PATTERNS OF PLANT SUCCESSION ON
POISONED PRAIRIE DOG TOWNS

by

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Patterns of Plant Succession on Poisoned Prairie dog Towns

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Plant succession in above-ground vegetation and soil seed banks following the poisoning of black-tailed prairie dogs (*Cynomys ludovicianus*) was studied at Wind Cave National Park, South Dakota. Prairie dog towns that were poisoned four to eight years previously were compared to both active prairie dog towns and uncolonized mixed-grass prairie.

Successional processes had occurred on the poisoned prairie dog towns as evidenced by significant increases in average vegetation height, percent cover of litter, and importance of exotic plants over the active prairie dog towns. The poisoned prairie dog towns were also significantly different than the uncolonized prairie having a shorter vegetation height, less importance of perennial grasses, and a greater importance of monocarpic plants.

Seed banks of all three treatments were studied using greenhouse germination. The poisoned prairie dog towns had a minimum of 256 seeds/l (12,806 seeds/m^2) in the top 5 cm of soil. Active prairie dog towns had a seed density of 294 seeds/l (14,706 seeds/m^2), and seeds/m^2). The seed banks of the active prairie dog towns and the poisoned prairie dog towns were similar in both density and composition, being dominated by native annual forbs such as *Veronica peregrina*, *Androsace occidentalis*, and *Hedeoma hispidum*. The uncolonized prairie had significantly smaller seed banks than the other two treatments and also had a greater percentage of graminoids, exotics, and polycarpic plants.

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CHAPTER I

INTRODUCTION

Ecology of Prairie Dog Towns

Black-Tailed Prairie Dogs

Description. Black-Tailed prairie dogs (*Cynomys ludovicianus*) are large, herbivorous, burrowing rodents weighing approximately 750 g as adults (Koford 1958). The original distribution of the black-tailed prairie dog spanned the short and mid-grass areas of the Western Great Plains from Montana to western Texas (Koford 1958). These prairie dogs are colonial animals and have a highly evolved social structure (Hoogland 1982, 1985). The locations of prairie dog colonies are called prairie dog towns. These prairie dog towns can range from several acres to nearly 25,000 square miles (Merriam 1901).

Current populations of prairie dogs are less than two percent of what they were fifty years ago due to widespread reduction programs aimed at reducing competition with livestock (Summers and Linder 1978). This prairie dog reduction program has largely been carried out through poisoning with zinc phosphide and has been shown not to be cost effective for increasing cattle production (Collins et al. 1984).

Diet. Early studies of prairie dog diets focused on whether the main component was grasses or forbs and conflicting results were found. One group (Clements and Clements 1940, Bond 1945, King 1955) found that prairie dogs prefer forbs, while the other group (Kelso 1939, Koford 1958) found that grasses were the most important part of the diet. Later studies found a wide range of dietary preferences depending upon available forage, but the general consensus is that graminoids are slightly preferred when available.

Fagerstone et al. (1977) showed that prairie dogs are opportunistic foragers capable of altering their diet to exploit a wide range of plant communities. They studied the effects of a prairie dog reduction program that used a selective herbicide (2,4-D) to kill forbs on prairie dog towns. The herbicide treatment greatly decreased forb cover on the towns without affecting graminoid cover. Before the treatment prairie dogs consumed 73% forbs and 5% grasses compared to 9% forbs and 82% grasses after the application. The major shift in diet seemed to have no effect on prairie dog weights or population sizes.

Despite being opportunistic feeders, prairie dogs are selective in their dietary habits. Careful studies of diet contents and vegetation availability have found a 25% (Uresk 1984) to 36% (Fagerstone et al. 1981) annual similarity between diet and plant cover. Preferences for individual plant species have been found as high as 65 times the availability in the vegetation while other available species are not eaten (Fagerstone 1979).

Although it has been hypothesized that selective herbivores should avoid plants with the C_4 photosynthetic pathway (Caswell et al. 1973), prairie dogs seem to select C_4 species equally with C_3 species. Fagerstone (1979) found that C_3 and C_4 species were equally preferred in the annual diet. Tieszen et al. (1988) used stable carbon isotopes to determine the percentage of C_4 plants in the diets of several herbivores at Wind Cave National Park. They found that the prairie dogs had the highest percentage use of C_4 plants out of all the herbivores studied.

Several studies have shown that prairie dog diets can have a large seasonal variation. Prairie dogs seem to prefer plants when they are actively growing, eating more C_3 grasses and spring annuals during spring and early summer, switching to C_4 plants in the late summer (Fagerstone 1979, Uresk 1984). Prairie dogs have also been found to eat cacti during the winter months, presumably to counter water stress (Kelso 1939, Tileston and Lechleitner 1966, Fagerstone 1979).

Other Impacts. Prairie dogs alter vegetation on their towns in ways other than herbivory. Prairie dogs create mounds of excavated soil at the entrances to their burrows that are 1 to 2m in diameter. These mounds are generally bare of vegetation and can number from 50 to 300/ha (Whicker and Detling 1988). Prairie dogs will also clip vegetation for nesting material or as an aid in predator detection (Koford 1958).

Population Fluctuations. Factors that have been found to influence prairie dog populations include degree of grazing by hoofed mammals, amount of time since prairie dog colonization, epidemic disease, poisoning by humans, and climatic variations. It has long been understood that severe amounts of grazing by large herbivores facilitates prairie dog colony expansion (Koford 1958). This expansion occurs because tall grasses that would normally inhibit prairie dog expansion are reduced by these other herbivores. In northeastern Montana, Knowles (1986) found that prairie dog colonies were significantly correlated with livestock grazing and other human disturbances.

When prairie dog towns are occupied for long periods of time the ground becomes denuded of vegetation. Coppock et al. (1983b) measured population densities of prairie dogs in a long occupied town at 50% of the densities of recently occupied areas and Archer et al. (1987) stated that prairie dogs abandon large portions of colonies after graminoids are reduced. Climatic fluctuations can accelerate changes due to occupation and grazing. Periods of drought should facilitate prairie dog town expansion at the perimeters of towns due to a reduction in vegetation height and an abandonment of older town centers because of reduced forage availability. Conversely, wetter periods should cause prairie dog town contraction, and recolonization of town centers (Koford 1958, White 1986, Klukas 1987).

Prairie dogs occasionally experience rapid population decimations. Because of their communal lifestyle prairie dogs are susceptible to epidemic diseases. Historically the most common disease is sylvatic plague which can destroy a town of prairie dogs in a single year (Koford 1958, Hansen and Gold 1977). Poisoning programs in the last century have also been very effective in reducing prairie dog numbers on a large scale (Collins et al. 1984).

Animals Associated With Prairie Dog Towns

Native Ungulates. The activities of prairie dogs alter vegetation structure and composition to such an extent that the towns become recognizably different to other species of animals and therefore receive different amounts of use by these animals. Koford (1958) early recognized that although prairie dogs compete with other animals for available forage, there may be beneficial relationships between prairie dogs and other animals.

In areas where they are present, bison (*Bison bison*)are conspicuous associates on prairie dog towns. Koford (1958) stated that there was "a reciprocal ecologic relationship between bison and prairie dogs each tending to maintain habitat ideal for the other". This statement was supported by more recent research. Coppock et al. (1983b) and Whicker and Detling (1988) found that bison strongly select prairie dog towns over uncolonized prairie, at least in the summer months. Analysis of foraging behaviors reveal that prairie dogs and bison have mutually beneficial effects on vegetation due to their grazing (Krueger 1986). Prairie dog towns are also preferred areas of bison wallowing (King 1955, Coppock et al. 1983b, Wydeven and Dahlgren 1985). These bison wallows are relatively bare depressions that contain unique vegetation assemblages (Koford 1958, Uno 1989).

Other native ungulates that have been found to feed on prairie dog towns are pronghorn antelope (*Antilocarpa* *americana*) and elk (*Cervus elaphus*). Pronghorn select prairie dog towns for feeding more often than bison while elk feed on prairie dog towns but to a lesser degree than bison (Wydeven and Dahlgren 1985). Analysis of foraging behavior show that pronghorns prefer prairie dog towns to uncolonized prairie and prairie dogs have neither a positive or negative response to pronghorn grazing (Krueger 1986).

Other Animals. Studies that have examined the populations of various other species in relation to prairie dog towns generally have found significant differences on and off towns. Studies of small mammal populations (Agnew et al. 1986, O'Meilia 1982) have found an increase in density but a decrease in species richness on prairie dog towns. Species that increased on prairie dog towns included grasshopper mice (*Onychomys leucogaster*) and deer mice (*Peromyscus maniculatus*), while hispid pocket mice (*Perognathus hispidus*) and Prairie voles (*Microtus ochrogaster*) decreased on prairie dog towns. Agnew et al. (1986) found that 13-lined ground squirrels decreased on prairie dog towns while O'Meilia (1982) found that they increased.

Agnew et al. (1986) also examined bird populations on and off prairie dog towns and found an increased bird density and species richness on the prairie dog towns.

These results contradict preliminary findings by Webb, Bennett and Preston (unpubl.) that found bird densities on prairie dog colonies to be less than in six other uncolonized grassland types. Bird species that Agnew et al. (1986) found to be significantly more abundant on prairie dog towns were horned larks (*Eremophila alpestris*), mourning doves (*Zenaidura macroura*), killdeers (*Charadrius vacitenus*), barn swallows (*Hirundo rustica*), and burrowing owls (*Athene cunicularia*).

Two separate studies have found that the desert cottontail (*Sylvilagus audubonii*) is strongly attracted to prairie dog towns. Dano (1952) found cottontail densities to be seven times greater on prairie dog towns and Hansen and Gold (1977) found populations approximately 20 times greater on prairie dog towns. Cottontails prefer prairie dog towns presumably for improved forage and for use of prairie dog burrows as shelter (Koford 1958).

Invertebrate animals can have a large impact on grasslands but have been poorly studied. Two studies have examined arthropod biomass in relation to prairie dog towns. O'Meilia (1982) found three times less biomass on prairie dog towns than off, but Agnew (1983) found no significant difference. Neither study examined differences of individual species or of species groups. Ingham and Detling (1984) measured populations of soil nematodes on and off prairie dog towns and found 3.5 times more individuals on prairie dog towns. Consumption of roots by nematodes averaged 12.6% of the annual net root production on prairie dog towns compared to 5.8% off of towns.

Vegetation on Prairie Dog Towns

Plant Communities. Describing a vegetation type typical of prairie dog towns can be difficult because many different vegetation types are associated with prairie dog towns. Often this variability is contained within a single town and is related to the amount of time the area has been colonized (Whicker and Detling 1988). Osborn and Allen (1949) listed seven concentric zones of vegetation that were similar to successional stages of abandoned farmland in the same area. The center of the town was described as a mat forb stage with the outer zones becoming more similar to the native prairie.

A common effect of prairie dog grazing is a decrease in the graminoid:forb ratio (Bohnam and Lerwick 1976, Agnew 1983, Coppock et al. 1983a, Archer et al. 1987, Whicker and Detling 1988) or an increase in forb cover (Agnew et al. 1986). This replacement of graminoids by forbs is moderate during the first eight years of prairie dog colonization but can be almost complete on areas colonized for more than 26 years (Coppock et al. 1983a).

Several studies have shown that plant species richness and diversity are greater on prairie dog towns than off (Koford 1958, Bohnam and Lerwick 1976, Archer et al. 1987), but Agnew et al. (1986) found a decrease in species richness on prairie dog towns. Collins and Barber (1985) concluded that plant diversity on prairie dog towns was greater than in grazing exclosures but less than on lightly grazed prairie. Age of prairie dog towns also has an impact with young towns being more diverse than old towns and town edges (Coppock et al. 1983a).

Vegetation Structure. The vegetation structure of prairie dog towns is often so different from the surrounding prairie that it creates a strong visual patch (Whicker and Detling 1988a). One reason for the visual impact is that prairie dog towns have a greatly reduced amount of litter and standing dead vegetation (Coppock et al. 1983a, Agnew et al. 1986, Archer et al. 1987). This makes green plant tissue more visible. Although more visible, there is generally a decrease in plant cover on prairie dog towns (Agnew et al.1986, Archer et al. 1987).

The height of vegetation on prairie dog towns is shorter than that on surrounding prairie due to both increased grazing, and clipping of unpalatable vegetation (Koford 1956, Agnew et al. 1986, Archer et al. 1987, Whicker and Detling 1988b). Agnew (1983) observed that during a wet year the height of vegetation on uncolonized prairie was much greater than in previous years but there was no change in the height on the prairie dog town suggesting that the prairie dogs keep a cap on the height of the vegetation.

Effects of Removal of Prairie Dogs on Vegetation

There have been a few studies that have examined plant successional changes in the first five years following removal of prairie dogs. Cid et al. (1991) measured vegetation in prairie dog exclosures for two years but did not measure pre-exclosure vegetation. Uresk (1985) measured plant production both before poisoning and 1 and 4 years after poisoning. Klatt and Hein (1978) examined vegetation on three prairie dog towns that had been poisoned 1, 2, and 5 years and compared those towns to an active town. Osborn and Allen (1949) examined a prairie dog town that had been naturally abandoned one year before.

These studies, in general, have either been inconclusive or contradictory. Cid et al. (1991) found an increase in both graminoid and total plant biomass two years after exclusion, but Uresk (1985) found no significant change in either measure and Klatt and Hein (1978) found a decrease in graminoid and total plant cover. Klatt and Hein (1978) found a slight increase in western wheat grass cover, and Uresk (1985) also found an increase in western wheatgrass production but he used a significance level of .20. Koford (1958) observed that after prairie dogs were removed from some areas, previously stunted shrubs grew rapidly. He also observed vegetative differences between a town that had been poisoned seven years earlier and adjacent prairie.

Soil Seed Banks

Introduction

> For too long ecologists and other field workers have tended to give greater emphasis to aboveground phenomena and pay less attention to the hidden life below the surface. (Baker 1989, pg. 21)

The soil seed bank is the total of all viable seeds present on or in the soil or associated litter (Simpson et al. 1989). Seed banks have been studied since Darwin (1859), but often they are ignored in studies of plant populations and communities where they may play an important role. Many studies of soil seed banks have been conducted in the last 25 years, but comparisons among the studies is often difficult because of the differences in methods (Simpson et al. 1989).

Methods Used to Study Seed Banks

Soil Sampling. The method of collecting soil samples can potentially have a large influence on the results of a seed bank experiment. Since seed numbers tend to decrease with soil depth (Kemp 1989), the depth of soil samples will affect the relationship between volume and area measurements of seed densities. Deeper soil samples will increase seed densities expressed in units of area, but will decrease seed densities expressed in units of volume. Plant litter potentially contains many seeds, and its inclusion or exclusion can alter seed densities.

Seed banks of many species are spatially clumped so that a large number of samples may be necessary to get a reasonable estimate of seed densities (Thompson 1986, Bigwood and Inouye 1988). Determination of seed bank composition is time consuming so it is often recommended that a large number of small samples is the most reliable method of seed bank sampling. The time of year the soil was sampled will also have an influence on the seed bank contents, especially in temperate climates (Thompson and Grime 1979).

Determining seed bank composition. Two types of methods are used to determine seed bank composition; the bioassay method of germinating seeds in the soil, and separation of seeds from the soil. The bioassay method involves placing the seeds in a greenhouse or other controlled environment and simulating conditions favorable to germination. Dormancy breaking methods such as cold stratification or soil mixing are often used, but it is often impossible to satisfy the germination requirements of all seeds in a sample, so bioassays generally underestimate the size of a seed bank (Simpson et al. 1989).

Two methods have been used to separate seeds from the soil for counting. Soils can be dissolved in aqueous solutions and the seeds "floated out" (Malone 1967), or soils can be passed through fine mesh sieves that trap the seeds. Both of these methods just count the number of seeds in the soil, but if information on viability is wanted then further tests must be done by either germinating the seeds or staining with tetrazolium.

