Weed Science 2013 61:283–288

Glyphosate Resistance Does Not Affect Palmer Amaranth (*Amaranthus palmeri*) Seedbank Longevity

Lynn M. Sosnoskie, Theodore M. Webster, and A. Stanley Culpepper*

A greater understanding of the factors that regulate weed seed return to and persistence in the soil seedbank is needed for the management of difficult-to-control herbicide-resistant weeds. Studies were conducted in Tifton, GA to (1) evaluate whether glyphosate resistance, burial depth, and burial duration affect the longevity of Palmer amaranth seeds and (2) estimate the potential postdispersal herbivory of seeds. Palmer amaranth seeds from glyphosate-resistant and glyphosate-susceptible populations were buried in nylon bags at four depths ranging from 1 to 40 cm for intervals ranging between 0 and 36 mo, after which the bags were exhumed and seeds evaluated for viability. There were no detectable differences in seed viability between glyphosate-resistant and glyphosate-susceptible Palmer amaranth seeds, but there was a significant burial time by burial depth interaction. Palmer amaranth seed viability for each of the burial depths declined over time and was described by exponential decay regression models. Seed viability at the initiation of the study was $\geq$ 96%; after 6 mo of burial, viability declined to 65 to 78%. As burial depth increased, so did Palmer amaranth seed viability. By 36 mo, seed viability ranged from 9% (1-cm depth) to 22% (40-cm depth). To evaluate potential herbivory, seed traps with three levels of exclusion were constructed: (1) no exclusion, (2) rodent exclusion, and (3) rodent and large arthropod exclusion. Each seed trap contained 100 Palmer amaranth seeds and were deployed for 7 d at irregular intervals throughout the year, totaling 27 sample times. There were seasonal differences in seed recovery and differences among type of seed trap exclusion, but no interactions. Seed recovery was lower in the summer and early autumn and higher in the late winter and early spring, which may reflect the seasonal fluctuations in herbivore populations or the availability of other food sources. Seed recovery was greatest (44%) from the most restrictive traps, which only allowed access by small arthropods, such as fire ants. Traps that excluded rodents, but allowed access by small and large arthropods, had 34% seed recovery. In the nonexclusion traps, only 25% of seed were recovered, with evidence of rodent activity around these traps. Despite the physically small seed size, Palmer amaranth is targeted for removal from seed traps by seed herbivores, which could signify a reduction in the overall seed density. To be successful, Palmer amaranth management programs will need to reduce soil seedbank population densities. Future studies need to address factors that enhance the depletion of the soil seedbank and evaluate how these interact with other weed control practices.

Nomenclature: Palmer amaranth, *Amaranthus palmeri* (S.) Wats. AMAPA.

Key words: Biological control, glyphosate resistance, herbicide resistance, predation, seed burial, soil seedbank.

Palmer amaranth has become one of the most important weeds of agronomic crops in the southern United States, in part because of its proclivity to develop resistance to many commonly used herbicides (Culpepper et al. 2006; Heap 2012; Vencill et al. 2008; Wise et al. 2009). Greater understanding of ecological factors that regulate population dynamics of Palmer amaranth is needed so that growers can leverage these factors in their management strategies.

Weed escapes are capable of affecting both current and future crop yields; the offspring derived from surviving plants will be available to compete with subsequent crops for available resources. Mature female Palmer amaranth plants produce prodigious amounts of seed. Mean seed production of Palmer amaranth plants in California ranged from 200,000 to 600,000 seed for plants that emerged between March and June, whereas those in Missouri produced greater than 250,000 seed per plant (Keeley et al. 1987; Sellers et al. 2003).

The success of weed management systems in a given year is often a function of the efficacy of weed control systems applied the previous year (Mortensen et al. 2000). Herbicide performance can be diminished greatly in the years after weed control failures (Dieleman et al. 1999; Hartzler and Roth 1993; Webster et al. 1998). Sparks et al. (2003) reported that increased Palmer amaranth seed density in the soil seedbank required higher rates of PRE herbicides to achieve acceptable weed control.

Weed management (e.g., PRE and POST herbicides, cultivation, etc.) historically has focused on the prevention of seedling establishment and growth, but little attention has been provided to practices that minimize seed return and maximize seed depletion from the soil seedbank (Anderson 2007; Cardina et al. 1999; Gallandt 2006). As weeds have developed resistance to commonly used herbicides, alternative management programs that integrate various cultural practices along with herbicides have been advocated as a means to reduce the weed population and assist growers in successful weed control (Norsworthy et al. 2012). Perhaps 90% or more of plant mortality occurs in the seed stage (Cavers 1983; Forcella et al. 1992), with losses occurring due to herbivory, pathogens, aging, and fatal germination (Forcella 2003). Sensitivity analysis from a crop rotation model on the soil seedbank suggested value in reducing the overwintering weed seed populations (Jordan et al. 1995). A model of Palmer amaranth predicted that population size is one of the most important factors in regulating the occurrence of glyphosate resistance and presumably other herbicide resistance issues (Neve et al. 2011).

