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COLORADO STATE UNIVERSITY

Ecological Evaluation of the Abundance and Effects of Elk Herbivory in Rocky Mountain National Park, Colorado, 1994–1999

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Introduction

Scientific Input and Study Design

Several National Park Service units in the Intermountain region possess a number of closely related management needs relative to the abundance of wild ungulates and their herbivory effects on plants and ecosystem processes. In 1993, the then National Biological Service (NBS) – now U.S. Geological Survey, Biological Resources Discipline (USGS, BRD) – initiated a series of research studies in four park units in the Intermountain West, into the abundance and effects of ungulates on park ecosystems. Each of these parks received a number of similar research study elements including: (a) a number of new ungulate grazing exclosures ($n = 12–21$ exclosures per park); (b) aerial survey sightability models to estimate population sizes of ungulates; (c) measures of biomass production and consumption rates near the exclosures and across the landscape; (d) studies of the effects of the grazing on plant abundance, species diversity, and ecosystem effects; and (e) computer model simulations (SAVANNA) of the effects on the ecosystem and plant resources of different ungulate management scenarios. One park unit, Rocky Mountain National Park, Colorado, received funding from the U.S. Geological Survey (USGS, BRD) and parallel funding from NPS for an intensive research study of the effects of elk on the park ecosystems.

Elk were extirpated, or nearly so, from Rocky Mountain National Park by human exploitation in the late 1800s, but were then reintroduced in 1913 and 1914. Elk steadily increased until they reached an estimated 1,000 animals within the park boundaries in 1944 (Packard 1947). Due to concerns over increasing elk numbers and potential effects on the park winter range, elk in the park were artificially reduced from 1943–1968. During this period, a total of 1,664 elk were removed from the park with the goal of reducing the park herd to about 500 on the eastern boundary winter range. In 1968 elk were no longer controlled within the park's boundaries with a NPS change in management policy to one of natural regulation that occurred in Yellowstone National Park at the same time. From 1968 to the present time, herd limitation was attempted through natural regulation within the park and harvests outside of the park. Interagency goals of the NPS, Colorado Division of Wildlife (CDOW), and U.S. Forest Service (USFS) included use of both regular and late season hunts outside of the park boundaries to limit the elk population by harvesting 500–600 elk each year. The harvest goal was nearly achieved prior to 1987 when an average of 442 ± 78 elk were harvested each year, but after 1987, increasing restrictions to private lands outside the park reduced the harvest. Elk harvests declined to 302 ± 36 after 1987. In either case, these harvests were insufficient to limit the growth of the elk population and elk steadily increased in the park and then later in the town of Estes Park. Concerns over possibly overabundant elk resulted in criticisms of the park elk policy (Hess 1993) and calls for the agencies to reevaluate their interagency elk management efforts. In 1993, the park superintendent, James Thompson, requested F. J. Singer of the National Biological Service (now USGS-BRD), to conduct a problem analysis of the elk situation.

The goals of the study included determination of whether elk densities had exceeded those expected in a natural system, whether unnatural concentrations of elk were occurring, what the effects of elk herbivory were, and whether the effects of the elk herbivory were acceptable or unacceptable. At the onset of the study, it was recognized that a number of human influences had occurred in the system that might confound the interpretation of the effects of elk alone. For example, any climate change or unnatural succession due to fire suppression might have influenced plant communities. A number of meadows in the winter range had been drained for a golf course located in the park until the 1960s and a number of other park meadows had been drained for cultivation. Beaver had apparently declined on at least part of the winter range and for unknown reasons. The presence of the rapidly growing town of Estes Park, located within the edge of the winter range, might have altered or abbreviated elk migrations. The major predators of the system, wolves and grizzly bears, had long since been extirpated and considerable debate and speculation surrounded what their effects might have been on possible limitation of elk.

Study design input included the problem analysis prepared in 1993 and proposals submitted to BRD and the NPS in 1993 by F. Singer, and three peer reviews of the study design conducted in 1994 (Table 1). The study also built upon earlier peer reviews of the similar problem in Yellowstone National Park (Table 1). The study design included key elements of those review suggestions, including: census methodology and demographic analysis of the elk population, studies of vegetative biomass produced in grazed and ungrazed areas and elk offtake, studies of effects on ecosystem processes, GIS-based ecosystem model (SAVANNA) experiments to test hypotheses, and evaluation of grazing effects on plant

Table 1. List of proposals and peer reviews of this study in Rocky Mountain National Park and for the closely related elk management situation in Yellowstone National Park.

Proposals:

Singer, F. J. 1993. Elk-vegetation relationships in Rocky Mountain National Park: A problem analysis of the existing data and recommendations for future research and monitoring. U.S. Department of the Interior, National Park Service, Fort Collins, Colo. 23 pp.

National Biological Service. 1994. Draft work study plan, ungulate-plant interactions in five national parks in the Rocky Mountain region. Northern Rocky Mountain Section, Midcontinent Ecological Science Center, Fort Collins, Colo. 11 pp.

Singer, F. J., M. B. Coughenour, T. Johnson, and R. Cates. 1993. Population estimation, plant interactions, forage biomass, and offtake and carrying capacity estimation of elk in the Estes Valley. Proposal to National Park Service, Denver, Colo. 23 pp.

Peer Reviews for Rocky Mountain National Park:

Smith, M., J. Dodd, and J. Mitchell. 1994. Unpublished peer reviews of Rocky Mountain National Park elk research study plan to National Biological Service (now USGS-BRD), Fort Collins, Colo.

Hobbs, N. T. 1994. Unpublished peer reviews of Rocky Mountain National Park elk research study plan.

Unsworth, J., G. C. White, D. C. Bowden, S. Steinert, and G. Schoenveld. 1994. Correction of elk counts in and near Estes Park and Rocky Mountain National Park: A problem analysis. April 26, 1994 memorandum, National Biological Survey (now U.S. Geological Survey), 4512 McMurry Avenue, Fort Collins, Colo.

Peer Reviews for Yellowstone National Park:

Garton, E. O., and D. Goodman. 1986. Recommendations concerning northern Yellowstone elk: Aerial survey and population analysis. November 26, 1986, Yellowstone National Park files. 14 pp.

McNaughton, S. J., J. Detling, and L. Wallace (D. Houston ex officio member). 1986. Yellowstone elk research: Consultant's report. Yellowstone National Park files. 3 pp.

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species diversity. Three peer-reviews of the initial study design were obtained in 1994 (Hobbs 1994; Smith et al. 1994; Unsworth et al. 1994). A statistical analysis of field data collected from 1968–1992 was completed (Zeigenfuss et al. 1999). A mid-study science based assessment of vegetation management goals for elk winter range was conducted (Berry et al. 1997). Modifications to the original plan were made to meet some of the concerns of Berry et al. (1997) and through introspection by the study team investigators and unanswered questions brought out during analysis of the first two years of data. These modifications included: (1) an analysis of long-term climate trends to evaluate vegetation changes; (2) one more year of offtake measures to reduce high variances observed during years one and two; (3) measures of biomass and offtake in town since it became obvious after two years of research that more elk were wintering in town than in the park; (4) the earlier proposed study of total N cycle and sustainability was funded by the USGS-NRPP fund program; (5) the long-term trends of willows were determined from sequences of aerial photos and GIS analyses; and (6) a population-based estimate of *K* for elk (ecological carrying capacity) in both town and in the park was conducted. A regional study of the effects of elk on plant species diversity with a multi-scale perspective was funded for a number of study sites, that opportunistically included the RMNP winter range (Stohlgren et al. 1999). Thus, all of the elements of the ideal research study were achieved, including: (a) a study design and plans were prepared at the outset; (b) these were peer-reviewed; and (c) a mid-study assessment and changes in response to that assessment were accomplished.

The study also included additional characteristics of a strong research initiative. There was an emphasis on an ecosystem approach to the study (Fig. 1), including the involvement of an interdisciplinary study team of six scientists. Riparian willow and upland shrub communities were selected for the focus of field data collection. A GIS was used to randomly locate study plots on a landscape scale. A strong experimental nature to the project was developed, in order to control for a large number of potentially confounding variables (Fig. 2). Sixteen exclosures were constructed to exclude herbivory to simulate the effects of no elk, and clipping treatments were conducted inside portions of exclosures to simulate more elk or the invasion of moose to the system (Fig. 2). The question of whether willows and wet site herbaceous vegetation were responding to elk herbivory alone, or also responding to climate change, hydrologic changes, beaver declines, succession, or other factors was addressed. Check dams were used to add water to some study plots to simulate hydrologic change, in particular the return of beaver and their dams. Prescribed burns were conducted inside and outside upland shrub exclosures to evaluate fire effects. Measurements were also made within three 35-year old exclosures to assess the effects of herbivore exclusion over a longer time period.

First, a brief executive summary keynotes the key findings. In the following sections, we present the methodology and findings for each study of the various ecosystem components. The final section summarizes model findings against various ecological paradigms to assist staff of RMNP in their assessment of the appropriate number of elk. In a separate modeling report, the SAVANNA modeling effort uses a GIS-based, spatially-explicit model to draw together the findings of these various study components into a single, predictive ecosystem model (Coughenour 2001).

The chronological timetable of the planning for this initiative and the peer reviews and study elements are presented in Table 2. The specific measures that were gathered during this study, number of plots, and measures at each plot and the rationale for each measure or group of measures is presented in Table 3.

Literature Cited

Berry, J., D. Decker, J. Gordon, R. Heitschmidt, D. Huff, D. Knight, W. Romme, and D. Swift. 1997. Science-based assessment of vegetation management goals of elk winter range, Rocky Mountain National Park. Environment and Natural Resources Policy Institute, Colorado State University, Fort Collins, Colo. 16 pp.

Coughenour, M. 2001. A spatially explicit ecosystem model (SAVANNA) of different ungulate management scenarios. Final report to U.S. Geological Survey and National Park Service.

Hess, K. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot. 167 pp.

Hobbs, N. T. 1994. Unpublished peer reviews of Rocky Mountain National Park elk research study plan.

Packard, F. M. 1947. A study of the deer and elk herds of Rocky Mountain National Park, Colorado. Journal of Mammology 28:4–12.

Smith, M., J. Dodd, and J. Mitchell. 1994. Unpublished peer reviews of Rocky Mountain National Park elk research study plan.

Stohlgren, T. J., L. D. Schell, and B. V. Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9:45–64.

Unsworth, J., G. C. White, D. C. Bowden, S. Steinert, and G. Schoenveld. 1994. Correction of elk counts in and near Estes Park and Rocky Mountain National Park: A problem analysis. April 26, 1994 memorandum. National Biological Survey (now U.S. Geological Survey), 4512 McMurry Avenue, Fort Collins, Colo.

Zeigenfuss, L. C., F. J. Singer, and D. Bowden. 1999. Vegetation responses to natural regulation of elk in Rocky Mountain National Park. Biological Science Report USGS/BRD/BSR-1999-0003. U.S. Government Printing Office, Denver, Colo. 23 pp.

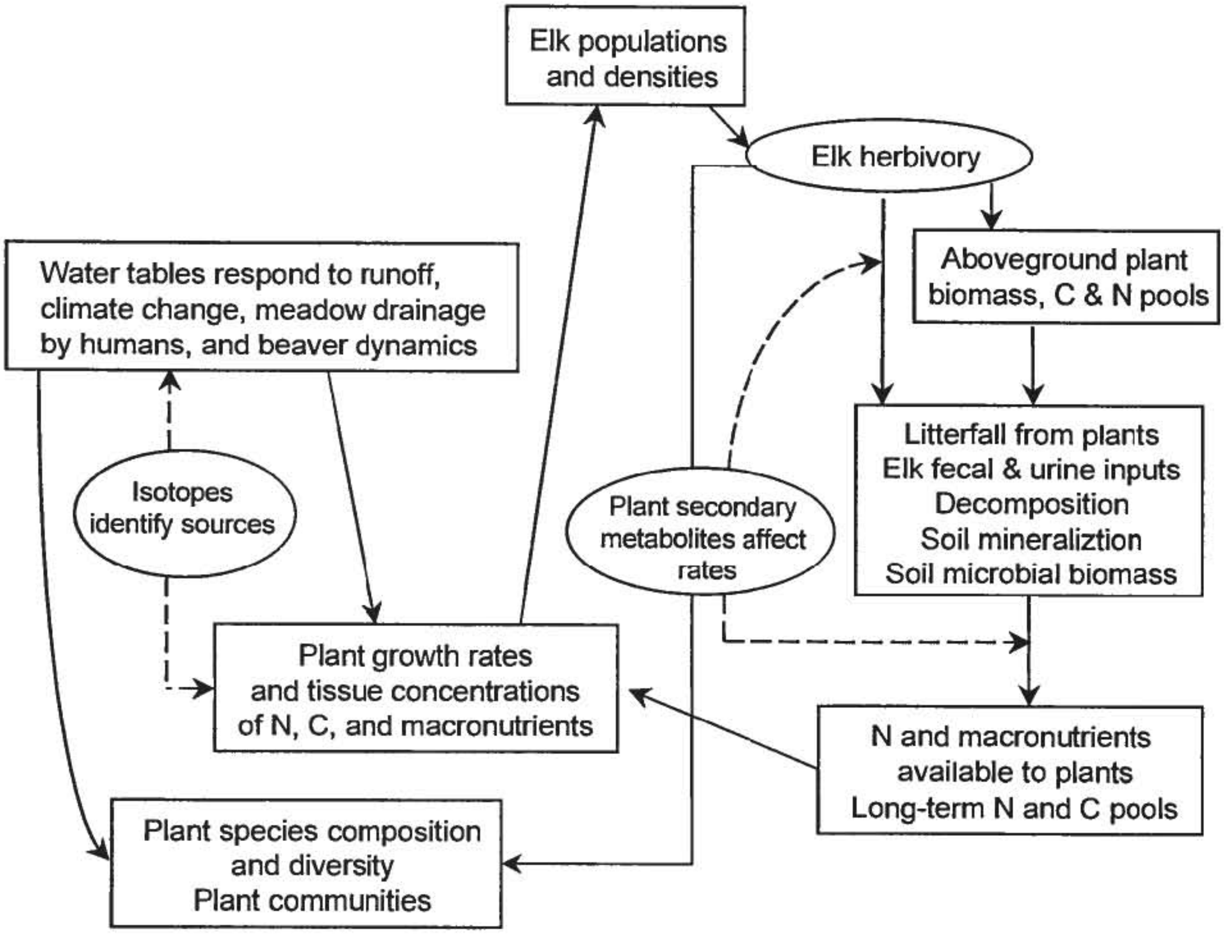
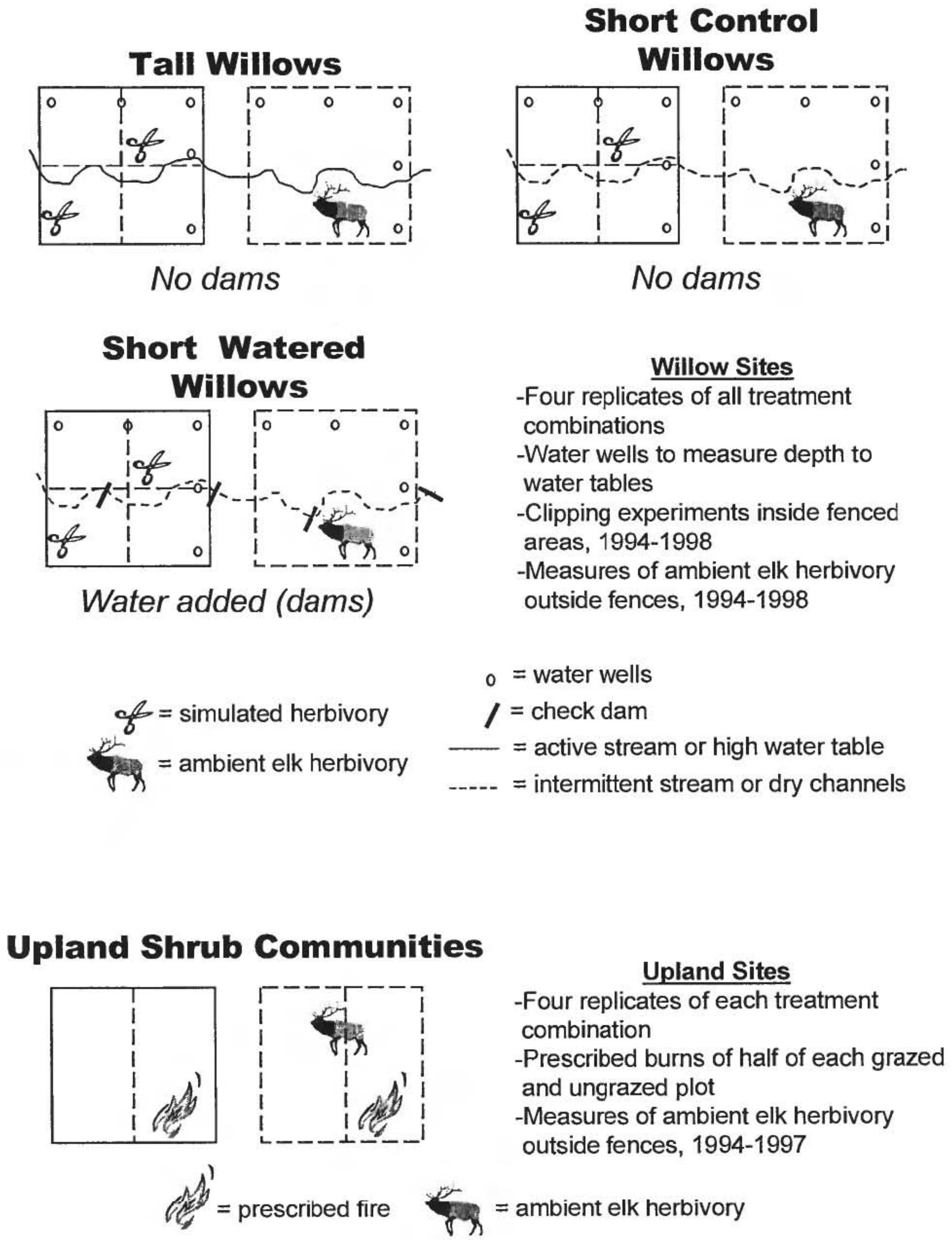