Santanachote (1991) compared two methods of seed bank analysis; bioassay, and floatation. Her results show that neither of the methods is able to determine the complete composition of a grassland seed bank. Each of the methods revealed similar densities of seeds, but the species composition was different.

Seed Dormancy and Germination Requirements

There is a large variation in the length of time that a seed can remain dormant in the soil. Some trees, such as the para rubber tree (*Hevea braziliensis*) and quaking aspen (*Populus tremuloides*), must germinate within days or loose their viability, while others can remain viable for many years (Fenner 1985). There have been many studies attempting to determine maximum longevity of seeds, and some have been consequently found to be fraudulous (Priestly 1986, Baker 1989). The current record seems to be 10,000 year old *Lupinus arcticus* seeds from Canada (Porsild et al. 1967).

The physiological mechanisms of seed dormancy are complex and variable among plant species (Baskin and Baskin 1989). The environmental cues that stimulate germination are not only different among species, but can be variable within species or even change with time within an individual seed. Some of the environmental conditions that have been found to influence seed germination are moisture regimes, temperature regimes, light regimes, seed age, physical scarification, chemicals (both stimulatory and inhibitory), and biotic influences such as passing through an animal gut, presence of mycorrhizae, or proximity to a host plant root (Wells 1981, Fenner 1985, Baker 1989).

Evolutionary Considerations of Seed Banks

The presence of a large persistent seed bank can have a large evolutionary significance for a population. Germinating seeds from a persistent seed bank will be from parents existing at widely different times, giving these species an "evolutionary memory" (Fenner 1985). The presence of a large seed bank increases the size of the effective breeding population, increases genetic variation, and buffers a population against genetic drift and selection (Baskin and Baskin 1987, Levin 1990). Levin (1990) theorized that since mutation rates are known to increase with seed age, persistent seed banks may also be a source of genetic novelty and evolutionary potential.

Brown and Venable (1988) described with a mathematical model how seed bank "strategy" varies with the predictability of climatic conditions in desert annuals. They reasoned that annuals having a smaller persistent seed bank would have a more "conservative" growth form. Annuals with a larger seed bank can be more "mesic", being able to afford high mortality in bad years in exchange for "big bang" seed production in good years.

Seed Banks in Relation to Succession

Successional stage has been found to be very important in relation to the quanity of seeds in the soil. Early successional communities generally have larger seed banks than later successional communities (Donelan and Thompson 1980). Colonizing species usually have the largest seed banks within a community with climax species often underrepresented (Oosting and Humphrey 1940, Thompson 1978, Fenner 1985).

Some species with persistent seed banks are adapted to colonize a certain type of disturbance (Pickett and McDonnell 1989). In tropical forests seed banks often consist of gap colonizing species that are adapted to particular gap conditions such as treefall pits (Putz 1983, Lawton and Putz 1988). Other seed banks are adapted to larger scale disturbances such as fire (Marks 1974, Rundel and Parsons 1984, Parker and Kelly 1989).

CHAPTER II

STUDY SITE

Wind Cave National Park

Description

Wind Cave National Park is an 11,355 ha site on the southeastern edge of the Black Hills in western South Dakota. The Park ranges in elevation from 1,111m to 1,528m and is 20 - 25% ponderosa pine (*Pinus ponderosa*) forest and about 75% northern mixed-grass prairie (Coppock et al. 1983a). The Park originally was established for the underground cave system but is now also known for its native prairie ecosystem. Domestic animals have been excluded since 1946 and a 2.4m high fence encircles the Park, containing 350 - 400 bison, 300 - 500 elk, 75 - 150 pronghorn, and 80 - 125 mule deer (Coppock et al. 1983a, Wydeven and Dahlgren 1985, Cid et al. 1991).

Previous Ecological Work

Wind Cave National Park has long been the focus of prairie dog ecological research. Koford's (1958) extensive studies of prairie dogs took him all over the Great Plains, but Wind Cave was a principal area of study for him. Since that time, prairie dogs at Wind Cave have been used to study vegetation responses (Coppock et al. 1983a, Detling and Painter 1983, Archer et al. 1987, Whicker and Detling 1988a, 1988b, Cid et al. 1991), interspecific interactions with other animals (Coppock et al. 1983b, Ingham and Detling 1984, Wydeven and Dahlgren 1985, Krueger 1986), diet (Tieszen et al. 1988), mound histories and soil structure (Carlson and White 1987), behavior and dispersal (Garrett et al. 1982, Hoogland 1982, 1985), and management considerations (Dalsted et al. 1981, Coppock and Detling 1986, Klukas 1987). Wind Cave is also near Conata Basin and Badlands National Park, two other western South Dakota locations that have been used for prairie dog research.

Weather

Wind Cave National Park averages 44.2 cm of precipitation a year, almost two thirds of which falls as rain between April and August. During the period of vegetation measurements in 1989 the area was in the third year of a dry cycle. 1988 was the driest year since 1964

Table 2.1. Cumulative total precipitation in cm. at Wind Cave National Park headquarters for 1988-1990 and 26 year average.

	apr	may	jun	jul	aug	tot
1988	3.4	9.4	17.7	21.5	26.4	32.2
1989	9.1	15.6	18.5	26.0	29.2	41.6
1990	10.5					
avg	9.3	16.8	24.1	30.4	34.4	44.2

with 32.2 cm precipitation, and 1987 was the fourth driest year since 1964 with 36.5 cm. Total precipitation for 1989 (41.6 cm) was closer to the yearly average but the cumulative average during the summer was far below normal until heavy september rains (Table 2.1). Heavier than normal precipitation fell in spring 1990 with the cumulative total on May 1 (10.5 cm) greater than average (9.3 cm).

Prairie Dog Management Practices

Although some prairie dog towns at Wind Cave National Park are likely to have been occupied at least 7,000 years ago (Carlson and White 1987), Park personnel believed that populations in 1982 exceeded those of the past (WCNP 1982). Aerial photographs from 1938 were used to determine that prairie dog towns, at the time, covered less than 283 ha (ibid.). A prairie dog poisoning program from the mid 1940s to mid '50s reduced the area covered by prairie dogs to 134 ha.

No prairie dog management activities were undertaken from the mid 50's to 1982 and prairie dog populations expanded to cover 729 ha. by 1982 (WCNP 1982). It was believed that this large population of prairie dogs was an unnatural condition brought about by heavy grazing of captive ungulates. A prairie dog management plan was drafted in 1982 to reduce the area of prairie dog towns to 283 ha using zinc phosphide treated oats as poison. The prairie dog poisoning was undertaken from 1982 to 1987 along with some population "reduction by rifle". The poisoning was effective in reducing prairie dog town area to 283 ha, but with the cessation of management efforts in 1987 the expansion of prairie dog towns was renewed.

Site Selection and Histories

Protocol for Selecting Sites

In order to examine the patterns of secondary succession on poisoned prairie dog towns, the vegetation on the poisoned towns was compared with both active prairie dog towns and prairie that had no evidence of prairie dog colonization. Pre-poisoning vegetation data on the poisoned towns was unavailable, so locations of poisoned towns were different from active towns. An experimental design was used that had eight replicate transects in each of three treatments: Active, Poisoned, and Uncolonized. The 24 transects were selected in May 1989 and certain protocols were used to select transects within each treatment.

The number of possible locations for transects on poisoned towns limited the number of replicates per treatment. Poisoned towns were located from park documents and surveyed by foot. The 90 m transects were placed in areas that had no evidence of prairie dog activity but that did have inactive mounds with furthur evidence from vegetation and spider webs over old entrances. The transects were placed near the geographical center of the poisoned towns, or, where possible, more than one transect was used per town.

Transects for the active town treatment were located through areas that had current prairie dog activity. As with the poisoned towns, centers of smaller towns were used and larger towns often were split into more than one transect. An attempt was made to match geographical localities with the poisoned towns whenever possible, but because the poisoning was concentrated on the perimeter of the Park, this was not always possible.

The uncolonized prairie transects were the most difficult to select and potentially included the most observer bias. An effort was made to find prairie locations similar in slope, aspect, and soil to prairie dog towns but that had no known history of prairie dog occupation.

Transect Locations and Histories

The names of the 24 transects, their abbreviations, and the figure they are graphed on, are summarized in Table 2.2. The transects have different histories of prairie dog occupation and human disturbance, as well as different environmental conditions that have had an effect on the vegetation and seed banks at those sites.

Southwest Region. Ten transects are located in the southwest portion of the Park near the Park headquarters and cave system (fig. 2.1). The Bison Flats area south of the Park headquarters contains a small area of ancient mounds and had a 12 ha prairie dog town in 1938. This praire dog town expanded to 261 ha by 1982 and to 421 ha by 1986. In March, 1986 the prairie dog town was reduced to 77 ha. The Bison Flats (1A) transect is located in an area of ancient mounds and has been occupied at least since 1938. Sites 1P (Windy Point) and 2P (E Bison Flats) are located near the perimeter of the prairie dog

Table 2.2. Names, abbreviations, and Figure locations for the 24 transects used in the study.

Transect Name	Abbr.	Fig.
Active Towns		
Bison Flats	1A	2.1
Wind Cave Canyon	2A	2.1
Research Reserve	3A	2.1
Norbeck	4A	2.1
Pringle Cut-off	5A	2.2
Rankin Ridge	6A	2.2
Central Highlands	7A	2.3
Southeast	8A	2.4
Poisoned Towns		
Windy Point	1P	2.1
East Bison Flats	2P	2.1
North Boundary	3P	2.1
Southeast Norbeck	4P	2.2
South Sanctuary	5P	2.2
North Sanctuary	6P	2.2
West Boland	7P	2.5
Southeast Boland	8P	2.5
Uncolonized Prairie		
Southwest of Bison Flats	1U	2.1
Shirttail Trailhead	2U	2.1
Beaver Creek	3U	2.1
Northwest of Sanctuary	4U	2.2
Southwest of Central Highlands	5U	2.3
Upper Highlands	6U	2.3
Northeast of Southeast	7U	2.4
Northwest of Boland	8U	2.5

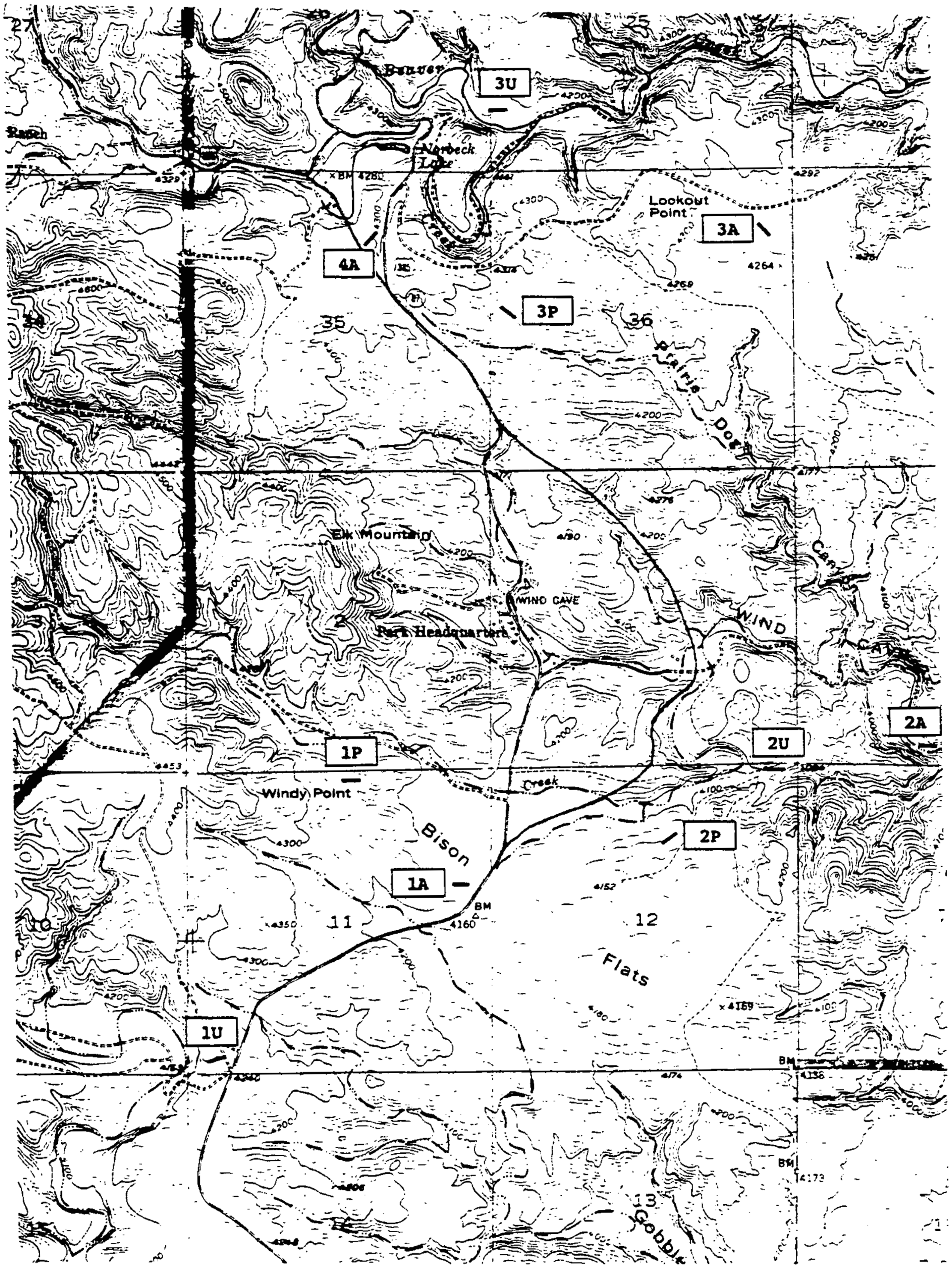

Figure 2.1. Locations of transects in the southwestern regions of the park.

