Research Article

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Influence of flooding period and seed burial depth on Palmer amaranth (*Amaranthus palmeri*) seed germination

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Abstract

BACKGROUND: Flooding throughout fall and winter months is an effective practice for rice (*Oryza sativa* L.) straw decomposition, soil seedbank depletion, and waterfowl habitat in Mississippi. Nevertheless, limited research is available regarding the effects of fall–winter flooding and seed burial depth on Palmer amaranth (*Amaranthus palmeri* S. Wats.) seed germination. The objective of this study was to evaluate the effect of flooding period and seed burial depth on *A. palmeri* seed damage and germination in three different soil textures in Mississippi.

RESULTS: *Amaranthus palmeri* seed damage was greater when seeds were buried in sandy loam compared to silt loam soil textures. An interaction between flooding period and seed burial depth was present for *A. palmeri* seed germination. Flooding periods of 1-month (at 0 and 15 cm burial depth) and 2 months (at 0 cm burial depth) provided similar *A. palmeri* seed germination compared to no-flooding (at 0 cm burial depth). In addition, flooding periods of 3, 4, and 5 months reduced *A. palmeri* seed germination by 10, 10 and 14 percentage points at 0 cm burial depth, and 36, 40, and 41 percentage points when seeds were buried at 15 cm, respectively, across all soil textures.

CONCLUSION: This research demonstrates that flooding for 3, 4, and 5-months throughout fall and winter is an effective cultural practice to increase soil seedbank depletion through reduced germination potential to help manage herbicide-resistant *A. palmeri* populations in sandy loam, silt, and silt loam soil textures.

Keywords: flooding period; seed burial depth; germination; Palmer amaranth; weed management

1 INTRODUCTION

Palmer amaranth (*Amaranthus palmeri* S. Wats.) is a C4, summer annual, dioecious weed species native to north-western Mexico, southern California, New Mexico and Texas.[1] As *A. palmeri* originated in a xeric environment, it is naturally opportunistic and adapted for rapid germination and a complete life cycle in response to available moisture and temperature.[2] Normally, *A. palmeri* flowers during September and October, but decreasing day lengths may expedite the flowering process.[3] Seeds are smooth, round or disc-shaped, 1 to 2 mm in diameter, and are usually dispersed by gravity; although, seed dispersal has been reported as a result of animal movement and agricultural practices such as irrigation, plowing, mowing, and harvest.[4]

Amaranthus palmeri is an extremely prolific seed producer with one female plant capable of producing up to 600 000 seeds under favorable conditions.[3] Although interspecific and intraspecific competition may reduce seed production of several plant species, *A. palmeri* seed production remains high in competition with agronomic crops, allowing for its rapid dissemination.[4] In North Carolina, *A. palmeri* density of 5 plants m^{-1} within a peanut (*Arachis hypogaea* L.) row produced 124 000 seeds m^{-2}.[5] Research conducted in Georgia reported that *A. palmeri* produced 312 000 and 446 000 seeds per plant when competing with cotton (*Gossypium hirsutum* L.) and in absence of the crop, respectively.[6] Additionally, total loss of a cotton field due to *A. palmeri* infestation has been reported 3 years after initial introduction of the species.[7]

Several factors influence seed germination and dormancy such as moisture, temperature, oxygen availability, temperature, light exposure, and microbial activity.[8] Seed dormancy is also determined by genetic factors and contributes to plant adaptation to

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a diversity of habitats.[9] When determined by genetic factors, seed dormancy is classified as primary dormancy. Secondary dormancy occurs when unfavorable conditions related to the environment are the determining factor.[10] Different classes of seed dormancy have been reported among plant species and can be divided into physiological, morphological, morphophysiological, and combinational dormancy.[10–12] Physiological and morphological dormancies are the most common mechanisms of weed seed persistence in the soil seedbank.[12] Previous research reported that differences in *A. palmeri* seed dormancy levels are due to variability in seed physiology in response to selection pressure events such as continuous herbicide applications and tillage practices.[13,14]

Typically, *A. palmeri* emerges from shallow depths and often requires light for breaking dormancy and triggering germination.[15–17] Small-seeded broadleaves such as *A. palmeri* may not survive germination from deeper in the soil profile.[18] Therefore, the necessity for light is considered an evolutionary advantage. The quality and quantity of light reaching the soil surface is deeply dependent on the presence of crop canopy, plant residue, and water. Generally, in the presence of crop canopy, the light passing through green leaves is filtered and depleted in red light and enriched in far-red wavelengths, which inhibits germination of many small-seeded broadleaf species, such as *A. palmeri*.[19]

