

Debiting the seedbank: priorities and predictions

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Summary

There are four general fates of seeds in seedbanks: persistence, germination, death and emigration. The latter three fates represent seedbank losses, and they are the topics examined in this paper. Seed death in the seedbank typically is caused by granivores and seed pathogens, but general seed deterioration via ageing also is important, especially for deeply buried seeds. Dormant seeds may be more resistant to pathogens and less palatable to granivores than non-dormant seeds. Losses through seed death can be large, but typically affect < 50% of seeds, unless seeds are buried deeply. Emigration occurs through runoff and erosion, but probably does not represent a major loss from seedbanks. Generally, seed germination accounts for the majority of seedbank losses. Consequently, understanding the timing and magnitude of seed dormancy release, seed germination and seedling emergence is still critical for future research and increasing the efficacy of management operations and alternatives. This does not diminish the importance of studying seed death and emigration, but merely lends perspective to such research.

Key words: Germination, granivory, seed ageing, seed loss, seed pathogen, seed persistence, seed survival

Introduction and Banking Economics

Losses from seedbanks obviously play important roles in seedbank ecology and dynamics. However, these losses are equally important in the management and economics of seedbanks. This importance can be illustrated nicely through the simulations of Jones *et al.* (2002). These authors developed "numerical optimal control" models wherein future values of seed losses (or gains) could be simulated for varying management scenarios. For example, Fig. 1 depicts the benefit (or cost) of decreasing (or increasing) seedbanks by one seed m^{-2} of either *Avena fatua* L. or *Raphanus raphanistrum* L. under postemergence herbicide control scenarios given differing initial seedbank densities.

There are two major features within Fig. 1. The first is obvious; that is, decreases in seedbank densities are always of value. The second point, however, is less intuitive; that is, the value of decreasing a seedbank is much greater when seedbank densities are low than when they are high. In other words, when seedbanks are sparse, the loss of an additional seed has considerable future impact because each lost seed appreciably reduces the proportional potential of the seedbank to generate progeny. In contrast, when seedbanks are densely populated, loss of an individual seed is almost inconsequential in terms of generating progeny. The "breaks" in the curves (i.e., where the slopes change rapidly) in Fig. 1, which are between 500 and 1000 seeds m^{-2} , probably define the densities at which the population dynamics of the two weed species are seed-limited or site-

limited. That is, when densities are less than the break point, the populations are not constrained by density and thereby are seed-limited. In contrast, at densities above the break point, density-dependence occurs and, consequently, the populations are limited by the capacity of the site.

A recent experiment on seedbank augmentation of *Helianthus annuus* L. (Cummings & Alexander, 2002) confirms at least part of the principle illustrated in Fig. 1. This experiment was a 2×2 factorial: small or large seedbanks and absence or presence of vertebrate granivores. Plots were augmented with 500 or 2500 seeds m^{-2} and nets excluded vertebrates in half of the plots. Plant densities the following spring were about 100 or 400 seedlings m^{-2} where granivores were excluded, and about 75 or 300 seedlings m^{-2} where granivores had over-winter access to the seeds. Although some density-dependent seedling mortality occurred during the growing season, at the time of seed shed all treatment combinations produced similarly, about 2500 seeds m^{-2} . This indicates that the *H. annuus* seedbank was not seed-limited at the lowest density (500 seeds m^{-2}), which produced about 75 to 100 plants m^{-2} , each of which potentially can grow 1 to 2 m tall. Clearly, this species was site-limited even at the lowest experimental seedbank density, highest level of granivory and associated plant population. As a consequence, the simulated 80% reduction of the initial seedbank, from 2500 to 500 seeds m^{-2} , had no effect on ensuing seed production. By extension, such a reduction in a *H. annuus* seedbank probably would have no influence on subsequent management decisions and outcomes in a cropped field. A smaller seedbank would have impact on management and population dynamics only if the initial density was lower than the break point (Fig. 1), which probably is < 500 seeds m^{-2} for *H. annuus*.