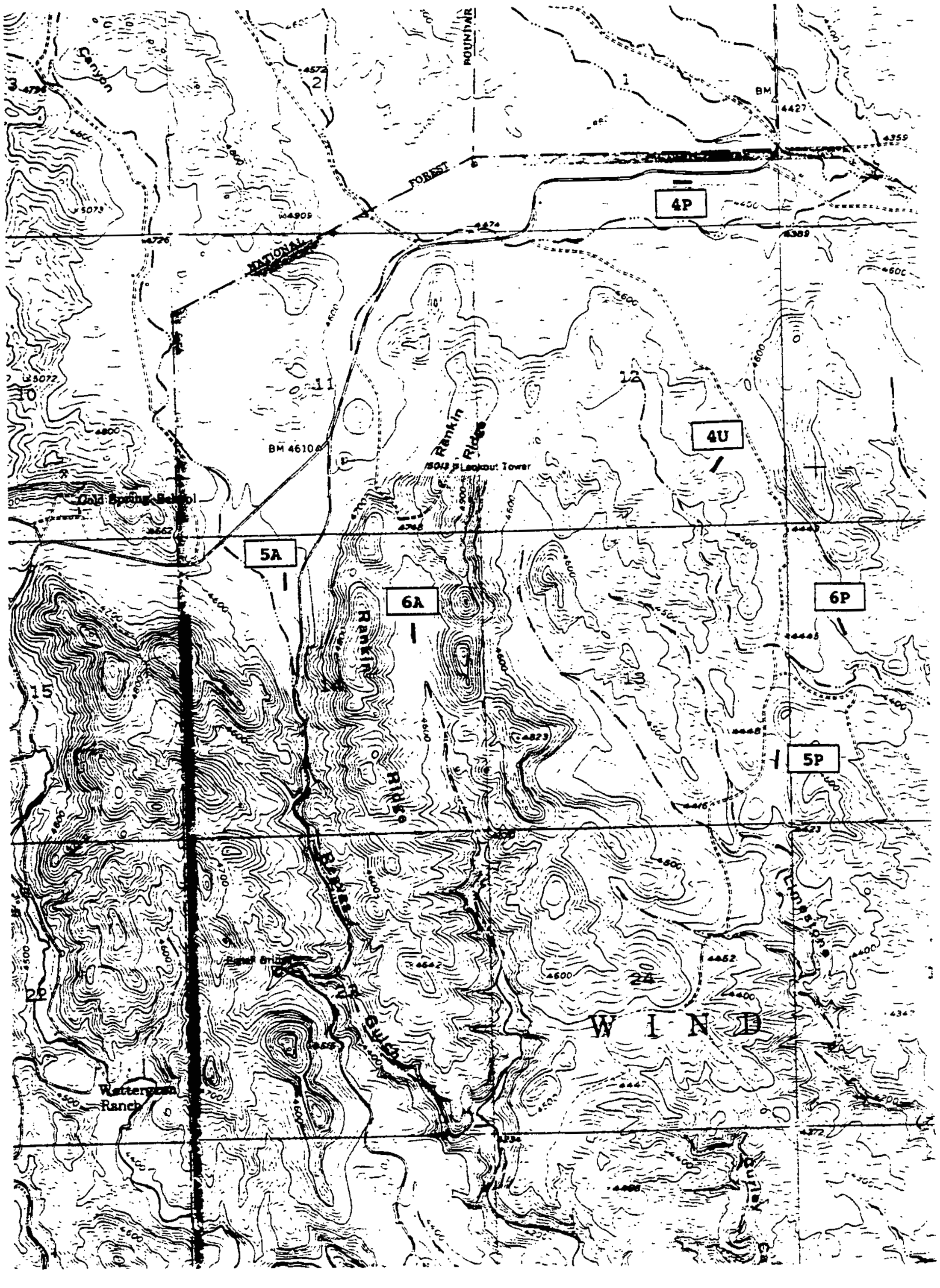

Figure 2.2. Locations of transects in the northwestern region of the park.

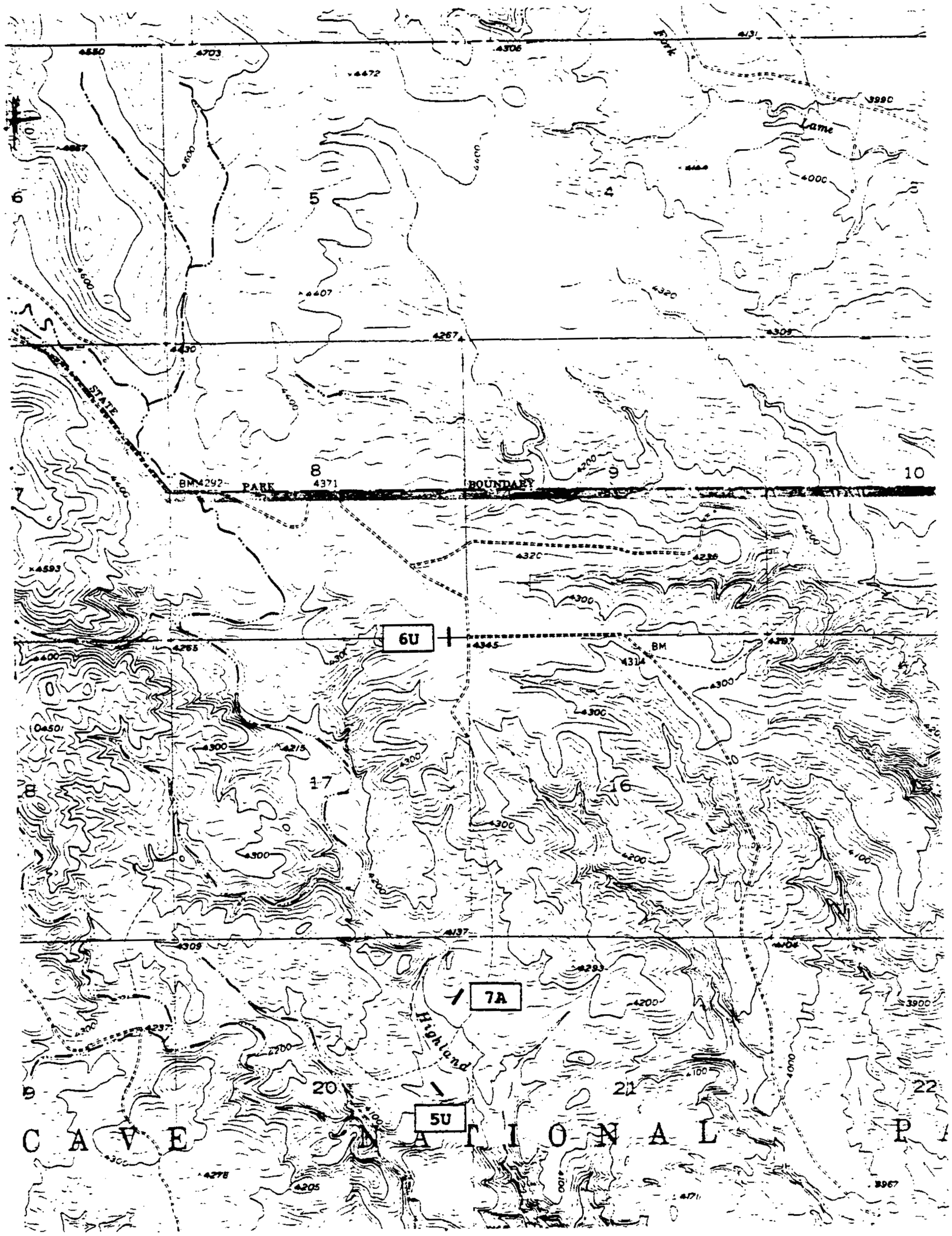

Figure 2.3. Location of transects in the central region of the park.

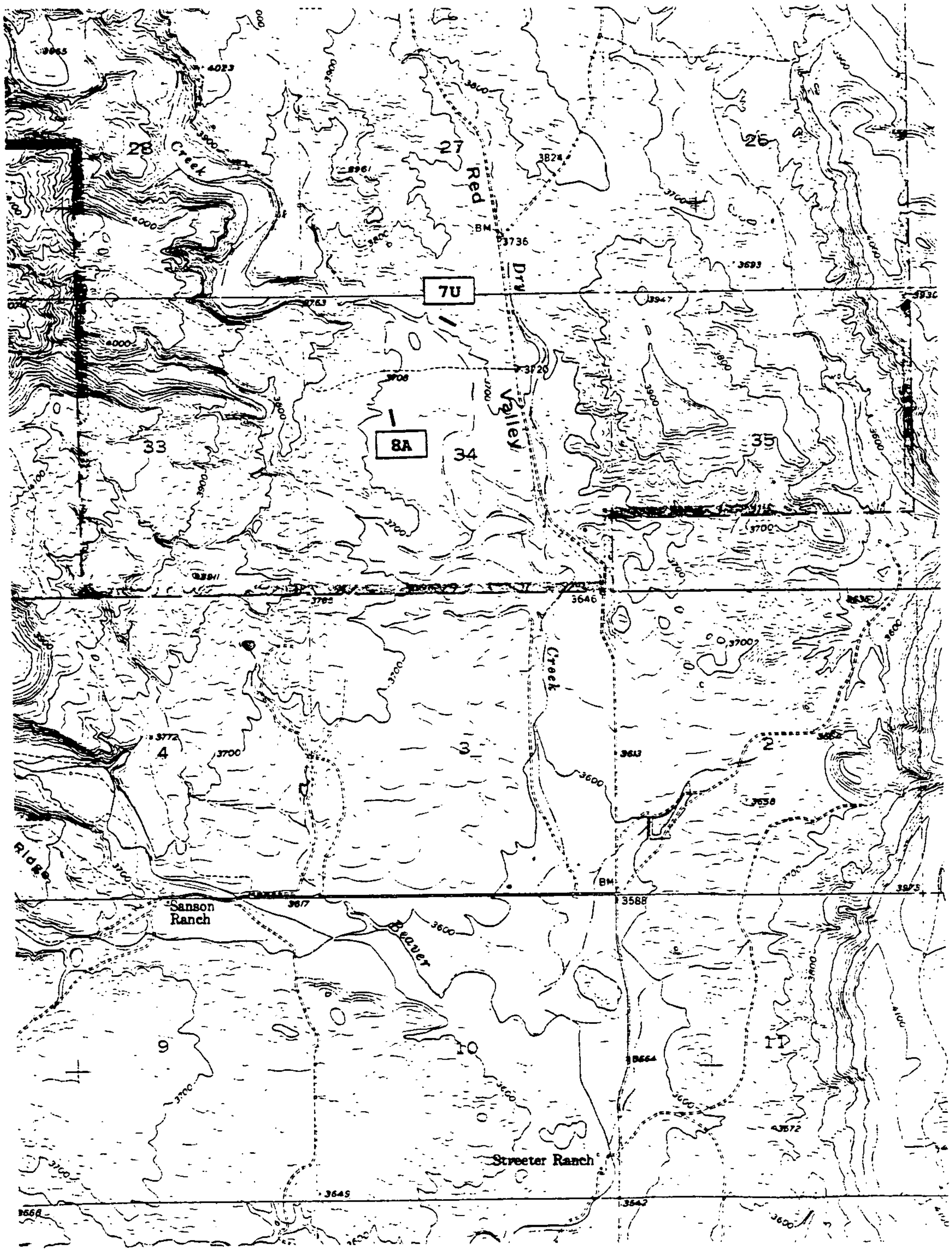

Figure 2.4. Location of transects in the southeastern region of the park.

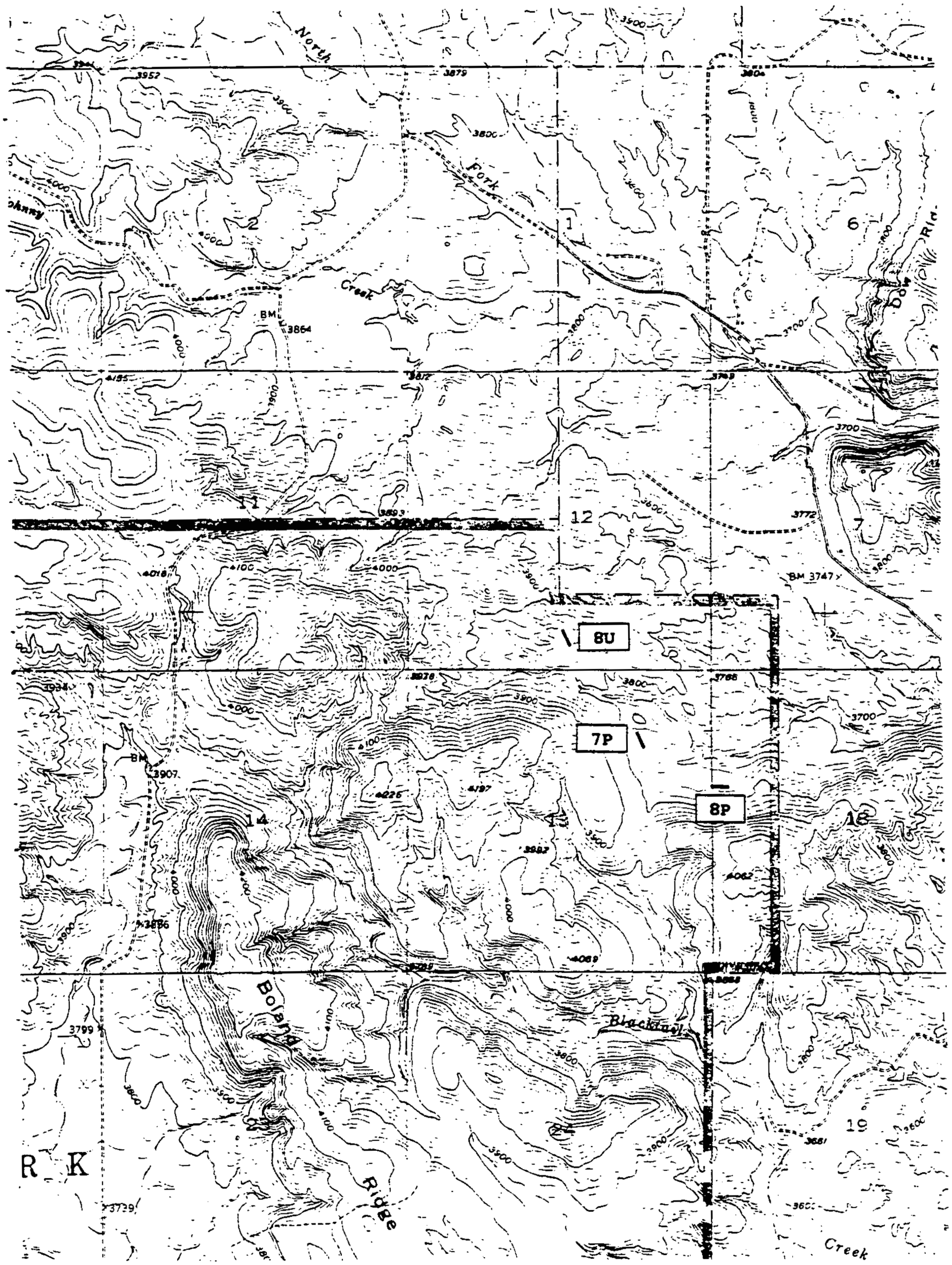

Figure 2.5. Location of transects in the northeastern region of the park.

town as it existed in 1982. These sites were probably only occupied 5-10 years before being poisoned and were in the fourth year of succession since the prairie dogs were removed. Sites 1U (SW Bison Flats) and 2U (NE Bison Flats) are both located on the edge of Bison Flats and have no evidence of any prairie dog use.

The Wind Cave Canyon prairie dog town (2A) is a small town (2 ha) located at the bottom of a canyon. This town was first colonized in 1976 and has been continuously occupied since. Birth control experiments were carried out on this town from 1980 to 1984 and may have kept this town to its small size. The Research Reserve (3A) transect is located on an area that has been occupied by prairie dogs at least since 1938. This area may be very old but it shows less evidence of ancient mounds compared to other areas of the Park.

The Norbeck prairie dog town, like Bison Flats, was a small town (14 ha) in 1938 that expanded to 95 ha at the time it was first reduced by poisoning in 1985 to 8 ha. Transect 4A (Norbeck) was probably first colonized around 1938 and is part of the remaining 8 ha. Transect 3P (SE Norbeck) was colonized sometime between 1938 and 1982 and the prairie dogs were removed 4 1/2 years before this study. The Beaver Creek (3U) transect is located at the bottom of a canyon with a similar topography as the Wind Cave Canyon prairie dog town but it has no evidence of prairie dog use.

Northwest Region. The northwest region (fig. 2.2) is in the highest and most forested portion of the Park. There are four areas in this region that have been historically used by prairie dogs. The Pringle Cut-off town is a location of some ancient mounds (>500 yrs. White 1986). The town was last colonized in 1967 and covered 61 ha in November 1987 when the town was reduced to 28 ha. Transect 5A (Pringle Cut-off) is located on an active part of the town that is away from the identified ancient mounds.

The Rankin Ridge prairie dog town (transect 6A) was colonized in the late 1940's, poisoned out in 1953, and recolonized in 1967 (Coppock et. al. 1983a). Transect 4P (North Boundary) is located on ancient mounds. The town expanded from 12 ha in 1938 to 69 ha in November 1982 when the entire town was poisoned. The area has been retreated several times between 1983 and 1987, and some recolonization along this transect occurred during the course of this study.

