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Seed viability and dormancy of 17 weed species after 19.7 years of burial in Alaska

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A study at Fairbanks, AK, was started in 1984 to determine soil seed longevity of 17 weed species. Seeds were buried in mesh bags 2 and 15 cm deep and were recovered 0.7, 1.7, 2.7, 3.7, 4.7, 6.7, 9.7, and 19.7 yr later. Viability was determined by germination and tetrazolium tests. Seed viability data were fit to an exponential model, separately for each depth, and the likelihood-ratio test was used to determine whether seed-viability decline was affected by burial depth. Depth of burial had a significant effect on viability decline of prostrate knotweed, marsh yellowcress, bluejoint reedgrass, and wild oat. By 19.7 years after burial (YAB), all seeds of common hempnettle, quackgrass, wild oat, foxtail barley, and bluejoint reedgrass were dead. Seeds of 12 other species were still viable: corn spurry (0.1%), prostrate knotweed (0.3% at 2 cm, 0.8% at 15 cm), flixweed (0.5%), pineapple-weed (0.6%), shepherd's-purse (1.3%), wild buckwheat (1.5%), common chickweed (1.6%), rough cinquefoil (1.8%), common lambsquarters (3.0%), Pennsylvania smartweed (3.3%), marsh yellowcress (8.5% at 2 cm, 0.3% at 15 cm), and American dragonhead (62.2%). Seed dormancy at 19.7 YAB was very low for all species (< 4%) except for American dragonhead, common lambsquarters, Pennsylvania smartweed, and shepherd's-purse, which had seed dormancies of 100, 27, 25, and 38%, respectively. Seed longevity was not increased by cold, subarctic temperatures.

Nomenclature: American dragonhead, *Dracocephalum parviflorum* Nutt. DRAPA; bluejoint reedgrass, *Calamagrostis canadensis* (Michx.) Beauv. CLMCD; common chickweed, *Stellaria media* (L.) Vill. STEME; Common hempnettle, *Galeopsis tetrahit* L. GAETE; common lambsquarters, *Chenopodium album* L. CHEAL; corn spurry, *Spergula arvensis* L. SPRAR; flixweed, *Descurainia sophia* (L.) Webb ex Prantl DESSO; foxtail barley, *Hordeum jubatum* L. HORJU; marsh yellowcress, *Rorippa islandica* (Oeder) Borbas RORIS; Pennsylvania smartweed, *Polygonum pensylvanicum* L. POLPY; pineapple-weed, *Matricaria matricarioides* (Less.) C.L. Porter MATMT; prostrate knotweed, *Polygonum aviculare* L. POLAV; quackgrass, *Elytrigia repens* (L.) Nevski AGRRE; rough cinquefoil, *Potentilla norvegica* L. PTLNO; shepherd's-purse, *Capsella bursa-pastoris* (L.) Medicus CAPBP; wild buckwheat, *Polygonum convolvulus* L. POLCO; wild oat, *Avena fatua* L. AVEFA.

Key words: Buried seed, seed longevity, weed seed decline, logarithmic model, subarctic.

Weed management is aided by knowledge of soil seed longevity. Weeds continue to emerge and compete with desirable plants as long as a viable propagule bank exists. To eradicate plants without long-lived vegetative propagules, seed production must be prevented for the length of time that seeds survive in soil (Zamora et al. 1989). Knowledge of seed-bank persistence is needed to determine how long control measures must be continued and to determine the feasibility of eradication (Panetta and Timmins 2004). Seed longevity data are also commonly used as one of the criteria for assessing weed invasiveness potential (Daehler et al. 2004; Hiebert 1997).

Despite the need for seed longevity data, relatively few seed-bank studies have been conducted that have lasted 15 yr or more. Beal's ongoing study of soil seed longevity of 21 species at Michigan State University has spanned more than 120 yr (Darlington 1951; Telewski and Zeevaart 2002), and the Duvel study with 107 crop and weed species in Virginia lasted 39 yr (Toole and Brown 1946). Burnside et al. (1996) in Nebraska studied seed longevity of 41 species at two locations, and Lewis (1973) determined the soil seed longevity of 39 crop and weed species in Wales over a 20-yr period.