Depending on weed species and environmental conditions, seed burial depth may be advantageous for germination and emergence.[20] The overlay of soil creates a mulch that sustains high humidity allowing for rapid seed germination. Furthermore, the soil protects seeds and seedlings from abnormal air temperatures as well as damage from granivores and herbivores that feed on near the soil surface.[19,21] *Amaranthus palmeri* seed viability decreases as burial time increases; conversely, seed viability increases with burial depth.[22] Previous research reported that spiny amaranth (*Amaranthus spinosus* L.) and slender amaranth (*Amaranthus viridis* L.) emergence did not occur when seeds were buried at 4 and 6 cm, respectively.[23]

Flooding is a common practice in most rice (*Oryza sativa* L.) fields in the United States.[24] On average, 96% of all rice produced in the United States is grown on silt loam and clay loam soils, and 99.5% utilizes flooding as part of a weed management program.[25] The presence of water creates an unfavorable environment for most weed species, typically resulting in reduced emergence after permanent flooding is established.[26] Flooding through fall and winter months has proven to be an effective practice for rice straw decomposition, soil seedbank depletion, and waterfowl habitat in the Mississippi Alluvial Valley.[27,28] In addition, fall–winter flooding may reduce soybean and rice production costs related to managing rice straw from previous growing season, winter weeds, and red rice infestation (*O. sativa* L.).[28,29] Nevertheless, limited research is available regarding the effects of fall–winter flooding and seed burial depth on *A. palmeri* germination in Mississippi. Hence, the objective of this experiment was to evaluate the effect of flooding period and seed burial depth on *A. palmeri* seed damage and germination in three different soil textures.

2 MATERIALS AND METHODS

2.1 Experiment design and establishment

Experiments were conducted at the R. R. Foil Plant Science Research Center near Starkville, MS (33°28′14″ N; 88°46′50″ W) from October through February in 2016–2017 and 2017–2018. The *A. palmeri* population selected for this research was confirmed resistant to 5-enolpyruvylshikimate-3-phosphate synthase (EPSPs) and acetolactate synthase (ALS) or acetohydroxyacid synthase (AHAS) inhibiting herbicides.[30–32] Prior to study initiation, a germination test was conducted at the Mississippi State Seed Testing Laboratory in Percival™ GR41L growth chambers (Percival Scientific, Inc., Perry, IA, USA) to determine the germination rate of the selected *A. palmeri* population. One hundred *A. palmeri* seeds were placed on moist filter paper inside 18 cm diameter petri dishes. Day and night temperatures were set at 35 °C/30 °C and 14-h/10-h day/night periods. Temperature and light cycles were selected in order to maximize *A. palmeri* seed germination as described by Guo and Al-Khatib.[33] Seeds were considered successfully germinated when the radicle reached 1 mm in length [Fig. 1(A)]. In order to account for potential seed dormancy, germinated seeds were enumerated and removed daily for 15 days.

Three soil textures were used in this experiment, which included sandy loam (2.8% clay, 28.4% silt, and 68.8% sand) from Starkville, MS (33°28′44″ N; 88°46′53″ W); silt (2.8% clay, 84.2% silt, and 13% sand) from Stoneville, MS (33°25′18″ N; 90°55′7″ W); and silt loam (18% clay, 64.2% silt, and 17.8% sand) from Brooksville, MS (33° 15′32″ N; 88°33′31″ W). Soils were collected from aforementioned areas, brought to the R. R. Foil Plant Science Research Center and allowed to air dry for 7 days. Soils were sieved and screened using a 112 Royer™ soil grinder (Royer Industries Inc., Oshkosh, WI, USA) to eliminate large soil particles. In order to avoid germination of any previous weed seed present in selected soils, soil samples (1 kg) of each soil texture were collected and

