Weed Science

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Tillage and Cover Crop Effects on Weed Seed Persistence: Do Light Exposure and Fungal Pathogens Play a Role?

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Research Article

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Abstract

In a series of seed burial studies, we tested the hypothesis that reduced tillage and cereal rye (*Secale cereale* L.) cover cropping influence seed persistence and that these effects are mediated by differences in fungal pathogens and exposure to light. Seeds of Powell amaranth (*Amaranthus powellii* S. Watson) and large crabgrass [*Digitaria sanguinalis* (L). Scop.] were buried in mesh bags in a long-term experiment with two levels of tillage (full-width tillage [FWT] or strip tillage [ST]) and two levels of cover cropping (none or cereal rye). In Experiment 1, seeds were exhumed each spring for 3 yr and tested for viability. In Experiment 2, untreated and fungicide-treated seeds were buried, exhumed at shorter intervals, and tested for viability. In addition, a subset of seeds in FWT treatments were exhumed and stored in either light or darkness during tillage operations and evaluated for persistence at 8.5 mo after burial (MAB). In Experiment 1, the persistence of *D. sanguinalis* seeds declined by 80% at 7 MAB regardless of cover crop or tillage treatment. The persistence of *A. powellii* seeds at 19 MAB declined by 95% in FWT compared with only 50% in ST. In Experiment 2, seed persistence of both species was greater in ST compared with FWT treatments, for seeds that had been exposed to light, but not for those that were maintained in darkness. Rye cover cropping resulted in a 2-fold increase in overwinter persistence of seeds of *D. sanguinalis* regardless of fungicide treatment. These results demonstrate that increased persistence under ST was primarily due to reductions in light-induced fatal germination and that increased overwinter persistence of *D. sanguinalis* in rye cover crop treatments could not be explained by differences in decay due to fungal pathogens controlled by the seed treatment.

Introduction

Conservation agricultural systems—those that include residue retention, reduced tillage, and diverse crop rotations—have received considerable attention for their potential soil-improving benefits (Hobbes et al. 2008; Reicosky 2015). However, adoption of these systems is often constrained by the increased difficulty and expense associated with weed management (Hoyt et al. 1994; Luna et al. 2012). Although many studies have characterized shifts in weed seedbank diversity and abundance under conservation agriculture (e.g., Brainard et al. 2013; Buhler 1995; Cardina et al. 1991; Gomez et al. 2014; Pollard and Cussans 1981), the mechanisms responsible for those shifts are poorly understood. These mechanisms may include changes in seed production and dispersal, as well as mechanisms of loss from the weed seedbank, including germination, predation, and decay. The persistence of weed seeds in the soil depends on their inherent resistance to fatal germination or death and on their exposure to environmental conditions that influence those fates (Long et al. 2015). Differences in seedbank persistence and their causes are challenging to quantify, but are important for predicting shifts in weed species communities and identifying efficient weed management strategies that target weak points in weed life cycles (Cousens and Mortimer 1995; Gomez et al. 2014).

Conservation agricultural practices, including reduced tillage and cover cropping, may influence weed seed persistence through changes in soil biology that affect seed mortality (Gallandt et al. 2004; Long et al. 2015; Schafer and Chilcote 1970) and species-specific genetic differences in seed resistance to decay (Long et al. 2015). For example, Fennimore and Jackson (2003) found shepherd's-purse [*Capsella bursa-pastoris* (L.) Medik.] emergence and seedbank density were lower in treatments with higher levels of cover cropping and compost addition,

and speculated that changes in microbial populations associated with higher levels of organic matter may have been responsible. In contrast, Davis et al. (2006) found that seed mortality of giant foxtail (*Setaria faberi* Herrm.) and velvetleaf (*Abutilon theophrasti* Medik.) was lower in long-term cropping systems with higher levels of cover crop and compost addition and that mortality of these species was associated with shifts in microbial community composition. However, Ullrich et al. (2011) and Gomez et al. (2014) found only small and inconsistent differences in persistence of weed seeds in soils from long-term cropping systems that differed in organic matter inputs and soil microbial biomass. Such contrasting responses of weed seed persistence to broadly similar organic matter additions are not surprising, given the diversity of potential factors influencing persistence and the variability in those factors and their impacts across soil types, weather conditions, and weed species (Long et al. 2015).

Differences in weed seed persistence across cropping systems may be explained in part by differences in fungal communities that influence seed decay (Chee-Sanford et al. 2006; Davis et al. 2006; Gallandt et al. 2004; Gomez et al. 2014; Kremer 1993; Pitty et al. 1987) and species differences in seed resistance to decay agents (Long et al. 2015). Many saprophytic and pathogenic fungi are present in the soil and isolated from seeds (Gomez et al. 2014; Mitschunas et al. 2009), and several studies have used soil sterilization or fungicide seed treatment to evaluate the role of microorganisms as a cause of seed mortality (Gallandt et al. 2004). In a review of 14 such studies, fungicide treatments increased persistence in most cases, with results varying by study, weed species, and duration of burial (Wagner and Mitschunas 2008). Several researchers have used this approach to evaluate whether differences in fungal decay varied based on tillage or cover crop practices. For example, Gallandt et al. (2004) detected no interaction between tillage and fungicide treatment on decay of wild oat (*Avena fatua* L.). Similarly, Kumar et al. (2011) found that although fungicides increased overwinter persistence of Powell amaranth (*Amaranthus powellii* S. Watson) and barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.], there were no differences in these fungicide effects in buckwheat (*Fagopyum esculentum* Moench) cover crop treatments compared with the no cover crop control. On the other hand, higher populations of fungal pathogens such as *Pythium*, *Rhizoctonia solani*, *Fusarium*, and *Thielaviopsis* spp. were found following incorporation of cover crops (Dabney et al. 1996; Mohler et al. 2012; Rothrock et al. 1995; Toussoun et al. 1963), and these have been associated with reductions in emergence (Mohler et al. 2012) or persistence (Davis et al. 2006) of common weed species.

