Weed Science

cambridge.org/wsc

Weed Biology and Ecology

Cite this article: Mohler CL, Taylor AG, DiTommaso A, Hahn RR, and Bellinder RR (2018) Effects of Incorporated Rye and Hairy Vetch Cover Crop Residue on the Persistence of Weed Seeds in the Soil. Weed Sci 66: 379–385. doi: 10.1017/wsc.2017.80

Received: 6 September 2017
Accepted: 5 December 2017

Associate Editor:
Adam Davis, USDA-ARS

Key words:
Fatal germination; green manure; nitrate; seedbanks; seed survival.

Author for correspondence:
Charles L. Mohler, Section of Soil and Crop Sciences, School of Integrative Plant Science, 907 Bradfield Hall, Cornell University, Ithaca, NY 14853. (Email: clm11@cornell.edu)

Effects of Incorporated Rye and Hairy Vetch Cover Crop Residue on the Persistence of Weed Seeds in the Soil

Charles L. Mohler[1], Alan G. Taylor[2], Antonio DiTommaso[3], Russell R. Hahn[4] and Robin R. Bellinder[2,✠]

[1]Senior Research Associate, Section of Soil and Crop Sciences, School of Integrative Plant Science, Cornell University, Ithaca, NY, USA, [2]Professor, Section of Horticulture, School of Integrative Plant Science, Cornell University, New York State Agricultural Experiment Station, Geneva, NY, USA, [3]Professor, Section of Soil and Crop Sciences, School of Integrative Plant Science, Cornell University, Ithaca, NY, USA, [4]Associate Professor, Section of Soil and Crop Sciences, School of Integrative Plant Science, Cornell University, Ithaca, NY, USA
✠Deceased.

Abstract

Incorporation of cover crop residue into the soil has been suggested as a means for reducing weed seedbanks. To explore this hypothesis, we buried mesh bags of seeds mixed with sand at 15-cm depth in late fall in plots that had been planted with rye (*Secale cereale* L.) or hairy vetch (*Vicia villosa* Roth.) or left unplanted. Separate bags contained either velvetleaf (*Abutilon theophrasti* Medik.), giant foxtail (*Setaria faberi* Herrm.), Powell amaranth (*Amaranthus powellii* S. Watson), or common lambsquarters (*Chenopodium album* L.). The experiment used a randomized complete block design with five replications, and enough bags were buried to allow a final recovery in each of the following three springs. Each spring, bags were exhumed, and seeds were either counted and tested for viability or mixed with chopped cover crop material or simply stirred for control bags, and the material was reburied. The experiment was completed twice with initial burials in fall of 2011 and 2013. Rye had no consistent effect on persistence of seeds of any of the species. For two observation intervals, rye increased persistence of a species; for another two intervals, it decreased persistence relative to the control; but mostly rye did not affect persistence. Hairy vetch decreased persistence of *C. album* and *A. powellii* in both runs of the experiment but had no effect on persistence of *A. theophrasti* and *S. faberi*. Germination of the first two species is promoted by nitrate, whereas *A. theophrasti* germination is not sensitive to nitrate, and *S. faberi* is only rarely nitrate sensitive. We suggest that nitrate released during decomposition of hairy vetch may have promoted fatal germination of *C. album* and *A. powellii*. Incorporation of legume cover crops like hairy vetch may provide a means for decreasing the seedbanks of the many weed species whose germination is promoted by nitrate. The lack of any reduction of *A. theophrasti* and *S. faberi* seed persistence in response to hairy vetch and the inconsistent and mostly negligible effect of rye indicate that a general increase in readily decomposable organic matter through incorporation of cover crops may be ineffective at reducing weed seedbanks.

Introduction

The need for management of weed seedbanks is widely recognized (Davis et al. 2005; Gallandt et al. 1999; Jordan et al. 1995; Liebman and Mohler 2001). Many studies have shown a decrease in weed seed density in the soil in response to tillage (Lueschen et al. 1993; Roberts and Feast 1972; Schweizer and Zimdahl 1984), and to date, tillage coupled with the elimination of seed rain has been the most effective means for decreasing weed seedbanks. However, because of potential soil degradation associated with frequent tillage, other methods are needed for reducing weed seedbanks.