Previous studies on seed longevity have documented seed viability for some weed species after approximately 20 yr of soil burial in porous packets (Conn et al. 2006; Lewis 1973). In the Beal burial study, which was initiated in 1879, seed viability was detected in two species that were buried for 120 yr (Telewski and Zeevaart 2002). Despite these extreme and unique occurrences, many species rapidly lose seed

DOI: 10.1614/WS-D-12-00111.1

* First and third authors: Research Professional and Professor, University of Georgia, Tifton, GA 31794; second author: Research Agronomist, Crop Protection and Management Research Unit, USDA-ARS, Tifton, GA 31794. Current address of first author: Project Scientist, University of California, Davis, CA 95616. Corresponding author's E-mail: ted.webster@ars.usda.gov

viability within the first few years of burial (Conn et al. 2006; Egley and Chandler 1983; Lewis 1973; Lutman et al. 2002). A study in Mississippi with agronomic weeds revealed that only 5 of the 20 tested species had > 50% viability after 42 mo of burial (Egley and Chandler 1983). Of the 41 weed species buried in a Nebraska study, 12 and 17 species had > 30% seed viability after 36 mo of burial at two experimental locations, respectively (Burnside et al. 1996).

Seed herbivory also may represent an important means of regulating weed seed populations (Cardina et al. 2002; Gallandt 2006). Previous studies in agricultural systems have documented high rates of seed removal from seed traps, suggesting that various animals potentially can prevent seeds from entering the soil seedbank (Gallandt et al. 2005; Menalled et al. 2007; Spafford Jacob et al. 2006). To implement management strategies that target the reduction of soil seedbank density, awareness of the factors that regulate its persistence is necessary. Our objectives were to quantify the potential longevity of both glyphosate-resistant (GR) and glyphosate-susceptible (GS) Palmer amaranth soil seedbanks over a 3-yr period when buried at four depths and evaluate if herbivores will target Palmer amaranth seeds.

Materials and Methods

Burial Studies. Field studies were initiated in January 2008 and 2009 at the U.S. Department of Agriculture–Agricultural Research Service (USDA-ARS) Jones Research Farm in Chula, GA (31.513941°N, 83.544967°W) to evaluate the potential longevity of Palmer amaranth seeds in the soil seedbank. Seeds used in the study were collected in the late autumn of 2007 and 2008 from a naturally senescent GS population of Palmer amaranth in Attapulgus, GA and a GR population in Ideal, GA. Seeds were stored in a nonheated greenhouse until burial. Seed packets consisted of water-permeable nylon bags (50-µm mesh, 5 cm by 10.5 cm) containing 100 Palmer amaranth seed and 10 g of sterilized sand, which facilitated recovery of seeds and provided a means of minimizing seed-to-seed contact in the bag (Van Mourik et al. 2005). Treatments were in a factorial arrangement with two levels of Palmer amaranth seed (GR and GS), four burial depths (1, 2.5, 10, and 40 cm), and nine burial durations (0, 3, 6, 9, 12, 18, 24, 30, and 36 mo). The study was a randomized complete block design with four replications and was repeated over time.

After packets were exhumed, seeds were evaluated for viability in the laboratory. Seed viability was initially evaluated by putting gentle pressure on the seed coat to test for firmness (Forcella et al. 2003); decayed seeds were marked as nonviable and discarded following this test. Intact seeds were placed on moistened germination paper in petri dishes for 28 d at a 30/20 C day/night temperatures. All nongerminated seeds after this time period were again tested for firmness, with decayed seeds scored as nonviable (Borza et al. 2007; Forcella et al. 1992; International Seed Testing Association 1985; Sawma and Mohler 2002).

Data were analyzed using a mixed model with burial longevity, burial depth, and Palmer amaranth population as fixed effects, whereas replications and initiation years were random effects. Data on Palmer amaranth seed viability (*y*) over time were fit to an exponential decay regression model that includes the *y*-intercept (*a*) and rate of decay (*b*) over time (*x*):

$$y = ae^{-bx} \qquad [1]$$

Differences among estimates of parameters *a* and *b* among burial depths were determined using a *t* test with a critical $t_{0.05} = 1.96$ (Glantz and Slinker 2001).

Seed Herbivory. Field studies were conducted at the USDA-ARS Sanders Research Farm near Tifton, GA (31.504422°N, 83.559337°W) to determine the level of potential Palmer amaranth seed herbivory between August 2008 and October 2010. The field had a naturalized infestation of Palmer amaranth with a seedbank population at the initiation of the study of approximately 9,000 seeds m^{-2}, determined through germination tests following the procedures detailed in Forcella et al. (2003). Petri dishes (8.75 cm diam by 1.3 cm tall) were filled with sand and 100 Palmer amaranth seeds placed on the surface (16,600 seeds m^{-2}). Previous studies have estimated Palmer amaranth seed production in excess of 100,000 seeds m^{-2} in cotton (*Gossypium hirsutum* L.) (Webster unpublished) and in peanut (Burke et al. 2007), with seedbank densities up to 35,000 germinable seeds m^{-2} in the top 5 cm of soil (Sosnoskie unpublished). Seeded petri dishes were placed in each of three trap types that were designed to: (1) permit all herbivores, (2) exclude rodents through the use of metal wire with a mesh size of 0.39 cm^2, and (3) exclude large arthropods and rodents with metal wire with a mesh size of 0.028 cm^2. Five seed traps were placed in both horizontally rolled rye (*Secale cereale* L.)residues and winter fallow areas of the same agronomic field. Rye ('Wrens Abruzzi') was planted in 18-cm rows in November at 100 kg ha^{-1} and rolled horizontally at anthesis. The winter fallow area was treated with glyphosate at 0.84 kg ae ha^{-1} to eliminate weeds in December and April. Cotton was planted into strip-tilled rows in April using recommended practices for Georgia (Collins et al. 2010). Seed trap evaluation began the last week of September, which corresponds with the early (< 10%) cotton harvest in Georgia (Shurley et al. 2004). Seed traps were deployed for 7 d at irregular intervals throughout the year for a total of 27 sample times for the study.