Because soil temperature can greatly influence longevity of seeds (McGraw et al. 1991; Shafer and Chilcote 1970), a 50-yr buried-seed study was started at Fairbanks, AK, in 1984, to determine seed longevity and dormancy patterns of 17 plant species under subarctic conditions. Earlier results of this study showed no significant relationship between initial dormancy and longevity (Conn and Farris 1987). Dormancy was initially high but rapidly decreased for most species. By 4.7 YAB only two species, common hempnettle and quackgrass, had lost all seed viability (Conn 1990), and it required > 6.7 yr and ≤ 9.7 yr for all viability of foxtail barley and wild oat to be lost (Conn and Deck 1995). By 9.7 YAB, < 1% seed viability remained for bluejoint reedgrass, corn spurry, pineapple-weed, prostrate knotweed, and wild buckwheat. From 2 to 5% of seeds from common chickweed, common lambsquarters, flixweed, Pennsylvania smartweed, rough cinquefoil, marsh yellowcress, and shepherd's-purse were viable, whereas 62% of American dragonhead seeds were still alive (Conn and Deck 1995).

In the original design of this study, seeds were scheduled to be exhumed at 11.7, 13.7, and 15.7 YAB. However, clo-

TABLE 1. Mean and standard errors of seed viability (TOTAL) and dormancy (PDORM) 19.7 years after burial at Fairbanks, AK. Data from 2- and 15-cm depths were combined when it was found that residual sums of squares for the fitted model for each depth were not significantly different using the likelihood-ratio statistic.

Common name	Depth	TOTAL	PDORM
	cm	# seeds	%
American dragonhead	2 + 15	62.3 ± 12.8	99.6 ± 0.7
Bluejoint reedgrass	2	0	0
	15	0	0
Common chickweed	2 + 15	1.6 ± 4.6	0
Common hempnettle	2 + 15	0	0
Common lambsquarters	2 + 15	3.0 ± 5.0	26.7 ± 37.9
Corn spurry	2 + 15	0.1 ± 0.4	0
Flixweed	2 + 15	0.3 ± 0.5	0
Foxtail barley	2 + 15	0	0
Marsh yellowcress	2	8.5 ± 14.4	0
	15	0.3 ± 0.5	0
Pennsylvania smartweed	2 + 15	3.3 ± 3.2	25.0 ± 46.3
Pineapple-weed	2 + 15	1.6 ± 2.4	3.6 ± 10.1
Prostrate knotweed	2	0.3 ± 0.5	0
	15	0.8 ± 1.5	0
Quackgrass	2 + 15	0	0
Rough cinquefoil	2 + 15	1.4 ± 1.7	0
Shepherd's-purse	2 + 15	1.9 ± 2.1	37.5 ± 46.3
Wild buckwheat	2 + 15	1.5 ± 1.7	0
Wild oat	2	0	0
	15	0	0

sure of the U.S. Department of Agriculture–Agricultural Research Service (USDA–ARS), Subarctic Agriculture Research Unit in Alaska from 1995 to 2002 interrupted the study. This article reports results on the viability and dormancy of the buried seeds 19.7 YAB and examines the effect of burial depth on seed longevity over the course of the study.

Materials and Methods

Burial and Viability Methods

A complete description of seed burial and viability testing procedures was given in previous papers (Conn 1990; Conn and Deck 1995; Conn and Farris 1987). On October 2, 1984, 100 seeds of each weed species were buried in mesh bags at 2- and 15-cm soil depth. Enough bags were buried to allow for four replicates (blocks) of each species and burial depth to be recovered on 15 dates spanning 50 yr. Seeds were previously recovered in mid-May 0.7, 1.7, 2.7, 3.7, 4.7, 6.7, and 9.7 YAB.

Seeds were recovered May 19 to 21, 2004, 19.7 YAB. Immediately after seeds were exhumed, intact seeds were removed from the bags and were placed on moist filter papers and incubated for 2 wk at temperatures favorable for germination (Conn and Farris 1987). Seed coats of seeds that did not germinate were scarified and incubated for an additional 7 d. Nongerminated seeds were then placed in a 3,000-ppm 2,3,5-triphenyltetrazolium chloride (TTC) solution (pH 7.0) for 7 to 14 d. Seeds were then dissected, and seeds with pink-to-red embryos were recorded as viable.

