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Effects of ungulates and prairie dogs on seed banks and vegetation in a North American mixed-grass prairie

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Abstract

The relationship between vegetation cover and soil seed banks was studied in five different ungulate herbivore-prairie dog treatment combinations at three northern mixed-grass prairie sites in Badlands National Park, South Dakota. There were distinct differences in both the seed bank composition and the aboveground vegetation between the off-prairie dog colony treatments and the on-colony treatments. The three on-colony treatments were similar to each other at all three sites with vegetation dominated by the forbs *Dyssodia papposa, Hedeoma* spp., *Sphaeralcea coccinea, Conyza canadensis*, and *Plantago patagonica* and seed banks dominated by the forbs *Verbena bracteata* and *Dyssodia papposa*. The two off-colony treatments were also similar to each other at all three sites. Vegetation at these sites was dominated by the grasses *Pascopyrum smithii, Bromus tectorum* and *Bouteloua gracilis* and the seed banks were dominated by several grasses including *Bromus tectorum, Monroa squarrosa, Panicum capillare, Sporobolus cryptandra* and *Stipa viridula*. A total of 146 seedlings representing 21 species germinated and emerged from off-colony treatments while 3069 seedlings comprising 33 species germinated from on-colony treatments. Fifteen of the forty species found in soil seed banks were not present in the vegetation, and 57 of the 82 species represented in the vegetation were not found in the seed banks. Few dominant species typical of mixed-grass prairie vegetation germinated and emerged from seed banks collected from prairie dog colony treatments suggesting that removal of prairie dogs will not result in the rapid reestablishment of representative mixed-grass prairie unless steps are taken to restore the soil seed bank.

Introduction

Black-tailed prairie dogs (*Cynomys ludovicianus*) have profound effects on numerous structural and functional aspects of grassland vegetation. Although predominantly grass feeders (Summers and Linder 1978; Fagerstone et al. 1981; Uresk 1984), these colonial animals indiscriminately clear large quantities of vegetation, ostensibly as a predator avoidance mechanism and to facilitate visual communication among individuals (Hoogland 1995; Detling 1998). Prairie dogs also change many soil and belowground properties through their grazing and burrowing activities (Ingham and Detling 1984; Holland and Detling 1990; Munn 1993). Consequently, plant species composition and mineral nutrition of the vegetation in prairie dog colonies changes as time since colonization increases (Osborn and Allan 1949; Coppock et al. (1983a, 1983b); Archer et al. 1987). As a result, these prairie dog colony patches often become preferential areas for grazing and resting by ungulate herbivores, such as bison (*Bison bison*), elk (*Cervus elaphus*), and pronghorn (*Antilocapra americana*) (Coppock et al. 1983a; Wydeven and Dahlgren 1985;

Krueger 1986). The consequences of this intense biological activity are large differences in above- and belowground plant biomass, decomposition and nutrient cycling rates, nutrient distribution, species composition, and vegetation structure between active colony patches and uncolonized prairie (Koford 1958; Coppock et al. (1983a, 1983b); Archer et al. 1987; Whicker and Detling (1988, 1993); Detling 1998; Fahnestock and Detling 2002).

Prairie dogs often are thought to compete with cattle for forage (Uresk 1985) and increase the potential for economic loss on range and pasture lands. For this reason, several states, including South Dakota where our study took place, have declared prairie dogs a pest and have subjected them to control via poisoning or other means on both public and private lands (e.g., http://www.state.sd.us/doa/das/pd_mngt.htm). Despite the perceived conflict between prairie dogs and cattle, prairie dog colonies provide the only habitat of the endangered black-footed ferret (*Mustela nigripes*). Thus, the elimination of prairie dogs and the potential for subsequent grassland succession is of considerable interest. Furthermore, because of the potential for significant interactive effects on vegetation and ecosystem processes by prairie dogs and native ungulates, understanding their independent and combined influence is important for predicting the likelihood of colonized land returning to vegetation reminiscent of uncolonized grassland.

The disturbance caused to soils and vegetation through the independent and combined activity of prairie dogs and ungulate herbivores may be an important mechanism providing microsites for seedling recruitment, and may be critical to maintaining plant species richness and diversity in grassland ecosystems (Crawley 1990; Lavorel et al. 1994; Edwards and Crawley 1999). Seedling recruitment in these disturbed areas may come from seeds present in the soil prior to the disturbance or from recently produced seeds (i.e., seed rain and transport). Plant growth in colonies may also occur through vegetative reproduction (stolons and rhizomes), as is common in many perennial grass species. Because seed banks rarely reflect current plant species composition (Thompson and Grime 1979; Coffin and Lauenroth 1989; Willms and Quinton 1995), quantifying the composition of the seed bank is important if one wishes to predict the potential successional trend of the vegetation following initiation or cessation of a disturbance (Willms and Quinton 1995; Perez et al. 1998).

The overall objective of this study was to characterize the soil seed banks in mixed-grass prairie in Badlands National Park, South Dakota, USA, under various ungulate herbivore – prairie dog treatment combinations, and to compare the seed bank with existing vegetation. Studies were carried out on three separate prairie dog colonies and on nearby, uncolonized grassland that was grazed by ungulate herbivores or was recently (< 3 years) exclosed from vertebrate herbivore activity. The study addressed three related questions: 1) How similar is the composition of the vegetation and soil seed bank in prairie dog colonies to those in adjacent uncolonized mixed-grass prairie? 2) Does the species composition of existing vegetation reflect species present in the soil seed bank? 3) Are their significant differences in vegetation and seed banks in areas that are occupied only by prairie dogs compared to areas occupied only by ungulate herbivores or by both ungulates and prairie dogs?