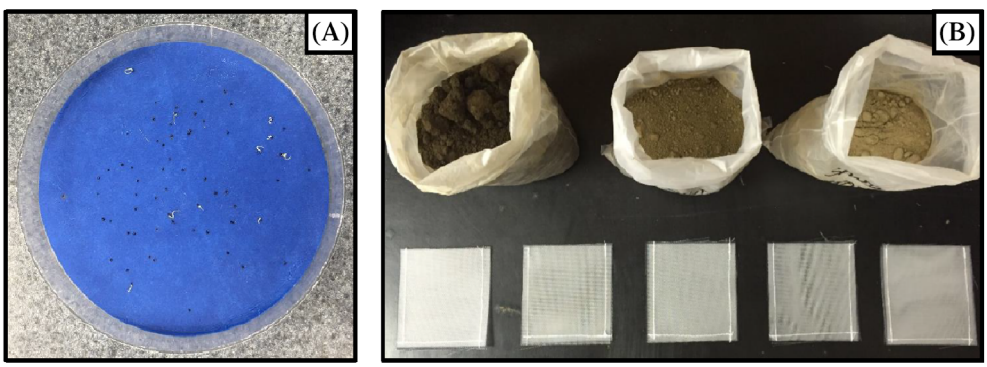

Figure 1. Germinated *Amaranthus palmeri* seeds during germination test at Mississippi State Seed Testing Laboratory (A). Silt loam (left), silt (center), and sandy loam (right) soil textures with 500 µm pore opening polyethylene mesh bags (bottom) (B). [Color figure can be viewed at wileyonlinelibrary.com]

autoclaved (100 °C) for 2 h using a Market Forge Sterilmatic® autoclave (Market Forge Inc., Burlington, VT, USA). Polyethylene mesh bags (64 cm^2) with 500 μm pore opening (Elko Filtering Co., Miami, FL, USA) were utilized for seed storage throughout the duration of the experiment [Fig. 1(B)]. One hundred *A. palmeri* seeds plus sterilized soil (20 g) were placed inside each bag. Two polyethylene bags containing seeds and sterilized soil were placed in each bucket. One bag was buried at 15 cm and the other placed on the soil surface.

Each soil texture was placed into 27 L plastic buckets (U-LINE Company, Pleasant Prairie, WI, USA) and buried at 38 cm depth (Fig. 2). Buckets were covered with a plastic mesh to prevent plant residue from falling into the buckets and to protect seeds from eventual damage from small rodents and birds. Flooding simulation was conducted by adding water (15 cm) above soil surface for one of five flooding periods. In order to maintain a uniform flood level and reduce the impact of precipitation on water depth, holes were drilled on each bucket at the 15 cm above soil level. Flood level was checked every 2 days and water was added every time flood level was lower than 13 cm above soil surface. Flooding periods were as follows: 5 months (October through February); 4 months (October through January); 3 months (October through December); 2 months (October through November); 1 month (October); and no-flooding (October through February). A single no-flooding treatment was utilized to maximize potential differences between presence and absence of water. Experimental design was a split-plot with three replications. Buckets were placed 3 m by 3 m apart, and main plot factors were flooding period and soil texture, and sub-plot factor was seed burial depth.

2.2 Data collection and analyses

At the day of completion of each flooding period, polyethylene mesh bags were removed from buckets and seeds were separated from soil using a N°35, 500 μm mesh sieve (VWR™ International, Radnor, PA, USA). Under a microscope, *A. palmeri* seeds were enumerated and characterized as normal or damaged. Seeds were classified as damaged when seeds were hollow, presenting substantial damage to the seed coat, and/or with visible signs of tissue decaying (Fig. 3). After seed characterization, a post-treatment germination test was conducted using normal and damaged seeds at the Mississippi State Seed Testing Laboratory following the aforementioned procedure described by Guo and Al-Khatib.[33] Seed characterization and germination values were analyzed using PROC MIXED procedure in SAS v.9.4 (SAS® Institute Inc., Cary, NC, USA). Flooding period, soil texture, and burial depth were analyzed as fixed effects, and random effects were year and replication nested in year.