The Sanctuary town was first colonized between 1938 and 1982. In 1982 it covered 55 ha and the entire town was poisoned in 1983. Further reduction of prairie dogs occurred 1984 to 1986 and a small colony was present in 1989. Transects 5P (S Sanctuary) and 6P (N Sanctuary) were both located away from this small colony. Transect 4U (NW of Sanctuary) was located north west of the Sanctuary town and has no evidence of any prairie dog use.

Central Region. In 1938, the central region (fig. 2.3) had the two largest prairie dog towns in the park, the Upper Highland and Central Highland Creek towns which together covered 107 ha. The towns were poisoned in the 1940's and 1950's. The Central Highlands town re-activated in 1970 and had grown to 37 ha by 1986 without any controls. Transect 7A (Central Highlands) is located near the center of this town. Transect 5U (SW of Central Highlands) was an active prairie dog town in the 1950's but has not been colonized in the last 30 years. Transect 6U (Upper Highlands) is near ancient mounds, was briefly cultivated in the 19th century and was part of the Upper Highland town before being poisoned in the late 1940's.

Eastern. The eastern region is located towards the edge of the Black Hills and has soils that are different than the rest of the Park. The Southeast prairie dog town (fig. 2.4) was once cultivated and was first colonized in 1952 or 1953. The town covered 105 ha in October of 1983 when the entire town was poisoned. Further reduction was carried out between 1983 and 1986. Transect 8A (Southeast) is on a re-established town of about 8 ha. Transect 7U (NE of Southeast) is in an area never utilized by prairie dogs.

The Boland Ridge (or Northeast) prairie dog town (Fig. 2.5) shows evidence of cultivation in the late 1800's and was colonized with prairie dogs by 1938. The town was later poisoned and re-activated in 1967. The entire town was again poisoned in 1982 but recolonized by 1984. Heavy rifle reduction from 1984 to 1987 removed most of the prairie dogs and I observed only two occupied burrows there during my study. Transects 7P (NW Boland) and 8P (SE Boland) are on the eradicated town and transect 8U (NW of Boland) is on adjacent grassland.

CHAPTER III

VEGETATION PATTERNS

Materials and Methods

Field Methods

Each of the 24 transects that were established in May 1989 were sampled for above-ground vegetation composition four times between May 1989 and June 1990. Two of the sampling periods, May '89 (5/20/89 - 5/30/89) and May '90 (5/26/90 - 6/1/90), were done in the spring to detect spring annuals and C^3 grasses. The other two sampling periods, July '89 (7/2/89 -7/12/89) and August '89 (8/4/89 - 8/12/89), were done in the summer to detect C^4 grasses, and late summer annuals and perennials.

A regularly spaced quadrat technique (Kershaw and Looney 1985) was used to measure the vegetation on all transects. This method consisted of placing $1m^2$ quadrats every ten meters along the 90 meter transect, resulting in ten quadrats per transect per sampling period. At each of the 960 quadrats studied (10 quadrats X 24 transects X 4 sampling periods), every species present in the quadrat was recorded. If a certain species was unidentifiable it was placed into a category such as perennial grass or dicot seedling. For each species in a quadrat estimates were made of percent cover, number of individuals and average height. Estimates also were made of the percent of the quadrat covered by bare ground and litter. Plant cover was defined as green plant tissue or woody stems supporting green plant tissue. Litter was defined as dead plant tissue and bare ground as exposed soil.

Statistical Methods

Importance Values. Importance values were created for each species in each transect. These importance values are similar in nature to those used by Curtis and MacIntosh (1951). The importance value of a species equals the average of the relative frequency, relative density and relative cover. Relative frequency was defined as the number of quadrats a species was found in during the four sampling periods divided by the total frequency of all species in a given transect. Relative density was defined as the number of individuals of a species divided by the total number of individuals in a transect. Relative cover was the total percent cover of a species divided by the total cover of all plants (excluding bare ground and litter). All three measures are frequencies so that a summation of all species in a transect will equal one. The importance value, being an average of the three, is also a frequency and can be expressed either as a decimal frequency or as a percentage.

The benefit of importance values is that they reduce the dimensionality of a large data set without underrepresenting important components of the community. For example, species that are characterized by large individuals may account for a large proportion of cover but have a very low density while small annual forbs may have high densities with very little cover. Frequency is a way of recognizing species that are consistently distributed throughout the community in space and time.

Vegetation Height. Average height of the vegetation was determined by averaging the height of all species in a quadrat weighted by the cover of each species. Since bare ground and litter were excluded from this analysis, this is a measure of vegetation height and not quadrat height. Transect height for a sampling period was determined by averaging the height of the ten quadrats.

Plant diversity. Plant diversity was measured using the formula EXP(H′). This measure is a modification of the Shannon-Weaver index (Shannon and Weaver 1949) of information theory. The exponential form is used to simplify interpretation because it is equivalent to the number of equally common species (MacArthur 1965, Peet 1974). The measure also is beneficial because the results are the same at all bases of logarithms. The species importance values from each transect were used in computing the diversity formula.

The diversity of plants was also described using two measures of species richness. Richness/m^2 was computed as the average number of species per quadrat and total richness as the total number of species encountered in a transect over the four sampling periods.

Species Groups. To reduce the amount of data for some analyses, species with similar traits were grouped together. Three dichotomous divisions were made for all of the species: graminoid:forb, monocarpic:polycarpic, and native:exotic. Graminoids were defined as all species belonging to the families Poaceae, Cyperaceae, and Juncaceae, while all other species were defined as forbs. Monocarpic plants flower only once in their lifetime, which in this study only included annual and biennial plants. Polycarpic plants flower more than once in their lifetime and are equivalent to perennial plants in this study. Exotic plants were plants not known to grow on the study site in historical times. Exotic plants were determined by referencing several floras (Weber 1976, Dorn 1977, Great Plains Flora Association 1986), if none of the floras mentioned that the plant was exotic, introduced, etc. then the species was considered native. These dichotomous variables can be expressed either as percentages or ratios.

Univariate Analyses. Tests for significance among treatments for single variables were done with a oneway anova and a Duncan's multiple range test using the SPSS computer program (SPSS-X 1988). To improve the accuracy of the anova analysis, most variables were transformed to improve normality and homogeneity of variances (Sokal and Rohlf 1981). Proportional data (importance values and cover) were transformed using the angular transformation (arcsin(sqrt(p))) and other data (ratios and height) were transformed using a logarithmic transformation. All transformed variables were retested for normality and homogeneity of variances and only those transformations that reduced Cochran's C (more homogeneous variances) and Kolmogorov-Smirnov's D (more normal distribution) (Sokal and Rohlf 1981) were used.

Multivariate Analyses. Two different multivariate analyses were used to describe the data set in reduced dimensions, principal components analysis and discriminant function analysis. Principal components analysis is a method that produces linear combinations of variables (factors) that maximally separate objects (transects). Successive factors are constructed to be uncorrelated with previous ones (James and McCulloch 1990). The method allows data to be described with a fewer number of variables, but the variables themselves become more difficult to explain. Principal components analysis requires no formal assumptions (James and McCulloch 1990) but results are generally improved when the data are normal and variances are homogeneous. For this reason, transformed variables were used for analysis.

Discriminant function analysis is similar to principal components analysis but *a priori* groups are defined and the analysis determines functions that best discriminate between the groups. Discriminant function analysis is most robust with many objects and few variables. Williams and Titus (1988) arbitrarily recommended that group size be three times the number of variables. Other limitations to discriminant function analysis can be avoided with cautious interpretation.

Results

Community Attributes

Vegetation Height. The mean height of the vegetation on the poisoned prairie dog towns was both significantly taller than on active towns and significantly shorter than on uncolonized prairie (Table 3.1). This relationship of intermediate height occurred during all four sampling periods. The vegetation heights on both the poisoned and uncolonized treatments were higher in May 1990 than in May 1989, probably due to increase moisture availability. The active colony sites showed no increase in height during the same period which corroborates with similar findings of Agnew (1983).

Table 3.1. Mean vegetation height in cm for the three treatments during each sampling period weighted by percent cover. Means of all three treatments significantly different each month and total using Duncan's procedure at $\alpha = 0.01$.

		May '89	July '89	Aug '89	May '90	Mean
Active	X	6.0	5.4	6.3	5.9	5.9
	SE	0.4	0.5	0.4	0.4	0.4
Poisoned	X	9.2	6.9	9.2	11.2	9.1
	SE	0.7	0.5	0.6	1.2	0.6
Uncolonized	X	10.9	10.3	11.1	15.7	12.0
	SE	1.1	1.2	0.8	1.5	1.1
Mean	X	8.7	7.5	8.8	10.9	
	SE	1.0	1.1	0.9	1.8	

Plant Diversity. Plant diversity and species richness for the three treatments are summarized in Table 3.2. The poisoned prairie dog towns had a slightly lower mean diversity and species richness than both the active towns and uncolonized prairie, but this difference was not significant at $\alpha = .05$. It appears from this study that prairie dogs have no significant effect on total plant diversity or richness.

Species Groups.

The four main categories of quadrat cover are summarized in Figure 3.1. In all cases the mean values of the poisoned treatment fell between the values of the other two treatments. For all four of the categories, the active and uncolonized treatments were significantly different ($\alpha = .05$). The effects of prairie dog occupation were a decrease in graminoids and litter, and an increase in

Table 3.2. Plant diversity and species richness (±SE) for the three treatments. Plant diversity is measured as EXP(H′) and richness as number of species encountered. No means are significantly different among treatments at $\alpha = .05$.

	Diversity	Richness/m^2	Total Richness
Active	17.5(±1.3)	7.3(±0.3)	46.2(±2.4)
Poisoned	15.0(±1.4)	6.4(±0.3)	40.5(±2.3)
Uncolonized	17.0(±1.5)	6.8(±0.4)	44.3(±2.7)

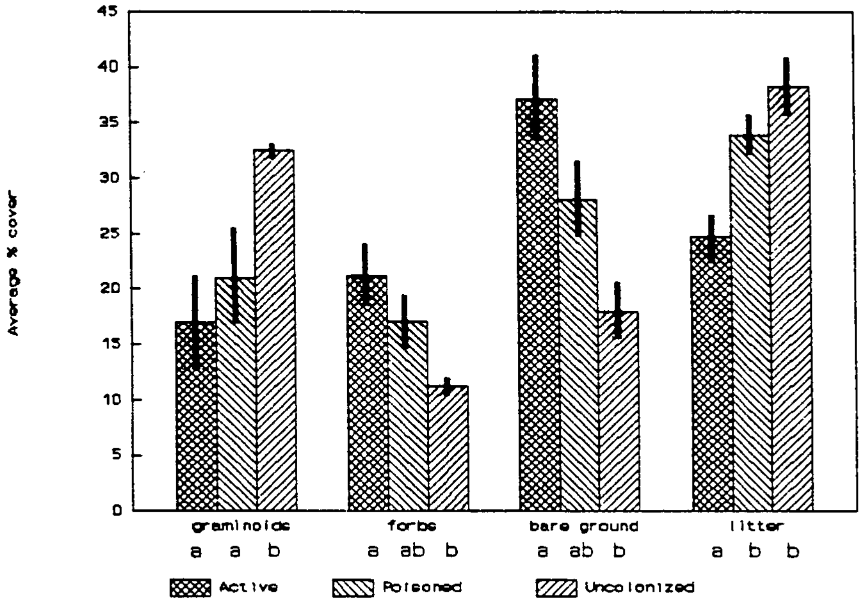

Figure 3.1. Distribution of the four main categories of cover pooled across the four sampling periods. Error bars are ± 1 SE. Different letters among treatments within a group are significantly different ($\alpha = .05$).

forbs and bare ground. The poisoned treatment had significantly fewer graminoids than the uncolonized treatment and more litter than the prairie dog towns.

The relative importance of the three main species divisions is shown in Figure 3.2. The percentage importance of graminoids was significantly higher on the uncolonized prairie than on the active towns, while the poisoned town had a mean value that was intermediate to the other two treatments. The poisoned town had the greatest importance of monocarpic plants, significantly

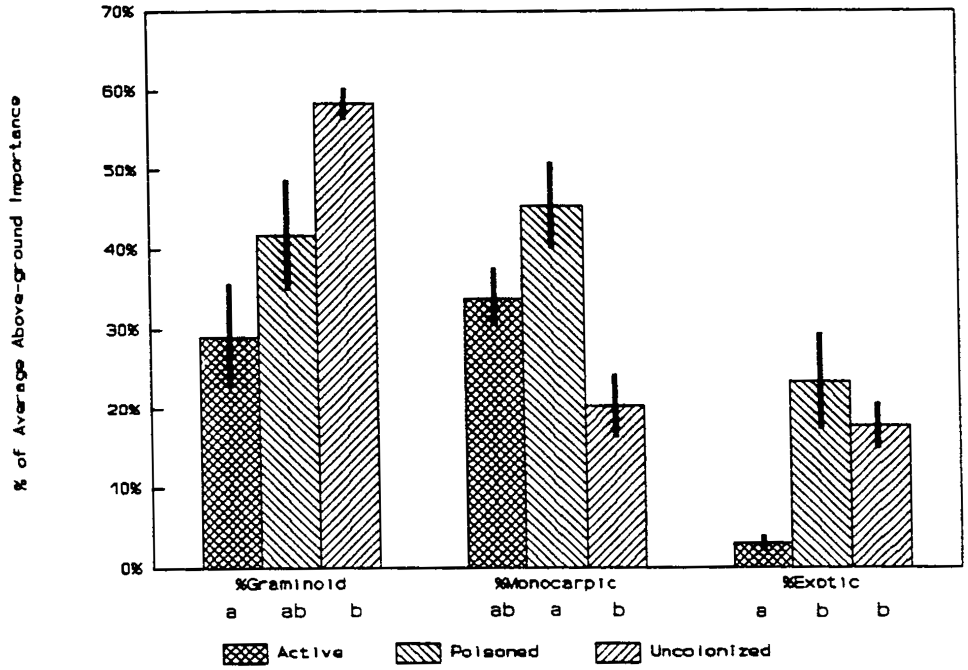

Figure 3.2. Percent of the above-ground importance for graminoids, monocarps and exotic plants. Error bars are ± 1 SE. Different letters among treatments within a group are significantly different ($\alpha = .05$).

more than the uncolonized prairie. The percent importance of exotics on the prairie dog towns was very low, ranging from 0 to 8% on the eight transects studied. The average of 3.0% exotics was significantly lower than the other two treatments.

