DISSERTATION

PLAGUE AND THE BLACK-TAILED PRAIRIE DOG: AN INTRODUCED DISEASE MEDIATES THE EFFECTS OF AN HERBIVORE ON ECOSYSTEM STRUCTURE AND FUNCTION

Submitted by
Laurel M. Hartley
Graduate Degree Program in Ecology

In partial fulfillment of the requirements
For the Degree of Doctor of Philosophy
Colorado State University
Fort Collins, CO
Fall 2006

COLORADO STATE UNIVERSITY

September 26, 2006

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISON BY LAUREL M. HARTLEY ENTITLED "PLAGUE AND THE BLACK-TAILED PRAIRIE DOG: AN INTRODUCED DISEASE MEDIATES THE EFFECTS OF AN HERBIVORE ON ECOSYSTEM STRUCTURE AND FUNCTION" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILSOPHY.

Committee on Graduate Work

Adviser

Department Head

ABSTRACT OF DISSERTATION

PLAGUE AND THE BLACK-TAILED PRAIRIE DOG: AN INTRODUCED DISEASE MEDIATES THE EFFECTS OF AN HERBIVORE ON ECOSYSTEM STRUCTURE AND FUNCTION

I investigated the effects of black-tailed prairie dogs (*Cynomys ludovicianus*) on plant communities and nutrient cycling on the shortgrass steppe of Colorado, and how colony age and activity (active or plague-extirpated) influence the effects of prairie dogs in this system. Plague, caused by the bacterium *Yersinia pestis*, was first noted in prairie dog colonies in the 1940s. I suggest that this introduced disease has altered the role of prairie dogs in shaping ecosystem structure and function on the shortgrass steppe.

Plague causes periodic die-offs of entire colonies. During periods of inactivity, vegetation may recover from the effects of heavy grazing. Using 25 years of size and activity data about each colony on the Pawnee National Grassland, I found that most colonies (98%) experienced a plague-outbreak within 15 years of activity, and that over half (55%) of all colonies were inactive for at least five years after an outbreak. Furthermore, the probability of a colony attaining its pre-outbreak size within 5 years was low (28%).

I first studied five colonies (5-17 years of age) both before (1997-1999) and after (2000-2001) a plague-outbreak. Mean total plant canopy cover and cover of functional groups (forb, graminoid, shrub, cactus) did not differ significantly ($P \leq 0.05$) between on- and off-colony sites either before or after the plague-outbreak. However, mean total live plant biomass and graminoid biomass were lower on than off of colonies before, but not after the plague-outbreak, while forb biomass did not differ significantly between on- and off-colony sites either before or after the outbreak.

Using herbivore exclosure cages on the same five colonies, I estimated the relative amounts of plant biomass removed by cattle and prairie dogs on the shortgrass steppe in 1998 and 1999. I found that cattle and prairie dogs had similar and additive effects on plant biomass. Cattle consumed about the same amount of plant biomass on and off of colonies. Also, total aboveground plant production was not significantly different between on- and off-colony sites, but graminoid production decreased and forb production increased with prairie dog grazing.

To further elucidate how colony age and activity influence the role of prairie dogs on the shortgrass steppe, I studied plant communities on and off of three young (3-7 years since colonization), three old (~ 20 years since colonization), and three plague-extirpated (7-12 years old when extirpated) colonies from 2002 through 2004. I found that both young and old colonies, but not plague-extirpated colonies, had a significantly shorter canopy and lower graminoid cover and biomass than paired uncolonized sites. Although all three colony types showed the same trend, bare ground cover and forb cover and biomass were significantly greater on- than off-colony for only the old colony type. Biomass of standing dead plants (previous year's growth) and litter were lower only on the old colonies compared to off-colonies. Root biomass was not significantly different on than off of colonies for any colony type. Total plant species richness was greater only on old and plague-extirpated colonies, and greater species richness was due to greater numbers of forb species rather than graminoid species.

To understand how aboveground effects of prairie dogs influence belowground processes, I studied differences in N cycling on and off the same young, old, and plague-extirpated colonies in 2003 and 2004. Shoot N concentrations of the dominant graminoid (*Bouteloua gracilis*) and forb (*Sphaeralcea coccinea*) were significantly greater on than off of active, but not plague-extirpated colonies. Despite greater shoot N concentrations, total standing crop N was lower on than off of active colonies for *B. gracilis* because the increase in shoot N was not great enough to offset the decrease in aboveground biomass. Although there was a trend toward higher root N concentration on than off of colonies, it was statistically significant when colonies were considered collectively, but not when considered by colony type. Intermound spaces on prairie dog colonies did not have significantly higher rates of net N mineralization than uncolonized grassland for any colony type, but prairie dog mounds on active colonies had greater rates of N mineralization compared to off-colony sites or intermound spaces on colonies, suggesting that mounds may be sites of high nutrient turnover. Soil organic matter pools (total C and N, particulate organic matter C and N) appear to be relatively unaffected by prairie dogs, with differences seen only in the older colonies. Both mound and intermound areas on old colonies had lower total organic C than off of old colonies.

My results suggest that the above- and belowground effects of prairie dogs on the shortgrass steppe are generally similar to, but of lower magnitude than, their effects on the more mesic mixed-grass prairie where they have been most studied. My research also supports the hypothesis that the introduction of plague to North America may be altering the role of prairie dogs in shaping ecosystem structure and function because plague-extirpated colonies were rarely different from their associated off-colony sites. Also, effects of prairie dogs appear to increase with colony age, but because of plague, few colonies now persist for multiple decades.

Laurel M. Hartley
Graduate Degree Program in Ecology
Colorado State University
Fort Collins, CO 80523
Fall 2006

ACKNOWLEDGEMENTS

I am fortunate to have had committee members who are excellent scientists, role models, and mentors. They have taught me fundamentals of my discipline, explored ideas with me, and allowed me to make and learn from mistakes. I thank Indy Burke for what she has taught me about biogeochemistry and for all of the doors she has opened for me. Many of the positive events in my career came about because Indy told me about an opportunity and encouraged me to go for it. Indy treated me as an individual and helped me explore my personal strengths and work on my weaknesses. The conversations I have had with Daniel Milchunas in the years I have been associated with SGS-LTER have given me a better understanding of and enthusiasm for grasslands. There are few people who know as much about the shortgrass steppe as Daniel, and I appreciate that he was always approachable and willing to answer my questions. David Steingraeber is one of the most thoughtful and thorough professors I have had in my college career. I learned fundamentals about ecology and plant morphology from his classes. Last but not least, I must acknowledge The Great One. I couldn't have asked for a better advisor than Jim Detling. During my tenure as his student, he was always approachable, always fair, and always fun. I am grateful for all that Jim taught me about plant-herbivore interactions, about being a scientist in general, and for his support of my interests in both education and ecology. I only hope that I can someday help "make him even more famous".

My lab mates over the years have made the Detling lab an enjoyable place to be. Kelly Hardwicke, Nikki Grant-Hoffman, and Chrissy Alba-Lynn helped me both in the lab and field, and I hope we will remain life-long friends and colleagues. J.P. Farrar,

Kim Magraw, and Heather Blackburn were excellent academic siblings and provided stimulating conversation during our lab meetings at the Crown Pub.

The Shortgrass Steppe LTER has been a wonderful group with which to be associated. My years on the LTER field crew gave me a great appreciation for the shortgrass steppe and an idea for a dissertation project. I am grateful to Nicole Kaplan and Mark Lindquist for their support and friendship over the years. Working with them and learning about the steppe was so much fun, I can't believe I was paid for it. I appreciate the many members of the LTER field crews who helped gather data for this dissertation. Sallie Sprague helped me sort out any issue from renting a field vehicle to printing a poster. Jeri Morgan has been a great help with LTER logistics, as well as, a good friend and confidant to me. Judy Hendryx gave me invaluable advice in the lab and became a friend. Gene Kelly, Bob Flynn, Mike Antolin, Dan Tripp, Lisa Savage, Mary Ashby, Jeff Thomas, and Becky Riggle provided guidance regarding various aspects of my data design, collection, and analysis.

My graduate work was supported in part by a National Science Foundation GK-12 Fellowship. I thank John Moore and Dave Swift for allowing me to be part of the GK-12 program. The teachers I worked with were inspiring. Carol Seemueller, Tom Creegan, Tamara Driskill, and Dave Swartz from Rocky Mountain High School helped me to become a better teacher and communicator of science. Carol Seemueller (and sons Eric and Jonathan), Jenny Kaiser, Angie Moline, Shawn Kelly, Cindy Keesis, Jason McLaughlin, and Cathy Hoyt were GK-12 teachers and fellows who helped me gather field data for this dissertation.

Gary and Kathy Packard advised my M.S. thesis work and what I learned from them about study design, statistics, and writing was very helpful to me in finishing this dissertation.

My family, Jim, Cindy, and Jen Hartley, have played a big role in my completing this dissertation. They loaned me money, loaned me a field vehicle, and told me that thirty was the new twenty when I wondered why I was still in school.

Deb Guenther, Deb Finn, Cindy & John Crosby, Erin Lehmer, and Brook Byerley were graduate students who became great friends and were always there to lend a hand or offer words of advice. Finally, my best friend and partner, Jamie Lehmer helped me pound soil cores, wash roots, sieve soils, and carry bags of samples. I am grateful for his patience and the fact that he could listen (or pretend to listen) to me go on and on about how much I loved or hated prairie dogs, soil, trying to measuring nitrogen, studying roots etc.

TABLE OF CONTENTS

CHAPTER 1

INTRODUCTION TO THE DISSERTATION

In grassland ecosystems, herbivores may consume more than half of aboveground annual net primary production and thus significantly influence ecosystem structure and function (McNaughton 1983, Milchunas and Lauenroth 1993). The central North American grasslands have a long evolutionary history of grazing, but most literature focuses on influences of only large generalist herbivores such as bison (*Bison bison*), elk (*Cervus elaphus*), and pronghorn antelope (*Antelocapra americana*) (Stebbins 1981, Mack and Thompson 1982, Milchunas et al. 1988). Prairie dogs (*Cynomys* spp.) have undoubtedly also played a role in shaping plant communities of the Great Plains. Prairie dogs are herbivorous, colonial, large (~ 1 kg) rodents whose impacts on vegetation are characteristically localized, intensive, and sustained. Their influence may be considered far reaching in both space and time because they are distributed widely in North America (Fig. 1.1) and have been inhabitants of the plains since the Pleistocene (Goodwin 1995).

I first became interested in black-tailed prairie dogs (*Cynomys ludovicianus*) while working for the Shortgrass Steppe Long Term Ecological Research (SGS-LTER) program. In 1997, the SGS-LTER began a study of the effects of prairie dogs on vegetation. While collecting field data for that study, I made several anecdotal observations: 1) generalizations about the effects of prairie dogs on vegetation, as observed in the mixed-grass prairie, did not appear to be true for prairie dogs on the shortgrass steppe, 2) areas heavily grazed by prairie dogs (i.e. colonies) are visibly more different from the surrounding grassland than are areas that are heavily grazed by cattle, and 3) after a plague outbreak, changes induced by prairie dogs quickly became less apparent.

Because prairie dogs are found along a climatic gradient in North America, they are an excellent study organism for assessing the context dependent effects of a native herbivore on vegetation. In the mixed-grass prairie, prairie dog activities result in a sizeable (~ 60 %) reduction of canopy height, a decrease in above- and belowground biomass and a change in plant community composition from grass-dominated to forb-dominated (Coppock et al. 1983, Archer and Detling 1987, Whicker and Detling 1988, Johnson-Nistler et al. 2004). However, even though prairie dogs on the mixed-grass prairie reduce the quantity of forage on their colonies, the reduction is partially offset by an increase in forage quality because plants on colonies tend to have higher nitrogen concentrations and are more readily digested (Coppock et al. 1983, Detling 2006). Nitrogen cycling rates have also been shown to be accelerated on prairie dog colonies (Holland and Detling 1990, Fahnestock and Detling 2002). In the mixed-grass prairie, most of the effects of prairie dogs are evident soon (3-8 years) after colonization, and the magnitude of prairie dog-induced changes subsequently increases with colony age (Coppock et al. 1983, Archer and Detling 1987, Holland and Detling 1990).

One of the aims of my dissertation is to assess how prairie dogs affect plant communities and nutrient cycling on the shortgrass steppe and to compare those effects to effects found in previous studies on the mixed-grass prairie. Because of the paucity of studies of prairie dogs on the shortgrass steppe, definitive comparisons between the effects of prairie dogs on the two grassland types have not been made. Prairie dogs may have less dramatic effects on the shortgrass steppe than they do in the mixed-grass prairie. One reason is that the shortgrass steppe is unusually tolerant of heavy grazing (Klipple and Costello 1960, Milchunas et al. 1989, Burke et al. 1999). Milchunas et al.

(1988) suggested that this unusual tolerance may be due to the convergent selection pressures of herbivory and semi-aridity. Although both the shortgrass steppe and mixed-grass prairie presumably have long evolutionary histories of grazing (Milchunas et al. 1988, 1989), the shortgrass steppe is a drier grassland than the mixed-grass prairie (Coupland 1992, Lauenroth and Milchunas 1992). Adaptations to aridity such as drought-deciduous leaves, basal meristems, and short stature are exaptations (sensu Gould and Vrba 1982) that also may confer advantages for resistance to or tolerance of herbivory (Coughenour 1985).

Chapter 2 of this dissertation includes an analysis of plant community data collected by the SGS-LTER on and off of five prairie dog colonies from 1997 to 2001. Results of this analysis support the hypothesis that the effects of prairie dogs on plant community composition and biomass are qualitatively similar, but quantitatively less, than their effects on the mixed-grass prairie. However, the LTER data set did not include older colonies and, in the mixed-grass prairie, effects of prairie dogs increased with colony age. In Chapter 3, I address the extent to which impacts of prairie dogs on plant community composition and biomass are a function of colony age in the shortgrass steppe. Results suggest that effects of prairie dogs are greater on older (~ 20 years) than on younger colonies (~ 5 years).

In the mixed-grass prairie, prairie dogs influenced nutrient cycling on their colonies by increasing forage N concentration and net N mineralization (Coppock et al. 1983, Holland and Detling 1990, Fahnestock and Detling 2002). In Chapter 4, I address the effects of prairie dogs on N cycling in the shortgrass steppe. Effects of prairie dogs on N concentration of individual plants and N mineralization on the shortgrass steppe appear to be similar in both direction and magnitude to effects seen on the mixed-grass prairie.

A major theme throughout the dissertation concerns how an introduced disease of prairie dogs, sylvatic plague, mediates their effects on plant communities and nutrient cycling. Around the middle of the 20th century, large die-offs of prairie dog colonies began to occur west of the 102nd meridian, and these die-offs were attributed to sylvatic plague (Eskey and Haas 1940, Ecke and Johnson 1952). The plague that affects prairie dogs is the same plague that resulted in infamous pandemics in humans, most notably the Black Death of medieval Europe in the 17th century (Poland and Dennis 1998). Plague, caused by the bacterium *Yersinia pestis*, is transmitted via flea bites or direct contact with infected individuals (Inglesby et al. 2000). The prevailing theory is that plague was introduced from Asia into multiple ports on the Western coast of the United States around 1900. Infected ship rats (*Rattus rattus*, *R. norvegicus*) and their fleas (*Xenopsylla chopis*) passed the disease to local populations of rodents and fleas (Levy and Gage 1999). The disease rapidly spread across the United States and was first noted in prairie dog populations in Kansas, New Mexico, Texas, and Colorado in the 1940s (Eskey and Haas 1940, Ecke and Johnson 1952, Cully et al. 2000). Prairie dogs are highly susceptible to plague with at or near 100% mortality within a colony (Barnes 1993, Cully and Williams 2001, Stapp et al. 2004). Because of plague, prairie dogs now exhibit classic metapopulation dynamics in that colonies are subject to periodic extinction events and are repopulated by individuals from neighboring colonies (Roach et al. 2001). To date, there is little evidence that prairie dogs are evolving resistance to the disease (Antolin et al. 2006). It is well recognized that plague has had important effects on prairie dog population genetics (Roach et al. 2001, Antolin et al. 2002, 2006), but I suggest that plague has, and will continue to have, important mediating effects on the role of prairie dogs in influencing plant communities on the shortgrass steppe.

I used long-term monitoring data collected by the U. S. Forest Service to estimate the frequency of plague outbreaks on the Pawnee National Grassland (PNG) and the rate of recovery of colonies following an outbreak. Data on colony size and activity (active or inactive) have been collected for colonies known to exist within the boundaries of the PNG from 1981 to present (Fig. 1.2). Based on these data, the median length of continuous activity before which a colony experienced an outbreak was 6.6 years and the probability of a colony experiencing at least one plague outbreak within a 20 year period was 98% (Fig. 1.3). In areas of the prairie dog distribution where plague is not present, such as South Dakota, colonies can persist for multiple decades in one location (Hoogland 1995, Antolin et al. 2002), and prior to the introduction of plague, the average age of prairie dog colonies on the shortgrass steppe was almost certainly higher. Not only are plague outbreaks frequent on the shortgrass steppe, they are most often followed by a period of inactivity during which vegetation might recover from the influence of prairie dogs. Data from the PNG suggest that nearly half of the colonies will be inactive for at least 5 years following an outbreak (Fig. 1.4). Antolin et al. (2002) reported that plague has reduced the average size of colonies. My analysis of the PNG data supports this assertion because less than half of the plague-extirpated colonies had attained their pre-plague size within 10 years of an outbreak (Fig. 1.5). Thus, even though prairie dog colonies can expand quickly (Stapp et al. 2004), expansion rates on an individual colony are apparently not great enough to offset the influence of plague extirpations.

In Chapters 3 and 4, in addition to addressing the extent to which effects of prairie dogs on vegetation and nutrient cycling are influenced by colony age, I also address the degree to which colonies recover from the effects of prairie dogs during periods of inactivity after a plague outbreak. Many of the effects of prairie dogs on the shortgrass steppe appear to increase with colony age, but because of plague, colonies on the shortgrass steppe no longer reach "old" age. Most colonies will experience periodic episodes of inactivity because of plague, and I found that plague-extirpated colonies were rarely significantly different from uncolonized grassland.

Prairie dogs are species of special concern because their numbers have been greatly reduced over the last century due to loss of habitat, poisoning, recreational shooting and disease (Luce 2003, Antolin et al. 2002). Some argue that prairie dogs are ecosystem engineers (sensu Jones et al. 1994) because they modify their environment in ways that influence resource availability to other organisms (Ceballos et al. 1999) and some consider prairie dogs to be keystone species (sensu Paine 1969, Power et al. 1996) because their influence on plant and animal communities is disproportionately large compared to their relative abundance (Miller et al. 1994, Kotliar et al. 1999, Kotliar 2000, but see Stapp 1998). My results suggest that plague outbreaks mediate the effects of prairie dogs on their physical environment. This could have important implications for the plants and animals associated with prairie dog colonies (Hardwicke 2006, Kotliar et al. 1999, Ceballos et al. 1999). Furthermore, plague has important implications in the debate about how prairie dogs influence cattle production. In general, the effects of prairie dogs on standing plant biomass are less on younger colonies and not significant on plague-extirpated colonies. Ranchers can thus expect the effects of prairie dogs on forage quantity in their pastures to be periodically alleviated when inevitable plague outbreaks occur.

LITERATURE CITED

Antolin, M. F., P. Gober, D. Luce, D. E. Biggins, W. E. Van Pelt, D. B. Seery, M. Lockhart, and M. Ball. 2002. The influence of sylvatic plague on North American wildlife at the landscape level, with special emphasis on black-footed ferret and prairie dog conservation. Transactions of the 67th North American Wildlife and Natural Resources Conference 67:104-127.

Antolin, M. F., L. T. Savage, and R. J. Eisen. 2006. Landscape features influence genetic structure of black-tailed prairie dogs (*Cynomys ludovicianus*). Landscape Ecology 21:867-875.

Archer, S. R., M. G. Garrett, and J. K. Detling. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio 72:159-166.

Barnes, A. M. 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. Pages 28-37 *in* J. L. Oldemeyer, D. E. Biggins and B. J. Miller, (Editors), Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret. U.S. Department of Interior Biological Report 13.

Burke, I. C., W. K. Lauenroth, R. Riggle, P. Brannen, B. Madigan, and S. Beard. 1999. Spatial variability of soil properties in the shortgrass steppe: the relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. Ecosystems 2:422-248.

Ceballos, G., J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. Journal of Arid Environments 41:161-172.

Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1-9.

Coughenour, M. B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations and interacting processes. Annals of the Missouri Botanical Garden 72:852-863.

Coupland, R. T. 1992. Mixed Prairie. Pages 151-182 *in* R. T. Coupland (Editor), Ecosystems of the World 8A. Natural Grasslands. Introduction and Western Hemisphere. Elsevier, New York, New York.

Detling, J. K. 2006. Do prairie dogs compete with livestock? Pages 65 – 88 *in* J. L. Hoogland (Editor), Conservation of The Black-Tailed Prairie Dog: Saving North America's Western Grasslands. The University of Chicago Press. Chicago, Illinois.

Cully, J. F, L. G. Carter, and K. L. Gage. 2000. New records of sylvatic plauge in Kansas. Journal of Wildlife Diseases 36:389-392.

Cully, J. F. and E. S. Williams. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. Journal of Mammalogy 82:894-905.

Ecke, D. H. and C. W. Johnson. 1952. Plague in Colorado and Texas. Part I. Plague in Colorado. Public Health Monograph No. 6 U.S. Government Printing Office, Washington, D.C.

Eskey, C.R. and V. H. Haas. 1940. Plague in the Western Part of the United States. U.S. Public Health Service Bulletin No. 254 U.S. Government Printing Office, Washington, D.C.

Fahnestock, J. T. and J. K. Detling. 2002. Bison-prairie dog –plant interactions in a North American mixed-grass prairie. Oecologia 132:86-95.

Goodwin, H. T. 1995. Systemic revision of fossil prairie dogs with descriptions of two new species. University of Kansas Museum of Natural History Miscellaneous Publications 86:1-38.

Gould, S. J. and E. S. Vrba. 1982. Exaptation – a missing term in the science of form. Paleobiology 8:4-15.

Hardwicke, K. 2006. Tri-trophic interactions affect plant-insect floral visitor webs of the shortgrass steppe: prairie dogs, plant, and pollinators. Ph.D. Dissertation, Colorado State University, Fort Collins, Colorado.

Holland, E. A. and J. K. Detling. 1990. Plant responses to herbivory and belowground nitrogen cycling. Ecology 71:1040-1049.

Hoogland, J. L. 1995. The Black-Tailed Prairie Dog: Social Life of a Burrowing Animal. The University of Chicago Press. Chicago, Illinois.

Inglesby, T. V., D. T. Dennis, D. A. Henderson, J. G. Bartlett, M. S. Ascher, E. Eitzen, A. D. Fine, A. M. Friedlander, J. Hauer, J. F. Koerner, M. Layton, J. McDade, M. T. Oserholm, T. O'Toole, G. Parker, T. M. Perl, P. K. Russel, M. Schoch-Spana and K. Tonant. 2000. Plague as a biological weapon. Journal of the American Medical Association 283:2281-2290.

Johnson-Nistler, C. M., B. F. Sowell, H. W. Sherwood, and C. L. Wambolt. 2004. Black-tailed prairie dog effects on Montana's mixed-grass prairie. Journal of Range Management 57:641-648.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373-386.

Klipple, G. E. and D. F. Costello. 1960. Vegetation and cattle responses to different intensities of grazing on shortgrass ranges on the central Great Plains. Technical Bulletin 1216. U.S. Department of Agriculture. U. S. Government Printing Office, Washington D.C.

Kotliar, N. B., B. W. Baker, A. D. Whicker, and G. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management 24:177-192.

Kotliar, N. B. 2000. Application of the new keystone-species concept to prairie dogs: how well does it work? Conservation Biology 14:1715-1721.

Lauenroth, W. K. and D. G. Milchunas. 1992. Short-grass steppe. Pages 183-226 *in* R. T. Coupland, (Editor), Natural grasslands I. Introduction and Western Hemisphere. Elsevier, New York, New York.

Levy, C. E. and K. L. Gage. 1999. Plague in the United States, 1995-1997. Infections in Medicine. 16:54-64.

Luce, R. J. 2003. A Multi-State Conservation Plan for the Black-Tailed Prairie Dog, *Cynomys ludovicianus*, in the United States – An addendum to the Black-tailed Prairie Dog Conservation Assessment and Strategy, November 3, 1999.

Mack, R. N. and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. American Naturalist 119:757-773.

McNaughton, S. J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecological Monographs 53:291-320.

Milchunas, D. G. and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs. 63:327-366.

Milchunas, D. G., O. E. Sala, and W. K. Lauenroth.1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. The American Naturalist 132:87-106.

Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. Vegetatio 80:11-23.

Miller, B. K., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology 8:677-681.

Paine, R. T. 1969. A note on trophic complexity and species diversity. American Naturalist 100:91–93.

Poland, J. D. and D. T. Dennis. 1998. Plague. Pages 545-558 *in* A. S. Evans and P. S. Brachman, (Editors), Bacterial Infections in Humans, Epidemiology and Control, 3rd ed. Plenum Publishing Corporation, New York, New York.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. BioScience 46:609-620.

Roach, J. L., P. Stapp, B. Van Horne, and M. F. Antolin. 2001. Genetic structure of a metapopulation of black-tailed prairie dogs. Journal of Mammology 82:946-959.

Stapp, P., M. F. Antolin, and M. Ball. 2004. Patterns of extinction in prairie dog metapopulations: plague outbreaks follow El Niño events. Frontiers in Ecology and the Environment 2:235-240.

Stapp, P. 1998. A reevalutaion of the role of prairie dogs in Great Plains grasslands. Conservation Biology 12:1253-1259.

Stebbins, G. L. 1981. Coevolution of grasses and large herbivores. Annals of the Missouri Botanical Garden 68:75-86.

Whicker, A. D. and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. Bioscience 38:778-785.

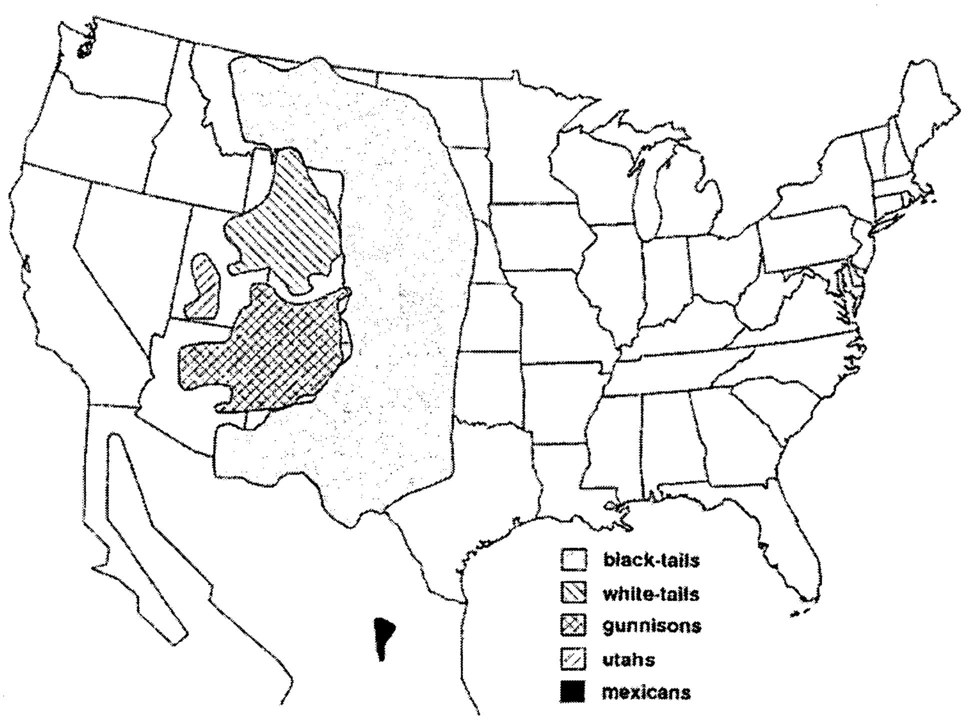

Figure 1.1 - Distributions of the five species of prairie dog in North America (from Hoogland 1995).

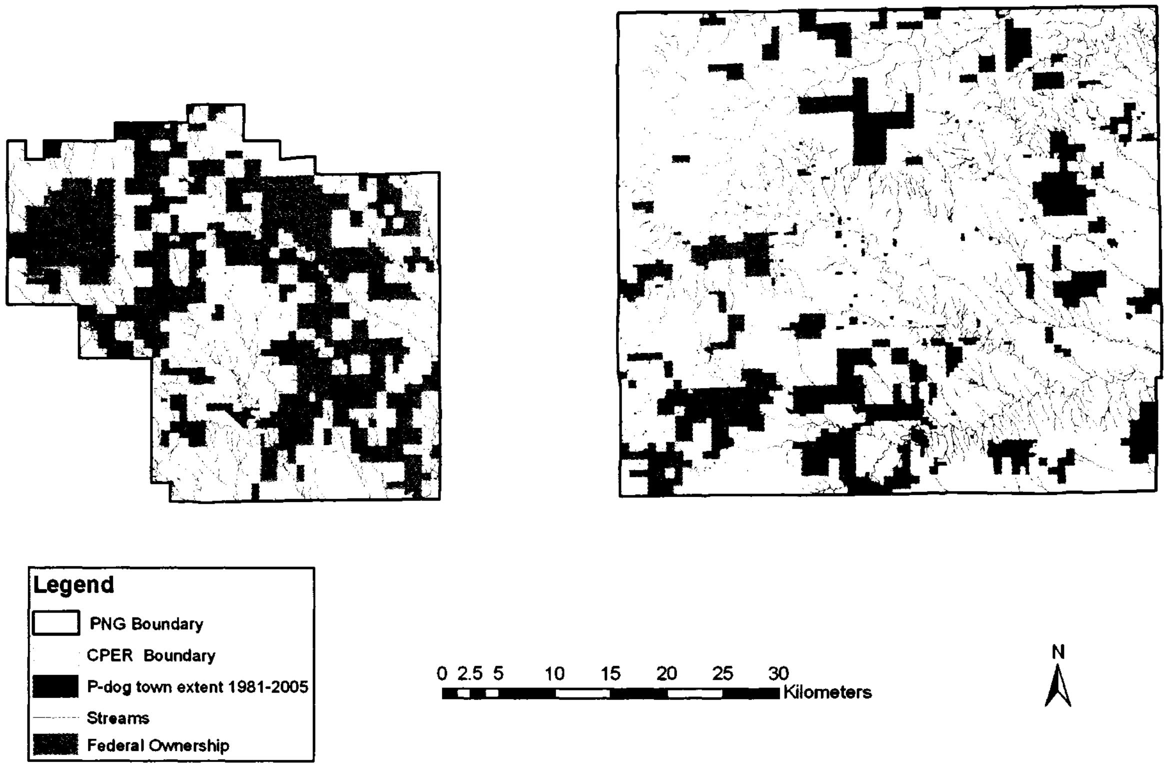

Figure 1.2 - Map of the 70 + colonies that have been known to exist on Pawnee National Grassland (U. S. Forest Service) and Central Plains Experimental Range (U.S. Department of Agriculture). Although colonies were present on private land, monitoring and mapping was conducted only within the boundaries of the Pawnee National Grassland.