Statistical Analysis

Total seed viability (TOTAL) was calculated as the sum of seeds that germinated before scarification plus seeds that germinated after scarification (GAS) plus nongerminated seeds with TTC-stained embryos (STAINED). The percentage of seeds that were dormant (PDORM) was calculated as {[(GAS + STAINED)/TOTAL] × 100}.

Analysis of variance, used to analyze earlier data for this experiment, could not be used for this data set because analysis of residuals showed that the underlying assumptions of ANOVA, homogeneity of variance and normality, could not be met. A nonlinear regression approach was used to fit the data on seed viability over time to an exponential model. This model has been widely used for analyzing seed viability decline and, even though not optimal for every species, provides a means for comparing decline rates for different species (Conn 1990; Lutman et al. 2002; Taylor et al. 2005). Exponential decline rates were calculated using the formula:

$$Y = A + BR^X \qquad [1]$$

where $A + B =$ the initial number of viable seed at the time of burial, A is the minimum number of seeds at infinite time, R is the proportion of seeds surviving each year, and $X =$ years. Because the minimum number of seeds (A) is zero, the equation becomes

$$Y = BR^X \qquad [2]$$

The logarithmic model was fit for each species and burial depth over time using PROC NLIN of SAS (SAS 1999). For each species, the importance of burial depth as a predicting factor of viability was tested using a likelihood-ratio test (Haddon 2001). The test used is an overall test of coincident curves and is defined as

$$\chi^2_k = -N \times \ln\left(\frac{RRS_\Omega}{RRS_\varpi}\right) \qquad [3]$$

where k is the degrees of freedom (the number of parameters assumed equal), N is the total number of observations, RRS_Ω is the total sum of squared residuals calculated by fitting curves