Methods

Study sites and treatments

Our study was conducted in the north unit of Badlands National Park (BNP), South Dakota, USA. About one-third of the landscape in the park consists of highly eroded and nearly barren soils (“badlands”) and the remainder is northern mixed-grass prairie interspersed with woody draws (Von Loh et al. 1999). Cool- (C_3) and warm-season (C_4) grasses – blue grama (*Bouteloua gracilis*), needle-and-thread (*Stipa comata*), western wheatgrass (*Pascopyrum smithii*), cheatgrass (*Bromus tectorum*) and side-oats grama (*Bouteloua curtipendula*) – and numerous forb species dominate the vegetation in the park. Shrubs, such as yucca (*Yucca glauca*) and silver sagebrush (*Artemisia cana*), are conspicuous and juniper (*Juniperus spp.*) groves and cottonwood (*Populus deltoides*) trees can be found in wetter areas of the landscape.

Bison are the most conspicuous ungulate herbivores in BNP, numbering over 300 individuals at the time of this study. Other less common ungulates include pronghorn, mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*). The north unit of the park also supports large populations of black-tailed prairie dogs located in several distinct colonies (Langer 1998) into which many dozen black-footed ferrets have been reintroduced.

For this study we used treatments established in the fall and winter of 1994 at three active prairie dog colony sites – Hay Butte, Kalchbrenner, and Kocher Flats (Fahnestock and Detling 2002). The three study sites are separated from each other by about eight kilometers ant are located within the Sage Creek Wilderness Area, a 26,000 ha portion of the north unit of BNP. These three sites were chosen because they had similar soil characteristics, had large active prairie dog colonies, and because there were large expanses of mixed-grass prairie adjacent to the colonies that were regularly utilized by ungulates, primarily bison (Fahnestock and Detling 2002). At each prairie dog colony, two permanent 50 m by 50 m exclosures were constructed in the fall and winter of 1994 in active areas of the colony – one excluded bison and other ungulate herbivores but allowed for the continued use of the area by prairie dogs, the other excluded all ungulate herbivores as well as prairie dogs. These exclosures were within 50 m of uncolonized mixed-grass prairie seed bank sources. Adjacent to each prairie dog colony, an additional 50 m by 50 m exclosure was built on native mixed-grass prairie to exclude ungulates. Plots of the same size, but lacking the exclosure, also were established both on and off each colony to serve as controls. Thus, at each of the three study sites there were two off-colony treatments, (1) bison and other ungulates excluded (−B) and (2) continued utilization by ungulates (+B), and three on-colony treatments, (3) continued ungulate and prairie dog utilization (+B+P), (4) only prairie dog utilization (−B+P), and (5) all herbivores excluded (−B−P). All treatments were in place for three years prior to the initiation of this study.

Exclosures were built with 4 m tall by 15 cm diameter wooden poles spaced every 5 m and placed in the ground to a depth of 1 m. Multiple strands of fencing wire surrounded the poles from the ground to 3 m to exclude all ungulates. On the exclosure that excluded ungulates and prairie dogs, we also wrapped 0.5 m of chicken wire around the lowest aboveground portion of the fence and to a depth of 0.5 m below the soil surface, and we installed 0.5 m of sheet metal flashing above the chicken wire. Despite these efforts, some prairie dogs stilled gained access to the exclosures and had to be periodically removed. We do not believe that the design of the exclosures prevented wind or water dispersal of seeds into the exclosure areas, but obviously restricted potential seed transport by ungulates.

Vegetation survey

Plant species composition and cover were assessed in all five herbivore treatments at each of the three sites in June and July 1997. Measurements were made in both months to ensure documentation of both early and late emerging plant species and monthly data were averaged by species prior to statistical analyses. In each 50 m by 50 m treatment, we placed twenty 0.10 m^2 quadrats every two meters along the diagonal axis of the site and visually estimated live and standing dead canopy coverage of each species (Daubenmire 1959). We also estimated the percent of exposed soil and litter in each quadrat. While this method was not sensitive to detecting rare plant species (Stohlgren et al. 1998), we have used it successfully to monitor species composition and trends in cover of dominant plant species in this (Fahnestock and Detling 2002) and other grassland-grazer systems (Fahnestock and Detling 1999). We have also found that twenty replicate quadrats are adequate for detecting trends and monitoring species composition in this type of grassland (Fahnestock, unpublished data). Voucher specimens of each species encountered were collected and identification was verified at the Colorado State University herbarium.

Seed bank samples and recruitment

To survey seed banks we collected 5.0 cm-diameter soil cores to a depth of 3.0 cm at 20 random locations within each 50 m by 50 m treatment in the three sites. Space constraints in the screen house (see below) restricted the amount of soil we could process, and so only 20 replicate cores could be collected in each treatment at each site, potentially limiting our ability to fully document the seed bank at each site. Sampling was conducted over 3 days in mid-April 1997 just after the ground had thawed. No samples were collected within 5 -m of the edge of any treatment to reduce edge effects. For each site, the 20 soil samples were composited by herbivore treatment, thoroughly mixed, and kept refrigerated until 3 June 1997. At that time, we broke up any aggregated soils, removed litter, and spread soil from each treatment plot over three (25 cm by 52 cm) greenhouse trays into which we first had placed 2.5 cm of vermiculite covered by a single layer of paper toweling. Depth of the sampled soil was approximately 2.5 cm in each tray. Since we were interested in the potential vegetation at each site, we also left stolon and rhizome fragments in the soil samples, given that many perennial grass species reproduce vegetatively.