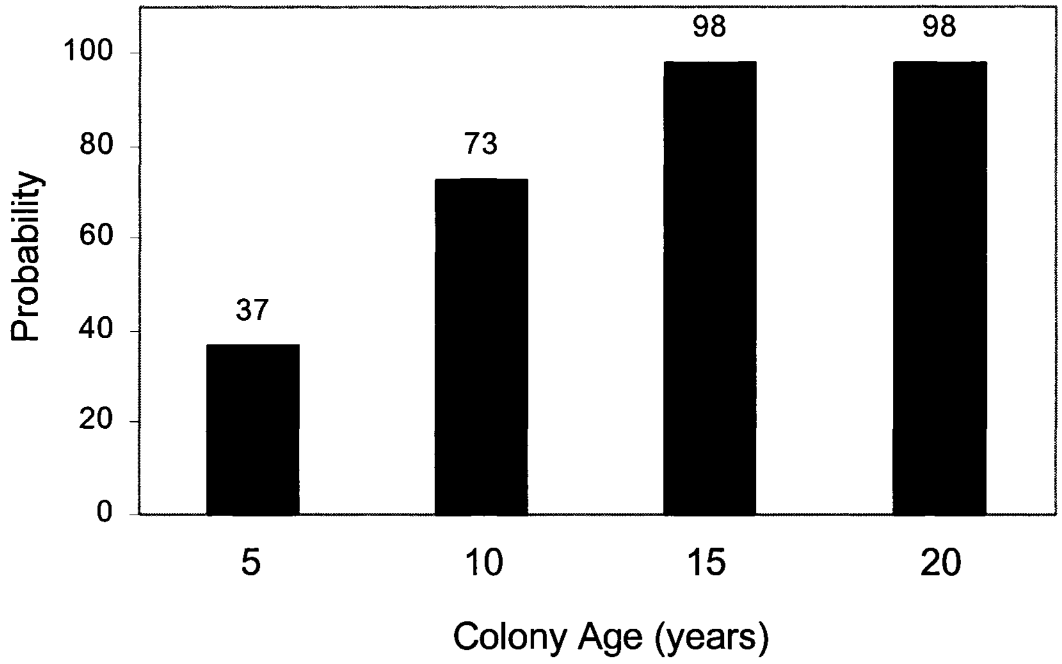

Figure 1.3 - The probability that an individual colony on the Pawnee National Grassland will experience a plague outbreak within 5, 10, 15, or 20 years of continuous activity.

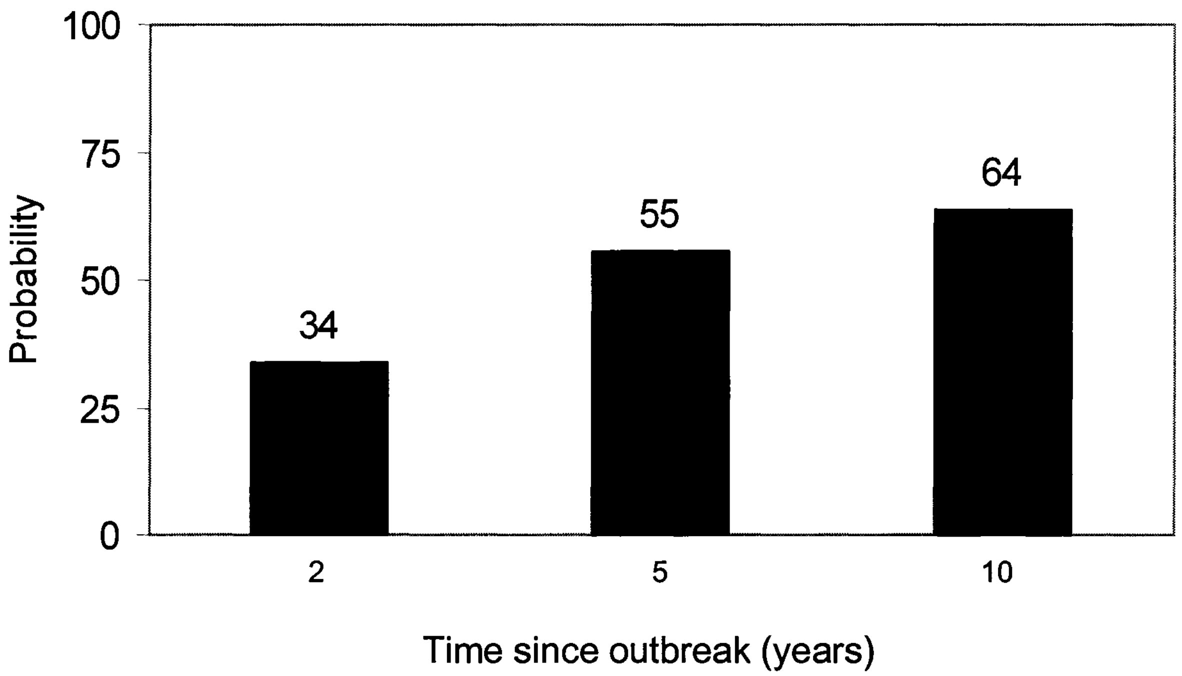

Figure 1.4 - The probability that a colony on the Pawnee National Grassland will be recolonized within 2, 5 or 10 years of a plague outbreak.

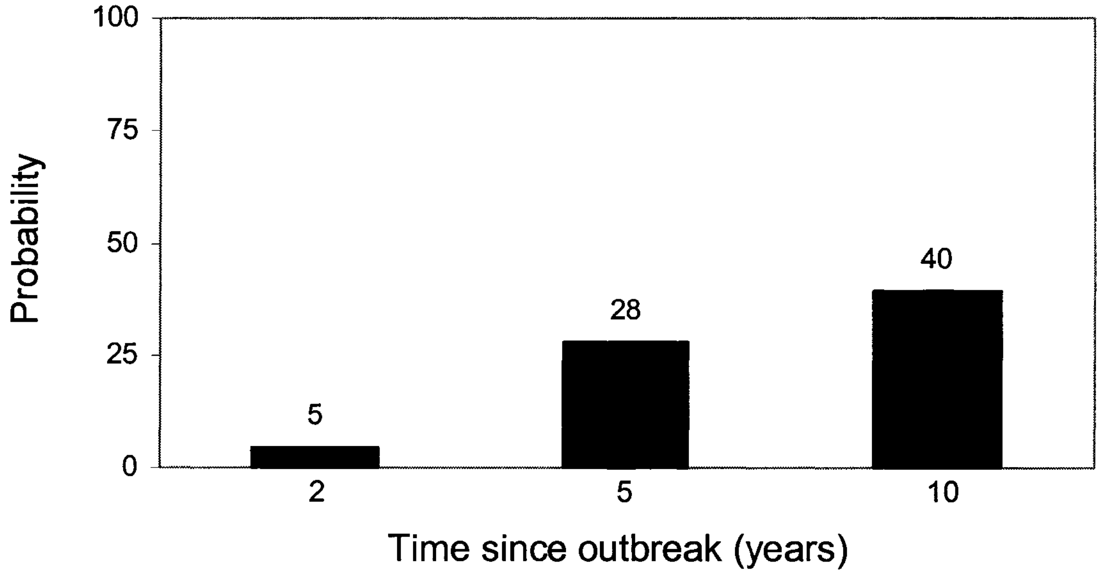

Figure 1.5 – The probability that a colony on the Pawnee National Grassland will attain its pre-plague size within 2, 5 or 10 years of a plague outbreak.

CHAPTER 2

EFFECTS OF PRAIRIE DOGS AND CATTLE ON PLANT COMMUNITIES OF THE SHORTGRASS STEPPE

Abstract. --- I studied the effects of black-tailed prairie dogs (*Cynomys ludovicianus*) and cattle (*Bos taurus*) on plant communities of the shortgrass steppe in northeastern Colorado. I estimated plant cover and biomass on and off of five colonies from 1997 through 2001. All of the colonies were active from 1997 through 1999, but because of a plague outbreak in late 1999, 4 of the colonies were inactive in 2000 and 2001. Mean total plant canopy cover and cover of functional groups (forb, graminoid, shrub, cactus) did not differ significantly between on- and off-colony sites either before or after the plague outbreak. Mean total current-year plant biomass and biomass of both C3 and C4 graminoids was lower on colonies before, but not after the plague-outbreak. Forb biomass did not differ significantly between on- and off-colony sites either before or after the outbreak, but forbs accounted for 22% of the biomass on-colonies before, but only 6% after the outbreak. Root biomass did not appear to be affected by prairie dog herbivory, supporting the idea that belowground biomass is resistant to effects of heavy grazing on the shortgrass steppe. Mean total plant species richness was greater on than off of colonies before, but not after the outbreak. Total plant species diversity did not differ between on- and off-colony sites before or after the outbreak. In 1998 and 1999, I estimated mean total live plant biomass and biomass of graminoids and forbs under cages intended to exclude cattle or cattle and prairie dogs. In general, exclusion of one or both herbivores resulted in increases in graminoid biomass and decreases in forb biomass. Cattle and prairie dogs appear to have similar and additive effects on plant biomass.

Key words: Cynomys ludovicianus, Bos taurus, *grazing, plague, shortgrass steppe, roots, plant diversity*

INTRODUCTION

In grassland ecosystems, herbivores influence plant community composition, physiognomy, and productivity (Whicker and Detling 1988, Mack and Thompson 1982, Milchunas and Lauenroth 1993, Adler et al. 2004). However, the specific responses of a grassland plant community to herbivory depend upon many factors, including herbivore densities, herbivore size, climate, and the length of evolutionary time that the grassland has been occupied by grazers (Mack and Thompson 1982, Coughenour 1985, Milchunas et al. 1988, Adler et al. 2004). The shortgrass steppe is characterized by a long evolutionary history of grazing, a semi-arid climate, high winds, short-statured plant species, and a low ratio of aboveground to belowground biomass (Lauenroth and Milchunas 1992). Even when compared to other grasslands with long evolutionary histories of grazing, the shortgrass steppe is unusually tolerant of herbivory (Milchunas et al. 1988, 1989). This high tolerance has been attributed to the idea that the predominant selection pressures on the shortgrass steppe, grazing and semiaridity, are convergent while the selection pressures on more mesic grasslands, grazing and canopy competition, are divergent (Milchunas et al. 1988).

The black-tailed prairie dog (*Cynomys ludovicianus*) is an iconic herbivore native to the Great Plains of North America. Prairie dogs are found in the relatively more mesic northern mixed-grass prairie, the semi-arid shortgrass steppe, and the sub-humid southern mixed-grass prairie (Hoogland 1995) and are an excellent study organism for comparing the effects of herbivory across climatic gradients. In the mixed-grass prairies of South Dakota and Texas, grazing by prairie dogs results in decreases in standing biomass, canopy height, litter, and cover and biomass of graminoids relative to forbs (Coppock et al. 1983a, Archer et al. 1987, Whicker and Detling 1993, Weltzin et al. 1997a,b, Fahnestock and Detling 2002). The effects of prairie dogs on shortgrass steppe vegetation have been less studied (Bonham and Lerwick 1976, Hansen and Gold 1977, Winter et al. 2002). Currently, data from studies of prairie dogs on the mixed-grass prairie are being used to make management decisions for prairie dogs across the plains and including the shortgrass steppe, but because the shortgrass steppe is so tolerant of heavy grazing, effects of prairie dogs may be less dramatic in the shortgrass steppe than they are on the mixed-grass prairie. The first objective of this research is to quantify the effects of prairie dogs on standing crop biomass and plant community composition on the shortgrass steppe and to compare these effects to those observed on the mixed-grass prairie.

The second objective of this study is to examine whether any effects of prairie dogs on aboveground biomass and plant community composition between on- and off-colonies persist after a colony is extirpated by an introduced disease, sylvatic plague. Plague is not present in all parts of the black-tailed prairie dog's range and was not present in the shortgrass steppe until the mid-1940s (Eskey and Haas 1940, Ecke and Johnson 1952, Cully and Williams 2001). Prairie dogs are highly susceptible to plague, with essentially 100 % mortality of infected individuals (Cully and Williams 2001, Stapp et al. 2004). After an outbreak occurs on a colony, the colony typically will be inactive for at least several years before immigrant prairie dogs begin to recolonize the area (Chapter 1). During the course of this five year study, the majority of the focal colonies were extirpated due to plague. Because plague epizootics are frequent and widespread on the shortgrass steppe and there is no evidence that prairie dogs are developing resistance to the disease (Antolin et al. 2006), an understanding the role of plague in mediating the effects of prairie dogs on vegetation is needed . Some studies suggest that the effects of prairie dogs on grassland ecosystems are rapidly (within several years) reversed once prairie dogs are removed or excluded from grazing (Osborn and Allan 1949, Cid et al. 1991), while others have shown no reversal of the effects of prairie dogs within several years of removal (Klatt and Hein 1978, Uresk 1985).

The changes in plant communities caused by prairie dog activities may have competitive, neutral, or beneficial effects on large ungulate herbivores (O'Meilia et al. 1982, Coppock et al. 1983b, Krueger 1986, Guenther and Detling 2003, Derner et al. *in press*). In the mixed-grass prairie, bison (*Bison bison*) preferentially graze on prairie dog colonies during the growing season, when forage protein and in vitro digestibilities are greater on than off of colonies (Coppock et al. 1983a,b), and mathematical modeling suggests that bison that feed on prairie dog colonies during the summer could have significantly greater weight gains than bison that feed off of colonies (Vanderhye 1985).

Domestic cattle (*Bos taurus*) have replaced bison as the dominant ungulate herbivore in most of the Great Plains, including the shortgrass steppe. The interactions between prairie dogs and cattle are of socio-economic interest because prairie dogs are often viewed by ranchers as intolerable competitors with livestock for forage. Based on fecal analysis, Hansen and Gold (1977) observed a 64% overlap between the diets of prairie dogs and cattle on the shortgrass steppe and concluded that prairie dogs may reduce habitat suitability for cattle grazing. O'Meilia et al. (1982) reported lower biomass of cattle-preferred species on prairie dog colonies, but they did not find a statistically significant difference in cattle weight gain between on and off of colonies. Despite suggestions that prairie dogs may reduce available preferred forage for cattle, cattle apparently graze on prairie dog colonies of the shortgrass steppe in proportion to their areal coverage, which suggests that they neither prefer nor avoid them (Guenther and Detling 2003). In a recent study, Derner et al. (2006) reported that steers gained less weight on pastures with colonies, but that a tripling in colony size (from 20 to 60% of the pasture) resulted in only an additional 8.5 % decrease in cattle weight gain.

The third objective of this study is to estimate the relative amounts of standing crop biomass removed by cattle and prairie dogs on the shortgrass steppe. This information will be useful for interpreting potential competition between cattle and prairie dogs. Many researchers have suggested that the influences of small and large herbivores may be different because of differences in the frequency and intensity of grazing, patterns in distribution of feces, diet selectivity, and intensity of pedoturbation (Bakker et al. 2004, Cid et al. 1991, Olff and Ritchie 1998). Cid et al. (1991) found that, in spite of their different grazing patterns, bison and prairie dogs had similar and independent (i.e. additive) effects on plant biomass and community composition in mixed-grass prairie. However, this same relationship may not be true for cattle and prairie dogs on the shortgrass steppe for several reasons. The shortgrass steppe has lower annual net primary production than the mixed-grass prairie, and competition between herbivores has been shown to be greater when resources are more limited (Heske and Campbell 1991). Furthermore, cattle have slightly different dietary requirements and foraging behavior than bison (Hansen et al. 1973, Schwartz and Ellis 1981, Hartnett et al.

1996) and are not allowed to roam over large areas on the Pawnee National Grassland as bison were in the study conducted on the mixed-grass prairie.

METHODS

Site Description. --- I conducted this study from 1997 through 2001 on the Pawnee National Grassland located in northeastern Colorado. The dominant plants are *Bouteloua gracilis* (blue grama), *Buchloe dactyloides* (buffalo grass), and (*Opuntia polyacantha* (prickly pear cactus). Long term mean annual precipitation is 322 mm, with approximately 70% of precipitation falling between April and September (Lauenroth and Milchunas 1992). Mean annual temperature is 8.6 C. As is typical for the shortgrass steppe, precipitation was highly variable among years. Total precipitation from April through July was 278 mm in 1997, 207 mm in 1998, 359 mm in 1999, 102 mm in 2000, and 220 mm in 2001 (National Science Foundation Shortgrass Steppe Long Term Ecological Research Program, Colorado State University, Fort Collins, CO).

I studied five prairie dog colonies and an associated off-colony site for each. Paired colony and control sites had similar potential vegetation, soil characteristics, and topography. All of the sites were native vegetation and had never been cultivated or seeded according to historical records (U. S. Forest Service, Pawnee National Grassland, Greeley, CO). At the beginning of the study, the ages of the five colonies were 5, 5, 8, 10, and 17 years. However, the 17 year old colony was inactive from 1991 through 1992 due to plague and therefore had been continuously active for only 5 years prior to this study. All five colonies were active from 1997 to 1999. In 1999, a plague outbreak occurred and all but one of the colonies was extirpated.

Plant Community Composition. --- I estimated canopy cover of each plant species, bare ground, and litter at 20 random coordinates within a 150 x 80 m plot located in the center of each colony and off-colony site using Daubenmire quadrats (0.2 x 0.8 cm) (Daubenmire 1970). I collected data annually in late July or early August and used data to assess the relative cover of functional groups (C3 and C4 graminoids, forbs, shrubs, and cactus) and the dominant grasses on the shortgrass steppe (*Bouteloua gracilis* and *Buchloe dactyloides*). I also calculated species richness (# of species per site), Shannon-Weiner diversity (H'), and Jaccard's index of similarity (S_j) between on- and off- colony sites for forbs, graminoids, and total vegetation (Gurevitch et al. 2002).

Plant Biomass. --- I clipped aboveground biomass on 5 randomly located quadrats (0.25 m^2) on each colony and control site at the time of estimated peak biomass each year. Current year's growth was separated by species, but previous year's growth was not. I dried samples at 55 °C and weighed them. Prior to statistical analysis, I summed plant biomass estimates by functional group.

In early summer 1998 and 1999, I collected five soil cores (6.35 cm diameter) at each colony and control site and divided the cores into 0-15, 15-30, and 30-45 cm depth increments. I mixed each sample with water and agitated them to separate root material from soil (Lauenroth and Whitman 1971). As roots floated to the surface, I decanted them onto a 0.5 mm mesh sieve. I then dried root samples at 55 °C, hand-picked non-root materials (e.g. seeds, pebbles, feces) from each sample, and weighed them. I corrected for soil contamination in each sample by multiplying the mass of the original sample by the organic matter (%) in the sample. I calculated organic matter (%) by grinding root samples into a fine powder and then combusting a 0.5 g subsample in a muffle furnace at 600 °C for 4 hours.

Consumption by Prairie Dogs and Cattle. --- To estimate consumption of aboveground biomass by cattle and prairie dogs, I installed five (1 m x 1 m) cattle exclosure cages at each colony and control site and five prairie dog exclosure cages (1 m x 1 m) at each colony site. All exclosure cages were fashioned out of hardware cloth, and prairie dog exclosure cages were covered with chicken wire. I installed cages at the beginning of the growing seasons in 1998 and 1999. At the time of peak biomass, I clipped aboveground biomass by species in a 0.25 m^2 area under the cages dried samples at 55 °C, and weighed them.

Statistical Analyses. --- I used a repeated measures, mixed model analysis of variance (ANOVA) to test the effects of colony (site), location (on- versus off-colony), and year on cover, richness, and diversity (H') of functional groups, aboveground biomass of functional groups, and total belowground biomass. Colony was treated as a random effect. Location and year were fixed effects. I also examined interactions between the main effects. In 1999, four of the five colonies experienced a plague outbreak near the end of the growing season. Therefore, I analyzed data collected prior to the plague outbreak (1997-1999) separately from data collected after the plague outbreak (2000-2001). I used t-tests to examine whether similarity indices (S_j) for each functional group were different before and after the plague outbreak.

I also used ANOVAs to examine differences in consumption of aboveground biomass by cattle and prairie dogs on and off of active prairie dog colonies. In these ANOVAs, I used the response variables of total aboveground biomass and biomass by functional group. Colony was again used as a random effect while year and location were fixed effects. The location variable included not only on- versus off- colony, but also the three exclosure cage types (cattle excluded from off-colony sites, cattle excluded from on-colony sites, and prairie dogs excluded from on-colony sites).

For all models, I analyzed differences between on- and off- colonies by considering colonies, rather than individual quadrats, as replicates. Residuals of all models were examined for normality and, if necessary, data were square-root transformed and reanalyzed. All tables and figures depict untransformed data. I used SAS statistical software to perform all analyses (SAS Institute 1999, Cary, NC, USA). All differences reported are statistically significant at $P \leq 0.05$.

RESULTS

Plant Cover. --- Mean plant cover did not differ significantly between on- and off-colony sites either before (on = 41%, off = 41%) or after (on = 52%, off = 56%) the plague outbreak (Table 2.1). Bare ground cover did not differ significantly between on- and off-colonies prior to the outbreak, but was slightly greater on-colonies after the outbreak (Fig. 2.1, Table 2.1). There were no significant differences between off- and on-colonies with respect to the graminoid, forb, and cactus functional groups either before or after prairie dogs were extirpated (Fig. 2.1, Table 2.1). Shrub cover was not significantly different between on- and off-colonies in any year except 1998 (Fig. 2.1, Table 2.1). Mean C3 plant cover was significantly lower on- than off-colonies prior to the plague outbreak, but not after (Fig. 2.1, Table 2.1). Differences in C3 cover were primarily due to a lower cover of the graminoid species, *Sitanian hystrix* on colonies (on = 0.3 %, off = 2.5 %, F = 9.84, P = 0.01). Colonies had significantly lower litter cover than control sites prior to the outbreak and in the first year after the plague outbreak, but not in the second year after the outbreak (Fig. 2.1, Table 2.1). Mean cover of *B. gracilis* did not differ significantly between on- and off-colony sites either before (on = 22 %, off = 24 %) or after (on = 32 %, off = 31 %) the outbreak (Table 2.1). Similarly, mean cover of *B. dactyloides* did not differ significantly between on- and off-colonies either before (on = 8.4 %, off = 6.3 %) or after (on = 8.9 %, off = 11.3 %) the outbreak (Table 2.1).

Plant Biomass. --- Mean total aboveground plant biomass (current year's growth) was significantly lower on (65 g/m^2) than off (81 g/m^2) colonies prior to the plague outbreak, but after the plague outbreak, it did not differ significantly between on (60 g/m^2) and off (71 g/m^2) of colonies (Table 2.2). Compared to uncolonized sites, prairie dog colonies had significantly lower biomass of both C3 and C4 graminoids prior to, but not after, the outbreak (Fig. 2.2a, Table 2.2). Forb biomass did not differ significantly between on and off of colonies before or after the outbreak (Fig. 2.2a, Table 2.2). However, forbs accounted for almost 22% of plant biomass before the outbreak, but only 6% after the outbreak, compared to 5 – 8% off of colonies. Biomass of shrubs did not differ significantly between on and off of colonies before or after the outbreak (Fig. 2.2b, Table 2.2). Although there was a trend toward lower biomass of standing dead plants on than off of colonies both prior to (on = 1.5 g/m^2, off = 4.2 g/m^2) and after (on = 1.7 g/m^2, off = 6.6 g/m^2) the plague outbreak, the trend was not significant (Table 2.2). Statistical analyses were not performed for the cactus functional group because of high variability in cactus biomass. Biomass of *B. gracilis* was lower on (33.2 g/m^2) than off (46.3 g/m^2) of colonies before, but not after the outbreak (on = 28.4 g/m^2, off = 31.7 g/m^2) (Table 2.2). Biomass of *B. dactyloides* did not differ significantly between on and off of colonies before (on = 7.9 g/m^2, off = 7.4 g/m^2) or after (on = 11.9 g/m^2, off = 11.6 g/m^2) the outbreak (Table 2.2). Live plant biomass was correlated with precipitation (Pearson correlation coefficient $r = 0.65$, $P < 0.001$). However, there were no significant interactions between location (on versus off of colony) and year for any of the ANOVA procedures.

Root biomass did not differ significantly between on- and off-active colonies for any of the depth increments measured (0 to 15 cm, 15 to 30 cm, or 30 to 45 cm) or for the sum of all depth increments (0 to 45 cm) (Fig 2.3). Mean root biomass for the two years sampled was greatest for the 0 to 15 cm depth increment (off = 917 g/m^2, on = 931 g/m^2) and least for the 30 to 45 cm depth increment (off = 185 g/m^2, on = 170 g/m^2) (Fig. 2.3). Root biomass was not estimated in the years after the plague outbreak.

Plant Species Richness, Diversity, and Similarity. --- Mean total plant species richness and forb species richness were greater on than off of colonies prior to, but not after, the outbreak (Table 2.3). Both before and after the outbreak, graminoid species richness was similar between on- and off-colony sites (Table 2.3). The trends for total plant diversity and diversity of graminoids were not consistent between years, and in no year were trends significant (Table 2.3). However, forb diversity was higher on than off colonies prior to the outbreak, but not after (Table 2.3). Similarity indices (S_j) showed greater overlap between on- and off-colony sites with respect to graminoids and cactus than with respect to forbs or shrubs (Table 2.4). Colonies were not more or less similar to their paired off-colony sites after the plague outbreak than they were before the outbreak with respect to all plants and forbs (Table 2.4). However, similarity between on- and off- colony sites with respect to graminoid species composition was significantly greater after the plague outbreak (Table 2.4).

Consumption by Prairie Dogs and Cattle. --- Off of colonies, cattle grazing reduced total standing crop biomass by 28 %. On colonies, total standing crop biomass was reduced 27% by cattle and an additional 13% by prairie dogs (Fig. 2.4). Off of colonies, cattle grazing reduced graminoid biomass by 26 %. On colonies, graminoid biomass was reduced 32 % by cattle and an additional 19 % by prairie dogs (Fig. 2.4). There were trends toward higher forb biomass in plots where cattle and cattle + prairie dogs were allowed to graze (Fig. 2.4), but the trends were not significant. There were no significant differences between exclosure types for cactus (F = 0.22, P = 0.924), shrubs (F = 0.56, P = 0.691), or standing dead plant biomass (F = 1.26, P = 0.307). There were also no significant differences between sampling locations for any individual plant species except for the dominant graminoid, *B. gracilis* (F = 5.35, P = 0.002). The patterns in biomass reduction of *B. gracilis* with cattle and prairie dog grazing were similar to those of the graminoid functional group. *B. gracilis* accounted for 50-60% of the graminoid biomass in all exlcosure types.

DISCUSSION

My first goal was to quantify the effects of prairie dogs on plant community composition and biomass and to compare the effects of prairie dogs on the shortgrass steppe to their effects on the mixed grass prairie. In the mixed-grass prairie, grazing by prairie dogs results in large decreases in cover of graminoids (~ 70 → 20 %) and litter (~ 20 → 10%) and large increases in cover of forbs (~ 10 → 50 %) and bare ground (~ 10 → 35%) (Archer et al.1987). I found similar trends to those observed in the mixed-grass prairie, but prairie dog-induced changes to plant cover were much smaller in magnitude on the shortgrass steppe and were, for the most part, not statistically significant. Differences between on- and off- colony sites were apparent within 2 to 4 years of colonization in the mixed-grass prairie and increased thereafter as a function of colony age (Archer et al. 1987). My study was restricted to colonies that were active for less than 20 years. Older colonies on the shortgrass steppe may exhibit greater changes than younger colonies. More information is needed about whether effects of prairie dogs on plant cover increase with colony age on the shortgrass steppe. This information is especially important because average colony age has been reduced on the shortgrass steppe, due to plague, with few colonies now persisting for multiple decades (Antolin et al. 2002, Chapter 1).

I found the effects of prairie dogs on aboveground plant biomass on the shortgrass steppe to be greater than their effects on plant cover (Figs. 2.1 and 2.2). The reduction in total plant biomass observed in this study was similar in direction, but lower in magnitude, than the reduction noted for the mixed-grass prairie. On the mixed-grass prairie, prairie dog grazing reduced standing crop biomass by more than 50% on colonies occupied for 3 to 8 years (Coppock et al. 1983a). In this study on the shortgrass steppe, prairie dog grazing reduced biomass by only 20% on similarly aged colonies. For young colonies (3-8 years) in the mixed-grass prairie, graminoids comprised 70% of total plant biomass on-colony and 85% off-colony while forbs comprised 25 % of the biomass on-colony and 15% off-colony (Coppock et al. 1983a). I observed a similar pattern for active colonies on the shortgrass steppe, with graminoids comprising 77 % of biomass on-colony and 90% off-colony, and forbs comprising 22% of biomass on-colony and 8% of biomass off-colony. In the mixed-grass prairie, the effect of prairie dogs on the relative proportions of graminoids and forbs increased with colony age while the effect of prairie dogs on total plant biomass decreased with colony age (Coppock et al. 1983a). This occurs because forb biomass increases as graminoid biomass decreases. Because this study on the shortgrass steppe did not include older colonies, I cannot address how colony age influences the effects of prairie dogs on plant biomass.

Unlike on the mixed-grass prairie, prairie dog grazing on the shortgrass steppe did not result in a decrease in belowground plant biomass. The shortgrass steppe has a very low (1:10) ratio of aboveground to belowground biomass, and belowground biomass has been very resistant to reductions by heavy grazing (Milchunas and Lauenroth 1989). It is possible that reductions of belowground biomass would only be seen in colonies that have been heavily grazed by prairie dogs for much longer periods of time (> 20 years).

The second goal of this study was to assess the role of plague in mediating the effects of prairie dogs on the shortgrass steppe. Almost all prairie dog-induced changes in vegetation were reversed within one to two years of the plague epizootic that occurred at the end of the 1999 growing season. Thus, bubonic plague may be profoundly altering the potential long-term role prairie dogs play in shaping shortgrass steppe plant communities. Colonies represent unique patches of habitat within the larger grassland matrix and differences in vegetation structure and composition on- and off-colonies have been cited as reasons why some animal species are found in greater abundance on prairie dog colonies (Miller et al. 1994, Kotliar 2000, Hardwicke 2006) and as reasons why cattle production may be detrimentally affected by the presence of a prairie dog colony in a pasture (O'Meilia et al. 1982, Vermiere et al. 2004). Periodic die-offs of colonies due to plague may have important implications for the animal species that preferentially utilize prairie dog colonies and for the highly politicized debate about whether prairie dogs should be exterminated on rangeland to facilitate cattle production (e.g. Vermiere et al. 2004 vs. Forrest 2005). Ranchers may chose not to spend time and money to eradicate prairie dogs on their pastures because most, if not all, colonies on the shortgrass steppe will experience a plague outbreak at least once every twenty years and most colonies will likely be inactive for at least several years after an outbreak (Stapp et al. 2004, Chapter 1).

The final goal of this study was to estimate the amount of standing crop biomass removed by cattle, prairie dogs, and cattle + prairie dogs. Exclusion of cattle and cattle + prairie dogs each significantly increased plant biomass. Unfortunately, on-colonies, I was unable to exclude prairie dogs, but leave cattle. Cattle consumed statistically similar amounts of total annual net primary production (ANPP) on versus off of colonies. Even though graminoid ANPP was lower on than off of colonies, total ANPP did not differ between on- and off-colony sites. Exclusion of cattle and cattle + prairie dogs both resulted in an increase in graminoid biomass and a decrease in forb biomass, suggesting dietary overlap in functional group preference. These results are similar to those reported for bison and prairie dogs on the mixed-grass prairie in that cattle and prairie dogs had similar and additive effects on plant biomass reduction (Cid et al. 1991).

In summary, the effects of prairie dogs on the shortgrass steppe are similar in direction to their effects on the mixed-grass prairie: prairie dogs reduce plant biomass and shift composition toward forbs and away from graminoids. However, the magnitudes of many of the changes (i.e. plant cover by functional group, total biomass, belowground biomass) are much less on the shortgrass steppe than on the mixed-grass prairie and, in many cases, differences between on- and off-colony are not statistically significant. More data are needed to assess whether the effects of prairie dogs on shortgrass steppe vegetation increase as a function of colony age as has been found on the mixed-grass prairie. Plague was not present in most of the previously studied prairie dog colonies. I found that after a plague outbreak, colonies on the shortgrass steppe quickly recover from the effects of prairie dogs and this quick recovery may have important implications for species associated with prairie dog colonies. Finally, cattle and prairie dogs appear to have similar and additive effects on plant biomass removal and cattle remove about the same amount of forage on- colony as they do off-colony.

LITERATURE CITED

Adler, P. B., D. G. Milchunas, W. L. Lauenroth, O. E. Sala, and I. C. Burke. 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. Journal of Applied Ecology 41:653-663.

Antolin, M. F., L. T. Savage, and R. J. Eisen. 2006. Landscape features influence genetic structure of black-tailed prairie dogs (*Cynomys ludovicianus*). Landscape Ecology 21:867-875.

Antolin, M. F., P. Gober, D. Luce, D. E. Biggins, W. E. Van Pelt, D. B. Seery, M. Lockhart, and M. Ball. 2002. The influence of sylvatic plague on North American wildlife at the landscape level, with special emphasis on black-footed ferret and prairie dog conservation. Transactions of the 67th North American Wildlife and Natural Resources Conference 67:104-127.