By combining the three species divisions, species groups were developed. The six main species groups are graphed in figure 3.3. The significant effects of prairie dog colonization are a decrease in both native and exotic perennial grasses and an increase in both

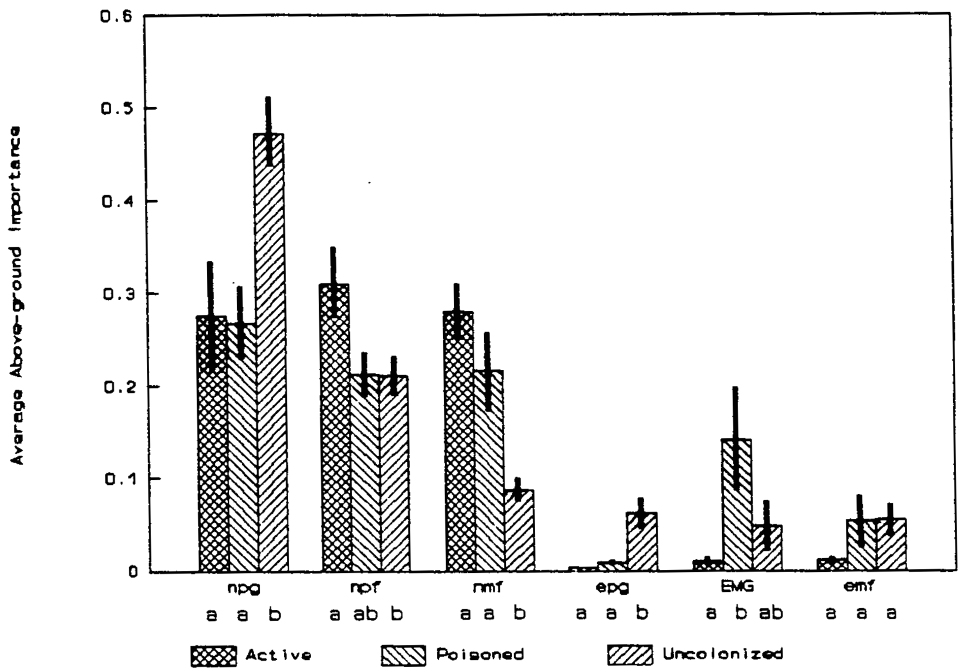

Figure 3.3. Average above-ground importance for the six main species groups. Different letters among treatments within a group are significantly different ($\alpha = .05$). Key: N=native, E=exotic, P=polycarpic, M=monocarpic, G=graminoid, F=forb.

towns had a significant increase in exotic monocarpic graminoids and a near significant decrease in native polycarpic forbs when compared to the active towns. When compared to the uncolonized prairie, the poisoned towns had significantly fewer perennial grasses and significantly more native monocarpic forbs.

Selected Autecology

Native Graminoids. The two most common grasses on

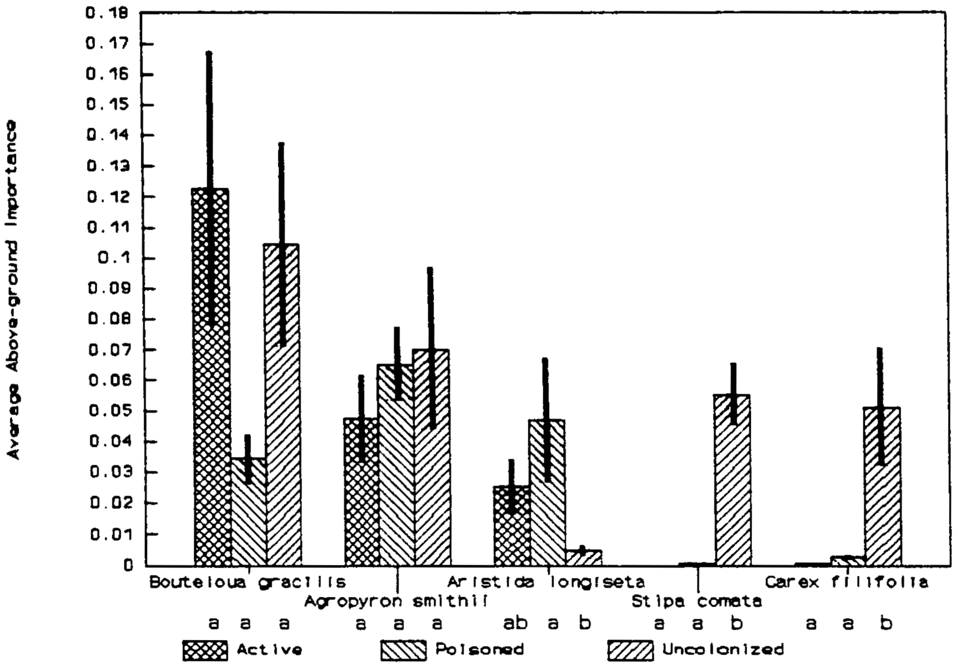

Figure 3.4. Relative importance of selected native graminoids. Error bars are ± 1 SE. Different letters among treatments within a species are significantly different ($\alpha = .05$).

prairie dog towns, *Bouteloua gracilis* (blue grama) and *Agropyron smithii* (western wheat grass), showed no significant differences among the three treatments (Figure 3.4). Blue grama did show a dramatic reduction on the poisoned towns but this was possibly due to random fluctuations. *Aristida longiseta* (red three-awn) had the greatest importance on the poisoned town, significantly greater than on the uncolonized prairie. This species is known to be associated with prairie dog towns and to be fairly unpalatable to prairie dogs (Koford 1958,

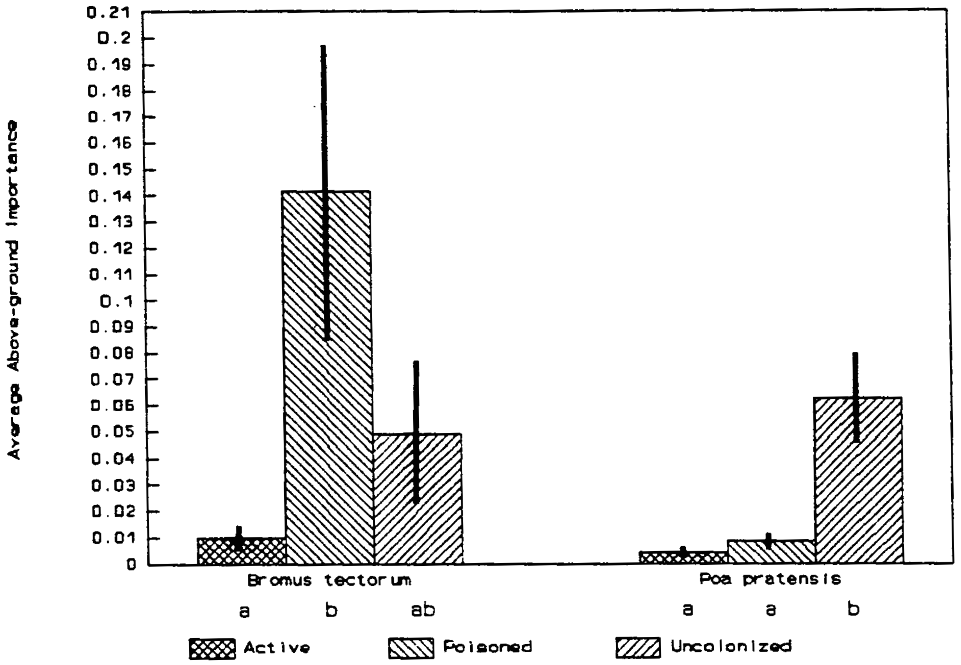

Figure 3.5. Relative importance values of selected exotic graminoids. Error bars are ± 1 SE. Different letters among treatments within a species are significantly different ($\alpha = .05$).

Fagerstone 1979). *Stipa comata* (needle and thread) and *Carex filifolia* (threadleaf sedge) are both much more common on uncolonized prairie than on prairie dog towns. Neither of these species showed a significant increase on the poisoned towns.

Exotic Graminoids. Only two exotic graminoids were found in moderate amounts in the above-ground vegetation. *Bromus tectorum* (cheatgrass) is an annual grass that is known as a noxious weed (USDA 1937). Its highest impor-

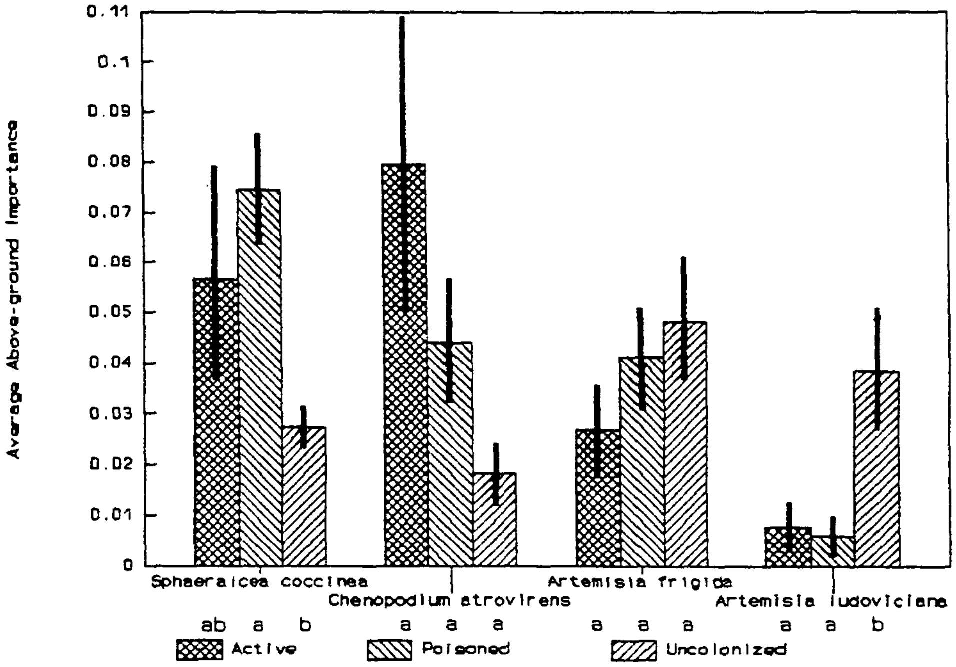

Figure 3.6. Relative importance values for selected native polycarpic forbs. Error bars are ± 1 SE. Different letters among treatments within a species are significantly different ($\alpha = .05$).

tance value was on the poisoned treatment, where it was significantly greater than on the active towns (Figure 3.5). *Poa pratensis* (Kentucky blue-grass), a perennial grass, had a similar distribution to needle and thread and threadleaf sedge, with importance values large only on uncolonized prairie.

<u>Native Polycarpic Forbs</u>. Of the four main native polycarpic forbs, none showed any significant change after poisoning of prairie dogs (Figure 3.6).

Sphaeralcea coccinea (scarlet globe-mallow) was significantly more important on the poisoned towns than on the uncolonized prairie and *Artemesia ludoviciana* (prairie sage) was more important on the uncolonized prairie than the other two treatments. Neither *Chenopodium atrovirens* (goosefoot) nor *Artemesia frigida* (pasture sagebrush) showed significant differences among the treatments.

Native Monocarpic Forbs. *Lappula redowskii* (stickseed) had the highest mean importance value of all monocarpic forbs for all three treatments. The importances of stickseed and *Hedeoma hispidum* (rough pennyroyal) were significantly greater on both the active and poisoned treatments than on the uncolonized prairie (Fig. 3.7). *Plantago patagonica* (wooly plantain) had greater importance values on active towns than on uncolonized prairie, and *Androsace occidentalis* (Carolina whitlow-grass) showed no significant differences among the treatments.

Multivariate Ordinations

Principal Components Analysis. A principal components analysis was run on the seven variables shown in Table 3.3. Three factors extracted by the analysis were used for study. The first principal component factor

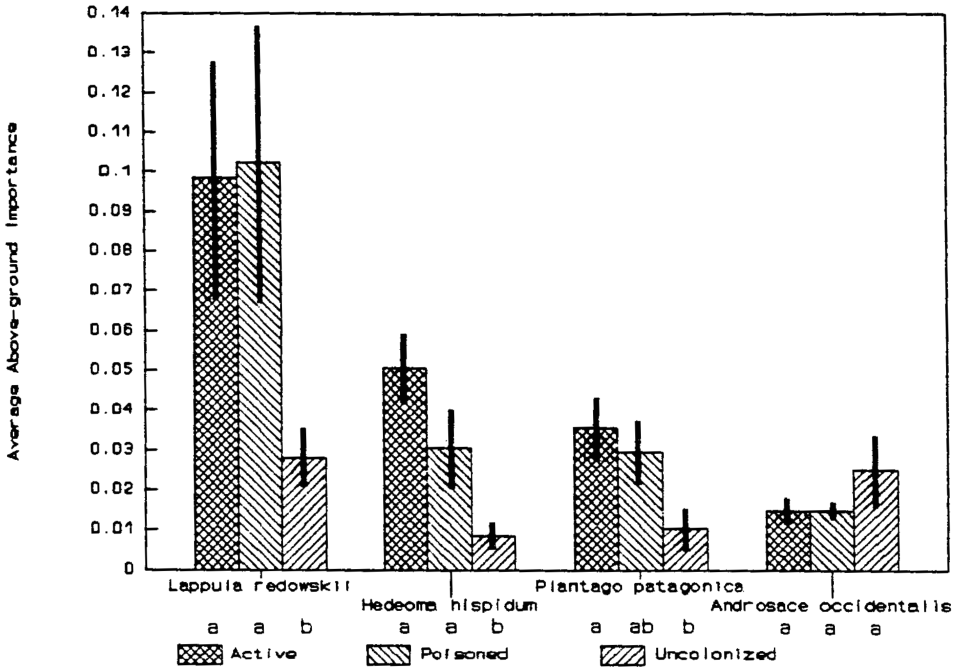

Figure 3.7. Relative importance values of selected native monocarpic forbs. Error bars are ± 1 SE. Different letters among treatments within species are significantly different ($\alpha = .05$).

explained 49.3% of the variation in the data set, the second factor 20.3%, and the third factor 13.3%. The three factors together explained 82.8% of the variation.

The values in Table 3.3 are "loadings" of variables on the three factors. For example, factor 1 has large positive loadings on gram:forb and total cover, and large negative loadings on monocarp:polycarp and bare:litter. These variables taken together describe a gradient from monocarpic forbs, with bare ground and low cover to polycarpic graminoids with litter and high cover. This

Table 3.3. PCA factor loadings using the rotated factor matrix for the first three factors.

	Factor 1	Factor 2	Factor 3
Mono:Poly	-.8077	.1330	-.2282
Gram:Forb	.7985	.3613	-.3442
Tot. Cover	.7693	.2916	.0270
Bare:Lit	-.6280	-.6069	.2848
Exot:Native	.0601	.9460	-.0172
Avg. Height	.2059	.8644	-.1461
Diversity	.0357	-.1012	.9735

gradient is similar to a grassland successional gradient.

Factor 2 has large positive loadings on exotic:native and average height with a large negative loading on bare:litter. This describes a gradient from short natives with bare ground, to tall exotics with litter. Factor three loads strongly only with plant diversity, describing a gradient from low diversity to high diversity.

Using the principal component factors as new variables, the vegetation transects can be graphed to show relationships among the transects. The ordination for the first two factors is shown in Figure 3.8. The first factor separates the poisoned towns from the uncolonized transects with the active towns overlapping the other two treatments. The second factor separates the active towns from the other two treatments. The third principal

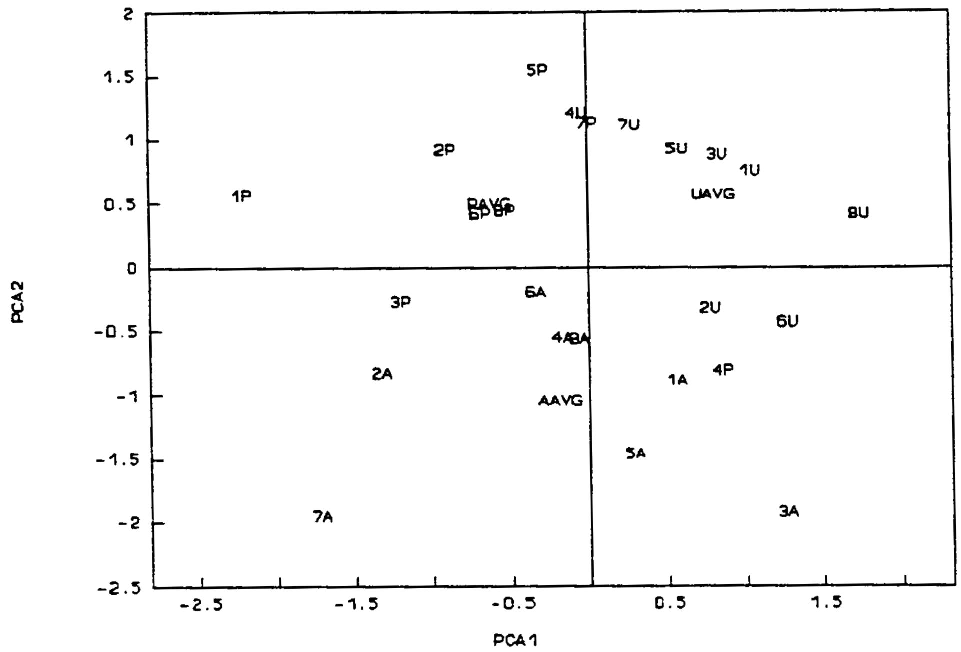

Figure 3.8. Principal components ordination of the 24 transects and the average values for each treatment using above-ground variables. Factor scores 1 and 2 are used as axes. See Fig. 2.2 for transect names.

component axis is shown graphed with the first axis (Figure 3.9). This axis partially separates the poisoned towns from the other two treatments, but the amount of overlap is large.