Data were analyzed using a mixed-model ANOVA with presence of cover crop, time of year, and seed trap type as fixed effects, whereas replications were random effects. Treatment means were separated using Fisher's Protected $LSD_{0.05}$.

Results and Discussion

Burial Studies. There were no detectable differences in seed viability between GS and GR Palmer amaranth populations; therefore data were combined over populations and years for regression analysis. There were significant interactions between burial time and depth of burial; the relationship between Palmer amaranth seed viability and time was satisfactorily described by exponential decay regression models for each of the burial depths (Figures 1 to 4). There were no differences in the *y*-intercept parameters among burial depths, but there were differences in rate of decline in seed viability (Table 1). The shallowest burial depth had a higher rate of viability loss than seed buried at 10 and 40 cm. Palmer amaranth seed viability at the initiation of the study was ≥ 96%, declining to 65 to 78% across all depths after 6 mo

https://doi.org/10.1614/WS-D-12-00111.1

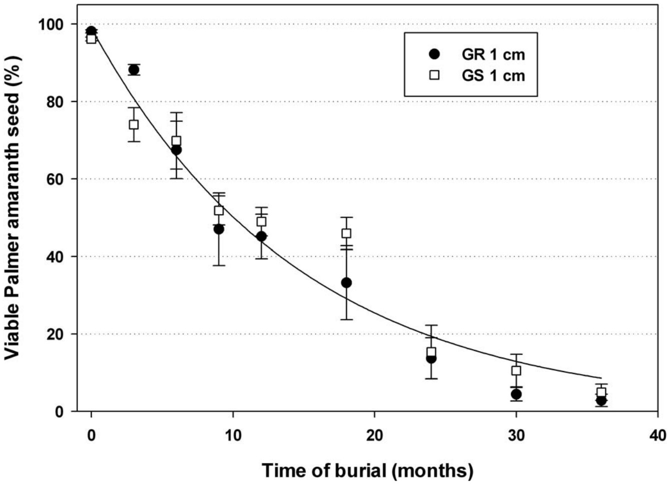

Figure 1. Influence of burial duration at 1 cm on viability of Palmer amaranth seeds. There were no differences between glyphosate-susceptible (GS) and glyphosate-resistant (GR) populations of Palmer amaranth; therefore data were combined for regression analysis. Values shown represent the mean of the two study initiation dates and four replications. $y = 98.9e^{-0.068x}$, $P < 0.0001$, $r^2 = 0.82$.

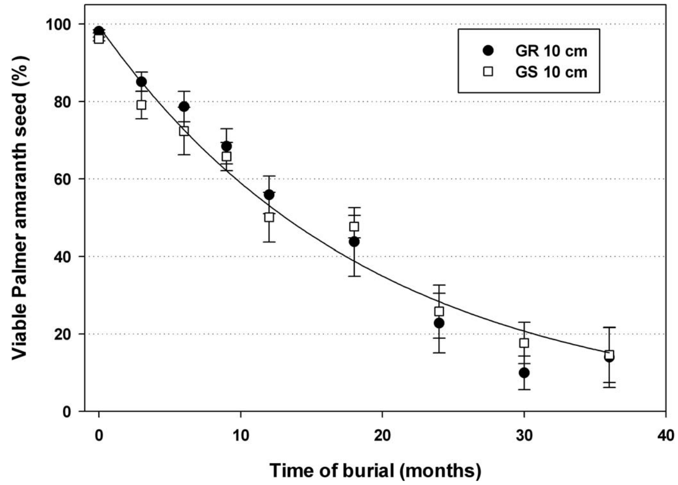

Figure 3. Influence of burial duration at 10 cm on viability of Palmer amaranth seeds. There were no differences between glyphosate-susceptible (GS) and glyphosate-resistant (GR) populations of Palmer amaranth; therefore data were combined for regression analysis. Values shown represent the mean of the two study initiation dates and four replications. $y = 99.5e^{-0.050x}$, $P < 0.0001$, $r^2 = 0.80$.

of burial. Seed viability of a similar species, redroot pigweed (*Amaranthus retroflexus* L.), after 6 mo of burial at 8- to 38-cm depths was 75 to 80%, compared with initial viability of 94% (Egley and Chandler 1978).

Over time, Palmer amaranth seed retained higher viabilities with increasing burial depth. After 12 mo, seeds buried at depths of 1, 2.5, 10, and 40 cm were 44, 48, 53, and 61% viable, respectively. Previous burial studies with redroot pigweed and South American amaranth (*Amaranthus quitensis* H.B. & K.) determined that viability of exhumed seed ranged from 62 to 90% when buried at depths ≤ 10 cm for 12 mo and 68 to 81% when buried at depths ≤ 4 cm for 11 mo, respectively (Faccini and Vitta 2005; Omami et al. 1999). Seed viability of redroot pigweed declined rapidly at 18 mo, ranging from 2 to 11% viability at all burial depths (Egley and Chandler 1978). In contrast, after 24 mo of burial, Palmer amaranth viability in the current study was 19, 24, 28, and 37% at the 1-, 2.5-, 10-, and 40-cm burial depths, respectively.

