

Effect of tillage, fungicide seed treatment, and soil fumigation on seed bank dynamics of wild oat (*Avena fatua*)

Eric R. Gallandt

Corresponding author. Department of Plant, Soil and Environmental Sciences, University of Maine, 5722 Deering Hall, Orono, ME 04469-5722; gallandt@maine.edu

E. Patrick Fuerst

Department of Crop and Soil Sciences, Washington State University, Pullman, WA 99164-6420

Ann C. Kennedy

USDA-ARS, Department of Crop and Soil Sciences, Washington State University, Pullman, WA 99164-6420

No-tillage offers potential for improved soil quality, reduced erosion, and equal or increased crop yields. We hypothesized that, compared with conservation tillage (CT), no-tillage (NT) offers conditions more conducive to microbial decay of weed seed. In NT systems seed remain at or near the soil surface where crop residues, moisture, and lack of disturbance create an environment with greater soil microbial diversity. In late fall of 1998 and 1999, dormant seed of wild oat, either individually glued to plastic toothpicks or mixed with soil and placed in mesh bags, were buried (mean seed depth of 2.5 cm) in replicated field plots managed by NT or CT since 1982. Treatments including fungicide seed treatment (thiram + metalaxyl + captan) and soil fumigation (propylene oxide) provided estimates of the contribution of microorganisms to observed mortality. Seed were retrieved in May and August, 1999 and 2000. Contrary to our original hypothesis, the proportion of dead seed was generally similar in NT and CT systems. Lack of tillage system by seed or soil treatments affecting the proportion of dead or decayed seed suggests that the contribution of microorganisms to seed fate is similar in these tillage environments. However, the proportion of dormant seed was consistently lower in the NT compared with CT treatments; there was a corresponding increase in the proportion of germinated seed. Overall, more than half of the wild oat seed bank losses could be directly attributed to germination whereas losses due to decay were relatively minor by comparison. Despite favorable distribution of seed and improved quality of the surface-strata of soil in NT systems, this study fails to provide evidence that enhanced microbial decay will contribute to a “weed-suppressive” capacity in such cropping systems.

Nomenclature: Captan, N-trichloromethylthio-4-cyclohexene-1,2-dicarboximide, metalaxyl, N-(2,6-dimethylphenyl)-N-(methoxyacetyl)alanine methyl ester; propylene oxide; thiram, tetramethylthiuram disulfide; wild oat, *Avena fatua* L. AVEFA; wheat, *Triticum aestivum* L. ‘Madsen’.

Key words: Conservation tillage, no-tillage, weed population dynamics, weed seed bank, seed dormancy, seed mortality.

Dormancy and resistance to decay enable seed of many species to persist in the seed bank for several years or even decades, thereby dispersing the population with time (Cavers and Benoit 1989). Seed bank decline is a function of losses due to germination and mortality. Lacking input, seed banks commonly decline at a constant percentage annual loss that is known to differ among species (Cook 1980), among seed sources within a species (Donald 1993), and among locations (Burnside et al. 1977). Mechanistic explanations of species- and location-specific decay rates are not available. However, the large variation in seed survivorship suggests that there is opportunity to manipulate seed banks through practices that influence seed germination, dormancy, and mortality. Repeated shallow tillage stimulates germination (Ogg and Dawson 1984) but causes soil erosion, which limits widespread recommendation of this practice. Various chemicals stimulate germination by breaking dormancy (Egley and Duke 1985) but this approach has not been widely adopted for various reasons, including limited efficacy.

To effectively manage the seed bank, we must consider all possible causes of seed mortality, including: fatal germination;

predation by vertebrates and invertebrates; environmental stresses, such as the effect of fluctuating temperatures and moisture near the soil surface; aging, such as the gradual loss of viability of dry seed; and invasion and decay by microorganisms. The interaction of these factors, such as damage by predation and subsequent microbial invasion (Kremer and Spencer 1989) may also increase mortality. Seed mortality in situ has rarely, if ever, been successfully partitioned into categories of fatal germination, predation, environmental stress, aging, and decay.

Conservation tillage (CT), including no-tillage (NT), has been widely adopted in many cropping areas as a means of reducing soil erosion, increasing soil organic matter, and improving soil structure, as well as improving production efficiency (Uri 1999). Elimination of intensive soil disturbance has resulted in greater reliance on herbicides for weed control and changes in weed communities in CT systems. On the basis of experiences in the Midwestern United States, Forcella et al. (1994) found annual grass and perennial weeds to increase in importance in CT systems whereas larger-seeded broadleaf weeds were more prominent in moldboard-plow systems. Smaller-seeded broadleaf species

were variable in their response to reduced tillage. Under NT, the soil surface layer has a high proportion of weed seed (Yenish et al. 1992), a higher moisture level (Papendick and Parr 1997), and greater microbial diversity (Lupwayi et al. 1998). These characteristics contribute to observed changes in weed communities and seemingly would favor microbial seed decay.