Fig. 1. Ecosystem approach to the study of elk abundance and herbivory effects on winter range of Rocky Mountain National Park, Colorado, 1994–1999.



Willow Sites

- -Four replicates of all treatment combinations
- -Water wells to measure depth to water tables
- -Clipping experiments inside fenced areas, 1994-1998
- -Measures of ambient elk herbivory outside fences, 1994-1998

Upland Sites

- -Four replicates of each treatment combination
- -Prescribed burns of half of each grazed and ungrazed plot
- -Measures of ambient elk herbivory outside fences, 1994-1997

Fig. 2. Experimental design used to study impacts of elk herbivory and water availability on elk winter range of Rocky Mountain National Park, Colorado.

Table 2. Chronology of significant events, Rocky Mountain National Park elk ecology study, 1992–2001.

1992	Final report on 25 years of elk research submitted by D. Stevens.
1993	Problem analysis and review of earlier work by F. Singer. Parallel proposals to NBS (now USGS-BRD) and NPS written by F. Singer.
1994	Three peer reviews of study designs. Pre-treatment vegetation biomass data collected. Exclosures and treatments put in place.
1995	Radiocollars placed on 73 elk. Dams and clipping treatments put in place.
1995–1997	Prescribed burns conducted. Post-treatment field data collected by BRD, NREL (Natural Resource Ecology Lab), and NPS crews.
1997	Berry et al. (1997) science-based assessment of vegetation goals occurs at mid-study. Study modifications according to Berry et al. (1997) and research team analysis.
1998	Additional year of offtake measures, climate analysis, and sustainability study.
1999	Release of statistical analysis of 25 years of long-term vegetation responses (Zeigenfuss et al. 1999).
2001	Planned release of final BRD-NREL report to the park on 1994–1999 study.

Table 3. Study variables measured, locations and rationale for their measurements, Rocky Mountain National Park, Colorado, 1994–1999.

Variable measured	Rationale for studying the topic	Location
Nutrient processes	Nitrogen is single most important factor to plant growth	
Biogeochemical processes		
% nitrogen in plants and soil		
Nitrogen mineralization rates		12 new willow exclosures
Elk fecal/urine deposition rates		Three 35-year-old exclosures
Nutrient flows and inputs and outputs of N by elk vs. litterfall		
Production and offtake	Evaluate effects on plants and to determine allowable use.	16 new exclosures Three 35-year-old exclosures
Plant species composition	To evaluate whether species shifts to exotics or grazing-resistant species are occurring.	16 new exclosures One 35-year-old exclosure
Water table levels	To examine whether hydrological manipulations were successful at increasing water on sites, and to correlate water availability to plant growth and biogeochemistry.	12 new willow exclosures
Plant physiological measures Plant water balance Photosynthesis and carbon gain	To evaluate impact of herbivory on water balance and individual plant processes.	12 new willow exclosures
Secondary metabolites	Plants which are heavily browsed may return to a juvenile phase, producing higher concentrations of defensive compounds, and thereby influencing nitrogen cycling through quality of litterfall.	12 new exclosures One 35-year-old exclosure
Elk movements, population dynamics, and census		
Elk density in park and town	To correlate with plant abundance.	Winter range on park east slope and town of Estes Park
Elk trends and density-dependent population processes	To determine if elk will regulate their numbers.	Throughout elk winter range in the park and the town of Estes Park.
Estimate ecological carrying capacity (food-limited) for elk in town and park	To determine at what density elk numbers might stabilize.	Throughout elk winter and summer range in the park and the town of Estes Park.
Macronutrient analysis	To determine whether herbivory, water availability, or fir affect nutrient concentrations in plants consumed by elk.	16 new exclosures Three 35-year-old exclosures
Measures of willow cover, morphology, seed production, and demography	Seed production may decrease under high levels of herbivory. Willow morphology may shift to shorter, more compact crowns under high herbivory levels.	12 new exclosures One 35-year-old exclosure

Executive Summary of Empirical Findings

Francis J. Singer

Introduction

A research initiative was conducted from 1994 to 1999 in Rocky Mountain National Park (RMNP), Colorado, to evaluate the numbers, trends, and ecological effects of elk (*Cervus elaphus*) in the park and the adjacent Estes Valley. Concerns were expressed that perhaps too many elk inhabited the area, that animals were over-concentrated in certain locales, and that certain vegetative changes were taking place. In particular, concerns were expressed over the visual appearance of short, hedged willows in the open wet meadows on the park primary elk winter range.

Elk were extirpated, or nearly so, from RMNP by human exploitation in the late 1800s, but were reintroduced in 1913 and 1914. Elk steadily increased until they reached an estimated 1,000 animals within the park boundaries in 1944 (Packard 1947). Due to concerns over increasing elk numbers and potential effects on the park winter range, elk in the park were artificially reduced from 1943 to 1968. During this period, 1,664 elk were removed from the park with the goal of reducing the park herd to about 400–500 on the winter range on the eastern side of the park. In 1968, elk were no longer controlled within the park's boundaries, in concert with an NPS change in management policy to one of natural regulation that occurred in Yellowstone National Park at the same time. From 1968 to the present time, increasing reliance to limit the herd was placed on harvests outside of the park. Interagency goals of the National Park Service (NPS), Colorado Division of Wildlife (CDOW), and U.S. Forest Service (USFS) included use of both regular and late season hunts outside of the park boundaries to limit the elk population. A goal was set to harvest 500–600 elk each year that was based on a population reconstruction harvest model (called POP-II). This goal was set with the intent to limit growth of the elk population. This goal of harvesting 500–600 elk was nearly achieved prior to 1987, when an average of 442 ± 78 elk were harvested each year, but after 1987, increasing restriction to private lands outside the park functioned to reduce the ability to harvest the desired number of elk. Elk harvests declined to 302 ± 36 following 1987 through 1996. The more recent use of the town area, and habituation of elk to humans there, have also made elk increasingly inaccessible to sport hunters. Although the harvests may have slowed elk population growth, the desired limitation was never achieved and elk steadily increased both in the park since 1968 and in the town of Estes Park after elk pioneered the town area in the late 1970s (Chapter 1). By 1993, concerns over high elk numbers resulted in criticism of the park elk policy (Hess 1993) and led the agencies to re-evaluate their interagency elk management efforts. In 1993, the park superintendent, James Thompson, requested F. J. Singer (of the U.S. Geological Survey, Biological Resources Division, then the National Biological Service) to conduct a problem analysis of the elk situation and then to write a proposal to research the elk situation.

The goals of the study included providing park managers with information on the effects that elk were having on plant species and the ecosystem. At the onset of the study, it was recognized that a number of human influences had occurred in the system that might confound the interpretation of the effects of the elk abundance alone. For example, any climate change or unnatural succession due to fire suppression by park management might have influenced plant communities. A number of meadows in the winter range had been drained for a golf course in the park (now gone since the 1960s) and for agriculture at a few homesteads within the park. Beaver had apparently declined both on and off the winter range, for unknown reasons. The presence of the rapidly growing town of Estes Park, located within the winter range, might have altered or abbreviated elk migrations. The major predators of the system, wolves and grizzly bears, had long since been extirpated and considerable debate and speculation surrounded what their effects might have been on ungulate populations in a pristine system.

National Park Service (NPS) policy states that natural processes should be relied upon to the largest extent possible to manage wildlife populations within national parks, but that high populations of animals may be managed, if those over-concentrations are due to human activities (NPS 2001). Human activities may have altered some national park ecosystems from their pre-existing, unaltered, naturally functioning state. Native predators have been eliminated from many national parks, migrations of ungulates have been altered by developments and activities outside of parks, keystone predators have been eliminated, and climate change potentially due to human activities may have altered ecosystems (Wagner et al. 1995; Wright 1996; Singer et al. 1998a). NPS guidelines do not provide specific criteria by which to evaluate potential ungulate overabundance.

The assessment of what constitutes an overconcentration or too much grazing by ungulates in a national park is a very complex question. Overgrazing is typically defined as any excess of herbivory that leads to degradation of plant and soil resources. However, even in this simplest of definitions, the word "excess" is a value-laden term that may be defined differently depending upon one's objectives in managing an ecosystem. A range manager, wildlife manager, ecologist, or park manager might have very different management objectives for ungulates and each might define an "excess" differently. Ungulate grazing nearly always results in some effects on the plant and the ecosystem, but when do those effects become too much?

The purpose of this research was to document the influences that elk had on the RMNP ecosystem for managers, but not to make any judgments as to what effects were acceptable or unacceptable. The criteria for five commonly-used ecological approaches to evaluate the abundance of ungulates (the population based-predator limitation, the allowable use, the overgrazing, the grazing optimization/sustainability, and the biodiversity approaches) are presented in Chapter 12 and their potential for ease of application to park management situations is discussed. Each one of these approaches has some potential for application to the RMNP elk assessment.

In 1993 and through 1999, the Biological Resources Division of the U.S. Geological Survey, Midcontinent Ecological Science Center (then the National Biological Service), in conjunction with the National Park Service Natural Resources Preservation Program and RMNP, conducted a series of research studies into the question of the possible overabundance of elk in the park. The broad objectives addressed in the initiative included the following: (1) to determine the current status and trends, population demography (survival and recruitment), and distributions of elk on winter range in both the park and in town; (2) to determine current vegetation conditions and trends on the winter range; (3) to evaluate the relative effects of elk herbivory, water additions, artificial clipping, and fire on vegetative conditions; (4) in a general sense, to assess the role of water availability and precipitation patterns; (5) to evaluate the long-term effects of grazing on soil fertility and the sustainability of the system; and (6) to conduct modeling experiments to predict effects resulting from different management scenarios.

Specific projects addressed in the combined USGS-NPS initiative included the following:

Elk Population Studies

1. Aerial and ground estimations of elk densities were conducted in the park and town, assisted with information from marked animals from the capture and radiocollaring of 73 elk during 1995 (Chapter 1). An aerial sightability model was developed in the park and a mark-resight model in the town to estimate elk numbers.
2. Estimates of elk survivorship and recruitment were developed from these population estimates and the radiocollared animals. Population models were developed for the park and town elk subpopulations. These models were then used to develop population-based estimates of food-limited ecological carrying capacity (ECC or K)[a] for elk in both sectors. (Chapter 1).
3. In order to calculate an independent forage-based estimate of K for elk in the town sector, forage biomass was sampled in 1997, 1998, and 2000 in town (Chapter 12). A prior estimate of the park's capability of vegetation and forage nutrition to support elk was provided in earlier research by the Colorado Division of Wildlife (Hobbs et al. 1982).

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[a] Food-limited carrying capacity (K) is defined as the ungulate-vegetation ceiling for an area. This is the number of ungulates that the area can support, where the ungulates are regulated by density-dependent processes set by per capita restrictions in food availability. Density-dependent processes that can act to regulate the population might include decreased survival, decreased recruitment, or increased dispersal at higher densities. Predators limit ungulates below K in many ecosystems. Evidence has been reported for multi-predator (usually wolves and bears together) limitation of ungulates (Gasaway et al. 1992; Messier 1994; Orians et al. 1997; Peterson 1999). Limitation is more likely when there is more than one species of major predator (Orians et al. 1997).

Landscape Level Measures

1. Long-term trends in vegetation were determined on the open winter range using the long-term plots monitored from 1968 to 1992 (Chapter 3).
2. A series of 25 additional willow plots were randomly located across the landscape of the winter range and monitored during the study for condition and trend (Chapter 12).
3. The historical trends in stream channel patterns and willow cover since the 1940s were assessed using GIS, photo interpretations, and ground truthing (Chapter 2). The historical trends in the abundance of beaver and their ponds were assessed from repeated ground surveys of active dams, food caches, and lodges since 1939 (Chapter 4).

Treatments and Experiments[b]

1. Twelve new exclosures were erected in willow communities (stratified into short and tall willows) in 1994. Check dams were placed in streamside channels at some of the sites, and artificial clipping was used to simulate higher levels of herbivory inside the exclosures. A control, or undisturbed, plot was maintained inside of each exclosure. An additional four new exclosures were erected in upland shrub communities in 1995. Prescribed burns were conducted inside and outside portions of these exclosures in 1995–1996 (Chapter 4).
2. A large number of variables were measured for each treatment, including any changes in depth to the water table, plant species composition, plant production, responses in willow morphology and community structure, and responses in nutrient concentrations of plants (Chapters 4 and 5); plant ecophysiology responses (Chapters 6 and 8); secondary metabolites or plant defense compounds (Chapter 9); and patterns in isotopic signatures of carbon and oxygen (Chapter 7).
3. Measurements of plant, soil, and process responses were taken at three long-term (35-year) exclosures and adjacent grazed sites on the elk winter range in the park (Chapters 10 and 11).
4. Climate and stream flows were monitored during the study. An analysis of long-term trends in climate patterns for the area was reported in an earlier publication (Singer et al. 1998b).

Ecosystem Sustainability to Grazing by Ungulates

1. The effect of elk upon soil fertility and long-term sustainability of the ecosystem was also assessed. The dynamics of nitrogen (N), a nutrient often in limited supply that may strongly influence plant growth, and carbon (C), in response to elk activity was documented. We studied the removal of N and C by elk grazing, the annual inputs of N and C by the plants following the grazing removals, the annual inputs of N and C from elk urine and feces, the transport of N from the summer range, and the loss of N and C from certain vegetation types on the winter range due to elk herbivory (Chapter 11).
2. The CENTURY soil model was used in the sustainability analysis to predict the responses of N and C to elk herbivory (Chapter 11).