Archer, S. R., M. G. Garrett, and J. K. Detling. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio 72:159-166.

Bakker, E. S., H. Olff, M. Boekhoff, and J. M. Gleichman. 2004. Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. Oecologia 138:91-101.

Bonham, C. D. and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. Journal of Range Management 29:221-225.

Cid, M. S., J. K. Detling, A. D. Whicker, and M. A. Brizuela. 1991. Vegetational responses of a mixed-grass prairie site following exclusion of prairie dogs and bison. Journal of Range Management 44:100-105.

Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983a. Plant-herbivore interactions in a North American mixed-grass prairie I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1-9.

Coppock, D. L., J. E. Ellis, J. K. Detling, and M. I. Dyer. 1983b. Plant-herbivore interactions in a North American mixed-grass prairie II. Responses of bison to modification of vegetation by prairie dogs. Oecologia 56:10-15.

Coughenour, M. B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations and interacting processes. Annals of the Missouri Botanical Garden 72:852-863.

Cully, J. F. and E. S. Williams. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. Journal of Mammalogy 82:894-905.

Daubenmire, R. 1970. Steppe vegetation of Washington. Washington Agricultural Experiment Station Technical Bulletin 62.

Derner, J. D., J. K. Detling, and M. F. Antolin. 2006. Are livestock weight gains affected by black-tailed prairie dogs? Frontiers in Ecology and the Environment 4:459-464.

Ecke, D. H. and C. W. Johnson. 1952. Plague in Colorado and Texas. Part I. Plague in Colorado. Public Health Monograph No. 6 U.S. Government Printing Office, Washington, D.C. 37 pp.

Eskey, C.R. and V. H. Haas. 1940. Plague in the Western Part of the United States. U. S. Public Health Service Bulletin No. 254 U.S. Government Printing Office, Washington, D. C. 83 pp.

Fahnestock, J. T. and J. K. Detling. 2002. Bison-prairie dog –plant interactions in a North American mixed-grass prairie. Oecologia 132:86-95.

Forrest, S. 2005. Getting the story right: A response to Vermeire and colleagues. BioScience 55:526-530.

Guenther, D. A. and J. K. Detling. 2003. Observations of cattle use of prairie dog towns. Journal of Range Management 56:410-417.

Gurevitch, J, S. M. Scheiner, and G. A Fox. 2002. The ecology of plants. Sinauer Associates, Inc, Sunderland, Massachusetts.

Hansen, R. M., D. G. Peden, and R. W. Rice. 1973. Discerned fragments in feces indicated diet overlap. Journal of Range management 26:103-105.

Hansen, R. M. and I. K. Gold. 1977. Blacktail prairie dogs, desert cottontails, and cattle trophic relations on shortgrass range. Journal of Range Management 30:210-213.

Hardwicke, K. 2006. Tri-trophic interactions affect plant-insect floral visitor webs of the shortgrass steppe: prairie dogs, plant, and pollinators. Ph.D. Dissertation, Colorado State University, Fort Collins, Colorado.

Hartnett, D. C., A. A. Steuter, and K. R. Hickman. 1996. Comparative ecology of native and introduced ungulates. Pages 72-101 *in* F. L. Knopf and F. B. Samson, (Editors), Ecology and conservation of Great Plains vertebrates. Springer-Verlag, Berlin.

Heske E. J. and M. Campbell. 1991. Effects of an 11-year livestock exclosure on rodent and ant numbers in the Chihuahuan Desert, southeastern Arizona. Southwestern Naturalist 36:89–93.

Hoogland, J. L. 1995. The Black-Tailed Prairie Dog: Social Life of a Burrowing Animal. The University of Chicago Press. Chicago, Illinois.

Klatt, L. E. and D. Hein. 1978. Vegetative differences among active and abandoned towns of black-tailed prairie dogs (*Cynomys ludovicianus*). Journal of Range Management 31:315-317.

Kotliar, N. B. 2000. Application of the new keystone-species concept to prairie dogs: how well does it work? Conservation Biology 14:1715-1721.

Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. Ecology 67:760-770.

Lauenroth, W. K. and D. G. Milchunas. 1992. Short-grass steppe. Pages 183-226 *in* R. T. Coupland, (Editor), Natural grasslands I. Introduction and Western Hemisphere. Elsevier, New York, New York.

Lauenroth, W. K. and W. C. Whitman. 1971. A rapid method for washing roots. Journal of Range Management 24:308-309.

Mack, R. N. and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. American Naturalist 119:757-773.

Milchunas, D. G. and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327-366.

Milchunas, D. G. and W. K. Lauenroth. 1989. Three-dimensional distribution of plant biomass in relation to grazing and topography in the shortgrass steppe. Oikos 55:82-86.

Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. Vegetatio 80:11-23.

Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. The American Naturalist 132:87-106.

Miller, B. G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology 8:677-681.

Olff, H. and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution 13:261-265.

O'Meilia, M. E., F. L. Knopf, and J. C. Lewis. 1982. Some consequences of competition between prairie dogs and beef cattle. Journal of Range Management 35:580-585.

Osborn, B. and P. F. Allan. 1949. Vegetation of an abandoned prairie dog town in tall grass prairie. Ecology 30:322-332.

SAS Institute. 1999. SAS version 8.02. SAS Institute, Inc. Cary, North Carolina.

Schwartz, C. C. and J. E. Ellis. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. Journal of Applied Ecology 18: 343-353.

Stapp, P., M. F. Antolin, and M. Ball. 2004. Patterns of extinction in prairie dog metapopulations: plague outbreaks follow El Niño events. Frontiers in Ecology and the Environment 2:235-240.

Uresk, D. W. 1985. Effects of controlling black-tailed prairie dogs on plant production. Journal of Range Management 38:466-468.

Vanderhye, A. V. R. 1985. Interspecific nutritional facilitation: Do bison benefit from feeding on prairie dog towns? M. S. Thesis, Colorado State University, Fort Collins, Colorado.

Vermiere, L. T., R. K. Heitschmidt, P. S. Johnson, and B. F. Sowell. 2004. The prairie dog story: do we have it right? BioScience 54:689-695.

Weltzin, J. F., S. Archer, R. K. Heitschmidt. 1997a. Small-mammal regulation of vegetation structure in a temperate savanna. Ecology 78:751-763.

Weltzin, J. F., S. L. Dowhower, and R. K. Heitschmidt. 1997b. Prairie dog effects on plant community structure in a southern mixed-grass prairie. The Southwestern Naturalist 42:251-258.

Whicker, A. D. and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. Bioscience 38:778-785.

Whicker, A. D. and J. K. Detling. 1993. Control of grassland ecosystem processes by prairie dogs. From: Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret. Biological Report 13:18-27.

Winter, S. L., J. F. Cully, and J. F. Pontius. 2002. Vegetation of prairie dog colonies and non-colonized shortgrass prairie. Journal of Range Management 55:502-508.

Table 2.1 – ANOVA results for plant canopy cover (%) on and off of prairie dog colonies on the Pawnee National Grassland before (1997-1999) and after (2000-2001) a plague outbreak. In cases where there were significant interactions between main effects, I report means and P values for each year as footnotes.

Response	Study Years	Factor					
		Location (On vs. Off Colony)		Year		Location X Year	
		F	P	F	P	F	P
Total Plant	1997 – 1999	0.01	0.949	4.74	0.439	1.44	0.275
	2000 – 2001	1.73	0.225	7.96	0.048	0.32	0.584
All Graminoids	1997 – 1999	0.94	0.352	4.97	0.040	1.34	0.298
	2000 – 2001	3.81	0.087	2.57	0.184	1.36	0.278
C3 Graminoids	1997 – 1999	5.91	0.312	13.33	0.003	1.92	0.189
	2000 – 2001	0.92	0.367	21.60	0.010	3.11	0.117
C4 Graminoids	1997 – 1999	0.01	0.927	4.11	0.059	1.27	0.316
	2000 – 2001	0.22	0.653	0.25	0.642	5.34	0.050[A]
Forbs	1997 – 1999	1.40	0.260	3.45	0.083	1.09	0.367
	2000 – 2001	0.07	0.793	8.89	0.041	0.00	0.975
Cactus	1997 – 1999	0.92	0.357	0.23	0.800	0.17	0.848
	2000 – 2001	1.29	0.289	0.14	0.728	5.07	0.055
Shrubs	1997 – 1999	1.41	0.260	0.20	0.822	5.61	0.020[B]
	2000 – 2001	2.81	0.132	2.29	0.205	0.11	0.752
Bare Ground	1997 – 1999	4.11	0.065	35.34	0.001	2.79	0.101
	2000 – 2001	5.87	0.042	7.29	0.054	0.71	0.423
Litter	1997 – 1999	8.84	0.012	7.25	0.016	2.23	0.150
	2000 – 2001	4.30	0.072	121.23	0.001	10.35	0.012[C]
Bouteloua gracilis	1997 – 1999	0.28	0.609	0.92	0.437	0.79	0.476
	2000 – 2001	0.05	0.827	0.16	0.708	0.24	0.635
Buchloe dactyloides	1997 – 1999	1.36	0.266	2.58	0.137	1.10	0.365
	2000 – 2001	0.03	0.877	1.95	0.235	0.04	0.847

[A] 2000 Off = 43.6 On = 44.2 (P = 0.839), 2001 Off = 48.5 On = 43.7 (P = 0.301)

[B] 1997 Off = 0.24 On = 0.59 (P = 0.990), 1998 Off = 0.00 On = 1.80 (P = 0.033), 1999 Off = 0.52, On = 0.99 (P = 0.55)

[C] 2000 Off = 32.5 On = 26.8 (P = 0.016), 2001 Off = 17.9 On = 16.3 (P = 0.422)

Table 2.2 – ANOVA results for plant biomass (g/m^2) on and off of prairie dog colonies on the Pawnee National Grassland before (1997-1999) and after (2000-2001) a plague outbreak.

Response	Study Years	Factor					
		Location (On vs. Off Colony)		Year		Location X Year	
		F	P	F	P	F	P
Total Plant	1997 – 1999	4.80	0.049	19.05	< 0.001	0.50	0.620
	2000 – 2001	1.81	0.215	5.15	0.086	0.10	0.758
All Graminoids	1997 – 1999	8.37	0.014	9.29	0.008	0.18	0.840
	2000 – 2001	2.34	0.165	5.77	0.074	0.19	0.672
C3 Graminoids	1997 – 1999	6.77	0.023	4.96	0.040	0.11	0.898
	2000 – 2001	1.56	0.025	9.76	0.035	1.49	0.257
C4 Graminoids	1997 – 1999	5.05	0.004	8.02	0.012	0.44	0.655
	2000 – 2001	2.70	0.139	2.59	0.183	0.00	0.988
Forbs	1997 – 1999	2.69	0.127	7.12	0.017	0.09	0.912
	2000 – 2001	0.44	0.526	3.11	0.153	2.15	0.181
Shrubs	1997 – 1999	1.89	0.194	1.15	0.365	2.20	0.154
	2000 – 2001	0.74	0.414	0.01	0.937	3.01	0.121
Standing Dead	1997 – 1999	3.18	0.099	21.03	0.001	2.56	0.118
	2000 – 2001	1.64	0.236	1.70	0.262	1.99	0.196
Bouteloua gracilis	1997 – 1999	7.75	0.017	8.67	0.010	0.61	0.559
	2000 – 2001	0.41	0.539	1.55	0.281	0.16	0.703
Buchloe dactyloides	1997 – 1999	0.93	0.353	1.46	0.289	1.52	0.257
	2000 – 2001	0.00	0.960	1.23	0.329	0.04	0.843

Table 2.3 – Plant species richness (mean number of species per site) (± SE) and diversity (H') (± SE) off and on prairie dog colonies on the Pawnee National Grassland before (1997-1999) and after (2000-2001) a plague outbreak. In cases where there are significant interactions between main effects, I report means and P values for each year as footnotes.

Response	Study Years	Means		Factor					
				Location (On vs. Off Colony)		Year		Location X Year	
	Sample Years	Off ± SE	On ± SE	F	P	F	P	F	P
RICHNESS									
Graminoids	1997-1999	6.07 ± 0.54	6.53 ± 0.50	0.61	0.449	2.02	0.196	2.84	0.100
	2000-2001	6.50 ± 0.54	6.90 ± 0.65	0.23	0.648	2.67	0.178	0.17	0.694
Forbs	1997-1999	4.60 ± 0.90	8.40 ± 1.20	10.15	0.008	2.56	0.138	0.31	0.735
	2000-2001	4.50 ± 1.05	6.40 ± 0.69	2.85	0.129	20.99	0.010	0.56	0.476
All Plants	1997-1999	12.33 ± 1.33	16.33 ± 1.49	5.00	0.045	3.00	0.106	1.75	0.216
	2000-2001	12.50 ± 1.40	15.10 ± 0.81	2.39	0.161	35.77	0.004	2.60	0.146
DIVERSITY									
Graminoids	1997-1999	0.92 ± 0.17	0.90 ± 0.07	0.02	0.903	3.62	0.08	7.04	0.010[A]
	2000-2001	0.93 ± 0.01	0.91 ± 0.10	0.02	0.885	2.10	0.221	13.07	0.010[B]
Forbs	1997-1999	1.03 ± 0.19	1.58 ± 0.14	6.96	0.022	2.07	0.189	0.43	0.659
	2000-2001	0.96 ± 0.20	1.16 ± 0.13	1.11	0.322	11.35	0.028	0.07	0.805
All Plants	1997-1999	1.30 ± 0.21	1.47 ± 0.10	0.56	0.467	2.15	0.179	6.62	0.012[C]
	2000-2001	1.20 ± 0.19	1.26 ± 0.07	0.12	0.739	8.84	0.041	5.98	0.040[D]

[A] 1997 Off = 0.95 On = 0.63 (P = 0.137), 1998 Off = 0.86 On = 0.98 (P = 0.548), 1999 Off = 0.95, On = 1.08 (P = 0.549)

[B] 2000 Off = 0.90 On = 0.70 (P = 0.397), 2001 Off = 0.94 On = 1.06 (P = 0.272)

[C] 1997 Off = 1.44 On = 1.34 (P = 0.827), 1998 Off = 1.15 On = 1.48 (P = 0.245), 1999 Off = 1.29, On = 1.58 (P = 0.069)

[D] 2000 Off = 1.14 On = 1.03 (P = 0.543), 2001 Off = 1.26 On = 1.48 (P = 0.240)

Table 2.4 - Jaccard's similarity indices (J_s) for between on and off prairie dog colonies on the Pawnee National Grassland prior to (1997 – 1999) and after (2000 – 2001) a plague outbreak.

Vegetation Category	Sample Periods		Factor	
	1997 - 1999	2000 – 2001	Before vs. After Plague	
	J_s between on and off colonies	J_s between on and off colonies	F	P
Graminoids	0.53	0.69	6.15	0.023
Forbs	0.34	0.29	0.83	0.373
All Plants	0.41	0.47	0.49	0.493

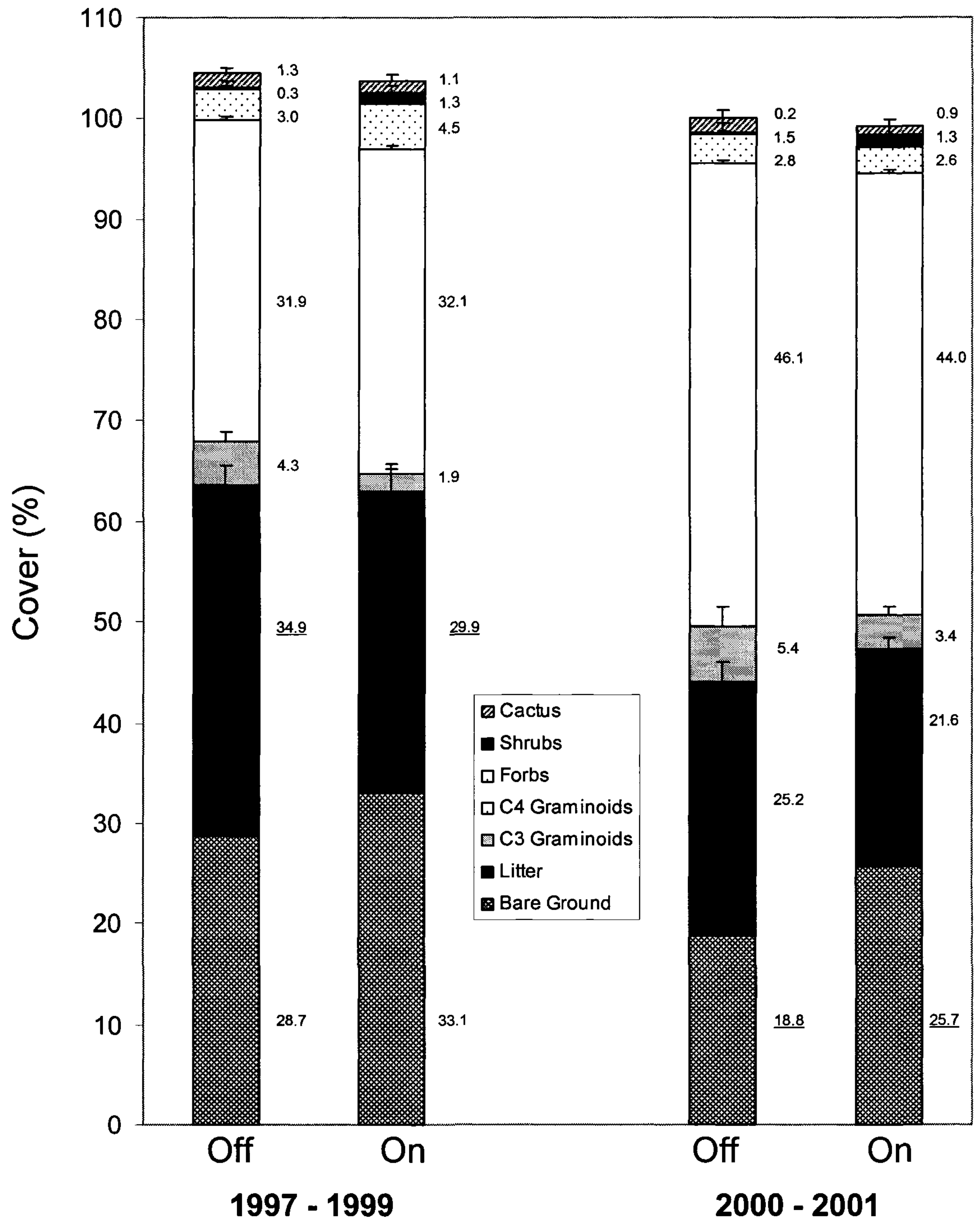

Figure 2.1 – Mean cover (%) + 1 SE of plant functional groups, litter, and bare ground on and off of prairie dog colonies (N = 5) on the Pawnee National Grassland for the three years before (1997 – 1999) and two years after (2000 – 2001) a plague outbreak. Underlined values indicate a significant difference between an on- and off-colony pair.

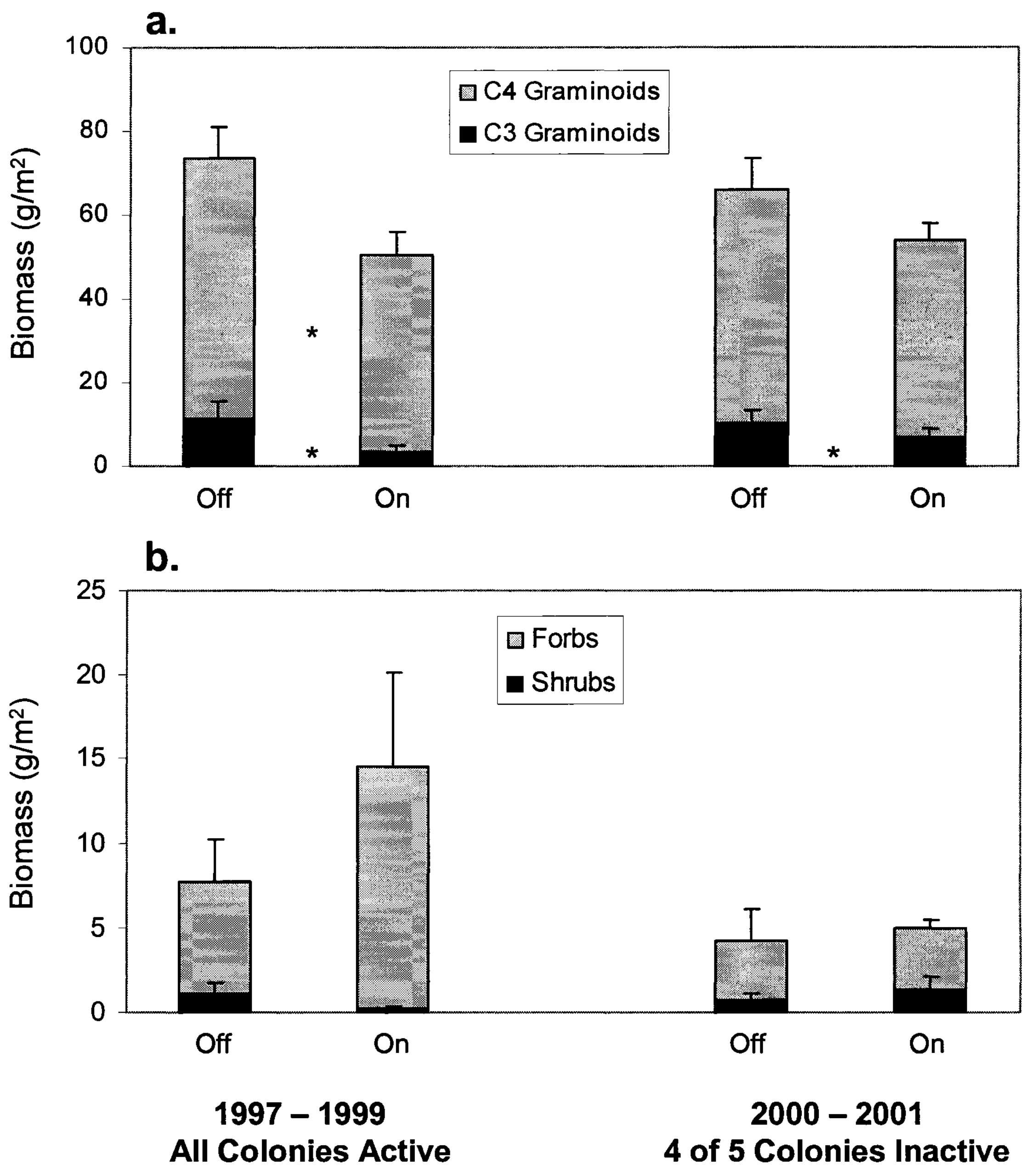

Figure 2.2 – Mean aboveground biomass (g/m^2) of (a.) graminoids and (b.) forbs and shrubs off an on prairie dog colonies (N = 5) on the Pawnee National Grassland for the three years before (1997 – 1999) and two years after (2000 – 2001) a plague outbreak. . Asterisks indicate a significant difference between an on- and off-colony pair.

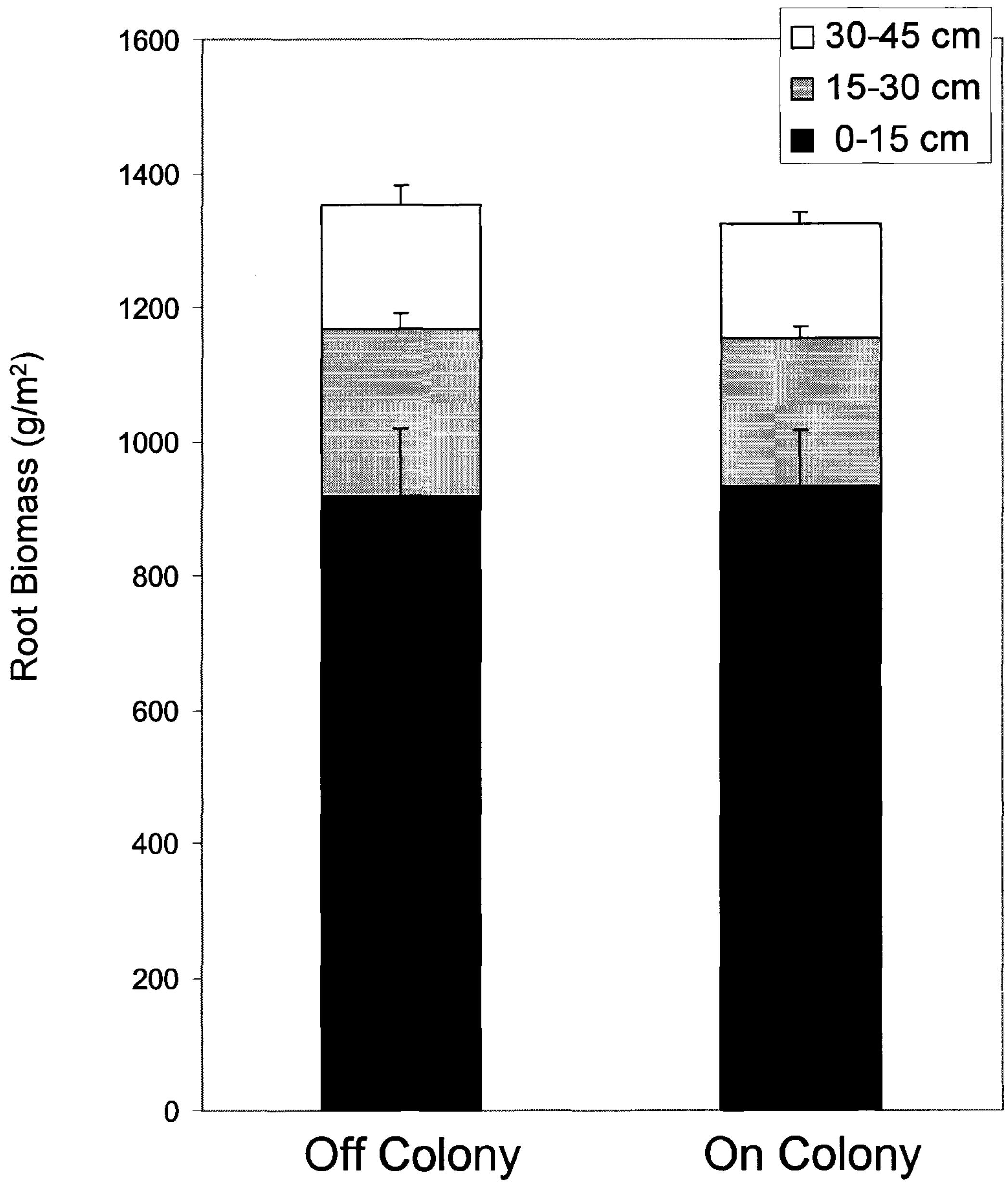

Figure 2.3 – Mean root biomass averaged for 1998 and 1999 on and off of colonies (N = 5) on the Pawnee National Grassland at three depth increments. There were no significant differences between on- and off-colony sites for any depth increment (0-15 cm [F = 0.03, P = 0.869]; 15-30 cm [F = 1.65, P = 0.234]; 30-45 cm [F = 0.34, P = 0.574]; 0-45 [F = 0.08, P = 0.789]).

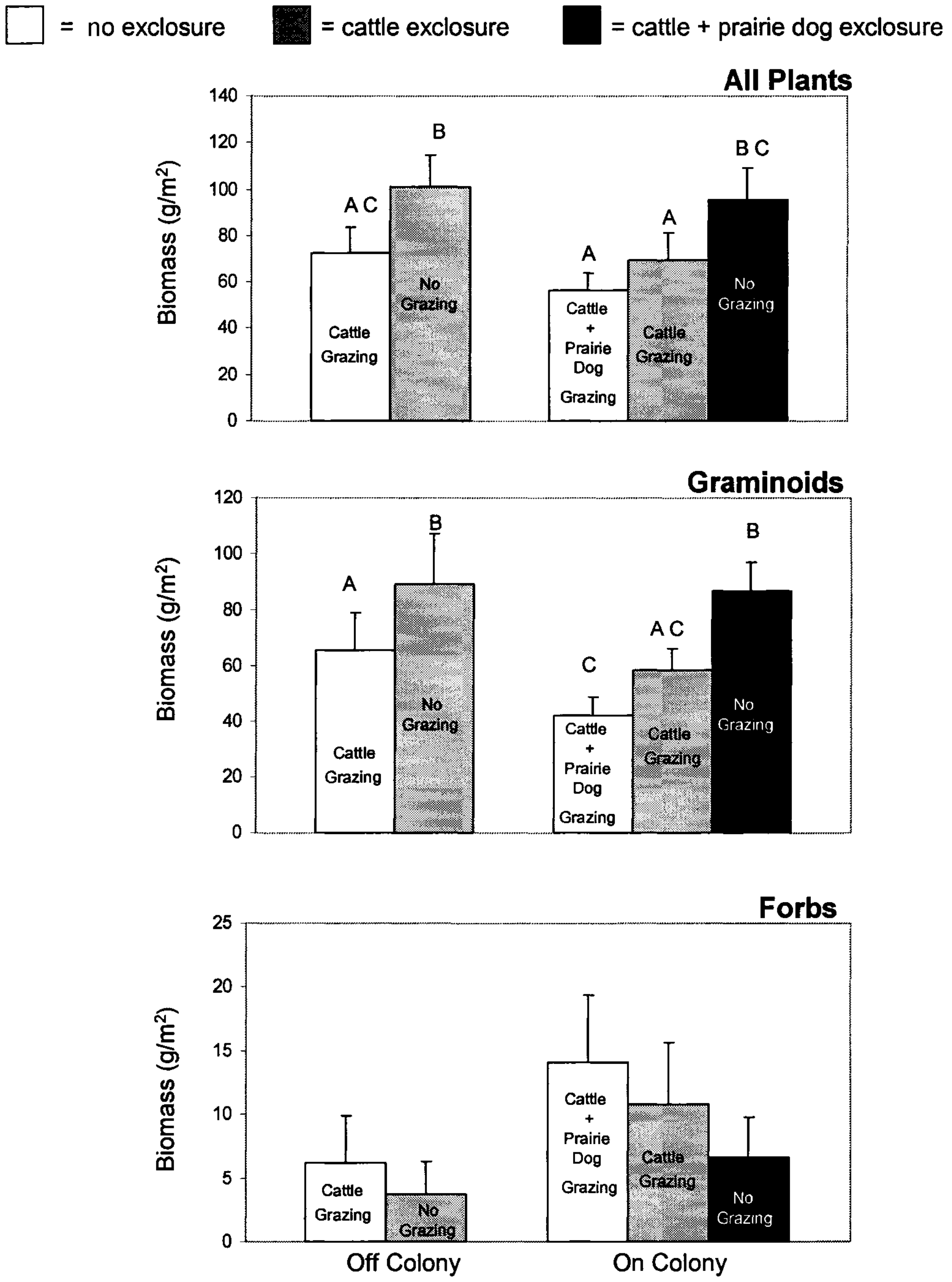

Figure 2.4 – Mean biomass (+ 1 SE) averaged over 1998 and 1999 for all plant species (excluding cactus), graminoids, and forbs off and on prairie dog colonies (N = 5) with no exclosure cages, cattle exclosure cages, and prairie dog exclosure cages. Exlcosure cages were erected at the beginning of the growing season each year. Within each graph, bars with the same letters were not significantly different ($P \leq 0.05$). The main effect of sampling location was significant for total biomass ($F = 4.19$, $P = 0.008$) and graminoid biomass ($F = 7.58$, $P < 0.001$), but not forb biomass ($F = 0.91$, $P = 0.471$).

CHAPTER 3

EFFECTS OF PRAIRIE DOGS ON SHORTGRASS STEPPE PLANT COMMUNITIES: INFLUENCES OF COLONY AGE AND PLAGUE OUTBREAKS

Abstract. --- The goal of this study was to examine the effects of black-tailed prairie dogs (*Cynomys ludovicianus*) on plant communities on young (3 -8 years), old (~ 20 years), and plague-extirpated colonies on the shortgrass steppe of Colorado. Averaged across all three types of colonies and compared to uncolonized grassland, prairie dog colonies had a shorter mean canopy height, lower graminoid cover and biomass, greater forb cover and biomass, and greater bare ground cover ($P \leq 0.05$). Colonies also had greater total and forb species richness and greater total plant diversity (H') than off-colony sites. Belowground biomass was not significantly different between on- and off-colony sites. Differences between on- and off-colony sites were most pronounced for older colonies. Plague-extirpated colonies were not significantly different from their associated off-colony sites for most variables measured. Results of this study suggest that the effects of prairie dogs on the shortgrass steppe are similar to, but of lower magnitude than, their effects on the mixed-grass prairie. Results also suggest that the recently introduced disease, sylvatic plague, may mediate the effects of prairie dogs on the shortgrass steppe because (1) during periods of inactivity after plague outbreaks, plant communities recover from the effects of heavy grazing and (2) effects of prairie dogs increase with colony age, but because of plague, fewer colonies now persist for substantial (20+ years) periods of time.