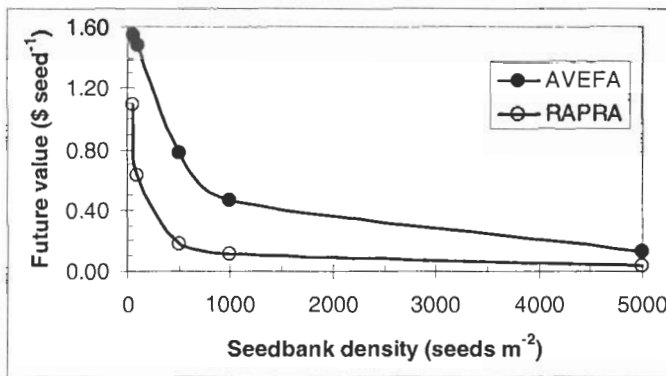


Fig. 1. Simulated financial values of individual seeds of *Avena fatua* (AVEFA) and *Raphanus raphanistrum* (RAPRA) in seedbanks in Australian wheat crops as functions of seedbank densities. Adapted from Jones *et al.* (2002).

Debiting the Seedbank through Granivory

One of the most fascinating topics in recent seedbank research is seed movement and loss via seed-caching and seed-eating animals. For instance, in the study by Cummings & Alexander (2002), mentioned above, about 25% of the seedbank of *H. annuus* was removed by vertebrates between seed shed in autumn and seed germination in spring. This experiment was of the "exclusion" type, whereby seeds were sown and netting erected on half the seeded plots to exclude vertebrates. The effects of vertebrate granivores then were demonstrated by comparing numbers of emerged seedlings in plots with and without netting.

An alternative method of examining granivory is the seed "buffet." In this type of experiment, known numbers of seeds are placed onto various styles of trays and left in the field. Differing types of enclosures sometimes are used to dissect impacts of granivorous guilds, i.e. differing groups of seed-eating insects, rodents, birds, etc. In buffet-type experiments seed losses typically are very high, with considerable seed removal usually occurring within only a few days (e.g., Menalled *et al.*, 2000), which suggests that the potential is substantial for seedbank losses through granivores.

Unfortunately, interpretation of results from buffet experiments is not simple in terms of impacts on seedbanks. Because of granivore behaviour, complexity of granivore guilds and the nature of the experiments, extrapolation of seed loss data from buffet experiments to reality is challenging. What buffet experiments can show, however, is differential seed removal across various management practices, locations, etc. For example, buffet experiments can be used to test the effect of distance from field margins on granivore-mediated seedbank depletion. (In this example, no effects were observed in wheat fields managed organically in Holland (Westerman *et al.*, 2003) or traditionally in the UK (Tooley *et al.*, 1999).)

Menalled *et al.* (2000) examined whether granivory of weeds in Michigan, USA, maize fields was affected by landscape complexity, field identity and granivore guild. Granivory was only slightly higher (11% of seeds removed day⁻¹) in complex compared to simple landscapes (9% day⁻¹). More variation in seed removal rates occurred among fields within landscapes than between landscapes. Weed seed removal rates averaged about 13, 11 and 4% day⁻¹ without enclosures, with vertebrate enclosures and with combined vertebrate plus invertebrate enclosures, respectively. These loss rates, if linear over time, would equate to seedbank residence times of merely 8, 9 and 25 days. Such high rates of animal-mediated loss from seedbanks suggest that seeds in soil disappear too quickly to form seedbanks. The fact that persistent seedbanks occur almost universally in arable fields gives indication that data from buffet experiments are interesting for comparative purposes but cannot be used to debit seedbanks realistically.

Another buffet study reported rates of seed loss for *Abutilon theophrasti* Medik. in maize in Ohio, USA (Cardina *et al.*, 1996). Several factors were tested, including tillage system, granivore guild and seedbank density. Tillage had no influence on seed loss. Unlike the Dutch buffet study (Westerman *et al.*, 2003) and a similar study in Sweden (Andersson, 1998), small granivores (insects) removed more seeds than larger granivores (rodents). Rate of granivory decreased exponentially with seedbank density when rate was reported as percentage of seedbank lost per day (Fig. 2). If seed losses are reported more simply as numbers of seed lost per day, the relationship between seedbank density and seed loss was linear. That is, the amount of seeds removed by granivores is a simple and constant function of seed availability (Fig. 2). The slope of this linear relationship suggests that about 5% day⁻¹, on average, of seeds are lost through granivory regardless of seedbank density.