Manipulation of bacterial, fungal, and macrofaunal populations that attack seeds in the soil offers a potential alternative to tillage as a means for managing weed seedbanks (Gallandt et al. 2005; Kremer 1993). Soil has been experimentally inoculated with bacterial and fungal populations known to attack weed seeds (Kremer 1993), but this approach faces the many problems associated with bioherbicides (Auld et al. 2003; Ghosheh 2005). A more promising approach is to use cover crops, later incorporated as green manures, to promote animal and microbial populations that attack weed seeds. While the cover crop is growing, it can provide habitat beneficial to seed predators (Gallandt et al. 2005). Once incorporated, the cover crop residue feeds microorganisms that could potentially attack weed seeds. However, studies comparing cropping systems with and without green manures have shown contradictory effects on weed seed populations. Fennimore and Jackson (2003) found reduced burning nettle

(*Urtica urens* L.) and shepherd's purse [*Capsella bursa-pastoris* (L.) Medik.] seedling densities in treatments amended with green manures and compost compared with control treatments. They further found lower densities of *C. bursa-pastoris* seeds in the amended treatments and a negative correlation between microbial biomass and density of *U. urens* and *C. bursa-pastoris* seedlings. Similarly, Dyck and Liebman (1994) found lower emergence of common lambsquarters (*Chenopodium album* L.) following incorporation of crimson clover (*Trifolium incarnatum* L.). The reduced emergence could potentially have been due to either suppression of germination or to increased death of seeds and of seedlings before emergence. Suppression of germination is unlikely, however, because nitrate released during decomposition of a legume would tend to promote germination of *C. album* (Henson 1970; Roberts and Benjamin 1979; Vincent and Roberts 1977). Mohler et al. (2014) found that incorporation of pea (*Pisum sativum* L.) reduced emergence of several common weed species and that this was associated with infection of seeds by *Fusarium* species.

In contrast with these studies, Davis et al. (2006) found that after 10 yr of cropping system history, seed mortality of velvetleaf (*Abutilon theophrasti* Medik.) and giant foxtail (*Setaria faberi* Herrm.) was greater in conventional systems than in a system that received only compost as a nutrient source. Moreover, *S. faberi* mortality was also greater in a conventional system than in a system with red clover (*Trifolium pratense* L.) green manure. They also showed that seed mortality rates were correlated with the composition of the microbial community. Davis (2007) found that addition of corn stover to soil had no effect on seed mortality of five species and decreased the mortality of *A. theophrasti* compared with a control without corn stover. For giant ragweed (*Ambrosia trifida* L.) and wooly cupgrass [*Eriochloa villosa* (Thunb.) Kunth], corn stover increased or decreased weed persistence, depending on whether or not inorganic nitrogen was added. Thus, the overall addition of organic matter mostly either had no effect on seed mortality or decreased mortality. Similarly, Gallandt et al. (2004) found that whether crop residues were left on the soil surface in a no-tillage system or incorporated in a conservation tillage system had no effect on decay of wild oat (*Avena fatua* L.) seeds.

Incorporated cover crops can potentially affect weed seed populations in three ways. First, cover crops can attract macrofauna like earthworms that consume weed seeds. Earthworm population density is correlated with soil carbon (Edwards 1983), and earthworms consume weed seeds (McRill and Sagar 1973; Shumway and Koide 1994). Second, incorporation of cover crop residue promotes growth of microbial populations, which could potentially damage weed seeds. This was the focus of much of the work discussed earlier.

Finally, incorporated cover crops can potentially promote or inhibit germination of weed seeds, thereby decreasing or increasing the persistence of seedbanks. If the seed germinates but the seedling dies before emergence because it is too deep in the soil or is killed by some agency, then this fatal germination is essentially indistinguishable from seed mortality. Legume cover crop residue generally has a low carbon to nitrogen ratio, and consequently, decomposition of this material releases nitrogen, which is quickly converted to nitrate. About half of all weed species have increased germination under at least some conditions when nitrate is present in the germination environment (Steinbauer and Grigsby 1957). Thus, an incorporated legume could promote germination and thereby reduce seed persistence of nitrate-sensitive species. Conversely, incorporation of materials with a high carbon to nitrogen ratio, such as nearly mature cereal grain and grain straw, can be expected to promote microbial sequestration of nitrogen, thereby reducing potential germination in response to nitrate released during decomposition of soil organic matter. Similarly, allelopathic chemicals released from decomposing crop residue sometimes inhibit or promote germination (Altieri and Doll 1978; Chung and Miller 1995; Reigosa et al. 1999), and that could affect seed persistence. Allelopathic chemicals rarely kill seeds before germination but can act as one of the several factors preventing successful emergence. Many factors associated with tillage promote germination, including exposure to light (Sauer and Struik 1964), increased diurnal temperature fluctuations (Fausey and Renner 1997; Henson 1970), and the venting of volatile germination inhibitors (Holm 1972), and these processes can deplete seedbanks. However, these processes will act about equally whether residues are incorporated during tillage or not. The present study explored the second and third possible source of changes in seed persistence associated with the incorporation of cover crops. Because the experiment was conducted with the seeds confined in bags, macrofauna were excluded.

