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Relative Canopy Height Influences Wild Oat (*Avena fatua*) Seed Viability, Dormancy, and Germination

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The environment in which a plant grows (maternal environment) can affect seed viability, germination, and dormancy. We assessed the effects of maternal environment on wild oat seed viability, germination, dormancy, and pathogen infection by collecting and analyzing wild oat seed from above and below a barley canopy at three field sites in Montana. The viability of wild oat seed collected below a crop canopy was consistently less than it was for seed from the overstory but varied among sites and years. Reductions in viability because of relative canopy position ranged from 10% to 30%. Effects of position relative to crop canopy on weed seed germination/dormancy rates varied by site and suggest that the direction and magnitude of the effects of maternal environment on dormancy depend on environmental conditions. These effects may be driven by crop competition or by changes in seed pathogen pressure or both. Seven species each of fungi and bacteria were isolated from wild oat seeds. The only fungi causing reductions in seed viability (15%) was isolated from understory seeds, and several bacteria from both overstory and understory sources reduced seed germination. Results suggest that, in addition to the known weed-suppressive effects of using taller or earlier emerging varieties of crops, such crops can reduce weed spread through effects on weed seed demography because weeds growing beneath the crop canopy produce a reduced amount of viable seed that is less likely to germinate in the following year.

Nomenclature: Wild oat, *Avena fatua* L. AVEFA; barley, *Hordeum vulgare* L.

Key words: Cereals, crop height, maternal effects, microclimate, pathogens, seedbank, seed decay, weed demography, weed management.

Wild oat is one of the most economically harmful weeds in small-grain production in North America, where more than $500 million is spent annually on herbicides to control it. In the United States, wild oat infests more than 11 million ha of cropland, causing more than $1 billion in crop losses (Beckie et al. 2012). In annual cropping systems, it is particularly difficult to manage because of its seed dormancy, which allows seed germination to occur throughout the growing season as well as in sequential years (Sharma and Vanden Born 1978). In addition, multiple wild oat populations around the globe have evolved resistance to one or more of commonly used herbicide mechanisms of action (Heap 2013). Multiple herbicide-resistant biotypes have been found most frequently in the northern Great Plains (80% of cases in Heap 2013), and new biotypes have recently been documented in this region (Lehnhoff et al. 2013). These herbicide-resistant biotypes add to the need to understand how integrated weed-management practices can contribute to the control of this weed.

Effective management of a weed species in agricultural systems requires an understanding of the species' population dynamics (Cousens and Mortimer 1995), in which seed fate is a critically important component. Seed dynamics depend on the rate of seed viability and dormancy (Venable and Brown 1988) that alter other processes, such as mortality in the seedbank, including senescence and decay (Pakeman et al. 2012), predation (Westerman et al. 2003), and fatal germination (Davis and Renner 2007). The environment in which the mother plant grows (maternal environment) during seed production and maturation can influence seed viability, seed dormancy, and survival in the seedbank (Baskin and Baskin 1998; Kegode and Pearce 1998; Luzuriaga et al. 2006; Williams et al. 2012). This phenomenon also occurs within individual plants where seeds maturing in different positions on the plant may experience different environmental conditions (Baskin and Baskin 1998). On a given plant, seeds produced in shaded conditions may be immature or may exhibit less dormancy than those exposed to full sunlight (Brainard et al. 2005), possibly because shaded conditions lead to reduced photosynthate for seed-coat development (Nurse and DiTommaso 2005). Alternatively, seeds produced in shade may have decreased germination ability (i.e., higher dormancy) as an adaptive mechanism to avoid germination in a light-limited environment (Jha et al. 2010).

In addition, differences in microenvironment above and below a plant canopy can influence the habitat suitability for microflora (e.g., fungi and bacteria), with shaded, moister sites being more favorable (Juroszek and von Tiedemann 2011), and this in turn may affect seed infection by pathogen and survival in the seedbank. Predation or infection of seed by microflora can reduce seed viability (Kiewnick 1964). Fungi invade seeds during their development on plants in the field, and 52 species of fungi have been found on wild oat (Kiewnick 1963). Mortensen and Hsiao (1987) assessed seeds from several lines of wild oat for fungi, and no relationship was found between viability of seeds and the fungi carried on the seeds. However, (Kiewnick 1964) found that plants attacked by *Fusarium culmorum* produced sterile seeds and that there were correlations between the amount of rainfall, the number of microorganisms, and the germination capacity of wild oat. Regardless, for dormant seeds to persist in the seedbank, resistance to decay by microorganisms is required (Fuerst et al. 2011), and such resistance may be related to seed maturity.