By 36 mo, Palmer amaranth seed viability at 40 cm (22%) was more than double that at 1 cm (9%), with 12 and 15% seed viability at 2.5 and 10 cm, respectively. Giant ragweed (*Ambrosia trifida* L.) seed persistence in the soil seedbank was proportional to burial depth, with seed buried at 20 cm maintaining greater viability after 4 yr than those buried at 0, 5, and 10 cm (Harrison et al. 2007). Exhumed after 36 mo of burial, seeds of redroot pigweed and tall waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer] had viabilities that ranged from 5 to 40% and 7 to 14%, respectively (Burnside et al. 1996). Although these values are similar to those of Palmer amaranth is the current study, viable seeds of redroot pigweed and tall waterhemp were recovered after 17 yr (≤ 1% for

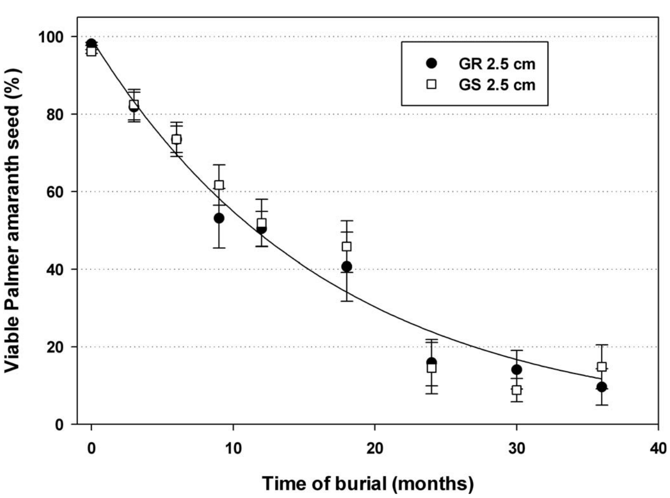

Figure 2. Influence of burial duration at 2.5 cm on viability of Palmer amaranth seeds. There were no differences between glyphosate-susceptible (GS) and glyphosate-resistant (GR) populations of Palmer amaranth; therefore data were combined for regression analysis. Values shown represent the mean of the two study initiation dates and four replications. $y = 99.0e^{-0.060x}$, $P < 0.0001$, $r^2 = 0.81$.

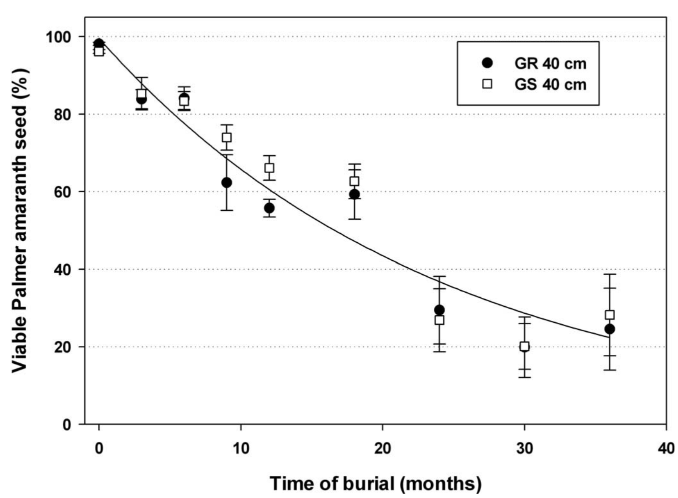

Figure 4. Influence of burial duration at 40 cm on viability of Palmer amaranth seeds. There were no differences between glyphosate-susceptible (GS) and glyphosate-resistant (GR) populations of Palmer amaranth; therefore data were combined for regression analysis. Values shown represent the mean of the two study initiation dates and four replications. $y = 99.6e^{-0.042x}$, $P < 0.0001$, $r^2 = 0.70$.

Table 1. Parameter estimates of the exponential decay regression models fit to the seed viability over time data in Figures 1 through 4.[a]

Depth	Parameter a (std.error)		Rate of decay (std. error)		
cm					
1.0	98.9	(2.9)	−0.068	(0.0040)	a
2.5	99.0	(2.8)	−0.060	(0.0034)	b
10.0	99.5	(2.7)	−0.050	(0.0031)	c
40.0	99.6	(3.1)	−0.042	(0.0029)	c

[a] Differences in parameter estimates were determined using a t test, with a $t_{0.05}$-critical value of 1.96. There were no differences among depths for parameter a. Letters were used to signify differences among parameter estimates for rate of decay.

redroot pigweed and ≤ 3% for tall waterhemp) (Burnside et al. 1996). The viability of Palmer amaranth beyond 36 mo of burial in soil is not known.

As the duration of the current study did not exhaust seed viability, there is potential for a rapid recolonization of Palmer amaranth as long as some viable seed remain in the soil seedbank, as has been previously noted with other species (Burnside et al. 1986). Menges (1987) reported that, in the absence of chemical or cultural management efforts, Palmer amaranth seedbank densities grew from 173 million seeds ha^{-1} to 1.1 billion seeds ha^{-1} within 6 yr. Although weed management practices were able to reduce the seedbank size by 98% relative to the control, approximately 18 million seed ha^{-1} remained in the soil of the treated plots at the end of the study (Menges 1987). Harrison et al. (2007) suggested that tillage, which brings buried seed closer to the soil surface, could reintroduce a weed into a cropping system that had previously been eliminated from the surface seed bank. In the current study, Palmer amaranth seeds were buried throughout the plow layer to estimate the length of time needed to exhaust the soil seedbank, given current management recommendations.