Materials and Methods

The experiment was conducted in a Cornell University Agricultural Experiment Station field adjacent to the Cornell University campus in Ithaca, NY (42.450°N, 76.460°W). The soil was a Williamson very fine sandy loam (coarse-silty, mixed, active, mesic, Typic Fragiudepts). The field had been fallow before the experiment. On August 23, 2011, the field was sprayed with glufosinate ammonium at 0.25 kg ai ha^{-1}, mowed 8 d later, disked, and on September 1, 2011, planted with cover crops. The experiment was laid out in a replicated block design with five replications and three treatments: bare control, rye (*Secale cereale* L.), and hairy vetch (*Vicia villosa* Roth.). 'Aroostook' rye was drilled at 123 kg ha^{-1} and hairy vetch at 67 kg ha^{-1} in this and subsequent years using a Great Plains model 3P1006NT grain drill (Great Plains Manufacturing, Salina, KS). Plots were 3.0 by 13.7 m.

The basic approach of the experiment was to bury bags of weed seeds mixed with sand in the late fall when cool soil temperatures prevented germination. Each succeeding spring for the next 3 yr, all bags were exhumed and opened. Some samples were retained for testing; the remaining samples had chopped cover crop material mixed with the sand and seeds or, in the case of the control treatment, the sample was simply stirred. The samples were then rebagged and buried until the next spring. This procedure was intended to simulate spring tillage for incorporation of cover crops. The entire experiment was conducted twice, with initial burials in 2011 and 2013.

Seeds of *C. album*, Powell amaranth (*Amaranthus powellii* S. Watson), and *S. faberi* were collected from agricultural populations in central New York state. Mature whole plants of *C. album* and *A. powellii* were cut near the plant base and allowed to dry at room temperature in large paper bags. Ripe seeds of *S. faberi* were shaken from the inflorescences into a bucket and allowed to further dry at room temperature. Fully black capsules of *A. theophrasti* were collected from buffer areas of a nutrient rate experiment (Little et al. 2014) and allowed to dry at room temperature. When seeds were judged to be dry, they were threshed out from other plant material and thoroughly cleaned. Seeds were collected the same fall they were buried, except that the 2011 *A. theophrasti* seeds were also used in 2013. These were stored dry at 4 C until used.

https://doi.org/10.1017/wsc.2017.80 Published online by Cambridge University Press

Table 1. Number of seeds per bag.

Species	2011 initiation	2013 initiation
Abutilon theophrasti	200	400
Setaria faberi	250	500
Amaranthus powellii	200	400
Chenopodium album	200	400

Seeds were counted into coin envelopes using a Model 801-7/B Seedburo seed counter (Seedburo Equipment, Des Plaines, IL) with an accuracy of 1% to 3% (Table 1). Just before burial, seeds were mixed with 57 ml (83 g) of silica sand that had passed a 0.5-mm sieve and were placed into 7.5 by 10 cm organza bags (Uline, Pleasant Prairie, WI). The bags were stapled shut and placed into a second bag, and this too was stapled shut. Bags were tied to approximately 40 cm of nylon cord. A plastic label stating the species, treatment, replication, and year to be recovered for testing was threaded onto the cord, and the end was tied to three 2.5-cm (inside diameter) steel washers. Seed bags were buried initially on October 31, 2011, and November 21, 2013, at a depth of 15 cm in individual holes. Holes were made with an 18 by 7 cm diameter bulb planter. The washers were placed at the bottom of the hole, then the plastic tag, a dusting of soil, and finally the bag containing the sand and seeds. Holes were spaced 90 cm apart along a line 1 m from the plot edge to avoid wheel traffic.

In mid-May of each year from 2012 through 2015, weeds in the control treatments were sprayed with glyphosate (1.5 kg ai ha^{-1}) or hoed, and hairy vetch or rye plants that were in the wrong plot due to imprecision during planting were removed to bare spots in plots of the appropriate treatment. A few days before the bags were to be excavated, aboveground cover crop biomass was sampled by clipping and separately bagging cover crops and weeds in two randomly placed 33 by 76 cm (0.25-m^{-2}) quadrats. This material was weighed, dried for 3 d at 60 C, and weighed again. This provided both an estimate of cover crop biomass and the ratio of fresh to dry weight. Additional cover crop material was collected and chopped into approximately 0.5-cm pieces. The chopped material was weighed out into small plastic bags that contained the amount of material corresponding to the incorporation of 600 dry g m^{-2} of cover crop incorporated to a depth of 15 cm that would be contained in 57 ml of soil (the volume of sand in the bag). Previous experiments have shown that 600 g m^{-2} of aboveground cover crop material is about the maximum that can be grown between September and late May in central New York state.

During the last week in May of each year, cover crops were mowed with a Mott 74 flail mower (Alamo Industrial, Seguin, TX). Each bag was located with a metal detector and marked with a flag. The next day, all bags were exhumed. Bags were immediately placed in an ice chest to keep them at close to soil temperature. In the laboratory, soil was brushed off of the bags, and bags were opened into a pan. Samples that were destined for reburial were stirred (control) or mixed with the appropriate type of cover crop material, rebagged, and returned to an ice chest. While samples were being processed, the field plots were tilled to a depth of about 12 cm with a Maschio 155 rotary tiller (Machio Gaspardo North America, DeWitt, IA) to incorporate cover crops. The next day, bags were reburied as before. Samples that were to be analyzed for seed viability were spread in 15-cm aluminum pie pans and dried for 24 h at 40 C. The seeds were then separated from sand by sieving and stored at 5 C and 30% relative humidity until testing.