Crop height can increase crop competitive ability and reduce growth and seed production by weedy species. For example, (Blackshaw 1994) showed that taller varieties of winter wheat (*Triticum aestivum* L.) were more competitive with downy brome (*Bromus tectorum* L.), producing higher yields and suppressing weed seed production compared with shorter varieties. Differences in crop canopy heights often develop late in the growing season and thus may only affect

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Table 1. Climate data summary for three study sites in Montana: mean temperature during wild oat flowering and seed maturation and percentage of normal precipitation during growing season for 3 yr.

	Mean temperature	Precipitation (% of normal)
Location and year	July–August	April–September
	C	Cm
Bozeman, MT		
Mean	19.2	31
1992	17.4	41.2 (+ 33)
1993	15.4	50.2 (+ 62)
1994	20.4	27 (− 13)
Creston, MT		
1992	16.3	31.9 (+ 47)
Moccasin, MT		
1994	19.1	21.6 (− 26)

later stages of weed development, e.g., seed production and maturation. However, the weed demographic responses to canopy height are not well known. Understanding the effects of biotic and abiotic factors on weed population seed viability and dormancy could improve management.

Levels of seed dormancy in wild oat have been associated with diverse factors, including genetic traits (Foley and Fennimore 1998), metabolic rate (Hilton and Thomas 1986), seed position, and the effects of environment on the maternal plant (Jones et al. 1997). Mechanisms enforcing wild oat seed dormancy have been shown to include floret structures, seed coat, immature embryo, and unfavorable environmental conditions (Sawhney and Naylor 1982; Sawhney et al. 1986). The seed coats or maternal structures can interfere with water uptake or gas exchange and act as mechanical barriers that regulate the movement of inhibitor chemicals to and from the embryo.

An addition series experiment at three locations in Montana for three cropping seasons, 1992, 1993, and 1994, to determine the long-term wild oat density threshold (economic injury level) in spring barley (Maxwell et al. 1994), provided insight into an additional factor affecting wild oat seed dynamics. A portion of the wild oat seedlings that emerged more than 7 d after the barley or under intense competition matured and set seed below the barley canopy, whereas those that emerged before or at the same time and under less-competitive environments produced a panicle above the canopy. Understory (maturing below the canopy) seeds generally appeared to be lighter in color and reduced in weight and size relative to seeds from overstory plants. Understory seed demonstrated lower viability and higher dormancy and had greater microbial growth during preliminary laboratory germination tests (unpublished data). It was unknown whether these differences were related simply to seed maturity or whether differences in the pathogen community above vs. below the canopy affected viability and dormancy, but evidence suggested that seed germinability was related to the microenvironment in which it matured. These observations were interesting in light of the increased planting of dwarf and semidwarf cultivars of wheat and barley that may not provide a canopy over wild oat and suggested that wild oat panicle position with respect to the crop canopy could alter wild oat population dynamics. Based on these observations, two objectives for this study were formulated: to investigate the effects of (1) wild oat panicle position with respect to crop canopy, and (2) the extant microflora on wild oat seed viability, germination, and dormancy.

Materials and Methods

Study Sites. The study was conducted with wild oat seeds collected from fields in Bozeman, MT (45°47′N, 111°9′W), Creston, MT (48°11′N, 114°8′W), and Moccasin, MT (47°3′N, 109°54W). Mean growing season temperature and precipitation were 19.2 C (66.6 F) and 31 cm (12.2 in) for Bozeman, MT; 17.6 C and 21.7 cm for Creston, MT; and 18.5 C and 29.2 cm for Moccasin, MT (Table 1).