In the seedbank, potential causes for the loss of seed viability over time include: herbivory, germination, fungal and bacterial pathogens, or seed aging (Gallandt 2006). In the current burial study, herbivory by rodents and invertebrates was nonexistent because of burial and the protective mesh bag. Seeds that did germinate in response to environmental cues were not able to grow through the mesh bag and become established. Pathogens may have reduced seed viability in the packets, but the inclusion of sand (10 g) in the packets with the Palmer amaranth seed (~0.027 g for 100 seed) may have minimized the spread of disease from seed to seed (Van Mourik et al. 2005).

Seed Herbivory. There was no effect of the presence of rye (which was rolled to form a horizontal mulch in mid-May, with an average dry biomass of 2,800 kg ha^{-1}) or its absence in the winter fallow on level of seed removal from the traps. Previous research has suggested that cover crops enhance populations of weed seed herbivores (Gallandt et al. 2005; Heggenstaller et al. 2006). In the current study, the field was in a reduced tillage system with permanent grassways spaced every 11 m through the fields, which may have provided habitats for various seed herbivores, regardless of in-field cover (Kromp 1999).

There were seasonal differences in seed recovery and differences among type of seed trap exclusion, but there were no interactions between these factors. Although Palmer amaranth seeds are small, they were targeted for removal

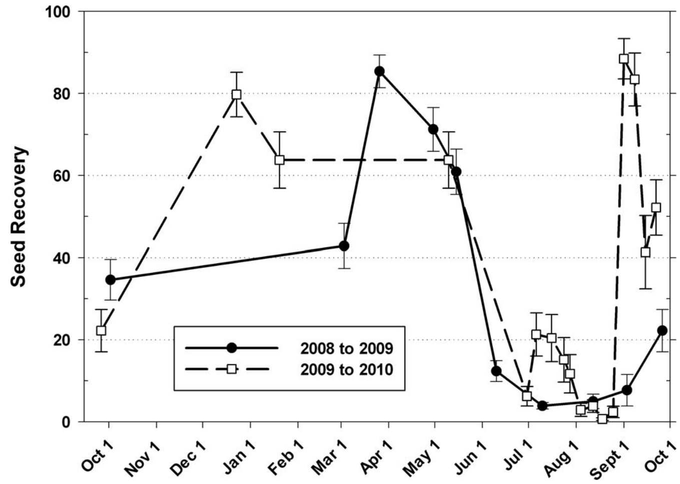

Figure 5. Seasonal pattern of Palmer amaranth seed recovery averaged over the three types of seed traps meant to exclude various herbivores. High values of seed recovery indicate that the seed were not removed from the trap, whereas low amounts of recovery suggest that seed were removed by a herbivores.

from the seed traps. Seed recovery (the inverse of seed removal or potential herbivory) was lowest in the summer and early autumn and highest in the late winter and early spring (Figure 5). High variability occurred in September seed recovery. The seasonal changes may reflect fluctuations in herbivore populations and the availability of other food sources. Previous research in Iowa determined that seed herbivory of velvetleaf (*Abutilon theophrasti* Medik.) and giant foxtail (*Setaria faberi* Herrm.) in summer annual crops was highest in the summer and lower in both the spring and autumn (Heggenstaller et al. 2006). Palmer amaranth flowering in south Georgia initiates in early June; however, information on rate at which viable seed is produced has not been reported. A related species, tall waterhemp, was capable of producing viable seed within 9 d of pollination (Bell and Tranel 2010). The seed rain pattern for Palmer amaranth over its life cycle also has not been quantified, so how much freshly produced and dispersed seed is available for herbivory during the summer months is not known.

There were differences in seed recovery among types of traps, when averaged over time. Seed recovery was greatest (44%, Fisher's Protected $LSD_{0.05}$ = 6%) from the most restrictive traps, which only allowed access to small arthropods, such as red imported fire ant (*Solenopsis invicta* Buren). Fire ants were plentiful in the field and were observed to remove Palmer amaranth seeds from the traps. In a previous study, redroot pigweed seeds were consumed preferentially by fire ants when given a choice of weed seeds of various sizes and plant families (Seaman and Marino 2003). Ants are known to be important in seed dispersal in desert habitats in which Palmer amaranth is native (Brown and Davidson 1977).

Seed traps that excluded rodents but allowed access to small and large arthropods had 34% seed recovery. In addition to fire ants, field crickets (*Gryllus* spp.) and ground beetles (e.g., *Harpalus pensylvanicus* De Geer) were potential seed herbivores captured in pitfall traps (Webster, unpublished data). In the nonexclusion traps, only 25% of seed were recovered, with evidence of rodent activity around these traps. Previous studies have reported that rodents were capable of dispersing large caches of seeds, as an individual can fill its cheek pouches

https://doi.org/10.1614/WS-D-12-00111.1

with seeds (Brown et al. 1975); conversely, ants will not remove seeds as quickly, because they harvest a single seed at a time (Brown et al. 1975); however, a single seed trap was emptied of Palmer amaranth seeds by fire ants within 30 min (Thomas Sklany, personal communication). Neither Palmer amaranth nor red imported fire ants are native to Georgia or the southeast United States, and even though their native ranges do not overlap, apparently one nonnative species (imported red fire ant) consumes (or at least relocates) another nonnative species (Palmer amaranth) in this system.