Differences in seed persistence across tillage and cover-cropping systems may also be strongly influenced by effects on dormancy loss and fatal germination (Long et al. 2015; Wagner and Mitschunas 2008). For example, tillage-induced exposure of seeds to light, fluctuating soil temperatures, oxygen, and inorganic nitrogen may contribute to dormancy release and stimulation of germination of seeds that fail to successfully establish (Baskin and Baskin 1998; Finch-Savage and Footitt 2017). Many short-term studies have shown lower rates of weed emergence under reduced-tillage systems (e.g., Brainard and Noyes 2012; Hendrix et al. 2004; Wang and Ngouajio 2008), suggesting that—other things being equal—fatal germination may also be reduced in conservation tillage systems. However, this relationship is complicated by differences in the vertical distribution of seeds in the soil and other biological factors influencing recruitment following germination (Haramoto and Brainard 2017; Long et al. 2015). Tillage redistributes seeds by depth in the soil, which alters light, temperature, and moisture conditions that affect seed dormancy, germination, and persistence (Long et al. 2015; Mohler 2001). Despite the well-established observation that seeds are more shallowly distributed in reduced-tillage systems, surprisingly few studies have evaluated the effects of tillage on germination, emergence, or persistence independent of depth of seed burial. Roberts and Feast (1972) found that for a given depth of weed seed burial, the emergence of weeds was lower and the persistence of weed seeds higher in undisturbed compared with cultivated soils. However, when controlling for seed depth, Haramoto and Brainard (2017) found that emergence of *A. powellii* was sometimes higher in undisturbed soil with surface cover crop residue, presumably due to higher moisture retention at the soil surface.

The importance of tillage-induced light exposure on germination of annual weeds is well known, but its relative importance in explaining differences in persistence across tillage systems has not been extensively explored in previous studies (Wagner and Mitschunas 2008). Light exposure increases seed germination for many weed species (Baskin and Baskin 1998; Wesson and Wareing 1967), including southern crabgrass [*Digitaria ciliaris* (Retz.) Koeler] (Tang et al. 2010), common lambsquarters (*Chenopodium album* L.) (Milberg et al. 1996), large thornapple (*Datura ferox* L.) (Scopel et al. 1991), and redroot pigweed (*Amaranthus retroflexus* L.) (Gallagher and Cardina 1998a). As a consequence of this light sensitivity, cultivation or tillage events occurring at night result in lower rates of emergence for many important weed species (Botto et al. 1998; Buhler 1997; Fogelberg 1999; Scopel et al. 1991, 1994). However, the relationship between light-induced increases in emergence, fatal germination, and seed persistence is not well established.

Previous studies evaluating tillage effects on seed persistence rarely control for light exposure, so it is often unclear whether observed tillage effects are due to long-term changes in soil conditions influencing seed decay or predation or short-term changes in other factors—including light exposure—that strongly influence dormancy release, fatal germination, and persistence. For example, studies evaluating seed persistence in tilled systems using buried mesh bags often remove bags temporarily during tillage operations to avoid destruction of the seed bags (e.g., Hill et al. 2016; Ullrich et al. 2011). While often necessary, this approach may expose seeds to light, higher oxygen levels, and other stimuli that their ambient seed counterparts may not experience, depending on the timing and type of tillage used.

The objectives of this study were to evaluate the effects of tillage and cereal rye (*Secale cereale* L.) cover cropping on weed seed persistence and to investigate the extent to which these effects are mediated by fungal pathogens and exposure to light. We hypothesized that (1) weed seed persistence is influenced by historic cover-cropping and tillage practices; (2) tillage and cover crop effects on seed persistence are mediated in part by fungal pathogens; and (3) tillage effects on weed seed persistence depend on the level of light exposure experienced by those seeds during tillage. To test these hypotheses, persistence was first evaluated in a seed burial study (Experiment 1) within a long-term cropping systems trial with two levels of tillage (strip tillage vs. full-width tillage) and cover cropping (none vs. cereal rye). To better understand the possible mechanisms responsible for observed differences in persistence, we designed a second set of experiments (Experiments 2A and 2B) with more frequent exhumations

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and additional treatments to evaluate the potential role of fungal pathogens (Experiment 2A) or light (Experiment 2B) in mediating tillage and cover crop effects.

Materials and Methods

Long-Term Trial Experimental Treatments and Design

Three weed seed burial experiments (Experiment 1, Experiment 2A, and Experiment 2B) were conducted within a subset of treatments in a long-term tillage trial initiated in September 2008 on Oakville fine sand (mixed, mesic Typic Udipsamments) at the Southwest Michigan Research and Extension Center (SWMREC) in Benton Harbor, MI (42.085244°N, 86.358736°W). These treatments consisted of all combinations of two factors: tillage (strip tillage [ST] vs. conventional full-width tillage using a moldboard plow [FWT]) and cover crop (no cover crop [no cover] vs. cereal rye [rye]). Treatments were imposed in the same plots each year with crops following a 3-yr rotational sequence of sweet corn (*Zea mays* L.)–snap bean (*Phaseolus vulgaris* L.)–cucurbit crop (butternut squash (*Cucurbita moschata* Duchesne) in 2011 and pickling cucumber (*Cucumis sativa* L.) in 2014. Plots were arranged in a split-split plot design with tillage as the main plot factor and cover crop as the subplot factor. Tillage main plots measured 11.4 m by 18.3 m and were arranged in a randomized complete block design with four replications. Cover crop split plots were 3.8 m by 18.3 m with either 2 (winter squash) or 5 rows (all other crops) per plot.