Seed Collection. Wild oat seeds were collected after seed maturation and before seed shatter, above and below the barley canopy in all plots of wild oat–barley addition-series experiments for 3 yr at the Bozeman, MT, site and 1 yr at the Creston, MT (1992), and Moccasin, MT (1994), sites (see Table 2). Understory seeds were collected from panicles that were the same height or shorter than the barley heads, as measured from the top of crop and weed seed heads. Overstory seeds were collected from panicles that were taller than the barley heads. Within each position, all seeds were collected from the entire panicle.

Seed Viability, Germinability, and Dormancy. Wild oat seeds from each treatment (collection position, year, and storage location) were placed on germination paper (Anchor Paper Co., St. Paul, MN), moistened with distilled water in petri dishes, and incubated at 19 C for 30 d in the dark. Additional distilled water was added to each petri dish as required to maintain visible moisture on the paper. During incubation, the number of germinated seeds in each petri dish was recorded every 2 d, and seed germination was determined by the appearance of the coleoptile. To reduce microbial growth, a 1% solution of Captan 400-D (Bayer Crop Science, Research Triangle Park, NC) was added to the seed germination dishes where microbial growth was visible. At the end of the germination test period, seeds that did not germinate were tested for viability (Baskin and Baskin 1998). Each caryopsis was bisected dorsal–ventral to expose the embryo. Seeds were considered dead when no solid material was found within the seed coat (Baskin and Baskin 1998). Solid caryopses were placed cut-side down on anchor paper saturated with a 1% tetrazolium chloride solution and stored at 24 C for 12 h in the dark (Simpson 1990). Seeds were considered dead if the tetrazolium test produced no staining or the treatment stained the entire contents within the seed coat. Seeds containing a stained embryo were recorded as viable, but dormant.

The proportion viable seed was calculated as follows:

$$PV = [(S_t - S_d)/S_t] \quad [1]$$

where S_t was the total seed in the test, and S_d was the number of dead seed. Proportion germinated for each treatment was calculated as the proportion of the viable seed that germinated. This measure is equivalent to the germination rate of viable seeds or 1 − *dormancy rate*.

Statistical analysis was performed on logit-transformed rate (percentage) data to homogenize the variance. Effects of canopy position and site–year were tested using a full-factorial ANOVA model. Differences in wild oat seed responses

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Table 2. Overstory and understory wild oat seed characteristics at three sites in Montana. Results are mean (± SE); n = number of replicate petri dishes; 20 seeds replicate^{-1}.

Year	Location	% viability[a]		% germination[a]	
		Overstory	Understory	Overstory	Understory
		%			
1992	Bozeman (n = 24)	94 (1) a	68 (3) b	71 (4) a	39 (4) b
1993	Bozeman (n = 18)	78 (4) a	62 (7) b	8 (2) a	3 (1) a
1994	Bozeman (n = 104)	96 (1) a	91 (1) b	34 (2) a	16 (1) b
1992	Creston (n = 10)	93 (3) a	56 (5) b	26 (6) a	25 (6) a
1994	Moccasin (n = 60)	84 (2) a	74 (2) b	39 (3) b	52 (3) a

[a] Means for percentage of viability or percentage of germination followed by the same letter between columns (overstory vs. understory) were not different at P = 0.05.

between relative canopy positions were tested using Fisher's Protected LSD test (a priori or planned comparisons). Differences among site–years were determined using Tukey's Honestly Significant Difference test.

Assessing Effect of Storage Condition on Response Variables. Seeds used to estimate viability and dormancy rates were stored at room temperature. However, that may not accurately reflect the viability and dormancy rates under field conditions, i.e., where seeds reside in the soil seedbank. To test whether storage at room temperature altered those rates relative to the field, seeds stored at room temperature (24 C) over winter were compared with seeds buried in the field over winter. Seeds collected from overstory and understory plants in the field in 1993 were divided into two groups. Half of the seeds were returned to the field in the fall of 1993 and buried in nylon mesh bags 4 cm deep in the soil. The remaining seeds were stored at 24 C in the dark in the laboratory. After 5 mo, seeds were retrieved from the soil and for both sets of seeds viability, germinability, and dormancy rates were measured and analyzed using the methods described above.