Sorghum-sudangrass [*Sorghum bicolor* (L.) Moench. ssp. *drummondi* (Nees ex Steud.) de Wet & Harlan] was planted at a rate of 73 kg ha^{-1} on the whole field just before or after the bags were reburied. Sorghum-sudangrass was harvested using a John Deere 972 forage chopper (John Deere, Moline, IL) in early September and removed from the field. The plots were sprayed with glyphosate at 2.3 kg ai ha^{-1}, and the cover crop plots were no-till planted with rye and hairy vetch, as in 2011.

The original seed lots of each species were tested at selected temperature and light regimens to determine which gave the highest percentage of germination. All species were tested on two layers of moistened blue germination blotters (Anchor Paper, St Paul, MN) in 9 by 9 by 3.5 cm germination boxes. Germination tests were performed in a growth chamber (Model I-36LL, Percival Scientific, Perry, IA). Germination of *A. theophrasti* was tested at 35 C in the dark for 7 d. Dormancy in *A. theophrasti* is maintained by an impermeable seed coat (Horowitz and Taylorson 1985), so viability of hard seeds was then determined by piercing the hilum with a needle and allowing the seeds to germinate for another 7 d.

Germination of *A. powellii* seeds was tested with 14/10 h light/dark at 35/20 C for 14 d (Weaver and Thomas 1986). Germination of *C. album* and *S. faberi* was tested with 8/16 h light/dark at 30/20 C for 14 d. Viability of nongerminated *C. album* and *A. powellii* seeds was evaluated by staining with a 1.0 % solution of 2,3,5-triphenyl tetrazolium chloride (USB, Cleveland, OH), and *S. faberi* viability was evaluated using a 0.1% tetrazolium solution (AOSA/SCST 2010). Viability of the original seed lots was tested using a minimum of five replicates of 50 seeds each. Tests on recovered seeds were done on 50 randomly selected seeds from each replicate bag unless fewer than 50 seeds were present, in which case all seeds were tested.

Data Analysis

The numbers of viable seeds (germinable plus dormant) present in succeeding years were analyzed with general linear mixed models assuming a Poisson distribution with overdispersion (SAS PROC GLIMMIX, Statistical Analysis System, Cary, NC). Treatment, year, and their interaction were treated as fixed effects, and replication and treatment within replication were treated as random effects. To allow for overdispersion, the interaction between treatment, replication, and year was also treated as a random effect. The significance of difference between treatments of the change in number of viable seeds in succeeding years was determined by predefined contrasts and was used to indicate the significance of differences in seed persistence between treatments. Since the algorithm used a natural log link, estimates of the difference between years in least-squares means were back-transformed by exponentiation to provide estimates of seed persistence.

Results and Discussion

Incorporation of hairy vetch produced substantial reductions in the survival of *C. album* and *A. powellii* over the 2.5-yr period from initial burial to final exhumation (Table 2). For these species, seed persistence was reduced two-thirds to 1/4 that of the control treatment. The decreased persistence of *C. album* and

https://doi.org/10.1017/wsc.2017.80 Published online by Cambridge University Press

Table 2. Persistence rates of weed seeds buried at two times, fall 2011 and fall 2013, and recovered for analysis 2.5 yr later following additions of rye, hairy vetch, or no (control) cover crop residue each subsequent spring.[a]

	Control	Rye	Hairy vetch	C vs. R	C vs. V
				——P values[b]——	
Abutilon theophrasti					
F2011–S2014	0.57	0.55	0.57	0.65	9.68
F2013–S2016	0.57	0.55	0.57	0.56	0.88
Setaria faberi					
F2011–S2014	0.06	0.12	0.06	**0.001**	0.62
F2013–S2016	0.14	0.08	0.05	0.52	0.17
Amaranthus powellii					
F2011–S2014	0.13	0.14	0.03	0.74	**<0.001**
F2013–S2016	0.04	0.05	0.02	0.15	**0.08**
Chenopodium album					
F2011–S2014	0.38	0.33	0.16	0.52	**0.004**
F2013–S2016	0.03	0.06	0.02	**0.004**	**0.004**

[a]Abbreviations: C, control; F, fall; R, rye; S, spring; V, hairy vetch.
[b]P values for predefined comparisons that are significant ($P < 0.05$) or nearly significant ($0.05 < P < 0.1$) are shown in bold.