In contrast to many studies on weed seed granivory, the buffet study by Cardina *et al.* (1996) took the wise precaution of seeding the general study area with the target weed species. Consequently, the Petri dishes used to hold the measured seeds did not represent an anomalous high-density seed cache that would attract unusually high numbers of granivores. (Analogously, Andersson (1998) used empty dishes scattered among seeded dishes to dilute the effect of seeded dishes serving as feeding stations.) Another important facet of this study was the observation that insects usually consumed only imbibed seeds of *A. theophrasti*, which is a hard-seeded species of the Malvaceae. Seeds that were not imbibed rarely were consumed.

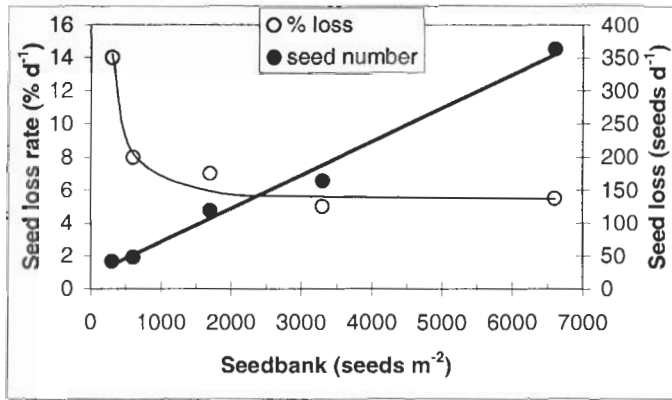


Fig. 2. Rate of seed loss (% seeds per day) of *Abutilon theophrasti* as a function of seedbank density (adapted from Cardina *et al.*, 1996), as depicted by the open circles and thin line, also can be expressed more simply as absolute numbers of seeds lost per day (closed circles and heavy line).

A study from Ontario, Canada (Cromar *et al.*, 1999) measured granivory rates that were at least twice as high ($> 22\% \text{ day}^{-1}$) as in the Ohio study ($11\% \text{ day}^{-1}$). However, similar to the Ohio study, the study from Ontario showed that insects were the main granivores, tillage intensity had no consistent trend regarding rates of granivory of weed seeds (*Echinochloa crus-galli* [L.] Beauv. and *Chenopodium album* L.), levels of residue from the previous crop were not related to granivore densities or seed losses, and density-dependent granivory was evident if seed losses were expressed in absolute numbers. There was a trend for granivory to be greater in autumn than spring, with autumn being the time of natural seed shed for summer annual weeds. In contrast, the Ohio study found no consistent seasonal trend in granivory, except that granivory was low in very early spring or very late autumn, when temperatures probably were low enough to inhibit insect activity.

Debiting the Seedbank via Seed Pathogens

Surprisingly little information exists regarding effects of microorganisms on weed seedbanks. This may reflect difficulties in experimental methodologies, which do not seem to have been developed rigorously yet by weed biologists.

Effects of pathogens on seeds of *Sorghum bicolor* (L.) Moench were examined in the field in Nebraska, USA (Fellows & Roeth, 1992). A seed of *S. bicolor* is composed of a caryopsis incompletely surrounded by two indurated glumes. The glumes were suspected of having antimicrobial properties. Glumes were removed from some seeds and the isolated caryopses were treated or not treated with the fungicides, carboxin and thiram. These caryopses, as well as non-treated seeds, were buried in November in each of two years, exhumed the following April, and then tested for viability. Although results differed between years, the impact of microbes on seed viability was clear. Germination of untreated seeds before and after burial decreased from 83 to 5% in year 1 and 79 to 53% in year 2. Untreated caryopsis germination fell from 95 to $<1\%$ in year 1 and 97 to 17% in year 2. Lastly, germination of fungicide-treated caryopses decreased from 95 to 17% in year 1 and 96 to 40% in year 2.