Fungi Isolation and Inoculated Seed Germination Tests. Fungi were isolated from 20 understory and 20 overstory seeds from the Bozeman, MT, location in 1994. The seeds were surface-sterilized with a 10% bleach solution with one drop of Tween 20 (Thermo Fisher Scientific, Rockford, IL), thereby limiting our study to pathogens within seeds as opposed to seed surface pathogens. The solution and seeds were placed in a beaker and stirred for 3 min. Seeds were placed on acidified potato dextrose agar (PDA; Difco, BD, Franklin Lakes, NJ) petri plates (5 seeds plate^{-1}) using sterile forceps. These plates were then incubated at 24 C and observed daily for the growth of fungus. Once there was fungal growth, a small piece of PDA was taken from the edge of the growing fungus and was placed on a clean PDA plate. After pure cultures were created, they were grown on autoclaved oat (*Avena sativa* L.) kernels, which served as a media for the fungal growth. When the fungal growth had increased, the colonized kernels were spread out to dry. The dried spores/hyphae for each fungal isolate were then used as inoculum to test their effects on germination.

Firm, plump, mature (brown) wild oat seeds collected from the Bozeman, MT, location in 1994 were used for the fungi-inoculation germination tests. The experimental design consisted of seven fungi treatments, three infection rates, and five seeds per treatment, with eight replications. The rates of infection were a control (no fungi), one colonized kernel per petri dish seed, and two colonized kernels per petri dish. In a second experiment, two of the fungi identified in the first experiment were retested using eight replications of five seeds each.

The seeds were germinated in a growth chamber at 19 C for 30 d in the dark. Daily observations were made on the seeds, and seed germination was determined by the appearance of the coleoptile. At the end of the 30 d, the seeds that had not germinated were tested for viability using the tetrazolium assay described above.

Bacteria Isolation and Seed Germination Tests. Bacteria were isolated from wild oat seeds hand-collected from above or below the barley canopy, as well as from combine-harvested seeds at the Bozeman, MT, location in 1994. Nonsurface sterilized seeds were stirred in a phosphate buffer and the solution was streaked on nutrient agar (NA) and Kings B (KB) agar (Sigma-Aldrich, St. Louis, MO). The bacteria isolates were purified from a single colony, increased on media, and used as the inocula in the wild oat germination test.

Bacterial inoculation used seeds from the same seed lot as the fungal inoculations (mature seeds collected from Bozeman, MT, in 1994). The experimental design consisted of four bacteria treatments, two infection rates (infected or control), five seeds per treatment, and four replications. The control seeds were soaked in 40 ml of phosphate buffer and were placed in petri dishes. The bacteria-treated seeds were inoculated by adding phosphate buffer to the purified bacterial isolates and coating each wild oat seed from the field with the solution. Seeds were then placed in petri dishes for germination, following the procedure for the fungi-inoculated seeds. A second experiment was performed using five of the bacterial isolates identified in the first experiment, which was replicated 10 times with five seeds each. Effects of fungal and bacterial inoculation on viability and germination were evaluated via ANOVA using logit-transformed data.

Results and Discussion

Climate. Mean temperatures during wild oat flowering were similar among sites and years (range = 5 C; Table 1). Mean monthly precipitation varied among sites and years. In 1993, the Bozeman, MT, site received above normal precipitation and more precipitation late in the growing season than did the other site–years. More than 23 cm of rain fell in Bozeman, MT, in June and July. The Moccasin, MT, site was drier than the other sites, with 7 cm of rain falling in June and July. Precipitation at the remaining sites (Creston, MT, in 1992; Bozeman, MT, 1992 and 1994) was similar, ranging from 13 to 16 cm of precipitation during the 2 mo.

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Table 3. Bozeman, MT, 1993 wild oat seed characteristics when stored for 5 mo at room temperature (24 C) and for 5 mo in the field in soil. Results are mean (± SE); n = 18 replicates for each treatment; 20 seeds replicate^{-1}.

	% viable[a]		% germination[a]	
Storage	Overstory	Understory	Overstory	Understory
	%			
Room	73 (4) a	64 (5) a	23 (3) a	28 (5) a
Soil	85 (2) a*	55 (6) b	45 (4) a*	37 (7) a

[a] Means for percentage of viability or percentage of germination followed by the same letter between columns (overstory vs. understory) were not different at P = 0.05. An asterisk (*) indicates differences in percentage of viability of percentage of germination between storage locations at P = 0.05.