Field Management

Cereal rye was drilled at 125 kg ha^{-1} in mid-September of each year using a grain drill with 19-cm between-row spacing. The following spring of each year, the entire experimental area was treated with glyphosate (0.84 kg ae ha^{-1}) in mid-May to terminate both cereal rye and winter annual weeds before tillage. Immediately before glyphosate application, mean aboveground shoot dry weight of both rye and weeds was estimated from tissue sampled from two 0.25-m^2 quadrats per plot. Dry shoot weight at the time of termination ranged from approximately 300 to 700 g m^{-2} for rye and 0 to 250 g m^{-2} for weeds depending on the year and treatment, with far lower weed biomass in rye treatments (see details in Brainard et al. 2016). Tillage occurred in late May or early June depending on the crop. FWT consisted of moldboard plowing followed by disking and field cultivating. ST was accomplished using either a Hiniker 6000 strip-tiller (for sweet corn, snap beans, and cucumbers) or an Unverferth 120 subsoiler (for winter squash). Both strip-tillage implements were equipped with a row cleaner (to remove cover crop residue), a shank, offset disks, and a rolling basket. ST resulted in an approximately 25-cm-wide by 30-cm-deep zone of disturbed soil into which crops were planted.

Experiment 1: Tillage and Cover Crop Effects on Seed Persistence

Experimental Design

This experiment evaluated the effects of cover crop (no cover vs. rye) and tillage (ST vs. FWT) on seed persistence of *A. powellii* collected in 2011 from agricultural fields at the Kellogg Biological Station in Hickory Corners, MI, and *D. sanguinalis*, collected in 2011 from SWMREC, Benton Harbor, MI. Seeds were separated from chaff, counted, and stored in glass jars in a laboratory at 20 C until the time of burial (~1 mo after seed collection). Before burial, seed viability (determined via germination with gibberellic acid [GA_3]) was 84% and 92% for *D. sanguinalis* and *A. powellii*, respectively.

Seeds were buried following winter squash harvest in each cover crop subplot of the long-term trial described earlier (Table 1). Therefore, for each weed species, the design was a split-plot design with tillage as the main plot factor and cover crop as the subplot factor.

Seed Preparation and Burial

Mesh bags (~8 cm by 10 cm) were constructed from 20D polyester "no-see-um" permeable mesh (Outdoor Wilderness Fabrics, 123 E Simplot Blvd, Caldwell, ID 83605, USA) using nylon thread. Bags were filled with 100 g of sand that had been sieved through a 500-micron sieve (smaller fraction kept) mixed with either 100 seeds of *A. powellii* or 200 seeds of *D. sanguinalis*. Silica sand was used for ease of subsequent seed separation and because it mimicked the soil texture (Oakfield fine sand; 94% sand; 1% to 2% soil organic matter) at our experimental site. One drawback of this approach is that buried seeds were not initially in direct contact with field soil and hence may have experienced different edaphic conditions than seeds in the ambient seedbank. To minimize such differences, we used a small volume of sand and flattened each bag such that seeds were in close proximity to ambient soil. Flattened bags were only 1.5-cm thick, so colonization by soil microbes was likely. Seed densities were chosen to roughly mimic the proportion of these species in the ambient weed seedbank. Bags were buried 15-cm deep in all four cover crop by tillage (FWT + no cover, FWT + rye, ST + no cover, FWT + rye) combinations in November 2011 (Table 2). Seed bags in ST treatments were buried in the between-row zone and therefore were not subject to disturbance from the ST operation.

Table 1. Trial design and treatments.

	Factor	Treatment	Levels
Experiment 1			
	Whole plot	Tillage	Strip-till Conventional moldboard plow
	Subplot	Cover crop	No cover crop Cereal rye
Experiment 2A			
	Whole plot	Tillage	Strip-till Conventional moldboard plow
	Subplot	Cover crop	No cover crop Cereal rye
	Sub-subplot	Fungicide	Triple-fungicide coating No fungicide
Experiment 2B			
	Whole plot	Tillage	Conventional moldboard plow
	Subplot	Cover crop	No cover crop
	Sub-subplot	Exhumation conditions	Light exposure No light exposure

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Table 2. Timing of relevant field operations and experimental procedures.

Date		Field operation	Experiment operation
2011			
	August 29	Winter squash harvest	
	September 8	Rye seeding	
	November 9		Experiment 1 seed bag burial
2012			
	May 17	Rye termination	
	June 4	Tillage and sweet corn planting	Exhumation 1; bag reburial
	August 21	Sweet corn harvest	
	September 5	Rye seeding	
2013			
	May 16	Rye termination	
	May 29	Tillage and snap bean planting	Exhumation 2; bag reburial
	July 23	Snap bean harvest	
	September 1	Rye seeding	
2014			
	May 28	Rye termination	
	June 5	Tillage and cucumber planting	Exhumation 3 (end of Experiment 1)
	July 28	Cucumber harvest	
	September 2	Rye seeding	
2015			
	May 20	Rye termination	
	June 3	Tillage and sweet corn planting	
	August 24	Sweet corn harvest	
	September 4	Corn residue disking	
	September 10	Rye seeding	
	October 27		Experiment 2A and 2B seed bag burial, soil sample collection
	December 1		Exhumation 1, soil sample collection
2016			
	March 22		Exhumation 2, soil sample collection
	May 19	Rye cover termination	
	June 1	Tillage and snap bean planting	Exhumation 3, soil sample collection, remove and rebury all CT bags
	July 27		Exhumation 4, soil sample collection
	Jul 28	Beans harvest	
	August 17	Bean residue disking	
	August 23	Rye seeding	
	September 8		Exhumation 5, soil sample collection

Bags were buried by using a golf-cup hole cutter to first remove a cylindrical soil core (10.2-cm deep with an 11.4-cm diameter) and then restore the core into the hole.

Seed Retrieval and Viability Assessment

One bag of each species from each plot was exhumed in June 2012, May 2013, and June 2014 (7, 19, and 31 mo after burial [MAB]). Bags were stored at 4 C until viability testing. Seeds were removed from bags by sieving through a 500-micron sieve. Seeds of *A. powellii* were then germinated in petri dishes with 2 µM GA_3, while *D. sanguinalis* seeds were germinated with deionized water. These seeds were placed in a 16-h day/8-h night growth chamber set at 30/25 C with incandescent bulbs that provided approximately 28 µmol m^{-2} s^{-1} of light. These treatments and conditions were chosen based on the stimulation of high germination rates in preliminary studies with nonburied seeds from the same seed lots. Ungerminated seeds were assessed for viability by a combination of squeeze testing with forceps and using a 0.1% 2,3,5-tretrazolium chloride (TZ) solution in accordance with methods outlined by the Tetrazolium Subcommittee of the Association of Official Seed Analysts (Peters and Lanham 2000).