The influence of microorganisms on seed germination and viability has been studied both in vitro and in situ. In the laboratory, microbial isolates can inhibit seed germination and cause seed mortality (Kennedy et al. 1991). A few studies have used methods such as soil sterilization or fungicide seed treatment that implicate microorganisms as a cause of seed mortality in situ (Gallagher and Fuerst 2004). For example, wild oat seed germination was reduced in untreated soil compared with steam-sterilized soil (Kiewnick 1964). Similarly, fungicide seed treatments increased the survival of shattercane [*Sorghum bicolor* (L.) Moench] (Fellows and Roeth 1992) and catclaw mimosa (*Mimosa pigra* L.) (Lonsdale 1993). Field germination of black medic (*Medicago lupulina* L.), field bindweed (*Convolvulus arvensis* L.), and birdsfoot trefoil (*Lotus corniculatus* L.), but not European blackberry (*Rubus fruticosus* L.), increased in response to a combination of seed and soil-applied fungicides during a 2-yr period (Leishman et al. 2000). In field studies, fungal colonization of *Setaria* spp. caryopses was related to crop residue placement in soil (Pitty et al. 1987). In NT plots, colonization occurred predominately on seed near the soil surface whereas moldboard plowing and deeper residue incorporation resulted in increased colonization of seed at greater depths. Although these studies lack a direct assessment of seed decay, they indicate that microorganisms may be a factor in weed seed mortality in situ.

To better understand and perhaps more fully exploit the relationships between soil microorganisms and weed seed decay, we evaluated the effects of tillage, soil fumigation, and fungicide seed treatment on the overwinter germination, dormancy, mortality, and decay of wild oat. We evaluated the hypotheses that seed decay would be more rapid in plots subjected to long-term NT relative to plots subject to long-term CT and that decay would be reduced by soil fumigation or fungicide seed treatment or both. Furthermore, we directly measured the decay component of mortality, which thus far has usually been implicated only indirectly in other field studies.

Materials and Methods

Experiments were conducted in each of the 2 yr (1998 to 1999, 1999 to 2000) at the USDA-ARS Conservation Research Farm near Pullman, WA. Soil at this site is a Palouse silt loam (fine-silty, mixed mesic, Pachic Ultic Haploxerolls), and average annual precipitation is 564 mm. Two field experiments, featuring contrasting methods of seed burial and referred to as the "mesh bag" and "toothpick" experiments, were conducted each year. The former experiment relied on a commonly used method in which seed were mixed with sieved soil, placed in mesh bags, and buried (e.g., Zorner et al. 1984). Although plot establishment and seed recovery are expedient with this method, established fungal hyphae networks, likely to predominate NT systems (Kladivko 2001), are destroyed and viable seed losses due to

germination are difficult to distinguish from other causes of mortality. Consequently, in the latter experiment, we developed an alternative, albeit more labor intensive, method in which seed were individually glued to toothpicks and inserted into the soil. This method minimized disruption of indigenous fungi and allowed monitoring of seed germination. The scope of the work required to establish and process samples from these experiments precluded an experimental design combining the two assay methods; consequently, the mesh bag and toothpick experiments were conducted, and therefore must be interpreted, individually.

The mesh bag and toothpick experiments were established within a long-term tillage study that contained four replicates of two tillage systems (CT vs. NT) arranged in a random design (see Petersen et al. 2002). Each tillage treatment (main plot) had been maintained as such for 15 yr. CT main plots were chisel plowed 15 to 20 cm deep. 'Madsen' winter wheat was planted across all main plots on October 2, 1998, and November 1, 1999, with a low-disturbance Cross-Slot® drill.¹

Wild oat was selected for this study for several reasons: it is a major weed of cereals worldwide (Holm et al. 1977), its germination and dormancy are relatively well characterized (Simpson 1990), pure genetic lines are available, and large seed size simplifies seed handling. Wild oat line AN265 was selected on the basis of its high level of dormancy and low level of germination during extended cold periods (Naylor and Fedec 1978); these traits were essential to minimize losses due to germination and to maximize opportunity for microbial decay. AN265 seed were raised in the field so that the microbial community on the seed would be representative of that which normally occurs in the field. Plants were watered to minimize the decrease in dormancy caused by drought stress in wild oat (Sawhney and Naylor 1982). Seed were harvested as they matured in July each year (1998, 1999) and stored for 3 to 4 mo at $-+ 20$ C before use, to preserve dormancy and viability (Foley 1994). Seed viability was $> 98\%$ on the basis of germination of caryopses on 5 mM gibberellic acid (data not shown). Sterile practices were used in all seed-handling procedures to prevent contamination by nonindigenous microorganisms.