We had a total of 45 germination trays (3 sites × 5 treatments × 3 trays/treatment). Trays were arranged randomly in a screen house at Badlands National Park where samples were subjected to prevailing temperatures and humidity levels typical of the sites from which they had been collected. An additional fifteen trays containing only vermiculite were used as controls to test for seed rain contamination within the screen house. We kept the soil moist by watering from beneath to the depth of the vermiculite, using water from a local well. Counts were made weekly, and representatives of any seedlings that did not thrive in the trays were transplanted into peat pots until they developed enough to identify. Care was taken to ensure that all seedlings that germinated during the experiment were counted only once. A final count was made on 17 July 1997 and all plants were harvested. Soil was allowed to dry for two weeks and then rewatered. We observed no further germination. All the seedlings that emerged were summed by species and the seeds that germinated from each of the three replicate trays were averaged for each treatment prior to analyses. Voucher specimens were collected for each species and sent to Dr Gary Larson at South Dakota State University for verification of species identification.

Statistical analysis

Differences ($P < 0.05$) in vegetation cover among the five herbivore treatments were tested using a randomized block design and the General Linear Model procedure (SAS Institute 1989), using site as a block. Prior to analyses, cover data for all sites were transformed for analyses as: cover = arcsine [square root (% cover of the individual species)], and all June and July quadrat data for each treatment at each site were averaged by species. Because there was a significant ($P < 0.05$) treatment effect, we set up specific contrasts to test for differences ($P < 0.05$) in vegetation cover between the off- and on-colony treatments, between the two off-colony treatments, and among the three on-colony treatments. There were few significant differences between the off-colony treatments and few differences among the on-colony treatments; therefore, we categorized treatments as either off- or on-colony for data presentation.

Non-metric multidimensional scaling (NMS; Ludwig and Reynolds (1988)) was used to examine and compare species composition patterns in the vegetation and in the seed banks among the various treatments and sites (PC-ORD Version 3.0; McCune and Mefford (1997)). NMS, which uses ranked distances, is appropriate when data are not linearly distributed along an environmental gradient (McCune and Mefford 1997). Unlike principal components, axes are numbered arbitrarily, so that the first axis does not necessarily account for the greatest variance. Pearson correlation coefficients and axes of the non-metric multidimensional scaling analysis were computed for the individual species comprising the vegetation and the germinated seed banks.

For both vegetative cover and seed bank data we calculated community parameters, including species richness (number of species, N), Shannon diversity ($H' = -\Sigma p_i \log p_i$, where $P_i = -n_i/N$), and evenness ($J' = H'/H_{max}'$) (Brower et al. 1990). The extent to which species composition of vegetation and seed banks diverged between each pair of treatment combinations was also quantitatively compared using Morisita's similarity index (Morisita 1959).

Results

Vegetation

Total plant cover did not vary between off-colony treatments (59% cover) and on-colony treatments (58% cover). However, litter cover was significantly higher in off-colony treatments (49%) than in on-colony treatments (14%) and bare ground was much lower off- than on-colonies at 4% and 26%, respectively (Table 1). Species composition was very different between the off-colony and on-colony treatments. There were a total of 82 species represented in the vegetation (see Table 3 for species listing). Of these, 36 were found in off-colony treatments and 72 were found on prairie dog colonies (Table 1). There were 26 species that were found in the vegetation of both off- and on-colony treatments, 10 plant species found in the vegetation off-colonies but not found on-colonies, and 46 species unique to the prairie dog colonies that were not found on the adjacent uncolonized grassland.

Grasses accounted for 82% of the vegetative cover off the prairie dog colonies (Table 1). Seven plant species had cover values one percent or greater off the colonies and five of these were grasses. Two grasses, *Pascopyrum smithii* and *Bromus tectorum*, accounted

Table 1. Plant species composition (for those species exceeding 1% cover) and mean canopy coverage ± 1 SE (live plus standing dead), and other plant community characteristics off and on prairie dog colonies in summer (June and July, averaged) 1997 in Badlands National Park. Data are transformed mean percent cover ± 1 SE for three separate sites each comprising two off-colony treatments and three on-colony treatments. Data are transformed as mean percent cover = arcsine [square root (% cover of the individual species)]. All off- vs. on-colony comparisons of species and other community characteristics are significantly ($P < 0.05$) different except for *Hedeoma* spp. Grass species are indicated by[g] and exotic species by[e].

OFF COLONY Species	% Cover	ON COLONY Species	% Cover
Pascopyrum smithii[g]	23.0 ± 1.5	*Hedeoma spp.*	3.8 ± 2.3
Bromus tectorum[ge]	17.6 ± 1.7	*Dyssodia papposa*	3.0 ± 1.2
Bouteloua gracilis[g]	4.2 ± 0.8	*Conyza canadensis*	2.2 ± 1.2
Stipa viridula[g]	2.9 ± 0.8	*Sphaeralcea coccinea*	2.2 ± 1.3
Hedeoma spp.	1.7 ± 1.2	*Plantago patagonica*	2.1 ± 1.1
Tragopogon dubius[e]	1.5 ± 1.1	*Pascopyrum smithii*[g]	2.0 ± 1.7
Bouteloua curtipendula[g]	1.0 ± 1.0	*Convolvulus arvensis*[e]	1.9 ± 1.1
		Hedeoma hispidum	1.9 ± 1.4
Total plant cover	59.4 ± 5.4	*Salsola iberica*[e]	1.7 ± 1.1
Total grass cover	49.0 ± 3.2	*Euphorbia stictospora*	1.6 ± 0.9
Exotic plant cover	20.2 ± 3.8	*Verbena bracteata*	1.5 ± 0.8
Litter	48.9 ± 5.7	*Lactuca serriola*[e]	1.4 ± 1.3
Bare ground	4.1 ± 3.6	*Schedonnardus paniculatus*[g]	1.3 ± 0.2
		Festuca octoflora[g]	1.2 ± 1.1
Total species richness	36	*Bromus tectorum*[ge]	1.2 ± 0.7
Exotic species richness	7	*Melilotus officinalis*[e]	1.1 ± 0.8
Species diversity (H')	0.71	*Zigadenus venonosus*	1.1 ± 0.6
Species evenness (J')	0.46	*Lappula redowskii*	1.1 ± 1.0
		Draba reptans	1.0 ± 0.6
		Descurainia sophia[e]	1.0 ± 0.5
		Total plant cover	57.8 ± 6.0
		Total forb cover	48.6 ± 6.4
		Exotic plant cover	11.0 ± 2.1
		Litter	13.9 ± 1.3
		Bare ground	26.3 ± 2.3
		Total species richness	72
		Exotic species richness	12
		Species diversity (H')	1.40
		Species evenness (J')	0.75

