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Postdispersal Loss of Important Arable Weed Seeds in the Midsouthern United States

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Postdispersal processes play an important role in the regulation of weed population dynamics. Experiments were conducted at two locations in Arkansas to understand postdispersal loss of five arable weed species important to this region—barnyardgrass, johnsongrass, pitted morningglory, Palmer amaranth, and red rice—between seed dispersal in autumn and the production of fresh seeds the subsequent autumn. Total seed loss through predation, decay, germination (fatal or successful), and loss in viability was estimated, and the influences of residue level and seed burial depth (near ground vs. 5 cm deep) were also examined. On average, the active (i.e., viable) seedbank proportion in spring (5 mo after dispersal) ranged from 8 to 11% (barnyardgrass), 10 to 11% (johnsongrass), 20 to 23% (pitted morningglory), 4 to 6% (Palmer amaranth), and 5 to 10% (red rice) across the two locations. At 1 yr after dispersal, 0.7 to 1.5% of barnyardgrass, 7 to 8% of johnsongrass, 5 to 9% of pitted morningglory, about 1.5% of Palmer amaranth, and 0.2 to 0.7% of red rice were part of the active seedbank for the two locations. There was no evidence to suggest that establishing a vegetation cover (such as a rye cover crop) after harvest of the main crop could accelerate seed predation. Burial depth did not influence seed decay, but most (45 [pitted morningglory] to 99% [Palmer amaranth]) of the seeds retrieved from the predator feeding stations were found buried in the soil substrate, and thus, not available for most predator species. This suggests that practices that allow weed seeds to lie on the soil surface (such as no-till planting in autumn) are highly valuable in encouraging seed predation. The high levels of seed loss observed in this study indicate that seedbank management should be a vital component of integrated weed management strategies.

Nomenclature: Barnyardgrass, *Echinochloa crus-galli* (L.) Beauv.; johnsongrass, *Sorghum halepense* (L.) Pers.; Palmer amaranth, *Amaranthus palmeri* S. Wats.; pitted morningglory, *Ipomoea lacunosa* L.; red rice, *Oryza sativa* L; cereal rye, *Secale cereale* L.

Key words: Microbial decay, seedbank, seed predation, viability loss,weed population dynamics, weed seed burial.

Postdispersal weed-seed loss, facilitated through predation, microbial seed/seedling decay, and loss in viability (i.e., senescence and physiological aging), is an important process regulating weed population dynamics in arable crop fields (Forcella 2003; Gallandt 2006; Kremer 1993; Liebman et al. 2001; Menalled et al. 2000; Westerman et al. 2003). The time between seed dispersal and seedling recruitment is particularly vulnerable for loss (Grubb 1977; Harper 1977), wherein enormous mortality could be achieved through biological interventions (Honek et al. 2009). Weed seeds are important food sources for several specialist or generalist granivorous fauna (invertebrates, such as ants and carabids, and vertebrates, such as rodents and birds) inhabiting agricultural landscapes (Liebman et al. 2001). Likewise, pathogenic microorganisms (such as deleterious rhizobacteria and fungi) can attack weed seeds (Kremer 1993) and seedlings before emergence (i.e., fatal germination) (Davis and Renner 2007). Successful seedling emergence is also considered a seedbank-loss process (Forcella 2003), but it will be a permanent loss only if weed escapes are prevented and fresh seeds are not allowed to replenish the seedbank. Additionally, loss in seed viability due to physiological aging and senescence can also affect the longevity of weed seedbanks (Forcella 2003). Among the seedbank processes, predation and decay are considered the two most important processes for depleting soil seedbanks (Thompson 1992).

Studies have documented high levels (exceeding 25 to 50%) of weed-seed loss associated with granivores (e.g., Cardina et al. 1996) or microbial organisms (e.g., Bridgemohan et al. 1991), levels often sufficient to slow down population growth rates (Davis et al. 2004; Westerman et al. 2005). The role of beneficial organisms in seedbank management has been widely recognized in organic and other low-input agricultural systems (O'Rourke et al. 2006: Westerman et al. 2003). In herbicide-intensive weed management systems, seedbank management is becoming increasingly important, especially where herbicide resistance is a threat. With the widespread occurrence of herbicide-resistant weeds, particularly in the midsouthern United States, there is a growing recognition that adoption of diverse strategies, including the use of beneficial organisms for seedbank management, is crucial for achieving sustainable weed management (Norsworthy et al. 2012). Models simulating herbicide resistance have shown that postdispersal seed loss and annual seedbank loss were two important parameters for which the models were highly sensitive, with reduction in resistance risk for every increase in seed loss and vice versa (Bagavathiannan et al. 2013; Neve et al. 2011).

A key question is how the depletive seedbank processes could be manipulated and encouraged as effective control tools through management practices. Some studies have found that establishing residue cover, such as mulches and cover crops, can provide foraging habitat and thereby promote predation (Gallandt 2006; Meiss et al. 2010). For instance, Shearin et al. (2008) showed that ground beetles preferred fields with cover crops compared with open, cultivated plots. Rye cover crops included in the residue management program can greatly promote beneficial granivores, such as carabids (Shearin et al. 2008). When seeds are buried because of tillage or other processes, they are typically unavailable for most epigeic predators. Buried seeds can, however, be attacked by microbial pathogens and subsequently lost from the active seedbank (Kremer 1993). The depth of seed burial can be an important consideration in that regard. In a 4-yr study of giant ragweed (*Ambrosia trifida* L.) seed decay in Ohio, Harrison et al. (2007) found that the rates of seed demise were

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inversely proportional to the depth of seed burial. Likewise, in Adelaide, Australia, Chauhan et al. (2006) reported that rigid ryegrass (*Lolium rigidum* Gaudin) seed decay was greater on the soil surface, compared with deep burial, suggesting that reduced tillage practices can promote weed seed loss through decay. Several microbial-decay studies reported final viable proportions, but did not explicitly test or discuss whether the loss in viability *per se* was affected by the treatments included in their studies (e.g., Egley and Chandler 1978; Noldin et al. 2006). Moreover, little is understood on how the soil physical environment may influence loss in viability (Forcella 2003). In one of the few experiments in which seed loss due to physiological aging was tested (Burnside et al. 1996), loss was greater in a mesic site than in an arid site in Nebraska, suggesting that high soil moisture conditions may accelerate seed aging.