Seed Viability, Germination, and Dormancy. The overstory wild oat seed consistently exhibited increased viability compared with understory seed ($P < 0.05$), but the magnitude of the differences varied by site–year (interaction of site–year and canopy position $F_{4,423} = 11.3$, $P < 0.01$, Table 2). The effects on relative canopy position were greater in both sites in 1992 than it was in other site-years ($P < 0.05$) and similar between sites in this year. On average, seed viability below the crop canopy was 30% (95% confidence interval [CI] = ± 5%) lower than it was above the crop canopy. Differences in seed viability between canopy positions were significant (canopy effect, $F_{1,358} = 36.7$; $P < 0.001$) and similar among remaining site-years (interaction of site-year and canopy position $F_{2,358} = 0.04$; $P > 0.9$), averaging 10% (95% CI = ± 2%) lower viability below than above the crop canopy. The reduced viability for the understory seed may be because of deficient resources, such as light and water, which resulted in poorly developed seed, although this is in contrast with Brainard et al. (2005) who found that the competitive environment in which Powell amaranth (*Amaranthus powellii* S. Watts.) was grown had little effect on seed viability. Variability in effects may be due to differences in climate or wild oat biotypes. Interestingly, canopy position appears to have greater effects in wet years than it does in dry ones. The effects of canopy position were relatively minor in 1994, where summer precipitation was an average of 15% below normal, and in 1993, when abundant late-season precipitation allowed weeds to continue growing after crop had senesced. In 1992, abundant spring precipitation was followed by relatively dry conditions, and presumably, the precipitation increased the rate of crop growth, leading to a taller, denser crop canopy. As a result, the effects of canopy position on the viability of weed seed were relatively large.

The direction and significance of seed position, relative to the crop canopy, on seed germination varied across sites and were not related to the canopy effects on seed viability. Note that dormancy rates are not presented but would be calculated as 100% − *percentage of germination*. Overstory seed exhibited 18% (mean of 1992 and 1994) more germination than did understory seed ($P < 0.05$) in 1992 and 1994 at the Bozeman, MT, site. Germination rates were similar between canopy positions in Bozeman, MT, in 1993 and for Creston, MT, in 1992. At the Moccasin, MT, site, germination rates of overstory seed were less than they were for understory seed ($P < 0.05$). (Note: results indicate additive changes in the percentage of germination or viability, *not* percent change.) Sawhney and Naylor (1982) demonstrated that water stress at time of seed maturation decreased dormancy in genetically pure lines of nondormant and dormant wild oats. Precipitation was well above normal during seed maturation at the Bozeman, MT, site in 1993 and the highest overall rates of dormancy were observed (Table 2). Regardless of the role of water stress, it is clear that, under some conditions, the position of wild oat panicles relative to the crop canopy affects germination and dormancy. Identifying the possible mechanisms, which may include both abiotic and biotic factors, will require further study.

The experiment described above showed that canopy position affects weed seed characteristics. For this experiment, weed seeds were stored in artificial conditions (indoors), whereas, in agricultural settings, weed seeds reside in the soil. The results of the experiment designed to assess the effects of storage environment suggest that effects of weed seed position relative the crop canopy on seed viability are greater under field conditions (i.e., experiments described above underestimate the effects of canopy position). Overstory seed viability was similar to understory seed when seeds were stored in the laboratory. When seeds were stored in soil, viability of understory seeds was 30% (± 19%) less than it was for overstory seeds ($P < 0.05$) (Table 3). These results indicate that overstory seeds are more likely to survive in the seedbank than understory seeds are. Germination of all seeds stored in soil was greater (i.e., dormancy was less) than it was when the seeds were stored at room conditions ($P < 0.05$), and germination not affected by canopy position. Under field conditions, where seeds received the required stratification, more overstory seeds germinated, whereas understory seeds remained dormant. These results indicate that our larger experiment with seeds stored in room conditions may have underestimated the effects of canopy position on wild oat viability. Overall, results suggest that wild oat seeds produced below a canopy of wheat or barley and subsequently entering the seedbank will contribute less to the weed populations in the following year than will seeds from above the crop canopy because they exhibit less viability and possibly greater dormancy. Dormancy, in some cases, may be an advantage, but the understory seeds in this experiment exhibited dormancy, even after stratification and when given ideal germination conditions. In this case, the extended dormancy was a disadvantage, leaving the nongerminated seeds susceptible to predators and pathogens. The increased differences between below-canopy and above-canopy seed viability in soil, relative to seed stored at room temperature, indicate that these understory seeds were more susceptible to decay in the soil.