Key words: *Cynomys ludovicianus*, plant-animal interactions, shortgrass steppe, plague, herbivory

INTRODUCTION

Black-tailed prairie dogs (*Cynomys ludovicianus*) are large (~1 kg), colonial, semi-fossorial rodents that are prevalent throughout the mixed and shortgrass prairies of North America (Hoogland 1995). Prairie dogs can have profound influences on grassland structure and function because they selectively consume large quantities of vegetation (60 to 80% of annual net primary production), indiscriminately clear taller vegetation to facilitate predator avoidance, and create extensive burrow systems (Whicker and Detling 1988, Hoogland 1995). Although estimates are hotly debated, prairie dogs may have occupied between 31 to 100 million ha of the North American grasslands in the late 19th century, but presently occupy only 350,000 to 791,000 ha (Mulhern and Knowles 1995, USFW 2004, Vermiere et al. 2004, Proctor et al. 2005). The drastic decline in prairie dog populations seen over the last century is due to habitat loss, recreational shooting, eradication via poisoning, and the introduction of sylvatic plague to rodent populations of North America (Van Putten and Miller 1999, Van Pelt 1999, Antolin et al. 2002, Luce 2003).

Although the black-tailed prairie dog is found in both the mixed-grass prairie and the shortgrass steppe, its effects on plant communities have been most extensively studied in the mixed-grass prairie. There, prairie dog grazing results in an overall lower canopy height, a decrease in litter, a decrease in above- and belowground biomass, and an increase in the ratio of live to dead standing biomass (Coppock et al. 1983, Ingham and Detling 1984, Archer et al. 1987, Whicker and Detling 1993, Weltzin et al. 1997a,b, Fahnestock and Detling 2002). Prairie dogs can also cause a shift in plant species composition by increasing the number, cover, and biomass of forb species and decreasing the number, cover, and biomass of grass species (Koford 1958, Bonham and Lerwick 1976, Dahlsted et al. 1979, Coppock et al. 1983, Archer et al. 1987). In the mixed-grass prairie, effects of prairie dogs on plant community composition increase with colony age (Coppock et al. 1983, Archer et al. 1987). In a study on the mixed-grass prairie, graminoids accounted for more than 85 % of total peak live biomass on uncolonized grassland, less than 70 % on the young (3 – 8 years) part of a colony, and less than 3 % on the oldest (> 20 years) part of a colony (Coppock et al. 1983). A limited number of studies on the mixed-grass prairie and the shortgrass steppe have indicated that grazing by prairie dogs may increase plant species richness and diversity (Bonham and Lerwick 1976, Coppock et al. 1983, Fahnestock and Detling 2002, Farrar 2002). On the mixed-grass prairie, plant species diversity is greater on prairie dog towns that have received moderate impact relative to uncolonized grassland or older colonies (Coppock et al. 1983, Archer et al. 1987).

Although there is a large body of literature related to the effects of prairie dogs on plant communities, our understanding of the effects of prairie dogs on North American grasslands is still incomplete. Most of the studies on prairie dogs and vegetation have been conducted on the mixed-grass prairie and those studies are being used to make management decisions for prairie dogs on the shortgrass steppe and other grassland types. However, there is reason to believe that the effects of prairie dogs on the shortgrass steppe may be quantitatively or qualitatively different than their effects on the mixed-grass prairie. The selection pressures that shape plant communities on the more mesic mixed-grass prairie, grazing and competition for light, are divergent, while selection pressures on the semiarid shortgrass steppe, grazing and competition for water, are convergent (Coughenour 1985, Milchunas and Lauenroth 1989, 1993). Compared to the mixed-grass prairie, the shortgrass steppe has proportionally more drought and grazing resistant plant species such as *Bouteloua gracilis,* proportionally more biomass belowground, and is notably resistant to changes in plant communities as a result of heavy grazing by cattle (Milchunas et al. 1989). In Chapter 2, I presented results from a study of prairie dog colonies on the shortgrass steppe which suggested that the effects of prairie dogs on plant community composition and biomass are qualitatively similar but quantitatively less than their effects on the mixed-grass prairie. However, the study did not include colonies ranging widely in age and, in the mixed-grass prairie, effects of prairie dogs increase with colony age (Coppock et al. 1983, Archer et al. 1987).

In addition to a lack of information about the effects of prairie dogs on the shortgrass steppe, we also do not understand how a recently introduced disease of the prairie dog, sylvatic plague, may alter its effects on ecosystem structure and function. The disease, caused by the same bacterium (*Yersinia pestis*) that caused global pandemics in humans, was first noted in the black-tailed prairie dog populations in the 1940s (Ecke and Johnson 1952, Barnes 1982, Barnes 1983, Cully and Williams 2001). Prairie dogs are highly susceptible to plague, with essentially 100% mortality within a colony (Barnes 1993, Cully and Williams 2001, Stapp et al. 2004). Because of plague, prairie dogs now exhibit classic metapopulation dynamics in that colonies are subject to periodic extinction events and are repopulated by individuals from neighboring colonies. On the Pawnee National Grassland, where this study was conducted, prairie dog activity has been monitored since 1981 and since that time, almost all of the original colonies experienced at least one plague outbreak and the majority of colonies were inactive for at least 5 years after an outbreak (Stapp et al. 2004, Chapter 1). I suggest that plague may mediate the effects of prairie dogs on plant communities because plague causes periodic episodes of inactivity on colonies. The increasing mobility of the human species has resulted in the relatively rapid and unprecedented translocations of species around the globe, and how introduced species influence ecosystem structure and function is arguably one of the most pressing issues in ecology. This research contributes to the understanding of how an introduced disease of an herbivore can influence that herbivore's effects on ecosystem structure and function.

The primary goals of this study are (1) to assess how the effects of prairie dogs on plant communities of the shortgrass steppe are influenced by colony age, (2) to assess how similar the effects of prairie dogs on the shortgrass steppe are to the effects of prairie dogs on the more mesic mixed-grass prairie, and (3) to assess how plague-induced colony die-offs impact plant communities on a colony.

METHODS

Site Description. --- I collected data from 2002 through 2004 in northeastern Colorado on the Pawnee National Grassland (PNG), a semi-arid shortgrass steppe with cold, dry winters. Long-term mean annual temperature is 8.6 C and long-term mean annual precipitation is 322 mm, with most precipitation falling during the growing season (April – September) as localized thunderstorms (Lauenroth and Milchunas 1992). Total precipitation from April through July was 91 mm in 2002, 214 mm in 2003, and 147 mm in 2004 (National Science Foundation Shortgrass Steppe Long-Term Ecological Research Program, Colorado State University, Fort Collins, CO).

In 1981, the U.S. Forest Service began collecting spatial data on prairie dog colony size and status (active or inactive) each year for colonies located on the PNG. Using information from that database, I chose the three colonies that had been occupied almost continuously since 1981, three of the most recently founded colonies (within the last 3-7 years), and three colonies that were 7 to 12 years old when plague outbreaks decimated them in 1999. For each prairie dog colony, I selected a nearby uncolonized control site that had similar slope, aspect, soil characteristics, and land-use history. My assumption was that the uncolonized sites were suitable habitat for prairie dogs. Indeed, after the conclusion of the study, some colonies spread into the areas I had chosen as control sites. Information about soil characteristics was obtained from the Soil Survey Geographic (SSURGO) database (Natural Resource Conservation Service). Information regarding land-use history was obtained from records kept by the U.S. Forest Service (Pawnee National Grassland Office, Greeley, CO). Records included aerial photographs and original deeds of sale. I made every effort to choose sites that had never been cultivated or seeded. In some cases, a single colony occupied some area that had been previously cultivated and some area that had not. I confined sampling efforts to the portion of the colony that had not been cultivated. In all cases, the land-use history of the colony and the control site were the same and any cultivation activities had ceased by 1938. All sites have been grazed seasonally by cattle since being purchased by the US Forest Service in the late 1930s to early 1940s. Pastures are grazed at "moderate" rates (1.74 ha/cow/month) (Bob Peterson pers. comm. in Guenther and Detling 2003). Based on a previous study that showed that cattle neither prefer nor avoid grazing on prairie dog colonies on the shortgrass steppe (Guenther and Detling 2003), I assumed that colonies and control sites were grazed similarly by cattle.

In 2004, one of the "old" colonies experienced a plague outbreak and was not sampled that year. Due to the lack of additional suitable sites, I did not replace this colony with another. In 2003 and 2004, several of the burrows at the margins of the "plague-extirpated" colonies were reoccupied by immigrant prairie dogs. I avoided sampling on the areas of the "plagued-extirpated" colonies that were being recolonized.

Plant Community Structure and Composition. --- I used US Forest Service spatial records (Pawnee National Grassland Office, Greeley, CO) of annual colony size (from 1981-present) to choose an approximately 100 m x 100 m polygon in the oldest part of the "old" colonies, the youngest part of the "young" colonies, and the center of the "plagued-extirpated" colonies. I generated 25 random coordinates within each polygon using ArcView (ESRI, Redlands, CA, USA). I layed a Daubenmire (1970) sampling frame (0.2 x 0.5 m) at each of the random coordinates and estimated foliar cover of each plant species, bare ground, and litter to the nearest percent. I also estimated average canopy height (cm) by placing a light styrofoam plank (0.1 m^2) atop the canopy and measuring the height of the plank through a hole cut in its center. These data were gathered twice (early and late season) in 2002 and 2003. I used canopy cover data to assess the relative cover of functional groups (graminoids, forbs, shrubs, and cactus) and several key species including *Spharaelcea coccinea,* the dominant forb, *Bouteloua gracilis*, *Buchloe dactyloides*, *Agropyron smithii* and *Carex eleocharis* which are important palatable graminoids and *Aristida longiseta*, a prevalent C4 bunchgrass that is not palatable to herbivores. Plant nomenclature follows Flora of the Great Plains (McGregor 1986). I also used cover data to calculate the frequency of occurrence of each species at each site and to calculate Shannon-Weiner diversity (H') at each site for graminoids, forbs, nonnative species and total vegetation. Shannon Weiner diversity was calculated as:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i \qquad \text{Eq. 1}$$

where p_i is the proportion (total cover) of species i in all samples from a site, and s is the total number of species collected at that site.

I used Modified-Whittaker multi-scale sampling plots (Stohlgren et al. 1995), to gather data for estimations of species richness and overlap. The Modified-Whittaker technique has been shown to detect more plant species in grasslands than other techniques (Stohlgren et al. 1998). A Modified-Whittaker plot (1000 m^2) was established in the center of the sampling polygon in each prairie dog colony and off-colony site in June, 2002 and 2003. Modified-Whittaker plots are 20 x 50 m plots with ten 0.5 x 2 m (1 m^2) nested subplots placed at intervals along the inside border, two 2 x 5 m (10 m^2) subplots in alternate corners, and a 5 x 20 m (100 m^2) subplot in the center. In the 1 m^2 subplots, I estimated foliar cover for each species and bare ground. In the 10 m^2 and the 100 m^2 supblots and the entire 1000 m^2 plot, I recorded each of the plant species present.

Using data from the Modified-Whittaker plots, I calculated species richness at each site for total vegetation, forbs, graminoids, and non-native species. I also calculated species overlap between paired on- and off-colony sites for total vegetation, forbs, and graminoids using Jaccard's Coefficient (Gurevitch et al. 2002), which is the percentage of species contained in two sites that are shared by those sites:

$$S_j = \frac{a}{a + b + c} \qquad \text{Eq. 2}$$

where a is the number of species in both sites, b is the number of species in the second site only and c is the number of species in the first site only. Jaccard's Coefficient ranges from 0 to 1, with 0 meaning that the sites are completely distinct and 1 meaning that the sites are identical.

Plant Biomass. --- I clipped aboveground biomass by species on five randomly selected plots (0.25 m^2) within the sampling polygon on each colony and off-colony site at the time of estimated peak biomass each year. Standing dead plants and litter were also collected. Samples were dried at 55 °C and weighed. I pooled masses by functional group prior to statistical analysis. I analyzed the graminoid and forb functional groups, but not the cacti and shrub functional groups because they were more patchily distributed and therefore were not adequately sampled. I also analyzed biomass of *Sphaeralcea coccinea, Bouteloua gracilis, Buchloe dactyloides, Agropyron smithii, Carex eleocharis* and *Aristida longiseta.*

The plague-extirpated colonies that I sampled were also sampled by the Shortgrass Steppe Long-Term Ecological Research Program in the years prior to the plague-outbreak (data in Chapter 2). Estimates of graminoid, forb, and total aboveground plant biomass on- and off-colony were made from 1997 to 2001 using the same method described above in approximately the same areas that I located my sampling polygons. I used these data to compare trends on these colonies both before and after the 1999 plague-outbreak.

I collected belowground plant biomass samples to a depth of 20 cm using a 6.35 cm diameter soil core. Sampling to a depth of 20 cm likely includes 75% of the root biomass in this grassland (Leetham and Milchunas 1985). At each colony and off-colony site, I collected 5 cores in 2003 and 8 cores in 2004. I mixed each sample with water and agitated it to separate soil from roots. As roots floated to the surface, I decanted them onto a 0.5 mm mesh sieve. I rinsed the collected roots thoroughly, dried them at 55 °C, hand-picked out any non-root material (e.g. seeds, pebbles), and weighed them. I ground each sample to a fine powder using a ball mill and determined its ash content by combusting a 0.5 g subsample in a muffle furnace at 600 °C for 4 hours. I corrected for soil contamination in each sample by multiplying the mass of the original sample by the % organic matter in the subsample.

Statistical Analyses. --- I used mixed-model, repeated measures analyses of variance to test the main effects of location (on- versus off-colony), year, season (early or late), colony (site), and type (young, old, plague-extirpated) on each response variable. I also tested for interactions between main effects. Because I chose specific off-colony sites for each colony, I linked each pair together in the programming code. I examined differences between on- versus off-colony pairs by colony type using Least Squares Means, and I examined on- versus off-colony pairs by type and year using paired t-tests. I averaged data by site prior to analysis, i.e. colonies were considered to be replicates rather than the individual samples collected.

Residuals of all models were examined for normality and, if necessary, data were square-root transformed and reanalyzed. All figures and tables depict untransformed data. I used SAS statistical software to perform all analyses (SAS Institute Inc., 1999, Cary, NC, USA).

RESULTS

Plant Height, Cover, and Biomass. --- I report height, cover, and biomass data as means of the years and seasons sampled unless the trends between on- and off-colony differed between years or seasons (i.e. there were significant ($P \leq 0.05$) interactions between the main effects) (see also Appendix A). Averaged across all colony types, canopy height was lower on (5.38 cm) than off (7.38 cm) of colonies ($F = 22.73$, $P = 0.003$). However, the trend was significant for active (young and old) colonies, but not for plague-extirpated colonies (Fig. 3.1). Bare ground was greater on than off of colonies (Table 3.1), but the trend was significant only for older colonies and not for young or plague-extirpated colonies (Fig. 3.2).

Averaged across all colony types, cover and biomass of graminoids was lower on than off of colonies (Table 3.1). The trend of lower graminoid cover on- than off-colonies was significant for all three colony types (Fig. 3.2), but the trend of lower graminoid biomass was significant only for the young and old colonies (Fig. 3.3). Averaged across all colony types, cover and biomass of forbs were greater on than off of colonies (Table 3.1). The trends of greater forb cover and biomass on colony were significant only for old colonies (Figs 3.2 and 3.3). There were no significant trends between on- and off-colony sites for cover of shrubs or cacti when colonies were considered collectively or by type (Table 3.1, Fig. 3.2). Shrub and cactus biomass were not statistically analyzed.

In the years prior to the plague-outbreak that occurred in late summer 1999, the "plague-extirpated" colonies were significantly different from their paired off-colony sites with respect to total plant biomass and graminoid biomass (Fig 3.4). Forb biomass was significantly different between on- and off-colonies in the year of the plague-outbreak (1999), but not in the years prior to (1997-1998) or the years (2000-2004) following the outbreak (Fig. 3.4).

The trends for litter cover were not consistent between years (2002 on = 26.0 %, off = 30.2 %; 2003 on = 21.6 %, off = 18.8 %), but in neither year were the trends significant (P = 0.059, P = 0.208 respectively). For old colonies, litter cover was not significantly different between on- and off-colony sites in 2002, but was greater off-colony in 2003 (Fig. 3.2). There were no significant trends in litter cover between on and off of colonies for young or plague-extirpated colonies in either year (Fig. 3.2). Litter biomass was not significantly different between on- and off-colony sites when colony types were considered collectively (Table 3.1). Litter biomass was not significantly different between on- and off- colonies for young or plague-extirpated colonies, but litter biomass was lower on than off of old colonies (Figure 3.3).

Averaged across all colony types, cover and biomass of *Bouteloua gracilis* and *Carex eleocharis* were lower on than off of colonies while cover and biomass of *Sphaeralcea coccinea* were greater on than off of colonies (Table 3.2). Cover of *Aristida longiseta* was greater on than off of colonies, but biomass was not significantly different

(Table 3.2). There were no significant trends for cover and biomass of *Buchloe dactyloides* or *Agropyron smithii* (Table 3.2). Compared to their paired off-colony sites, old colonies had significantly lower cover and biomass of *B. gracilis* and *C. eleocharis*, and significantly greater cover and biomass of *A. longiseta* and *S. coccinea* (Figs. 3.5 and 3.6). There were no significant trends between on- and off- old colonies for cover and biomass of *B. dactyloides* or *A. smithii* (Figs. 3.5 and 3.6). Compared to their paired off-colony sites, young colonies had lower biomass of *B. gracilis*, but not significantly lower cover (Figs. 3.5 and 3.6). For young colonies, cover and biomass of *C. eleocharis*, *B. dactyloides*, *A. smithii*, and *A. longiseta* were not significantly different between on- and off-colony (Figs. 3.5 and 3.6). Young colonies did have greater cover, but not biomass, of *S. coccinea* (Figs. 3.5 and 3.6). Cover, but not biomass, of *B. gracilis* was greater off than on plagued-extirpated colonies. There were no significant differences between on-and off-colonies with respect to cover or biomass of *B. dactyloides, C. eleocharis*, *A. smithii*, or *A. longiseta* (Figs. 3.5 and 3.6). Biomass, but not cover, of *S. coccinea* was greater on than off of plague-extirpated colonies.

Averaged across all colony types and years, root biomass was lower on (1165 g/m^2) than off (1441 g/m^2) of colonies ($F = 4.86$, $P = 0.043$). Unlike aboveground biomass, belowground biomass did not differ significantly between the years sampled ($F = 0.73$, $P = 0.405$). When considering colonies by type, all types showed a trend of higher root biomass off- than on- colony, but the trends were not significant (Fig. 3.7).

Species richness, diversity, similarity, and frequency. --- Averaged across all colony types and years, mean total species richness per site (on = 26.4, off = 22.3) and forb species richness (on = 15.9, off = 11.7) were greater on than off of colonies (F = 19.63, P < 0.001; F = 49.37, P < 0.001). However, species richness of graminoids (on = 6.7, off = 6.6) and non-native species (on = 1.9, off = 1.9) did not differ significantly between on- and off-colony sites (F = 0.01, P = 0.912; F = 0.26, P = 0.775). Total and forb species richness were greater on than off of colonies for old and plagued-extirpated colonies, but not for young colonies (Table 3.3). Graminoid and nonnative species richness were not significantly different for any colony type (Table 3.3).

Averaged across colony types and years, total diversity (H') was greater on (1.65) than off (1.41) of colonies (F = 5.72, P = 0.028). However, graminoid diversity (off = 1.02, on = 1.17) and forb diversity (off = 1.51, on = 1.49) did not differ significantly between on- and off-colony sites (F = 1.71, P = 0.207; F = 0.08, P = 0.855). There were no significant differences in diversity (total, graminoid, or forb) between on- and off-colony for any of the colony types (Table 3.3).

For all functional groups tested, Jaccard's index of species overlap between on- and off-colonies showed no significant differences between the colony types (young, old, plagued-extirpated), i.e. young colonies were no less similar to their paired off-colony sites than old or plagued colonies were to their paired off colony sites (Graminoids F = 1.36, P = 0.35; Forbs F = 2.45, P = 0.17; All plants F = 3.89, P = 0.08) (Table 3.3).

There were a total of 15 graminoid, 67 forb, 4 cactus, and 6 shrub species identified on and off prairie dog colonies of the PNG (Appendix B). *Bouteloua gracilis*, *Buchloe dactyloides*, *Carex eleocharis*, *Aristida longiseta*, *Agropyron smithii*, *Sphaeralcea coccinea*, and *Opuntia polyacantha* had the greatest frequencies both on- and off-colonies of all types (Table 3.4). For the ten most frequently encountered species on and off of colonies by type (Table 3.4), there were no significant differences for any species between on and off of young colonies or between on and off of plague-extirpated colonies. For old colonies, *B. gracilis* and *C. eleocharis* were encountered less frequently on- than off-colony while *A. longiseta*, *S. coccinea*, and *Chrysopsis villosa* were more frequently encountered on- than off-colony (Table 3.4).

DISCUSSION

The goals of my research were to (1) assess how the effects of prairie dogs on plant communities of the shortgrass steppe are influenced by colony age, (2) to assess how similar the effects of prairie dogs on the shortgrass steppe are to their effects on the more mesic mixed-grass prairie and (3) to assess how plague-induced colony die-offs impact plant communities on the colony. Compared to younger colonies (3-8 years), older colonies (~ 20 years) were more different than their paired off-colony sites with respect to species composition, suggesting that colony age is an important factor for understanding how prairie dogs influence the shortgrass steppe. Although effects of prairie dogs on the shortgrass steppe are qualitatively similar to their effects on the mixed-grass prairie, the magnitude of differences between on and off of active colonies is less, supporting the idea that the shortgrass steppe is unusually tolerant to heavy grazing (Milchunas and Lauenroth 1989, Milchunas et al. 1989). Plagued-extirpated colonies were rarely significantly different than their associated off-colony sites, suggesting that the changes in plant community resulting from prairie dog occupation quickly begin to reverse when colonies are abandoned.

Although average canopy height on uncolonized areas of the mixed-grass prairie (10-20 cm) (Archer at al. 1987) is higher than average canopy height on uncolonized areas of the shortgrass steppe (6 -15 cm in my study), prairie dogs in both grassland types graze vegetation to similar heights (6-8 cm) (Archer et al. 1987). However, I used a different method for measuring average canopy height than was used by Archer et al. (1987). I found similar cover of bare ground on colonies of the shortgrass steppe to what has been estimated for colonies on the mixed-grass prairie (Archer et al. 1987) even though off-colony sites on the mixed-grass prairie have greater bare ground cover (Archer et al. 1987) than I found for off-colony sites on the shortgrass steppe.

On the mixed-grass prairie, litter cover is lower on than off of colonies and decreases as a function of colony age (Archer et al. 1987, Coppock et al. 1983). In my study, differences in litter cover and biomass between on- and off-colony sites were only seen on older colonies. However, this study was conducted during years of below average precipitation and litter cover was likely lower than average due to low primary production.

As with the mixed-grass prairie, grazing by prairie dogs results in a decrease in cover and biomass of graminoids and an increase in cover and biomass of forbs, and these changes appear to be a function of colony age (Archer et al. 1987, Coppock et al. 1983). Forbs almost totally replace graminoids on the oldest parts of a mixed-grass prairie colony, but the changes are not as dramatic on the shortgrass steppe. On the oldest part (> 20 years) of a mixed-grass prairie colony, forbs covered almost 95% of the ground (Coppock et al. 1983) as opposed to a high of 12% on the oldest colonies (~ 20 years) I studied.

Species that exhibit relative and absolute increases, i.e. increasers (Heady and Child 1994), are those that are not preferred forage, are tolerant of defoliation, or are capable of exploiting gaps left by competitors that decreased in abundance with grazing. I observed a significant decrease in most graminoid species that are common dietary components of prairie dogs (Hansen and Gold 1977, O'Meilia et al. 1982). *Aristida longiseta*, a low forage quality, unpalatable grass, is the only graminoid that was found to be more abundant on than off of colonies. Although the forb *Sphaeralcea coccinea* is palatable to prairie dogs, the cover and biomass of this forb increased on colonies. *Bouteloua gracilis* is, by far, the most dominant species on the shortgrass steppe and its importance to ecosystem structure and function has been much discussed (Milchunas et al. 1989, Milchunas et al. 1990, Hook et al. 1991, Coffin et al. 1996). A previous study of heavy grazing by cattle indicated that *B. gracilis* basal cover increased with heavy grazing on swales (Milchunas et al. 1989). I found that canopy cover of *B. gracilis* decreased with heavy grazing by prairie dogs, but the decrease was most pronounced for older colonies. There were no significant differences in frequency for *B. gracilis* between on and off of young and plague-extirpated colonies, but *B. gracilis* was much less frequent on (0.27) than off (0.68) of old colonies. Compared to cattle grazing on the shortgrass steppe, long-term heavy grazing by prairie dogs may have a more negative influence on *B. gracilis*. Prairie dogs dig burrow systems and create bare ground runways between burrows. As a colony, they may consume greater amounts of dry matter than cattle, and their presence is more localized and sustained. Although not directly tested, my observations of prairie dog colonies on the shortgrass steppe suggest that the selective removal of *Bouteloua gracilis*, a preferred forage for prairie dogs

(Hansen and Gold 1977), may facilitate the shift in species composition to more forb-dominated vegetation.

Belowground biomass was lower on than off of colonies and the trend was the same for all colony types. Although the trend of lower root biomass on than off of colonies is the same as on the mixed-grass prairie, the magnitude is considerably less. On the mixed-grass prairie, the oldest parts of the colony have only about 25 % as much root biomass as off-colony (Whicker and Detling 1988). Heavy grazing by cattle on the shortgrass steppe also results in only small decreases in belowground biomass (Milchunas and Lauenroth 1989).

Some studies report greater species richness on colonies than off (Bonham and Lerwick 1976, Archer et al. 1987, Coppock et al. 1983, Collins and Barber 1985) while others have reported lower richness on-colony (Agnew 1986, Johnson-Nistler et al. 2004). I found that species richness was greater for forbs and total vegetation on the plague-extirpated and old colonies, but not the young colonies. This suggests that increases in species richness associated with prairie dogs take time to occur and may persist for some time after extirpation of a colony. I also found that species diversity (H') was little affected by prairie dogs. In the mixed-grass prairie, Coppock et al. (1983) and Archer et al. (1987) found that vegetation on prairie dog colonies becomes more dissimilar with time since colonization. In my study, species overlap was less between on and off of old colonies compared to on and off of young or plagued colonies, but the trend was not significant.

This research suggests that the changes in plant community structure and composition caused by prairie dogs are relatively rapidly reversed following abandonment of colonies. Comparisons between on and off of plague-extirpated colonies showed the same trends as comparisons between on and off of active colonies, but the trends were not significant for any attributes measured but species richness and graminoid canopy cover. However, evaluation of the data must be tempered by the fact that, when the plague-extirpated colonies were abandoned, they were not as old as the "old" colonies. Nevertheless, I suggest that plague has profoundly altered the effects of prairie dogs on shortgrass steppe plant communities. Plague appears to serve as a temporary release from intensive grazing pressure during which time a colony can recover from prairie-dog induced changes. Furthermore, vegetation changes induced by prairie dogs seem to increase as a function of colony age, but because plague cycles are so frequent, the probability of a colony becoming "old" is small (Chapter 1). The age of the colony at the time of a plague outbreak and the weather conditions following the outbreak may also have a strong influence on the rate at which colonies recover from colonization and explain why previous research on extirpated colonies has produced varying results (Osborn and Allen 1949, Uresk 1985, Cid et al. 1991).

My research raises several follow-up questions. Although I found lower graminoid biomass on- than off-colony, I cannot address whether this effect was due solely to removal of biomass by prairie dogs or to a combined influence of greater removal and lower annual net primary production (ANPP). While data from Chapter 2 of this dissertation suggest that prairie dogs do reduce graminoid ANPP, we have no information about whether the reduction of ANPP is influenced by colony age. Another question, addressed in the next chapter of this dissertation, is how do changes in plant community structure and composition influence nutrient cycling? In the mixed-grass prairie, shoot nitrogen concentration is greater on than off of colonies (Coppock et al. 1983), as is potential net nitrogen mineralization (Holland and Detling 1990) and in-situ net nitrogen mineralization (Fahnestock and Detling 2002). A third question is how do prairie dogs influence the grazing patterns of other herbivores on the shortgrass steppe, both large and small, mammalian and arthropod, and above- and belowground? Most published studies on the shortgrass steppe have examined only how prairie dogs influence domestic cattle (Hansen and Gold 1977, Guenther and Detling 2003, Derner et al. 2006). Finally, how do plague-induced colony die-offs influence population dynamics of plants and animals associated with prairie dog colonies? For example, it is well-known that the endangered black-footed ferret (*Mustela nigripes*) is dependent upon prairie dogs and has been negatively affected by plague-outbreaks on colonies (Roelle et al. 2006, Barnes 1993, Biggins et al. 1993). However, population dynamics of other species may be influenced positively or negatively by periodic episodes of inactivity on colonies of the shortgrass steppe.

LITERATURE CITED

Agnew, W. D., W. Uresk, R. M. Hansen. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. Journal of Range Management 39:135-139.

Antolin, M. F., P. Gober, D. Luce, D. E. Biggins, W. E. Van Pelt, D. B. Seery, M. Lockhart, and M. Ball. 2002. The influence of sylvatic plague on North American wildlife at the landscape level, with special emphasis on black-footed ferret and prairie dog conservation. Transactions of the 67th North American Wildlife and Natural Resources Conference 67:104-127.

Archer, S. R., M. G. Garrett, and J. K. Detling. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio 72:159-166.

Barnes, A. M. 1982. Surveillance and control of the bubonic plague in the United States. Symposium of the Zoological Society of London. 50:237-270.

Barnes, A. M. 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. Pages 28-37 *in* J. L. Oldemeyer, D. E. Biggins and B. J. Miller, (Editors), Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret. U.S. Department of Interior Biological Report 13.

Biggins, DE, B. J. Miller, L. R. Hanebury, B. Oakleaf, A. H. Farmer, R. Crete, and A. Dood. 1993. A technique for evaluating black-footed ferret habitat. Biological report. U.S. Fish and Wildlife Service. Washington, D.C.

Bonham, C. D. and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. Journal of Range Management 29:221-225.

Cid, M. S., J. K. Detling, A. D. Whicker, and M. A. Brizuela. 1991. Vegetational responses of a mixed-grass prairie site following exclusion of prairie dogs and bison. Journal of Range Management 44:100-105.

Coffin, D. P., W. K. Lauenroth, and I. C. Burke. 1996. Recovery of vegetation in semiarid grassland 53 years after disturbance. Ecological Applications 6:538-555.

Collins, S. L. and S. C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetatio 64:87-94.

Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1-9.

Coughenour, M. B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations and interacting processes. Annals of the Missouri Botanical Garden 72:852-863.

Cully, J. F. and E. S. Williams. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. Journal of Mammalogy 82:894-905.

Dahlsted, K. J., S. Sather-Blair, and B. K. Worcester. 1979. Application of remote sensing to prairie dog management. Unpublished Report to the National Park Service, Wind Cave National Park, South Dakota. Remote Sensing Institute, South Dakota State University, Brookings.

Daubenmire, R. 1970. Steppe vegetation of Washington. Washington Agricultural Experiment Station Technical Bulletin 62.

Derner, J. D., J. K. Detling, and M. F. Antolin. 2006. Are livestock weight gains affected by black-tailed prairie dogs? Frontiers in Ecology and the Environment 4:459-464.

Ecke, D. H. and C. W. Johnson. 1952. Plague in Colorado and Texas. Part I. Plague in Colorado. Public Health Monography No. 6 U.S. Government Printing Office, Washington, D.C..