Air temperature and cumulative precipitation were monitored on site. Soil temperature and matric potential at 1-cm depth were measured using calibrated line heat dissipation sensors² (Reece 1996). To evaluate soil characteristics, 40 stratified soil cores (0 to 2 cm and 2 to 4 cm deep) were collected and pooled within each main plot. Parameters measured included soil pH and electrical conductivity³ (Smith and Doran 1996), total C and N⁴, and dehydrogenase activity (Tabatabai 1994). Soil quality data were analyzed by analysis of variance (ANOVA) using Fisher's Protected LSD ($\alpha = 0.05$) (SAS 1988).

Mesh Bag Experiment

To improve the accuracy of our measurements within the two tillage treatments (main plots), four subplots were established within each main plot. Each subplot contained three randomized microbial treatments as "microplots" including: fumigated soil (untreated seed), fungicide-treated seed (untreated soil), and control (untreated seed and untreated soil). There were thus 32 microplots of each microbial treatment per year (two tillage systems by four replicates

by four subplots). Microplots were placed in a new location each year and were protected by enclosures made from 6-mm hardware cloth to eliminate losses due to vertebrate seed predators. The mesh-bag experiment did not include the fumigated treatment in the first year.

Surface soil (0 to 5 cm deep) from each main plot was sieved (2 mm) to remove debris and resident wild oat. To fumigate soil (second year only), 1,200 g of sieved soil from each main plot was sealed in a plastic bag and 15-ml propylene oxide (Smith 1947) was injected. The seal was broken after 48 h, and soil was ventilated 48 h before dispensing soil into mesh bags. For the fungicide seed treatment, an aqueous suspension containing commercially formulated metalaxyl at 160 $\mu\text{g ai g}^{-1}$ seed, captan at 810 $\mu\text{g ai g}^{-1}$, and thiram at 410 $\mu\text{g ai g}^{-1}$ was applied to wild oat seed and dried. This fungicide mixture was not phytotoxic (data not shown).

One hundred grams of soil and 75 wild oat seed were placed in each 10- by 12-cm nylon mesh bag. On October 30, 1998, and November 8, 1999, mesh bags were placed in microplots, within the main plots from which their soil had been taken. Two mesh bags (one per retrieval date) were placed side by side under approximately 1 cm of soil in each microplot. Filled mesh bags were 1.5 to 2.0 cm thick, and seed were thus positioned in the upper 1 to 3 cm of the soil profile.

Mesh bags were retrieved on May 16 and August 31, 1999, and May 8 to 11 and August 8 to 10, 2000. Each mesh bag was placed in a zip-lock bag. Samples were stored at 4 C and processed as described below within 5 d. Seed were recovered on a 2-mm sterilized sieve. Germinated seed were counted and discarded. Hulls were removed from the remaining seed. Caryopses were categorized as "germinated," "dead," or "possibly viable." Germinated caryopses included those with partially decayed roots and shoots. Dead caryopses included those where the hull was empty with no caryopsis, those with a flat caryopsis, and those where the caryopsis was discolored, sometimes swelled or soft, and obviously nonviable; the latter were considered "dead, decayed." Possibly viable caryopses, including some that were partially discolored, were tested for viability. Such caryopses were transferred to 100-mm-diam petri dishes containing two germination blotters moistened with 12 ml of germination suspension. The suspension contained 5 mM gibberellic acid (to induce germination of dormant caryopses) and 10 ppm (wt/v) penicillin, 10 ppm streptomycin, 20 ppm metalaxyl, 156 ppm captan, and 78 ppm thiram (to suppress microbial growth and caryopsis decay during the assay). Virtually all caryopses that were normal in appearance germinated within 4 wk. Such viable caryopses were categorized as "dormant." Caryopses that did not germinate and showed discoloration or severe decay were categorized as dead, decayed. Data analysis was subsequently performed on the following dependent variable categories: germinated, dormant, dead, and "decayed"; decayed was thus a subset of dead.

Toothpick Experiment

Four subplots were established within the two tillage treatments as described previously for the mesh bag experiment. As before, each subplot contained three randomized microbial treatments as microplots including: fumigated soil

(untreated seed), fungicide-treated seed (untreated soil), and control (untreated seed and untreated soil), and the microplots were protected by enclosures and placed in a new location each year. For the toothpick experiment, each microplot consisted of a 15-cm-diam by 10-cm-deep piece of black polyvinyl chloride (PVC) pipe that was driven into the soil to a depth of 9 cm. The ring was covered with 6-mil plastic and sealed before fumigation. Fumigation and ventilation were conducted as described previously. Tests for the efficacy of fumigation within the PVC rings were conducted in 1998. Dilutions were plated onto tryptic soy agar with cycloheximide to inhibit fungi and potato dextrose agar with streptomycin to inhibit bacteria (Wollum 1982). Colony-forming units per gram dry weight soil were reduced from 7.5 to 4.5 log units on tryptic soy agar and from 5.7 to 0.0 log units on potato dextrose agar. This confirmed that fumigation had reduced microbial populations substantially.

