

CHAPTER 10

Impacts of Seed Banks on Grassland Community Structure and Population Dynamics

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I. Introduction

At first glance, the structure of most grassland communities appears dominated by a single type of plant morphology. The more careful observer comes to know the diversity of structure and life history that exists within the grasses. In addition, closer inspection reveals a large number of dicot species that are quite diverse in morphology, phenology, and ecology. Very few people, however, come to appreciate the complexity hidden in the soil beneath a grassland community.

The seed banks in grasslands have generated a long-standing interest in basic and applied ecology. The economic necessities of understanding the potential of a seed bank to alter grassland composition and productivity have motivated researchers to compare the composition of the surface vegetation to seed reserves hidden in the soil. In this review, several questions motivated my examination of differences and similarities between above- and belowground composition. For example, if differences exist between the composition of the seed bank and the vegetation, what factors affect the magnitude of this difference? Are rates of disturbance important? Do dominant species within the vegetation play a large part in causing differences between above- and belowground flora? Are differences in seed bank composition among grasslands determined by the relative abundance of certain groups of species with long-lived seed banks?

I also consider the implications of seed banks for the population dynamics of grassland species. Survival in belowground seed populations is poorly understood. What might be the potential impact of granivory, microenvironment, and genetic variation on seed bank decay patterns? How might germination cueing in response to environmental heterogeneity affect the spatial distribution of seed banks? How much do we know about the effects of seed aging on the relative vigor of seedlings emerging from differently aged seed cohorts?

Finally, some modeling results on the population dynamics of annual plants with a seed bank are presented to illustrate demographic implications of seed bank age structure. Specifically, how might qualitative variation in seed carry-over and reproductive patterns among seed bank cohorts affect the dynamics of age structure in a seed bank?

II. Seed Banks and Community Structure in Grasslands

A. Aboveground versus Belowground Botanical Composition

Species composition in the grassland seed bank flora and the aboveground plant community is strikingly dissimilar (Chippendale and

Milton, 1934; Champness and Morris, 1948; Douglas, 1965; Major and Pyott, 1966; Johnston *et al.*, 1969; Roberts, 1972b; Hayashi and Numata, 1975). The implications of this difference in species composition depend on the research objectives and orientation of a particular study. Discrepancies between above- and belowground composition can make the description of a grassland flora for a particular locale extremely difficult (Major and Pyott, 1966), because a complete description of the plant community should include the seed bank. The relative accuracy of seed bank estimates depends on a number of factors, such as the number of samples, the density and distribution patterns of the species within the vegetation, and the season during which samples are taken (Major and Pyott, 1966). For example, the correspondence between the above- and belowground flora in a sagebrush grassland depended on the season of sample collection, whether the sample was collected under shrub canopy, whether the sample site had been recently burned, and, if recently burned, the relative intensity of the fire (Hassan and West, 1986). In applied ecological studies, differences between above- and belowground populations of a desirable forage species can indicate potential management problems. Douglas (1965) found that an important pasture grass, *Lolium perenne*, was not present in the seed bank despite its vegetative dominance in the standing vegetation. He suggested that any attempts to use aboveground composition to assess the success of sward renewal by cultivation or herbicide application would be grossly inaccurate because the seed bank was dominated by indigenous grasses and weeds.

In British perennial grasslands, Brenchley (1918) noted that only in permanent grassland was there a good correlation between seed in the soil and aboveground vegetation. Differences in composition between the seed bank and the standing vegetation were caused by arable weed species and generally decreased with age of the pasture or grassland. In moderately aged pastures (60 yr old), seed banks of arable weeds, although still present, are smaller than in pastures recently (10 yr old) released from cultivation (Brenchley, 1918; Chippendale and Milton, 1934; Douglas, 1965).

The degree of divergence between the species composition of the seed bank and the vegetation may vary among grassland types. This may depend on the size of the seed bank formed by the dominant taxa. Canopy dominants, such as *Lolium perenne* or *Dactylis glomerata*, often are poorly represented within the seed bank, while other indigenous grasses, such as *Agrostis* spp. and *Poa* spp., form substantial seed reserves (Chippendale and Milton, 1934; Champness and Morris, 1948; Douglas, 1965; Jalilo, 1975). In Japan, the vegetation of meadows dominated by *Miscanthus sinensis* or *Arundinella hirta* is poorly correlated with seed bank composition, while in meadows dominated by *Zoysia japonica* there is a general correspondence (Hayashi and Numata, 1975). In Great Britain, upland pastures dominated by *Agrostis tenuis* exhibit closer cor-

relation between seed bank composition and surface vegetation than do lowland sites (Champness and Morris, 1948).

B. Seed Bank Longevity in Annuals versus Perennials

In grasslands, annuals are more likely than perennials to produce a seed bank. In a bunchgrass community in California, Major and Pyott (1966) found that the relative contribution of annuals and perennials to the seed bank was substantially different. Seed banks for the perennial grasses (primarily *Stipa* spp.) were absent (Fig. 1). In contrast, annual grasses had well-developed seed banks despite their relatively minor contribution ($< 10\%$) to total cover. A survey of a variety of grazed lands in Great Britain indicated that species with a large contribution to surface vegetation cover and a small contribution to the seed bank were almost exclusively perennials (Champness and Morris, 1948). A similar survey of grasslands and meadows in Japan suggests that annuals and biennials consistently formed more extensive seed banks than did perennials (Hayashi and Numata, 1975).