Fahnestock, J. T. and J. K. Detling. 2002. Bison-prairie dog –plant interactions in a North American mixed-grass prairie. Oecologia 132:86-95.

Farrar, J. P. 2002. Effects of prairie dog mound-building and grazing activities on vegetation in the central grasslands. MS Thesis Colorado State University, Fort Collins, Colorado.

Guenther, D. A. and J. K. Detling. 2003. Observations of cattle use of prairie dog towns. Journal of Range Management. 56:410-417.

Gurevitch, J, S. M. Scheiner, and G. A Fox. 2002. The ecology of plants. Sinauer Associates, Inc, Sunderland, Massachusetts.

Hansen, R. M. and I. K. Gold. 1977. Blacktail prairie dogs, desert cottontails, and cattle trophic relations on shortgrass range. Journal of Range Management 30:210-213.

Heady, H. F. and R. D. Child. 1994. Rangeland ecology and management. Westview Press, Boulder, Colorado.

Holland, E. A. and J. K. Detling. 1990. Plant responses to herbivory and belowground nitrogen cycling. Ecology 71:1040-1049.

Hoogland, J. L. 1995. The Black-Tailed Prairie Dog: Social Life of a Burrowing Animal. The University of Chicago Press. Chicago, Illinois.

Hook, P. B., I. C. Burke, and W. K. Lauenroth. 1991. Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. Plant and Soil 138:247-256.

Ingham, R. E. and J. K. Detling. 1984. Plant-herbivore interactions in a North American mixed-grass prairie III. Soil nematode populations and root biomass on *Cynomys ludovicianus* colonies and adjacent uncolonized areas. Oecologia 63:307-313.

Johnson-Nistler, C. M., B. F. Sowell, H. W. Sherwood, and C. L. Wambolt. 2004. Black-tailed prairie dog effects on Montana's mixed-grass prairie. Journal of Range Management 57:641-648.

Koford, C. B. 1958. Prairie dogs, whitefaces, and blue grama. Wildlife Monographs. 3:6-78.

Lauenroth, W. K. and D. G. Milchunas. 1992. Short-grass steppe. Pages 183-226 *in* R. T. Coupland, (Editor), Natural grasslands I. Introduction and Western Hemisphere. Elsevier, New York, New York.

Leetham, J. W. and D. G. Milchunas. 1985. The composition and distribution of soil microarthropods in the shortgrass steppe in relation to soil water, root biomass, and grazing by cattle. Pedobiologia 28:311-325.

Luce, R. J. 2003. A Multi-State Conservation Plan for the Black-Tailed Prairie Dog, *Cynomys ludovicianus*, in the United States – An addendum to the Black-tailed Prairie Dog Conservation Assessment and Strategy, November 3, 1999.

McGregor, R. L. 1986. The flora of the Great Plains. T. M. Barkley, R. E. Brooks, and E. K. Schofield, (Editors). University of Kansas, Lawrence, Kansas.

Milchunas, D. G. and W. K. Lauenroth. 1989. Three-dimensional distribution of plant biomass is relation to grazing and topography on the shortgrass steppe. Oikos 55:82-86.

Milchunas, D. G. and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs. 63:327-366.

Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. Vegetatio 80:11-23.

Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1990. Community attributes along a perturbation gradient in a shortgrass steppe. Journal of Vegetation Science 1:375-384.

Mulhern, D. W. and C. J. Knowles. 1995. Black-tailed prairie dog status and future conservation planning. Pages 19-29 *in* Uresk, D., G. L. Schenbeck, and J. O'Rourke, (Editors), Conserving Biodiversity on Native Rangelands. Fort Collins, Colorado. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station. Technical Report RM-GTR-298.

O'Meilia, M. E., F. l. Knopf, and J. C. Lewis. 1982. Some consequences of competition between prairie dogs and beef cattle. Journal of Range Management 35:580-585.

Osborn, B. and P. F. Allan. 1949. Vegetation of an abandoned prairie dog town in tall grass prairie. Ecology 30:322-332.

Proctor, J. D., S. C. Forrest, B. Haskins. 2005. Focal areas for black-tailed prairie dog restoration. *in* Hoogland J.L., (Editor), Conservation of the Prairie Ecosystems. Island Press, Washington, D.C..

Roelle, J. E., B. J. Miller, J. L. Godbey, and D. E. Biggins (Editors). 2006. Recovery of the black-footed ferret – progress and continuing challenges: U.S. Geological Survey Scientific Investigations Report 2005-5392, 288 pp.

SAS Institute. 1999. SAS version 8.02. SAS Institute, Inc. Cary, North Carolina.

Stapp, P., M. F. Antolin, and M. Ball. 2004. Patterns of extinction in prairie dog metapopulations: plague outbreaks follow El Niño events. Frontiers in Ecology and the Environment 2:235-240.

Stohlgren, T. J., M. B. Falkner, and L. D. Schell. 1995. A modified-Whittakter nested vegetation sampling method. Vegetatio 117:113-121.

Stohlgren, T. J., K. A. Bull, and Y. Otsuki. 1998. Comparison of rangeland vegetation sampling techniques in the Central Grasslands. Journal of Range Management 51:164-172.

Uresk, D. W. 1985. Effects of controlling black-tailed prairie dogs on plant production. Journal of Range Management 38:466-468.

[USFW] US Fish and Wildlife Service. 2004. Endangered and Threatened Wildlife and Plants: Finding for the Resubmitted Petition to the List the Black-tailed Prairie Dog as Threatened, August 18, 204. Federal Register 69:51217-51226.

Van Pelt, W. E. 1999. The black-tailed prairie dog conservation assessment and strategy. Nongame and Endangered Wildlife Program, Arizona Game and Fish Department, Phoenix, Arizona. 55 pp.

Van Putten, M. and S. D. Miller. 1999. Prairie dogs: The case for listing. Wildlife Society Bulletin 27:113-120.

Vermiere, L. T., R. K. Heitschmidt, P. S. Johnson, and B. F. Sowell. 2004. The prairie dog story: do we have it right? BioScience 54:689-695.

Weltzin, J. F., S. Archer, R. K. Heitschmidt. 1997a. Small-mammal regulation of vegetation structure in a temperate savanna. Ecology 78:751-763.

Weltzin, J. F., S. L. Dowhower, and R. K. Heitschmidt. 1997b. Prairie dog effects on plant community structure in a southern mixed-grass prairie. The Southwestern Naturalist 42:251-258.

Whicker, A. D. and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. BioScience 38:778-785.

Whicker, A. D. and J. K. Detling. 1993. Control of grassland ecosystem processes by prairie dogs. From: Proceedings of the symposium on the management of prairie dog complexes for the reintroduction of the black-footed ferret. Biological Report 13:18-27.

Table 3.1 - Means and ANOVA results for cover and biomass of functional groups off and on prairie dog colonies (N = 9) on the Pawnee National Grassland. Sampling methods were not appropriate to assess the differences between off- and on-colony sites with respect to the biomass of cacti and shrub functional groups because of their patchy distribution on the landscape. Cover of standing dead was not measured.

Response		Means		Factor			
		Off-Colony	On-Colony	Colony (Off vs. On)		Year	
		Mean ± SE	Mean ± SE	F	P	F	P
Graminoids	Cover (%)	44.59 ± 3.39	33.02 ± 3.72	37.74	0.001	1.63	0.210
	Biomass (g/m^2)	33.58 ± 4.34	18.73 ± 2.45	27.47	< 0.001	20.48	< 0.001
Forbs	Cover (%)	2.20 ± 0.39	4.74 ± 1.01	19.99	0.004	88.94	< 0.001
	Biomass (g/m^2)	4.44 ± 1.56	8.33 ± 2.30	6.71	0.015	21.42	< 0.001
Shrubs	Cover (%)	0.81 ± 0.20	0.94 ± 0.42	0.04	0.550	4.58	0.039
Cacti	Cover (%)	3.03 ± 0.62	1.05 ± 0.23	4.24	0.085	0.76	0.388
Standing Dead	Biomass (g/m^2)	3.72 ± 1.36	2.15 ± 1.41	0.95	0.337	5.44	0.010
Litter	Cover (%)	23.22 ± 2.13	23.84 ± 1.84	0.20	0.670	28.48	< 0.001
	Biomass (g/m^2)	46.58 ± 9.36	41.00 ± 9.27	1.16	0.290	18.25	< 0.001
Bare ground	Cover (%)	23.90 ± 1.51	33.99 ± 1.52	21.01	0.004	8.10	0.007

Table 3.2 - ANOVA results for cover and biomass of prevalent species off and on prairie dog colonies (N = 9) on the Pawnee National Grassland. To account for very dissimilar variances from year to year, cover of *Aristida longiseta*, *Agropyron smithii*, and *Sphaeralcea coccinea* were grouped by year in the ANOVA.

Response		Means		Factor			
		Off-Colony	On-Colony	Colony (Off vs. On)		Year	
		Mean ± SE	Mean ± SE	F	P	F	P
Bouteloua gracilis	Cover (%)	26.94 ± 2.98	16.42 ± 2.59	22.85	0.003	0.06	0.803
	Biomass (g/m^2)	18.59 ± 2.46	9.27 ± 1.50	10.50	0.003	17.30	< 0.001
Buchloe dactyloides	Cover (%)	11.89 ± 1.94	9.94 ± 1.17	0.51	0.503	0.31	0.578
	Biomass (g/m^2)	5.23 ± 1.15	4.76 ± 0.81	0.00	0.946	4.52	0.020
Aristida longiseta	Cover (%)	1.60 ± 0.47	3.73 ± 0.74	19.15	0.001	14.42	0.003
	Biomass (g/m^2)	0.97 ± 0.32	2.02 ± 0.49	3.35	0.078	0.11	0.894
Carex eleocharis	Cover (%)	1.41 ± 0.35	0.70 ± 0.24	6.17	0.048	4.53	0.040
	Biomass (g/m^2)	4.02 ± 0.91	1.05 ± 0.24	9.88	0.004	14.21	< 0.001
Agropyron smithii	Cover (%)	0.71 ± 0.20	0.88 ± 0.40	0.03	0.863	0.08	0.782
	Biomass (g/m^2)	1.94 ± 0.78	0.93 ± 0.56	1.82	0.188	1.82	0.181
Sphaeralcea coccinea	Cover (%)	0.90 ± 0.21	1.93 ± 0.46	28.31	< 0.001	39.80	< 0.001
	Biomass (g/m^2)	1.64 ± 0.60	2.55 ± 0.44	47.99	< 0.001	15.27	< 0.001

Table 3.3 - Mean species richness and diversity (H') (± 1 SE) of plant functional groups off and on young (n = 3), old (n =3), and plague-extirpated (n = 3) prairie dog colonies and mean species overlap (Sj) (± 1 SE) between off and on-colony pairs for young, old, and plague-extirpated colonies on the Pawnee National Grassland. For species richness and diversity, an asterisk indicates a significant difference between an off and on colony pair (P < 0.05).

	Young		Old			Plagued		
	OFF	ON	OFF		ON	OFF		ON
Richness	Mean ± SE	Mean ± SE	Mean ± SE		Mean ± SE	Mean ± SE		Mean ± SE
Graminoid	6.3 ± 0.7	5.8 ± 0.4	6.2 ± 0.8		5.5 ± 0.5	7.5 ± 0.6		8.83 ± 0.4
Forb	13.2 ± 1.3	13.5 ± 1.2	11.7 ± 1.1	*	17.3 ± 2.0	10.2 ± 0.7	*	16.8 ± 0.8
All Plants	23.8 ± 1.9	24.2 ± 1.0	21.0 ± 1.9	*	25.7 ± 1.7	22.0 ± 1.5	*	29.3 ± 1.6
Non-native	1.6 ± 0.5	1.8 ± 0.6	2.5 ± 0.5		2.2 ± 0.5	1.5 ± 0.3		1.6 ± 0.3
Diversity (H')	Mean ± SE	Mean ± SE	Mean ± SE		Mean ± SE	Mean ± SE		Mean ± SE
Graminoid	1.1 ± 0.1	1.1 ± 0.1	1.3 ± 0.1		1.3 ± 0.1	0.7 ± 0.1		1.1 ± 0.1
Forb	1.5 ± 0.1	1.5 ± 0.2	1.4 ± 0.2		1.4 ± 0.2	1.6 ± 0.2		1.6 ± 0.2
All Plants	1.5 ± 0.1	1.6 ± 0.1	1.7 ± 0.1		1.7 ± 0.1	1.1 ± 0.2		1.4 ± 0.1
Species Overlap (S_j)	Mean ± SE		Mean ± SE			Mean ± SE		
Graminoid	0.74 ± 0.07		0.59 ± 0.07			0.65 ± 0.07		
Forb	0.52 ± 0.05		0.34 ± 0.10			0.44 ± 0.05		
All Plants	0.59 ± 0.05		0.43 ± 0.06			0.55 ± 0.03		

Table 3.4 – Most frequently encountered species on and off of young, old, and plague-extirpated prairie dog colonies on the Pawnee National Grassland. Significant differences (P ≤ 0.05) in frequency of encounters between an on- and off-colony pair are indicated by an underlined species name.

Young		Old		Plague-extirpated	
Off-colony species (frequency)	On-colony species (frequency)	Off-colony species (frequency)	On-colony species (frequency)	Off-colony species (frequency)	On-colony species (frequency)
Bouteloua gracilis (0.67)	*Bouteloua gracilis* (0.74)	*Bouteloua gracilis* (0.68)	*Aristida longiseta* (0.57)	*Bouteloua gracilis* (0.87)	*Bouteloua gracilis* (0.87)
Buchloe dactyloides (0.53)	*Sphaeralcea coccinea* (0.47)	*Buchloe dactyloides* (0.54)	*Buchloe dactyloides* (0.51)	*Buchloe dactyloides* (0.25)	*Buchloe dactyloides* (0.37)
Sphaeralcea coccinea (0.31)	*Buchloe dactyloides* (0.36)	*Carex eleocharis* (0.44)	*Sphaeralcea coccinea* (0.46)	*Sphaeralcea coccinea* (0.24)	*Carex eleocharis* (0.29)
Carex eleocharis (0.23)	*Carex eleocharis* (0.25)	*Agropyron smithii* (0.24)	*Bouteloua gracilis* (0.27)	*Opuntia polyacantha* (0.21)	*Sphaeralcea coccinea* (0.28)
Aristida longiseta (0.22)	*Aristida longiseta* (0.21)	*Opuntia polyacantha* (0.21)	*Artemisia frigida* (0.22)	*Carex eleocharis* (0.21)	*Aristida longiseta* (0.27)
Agropyron smithii (0.19)	*Agropyron smithii* (0.13)	*Aristida longiseta* (0.20)	*Agropyron smithii* (0.20)	*Aristida longiseta* (0.19)	*Lepidium densiflorum* (0.19)
Opuntia polyacantha (0.15)	*Opuntia polyacantha* (0.13)	*Vulpia octoflora* (0.16)	*Carex eleocharis* (0.09)	*Agropyron smithii* (0.18)	*Talinum parviflorum* (0.14)
Gutierezia sarothrae (0.10)	*Lepidium densiflorum* (0.03)	*Artemisia frigida* (0.15)	*Chrysopsis villosa* (0.09)	*Talinum parviflorum* (0.18)	*Vulpia octoflora* (0.13)
Sporobolus cryptandrus (0.09)	*Gutierezia sarothrae* (0.03)	*Sporobolus cryptandrus* (0.11)	*Schedonnardis paniculatus* (0.04)	*Lepidium densiflorum* (0.15)	*Opuntia polyacantha* (0.08)
Lepidium densiflorum (0.09)	*Talinum parviflorum* (0.03)	*Sphaeralcea coccinea* (0.11)	*Vulpia octoflora* (0.03)	*Vulpia octoflora* (0.11)	*Agropyron smithii* (0.06)

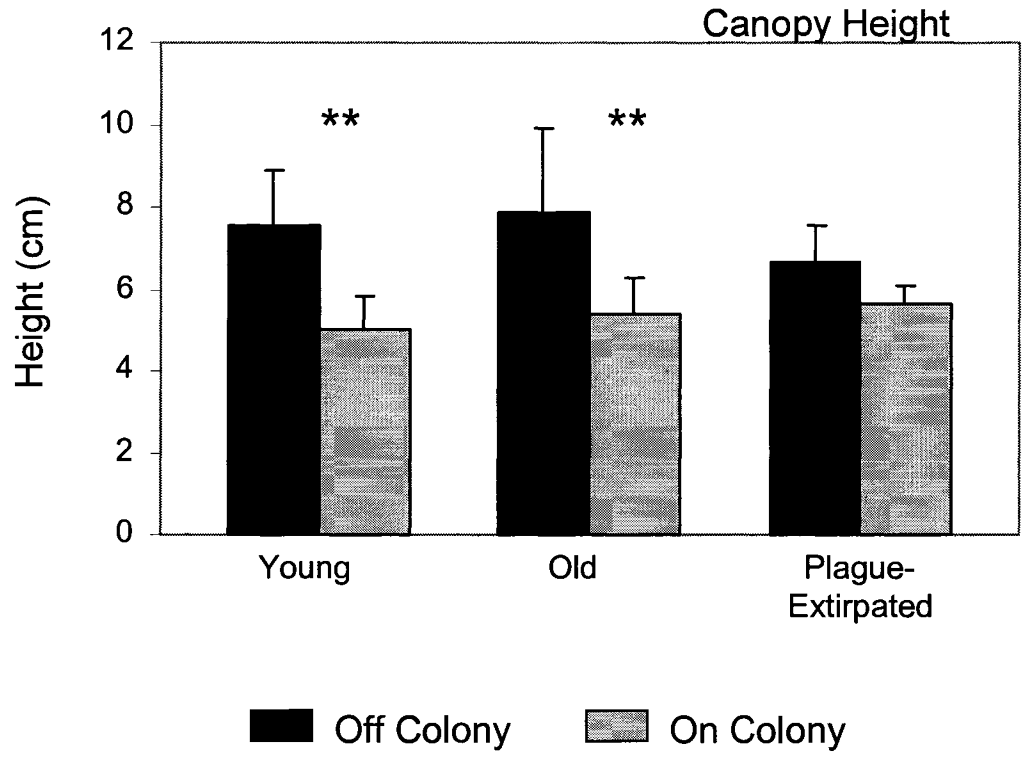

Figure 3.1 - Mean canopy height (cm) off and on prairie dog colonies on the Pawnee National Grassland, averaged across both seasons (early and late) and years (2002-2003) and presented by type (young, old, plagued). Asterisks (**) indicate a significant difference ($P \leq 0.01$) between an off- and on-colony pair.

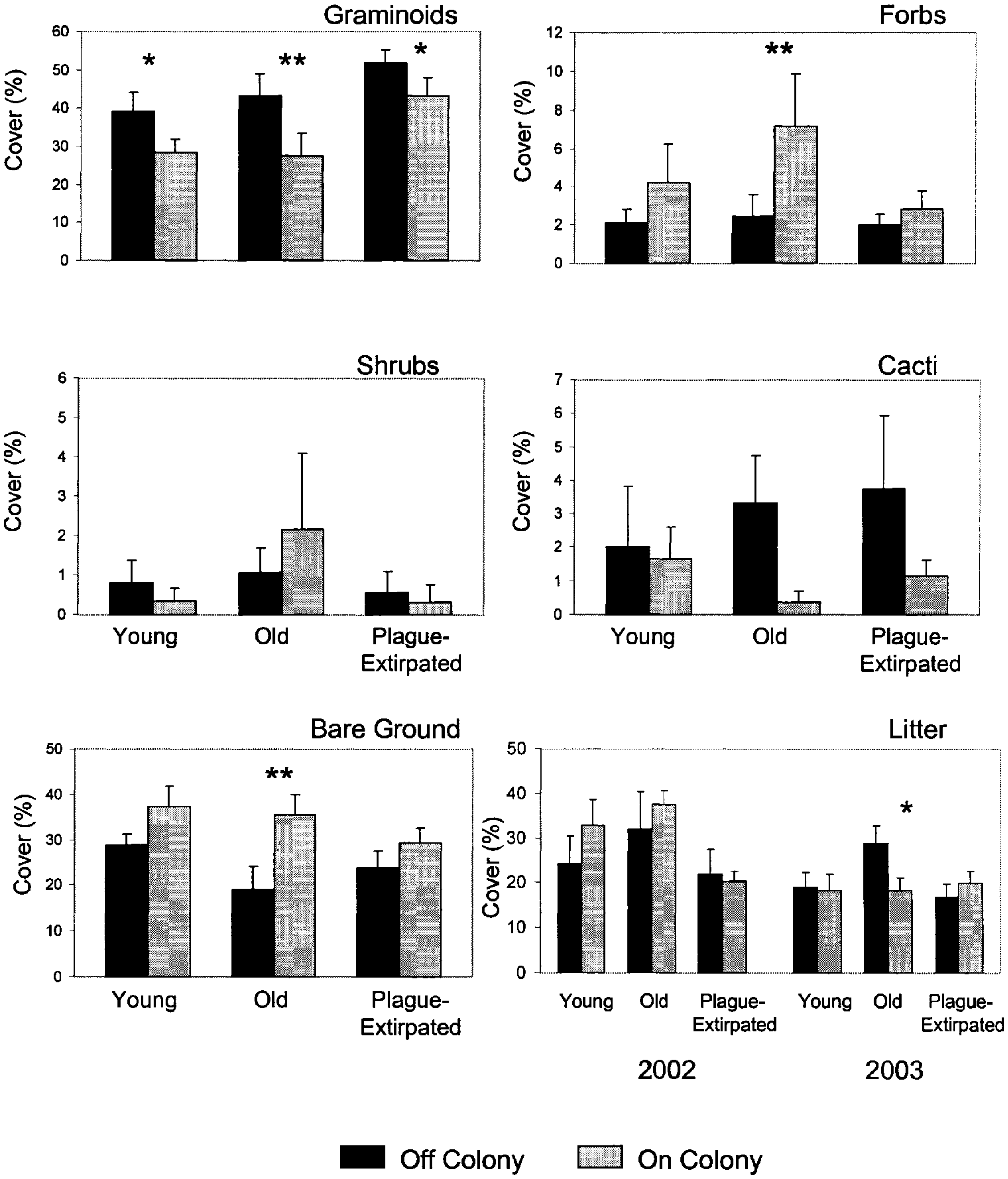

Figure 3.2 – Mean cover (%) of plants (by functional group), bare ground, and litter off and on prairie dog colonies of the Pawnee National Grassland, averaged across both seasons (early and late) and years (2002-2003) and presented by type (young, old, plague-extirpated). Cover of litter was not averaged over years because trends were not consistent between years. Significant differences between on- and off-colony pairs are indicated by asterisks ("*" denotes P ≤ 0.05, "**" denotes P ≤ 0.01).

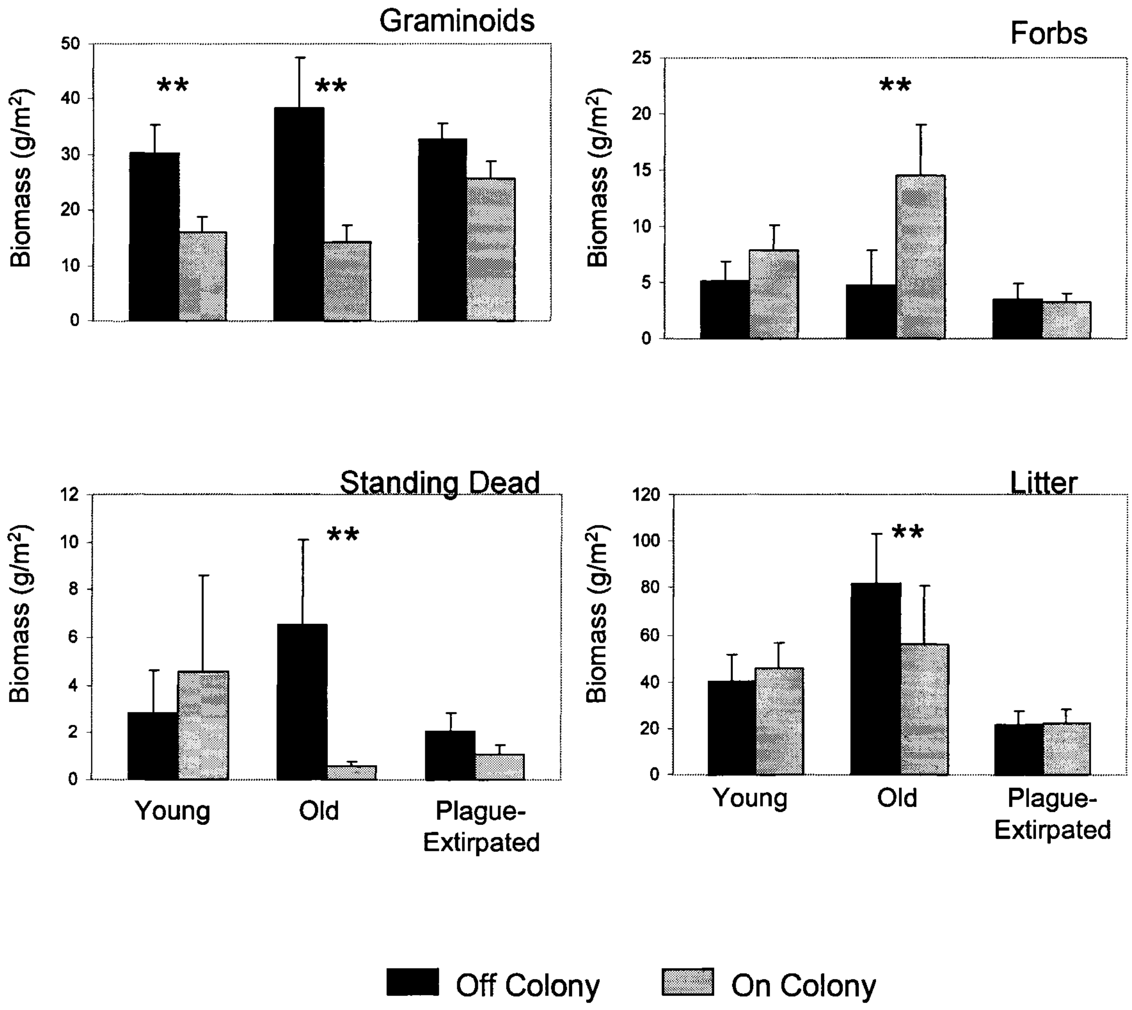

Figure 3.3 – Mean biomass (g/m^2) of graminoids, forbs, standing dead, and litter off and on prairie dog colonies on the Pawnee National Grassland, averaged over and years (2002-2004) and presented by type (young, old, plague-extirpated). Significant differences between on- and off-colony pairs are indicated by asterisks ("*" denotes $P \leq 0.05$, "**" denotes $P \leq 0.01$).

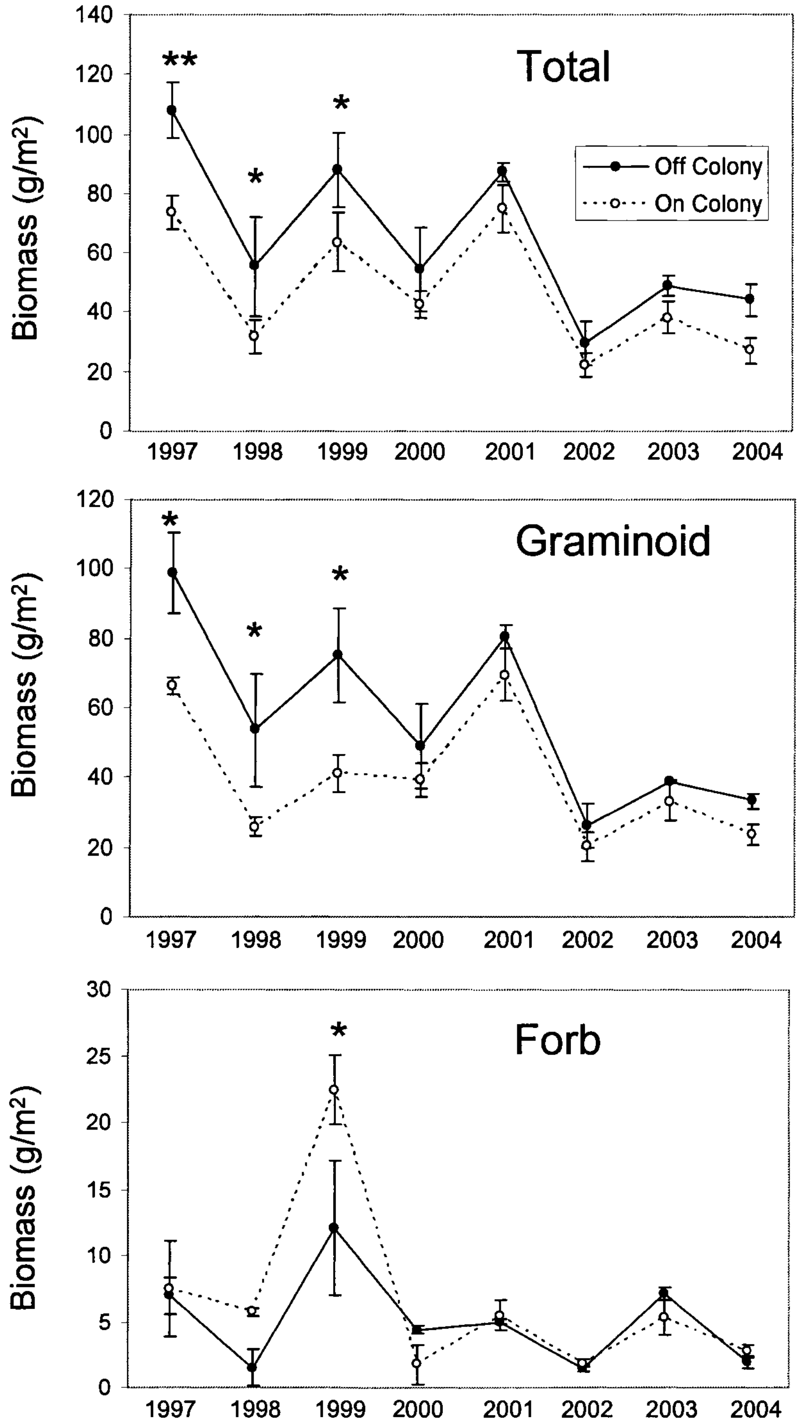

Figure 3.4 – Mean total, graminoid, and forb biomass (g/m^2) on "plague-extirpated" colonies (N = 3) on the Pawnee National Grassland both before and after a plague outbreak that occurred late in 1999. Total biomass includes all species except *Opuntia polyacantha*. Significant differences between on- and off-colony pairs are indicated by asterisks ("*" denotes $P \leq 0.05$, "**" denotes $P \leq 0.01$).