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Seeds were characterized as germinated, dormant (did not germinate but were TZ viable), or dead; germinated and dormant seeds were considered viable.

Seed Reburial

In FWT treatments, all bags in each plot were removed from the soil before spring tillage and reburied following tillage and planting the next day. During this removal period, no attempt was made to exclude seeds from light, although seeds were mixed with sand, which may have limited light exposure. For FWT treatments with rye residue, bags were supplemented with rye residue that had been collected before termination, dried down, and coarsely ground into 5- to 10-mm-long segments. Each bag received a quantity of rye residue chosen to reflect actual dry matter yields produced in the field that year, divided by the assumed depth of incorporation. Using this approach, 0.30 g of residue was added per bag in 2012 and 0.13 g of dry rye residue was added per bag in 2013.

Statistical Analysis

The total number of viable seeds for each seed bag for each exhumation date t ($N_{v,t}$) was calculated according to the equation:

$$N_{v,t} = N_{g,t} + N_{tz,t} \quad [1]$$

where $N_{g,t}$ is the total number of seeds retrieved at a time t that germinated in the growth chamber postexhumation, and $N_{tz,t}$ is the total number of seeds retrieved at time t that did not germinate, but tested TZ positive. The persistence of seeds at a given exhumation date t ($P_{i,t}$) was defined as:

$$P_{i,t} = N_{v,t} / N_{v,i} \quad [2]$$

where $N_{v,i}$ is the total number of viable seeds initially buried (t = initial).

For the 7-, 19-, and 31-month exhumation dates, the effects of tillage and cover crop on $N_{v,t}$ and $P_{i,t}$ were analyzed using the PROC GLIMMIX procedure in Statistical Analysis System v. 9.4 (SAS Institute, Cary, NC). For these exhumation dates, data were analyzed as a split-plot design with tillage as fixed main plot factor, cover crop as fixed subplot factor, and replicate as a random effect. Where main or interactive effects were significant, treatment mean separation occurred using Fisher's Protected LSD at $\alpha = 0.05$.

Experiment 2A: Tillage and Cover Crop Effects on Seed Persistence within a Year

Experimental Design

This experiment evaluated the effects of tillage (ST vs. FWT), cover crop (no cover vs. rye), and seed treatment (fungicide treated vs. untreated) on seed persistence of *A. powellii* collected in 2011 from Hickory Corners, MI, and *D. sanguinalis* collected in 2012 from Benton Harbor, MI. Both fungicide-treated and untreated seeds were buried in cover crop subplots of the long-term trial described earlier (Table 1). Therefore, for each weed species, the design was a split-split-plot design with tillage as the main plot factor, cover crop as the subplot factor, and fungicide as the sub-subplot factor.

Seed Preparation

During the winter of 2012, a subset of seeds of both species were coated with a triple-fungicide treatment used in previous studies to protect weed seeds against fungi including *Rhizoctonia*, *Fusarium*, *Pythium*, and *Phytophthora* (Kumar et al. 2008, 2011). This coating contained captan (Captan Fungicide, 71 mg ai per 100 g seed, Southern Agricultural Insecticides), trifloxystrobin (Flint®, 10 mg ai per 100 g seed, Bayer CropScience), and metalaxyl (Apron XL® 350ES, 15 mg ai per 100 g seed, Syngenta Crop Protection). Untreated seeds were from the same seed lot but received no fungicide coating. Both treated and untreated seeds were stored in glass vials in a laboratory at 20 C (±2 C) until the initiation of the experiment. Despite the relatively long storage period under these conditions, seed viability at the time of Experiment 2 (determined via germination in petri dishes) was approximately 75% and 90% for *D. sanguinalis* and *A. powellii*, respectively (compared with 84% and 92%, respectively, in Experiment 1). Germination testing at this time also confirmed that fungicide treatment did not affect germination of *D. sanguinalis* . However, fungicide treatment increased *A. powellii* germination by approximately 11% in light, but had no effect in darkness (unpublished data).

Seed Burial

For each species and fungicide treatment combination, 100 seeds were mixed with 125 g of sieved silica sand and placed in no-see-um mesh bags. In October of 2015, after cover crop planting (Table 2), seed bags were buried at a depth of 10.2 cm in all four cover crop by tillage treatments (FWT + no cover, FWT + rye, ST + no cover, FWT + rye). Seed bags in ST treatments were buried in the between-row zone and therefore were not subject to disturbance from the ST operation. For bags containing seeds without fungicide treatment, 8 bags of each species were buried in each of the 16 cover crop subplots so that 2 bags per plot could be removed for each of four subsequent exhumation dates. For bags containing fungicide-treated seeds, 4 bags of each species were buried in each plot so that 2 bags could be pulled at two subsequent exhumation dates to assess fungicide effects. Only two exhumation dates were evaluated for fungicide effects because of the likely limited persistence of the fungicides themselves. Bags were buried by using a golf-cup hole cutter to first remove a cylindrical soil core (10.2-cm deep with an 11.4-cm diameter) and then restore the core into the hole. In treatments containing rye surface residue, the residue was carefully removed before burial and replaced after burial. In FWT treatments, all seed bags (other than those used in Experiment 2B) were retrieved in the morning before tillage, placed in paper bags, stored in a cooler at 4 C, and reburied that same afternoon after tillage operations were complete. This process was necessary to avoid disturbance of the seed bags during tillage. The day of tillage was partly cloudy with a high temperature of 26 C, and the duration of bag storage was 6 h.