Obviously, the sharpness of this distinction between perennials and annuals may depend on the relative allocation of the perennials to seed production. As noted above, dominant grasses, such as *Lolium perenne*, that reproduce primarily by vegetative means are almost completely absent from the seed bank (Chippendale and Milton, 1934; Champness and Morris, 1948; Douglas, 1965; Jaliloq, 1975). In contrast, well-developed seed reserves are found for perennial grasses that reproduce pri-

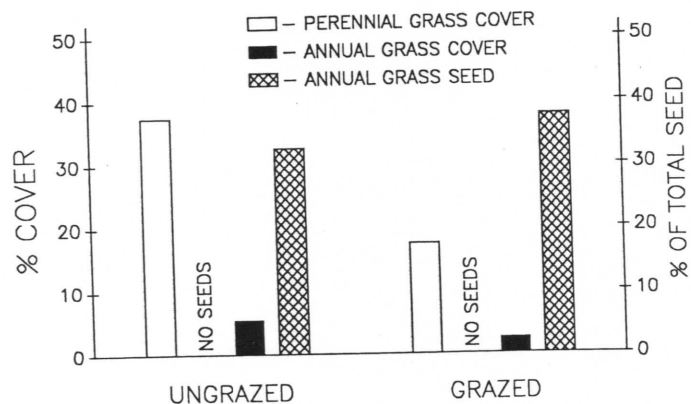


Figure 1. Differences between vegetative cover and seed bank composition for perennial and annual grass species in a California perennial bunchgrass (*Stipa* spp.) community (data from Major and Pyott, 1966).

marily by seed, such as *Zoysia japonica*, *Poa trivialis*, *Poa pratensis*, and *Agrostis* spp. (Chippendale and Milton, 1934; Champness and Morris, 1948; Hayashi and Numata, 1975).

C. Seed Bank Longevity in Grasses versus Forbs

As a group, forbs (i.e., any herbaceous dicot that is not a legume) seem more likely to form seed banks than do grass species. In a broad survey of seed banks, Roberts (1981) examined the relative contributions of different plant groups to the seed banks of several grassland communities. Averages taken across 13 different communities indicated that grasses contributed approximately 30% of the total viable seeds, while forbs dominated, contributing 50%. In a description of the persistent seed bank of a Californian annual grassland, Young *et al.* (1981) estimated rates of seed carry-over from one year to the next for annual grasses, annual forbs, and annual legumes (Fig. 2). Within the annual flora, carry-over rates were low, but data over the 5 yr of the study indicated that annual forbs produced a more persistent seed bank than did annual grasses. The increased carry-over (percentage) for all three types of annuals in the final year of the study suggests that seed bank persistence may vary over time. Among colonizing species that invade molehills in British perennial grasslands (Fig. 3), the weedy forbs have more extensive seed banks than do the weedy grasses or rushes and sedges (Jalloq, 1975). Champness and Morris (1948) also commented on the dominance of seed banks by forbs that often were rare in the surface vegetation. In contrast, Chippendale and Milton (1934) found that in certain types of

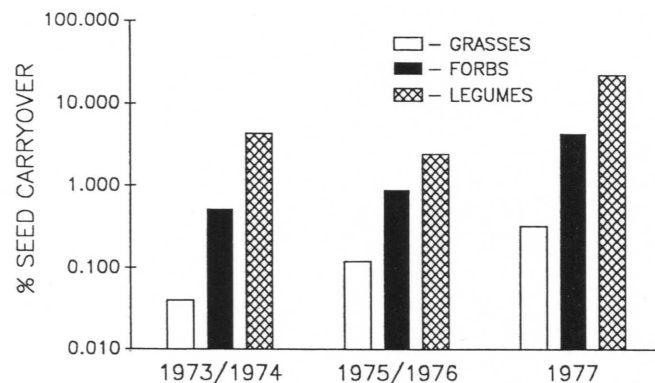


Figure 2. Seed carry-over for different annual species groups within a California annual grassland (note log scale). Numbers of germinable seed from soil samples taken after autumn germination were used to estimate potential rates of seed carry-over (data from Young *et al.*, 1981).

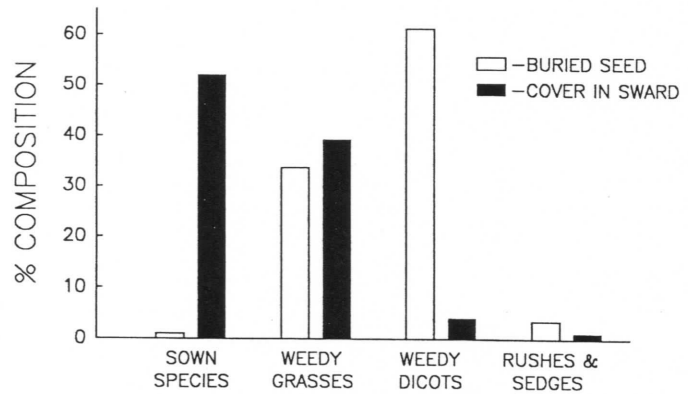


Figure 3. Comparison of the vegetative cover of sown and indigenous grassland species in undisturbed sward and the seed bank composition of these species in soil disturbances (molehills) (data from Jalloq, 1975).

grasslands the germinable seed banks of many forbs were low relative to seed pools of the dominant grasses (*Poa annua*, *Poa trivialis*, *Holcus lanatus*, and *Agrostis* spp.). The reliance of these particular grass species on reproduction by seed may explain this reversal in numerical dominance.