There are some important methodological considerations when estimating seedbank loss. Firstly, most studies have quantified either predation (Cardina et al. 1996; Harrison et al. 2007) or microbial decay (Bridgemohan et al. 1991; Colosi et al. 1988), but not both, simultaneously. When seed viability was estimated in burial studies, viability was not explicitly tested. Although these studies provide great insights into seed loss through predation or decay, there is a benefit in studying them simultaneously under the same environmental and experimental conditions to better estimate total seedbank loss facilitated by those processes. Secondly, a number of predation studies used seed cards for simulating weed seed presence on the soil surface. It has been well established that experimental substrate can affect the rate of predation (Gallandt 2005) and that a soil substrate that closely resembles natural field conditions is important for realistic estimation of predation rates (Shuler et al. 2008). Finally, density dependence, which can be positive (Cromar et al. 1999), negative (Cardina et al. 1996), or change from negative to positive with increasing mobility of predators (Westerman et al. 2008), can greatly regulate predation rates (Marino et al. 2005; Reichman 1979). It is, therefore, important to consider natural seed densities in studies of weed seed predation (Saska et al. 2008). To our knowledge, this is the first study that considered these factors in estimating seedbank loss.

Little is known about the postdispersal fate of some of the problematic weeds in the midsouthern United States or about the ways to promote seedbank loss. The present study focuses on determining the postdispersal loss of barnyardgrass, johnsongrass, pitted morningglory, Palmer amaranth, and red rice (straw-hull biotype), five of the most problematic weeds in the midsouthern U.S., arable crop production systems (Norsworthy et al. 2013; Riar et al. 2013). The total seed loss was estimated through two field experiments aimed at (1) evaluating the effect of residue level on predation, decay, and loss through physiological aging (autumn to spring), and (2) understanding the influence of burial depth (near the ground or 5 cm deep) and duration (up to spring [5 mo] or autumn [1 yr]) on decay, germination (successful or fatal), and loss via aging.

Materials and Methods

Study Sites. The field experiments were performed between early November 2010 and late October 2011 at two locations in Arkansas: the Agricultural Experiment Station at Fayetteville (36.1°N, 94.17°W; elevation: 427 m), with a Taloka silt loam soil type, and the Northeast Research and Extension Center at Keiser (36.12°N, 90.15°W; elevation: 71 m), characterized by a Sharkey clay soil type. The locations lie in the humid, subtropical climate zone, with mild winters and warm summers, but microclimatic conditions varied between these two experimental sites during the course of the study (Figure 1). The Fayetteville study location was situated in the Ozark mountain valley, with the predominant agricultural land use in the region being pasture/grazing lands and specialty crops, whereas the Keiser research station was located in the Mississippi Delta region, a major agricultural area with cotton, soybean, corn, and rice as important crops. In each location, the trials were established in soybean [*Glycine max* (L.) Merr.] fields immediately after crop harvest in late autumn, and the experimental area measured about 1 ha in each research site.

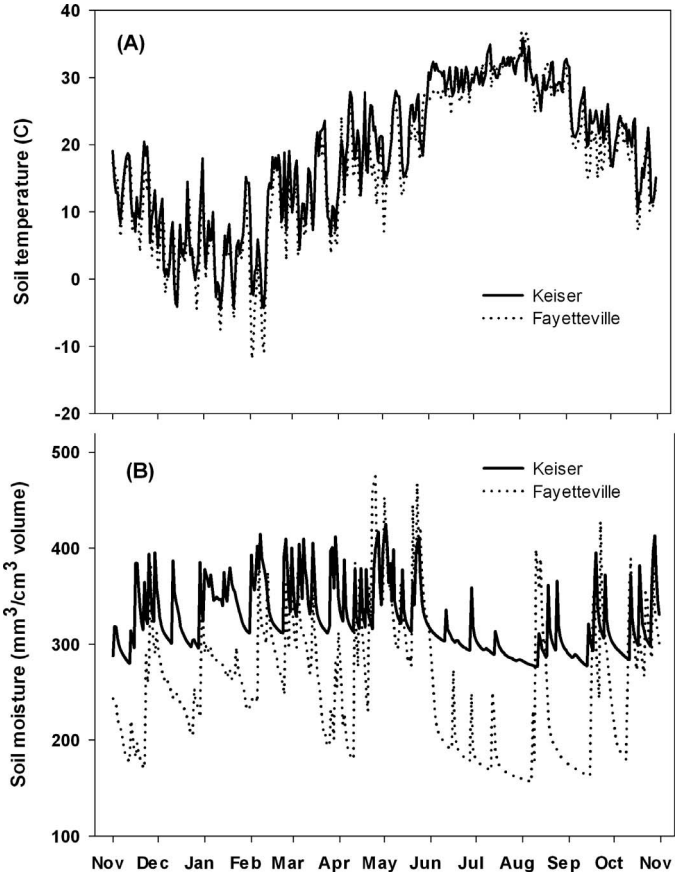

Figure 1. (A) Soil temperature and (B) moisture conditions estimated for the entire study period at the experimental sites in Fayetteville and Keiser, AR. The soil temperature and moisture conditions were simulated using the STM^2 model (Spokas and Forcella 2009).