Figure 2. Experimental area at the R. R. Foil Plant Science Research in Starkville, MS. [Color figure can be viewed at wileyonlinelibrary.com]

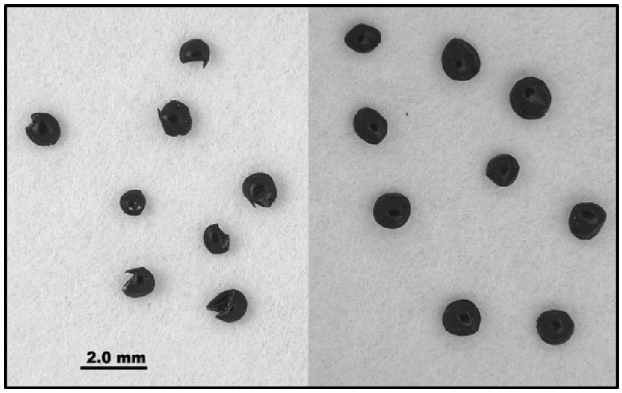

Figure 3. Visual aspects adopted for damaged (left) and normal (right) *Amaranthus palmeri* seed characterization.

Data means were separated using Fisher's Protected LSD (least significant difference) at 0.05 level of significance.

3 RESULTS AND DISCUSSION

3.1 *Amaranthus palmeri* seed characterization

Air temperature monthly averages and precipitation totals throughout experiment duration in 2016–2017 and 2017–2018 in Starkville, MS are shown in Table 1. Despite precipitation differences, air temperature monthly averages were similar between years. Analysis of variance (ANOVA) for *A. palmeri* seed characterization is presented in Table 2. The absence of a significant interaction between sources of variability allowed for individual analysis of fixed factors. However, it is important to highlight the low significance level observed for the flooding period and seed burial depth interaction ($P = 0.0677$). Although a *P*-value greater than 0.05 was observed, it demonstrates the potential impact of this interaction on seed decaying, especially in layers close to the soil surface.[34] Previous research conducted by Korres *et al.*[35] reported that seed burial had a greater impact on *A. palmeri* seed damage when seeds were placed closer to the soil surface. The presence of a layer of soil above the seed may reduce the adverse effects of seed weathering and insect predation, which may lead to greater seed longevity.[36] Nevertheless, in this research, the high volumetric water content of soils could have benefited the development of fungal pathogens across burial depths, which could have reduced the damage protection effect typically provided by seed burial.[35,37] *Amaranthus palmeri* seed characterization was influenced by soil texture ($P = 0.0419$) and flooding period ($P < 0.0001$). The greatest amount of damaged *A. palmeri* seeds was observed in the sandy loam soil texture (Fig. 4). Although greater seed damage level was observed in the sandy loam soil texture, damage did not differ when seeds were placed in silt soil texture. Differently, 5 percentage points less damaged seeds were observed when placed in silt loam soil texture (Fig. 4). Differences in seed characterization could be correlated to the microbial diversity present in each soil texture. Van Elsas *et al.*[38] reported that different soil management practices have a strong impact on soil bacterial and microbial populations, which can alter soil seedbank viability.

The influence of flooding period on *A. palmeri* seed damage is shown in Fig. 5. Flooding periods of 4 and 5-months resulted in the greatest amount of damaged *A. palmeri* seeds. Conversely, flooding period of 2-months had the least amount of seed

Table 1. Average air temperature and total monthly precipitation in Starkville, MS during field experiment duration in 2016–2017 and 2017-2018[a]

Year	Month	Air temperature (°C)	Precipitation (mm)
2016	October	20	28
	November	14	58
	December	8	128
2017	January	7	93
	February	12	174
2017	October	19	56
	November	13	29
	December	8	139
2018	January	3	52
	February	12	262

[a]Source: National Oceanic and Atmospheric Administration (NOAA).

Table 2. Analysis of variance (ANOVA) probability values for *Amaranthus palmeri* seed characterization

Fixed effects	Seed characterization (normal/damaged) *P*-Values[a]
Flooding period	<0.0001
Soil texture	0.0419
Flooding period*soil texture	0.9993
Seed burial depth	0.4303
Flooding period*seed burial depth	0.0677
Soil texture*seed burial depth	0.9520
Flooding period*soil texture*seed burial depth	0.8182

[a]Probability values calculated based on data pooled across years.