Discriminant Function Analysis. A discriminant function analysis was run on the same variable set as the principal components analysis with the inclusion of a treatment variable that the discriminant function analysis used as an *a priori* grouping variable. The analysis

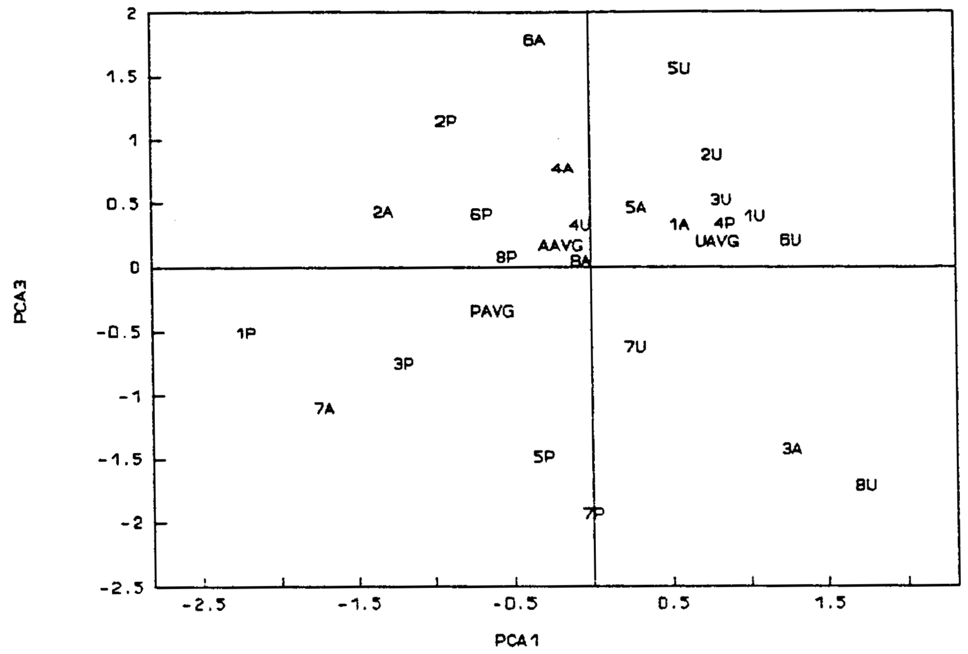

Figure 3.9. Principal components ordination of the 24 transects and the average values for each treatment using above-ground variables. Factor scores 1 and 3 are used as axes. See Fig. 2.2 for transect names.

described 74.7% of the data set variability with the first function and the remaining 25.3% with the second function. The loadings of the two functions are shown in table 3.4. The first function loads strongest positively with average height and negatively with bare:litter describing a gradient from short and bare to tall and litter. The smaller loadings include a gradient from natives, monocarps, forbs and decreased cover to exotics, polycarps, graminoids and increased cover. The direction of these gradients is equivalent to a combination of the

Table 3.4. Pooled within-groups correlations between discriminating variables and canonical discriminant functions.

	Function 1	Function 2
Avg. Height	.7855	-.3881
Bare:Litter	-.5152	.1561
Gram:Forb	.3958	.0444
Veg. Cover	.2564	.1900
Exotic:Native	.4710	-.6808
Mono:Poly	-.3503	-.6243
Diversity	-.0125	.3041

first two principal component axes. The second discriminant function has strong negative loadings on exotic:native and monocarpic:polycarpic, describing a gradient from exotic monocarps to native polycarps.

The scatterplot of the discriminant function scores of each transect (Fig. 3.10) shows good separation of all treatments except for the North Boundary (4P) poisoned treatment. The first axis describes a gradient from active towns through poisoned towns to uncolonized prairie. The second axis separates the poisoned towns from the other two treatments.

By examining how discriminant function analysis reclassifies transects based on its derived functions, relationships among the treatments can be deduced. The discriminant function analysis was able to correctly re-

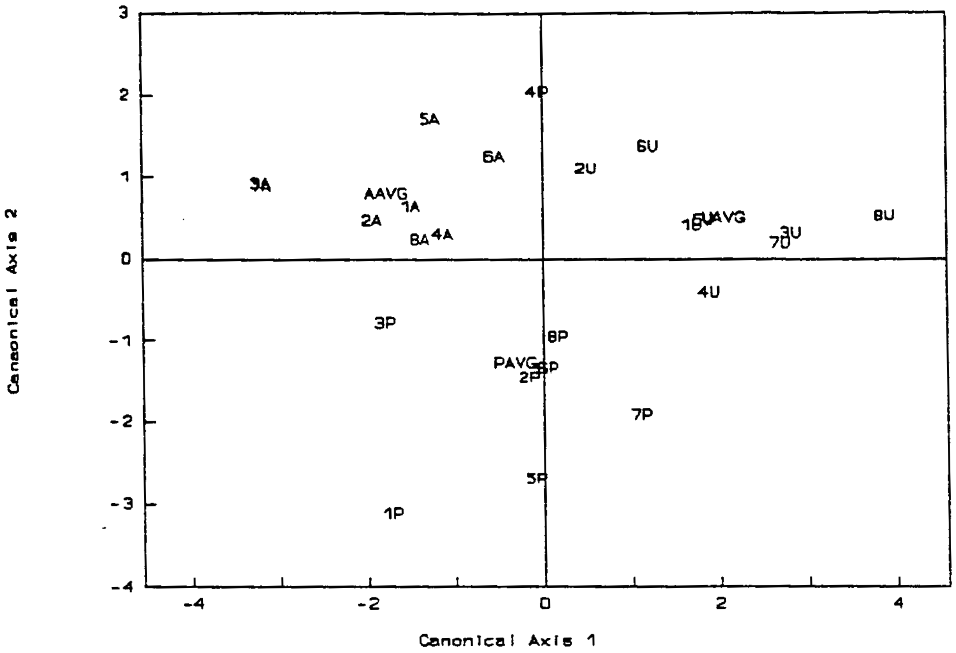

Figure 3.10. Discriminant function analysis ordination of the 24 transects and the average values for each treatment using above-ground variables. Canonical discriminant scores 1 and 2 were used as axes. See Fig. 2.2 for transect names.

classify all transects except for North Boundary (4P) (Table 3.5). The second highest probability helps describe the group that is the most similar to the selected group. All of the active towns had a second classification as poisoned towns while the poisoned town were almost equally reclassified as active and uncolonized (table 3.5). Of the uncolonized transects, 75% had a second classification of poisoned towns while 25% were more similar to the active towns.

Table 3.5. Percent re-classification by discriminant function analysis for the most probable group and the second most probable group.

	Highest Prob.			2nd Highest Prob		
	A	P	U	A	P	U
Active	100	0	0	0	100	0
Poisoned	12.5	87.5	0	37.5	0	62.5
Uncolonized	0	0	100	25	75	0

Discussion

The ordination of the discriminant function analysis (Fig. 3.10) summarizes the successional status of the poisoned prairie dog towns. The main direction of succession is explained by the first axis (75% of variation) which places the poisoned towns between the active towns and uncolonized prairie, slightly closer to the active towns. The variables most responsible for this gradient are plant height and bare:litter ratio. Within this successional gradient, some variables change more rapidly than others. Litter accumulates relatively rapidly (Fig 3.1), but perennial plants that are not associated with prairie dog towns (*Stipa comata*, *Carex filifolia*, *Poa pratensis*, and *Artemesia ludoviciana*) are slow to invade after prairie dog poisoning (Figs. 3.4, 3.5, and 3.6).

The second discriminant function axis describes a successional gradient in which the poisoned towns diverge from both the active and uncolonized treatments (Fig. 3.10). This axis describes 25% of the variation and the loadings on exotic, monocarpic plants correlates with the invasion of annual weeds such as *Bromus tectorum*.

While discriminant function analysis is effective in maximizing group separation and explaining large amounts of variability with few factors, principal components analysis is effective in examining the cohesiveness of groups because no *a priori* group assumptions are made. The ordination of the first two principal component axes (Fig. 3.8) show a reasonable separation of the three treatments. Non-overlapping lines could be drawn to separate the treatments except for two deviations. There is a small amount of overlap between the poisoned and uncolonized towns (4U and 7P) and the North Boundary poisoned town (4P) is disjunct from the other poisoned towns. The disjunction of this town is also described by the fact that it was not able to be reclassified by the discriminant function analysis (Table 3.5). The reasons for the unique vegetation on this town are likely due to the fact that it was partially recolonized by prairie dogs during the study and it contained ancient prairie dog mounds.

Previous studies comparing vegetation on and off prairie dog towns have found that the prairie dog towns have more forb cover, less graminoid cover, less litter, and shorter vegetation. The results of this study agree with these findings and also include the finding of decreased exotic plants on prairie dog towns. Contradictory results have been found in previous studies concerning the effect of prairie dogs upon plant diversity (Collins and Barber 1985, Agnew et al. 1986, Archer et al. 1987). The results here show a nearly identical level of plant diversity on and off prairie dog towns (Table 3.2).

CHAPTER IV

SEED BANKS

Materials and Methods

Field Methods

During vegetation sampling in August, 1989, soil samples were taken for analysis of viable seed banks. Samples were taken from the same corner of each of the 240 quadrats. In a few cases, the quadrat corner was over a dense grass sod and the sample was taken from the closest accessible soil. Soil samples were 5 by 8 cm in area and 5 cm deep. Plant litter lying on the soil was included but standing dead vegetation and large rocks were excluded. Samples were placed in zip-lock bags and taken to Boulder.

Greenhouse Methods

On September 13, 1989, the soil samples were placed under a misting system at a University of Colorado greenhouse. For each sample, the soil was mixed and 100 ml was removed and placed upon 50 ml of sterile sand in a 7.5 by 7.5 cm pot. This created a sample with effective dimensions of 20 cm^2 and 5 cm depth. Twenty-four additional pots were filled with 50 ml sand and 100 ml of soilless mixture to serve as a control for greenhouse contaminants. Pots were randomly placed into trays, and trays were rotated around the greenhouse under the misting system.

As seedlings germinated, they were removed from the pot, and if unidentifiable they were transplanted into a separate pot. These seedlings were grown until a positive identification to species could be determined. After eight weeks, when germination had slowed down, all samples were mixed and returned to the misting system. The germination process was continued for one year, during which soil samples were dried and remoistened and occasionally mixed. At the end of one year very little germination occurred.

Statistical Methods

Seeds germinating from each sample were pooled within transects to create densities per liter. Seed Bank diversity was computed using EXP(H′) using relative seed numbers within each transect. Richness/100ml was the average number of species per sample, and richness/l the number of species germinating for the whole transect. All other statistics were similar to those used in the vegetation analysis.

Results

Seed Number

The pots with soilless mixture that were used for greenhouse contaminants had large numbers of *Oxalis sp.* throughout the study. This was the only species to germinate in the control pots except for a brief period of cottonwood (*Populus sargentii*) germination. *Oxalis stricta* was found in the vegetation at Wind Cave and likely was present in the seed bank, but because of the greenhouse contamination, *Oxalis sp.* seeds were discounted from all analyses.

A total of 5,076 seeds were germinated from 24 liters of soil of which 96% were positively identified. The number of seeds germinated from each treatment is shown in Table 4.1. The prairie dog towns and poisoned towns both had significantly more seeds than the uncolonized prairie treatment ($\alpha = .05$), but were not significantly different from each other. The seed totals for each transect are shown in Table 4.2. There was an

Table 4.1. Mean number of seeds (±SE) germinated from the top 5 cm. of soil by volume and area for the three treatments. Different letters among treatments are significantly different using Duncan's ($\alpha = .05$).

	Seeds/l.	Seeds/m^2
Active	294(±48)a	14,706(±2,414)a
Poisoned	256(±45)a	12,806(±2,256)a
Uncolonized	84(±26)b	4,212(±1,304)b

unusually large seed total for the Northwest of Sanctuary uncolonized transect (4U).

Seed Types

Seed bank diversity was lowest on the active towns and highest on the uncolonized prairie (Table 4.3). The uncolonized treatments had the lowest levels of species richness while the active and poisoned towns had similar richness values.

The percentages of seeds from the three species divisions are shown in Figure 4.1. In all cases the uncolonized treatment was significantly different from the other two treatments, having fewer forbs, monocarps, and natives by percentage. The totals for species groups (Fig. 4.2) show a predominance of native monocarpic forbs for all treatments, but the uncolonized treatment had significantly fewer native monocarpic forbs and more

Table 4.2. Mean number of seeds (±SE) germinated per liter of soil for each of the 24 transects. See table 2.2 for transect names.

Transect #	Active	Poisoned	Uncolonized
1	125(±18)	101(±25)	78(±18)
2	425(±71)	261(±49)	48(±10)
3	412(±65)	109(±29)	34(±5)
4	159(±21)	113(±21)	267(±41)
5	236(±53)	408(±70)	74(±17)
6	451(±61)	308(±32)	61(±9)
7	386(±149)	448(±80)	52(±7)
8	103(±22)	297(±47)	45(±11)

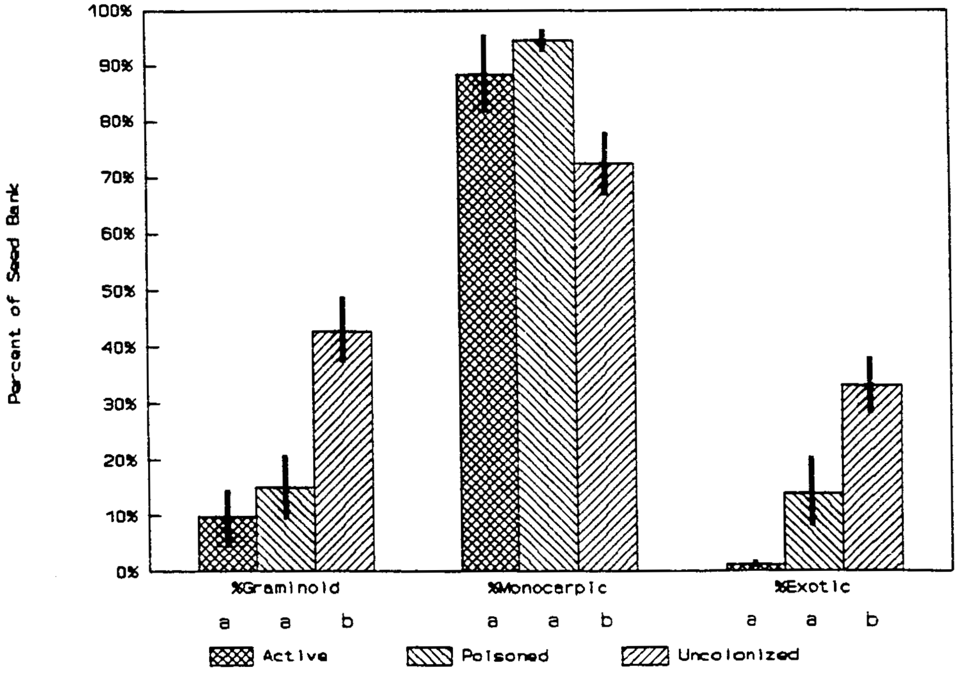

Figure 4.1. Percentages of seeds germinating from each of the three treatments for each of the three species divisions. Error bars are ± 1 SE. Different letters among treatments within a division are significantly different ($\alpha = .05$).