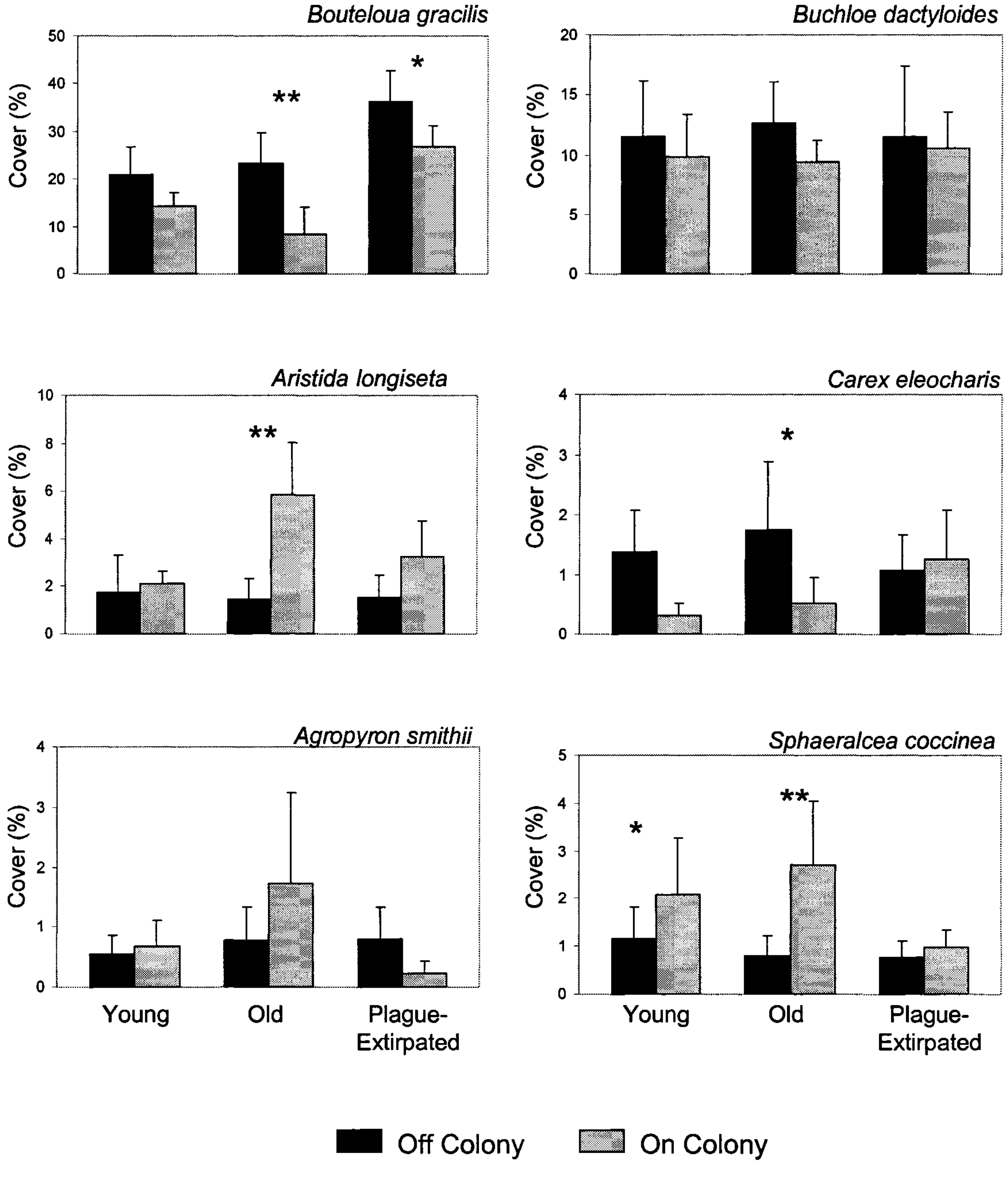

Figure 3.5 – Mean cover (%) of important plant species off and on prairie dog colonies on the Pawnee National Grassland, averaged over both seasons (early and late) and years (2002-2003) and presented by type (young, old, plague-extirpated). Significant differences between on- and off-colony pairs are indicated by asterisks ("*" denotes P ≤ 0.05, "**" denotes P ≤ 0.01).

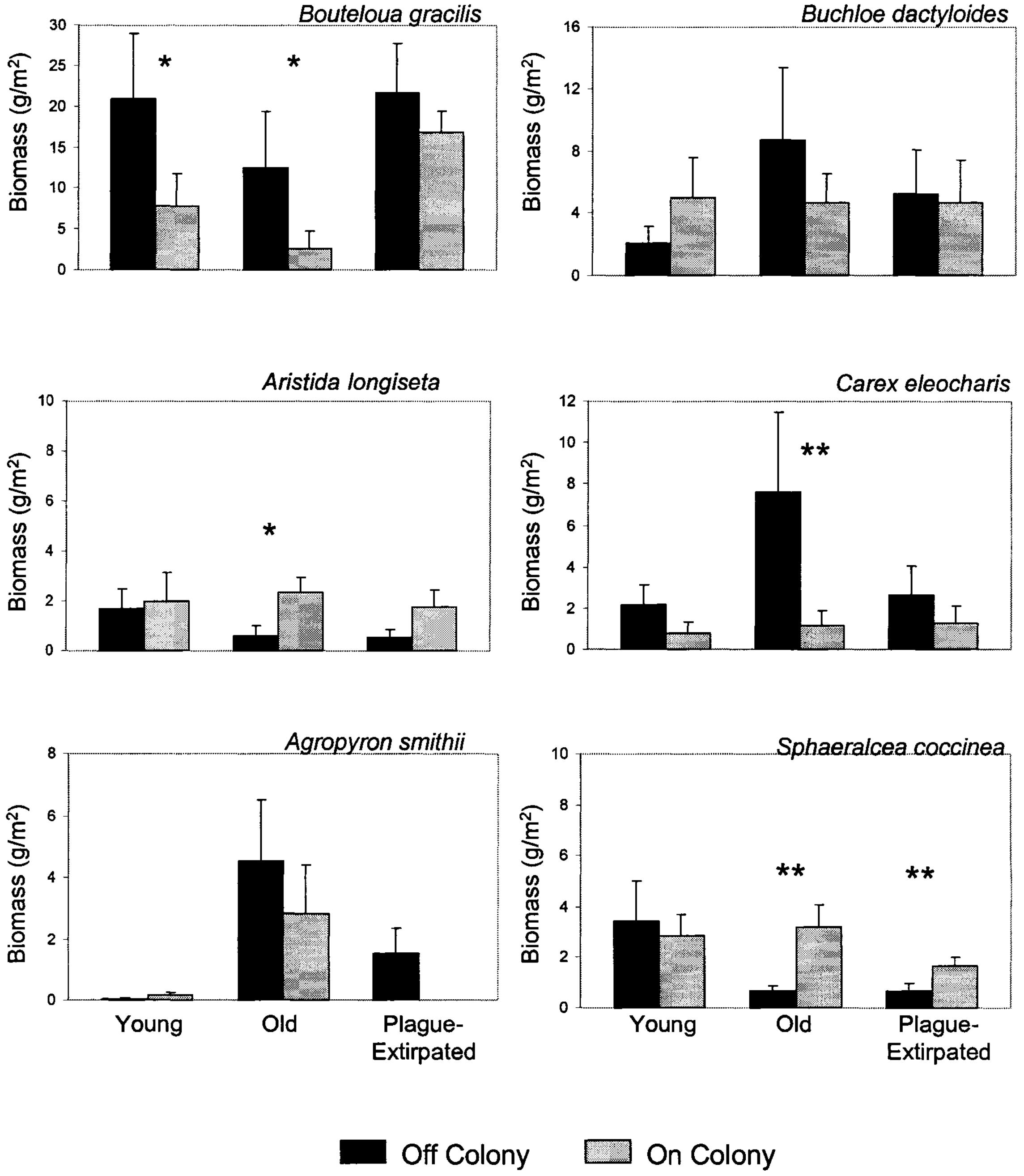

Figure 3.6 – Mean biomass (g/m^2) of important plant species off and on prairie dog colonies on the Pawnee National Grassland, averaged over all years (2002-2004) and presented by type (young, old, plague-extirpated). Significant differences between on- and off-colony pairs are indicated by asterisks ("*" denotes $P \leq 0.05$, "**" denotes $P \leq 0.01$).

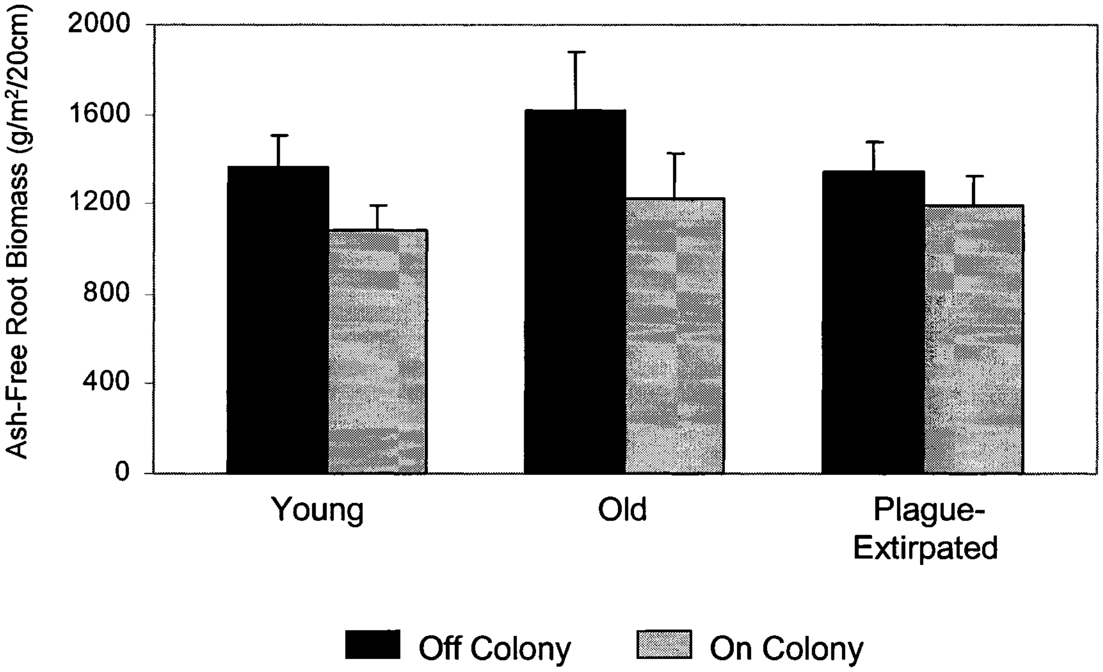

Figure 3.7 – Mean root biomass (g/m^2/20cm) off and on prairie dog colonies on the Pawnee National Grassland, averaged over all years and presented by type (young, old, plague-extirpated). There were no significant ($P \geq 0.05$) differences between on- and off-colony pairs for any colony type.

CHAPTER 4

EFFECTS OF PRAIRIE DOGS ON NUTRIENT CYCLING: INFLUENCES OF COLONY AGE AND PLAGUE OUTBREAKS

Abstract. --- Black-tailed prairie dogs (*Cynomys ludovicianus*) are colonial rodents whose burrowing, vegetation clipping, and intensive herbivory influence plant biomass and community composition on their colonies. I studied how these effects of prairie dogs influence belowground processes on the shortgrass steppe, and how differences in nutrient cycling on- and off- colonies are influenced by colony age and activity (active or plague-extirpated). I measured shoot and root N concentration, net N mineralization, and soil organic matter on and off of young (3-8 years), old (~ 20 years), and plague-extirpated prairie dog colonies. Shoot N was significantly greater on than off of active colonies, but not on than off of plague-extirpated colonies. Differences between on- and off-colony sites were slightly greater for older colonies. Root N concentration did not differ significantly between on- and off-colony sites for any of the colony types. Intermound spaces on prairie dog colonies did not have significantly higher rates of net N mineralization than uncolonized grassland. However, prairie dog mounds appear to be sites of high nutrient turnover. Mounds on active colonies had greater rates of net N mineralization compared to intermound sites on the colonies or to uncolonized sites. There were no significant trends for net N mineralization between on and off of plague-extirpated colonies. Soil organic matter (total C and N, particulate organic matter C and N) pools appear to be relatively unaffected by prairie dog activity. Differences between on- and off-colony sites were seen only in the older (~ 20 years) colonies.

Key words: *prairie dogs, herbivory, nitrogen cycling, soil organic matter, ecosystem engineers, grazing, pedoturbation, shortgrass steppe*

INTRODUCTION

Black-tailed prairie dogs (*Cynomys ludovicianus*) are semi-fossorial, colonial rodents that are prevalent in the short- and mixed-grass prairies of North America. Compared to uncolonized grassland, prairie dog colonies have shorter vegetation, less standing plant biomass, greater bare ground cover and a lower ratio of graminoid to forb biomass (Coppock et al. 1983a, Archer et al. 1987, Chapters 2 and 3). Another noticeable feature of colonies is the presence of burrow entrances (30 – 300 per hectare) that are surrounded by soil mounds as high as 1 m and as wide as 2 m (King 1955, Sheets et al. 1971, Archer et al. 1987, Whicker and Detling 1988, Cid et al. 1991, Hoogland 1995). The effects of prairie dogs on vegetation, along with their substantial pedoturbation, may influence nutrient cycling rates on their colonies by changing the quantity or quality of resources for microbes or by changing abiotic conditions (i.e. soil moisture, temperature, and aeration) that affect microbial process rates (Table 4.1).

On colonies, a large proportion of aboveground net primary production (ANPP) (60 – 80%) is consumed by prairie dogs (Whicker and Detling 1988). Prairie dog grazing may increase nutrient cycling because much of the biomass that is consumed by herbivores is decomposed in the fast rather than the slow cycle of decomposition (Bardgett et al. 1998, Bakker et al. 2004) (Figure 4.1). In the slow cycle, plants die and their nutrients are returned to the soil via decomposition of litter. In the fast cycle, herbivores consume vegetation and return any unassimilated nutrients to the soil as dung or urine. This shortens the length of time for decomposition because dung and urine are rich in labile nutrients and are more easily decomposed than litter (Reuss and McNaughton 1987, Day and Detling 1990, Bardgett et al. 1998).

Prairie dogs may affect nutrient cycling indirectly by increasing or decreasing litter quality, which is positively related to litter decomposition (Enriquez et al. 1993, Gholz et al. 2000). On the mixed-grass prairie, grazing by prairie dogs results in an increase in N concentration of standing plant biomass (Coppock et al. 1983a). An increase in plant N concentration is a common response to grazing, in part because repeated defoliation and regrowth reduces average leaf age. Younger leaves have less lignified tissue, and hence, lower C to N ratios than older leaves (Kamstra et al. 1968, Coughenour et al. 1990, McNaughton et al. 1997). Conversely, litter quality could decrease if herbivory induces plants to produce defense compounds. For example, concentrations of SiO_2, a putative anti-herbivore defense compound (McNaughton and Tarrants 1983), were higher in grasses on than off of colonies of the mixed-grass prairie (Brizuela et al. 1986, Cid et al. 1989).

Prairie dogs may also affect litter quality through changes in plant community composition. Colonies tend to have lower ratios of graminoid to forb biomass, which could result in higher litter quality since forb species tend to have lower C:N ratios than graminoids. However, cover of some unpalatable, nutrient poor species may also be higher on than off of colonies (Chapter 3), which could have a negative influence on plant litter quality.

Grazing and burrowing can influence abiotic soil properties (i.e. moisture, temperature, aeration) that control microbial process rates (Bardgett 2005) (Table 4.1). Soil temperature in the mixed-grass prairie was higher on than off of colonies, perhaps because of an increase in bare ground (Archer and Detling 1986). Prairie dog grazing may be expected to alter soil water balance through a variety of complex and counteracting effects. Reduction in total leaf area and cover of litter on colonies could translate to greater soil moisture because of reduced transpiration and canopy interception. However, an increase in bare ground could result in greater evaporative loss and thus a decrease in soil moisture. One study on the mixed-grass prairie reported higher gravimetric soil moisture on than off of colonies (Archer and Detling 1986) while another reported lower gravimetric soil moisture on than off of colonies (Holland and Detling 1990).

Effects of prairie dogs on nutrient cycling may be most pronounced on the soil mounds surrounding their burrow entrances. Mounds have less plant cover than the rest of the colony (Farrar 2002), which could increase surface soil temperatures. Canals et al. (2003) found soil temperatures of gopher mounds to be higher than those of vegetated soils. Lower plant cover on mounds could result in accumulation of inorganic N in bare mound soils due to lower N uptake by plants (Canals et al. 2003). Prairie dog feces are also concentrated in the vicinity of mounds, as is the subsurface soil that was translocated to the surface by prairie dogs during burrow creation (Sheets et al. 1971). Prairie dogs, like other burrowing animals, may break up soil aggregates and increase soil aeration, thereby stimulating microbial activity (Green et al. 1999). Frequent digging around burrows could also bury litter, and buried litter decomposes at a faster rate than surface litter (Cortinas and Seastedt 1996).

On the mixed-grass prairie, prairie dogs have been shown to stimulate net N mineralization (Holland and Detling 1990, Fahnestock and Detling 2002) and increase N concentration of standing plant biomass (Coppock et al. 1983a). How prairie dogs influence nutrient cycling is potentially important in the debate about whether prairie dogs reduce habitat suitability for livestock because increases in quality of available forage could potentially offset decreases in quantity (Detling 2006a). Higher N concentration in plants on versus off of colonies in the mixed-grass prairie has been cited as a possible explanation for why bison (*Bison bison*) and pronghorn (*Antelcapra americana*) preferentially graze on prairie dog colonies during the growing season (Coppock et al. 1983b, Krueger 1986). There is little information available to assess the influence of prairie dogs on nutrient cycling on the shortgrass steppe. Differences in forage nitrogen between on- and off-colony sites may be less pronounced in the shortgrass steppe than in the mixed-grass prairie because the shortgrass steppe is a drier and less productive system with inherently slower rates of N mineralization (Burke et al. 1997). Compared to the mixed-grass prairie, prairie dog grazing on the shortgrass steppe causes proportionately less of a reduction in litter and biomass, and the shift in plant community composition from graminoid- to forb-dominated is less pronounced (Chapter 3). Furthermore, changes in plant community composition, biomass, and nutrient cycling tend to increase with colony age (Holland and Detling 1990, Archer et al. 1987, Coppock et al. 1983a, Chapter 3) and colonies on the shortgrass steppe are much less likely to persist for multiple decades than they were in the past because of an introduced disease, bubonic plague (Antolin et al. 2002). Plague, first noted in prairie dogs in the 1940s, may have profound influences on the role of prairie dogs in shaping grassland structure and function because colonies periodically are extirpated by the disease and are subsequently recolonized by individuals from neighboring colonies (Antolin et al. 2002). On the

Pawnee National Grassland, where I conducted this study, almost all colonies experienced at least one plague outbreak within a 20 year period and colonies were typically inactive for several years after an outbreak (Stapp et al. 2004, Chapter 1).

The goals of this chapter are 1) to assess how prairie dogs influence plant N concentration, net N mineralization, and soil characteristics on the shortgrass steppe, 2) to assess the influence of colony age and activity (active versus plague-extirpated) on the magnitude of prairie dog-induced changes in nutrient cycling, and 3) to compare effects of prairie dogs on the shortgrass steppe to previously reported effects of prairie dogs on the mixed-grass prairie.

METHODS

Site Description. --- I conducted this study in 2003 and 2004 on the Pawnee National Grassland (PNG) located in northeastern Colorado. Long-term mean annual air temperature is 8.6 C and mean annual precipitation is 322 mm, with approximately 70 % of precipitation falling between April and September (Lauenroth and Milchunas 1992). Precipitation, averaged across four PNG sites, from April through July was 214 mm in 2003 and 147 mm in 2004 (National Science Foundation Shortgrass Steppe Long Term Ecological Research Program, Colorado State University, Fort Collins, CO).

I chose three colonies on the PNG that had been occupied almost continuously for the past 25 years, three that were among the most recently colonized (within the last 3-7 years), and three that had been recently extirpated due to a plague outbreak in 1999. For each prairie dog colony, I chose a nearby uncolonized site with similar slope, aspect, soil characteristics (NRCS-SSURGO), and land-use history (U.S. Forest Service, Pawnee National Grassland Office, Greeley, CO). If a single colony occupied some area that had been previously cultivated (before 1938), I confined sampling efforts to the portion of the colony that had not been cultivated. All sites were grazed seasonally and moderately by cattle.

In 2004, one of the "old" colonies experienced a plague outbreak and was not sampled that year. Due to the lack of additional suitable sites, I was unable to replace this colony with another. In 2003 and 2004, several burrows at the margins of the "plague-extirpated" colonies were reoccupied by immigrant prairie dogs. I confined my sampling on the plague-extirpated colonies to areas with the fewest signs of recent prairie dog activity.

Shoot Nitrogen Concentration. --- Each year, I collected three composite samples of live plant material of *Bouteloua gracilis*, the dominant grass, and *Sphaeralcea coccinea*, the dominant forb, on each colony and control site in June, July, and August. I dried samples at 55 °C, ground them through a 40-mesh screen in a Wiley mill, and analyzed a subsample for total C and N content using an automated combustion element analyzer (LECO, St. Joseph, MI, USA). To calculate potential standing crop N (g/m^2) for each species, I multiplied the highest monthly estimate of N concentration at each site by the mean peak biomass (reported in Chapter 3) for that species (g/m^2) at each site. I used the highest monthly estimate of N concentration and peak biomass to get the highest possible estimate of standing crop N.

Root Nitrogen Concentration. --- I collected root cores (6.35 cm diameter) to a depth of 20 cm. At each colony and off-colony site, I collected 5 cores in 2003 and 8 cores in 2004. I mixed each sample with water and agitated it to separate root material from soil (Lauenroth and Whitman 1971). As roots floated to the surface, I decanted them onto a 0.5 mm mesh sieve. I dried root samples at 55 °C, hand-picked non-root materials from each sample, and weighed them. I ground root samples in a ball mill and determined ash content of the ground sample by combusting a 0.5 g subsample in a muffle furnace at 600 °C for 4 hours. I analyzed a 0.2 g subsample of the ground root biomass samples for total C and N content. I corrected root biomass and root C and N content estimates using the known ash content for each sample in order to report results on an organic matter basis.

In-Situ Nitrogen Availability. --- I used Plant Root Simulator Probes™ (WesternAg Innovations (WAI), Saskatchewan, Canada) to estimate in-situ nitrogen availability. Unlike resin bags, the anion- and cation-exchange resin impregnated membranes on the PRS probes have a well-defined surface area (10 cm^2) and offer a specific geometry for calculating plant-available nutrients (Lajtha et al. 1999). Also, the flat exchange surface can be in direct contact with soil particles which eliminates potential interference from mesh bag material, the membranes on the probes are less likely than the resin bags to disrupt the flow of soil water, and insertion of the probes into the soil is less disruptive to soil structure than is the burial of resin bags (Lajtha et al. 1999).

At each colony and off-colony site, I established a 100 x 150 m grid with a sampling point every 50 m (total of 12 sampling points). At each point, I trenched a 10 x 10 cm square using a shovel and clipped the aboveground vegetation from the square. This was intended to greatly reduce or eliminate plant uptake of N and provide an estimate of net N mineralization by the decomposer community. At the center of each square on the grid, I inserted a pair of PRS™-probes (one cation and one anion). On the colonies, sampling points were located at least 2 m from a prairie dog mound. A cumulative measure of nutrient supply throughout the growing season was measured by removing buried PRS™-probes after 30 days and then re-inserting fresh probes in the same soil slot. This also allowed for the assessment of temporal changes in nutrient supply due to changing environmental conditions (Jowkin and Schoenau 1998). After removal, probes were washed thoroughly in the field with deionized water, and bulked together in groups of 4 to make 3 composite samples per site. Samples were packed on ice and shipped overnight to the laboratory at WAI where they were eluted for one hour using 0.5 N HCl/2 M KCl. The eluate was then analyzed for ammonium (NH_4^+) and nitrate (NO_3^-) using automated colorimetry.

In both years, samples were gathered on and off each colony from June 15 to July 15, July 15 to August 15, and August 15 to September 15. In 2004, I also measured net N mineralization on prairie dog burrow mounds by installing an additional pair of probes on the mound nearest each point on the sampling grid.

Soil Analysis Methods. --- In 2004, I collected eight soil cores to a depth of 20 cm at each off- and on-colony site and on eight mounds on each colony. Soil cores were dried at 55 °C and sieved through a 2 mm mesh sieve. I hand-picked large roots that fell length-wise through the sieve and mixed the sample thoroughly. I calculated soil bulk density as the ratio of the mass of oven-dried, sieved soil to core volume. I ground a subsample of the soil using a ball mill and analyzed if for total soil C and N.

Soil particle fractionation and particulate organic matter (POM) C and N were estimated using a combined procedure. I first suspended 50 g of soil in 100 mL of sodium hexametaphosphate (5%). I used an automated shaker to shake the suspension for 18 h at room temperature in order to disperse soil particles, transferred contents to a 1 L graduated cylinder, and brought the cylinder to volume with deionized water at room temperature. I plunged the soil and water solution for 10 seconds. After 2 hours, I measured the density using a standard hydrometer with a Bouyoucos scale (g/L) and used the density to estimate clay content of the soil. I then passed the contents of the graduated cylinder through a 500 μm sieve to collect the coarse sand fraction and finally through a 53 μm sieve to collect the fine sand fraction. I rinsed the coarse and fine fractions, collected them in aluminum pans, dried them at 55 °C, and weighed them. I then ground the fractions in a ball mill and analyzed them for POM C and N. I bulked the coarse POM fractions into 2 samples per site before grinding because of the small size of the samples (Burke et al. 1999). I estimated mineral-associated C and N by subtracting POM C and N from total C and N (Hook and Burke 2000). I calculated the average % C and N for each site and each soil fraction (whole soil, fine POM, coarse POM, and mineral-associated POM) and multiplied that by the average bulk density for the site to get total C and N (g/m^2) to 20 cm.

Statistical Analysis. --- I used mixed model analyses of variance to test the effects of site (colony), location (off-colony, on-colony, on-mound), month (if applicable), year (if applicable), and type (young, old, plagued-extirpated), on each response variable. Site was treated as a random effect while location, month, year, and type were fixed effects. I also examined interactions between main effects. Because I chose specific off-colony sites for each colony, I linked pairs together in the programming code. To avoid pseudoreplication, I averaged data by site prior to analysis, i.e. colonies, rather than the individual samples collected, were considered to be the replicates. I examined differences between on- versus off-colony pairs by type (young, old, plagued-extirpated) using LSMEANS and examined on- versus off-colony pairs by type and date (month or year) using paired t-tests. I square-root transformed data if residuals were not normally distributed. All figures and tables depict untransformed data. I used SAS statistical software to perform all analyses (SAS Institute 1999, Cary, NC, USA). Statistical significance was set at $P \leq 0.05$.

RESULTS

Shoot Nitrogen Concentration. --- For both *B. gracilis* and *S. coccinea,* N concentration varied significantly between site (off- versus on-colony), between years, and between months, but there were no significant interactions between main effects. Averaged across all colony types and sample dates, mean N concentration of *B. gracilis* was ~15 % higher on (2.51 %) than off (2.17 %) of colonies ($F = 7.51$, $P = 0.03$) and mean N concentration of *S. coccinea* was ~ 14 % higher on (2.80 %) than off (2.48 %) of colonies (F = 7.02, P = 0.04). For both species, N concentration was lowest in August, as was the difference between on- and off- colony pairs (Fig. 4.2). When considering colonies by type and averaged over all months, all types showed trends of higher nitrogen concentration on- than off- colony, but these trends were rarely statistically significant (Fig. 4.3). Averaged across all colony types, despite the fact that N concentration was higher on- than off-colonies for *B. gracilis*, total standing crop N was lower on (0.27 g/m^2) than off (0.52 g/m^2) colonies (F = 7.19, P = 0.04). Total standing crop N was higher on (0.09 g/m^2) than off (0.06 g/m^2) colonies for *S. coccinea* (F = 10.34, P = 0.03). When considering colonies by type, potential standing crop N of *B. gracilis* was significantly lower on than off old and young colonies, but not on than off plague-extirpated colonies (Table 4.2). Potential standing crop N of *S. coccinea* was significantly higher on than off old colonies, but not on than off young or plague-extirpated colonies (Table 4.2).

Root Nitrogen Concentration. --- Averaged across all colony types and years, root nitrogen concentration (%) was ~12% higher on (1.98 %) versus off (1.76 %) colonies (F = 6.22, P = 0.047). Root nitrogen concentration did not vary between sample years (F = 0.40, P = 0.542) . All colony types (young, old, plague-extirpated) exhibited a trend of higher root N concentration on- versus off-colony, but the trend was not statistically significant for any type (Fig. 4.4).

In-Situ Nitrogen Availability. --- The majority of the plant available inorganic N was in the form of NO_3^- and relatively little was in the form of NH_4^+ (Fig. 4.5). In 2003, there were no significant differences in monthly (Table 4.3) or cumulative (June 15th - September 15th) (Fig. 4.5) supply rates of inorganic N (total, NO_3^-, or NH_4^+) between on- and off-colonies for any of the colony types. In 2004, for young and old colonies, the cumulative supply rates for total inorganic N and NO_3^- were greatest on the mounds, intermediate on the intermound areas on the colonies, and lowest off of the colonies, but differences among sampling locations were statistically significant for only the young colonies (Fig. 4.5). In 2004, the cumulative supply rates for NH_4^+ were greater off-colony than on either sampling position on-colony for young colonies (Fig. 4.5). On plague-extirpated colonies, NH_4^+ was greater on intermound areas than on-mound or off-colony (Fig. 4.5). For all colony types, plant available inorganic N (total and NO_3^-) was greatest on the prairie dog mounds early in the season, but there were no differences in inorganic N (total, NO_3^-, or NH_4^+) supply rates between sampling locations later in the 2004 season (Table 4.4).

Soil Characteristics. --- Prairie dogs had little effect on soil organic matter on the colonies I studied (Table 4.5). There were very few notable or significant differences between on- and off-colonies with respect to C (g/m^2) or N (g/m^2) of the total, fine POM, coarse POM, or mineral-associated organic matter (Table 4.5). However, old colonies, both on- and off-mounds, had less soil carbon (total and coarse POM) than their off-colony sites and less coarse POM nitrogen on- than off-mounds (Table 4.5). Sand (%) and silt (%) did not vary between sampling positions (off-colony, on-colony, on-mound) for any of the colony types (Table 4.5). Clay (%) was significantly lower on mounds of old and plagued colonies compared to their paired off-colony sites, and clay was also lower on than off of plagued colonies (Table 4.5). There were no significant differences in fine soil bulk density between the sampling positions (Table 4.5).

DISCUSSION

On the shortgrass steppe, cattle (*Bos taurus*) neither prefer nor avoid grazing on prairie dog colonies (Guenther and Detling 2003). However, in the mixed-grass prairie, bison (*Bison bison*) and pronghorn (*Antelocapra americana*) have been observed to preferentially graze on colonies during the growing season (Coppock et al. 1983b, Krueger 1986), and the same may be true there for cattle (Detling 2006b). My results provide one possible explanation for why ungulate grazing preferences differ between the two grassland types. The increases in shoot N that I observed on the shortgrass steppe were smaller in magnitude than the increases observed on the mixed-grass prairie (Coppock et al. 1983a). Derner et al. (2006) found that cattle weight gain on the shortgrass steppe was lower in pastures colonized by prairie dogs, but as the amount of colonized pasture increased, the rate of decrease in cattle weight gain decreased. Lower weight gains of cattle in prairie dog-occupied pastures are consistent with my observation that the increases in forage N of *Bouteloua gracilis*, the dominant plant species on the shortgrass steppe, are not great enough to offset the decreases in forage biomass. However, I conducted this study in years with below average precipitation, and differences in forage N between between on- and off-colony sites could be greater in years with more rainfall.

On the mixed-grass prairie, potential net N mineralization was greatest in soils from the oldest part of a colony and least in soils from adjacent uncolonized grassland, and extractable nitrate was also greater on than off of colonies (Holland and Detling 1990). In-situ N mineralization did not show conclusive patterns in one study (Holland and Detling 1990), but was greater on- than off-colony in another study (Fahnestock and Detling 2002). Caution must be exercised in comparing my results to results from the mixed-grass prairie. I used resin strips while one study on the mixed-grass prairie used buried soil bags (Holland and Detling 1990) and the other used resin beads (Fahnestock and Detling 2002). Because units of measure are not the same, I can only compare relative differences (i.e. prairie dog colonies have higher or lower N mineralization rates than off-colony sites). Furthermore, the different ways soils are manipulated to install instruments needed for testing via the various methods (bags, probes, PVC pipe etc.) have a bearing on the results obtained, as do the relative sink strengths of the resins, in strips or beads, to the sink strength of plant roots or microbes. Using PRS probes in the field, I observed the same trends in net N mineralization as were observed for net N mineralization on the mixed-grass prairie (Holland and Detling 1990, Fahnestock and Detling 2002). However, the differences between on- and off-colony that I observed were minimal and not statistically significant. Further, differences did not increase with colony age as they did for potential net N mineralization on the mixed-grass prairie (Holland and Detling 1990).

A previous study of the effects of heavy grazing on the shortgrass steppe showed that cattle have little influence on potential N mineralization (Burke et al. 1999). Even though areas heavily grazed by prairie dogs are visibly more different from the surrounding grassland than are areas heavily grazed by cattle, prairie dogs do not appear to have greater effects on biogeochemical cycling. This lends further support to the idea that the shortgrass steppe is unusually tolerant of heavy grazing (Milchunas et al. 1989, Burke et al. 1999).