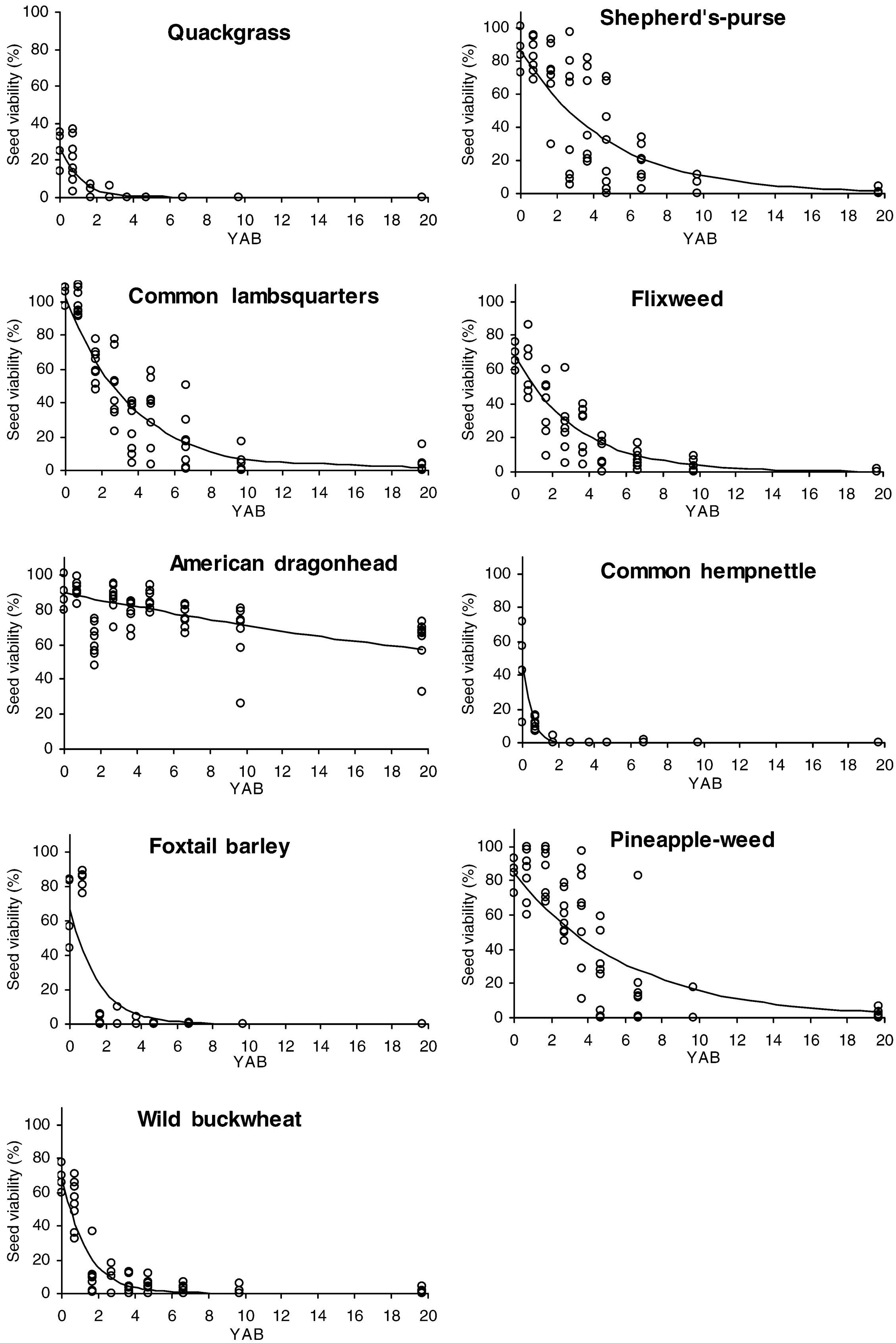

Figure 1. Seed viability decline of 17 weed species at Fairbanks, AK, over 19.7 years. The exponential function $Y = BR^X$ was used to fit to data from seeds recovered from both 2-cm and 15-cm burial depths. Data from both depths were combined if curves for the two depths were found not to be significantly different using the likelihood-ratio test.