D. Legumes in Seed Banks

Seed coat impermeability to water (hard seed) is a form of seed dormancy (see Baskin and Baskin, Chapter 4, this volume) widespread in legumes (Rolston, 1978) and is a major factor in promoting the formation of legume seed banks (Quinlivan, 1968). In California annual grasslands, carry-over rates in annual legumes (Fig. 2) are an order of magnitude greater than in the other dicots and two orders of magnitude greater than in annual grasses (Young *et al.*, 1981). Legume genera, such as *Lotus*, *Trifolium*, and *Medicago*, had consistently higher seed populations than would be expected from their occurrence in British grassland vegetation, and no legume species were present among those that had a disproportionately low contribution to the seed bank (Champness and Morris, 1948).

Seed longevity may explain, in part, the abundance of legumes in grassland seed banks. Hull (1973) compared the germination rates for a number of North American rangeland species that had been stored in unheated sheds for 14 to 41 yr. Seeds of legumes retained their viability longer and had higher rates of germination than did most of the grass and forb species tested, regardless of storage time. A study by Lewis (1973) on the effects of soil type and burial depth on the viability of seeds

enclosed in mesh bags indicated that only a few weed species had higher longevity than legumes. At least some seeds of most legumes persisted the length of the experiment (20 yr). Longevity of legume seed was slightly higher in loam soil than in acid peat and also increased with burial depth.

Differences among legumes in seed bank longevity can often be related to variation in seed dormancy. High persistence of *Lotononis bainesii* and *Trifolium repens* in subtropical pastures corresponded with high percentages of hard seed, 97% and 70%, respectively (Jones and Evans, 1977). In contrast, *Desmodium intortum* had a low percentage of hard seed, 9%, and was absent from heavily grazed areas where replenishment of seed reserves by seed production was severely reduced. Differences in seed bank longevity caused by differences in hard seed percentages may also exist among cultivars of a single legume species. The potential management implications of such differences are illustrated by an Australian study of *Trifolium subterraneum* cultivars (Beale, 1974). The Yarloop cultivar of *Trifolium subterraneum* was the primary cultivar in seed mixtures from 1957 to 1963 because it was a superior forage. After the Yarloop cultivar was found to induce infertility in sheep and to be susceptible to clover scorch (*Kabatiella caulivora*), many pastures were ripped up and replanted to other cultivars. Although many of these replanted pastures showed successful establishment of the new cultivars in the year of resowing, a reversion to the Yarloop cultivar often occurred in the following year. Beale (1974) demonstrated that this reversion was caused by regeneration from persistent seed reserves in the soil and that these well-developed seed banks would make conversion to the new cultivars extremely difficult.

E. Weedy Species in Seed Banks

Weedy or fugitive species, those that establish principally after disturbance, are among the largest component of grassland seed banks. As noted above, a large portion of the resident seed bank in a grassland may be arable weeds persistent from previous periods of cultivation (Brenchley, 1918; Chippendale and Milton, 1934; Champness and Morris, 1948; Douglas, 1965). In addition to arable weeds, native weedy species in grasslands also are characterized by large seed banks. For example, badger mounds in native tallgrass prairie create gaps in the vegetation that are colonized frequently by *Oenothera biennis* (Platt, 1975). Seeds of this species can remain viable in the soil for 80–100 yr (Kivilaan and Bandurski, 1973). Another prairie species, *Sporobolus cryptandrus*, can create extensive seed reserves in the soil (up to 20,000 seeds m^{-2}) following invasion after disturbance (Lippert and Hopkins, 1950). A series of defoliation experiments conducted in permanent grassland in

Great Britain demonstrated that seedling establishment of the grassland daisy, *Bellis perennis*, is enhanced significantly if the resident vegetation is disturbed by clipping or herbicide treatments (Foster, 1964, cited in Harper, 1977). Large and persistent seed bank populations of *Bellis perennis* (Chippendale and Milton, 1934; Champness and Morris, 1948), *Oenothera biennis*, and *Sporobolus cryptandrus* illustrate a temporal disperser colonization strategy. However, studies on the population dynamics of three *Ranunculus* species indicate that there is not always a consistent correlation between seed bank persistence and the ability to colonize soil disturbances or vegetation gaps (Sarukhán, 1974; Sarukhán and Gadgil, 1974). Demographic and mathematical analyses suggest that *Ranunculus repens* inhabits relatively stable environments with little variation in population growth rates in space and time, in contrast to *Ranunculus bulbosa*. However, seed bank longevity for the fugitive species, *Ranunculus bulbosa*, is much shorter than for *Ranunculus repens*, the species found growing in less disturbed habitats.