Three conclusions arise from these results. First, substantial losses in viability can occur over winter regardless of treatment. Second, glumes suppress initial germination but partially protect caryopses from over-winter microbial attack. Third, fungicides protect caryopses from microbial attack, which was substantial. Unfortunately, the full impact of microbes on *S. bicolor* seeds could not be assessed in this study because the fungicides had half-lives shorter than the residence times of the seeds in the soil. Caryopses would have to have been treated repeatedly with fungicide to determine the complete effect of fungi on *S. bicolor* seeds. Even then, the impacts would be only for those of fungi and some bacteria, because carboxin and thiram have limited effects on bacteria.

Viable hard seeds, which are impermeable to water, appear more resistant to pathogens than imbibed non-dormant seeds. In other words, when seeds gain the ability to imbibe water they simultaneously become more susceptible to pathogens. This can be illustrated with the studies on *Abutilon theophrasti* and the soil borne seed pathogen *Fusarium oxysporum* (Kremer & Schulte, 1989). After incubation in sterile medium, 2% of *A. theophrasti* seeds were not viable. This percentage was about the same, 5%, if the medium was infused with the pathogen. However, if seeds were incubated with dormancy-breaking chemical agents, such as nitrate or ethephon, then in the presence of *Fusarium* the percentages of non-viable seeds increased appreciably to 25 and 40%, respectively, but remained $\leq 5\%$ in sterile medium. Thus, imbibed seeds were more likely to be attacked by pathogens than dry seeds.

Another hardseeded weed is *Mimosa pigra* L. During the "winter" dry season in northern Australia, viability of *M. pigra* seeds declined to about 60% (Lonsdale, 1993). Viability of benomyl-treated seeds was about 13% higher than non-treated seeds. Highly fluctuating soil temperatures were thought to be the primary cause of seed loss, probably through their effect on seed softening (Dillon & Forcella, 1985) and facilitating entry of soil-borne pathogens (Lonsdale, 1993).

Seed-borne microorganisms not only reduce seedbanks directly through seed death, but also through decreased plant vigour and fecundity. Thus, in pastures with seeds of *Medicago polymorpha* L. initially infected with alfalfa mosaic virus in year 1, realised by year 4 a smaller *M. polymorpha* seedbank and a much greater population of the weed, *Arctotheca calendula* (L.) Levyns, which competed with *M. polymorpha* and suppressed its production of seeds (Jones & Nicholas, 1998).

Soil borne bacteria also infect weeds, such as *Pseudomonas fluorescens* infection of *Bromus tectorum* L. (Kennedy *et al.*, 1991), but in this case the infection occurs on roots after germination. Technically, this is an example of a seedling pathogen rather than a seed pathogen and, consequently, *B. tectorum* seedbanks are affected only indirectly by *P. fluorescens*.

Seed pathogens and seed-feeding insects can interact to influence seedbanks (Kremer, 2000). The best example is that of pre-dispersal seed feeding by the bug, *Niesthrea louisianica*, which facilitates infection by pathogenic fungi (Kremer & Spencer, 1989). Infection level was negatively correlated ($r^2 \geq 0.8$) with seed viability for each of three years of study. When infection levels reached $\geq 70\%$, seed viability was only 10 to 40%.

Debiting the Seedbank through Emigration

Seeds also can be lost from seedbanks via transport by external agents. In the case of animal dispersal agents, seeds are collected from one seedbank and cached in another at some distance from the original seedbank. Emigration from seedbanks typically is conceived with animal dispersal agents in mind. However, abiotic forces also are involved, especially in arable landscapes. For example, in furrow-irrigated fields, irrigation water scours seeds from the seedbank and transports them "down stream." Losses from such causes can be as high as 1000 seeds m^{-2} (Sojka *et al.*, 2003). Other sources of seed emigration include movement of seed-laden surface soils by natural means (e.g., soil erosion) or anthropogenic, such as soil moved during

harvest and transport of sugarbeet (Hodkinson & Thompson, 1997). However, there are very few studies that document these types of losses from seedbanks, and more information on this topic would be welcome additions to the literature.

Debiting the Seedbank through Seed Ageing

A vast literature exists for seed ageing, especially for seeds of crop species. Very exciting research is occurring on this topic, e.g. diminished ability for DNA repair in ageing seeds (Baskin & Baskin, 1998). However, much of this new research, as well as older research, is related only marginally to weeds and weed management. For instance, research on accelerated ageing is primarily laboratory-based and typically devoted strictly to testing the effects of storage on the viability and vigour of crop seeds. Although these types of experiments help us understand potential mechanisms of seed loss in soil, most of these tests may not be realistic regarding viability of weed seeds.