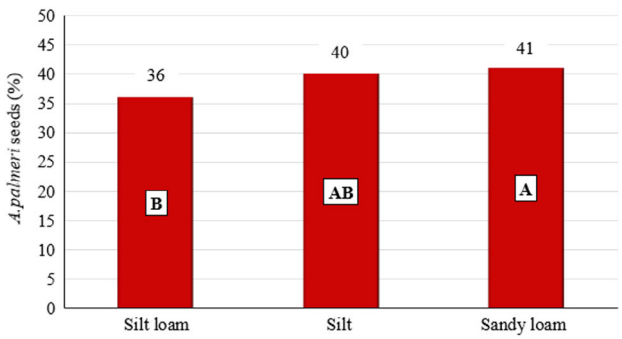

Figure 4. Damaged *Amaranthus palmeri* seeds with respect to soil texture. Means within the same color followed by the same letter are not significantly different according to Fisher's Protected LSD ($\alpha = 0.05$). [Color figure can be viewed at wileyonlinelibrary.com]

damage. Flooding for 1-month and 3-months resulted in more damaged seeds compared to 2-months. Furthermore, no-flooding resulted in similar levels of seed damage compared to flooding periods of 4 and 5-months. In this experiment, no-flooding was kept in the field throughout the study duration to evaluate the benefit of flooding for shorter periods compared to an extended no-flooding field condition. The amount of damaged *A. palmeri* seeds observed in no-flooding may be a result of

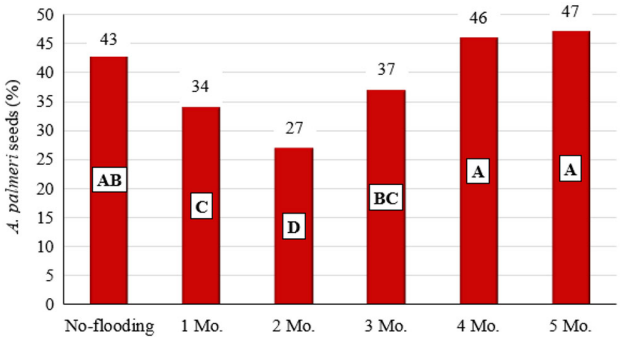

Figure 5. Damaged *Amaranthus palmeri* seeds in response to flooding period. Means within the same color followed by the same letter are not significantly different according to Fisher's Protected LSD ($\alpha = 0.05$). [Color figure can be viewed at wileyonlinelibrary.com]

extended exposure to adverse weather conditions throughout the experiment (Table 1). Less seed damage would be expected in no-flooding compared to flooding periods of 4 and 5-months had no-flooding been removed earlier. Nevertheless, the influence of flooding period on *A. palmeri* seed characterization remains unclear as greater seed damaged was observed on 1-month flooding period compared to 2-months. Factors other than time exposure to flooding must be further evaluated in future research to better address the impact of flooding period on seed characterization, especially in flooding periods less than 3-months.

3.2 Total *Amaranthus palmeri* seed germination

Analysis of fixed effects for total *A. palmeri* seed germination are presented in Table 3. *Amaranthus palmeri* seed germination did not differ due to soil texture. Although distinct seed characterization was previously reported, this did not translate into germination differences across soil textures. The abiotic and biotic factors that contributed to the differences previously shown in seed characterization may not have led to significant seed embryo damage.

The interaction of flooding period and seed burial depth affected total *A. palmeri* seed germination ($P < 0.0001$) (Table 3). *Amaranthus palmeri* seed germination was 23 percentage points greater when seeds were buried at 15 cm in no-flooding conditions compared to seeds placed on the soil surface (Table 4). Previous research reported increased *A. palmeri* and common

Table 3. Analysis of variance (ANOVA) probability values for total *Amaranthus palmeri* seed germination

Fixed effects	Total AMAPA[a] seed germination *P*-Values[b]
Flooding period	<0.0001
Soil texture	0.1470
Flooding period*soil texture	0.9523
Seed burial depth	0.5739
Flooding period*seed burial depth	<0.0001
Soil texture*seed burial depth	0.5779
Flooding period*soil texture*seed burial depth	0.9994

[a]AMAPA, *Amaranthus palmeri* S. Wats., Palmer amaranth.
[b]Probability values calculated based on data pooled across years.