Seeds of fugitive species are able to use various environmental cues, such as temperature and light quality, to detect gaps in the vegetation (Wesson and Wareing, 1967; Grime and Jarvis, 1975; Thompson *et al.*, 1977; Fenner, 1978; Silvertown, 1980a; Rice, 1985). Because of the sensitivity and specificity of germination cueing behavior, many of the traditional techniques for estimating seed reserves may be inaccurate. An example is provided by an annual forb, *Erodium botrys* (Rice, 1985, 1986). Germination tests of soil cores collected in early autumn before field germination indicated that large numbers of germinable seeds were present (Fig. 4). Plant number in the spring roughly correlates with

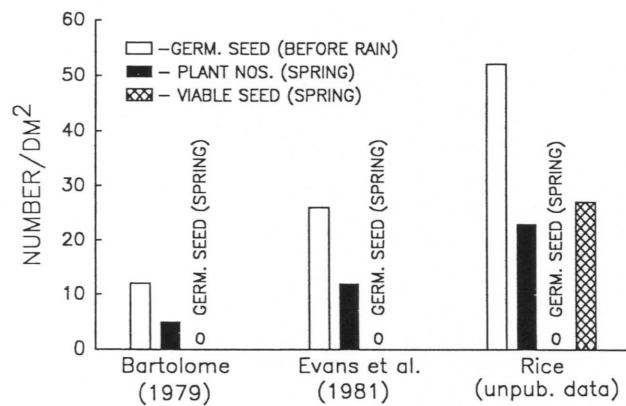


Figure 4. Seasonal variation in numbers of germinable seed of *Erodium botrys*. The presence of viable but not germinable seed in spring soil samples provides evidence for a persistent *Erodium* seed bank.

these estimates of germinable seed. In contrast to the autumn results, soil cores collected in the spring lacked germinable seed (Fig. 4), suggesting that there is little carry-over from one year to the next. However, when soil from cores collected in the spring was sieved, a large number of viable *Erodium botrys* seeds were recovered (Fig. 4) that germinated only when mechanically scarified (K. Rice, unpublished data). *Erodium* seed dormancy is caused by a seed coat impermeability to water and is broken by wide diurnal temperature fluctuations that exist only during the rainless summer months (Rice, 1985). Thus, the pool of germinable seeds increases through the summer until the cooler temperatures that begin with the onset of winter rains. Temperature fluctuations within a greenhouse during germination testing of soil cores are unlikely to break *Erodium* seed dormancy.

A summary of the composition of the seed banks of several grassland communities illustrates wide variation in both seed density and the number of species present in the seed pool (Table 1). Although much of this variation may be caused by the particular sampling protocol of a study (e.g., time of year sample was taken), some general trends are apparent. Although dominant in the vegetation, grasses are relatively underrepresented in the seed bank. On the other hand, dicots and grasslike plants (when present at all) are major contributors to seed pools in grasslands. Seed bank species diversity, as measured by number of species, also appears higher for dicots than in the grasses.

III. Seed Banks and Population Dynamics in Grasslands

A. Patterns of Seed Bank Depletion

Patterns of seed mortality in collections kept under air-dry storage (Harrington, 1972) indicate that the loss of viability during shelf storage follows a negative cumulative normal distribution. A depletion curve with this functional form suggests the importance of seed senescence where the probability of mortality depends on seed age. Roberts (1972b) suggests that such curves may result from the gradual accumulation of random cell deaths to some critical threshold after which the seed becomes inviable. In contrast, several studies on the depletion patterns of weed seeds in the soil (Roberts and Dawkins, 1967; Roberts and Feast, 1973a; Warnes and Andersen, 1984) suggest that the rate of seed bank depletion is constant, resulting in a negative exponential distribution for seed loss. This type of depletion pattern indicates that the probability of seed loss is independent of seed age. A constant depletion rate suggests that age-independent losses to germination, granivory, and disease are more important than losses caused by senescence.

Table 1
Contributions of different taxa to seed bank density (germinable seed)
and species diversity in several types of grassland communities

Location	Grassland type	Number of species per sample ^a				Total
		Grasses	Rushes and sedges	Legumes	Other dicots	
Kansas	Short-grass prairie	6	0	1	9	16
	Mixed grass prairie	10	0	1	10	21
	Mid-grass prairie	1	0	0	11	12
Missouri	Tall-grass prairie	7	2	0	15	24
Saskatchewan	Mid-grass prairie	1	6	1	7	15
Alberta	Fescue prairie	4+	0	0	4+	16+
	Mixed-grass prairie	4+	1+	0	2+	11+
California	<i>Stipa</i> grassland (ungrazed)	5	0	0	5	10
	(grazed)	6	0	3	8	17
California	Annual grassland Before autumn germination	7	0	4+	5+	16+
	After autumn ger- mination	3	0	3+	1+	7+
Wales	Acid grassland	9	2	0	7	18
Wales	<i>Molinia</i> grassland	6	6+	2	5	19+
	<i>Nardus</i> grasslands	4	5+	0	6	15+
	<i>Calluna</i> grassland	1+	6+	0	4	11+
	Marsh grassland	9+	10+	3	29	51+
Bohemia	Peat meadows (mean of 8 sites)	10+	2+	7	43	62+
Tasmania	<i>Poa gunnii</i> grassland	2	3	0	8	13
Japan	<i>Zoysia</i> grassland	2	4	1	9	19

^aSpecies numbers followed by a plus sign represent minimum estimates.

For many weedy grassland species the survivorship of seeds in storage is often a very poor predictor of potential longevity in the field. Seeds of *Ranunculus repens* and *Chenopodium album* were completely inviable after 20 yr of storage under granary conditions, but after 20 yr in mineral soil, viability estimates were 51 and 32%, respectively (Lewis, 1973). Conversely, viability remained high in granary collections of *Geranium dissectum* and *Geranium molle*, but longevity in buried populations of these species was less than 4 yr. Collections of *Bromus tectorum* stored for 10 yr showed virtually no loss of viability (Hull, 1973); however demographic studies in steppe communities indicated very little carry-over from one year to the next (Mack and Pyke, 1983).