Experimental Setup and Data Collection. There were two separate experiments to collectively estimate seed loss through predation, microbial decay, germination (successful or fatal), and physiological aging in the two study locations, but both experiments were conducted simultaneously in each site under the same environmental and experimental conditions. The first experiment (experiment 1) was carried out between early November and early April, and the second experiment (experiment 2) was established at the same time as experiment 1 in late autumn but had two observation times in the

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following year (early April 2011 and late October 2011). The focus of experiment 1 was to estimate total seed loss, when seeds are left on the soil surface after dispersal, and to understand how seed loss was influenced by residue level, whereas the aim of the experiment 2 was to understand the effects of burial depth and duration on the levels of seed loss. Two burial depths (near the ground and 5 cm deep) were chosen to represent subtle burial in the top soil layer by natural forces and shallow burial by a tillage operation typically used to establish a crop, respectively. The two observation times in experiment 2 were chosen to estimate seed loss before crop planting in early spring and before fresh seed return in late autumn. Seed loss through germination (successful or fatal) was less likely in experiment 1 and up to the first observation time in experiment 2 because weather conditions were not suitable for germination of the study species during that period (early November to early April, see Figure 1). The following section describes the methodology used in the two experiments.

Experiment 1. Experiment 1 was set up using plastic trays (i.e., predator feeding stations) measuring 113 cm^2 surface area and 5 cm deep. The bottom of the trays were removed and replaced with polyethylene mesh cloth (SEFAR Inc., Buffalo, NY) characterized by 500-µ pore spacing and 38% mesh opening. The trays were filled with soil (about three-quarters of the volume) collected from the experimental sites. Before filling, the soil substrate was examined in the laboratory and the seeds, if any, of the study species and other noticeable weed seeds were eliminated. Initial tests with the trays confirmed that the setup was sufficient to allow drainage of rainwater and to prevent escape of seeds through rain splash. Further, the trays were accessible, even for small invertebrates such as ants. The trays were then buried in the field such that the soil had a continuous surface between the trays and surrounding area. The soil was also compacted to match the surrounding field so that the soil substrate provided a closest resemblance to natural field conditions.

The experiment was arranged in a split-plot design, with three replications. Residue level (three levels: low, medium, and high) was considered as the whole-plot factor, and the plots were arranged in randomized complete blocks. Weed species (five levels: barnyardgrass, johnsongrass, pitted morningglory, Palmer amaranth, and red rice) was regarded as the subplot factor. Each whole-plot measured 25 m × 40 m and each subplot (1 m^2) was randomly assigned within the whole-plot such that they were at least 5 m apart from each other. Because of high variability anticipated, each subplot was replicated thrice within each whole-plot. In each whole-plot and for each weed species, three predator exclusion stations (i.e., control trays) were also set up to estimate seed loss in feeding stations caused by factors other than predation (typically microbial decay and loss in viability through aging). The Predator exclusion was accomplished by covering the seed trays with the polyethylene mesh cloth so that the predators would not have any access to the trays.

The soybean stubble present in the field after crop harvest represented a low-residue treatment (these plots were sprayed with labeled rates of glyphosate and flumioxazin to prevent the establishment of winter annual weeds), plots that consisted of naturally occurring winter annual weeds represented a medium residue level, and a no-till rye cover crop represented a high residue level. The rye crop was established at a seeding rate of 67 kg ha^{-1} and a row spacing of 18 cm. The crop was grown as a rain-fed, no-input culture. Residue level (total mass and ground cover) was determined for each plot before the initiation of the experiment in early November and again at the termination of the experiment in early April. Ground cover was visually estimated from four randomly placed quadrates (50 cm × 50 cm) in each plot. Soybean stubble and other plant residue present in each quadrate were collected/harvested, air dried, and weighed to estimate total residue mass. The residue levels were similar among the treatments before the initiation of the study (approximately 0.5 kg m^{-2} with 10 to 15% ground cover), whereas the residue levels for the low, medium, and high residue treatments at the termination of the experiment ranged from 0.5 to 0.7 kg m^{-2} with 10 to 15% ground cover, 0.8 to 1 kg m^{-2} with 70 to 85% cover, and 2 to 2.5 kg m^{-2} with 90 to 100% cover, respectively.

We aimed to simulate seed densities produced by random escapes within a weed patch, as expected in a typical production field. Within each subplot, respective weed seeds were dispersed around each tray to reflect natural seed densities that might be expected after harvest. About 20,000 barnyardgrass seeds (250 in the tray), about 250,000 Palmer amaranth (tray: 2500), about 10,000 johnsongrass (tray: 100), about 2,500 red rice (tray: 50), and about 7,500 pitted morningglory (tray: 100) seeds were dispersed with the known number of seeds taken in each tray to correspond to the surrounding seed density on an area basis. In the predation exclusion trays, 100 seeds of respective weed species were placed. The weed seeds used in all experiments were sourced locally from freshly harvested plants.

Before initiation of the study, initial seed germination and viability levels were characterized for each weed population. A subsample was drawn from each seed lot and six replications of 25 seeds each were placed on a filter paper (Whatman's No. 1, Fisher Scientific, Suwanee, GA) and soaked with deionized water and a fungicide (1% captan solution) in a 55-mm-diam petri dish. The seed samples were incubated at 30 C under white-fluorescent tubes with a 12-h photoperiod, and germination was evaluated after 14 d. Following that, the viability of the nongerminated seeds was estimated using the tetrazolium seed testing procedure (Peters, 2000). For that purpose, the seed coats were pierced to allow for imbibition of the tetrazolium chloride solution. The final viable proportion was calculated as the combination of the number of seeds germinated plus the number of seeds that tested positive in the tetrazolium seed test, out of the total seeds examined. Additionally, the background seedbank level in the experimental field (on the thin soil surface layer) was assessed before the initiation of the study, by collecting 10 random soil cores in each whole-plot at a depth of 1 cm. The core samples from each plot were pooled and washed in running water, and the retrieved seeds were weighed to estimate preexisting food source in each plot.

The feeding trays were collected from the experimental fields before seed germination in early April 2011. In each tray, the number of seeds left over on the soil surface was counted, removed, and the soil was subsequently washed in running water to document seed burial within the trays. To establish a relationship between seed size and burial rates in the feeding trays, average seed sizes (vertical diameter at the landing position) were established for each species based on 10 random seeds using a vernier caliper. Any decayed seed

(lack of seed contents when pressed) was counted and excluded from predation estimates, but the level of seed loss in predator exclusion trays provided a better means for estimating decay. The intact seeds retrieved from predator exclusion trays, which were placed within various residue treatments, were subjected to tetrazolium viability test as described above to estimate seed loss due to aging. The final viable proportions are corrected for initial viability of the seed lot before the initiation of the study.

