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Grazing effects on germinable seeds on the fescue prairie

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Abstract

The germinable seed bank in a grassland affects the succession of degraded range and the recolonization of disturbed sites, and must be understood to predict potential responses to management. The germinable seed bank on the fescue prairie was characterized and its relationship to grazing, season, and depth of burial determined. The study was conducted in the fescue prairie of southwestern Alberta in livestock exclosures and on paddocks that, since 1949, have been stocked at fixed rates to achieve light, moderate, or heavy grazing pressures. Surface debris was sampled in fall and spring, and soil was sampled to a depth of 6 cm in spring. The samples were spread on vermiculite in trays and the seeds allowed to germinate over a 90-day period. In fall, total surface seed numbers m^{-2} increased from 1,785 to 7,783 from the ungrazed to heavily grazed site, and most of the differences were accounted for by whitlow-grass (*Draba* spp.) and Kentucky bluegrass (*Poa pratensis* L.). These species also contributed most to differences between fall and spring on the grazed sites. Total seed numbers were similar (1,790 vs 1,803) in spring and fall on ungrazed sites. The species composition of the seed bank did not change with depth. In the soil, the annual forb pygmyflower (*Androsace septentrionalis* L.) was the most common seed but was not detected in a vegetation survey. Soil disturbance in the fescue prairie is more likely to lead to a seral community dominated by annual forbs, than a rough fescue (*Festuca campestris* Rydb.) dominated grassland.

Key Words: soil depth, season, native species, introduced species

The seed bank is an integral component of a grassland community that can influence ecological stability. Seeds in the bank can colonize disturbed sites and can result in successional trends that differ from the existing vegetation since the composition of seedbank and vegetation are often not complementary (Thompson and Grime 1979). This discrepancy is due to the pulsed input of long-lived seeds (Rabinowitz 1981) and variable dormancy and persistence among species (Williams 1983).

The composition of viable seeds in the soil is affected by various factors including grazing by cattle (Johnston et al. 1969), tillage (Forcella and Gill 1986), seed predation and storage by animals (Reichman 1979, Ryser and Gigon 1985), and time since dispersal (Roberts 1986). The effects of these factors are modified by species (Roberts 1986) and burial (Howe and Chancellor 1983).

The species composition of the fescue prairie is readily modified by livestock grazing. Rough fescue (*Festuca campestris* Rydb.), the dominant species, is sensitive to grazing during the growing season and is replaced by seral species (Willms et al. 1985). Consequently, the seed bank is altered (Johnston et al. 1969), affecting the importance of this source for range recovery and dictating the trend following soil disturbances from burrowing animals, livestock impact, or machines.

Johnston et al. (1969) examined the viable seeds in the top 2.5 cm on fescue prairie after 19 years of fixed stocking rates. However, that study examined only the effects of grazing and appeared to overestimate the number of rough fescue seeds in the bank. This species produces relatively few seeds yet was reported to contribute more than 50% of the total number of grass seeds in the bank.

The character of the seed bank must be understood in order to predict the effects of managed or accidental disturbances. Therefore, this study was conducted to determine the effect of grazing, season, and depth of burial on the germinable seed bank of the fescue prairie.

Materials and Methods

Site Description

The study was conducted 85 km northwest of Lethbridge near Stavely (50°12' latitude, 113°57' longitude) in the Porcupine Hills of southwestern Alberta. The vegetation is representative of the Rough Fescue Association described by Moss and Campbell (1947). Parry oat grass (*Danthonia parryi* Scribn.) is a co-dominant with rough fescue on more xeric sites. The soils are classified as Orthic Black Chernozemic (*Udic haploboroll*) developed on till overlying sandstone. The elevation varies from 1,280 to 1,420 m above sea level and annual precipitation has averaged 614 mm over a 30-year period.

In 1949, 3 paddocks were fenced to enclose areas of 65, 32, and 16 ha and a single 0.4 ha exclosure was constructed within or

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contiguous to each. Each paddock was stocked annually with 13 cows and calves for a 6-month period to achieve light, moderate, and heavy grazing pressures by stocking at rates of 1.2, 2.4, or 4.8 animal unit months (AUM) ha^{-1}, respectively. The high stocking rate was not maintained after 1959 due to overgrazing and reduced forage production. However, heavy grazing pressure was maintained at about 80% utilization by stocking at rates that varied from 2.4 to 4.8 AUM ha^{-1} (Willms et al. 1986).