Number of germinable seeds per m ²						Reference
Grasses	Rushes and sedges	Legumes	Other dicots	Unknown	Total	
377	0	4	380	0	761	Lippert and Hopkins (1950)
122	0	11	273	0	406	
7	0	0	280	0	287	
492	3026	0	1488	1362	6368	Rabinowitz (1981)
2697	0	0	5533	0	8230	Major and Pyott (1966)
4743	0	326	7208	0	12,227	
18,050	0	6350	3000	0	27,400	Young <i>et al.</i> (1981)
700	0	900	100	0	1700	Archibold (1981)
207	445	64	675	0	1391	
1303	0	0	1752	0	3055	Johnston <i>et al.</i> (1969)
566	0	0	474	0	1040	
5570	85	0	3458	72	9185	King (1976)
484	1184	32	9612	0	11,312	Chippendale and Milton (1934)
430	9020	0	5737	0	15,187	
43	1421	0	8396	0	9860	
3143	20,387	2260	5554	0	31,344	Mika (1978)
1102	408	172	1585	0	3267	
351	781	0	1072	0	2204	Howard (1974)
9770	4460	10	9160	30	23,430	Hayashi and Numata (1975)

B. Effects of Germination Cueing on Seed Bank Depletion

Although depletion rates in weed seed populations may remain constant for a particular environment, seed bank depletion rates are sensitive to the frequency of soil disturbance (Roberts and Feast, 1973a). This suggests that the ability of many grassland species to germinate in response to soil disturbance or gap formation may result in a coupling between rates of seed bank depletion and spatial variation in germination cues such as temperature and light.

In certain grassland species, germination depends on variation in light quantity and quality. Wesson and Wareing (1967) contributed

much of the earlier information on light-promoted germination and the induction of a light requirement by seed aging. Later studies by Grime and Jarvis (1975) support the generalization that many grasses do not require light for germination. In contrast, germination of many forb species is significantly reduced in the dark or under light filtered by plant canopy. This response is especially pronounced in species that colonize bare ground and emphasizes the importance of light quality as a germination cue in plants that require vegetation gaps for successful establishment. Silvertown (1980a) found that 17 of the 25 grassland dicot species he tested had significantly lower germination under light filtered by a leaf canopy than in the dark.

In a survey of 112 native herbaceous species, Thompson *et al.* (1977) found that germination of grassland species with persistent seed banks was often sensitive to temperature fluctuations in darkness. They speculated that such sensitivity allows buried seeds to detect canopy gaps. Rice (1985) reported that variation in diurnal temperature range for three types of microsites in annual grassland (under grass litter, bare soil, and buried under gopher mounds) significantly affected rates of dormancy release in *Erodium botrys*. Microsite variation in germination cues might have a strong influence on seed bank depletion by affecting the loss rate due to germination. Using data from Rice (1985) and assuming a constant depletion rate for each type of microsite, one would predict much more persistent *Erodium* seed banks under gopher mounds than in bare soil areas (Fig. 5). Thus, a large amount of spatial heterogeneity in physical parameters, such as temperature and light, may create a parallel amount of spatial variation in the longevity of a species' seed bank.

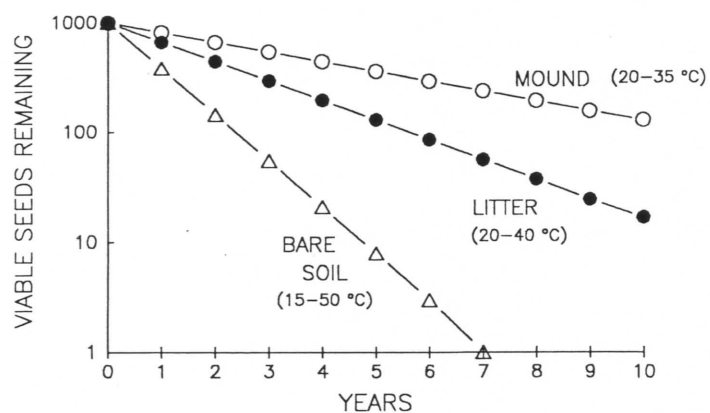


Figure 5. Predicted effects of varying microsite temperature regimes on seed bank longevity in *Erodium botrys* within California annual grasslands (note log scale) (data from Rice, 1985).

C. Impacts of Granivory on Seed Banks

Beginning with the work of Chippendale and Milton (1934), there has been much speculation on the importance of granivory in the spatial and temporal dynamics of grassland seed banks. Unfortunately, the general difficulty in identifying sources of seed mortality has forced much of the discussion to remain highly speculative. A notable exception is provided by a study of small mammal grazing on the seed banks of *Avena fatua* and *Avena barbata* in California annual grasslands (Marshall and Jain, 1970). Rates of loss to predation were highly variable. At one site there were no detectable losses, but at another site 65% of the seed reserve was consumed. Variation was such that at one site the degree of predation was independent of species while at another rates of seed loss were higher for *Avena barbata* than for *Avena fatua*.