A. powellii seeds in the presence of decomposing hairy vetch relative to the control could be related to the sensitivity of seeds of these two species to nitrate in the soil solution. Hairy vetch is a nitrogen-fixing legume and tissues have a high nitrogen content and release substantial amounts of nitrogen during decomposition (Sarrantonio and Scott 1988). As the vetch decomposes, it releases this nitrogen, which is quickly oxidized to nitrate by soil bacteria. Weak solutions of nitrate have been shown to increase the germination of *C. album* (Henson 1970; Roberts and Benjamin 1979; Vincent and Roberts 1977) and *A. powellii* and related pigweed (*Amaranthus*) species (Brainard et al. 2006; Costea et al. 2004). In the present experiment, seeds were placed too deeply in the soil for successful emergence of any of the four species, even if they had not been confined to bags. Thus, in the experiment, any nitrate-promoted germination was fatal and a similar promotion of fatal germination could be expected to work against seeds of *C. album* and *A. powellii* exposed to decomposing hairy vetch in the soil of a farmer's field. One might argue that the nitrate released from decomposing hairy vetch might also promote germination that leads to greater emergence of these species. However, we have demonstrated elsewhere that incorporated legumes decrease emergence of these and other species, probably by promoting a short-term increase in pathogenic fungi (Mohler et al. 2014). In results similar to ours, Hill et al. (2016) found that seeds of *C. album* buried with red clover residue were less persistent than seeds buried without residue in 1 of 2 yr. They showed that the clover residue released substantial amounts of inorganic nitrogen. This nitrogen could have triggered fatal germination of *C. album*.

In contrast with *C. album* and *A. powellii*, *A. theophrasti* and *S. faberi* showed no significant decrease in persistence associated with incorporation of hairy vetch relative to the control. Germination of *A. theophrasti* is not promoted by nitrate (Fawcett and Slife 1978; Sweeney et al. 2008). Consequently, fatal germination in response to nitrate released from decaying hairy vetch would not be expected to affect persistence of *A. theophrasti*. *Setaria faberi* similarly showed no significant reduction in persistence with hairy vetch relative to the control. However, apparent persistence of *S. faberi* with hairy vetch was only 36% that for the control, so the lack of a significant response to hairy vetch may be due to insufficient sample size in the face of extreme variability. Data on the germination response of *S. faberi* to nitrate are ambiguous. Fawcett and Slife (1978) found no response of *S. faberi* emergence to applications of nitrogen. Sweeney et al. (2008) did observe increased emergence of sown *S. faberi* following nitrogen application but found no increase in emergence of *S. faberi* from the seedbank in response to nitrogen. Schimpf and Palmblad (1980) found a weak germination response to nitrogen for fresh seeds, but no response to nitrogen for seeds that had been chilled. Dekker (2003) reviewed the literature on germination responses of foxtails (*Setaria* spp.) but did not mention any effect of nitrogen on germination. He did note, however, that germination responses of all species in the genus are highly variable and change with environmental conditions. In a study similar to ours, Hill et al. (2016) found that incorporated red clover had no effect on persistence of *S. faberi*. We conclude that incorporated legume cover crops are likely to have a weak or inconsistent effect on the persistence of *S. faberi*.

Because samples were collected for analysis at multiple times following the initial seed burial, additional insights can be gained by examining seed persistence over specific intervals (Table 3). The number of viable seeds varied greatly among replicates, indicating that seed survival rates are strongly affected by microvariation in soil conditions. Occasionally, this variation led to a few more seeds being present in a later sample than were present in the sample drawn from that plot the previous year. The general linear model algorithm, however, handled such cases without problems. For two species by interval cases, the later year had consistently more viable seeds than the previous year. This situation could not occur if the number of viable seeds present in a later sampling year were determined primarily by seed survival. Specifically, more *A. theophrasti* seeds were present for all plots in 2013 than 2012, and more *S. faberi* seeds were present in most samples in 2015 than 2014. As such situations could only occur due to some problem with handling or storage of the seeds during or after exhumation, the data for the earlier of the 2 yr were discarded for these cases.

Treatment had no effect on seed persistence during the first winter the seeds were in the soil (Table 3). This was as expected, because no cover crop material had been incorporated into the bags at the initial burial. Some fine roots did grow into the bags, and these could have potentially affected seed persistence. However, the degree of root penetration into the bags varied greatly between bags, apparently without pattern. Consequently, any effect the cover crop roots may have had on seed persistence was masked by the high variability in persistence.