Experimental Approach

Single sampling sites, representing light, moderate, or heavy grazing pressure, were located within a 10-m wide belt adjacent to the exclosure of their respective paddock. Areas of high impact from livestock in the immediate vicinity of the exclosures were avoided. For the heavily grazed paddock, a second sampling site about 200 m from the exclosure was used only in the examination of buried seed. Therefore, a total of 7 sites was sampled.

In each of 5 sampling periods, spring (April) and fall (October) in 1986 and 1987, and spring, 1988, 10 plots were randomly located in each site. On each plot, the herbage was cut to about 3 cm and discarded except for inflorescences which were retained with the sample. The surface seed was sampled with an insect vacuum having a nozzle area of 290 cm^2. The nozzle was placed about 5 cm from the ground while the surface was agitated by hand. This action removed all loose organic debris to the mineral soil. In the spring of 1986 and 1987, the soil was also sampled to a depth of 6 cm using a golf-hole cutter with an area of 87 cm^2. The soil core was taken from the center of the vacuumed sub-plot and partitioned into 2-cm increments.

Surface samples were hand sorted to remove coarse plant material and inflorescences were crushed to free seeds. The sampled material was distributed onto a 4-cm deep vermiculite base in 25 × 50 cm trays. The trays were placed in a greenhouse; temperatures were controlled at about 20°C and natural light was supplemented with artificial light to extend the day length to about 18 hours. The trays were watered daily to keep the surface moist.

Emerging seedlings were categorized by morphology, counted, and removed. Representatives of each group were transplanted into pots to allow further development and identification to genus and, where possible, to species. Seedlings were removed weekly over a 90-day period.

Seedlings were classified into 1 of 10 plant classes (Table 1) according to biological characteristics: plant form [graminoid (G), forb (F), or shrub], longevity [annual (A) vs perennial (P)], growth form [tufted (T) vs rhizomatous (R) vs either (E)], and source [native (N) vs introduced (I)]. The classes were thus: GPRN, GPRI, GPTN, GPEN, FPRN, FAN, FAI, FPNN, FPNI, and SHRUB. Tests were made to compare the effects of grazing treatments, season, and soil depth. For the grazing treatment effect, comparisons were made on the basis of the surface sampled seed bank in fall, 1986 to 1987 (n=10 plots × 2 years × 3 or 1 sites). For the effect of season, the data were analyzed separately by ungrazed treatment and by grazing treatments combined for fall, 1986 and 1987 vs spring, 1987 and 1988 (n=10 plots × 2 years × 3 sites). For the effect of soil depth, the data were analyzed separately by ungrazed treatment, light and moderate grazing treatments combined, and heavy grazing treatment, represented by 2 sites combined, in spring, 1986 and 1987 (n=10 plots × 2 years × 2 sites).

Important species that distinguished between or among treatments were identified using forward selection in stepwise discriminant analysis (SAS Institute 1982). This procedure selects a subset of the species variables to produce a discrimination model which defined the treatments. Inclusion in the discriminant model required a probability of less than 0.10. Similarity indices were calculated for germinable seed of species in the seed bank using Spatz's quantitative modification of Jaccard's index as described by Mueller-Dombois and Ellenberg (1974). Indices were calculated for the combinations of paired comparisons of ungrazed, light and moderate grazing treatment combined, and heavy grazing treatment.

The species composition of the vegetation at each site was estimated from basal area. Basal area was determined by sampling 4,800 points using a 30-pin frame with pins spaced 2.5 cm apart. The data were transformed to a percent of total "hits". The compositions of the vegetation and seed banks were compared on the basis of similarly ranked species (Rabinowitz 1981) and the Pearson product-moment correlation.

Table 1. Description for codes of species classes. Nomenclature follows Moss (1983).