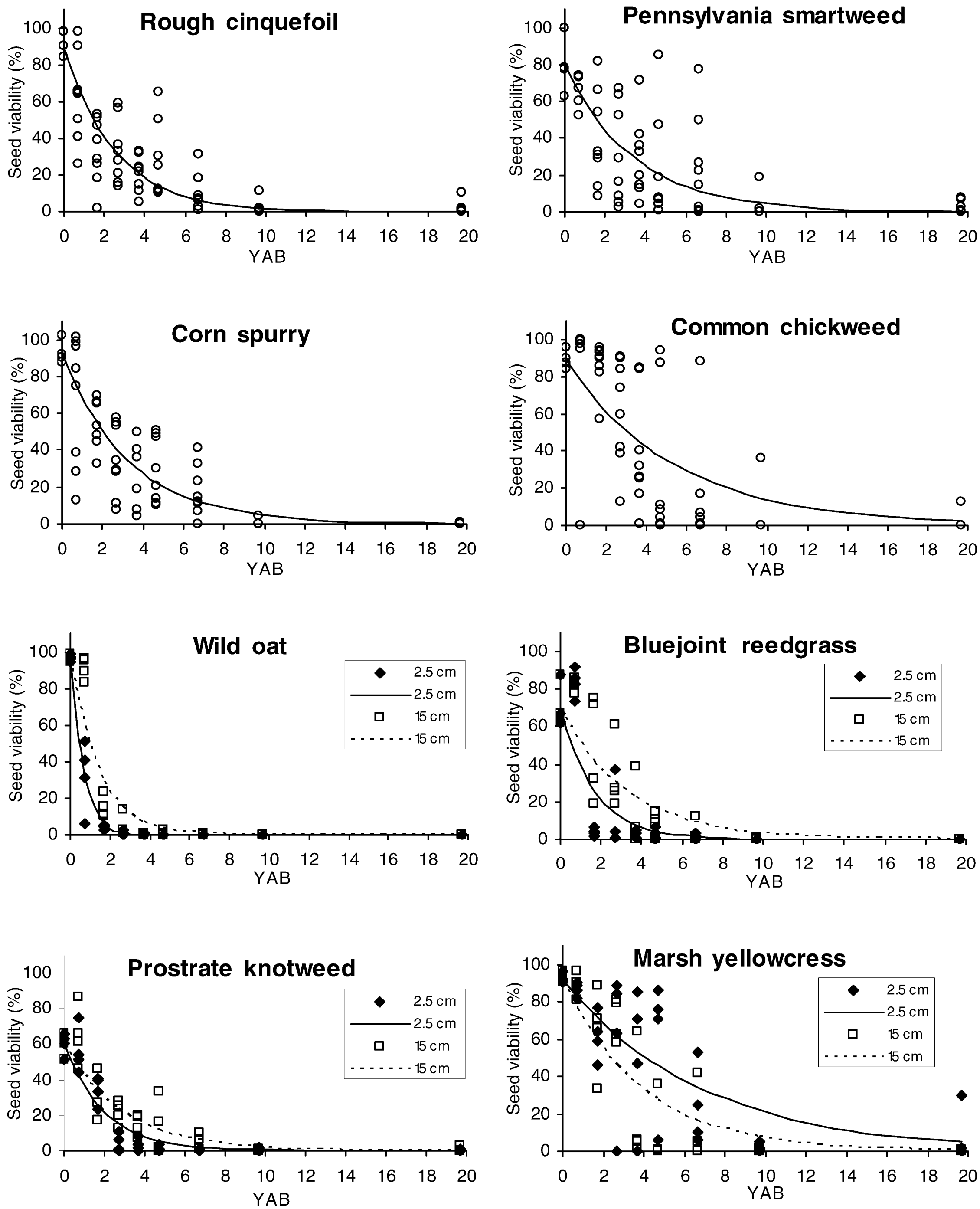

FIGURE 1. Continued.

separately for each burial depth; and RRS_{ϖ} is the total sum of squared residuals derived from fitting a curve for both depths combined. For this test, depth was included as an additional parameter. When the hypothesis of equal viability at both depths was rejected ($P \leq 0.05$), models created for each depth are presented. When the hypothesis was not rejected, depth had no effect on seed viability decline, so models fit to each depth were coincident, and a single model is presented.

Results and Discussion

Bluejoint reedgrass was the only species to lose viability during the 10-yr period since seeds were last exhumed (Table 1). At 19.7 YAB, less than 1% seed viability was observed for corn spurry, prostrate knotweed, and flixweed. Higher seed viability was found for rough cinquefoil (1.4%), wild buckwheat (1.5%), common chickweed (1.6%), pineapple-weed (1.6%), shepherd's-purse (1.9%), common lambsquarters (3.0%), Pennsylvania smartweed (3.3%), and marsh yellowcress (8.5% at 2 cm, 0.3% at 15 cm). American dragonhead still had 62.3% seed viability. Most species had very low dormancy (< 4%) and germinated without scarification. Exceptions to this were American dragonhead (99.6% dormant), shepherd's-purse (37.5% dormant), common lambsquarters (26.7% dormant), and Pennsylvania smartweed (25.0% dormant).

TABLE 2. Parameters estimated using nonlinear regression with the exponential function $Y = BR^X$, where B is the initial number of viable seed at the time of burial, R is the proportion of seeds surviving each year, and X is the number of years. Viability data for 17 species from the first 19.7 yr of a buried-seed study at Fairbanks, AK, were used for the estimations. Data from both burial depths (2 and 15 cm) were combined when it was found that residual sums of squares for the fitted model for each depth were not significantly different using the likelihood-ratio statistic.

		Estimated parameters		
Species	Burial depth	B	R	Annual decline rate[a]
	cm	#		%
American dragonhead	2 + 15	89.5	0.98	2
Bluejoint reedgrass	2	70.0	0.55	45
	15	70.0	0.74	26
Common chickweed	2 + 15	89.3	0.83	17
Common hempnettle	2 + 15	46.0	0.12	88
Common lambsquarters	2 + 15	102.0	0.76	24
Corn spurry	2 + 15	93.0	0.74	26
Flixweed	2 + 15	67.5	0.75	25
Foxtail barley	2 + 15	67.0	0.52	48
Marsh yellowcress	2	92.3	0.86	14
	15	92.3	0.77	23
Pennsylvania smartweed	2 + 15	79.5	0.75	25
Pineapple-weed	2 + 15	84.5	0.85	15
Prostrate knotweed	2	60.0	0.60	40
	15	60.0	0.71	29
Quackgrass	2 + 15	26.8	0.41	59
Rough cinquefoil	2 + 15	89.0	0.68	32
Shepherd's-purse	2 + 15	86.8	0.81	19
Wild buckwheat	2 + 15	68.5	0.48	52
Wild oat	2	96.5	0.20	80
	15	96.5	0.50	50

[a] The equation used to determine annual decline rate is $100 \times (1 - R)$.