The potential effects of earthworm foraging on grassland seed banks was explored by examining the selectivity of earthworms (*Lumbricus terrestris*) and the viability of seeds recovered from earthworm casts (McRill and Sagar, 1973). Ingestion rates and the percentage of ingested seeds recovered from casts varied widely among plant species. For example, earthworms ingested 60% of the *Poa annua* seed offered but only 3% of *Lolium perenne*. In addition, the recovery rate of seeds from earthworm casts was lower for *Poa annua* (28%) than for *Lolium perenne* (67%). Even among species preferred by the earthworms, large differences occurred in the survival of ingested seeds. *Agrostis tenuis* was the second most preferred species (50% of offered seeds ingested), and no seeds of this species were ever recovered from worm casts. Additional germination trials in this study suggested that earthworms also may deplete seed banks by increasing germination rates. Germination rates of *Poa trivialis*, *Bellis perennis*, and *Trifolium repens* increased significantly after passage through the earthworm gut.

Taken together, these studies suggest the potential importance of vertebrate and invertebrate consumers on the longevity of seed banks and the spatial distribution of seed reserves. There is a critical shortage of field studies that examine selective seed predation, differences among microhabitats in probability of predation, and seasonal or annual variation in predation pressure.

D. Genetic Variation in Seed Bank Depletion Rates

Few studies have focused on the genetic basis of variation in seed bank longevity as it relates to seed dormancy. Interpopulational variation for seed dormancy within a species is often substantial. For several annual grassland species, Jain (1982) detected significant intraspecific differ-

ences in seed dormancy among populations located along a rainfall gradient in California. In addition, heritability estimates suggested significant within-population variability for *Trifolium hirtum* seed dormancy. Sexsmith (1967) reported significant differences in degree of seed dormancy both among and within varieties of *Avena fatua*, and phenotypic expression of these genetic differences was affected by the physical environment during seed maturation. Seed dormancy variation in *Taeniatherum caput-medusae* results from an interaction of environmental conditions during seed maturation and genetic differences between populations (Nelson and Wilson, 1969). Varietal differences in seed dormancy also is well documented for several annual grassland legumes (Cameron, 1967; Quinlivan, 1966, 1968). Quinlivan (1968) found that for *Trifolium subterraneum*, an interaction of variety and temperature determined the rate at which the seed coat became permeable. Data from germination trials conducted under one daily temperature fluctuation regime (15–40°C) illustrate how varietal variation in seed dormancy could affect seed bank depletion rates (Fig. 6). Assuming that losses from the seed bank result only from germination of permeable seeds and that the rate of such losses remains constant, there are large potential differences in seed bank longevity among the four cultivars (Fig. 6). In addition, genotype and environment interactions also are suggested because changes in diurnal temperature regimes had differential effects on loss of dormancy. Though limited in number, these studies suggest that patterns of seed bank depletion in many grassland species may result from a complex interplay of genetics and spatial variation in the seed microenvironment.

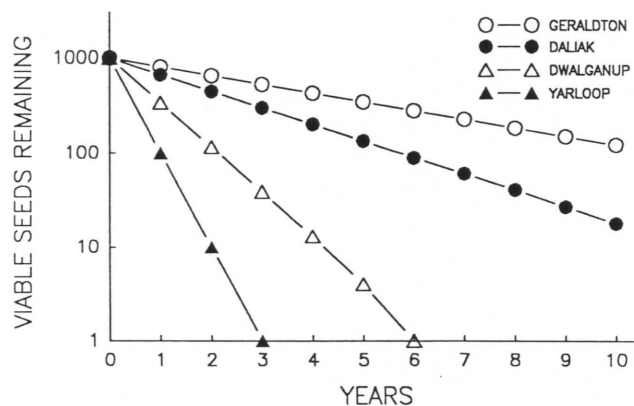


Figure 6. Predicted effects of varietal variation in seed dormancy on *Trifolium subterraneum* seed bank longevity (note log scale) (data from Quinlivan, 1968).

E. Variation in Vigor among Seed Bank Cohorts

Only a handful of studies provide any data on the effects of seed age on postgermination plant growth, development, and reproduction. How germination rate or the growth rate of emergent seedlings may vary with respect to seed age are questions that are not considered. Seeds of grasses, legumes, and weedy species that survived 20 yr of burial in undisturbed soil produced plants that were apparently normal in development and reproduction (Lewis, 1973). Hull (1973), however, found that, in addition to differences between species, speed of germination within each species is affected significantly by seed age. Seedlings emerged more rapidly from younger seeds than from older ones. Villiers (1973) speculated that such delays in emergence may be caused by the necessity, upon hydration, for repair of membrane damage accumulated during dormancy before further cell elongation and development can occur. Given that even small delays in emergence can result in a significant competitive disadvantage in dense populations (Black and Wilkinson, 1963), the demographic consequences of delayed emergence in older seed bank cohorts deserve further study.

IV. Annuals with Seed Banks: Modeling the Implications of Age Structure

Carry-over of seed in an annual plant population between years has highly significant demographic consequences. Seed carry-over in persistent seed banks results in overlapping generations and creates age structure within the seed bank cohorts. The population dynamics of annuals with a seed bank were modeled by Schmidt and Lawlor (1983) using a matrix projection technique developed by Leslie (1945). They studied the sensitivity of the finite rate of increase (dominant positive eigenvalue of the matrix) to variation in life history parameters. The finite rate of increase represents the rate of exponential growth when the population reaches a stable age distribution. They found the finite rate of increase to be more sensitive to plant survival and fecundity than to germination fraction. Their analysis also demonstrates the formal equivalence of a seed bank annual matrix to the matrix form developed by Leslie (1945) for an iteroparous organism. By focusing on the response of the finite rate of increase, the analysis of Schmidt and Lawlor (1983) is based upon what is known as the limiting behavior of the population (i.e., the population growth rate attained in the limit as time increases and a stable age distribution is realized).