GPRN	graminoids–grass, perennial, rhizomatous, native (*Agropyron dasystachyum, Agropyron smithii*)
GPRI	graminoids–grass, perennial, rhizomatous, introduced (*Bromus* spp., *Phleum pratense, Poa pratensis*)
GPTN	graminoids–grass, perennial, tufted, native (*Agropyron trachycaulum, Agrostis scabra, Danthonia parryi, Festuca idahoensis, F. campestris, Poa canbyi, P. cusickii, P. interior, P. palustris, Koeleria macrantha, Puccinellia nuttalliana, Stipa comata, S. viridula*)
GPEN	graminoids–nongrass, perennial, either tufted or rhizomatous, native (*Carex* spp., *Juncus* spp.)
FPRN	forbs, perennial, rhizomatous, native (*Achillea millefolium, Artemisia ludoviciana, Aster laevis, Cirsium arvens, Galium boreale, Mentha arvensis, Monarda fistulosa, Ranunculus abortivus, R. cymbalaria, Solidago missouriensis, S. mollis, S. spathulata, Thermopsis rhombifolia*)
FAN	forbs, annual, native (*Androsace septentrionalis, Barbarea orthoceras, Chenopodium rubrum, Chrysopsis villosa, Draba nemorosa, D. reptans, Mimulus* spp.)
FAI	forbs, annual, introduced (*Capsella bursa-pastoris, Chenopodium album, Cirsium vulgare, Descurainia sophia, Lappula squarrosa, Lepidium densiflorum, L. ramosissimum, Polygonum arenastrum, Salsola kali, Senecio vulgaris, Silene noctiflora, Sisymbrium altissimum, Thlaspi arvense*)
FPNN	forbs, perennial, non-rhizomatous, native (*Agoseris* spp., *Allium cernuum, Anemone multifida, Antennaria rosea, Arabis drummondii, Arabis lemonii, A. nuttallii, Artemisia biennis, A. camporum, A. frigida, Aster ericoides, Atriplex nuttalli, Atriplex rosea, Campanula rotundifolia, Cerastium arvense, Epilobium angustifolium, E. ciliatum, Erigeron glabellus, E. speciosus, Fragaria virginiana, Gaillardia aristata, Geranium viscosissimum, Heuchera richardsonii, Hieracium umbellatum, Lupinus argenteus, Potentilla drummondii, Sisyrinchium montanum, Veronica americana, Vicia americana, Viola* spp., *Zizia aptera*)
FPNI	forbs, perennial, non-rhizomatous, introduced (*Plantago major, Potentilla argentea, Taraxacum officinale, Tragopogon dubious*)
SHRUB	(*Amelanchier alnifolia, Juniperus horizontalis, Potentilla fruticosa, Rosa* spp., *Symphoricarpos occidentalis*)

Results

Ninety-three species or genera were identified and assigned to

Table 2. Effect of grazing pressure on the average number of germinable seeds of important species by classes. The class codes for species are described in Table 1.

Class and species	Partial[1] R^2	Grazing pressure Ungrazed (n=60)	Light (n=20)	Moderate (n=20)	Heavy (n=20)
		------------- (no. m^{-2})			-------------
GPRN		3	5	0	2
Agropyron dasytachyum	0.06	0	2	0	2
GPRI		167	1,744	1,248	1,127
Bromus inermis	0.07	0	0	0	3
Poa pratensis	0.20	138	1,730	1,238	1,115
Phleum pratense		29	14	10	9
GPTN		324	326	1,077	1,200
Agrostis scabra	0.06	0	5	0	3
Danthonia parryi		14	10	36	10
Festuca campestris	0.09	59	55	10	2
F. idahoensis		87	72	22	86
Koeleria macrantha	0.22	2	3	485	780
Poa spp.	0.06	148	176	509	318
Stipa comata		12	3	14	3
S. viridula		3	0	0	0
GPEN		17	0	0	9
Carex spp.		17	0	0	3
FPRN		387	312	283	269
Achillea millifolium	0.06	71	211	128	10
Aster laevis		222	43	5	2
Solidago missouriensis		6	0	93	214
FAN		69	60	397	.4,660
Androsace septentrionalis		8	17	48	21
Draba spp.	0.32	61	43	349	4,639
FAI		375	7	174	347
Capsella bursa-pastoris		230	2	0	3
Chenopodium album		5	0	0	0
Lappula squarrosa		20	5	174	257
Senecio vulgaris		112	0	0	79
Silene noctiflora		8	0	0	7
FPNN		290	135	214	129
Antennaria rosea		1	0	5	12
Arabis drummondii		47	5	10	59
A. nuttallii		0	0	74	0
Aster ericoides	0.06	3	33	0	0
Cerastium arvense		3	5	0	0
Epilobium ciliatum		16	2	0	2
Erigeron glabellus		4	7	14	0
E. speciosus	0.13	0	0	10	0
Heuchera richardsonii		83	0	0	7
Hieracium umbellatum		6	0	0	2
Potentilla drummondii		2	0	14	17
Viola spp.		118	81	36	34
FPNI		69	114	166	40
Potentilla argentea		29	71	129	12
Taraxacum officinale		43	43	100	29
SHRUB					
(*Potentilla fruticosa*)		84	59	36	0
Total		1,785	2,762	3,595	7,783