Depth of burial had a significant effect on seed viability decline over 19.7 yr for wild oat, prostrate knotweed, bluejoint reedgrass, and marsh yellowcress. Viability declined faster at 2 cm than at 15 cm for all these species except marsh yellowcress, where viability declined faster at the deeper depth (Figure 1; Table 2). Miller and Nalewaja (1990) also found that wild oat maintained viability longer with increased soil depth. When soil depth has been found to affect seed longevity, the usual case is that longevity is increased when seeds are buried deeper (Egley and Chandler 1983). Instances where seed longevity is greater near the soil surface are rare. Taylor et al. (2005) found that persistence of awned canary grass (*Phalaris paradoxa* L.) seeds was greater when placed on the soil surface than when buried.

There were three distinct patterns of seed viability decline displayed by the 17 species seen in Figure 1. Five of the species (quackgrass, foxtail barley, wild oat, bluejoint reedgrass, and common hempnettle) lost ≥ 80% of initial seed viability in the first 3.7 yr of the study and lost all viability before 19.7 YAB. A second pattern was exhibited by American dragonhead, with a very slow, constant decline in viability and 62% of seeds still viable at 19.7 YAB. The third pattern was exhibited by the other 10 species and was characterized by a rapid loss of seed viability within the first 9.7 years of the study, followed by a slower rate of decline with a low proportion of seeds remaining viable at 19.7 YAB.

The four grasses in this study had relatively short viability compared with the broadleaf species, a pattern also found by Lewis (1973). Seed size and longevity of species in this study did not appear to be related. Wild oat and common hempnettle have large seeds that were short-lived; however, American dragonhead, wild buckwheat, and prostrate knotweed have relatively large seeds, compared with the other broadleaf weeds in the study, but were long-lived. Seeds of herbaceous plants in Britain persisted longer in soil if seeds were small than if they were large (Bekker et al. 1998; Thompson 1987). In contrast, the relationship between seed size and soil persistence was not found for species studied in Australia (Leishman and Westoby 1998) or New Zealand (Moles et al. 2000).

The annual decline rates ($1 - R$) shown in Table 2 can be used to compare overall rates of seed-bank decline among the 17 species in this study. The annual decline rate of the American dragonhead seed bank was the slowest in this study (2%), whereas common hempnettle had the fastest decline (88% loss each year). The decline rates from the modeled data can also be used to nonstatistically compare common species between different seed-bank studies. Lutman et al. (2002) studied the persistence of 16 weed species over 6 yr at two locations in England. Seeds were broadcast on the soil surface, were tilled in as part of ordinary farming procedures, and were recovered annually by soil sampling and seed extraction. Common hempnettle had an annual decline rate of 61% in the Lutman et al. (2002) study, 17% less than what we found in Alaska. This difference is interesting because mesh bags in our study should have stopped seed predation and resulted in greater survival. The decline rate for prostrate knotweed was also higher for our study (40% at 2 cm and 29 % at 15 cm in Alaska vs. 23% for Lutman et al. [2002]). Decline rates for common lambsquarters were nearly identical (24% Alaska, 28% Lutman et al. [2002]) and were higher for common chickweed in the Lutman et al. (2002) study (35% Lutman et al. [2002], 17% Alaska).

Table 3 shows seed viability of species that were jointly studied here and in the long-term seed viability experiments of Beal (Darlington 1951; Telewski and Zeevaart 2002), Duval (Toole and Brown 1946), Lewis (1973), and Burnside et al. (1996). There was no consistent pattern of increased seed longevity with decreasing mean annual temperature. Although seed viability for common chickweed, shepherd's-purse, common lambsquarters, and Pennsylvania smartweed had all reached 0% by 21 YAB in Virginia, all of these species were still viable in Alaska; however, 83% of rough cinquefoil seeds were still viable in Virginia vs. 1.4% in Alaska. Moreover, longevity of common chickweed and shepherd's-purse seeds was greater in Michigan than in Alaska, and common lambsquarters seeds persisted longer in Wales and Nebraska than in Alaska.

Comparing the results of this study to other long-term seed longevity experiments is difficult because of differences in experiments in burial methods, such as seed containers; burial depths; recovery intervals; and procedures for viability testing. Conditions under which the seeds were produced could also have influenced seed dormancy and longevity.