For information on ageing of weed seeds, one typically must turn to studies of the viability of weed seeds buried for many years. An example is that of Burnside *et al.* (1996) who monitored responses of 41 weed species whose seeds were buried for 17 years at two sites in Nebraska, USA. One site was mesic, averaging 73 cm precipitation annually and the other site was arid, averaging only 34 cm precipitation per year. Burial containers prevented attack by granivores, but not pathogens. Because the seeds were buried deeply, 20 cm, little loss of seeds to fatal germination was anticipated, especially for a species such as *Datura stramonium* L. (see following section on 'Fatal Germination'). Consequently, seed ageing may have accounted for a large portion of the observed seed losses.

Across all species, fewer seeds were lost (due to ageing) at the arid site than at the mesic site, although some exceptions occurred, as with *Chenopodium album* (Fig. 3). This general phenomenon probably is associated with the known debilitating effect on seed viability of high humidity during seed storage (Baskin and Baskin, 1998). *D. stramonium* was the most dramatic example of a species that lost all of its seeds quickly, within 4 years, at the mesic site (Fig. 3), but suffered hardly any losses at the arid site even after 17 years in the soil. Although the seeds of *D. stramonium* persisted much longer in dry than moist soil, this species is a much greater problem as a weed in mesic than arid regions. We still have too little understanding of how the soil physical environment influences seed ageing and seed death. This remains an important topic for future research. Physically based models that simulate seed germination must be complemented by models that predict seed death.

Debiting the Seedbank through Germination

Fatal germination

One form of seed loss is fatal germination, that is germination at soil depths from which seedlings cannot emerge successfully. Tillage, especially deep tillage, hopefully promotes this form of preemergence mortality, which Benvenuti (2003) refers to as "suicide germination". However, deep germination is not documented very well, even though it is perceived to be common. The reports listed by Baskin & Baskin (1998) for fatal germination tend to be for species other than arable weeds, except *Avena fatua* (Zorner *et al.*, 1984).

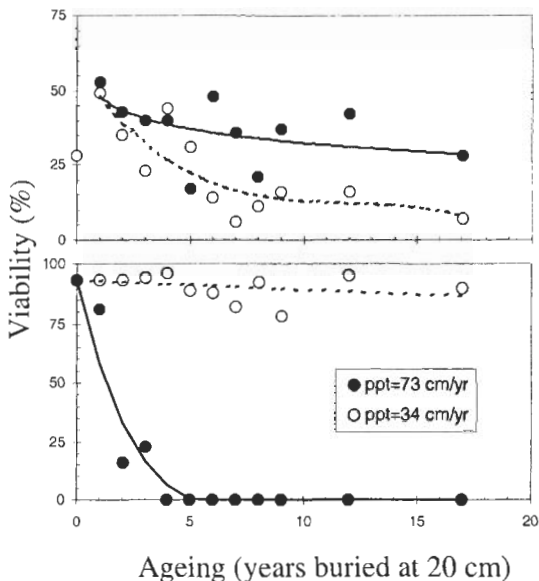


Fig. 3. Loss of seed viability through probable seed ageing of *Chenopodium album* (top) and *Datura stramonium* (bottom) during 17 years of soil burial at two sites with contrasting annual precipitation (ppt) regimes. Grey value for *C. album* at 0 years indicates that the initial seed lot was partially dormant, with 28% germination. Drawn from tabular data in Burnside *et al.* (1996).

Germination of deeply buried seeds is not a common occurrence in *Datura stramonium*. Benvenuti (2003) suspected that seeds of this species somehow sense the gaseous soil environment and regulate germination so that deeply buried seeds never germinate. Experimental irrigation of soil and deeply buried seeds with oxygen-rich air allowed germination to proceed. Deep germination also appeared to be uncommon for a group of 20 weed species (Benvenuti *et al.*, 2001), although these species were not investigated as thoroughly as was *D. stramonium*. A substantial investigative burden will have been removed from the shoulders of weed seedbank biologists if results for *D. stramonium* can be extrapolated to other species.