Large reductions in seed persistence relative to the controls occurred for *C. album* following the first incorporation of hairy vetch, that is, from 2012 to 2013 for the 2011 initial burial and 2014 to 2015 for the 2013 initial burial (Table 3). Hairy vetch had no effect on *C. album* persistence following the second input of hairy vetch residue. Only a portion of the seeds in any seed lot of *C. album* are sensitive to nitrate (Henson 1970; Roberts and Benjamin 1979; Vincent and Roberts 1977). Possibly, the nitrate-sensitive individuals germinated following the first incorporation of hairy vetch and thus were not present to be affected by the second incorporation.

https://doi.org/10.1017/wsc.2017.80 Published online by Cambridge University Press

Table 3. Persistence rates of weed seeds buried at two times, fall 2011 and fall 2013, and recovered for analysis the following three springs.[a]

	Fall to spring (no residue)[b]		With incorporated residue[b]			
			Initiated fall 2011		Initiated fall 2013	
Treatment	F2011–S2012	F2013–S2014	S2012–S2013	S2013–S2014	S2014–S2015	S2015–S2016
Abutilon theophrasti[c]						
Control	NA	0.39	NA	0.99	1.00	0.46
Rye	NA	0.44	NA	0.79	0.77	0.62
Hairy vetch	NA	0.45	NA	0.93	0.43	1.00
C vs. R		0.40		**0.02**	0.48	0.63
C vs. V		0.33		0.53	0.06	0.15
Setaria faberi						
Control	0.89	NA	0.28	0.24	NA	0.14
Rye	0.88	NA	0.32	0.42	NA	0.10
Hairy vetch	0.97	NA	0.32	0.18	NA	0.05
C vs. R	0.94		0.42	0.10		0.63
C vs. V	0.28		0.40	0.36		0.17
Amaranthus powellii						
Control	0.86	0.90	0.55	0.32	0.12	0.29
Rye	0.86	0.96	0.20	0.60	0.17	0.09
Hairy vetch	0.91	0.84	0.30	0.08	0.09	0.06
C vs. R	0.46	0.26	**0.03**	0.31	0.48	0.22
C vs. V	0.33	0.34	0.14	**0.05**	0.56	**0.**08
Chenopodium album						
Control	0.61	0.72	0.78	0.80	0.22	0.21
Rye	0.71	0.72	0.51	0.89	0.30	0.25
Hairy vetch	0.68	0.83	0.33	0.68	0.07	0.25
C vs. R	0.42	0.98	0.21	0.73	0.26	0.70
C vs. V	0.54	0.25	**0.02**	0.60	**0.001**	0.69

[a]Abbreviations: C, control; F, fall; R, rye; S, spring; V, hairy vetch; NA, data not available.
[b]P values for predefined comparisons are given below the proportion of seeds persisting during the interval. P-values that are significant ($P < 0.05$) or nearly significant ($0.05 < P < 0.1$) are shown in bold.
[c]Survival rates of 1.00 were substituted for estimates slightly greater than 1 for *A. theophrasti* in the control treatment for S2014–S2015 and *A. theophrasti* in the hairy vetch treatment for S2015–S2016.

In contrast with *C. album*, the reduction in *A. powellii* seed persistence with hairy vetch compared with the control followed the second incorporation of hairy vetch rather than the first. Although the reduction in seed persistence in the 2015 to 2016 interval did not quite reach statistical significance ($P = 0.08$), only 21% as many seeds persisted in the presence of hairy vetch compared with the control. Conceivably, the *A. powellii* seeds aged into a sensitivity to nitrate, but the literature provides no basis for this hypothesis. Consequently, why the effect of the hairy vetch was delayed until the second addition of residue is unknown.

The effect of incorporated rye residue on seed persistence was mostly negligible and without obvious pattern when it did occur. Rye about doubled persistence relative to the control of *S. faberi* from fall 2011 to spring 2014 and *C. album* from fall 2013 to spring 2016. This increase in persistence due to rye is similar, though less consistent, to that observed by Davis (2007) when corn stover, another residue with high carbon to nitrogen ratio, was incorporated. Balancing the observed increase in persistence due to rye for *S. faberi* and *C. album*, however, was a decrease in persistence in the presence of rye relative to the control for *A. theophrasti* from 2014 to 2015 and *A. powellii* from 2012 to 2013. Unlike the effects of hairy vetch on persistence of *C. album* and *A. powellii*, the effects of rye over the 2.5-yr intervals (Table 2) are not easily related to persistence in the three shorter intervals (Table 3).

https://doi.org/10.1017/wsc.2017.80 Published online by Cambridge University Press

The frequently negligible and sometimes positive effect of rye on seed persistence and the lack of an effect of hairy vetch on the two species with low or no sensitivity to nitrate indicates that attempting to promote microbial attack on weed seeds by incorporation of cover crop residue may be a poor strategy for reducing weed seedbanks. However, we do not discount the potential importance of microbes in affecting the persistence of seeds in the soil. The density and composition of the microbial community probably varies greatly on small scales within the soil and may contribute to the high variability in seed persistence between replicates observed in this study. Nevertheless, the present study, in conjunction with published literature, indicates that a general promotion of microbial activity through the incorporation of cover crops is not an effective method for the management of weed seedbanks.