[1]Partial R^2's are associated with the species selected for the discrimination model by stepwise discriminant analysis ($P<0.10$); they denote the contribution of the species to the discrimination model when the effects of previously selected species are controlled.

one of 10 plant classes (Table 1). In fall, the most common seeds on the soil surface were yellow whitlow-grass (*Draba nemorosa* L.) and creeping whitlow-grass (*D. reptans* (Lam.) Fern.), which are annual native forbs, and Kentucky bluegrass (*Poa pratensis* L.) which is a perennial, rhizomatous grass that was possibly introduced (Table 2). The surface germinable seed bank of Kentucky bluegrass was greatest on the lightly grazed paddock while whitlow-grasses increased over 100 times from the lightly to the heavily grazed paddocks (Table 2). However, greatest numbers of most perennial forbs, either native or introduced, were found at less than heavy grazing pressure (Table 2). Seed of rough fescue, the climax dominant, was eliminated with heavy grazing pressure as was shrubby cinquefoil (*Potentilla fruiticosa* L.), the only important shrub on the grassland (Table 2).

About twice as many germinable seeds were found on the surface in the fall as in spring (4,734 and 2,407 seeds m^{-2}, respectively) on grazed sites and similar numbers were found on ungrazed sites (1,803 seeds m^{-2}, and 1,790 seeds m^{-2}, respectively) (Table 3). On the grazed sites, however, the germinable seeds of some species increased from fall to spring, including sedge (*Carex* spp.), cut-leaved anemone (*Anemone multifida* Poir.), chickweed (*Cerastium arvense* L.), and dandelion (*Taraxacum officinale* Weber) (Table 3). Kentucky bluegrass and whitlow-grasses contributed most to the reduction in seed number over this period (Table 3). On the ungrazed sites, the greatest differences between fall and spring were in silvery cinquefoil (*Potentilla argentea* L.), which decreased, and needle-and-thread (*Stipa comata* Trin. + Rupr.) and northern bedstraw (*Galium boreale* L.), which increased (Table 3). On these sites, neither Kentucky bluegrass nor whitlow-grasses were significantly different ($P>0.10$) between seasons.

The greatest number of germinable seeds below the soil surface of all sites was mostly of the native annual forb and perennial non-rhizomatous native forb classes (Table 4), while differences in their distribution with depth were defined ($P<0.10$) by 15 or more species in the stepwise discriminant analysis, representing 7 or more classes, depending on the grazing treatment (Table 5). Germinable seeds of most species decreased from the surface to each successive 2-cm increment to a depth of 6 cm. Important exceptions were needle-and-thread, pygmyflower, violet (*Viola* spp.), and silvery cinquefoil which were usually more common below the soil surface to 2-cm depth than on the surface (Table 4). Pygmyflower and violets were the most significant ($P<0.10$) and consistent representatives of the native annual forb and perennial non-rhizomatous native forb classes, respectively, that distinguished among sampling depths (Table 5). Germinable seed numbers of most grasses tended to be greatest at the surface.

Similarity indices for the composition of germinable seeds between ungrazed vs lightly and moderately grazed, ungrazed vs heavily grazed, and lightly and moderately grazed combined vs heavily grazed sites were, for the surface banks in spring, 32.7, 18.9, and 30.7%, respectively, and for the buried seed, 35.1, 28.0, and 32.5%, respectively.

The vegetation was represented primarily by perennial tufted native grasses and secondly by perennial rhizomatous introduced grasses (Table 6) with native annual forbs unrepresented. The Pearson product-moment correlations between the class-composition of vegetation and surface-germinable seed were significant ($P<0.05$) only for the moderately grazed site where the correlation was 0.85 ($P=0.002$) in fall, and 0.92 ($P<0.001$) in spring. On all other sites, by season, the correlations were 0.34 or less ($P>0.05$). When sites were pooled in the analysis, the correlations

Table 3. Effect of season on the average number of germinable seeds of important species, by classes, on the soil surface of both grazed and ungrazed sites. The class codes for species are described in Table 1.