Although trends of higher net N mineralization on versus off of colonies were not statistically significant, differences between mounds and off-mound sites were highly significant early in the growing season. A substantial body of literature is amassing in support of the idea that animal mounds greatly influence biogeochemical cycling (Mun and Whitford 1990, Cortinas and Seastedt 1996, Liator et al. 1996, Ayarbe and Kieft 2000, Canals and Sebastia 2000, Sherrod and Seastedt 2001, Canals et al. 2003). My study did not explicitly test the possible mechanisms for why net N mineralization could be higher on than off of mounds. One possible explanation is that mound soils have a greater proportion of labile nutrients because feces are concentrated in the vicinity of burrow entrances. Mounds could also have higher temperature or moisture due to more bare soil. Soil aeration could also be greater due to frequent digging by prairie dogs, however, bulk densities were not significantly different on and off of mounds. There were no substantial differences in total N or C on and off of mounds, suggesting that the quantity of substrate for microbes did not differ between the microsites. Even though mounds appear to be hot-spots of nutrient turnover, their importance to the overall picture of nutrient cycling on a colony may be minimal because mounds and the denuded area around them account for only about 4-6 % of a colony's overall area (Farrar 2002, Detling 2006a).

Soil organic matter pools have been notably resistant to heavy grazing in the shortgrass steppe (Burke et al. 1999). However, I hypothesized that prairie dogs might have a greater influence on soil nutrients than cattle because, as a colony, prairie dogs may graze more intensively than cattle for a more prolonged period of time, and prairie dogs are also agents of extreme pedoturbation. I noted few differences between on- and off- colony sites. However, older colonies had significantly less soil C (total, fine POM, coarse POM) than off-colony sites. In this study, the old colonies had been heavily grazed by prairie dogs for almost 20 years and had the greatest change in plant species composition and biomass. Decreased carbon inputs over 20 years could have resulted in less stored C belowground. I did not observe any notable differences in soil N between on- and off-colony and on- and off-mounds. Prairie dogs consume both C and N. Respiration releases much of the C they ingest to the atmosphere while defecation returns much of the N they ingest to the soil.

One of the aims of this study was to assess whether the effects of prairie dogs on nutrient cycling are influenced by plague-extirpations. The probability of a colony experiencing a plague outbreak within 20 years of activity is almost 100% and most colonies will be inactive for at least a few years after an outbreak (Stapp et al. 2004, Chapter 1). Because there were more differences in shoot N and net N mineralization between on- and off-colony sites for the active (young and old) colonies than the plague-extirpated colonies, I conclude that plague may have important mediating effects on the role of prairie dogs in influencing these response variables. With respect to SOM, the difference between on and off of plague-extirpated colonies may have been minimal not because of recovery from the effects of prairie dogs, but perhaps because the colonies were not as old as the "old" colonies when they were extirpated and may not have had time for losses in SOM to accrue.

In summary, grazing and burrowing by prairie dogs does appear to have small effects on nutrient cycling in the shortgrass steppe. Qualitative trends in forage N between on and off-colony were similar to those seen on the mixed-grass prairie, but differences were only significant for the active colonies. The trends for net N mineralization were similar to those seen for net N mineralization on the mixed-grass prairie, but differences were smaller in magnitude and not a function of colony age. I found the influence of prairie dogs on net N mineralization on their colonies was greatest on soil mounds surrounding burrow entrances, suggesting that mounds may be "hot-spots" for nutrient turnover. Changes in soil organic matter were only evident for colonies that had been occupied for the longest time (~ 20 years), supporting the idea that the shortgrass steppe is highly resistant to changes in SOM due to heavy grazing.

LITERATURE CITED

Antolin, M. F., P. Gober, D. Luce, D. E. Biggins, W. E. Van Pelt, D. B. Seery, M. Lockhart, and M. Ball. 2002. The influence of sylvatic plague on North American wildlife at the landscape level, with special emphasis on black-footed ferret and prairie dog conservation. Transactions of the 67th North American Wildlife and Natural Resources Conference 67:104-127.

Archer, S. and J. K. Detling. 1986. Evaluation of potential herbivore mediation of plant water status in a North American mixed-grass prairie. Oikos 47:287-291.

Archer, S. R., M. G. Garrett, and J. K. Detling. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio 72:159-166.

Ayarbe, J. P. and T. L. Kieft. 2000. Mammal mounds stimulate microbial activity in a semiarid shrubland. Ecology 81:1150-1154.

Ayres, E., J. Heath, M. Possell, H. I. J. Black, G. Kerstiens, and R. D. Bardgett. 2004. Tree physiological responses to above-ground herbivory directly modify below-ground processes of soil carbon and nitrogen cycling. Ecology Letters 7:469-479.

Bakker, E. S., H. Olff, M. Boekhoff, J. M. Gleichman, and F. Berendse. 2004. Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. Oecologia 138:91-101.

Bardgett, R. D., D. A. Wardle, and G. W. Yeates. 1998. Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. Soil Biology and Biochemistry 30:1867-1878.

Bardgett, R.D. 2005. The Biology of Soils: A Community and Ecosystem Approach. Oxford University Press.

Brizuela, M. A., J. K. Detling, and M. S. Cid. 1986. Silicon concentration of grasses growing in sites with different grazing histories. Ecology 67:1098-1101.

Burke, I.C., W. K. Lauenroth, and W. J. Parton. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. Ecology 78:1330-1340.

Burke, I. C., W. K. Lauenroth, R. Riggle, P. Brannen, B. Madigan, and S. Beard. 1999. Spatial variability of soil properties in the shortgrass steppe: the relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. Ecosystems 2:422-248.

Canals, R. M. and M. T. Sebastia. 2000. Soil nutrient fluxes and vegetation changes on molehills. Journal of Vegetation Science 11:23-30.

Canals, R. M., D. J. Herman, and M. K. Firestone. 2003. How disturbance by fossorial mammals alters N cycling in a California annual grassland. Ecology 84:875-881.

Cid, M. S., J. K. Detling, M. A. Brizuela, and A. D. Whicker. 1989. Silicon concentration of grasses growing in sites with different grazing histories. Ecology 67:1098-1101.

Cid, M. S., J. K. Detling, A. D. Whicker, and M. A. Brizuela. 1991. Vegetational responses of a mixed-grass prairie site following exclusion of prairie dogs and bison. Journal of Range Management 44:100-105.

Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983a. Plant-herbivore interactions in a North American mixed-grass prairie I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1-9.

Coppock, D. L., J. E. Ellis, J. K. Detling, and M. I. Dyer. 1983b. Plant-herbivore interactions in a North American mixed-grass prairie II. Responses of bison to modification of vegetation by prairie dogs. Oecologia 56:10-15.

Cortinas, M. R. and T. R. Seastedt. 1996. Short- and long-term effects of gophers (*Thomomys talpoides*) on soil organic matter dynamics in alpine tundra. Pedobiologia 40:162-170.

Coughenour, M. B., J. K. Detling, I. E. Bamberg, and M. M. Mugambi. 1990. Production and nitrogen responses of the African dwarf shrub *Indigofera spinosa* to defoliation and water limitation. Oecologia 85:546-552.

Day, T. A. and J. K. Detling. 1990. Grassland patch dynamics and herbivore grazing preference following uring deposition. Ecology 71:180-188.

Derner, J. D., J. K. Detling, and M. F. Antolin. 2006. Are livestock weight gains affected by black-tailed prairie dogs? Frontiers in Ecology and the Environment 4:459-464.

Detling, J. K. 2006a. Do prairie dogs compete with livestock? Pages 65-88 *in* J. L. Hoogland (Editor), Conservation of The Black-Tailed Prairie Dog: Saving North America's Western Grasslands. Island Press, Washington D.C.

Detling, J. K. 2006b. Black-tailed prairie dog interactions with other herbivores: mediation via alterations of vegetation. Pages 111-118 *In* J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, (Editors), Recovery of the black-footed ferret – progress and continuing challenges: U. S. Geological Survey Scientific Investigations Report 2005-5293, 288 pp.

Enriquez, S., C. M. Duarte, and K. Sand-Jensen. 1993. Patterns in decomposition rates among photosynthetic organisms: The importance of detritus C:N:P content. Oecologia 94:457-471.

Fahnestock, J. T. and J. K. Detling. 2002. Bison-prairie dog –plant interactions in a North American mixed-grass prairie. Oecologia 132:86-95.

Farrar, J. P. 2002. Effects of prairie dog mound-building and grazing activities on vegetation in the central grasslands. M. S. Thesis, Colorado State University, Fort Collins, Colorado.

Findlay, S., M. Carreiro, V. Krishik, and C. G. Jones. 1996. Effects of damage to living plants on leaf litter quality. Ecological Applications 6:269-275.

Frank, D. A., and P. M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79:2229-2241.

Gholz, H. L., D. A. Wedin, S. M. Smitherman, M. E. Harmon, and W. J. Parton. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: Toward a global model of decomposition. Global Change Biology 6:751-765.

Green, W. P., D. E. Pettry, and R. E. Switzer. 1999. Structure and hydrology of mounds of the imported fire ants in the southeastern United States. Geoderma 93:1-17.

Guenther, D. A. and J. K. Detling. 2003. Observations of cattle use of prairie dog towns. Journal of Range Management 56:410-417.

Gutterman, Y. 1997. Spring and summer daily subsurface temperatures in three microhabitats in a flat natural loess area in the Negev Desert, Israel. Journal of Arid Environments 36:225-235

Hamilton, E. W. and D. A. Frank. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82:2397-2402.

Holland, E. A. and J. K. Detling. 1990. Plant responses to herbivory and belowground nitrogen cycling. Ecology 71:1040-1049.

Hoogland, J. L. 1995. The Black-Tailed Prairie Dog: Social Life of a Burrowing Animal. The University of Chicago Press. Chicago, Illinois.

Hook, P. B. and I. C. Burke. 2000. Biogeochemistry in a shortgrass landscape: control by topography, soil texture, and microclimate. Ecology 81:2686-2703.

Jowkin, V. and J. J. Schoenau. 1998. Impact of tillage and landscape position on nitrogen availability and yield of spring wheat in the Brown soil zone in southwestern Saskatchewan. Canadian Journal of Soil Science 78:563-572.

Kamstra L.D., D.L. Schentzel, J.K. Lewis, and R.L. Elderkin. 1968. Maturity studies with western wheatgrass. Journal of Range Management 21:235-239.

King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contributions from the Laboratory of Vertebrate Biology. No. 67. University of Michigan, Ann Arbor.

Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: An experimental analysis. Ecology 67:760-770.

Lajtha, K., W. M. Jarrell, D. W. Johnson, and P. Sollins. 1999. Collection of soil Solutions. Pages 166-182 *in* G. P. Robertson, D. C. Coleman, C. S. Bledsoe, and P. Sollins, (Editors), Standard soil methods for long-term ecological research. Oxford University Press Inc., New York, New York.

Lauenroth, W. K. and D. G. Milchunas. 1992. Short-grass steppe. Pages 183-226 *in* R. T. Coupland (Editor), Ecosystems of the World 8A. Natural Grasslands. Introduction and Western Hemisphere. Elsevier, New York, New York.

Lauenroth, W. K. and W. C. Whitman. 1971. A rapid method for washing roots. Journal of Range Management 24:308-309.

Liator, M. I., R. Mancinelli, and J. C. Halfpenny. 1996. The influence of pocket gophers on the status of nutrients in Alpine soils. Geoderma 70:37-48.

McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278:1978-1800.

McNaughton, S. J., and J. L. Tarrants. 1983. Grass leaf silification: Natural selection for an inducible defense against herbivores. Proceedings of the National Academy of Science 80:790-791.

Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. Vegetatio 80:11-23.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327-366.

Mun, H. T. and W. G. Whitford. 1990. Factors affecting annual plants assemblages on banner-tailed kangaroo rat mounds. Journal of Arid Environments 18:165–173.

Rhoades, D. F. 1985. Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. American Naturalist 125:205-238.

Ritchie, M. E., D. Tilman, and J. M. H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in Oak savanna. Ecology 79:165-177.

Ruess, R. W. and S. J. McNaughton. 1987. Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. Oikos 49:101-110.

SAS Institute. 1999. SAS version 8.02. SAS Institute, Inc. Cary, North Carolina.

Sheets, R. G., R. L. Linder and R. B. Dahlgren. 1971. Burrow systems of prairie dogs in South Dakota. Journal of Mammalogy 52:451-453.

Sherrod, S. K. and T. R. Seastedt. 2001. Effects of the northern pocket gopher (*Thamomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. Biogeochemistry 55:195-218.

Sirotnak, J. M. and N. J. Huntly. 2000. Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. Ecology 81:78-87.

Stapp, P., M. F. Antolin, and M. Ball. 2004. Patterns of extinction in prairie dog metapopulations: plague outbreaks follow El Niño events. Frontiers in Ecology and the Environment 2:235-240.

Steinauer, E. M. and S. L. Collins. 1995. Effect of urine deposition on small-scale patch structure in prairie vegetation. Ecology 74:1195-1205.

Whicker, A. D. and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. BioScience 38:778-785.

Whitford, W. G. and F. R. Kay. 1999. Biopedturbation by mammals in deserts: a review. Journal of Arid Environments 41:203-230.

Table 4.1 - Mechanisms through which grazing and burrowing can accelerate or decelerate nutrient cycling.

Positive effects on nutrient cycling rates	**Negative effects on nutrient cycling rates**
• **Digestion of plant material in the herbivore gut** (Steinauer and Collins 1995, McNaughton et al. 1997, Bardgett et al. 1998, Frank and Groffman 1998).	• **Loss of nutrients from feces via leaching or volatilization** (Ruess and McNaughton 1987)
• **Increased primary production** (Milchunas and Lauenroth 1993)	• **Decreased primary production** (Milchunas and Lauenroth 1993)
• **Increased root exudation** (Hamilton and Frank 2001, Ayres et al. 2004).	• **Decreased litter quality** (Rhoades 1985, Findlay et al. 1996, Ritchie et al. 1998, Sirotnak and Huntly 2000)
• **Increased litter quality** (Holland and Detling 1990, Hamilton and Frank 2001)	• **Decreased soil temperature** (Gutterman 1997)
• **Increased soil temperature** (Archer and Detling 1986)	• **Decreased infiltration or soil moisture** (Holland and Detling 1990, Mun and Whitford 1990)
• **Increased infiltration or soil moisture** (Whitford and Kay 1999, Archer and Detling 1986)	• **Decreased aeration**
• **Increased aeration** (Green et al. 1999)	

Table 4.2 - Differences between on and off of young (N = 3), old (N = 3), and plague-extirpated (N = 3) prairie dog colonies on the Pawnee National Grassland with respect to standing biomass, nitrogen concentration (%), and standing crop N (g/m^2) for *Bouteloua gracilis* and *Sphaeralcea coccinea*. Biomass was measured at the time of estimated peak standing biomass (late July/earlyAugust). Nitrogen concentrations used were those from samples taken in June when nitrogen concentration was higher than at any other point in the growing season. Data depicted are averages for the two sample years (2003 and 2004). Shading indicates a significant ($P \leq 0.05$) difference between an on- and off-colony pair.

		Bouteloua gracilis			*Sphaeralcea coccinea*		
Colony Type		Biomass (g/m^2)	%N	N (g/m^2)	Biomass (g/m^2)	N (%)	N (g/m^2)
Young	Off	29.61	2.22	0.65	4.80	2.55	0.12
Young	On	10.35	2.55	0.27	3.64	2.90	0.11
	% Change	*- 65 %*	*+ 15 %*	*- 59 %*	*- 24 %*	*+ 14 %*	- 13 %
Old	Off	17.34	2.09	0.35	0.96	2.42	0.02
Old	On	3.96	2.54	0.11	4.64	2.87	0.13
	% Change	*- 77 %*	*+ 21 %*	*- 69 %*	*+ 382 %*	*+ 19 %*	+ 448 %
Plagued	Off	23.29	2.25	0.53	1.03	2.77	0.03
Plagued	On	17.47	2.28	0.40	1.66	2.79	0.05
	% Change	*- 24 %*	*+ 1 %*	*- 25 %*	*+ 60 %*	*+ 0.5 %*	+ 59 %

Table 4.3 - Supply rate (μg/10cm^2/1month) of net nitrogen mineralized on and off of young (N = 3), old (N = 3), and plague-extirpated (N = 3) prairie dog colonies on the Pawnee National Grassland in 2003. There were no significant differences ($P \leq 0.05$) between on- and off-colony pairs for any colony type or date.

		Total N			NO_3^-			NH_4^+		
		X		SE	X		SE	X		SE
June 15 - July 15										
Young	Off colony	68.82	±	18.59	64.24	±	18.69	4.58	±	0.56
	On colony	66.51	±	7.71	63.16	±	8.20	3.36	±	0.80
Old	Off colony	56.91	±	6.48	52.22	±	5.10	4.69	±	1.31
	On colony	63.69	±	12.16	59.22	±	11.08	4.47	±	1.41
Plagued	Off colony	33.12	±	12.01	29.34	±	11.78	3.77	±	0.32
	On colony	41.18	±	5.70	35.39	±	5.03	5.79	±	0.69
July 15 – August 15										
Young	Off colony	315.04	±	23.14	313.66	±	22.70	1.77	±	0.53
	On colony	335.47	±	19.24	331.93	±	19.31	3.53	±	0.08
Old	Off colony	224.53	±	26.12	221.93	±	26.20	2.60	±	0.93
	On colony	248.43	±	47.09	243.30	±	45.90	5.13	±	0.09
Plagued	Off colony	183.70	±	56.52	177.05	±	55.85	6.65	±	1.66
	On colony	195.29	±	20.94	187.09	±	21.74	8.20	±	0.86
August 15 – September 15										
Young	Off colony	215.05	±	27.25	210.86	±	27.69	4.19	±	1.25
	On colony	273.68	±	25.69	269.23	±	24.92	4.46	±	0.81
Old	Off colony	165.15	±	16.91	161.32	±	16.91	3.83	±	0.57
	On colony	149.23	±	18.62	145.93	±	18.67	3.29	±	0.59
Plagued	Off colony	226.44	±	15.02	215.98	±	15.32	10.45	±	10.81
	On colony	218.71	±	16.38	199.81	±	15.17	18.90	±	1.67

Table 4.4 - Supply rate (μg/10cm^2/1month) of net nitrogen mineralized on-colony, on-mounds, and off-colony on young (N = 3), old (N = 3), and plague-extirpated (N = 3) prairie dog colonies on the Pawnee National Grassland in 2004. Within each colony type and date, values with the same superscript letter are not significantly ($P \leq 0.05$) different among sampling positions. For groups with no superscript letters, there were no significant differences among sampling positions.

		Total N		NO_3^-		NH_4^+	
		X	SE	X	SE	X	SE
June 15 - July 15							
Young	Off colony	241.43^{a}	± 63.68	236.49^{a}	± 62.77	4.94	± 1.01
	On colony	270.35^{a}	± 32.94	266.68^{a}	± 33.09	3.67	± 0.76
	On Mound	461.05^{b}	± 14.47	458.61^{b}	± 14.11	2.43	± 0.61
Old	Off colony	214.33^{a}	± 8.39	208.47^{a}	± 7.70	5.86	± 0.69
	On colony	339.81^{b}	± 18.42	332.41^{b}	± 19.42	7.40	± 0.99
	On Mound	400.78^{b}	± 2.46	397.06^{b}	± 1.79	3.72	± 0.66
Plagued	Off colony	227.50^{a}	± 18.84	218.99^{a}	± 21.30	8.51^{a}	± 2.79
	On colony	257.79^{a}	± 41.53	237.95^{a}	± 36.77	19.83^{b}	± 5.72
	On Mound	393.46^{b}	± 59.73	384.74^{b}	± 61.65	8.72^{a}	± 3.44
July 15 – August 15							
Young	Off colony	259.43	± 58.34	250.55	± 59.20	8.87	± 1.33
	On colony	310.42	± 37.82	304.73	± 37.80	5.68	± 0.95
	On Mound	330.29	± 64.33	325.42	± 63.68	4.86	± 1.10
Old	Off colony	192.13	± 10.75	188.30	± 10.91	3.83	± 0.16
	On colony	205.25	± 6.58	200.88	± 7.48	4.37	± 0.91
	On Mound	210.10	± 11.94	206.38	± 10.98	3.72	± 0.96
Plagued	Off colony	221.93	± 5.68	212.43	± 4.78	9.50	± 0.95
	On colony	119.93	± 24.42	109.31	± 27.24	10.61	± 2.78
	On Mound	217.01	± 96.25	211.11	± 95.83	5.98	± 0.58
August 15 – September 15							
Young	Off colony	157.79	± 15.05	153.43	± 15.15	4.36	± 0.86
	On colony	189.27	± 6.14	186.41	± 5.74	2.86	± 0.41
	On Mound	264.19	± 8.41	262.52	± 8.05	1.67	± 0.42
Old	Off colony	139.42	± 4.54	136.02	± 2.86	3.40	± 1.70
	On colony	113.93	± 0.30	112.47	± 0.66	1.46	± 0.19
	On Mound	176.81	± 29.17	175.46	± 29.19	1.35	± 0.01
Plagued	Off colony	258.44	± 20.19	251.94	± 21.19	6.49	± 0.93
	On colony	272.43	± 53.20	267.20	± 52.11	5.22	± 1.98
	On Mound	265.10	± 62.31	259.60	± 62.63	5.41	± 0.82

Table 4.5. Effects of prairie dogs (± 1 SE) on soil characteristics (to 20 cm depth) for three sample positions (Off, On, Mound) and for three colony types (Young, Old, Plague-extirpated) on the Pawnee National Grassland in 2004. Within each colony type, values with the same superscript letter are not significantly ($P \leq 0.05$) different among sampling positions. For groups with no superscript letters, there were no significant differences among sampling positions.

	Total N (g/m^2)			Fine N (g/m^2)			Coarse N (g/m^2)			MOAN (g/m^2)		
Young												
Off colony	213	±	15	52	±	5	11.0	±	1.5	151	±	10
On colony	232	±	13	51	±	1	10.6	±	0.6	170	±	13
On Mound	218	±	14	50	±	1	10.7	±	1.2	157	±	16
Old												
Off colony	303	±	13	48	±	2	12.9^{a}	±	1.5	242	±	17
On colony	269	±	1	47	±	3	9.8^{ab}	±	0.3	212	±	02
On Mound	276	±	15	40	±	2	8.9^{b}	±	0.6	227	±	17
Plagued												
Off colony	192	±	12	36	±	2	9.3^{a}	±	0.9	147	±	11
On colony	214	±	28	44	±	3	12.3^{b}	±	0.7	158	±	29
On Mound	212	±	12	43	±	6	10.8^{a}	±	0.2	158	±	9
	Total POM C (g/m^2)			**Fine POM C (g/m^2)**			**Coarse POM C (g/m^2)**			**MOAC (g/m^2)**		
Young												
Off colony	2108	±	115	559	±	13	212	±	33	1337	±	81
On colony	2218	±	93	554	±	18	219	±	16	1446	±	106
On Mound	2068	±	105	558	±	33	199	±	18	1312	±	98
Old												
Off colony	3005^{a}	±	83	622^{a}	±	74	242^{a}	±	23	2141	±	13
On colony	2452^{b}	±	109	511^{ab}	±	70	163^{b}	±	12	1778	±	28
On Mound	2502^{b}	±	28	479^{b}	±	51	148^{b}	±	11	1875	±	68
Plagued												
Off colony	1842	±	140	533	±	47	209	±	16	1101	±	90
On colony	2017	±	139	542	±	3	233	±	9	1242	±	138
On Mound	2058	±	95	605	±	48	193	±	14	1260	±	34
	% Sand			**% Silt**			**% Clay**			**Bulk Density**		
	X		SE	X		SE	X		SE	X		SE
Young												
Off colony	70.7	±	3.4	13.0	±	2.3	16.3	±	1.0	1.18	±	0.07
On colony	65.9	±	1.3	14.7	±	1.3	19.4	±	0.2	1.16	±	0.01
On Mound	66.8	±	0.6	14.0	±	0.9	19.2	±	0.6	1.18	±	0.06
Old												
Off colony	48.0	±	0.3	24.5	±	1.8	27.5^{a}	±	1.5	1.05	±	0.01
On colony	48.7	±	0.1	27.9	±	0.3	23.4^{ab}	±	0.2	1.07	±	0.01
On Mound	48.5	±	0.3	28.9	±	1.4	22.5^{b}	±	0.2	1.17	±	0.01
Plagued												
Off colony	67.2	±	2.7	11.6	±	1.7	21.2^{a}	±	1.3	1.11	±	0.10
On colony	69.5	±	2.5	14.2	±	1.8	16.4^{b}	±	1.2	1.17	±	0.12
On Mound	70.7	±	1.7	13.0	±	1.5	16.3^{b}	±	1.0	1.29	±	0.06

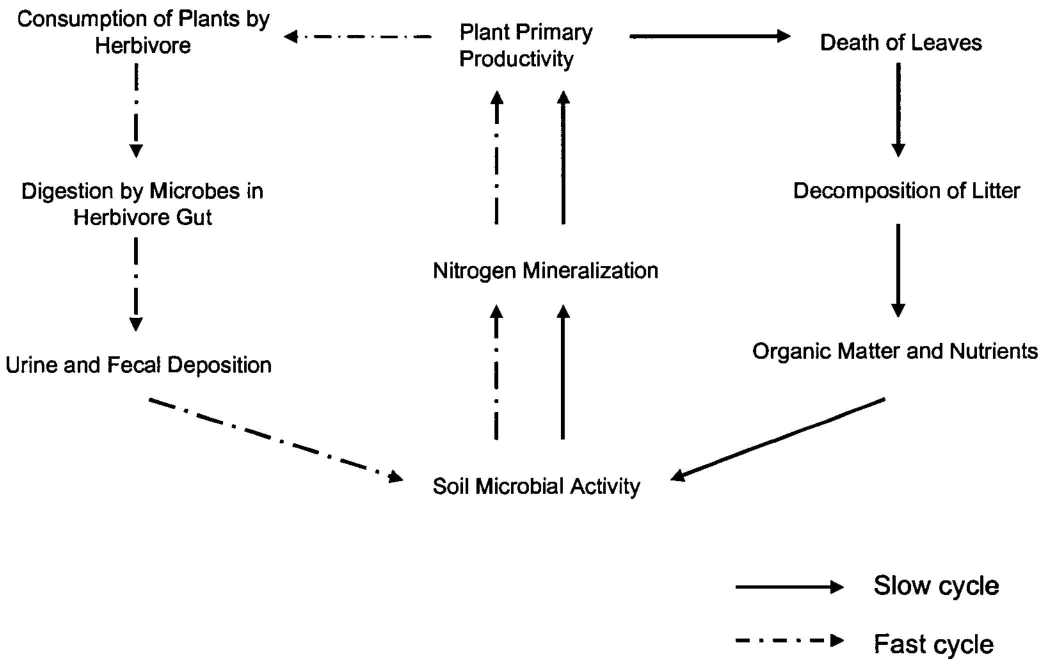

Figure 4.1 - Conceptual diagram of the slow and fast cycles of nutrient cycling. Modified from Bakker et al. (2004).

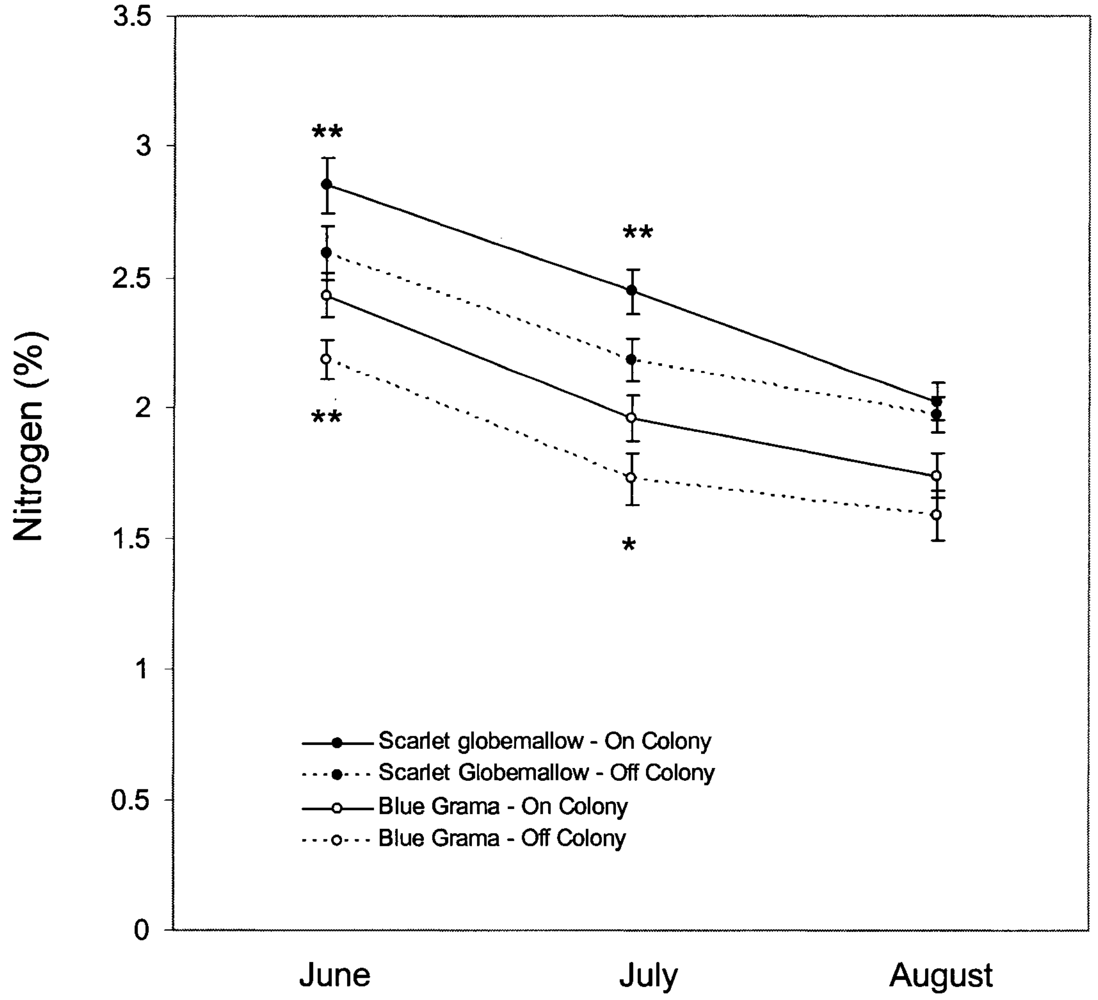

Figure 4.2 - Mean monthly nitrogen concentration (%) in shoots of scarlet globemallow (*Sphaeralcea coccinea*) and blue grama (*Bouteloua gracilis*) on versus off prairie dog colonies on the Pawnee National Grassland averaged over both years (2003 and 2004). N = 9 in 2003 and N = 8 in 2004. Asterisks indicate a significant difference between on and off colony for a specific month and species ("*" denotes $P \leq 0.05$, "**" denotes $P \leq 0.01$).