Experiment 2. Experiment 2 was a seed burial study carried out in an area immediately adjacent to the experiment 1. The study was conducted using seed bags made of the same polyethylene mesh cloth material used in experiment 1, with each bag measuring 15 cm × 15 cm. The bags provided a convenient means to prevent predation and seed emigration, while allowing the passage of water and solutes. The study was conducted in a factorial, randomized complete-block design (block area: 10 m × 10 m) with four replicates per treatment. The first factor included two burial depths (near the ground and 5 cm deep), and weed species (five levels) was considered as the second factor. The retrieval time/burial duration (early April 2011 [5 mo] and late October 2011 [1 yr]) was added as a third factor to determine seed demise at those intervals. The experiment also included two control treatments. In the first, eight soil-filled seed bags (four for each retrieval time) for each weed species were stored in a cold room at 4 C. In the second, the seed samples were stored in storage containers under room temperature (25 C) to estimate the natural changes in viability during the course of the experiment. A total of 200 seed bags were used in the experiment. In each location, weather conditions, including daily maximum and minimum air temperatures and precipitation, were recorded throughout the duration of the study. Daily soil temperature and moisture levels were estimated for each experimental site using the STM^2 model (Spokas and Forcella 2009).

To create an artificial seedbank that mimics natural conditions as closely as possible, soil collected from each experimental site was used as a carrier material in the seed bags, as suggested by Chee-Sanford and Fu (2010). The soil material was carefully processed to remove weed seeds, plant residues, and other particulates to create uniform starting conditions. Two hundred, even-sized seeds were thoroughly mixed with the soil, placed in each bag, and sealed. This setup greatly avoided seed-to-seed contact in the bags, which otherwise can overestimate depletion rates (Van Mourik et al. 2005), and simulated conditions natural to each soil type. At each retrieval time, the seed bags were removed from the experimental site and were stored at 4 C while being processed. The seed bags were opened, and the contents were transferred to a container. Germinated seeds (radicle present), if any, were counted and removed, and the rest of the material was washed in running water to extract the seeds. The seeds were then carefully hand-sorted and categorized either as intact seeds with no visible signs of damage or decayed seeds (devoid of seed contents).

The decayed seed proportion in the seed bags also included any fatally germinated seeds from pathogenic attack (Davis et al. 2005) and seedling death caused by the physical barrier provided by the bags (otherwise successful recruitment). It is difficult to differentiate seed loss caused by those pathways because of the rapid degradation of dead seedling tissue (Schafer and Chilcote 1969); thus, the total seed loss in the seed bags is presented as a pooled estimate of loss through decay and germination (fatal or successful). As mentioned above, it was less likely that germination occurred in seed bags at the spring retrieval because the environmental conditions were not conducive. The retrieved seeds, along with the seeds stored in the cold room and under room temperature, were tested for viability and germination as described above.

Data Analysis. The proportion of seed loss through predation was calculated as,

$$P = \{[(T - I)/T] \times 100\} - D_e \quad [1]$$

where P is the proportion of predation from each feeding tray, T is the total number of seeds placed in each tray, I is the total number of intact seeds retrieved, and D_e is the proportion of decayed seeds in the predation exclusion trays, which was calculated as,

$$D_e = [(T_e - I_e)/T_e] \times 100 \quad [2]$$

where T_e and I_e represent, respectively, the total number of seeds placed and the number of intact seeds retrieved in the predation exclusion trays. The proportion of decay in the seed bags was calculated similar to D_e, as described above.

Those data pertaining to seedbank loss were analyzed using the generalized linear mixed model procedure (PROC GLIMMIX) in SAS (version 9.3, SAS Institute, Cary, NC), which is robust for nonnormal response variables and where data distribution pertains to the exponential family. Initial seedbank densities estimated from different plots were considered as covariates in analyzing predation levels. There was high variability in the response variables, resulting in overdispersion of the data. For count data, overdispersion can be adequately considered with a negative binomial distribution. An effective alternative to that is the generalized Poisson distribution, as shown by Joe and Zhu (2005). A log–link function and Poisson distribution were assigned to the GLIMMIX model to account for the overdispersion of data. Following the model analysis, mean separation was performed using the Fisher's Protected LSD test ($\alpha = 0.05$). The association between weed-seed size and the level of burial was tested using the Pearson correlation coefficient analysis using PROC CORR in SAS.

Results and Discussion

Experimental Setup. The study design and setup allowed us to collectively estimate postdispersal weed-seed loss as affected by predation, decay, germination, and loss in viability. We believe that the levels of cumulative seed loss estimated here are more realistic than they are in experiments involving separate studies to estimate each of the seedbank processes. The study setup sufficiently simulated natural seed density and spatial patterns typical of random weed escapes. Further, the use of soil substrate in predation trays provided a close representation of field conditions. Although it was laborious and tedious to extract seeds from each tray, particularly those of Palmer amaranth, doing so allowed the quantification of seed burial, a vital process that may greatly affect the fate of dispersed weed seeds.