Classes and species	Grazed (n=60) Partial[1] R^2	Grazed Fall	Grazed Spring	Ungrazed (n=60) Partial R^2	Ungrazed Fall	Ungrazed Spring
		-------- (no. m^{-2}) --------			-------- (no. m^{-2}) -------	
GPRN (*Agropyron* spp.)		2	1		3	0
Agropyron dasytachyum		1	1		0	0
GPRI		1,373	336		167	57
Bromus inermis		1	0		0	0
Phleum pratense		11	9		29	2
Poa pratensis	0.13	1,361	326		138	55
GPTN		867	674		324	468
Agrostis scabra		2	9		0	2
Danthonia parryi		19	108		14	54
Festuca campestris		22	22		59	54
F. idahoensis		60	43		87	75
Koeleria macrantha	0.08	423	34		2	1
Poa spp.		334	388		148	255
Stipa comata		7	44	0.05	12	28
S. viridula		0	20	0.03	0	3
GPEN		3	244		17	2
Carex spp.	0.10	1	244		17	1
FPRN		288	129		387	521
Achillea millifolium		116	45		71	55
Aster laevis		17	25		222	304
Galium boreale		11	27	0.05	0	22
Solidago missouriensis		102	0		6	8
FAN		1,706	334		69	40
Androsace septentrionalis		29	13		8	3
Draba spp.	0.07	1,677	318		61	36
FAI		176	225		375	470
Capsella bursa-pastoris		2	0	0.03	230	0
Chenopodium album		0	0		5	1
Lappula squarrosa		146	102		20	144
Senecio vulgaris		26	62		112	312
Silene noctiflora		2	32		8	7
FPNN		159	243		290	175
Anemone multifida	0.05	1	15		0	5
Antennaria rosea		6	139		1	0
Arabis drummondii		25	2		47	14
A. nuttallii		25	0		0	0
Aster ericoides		11	10		3	10
Cerastium arvense	0.03	2	27	0.03	3	1
Epilobium ciliatum		1	1		16	1
Erigeron glabellus		7	0		4	0
E. speciosus		3	0		0	0
Heuchera richardsonii		2	2	0.03	83	9
Hieracium umbellatum		1	0		6	0
Potentilla drummondii		10	0		2	0
Viola spp.		51	28		118	84
FPNI		128	189		74	42
Potentilla argentea		70	58	0.06	29	5
Taraxacum officinale	0.04	58	130		43	36
SHRUB (*Potentilla fruticosa*)		32	32		84	28
Total		4,734	2,407		1,790	1,803

[1]Partial R^2's are associated with the species selected for the discrimination model by stepwise discriminant analysis (P<0.10); they denote the contribution of the species to the discrimination model when the effects of previously selected species are controlled.

were 0.17 (P=0.279) and 0.42 (P=0.008) in fall and spring, respectively.

Five of the 10 most common species in the vegetation on the ungrazed sites were also among the 10 most common species in the surface seed bank. Similar comparisons for the lightly and moderately grazed sites combined and the heavily grazed site

Table 4. Effect of burial depth on the average number of germinable seeds in spring of important species, by classes[1], and grazing pressure (species selected by stepwise discriminant analysis (P<0.10) are shown in Table 5)[1]. The class codes for species are described in Table 1.

