Weed Science 2016 64:80–86

Invertebrate Seed Predators Reduce Weed Emergence Following Seed Rain

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Weeds are selected to produce overwhelming propagule pressure, and while vertebrate and invertebrate seed predators destroy a large percentage of seeds, their ecosystem services may not be sufficient to overcome germination site limitations. Cover crops are suggested to facilitate seed predation, but it is difficult to disentangle reductions in weed recruitment attributable to granivores from those due to plant competition. Using common lambsquarters as a focal weed species, we used experimental seed subsidies and differential seed predator exclusion to evaluate the utility of vertebrate and invertebrate seed predators in fallow, killed cover crop, and living mulch systems. Over two growing seasons, we found that seed predators were responsible for a 38% reduction in seedling emergence and 81% reduction in weed biomass in fallow plots following simulated seed rain, suggesting that granivory indeed overcomes safe-site limitation and suppresses weeds. However, the common lambsquarters densities in ambient seedbanks across fallow and cover crop treatments were high, and seed predators did not impact their abundance. Across the study, we found either neutral or negative effects of vertebrate seed predators on seed predation, suggesting that invertebrate seed predators contribute most to common lamnsquarters regulation in our system. These results imply that weed seed biocontrol by invertebrates can reduce propagule pressure initially following senescence, but other tools must be leveraged for long-term seedbank management.

Nomenclature: Common lambsquarters, *Chenopodium album* L. CHEAL.

Key words: *Chenopodium album*, cover crops, seed limitation, weed seed predation.

Seed predators, including ants, crickets, ground beetles, and small mammals are ubiquitous residents of crop environments, and all contribute to weed seed biological control. Their capacity to limit weed recruitment is frequently examined, particularly in organic systems where weed management is labor-intensive (Landis et al. 2005). Seed predators destroy a large percentage of weed seeds each year, but weeds are selected to produce overwhelming propagule pressure. For example, a single annual weed can approach 176,000 seeds per plant (Clements et al. 1996), and thus weed seed biological control can only have an agriculturally relevant impact if seed predators allow fewer escaped propagules than available germination sites (Lundgren 2009). Studies have shown that seed predation can reduce plant recruitment in natural systems (Crawley 1992; Turnbull et al. 2000). Yet, seed limitations have not been clearly established in agroecosystems (Boyd and Van Acker 2004).

Numerous studies document high seed predation rates using episodic point estimates of seed removal (Fox et al. 2013; Gallandt et al. 2005; O'Rourke et al. 2006), and simulation models suggest that seed predation is an important factor limiting seedbank flux (Westerman et al. 2006), but few connect the action of seed predators with subsequent weed growth (Brust 1994; White et al. 2007). Due to seasonal tillage requirements in most working agricultural systems, it is difficult to directly measure the impact of weed seed predators on seedling emergence at a particular site, limiting our ability to precisely evaluate how seed predators ultimately drive weed demography (but see White et al. 2007). Nonetheless, the current body of literature has helped to identify local habitat factors that affect seed predator foraging. These include insecticide use, tillage regimes, proximity to untilled margins, and vegetative cover (Landis et al. 2000).

Both vertebrate and invertebrate seed predators utilize available vegetative resources like cover crops, and cover may facilitate weed seed destruction (Gallandt et al. 2005; Meiss et al. 2010; Pullaro et al. 2006). However, it is difficult to disentangle reductions in weed recruitment attributable to the indirect effect of habitat provisioning for granivores from the direct effect due to competition with cover crops. Living mulches consistently harbor higher activity densities of weed seed predators than exposed habitats (Carmona and Landis 1999; Davis and Liebman 2003; Shearin et al. 2008), but killed cover crop

DOI: 10.1614/WS-D-15-00111.1

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https://doi.org/10.1614/WS-D-15-00111.1 Published online by Cambridge University Press

mulches have mixed effects on seed predator recruitment (Blubaugh and Kaplan 2015; Pullaro et al. 2006; Ward et al. 2011). Structural habitat complexity may provide shelter and improved microclimate for seed predators, but alternative food resources associated with living plant biomass are also important (Diehl et al. 2012). Despite evidence for stronger pressure by seed predators in vegetated habitats, cover may neutralize their effect on seedling emergence by reducing the availability of suitable germination sites (Calvinõ-Cancela 2007; Reader 1993).