Computer Simulation Modeling

1. The SAVANNA ecosystem model was applied to predict the effects that human alterations have had on the ecosystem and to project the effects of different management scenarios (Coughenour 2001).

The majority of the research was conducted by scientists from the Natural Resource Ecology Laboratory at Colorado State University. Researchers also represented the Statistics and Fisheries and Wildlife Departments of Colorado State University, the Botany and Range Science Department of Brigham Young University, and the Midcontinent Ecological Science Center of the U.S. Geological Survey. The chapters in this final report consist of individual manuscripts that address all of the empirical findings from the 1993–1999 elk initiative. The full results from the ecosystem simulation modeling are presented independently, in a technical report to the USGS-BRD and the NPS

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[b] The purpose of the experiments was to control for all other potentially confounding influences and factors such as herbivory by small mammals and insects, succession, and others, by applying the main treatment effect (fencing, damming, clipping, burning) to one of two similar macro plots. In this study, both the study site and the macro plot that received the treatment were selected by random procedures.

(Coughenour 2001); however, the executive summary from that report is included at the end of this final report.

This executive summary features key findings from the empirical studies. Space in this summary is insufficient to review each and every one of the findings here. Please refer to the specific chapters in the report for greater details.

Key Findings

Elk Populations and Distributions

The studies revealed three largely distinct subpopulations of elk on the primary winter range: (a) the Moraine Park-Beaver Meadows; (b) the Horseshoe Park; and (c) the town of Estes Park subpopulations. A few animals wintered in the small Cow Creek area, also part of the park winter range, and another 125 or so animals spent the winters on windswept alpine meadows of Trail Ridge (Chapter 1). Elk densities were about three times higher in the Moraine Park-Beaver Meadows area than in the Horseshoe Park area, both which are within park boundaries. Average elk densities across the winter range varied dramatically. Average elk densities in the park during all aerial surveys, 1994–1999, were very high, >65 elk/km^2 (range = 66–110 elk/km^2) on 2.9 km^2 (3%) of the winter range; high, 30–65 elk/km^2 on 4.0 km^2 (4%) of the winter range; but medium, 10–29 elk/km^2 or low, <1–9 elk/km^2 on the remaining 92.5km^2 (93%) of the winter range (Chapter 12).

The park elk population grew rapidly following release from controls in 1968, but the elk population growth began to slow about 1980, and stabilized ($\lambda \cong 1.0$) at about 1,000 animals in 1990 due to lowered calf and yearling survival rates. The population based K for the park subpopulations was 1,069 $\pm$ 55 ($\bar{x} \pm$ SE) elk (Chapter 1). This estimate compares favorably with the forage-nutritional based average estimates of 991 $\pm$ 102 for a slightly dry year and 1,481 $\pm$ 261 elk for a wet year reported by Hobbs et al. (1982) for the park area.

The 2001 modeled population estimate for the Estes Park town subpopulation was 1,975 $\pm$ 150 elk (Chapter 1). This sector of the elk population was still growing at about 5.2% per year at the end of the study. The population-based estimate of K for the town, i.e., its potential largest size at the vegetation ceiling, is 2,869 $\pm$ 415 elk (Chapter 1). This compares favorably with independent forage based maximum elk potential estimates of 2,330 ± 78 to 2,563 $\pm$ 85 elk for a dry year and 3,082 ± 103 to 3,391 $\pm$ 113 elk for a normal year (Chapter 12). These potentials for elk populations in town will continue to decline as human developments remove useable elk habitat. I concluded K for elk were well approximated for both the park and the town sectors, due to the application of the various methods, but the reader should be reminded that these are estimates only and also that K will vary due to climatic conditions. Ecological carrying capacity for the potential largest size for the entire population was about 3,938 $\pm$ 419 elk (Chapter 12). Adult annual survival rates for cows were about 0.913 in both the park and the town sectors. Adult bull survival was 0.79 in the park, but only 0.42 in town due to sport harvests (Chapter 1).

Current Vegetation Conditions and Trends

The USGS-CSU study team generally found no effect on plant species diversity in upland shrub and willow communities in the 4-year exclosures (no differences were found in the six treatment types; Chapter 12). This finding of no or few diversity differences was also supported by two independent samplings at the older, 35-year exclosures by Tom Stohlgren (USGS-MESC) and his coworkers in 1997 (Stohlgren et al. 1999) and at these older exclosures by our study team in 1998 (Chapter 12). The wet meadow, willow, upland shrub, and Ponderosa pine/shrub types were well represented by these samplings. However, in contrast to our samplings, Dave Stevens, (now retired NPS) found that, following more than 25 years of grazing, three less palatable plants (*Carex* spp., *Selaginella densa*, *Phleum pratense*) increased on heavily grazed and dry open upland grass/shrub and meadow sites (Chapter 3, also see Stevens [1992]). This latter study, however, did not include sampling in control, i.e., ungrazed sites, and thus, effects of confounding variables such as climate and succession cannot be ruled out. The upward trends of several less palatable plant species through time on these grazed sites may warrant further consideration.

Based on published information from similar ecosystems, the elk consumption rates (~60%) on herbaceous vegetation in the upland grass/shrub type appeared relatively high from the viewpoint of conventional guidelines for allowable use (Chapter 12). A general guideline for sustainable range management is for maximum consumption of herbaceous vegetation to be about 50%, while substantially higher levels result in species and ecosystem alterations (see Biondini et al. [1998] for results of a test of the 50% rule). There was little predictability from the literature of the effects from shrub use values in any of the types we studied, since so many of the studies used artificial clipping to simulate herbivory. We found the effects of natural elk herbivory were much greater than clipping, apparently due to the stripping of bark and the rough breakage of willow stems by elk (Chapters 4 and 6). Willow structure and growth declined noticeably at use levels of about 37% by the wild elk and greater (Chapter 12). The structural changes attributed to elk herbivory at these higher use levels in the willow type were quite large (Chapters 4, 5, and 11). Overall, consumption of willows on the winter range averaged 33% by elk (Chapter 12).

A number of additional plant community alterations were also attributed to elk herbivory. At the 4-year exclosures in the willow type, there was 4.6% more bare ground on the grazed sites (7.7% grazed vs. 3.1% ungrazed), herbaceous production declined 22%, and there were less bluebell (*Mertensia ciliata*) and more *Solidago* spp. on the grazed sites. In grazed upland grass/shrub sites, cover of *Artemisia ludoviciana* was reduced 62% and cover of *Eriogonum umbellatum* was 50% less on grazed sites (Chapter 12). At the 35-year exclosures, the size and production of big sagebrush (*Artemisia tridentata*), an upland shrub that covers about 5–8% of the winter range, was reduced by two-thirds. However, size and production of the much more ubiquitous bitterbrush (*Purshia tridentata*) increased on grazed sites. The trend toward slightly more bare ground continued at the 35-year exclosures where there was 6.4% more bare ground on grazed sites compared to ungrazed sites (this difference, however, was not statistically significant; Chapter 12).

Willow production was reduced 66% by year 4 of the study (Chapter 4). There were no effects on willow production in years 1–3 (Chapters 4 and 5), which were years with heavy snowpacks and high stream runoff. In year 4 (1998), following a more normal spring stream runoff, willow community production was significantly less in grazed treatments compared to the ungrazed controls (Chapter 4). I attribute the differences in reported findings either to the difference in years of measurements (Raul Peinetti did not sample in 1998) or to the individual-willow-based sample of Peinetti et al. (Chapter 5) vs. the plot-based sample of Zeigenfuss et al. (Chapter 4). Additionally, willow catkins were reduced 70%, there were fewer shoots/grazed stem, and there were fewer leaves/grazed stem (228 vs. 411) in grazed willows (Chapters 4 and 5). Another effect of elk herbivory was that grazed willows obtained less of their water from groundwater than did ungrazed willows based on isotope analysis (Chapter 8). These authors concluded from the isotopic signatures that willows growing on sites further removed from streamsides likely possessed reduced rooting depths and thus were less able to compensate for the effects of the intense herbivory than streamside and ungrazed willows.

Grazed willows also possessed heavier and longer shoots, more shoots and more leaves per unit of biomass, and there was more current biomass (n) per unit of previous year's (n-1) biomass. There were few physiological differences, but large morphological and canopy architecture structural differences between grazed and ungrazed willows. Vigorously grazed willows tended to "catch-up" in size during the growing season to ungrazed willows (Chapter 5), but overall, grazed willows were significantly shorter than ungrazed willows by the end of the study (Chapters 4 and 5). Grazing optimization, a curvilinear relation with peak values at moderate herbivory, was verified for eight different willow growth parameters on the RMNP winter range. The evidence for this grazing optimization included the following. At moderate levels of willow consumption (about 21 ± 0.4% annual use), willow growth parameters exceeded those for ungrazed willows, but at high levels of use (>37 ± 3% use) willow growth parameters declined. Moderately browsed willows (browsed at about 21% of current annual growth) produced substantially more current annual growth, stems were more dense, plants were taller on the average, and canopy volume was greater than for their unbrowsed counterparts (Chapter 12).

The high consumption rate of 37% of the annual growth of willows corresponded to a high density of ~32 ± 1 elk/km^2. At these and higher elk densities and herbivory levels, elk were having a negative influence on willows (Chapter 12). These negative effects were occurring on large portions of Moraine Park where elk densities were very high, and on some portions of Horseshoe Park (Chapter 12).

The Relative Role of Elk Herbivory, Water, and Prescribed Fire Evaluated from Experiments

The experiments with exclosures, indicated elk herbivory suppressed willow heights, leader lengths, and annual production in the short willow type, as well as reduced herbaceous biomass production by about 22%. The water impoundment treatments increased graminoid production over controls on the drier sites, but the impoundment treatments did not significantly influence shrub production. The researchers suspected that the impoundment treatment was of too short duration in the growing season (only about six weeks of dam effects) and the natural water tables were high (no water table fell below 1 m even in late summer on any site), even on sites formerly occupied by beaver and with no active impoundments, to influence the shrubs (Chapter 4).

Prescribed burning in the upland bitterbrush communities decreased the amounts of shrub cover and production, at least in the short-term of the study, but there was no effect on herbaceous standing biomass, except that biomass of *Stipa comata* declined. However, grazing in the upland grass/bitterbrush type reduced herbaceous biomass, increased N content of grasses, and increased digestibility of grasses and forbs (Chapter 4).

Isotopic analysis provided important insights into the autecology of willows and sedges, without requiring the destructive sampling of entire plants or root systems. The isotope research suggested willows received about 80% of their water from stream-related underground flows, while sedges received 50% of their water from rainfall (Chapter 7). Several lines of evidence suggested willow plant-root balances were being modified by herbivory. The improved physiological performance of browsed willows suggested improved root:shoot ratios (i.e., the aboveground area of willows were decreased faster than the belowground due to browsing, Chapter 7). But browsed willows growing away from streamside sites may have given up rooting depth and root biomass, based on their changes in isotopic signatures, thus reducing their access to groundwater compared to either protected willows or to willows growing on streamside sites (Chapters 7 and 8). Repeatedly browsed willows located away from streamsides thus likely became more vulnerable to intense herbivory through time.

Secondary metabolites of plants, including phenolics and tannins in willows, may function as a defense to plants against herbivores by binding with metabolites such as nitrogen-containing proteins, amino acids, DNA and RNAs, making them difficult to digest. Phenolics may be toxic and/or act as feeding deterrents (Robbins 1993). The research team, especially Brigham Young University scientists, studied the responses of tannins and phenolics to water amendment, clipping treatments, and ambient levels of browsing. The responses of secondary metabolites in willows to a variety of stratifications (tall, short; deeper vs. shallow water tables) and treatments (clipping, water amendments) are presented in Chapter 9. In general, willows clipped at intermediate (for clipping treatments) levels of 50% inside of one long-term exclosure in RMNP were able to respond in a predicted fashion by increasing production of tannins and phenolics over unclipped controls, but willows clipped at 100% removal of current annual shoot growth could not increase production of the secondary metabolites (Singer et al. 1998b). Less vigorous willows in Yellowstone National Park, growing on drier and less favorable sites, were not able to increase production of metabolites at either clipping treatment (Singer et al. 1998b).

The Role of Water Availability and Precipitation

There was compelling evidence for the large importance of water availability to the status of riparian plants on the RMNP winter range. The best evidence for this is descriptive and correlational, and the statistical model evidence, although present, is weak. Our check dams, although their effects were of shorter duration (only about six weeks) and of lesser magnitude than a beaver dam, resulted in a near doubling of herbaceous biomass and verified the importance of water (Chapter 4). Since 1946, total stream length declined 44–56% and surface area of water declined 47–69% on the elk winter range (Chapter 2); changes that were likely of enormous biological importance to the dewatering of large areas of willows and riparian vegetation. Rocky Mountain willows often regenerate in abandoned beaver ponds (Cottrell 1995) and the water and ice of the pond may have thwarted elk access to some willows and reduced herbivory. Shrub and herbaceous annual productions were correlated to March-September precipitation in a quadratic relationship, implying production increased with increasing precipitation to a threshold point, but above that point production did not further increase (Chapter 4). Stream flows and water tables were also higher following high winter snowpacks and high spring runoff and, therefore, streamside water tables were higher in those years. Shallower depths to the water table positively influenced herbaceous production. Depth to water was included in two best biological models that explained willow growth, but not in two other models (Chapters 4 and 12), although depth to the water table in June was correlated to willow growth (Chapter 12). These analyses present evidence for influence of depth to the water table to willow growth, even over the relatively narrow range of water tables that were investigated. The multivariate models suggested elk had a much larger influence on willow growth parameters than did depth to the water table for the range in water tables studied (based on better Akaike's Information Criteria values; Chapter 12).

Climate change might also have contributed to declines in willow growth and, ultimately, to declines in willow abundance. The winter range and the town of Estes Park have apparently experienced a minor, several-decade, warmer (0.89°C warmer) and drier (1 cm less precipitation) climate trend that was punctuated since 1995 with a wetter trend (Singer et al. 1998b). During our study, elk herbivory had the greatest negative effect on willows during a year with normal snowpack and runoff, but less effects during wetter years.

Ecosystem Sustainability and Fertility

The central question in the sustainability view of evaluating the abundance of ungulates is whether total plant production, both above and below ground, and soil fertility are maintained under the grazing level in question. The research indicated that elk were apparently depositing roughly equivalent amounts of N to what was being lost in the upland grass/shrub type. Additionally there was also slightly more root production and root N yield on grazed sites in this type, suggesting aboveground biomass was not being supported at the expense of the belowground biomass on grazed sites (Chapter 11). Soil bulk densities were higher on grazed sites (Chapter 10). The steeper slopes in the upland type might be vulnerable to accelerated soil loss due to ungulates since grazed sites exceeded the suggested thresholds (38% bare ground, 1.10 g/cm^2 bulk densities) of Packer (1963) for accelerated erosion. But this cannot be assessed, since we did not study sediment yields.

Elk activity apparently resulted in a loss of N from both the willow and aspen types. Nitrogen concentrations were higher in willow litter falling on grazed sites, but this did not compensate for other losses in the willow type (Chapter 11). Total biomass of leaf litter was less on grazed willow sites, willow sizes and production were reduced, herbaceous production was 22% less, and elk consumed 33% of the annual shrub biomass and 55% of the annual herbaceous biomass (Chapters 4 and 12). We calculated that total N inputs to the ground surface were only 5.79 g N/m^2/year on the grazed sites and 9.66 g N/m^2/year on ungrazed sites in the willow type. Apparently, because of the elk herbivory, N mineralization rates were substantially (79%) less and N pools (NO_3) were 78% less on grazed vs. ungrazed sites in the short willow type. Our analysis indicated elk activity also resulted in a net loss of N from the aspen type of 0.60 g N/m^2/year (1.13 g N/m^2/year was removed by elk grazing plus 0.53 g N/m^2/year was added in the form of elk urine and feces; Chapter 11). The evidence for declining fertility in grazed willow and aspen communities included: (1) the lower observed N mineralization and N pools; (2) the lower estimated N inputs to grazed sites; (3) the feeding behavior of elk; (4) CENTURY soil modeling of the observed parameters; and (5) the predictions of Biondini et al. (1998). Lowered N availability may reduce productivity and alter plant community composition.