In addition to the herbivores encountered in the seed traps in the current study, birds are also known to consume weed seeds. Although the top of the traps prevented birds from feeding on the seeds in this study, previous studies determined that Palmer amaranth seeds retained $>$ 60% viability after passing through avian intestinal tracts (DeVlaming and Vernon 1968), with viable seeds recovered after 2 to 15 h inside 11 different types of birds (Proctor 1968). Therefore, the data in the current study may underestimate the total amount of seed herbivory that potentially occurs.

Previous studies on seed herbivory from traps have reported high levels of seed removal (Cardina et al. 1996; Chauhan et al. 2010; Gallandt et al. 2005; Heggenstaller et al. 2006; Menalled et al. 2007), consistent with what was found in the current study. However, interpretation of these data is not clear, as results project rapid depletion of the soil seedbank, which, on the basis of the annual reoccurrence of weeds in these fields, clearly does not occur (Forcella 2003). Therefore, the value of the data from this and similar studies is likely related to the fact that multiple species of potential herbivores can and will remove or consume these small seeds.

Conclusions

Persistence of the soil seedbank will be regulated, in part, by the speed at which new seeds are incorporated into the soil (Egley and Williams 1990). Small seeds like Palmer amaranth are incorporated into the soil matrix more rapidly than larger seeds (Benvenuti 2007; Thompson et al. 1993; Westerman et al. 2009), and seeds are reported to be less susceptible to herbivory once they are buried in the soil (Hulme 1994; Thompson 1987; White et al. 2007). Although herbivory is believed to decline once seeds are buried in the soil, the current study indicates that depth of burial affects seed persistence in the absence of herbivory. Seeds near the soil surface will not be as persistent as those buried deeper. One of the proposed methods of reducing the potential seedling population within the seedbank is to reposition weed seeds that are near the soil surface to positions below optimal emergence zones through soil inversion (i.e., moldboard plow). The current study suggests that deep burial of Palmer amaranth seeds can mitigate problems, but only if the seeds stay buried below their germination zone for more than 36 mo, as 22% of the seeds in this study buried at 40 cm were still viable after 36 mo.

Palmer amaranth seeds were removed from seed traps in the current study, but their fate was not known. Many seed herbivores will not only consume weed seeds, but also actively disperse them (Seaman and Marino 2003; Zhang et al. 1997). Vander Wall et al. (2005) cautioned that seed removal from a trap should not be equated with seed herbivory, as seeds could be transported to microsites that favor seedling establishment. For instance, seeds of common ragweed (*Ambrosia artemisiifolia* L.) that were harvested by fire ants and relocated to their nutrient-rich mounds germinated and had greater abundance, plant heights, and plant biomass than adjacent plants not growing on the mounds (Seaman and Marino 2003). In light of the criticisms raised by Vander Wall et al. (2005) of equating seed removal and seed herbivory, additional studies are needed to characterize the fate of Palmer amaranth seeds once they are removed by potential herbivores from the seed traps and evaluate what factors in crop production systems can be altered easily to enhance seed herbivory.

Acknowledgment

Appreciation is expressed to Thomas Sklany for technical assistance.

Literature Cited

Anderson, R. L. 2007. Managing weeds with a dualistic approach of prevention and control. A review. Agron. Sust. Dev. 27:13–18.

Bell, M. S. and P. J. Tranel. 2010. Time requirement from pollination to seed maturity in waterhemp (*Amaranthus tuberculatus*). Weed Sci. 58:167–173.

Benvenuti, S. 2007. Natural weed seed burial: effect of soil texture, rain and seed characteristics. Seed Sci. Res. 17:211–219.

Borza, J. K., P. R. Westerman, and M. Liebman. 2007. Comparing estimates of seed viability in three foxtail (*Setaria*) species using the imbibed seed crush test with and without additional tetrazolium testing. Weed Technol. 21:518–522.

Brown, J. H. and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. Science 196:880–882.

Brown, J. H., J. J. Grover, D. W. Davidson, and G. A. Lieberman. 1975. Preliminary study of seed predation in desert and montane habitats. Ecology 56:987–992.

Burke, I. C., M. Schroeder, W. E. Thomas, and J. W. Wilcut. 2007. Palmer amaranth interference and seed production in peanut. Weed Technol. 21:367–371.

Burnside, O. C., R. S. Moomaw, F. W. Roeth, G. A. Wicks, and R. G. Wilson. 1986. Weed seed demise in soil in weed-free corn (*Zea mays*) production across Nebraska. Weed Sci. 34:248–251.

Burnside, O. C., R. G. Wilson, S. Weisberg, and K. G. Hubbard. 1996. Seed longevity of 41 weed species buried 17 years in eastern and western Nebraska. Weed Sci. 44:74–86.

Cardina, J., S. K. Harrison, E. E. Regnier, and J. T. Schmoll. 2002. Seeds as the targets for biological control of weeds. Pages 57–67 *in* Seminario International Departmento Do Ciencias Vegetales Semilas: Commercializacion, Producion y technologia 2002; Santiago, Chile. Cardina, J., H. M. Norquay, B. R. Stinner, and D. A. McCartney. 1996. Postdispersal predation of velvetleaf *(Abutilon theophrasti)* seeds. Weed Sci. 44: 534–539.

Cardina, J., T. M. Webster, C. P. Herms, and E. E. Regnier. 1999. Development of weed IPM: levels of integration for weed management. Pages 239–267 *in* D. D. Buhler, ed. Expanding the Context of Weed Management. New York: Haworth Press.