	Ungrazed (n=60)				Light and moderate (n=40)				Heavy (n=40)			
	Depth (cm)											
Class and Species	0	0-2	2-4	4-6	0	0-2	2-4	4-6	0	0-2	2-4	4-6
	(no. m^{-2})											
GPRN	0	0	0	0	1	0	0	0	0	0	0	0
GPRI	46	100	12	2	274	225	38	32	311	92	32	0
Phleum pratense	3	0	0	0	12	3	0	0	3	0	0	0
Poa pratensis	40	100	12	2	262	222	38	32	308	92	32	0
GPTN	445	311	50	14	588	346	84	12	945	170	12	12
Agrostis scabra	1	0	0	0	33	0	0	0	0	0	0	0
Danthonia parryi	50	8	0	4	36	3	3	0	165	32	0	3
Festuca campestris	54	19	2	0	32	0	0	0	1	0	0	0
F. idahoensis	62	6	0	0	19	32	0	0	66	3	0	0
Poa spp.	44	69	12	4	389	107	14	3	646	118	12	9
Stipa comata	44	202	37	6	47	167	66	9	53	14	0	0
Stipa viridula	0	8	0	0	29	12	0	0	0	0	0	0
GNG	3	12	12	2	236	136	17	11	129	32	66	3
Carex spp.	2	4	0	2	236	130	14	6	129	6	3	3
FRPN	247	212	38	6	139	43	14	6	76	75	3	6
Achillea millifolium	60	48	2	4	50	29	6	3	17	20	0	0
Aster laevis	43	44	23	2	15	9	0	0	3	3	0	0
Galium boreale	29	60	10	0	51	0	0	0	34	29	0	6
Solidago missouriensis	12	2	2	0	1	0	0	0	0	3	0	0
FAN	26	1,110	598	335	87	1,761	779	644	1,118	1,547	693	430
Androsace septentrionalis	10	991	541	289	60	1,732	759	583	75	805	609	398
Draba spp.	16	119	56	46	24	29	17	61	1,041	742	84	32
FAI	508	429	50	27	102	84	35	0	830	370	69	14
Capsella bursa-pastoris	27	69	2	2	0	0	0	0	0	0	0	0
Lappula squarrosa	146	12	4	0	29	0	3	0	505	78	0	6
Senecio vulgaris	317	277	19	17	60	6	0	0	117	219	26	0
Silene noctiflora	13	15	17	0	12	61	29	0	199	52	29	0
FPNN	272	1187	291	127	191	800	430	248	316	430	199	49
Anemone multifida	5	0	0	0	7	0	0	0	4	0	0	0
Artemisia frigida	0	0	0	0	1	0	0	0	5	78	3	0
Aster ericoides	24	27	4	0	16	0	0	0	1	0	3	0
Antennaria rosea	1	0	0	0	3	6	0	0	205	6	0	0
Cerastium arvense	7	17	8	10	13	72	9	0	54	52	3	3
Epilobium ciliatum	3	0	0	0	3	0	0	0	3	0	0	0
Geranium viscosissimum	44	73	29	8	14	231	81	14	11	23	9	0
Heuchera richardsonii	38	264	60	15	15	84	72	20	3	49	20	3
Viola spp.	135	724	181	90	104	407	254	202	14	205	156	43
FPNI	79	135	17	17	180	185	52	23	548	101	12	3
Potentilla argentea	41	110	17	17	89	124	26	9	31	40	9	3
Taraxacum officinale	37	23	0	0	91	58	26	3	517	61	3	0
SHRUB (*Potentilla fruticosa*)	97	2	0	0	9	3	6	0	4	0	0	0
Total	1,723	3,498	1,068	530	1,907	3,583	1,455	976	4,277	2,817	1,086	517

[1]Some species selected by the model (Table 5) are not shown due to the small number of seeds present in the sample.

were 4 and 3, respectively. Of the 10 most common species in the seed bank at the 2 to 4 cm increment, 9 also ranked with the top 10 species in the 0 to 2 cm increment on the ungrazed, lightly and moderately grazed combined, and on the heavily grazed sites.

Discussion

Grazing affected the surface-germinable seed bank by altering the characteristics of seed input through changes in the vegetation composition (Table 6). However, grazing also reduces litter quantity which alters seed losses to dormancy, germination, and predation, and thereby affects the germinable seed bank. Grazing the fescue prairie at a light stocking rate reduced litter from 12,403 to 9,186 kg ha^{-1} (Peake and Johnston 1965), and increasing grazing pressure from moderate to heavy reduced it from 1,181 to 327 kg litter ha^{-1} (Willms 1988). Reductions in litter quantity are associated with increased bare ground (Johnston 1962). Litter reduces

Table 5. Species selected ($P<0.10$) by the discrimination model, and their partial correlation coefficients1, for the effect of depth on the number of germinable seeds (Table 4) by grazing pressure. The class codes for species are described in Table 1.

Species	Ungrazed	Light and moderate	Heavy
	(partial R^2)		
GPRI			
Poa pratensis	—	0.05	0.05
GPTN			
Agrostis scabra	—	0.08	—
Danthonia parryi	0.07	—	—
Festuca campestris	0.16	0.08	0.04
Koeleria macrantha	0.03	—	0.11
Poa spp.	—	0.15	—
Stipa comata	0.10	0.11	—
Stipa viridula	—	0.05	—
GPEN			
Carex spp.	—	—	0.05
Juncus spp.	0.03	—	—
FRPN			
Achillea millifolium	—	0.05	—
Galium boreale	—	—	0.06
Monarda fistulosa	0.06	—	—
Solidago missouriensis	—	0.05	—
FAN			
Androsace septentrionalis	0.14	—	0.07
FAI			
Mimulus spp.	—	—	0.05
Cirsium vulgare	0.03	—	—
Senecio vulgaris	—	0.07	0.09
Thlaspi arvense	0.05	—	0.06
FPNN			
Allium cernuum	0.04	—	—
Arabis drummondii	0.08	—	—
Artemisia frigida	—	0.05	0.09
Aster ericoides	—	0.05	—
Antenaria rosea	—	0.06	—
Cerastium arvense	—	0.05	—
Epilobium ciliatum	0.07	0.07	—
Erigeron glabellus	—	0.05	—
E. speciosus	—	0.05	—
Heuchera richardsonii	—	—	0.04
Potentilla drummondii	—	—	0.04
Viola spp.	0.22	0.07	0.12
FPNI			
Potentilla argentea	0.03	—	0.05
Taraxacum officinale	0.05	—	0.08
SHRUB			
Potentilla fruticosa	—	0.11	—