Plants may compensate for tissue losses due to herbivory in a variety of ways. For example in grasslands grazed by native ungulates, increased rates of uptake of N by roots is often observed, as are increased N concentrations in shoots, increased N mineralization rates in the soil, and at times, increased N yield per unit of plant (Ruess 1984; Jaramillo and Detling 1988; Coughenour et al. 1990). These responses may be due to: (a) the conversion by ungulate grazing of less mobile N locked up in litter and standing dead vegetation, into more useable N in ungulate feces and urine; and/or (b) the reduction of soil microbial biomass due to reduced underground reserves. Grazed shrubs may possess an increased number of branched shoots, larger shoots that regrow following browsing, longer shoots, and more buds (Bergström and Danell 1987). These compensatory responses may be sufficient in some instances to result in higher net primary production (i.e., grazing optimization in moderately grazed vs. ungrazed controls (McNaughton 1979, 1983, 1993; Dyer et al. 1993; Frank and McNaughton 1993; Turner et al. 1993; Green and Detling 2000), but not in heavily grazed shrubs.

Compensatory processes were observed in browsed willows in the study. More willow shoots and more leaves were produced per unit of total biomass on browsed willows, more current year's biomass was produced per unit of the previous year's biomass, previously browsed shoots were longer and heavier, and a higher proportion of the total willow plant N was allocated to new leaves and new shoots in browsed plants (Chapter 5). Thus, RMNP supports a gradient of willow patches that vary in herbivory effects from some patches that are essentially unbrowsed, to some patches that are moderately browsed with high vigor, to other willow patches that are intensely browsed and negatively influenced by the browsing. Overall, 71% of all the willow patches on the park's winter range are now in the short willow type, an apparent browse-induced type, suggesting large areas of willows are browsed too much. The ecosystem functional, structural, and community alterations by ungulates of this shrub community are substantial.

Literature Cited

Bergström, R., and K. Danell. 1987. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. Journal of Ecology 75:533–544.

Biondini, M., B. D. Patton, and P. E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. Ecological Applications 8:469–479.

Cottrell, T. R. 1995. Willow colonization of Rocky Mountain mires. Canadian Journal of Forest Research 25:215–222.

Coughenour, M. B. 2001. Elk in Rocky Mountain National Park – an ecosystem modeling analysis. Unpublished technical report to the U.S. Geological Survey Biological Resources Division and the National Park Service.

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 83:546–552.

Dyer, M. I., C. L. Turner, and T. R. Seastedt. 1993. Herbivory and its consequences. Ecological Applications 3:10–16.

Frank, D. A., and S. J. McNaughton. 1993. Evidence for promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96:157–161.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 20:1–59.

Green, R. A., and J. K. Detling. 2000. Defoliation-induced enhancement of total aboveground nitrogen yield of grasses. Oikos 91:280–284.

Hess, K. 1993. Rocky Times in Rocky Mountain National Park. University Press of Colorado, Niwot. 167 pp.

Hobbs, N. T., D. L. Baker, J. E. Ellis, D. M. Swift, and R. A. Green. 1982. Energy and nitrogen based estimates of elk winter range carrying capacity. Journal of Wildlife Management 46:12–21.

Jaramillo, V. J., and J. K. Detling. 1988. Grazing history, defoliation, and competition: Effects on shortgrass production and nitrogen accumulation. Ecology 69:1599–1608.

McNaughton, S. J. 1979. Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. American Naturalist 11:691–703.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329–336.

McNaughton, S. J. 1993. Grasses and grazers, science and management. Ecological Applications 3:17–20.

Messier, F. 1994. Ungulate population models with predation: A case study with the North American moose. Ecology 75:478–488.

National Park Service. 2001. Management policies. U.S. Government Printing Office, Washington, D.C.

Orians, G., D. A. Cochran, J. W. Duffield, T. K. Fulla, R. J. Gutierrez, W. M. Hanemann, F. C. James, P. Karieva, S. R. Kellert, D. Klein, B. N. McLellan, P. D. Olson, and G. Yaska. 1997. Wolves, bears and their prey in Alaska. National Academy Press, Washington, D.C.

Packard, F. M. 1947. A study of the deer and elk herds of Rocky Mountain National Park, Colorado. Journal of Mammology 28:4–12.

Packer, P. E. 1963. Soil stability requirements for the Gallatin elk winter range. Journal of Wildlife Management 27:401–410.

Peterson, R. O. 1999. Wolf-moose interaction on Isle Royale: The end of natural regulation. Ecological Applications 9:10–15.

Robbins, C.T. 1993. Wildlife Feeding and Nutrition. Academic Press, San Diego, California. 351 pp.

Ruess, R. W. 1984. Nutrient movement and grazing: Experimental effects of clipping and nitrogen source in nutrient uptake in *Kyllinga nervosa*. Oikos 43:183–188.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998a. Thunder on the Yellowstone revisited: An assessment of management of native ungulates by natural regulation, 1968–93. Wildlife Society Bulletin 26:375–390.

Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998b. Elk, multiple factors, and persistence of willows in national parks. Wildlife Society Bulletin 26:419–428.

Stevens, D. R. 1992. Ungulate winter habitat conditions and management. Annual Reports. ROMO-N-08a.

Stohlgren, T. J., L. D. Schell, and B. V. Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain Grasslands. Ecological Applications 9:45–64.

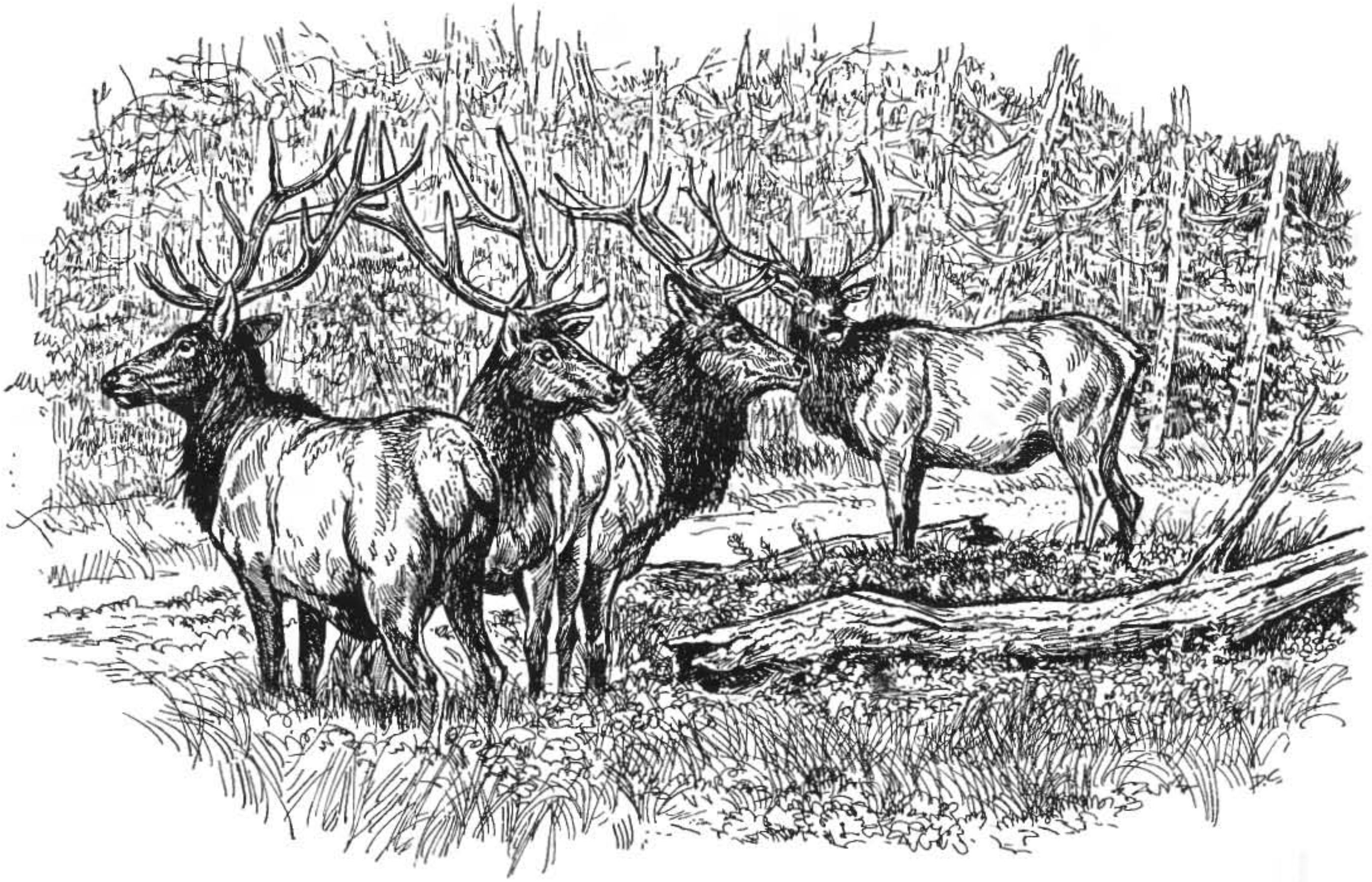
Turner, C. L., T. R. Seastedt, and M. I. Dyer. 1993. Maximization of above ground grassland production: The role of defoliation frequency, intensity, and history. Ecological Applications 3:175–186.

Wagner, F. H., R. Foresta, R. B. Gill, D. R. McCullough, M. R. Pelton, W. F. Porter, and H. Salwasser. 1995. Wildlife policies in the U.S. National Parks. Island Press, Washington, D.C.

Wright, R. G. 1996. National parks and protected areas: Their role in environmental protection. Blackwell Science, Cambridge, Massachusetts. 470 pp.

PART I

EMPIRICAL FINDINGS



CHAPTER ONE

Dynamics of Interacting Elk Populations Within and Adjacent to Rocky Mountain National Park

By

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Abstract. We studied population subdivision and density dependent and independent factors influencing population processes between 1965–2001 for elk (*Cervus elaphus*) inhabiting Rocky Mountain National Park and the adjacent Estes Valley, Colorado. Elk numbers within the park were held relatively constant by management controls until 1967, after which time they were allowed to increase without human interference. Radiotelemetry of 73 elk indicated limited exchange between the subpopulations; combined with clear distinctions in population dynamics, this suggests that these subpopulations are relatively independent despite the absence of physical barriers between them. The elk subpopulation within the park initially increased at 6.5%/year between 1968 and 1970, then growth gradually slowed, exhibiting density-dependent reductions both in calf survival and recruitment with increasing population size, and approached an estimated carrying capacity of 1,069 ± 55 ($\bar{x} \pm$ SE). Since 1991, this subpopulation has remained within ±5% of this equilibrium. The adjacent Estes Valley subpopulation grew at an estimated maximum 5-year average rate of 11.0% from 1979–1983 and is still increasing at 5.2%/year (1991–2001 average). Estimated town population is currently about 70% of our projected carrying capacity of 2,869 ± 415 elk based on projection of observed calf recruitment decline with increasing population. Both carrying capacity estimates are consistent with independent estimates based on forage biomass and energy considerations. Adult cow survival rate did not differ between park and town and we estimated a constant rate of 0.913 [95% CI = 0.911, 0.915]. Bull survival rates increased in the park from 0.52 to 0.79 between 1965–2001, but remained constant at 0.42 [0.35, 0.47] in the Estes Valley. Colder winter temperatures were correlated with reduced calf recruitment (calves:cow at age 0.5 yrs) and with reduced calf survival (between age 0.5–1.5 yrs) in town. Recruitment of town elk also increased with warmer summer temperatures and greater summer precipitation. No weather covariates were significantly correlated with calf recruitment or survival in the park. Declining calf recruitment has been nearly linear and similar in both the park and town. However, density response of calf survival in the park was abrupt near carrying capacity and has not yet been detected in town, suggesting that this mechanism of density dependence is difficult to detect until the population is near carrying capacity. We estimated current combined population size of 3,049 [2759, 3369] elk in 2001. Elk in the town sector currently outnumber elk in the adjacent national park by almost 2:1 and are projected to increase by 46% before being nutritionally limited, suggesting that human-elk conflicts will likely increase in the absence of active management intervention.

Keywords: *Cervus elaphus*, density dependence, elk, national parks, natural regulation, parameter estimation, population dynamics, population models, ungulates.

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Introduction

U.S. National Park Service (NPS) policy states that natural processes should be relied upon to the greatest extent possible to regulate ungulate populations (NPS 2001). However, the policy is flexible, resulting in different management approaches in different situations. Where natural controls have been altered by human activities, unnatural concentrations of ungulates may be managed by park staff (Huff and Varley 1999). This natural regulation management of ungulates in parks has been criticized as operationally vague (Kay and Wagner 1994; Wagner et al. 1995). Olmsted (1979) and Baker et al. (1997) have attributed vegetative changes, especially declines in willow (*Salix* spp.) and aspen (*Populus tremuloides*), to high ungulate populations resulting from this policy of natural regulation. Furthermore, management targeted toward park elk may have consequences for adjacent private lands. A growing elk population located amidst a large human population has important social implications (Berris 1987). Future management in both areas requires an understanding of factors affecting population growth and regulation.

Natural regulation relies on population regulation through predator or food limitation. There is growing evidence for predator limitation of ungulates in natural systems (Bergerud et al. 1988; Boutin 1992; Gasaway et al. 1992; Messier 1994; Mech et al. 1998; Singer et al. 1998); however, uncertainty remains over the level of predator limitation in pre-European systems (Boutin 1992; Singer et al. 1997). Predators have been eliminated from many parks, and even when all predators are still present, ungulate migration patterns or habitat often have been greatly altered. Food-limited populations are assumed to result from density-dependent processes related to per capita restrictions in food availability (Caughley 1976; Fryxell 1987; Dublin et al. 1990; Choquenot 1991). Although evidence exists for food limitation of ungulates in the absence or limited abundance of large predators (Houston 1982; Choquenot 1991; Coughenour and Singer 1996; Saether et al. 1996), regulation or limitation of ungulate populations in national parks by either food or predators remains controversial (Boutin 1992; Sinclair and Arcese 1995; Boyce and Anderson 1999; Peterson 1999).

Detecting density dependence in a population from time series data is difficult. Success often requires long term-monitoring, supplemental information on survival and recruitment, and a large initial reduction (75% is suggested) by management intervention or environmental catastrophe (Shenk et al. 1998). The northern elk population in Yellowstone National Park, following release from management regulation, has exhibited considerable evidence for density dependence as periodically updated by a variety of authors (Houston 1982; Dennis and Taper 1994; Coughenour and Singer 1996; Singer et al. 1997). Similar evidence has been compiled for the Jackson Wyoming elk herd despite supplemental winter feeding (Sauer and Boyce 1983; Boyce 1989) and for red deer (*Cervus elaphus*) on the Island of Rhum (Clutton-Brock et al. 1982). Elk were similarly released from management control in Rocky Mountain National Park (RMNP) in 1968, so this population provides an independent assessment of the roles of density dependent and independent factors in elk population dynamics.