Seed Retrieval and Viability Assessment

Two bags each of both fungicide and non–fungicide treated seeds were retrieved 1 and 4.5 MAB for *D. sanguinalis*, and after 1 and 7 mo for *A. powellii*. Additional sets of 2 bags of untreated seed were retrieved at 7 and 9 mo for *D. sanguinalis*, and 9 and 10.5 mo for *A. powellii*. Following the recommendation of Wagner and Mitschunas (2008), earlier retrieval dates for *D. sanguinalis* seeds were used to better characterize seed decay, which Experiment 1 demonstrated occurred more rapidly for *D. sanguinalis* than *A. powellii*. Upon retrieval, all bags were placed in cold storage at 4 C until being processed to evaluate seed viability. Seeds were separated from silica sand using a 500-micron sieve and tested for germination in either deioized water for *D. sanguinalis* or

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2 mL 2 µM GA_3 for *A. powellii*. These seeds were placed in a 16-h day/8-h night growth chamber set at 30/25 C with incandescent bulbs that provided approximately 28 µmol m^{-2} s^{-1} of light. After 2 wk, all ungerminated seeds were tested for viability as described for Experiment 1.

Statistical Analysis

The total number of viable seeds for each seed bag for each exhumation date t ($N_{v,t}$) was calculated according to Equation 1. The persistence of seeds at a given exhumation date t ($P_{1,t}$) was defined as:

$$P_{1,t} = N_{v,t} / N_{v,1} \quad [3]$$

where $N_{v,1}$ is the total number of viable seeds at the December exhumation time ($t = 1$) and $N_{v,t}$ is the number of viable seeds at exhumation date t. Persistence was calculated using December as the initial time point, because seeds buried in October experienced warm soil temperatures that resulted in fatal germination that was likely not reflective of natural populations of *A. powellii* or *D. sanguinalis* (which would have had a higher level of dormancy at this time). Mean values of these responses from the 2 bags recovered from each sub-subplot were used for subsequent analysis.

For the 1-, 4.5- (*D. sanguinalis* only), and 7-month (*A. powellii* only) exhumation dates, the effects of tillage, cover crop, and fungicide treatment on $N_{v,t}$ and $P_{1,t}$ were analyzed using the PROC GLIMMIX procedure in Statistical Analysis System v. 9.4 (SAS Institute). For these exhumation dates, data were analyzed as a split-split-plot design with tillage, cover crop, and fungicide treated as fixed effects, and replicate, replicate by tillage, and replicate by tillage by cover crop as random effects. For the 7- (*D. sanguinalis* only), 8.5-, and 10.5-mo (*A. powellii* only) exhumation dates, where fungicide treatments were not included, data were analyzed as a split-plot design with tillage and cover crops as fixed effects and replicate and replicate by tillage as random effects. Where main or interactive effects were significant, treatment mean separation occurred using Fisher's protected LSD at $\alpha = 0.05$.

Experiment 2B: Role of Light on Tillage-mediated Seed Persistence

Experimental Design

To evaluate the potential impact of light on seed persistence in FWT treatments, two exhumation treatments were evaluated: (1) exhumation as described for Experiment 2A (ambient light); and (2) exhumation in darkness (no light) (Table 1). To accommodate these treatments, 4 additional bags of untreated *A. powellii* and *D. sanguinalis* seeds were buried in all four FWT + no cover plots to allow for subsequent evaluation of 2 bags per light treatment at one additional sampling date.

Exhumation, Storage, and Reburial

For seed bags without exposure to light, an opaque plastic box with gloved openings (Figure 1) was placed upside-down over the soil. The edges of the box were buried carefully to exclude all light while bags were excavated by hand and placed in sealed tins contained within the box. Seeds were stored in tins at 4 C for 8 h in the same location as seed exposed to light. Reburial was managed by again excluding light using the box.

Retrieval and Viability Testing

All bags for this experiment were left in the field for 1.5 mo after reburial, at which point they were removed and tested for viability as described in Experiment 2A above.

Statistical Analysis

The effects of exhumation procedure on $N_{v,t}$ and $P_{v,t}$ were analyzed using PROC GLIMMIX in Statistical Analysis System v. 9.4 (SAS Institute) with exhumation procedure as a fixed effect and replicate as a random effect. The persistence of seeds from time period 3 (June) to 4 (July) was calculated according to:

$$P_{3,4} = N_{v,4} / N_{v,3} \quad [4]$$

where $N_{v,3}$ and $N_{v,4}$ are the total number of viable seeds at the June ($t = 3$) and July ($t = 4$) exhumation times, respectively. Persistence for Experiment 2B was defined based on the June time point to better evaluate seed persistence specifically after light exposure during the tillage event. Mean values of these responses from the 2 bags recovered from each sub-subplot were used for subsequent analysis.

Results and Discussion

Experiment 1: Tillage and Cover Crop Effects on Seed Persistence

The overwinter (7 MAB) persistence of *A. powellii* and *D. sanguinalis* was 77% and 20%, respectively, regardless of cover crop

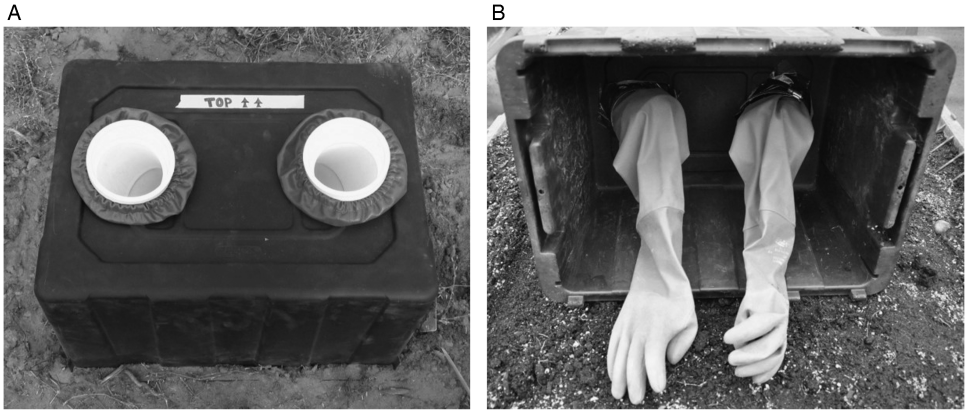

Figure 1. The outside (A) and underside (B) of the opaque plastic box with gloved openings that was placed upside-down over the soil to facilitate seed bag exhumation without light exposure.