Wild oat seed were individually glued with the longitudinal axis parallel to 7-cm-long plastic toothpicks. A 1.5- to 2.0-mm-diam droplet of hot glue⁵ was applied to the toothpick, and the lemma of a wild oat seed was immediately appressed to the glue droplet and toothpick. Gluing had no effect on seed viability. Microplots were established on October 16 to 23, 1998, and November 6, 1999. For each retrieval date, 75 seed on toothpicks were placed in each microplot. Seed were pushed through any litter present into the soil, embryo end pointing downward, until the embryo was positioned 1.5 to 2.5 cm below the soil surface. Microplots were monitored periodically and germinated wild oat were counted and removed. Seed were retrieved on May 16 and August 31, 1999, and May 23, 2000. Seed and toothpicks from each microplot were placed in a sealed container. Seed were processed and categorized as discussed previously.

Statistical Analysis

The number of germinated, dormant, dead, and decayed seed were expressed as a percent of the total recovered seed for each microplot. ANOVA was used to test for treatment and time effects. Levene's test (JMP 2002) indicated lack of homogeneity of variance for three of four dependent variables between years of the experiment. Subsequent analyses were therefore performed individually for each year. Tillage nested within replicates (main plots) provided the error term for *F*-tests of tillage. The interaction of main plots nested within subplots provided the error term for testing effects of microbial treatment and microbial treatment by tillage. Effects of time, and interactions including time, were tested using the residual error term. Means were separated using single degree of freedom contrasts or Fisher's Protected LSD.

Results and Discussion

Effects of Tillage and Microorganisms on Seed Fate

Mortality

We hypothesized that soil surface conditions in NT would favor microbial decay and mortality of wild oat seed. Accordingly, the proportion of recovered seed categorized as dead and particularly the subset that were decayed should

TABLE 1. Effects of long-term tillage system and microbial treatment (control vs. fungicide seed treatment vs. soil fumigation), on the fate of wild oat seed placed in soil within mesh bags, placed in the field in September 1998 and 1999, and retrieved in May and August 1999, and 2000, respectively.^a

Tillage system	Microbial treatment	Germinated		Dormant		Dead		Decayed ^c	
		1999 ^b	2000	1999	2000	1999	2000	1999	2000
%									
Conservation tillage (CT)	Control	27	51	35	41	39	7	12	1 b
	Fungicide	29	50	40	43	32	8	8	<1 b
	Fumigation	—	41	—	54	—	5	—	1 b
No-tillage (NT)	Control	40	55	25	36	35	9	9	1 b
	Fungicide	40	52	33	38	28	10	6	<1 b
	Fumigation	—	42	—	49	—	9	—	2 a
Main effects									
Tillage ^d	CT	27 b	47	37	46 a	35	7	10	1
	NT	40 a	50	29	41 b	31	10	7	1
Microbial treatment	Control	34	53 a	30 b	39 b	37 a	8	11 a	1
	Fungicide	34	51 a	36 a	40 b	30 b	9	7 b	<1
	Fumigation	—	42 b	—	51 a	—	7	—	1

^a Within column sections, means not followed by the same letter are significantly different ($P < 0.05$).

^b Data were averaged over the two retrieval times (May and August).

^c See text for a description of the distinction between the categories dead and decayed.

^d Main effects of tillage and experimental treatment were compared statistically when treatment interactions were not significant ($P > 0.05$).

have been greater in NT without fungicide or fumigation, i.e., NT “control” treatments, and lower with CT, fungicide or fumigation treatments (or both). Although not tested explicitly in our design, we expected to observe greater mortality in the toothpick experiment relative to the mesh bag method because, as discussed previously, this procedure reduces disruption of established fungal hyphae networks.

Contrary to our original hypothesis, the proportion of dead and decayed seed was generally similar in NT and CT (see Main effects: tillage, Tables 1 and 2), and the proportion of decayed seed was actually greater in CT than NT (9 vs. 4%, respectively; Table 2) in the 1999 toothpick experiment (Table 2). Also unexpected was the slightly greater proportion of decayed seed recovered in the fumigated NT

treatments (2%) compared with other treatment combinations ($\leq 1\%$) in the second year of the mesh bag experiment (Table 1). However, consistent with our original hypothesis, there was a significant reduction in mortality (37 to 30%) and decay (11 to 7%) in the first year of the mesh bag experiment (Table 1). The minimal effects of tillage, fungicide, and fumigation on the proportion of dead or decayed seed (Tables 1 and 2), suggest that the contribution of microorganisms to seed deterioration was generally similar in these contrasting environments.