In this paper, we examine the elk that winter in the eastern portion of RMNP and the adjacent Estes Valley, which includes the town of Estes Park, Colorado (Fig. 1), referring to these sectors as "park" and "town", respectively. All of the elk in these areas are thought to have descended from a reintroduction between 1913–1914. Bear (1989) and Larkins (1997) treat these elk as a single population; nevertheless, Larkins (1997) observed that even though elk wintering in town migrated through and used some of the same ranges as park-wintering elk, they did so independently at different times. Before 1968, elk in RMNP were controlled by culling and live removal to maintain a target population of approximately 400 individuals (Stevens 1980). We focused on the period after 1967 when control of elk numbers inside RMNP ended, thereby initiating the NPS policy of natural regulation (Stevens 1980). This change in policy constitutes a >35-year management experiment on the dynamics of a population growing from an initial size well below carrying capacity (K). Elk first appeared in the town sector in noticeable numbers about between 1975–1980 (N. T. Hobbs, Colorado Division of Wildlife, personal communication), about 8–13 years after management control of elk in the park ended. Harvests of both male and female elk have been a regular part of management in town.

In our analysis, we reconsider whether distinct subpopulations exist in this area, based on telemetry locations, differences in dynamics (survival and recruitment rates), and support in our data for either temporary movement or permanent dispersal of elk. We build a series of related models with alternative parameter sets and use information theoretic model selection techniques to identify those that best explain the available data. We look for evidence of density feedback, specifically, declining population growth, calf ratios, recruitment, and survival

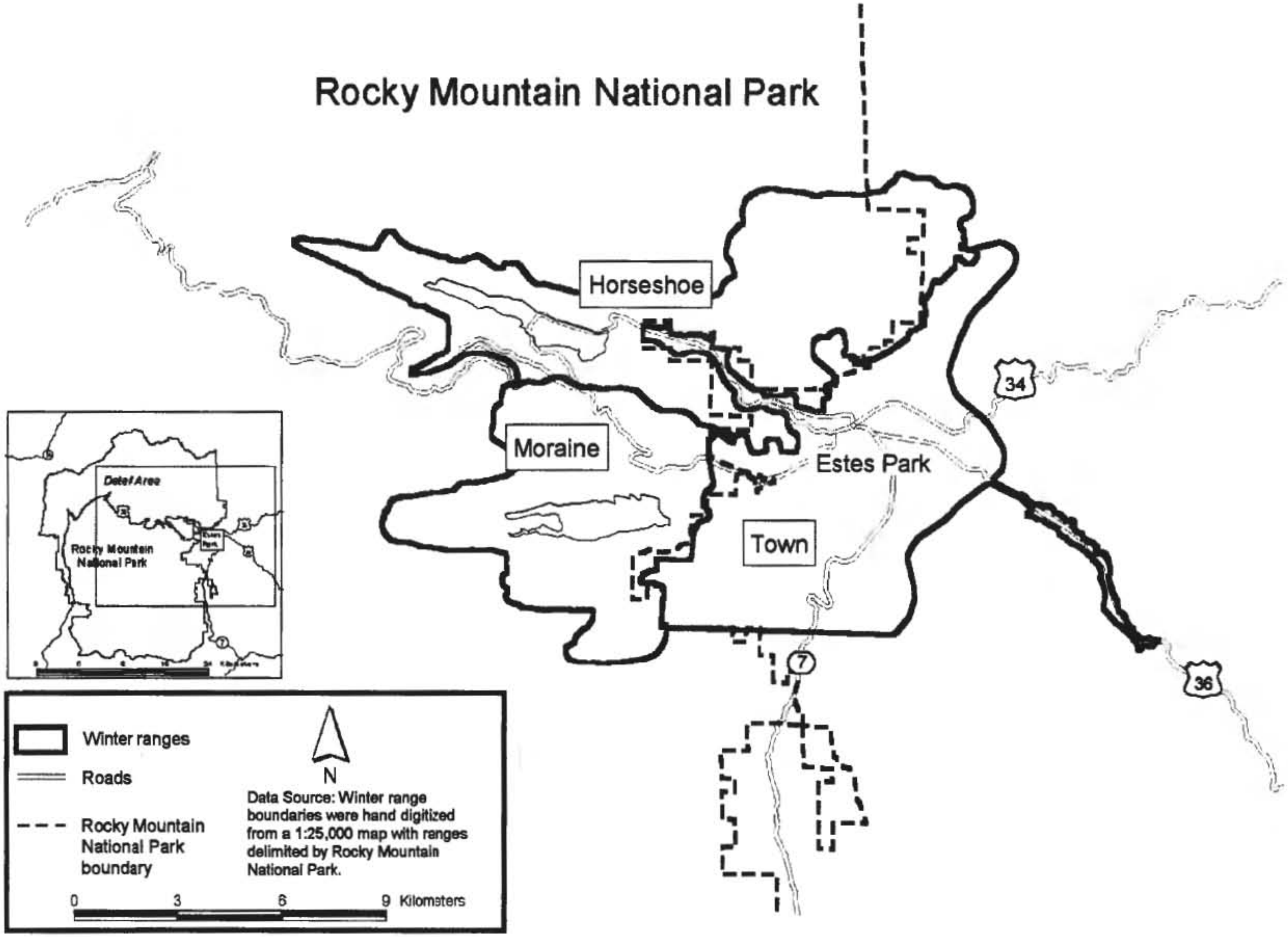

Fig. 1. Map of the study area, including the eastern portion of Rocky Mountain National Park and the Estes Valley which contains the town of Estes Park, Colorado, depicting the boundaries of three winter range areas based on all known elk locations determined by telemetry, aerial, and ground surveys. The winter range labeled "Horseshoe" also includes the Cow Creek drainage. The area labeled "Moraine" also includes Hallowell Park and Beaver Meadows.

rates inversely related to increasing elk population size. We also examine density independent correlations of calf recruitment and survival with precipitation and temperature statistics.

Methods

Several independent data sets were used in this study. Elk that winter inside RMNP have been monitored for most of this century (Packard 1947; Gysel 1959; Stevens 1980). Elk that winter in the Estes Valley outside RMNP have been monitored primarily from 1988 to the present. Elk population counts and composition data (ratios of bulls, spikes, and calves to cows) were collected in RMNP and in the Estes Valley by the Colorado Division of Wildlife (CDOW) and the NPS over the past several decades. To supplement these historical data, we collected data from 1994–2001 separately in the park and town sectors. We analyzed these multiple data sets in two phases: first we made direct estimates of population size, composition, and survival rate from the data; then we used these estimates to fit a series of alternative population projection models.

Direct Estimates

Movement and Survival

From early January through March 1995 we captured 73 elk (62 females and 11 males); each was aged, sexed, and fitted with a telemetry collar with activity monitor and an identifying tag. Elk were captured by net gun from a helicopter in the park and by dart gun from the ground in town. Elk were captured from each of the major wintering areas: 29 from the Estes Valley outside the park, 28 in Moraine Park and Beaver Meadows, and 16 in Horseshoe Park and Cow Creek. In a separate study (Larkins 1997), elk were located several times per month from the ground and fixed wing aircraft between February 1995 and November 1996. Monitoring for mortality at roughly monthly intervals continued through September 1998. Larkins (1997) provides additional details on the capture and monitoring of these elk.

We categorized all winter (defined for this analysis as November–April) locations for each elk with at least five independent telemetry locations during that period. Each elk location was assigned to one of three primary winter range areas (Fig. 1): Moraine Park (including Beaver Meadows and Hallowell Park), Horseshoe Park, or the Estes Valley. Frequent movements of elk between Moraine Park, Beaver Meadows, and Hallowell Park within the Big Thompson River drainage indicated that these areas belong to a single winter range (hereafter referred to as Moraine). Similarly, Horseshoe Park along the Fall River combined with the Cow Creek drainage comprises a separate winter range (hereafter referred to as Horseshoe). Counts of elk locations by winter range were used to summarize patterns of winter range use and fidelity.

Survival was estimated with the known fates model in program MARK (White and Burnham 1999). Specific dates when individuals were observed alive or dead were collapsed into observations for winter (January–March), spring/summer (April–August), and fall (September–December). Alternative models with differing numbers of parameters were considered and the best of these was chosen based on AIC_c (Burnham and Anderson 1998). Annual survival rates were computed by multiplying seasonal rates; standard errors were computed using the Delta method (Cox 1998).

Park Population Size and Composition

Counts and composition data for low elevation winter range areas within RMNP east of the Continental Divide 1965–1991 were provided by Stevens (1980 and personal communication). From 1980 to 1991, ground and air (both helicopter and fixed-wing) count and classification surveys were conducted. Surveys during this time period had no specific design; instead observers attempted to find as many animals in the park as possible. Classification data for this period were not recorded by group, only total counts were recorded. Ground counts and classification surveys were conducted in 1992 and 1993 by NPS employees. From 1994 to 2001, we conducted helicopter counts and classification surveys. Classification data were recorded by group (any collection of individuals appearing to move as a discrete unit) from 1992–2001. To confirm that ground and aerial methods gave consistent classification results, we used both methods on the same day and obtained nearly identical ratios for calves per 100 cows, differing by only $1.0 \pm 3.3\%$ ($\bar{x} \pm$ SE).

Helicopter surveys conducted in 1995–1998 were used to develop a sightability correction model following the methods of Samuel et al. (1987) and Steinhorst and Samuel (1989) supplemented by improved methods for variance estimation developed by Wong (1996) and implemented using PROC IML (SAS Institute 1989). The procedure does not take into account the possibility that the counted size of observed elk groups may be in error. Counting error may result in underestimation of elk population size (Cogan and Diefenbach 1998). However, we believe this potential bias is far less severe for RMNP, because numerous and extensive open areas exist where all elk can be seen and helicopter crews slowly herded large groups of elk from areas of cover into the open before counting commenced. Nevertheless, some unknown level of undercounting bias may still be present.

These surveys yielded 44 potential sighting observations of elk groups. We assumed that the collared elk could be considered a random sample of the elk population. We used PROC LOGISTIC (SAS Institute 1990) to fit logistic regression models to the data set. Sighting characteristics considered were total group size, the natural logarithm of group size, group activity (moving or not), percent tree cover, and percent snow cover, and snow^3/10,000, following Unsworth et al. (1994). Converting percent tree cover into the seven vegetation cover classes of Unsworth et al. (1994) did not meaningfully improve results.

Town Population Size and Composition

Classification data from 1979–2001 were unpublished counts made by CDOW and NPS personnel. Aerial classification surveys using a helicopter were made in August or September of 1980–1982 in Estes Park (G. Bear, personal communication). Classification data for 1979, 1984, and 1986 are based on aerial surveys made in January of Game Management Unit (GMU) 20, which includes Estes Park, but may not represent it accurately (Steve Steinert, CDOW, personal communication). From 1988 to 2001, CDOW or NPS biologists using three to four observers conducted ground counts and classification surveys during February in the town of Estes Park (Rick Spowart, CDOW, personal communication).

To get a better population size estimate than the above counts provided, we conducted a series of 10 mark-resight surveys (Bowden and Kufeld 1995) in the Estes Valley from 1995–1997. A fixed-wing flight was made to determine the number of radio-collared elk within the count area, based on radio signal locations. Ground crews counted elk observed while traversing designated routes within the Estes Valley. Routes were selected to maximize the total number of elk seen and to avoid multiple counts of the same elk on a given day. Additionally, ground counts were made on three consecutive days within 5 days of the flight. We attempted to identify each collared elk seen using the identifying number on its collar. Elk observed in the survey area during the ground count that had been previously classified as outside the area during the aerial survey were reclassified as available marked elk for the population estimate.

Mark-resight population estimates for 1995–1998 were developed from these data using the methods of Bowden and Kufeld (1995). These population estimates were then used as the basis for calibrating a model to estimate population size for other years based on ground count data collected during those years. This model was a linear regression of mark-resight population size estimates on the total number of elk observed during the 3-day ground count using SAS, PROC REG (SAS Institute 1990). Prediction precision was estimated for the regression. However, the residual mean square was reduced by the mean variance of the mark-resight estimates to account for this additional source of variation.

Population Composition Precision Estimates

We used a bootstrap procedure following Wong (1996:115) to compute confidence intervals for sex and age ratio estimates. Data for this analysis consisted of composition of individual elk groups sighted from 1992–2001. We generated an empirical population of elk groups using estimates of sightability based on group size, then resampled this population without replacement based on sighting probability to obtain 1,000 samples. Standard errors were computed as the standard deviation of ratios in these resampled data sets. For years lacking individual group composition data, we used the mean coefficient of variation estimated for years with adequate data, inflated by 50%. The arbitrary 50% adjustment was included to account for probable differences in methods and observers during earlier periods and served merely to place less weight on these estimates in the population model.

Supplemental Data: Weather and Harvest

Monthly precipitation and mean monthly temperature data were obtained from the weather station in Estes Park, Colorado. These data were summarized into summer (April–August) and winter (September–February) periods for use as covariates in our models of recruitment and calf survival. Harvest data were consolidated from CDOW reports and include all elk taken from Game Management Unit (GMU) 20. Unfortunately, GMU 20 encompasses a much larger area than our study and it was not possible to determine what portion of these animals were taken from the Estes Valley. Furthermore, these harvest data are based on telephone and mail surveys, rather than check-station counts and, thus, may be unreliable. Furthermore, no measures of precision were available for harvest estimates, making their reliability difficult to assess. Consequently, we chose to estimate survival rates after all mortality sources, natural and artificial, because of the difficulty of segregating the harvest effect.

Population Models

We fit a series of alternative population projection models with varying numbers of parameters to the direct parameter estimates. Models with fewer parameters assumed that some parameters in the general model were indistinguishable and could be represented by a single value--these models represent special cases of the most general model. Some of these special cases represented important hypotheses of interests, such as whether or not park and town populations could be considered a single population or whether significant dispersal migration was occurring between them. Information theoretic methods (Burnham and Anderson 1998) were used to select the best models from this set. Effects that were supported by the data were identified by their inclusion in the best model. Models were fit for the entire time period of interest despite some missing observations, thus producing a reconstruction of the population.

Model Specification

Our models covered the period from 1965–2001 for park elk, and 1978–2001 for town elk. The Horseshoe and Moraine subpopulations within the park were pooled into a single "park" subpopulation for this analysis. The most general model considered included different parameter values for park and town subpopulations. A more general model of the elk in our study area might have allowed for separate parameters for the two subpopulations that we identified within the park (Moraine and Horseshoe). This was not done for several reasons: (1) these herds had never been considered separate subpopulations before our study and so data were previously not recorded separately for them; (2) the habitats and entire history of management of these subpopulations has been indistinguishable; and (3) calf:cow and spike:cow ratios during the period of our study were virtually identical (estimates with 95% confidence intervals in Horseshoe and Moraine, respectively, were 25.3 [21.2, 34.1] and 25.8 [21.5, 31.6] for calf:cow ratio and 4.6[1.3, 9.6] and 4.1 [2.5, 5.1] for spike:cow ratios). Thus, pooling of data from these subpopulations for comparison to the distinctly different town subpopulation was well justified.

Each subpopulation (park and town) was modeled with five age/sex classes. Population segments were: calves (<1 year); yearling (1 < age <2) males (spikes) and females; and adult (age >2) males (bulls) and females (cows). Projections are made using a 1 year time interval referenced to the mid-winter (February–March) population survey.

Calves are recruited from the adult female segment of the population at a rate determined by a recruitment submodel and estimated sex ratio. Calf recruitment was defined as the number of calves per adult female in the mid-winter count. Calf survival was defined as the proportion of those recruited calves that survived until the following year's mid-winter count when they are reclassified as yearlings. Separate survival rates for each age and sex segment within each subpopulation were considered. Calf survival, S_c, for each subpopulation was related to local population size and four weather statistics through a logistic model:

$$\ln\left(\frac{S_c}{1 - S_c}\right) = \beta_0 + \beta_1 N_T + \beta_2 T_s + \beta_3 T_w + \beta_4 P_s + \beta_5 P_w$$

where N_T is the total subpopulation size; T_s and T_w are average summer (April–August) and winter (September–February) temperature deviations from the mean over all years of the study; P_s and P_w are average summer and winter precipitation deviations from the mean over all years of the study; and the B_i values are estimated parameters. Recruitment rate for each subpopulation was also modeled using a similar logistic function incorporating these density and weather covariates. Each winter range remained a constant size, therefore we consider correlations to population size equivalent to correlations with elk density.