Another approach to the dynamics of age-structured populations is to examine the transient dynamics of the population that occur before

the population reaches a stable age distribution. This form of analysis is especially appropriate for colonizing plant (Caswell and Werner, 1978) or insect (Taylor, 1979) species because changes in environmental conditions often prevent such populations from ever reaching a stable age distribution. Using the number of generations required to reach a stable age distribution as an index, one can examine how changes in life history parameters influence transient population dynamics (Taylor, 1979). Increased time required to reach a stable age distribution reflects a tendency within a population for more prolonged oscillations in age structure before reaching a stable age distribution (Lefkovich, 1971).

To examine how changes in seed bank life history parameters might influence oscillations in seed age structure, I used a form of the matrix model developed by Schmidt and Lawlor (1983) that contained five different seed age classes. Probabilities of germination, seedling survival, and reproductive output for a particular seed age class were varied. This allowed examination of the effects of qualitative changes in reproductive patterns on transient behavior in seed age structure. Seed carry-over patterns were also varied to explore their impact on transient behavior. Using the number of generations required to reach a stable age distribution as an index of oscillatory behavior, the interaction of seed carry-over and delays in reproduction on transient dynamics of seed bank age structure can be studied. Four types of reproductive patterns were examined (Fig. 7): (1) no delay (constant)—no delay in constant reproduction (i.e., true annual pattern) such that newborn seeds (age class 0) survive after germination to reproduce at rates comparable to other seed age classes, and rates of reproduction are constant among all seed age

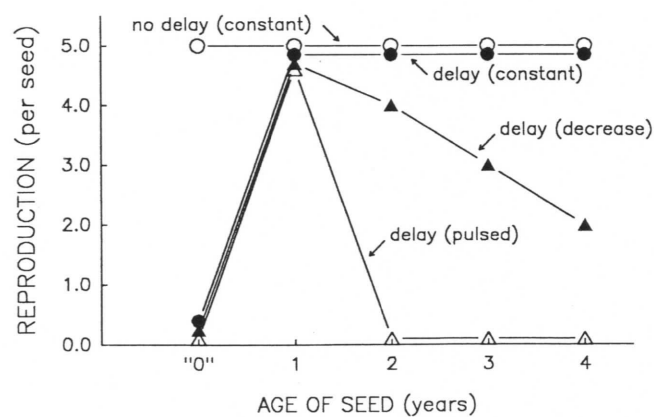


Figure 7. Reproductive patterns for seed age cohorts used in the matrix model of the transient dynamics of age structure. The 0 age class represents newborn seed. (See text for details.)

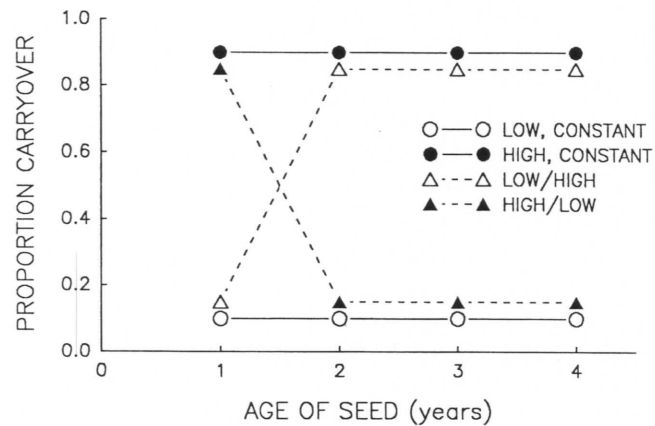


Figure 8. Patterns of seed carry-over used in the matrix model of the transient dynamics of age structure. (See text for details.)

classes; (2) delay (constant)—1-yr delay where seedling survival and reproduction in newborn seed is relatively lower than in other age classes, but reproduction is constant beginning with 1-yr-old seed; (3) delay (pulsed)—1-yr delay that is similar to (2) but where reproduction is concentrated in the 1-yr-old age class; and (4) delay (decrease)—1-yr delay that is also similar to (2) but where reproduction after the 1-yr-old age class gradually decreases. There were also four types of carry-over patterns examined (Fig. 8): (1) low and constant rates of seed carry-over; (2) high and constant rates of seed carry-over; (3) low rate of carry-over in the first year followed by high rates in succeeding years; and (4) a high rate of carry-over in the first year followed by low rates in older age classes. These particular patterns of reproduction and seed carry-over were chosen more for their qualitative differences in configuration than for any direct application to a particular species. Although the interaction of carry-over and reproductive patterns during convergence to a stable age distribution are complex (Fig. 9), certain general patterns emerge. Delays in reproduction, caused by either reduced reproduction in newborn seed or by high carry-over rates to later age classes, dramatically increase the time required to attain a stable age distribution. Given some delay in reproduction, oscillatory dynamics also are promoted by concentrating reproduction on a single seed age class. This effect is demonstrated by increased time to a stable age distribution in the pulsed reproductive pattern and in the high/low carry-over pattern where most germination occurs in the 1-yr-old seed age class. These results are similar to the those reported by Taylor (1979) in models of insect populations. He found that rates of convergence to a stable age distribution