Because we did not analyze microbial communities, we cannot rule out the possibility that microbial attack rather than fatal germination was responsible for the reduced persistence of *C. album* and *A. powellii* following incorporation of hairy vetch. We believe, however, that fatal germination is the more parsimonious explanation of the effect. Whether depletion of seedbanks of nitrate-sensitive species through incorporation of legume cover crops can be broadly applied in the field remains to be determined. Previous studies examined seedling emergence of nitrate-sensitive species following application of nitrate fertilizers and found no response or variable responses among years, weed populations, seed lots, and even position of seeds on the parent plant (Brainard et al. 2006; Fawcett and Slife 1978; Hilton 1985; Hurtt and Taylorson 1986). Although these studies focused on emergence, the effect or lack of effect of nitrate was presumably on germination rather than on seedling growth through the soil, and thus these studies are relevant to persistence of seedbanks. Nitrate sensitivity can also change as seeds age, are chilled over the winter (Schimpf and Palmblad 1980), or are affected by other environmental factors (Hilton 1984). Clearly, additional studies are needed to explore the causes and consistency of the decreased persistence of some species of weed seeds following incorporation of legume cover crops. Nevertheless, promotion of fatal germination of seeds of nitrate-sensitive species through incorporation of legumes may reduce weed seedbanks in some circumstances.

Acknowledgements. We thank S. Morris, P. Putriment, E. Kennedy, K. Ellis, X. Garcia Friere. K. Bitter, M. Harbert, V. Minares, D. Stauffer, M. Loos, S. Costello, C. Catranis, W. Huang. K. Walsh, J. Hunn, Q. Maqsood, Z. Kaufmann, M. Amirkhani, N. Brennan, A. Repka, C. Stokes, L. Woodruff, C. Jennison, E. Marino, M. Dias, P. Kikhao, J. Drennan, J. France, P. Tremel, D. Stauffer, F. Kordbacheh, C. Neumann, and E. Buck for assistance with the lab work and fieldwork, and R. J. Richtmyer for conducting the machinery operations. This work was supported by funds from the Cornell University and New York State Agricultural Experiment Station (Multi-State Hatch Projects NE-1026, and NE-1047, Project numbers 3120006036 NYC-145843 NE1026, and 231327 NYC-125800 NE1047). No conflicts of interest have been declared.

References

Altieri MA, Doll JD (1978) The potential of allelopathy as a tool for weed management in crop fields. Intl J Pest Manag 24:495–502

[AOSA/SCST] Association of Official Seed Analysts/Society of Commercial Seed Technologists (2010) Tetrazolium Testing Handbook. 2010 ed. Ithaca, NY: AOSA/SCST

Auld B, Hetherington SD, Smith HE (2003) Advances in bioherbicide formulation. Weed Biol Manag 3:61–67

Brainard DC, DiTommaso A, Mohler CL (2006) Intraspecific variation in germination response to ammonium nitrate of Powell amaranth (*Amaranthus powellii*) seeds originating from organic and conventional vegetable farms. Weed Sci 54:435–442

Costea M, Weaver SE, Tardif EJ (2004) The biology of Canadian weeds. 44. *Amaranthus retroflexus* L., *A. powellii* S. Watson and *A. hybridus* L. (updated). Can J Plant Sci 84:631–668

Chung I-M, Miller DA (1995) Natural herbicide potential of alfalfa residue on selected weed species. Agron J 87:920–925

Davis AS (2007) Nitrogen fertilizer and crop residue effects on seed mortality and germination of eight annual weed species. Weed Sci 55:123–128

Davis AS, Anderson KI, Hallett SG, Renner KA (2006) Weed seed mortality in soils with contrasting agricultural management histories. Weed Sci 54: 291–297

Davis AS, Cardina J, Forcella F, Johnson GA, Kegode G, Lindquist JL, Luschei EC, Renner KA, Sprague CL, Williams MM II (2005) Environmental factors affecting seed persistence of annual weeds across the U.S. corn belt. Weed Sci 53:860–868

Dekker J (2003) The foxtail (*Setaria*) species-group. Weed Sci 51:641–656

Dyck E, Liebman M (1994) Soil fertility management as a factor in weed control: the effect of crimson clover residue, synthetic nitrogen fertilizer, and their interaction on emergence and early growth of lambsquarters and sweet corn. Plant Soil 167:227–237

Edwards CA (1983) Earthworm ecology in cultivated soil. Pages 123–137 *in* Satchell JE, ed. Earthworm Ecology. London: Chapman and Hall

Fausey JC, Renner KA (1997) Germination, emergence, and growth of giant foxtail (*Setaria faberi*) and fall panicum (*Panicum dichotomiflorum*). Weed Sci 45:423–425

Fawcett RS, Slife EW (1978) Effect of field applications of nitrate on weed seed germination and dormancy. Weed Sci 26:594–596

Fennimore SA, Jackson LE (2003) Organic amendment and tillage effects on vegetable field weed emergence and seedbanks. Weed Technol 17:42–50