With separate models for calf recruitment and survival and for both park and town populations, up to 24 parameters could be estimated for this portion of the model in the most general case. In addition, the most general model allowed for separate estimates of survival and productivity for older elk of each sex in each sector (park or town), plus a linear time trend in each of these survival rates, resulting in eight potential parameters. A common survival rate was estimated for adult and yearling males and another for adult and yearling females, because data were insufficient to distinguish these individual rates.

We included parameters to account for temporary movements of elk from one sector to the other (elk that normally wintered in one sector, but were counted in the other due to temporarily moving across the park boundary in the area of winter range overlap noted earlier). Parameters for temporary migration were only considered in years when population data were available for both sectors. We also considered permanent dispersal at either a constant rate or varying linearly with either park or town population size. All parameters were constrained to biologically meaningful values.

Parameter Estimation by Model Fitting and Selection

The specified model of elk population dynamics contained various unknown variables, some of which had been measured directly in the field and others that had not. Model-based estimates of each of the quantities observed in the field were compared to the direct estimates. Following a procedure by White and Lubow (2002), we computed a sum of squared errors between the model estimate, $\hat{\theta}'_i$, and the direct estimate, $\hat{\theta}_i$, each weighted by the variance of the direct estimate, var($\hat{\theta}_i$),

$$\mathrm{SSE} = \Sigma_i \frac{(\hat{\theta}'_i - \hat{\theta}_i)^2}{\mathrm{var}(\hat{\theta}_i)}$$

We used the numerical optimizing tool in the Microsoft Excel® spreadsheet software to minimize the SSE by seeking optimum values of the model parameters. Assuming normality of errors, a log-likelihood was computed from this statistic. This approach enabled disparate direct estimates, including population size, population composition, and independently estimated survival rate, to all be included in estimating an overall population model. Notice that the model estimates, $\hat{\theta}'_i$, such as population ratios, used in the least squares fit do not need to be identical to model parameters, such as survival and recruitment rates, as long as the modeled values can be used to compute estimates of the same parameters observed in the field.

We compared the ability of alternative models to represent observed dynamics using Akaike's Information Criteria with small sample bias correction (AIC_c) to examine the relative support in the data for different ecological parameters involved in elk population dynamics. Results are stated as AIC weights, where the best model has a weight of 1.0 to show the relative strength of support for the alternative model (Burnham and Anderson 1998).

Profile likelihood confidence intervals for the selected model parameter estimates were computed by finding the pair of parameter values (one less and one greater than the maximum likelihood estimate) that resulted in reducing the log-likelihood by 1.92 (corresponding to a 95% confidence interval) from the maximum likelihood. Estimates of precision for derived parameters (i.e., those not part of the fitted model, but computed from them, such as *K*) were based on the Delta method (Cox 1998). This required computation of first and second derivatives of the log-likelihood with respect to each model parameter and inverting the matrix of second partial derivatives to get the variance-covariance matrix. These derivatives and all matrix computations were computed numerically in Microsoft Excel® and Microsoft Visual Basic® using numerical methods described by Abromowitz and Stegun (1970) and Press et al. (1992).

Results

Winter Range Locations

Classification based on winter telemetry locations, placed 85% of the 73 radio-collared elk in one of the three winter ranges (Fig. 1). Of the remaining elk, 4% used both Horseshoe Park and Estes Valley ranges, 8% used both Moraine and Estes Valley, and 3% used all three. Of the 11 elk that did not use a single winter range exclusively, only one was a male. Thus, 9% of marked males and 16% of marked females were migratory. The migratory male was age 7 at capture; ages of the 10 migratory females ranged from 1–10 years. Although some individuals were observed using multiple winter ranges, none were observed to switch winter range use between years.

Elk captured in Moraine Park were observed just outside the park boundaries in an area that is also used by the town subpopulation, although not at the same time. Therefore, some elk groups could be assigned to the wrong subpopulation during counts in some years, were it not for the presence of radio-collared animals. In summary, the data suggest that there are three distinct and cohesive subpopulations of elk with different, but slightly overlapping, winter ranges with boundaries that do not correspond precisely to park boundaries.

Direct Parameter Estimates

The best model of sighting probability contains group size, activity, tree cover, and snow cover covariates.

However, in this model the coefficient for tree cover was not significant ($P = 0.125$), hence we used the simpler model without this covariate ($\Delta AIC_c = 0.575$):

$$\ln\left(\frac{u}{1-u}\right) = 2.937 - 2.506(\text{activity}) + 0.0276\left(\frac{\%\ \text{snow cover}^3}{10{,}000}\right) + 0.0494(\text{group size})$$

where, u, is the probability of sighting a group. The model is significant ($P < 0.0001$) as are each of the slope coefficients ($P < 0.05$). Park subpopulation size estimates were made using several of the fitted sighting probability models and the Hiller 12E model of Unsworth et al. (1994). Further estimates were made for some models by applying adjustments only to groups of size less than 75. This assumed that groups of size 75 or more were always seen. All subpopulation size estimates for the same year were roughly similar regardless of which model was used (Table 1). Mean size of the park subpopulation estimates from 1995–1998 was 1,045 ± 100 ($\bar{x} \pm$ se) elk. Assuming similar sighting conditions were encountered during earlier surveys, regression of the sightability adjusted estimates versus raw counts provided a means of adjusting earlier park counts for which no covariates were available. This regression yielded:

$$\hat{N}_p = 42.442 + 1.0958\ (\mathit{count})$$

Precision of estimates based on this regression was given by the standard linear regression prediction precision formula plus a 50% inflation to account for methodological differences:

$$se(\hat{N}_p) = 1.5\sqrt{2448\left(1+\frac{1}{6}+\frac{(\text{count}-840)^2}{211958}\right)}$$

Town subpopulation size estimates for the 11 winter survey periods between 1995–1998 ranged from 942–2,494 ($\bar{x}$ = 1,734 ± 162; Table 2). Some movement of elk in and out of the count area during mark-resight periods was observed, however, if collared and uncollared elk move in or out of the count area at the same rate during this time period the estimation procedure remains an unbiased estimate of the number of elk in the count area at the time of the flight to locate radio-collared elk.

Using the mark-resight estimates to calibrate the raw counts in other years yielded the following relationships:

$$\hat{N}_t = 79.82 + 0.742\ (\text{3-day count})$$

$$\hat{N}_t = 160.4 + 2.35\ (\text{1-day count})$$

The linear regression accounted for 58.3% of the variation in the mark-sight subpopulation estimates in the 3-day ground count and 79.7% in the 1-day counts. Prediction precision for these two regressions (including a 50% inflation factor for the 1-day counts) are computed as:

$$se(\hat{N}_t) = \sqrt{147455\left(1+\frac{1}{10}+\frac{(3\_day\_count-2195)^2}{2997580}\right)}$$

$$se(\hat{N}_t) = 1.5\sqrt{44425\left(1+\frac{1}{4}+\frac{(1\_day\_count-715)^2}{2170896}\right)}$$

Corrected estimates and precision are reported in Table 1.

Composition counts are listed in Table 3 along with bootstrap precision estimates for years with individual group data. Precision estimates for other years were extrapolated based on assumed coefficients of variation for park and town, respectively, of 0.575 and 0.576 for bull:cow ratios, 0.437 and 0.204 for spike:cow ratios and 0.142 and 0.088 for calf:cow ratios. Each represents a 50% inflation of the mean CV for the years with available bootstrap estimates.

Based on direct estimation with program MARK, the best AIC_c model contained no survival differences between yearling and adult age classes or between sex classes within either the park or town populations. A single annual survival rate of 0.929 ± 0.023 adequately describes the park subpopulation. Two seasonal survival rates best describe the town subpopulation: 0.821 ± 0.043 for the 7-month winter period, and 0.97 ± 0.001 for the 5-month spring/summer period. The combined annual survival rate estimate for town elk is, therefore, 0.797 ± 0.043. This direct estimate of survival represents an average of male and female survival, weighted by the proportions of each in the sample, thus this result must be compared to a similarly weighted average of the separate male and female survival rates estimated for the fitted subpopulation model.

Table 1. Elk count data and population estimates for Rocky Mountain National Park (Park) and the adjacent Estes Valley including the town of Estes Park, Colorado (Town).

	Park			Town			
Year	Count[a]	Estimate[b]	SE[c]	1 day count	3 day count	Estimate[d]	SE[e]
1965	427	510	104				
1966	437	521	103				
1967	419	502	105				
1968	310	382	117				
1969	579	677	91				
1970	419	502	105				
1971	501	591	97				
1972	589	688	90				
1973	387	467	109				
1974	516	608	96				
1975	452	538	102				
1976	863	988	80				
1977	491	580	98				
1978	812	932	80				
1979	715	826	83				
1980	739	852	82				
1981	799	918	80				
1982	689	797	84				
1983	1,387	1,562	119				
1984	809	929	80				
1985	1,010	1,149	85				
1986	750	864	81				
1987	779	896	81				
1988	854	978	80	476		1,279	357
1989	702	812	83	303		872	364
1990	753	868	81	369		1,027	361
1991	1,022	1,162	85	532		1,410	356
1992	787	905	81	557		1,469	355
1993	648	753	86	528		1,401	356
1994	552	600	34	620		1,617	354
1995	1,027	1,221	193	568	1,741	1,178	154
1996	675	788	78	552	2,477	1,727	204
1997	784	988	139	992	3,116	2,474	286

(Continued on next page)

Table 1. Concluded.

Year	Park			Town			
	Count[a]	Estimate[b]	SE[c]	1 day count	3 day count	Estimate[d]	SE[e]
1998	1,075	1,184	83	748	2,612	1,983	298
1999	932	1,036	80		3,169	2,431	457
2000	694	730	30		3,167	2,430	457
2001	1,346	1,418	56		1,754	1,381	414

[a] Counts are from helicopter surveys only in 1994–2001 and from a mixture of ground and fixed-wing aerial surveys in earlier years.

[b] Estimates are based on sightability adjustment model, described in text, for 1994–2001. Earlier years' estimates are based on a regression of estimates versus raw counts for these 8 years.

[c] Standard errors are based on Wong (1996) for 1994–2001. Earlier years' precision is based on regression prediction interval inflated by 50% to account for methodological differences.

[d] Mark-resighting survey estimates from Table 2 for date closest to the date of park estimates were used in 1995–2001. Estimates for 1994 and earlier are based on regression of 1-day counts on mark-resight estimates.

[e] Standard errors for 1995–2001 estimates are based on mark-resighting analysis. For earlier years, standard errors are based on prediction error of the regression model inflated by 50% to account for methodological differences.

Table 2. Summary of results for mark-resight population size estimates for Estes Valley including the town of Estes Park, Colorado.

Dates	Total elk count	Collared elk in town	Count of collared elk	Estimated population size	Estimated standard error	95% confidence limits
April 3–5, 1995	1,741	31	45	1,178	154.38	913–1,575
May 8–10, 1995	2,208	49	67	1,644	178.30	1,334–2,075
October 10–12, 1995	918	18	16	942	266.35	536–1,990
December 11–13, 1995	2,400	44	41	2,494	436.86	1,788–3,711
January 16–18, 1996	2,017	29	46	1,245	179.21	941–1,719
February 16–20, 1996	2,477	29	41	1,727	203.72	1,371–2,239
March 20–22, 1996	2,321	34	65	1,208	81.91	1,057–1,395
January 31–February 2, 1997	2,559	31	37	2,103	289.05	1,610–2,855
February 19–21, 1997	3,116	33	41	2,474	286.34	1,974–3,185
March 10–12, 1997	2,128	31	31	2,073	329.74	1,524–2,971
March 9–12, 1998	2,612	31	41	1,983	297.80	1,483–2,778

Table 3. Elk population age and sex composition counts for Rocky Mountain National Park (Park) and the adjacent Estes Valley including the town of Estes Park (Town), Colorado expressed as ratio per 100 cows.

	Park[a]						Town[b]					
Year	Bulls	SE	Spikes	SE	Calves	SE	Bulls	SE	Spikes	SE	Calves	SE
1965	28	16.1	13	5.5	39	5.5						
1966	11	6.3	18	7.9	53	7.5						
1967	24	13.8	9	3.9	46	6.5						
1968	33	19.0	11	4.8	38	5.4						
1969	36	20.7	9	3.9	36	5.1						
1970	12	6.9	15	6.6	26	3.7						
1971	18	10.3	14	6.1	27	3.8						
1972	26	14.9	13	5.7	44	6.3						
1973	12	6.9	13	5.7	26	3.7						
1974	15	8.6	10	4.4	39	5.5						
1975	17	9.8	17	7.4	33	4.7						
1976	9	5.2	9	3.9	30	4.3						
1977	11	6.3	11	4.8	36	5.1						
1978	11	6.3	8	3.5	35	5.0	7	4.0			60	5.3
1979							50	28.8	6	1.2	42	3.7
1980							35	20.2	6	1.2	43	3.8
1981							52	30.0	14	2.9	60	5.3
1982							35	20.2	18	3.7	46	4.1
1983												
1984			10	4.4	39	5.5						
1985			8	3.5	30	4.3						
1986			11	4.8	35	5.0						
1987			5	2.2	40	5.7						
1988			14	6.1	39	5.5	3	1.6	8	1.5	55	1.8
1989			4	1.7	34	4.8	10	5.6	10	3.4	41	2.3
1990			7	3.1	37	5.3	5	2.2	10	1.4	43	2.7
1991			9	3.9	28	4.0	6	2.7	10	3.3	37	3.2
1992	46	14.1	10	3.3	36	4.0	7	2.3	13	1.5	42	1.0
1993	31	6.2	17	5.6	56	5.4	19	6.3	13	2.0	43	3.6
1994	14	4.7	5	0.7	32	1.6	13	5.4	12	1.0	28	1.3
1995	8	2.2	6	0.8	23	1.5	15	8.6	8	1.6	27	2.4
1996	24	6.9	7	1.5	15	0.8	12	4.2	11	1.3	41	1.6
1997	9	3.0	4	0.6	30	1.2	13	1.9	10	0.5	44	1.4
1998	33	11.8	6	2.1	37	4.2	8	2.7	11	1.0	33	1.3
1999	26	21.4	3	1.6	23	2.8	8	2.5	10	0.1	31	1.7
2000	8	4.5	7	4.3	26	3.6	7	2.9	10	0.5	31	4.5
2001	20	7.4	7	0.9	26	2.5	8	3.1	8	0.8	26	1.7

[a] Composition counts for 1994–2001 were made by helicopter survey for this study. Earlier counts were made by RMNP biologists using a mixture of ground, helicopter, and fixed-wing aerial surveys. Standard errors for 1992–2001 are based on 1,000 bootstrap resamples of elk groups. Earlier estimates are assumed to have error coefficients of variation 50% larger than the average calculated for the later period.

[b] Composition counts for 1988–2001 were conducted in February on the ground using 3–4 observers, led by CDOW biologist Rick Spowart. Standard errors for 1988–2001 are based on 1,000 bootstrap resamples of elk groups. Earlier estimates are assumed to have error coefficients of variation 50% larger than the average calculated for the later period.

Population Model

The best population model fits the estimated population size data well (Fig. 2), but shows considerable deviation from the estimated population composition data (Fig. 3). In large part, this reflects low precision of the ratio estimates and the superiority of the model estimates based on inferred survival and productivity. Thus, the variation in these ratio estimates is due primarily to sampling error and not to large annual fluctuations in the actual parameters. Total population size in the park rose rapidly during roughly the first third of the study (1968–1981), then appeared to rise gradually (1982–1990) and then remain near a dynamic equilibrium during the remainder (1991–2001). Model-based estimate of population size for the town subpopulation in 2001 was 1,975 [95% CI = 1,701; 2,292] elk and 1,074 [1,000; 1,154] elk for the park subpopulation (Fig. 2).