The number of dead and decayed seed was greater in 1999 than in 2000 in both the mesh-bag and toothpick experiments (Tables 1 and 2). The greater effect of year than of tillage on the proportion of both dead and decayed seed

TABLE 2. Effects of long-term tillage system and microbial treatment (control vs. fungicide seed treatment vs. soil fumigation), on the fate of wild oat seed attached to toothpicks, placed in the field in September 1998 and 1999, and retrieved in May and August 1999 and May 2000, respectively.^a

Tillage system	Microbial treatment	Germinated		Dormant		Dead		Decayed ^c	
		1999 ^b	2000	1999	2000	1999	2000	1999	2000
%									
Conservation tillage (CT)	Control	18 a	40	63 b	58	19	2	9	<1
	Fungicide	19 a	42	63 b	54	18	4	9	<1
	Fumigation	15 a	27	67 b	70	18	3	7	1
No-tillage (NT)	Control	37 c	48	45 a	49	18	4	5	<1
	Fungicide	35 c	44	50 a	52	15	4	5	1
	Fumigation	24 b	26	63 b	71	14	4	3	2
Main effects									
Tillage ^d	CT	17	36	65	61 a	19	3	9 a	1
	NT	32	39	52	57 b	16	4	4 b	1
Microbial treatment	Control	27	44 b	54	54 b	19	3	7	1
	Fungicide	27	43 b	56	53 b	17	4	7	1
	Fumigation	19	26 a	65	70 a	16	3	5	1

^a Within column sections, means not followed by the same letter are significantly different ($P < 0.05$).

^b Data from 1999 were averaged over the two retrieval times (May and August).

^c See text for a description of the distinction between the categories dead and decayed.

^d Main effects of tillage and experimental treatment were compared statistically when treatment interactions were not significant ($P > 0.05$).

(Tables 1 and 2) suggests that seed mortality may be affected more by environment than by tillage. It is also important to note that the number of dead seed was consistently lower in the toothpick experiments (Table 2) than in the mesh-bag experiments (Table 1). We attribute this to our ability to count and remove germinated seed during incubation in the field for the toothpick but not for the mesh-bag experiments. In the mesh-bag experiment, seed that germinated in late fall or early winter would have died and decayed to the point that root and shoot were not evident.

Germination and Dormancy

The proportion of dormant seed was consistently lower, and the proportion of germinated seed correspondingly higher, in the NT compared with the CT treatments (Tables 1 and 2). The reduced dormancy in NT may be due to hydrothermal properties in the NT environment (Allen et al. 2000). We observed differences in soil temperature and moisture between NT and CT as well as reduced daily temperature fluctuations in NT (data not shown) but it is not clear which environmental parameter(s) are responsible for this shift in dormancy and germination. Naylor and Fedec (1978) found that dormant genotypes of wild oat, including AN265, germinated to a greater extent at temperatures below 12 C. Despite differences in mean daily soil temperature approaching 2 C, the number of favorable germination days (i.e., < 12 C) on the basis of mean daily soil temperatures during the 1999 to 2000 field seasons did not differ between the NT and CT treatments (data not shown).

Soil fumigation consistently increased the proportion of dormant seed with a corresponding decrease in the proportion of germinated seed, but mortality and decay were not affected by fumigation (Tables 1 and 2). For example, in the 1999 toothpick study, 63% were dormant in the NT fumigated treatments compared with 45% in the NT control (Table 2); there was a corresponding decrease in germination in the NT fumigated treatment. In the CT treatments, dormancy was unaffected by fumigation. In the next year, although the interaction with tillage system was not detected, the main effect of fumigation was again noted; 70% of recovered seed were dormant in fumigation treatments compared with 54% in the control (Table 2). The fumigation treatment was not included in the first year of the mesh-bag experiment, but the 2000 fumigation treatment contained 51% dormant seed compared with 39% in the control (Table 2).