Table 4. Total *Amaranthus palmeri* seed germination as a result of flooding period and seed burial depth[a]

Flooding period	Seed burial depth (cm)	Total AMAPA seed germination (%)
Months		
No-flooding	0	21 ^{B}
	15	44 ^{A}
1	0	15 ^{BC}
	15	14 ^{BCD}
2	0	14 ^{BCD}
	15	13 ^{CD}
3	0	11 ^{CD}
	15	8 ^{CDE}
4	0	11 ^{CDE}
	15	4 ^{EF}
5	0	7 ^{DE}
	15	3 ^{F}

[a]Total *Amaranthus palmeri* seed germination pooled across soil texture and year.
Note: Means followed by the same letter are not significantly different according to Fisher's protected LSD at 0.05 level of significance.
AMAPA, *Amaranthus palmeri* S. Wats., Palmer amaranth.

waterhemp [*Amaranthus tuberculatus* (Moq.) J. D. Sauer] seed germination and longevity when seeds were buried at 17.5 cm compared to seeds placed at soil surface.[35] Furthermore, Sosnoskie *et al.*[22] reported greater *A. palmeri* seed viability when seeds were buried at 10 and 40 cm compared to 1 and 2.5 cm burial depths. However, results from this experiment show that seed burial depth did not influence *A. palmeri* seed germination under flooded conditions, regardless of flooding period (Table 4). The presence of water not only reduces light incidence, but also negatively impacts oxygen availability, which is essential to growth and development of higher plants such as *A. palmeri*.[39] Similar research reported that volumetric water content may be responsible for differences in *A. palmeri* seed persistence in different soils, which explains why the advantageous effect of burial on seed germination was only observed in no-flooding conditions.[38]

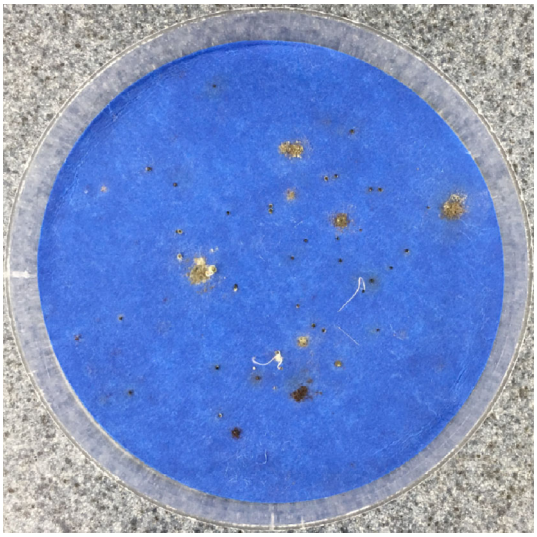

Figure 6. Fungi colonization on petri dish with *Amaranthus palmeri* seeds retrieved after 5-months under flooded condition. [Color figure can be viewed at wileyonlinelibrary.com]

Flooding periods of 3, 4, and 5 months reduced *A. palmeri* seed germination compared to no-flooding at both burial depths (Table 4). Flooding periods of 3, 4, and 5 months reduced *A. palmeri* seed germination by 10, 10, and 14 percentage points at 0 cm burial depth, and 36, 40, 41 percentage points at 15 cm burial depth (Table 4). Extended periods of oxygen deficiency has also reduced seed germination and viability of Texasweed (*Caperonia palustris* L.) and barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.].[40,41] In addition, increased soil moisture conditions favor the establishment and colonization of saprophytic fungi and bacteria, which exercise an important role in seed mortality.[42] In this research, the development of fungi colonies was observed, especially in seeds retrieved from flooded treatments (Fig. 6). Despite the fact that seed viability was not numerically estimated in this experiment, the presence of heavy fungi development may be used to indicate increased seed decaying, thus, reduced seed viability, other than increased seed dormancy. The findings of this research indicate that *A. palmeri* seed germination is strongly affected by edaphic conditions, especially under flooded conditions. Fall–winter flooding can be used to efficiently improve *A. palmeri* control practices that utilize soil seedbank depletion as part of an integrated weed management program.

4 CONCLUSION

The findings of this research demonstrate that flooding can be used to effectively reduce *A. palmeri* seed germination in sandy loam, silt, and silt loam soil textures. Flooding periods conducted for 3, 4, and 5 months resulted in the greatest *A. palmeri* seed viability reduction. Additionally, seed burial depth did not increase *A. palmeri* seed viability under flooded conditions. Coupled with a sustainable and economically viable in-season weed control program, fall–winter flooding could be adopted as a reliable and effective practice to optimize *A. palmeri* soil seedbank depletion, especially in areas infested with herbicide-resistant biotypes.

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CONFLICTS OF INTEREST

No conflicts of interest have been declared.