for nearly 70% of the vegetative cover off the prairie dog colonies. In contrast, forbs comprised 84% of the vegetative cover on the prairie dog colonies and there was much greater species evenness on colonies than off colonies (Table 1). There were 20 species that had cover values of one percent or greater on prairie dog colonies and only four of these were grasses. The most common species on colonies were forbs and included *Hedeoma* species (5.7% cover), *Dyssodia papposa* (3.0%), *Conyza canadensis* (2.2%), *Sphaeralcea coccinea* (2.2%) and *Plantago patagonica* (2.1%; Table 1). The most common grass species on prairie dog colonies was *P. smithii* with 2% cover.

Seven exotic species (i.e., not native to North America) accounted for 34% of the plant cover off the prairie dog colonies with *B. tectorum* accounting for 87% of this (Table 1). There were 12 exotic species on the prairie dog colonies but they comprised only 19% of the total plant cover on the colonies. Species diversity was 0.71 off of the prairie dog colonies and 1.40 on the colonies. Species evenness was 0.46 and 0.75 off- and on-colonies, respectively (Table 1).

The vegetation of the two off-colony treatments was very similar to each other 94%), but quite different from the three on-colony treatments (Table 2). Likewise, the vegetation of the three on-colony treat-

Table 2. Similarity (Morisita's index of community similarity; Morisita (1959)) of mixed-grass prairie vegetation and germinated seeds among five herbivore treatments in June and July 1997 (averaged) in Badlands National Park. Treatment abbreviations are off-colony, continued utilization by ungulates (+B), off-colony, bison and other ungulates excluded (−B), on-colony, only prairie dog utilization (−B+P), on-colony, continued ungulate and prairie dog utilization (+B+P), and on-colony, all vertebrate herbivores excluded (−B−P).

VEGETATION		OFF COLONY		ON COLONY		
	Treatment	+B	−B	−B+P	+B+P	−B−P
	+B	1.00	—	—	—	—
	−B	0.94	1.00	—	—	—
	−B+P	0.07	0.15	1.00	—	—
	+B+P	0.21	0.29	0.82	1.00	—
	−B−P	0.08	0.12	0.71	0.59	1.00
SEED BANKS		OFF COLONY		ON COLONY		
	Treatment	+B	−B	−B+P	+B+P	−B−P
	+B	1.00	—	—	—	—
	−B	0.92	1.00	—	—	—
	−B+P	0.23	0.24	1.00	—	—
	+B+P	0.24	0.24	0.99	1.00	—
	−B−P	0.28	0.27	0.97	0.98	1.00

ments shared some similarity (59–82%). There was slightly greater similarity between the treatment with continued ungulate and prairie dog grazing (i.e., +B+P) and the off-colony treatments (+B and −B) than between the other on-colony (i.e., −B+P and −B−P) vs. off-colony treatments (Table 2). This was due primarily to greater cover of *P. smithii* on +B+P (9.3%) than on −B+P and −B−P (1.2%) and about two-thirds less cover of C. *canadensis* and *S. coccinea* on +B+P than on −B+P and −B−P (data not shown).

The ordination also showed clear differences in species composition of the vegetation on-vs. off-colony, but little evidence of treatment differences (Figure 1). The two dimensional solution was selected, based on minimal change in stress beyond that dimension. The first axis represented an imperfect separation of Kalchbrenner from Hay Butte and Kocher Flats. It was strongly positively correlated with *Conyza canadensis, Festuca octoflora, Plantago patagonica*, and *Sphaeralcea coccinea*, species primarily found on prairie dog colonies and in greater abundance at Hay Butte and Kocher Flats than at Kalchbrenner, and negatively associated with *Pascopyrum smithii* (Table 3). The second axis separated on- and off-colony plots (Figure 1), based on positive associations with *Bromus tectorum* and *Pascopyrum smithii* and negative associations with *Dyssodia papposa, Euphorbia marginata, Solanum rostratum*, and *Verbena bracteata* (Table 3).

Seed banks

Seeds of 40 species germinated and emerged during this study (Table 3), 21 from off-colony plots and 33 from on-colony plots (Table 4). Thirteen grass species emerged in our study, 9 from off- and 11 from on-colony plots. Some of the perennial grasses may have sprouted from rhizome fragments. Seven of the plant species that germinated off-colony did not germinate from on-colony treatments, and 19 species of on-colony seedlings were not found among off-colony seedlings. Fourteen of the species that germinated and emerged were found in both off- and on-colony treatments. Fifty-eight percent of the off-colony and 65% of the on-colony species were annuals (Table 4). Four exotic species were found in off-colony plots and five in on-colony plots. Control flats averaged only 0.4 seedlings per flat, so we did not include any correction for seed contamination within the screen house in our analyses.