Although propylene oxide is known to reduce germination of plant seed (e.g., barley [*Hordeum vulgare* L.]; Ramakrishna et al. 1991), we anticipated that ≥ 48 h of ventilation would result in complete dissipation of the propylene oxide gas. However, it is apparent that residual inhibitory epoxides may persist even after vacuum degassing of treated soil (Skipper and Westermann 1973). If the proportion of dead seed had simply increased in response to fumigation, the conclusion that propylene oxide killed the wild oat would be a logical extension of the results of Skipper and Westermann (1973) and Ramakrishna et al. (1991) in which germination of wheat and barley, respectively, were reduced by this fumigant. However, our field results, confirmed by subsequent laboratory assays, consistently demonstrated that dormancy was greater in seed placed in propylene oxide-fumigated soils (ventilated ≥ 48 h) and that

viability was unaffected (unpublished data). This dormancy-enhancing residual effect of propylene oxide fumigation may be a useful tool in mechanistic studies of wild oat dormancy.

One of the reasons we chose wild oat to study seed decay was because of the availability of a thoroughly characterized dormant genotype. The high level of dormancy was viewed as essential because genetic lines or species lacking dormancy could only be assayed under environmental conditions that enforced dormancy (Fenner 1985); high levels of germination would cause difficulty in measuring levels of seed decay. However, it is possible that resistance to deterioration is genetically linked to dormancy in wild oat, resulting in an overly robust test of our hypothesis. For example, in one study, dormant wild oat lines generally had fewer endophytes and were less susceptible to fungal pathogen infection than nondormant wild oat (Mortensen and Hsiao 1987).

Seed Recovery

Without regard to treatments, seed recovery was high for both the toothpick and mesh-bag experiments (Figures 1A–D). The values over 100% suggest that background wild oat seed contaminating the experimental units were occasionally counted as germinated in the field or accidentally collected and counted in the lab. Recovery was more variable in the first year of the experiments (Figures 1A and C compared with 1B and D). Whether this variation was related to our own experience, differences in weather conditions, or some other factor is not known. However, ANOVA demonstrated that recovery was unaffected by tillage or seed-soil treatments (data not shown).

Most seed recovered at the May and August 1999 and 2000 retrieval dates were categorized as germinated, mostly identified in the field, or dormant (Figures 1A–D). There were relatively few cases of missing caryopses, i.e., empty hulls with only the lemma and palea present. Similarly, the decayed and dead categories each contained relatively few seed, particularly in comparison with the germinated and dormant categories. There were more dead seed in the first year of the study compared with the second, a trend that was consistent in both the mesh-bag (Figures 1A and 1B) and the toothpick studies (Figures 1C and 1D).

Time of Seed Retrieval

Time of seed retrieval (May vs. August) did not consistently affect the proportion of germinated, dormant, decayed, or dead seed (data not shown). This prompted us to eliminate the August retrieval date in the second year of the toothpick experiment; both retrieval times were included for the mesh-bag experiment. Both retrieval times were included in the analyses of the mesh-bag experiment and the first year of the toothpick experiment. The lack of time by treatment interactions (data not shown) affecting any of the seed fate categories suggests that processes affecting wild oat seed fate are similar in during winter and spring and the summer growing season periods that we assayed.

Site Characteristics and Environmental Conditions

NT treatments contained greater total C and N, at both 0 to 2 cm and 2 to 4 cm compared with CT treatments (Table 3). Because elevated total C, i.e., organic matter, can

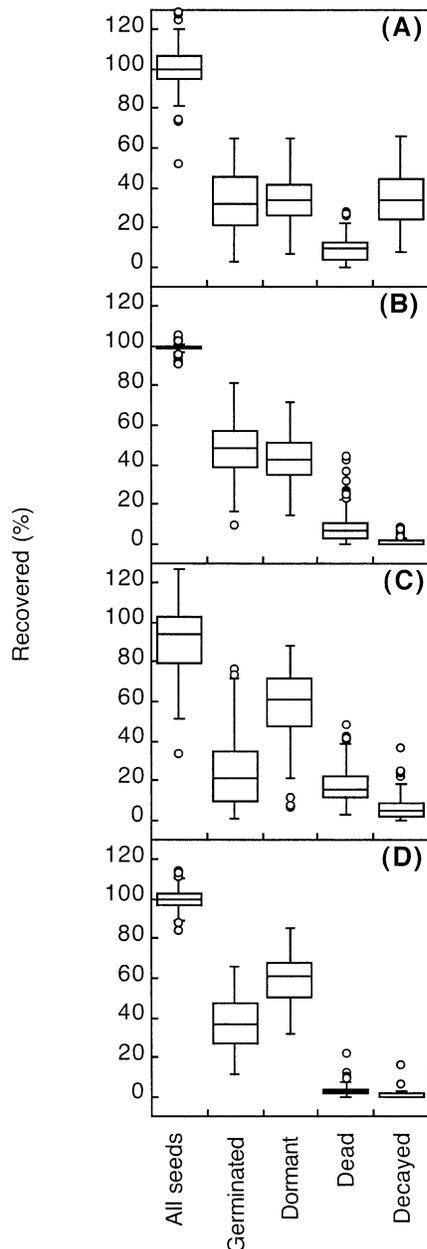


FIGURE 1. Box plots showing the recovery and fate of wild oat seed retrieved from mesh bags in May and August 1999 (A), and from toothpicks in May and August 1999 (C), and May 2000 (D). Seed fate was classified as germinated, dormant, dead, or decayed. Median values are displayed as a line with the top and bottom of the box marking the upper and lower quartiles; the "whiskers" extending above and below boxes are less than or equal to upper quartile + 1.5 × interquartile range, or equal to the lower quartile - 1.5 × interquartile range. Points lying outside this range are shown individually.