We did not attempt to characterize predator activity in the experimental fields because of resource limitations. Moreover,

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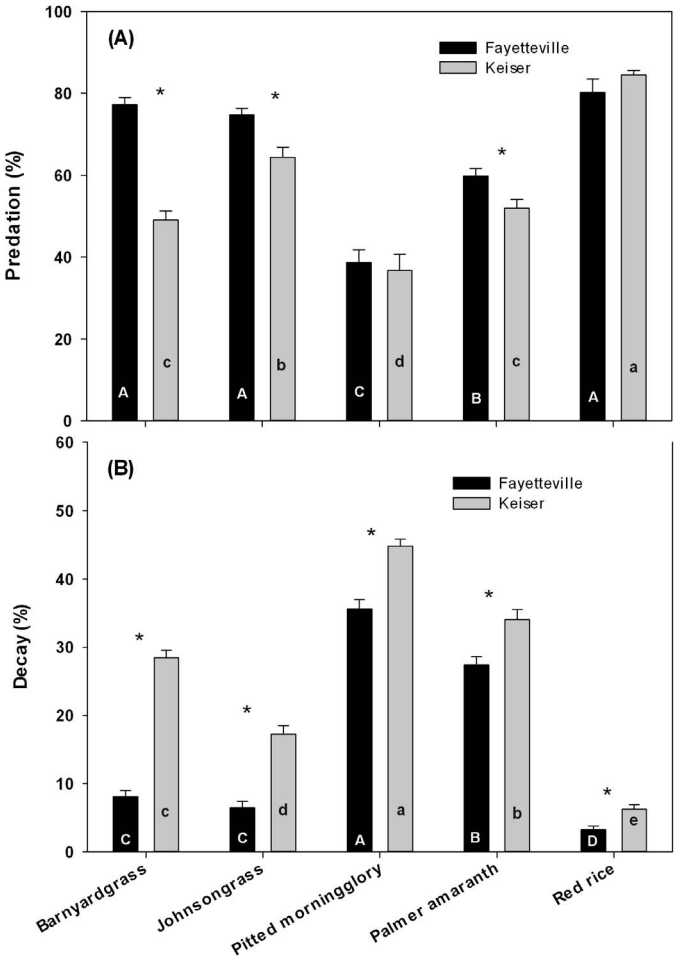

Figure 2. The level of seed loss caused by (A) predation and (B) decay for the various weed species in Fayetteville and Keiser, AR, for the period between autumn and spring. The lines above each bar indicate standard errors of the mean. Weed species denoted by the same capital (Fayetteville) or small (Keiser) letters were not significantly different based on Fisher's Protected LSD test ($\alpha = 0.05$), and the asterisks indicate significant differences between the locations.

it would be very difficult to establish associations with specific predator activity and predation rate in a long-term study like this one, where substantial temporal variations are expected in predator activities and predation rates and point estimates are required to establish such associations. We estimated seed predation based on seed number rather than seed mass removed. The amount of seed material available for predators in feeding trays differed among the weed species, depending on fecundity and seed size. Approximate seed masses taken in feeding trays were 0.37 g for barnyardgrass, 0.39 g for johnsongrass, 0.64 g for Palmer amaranth, 1.14 g for red rice, and 2.22 g for morningglory. Results could have been different if seed loss was estimated based on mass removed, but reduction in seed number is a more useful estimate for its influence on weed population dynamics.

There were also some challenges with the experimental setup that need to be considered in interpreting the results. The polyethylene mesh cloth used to achieve predator exclusion in feeding trays could have influenced microclimatic conditions, possibly favoring pathogen activity. The different residue treatments used in the study differed in quality (poor-quality soybean stubbles vs. high-quality rye cover crop) in addition to quantity. Cromar et al. (1999) indicated that seed predators prefer high-quality residues and that the quality of residue is as important as the quantity of residue cover in encouraging weed-seed predation. In the present study, there was a confounding of cover quality and quantity, which was not explicitly studied. One has to be cautious in interpreting the predation rates observed as a measure of seed removal. It has been suggested that not all removed seeds were consumed and lost; thus, predation may favor secondary seed dispersal (e.g., Chambers and MacMahon 1994; Vander Wall et al. 2005). The levels of secondary dispersal, however, are usually very low (Forget 1996; Levey and Bryne 1993), and it is reasonable to assume that seed removal in feeding stations is a useful estimate of actual seed loss. Furthermore, the present study was conducted in only 2 site–yr, and actual seed loss might vary across different environments. Yet, the study allows a reasonable estimation of the likely levels of postdispersal seed loss in the midsouthern U.S. region.

Table 1. Significance of various effects for predation, decay, seed burial, and viability loss, tested using the GLIMMIX model.

	P value			
Effect	Predation	Decay[a]	Seed burial[b]	Viability loss[c]
Location	< 0.0001	< 0.0001	0.0262	0.9505
Residue	0.6536	0.4548	0.9691	0.6969
Location × residue	0.0954	0.0663	0.9388	0.5109
Species	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Location × species	< 0.0001	< 0.0001	0.0422	0.4478
Residue × species	0.3799	0.3000	0.7485	0.7338
Location × residue × species	0.6539	0.0762	0.9728	0.1474

[a] For the period between autumn and spring.
[b] Buried proportion out of the total retrieved seeds.
[c] Loss in viability under field conditions from seed dispersal in autumn to the subsequent autumn.

Postdispersal Seed Loss. *Predation.* Results indicate that predation was the most important factor that accounted for most of the seed loss (Figure 2A), and such levels can be comparable to mechanical weed control (Westerman et al. 2003). The significance of various factors and their interactions are provided in Table 1. There was a significant location by species interaction ($P < 0.0001$). In the Fayetteville location, seed loss was the greatest for red rice (80%), barnyardgrass (77%), and johnsongrass (75%), followed by Palmer amaranth (60%) and by pitted morningglory (39%), whereas at the Keiser location, seed loss was observed in the following order: red rice (85%) > johnsongrass (64%) > Palmer amaranth (52%), barnyardgrass (49%) > pitted morningglory (36%) (Figure 2A). Comparisons between the locations for each species showed greater seed loss at the Fayetteville location for barnyardgrass, johnsongrass, and Palmer amaranth, and location differences were not significant for pitted morningglory and red rice. It was difficult to explain the differences in seed loss, especially given that the predator species were not identified. Landis and Marino (1999) suggested that weed seed predation would be greater in noncrop landscapes (the Fayetteville location in this study) but, as shown above, such an association was not consistent in our study. Seed predation is likely influenced by several spatially and temporally variable factors, weed species, and their interactions, and it is difficult to ascribe it solely to a particular landscape characteristic.