Only 25 species were found in common between the seed banks and the vegetation (Table 3). Fifteen species were found only in the seed banks and not the vegetation while 57 species were found only in the vegetation and not the seed banks. Differences in the number of species detected between vegetation and

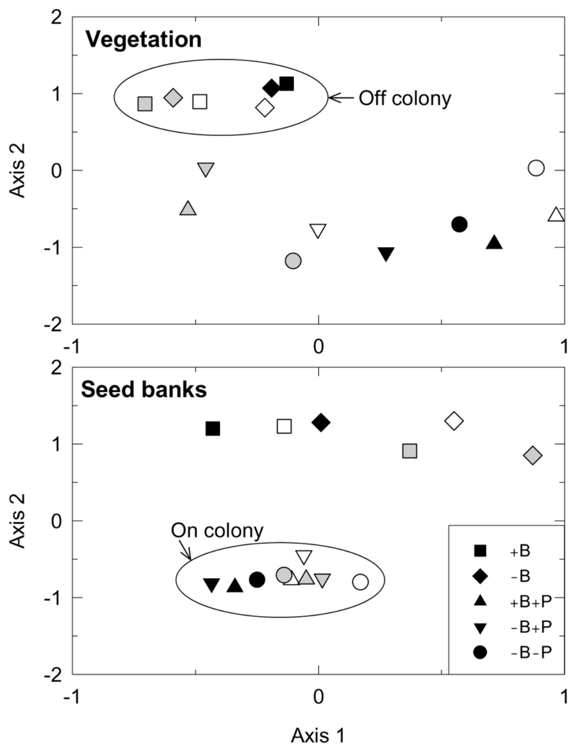

Figure 1. Ordination (non-metric multidimensional scaling) of vegetation and germinable seed banks on three prairie dog colonies and on adjacent mixed-grass prairie at Badlands National Park. Stress = 5.22 for vegetation and 5.55 for seed banks for the two dimensional solution. Symbol shape corresponds to treatment (see legend) and color indicates site – black is Hay Butte, shaded is Kalchbrenner, white is Kocher Flats.

the germinable seed bank may be explained in part by a greater sampling effort for the vegetative component than for the seed bank, which likely resulted in fewer species detected by the seed bank sampling.

The similarity in the germinated seed bank of the two off-colony treatments was very high (92%), but these treatments were quite dissimilar from the three on-colony treatments (23–28% similarity; Table 2). Likewise, seed bank composition of the three on-colony treatments was very similar (97–99%; Table 2). As in the vegetation, we found a clear difference in species composition of the seed banks on- vs. off-colony, but little evidence of treatment differences in the ordination (Figure 1). In the case of the seed banks, however, the first axis represented an imperfect separation of Hay Butte from Kalchbrenner and Kocher Flats. It was strongly positively correlated with *Euphorbia maculata, Medicago sativa* and *Stipa viridula*, species found off-colony primarily at Kalchbrenner and/or Kocher Flats, and was negatively associated with *Dyssodia papposa, Sporobolus cryptandrus*, and *Verbena bracteata* (Table 3). *V. bracteata* and *D. papposa* dominated the on-colony plots at all sites, but *S. cryptandrus* was most abundant at Hay Butte both off- and on-colony. The second axis separated on- and off-colony plots, based on negative associations with *Amaranthus albus, Dyssodia papposa*, and *V. bracteata* and a positive association with *B. tectorum* and *Stipa viridula* (Table 3). *B. tectorum* and *S. viridula* occurred only off-colony and *A. albus* occurred only on-colony (Table 4).

Analysis of variance revealed no differences among exclosure treatments on or off the colonies, nor any interaction between the two variables, with respect to community metrics. Therefore, we collapsed them into two treatments, either on- or off-colony, for subsequent analyses. We found significant colony by site interactions for mean number of germinated seeds ($F_{2,9}$ = 11.27; P = 0.0035), species richness ($F_{2,9}$ = 22.96; P = 0.0003), and H' ($F_{2,9}$ = 9.30; P = 0.0065). In contrast to the vegetation, evenness was greater off the colony than on it (least-squares means of 0.87 vs. 0.50; $F_{1,2}$ = 37.30; P = 0.0258); this relation did not vary with site. In general, the mean number of germinated seeds per species was much lower off-colony than on, as were the number of species, with the exception of Kalchbrenner (Figure 2). The abundance of only a few germinating species on the colonies, however, resulted in higher species diversity off-colony, with the exception of Kocher Flats (Figure 2).

Discussion

Both prairie dogs and bison prefer graminoids to other types of forage (Peden et al. 1974; Hansen and Gold 1977; Fagerstone et al. 1981). As a result, prairie dog colony patches generally have lower graminoid biomass and greater biomass of forbs and annual grasses relative to uncolonized prairie (Bonham and Lerwick 1976; Coppock et al. (1983a, 1983b); Archer et al. 1987). Our results are consistent with these earlier findings. Grasses dominated the vegetation in uncolonized mixed-grass prairie, accounting for over 80% of the vegetative plant cover, while they only accounted for about 15% of the vegetative plant cover on prairie dog colonies. The most abundant grasses represented in the vegetation in uncolonized mixed-grass prairie at our study sites were *Pascopyrum smithii* and *Bromus tectorum* with absolute cover val-

Table 3. Pearson correlation coefficients and axes of the non-metric multidimensional scaling analysis for vegetation and for germinated seedling species. Axis I of the vegetation separated Kalchbrenner from the other two sites, regardless of treatment, and Axis I of the seed bank data separated Hay Butte site from the other two sites. Axis II of both the vegetation and seed banks separated on- and off-colony plots, independent of site. Significance indicated by asterisks: * $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; *** $p < 0.001$; N=15. Grass species are indicated by[g] and exotic species by[e].