Microflora on Seeds. In addition to crop competition, these differences in seed viability could also be due to differences in the disease pressure on seeds above and below the canopy. Seven fungi and seven bacteria isolates were grown from wild oat seeds (Table 4) collected from the Bozeman, MT, location in 1994. Isolates were cultivated from both overstory and understory seeds as well as from the combine seed bin; however, each individual isolate identified was only found in

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Table 4. Identity and source of microflora isolated from wild oat seed collected at the Bozeman, MT, location in 1994.

Code	Microflora organism	Source of seed
F1	Dark mycelium fungus	Understory
F2	*Bispora* spp.	Overstory
F3	*Fusarium poae*	Understory
F4	*Nigrospora* spp.	Combine bin
F5	Dark mycelium fungus	Overstory
F6	*Cladosporium* spp.	Overstory
F7	*Fusarium culmorum*	Overstory
B1	Unidentified	Combine bin
B2	Unidentified	Combine bin
B3	*Ochrobactrum anthropi*	Combine bin
B4	Stenotrophomonas maltophilia	Combine bin
B5	*Pseudomonas cichorii*	Overstory
B6	*Pseudo putida*	Overstory
B7	*Pantoea agglomerans*	Understory

one source location (e.g., the same isolate was not found on both understory and overstory seed). This indicated that the microflora community differed with respect to canopy position.

There were no significant differences in wild oat viability, germination, or dormancy between seeds inoculated with one or two fungus-colonized oat kernels ($P < 0.05$). Wild oat viability, germination, and dormancy were not affected by the presence of the fungi in experiment 1 (Table 5). In experiment 2, we found that wild oat seed infected with *Fusarium poae* had significantly lower viability (15% lower) than the control did, but there were no differences in dormancy ($P < 0.05$). These results differed from Kiewnick (1963) who isolated 52 species of fungi from wild oat spikelets and found seven species, including three *Fusarium* species, to be pathogenic against seeds in the soil, causing loss of seed viability. However, our isolation techniques likely were not successful in isolating all species of fungi present on the collected wild oat seeds.

Wild oat seeds infected with bacteria were not different from the controls in viability, but they did have lower germination rates (0 to 59% compared with 70 to 96%) (Table 6). The role of bacteria in seed mortality has largely been unexplored (Wagner and Mitschunas 2008), but these data indicate that bacteria may have implications for long-term seed survival in the seedbank. Reduced germination and increased dormancy would result in increased risk of not only

Table 5. Effects of fungus infection on wild oat viability, germination, and dormancy. Results are mean (± SE); n = 8; 5 seeds replicate^{-1}.

Treatment	Viability[a]	Germination
Experiment 1		
Control	100 (0)	75 (7)
Dark mycelium	100 (0)	65 (11)
Bispora spp.	100 (0)	65 (8)
Fusarium poae	98 (2)	65 (13)
Nigrospora spp.	95 (3)	61 (9)
Dark mycelium	100 (0)	58 (7)
Cladosporium spp.	100 (0)	45 (12)
Fusarium culmorum	100 (0)	78 (6)
Experiment 2		
Control	100 (0)	85 (7)
Fusarium poae	85 (9)*	79 (6)
Cladosporium	100 (0)	70 (7)

[a] Means within a column (within an experiment) followed by an asterisk (*) are significantly different from the control ($P < 0.05$).

Table 6. Effects of bacterial infection on wild oat viability, germination, and dormancy. Results are mean (±standard error); n varied by experiment (see below); 5 seeds replicate^{-1}.