Correlative evidence from the current body of literature suggests that seed predators perform important ecosystem services, and may even regulate weed seedbanks (Bohan et al. 2011). However, without experimental validation of their impact, growers may be reluctant to adapt management programs to promote stable seed predator populations. To that end, we performed an experiment to explicitly examine the effects of seed predation on subsequent weed germination rates in common cover crop environments. We used seed additions of common lambsquarters and differential exclosure treatments to compare the effects of vertebrate and invertebrate seed predators on emergence, biomass, and seedbank density in undisturbed plots over multiple field seasons. This work clarifies the role of seed predators in weed population dynamics, documenting weed seed biological control in a comprehensive, agriculturally relevant framework.

Materials and Methods

Study System. The experiment was conducted at the Purdue University Meigs Horticulture Research Farm near Lafayette, IN, USA. We examined the effects of cover crop type (three treatments), seed predator exclosure (three treatments), and weed seed additions (two treatments), in a randomized block, split plot design. The main plot factor was cover crop type (rye/vetch, red clover, and fallow), and these were planted in eight replicated 9 by 12 m plots (24 plots total) following disc tillage in early September 2012. Rye/vetch mix (*Secale cereale* L., and *Vicia villosa* R., 2 : 1 by weight) and red clover (*Trifolium pratense* L.) were planted at rates of 60 kg ha^{-1} and 13 kg ha^{-1}, respectively. Plots had 4.5-m margins between them, which were planted to a perennial grass mix. The experimental plot matrix was surrounded on one side by a grassy margin and on three sides by conventionally managed soybeans. In May 2013, rye/vetch cover crops were killed at flowering when the stand was at a density of ca. 246 g dry biomass m^{-2} by flail mowing and left as mulch on the soil surface. Weeds in the system were managed with monthly mowing, and no chemical inputs were used throughout the study.

Four weeks after cover crops were sown, six circular, 0.5 m^2 subplots were established 2 m apart along a transect running lengthwise across the north side of main plots, 2 m from the border. Subplot treatments were the crossed combinations of seed subsidy treatments (presence/absence), and differential exclosure treatments (vertebrate exclosure, complete exclosure, and open control), randomized within each main plot. Small mammal access was reduced using 1 m tall hardware cloth fences (1 cm gauge); both small mammals and vertebrates were excluded using 80 cm aluminum flashing. Both fence types were buried 5 cm deep. Birds were not excluded from subplots because we assumed their contribution to weed seed predation would be minimal (Holmes and Froud-Williams 2005). To evaluate seed limitation in our system, we evenly sowed 10 g of common lambsquarters seeds (30,000 seeds m^{-2}) in half the subplots on October 19, 2012, and September 27, 2013. Seed additions were intended to approximate the timing and density of biologically relevant, yet intense seed rain in the fall (Davis and Raghu 2010), and were purchased from Azlin Seed Service (Leland, MS, USA). Germination rate for the seed batch used was 71.5%, and this was calculated from 500 seeds in five petri dishes (100 seeds each) on moistened filter paper over 14 d in a growth chamber. We chose common lambsquarters as a focal species because it was the most common weed at our research site, palatable to both invertebrate seed predators and small mammals (Lundgren and Rosentrater 2007), and also because of its global importance as a persistent weed in temperate agricultural systems (Holm et al. 1977).

Due to poor clover germination in fall 2012, installation of all clover subplot treatments were delayed until September 2013, when the red clover stand was ca. 288 g dry biomass m^{-2}. To account for this methodological difference, we established a second complete replication of subplot treatments in the fallow plots in 2013 to coincide with the delayed clover treatments for comparison. These were placed on the south side of fallow plots, which were tilled 2 wk prior. Thus, fallow plots were compared with killed rye/vetch treatments in 2012, and a second fallow replication paired with clover treatments in 2013. Due to time and resource constraints, six replicates (instead of eight) were used when the experiment was repeated in 2013.