REFERENCES

1 Sauer J, Recent migration and evolution of the dioecious amaranths. *Evolution* **1**:11–31 (1957).
2 Ehleringer J, Annuals and perennials of warm deserts, in *Physiological Ecology of North American Plant Communities*. Springer, Dordrecht, pp. 162–180 (1985).
3 Keeley PE, Carter CH and Thullen RJ, Influence of planting date on growth of palmer amaranth (*Amaranthus palmeri*). *Weed Sci* **35**: 199–204 (1987).
4 Sauer J, Revision of the dioecious amaranths. *Madrono* **13**:5–46 (1955).
5 Burke IC, Schroeder M, Thomas WE and Wilcut JW, Palmer amaranth interference and seed production in peanut. *Weed Technol* **21**:367–371 (2007).
6 Webster TM and Grey TL, Glyphosate-resistant Palmer amaranth (*Amaranthus palmeri*) morphology, growth, and seed production in Georgia. *Weed Sci* **63**:264–272 (2015).
7 Norsworthy JK, Griffith G, Griffin T, Bagavathiannan M and Gbur EE, In-field movement of glyphosate-resistant Palmer amaranth (*Amaranthus palmeri*) and its impact on cotton lint yield: evidence supporting a zero-threshold strategy. *Weed Sci* **62**:237–249 (2014).
8 Leon RG, Knapp AD and Owen MDK, Effect of temperature on germination of common waterhemp (*Amaranthus tuberculatus*), giant foxtail (*Setaria faberi*), and velvetleaf (*Abutilon theophrasti*). *Weed Sci* **52**:67–73 (2004).
9 Graeber KAI, Nakabayashi K, Miatton E, Leubner-Metzger GE and Soppe WJ, Molecular mechanisms of seed dormancy. *Plant Cell Environ* **35**:1769–1786 (2012).
10 Baskin JM and Baskin CC, A classification system for seed dormancy. *Seed Sci Res* **14**:1–16 (2004).
11 Finch-Savage WE and Leubner-Metzger G, Seed dormancy and the control of germination. *New Phytol* **171**:501–523 (2006).
12 Omani EN, Haigh AM, Medd RW and Nicol HI, Changes in germinability, dormancy and viability of *Amaranthus retroflexus* as affected by a depth and duration of burial. *Weed Res* **39**:345–354 (1999).
13 Jha P and Norsworthy JK, Soybean canopy and tillage effects on emergence of Palmer amaranth (*Amaranthus palmeri*) from a natural seedbank. *Weed Sci* **57**:644–651 (2009).
14 Jha P, Norsworthy JK and Garcia J, Depletion of an artificial seed bank of Palmer amaranth (*Amaranthus palmeri*) over four years of burial. *Am J Plant Sci* **5**:1599–1606 (2014).
15 Leon RG, Bassham DC and Owen MD, Germination and proteome analyses reveal intraspecific variation in seed dormancy regulation in common waterhemp (*Amaranthus tuberculatus*). *Weed Sci* **54**:305–315 (2006).
16 Baskin JM and Baskin CC, Temperature requirements for after-ripening in buried seeds of four summer annual weeds. *Weed Res* **27**:385–389 (1987).
17 Benech-Arnold RL, Sanchez RA, Forcella F, Kruk BC and Ghersa CM, Environmental control of dormancy in weed seed banks in soil. *Field Crop Res* **67**:105–122 (2000).
18 Gallagher RS and Cardina J, Phytochrome-mediated Amaranthus germination I: effect of seed burial and germination temperature. *Weed Sci* **46**:48–52 (1998) 1998.
19 Taylorson RB and Borthwick HA, Light infiltration by foliar canopies: significance for light-controlled weed seed germination. *Weed Sci* **17**:48–51 (1969).
20 Pons TL, Induction of dark dormancy in seeds: its importance for the seed bank in the soil. *Funct Ecol* **5**:669–675 (1991).
21 Forcella F, Arnold RLB, Sanchez R and Ghersa CM, Modeling seedling emergence. *Field Crop Res* **67**:123–139 (2000).
22 Sosnoskie LM, Webster TM and Culpepper AS, Glyphosate resistance does not affect palmer amaranth (*Amaranthus palmeri*) seed bank longevity. *Weed Sci* **61**:283–288 (2013).
23 Chauhan BS and Johnson DE, Germination ecology of spiny (*Amaranthus spinosus*) and slender amaranth (*A. viridis*): troublesome weeds of direct-seeded rice. *Weed Sci* **57**:379–385 (2009).