	Vegetation		Seed Banks	
SPECIES	Axis I (r)	Axis II (r)	Axis I (r)	Axis II (r)
Allium spp.	–0.109	0.259	—	—
Amaranthus albus	0.186	–0.131	–0.418*	–0.728***
Amaranthus retroflexus	—	—	0.012	–0.218
Ambrosia spp.	–0.071	–0.485*	—	—
Andropogon gerardii[g]	–0.241	0.283	0.012	–0.218
Argemone polyanthemos	0.286	–0.223	—	—
Aristida longiseta	0.297	–0.251*	—	—
Artemisia campestris	–0.351	0.274	—	—
Aslepias pumila	0.535*	–0.412*	—	—
Astragalus agrestis	0.363	–0.545*	—	—
Bouteloua curtipendula[g]	–0.401	0.621**	–0.329	0.344
Bouteloua gracilis[g]	–0.332	0.688**	—	—
Bromus inermis[ge]	–0.241	0.283	—	—
Bromus tectorum[ge]	–0.626**	0.761***	–0.064	0.779***
Buchloe dactyloides[g]	0.286	–0.223	—	—
Carex eleocharis[g]	0.209	0.079	—	—
Chenopodium desiccatum[a]	0.269	–0.558**	–0.212	–0.398
Cirsium arvense[c]	0.083	–0.340	—	—
Cirsium spp.	0.225	–0.345	—	—
Cirsium vulgare[e]	0.260	–0.400	—	—
Convolvulus arvensis[e]	–0.297	–0.122	0.012	–0.218
Conyza canadensis	0.751***	–0.647**	–0.337	–0.241
Conyza ramosissima	0.388	–0.513*	–0.084	–0.221
Coryphantha spp.	0.481*	–0.189	—	—
Cryptantha crassisepala	0.481*	–0.189	—	—
Descurainia sophia[e]	–0.109	–0.239	—	—
Draba reptans	0.527*	–0.664**	—	—
Dyssodia papposa	0.029	–0.740***	–0.488*	–0.773***
Eragrostis cilianensis[ge]	—	—	0.13	–0.228
Erigeron spp.	–0.051	–0.374	—	—
Euphorbia glyptosperma	—	—	0.267	0.098
Euphorbia maculata	—	—	0.661**	0.253
Euphorbia marginata	0.243	–0.783***	—	—
Euphorbia serrphyllifolia	—	—	–0.457*	–0.469*
Euphorbia stictospora	0.368	–0.781	–0.193	–0.227
Evax prolifera	0.362	–0.471**	—	—
Festuca octoflora[g]	0.809***	–0.310	–0.337	–0.241
Gaura coccinea	0.200	–0.410	—	—
Geranium carolinianum	–0.002	–0.242	—	—
Grindelia squarrosa	–0.052	–0.415*	—	—
Hedeoma hispidum	–0.158	–0.396	–0.368	–0.468*
Hedeoma spp.	0.588**	–0.608**	—	—
Helianthus annuus	–0.267	–0.296	0.278	0.262
Hordeum pusillum[g]	–0.002	–0.242	—	—

Table 3. Continued.

	Vegetation		Seed Banks	
SPECIES	Axis I (r)	Axis II (r)	Axis I (r)	Axis II (r)
Kochia scoparia[e]	—	—	–0.045	–0.126
Koeleria macrantha[g]	—	—	–0.045	–0.126
Krashininnikovia lanata	–0.241	0.283	—	—
Lactuca serriola[e]	0.350	–0.055	—	—
Lactuca spp.	–0.155	–0.251	—	—
Lappula redowskii	–0.092	–0.306	–0.302	–0.344
Lepidium densiflorum	0.685**	–0.132	—	—
Linum rigidum	–0.207	0.302	—	—
Lomatium macrocarpum	–0.295	0.299	—	—
Medicago sativa[e]	—	—	0.721**	0.314
Melilotus officinalis[e]	–0.351	–0.238	—	—
Monolepis nuttalliana	—	—	–0.174	–0.209
Monroa squarrosa[g]	—	—	–0.367	–0.141
Musineon divaricatum	–0.241	0.283	—	—
Opuntia polyacantha	–0.276	0.499*	—	—
Oxalis dellenii (stricta?)	0.440*	–0.451*	0.09	–0.269
Panicum capillare[g]	—	—	0.547*	0.419*
Pascopyrum smithii[g]	–0.756***	0.732***	0.425*	0.162
Physalis longifolia	0.356	–0.304	0.13	–0.228
Plantago patagonica	0.699***	–0.204	–0.039	–0.288
Polygala alba	0.251	–0.602**	—	—
Polygonum aviculare	0.038	–0.335	—	—
Psoralea cuspidata	0.481*	–0.189	—	—
Psoralea tenuiflora	0.286	–0.223	—	—
Salsola iberica[e]	0.457*	–0.629**	–0.252	–0.662**
Salvia reflexa	0.483*	–0.026	–0.084	–0.345
Schedonnardus paniculatus[g]	0.423*	–0.433*	–0.289	–0.516*
Setaria glauca[ge]	—	—	–0.193	–0.227
Sisymbrium altissimum[e]	–0.138	–0.068	—	—
Sisyrinchium montanum	—	—	0.001	0.361
Solanum rostratum	0.119	–0.754***	—	—
Sphaeralcea coccinea	0.778***	–0.343	—	—
Sporobolus cryptandrus[g]	0.441*	0.009	–0.499*	0.408
Stipa comata[g]	0.311	–0.288	—	—
Stipa viridula[g]	–0.528*	0.577**	0.763***	0.616**
Symphoricarpus spp.	0.356	–0.304	—	—
Taraxacum officinale[e]	0.156	–0.069	–0.025	0.340
Tradescantia spp.	0.520*	–0.542*	—	—
Tragopogon dubius[e]	–0.030	0.293	—	—
Verbena bracteata	0.295	–0.767***	–0.569**	–0.762***
Veronica arvensis[e]	0.137	–0.338	—	—
Vicia americana	–0.343	–0.350	—	—
Viola nuttallii	0.019	–0.328	—	
Zigadenus venonosus	0.492*	–0.292	—	—
Unknown grass 1[g]	—	—	–0.124	0.297
Unknown forb 1	–0.264	–0.164	—	—
Unknown forb 2	–0.264	–0.164	—	—
Unknown forb 3	–0.051	–0.374	—	—