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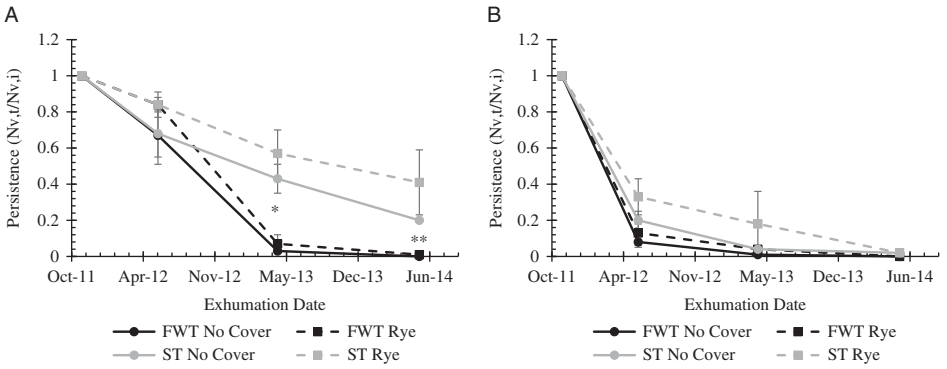

Figure 2. Effects of tillage (full-width tillage [FWT] or strip tillage [ST]) and cover crop (no cover or rye) from Experiment 1 on the persistence (mean ± SE) of (A) *Amaranthus powellii* and (B) *Digitaria sanguinalis* seeds between November 2011 and June 2014. Persistence is defined as the total number of viable seeds on a given date ($N_{v,t}$) divided by the total number of viable seeds initially buried ($N_{v,i}$). Asterisks indicate significant differences between tillage treatments within each species: *$P < 0.05$; **$P < 0.01$. The effects of cover crop and cover crop * tillage interactions were not significant for either species at any sampling date. The main effect of tillage was significant only for *A. powellii* at the May and June sampling dates ($P < 0.05$).

or tillage (Figure 2). By 19 MAB, *A. powellii* seeds in FWT treatments had only 5% persistence, while counterparts in ST treatments had 51% persistence, with no significant differences between cereal rye and the no cover treatment (Figure 2A). At 31 MAB, *A. powellii* seeds in FWT had only 0.6% persistence compared with 29% persistence in ST treatments. At 19 and 31 MAB, persistence of *D. sanguinalis* seeds was 15% and 2%, respectively, regardless of tillage or cover crop treatment (Figure 2B).

There are several possible explanations for the large effect of tillage on the persistence of *A. powellii* in this study. One explanation is that seeds in FWT treatments were temporarily removed from the field during tillage operations and were therefore exposed to stimuli (e.g., light, oxygen) that may have triggered fatal germination following reburial. In contrast, seeds in ST treatments remained continuously buried and did not experience such stimuli. Seeds of species closely related to *A. powellii* are well known for their germination response to light (Gallagher and Cardina 1998a, 1998b). In contrast, *D. sanguinalis* germination may be less affected by light, which may account for the lack of observed tillage effect on *D. sanguinalis* persistence, although the related species southern crabgrass [*Digitaria ciliaris* (Retz.) Koeler] is light sensitive in its germination response (Tang et al. 2010). In addition, tillage and cereal rye effects on *D. sanguinalis* seeds may have been difficult to observe in this experiment due to both the high variability and the rapid decline in *D. sanguinalis* viability that occurred before the first exhumation. An alternative explanation for reduced persistence of *A. powellii* under FWT in this study is that fungal pathogens responsible for seed decay were more prevalent in FWT treatments; this was tested in the subsequent experiment.

Experiment 2A: Tillage and Cover Crop Effects on Seed Persistence and the Potential Role of Fungal Pathogens

Effects of Tillage on Persistence

Consistent with Experiment 1, *A. powellii* seed persistence in Experiment 2A was influenced by tillage but not the cereal rye cover crop (Table 3). This tillage effect was only evident after at least 8.5 mo of burial and following removal and reburial to accommodate spring tillage in the FWT plots. The persistence of *A. powellii* seeds recovered in ST treatments did not differ between June and September following tillage. In contrast, the proportion of persistent *A. powellii* seeds in FWT treatments declined by approximately 60% during the same time period. Because the tillage effect on persistence did not occur until 8.5 MAB, and fungicide treatments were only evaluated at the 7-mo exhumation date, we could not evaluate the potential role of fungal pathogens in mediating this effect. This shortcoming could have been overcome by burying sufficient numbers of additional bags of fungicide-treated seeds to allow seed recovery and testing for a longer period, although the lack of persistence of the fungicides themselves over such longer periods limits the value of this approach (Kamrin 1997; Krieger 2001). Another alternative would have been to bury fresh bags of untreated and fungicide-treated seeds in the spring and evaluate differences in seed persistence over a shorter period following tillage. However, interpretation of results from this approach would be complicated by the fact that the seeds had not undergone stratification in the field.

Digitaria sanguinalis persistence was influenced by tillage (Table 4). As with *A. powellii*, the persistence of *D. sanguinalis* seeds was greater in ST compared with FWT treatments, but only following removal and reburial to accommodate spring tillage. Specifically, seed persistence declined by 63% between December and July in ST plots compared with 88% in FWT treatments.

Our finding that seeds of both *A. powellii* and *D. sanguinalis* had greater persistence under ST compared with FWT is consistent with several other studies demonstrating greater persistence of summer annual weeds under no-tillage conditions compared with conventional FWT (Davis et al. 2005; Roberts and Feast 1972; Steckel et al. 2007). Although weed seed persistence and weed seedbank dynamics under ST are in theory different from those under no-till due to greater spatial heterogeneity (Brainard et al. 2013), in practice they may be similar, especially in the between-row zone where seeds were buried in our experiments.