24 Manley SW, Ecological and agricultural values of winter-flooded rice fields in Mississippi (Doctoral dissertation), Mississippi State University, Department of Wildlife and Fisheries, (1999).
25 Hardke J, Schmidt L, Mazzanti R, Arkansas Rice Quick Facts. University of Arkansas Division of Agriculture, Research and Extension, Little Rock, AR, 2013. http://www.agriculture.org/crops/rice/quick_facts/2013_rice_quick_facts.pdf [10 February 2017].
26 Moldenhauer KE and Slaton N, *Rice Growth and Development. Rice Production Handbook*, Vol. **192**, pp. 7–14. 2301 S. University Little Rock, Arkansas 72204: University of Arkansas Division of Agriculture Cooperative Extension Service; (2001).
27 Manley SW, Kaminski RM, Reinecke KJ and Gerard PD, Agronomic implications of waterfowl management in Mississippi rice fields. *Wildl Soc Bull* **33**:981–992 (2005).
28 Emory J, Just add water. *Nat Conserv* **44**:11–15 (1994).
29 Muzzi D, Winter floods offer duck habitat and crop savings. *Rice J* **97**: 8–9 (1994).
30 Heap IM, The International Survey of Herbicide-Resistant Weeds 2019. http://www.weedscience.org/ [12 January 2019]
31 Nandula VK, Wright AA, Bond JA, Ray JD, Eubank TW and Molin WT, EPSPS amplification in glyphosate-resistant spiny amaranth (*Amaranthus spinosus*): a case of gene transfer via interspecific hybridization from glyphosate-resistant Palmer amaranth (*Amaranthus palmeri*). *Pest Manag Sci* **70**:1902–1909 (2014).
32 Molin WT, Nandula VK, Wright AA and Bond JA, Transfer and expression of ALS inhibitor resistance from Palmer amaranth (*Amaranthus palmeri*) to an *A. spinosus x A. palmeri* hybrid. *Weed Sci* **64**:240–247 (2016).
33 Guo P and Al-Khatib K, Temperature effects on germination of redroot pigweed (*Amaranthus retroflexus*), Palmer amaranth (*A. palmeri*), and common waterhemp (*A. rudis*). *Weed Sci* **51**:869–875 (2003).
34 Forcella F, Debiting the seedbank: priorities and predictions. *Asp Appl Biol* **69**:151–162 (2003).
35 Korres NE, Norsworthy JK, Young BG, Reynolds DB, Johnson WG, Conley SP *et al.*, Seedbank persistence of palmer amaranth (*Amaranthus palmeri*) and waterhemp (*Amaranthus tuberculatus*) across diverse geographical regions in the United States. *Weed Sci* **66**: 446–456 (2018).
36 Wijayratne UC and Pyke DA, Burial increases seed longevity of two *Artemisia tridentata* (Asteraceae) subspecies. *Am J Bot* **99**:438–447 (2012).
37 Crist TO and Friese CF, The impact of fungi on soils seed: implications for plants and granivores in a semi-arid shrub-steppe. *Ecology* **74**: 2231–2239 (1993).
38 Van Elsas JD, Garbeva P and Salles J, Effects of agronomical measures on the microbial diversity of soils as related to the suppression of soil-borne plant pathogens. *Biodegradation* **13**:29–40 (2002).
39 Counce PA and Burgos NR, Agronomic practices in addition to herbicides for improving weed control in dry-seeded flooded rice. *J Sustain Agric* **28**:145–156 (2006).
40 Abouziena HF, El-Awadi ME, EL-Saeid HM, El-Metwally IM, El-Desouki IR and Singh M, Influence of environmental factors, flooding period and seeding depth on germination and emergence of barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.]. *Int J ChemTech Res* **8**:459–467 (2015).
41 Koger CH, Reddy KN and Poston DH, Factors affecting seed germination, seedling emergence, and survival of texasweed (*Caperonia palustris*). *Weed Sci* **52**:989–995 (2004).
42 Pakeman RJ, Small JL and Torvell L, Edaphic factors influence the longevity of seeds in the soil. *Plant Ecol* **213**:57–65 (2012).