[1]Partial R^2's are associated with the species selected for the discrimination model by stepwise discriminant analysis ($P<0.10$); this denotes the contribution of the species to the discrimination model when the effects of previously selected species are controlled.

soil temperature fluctuations, evaporation, and light at the soil surface (Facelli and Pickett 1991), all of which affect the germination and dormancy of seeds (Roberts 1986).

Heavy grazing pressure nearly eliminated rough fescue, the climax dominant, from the germinable seed bank and greatly enhanced the early seral species, whitlow-grasses and June grass (*Koeleria macrantha* (Ledeb.) Schult.) (Table 2). These species produce numerous seeds and increase in abundance on disturbed areas (Moss 1983). On the other hand, rough fescue depends on vegetative reproduction rather than seed, which is characteristic of a dominant species in a late seral stage (Abrams 1988). Rough fescue plants were virtually absent from the heavily grazed site, but about 2 seeds m^{-2} (Table 2) were found on the soil surface. Seeds may have been imported by wind; it is not uncommon for the area to experience wind speeds of over 80 km $hour^{-1}$ which can carry seed. Johnston et al. (1969) found 58 seeds m^{-2} of rough fescue but no plants. This suggests either a large import or faulty identification.

Unlike native annual forbs, the surface germinable seed bank of Kentucky bluegrass was increased by grazing at all stocking rates. Increased grazing pressure enabled the vegetative expansion of Kentucky bluegrass (Table 6) but not in proportion to its surface seed bank (Table 2). The high number of germinable seeds on the lightly grazed site, in comparison with the moderately or heavily grazed sites (Table 2), may indicate that the large litter component leads to seed preservation by maintaining seed dormancy (Williams 1983), by preventing exposure to light, by keeping temperatures cool, and through chemical inhibition. The large seed bank of Kentucky bluegrass may, in part, account for the success of this grass, which may have been introduced by European settlers and now threatens to replace the dominant rough fescue community on more mesic sites. However, the rhizomatous character of Kentucky bluegrass also enables its expansion and provides resistance to heavy grazing pressure that virtually eliminates rough fescue (Willms et al. 1985).

The introduced annual forb class occurred consistently across grazing treatments (Table 2). Blue bur (*Lappula squarrosa* (Retz.) Dumort.) was the most abundant representative on the heavily grazed site and was commonly associated with common groundsel (*Senecio vulgaris* L.) and shepherd's-purse (*Cappella bursa-pastors* (L.) Medic.), which were equally common on the ungrazed site. Although seed numbers were not great relative to some other classes, representatives of introduced annual forbs are the earliest colonizers of cultivated fescue prairie and are some of the more troublesome weeds, persisting for many years after cultivation (Authors' observations). Although these species were likely introduced to the area by early homesteaders, their presence on the native grasslands indicates dispersal by wind or animals; establishment is predicated on disturbances that create bare ground. Coffin and Lauenroth (1989) also reported the greatest number of seeds in a short-grass prairie community were from annual species.

The difference in the germinable seed bank between fall and spring is a function of each species' dormancy and conditions for germination. Apparently, most grassland species are not innately dormant and germinate as soon as their requirements are met (Williams 1983, Roberts 1986). However, dormancy may be imposed through altered light and temperature conditions under the canopy of litter that is prevalent on ungrazed sites. The reduction in germinable seed number from fall to spring was accounted for almost entirely by Kentucky bluegrass and whitlow-grasses (Table 3). With these exceptions, the total number of seeds was, essentially, unchanged between seasons. Kentucky bluegrass and whitlow-grasses expend a considerable amount of energy in seed production, and whether the seeds are simply dormant or short-lived is not certain. Nevertheless, numbers of germinable seeds in spring were high and would not limit establishment from seed in spring.

The fall surface seed bank represents the sum of carry-over from previous years and the current seed rain less all losses to

Table 6. Percent basal area of major species in relation to stocking. The class codes for species are described in Table 1.