As populations have grown over the period of study, ratios of calves:100-cows have declined in both the park and town (Fig. 3). Model-based estimates show a decline from 36.0 to 28.4 calves:100-cows in the park between 1986 and 2001 and from 50.0 to 29.9 in town between 1978 and 2001. Spike ratios have also declined steadily, from 11.7 to 6.9 spikes:100-cows in the park, and from 11.0 to 5.1 in town, over the same periods. Bull ratio changes appear to be more complex, initially falling then slowly rising in the park, while remaining steady in town; however, large measurement errors and missing values in these observations make patterns difficult to detect. However, current ratios of bulls:100 cows are substantially higher in the park (22.2) than town (6.1), presumably reflecting the differential effect of legal harvest outside the park.

Of the models evaluated, one stood out as clearly superior to all others. This best model included different values between park and town for every parameter value (Table 4) except noncalf female survival. Models that set other park and town parameter values equal, received negligible AIC_c weight (<0.1%). Removing any of the non-weather parameters from this model lowered the weight to <0.1% relative to the best model. Other combinations of the same number or fewer weather covariates were clearly inferior, receiving <5% of the best model's weight.

Male survival in both park and town subpopulations differed from each other and from noncalf female survival (Table 4). In the park, male noncalf survival rate exhibited an increasing linear trend over time from 52% in 1965 to 79% in 2001, but no trend was supported by the town data. Sex ratios at recruitment favored females in both subpopulations, but by a larger margin in town. Calf recruitment was density dependent in both park and town, but with different slopes, reflecting the different carrying capacities of the two ranges. However, when recruitment is depicted relative to K, patterns in the park and town are nearly linear with similar slopes (Fig. 4). Calf survival differed between park and town and was negatively affected by density in the park, but not in town (Table 4). The effect of density on calf survival in the park was more abrupt than on recruitment, with about two-thirds of the reduction occurring between half of K and K. Average calf survival rates in the park and town were similar. Calf recruitment rates were unique for the subpopulations and appear to have been so throughout the period studied, however, the recruitment rates appear to be converging over time as the town subpopulation grows (Fig. 4).

Calf survival is not correlated with any of the weather covariates in the park elk. Town calf survival is correlated positively with winter temperature (Table 4). Recruitment is also positively correlated with winter temperature in the town subpopulation. Recruitment in town is also positively correlated with summer temperature and precipitation. All other weather covariate relationships tested were insufficiently supported to be included in the final model.

Evidence exists for 20 temporary cross-boundary movement events involving bulls 4 times, spikes 6 times, cows 5 times, and calves 5 times (Figs. 2 and 3). Before 2001, all temporary cross-boundary movements involved park elk being observed in the town sector, however, in 2001, calves and cows may have moved in the opposite direction for the first time. Data were insufficient to attempt estimation of temporary cross-boundary movements before 1988, so the absence of parameters from these years does not imply that it did not occur.

The park subpopulation estimates have remained within ±5% of projected K between 1991–2001 and exhibited minimal trend, increasing by only 55 animals or 0.5%/year. The town subpopulation, on the other hand, has continued to grow, averaging 5.2%/year between 1991–2001. Using parameter estimates from the best model, we extrapolated to equilibrium assuming that no significant changes in current management, including harvest regulations, occur and that male survival in the park will not continue to increase. These projections lead to estimates for $K = 1{,}069 \pm 55$ elk for the park and $2{,}869 \pm 415$ elk for town. Using estimates of winter range area from a related study (Singer et al. 2001), we computed corresponding densities at K of 10.1 elk/km² and 47.3 elk/km². Model projections predict that 90% of K will be reached in town in the year 2013.

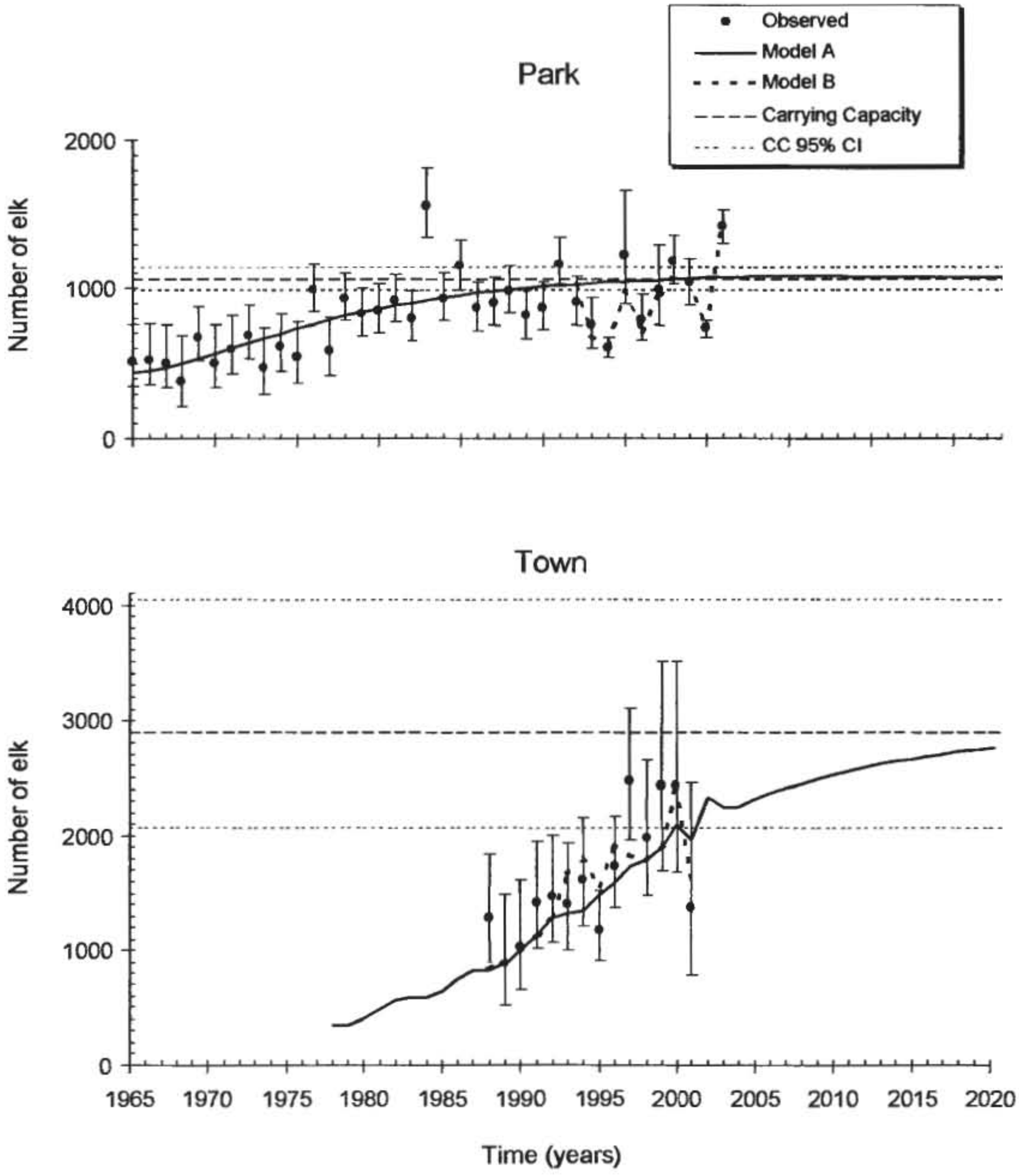

Fig. 2. Total size of elk population based on field observations and fitted models for Rocky Mountain National Park (park) and the adjacent Estes Valley, including the town of Estes Park, Colorado (town). Models include the effects of elk density, summer precipitation and temperature, and winter temperature on elk population dynamics (see Table 4 for parameter estimates). Model A depicts estimates for each actual subpopulation, Model B included the modeled effects on field estimates of 20 temporary cross-boundary movements of elk supported by the data, which resulted in miscounting some individuals belonging to the park subpopulation as town elk. Confidence intervals for population estimates are constructed from standard errors in Table 1 assuming normal errors. Ecological carrying capacity (K) is the equilibrium projected by the model with weather covariates set to their average values.

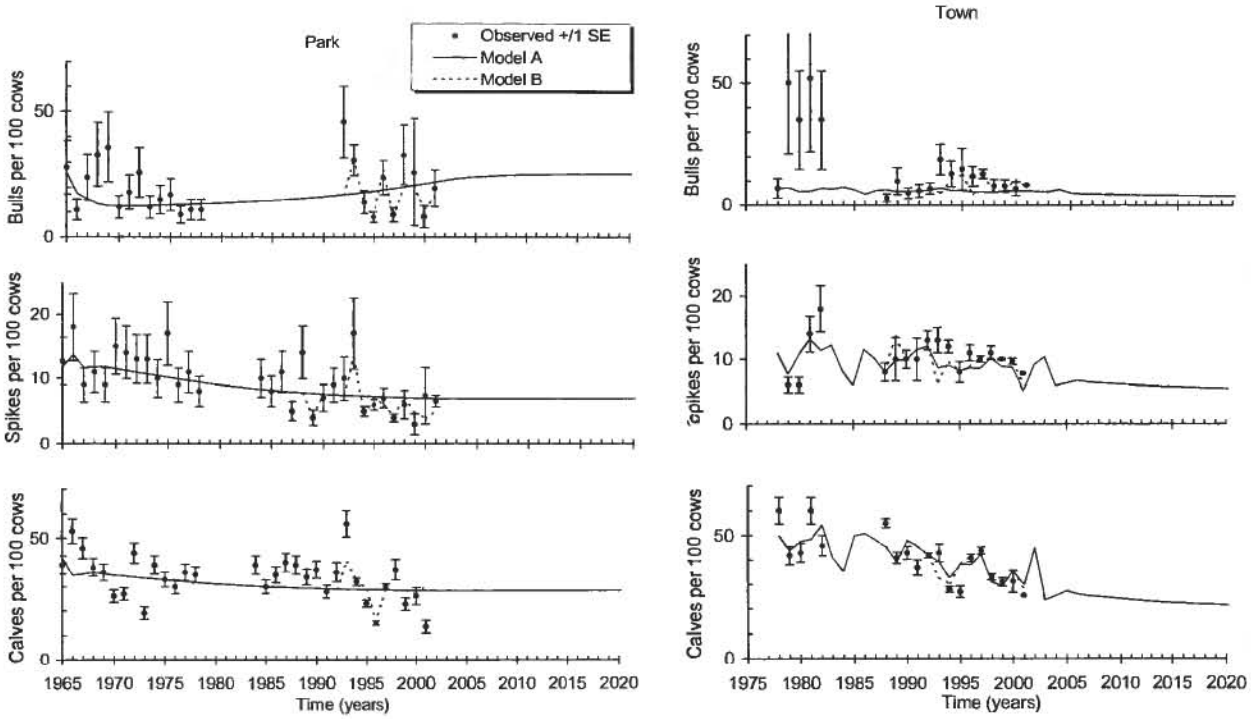

Fig. 3. Direct estimates and best fitted model for sex and age composition of elk bull:100 cow, spike:100 cow, and calf:100 cow ratios in both: (A) Rocky Mountain National Park (park); and (B) the adjacent Estes Valley including the town of Estes Park, Coloraod (town). Model A depicts estimates for each actual subpopualtion; Model B includes the modeled effects on field estimates of 20 temporary cross-boundary movements of elk that resulted in miscounting some individuals belonging to the park subpopulation as town elk. Precision of observations is shown as ±1 SE, based on values in Table 3.

Discussion

Elk were using two major migration routes during the time (1995–1996) of Larkin's (1997) study, suggesting two separate elk populations, one that wintered in Estes Valley and Horseshoe Park, and another that wintered in Moraine Park within RMNP. Timing of migrations also differed for Horseshoe Park and Estes Valley elk, confirming Bear's (1989) findings. Our reanalysis of Larkin's data confirms a strong philopatric pattern in winter range use, despite an absence of significant barriers between these winter ranges; however, we conclude that there are actually three distinct populations, based on winter range locations, and that the Horseshoe Park subpopulation is distinct from the other two.

Despite the distinct Horseshoe and Moraine subpopulations, our models pool these for the purpose of comparing them to the town subpopulation. Evidence of similar demography within the park, combined with identical management histories and habitats justify this approach. The distinctness of the town subpopulation and absence of permanent dispersal observed in the radio location data is confirmed by our population modeling. Different survival and recruitment rates can be distinguished between the park and town subpopulations, whereas dispersal migration parameters are not supported. Only recently are the calf recruitment rates of the two subpopulations beginning to converge as the town subpopulation approaches *K*. Thus, the town subpopulation appears to be growing independently of the park subpopulation. Although the origin of the town subpopulation was likely emigration from the park and some limited exchange may continue to take place, this mechanism does not appear to be important to its

Table 4. Parameter estimates for best (AIC_c) model for Rocky Mountain National Park (Park) and the town of Estes Park and surrounding Estes Valley (Town).

	Park			Town		
Parameter[a]	Estimate	LCL[b]	UCL[b]	Estimate	LCL[b]	UCL[b]
Male survival rate (age <1.5), intercept[c]	0.496	0.468	0.520	0.418	0.351	0.474
Male survival rate (age <1.5), time slope[c]	0.913	0.911	0.915	0.913	0.911	0.915
Adult (both sexes) survival rate (age >1.5)[d]	0.913	0.911	0.915	0.913	0.911	0.915
Calf survival, intercept	2.35	2.27	2.44	0.729	0.665	0.795
Calf survival, density slope	-0.00195	-0.00205	-0.00186			
Calf survival, winter temperature slope				0.392	0.337	0.449
Recruitment, intercept	0.349	0.307	0.392	0.878	0.782	0.974
Recruitment, density slope	-0.00111	-0.00115	-0.00106	-0.00074	-0.00080	-0.00068
Recruitment, winter temperature slope				0.105	0.081	0.129
Recruitment, summer temperature slope				0.261	0.238	0.284
Recruitment, summer precipitation slope				0.413	0.368	0.457
Recruitment sex ratio	0.444	0.431	0.457	0.374	0.368	0.379

[a] In addition to the 19 unique parameter estimates shown here, the best model contains 20 parameters for temporary cross-boundary movements and 2 for initial population size for a total of 41.

[b] Confidence intervals are based on profile likelihood method, i.e., parameter values are found that reduce the $\ln(L)$ by 1.92.

[c] Survival is computed as a linear function of the year, t, referenced to a base year of 1962.

[d] Common parameter for park and town.

sustained growth. This conclusion is consistent with those of Edge et al. (1986) and Van Dyke et al. (1998) who also observed strong range fidelity and herd cohesion in adjacent populations.

Although harvest data were not used in this analysis, our results are consistent with prior expectations that harvest of males should be greater for those that winter outside, rather than inside, the protection of the park. Low, but increasing, male survival in the park indicates that these individuals are also subject to harvest at some times, but that this effect has declined over time. Harvest of female elk does not appear to have a differential impact on park versus town survival rates. Many female elk that winter outside the park may remain in the park during hunting season, or, the low (1.7% from 1989–1997) female harvest rate may be too small to have a measurable effect.