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Data Collection. The variables we measured were spring weed emergence (given as stem counts per subplot), harvested weed biomass, and seedbank density of common lambsquarters. We counted seedlings on May 23, 2013, and June 8, 2014, and harvested biomass of all weed species on September 26, 2013, and June 8, 2014. Because weed emergence was negligible in cover crop plots the first year, all biomass was removed from the soil surface the following spring to allow for emergence in the absence of the physical barrier provided by the cover crop. Biomass was dried for 72 h then weighed. We had to remove two plots from our biomass analysis where the open control treatments were accidentally mowed. To avoid edge effects in subplots, seedlings within 10 cm of the fence boundaries were not counted nor harvested. After data were collected, all common lambsquarters plants were removed from subplots and surrounding areas to prevent seed rain.

Seedbank samples from all subplots (those established in both years of the study) were collected on October 1 and 2, 2014. Five soil samples were taken in each subplot using a soil core (5 cm depth, 10 cm diameter). No soil was collected within 10 cm of each subplot boundary to avoid edge effects. Common lambsquarters seeds were washed from a 625-ml subsample of the five homogenized cores using a 0.595-mm sieve. Prior to counting, we crushed dried seed samples against the sieve, eliminating decayed seeds. Unbroken seeds were separated from debris, identified, and counted using a dissecting microscope.

Statistical Analysis. Common lambsquarters seedling counts from fallow plots were analyzed using a mixed effect generalized linear model assuming a Poisson distribution with quasi-likelihood estimation (for overdispersion) using the glmmPQL function in the MASS package of R (R Development Core Team 2014). Red clover and rye/vetch plots were excluded from seedling and biomass models because we only observed quantifiable common lambsquarters growth in fallow plots. Fixed effects were exclosure type (open, invertebrates only, mammals + invertebrates excluded), seed subsidy, and year; main plot was a random effect. Common lambsquarters biomass values from fallow plots were natural log transformed and analyzed with a mixed effect model. Fixed and random effects were the same as they were for seedling counts, and the lme function in the nlme package of R was used. Seedbanks were analyzed using a separate model for each year of the study, since cover crop treatments could not be fully crossed within years due to poor clover germination in year 1 of the study. Common lambsquarters seedbank densities were natural log transformed and analyzed with mixed effect models, using the lme function in R. Fixed effects were cover crop type (fallow and rye vetch in 2012, fallow and red clover in 2013), seed subsidy, and exclosure type; random effects were main plot nested in block. Raw data from each subplot were analyzed for each response variable, but they were converted to normal metric units (seedlings m^{-2}, seeds ml^{-1}, etc) for presentation in figures.

Results and Discussion

Over repeated seasons, we found that seed predators overcame intense seed rain (30,000 seeds m^{-2}) and substantially reduced germination rates after fall tillage in fallow plots (Table 1a), demonstrating that granivores perform relevant services that improve weed biocontrol. In subplots with seed subsidies, common lambsquarters emergence rates were almost twice as high when seed predators were excluded as they were when insects or rodents had access (Figure 1). The impact of seed predators on weed biomass was lower in subplots with ambient seedbanks (Figure 2); we found a seed*exclosure interaction on common lambsquaretrs biomass (Table 1b), but the main effect of seed predator exclosure was significant overall for seedling emergence (Table 1a). The positive effect of seed addition on both germination and biomass (Tables 1a and 1b) indicates that weeds are indeed seed-limited in annual cropping systems (i.e., seed predators allowed fewer seeds to escape than the number of suitable germination sites in each subplot). The reduction in spring emergence due to weed seed predation that we observed was similar in magnitude to the only other study that explicitly measured it (White et al. 2007), even though the seed rain density we examined was 10 times higher; showing that seed predators are capable of intercepting a high volume of seeds before they enter the seedbank.

Surprisingly, there was no difference in weed emergence between the two types of seed predator exclosures (Figure 1), suggesting that small mammals contribute little to suppression of common lambsquarters in this system. The weak impact of vertebrates we observed is consistent with other work performed in US Midwestern field crop environments (Menalled et al. 2000; Westerman et al. 2008). However, other studies provide conflicting evidence that

https://doi.org/10.1614/WS-D-15-00111.1 Published online by Cambridge University Press

Table 1. Output from decomposed mixed models of common lambsquarters seedling counts (a), biomass (b), and seedbank density (c and d).