General germination

Seeds of some species have little persistence, and their entire seedbank is lost and must be replenished through seed production each year. Weeds species that lack persistent seedbanks are not rare, but they also are not typical, and they will not be discussed here. For species with persistent seedbanks, there are numerous examples in the literature of seedbank losses through germination. Indeed, there are so many examples that reviewing them is a daunting task. Consequently, what follows is a recent example, not yet published, of seed losses for three common summer-annual weed species as influenced by tillage system, burial depth and season. The results serve to cover the range of information on losses due to germination reported in the literature.

Summer-growing crops, such as maize, typically are subjected to pressure from summer-growing weeds. In the major maize-growing region of North America, which is known as the "Corn Belt," three important weed species are *Chenopodium album*, *Setaria, faberi* Herrm. and *Abutilon theophrasti*. Extensive literature exists regarding the biology of these species. On average, the percentage of the seedbank of these species that is lost through germination and seedling emergence each year is about 3, 31 and 28%, respectively (Forcella *et al.*, 1997). However, total annual losses are not known well. For this reason, a group of weed scientists, known as the NC-202 Regional Research Committee, initiated a network of experiments throughout the Corn Belt in 2001 to document total seedbank losses of the three species mentioned above. Preliminary results from one of these experiments, located in Morris, Minnesota (USA), are reported here.

Freshly harvested seeds (100 of each species) were placed in mesh bags and buried at three depths (0, 2 and 10 cm) in each of three long-term (> 20 years) tillage treatments (NT, no-till; FC, fall chisel = autumn tine plough; MP, autumn mouldboard plough). Two periods of time were examined: "over winter" (autumn to spring) and "over summer" (spring to autumn). Burial and retrieval times corresponded to dates of maize planting in spring and harvesting in autumn. Upon retrieval in spring, seeds were categorized as "germinated" (visible shoot or root), "survived" (firm and not germinated) or "dead" (soft and not germinated). In contrast, seeds were categorized only as "survived" and "dead," for seeds retrieved in autumn, as evidence of "germinated" seed had disappeared by that time. Percentage data were transformed ($[(x+1)^{0.5}]$) prior to statistical analyses and back-transformed for presentation of results.

Total seed loss over winter averaged 34, 20 and 22% for *C. album*, *S. faberi* and *A. theophrasti*, respectively (Fig. 4). These over-winter losses were comprised of seed death (12, 8 and 16%, respectively, for the same three species) and seed germination (22, 12 and 6%, respectively). A previously reported over-winter value for seed death of both *C. album* and *Setaria* spp. was 8% (Forcella, 1992). In contrast, over-summer total seed losses for *C. album*, *S. faberi* and *A. theophrasti* averaged 50, 91 and 33% for the same species (Fig. 4). The most striking contrast between over-winter and over-summer results is that for the grass, *S. faberi*. The very high over-summer losses are assumed to be from germination.

Effects of tillage and depth on seed death were not significant ($P > 0.05$) over winter. Loss through germination was affected by burial depth in all species, and by tillage in all but *C. album*. FC and MP tended to promote germination of *S. faberi* and *A. theophrasti*, especially when seeds were buried at 2 cm. Tillage significantly affected total losses over summer in all species ($P < 0.05$), and burial depth influenced losses in *C. album* and *S. faberi*, but not *A. theophrasti*. Generally, over-summer losses were lowest in NT.

Tillage had a similar effect on over-winter seed loss as burial depth. When averaged across burial depths, NT, FC and MP allowed 12, 26, 22%, respectively, over-winter seed loss of *S. faberi*, with the value for NT being smaller ($P < 0.05$) than those for FC and MP. These differences were about the same as those associated with burial depth: 8, 38 and 14% for 0, 2 and 10 cm, respectively for *S. faberi*. These results indicate that tillage exerts its effect on seed loss through seed burial and through the modification of soil structure and soil-seed contact. Indeed, the highest over-winter loss (55%) of *S. faberi* occurred in seeds placed at 2 cm depth in FC. Lowest over-winter loss of *S. faberi* seeds was in MP at 0 cm depth, probably because the seeds remained cold and dry in this treatment, and soil (residue)-seed contact was nil. Over-summer seed loss of *S. faberi* followed the same trend as with over-winter loss, but with dramatically higher values. The highest over-summer losses were about 98% at 2 cm depth in all tillage systems and in FC at 0 cm depth, and the lowest values were 83% in MP and 67% in NT, both at 0 cm burial depth. Lack of burial clearly prevented loss in MP and NT, probably because seeds were exposed to drier conditions than were buried seeds.