Table 3. Continued.

SPECIES	Vegetation Axis I (r)	Vegetation Axis II (r)	Seed Banks Axis I (r)	Seed Banks Axis II (r)
Unknown forb 4	–0.228	0.010	—	—
Unknown forb 5	0.137	–0.338	—	—
Unknown forb 6	0.286	–0.223	—	—
Unknown forb 7	0.137	–0.338	—	—
Unknown forb 8	—	—	–0.466*	–0.422*

ues of 23% and 18%, respectively. The most abundant forbs off prairie dog colonies were *Tragopogon dubius* and *Hedeoma* species, each making up < 2.0% of the total plant cover. In contrast, cover of *P. smithii* and *B. tectorum* was dramatically lower on prairie dog colonies (2% and 1%, respectively), while several species of forbs had cover values > 1% on prairie dog colonies.

Similar patterns were found in the germinated seed banks. For instance, grass species accounted for 9 of the 21 species (43%) represented in the seed banks from uncolonized portions of the landscape and grass seeds accounted for 108 of the 146 seedlings (74%) that emerged from off the colonies. Five grass species from off the colonies were represented by more than 10 seeds each while only one forb species was represented by > 10 seeds. In contrast, forbs accounted for 66% of the species and 91% of the seedlings that germinated from soil collected on prairie dog colonies. Ten forb species but only three grass species were represented by > 10 seeds each.

Non-native (i.e., exotic) plant species accounted for a much larger portion of the plant cover off of prairie dog colonies than on them. This was primarily the result of significant abundance of *Bromus tectorum*, an introduced annual grass commonly found in the diet of many ungulate grazers (Whitson et al. 1996). There were more species of exotic plants on prairie dog colonies and they included several undesirable forb species, including *Convolvulus arvensis* (field bindweed), *Salsola iberica* (Russian thistle), and *Lactuca serriola* (prickly lettuce). Prairie dog colonies were generally not, however, reservoirs for seeds of exotic species at our study sites. In fact, one of the exotic species with the highest number of seedlings, *B. tectorum*, germinated from seeds found only off the colony. Three native species (*Amaranthus albus, D. papposa*, and *V. bracteata*) and one exotic species (*S. iberica*) were most strongly associated with on colony plots in the NMS analysis on seed banks.

There were significant differences in the germinable seed banks on and off of prairie dog colonies. The reason for this appears to be related to the presence of several species of forbs on colonies that were not found in uncolonized mixed-grass prairie. At least one of the germinating species from the colonies (*D. papposa*) was not a preferred food of prairie dogs in a study of stomach contents done in areas near our study sites (Summers and Linder 1978); this may contribute to its abundance in both the vegetation and the seed banks. Food preference may be a factor in the abundance of other species as well.

The percentage of annual species represented in the seed banks of the on-colony vs. off-colony plots was similar. However, seedlings of the annual forb *Verbena bracteata* were twice as abundant on colony as all other species combined, even though this species accounted for only 1.5% of the vegetation cover. No species off the colony dominated the seed bank in such a way.

The significant reductions in plant litter cover and increases in bare ground that we observed on the prairie dog colonies have been documented in other systems as well (Coppock et al. 1983b; Archer et al. 1987). These changes in vegetation structure can substantially alter the microenvironment of patches and significantly impact ecosystem processes such as nutrient cycling, primary production, and plant-soil water relations (Knapp and Seastedt 1986; Day and Detling 1994; Detling 1998). The reduction in dominant grasses and increase in subordinate forbs and less palatable grasses as a result of prairie dog colonization can also have important ramifications for community recovery or succession.

One species that bears mentioning is *Sporobolus cryptandrus*. This species was very scarce (< 0.25% cover) in the vegetation of prairie dog colonies and

Table 4. Number of seedlings of each species that germinated and emerged from soils collected off and on prairie dog colonies in Badlands National Park. Grass species are indicated by[g], exotic species by[e], and species with annual life histories by[a].