Factor	Coefficient	SE	*t*	P	
a) Seedling counts (fallow plots only)					
Intercept	899.932	401.275	2.242	0.028	*
Seeds	0.548	0.186	2.934	0.004	**
Fence (invertebrate)	−0.475	0.228	−2.077	0.041	*
Fence (open)	−0.503	0.228	−2.201	0.030	*
Year	−0.446	0.199	−2.238	0.028	*
b) Biomass (fallow plots only)					
Intercept	209.542	82.309	2.545	0.014	*
Seeds	0.131	0.064	2.022	0.049	*
Fence (invertebrate)	0.003	0.064	0.057	0.954	
Fence (open)	0.011	0.066	0.1761	0.860	
Year	−0.104	0.040	−2.544	0.014	*
Seeds x fence (invert)	−0.142	0.091	−1.548	0.128	
Seeds x fence (open)	−0.189	0.094	−2.012	0.050	*
c) Seedbank density 2012 plots (rye/fallow)					
Intercept	4.661	0.315	14.768	< 0.001	**
Cover	0.463	0.334	1.388	0.207	
Seeds	0.434	0.206	2.103	0.038	*
Fence (invert)	0.382	0.219	1.747	0.084	
Fence (open)	0.356	0.219	1.625	0.108	
Seeds x fence (invert)	−0.668	0.253	−2.642	0.010	*
Seeds x fence (open)	−0.499	0.253	−1.972	0.052	
d) Seedbank density 2013 plots (clover/fallow)					
Intercept	4.402	0.273	16.081	< 0.001	**
Cover	0.184	0.367	0.501	0.637	
Seeds	0.273	0.100	2.725	0.008	**
Fence (invertebrate)	−0.005	0.122	−0.043	0.965	
Fence (open)	−0.049	0.122	−0.406	0.685	

$P < 0.1$; * $P < 0.05$; ** $P < 0.01$.

small mammals perform the majority of weed seed predation services (Baraibar et al. 2009; Westerman et al. 2003). Seed size is an important predictor of weed seed consumption (Brust and House 1988), especially for small mammals, which preferentially exploit larger-seeded species to minimize foraging investment per seed (Muñoz and Bonal 2008). Common lambsquarters seeds are relatively small compared to other common weed seeds (Lundgren and Rosentrater 2007), and this may partially explain the weak

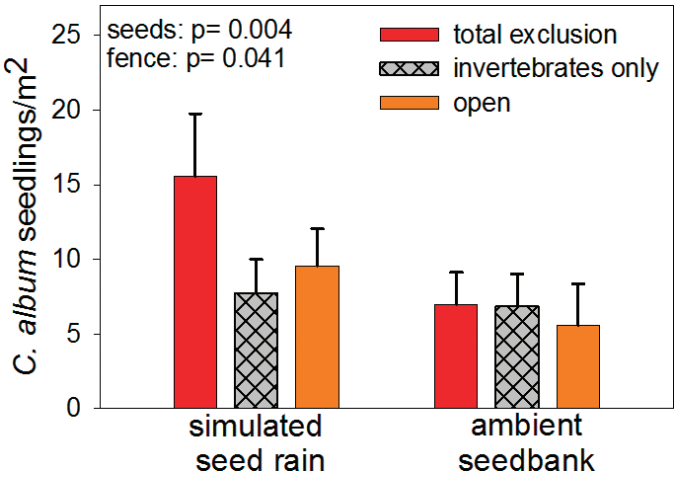


Figure 1. Common lambsquarters seedling counts m^{-2} (mean + SE) in fallow subplots pooled from spring 2013 and 2014. (Color for this figure is available in the online version of this article.)