Table 4.3. Diversity and richness of seed bank (±SE) separated by treatment. Different letters among treatments within a variable are significantly different ($\alpha = .05$).

	A	P	U
EXP(H′)	6.1(±.9)a	7.2(±.7)ab	9.1(±.6)b
Richness/100ml	5.7(±.4)a	5.5(±.3)a	3.6(±.5)b
Richness/liter	17.3(±1.0)a	18.7(±.8)a	15.5(±1.4)a

exotic perennial graminoids than the other two treatments.

The dominant species in the seed bank are shown in Table 4.4. *Veronica peregrina* had the highest densities of seeds in the study, but was noticeably deficient on the uncolonized prairie. Many species had small numbers of seeds on the uncolonized prairie, with notable exceptions of *Poa pratensis* and *Silene antirrhina*. These had the greatest densities on the uncolonized prairie. Only two species, *Myosurus minimus* and *Draba reptans*, had significantly different densities between the active and poisoned treatments. These are plants of low stature that had significantly fewer seeds on the poisoned towns than on the active towns.

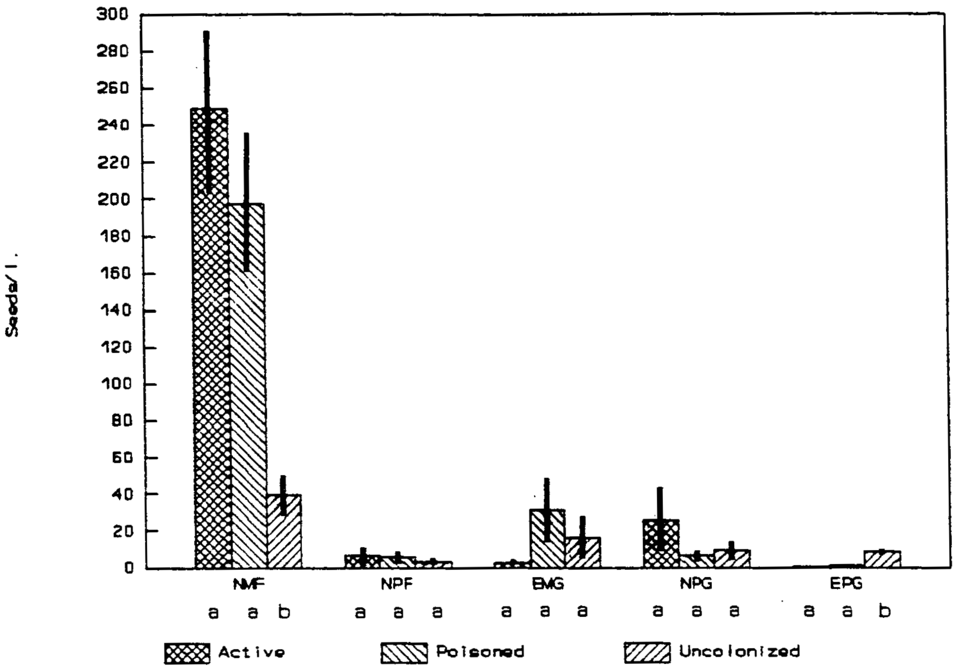

Figure 4.2. Densities of germinable seeds for the five main species groups. Different letters among treatments within a group are significantly different ($\alpha = .05$). Key: N=native, E=exotic, M=monocarp, P=polycarp, F=forb, G=graminoid.

Multivariate Analyses

Principal components analysis. A principal components analysis was run on the five variables shown in Table 4.5. The first factor extracted by the analysis explained 64.7% of the variance, and loaded positively on number of seeds and negatively on diversity describing a gradient from few seeds and high diversity to many seeds and low diversity. The second factor, explaining 19.8% of the variance, loaded on Exotic:Native and

Table 4.4. Germinable seeds per liter of soil of the main species separated by treatment. Different letters among treatments within a species are significantly different ($\alpha = .05$).

species	A	P	U
Veronica peregrina	150.6 a	74.3 a	1.8 b
Androsace occidentalis	21.4 ab	34.6 a	12.5 b
Hedeoma hispidum	19.6 a	33.1 a	2.9 b
Bromus tectorum	2.3 a	31.3 a	16.1 a
Verbena bracteata	18.5 a	24.9 a	4.5 a
Triodanis perfoliata	16.9 a	14.3 a	8.8 a
Juncus interior	20.4 a	1.3 a	2.6 a
Poa pratensis	0.8 a	0.9 a	8.6 b
Festuca ovina	3.8 a	2.6 a	3.5 a
Artemisia frigida	0.9 a	4.9 a	2.5 a
Silene antirrhina	1.4 a	1.4 a	4.5 b
Conyza canadensis	3.3 a	2.8 a	1.0 a
Potentilla sp.	5.8 a	0.3 a	0.9 a
Myosurus minimus	5.1 a	0.1 b	0.0 b
Plantago patagonica	1.5 a	2.4 a	1.3 a
Draba reptans	4.6 a	0.3 b	0.1 b

Table 4.5. PCA factor loadings on seed bank variables using the rotated factor matrix for the first three factors.

	Factor 1	Factor 2	Factor 3
Total Seeds	.9088	-.0594	.2213
Diversity	-.8444	.3087	-.1820
Exotic:Native	-.2104	.9046	-.2050
Graminoid:Forb	-.1577	.7546	-.6183
Mono:Poly	.3314	-.3013	.8896

Graminoid:Forb, explaining a gradient from native forbs to exotic graminoids. The third factor, explaining 8.7% of the variance, described a gradient from polycarpic graminoids to monocarpic forbs.

The ordinations of the first two axes (Fig. 4.3) both place the average values of the poisoned towns between the other two treatments, but there is considerable overlap on each axis. The third axis (Fig. 4.4) places the active treatment between the other two treatments but there is considerable overlap here also.

Discriminant function analysis. The discriminant function analysis described 97.53% of the variation with one function and only 2.47% with the second function. The largest loadings on the first function describe a gradient from exotic polycarpic graminoids to native monocarpic forbs (Table 4.6). The smaller loadings on

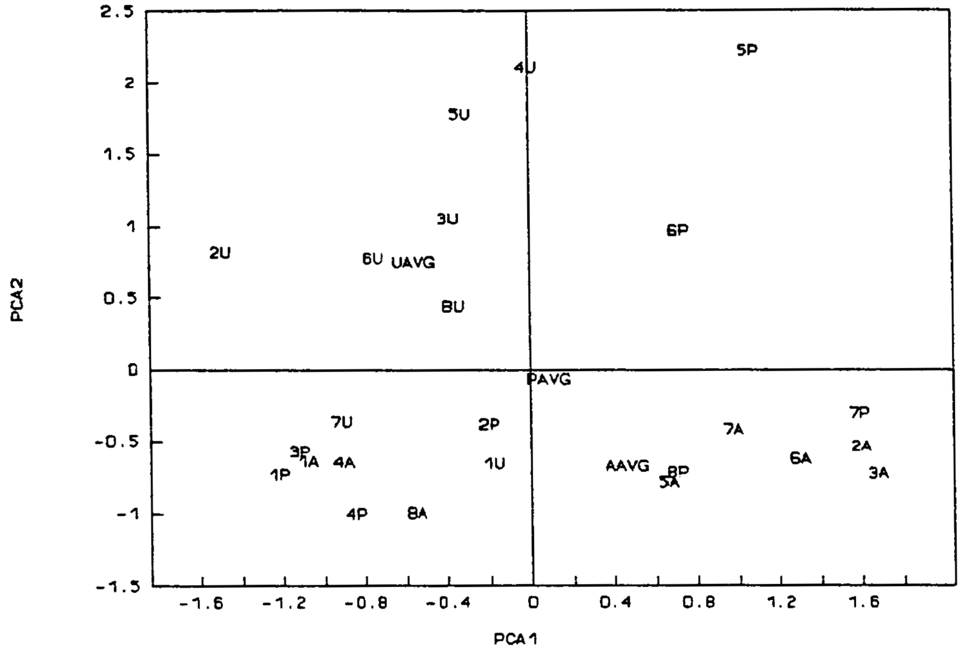

Figure 4.3. Principal components ordination of the 24 transects using seed bank data, and the average values for each treatment. Factor scores 1 and 2 are used as axes. See Fig. 2.2 for transect names.

the first axis describe a gradient from high diversity to high seed number. The second function mostly separates native polycarps from exotic monocarps.

The ordination of the discriminant function analysis shows that the first function separates the uncolonized transects from the other two treatments but does not discriminate between the prairie dog towns and poisoned towns (Fig. 4.5). The second axis provides a partial separation of the poisoned and active towns but there is still overlap and the amount of variance explained by the

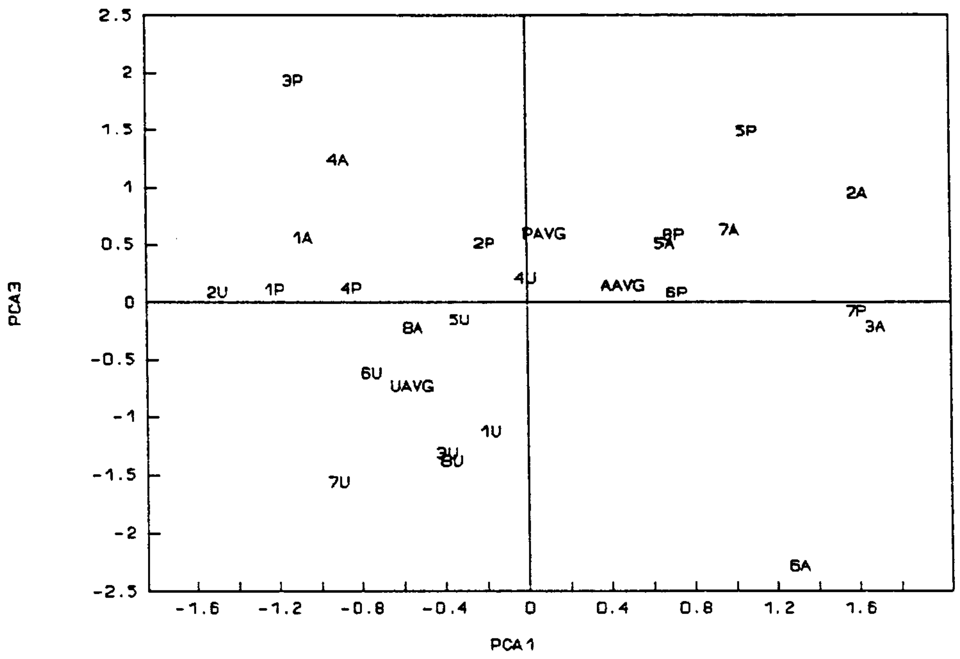

Figure 4.4. Principal components ordination of the 24 transects using seed bank data and the average values for each treatment. Factor scores 1 and 3 are used as axes. See Fig. 2.2 for transect names.

function is small.

The re-classification table (Table 4.7) shows that the discriminant function analysis is able to correctly re-classify all of the uncolonized transects but is not effective in re-classifying either the active or poisoned treatments. The treatment closest to the uncolonized treatment is the poisoned treatment for all eight of the transects.

Discussion

Table 4.6. Pooled within-groups correlations between discriminating seed bank variables and canonical discriminant functions.

	Function 1	Function 2
Exotic:Native	-.5525	.5908
Graminoid:Forb	-.5434	-.0162
Mono:Poly	.5340	.5975
Total Seeds	.3514	-.0903
Diversity (EXP(H′))	-.2635	.4072

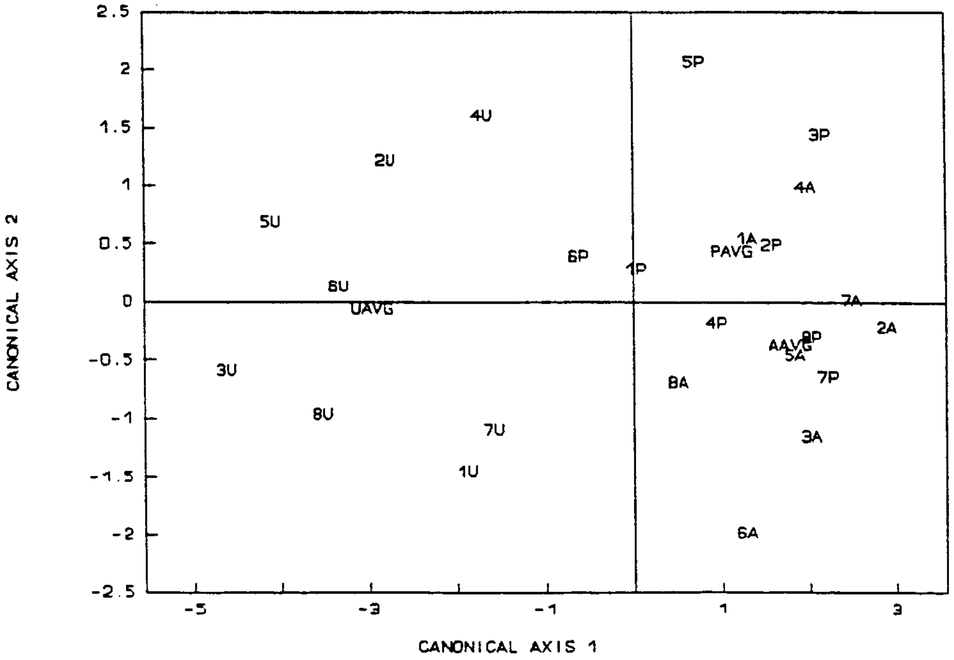

Figure 4.5. Discriminant function analysis ordination of the 24 transects and the average values of each treatment using seed bank data. See Fig 2.2 for transect names.

Table 4.7. Percent re-classification by discriminant function analysis for the most probable group and the second most probable group using seed bank data.

	Highest Prob.			2nd Highest Prob		
	A	P	U	A	P	U
Active	62.5	37.5	0	37.5	62.5	0
Poisoned	25.0	75.0	0	62.5	25.0	12.5
Uncolonized	0	0	100	0	100	0

The densities of germinable seeds found in this study are larger than have been found in most grassland studies (Rice 1989, pg.220), but less than other studies on annual California grasslands (Young et al. 1981), cultivated fields (Roberts 1981), and buffalo wallows (Uno 1989). Because seed bank estimations vary widely among studies, not too much significance should be placed on between-study comparisons.

The 3.5 fold increase of seed densities on active towns compared to uncolonized prairie is consistent with other studies showing large increases of seeds in earlier stages of succession (Donelan and Thompson 1980). The large number of seeds on the Northwest of Sanctuary transect (4U) may have been a result of previous unknown disturbance such as fire or previous prairie dog colonization. It is interesting that despite its large number of seeds, this transect was correctly re-classified by the discriminant function analysis.

The inability of the discriminant function analysis to effectively separate the active and poisoned transects seems to indicate that successional changes in the seed bank are insignificant during the first four to eight years after prairie dog removal. It is also possible that a different selection of variables for the analysis may have allowed for better discrimination. For example, the lumping of natives, monocarps, and forbs, may obscure the effects of different species within these divisions.

Analysis of seed bank communities is also difficult because of the clumped nature of seed banks (Bigwood and Inouye 1988). In this study, for example, three transects (5P, 6P ,and 4U) accounted for 80% of all *Bromus tectorum* seeds, and the Rankin Ridge praire dog town (6A) accounted for 70% of the *Juncus interior*, and 80% of the *Potentilla sp.* seeds.