benefit numerous soil physical and chemical functions (Boyle et al. 1989), the relatively high level found in the soil surface (2.6%) in the NT system is consistent with our premise that the soil surface environment in NT could influence seed deterioration.

In the first year of the study, the months of November, December, and February received considerably more precipitation (340 mm) than that which long-term averages would suggest is typical (200 mm); this wet fall and winter period was then followed by dryer than normal months of March,

April, and May (cumulative precipitation 50 mm; long-term average 129 mm). In the second year of the experiment, September was dryer than normal (2 mm precipitation; average 25 mm) with the remaining months being more similar to the long-term average precipitation at the site.

Measured only in second year of the experiment, soil temperature at 1.5 cm was $0.51\text{ C} \pm 0.04\text{ C}$ (mean daily average \pm standard error) warmer in NT than CT plots in November through January (data not shown). In contrast, the NT soil temperature was $0.36\text{ C} \pm 0.04\text{ C}$ cooler than CT treatments in the subsequent interval including February through July. Johnson and Lowery (1985) similarly found cooler spring soil temperatures in NT compared with CT, although the magnitude of difference was considerably greater at their Midwestern location. Through the late fall, winter, and early spring of 1999 and 2000, soil matric potential was near field capacity, approximately -0.01 MPa, and did not differ between the NT and CT treatments (data not shown). Considering that wild oat seed were placed in the field in October and recovered in May and that soil matric potential was generally similar in NT and CT treatments during this period, matric potential was not likely a factor affecting seed fate in these experiments. However, the warmer fall soil temperatures offer greater opportunity for microbial activity and greater frequency of conditions favorable for germination in the NT compared with the CT.

Implications for Weed Management and Future Research

The weed seed bank is a focal point in ecologically based weed management systems. In addition to managing for reduced seed inputs, a prominent goal is to manipulate the soil environment to accelerate the decline in the weed seed bank while considering larger goals related to maintenance or improvement in soil quality (Gallandt et al. 1999). Although our mechanistic hypothesis was not supported by these field studies, i.e., seed mortality and decay were generally similar in the NT and CT treatments (Tables 1 and 2), NT may nevertheless contribute to seed bank decline. Our results support the conclusions of Cook (1980) that "most mortality is due to the breakdown of dormancy mechanisms and subsequent germination while buried in the soil." In our studies, germination was increased and dormancy reduced in NT. From a management perspective, this NT system may result initially in greater densities of wild oat in crops; however, assuming effective management, the increased germination in NT would result in a less persistent seed bank.

The aim of this project was to evaluate the contribution of seed decay to seed mortality in situ. Our experiments included three relatively novel procedures that deserve some evaluative comments here. (1) Our procedure for evaluating decay was on the basis of visual inspection of caryopses. Caryopses that appeared healthy proved viable in the gibberellic acid test whereas those that showed signs of decay usually proved nonviable. Although removing the hull requires significant labor and although observations of decay were limited to those cases visible at the time of retrieval, we consider the data obtained an indispensable indicator of decay incidence. Therefore, we believe that similar approaches should be considered in future studies of seed de-

TABLE 3. Selected characteristics of soil from the long-term conservation tillage (CT) and no-tillage (NT) treatments at the USDA-ARS Palouse Conservation Field Station study site. Tillage treatments were initiated in 1983; soil samples were collected and analyzed in May 1999.^a

Tillage system	Depth cm	Dehydrogenase ug g soil ⁻¹ hr ⁻¹	pH	Electrical	Total	Total
				conductivity dSm ⁻¹	carbon %	nitrogen
CT	0-2	2.96 a	5.42 a	0.91 b	1.7 c	0.17 c
	2-4	2.46 b	5.33 b	0.88 b	1.7 c	0.17 c
NT	0-2	3.03 a	5.36 ab	1.12 a	2.6 a	0.24 a
	2-4	2.26 b	5.20 c	0.98 ab	2.0 b	0.20 b

^a Within a column, means ($n = 24$) not followed by the same letter are significantly different ($P < 0.05$).