The shallower burial depths at Fairbanks, AK (2 and 15 cm), vs. the deeper burial depths of the Beal (Darlington 1951; Telewski and Zeevaart 2002) (46 cm), Duvel (Toole

Table 3. A comparison of long-term seed viability of species held in common between this study and other long-term seed viability experiments performed by Beal (Telewski and Zeevaart 2002), Lewis (1973), Burnside et al. (1996), and Duvel (Toole and Brown 1946).

Study	Location	Mean annual temperature[a]	Burial depth	Years buried	Species: Common chick-weed	Shep-herd's-purse	Common lambs-quarters	Pennsyl-vania smart-weed	Rough cinquefoil
		C	cm	yr	Seed viability (%)				
Conn	Fairbanks, AK	−2.3	2 + 15	19.7	1.6	1.9	3.0	3.3	1.4
Beal	Lansing, MI	8.1	46	20	6	42	—	—	—
Lewis	Aberystwyth, Wales	9.7	13	20	—	—	32	—	—
Burnside	Mitchel, NE	9.1	20	17	—	—	7	2	—
Burnside	Lincoln, NE	10.7	20	17	—	—	28	7	—
Duvel	Rosslyn, VA	14.2	20	21	0	0	0	0	83

[a] Mean average air temperature (1971–2000) for U.S. locations were found in NOAA (2002) and for Aberystwyth, Wales, in U.K. Meteorological Office (2004).

and Brown 1946) (20 cm), and Burnside et al. (1996) (20 cm) studies may have predisposed the Alaska experiment to decreased seed longevity. Increased seed longevity with increasing seed burial depth has been found in other studies (Gleichsner and Appleby 1989; Roberts and Feast 1972; Wicks et al. 1971; Zorner et al. 1984).

Burial containers may also have influenced the results. In the Beal study, seeds were mixed with moist sand and placed in uncorked pint bottles for burial (Telewski and Zeevart 2002). For the Duvel study, seeds were mixed with sterilized soil and then placed in porous flowerpots before burial (Toole and Brown 1946). The Burnside study employed plastic cylinders to hold seeds mixed with soil. Cylinder ends were covered with a glass-fiber filter and a plastic screen (Burnside et al. 1981). Our study and the Lewis (1973) study used woven bags to contain the seeds. It is likely that the burial containers used in all of the studies would have reduced seed predation by larger insects, although Toole and Brown (1946) noted the presence of earthworms and ants in some of the pots in the Duvel study. The flowerpots of the Duvel study, the glass bottles of the Beal study, and the plastic cylinders employed in the Burnside study may have also buffered seeds inside from changes in soil moisture and temperature. Seeds in our study and the study of Lewis, which used mesh bags for burial, would have exposed enclosed seeds to conditions more resembling that of the surrounding soil.

The five long-term weed seed longevity experiments used different methods to determine seed viability after seed were exhumed. In the Beal, Lewis, and Burnside experiments, the number of seeds remaining and viability were determined by incubating soil (Beal experiment) or intact recovered seed (Lewis and Burnside studies) and counting seedlings. In the Duvel study, ungerminated seeds were separated from the soil and were scarified if they had not absorbed water, or were stratified at a lower temperature if they seemed imbibed but dormant (Toole and Brown 1946). In our study, seeds that did not germinate initially were scarified, and those seeds that did not then germinate were subjected to tetrazolium testing. The numbers of viable seeds remaining at recovery intervals in the Beal, Lewis, and Burnside experiments are probably underreported because dormant, viable seeds were not accounted for.

Artificial seed-bank studies may not accurately estimate seed longevity. These studies may overestimate seed longevity because burial containers decrease seed predation and may modify soil temperature and moisture fluctuations (Leon and Owen 2004). Artificial seed-bank studies also ignore the stimulatory effects of tillage on weed seed germination. On the other hand, seed longevity may be underestimated by artificial seed-bank studies because the densities of seeds in burial containers are artificially high, and mortality can be increased due to enhanced seed-to-seed contamination by pathogenic fungi (Van Mourik et al. 2005). For these reasons, the results of artificial seed bank should be interpreted with caution. Long-term artificial seed-bank studies do provide an indication of the absolute capability for seed survival in soil and are useful to those designing eradication programs and for those who want to know what the outer limits of seed survival might be. Even for economic threshold modeling, it is useful to know that viable seeds may be present, even at extremely low density, and can continue an infestation.

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