OFF COLONY Species	# Seeds	ON COLONY Species	# Seeds
Bromus tectorum[gea]	28	*Verbena bracteata*[a]	1973
Monroa squarrosa[ga]	21	*Dyssodia papposa*[a]	402
Panicum capillare[ga]	18	*Schedonnardus paniculatus*[g]	183
Sporobolus cryptandrus	17	*Euphorbia serrphyllifolia*[a]	129
Stipa viridula[g]	15	*Amaranthus albus*[a]	63
Verbena bracteata[a]	13	*Oxalis dellenii (stricta?)*	63
Medicago sativa[e]	5	*Salvia reflexa*[a]	52
Taraxacum officinale[e]	5	*Monroa squarrosa*[ga]	50
Dyssodia papposa[a]	4	*Salsola iberica*[ea]	28
Schedonnardus paniculatus[g]	4	*Euphorbia stictospora*[a]	20
Euphorbia glyptosperma[a]	3	*Monolepis nuttalliana*[a]	14
Pascopyrum smithii[g]	2	*Hedeoma hispidum*[a]	12
Salsola iberica[ae]	2	*Sporobolus cryptandrus*	11
Unknown grass 1[g]	2	*Panicum capillare*[ga]	8
Bouteloua curtipendula[g]	1	*Convolvulus arvensis*[e]	8
Euphorbia maculata[a]	1	*Lappula redowskii*[a]	7
Euphorbia serrphyllifolia[a]	1	Unknown forb 8	7
Helianthus annuus[a]	1	*Chenopodium desiccatum*[a]	5
Monolepis nuttalliana[a]	1	*Eragrostis cilianensis*[ge]	5
Sisyrinchium montanum	1	*Euphorbia glyptosperma*[a]	4
Unknown forb 8	1	*Kochia scoparia*[ae]	4
		Plantago patagonica	4
Total number of seeds	146	*Amaranthus retroflexus*[a]	3
Total number of grass seeds	108	*Taraxacum officinale*	3
Total number of species	21	*Conyza ramosissima*[a]	2
Total number of grass species	9	*Koeleria macrantha*[g]	2
		Andropogon gerardii[g]	1
		Conyza canadensis[a]	1
		Festuca octoflora[ga]	1
		Pascopyrum smithii[g]	1
		Physalis longifolia	1
		Setaria glauca[gea]	1
		Unknown grass[g]	1
		Total number of seeds	3069
		Total number of forb seeds	2805
		Total number of species	33
		Total number of forb species	22

was altogether absent off colonies. Yet several seeds of this species germinated from soils both on and off prairie dog colonies. *S. cryptandrus* is commonly abundant in the seed pool of North American grasslands, even when it is not a main constituent of the vegetation, and it is able to produce large quantities of seed even in dry years (Weaver and Mueller 1942; Lippert and Hopkins 1950; Abrams 1988). The presence of this species and other relatively poor forage species such as *Monroa squarrosa* and *Schedonnardus paniculatus* in the seed pool suggests that the more palatable forage species are being replaced and that the removal of prairie dogs will not result in the rapid reversion of colonies to representative mixed-grass prairie, but rather to communities composed of relatively poor nutritional quality species.

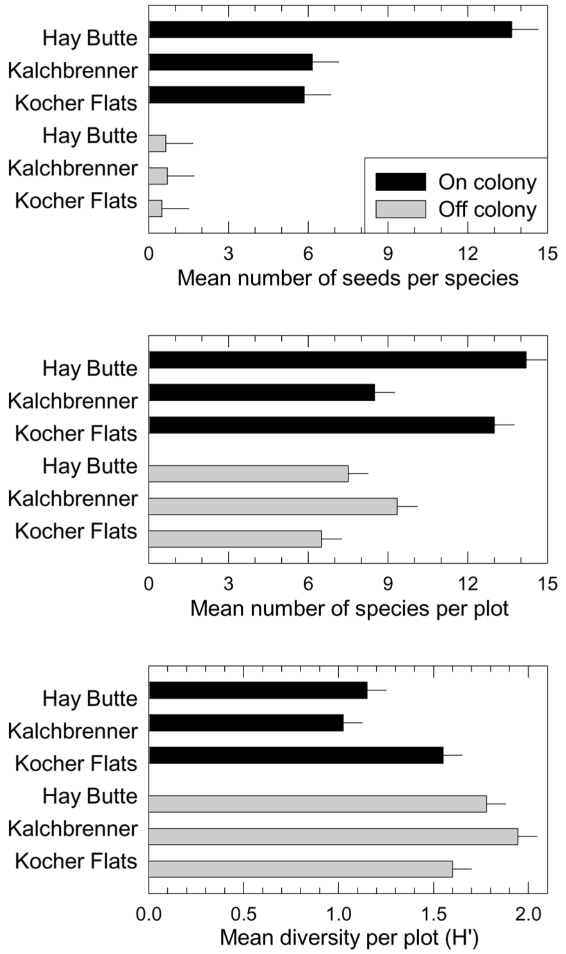

Figure 2. Community characteristics of the germinable seed bank on-colony (black) at 3 off-colony (shaded) at three sites at Badlands National Park. In each case, significant ($P < 0.05$) interactions were found between the sites and whether samples were collected on or off colony.

Across the historical range, the number and size of black-tailed prairie dog colonies have declined dramatically over the last century (Miller et al. 1994). Many times, the justification for prairie dog removal is the perceived competition between prairie dogs and cattle (Uresk 1985). Yet several studies suggest that ungulates may actually incur some nutritional advantage from feeding on colonies (Coppock et al. 1983a; Krueger 1986; Vanderhye 1985). Because ungulates spend more time on colonies than would be predicted by chance alone (Coppock et al. 1983a; Wydeven and Dahlgren 1985; Krueger 1986), they are likely to further impact colony patches above that already caused by the prairie dogs themselves. Continuous grazing and clearing of vegetation by prairie dogs and periodic grazing of colony patches by bison and other ungulates may be equally important in maintaining the vegetation characteristics of prairie dog colonies over short time periods (Cid et al. 1991), but the relative impact of prairie dog activity vs. ungulate activity on vegetation may change over longer periods of time. Our results suggest that, even if prairie dogs are extirpated from a colony, the likelihood is small that the land occupied by the colony will return to a successional state reflecting pre-colonization grassland unless steps are taken to restore the soil seed bank. Furthermore, even though ungulates can be important vectors for seed transport, it is likely that continued use of colony patches by native ungulates or livestock will delay the rate of recovery and prolong the time necessary for restoring colony patches to typical mixed-grass prairie.

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