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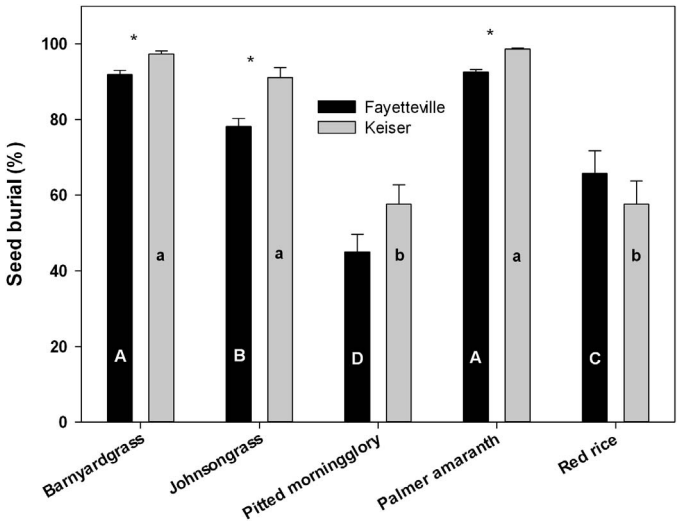

Figure 3. The proportion of seed burial observed among the retrieved seeds in feeding trays for the various weed species in Fayetteville and Keiser, AR. The lines above each bar indicate standard errors of the mean. Weed species denoted by the same capital (Fayetteville) or small (Keiser) letters were not significantly different based on Fisher's Protected LSD test ($\alpha = 0.05$), and the asterisks indicate significant differences between the locations.

The effect of residue treatments and their interactions with other factors were not significant. This observation corroborates other studies (e.g., Harrison et al. 2003; Jacob et al. 2006) that demonstrated that residue cover does not influence predation rates. It is likely that the amount of residue produced by winter annual weeds and rye cover crop were insufficient before spring regrowth to provide hideouts for large predators. However, the residue treatments were implemented such that they mimicked practices that can be adopted by growers after crop harvest. Planting a vegetation cover in autumn, such as a rye cover crop, may not be sufficient in influencing weed-seed predation in this region.

The levels of predation differed greatly among the weed species studied. Seed loss was greatest with red rice (up to 85%) and lowest (as low as 37%) with pitted morningglory across the two locations, which may suggest that some species are preferred more than others. Studies have established that larger animals prefer to feed on large seeds (Brust and House 1988) because small seeds are relatively harder to find and offer limited resources per seed compared with large ones (Shuler et al. 2008). Although large animals prefer large seeds, our anecdotal observations suggest that large seeds can also be predated by a group of small invertebrates, such as ants. Based on the present study, it appears that the relationship between seed size and predation rate is more complex than usually thought. For instance, predation in Palmer amaranth (average diameter: 0.69 mm) was greater than that of pitted morningglory (average diameter: 2.93 mm), but less than that of johnsongrass (average diameter: 1.45 mm) within the same experimental site. Other studies have suggested that seed attractiveness to predators, resulting from physical attributes, palatability, and nutritional status can also influence the levels of predation (e.g., Jorgensen and Toft 1997). It was difficult to establish weed species preferences based on observed predation rates (percentage of seed removal) because the consumption of a few large seeds could have been sufficient to a relatively small predator, even if that was a preferred seed.

An important observation is that most of the seeds (45 [pitted morningglory] to 99% [Palmer amaranth]) recovered from the feeding trays were found buried in the top soil layer (Figure 3). It is most likely that seed burial had prevented predation in the feeding trays. Although some predators can consume buried seeds (e.g., White et al. 2007), the likelihood of seed loss is much lower in buried seeds compared with the exposed ones (Puricelli et al. 2005). There was a significant location by species interaction ($P = 0.0422$) for seed burial (i.e., proportion of buried seeds out of total retrieved seeds), but burial was not influenced by residue cover (Table 1). In the Fayetteville location, seed burial was the greatest in Palmer amaranth (93% of retrieved seeds were buried) and barnyardgrass (92%) and was the lowest in pitted morningglory (45%). In the Keiser location, there was a clear distinction in seed burial levels between small-seeded (Palmer amaranth [99%], barnyardgrass [97%], and johnsongrass [91%]) and large-seeded (red rice [58%] and pitted morningglory [57%]) weeds (Figure 3). The trajectories of seed burial are likely to be robust in clay soil (a characteristic of the Keiser location), where fine texture can cause seed entrance into cracks and rapid incorporation in the soil matrix because of rain splash and runoff. A correlation analysis revealed a significant negative correlation between burial and seed size (Pearson's correlation coefficient: -0.6578, $P < 0.0001$). In general terms, seed burial occurred in the following order: Palmer amaranth (diameter: 0.69 mm) > barnyardgrass (0.98 mm) > johnsongrass (1.15 mm) > red rice (1.68 mm) > pitted morningglory (2.93 mm). Our findings indicate that smaller seeds can be easily buried in soil particles, supporting Westerman et al. (2009), who showed, using surrogate seeds (beads), that the rate of burial is a function of seed size.

Seed Decay and Germination. The levels of decay were similar between the predator exclusion trays and seed bags (both near the ground and 5 cm deep) for the period between autumn and spring; thus, data were pooled for each location. The significance of various factors and their interactions for seed decay and germination are provided in Table 1. There was a significant location by species interaction ($P < 0.0001$) for seed decay for this period. In the Fayetteville location, the decay of barnyardgrass (8%) and johnsongrass (6%) were comparable, but in the Keiser location, seed loss from decay was significantly greater in barnyardgrass (28%) than it was in johnsongrass (17%) (Figure 2B). It was not clear why there was such an interaction. However, comparisons between the two locations for each weed species show that seed decay was consistently greater in the Keiser location for all species (Figure 2B). The weather conditions (Figure 1) indicate that the relatively high organic matter (approximately 2.8%) clay soil in the Keiser site was slightly warmer, with substantially greater soil moisture content, than that of the low organic matter (approximately 1.8%) silt loam soil in the Fayetteville site. High soil moisture conditions (Pieczarka and Abawi 1978), warmer temperatures (Franzluebbers et al. 2001), and soil organic-matter enrichment (Marinari et al. 2000; Perucci 1990) may enhance soil microbial activity. Explicit studies are necessary to establish relationships between soil moisture, temperature, and organic matter content on the level of seed demise through microbial decay. The depth of seed burial (near the ground vs. 5 cm deep), however, did not influence

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Table 2. Viability levels after loss through physiological aging for five weed species after storage at cold (4 C) or room (25 C) temperature or after being exposed to field conditions for 5 mo or 1 yr.