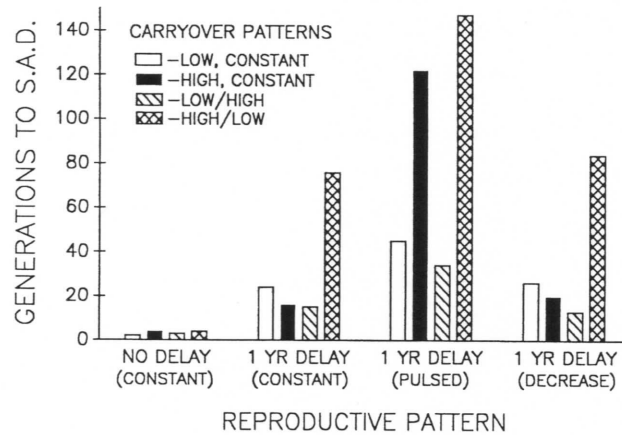


Figure 9. Interactive effects of reproductive patterns (Fig. 7) and carry-over (Fig. 8) on convergence to a stable age distribution (S.A.D.) in the matrix model of seed bank age structure.

were very sensitive to changes in the age of first reproduction and to changes in the variance of the age-specific birth rate. The importance of the pattern of the age-specific birth rate on the dynamics of these models further emphasizes the need for better information on the growth and reproductive vigor of different seed age cohorts within seed banks.

Delays in reproduction that result from the formation of seed banks effectively increase the generation time of an annual species. The qualitative relationship between generation time (T), net reproductive rate (R_0), and the finite rate of increase for the seed bank matrix model is shown in Fig. 10. The rapid decline in the finite rate of increase with increasing generation time would suggest little selective advantage for the formation of a seed bank. However, selection for delayed reproduction may depend on whether a population is increasing or decreasing (Mertz, 1971). From the equation in Fig. 10, it can be seen that in increasing populations ($\ln R_0 > 0$), any increase in generation time (T) will decrease the finite rate of increase. However, in a declining population ($\ln R_0 < 0$), an increase in T will slow the rate of population decline. Thus in populations that experience long periods of gradual increase in population size separated by brief, rapid periods of decline, one might expect selection to act against the formation of seed banks. In contrast, one might anticipate selection for a seed bank in populations (e.g., weedy species) that experience rapid bursts of population growth followed by long periods of population decline.

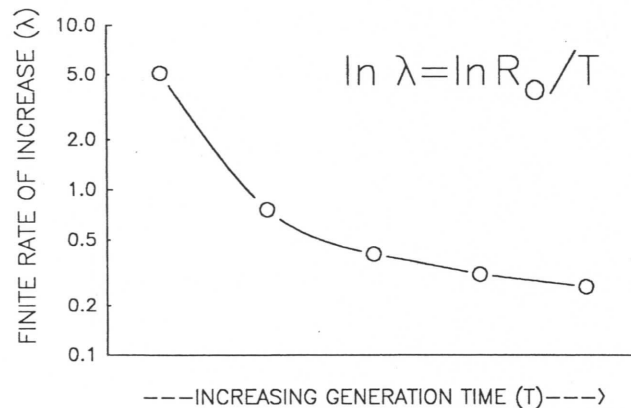


Figure 10. Effects of increasing generation time on the finite rate of increase in an annual species with a seed bank (data from the matrix model of seed bank age structure, Fig. 9.)

V. Summary

In many grassland communities there is a distinct difference between seed reserves and the surface vegetation. Dissimilarities between above- and belowground populations are caused, in part, by differences among taxa in the occurrence and persistence of seed banks. Seed banks appear to be (1) more developed in annuals than in perennials; (2) more extensive in forbs than in grasses; (3) widespread in leguminous species; and (4) common in weedy or fugitive species that colonize disturbances or gaps in the vegetation. These generalizations encompass designations that are by no means independent; the trend that forbs have more persistent seed banks than grasses may be related, in large part, to the weediness of many grassland forbs.

The demography of seed banks of most grassland species is still poorly understood. The work on arable weeds indicates that seed bank decay rates are constant within a particular environment; this possibility needs to be tested for typical grassland species before realistic models of seed bank dynamics can be created. How seed banks are affected by the interaction of genetic variation in dormancy and spatial variation in the microenvironment is poorly known even for important pasture species. The scant information available on the selectivity and intensity of granivory suggest that seed predation pressure is highly variable in space and time. There is a striking lack of information on the effects of seed

aging on the relative growth, reproduction, and competitive ability of differently aged seed cohorts. This information would be valuable especially because the behaviors of models of seed bank dynamics in annual plants are affected significantly by potential variation in reproductive output among seed bank cohorts. Finally, selection for a seed bank strategy in a population may depend on whether the population usually is increasing or decreasing in size. Seed banks might be expected to arise in weedy species that experience bursts of population growth in response to openings in the canopy by disturbance. After each isolated episode of rapid growth, the populations of the weedy species decline as sward vegetation slowly recovers from disturbance. In this situation, delays in reproduction caused by a seed bank might be selectively advantageous because an increase in generation time would slow rates of population decline.

Acknowledgment

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