Effects of Cover Crops on Persistence

We did not find a significant cereal rye cover crop effect on the persistence of *A. powellii* seeds (Table 3). There was, however, an effect of rye cover cropping on the proportion of persistent seeds of *D. sanguinalis*, independent of tillage (Table 4; no tillage by cover crop interaction). Contrary to our hypothesis, *D. sanguinalis* seed persistence was greater in cereal rye treatments compared with the no cover crop control at the March and June retrieval dates, although this effect had dissipated by July. For

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Table 3. Effects of tillage, cover crop, and fungicide treatment on the percentage of *Amaranthus powellii* seeds persisting at 7, 8.5, and 10.5 mo after burial ($N_{v,t}/N_{v,1}$*100) from Experiment 2A.

	June 2016	July 2016	September 2016
	7 mo	8.5 mo[a]	10.5 mo[a]
	%		
Tillage main effect[b]			
FWT	85.2	31.2b	34.6b
ST	88.3	77.6a	88.3a
Cover crop main effect			
No cover	82.5	60.6	55.4
Rye	91.0	48.2	67.5
Fungicide main effect			
With fungicide	90.2	na	na
Without fungicide	83.4	na	na
ANOVA[c]			
Tillage (T)	NS	*	**
Cover crop (C)	NS	NS	NS
Fungicide (F)	NS	na	na
T × C	NS	NS	NS
T × F	NS	na	na
C × F	NS	na	na
T × C × F	NS	na	na

[a]na indicates that the given effect or interaction is not applicable for that date.
[b]FWT, full-width tillage; ST, strip tillage.
[c]P-values are statistically significant at the following α: $^{+}<0.10$; $^{*}<0.05$; $^{**}<0.01$; $^{***}<0.001$; or not significant (NS).

Table 4. Effects of tillage, cover crop, and fungicide treatment on the percentage of *Digitaria sanguinalis* seeds persisting at 4.5, 7, and 8.5 mo after burial ($N_{v,t}/N_{v,1}$*100) from Experiment 2A.

	March 2016	June 2016	July 2016
	4.5 mo	7 mo[a]	8.5 mo[a]
	%		
Tillage main effect[b]			
FWT	51.2	55.4	11.7b
ST	61.5	61.4	36.6a
Cover crop main effect			
No cover	40.9b	41.7b	17.2
Rye	71.8a	75.1a	31.0
Fungicide main effect			
With fungicide	56.9	na[b]	na
Without fungicide	55.7	na	na
ANOVA[c]			
Tillage (T)	NS	NS	*
Cover crop (C)	**	**	NS
Fungicide (F)	NS	na	na
T × C	NS	NS	NS
T × F	NS	na	na
C × F	NS	na	na
T × C × F	NS	na	na

[a]na indicates that the given effect or interaction is not applicable for that date.
[b]FWT, full-width tillage; ST, strip tillage.
[c]P-values are statistically significant at the following α: $^{+}<0.10$; $^{*}<0.05$; $^{**}<0.01$; $^{***}<0.001$; or not significant (NS).

March and June sampling dates, *D. sanguinalis* viability was 2-fold greater in cereal rye compared with no cover crop treatments.

Our results are generally consistent with those of several other studies that also evaluated the impact of cereal rye on persistence of various summer annual weeds. Mohler et al. (2018) also found that the persistence of *A. powellii* was unaffected by rye cover crop residue. However, they found that in the grass species *S. faberi*, seed persistence (in one of two burial studies) was twice as high in the presence of rye compared with a bare-soil treatment. Similarly, Hill et al. (2016) found that cereal rye increased seed persistence of *S. faberi* and *A. theophrasti*.

In our bare-soil treatments, the decline in viability of *D. sanguinalis* seeds occurred most rapidly between December and February, with little change occurring between February and June. In contrast, the viability of *D. sanguinalis* seeds in ST treatments was relatively stable until June, declining most rapidly between the June and July sampling dates. *Digitaria sanguinalis* seeds had greater overwinter persistence in rye treatments regardless of tillage, implying that cereal rye residue affected viability regardless of whether the residue was left on the surface (ST) or incorporated into the soil (FWT) during the previous growing seasons.

Effects of Fungicide Treatment on Persistence

Fungicide treatment did not affect overwinter persistence of either *A. powellii* (Table 3) or *D. sanguinalis* (Table 4). Findings from other studies on the interactive effects of tillage or cover cropping on fungal-mediated seed persistence are mixed. Pitty et al. (1987) found greater fungal colonization of green foxtail [*Setaria viridis* (L.) P. Beauv] and *S. faberi* seeds at 0- to 7.5-cm depths of plowed plots as compared with reduced-tillage plots, presumably due to crop residue placement and organic matter accumulation. However, Gallandt et al. (2004) found no difference in fungal-mediated persistence of *A. fatua* in soils that differed in their historic tillage intensity.

We also found no evidence that the increased persistence of *D. sanguinalis* seeds in rye cover crop treatments (Table 4) was due to differences in fungal decay agents in rye versus bare-soil treatments. In particular, the effect of cereal rye on *D. sanguinalis* was independent of fungicide seed treatment. We cannot rule out the possibility that the fungicides used in our study were ineffective at providing protection from specific fungal pathogens, or strains of pathogens, responsible for decay of these species. When applied to soil, both captan and trifloxystrobin have reported half-lives ranging from only a few days to about 2 wk (Kamrin 1997; Krieger 2001), while metalaxyl has a reported half-life ranging from 7 to 170 d (Kamrin 1997). However, fungicides on seeds buried in the soil may have a longer half-life than those applied directly to the soil (Griffith and Mathews 1969), and many previous studies have shown positive effects of fungicides on seed persistence over periods greater than 4.5 mo, including those relying only on captan (reviewed in Wagner and Mitschunas 2008).