	Viability[a]					
	4 C		25 C		Field	
Species	5 mo	1 yr	5 mo	1 yr	5 mo	1 yr
	%					
Barnyardgrass	94.13 a (2.2)	87.85 b (1.2)	89.16 b (2.2)	79.87 b (2.0)	81.5 b (2.11)	10.44e (1.1)
Johnsongrass	97.27 a (1.0)	94.55 a (0.9)	95.22 a (1.5)	89.21 a (1.9)	76.7 c (2.08)	47.6 b (1.97)
Pitted morningglory	98.29 a (0.3)	96.26 a (0.7)	98.32 a (1.4)	94.91 a (2.1)	89.3 a (1.18)	78.9 a (1.0)
Palmer amaranth	98.88 a (1.9)	97.22 a (1.0)	97.87 a (2.6)	94.57 a (2.4)	56.3 d (1.22)	16.72 d (1.7)
Red rice	96.96 a (1.2)	95.61 a (0.6)	95.72 a (1.2)	90.14 a (1.9)	80.17 b (0.82)	31.37 c (2.1)

[a] The 5 mo and 1 yr periods represent, respectively, the period from seed dispersal in autumn to emergence in spring and the period to subsequent seed return in autumn. Values were corrected for initial viability levels and include germination proportion. Within each column, means followed by the same letters are not significantly different based on Fisher's Protected LSD test ($\alpha = 0.05$), and values in parenthesis indicate standard errors of the mean.

the rate of seed demise in the seed bags, irrespective of the location or species.

It is likely that in situ germination could have greatly contributed to the seed loss observed in seed bags between spring and autumn, which has been commonly observed and well documented (e.g., Schafer and Chilcote 1969). There were indications that seed dormancy levels played a vital role in the proportion of seedbank still active after 1 yr. In the present study, pitted morningglory and johnsongrass were the most persistent species, which corresponded to the levels of seed dormancy observed in our germination and viability tests (data not shown). There were indications that the dormancy was largely primary in nature caused by hard seed coats, as germination occurred when the seed coats were pierced for tetrazolium viability test (visual observations). This also explains why the seedbank longevity was the lowest in red rice; the straw-hull biotype used in this study, which is a predominant red rice biotype in the midsouthern United States, is known to lack seed dormancy (Noldin et al. 2006). Seedbank longevity due to impermeable seed coats was also observed elsewhere (e.g., Egley and Chandler 1978; LaCroix and Staniforth 1964). The levels of seed loss observed for red rice in the present study corroborates Noldin et al. (2006), who recovered < 1% viable red rice seeds 12 mo after burial at 0 cm or 0 to 12% viable seeds when buried at 12 cm in Texas. Egley and Chandler (1978) estimated seed loss of a number of weeds, including pitted morningglory, redroot pigweed (*Amaranthus retroflexus* L.), johnsongrass, and barnyardgrass, using a long-term burial study in Stoneville, MS. The reduction in seed longevity reported in the present study followed the general trend observed by Egley and Chandler (1978).

Physiological Aging. Quantification of natural loss in viability due to physiological aging revealed that the loss was the greatest under field conditions, followed by storage at 25 C and at 4 C (Table 2). The degree of viability loss due to aging was indirectly proportional to the duration (i.e., seed age) but was not influenced by residue cover, burial depth, or location (Table 1). Loss in seed viability differed among the weed species ($P < 0.0001$). When exposed under field conditions for 1 yr, seed viability conformed to the following order among the weed species studied: pitted morningglory (79%) > johnsongrass (48%) > red rice (31%) > Palmer amaranth (17%) > barnyardgrass (10%) (Table 2).

Seed aging causes deterioration and viability loss through various biochemical changes (Kerter et al. 1997; Spano et al. 2006). The differences among the weed species in the rate of decline in viability could be attributed to inherent genetic and physiological characteristics and their interactions with the physical environment. The high seed longevity under cold storage is generally attributed to low temperatures and low moisture conditions (Roberts 1972). High levels of seed viability loss observed under field conditions could have been due to high temperature and moisture conditions compared with cold storage. It has been recognized that high moisture (Burnside et al. 1996) and humidity (Baskin and Baskin 1998) may reduce seed viability. However, there is no indication from the present study on ways to increase the rate of physiological aging as a means of depleting the seedbank under field conditions. There needs to be experiments exclusively focused on understanding this process under a range of controlled and field conditions. Existing research in this area has largely focused on the effect of accelerated aging processes on the physiological changes in seeds under storage, specifically aimed at improving storage of various crop species (e.g., Dell'Aquila 1994; Kaewnaree et al. 2011). Forcella (2003) suggested that the accelerated aging experiments help us recognize some of the possible mechanisms of seed loss in soil, but those studies may not be directly applied to the viability loss of weed seeds.

The mean active seedbank proportion (after accounting for the various depletive seedbank processes) in spring ranged from 8 to 11% (barnyardgrass), 10 to 11% (johnsongrass), 20 to 23% (pitted morningglory), 4 to 6% (Palmer amaranth), or 5 to 10% (red rice) across the two locations (Figure 4A), and at 1 yr after seed dispersal the previous autumn, 0.7 to 1.5% of barnyardgrass, 7 to 8% of johnsongrass, 5 to 9% of pitted morningglory, about 1.5% of Palmer amaranth, and 0.2 to 0.7% of red rice were found comprising the active seedbank (Figure 4B).