Class and species	Stocking rate (AUM ha^{-1}) Ungrazed (0)	Light (1.2)	Moderate (2.4)	Heavy (4.8)
	(%)			
GPRN	1.3	1.7	6.6	5.6
Agropyron dasytachyum	1.1	1.7	4.4	5.1
GPRI	4.9	11.4	27.9	24.3
Bromus inermis	2.6	2.3	0.1	0.2
Poa pratensis	2.3	7.1	24.4	22.3
GPTN	65.1	60.6	42.3	32.2
Agropyron subsecundum	1.1	1.3	2.8	1.6
Agrostis scabra	0.6	1.3	2.8	1.6
Danthonia parryi	16.7	20.1	19.0	15.3
Festuca campestris	41.1	32.6	5.1	1.0
Festuca idahoensis	3.9	6.3	4.8	5.7
Stipa comata/viridula	1.7	0.3	10.6	7.9
GPEN	4.6	5.1	6.8	15.9
Carex spp.	4.6	5.1	6.8	15.9
FPRN	7.8	4.7	3.4	1.6
Achillea millefolium	2.0	1.0	1.4	0.5
Galium boreale	5.2	3.3	1.6	1.0
Thermopsis rhombifolia	0.3	0.3	1.6	3.0
FAN	0.0	0.0	0.0	0.0
FAI	0.3	0.0	0.1	0.2
FPNN	11.5	12.5	7.5	17.1
Artemisia frigida	0.0	0.0	0.1	8.8
Aster ericoides/laevis	5.5	4.2	0.6	0.9
FPNI	0.1	0.4	2.2	0.8
Taraxacum officinale	0.1	0.4	2.2	0.8
SHRUB	3.5	3.3	5.0	2.1
Potentilla fruticosa	1.5	2.3	2.3	1.5

dispersal agents, predation, and dormancy. Seed numbers could only decrease from fall to spring unless there was import from other areas. Germinable seeds of some species, notably sedges and needle-and-thread, however, increased between fall and spring (Table 3), suggesting that winter conditions might have released dormancy.

Some losses from the surface germinable bank would be into the soil via fissures resulting from drying and incorporation by animal activity. Since these processes are common to all species, there should be a good relationship between surface and below-ground germinable seeds. In fact, these seed banks were more similar than were surface seed and vegetation and the seed bank composition tended to be constant throughout the 6 cm profile. The data did not support the observation by Rabinowitz (1981) that the seed rain, which might be comparable to the fall surface seed bank of this study, more closely resembled the seed bank than the seed bank resembled the seed rain. In our data, the number of common species were the same in the ranked groups.

In spring, more germinable seed was in the soil than on the surface in the ungrazed to moderately grazed sites; however, in the heavily grazed sites the numbers were about equal (Table 4). Germinable seed below ground mainly belonged to the native annual forb class, mostly from the contribution of pygmyflower, a species not identified in the vegetation nor particularly abundant in the surface seed bank (Table 4). Only a few perennial non-rhizomatous native forb species were represented by germinable seed bank at the 4-6 cm depth and their numbers tended to diminish as grazing pressure increased. Of these, violets were the most abundant but purple geranium (*Geranium viscosissimum* Fisch. and Mey.) and alumroot (*Heuchera richardsoni* R. Br.) were also consistently present in the 4–6 cm depth (Table 4). Each of these species has a hard seed coat that prolongs seed survival. Similarly, the hard seed coat of needle-and-thread ensures its persistence in the soil despite the input of very few seeds from the surface in fall (Table 2).

Although more than twice as many seeds were present on the soil surface of the heavily grazed site as in the ungrazed to moderately grazed sites, fewer seeds were detected in the soil (Table 4). The apparent incorporation into the soil of fewer seeds on the heavily grazed sites compared to the other sites was possibly due to the near absence of litter and consequently greater exposure to predation and environmental hazards. Nevertheless, many species were common to each grazing treatment, both on the surface and in the soil, although the quantitative similarity was generally less than 35%. As might be expected, similarity was least between ungrazed and the heavily grazed sites; and, between sites, lower on the surface than in the soil.

Conclusions

Grazing altered the plant community and affected the germinable seed composition on the soil surface in fall. Heavy grazing pressure resulted in a large number of seeds of Kentucky bluegrass and whitlow-grasses and almost eliminated rough fescue. However, the high seed contribution from seral species was not reflected in the soil where numbers were approximately the same across grazing treatments. The most important change resulting from heavy grazing pressure was the loss of rough fescue, the climax dominant with the greatest forage value on this grassland. If grazing pressure were released, succession to a rough fescue dominated community would have to proceed from a severely restricted plant or seed population. On the other hand, disturbances of the soil surface are likely to produce similar responses over all grazing treatments, an increase of annual seral species and introduced invaders.

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