Given the lack of evidence for pathogen-mediated effects of rye on seed persistence, the mechanisms responsible for rye effects on persistence remain unclear. Perhaps rye changed soil edaphic conditions to disfavor decay agents of *D. sanguinalis*. For

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example, the presence of actively growing rye during the winter (regardless of tillage system) may have reduced soil moisture through transpiration, resulting in drier soil conditions that were less conducive to decay. Rye is also a well-known source of allelochemicals (Barnes et al. 1987) that may be toxic to decay agents of weed seeds. Another potential mechanism, suggested by both Hill et al. (2016) and Mohler et al. (2018), is that cover crops with high C:N ratios, like cereal rye, reduce fatal germination of seeds by lowering their exposure to soil nitrate. Because nitrate is well known to stimulate germination of many weed species, including both *A. powellii* (Brainard et al. 2006) and *D. sanguinalis* (Gallart et al. 2008), nitrogen immobilization following incorporation of high C:N cover crops may reduce fatal germination and hence increase persistence of these species.

Experiment 2B: Role of Light on Tillage-mediated Seed Persistence

Effects of Light on Persistence

In FWT treatments, seeds exposed to light during the spring-tillage exhumation event had a lower proportion of persistent seeds at a subsequent sampling date than seeds kept in darkness (Figure 3). After 1 mo of burial following tillage, *A. powellii* seeds that had been exposed to light had 48% lower persistence than those kept in darkness. Similarly, *D. sanguinalis* seeds exposed to light had 62% lower persistence than those kept in darkness.

These results suggest that light exposure that occurred in FWT treatments while seed bags were exhumed during tillage triggered subsequent fatal germination upon reburial, resulting in lower persistence. Petri dish germination trials supported this concept, with *D. sanguinalis* seeds showing a positive response in germination following exposure to light (unpublished data). However, the effect of light on *A. powellii* germination was less clear, with seeds tending to have higher germination in darkness when tested in a petri dish (unpublished data). Previous studies have shown that light exposure increases germination of *Digitaria* spp. (Tang et al. 2010) as well as species in the *Amaranthus* genus closely related to *A. powellii* (Gallagher and Cardina 1998a; Liebman et al. 2001). The discrepancy between our petri dish and field observations for *A. powellii* may be explained by the fact that light sensitivity of *Amaranthus* species changes with burial and prechilling (as would occur during overwinter burial and stratification) (Wesson and Wareing 1967, 1969), perhaps due to seasonal phytochrome sensitivity (Gallagher and Cardina 1998a, 1998b; Taylorson 1972).

We observed no difference in persistence between tillage types when we controlled for light exposure during FWT (Figure 3). This result suggests that light exposure was the only factor influencing tillage effects on seed persistence. In other words, long-term changes in soil conditions due to historic differences in tillage had no detectable effect on persistence of either species.

Our work has several important methodological implications for studies of this kind. First, to understand the influence of edaphic factors on seed persistence resulting from historic differences in management, it is important to control for short-term impacts of those practices. In the case of tillage, short-term exposure to light is clearly an important germination cue for many agricultural weed species and—as we have shown—may be the primary factor explaining tillage effects on persistence. However, mimicking the light exposure experienced by ambient weed seeds during tillage presents a challenge. Tracking the fate of known species and densities of seeds in mesh bags is a useful and well-established method for evaluating seed persistence, but removal of these bags during tillage—to minimize their destruction or loss—may result in light exposure that differs from that experienced by ambient seeds during tillage. Although many ambient seeds are likely to experience sufficient light exposure to trigger germination, others may be embedded in soil aggregates or insufficiently disturbed to experience such light cues (Pareja et al. 1985; Terpstra 1986). Our approach—removing and temporarily storing seeds in both light and darkness during tillage—provides a useful method for defining the range of plausible responses to light exposure.

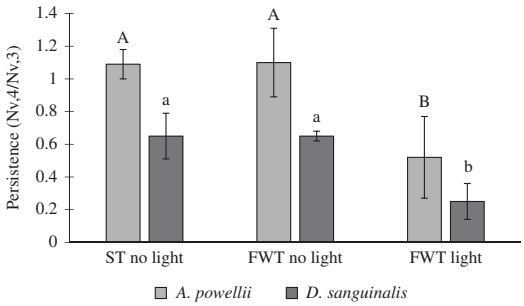

Figure 3. Effects of tillage (full width tillage [FWT] or strip tillage [ST]) and light condition during exhumation on seed persistence (mean ± SE) of *Amaranthus powellii* and *Digitaria sanguinalis* seeds 1.5 mo after tillage (8.5 MAB). Data are from Experiment 2B. Persistence is defined as the total number of viable seeds for each seed bag in July ($N_{v,4}$) divided by the total number of viable seeds at the June exhumation time ($N_{v,3}$). All seeds were placed within the no cover treatment. Different letters indicate significant differences between exhumation treatments within each species. Means were separated within each species using Fisher's protected LSD at $\alpha = 0.05$.

With respect to cover crop effects on seed persistence, our results are consistent with several recent studies suggesting that residues with high C:N ratios may increase seed persistence relative to residues with low C:N ratios or bare soil (Hill et al. 2016; Mohler et al. 2018). We found no evidence that cover crop–mediated changes in fungal pathogens were responsible for the observed increase in persistence of *D. sanguinalis*, but the mechanism and significance of this effect remains unclear. Future studies evaluating potential mechanisms responsible for the cover crop effects observed in this study would be valuable for understanding and managing *D. sanguinalis*, a major weed problem in both conventional and conservation agricultural systems.

In general, our results suggest that two key practices associated with conservation agriculture—reduced tillage and retention of crop or cover crop residue—may contribute to the persistence of important summer annual weed species and help explain observed increases in problematic species in these systems, including *D. sanguinalis*. Continued efforts to identify mechanisms responsible for these effects should help to identify complementary cover crop, tillage, or fertilization strategies that promote seed predation, decay, or fatal germination and lower weed management costs associated with these problematic weed species.

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