Treatment	Viability	Germination[a]
Experiment 1 (n = 4)		
Control	95 (5)	70 (13)
Unidentified bacteria 1	80 (12)	18 (11)*
Unidentified bacteria 2	75 (10)	36 (11)*
Ochrobactrum anthropi	55 (17)	0 (0)*
Stenotrophomonas maltophilia	75 (15)	5 (5)*
Experiment 2 (n = 10)		
Control	82 (3)	96 (3)
Ochrobactrum anthropi	86 (6)	36 (11)*
Stenotrophomonas maltophilia	90 (4)	39 (9)*
Pseudomonas cichorii	88 (5)	50 (7)*
Pseudo putida	92 (3)	59 (7)*
Pantoea agglomerans	84 (4)	22 (10)*

[a] Means within a column (within an experiment) followed by an asterisk (*) are significantly different from the control ($P < 0.05$).

further bacterial attack, but also fungal-induced decay and predation (Brown and Venable 1986; Pakeman et al. 2012).

Microflora on seeds during maturation of the mother plant may affect wild oat seed germination characteristics. Microclimate conditions in the overstory vs. the understory may select for different microflora, which, subsequently, influence germinability and dormancy in postdispersal seeds (e.g., *F. poae*, the only fungi isolate to affect wild oat seed viability in our study, was isolated from understory seeds). Understory seeds tend to be small and less developed; thus, the seed coat maybe more susceptible to infection by microbes.

Although we isolated microflora from several seed sources, we did not quantitatively assess the amount of infection for the environment (by canopy or by site) from which seeds were collected. Moister conditions (e.g., under a plant canopy) might harbor higher populations of microflora and might dictate lower viability, higher dormancy, or both (Creston, MT, 1992; Bozeman, MT, 1993). Water and heat stress may decrease populations of microflora, and dictate higher viability and lower dormancy (Bozeman, MT, 1992 and 1994; Moccasin, MT, 1994). Because of the nature of petri dish bioassays, 30 d of 19 C under moist conditions, we cannot uncouple inherent dormancy (mechanical or genetic) and enforced dormancy (bacteria). Other mechanisms that may be influencing differential viability and dormancy on overstory and understory panicles should be investigated.

Overall results indicate important relationships between wild oat panicle position relative to the barley canopy and subsequent seed viability and dormancy. Panicle position relative to the crop is a function of weed emergence time (i.e., different cohorts), and it is possible that emergence time is related to biotype, which would mean that panicle position was confounded with biotype in this study. However, it is known that different seeds produced from a mother plant can exhibit different viability and dormancy rates (Jha et al. 2010; Brainard et al. 2005; Baskin and Baskin 1998), and other factors, such as seed burial depth, landscape position, and crop residue, affect emergence time (Beckie 2012). Additionally, position relative to a crop canopy influences the pathogen community composition, which, in turn, may lead to differences in seed viability and dormancy. These factors make it unlikely that our results were a function of biotype, but rather, a variety of other biotic and abiotic factors

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determined the emergence time of the different cohorts resulting wild oat panicles above or below the barley canopy.

In conclusion, wild oat panicle position relative to the crop canopy plays an important role in wild oat seed maturation and in determining seed viability, germination rate, and dormancy. Furthermore, seed position relative to the crop canopy during maturation may influence the complex interactions of dormancy and susceptibility to pathogens in the soil seedbank (Dalling et al. 2011), with overstory seeds generally exhibiting greater viability and germinability and less dormancy. These seed traits may be exploited (Juroszek and von Tiedemann 2011) to manage wild oat populations by planting crop cultivars that provide greater canopy cover over wild oat or by planting early emerging crop varieties, so that wild oats emerge under a crop canopy. Dwarf and semidwarf cultivars of wheat and barley may be competitive with weeds; however, the consequences of their shorter stature on microflora populations, wild oat seed germination behavior, and subsequent population dynamics are unknown. Forcing more of the wild oat population to produce seed in the understory by use of taller crop varieties or early seeding of the crop may create a seedbank of fewer, lower viability, and more-dormant seeds. Future wild oat populations may then have less effect on the crop because of increased dormancy by spreading emergence of cohorts over a longer period, delaying emergence relative to the crop, and thus, decreasing the maximum proportional yield loss (Cousens et al. 1987; Maxwell and O'Donovan 2007).

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