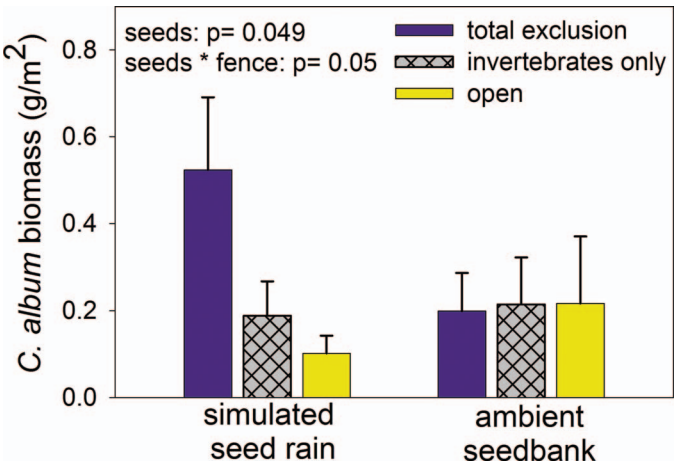


Figure 2. Common lambsquarters biomass m^{-2} (mean + SE) in fallow subplots pooled from spring 2013 and 2014. (Color for this figure is available in the online version of this article.)

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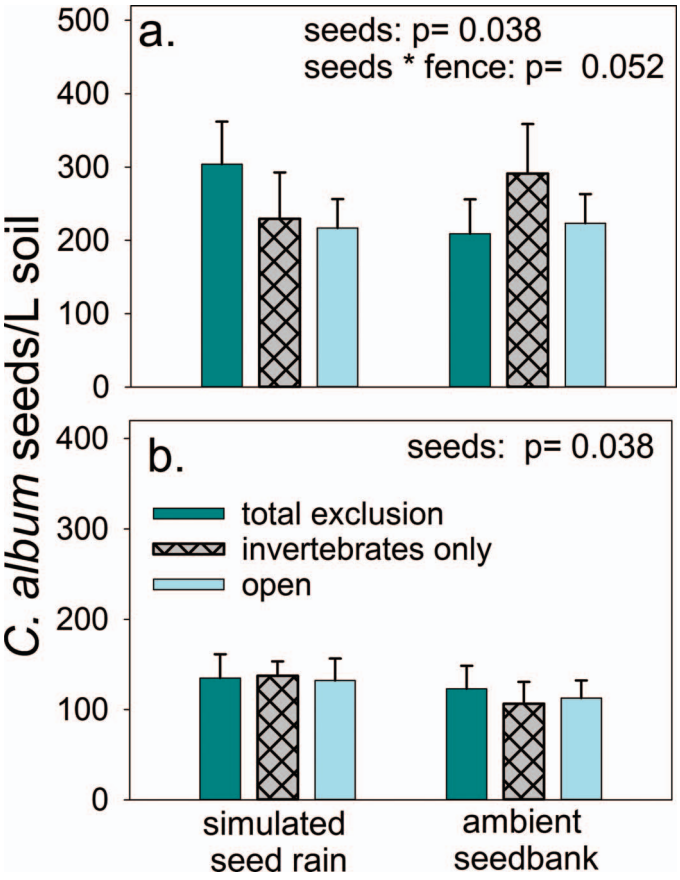


Figure 3. Common lambsquarters seed density (mean + SE) in soil samples from (a) pooled rye/vetch and fallow subplots established in 2012 and (b) pooled clover and fallow subplots established in 2013. Seedbank samples were collected from all subplots in September 2014. (Color for this figure is available in the online version of this article.)

contribution made by small mammals to weed seed biological control. When seasonally available, small mammals preferentially forage on spilled grain and invertebrate prey (Whitaker 1966), thus, alternative food availability in our system may have diverted vertebrate foraging on common lambsquarters. Still, several studies report substantial contributions by small mammals to common lambsquarters removal (Marino et al 1997; Mauchline et al 2005; Westerman et al 2003), and vertebrates are the only granivorous taxa whose seed predation services carry on over winter (Williams et al. 2009). Future research should identify environmental variables that predict their reliance on weed seed resources.