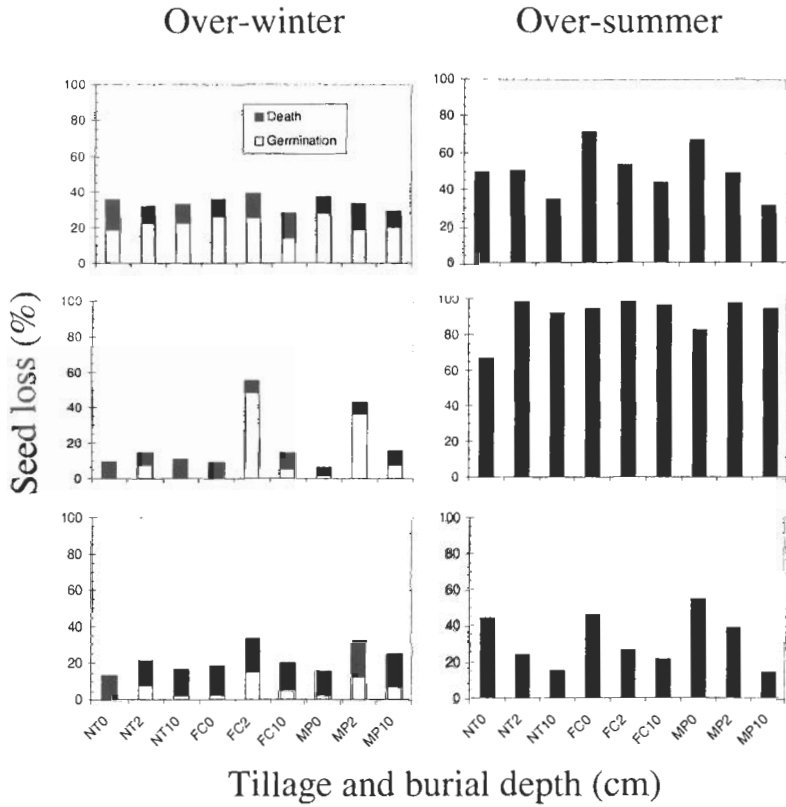


Fig. 4. Loss (death plus germination) of seeds of *Chenopodium album* (top), *Setaria faberi* (middle) and *Abutilon theophrasti* (bottom) in three tillage systems (NT, no-till; FC, fall chisel = tine ploughing in autumn; MP, mouldboard plough in autumn), three burial depths (0, 2 and 10 cm) and during two time periods: (winter) from seed shed in autumn 2001 to maize planting in spring 2002, and (summer) from maize planting in spring 2002 to maize harvest in autumn 2002.