Cavers, P. B. 1983. Seed demography. Can. J. Bot. 61:3578–3590.

Chauhan, B. S., T. Migo, P. R. Westerman, and D. E. Johnson. 2010. Postdispersal predation of weed seeds in rice fields. Weed Res. 50:553–560.

Collins, G., A. S. Culpepper, D. Day, G. Harris, R. C. Kemerait, P. Roberts, D. Shurley, A. Smith, and J. Whitaker. 2010. 2010 Georgia Cotton Production Guide. University of Georgia Cooperative Extension Service, public. no. CSS-10-01. Available at: http://commodities.caes.uga.edu/fieldcrops/cotton/2010cottonguide/2010CottonProductionGuide.pdf. Accessed: March 22, 2010.

Conn, J. S., K. L. Beattie, and A. Blanchard. 2006. Seed viability and dormancy of 17 weed species after 19.7 years of burial in Alaska. Weed Sci. 54:464–470.

Culpepper, A. S., T. L. Grey, W. K. Vencill, J. M. Kichler, T. M. Webster, S. M. Brown, A. C. York, J. W. Davis, and W. W. Hanna. 2006. Glyphosate-resistant Palmer amaranth (*Amaranthus palmeri*) confirmed in Georgia. Weed Sci. 54:620–626.

DeVlaming, V. and W. P. Vernon. 1968. Dispersal of aquatic organisms: viability of seeds recovered from the droppings of captive killdeer and mallard ducks. Am. J. Bot. 55:20–26.

Dieleman, J. A., D. A. Mortensen, and A. R. Martin. 1999. Influence of velvetleaf (*Abutilon theophrasti*) and common sunflower (*Helianthus annuus*) density variation on weed management outcomes. Weed Sci. 47:81–89.