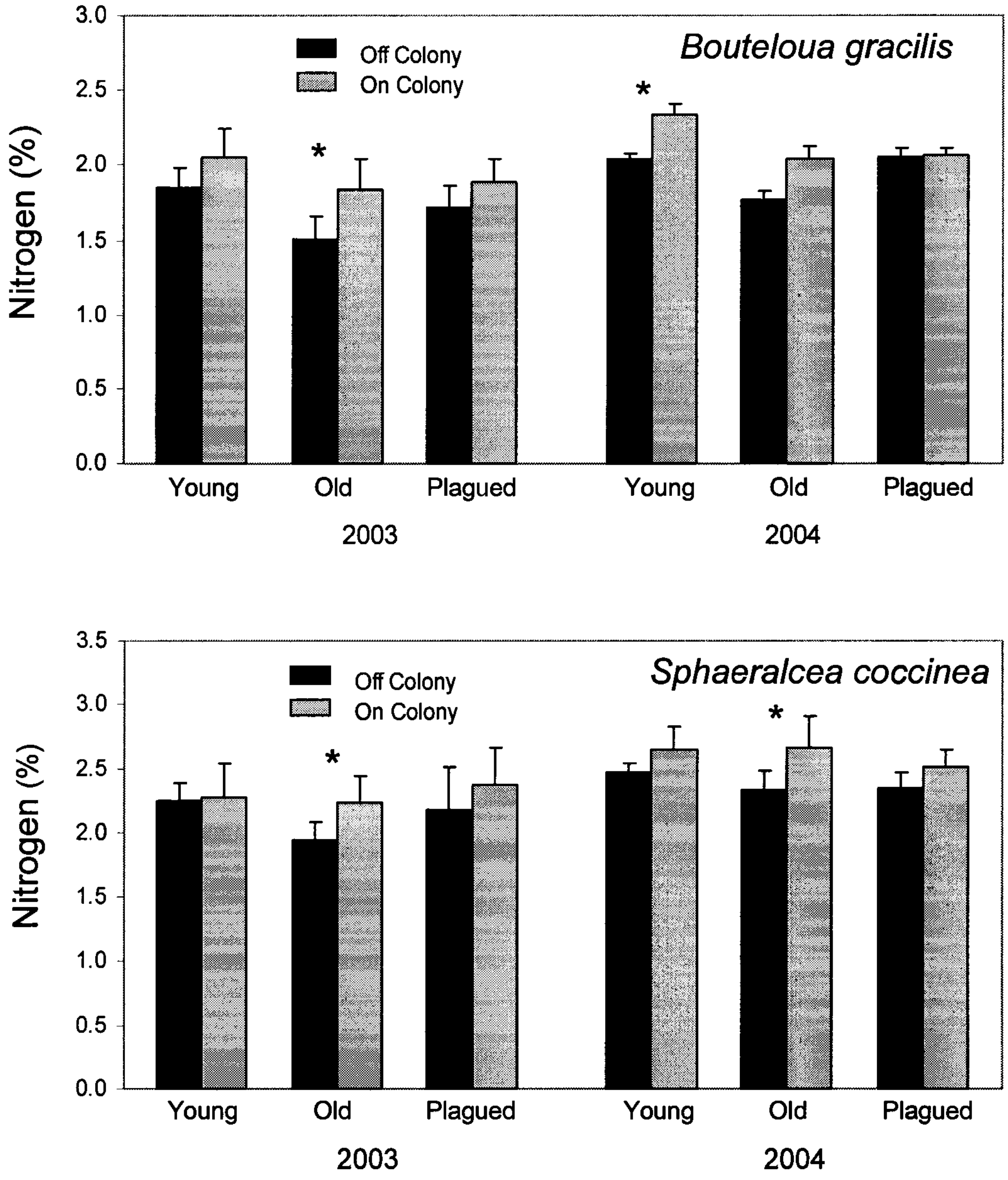

Figure 4.3 - Mean monthly nitrogen concentration in shoots on versus off of prairie dog colonies on the Pawnee National Grassland presented by type. N = 3 for all pairs except for Old colonies in 2004 for which N = 2. Asterisks (*) indicate a significant ($P \leq 0.05$) difference between an on- and off-colony pair.

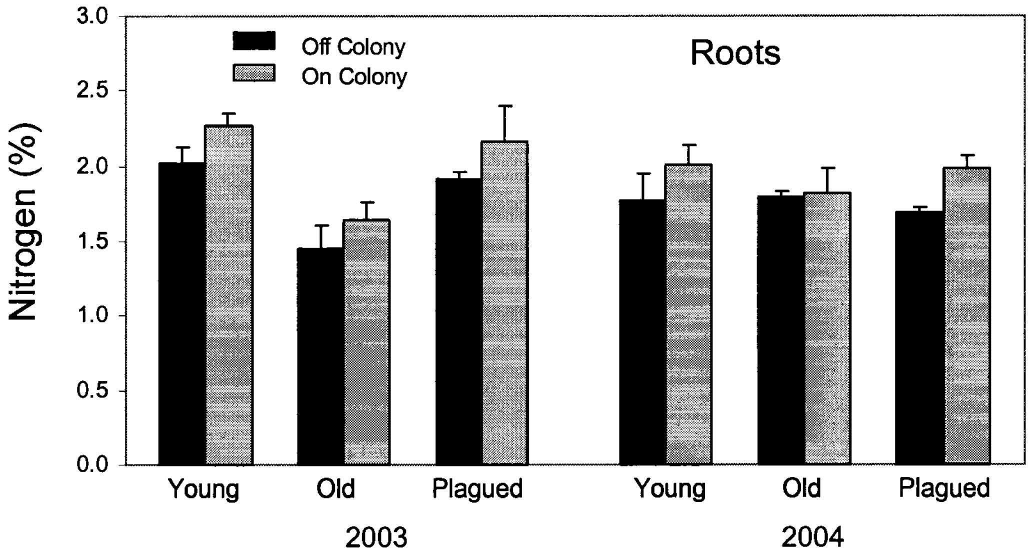

Figure 4.4 - Mean nitrogen concentration in roots on versus off of prairie dog colonies on the Pawnee National Grassland colonies presented by type. N = 3 for all pairs except for Old colonies in 2004 for which N = 2. The lack of asterisks indicates that there were no significant ($P \leq 0.05$) differences between an on- and off-colony pair.

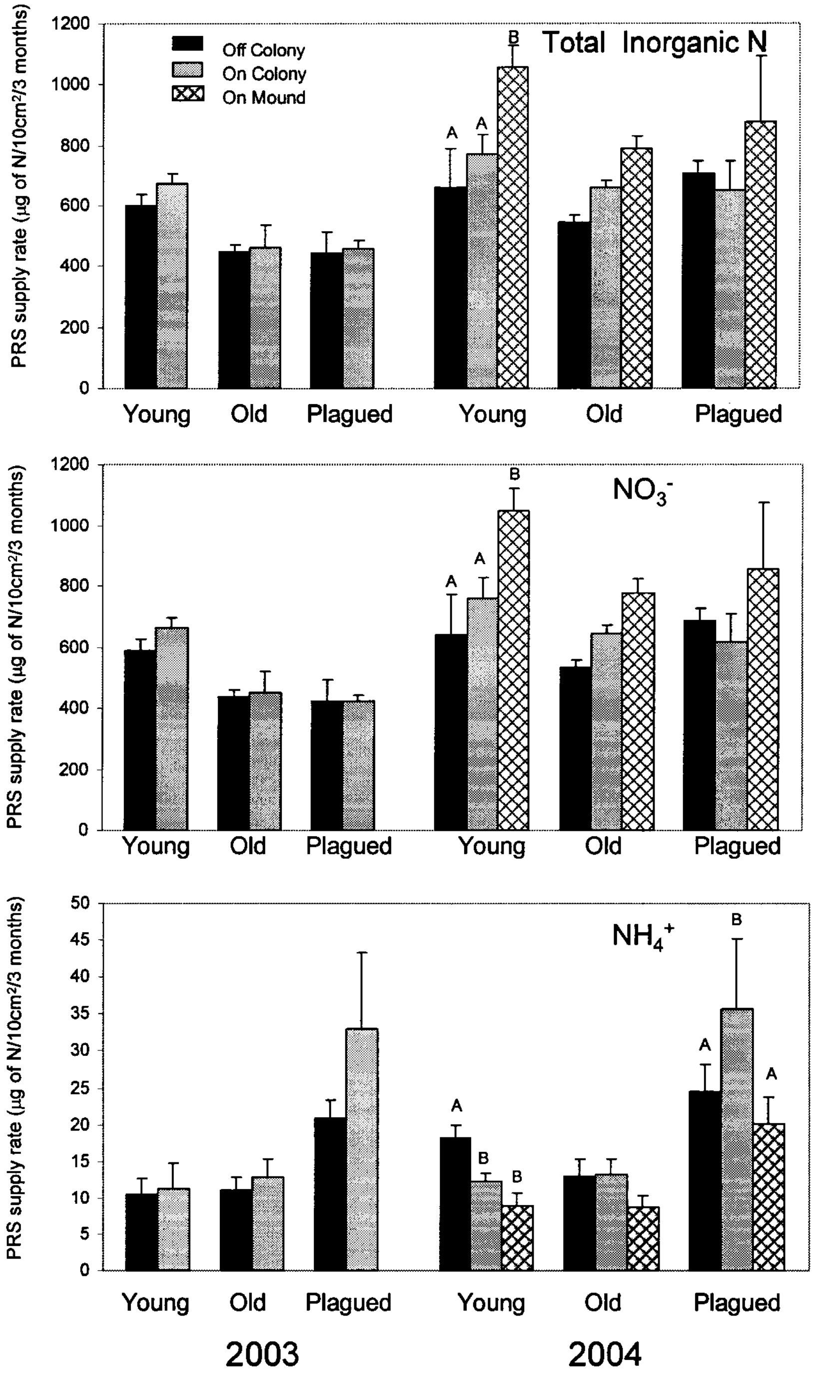

Figure 4.4 - Supply rate (µg/10cm^2/3months) of net N mineralized on-colony, on- mound, and off-colony for prairie dog colonies on the Pawnee National Grassland. Within each colony type and date, values with the same superscript letter are not significantly ($P \leq 0.05$) different among sampling positions. For groups with no superscript letters, there were no significant differences among sampling positions. N = 3 for all pairs except for Old colonies in 2004 for which N = 2.

APPENDIX A

Table A-1. Mean cover (%) of plant species on and off of prairie dog colonies on the Pawnee National Grassland in June and August of 2002 presented by type (young, old, plagued).

Graminoid Taxa	Month	Young		Old		Plagued	
		Off	On	Off	On	Off	On
Crested wheatgrass (*Agropyron cristatum*)	June	---	0.01	---	---	---	---
	August	---	---	---	---	---	---
Western wheatgrass (*Agropyron smithii*)	June	1.25	0.29	3.15	1.53	1.61	0.31
	August	0.20	0.33	0.21	0.25	0.16	0.28
Red threeawn (*Aristida purpurea*)	June	2.97	1.81	4.44	10.15	2.57	4.23
	August	3.20	2.17	0.68	6.80	2.04	3.80
Blue grama (*Bouteloua gracilis*)	June	23.69	15.65	12.45	4.32	36.05	28.43
	August	17.87	12.44	19.39	3.63	38.91	25.59
Buffalo grass (*Buchloe dactyloides*)	June	15.09	9.25	19.11	14.95	7.64	10.20
	August	12.53	7.33	10.75	9.73	9.44	14.28
Needleleaf sedge (*Carex eleocharis*)	June	1.17	0.71	4.81	0.25	0.87	0.41
	August	0.56	0.19	2.13	0.04	0.96	0.59
Inland saltgrass (*Distichlis spicata*)	June	---	0.27	---	---	---	---
	August	---	0.20	---	---	---	---
Ring muhly (*Muhlenbergia torreyi*)	June	---	---	---	0.73	---	0.73
	August	---	---	0.05	---	---	1.13
Tumblegrass (*Schedonnardis paniculatus*)	June	---	---	---	0.43	---	---
	August	---	---	---	---	---	0.03
Bottlebrush squirreltail (*Sitanion hystrix*)	June	0.51	---	0.16	0.40	0.13	0.23
	August	0.20	0.07	---	---	0.17	---
Sand dropseed (*Sporobolus cryptandrus*)	June	1.00	0.05	2.20	0.44	0.95	0.15
	August	0.40	---	0.01	0.00	0.31	0.17
Needle and thread (*Stipa comata*)	June	0.07	0.07	0.21	---	---	---
	August	0.63	---	---	---	---	0.04
Sixweeks fescue (*Vulpia octoflora*)	June	---	---	---	---	---	---
	August	0.08	0.04	0.40	0.13	0.01	0.37
Unidentified spp.	June	---	---	---	---	---	---
	August	0.80	1.04	6.31	0.84	---	---

Forb Taxa	Month	Young		Old		Plagued	
		Off	On	Off	On	Off	On
Milkvetch (*Astragalus spp.*)	June	---	---	---	0.01	0.19	---
	August	---	---	---	---	0.09	---
Hairy goldenaster (*Chrysopsis villosa*)	June	0.03	---	---	0.07	---	---
	August	0.05	0.05	0.03	0.04	---	---
Wavyleaf thistle (*Cirsium undulatum*)	June	---	0.01	0.03	---	---	---
	August	---	---	---	---	---	---
Scarlet gaura (*Gaura coccinea*)	June	0.03	0.01	---	---	---	---
	August	---	0.01	0.01	---	---	---
Curlycup gumweed (*Grindelia squarrosa*)	June	---	---	---	---	---	---
	August	0.01	0.08	---	---	---	---
Ironplant tansyaster (*Haplopappus spinulosus*)	June	---	---	---	---	---	---
	August	0.01	---	---	0.01	---	---
Prairie sunflower (*Helianthus petiolaris*)	June	---	---	---	---	---	---
	August	---	---	---	---	0.01	---
Prairie pepperweed (*Lepidium densiflorum*)	June	0.17	0.08	0.20	0.07	0.93	0.89
	August	0.08	0.00	0.01	0.00	0.00	0.00
Mountain lily (*Leucocrinum montanum*)	June	---	---	---	---	---	---
	August	---	---	---	---	---	---
Narrowleaf gromwell (*Lithosperma incisum*)	June	0.07	---	0.01	0.05	---	---
	August	---	---	---	---	---	---
Rush skeletonweed (*Lygodesmia juncea*)	June	---	---	0.03	0.04	---	0.03
	August	0.01	0.01	---	---	---	---
Tansyleaf aster (*Machaeranthea tanacetitofolia*)	June	0.08	0.04	0.08	0.01	---	---
	August	0.00	0.00	---	---	---	---
Linearleaved four-o'clock (*Mirabilis linearis*)	June	---	0.01	---	---	0.02	---
	August	0.01	0.01	0.01	0.01	0.01	0.09
Purple broomrape (*Orobanche fasciculata*)	June	---	---	---	0.04	---	---
	August	---	---	---	---	---	---
Plains bahia (*Picradeniopsis oppositifolia*)	June	0.03	0.03	---	---	0.03	0.05
	August	---	0.03	---	---	0.05	0.08
Common purslane (*Portulaca oleracea*)	June	---	---	0.01	0.08	---	---
	August	---	0.05	---	0.01	---	0.07
Wooly plantain (*Plantago patagonica*)	June	---	---	---	0.01	---	0.09
	August	---	---	---	---	---	---

Slimflower scurfpea (*Psoralea tenuiflora*)	June	---	---	0.03	---	---	0.03
	August	0.04	---	0.00	0.01	---	---
Russian thistle (*Salsola iberica*)	June	0.01	---	---	---	---	---
	August	---	---	---	---	---	---
Prairie groundsel (*Sencecio tridenticulatus*)	June	---	0.03	---	0.07	---	0.01
	August	---	---	---	---	---	---
Scarlet globemallow (*Sphaeralcea coccinea*)	June	0.53	0.76	0.20	1.13	1.27	1.01
	August	0.51	0.89	0.12	0.87	0.35	0.64
Prairie fameflower (*Talinum parviflorum*)	June	0.07	0.05	0.01	0.04	0.20	0.19
	August	---	---	---	---	0.21	0.17
Prairie spiderwort (*Tradescantia occidentalis*)	June	0.12	---	---	---	---	---
	August	---	---	---	---	---	---
Unidentified spp.	June	---	0.01	---	---	---	---
	August	---	0.01	0.01	0.03	---	---

Shrub Taxa	Month	Young		Old		Plagued	
		Off	On	Off	On	Off	On
Fringed sagewort (*Artemisia frigida*)	June	---	---	1.41	3.71	---	---
	August	0.01	---	0.41	2.11	---	---
Fourwing saltbush (*Atriplex canescens*)	June	---	---	---	---	0.93	---
	August	---	---	0.03	---	0.27	0.16
Douglas rabbitbrush (*Chrysothamnus viscidiflorus*)	June	0.20	---	---	---	---	0.13
	August	---	---	---	---	0.13	0.80
Spreading buckwheat (*Erioginum effusum*)	June	---	---	---	---	---	---
	August	---	---	---	---	0.01	---
Broom snakeweed (*Gutierrezia sarothrae*)	June	0.67	0.27	0.59	0.20	0.01	---
	August	2.01	0.53	---	0.01	0.61	---

Cactus Taxa	Month	Young		Old		Plagued	
		Off	On	Off	On	Off	On
Purple mammalaria (*Coryphantha vivipara*)	June	---	0.03	---	0.09	---	---
	August	---	---	---	0.13	---	---
Hedgehog cactus (*Echinocereus viridiflorus*)	June	---	0.08	---	---	---	---
	August	---	0.01	---	0.03	---	---
Plains prickly pear (*Opuntia polyacantha*)	June	0.96	2.09	0.91	0.20	3.23	1.20
	August	3.15	1.55	4.20	0.07	5.51	1.41

APPENDIX A

Table A-2. Mean cover (%) of plant species on and off of prairie dog colonies in June and August of 2003 presented by type (young, old, plagued).

Graminoid Taxa	Month	Young		Old		Plagued	
		Off	On	Off	On	Off	On
Crested wheatgrass (*Agropyron cristatum*)	June	0.16	---	0.19	---	---	---
	August	0.47	---	0.23	---	---	---
Western wheatgrass (*Agropyron smithii*)	June	0.59	1.12	1.43	4.23	0.28	0.32
	August	0.15	0.95	0.76	2.07	1.11	---
Red threeawn (*Aristida purpurea*)	June	---	2.04	0.12	3.84	0.60	3.40
	August	0.91	2.39	0.43	3.59	1.03	1.56
Blue grama (*Bouteloua gracilis*)	June	16.05	11.33	14.73	2.51	34.41	20.45
	August	26.24	17.76	21.23	6.63	35.85	32.45
Buffalo grass (*Buchloe dactyloides*)	June	12.03	9.05	10.01	7.09	11.47	11.52
	August	6.48	13.77	13.79	12.29	17.45	6.23
Needleleaf sedge (*Carex eleocharis*)	June	2.37	0.20	2.88	0.44	0.64	0.71
	August	1.44	0.16	1.75	0.84	2.40	2.81
Inland saltgrass (*Distichlis spicata*)	June	---	1.13	---	---	---	---
	August	---	---	---	---	---	---
Ring muhly (*Muhlenbergia torreyi*)	June	---	---	---	---	0.16	0.47
	August	---	---	---	---	---	0.01
Tumblegrass (*Schedonnardis paniculatus*)	June	---	---	---	---	---	---
	August	---	---	---	0.13	---	---
Bottlebrush squirreltail (*Sitanion hystrix*)	June	0.07	---	0.05	---	---	0.27
	August	0.05	---	---	---	---	---
Sand dropseed (*Sporobolus cryptandrus*)	June	0.33	0.28	0.32	0.36	0.29	0.47
	August	---	---	0.04	---	---	---
Needle and thread (*Stipa comata*)	June	0.05	---	---	---	---	---
	August	0.11	0.20	---	---	---	---
Sixweeks fescue (*Vulpia octoflora*)	June	2.84	0.63	4.28	1.23	0.16	0.76
	August	2.49	0.11	5.35	0.07	0.16	0.25
Unidentified spp.	June	---	---	---	---	---	---
	August	---	---	---	---	---	---

Forb Taxa	Month	Young		Old		Plagued	
		Off	On	Off	On	Off	On
Prairie onion (*Allium textile*)	June	0.03	---	0.13	---	---	---
	August	---	---	---	---	---	---
Milkvetch (*Astragalus spp.)*	June	0.05	0.05	0.75	---	0.21	---
	August	---	---	0.08	---	0.28	---
Lambsquarters (*Chenopodium album*)	June	0.51	0.05	0.29	0.12	0.71	0.49
	August	0.04	0.03	---	---	0.13	0.15
Ragleaf goosefoot (*Chenopodium incanum*)	June	0.01	0.03	---	---	---	---
	August	---	0.01	---	---	0.04	0.17
Narrowleaf goosefoot (*Chenopodium leptophyllum*)	June	0.15	---	0.61	0.03	0.04	0.01
	August	0.05	0.04	0.37	---	0.07	0.13
Hairy goldenaster (*Chrysopsis villosa*)	June	0.01	---	0.04	0.08	---	---
	August	0.03	0.07	---	0.53	0.01	---
Wavyleaf thistle (*Cirsium undulatum*)	June	---	---	---	0.05	---	---
	August	---	---	---	---	---	---
Horseweed (*Conyza candensis*)	June	---	---	---	---	---	---
	August	---	---	---	0.04	---	---
James cryptantha (*Cryptantha jamesii*)	June	---	---	---	---	---	---
	August	---	0.01	---	---	---	0.43
Plains cryptantha (*Cryptantha minima*)	June	---	0.31	---	0.60	---	---
	August	0.07	0.29	---	0.27	---	---
Western wallflower (*Erysimum asperum*)	June	---	---	0.08	0.04	---	---
	August	---	---	---	---	---	---
Ridgeseed euphorbia (*Euphorbia glyptosperma*)	June	---	---	---	---	---	---
	August	---	0.01	---	---	---	---
Scarlet gaura (*Gaura coccinea*)	June	---	---	0.04	0.01	0.01	---
	August	---	---	---	---	---	---
Curlycup gumweed (*Grindelia squarrosa*)	June	0.24	0.51	0.01	---	0.01	---
	August	0.03	0.03	0.03	---	0.04	---
Ironplant tansyaster (*Haplopappus spinulosus*)	June	0.01	---	---	---	---	---
	August	0.03	---	---	---	---	0.09
Looseflowered gilia (*Ipomopsis laxiflora*)	June	---	---	---	---	---	---
	August	---	0.01	0.08	---	0.01	---
Iran summer cyperus (*Kochia scoparia*)	June	---	---	---	---	0.01	---
	August	---	---	---	---	0.01	---

Blueburr stickseed (*Lappula redowskii*)	June	0.29	1.73	1.29	2.97	0.03	1.43
	August	0.01	---	---	---	0.01	0.03
Prairie pepperweed (*Lepdium densiflorum*)	June	0.17	0.51	0.04	0.49	0.43	0.35
	August	0.12	0.37	0.09	0.11	0.23	0.21
Mountain lily (*Leucocrinum montanum*)	June	0.03	---	0.01	---	0.03	---
	August	---	---	---	---	0.01	---
Narrowleaf gromwell (*Lithosperma incisum*)	June	---	---	---	---	---	0.04
	August	---	0.07	0.01	0.03	0.01	0.08
Rush skeletonweed (*Lygodesmia juncea*)	June	---	---	0.04	0.05	---	0.01
	August	---	0.04	0.19	0.04	0.03	----
Tansyleaf aster (*Machaeranthea tanacetitofolia*)	June	---	0.04	---	0.27	0.01	---
	August	0.07	0.21	---	---	0.01	---
Linearleaved four-o'clock (*Mirabilis linearis*)	June	---	---	0.01	0.01	---	---
	August	---	---	---	---	0.01	---
Large tongue evening primrose (*Oenothera caespitosa*)	June	---	---	---	---	---	---
	August	---	---	---	---	0.01	---
Coronopsus evening primrose (*Oenothera coronopifolia*)	June	0.07	---	---	---	---	---
	August	---	---	---	---	0.01	---
Evening primrose (*Oenotohera* spp.)	June	0.33	---	0.01	0.05	0.08	0.12
	August	---	0.03	0.01	---	0.01	0.01
Purple broomrape (*Orobanche fasciculata*)	June	---	---	---	0.01	---	---
	August	---	---	---	---	0.01	0.01
Lambert loco (*Oxytropis lambertii*)	June	---	---	---	---	---	---
	August	---	---	---	---	0.01	0.01
Plains bahia (*Picradeniopsis oppositifolia*)	June	0.03	0.51	---	0.13	0.08	0.05
	August	0.01	0.37	0.03	---	0.01	0.01
Common purslane (*Portulaca oleracea*)	June	---	0.21	0.03	1.32	---	0.13
	August	0.08	0.39	0.07	2.76	0.01	---
Wooly plantain (*Plantago patagonica*)	June	0.12	0.35	0.68	2.57	0.04	0.80
	August	0.03	0.19	0.13	0.79	0.08	0.57
Slimflower scurfpea (*Psoralea tenuiflora*)	June	0.13	0.01	0.03	0.03	---	0.05
	August	---	---	---	---	0.01	---
Russian thistle (*Salsola iberica*)	June	0.07	0.15	---	---	---	0.03
	August	0.05	0.11	0.12	0.03	0.01	---
Prairie groundsel (*Sencecio tridenticulatus*)	June	---	0.04	---	0.03	---	0.03
	August	---	0.09	0.01	0.28	0.01	---

Silky sophora (*Sophora nuttalliana*)	June	---	---	---	---	---	---
	August	---	---	---	0.01	0.01	---
Scarlet globemallow (*Sphaeralcea coccinea*)	June	2.64	4.24	1.52	6.24	0.95	1.48
	August	0.93	2.44	0.48	2.49	0.52	0.81
Prairie fameflower (*Talinum parviflorum*)	June	0.03	0.08	---	0.05	0.32	0.21
	August	0.05	0.04	---	0.03	0.09	0.01
Theadleaf greenthread (*Thelesperma filifolium*)	June	---	---	---	---	0.01	---
	August	---	---	---	---	0.01	---
Rayless greenthread (*Thelesperma megapotamicum*)	June	---	---	---	---	---	---
	August	---	---	---	---	0.01	---
Prairie spiderwort (*Tradescantia occidentalis*)	June	0.01	0.08	---	0.04	---	---
	August	---	---	---	---	0.01	---
Bigbract verbena (*Verbena bracteata*)	June	---	---	---	---	---	---
	August	---	0.85	---	1.53	0.01	---

Shrub Taxa	Month	Young		Old		Plagued	
		Off	On	Off	On	Off	On
Fringed sagewort (*Artemisia frigida*)	June	---	---	0.85	3.01	---	---
	August	---	---	0.76	3.15	---	---
Fourwing saltbush (*Atriplex canescens*)	June	---	---	0.67	---	0.16	---
	August	---	---	---	---	0.07	---

Douglas rabbitbrush (*Chrysothamnus viscidiflorus*)	June	---	---	---	---	---	---
	August	---	---	---	---	0.03	0.13
Spreading buckwheat (*Erioginum effusum*)	June	0.07	---	---	---	---	---
	August	0.27	---	---	0.07	---	---
Broom snakeweed (*Gutierrezia sarothrae*)	June	0.35	0.15	---	---	---	---
	August	0.05	0.45	---	0.01	---	---

Cactus Taxa	Month	Young		Old		Plagued	
		Off	On	Off	On	Off	On
Purple mammalaria (*Coryphantha vivipara*)	June	---	---	---	---	---	---
	August	---	---	0.04	---	---	---
Hedgehog cactus (*Echinocereus viridiflorus*)	June	---	---	0.01	---	---	---
	August	---	---	---	---	---	---
Flat prickly pear (*Opuntia compressa*)	June	0.20	---	---	0.20	---	0.03
	August	---	---	---	---	---	---
Plains prickly pear (*Opuntia polyacantha*)	June	3.45	1.92	3.01	---	4.84	0.91
	August	0.35	0.96	2.20	0.27	1.44	0.97

APPENDIX B

Table B-1. Species identified on prairie dog colonies and adjacent off-colony sites on the Pawnee National Grassland in 2002 and 2003.

Species	Common Name	On	Off
Graminoid Taxa			
Agropyron cristatum	Crested wheatgrass	X	X
Agropyron smithii	Western wheatgrass	X	X
Aristida purpurea	Red threeawn	X	X
Bouteoula gracilis	Blue grama	X	X
Buchloe dactyloides	Buffalo grass	X	X
Carex elecharis	Needleleaf sedge	X	X
Distichlis spicata	Inland saltgrass	X	X
Elymus elymoides	Bottlebrush squirreltail	X	X
Muhlenbergia asperifolia	Scratchgrass	X	
Muhlenbergia squarrosa	False buffalograss	X	X
Muhlenbergia torreyi	Ring muhly	X	X
Schedonnardis paniculatus	Tumblegrass	X	X
Sporobolus cryptandrus	Sand dropseed	X	X
Stipa comata	Needle and thread	X	X
Vulpia octoflora	Sixweeks fescue	X	X
Shrub Taxa			
Artemisia frigida	Fringed sagewort	X	X
Atriplex canescens	Fourwing saltbush	X	X
Ceratoides lanata	Common winter fat	X	X
Chrysothamnus viscidiflorus	Douglas rabbitbrush	X	X
Erioginum effusum	Spreading buckwheat	X	X
Gutierrezia sarothrae	Broom snakeweed	X	X
Cactus Taxa			
Coryphantha vivipara	Purple mammalaria	X	X

Echinocereus viridiflorus	Hedgehog cactus	X	X
Opuntia compressa	Flat prickly pear	X	X
Opuntia polyacantha	Plains prickly pear	X	X
Forb Taxa			
Allium textile	Prairie onion	X	X
Amaranthus spp.	Pigweed	X	
Argemone polyanthemos	Crested pricklypoppy	X	
Artemesia dracunculus	Tarragon sagewort	X	
Astragulus missouriensis	Missouri astragulus	X	X
Astragalus spp.	Milkvetch	X	X
Chenopodium album	Lambsquarters	X	X
Chenopodium incanum	Ragleaf goosefoot	X	X
Chenopodium leptophyllum	Narrowleaf goosefoot	X	X
Chrysopsis villosa	Hairy goldenaster	X	X
Cirsium arvense	Canadian thistle	X	X
Cirsium undulatum	Wavyleaf thistle	X	X
Cirsium spp.	Cirsium spp.	X	X
Cleome serrulata	Rocky mountain beeplant	X	X
Conyza candensis	Horseweed	X	X
Cryptantha jamesii	James cryptantha	X	X
Cryptantha minima	Plains cryptantha	X	X
Dyssodia papposa	Fetid marigold	X	
Erigeron pumilus	Shaggy fleabane	X	X
Erysimum asperum	Western wallflower	X	X
Euphorbia glyptosperma	Ridgeseed	X	X
Evolvulus nuttallianus	Nuttal's evolvulus	X	X
Grindelia squarrosa	Curlycup gumweed	X	X

Gaura coccinea	Scarlet gaura	X	X
Haplopappus spinulosus	Ironplant tansyaster	X	X
Helianthus annuus	Helianthus annuus	X	
Hedeoma hispidum	Hedeoma hispidum,	X	X
Helianthus spp.	Helianthus spp.	X	X
Ipomopsis laxiflora)	Looseflowered gilia	X	X
Kochia scoparia	Iran summer cyperus	X	X
Lappula redowskii	Blueburr stickseed	X	X
Lepdium densiflorum	Prairie pepperweed	X	X
Lesquerella ludoviciana	Lesquerella ludoviciana	X	
Leucocrinum montanum	Mountain lily	X	X
Lithosperma incisum	Narrowleaf gromwell	X	X
Linum rigidum	Stiffstem flax	X	X
Lygodesmia juncea	Rush skeletonweed	X	X
Machaeranthea tanacetitofolia	Tansyleaf aster	X	X
Mirabilis linearis	Linearleaved four-o'clock	X	X
Oenothera caespitosa	Large tongue evening primrose		X
Oenothera coronopifolia	Coronopsus evening primrose	X	X
Oenotohera spp.	Evening primrose	X	X
Orobanche fasciculata	Purple broomrape	X	X
Oxytropis lambertii	Lambert loco	X	X
Oxytropis spp.	Oxytropis spp.	X	
Penstemon albidus	White penstemon	X	X
Penstemon spp.	Penstemon spp.	X	
Picradeniopsis oppositifolia	Plains bahia	X	X
Plantago patagonica	Wooly plantain	X	X
Polygonum aviculare	Prostrate knotweed	X	

Portulaca oleracea	Common purslane	X	X
Psoralea tenuiflora	Slimflower scurfpea	X	X
Ratibida columnifera	Upright prairie coneflower	X	
Rumex venosus	Veiny dock	X	
Salsola iberica	Russian thistle	X	X
Sencecio tridenticulatus	Prairie groundsel	X	X
Solanum triflorum	Cutleaf nightshade	X	X
Sophora nuttalliana	Silky sophora	X	X
Sphaeralcea coccinea	Scarlet globemallow	X	X
Talinum parviflorum	Prairie fameflower	X	X
Thelesperma filifolium	Theadleaf greenthread	X	X
Thelesperma megapotamicus	Rayless greenthread		X
Townsendia grandiflora	Townsendia grandiflora		X
Tradescantia occidentalis	Prairie spiderwort	X	X
Tragopogon dubius	Yellow salsify		X
Tripterocalyx micranthus	Winged fruited sandverbena	X	
Verbena bracteata	Bigbract verbena	X	X
Unidentified spp.	Unidentified spp.	X	X