CHAPTER V

COMPARISONS BETWEEN SEED BANK AND ABOVE-GROUND VEGETATION

Plants Present in Seed Bank and Above-ground Vegetation

Twenty-one plant species were common to both the seed bank and the above-ground vegetation. For each of these species, a similarity index was created by converting seed bank data to relative frequencies within each transect, and then averaging the minimum value of seed bank frequency and above-ground importance for each transect within a treatment. The total similarity for the treatments ranged from 10.8% on the active towns to 17.6% on both the poisoned and uncolonized towns (Table 5.1). Individual transects varied from 4.7% (8P) to 42.4% (5P) similarity.

Bromus tectorum had the largest similarity values overall, and for the poisoned treatment (Table 5.1). This high similarity is partially a result of the timing of measurements. Soil was collected before autumn germination, and half of the vegetation measurements were done when cheatgrass is actively growing in May. The active

Table 5.1. Similarity indices of plants common to seed banks and above-ground vegetation.

	A	P	U
Total Similarity	10.8%	17.6%	17.6%
Bromus tectorum	0.5%	7.3%	4.5%
Hedeoma hispidium	3.9%	3.0%	0.7%
Poa pratensis	0.1%	0.1%	5.7%
Androsace occidentalis	1.5%	1.5%	2.5%
Artemesia frigida	0.2%	1.9%	2.2%
Plantago patagonica	0.6%	1.2%	0.8%
Veronica peregrina	1.1%	0.2%	0.0%
Draba reptans	1.1%	0.1%	0.0%
Verbena bracteata	0.6%	0.3%	0.1%
Sisymbrium altissimum	0.0%	0.8%	0.2%
Agropyron smithii	0.0%	0.2%	0.5%
Myosurus minimus	0.6%	0.0%	0.0%
Triodanis perfoliata	0.2%	0.2%	0.1%
Euphorbia stictospora	0.3%	0.1%	0.0%
Thlaspi arvensis	0.0%	0.1%	0.1%
Verbascum thapsus	0.0%	0.2%	0.0%
Conzya canadensis	0.1%	0.1%	0.1%
Potentilla sp.	0.1%	0.0%	0.1%
Oenothera coronopifolia	0.0%	0.1%	0.0%
Sphaeralcea coccinea	0.0%	0.1%	0.0%
Taraxacum officinale	0.0%	0.1%	0.0%

and uncolonized treatments are noticeably different in that the active treatment consisted mostly of native annual forbs and the uncolonized treatment had more exotic and perennial plants.

Plants Only in Vegetation or Seed Bank

The most notable exclusion from the seed bank was the most abundant forb in the vegetation, the annual *Lappula redowskii*. I observed this species setting abundant seed in all areas of the Park. It is likely that the seeds were present in the soil samples but did not germinate. Fenner (1985) mentions that this species germinates in late-winter and has a high level of dormancy. This species may be introduced from Eurasia, but I have treated it as a native because no flora mentioned it as being introduced, exotic, etc..

Native perennial graminoids in the vegetation were rare or absent in the seed bank. This result has been shared with most studies of grassland seed banks (Major and Pyott 1966, Rice 1989, Santanachote 1991).

Most species with large seed banks were present in the vegetation. A few of the graminoids such as *Juncus interior, Festuca ovina and Sporobolus cryptandrus* may have been present in the vegetation; but because they were not flowering, they were not identifiable during

Table 5.2. Pooled within-groups correlations between discriminating variables and canonical discriminant functions. Both seed band and vegetation variables used.

	Function 1	Function2
AG Vegetation Height	.2529	.3882
SB Exotic:Native	.2452	-.0183
SB Graminoid:Forb	.2352	-.1902
SB Mono:Poly	-.2219	.3520
AG Bare:Litter	-.1672	-.1759
SB Seed Number	-.1522	.0933
AG Exotic:Native	.1455	.5914
AG Graminoid:Forb	.1307	.0038
AG Mono:Poly	-.1238	.4649
SB Diversity	.1186	.0272
AG Total Cover	.0869	-.1266
AG Diversity	.0001	-.2445

vegetation measurements. The most numerous forbs in the seed bank that were not represented in the vegetation were *Silene antirrhina*, *Lepidum densiflorum*, and *Linaria canadensis*.

Multivariate Ordinations

A discriminant function analysis was run on the combined variables from the vegetation and seed bank analyses. The first discriminant function described 94.6% of the variance and the second function the remaining 5.4%. The loadings of the variables on the first

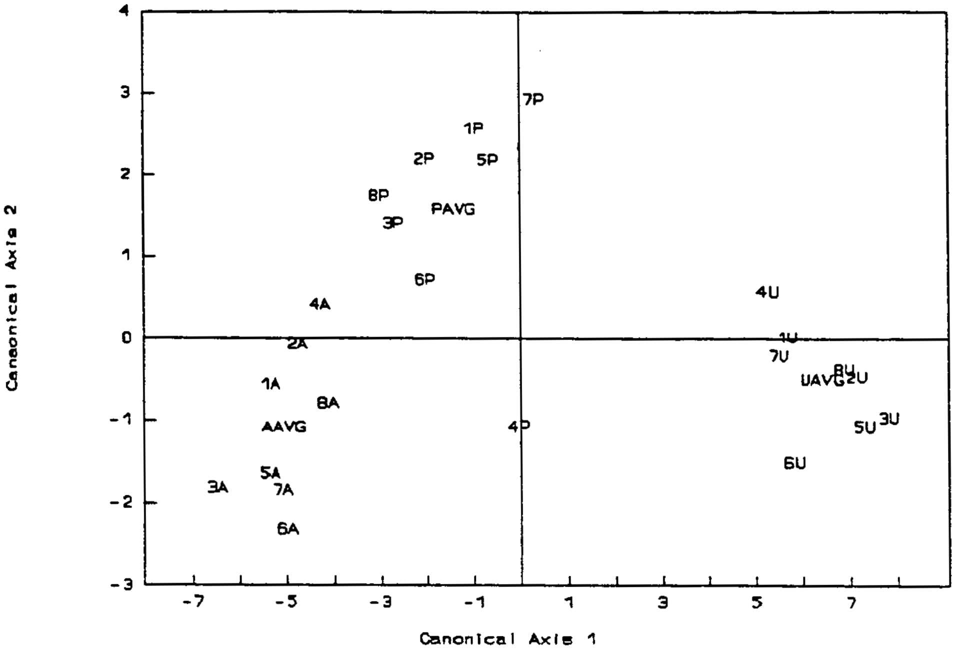

Figure 5.1. Discriminant function analysis ordination of the 24 transects, and the average values of each treatment using combined vegetation and seed bank data. See Fig. 2.2 for transect names.

function were small (Table 5.2). The largest loadings described a gradient from tall vegetation with native, monocarpic forbs in the seed bank to short vegetation with exotic, polycarpic graminoids in the seed bank. This factor alone was sufficient to separate the three treatments (Figure 5.1).

The second discriminant function separated the poisoned treatment from the other two treatments (Fig. 5.1) with the exception of the North Boundary transect (4P). This factor loaded most heavily on above-ground

Table 5.3. Percent re-classification by discriminant function analysis for the most probable and second most probable group, using combined vegetation and seed bank data.

	Highest Prob.			2nd Highest Prob		
	A	P	U	A	P	U
Active	100	0	0	0	100	0
Poisoned	0	100	0	100	0	0
Uncolonized	0	0	100	0	100	0

variables, describing a gradient from short vegetation with native polycarps to tall vegetation with exotic monocarps (Table 5.2).

The discriminant function analysis was able to re-classify all of the transects correctly (Table 5.3). All of the uncolonized transects were most similar to the poisoned transects and the poisoned and active transects were most similar to each other.

CHAPTER VI

CONCLUSIONS

No previous studies have examined seed banks on prairie dog towns. The large densities of seeds found on prairie dog towns in this study support previous grassland studies that show an increase in seed numbers with increasing disturbance.

The amount of successional changes in the seed banks of the poisoned towns were considerably less than for the above-ground vegetation. The similarity of the seed banks of towns abandoned for four to eight years to active towns, suggests that the seed bank stores a "successional memory" that is capable of restoring components of native, prairie dog adapted vegetation with the return of prairie dogs. The plant species in the seed bank are also mostly early successional species.

There have been no previous studies examining exotic plants on prairie dog towns. The results of this study show that exotic plants in the vegetation and seed bank are greatly reduced on prairie dog towns. The low levels of exotics on prairie dog towns occur despite the large amounts of disturbance that take place there. This may be due to the fact that the disturbance is not primarily anthropogenic and has occurred over large parts of the Great Plains for thousands of years, allowing native plant communities to evolve to adapt to local disturbance. The anthropogenic disturbance in this instance is the large scale reduction of the native prairie dogs from Great Plains rangeland. In this instance, it seems that the distinction between natural and anthropogenic disturbance determines the extent of exotic plant invasion.

My findings that compared prairie dog towns to uncolonized prairie are similar to results of previous studies. Prairie dog towns generally have more forb cover, less graminoid cover, less litter, and shorter vegetation. Previous studies examining abandoned prairie dog towns looked at towns that were abandoned for less than five years. These studies found little evidence of plant succession on these towns. The results of this study on towns abandoned for four to seven years show more evidence of plant succession. The main path of succession on the poisoned towns is towards the uncolonized prairie in most vegetation characteristics but there also was a divergent succession that was mostly determined by the invasion of exotic annual plants such as *Bromus tectorum*.

Areas of future research suggested by this study are an analysis of prairie dog towns that have been abandoned for a longer period of time, especially in relation to the persistence of a large seed bank. Comparisons of recolonized prairie dog towns to prairie dog expansion on uncolonized prairie would examine the importance of the persistent seed bank in restoring vegetation adapted to prairie dog towns. It also would be interesting to examine changes after prairie dog poisoning in the morphologies of plants such as *Bouteloua gracilis* and *Agropyron smithii* that have been shown to exhibit intraspecific variation on and off prairie dog towns (Detling and Painter 1983).

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Appendix A: Plant Species List

Exotic Monocarpic Forbs

Asteraceae	
Tragopogon dubius Scop.	Salsify
Brassicaceae	
Neslia paniculata (L.) Desv.	Ball Mustard
Sisymbrium altissimum L.	Jim Hill Mustard
Thlaspi arvense L.	Penny-cress
Fabaceae	
Medicago lupulina L.	Black Medic

Exotic Polycarpic Forbs

Asteraceae	
Taraxacum officinale Wiggers	Common Dandelion
Convolvulaceae	
Convolvulus arvensis L.	Small Bindweed

Native Monocarpic Forbs

Asteraceae	
Conyza canadensis (L.) Cronq.	Horseweed
Dyssodia papposa (Vent.) Hitchc.	Prairie Dog Weed
Boraginaceae	
Lappula redowskii (Hornem.) Greene	Stickseed
Brassicaceae	
Descurainia pinnata (Walt.) Britt.	Tansy Mustard
Draba reptans (Lam.) Fern.	Carolina Whitlow-grass
Draba stenoloba Ledeb.	
Lepidium densiflorum Schrad.	Pepper-grass

Roripa palustris (L.) Bess.	Cress
Campanulaceae	
Triodanis perfoliata (L.) Nieuwl.	Venus Looking-glass
Caryophyllaceae	
Silene antirrhina L.	Sleepy Catchfly
Chenopodiaceae	
Monolepis nuttaliana (R. & S.) Greene	Poverty Weed
Euphorbiaceae	
Euphorbia spathulata Lam.	
Euphorbia stictospora Engelm.	Mat Spurge
Hydrophyllaceae	
Ellisia nyctela L.	Ellisia
Lamiaceae	
Hedeoma hispidum Pursh	Rough Pennyroyal
Oxalidaceae	
Oxalis stricta L.	Yellow Wood Sorrel
Plantaginaceae	
Plantago patagoniga Jacq.	Wooly Plantain
Primulaceae	
Androsace occidentalis Pursh	Western Rock Primrose
Ranunculaceae	
Myosurus minimus L.	Mousetail
Scrophulariaceae	
Linaria canadensis (L.) Dum.	Blue Toadflax
Verbascum thapsus L.	Great Mullen
Veronica peregrina L.	Purslane Speedwell
Verbenaceae	
Verbena bracteata Lag. & Rodr.	Prostrate Vervain

Native Polycarpic Forbs

Asteraceae

Ambrosia psilostachya DC.	Western Ragweed
Antennaria sp.	Pussytoes
Artemisia frigida Willd.	Pasture Sagebrush
Artemisia ludoviciana Nutt.	Prairie Sage
Echinacea angustifoilia D.C.	Purple Cone-flower
Lygodesmia juncea (Pursh) Hook	Skeleton Weed
Ratibida columnifera (Nutt.)Woot. & Standl.	Prairie Cone-flower
Solidago missouriensis Nutt.	Smooth Goldenrod
Asclepiadaceae	
Asclepias pumila (Gray) Vail	Low Milkweed
Brassicaceae	
Erysimum asperum (Nutt.) DC.	Western Wallflower
Cactaceae	
Coryphantha vivipara (Nutt.) Britt. & Rose	Ball Cactus
Opuntia fragilis (Nutt.) Haw.	Little Prickly Pear
Opuntia polyacantha Haw.	Starvation Cactus
Caprifoliaceae	
Symphoricarpos occidentalis Hook.	Western Snowberry
Chenopodiaceae	
Chenopodium atrovirens Rydb.	Goosefoot
Commelinaceae	
Tradescantia bracteata (Britt.) Smyth	Spiderwort
Fabaceae	
Amorpha canescens Pursh.	Lead Plant
Astragalus missouriensis Nutt.	Milk Vetch
Astragalus spp.	Milk Vetch
Lupinus argenteus Pursh	Common Lupine
Psoralea tenuiflora Pursh	Slender Scurfpea
Vicia americana Muehl.	Vetch
Liliaceae	
Leucocrinum montanum Nutt.	Sand Lily

Zigadenus venenosus Wats.	Death Camas
Malvaceae	
Sphaeralcea coccinea (Pursh) Rydb.	Scarlet Globe-mallow
Onagraceae	
Oenothera coronopifolia T. & G.	Combleaf Evening Primrose
Polemoniaceae	
Phlox sp.	
Ranunculaceae	
Ranunculus rhomboideus Goldie	Prairie Buttercup
Rosaceae	
Potentilla sp.	Cinquefoil
Rosa arkansana Porter	Prairie Rose
Scrophulariaceae	
Penstemon albidus Nutt.	White Penstemon
Violaceae	
Viola nuttalii Pursh	Yellow Prairie Violet

Exotic Monocarpic Graminoids

Poaceae	
Bromus tectorum L.	Cheat-grass

Exotic Polycarpic Graminoids

Poaceae	
Poa pratensis L.	Kentucky Blue-grass

Native Polycarpic Graminoids

Cyperaceae	
Carex filifolia Nutt.	Threadleaf Sedge
Juncaceae	
Juncus interior Wieg.	Inland Rush
Poaceae	

Agropyron smithii Rydb.	Western Wheat-grass
Agrostis scabra Willd.	Ticklegrass
Aristida longiseta Steud.	Red Three-awn
Bouteloua curtipendula (Michx.) Torr.	Side-oats Gramma
Bouteloua gracilis (H.B.K.) Lag.	Blue Gramma
Buchloe dactyloides (Nutt.) Engelm.	Buffalo-grass
Dicanthelium oligosanthes (Schult.) Gould	
Festuca ovina L.	Sheep's Fescue
Munroa squarrosa (Nutt.) Torr.	False Buffalo-grass
Sporobolus cryptandrus (Torr.) Gray	Sand Dropseed
Stipa comata Trin. & Rupr.	Needle-and-thread