Management Implications. The comprehensive estimation of postdispersal seed loss in our study indicates that most weed seeds are lost from the system within a relatively short period. There was evidence from our study to suggest that postdispersal seed loss could be enhanced by some management strategies. A key strategy in this regard would be the prevention of weed seeds from being buried and incorporated into the soil because, once buried, they are largely unavailable for most seed predators and subsequent loss is dependent on other relatively less-important processes. Avoiding fall tillage is particularly critical and, in situations where a cover crop or a winter crop is established after harvest of the main-season

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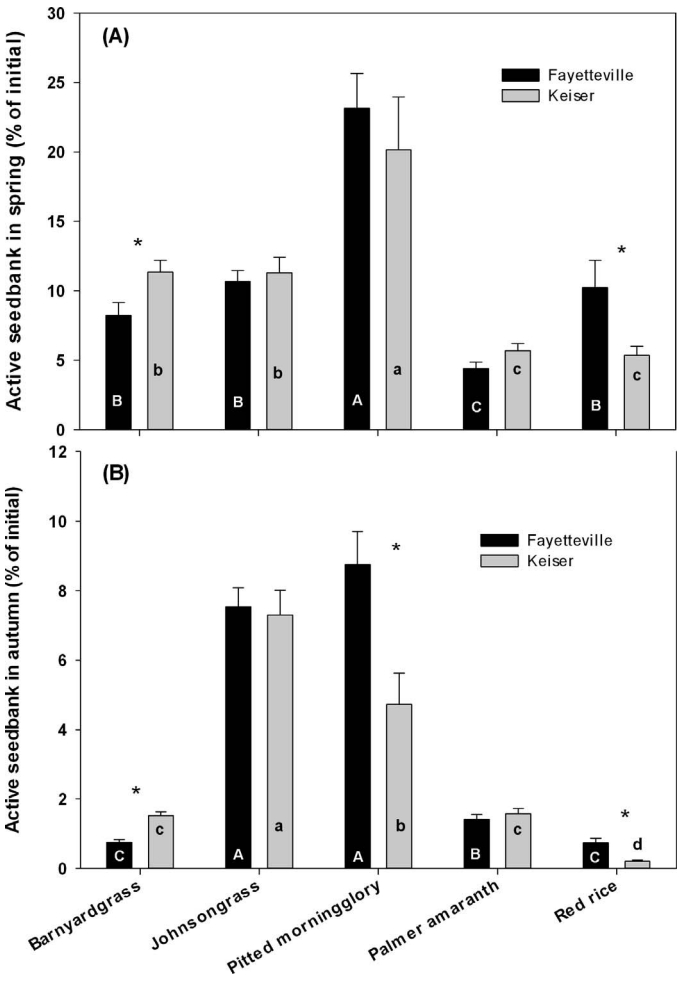

Figure 4. The proportion of active seedbank still present in (A) the subsequent spring and (B) autumn after dispersal in the previous autumn, for the various weed species in Fayetteville and Keiser, AR. The active seedbank in spring is the remnant seedbank after loss through predation, decay, and loss in viability, whereas the final active seedbank in autumn includes subsequent seed loss through decay, germination (successful or fatal), and loss in viability. The lines above each bar indicate standard errors of the mean. Weed species denoted by the same capital (Fayetteville) or small (Keiser) letters were not significantly different based on Fisher's Protected LSD test ($\alpha = 0.05$), and the asterisks indicate significant differences between the locations.

crop, reduced- or no-tillage practices should be preferred. Prevention of seed burial is particularly important for small-seeded weeds, such as Palmer amaranth, where the magnitude of seed burial can be high. Based on the limited evidence from this study, practices to improve soil temperature, organic matter and moisture conditions may promote microbial activity and result in pathogenic seed decay.

Although seed loss due to postdispersal processes is very high, the following factors need to be considered in interpreting the results for making management decisions. Firstly, the remaining seedbank proportion might still comprise numerous seeds in a field, given the profuse seed production by weeds. Secondly, the leftover seeds constitute the most persistent proportion of the seedbank. Forcella (2003) rightfully argued that the value of decreasing seedbank density is much greater when the seedbank size is low, because the proportional chance of the leftover seeds to sustain the population is much greater under low densities. This means that enough effort should be placed on depleting seedbanks to low levels, but even more effort should be invested in maintaining the seedbank size at those low levels or reducing them even further. Thirdly, the final seedbank size reported here (Figure 4B) represents the level before seed rain from the escapes (among the successful recruits). High seedling recruitment may rapidly deplete seedbank size, but that size can be sustained only if any seed return is prevented from weed escapes. Readers can consult Bagavathiannan and Norsworthy (2012) for a detailed discussion on late-season management considerations for weed escapes. The herbicide-resistance simulation models (Bagavathiannan et al. 2013; Neve et al. 2011) have shown that the risks of resistance evolution is greater when seedling recruitment is high because successful recruitment increases the probabilities of seed production and seedbank renewal, rather than being lost to seedbank processes. This possibly explains why barnyardgrass and red rice are still problematic in the midsouthern United States, even though they have a relatively short-lived seedbank, further stressing the importance of managing weed escapes and preventing seedbank renewal. Seed emigration can also be an important process leading to postdispersal seed loss (Forcella 2003), but it was not investigated in the present study, and research in that area is limited.

Overall, results suggest that postdispersal seed loss processes can greatly regulate the population dynamics of weeds and support the notion that the period between dispersal and recruitment is a highly vulnerable period in the life cycle of weeds. Thus, seedbank management should be an integral component of weed management programs. A strong focus on seedbank management can be a viable, nonchemical strategy that can be integrated into any weed management system, but is an underinvestigated and underused strategy. More research and extension efforts are necessary to better exploit the benefits offered by biotic interactions and other cultural strategies in weed seedbank management. Future research should also identify important weed-seed predators in the midsouthern U.S. region and investigate effective ways to promote seed loss.

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