cay in situ. (2) The toothpick procedure, although having the benefits of minimizing soil disturbance and allowing seed removal upon germination in situ, proved a very difficult and labor-intensive procedure, which we hesitate to recommend without modification. (3) We based our expectation that fumigation would control seed pathogens on the previously demonstrated control of root pathogens by methyl bromide soil fumigation (Cook 1982). Although our fumigation with propylene oxide reduced microbial numbers temporarily (discussed previously), this procedure had little effect on seed decay. It is possible that the ineffectiveness of this procedure was related to our choice of fumigant or the small size of our microplots. Because fumigation temporarily alters the microbial community, perhaps it could be followed by soil-applied treatments to extend suppression of decay organisms; for example, repeated treatment with soil-applied fungicides (without fumigation) has been used to provide extended control of fungi (Leishman et al. 2000).

In conclusion, germination and mortality accounted for 37 and 16%, respectively, of seed bank losses, whereas viable or dormant seed accounted for the 47% remaining in the seed bank, when averaged over the four mesh-bag and three toothpick experiments we conducted. Decay accounted for one-fourth of the mortality, i.e., only 4% of the total, and we attribute much of the remaining mortality to fatal germination. However, our procedure for measuring decay only allowed detection of seed that were decaying at the time of retrieval, and any that were completely decayed at that time would have been simply scored as dead. Our hope was that fungicide or fumigation treatments would allow detection of seed that decayed before retrieval, but as discussed, we observed little response to these treatments. Therefore, the measurable decayed seed were a small factor in seed bank decline in our studies.

There are a number of factors to consider before concluding that seed decay is generally a small factor in seed bank dynamics of wild oat or of weeds in general. (1) Our studies were limited to a 10-month duration but it is possible that the importance of decay is greater as duration increases. Seed surviving extended periods in the soil are subject to both aging and environmental stresses. In stored crop seed, a relationship among seed age, seed leakage, and vulnerability to seed decay has been demonstrated (Harman and Stasz 1986). The influence of aging and environmental stress on seed leakage and decay in weeds needs to be investigated. (2) Seed quality, as influenced by seed maturation environment, may influence decay. Our seed were raised in monoculture with irrigation to maximize dormancy (Sawhney and Naylor 1982). However, weed seed that mature

under reduced moisture, nutrient, or light conditions may have reduced seed quality characteristics and may be more vulnerable to decay (Gallagher and Fuerst 2004). (3) The species and biotype under study is likely to influence the incidence of decay. For example, many hard-seeded species belonging to the Leguminosae or Malvaceae possess high levels of dormancy and deterioration resistance (Kremer 1993). (4) As reviewed by Kennedy (1999), high levels of unexplained seed losses and enhanced survival with fungicide seed treatments are compelling evidence that soil microorganisms contribute to weed seed deterioration. We therefore conclude that inclusion of a greater variety of soil environments and weed species is warranted in future studies. Efficient assays of seed quality and seed decay would permit evaluation of a diversity of weed species under a wider range of soil environments. Correlation of microbial community and soil quality characteristics with weed seed deterioration is needed to comprehensively test the hypothesis that soil quality may affect the persistence of seed entering the weed seed bank.

Sources of Materials

¹ Cross Slot® No Tillage Seed Drill System, Cross Slot Technology Ltd, P.O. Box 22-717, Otahuhu, Auckland, New Zealand.

² 229 Heat Dissipation Matric Water Potential Sensor, Campbell Scientific, Inc., 815 West 1800 North, Logan, UT 84321.

³ Orion Research microprocessor pH/millivolt meter 811, Orion Research Inc., 529 Main Street, Boston, MA 02129.

⁴ CNS-2000 Elemental Analyzer, Leco Corp., 3000 Lakeview Avenue, St. Joseph, MI 49085-2396.

⁵ Thermogrip®, Black and Decker, Inc., 701 E. Joppa Road, Towson, MD 21286.

Acknowledgments

Support provided by USDA NRICGP, project no. 9800731 awarded to E.R.G., E.P.F., and A.C.K. We thank Dr. W. E. Dyer, Montana State University, for his generous gift of the AN265 wild oat, which was essential to the success of this project, and Dr. J. R. Alldredge, Washington State University, Professor of Statistics, for assistance with analyses of variance. We are also grateful for the expert technical assistance provided by P. Frohne, M. Thorne, S. Higgins, and C. Roche, and the dedication, perseverance, and the high quality work conducted by our student employees who made this labor-intensive project possible: B. Boyd, D. DuFault, G. Kauffman, P. Marston, A. Padgham, N. Pyle, and B. Russell. Lastly, we thank an anonymous reviewer whose critical review of an earlier version of this manuscript made this a better article.

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Received May 30, 2003, and approved February 23, 2004.