We intended to compare the effects of seed predators on common lambsquarters emergence rates between cover crop types, but found too few seedlings across all cover crop treatments for analysis, even after removing mulch from the soil surface in 2014 (data not presented). This suggests that competition with cover crops vastly outweighs seed predator effects on weed germination. Because we were unable to evaluate interactive effects of cover and seed predation on weed emergence, we examined their impacts on seedbanks. Surprisingly, cover crops had no effect on the seedbank in either year (Tables 1c and 1d). Episodic seed removal is often higher in sites with vegetative cover (Heggenstaller et al. 2006; Meiss et al. 2010), thus we expected that granivores would reduce seed density in the upper soil profile (0 to 5 cm) of cover crop treatments. With an average of ca. 15,000 seeds m^{-2}, the ambient common lambsquarters seedbank we observed was extremely high compared to those observed in other systems (Davis et al. 2012). This may have overwhelmed the effects of our cover crop treatments over the timescale of this study, as common lambsquarters has relatively high persistence in the seedbank (Davis et al. 2008). Additionally, it is important to note that the fallow plots were not devoid of cover for the entire study. At plot harvest, weed biomass in fallow plots was less than half that of both cover crop types (data presented elsewhere), but even sparse weed growth may provide habitat and food resources that facilitate seed predator activity (Blubaugh and Kaplan 2015).

We detected no effects of seed predators on the common lambsquaretrs seedbank in the 2013 subplots (Table 1d), which had only been installed for 1 yr at the time of soil sampling. In the 2012 subplots, we found a seed*exclosure interaction, 2 yr after treatments were applied (Table 1c). When seed subsidies were added, significantly fewer seeds were recovered in open subplots compared with both types of exclosure (Figure 3b). In unsubsidized subplots, however, more seeds were recovered where only invertebrate seed predators had access than in either of the other two exclosure treatments (Figure 3b). Invertebrate seed predators have a limited capacity to extract seeds from beneath the soil surface (Harrison and Gallandt 2012; White et al. 2007), and while they obviously reduce the number of seeds in the shallow germinable profile of common lambsquarters (2.5 cm, Weaver 1988; Figure 1) following seed rain, other processes (e.g., decay, germination, and successive cultivation) must target buried seeds.

Our analysis provides weak and inconsistent evidence of common lambsquarters seedbank regulation by granivores after 2 yr of continuous experimental exclosure. This contradicts the correlative evidence of Bohan et al. (2011), who regressed seasonal ground beetle pitfall trap captures with weed seedbank reduction. Notably, weed seedbank densities in that study were almost 10 times lower

https://doi.org/10.1614/WS-D-15-00111.1 Published online by Cambridge University Press

than those we observed (Heard et al 2003). We expect that seed predators may only have a detectable impact once underlying seedbanks are low enough such that annual flux composes a high proportion the total seedbank density. While the effects of our seed addition treatments were always positive and significant (Tables 1c and 1d), we were surprised that simulating intense seed rain only increased the 0- to 5-cm seedbank by 9% across both years of the study.

Our results validate the utility of beneficial seed-feeding insects by demonstrating a 38% reduction in weed emergence specifically attributable to seed predators. Still, seeds are only accessible by invertebrates as long as they remain on the soil surface, and while their ecosystem services are critical following seed rain (Figures 1 and 2), they become negligible once seeds are incorporated in the soil (Figure 3; Westerman et al. 2006). Our work suggests that high underlying seedbanks may overwhelm the impacts of seed predators over short timescales, thus other tools must be combined for long-term seedbank management (Davis 2006; Liebman and Gallandt 1997). Integrated management strategies that promote seed predator activity after seed inputs occur (Landis et al. 2005) while simultaneously targeting underlying seedbanks (Gallandt 2006) will lead to stronger suppression over time, and cover crops are critical tools for the task. They target weeds both above and below the soil surface by preventing emergence, promoting seed decay (Mohler et al. 2012), and providing optimal foraging habitat for seed predators (Landis et al. 2005).

Acknowledgments

This work was funded by a Ceres Trust and USDA OREI grant 10-51300-21305. We are grateful to Curt Hardin, Gareth Powell, Christie Shee, Ivy Widick, and Rob Blubaugh for technical assistance, and to Adam Davis, Kevin Gibson, and Carolina Zamorano for advice on methods.

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Received July 9, 2015, and approved September 2, 2015.

Associate Editor for this paper: Adam Davis, USDA-ARS

https://doi.org/10.1614/WS-D-15-00111.1 Published online by Cambridge University Press