Gallandt ER, Fuerst EP, Kennedy AC (2004) Effect of tillage, fungicide seed treatment, and fumigation on seed bank dynamics of wild oat (*Avena fatua*). Weed Sci 52:597–604

Gallandt ER, Liebman M, Huggins DR (1999) Improving soil quality: implications for weed management. J Crop Prod 2:95–121

Gallandt ER, Molloy T, Lynch RP, Drummond FA (2005) Effect of cover-cropping systems on invertebrate seed predation. Weed Sci 53:69–76

Ghosheh HZ (2005) Constraints in implementing biological weed control: a review. Weed Biol Manag 5:83–92

Henson IE (1970) Effects of light, potassium nitrate and temperature on the germination of *Chenopodium album* L. Weed Res 10:27–39

Hill EC, Renner KA, Sprague CL, Davis AS (2016) Cover crop impact on weed dynamics in an organic dry bean system. Weed Sci 64:261–275

Hilton JR (1984) The influence of light and potassium nitrate on the dormancy and germination of *Avena fatua* L. (wild oat) seed and its ecological significance. New Phytol 96:31–34

Hilton JR (1985) The influence of light and potassium nitrate on the dormancy and germination of *Avena fatua* L. (wild oat) seed stored buried under natural conditions. J Exp Bot 36:974–979

Holm RE (1972) Volatile metabolites controlling germination in buried weed seeds. Plant Physiol 50:293–297

Horowitz M, Taylorson RB (1985) Behaviour of hard and permeable seeds of *Abutilon theophrasti* Medic. (velvetleaf). Weed Res 25:363–372

Hurtt W, Taylorson RB (1986) Chemical manipulation of weed emergence. Weed Res 26:259–267

Jordan N, Mortensen DA, Prenzlow DM, Cox KC (1995) Simulation analysis of crop rotation effects on weed seedbanks. Am J Bot 82:390–398

Kremer RJ (1993) Management of weed seed banks with microorganisms. Ecol Appl 3:42–52

Liebman L, Mohler CL (2001) Weeds and the soil environment. Pages 210–268 *in* Liebman M, Mohler CL, Staver CP, eds. Ecological Management of Agricultural Weeds. Cambridge: Cambridge University Press

Little NG, Mohler CL, Ketterings QM, DiTommaso A (2014) Effects of organic nutrient amendments on weed and crop growth. Weed Sci 63:710–722

Lueschen WE, Andersen RN, Hoverstad TR, Kanne BK (1993) Seventeen years of cropping systems and tillage affect velvetleaf (*Abutilon theophrasti*) seed longevity. Weed Sci 41:82–86

https://doi.org/10.1017/wsc.2017.80 Published online by Cambridge University Press

McRill M, Sagar GR (1973) Earthworms and seeds. Nature 243:482
Mohler CL, Dykeman C, Nelson ER, DiTommaso A (2014) Reduction in weed seedling emergence by pathogens following the incorporation of green crop residue. Weed Res 52:467–477
Reigosa MJ, Souto XC, Gonzalez L (1999) Effect of phenolic compounds on the germination of six weed species. Plant Growth Regul 28:83–88
Roberts EH, Benjamin SK (1979) The interaction of light, nitrate and alternating temperature on the germination of *Chenopodium album*, *Capsella bursa-pastoris* and *Poa annua* before and after chilling. Seed Sci Technol 7:379–392
Roberts HA, Feast PM (1972) Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. Weed Res 12:316–324
Sarrantonio M, Scott TW (1988) Tillage effects on nitrogen availability to corn following a winter green manure crop. Soil Sci Soc Am J 52:1661–1668
Sauer J, Struik G (1964) A possible ecological relation between soil disturbance, light-flash, and seed germination. Ecol 45:884–886
Schimpf DJ, Palmblad IG (1980) Germination response of weed seeds to nitrate and ammonium with and without simulated overwintering. Weed Sci 28:190–193
Schweizer EE, Zimdahl RL (1984) Weed seed decline in irrigated soil after six years of continuous corn (*Zea mays*) and herbicides. Weed Sci 32:76–83
Shumway DL, Koide RT (1994) Seed preferences of *Lumbricus terrestris* L. Appl Soil Ecol 1:11–15
Steinbauer GP, Grigsby B (1957) Interaction of temperature, light, and moistening agent in the germination of weed seeds. Weeds 5:175–182
Sweeney AE, Renner KA, Laboski C, Davis A (2008) Effect of fertilizer nitrogen on weed emergence and growth. Weed Sci 56:714–721
Vincent EM, Roberts EH (1977) The interaction of light, nitrate and alternating temperature in promoting the germination of dormant seeds of common weed species. Seed Sci Technol 5:659–670
Weaver SE, Thomas AG (1986) Germination responses to temperature and atrazine-resistant and susceptible biotypes of two pigweed (*Amaranthus*) species. Weed Sci 34:865–870

https://doi.org/10.1017/wsc.2017.80 Published online by Cambridge University Press