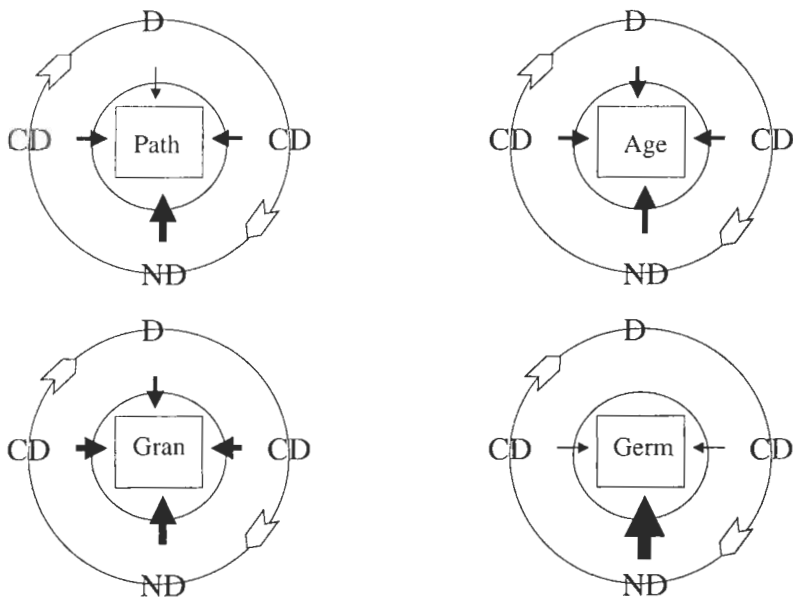


Fig. 5. Comparison of the relative effects (size of arrows) of seed pathogens (Path), granivores (Gran), ageing (Age), and germination (Germ) on losses from seedbanks at different times of the annual dormancy cycle (D, dormancy; CD, conditional dormancy; and ND, non-dormancy). The general cycle was adapted from Baskin & Baskin (1998).

Over-winter seed loss of *C. album* averaged 34%, was not affected by tillage system and was only slightly influenced ($P < 0.05$) by burial depth (from 36% at 0 cm to 30% at 10 cm). Over-summer loss averaged 50%, and it changed across tillage system and burial depth. Loss was greatest (67-71%) in MP and FC at 0 cm depth and least (31-35%) in MP and NT at 10 cm ($P < 0.05$). Over-summer loss of *C. album* was consistently less than that for *S. faberi*.

Despite the small range of values across tillage systems for over-winter seed losses of *A. theophrasti*, loss was less in NT than other systems ($P < 0.05$). Differences in over-winter losses also occurred with burial depth. Seeds buried at 2 cm had the highest loss ($P < 0.05$). High seed loss at 2 cm primarily was due to seed germination at the time of sampling in late April. With regard to over-summer losses, tillage had only a marginal effect ($P = 0.06$), but burial at 2 or 10 cm facilitated losses compared to surface seeds ($P < 0.05$). Highest over-summer loss was 55% at 0 cm in MP and lowest loss was 15% at 10 cm in NT.

As with many other studies of seed fate, the preliminary results from the NC-202 experiment show that deep seed burial tends to enhance persistence of seeds and that shallow burial tends to promote germination. Such seed fates, however, are conditioned somewhat by seed size and genetic affinity. Over summer, when the greatest seed losses occurred, the two broadleaf weeds responded monotonically to burial depth; that is, greater losses occurred with shallower burial, and fewer of the larger-seeded *A. theophrasti* were lost than the smaller-seeded *C. album*. For the grass weed, *S. faberi*, germination apparently was so much greater at 2 cm depth (cf. Mester & Buhler, 1991), that seed loss was consistently greater at this depth than when seeds were buried deeper or were on the soil surface.

The main effect of tillage on seedbanks in realistic field settings is seed burial (Grundy & Mead, 1998), as burial depth largely governs seed losses. However, tillage also creates soil environments that influence seedbank losses apart from burial. The high over-winter losses in FC and MP, but not NT, of *S. faberi* seeds buried at 2 cm, illustrate this point (Fig. 4). The specific factors of the soil environment that affect differential tillage-induced losses are not known with certainty and would entail useful future research projects.

Discussion

Losses from seedbanks obviously play important roles in seedbank dynamics. Curiously, however, quantification of seedbank losses are not well documented, except those occurring through seed germination or suspected of occurring through germination. Understandably, other forms of loss have not been investigated nearly as intensely as that for germination. However, the sparse literature that exists on these losses suggests that their magnitudes can be substantial at times. Fig. 5 crudely depicts the relative magnitudes of seedbank losses due to four causes: pathogens, granivores, ageing and germination; emigration is excluded because of too much uncertainty as to its importance. The magnitudes in Fig. 5 are based upon assessments of recent literature used to develop this report. By far, germination represents the major contributor to seedbank losses, but losses due to germination occur only during a relatively brief period of the year when seeds are non-dormant. Granivores can consume seeds all year, but seem to prefer soft rather than hard seeds. Pathogens affect seeds at all times, but much less when seeds are hardseeded than imbibed. Very little is known about seed ageing in natural seedbanks, but one might suspect that ageing is faster for soft seeds than for hard seeds.

The recurring dominance of germination as the primary means of seedbank losses reinforces the need to direct research efforts at this topic. This does not diminish the value of research on other aspects of seedbank losses, but merely helps place the importance of these topics in perspective.

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