Egley, G. H. and J. M. Chandler. 1978. Germination and viability of weed seeds after 2.5 years in a 50-year buried seed study. Weed Sci. 26:230–238.
Egley, G. H. and J. M. Chandler. 1983. Longevity of weed seeds after 5.5 years in the Stoneville 50-year buried-seed study. Weed Sci. 31:264–270.
Egley, G. H. and R. D. Williams. 1990. Decline of weed seeds and seedling emergence over five years as affected by soil disturbances. Weed Sci. 38:504–510.
Faccini, D. and J. I. Vitta. 2005. Germination characteristics of *Amaranthus quitensis* as affected by seed production date and duration of burial. Weed Res. 45:371–378.
Forcella, F. 2003. Debiting the seedbank: priorities and predictions. Aspects Appl. Biol. 69:151–162.
Forcella, F., T. M. Webster, and J. Cardina. 2003. Protocols for weed seed bank determination in agro-ecosystems. Pages 3–18 *in* R. Labrada, ed. Weed Management for Developing Countries. Rome: Food and Agriculture Organization of the United Nations, Plant Production and Protection Paper 120 (add.1).
Forcella, F., R. G. Wilson, K. A. Renner, J. Dekker, R. G. Harvey, D. A. Alm, D. D. Buhler, and J. Cardina. 1992. Weed seedbanks of the U.S. corn belt: magnitude, variation, emergence, and application. Weed Sci. 40:636–644.
Gallandt, E. R. 2006. How can we target the weed seedbank? Weed Sci. 54:588–596.
Gallandt, E. R., T. Molloy, R. P. Lynch, and F. A. Drummond. 2005. Effect of cover-cropping systems on invertebrate seed predation. Weed Sci. 53:69–76.
Glantz, S. A. and B. K. Slinker. 2001. Primer of Applied Regression and Analysis of Variance. New York: McGraw-Hill. Pages 25–28.
Harrison, S. K., E. E. Regnier, J. T. Schmoll, and J. M. Harrison. 2007. Seed size and burial effects on giant ragweed (*Ambrosia trifida*) emergence and seed demise. Weed Sci. 55:16–22.
Hartzler, R. G. and G. W. Roth. 1993. Effect of prior years weed control on herbicide effectiveness in corn (*Zea mays*). Weed Technol. 7:611–614.
Heap, I. M. 2012. International Survey of Herbicide Resistant Weeds (http://www.weedscience.org/in.asp). Accessed October 19, 2012.
Heggenstaller, A. H., F. D. Menalled, M. Liebman, and P. R. Westerman. 2006. Seasonal patterns in post-dispersal seed predation of *Abutilon theophrasti* and *Setaria faberi* in three cropping systems. J. Appl. Ecol. 43:999–1010.
Hulme, P. E. 1994. Postdispersal seed predation in grassland: its magnitude and sources of variation. J. Ecol. 82:645–652.
International Seed Testing Association. 1985. International rules for seed testing. Seed Sci. Technol. 13:300–520.
Jordan, N., D. A. Mortensen, D. M. Prenzlow, and K. C. Cox. 1995. Simulation analysis of crop rotation effects on weed seedbanks. Am. J. Bot. 82:390–398.
Keeley, P. E., C. H. Carter, and R. J. Thullen. 1987. Influence of planting date on growth of Palmer amaranth (*Amaranthus palmeri*). Weed Sci. 35:199–204.
Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. Agr. Ecosyst. Environ. 74:187–228.
Lewis, J. 1973. Longevity of crop and weed seeds—survival after 20 years in the soil. Weed Res. 13:179–191.
Lutman, P.J.W., G. W. Cussans, K. J. Wright, B. J. Wilson, G. M. Wright, and H. M. Lawson. 2002. The persistence of seeds of 16 weed species over six years in two arable fields. Weed Res. 42:231–241.
Menalled, F. D., R. G. Smith, J. T. Dauer, and T. B. Fox. 2007. Impact of agricultural management on carabid communities and weed seed predation. Agr. Ecosyst. Environ. 118:49–54.
Menges, R. M. 1987. Weed seed population dynamics during six years of weed management systems in crop rotations on irrigated soil. Weed Sci. 35:328–332.
Mortensen, D. A., L. Bastiaans, and M. Sattin. 2000. The role of ecology in the development of weed management systems: an outlook. Weed Res. 40:49–62.
Neve, P., J. K. Norsworthy, K. L. Smith, and I. A. Zelaya. 2011. Modelling evolution and management of glyphosate resistance in *Amaranthus palmeri*. Weed Res. 51:99–112.
Norsworthy, J. K., S. Ward, D. R. Shaw, R. S. Llewellyn, R. L. Nichols, T. M. Webster, K. W. Bradley, G. Frisvold, S. Powles, N. R. Burgos, W. W. Witt, and M. Barrett. 2012. Reducing the risks of herbicide resistance: best management practices and recommendations. Weed Sci. Spec. Iss. 31–62.
Omami, E. N., A. M. Haigh, R. W. Medd, and H. I. Nicol. 1999. Changes in germinability, dormancy and viability of *Amaranthus retroflexus* as affected by depth and duration of burial. Weed Res. 39:345–354.
Proctor, V. W. 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. Science 160:321–322.
Sawma, J. T. and C. L. Mohler. 2002. Evaluating seed viability by an unimbibed seed crush test in comparison with the tetrazolium test. Weed Technol. 16:781–786.
Seaman, R. E. and P. C. Marino. 2003. Influence of mound building and selective seed predation by the red imported fire ant (*Solenopsis invicta*) on an old-field plant assemblage. J. Torrey Bot. Soc. 130:193–201.
Sellers, B. A., R. J. Smeda, W. G. Johnson, J. A. Kendig, and M. R. Ellersieck. 2003. Comparative growth of six *Amaranthus* species in Missouri. Weed Sci. 51:329–333.
Shurley, D., C. Bednarz, S. Anthony, and S. M. Brown. 2004. Increasing cotton yield, fiber quality, and profit through improved defoliation and harvest timeliness. University of Georgia Collge of Agricultural and Environmental Sciences, Circ. No. AGECON-04-94. (http://www.ces.uga.edu/Agriculture/agecon/pubs/comm/increasingcot.pdf) Accessed June 1, 2012. 3 p.
Spafford Jacob, H., D. M. Minkey, R. S. Gallagher, and C. P. Borger. 2006. Variation in postdispersal weed seed predation in a crop field. Weed Sci. 54:148–155.
Sparks, O. C., J. L. Barrentine, N. R. Burgos, and M. R. McClelland. 2003. Effect of Palmer amaranth (*Amaranthus palmeri*) seedbank density on the performance of pendimethalin and fluometuron. Sum Ark. Cotton Res. Res. Ser. 521:167–172.
Telewski, F. W. and J.A.D. Zeevaart. 2002. The 120-yr period for Dr. Beal's seed viability experiment. Am. J. Bot. 89:1285–1288.
Thompson, K. 1987. Seeds and seedbanks. New Phytol. 106:23–34.
Thompson, K., S. R. Band, and J. G. Hodgson. 1993. Seed size and shape predict persistence in soil. Func. Ecol. 7:236–241.
Vander Wall, S. B., K. M. Kuhn, and M. J. Beck. 2005. Seed removal, seed predation, and secondary dispersal. Ecology 86:801–806.
Van Mourik, T. A., T. J. Stomph, and A. J. Murdoch. 2005. Why high seed densities within buried mesh bags may overestimate depletion rates of soil seed banks. J. Appl. Ecol. 42:299–305.
Vencill, W. K., T. L. Grey, A. S. Culpepper, C. Gaines, and R. Westra. 2008. Herbicide resistance in the *Amaranthaceae*. J. Plant Dis. Prot. Spec. Iss. 21:41–44.
Webster, T. M., J. Cardina, and M. M. Loux. 1998. The influence of weed management in wheat (*Triticum aestivum*) stubble on weed control in corn (*Zea mays*). Weed Technol. 12:522–526.
Westerman, P. R., P. M. Dixon, and M. Liebman. 2009. Burial rates of surrogate seeds in arable fields. Weed Res. 49:142–152.
White, S. S., K. A. Renner, F. D. Menalled, and D. A. Landis. 2007. Feeding preferences of weed seed predators and effect on weed emergence. Weed Sci. 55:606–612.
Wise, A. M., T. L. Grey, E. P. Prostko, W. K. Vencill, and T. M. Webster. 2009. Establishing the geographical distribution and level of acetolactate synthase resistance of Palmer amaranth (*Amaranthus palmeri*) accessions in Georgia. Weed Technol. 23:214–220.
Zhang, J. X., F. A. Drummond, M. Liebman, and A. Hartke. 1997. Insect Predation of Seeds and Plant Population Dynamics. Orono: University of Maine, Maine Agricultural Forest Experiment Station Technical Bulletin. 163. 32 p.

Received July 20, 2012, and approved November 29, 2012.