An area of overlap between the Moraine and Town subpopulations observed in the telemetry data, was confirmed by the modeling which found evidence that groups of elk from the park had occasionally crossed the national park boundary and been counted in the town sector, decreasing park and increasing town population estimates in those years. Evidence for such movements exist throughout the period (1988–2001) for which adequate data are available to detect them. Given the distinct dynamics of these two populations, lack of support for models with dispersal parameters, and the absence of contradictory telemetry data, we suspect that these movements are not resulting in substantial mixing of the populations or permanent emigration from the park. Instead, it is likely that these populations do use some of the same areas outside of the park at different times, but remain demographically isolated from each other

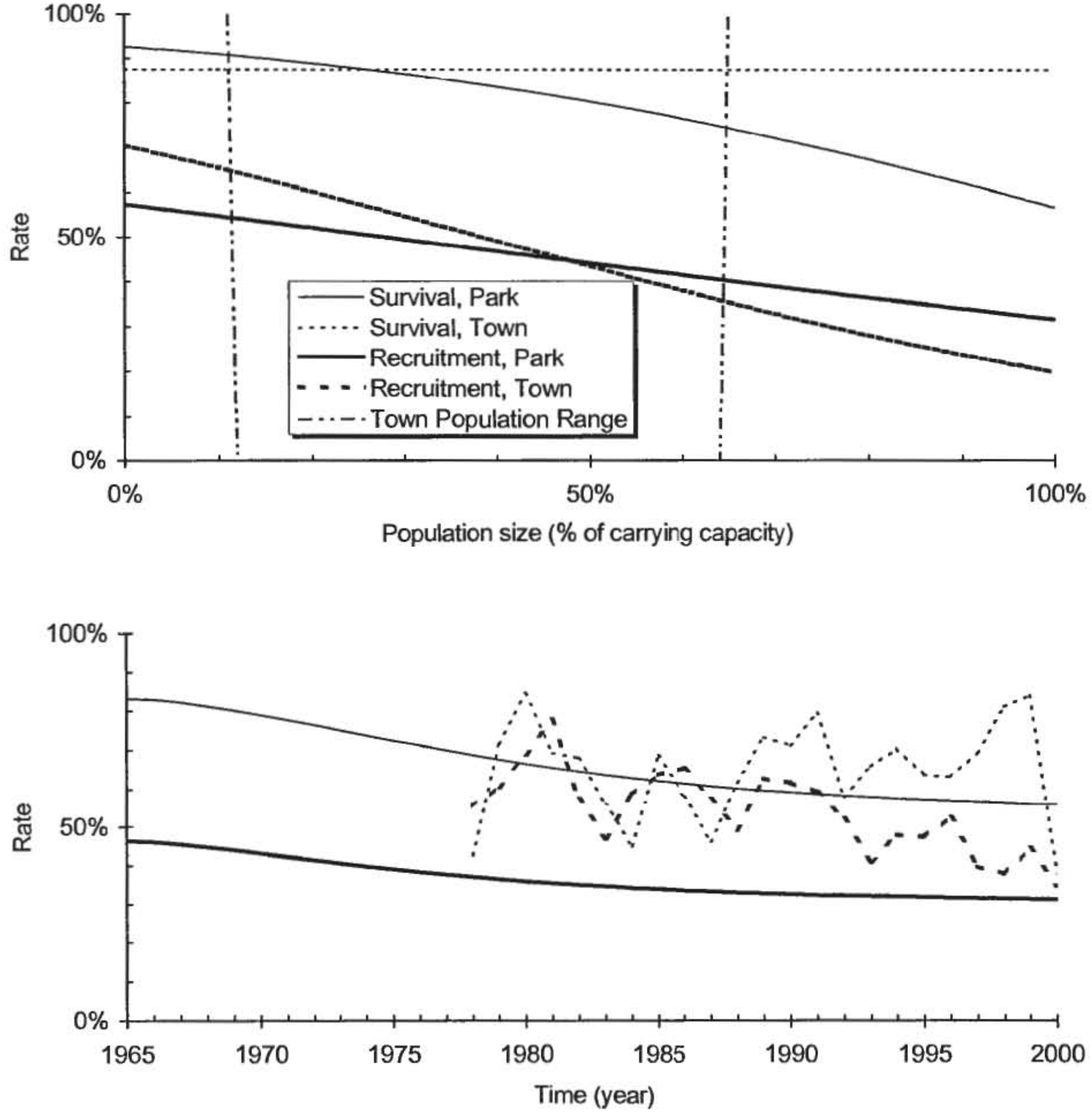

Fig. 4. Relationships between elk calf recruitment and survival rates in the park and town subpopoulations and population density relative to: (A) local carrying capacity (*K*) and (B) time. Relationships are based on the AIC$_c$ selected best model; however, weather covariates were set to their average values in (A) to clarify the density relationships.

through behavioral mechanisms. Until 2001, all temporary movements were from the park to town. However, the data suggest that movement from town to the park occurred in 2001. As the town population approaches *K*, we predict that movements in both directions will become nearly equal.

We concluded that the town subpopulation is still growing, even though the park subpopulation is no longer growing. We attribute the growth to higher recruitment and calf survival rates in town than in the park, rather than due to dispersal of elk from the park. Elk first appeared in the town sector in noticeable numbers about 1975–1980 (N. T. Hobbs, personal communication), or 8–13 years after elk in the park sector were released from artificial controls. This is also approximately the time at which population growth in the park slowed as it approached *K*, possibly providing the impetus for emigration. Thus, the town elk are chronologically behind the park elk subpopulation in occupying the available habitat.

Our estimated *K* for town assumes continuation of historic harvest levels which, so far, have not been adequate to maintain a stable population. Restrictions on hunting within town limits have undoubtedly provided the town elk subpopulation with a refuge. Our results indicate this projected equilibrium to be substantially higher than the current subpopulation size, although the projected equilibrium with continued harvest is undoubtedly lower than it would be in the absence of harvest. Thus, human-wildlife conflicts in the town, such as elk damage to ornamental shrubs, lawns, and golf courses, and potentially hazardous interactions with humans are likely to increase along with the expansion of both human and elk populations in the town sector.

We found strong evidence for density dependent feedback in the park elk subpopulation--only models that included population size feedback were supported by the AIC_c comparisons, and confidence intervals on density parameters are small. The primary mechanism of density feedback in both subpopulations was a nearly linear decline in calf recruitment, followed by more abruptly declining calf survival (Fig. 4). These mechanisms were also observed in the Yellowstone NP and Rhum examples (Clutton-Brock et al. 1982; Houston 1982; Coughenour and Singer 1996; Singer et al. 1997). Evidence for density dependence in the town subpopulation exists but is weaker, as demonstrated by the wider confidence intervals estimated for *K*. This is not surprising because this subpopulation has not yet reached *K*. The nearly linear decline in recruitment is similar to the relationship observed in the park (Fig. 4). Thus, there is no indication that density responses of these two subpopulations are qualitatively different, just that the threshold for a detectable effect on calf survival has not yet been reached in the town subpopulation, which first exceeded half of *K* only as recently as 1995. Because we were unable to measure the calf survival response to density in town, it is possible that the true value of *K* is lower than our projections due to the effect of this additional mechanism.

The RMNP elk population example met several conditions for demonstration of density dependence that were also met in the Yellowstone NP and Isle of Rhum examples: (1) the populations were released from artificially reduced population sizes taken well below (<1/2 of) *K*; (2) monitoring continued for several decades until each population had reached and remained near *K*; and (3) total population size data was supplemented by composition data. Failures to detect density dependence (Bartmann et al. 1992; Saether et al. 1996; Shenk 1998; Smith and Anderson 1998) have involved populations fluctuating near *K*, used a shorter time series (<10 years), used only total population size data, exhibited high density independent variation, or were confounded by artificial feeding.

Our results indicate that both calf recruitment and subsequent survival is affected by winter temperature in town, but not in the park. Since lower temperatures are associated with lingering snow cover, it is plausible that snow accumulation in early winter reduces calf recruitment (calves first counted at age 0.5) and snow in late winter reduces subsequent calf survival (from age 0.5 to 1.5 years). Failure to detect a similar effect in the park may be due to excessive noise (unidentified sources of temporal variation or measurement error), because our earlier analysis of these same data through 1999 did detect a positive effect of winter temperature on calf survival in the park. Consistent efforts to collect snow depth data on elk winter ranges would be worthwhile and could improve our understanding of this effect.

In town, increased calf recruitment was also correlated with both increasing summer (April–August) precipitation and temperature. Both effects are likely due to nutritional effects--warm temperatures reduce the period of snow cover and more summer precipitation promotes plant growth (Sims and Singh 1978; Webb et al. 1978; Sala et al. 1988; Merrill et al. 1993). However, the park subpopulation exhibited no similar correlation. Differences between these subpopulations in the timing of migrations from winter to summer range may explain the discrepancy. Or, this may simply reflect the difficulty of detecting an effect of weather with a time series of insufficient length in an environment with only moderate annual variation. To improve chances of discovering associations between weather and elk survival, direct estimates of calf recruitment and survival using calves captured and collared annually over long periods is required.

Our projected equilibrium *K* estimates for the two populations are not intended to imply that there is a single, static equilibrium for either subpopulation. Undoubtedly, changes in vegetation biomass due to variable weather patterns result in a fluctuating and possibly drifting *K*. Furthermore, long-term continued human alterations of the landscape in town could change carrying capacities. Since human domiciles in the town sector are currently only 30% of what is possible, (Theobold et al. 1997), we predict that human developments unusable to elk (pavement, buildings) will increase, eventually leading to reduced *K* for elk in the town sector. On the other hand, the annual fertilizations and irrigations of altered grasslands in the town sector may reduce annual fluctuations due to weather patterns.

The nearly 5-fold difference in absolute density of elk at *K* in the park and town is consistent with the analysis of forage availability. The area of grasslands in the town sector are twice as large as in the park, and many of the town's grasslands are enriched with fertilizers or irrigation (Singer et al., this volume). Thus, the forage base and potential habitat for elk in town is much larger than in the park, supporting much higher absolute elk densities. Our estimate of $K = 1{,}069 \pm 55$ elk in the park is remarkably close to that made >20 years ago by Hobbs et al. (1982) based on energy and nutritional considerations. Their estimates were 991 ± 102 and 1,481 ± 261 for a slightly dry and wet year, respectively. If carrying capacities do vary temporally as much as these results suggest, we would not expect the elk population to expand rapidly enough in good years to achieve the population size that a single year of forage availability would permit. Consequently, we expect that the observed average population would remain closer to the forage-based *K* imposed by poor years. The comparison of our estimate with the lower of the two estimates of Hobbs et al. (1982) suggest that this is precisely what has occurred. In a related study (Singer et al., this volume), an independent estimate of *K* in town, based entirely on forage biomass and quality, was 3,082 ± 103 elk, compared to our population projection estimate of 2,869 ± 415 elk. Given the substantial overlap in confidence intervals and the close agreement between these two methods for park elk, our confidence in these projections is high.

The data sets used in our analyses have been collected over several decades, by multiple investigators, and using varying methods. Consequently, the robustness of our conclusions must be evaluated in this context. Because the most reliable and consistent survey methods were used during the most recent 5 years, we lowered the weight given to earlier estimates by inflating their variance estimates. This would reduce the effect of any biases or inconsistencies on our conclusions. Although we found no undercounting of calves in the park by ground composition counts relative to aerial counts, many older males were missed by this method because they tend to forage in more densely vegetated areas. However, it is the dynamics of females that are of greatest interest in modeling a population. Furthermore, there is no noticeable discontinuity in the male composition ratios at the start of our 5-year study using aerial observations. The use of ground counts in town is less problematic because of fewer areas of dense cover and a more extensive road network. Although comparisons of absolute numbers between park and town may be biased by the survey methods, the patterns of change over time should be unaffected. Thus, the observation of continued population growth in town contrasted with relative stability in the park is not likely due to methodological differences. Nor are temporal correlations of vital rates with weather covariates in each subpopulation affected by any consistent bias. However, the differences in some estimates, such as sex ratios, could be due, in part, to such biases.

Fitting mechanistic population dynamics models to multiple sources of data is a valuable technique for extracting an understanding of a population from several noisy data sets. Although our individual data had large measurement errors, when combined with other data, reasonable estimates of vital parameters emerged. Undoubtedly, more precise data would provide better final estimates as would direct measurement of additional vital parameters, such as recruitment or calf survival. Detecting density dependence would be most easily accomplished by directly monitoring calf recruitment and survival, using radio marked calves. Because the density relationships lead to estimates of *K*, these would be improved as well by such data.

Management Implication

Correcting future population counts in town through our calibration relationship based on our mark-resighting estimates is undoubtedly an improvement over the raw counts. However, because of the small number of observations (11) used in developing this relationship, confidence intervals will be much wider than those for the mark-resight estimates made in this study. Furthermore, future changes in habitat or elk behavior could bias estimates based on this calibration. Thus, we recommend repeating the mark-resighting study about once each decade.

Similarly, the sighting probability model developed for the park was developed with a limited (n = 44) number of observations. The high elevation (8,000–9,000 ft), close proximity to the Continental Divide, and frequent high winds precluded obtaining the desired number of aerial sightings, despite 4 winters of efforts. Wong (1996) recommends 300 data points to develop independent sightability models such as these. We recommend that either: (a) additional data points are gathered, perhaps from nearby drainages; or (b) these data be combined with data from other studies (Samuel et al. 1987; Unsworth et al. 1994).

Undercounting of large elk groups by as much as 20% has been documented in Pennsylvania forests, however elk groups in the open were counted without error (Cogan and Diefenbach 1998). To minimize this potential bias, we slowly herded large elk groups to the nearest opening and counted while they were standing still. Nevertheless, we recommend that future sightability studies include tests for, and estimations of, group size undercounting.

Based on this study, management actions to reduce elk population in the park might reduce the occurrence or size of occasional temporary cross-boundary movements from park to town during winter caused by elk at *K* seeking better foraging. However, it is unlikely that such a reduction would substantially alter the growth rate of the town subpopulation or *K*. The effect of harvest outside of the park on elk inside the park is uncertain. Similar survival rates in both subpopulations suggest that harvest in town may affect both, however, the harvest rate of females has been so low that an effect may not have been detectable. Sensitivity estimates from our model predict that average equilibrium population in town can be reduced by 7% by a 1% reduction in adult female survival. Thus, harvest does appear to be a useful management tool for controlling the town subpopulation, so long as restrictions to harvesting near human settlements do not interfere with harvest goals.

We estimated food-limited *K* for elk in the park and town sectors and these compared very favorably with independently calculated forage and energy based estimates for the same sectors (Hobbs et al. 1982; Singer et al., this volume). While potentially useful, we consider these estimations only the first step in the process of determining appropriate numbers of elk for this ecosystem. NPS policy mandates that ungulates be managed under natural processes, but two major predators (wolves and grizzly bears) have been eliminated from this system, and the remaining predators that prey on elk--coyotes and mountain lions--are very likely reduced in the developed town sector. Other studies suggest that a naturally abundant assemblage of these four native large predators would have limited elk and other large ungulate numbers somewhere below food limitation for significant periods of time (Bergerud et al. 1988; Messier 1991, 1994; Gasaway et al. 1992; Mech et al. 1998). Therefore, we suggest to park management that the elk population levels at food-limited *K* that we estimated here are likely higher than elk population levels defined for natural process management of ungulates in U.S. national parks (NPS 2001). Unfortunately, there is considerable disagreement over the magnitude and duration that predator limitation might take (Boutin 1992; McLaren and Peterson 1994; Sinclair and Arcese 1995; Singer et al. 1998; Boyce and Anderson 1999). We propose that Yellowstone NP offers the most similar, well-documented example of the potential limitation of elk that may occur with recovery of all native predators. Thus, the Yellowstone NP experience may provide a guide to park managers of the effect of natural processes on elk for RMNP.

Literature Cited

Abromowitz, M., and I. A. Stegun. 1970. Handbook of mathematical functions. Ninth printing. Dover Publications, New York. 1046 pp.

Baker, W. L., J. A. Munroe, and A. E. Hessl. 1997. The effect of elk on aspen in the winter range of Rocky Mountain National Park, Colorado, USA. Ecography 20:155–165.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121. 39 pp.

Bear, G. D. 1989. Seasonal distribution and population characteristics of elk in Estes Valley, Colorado. Colorado Division of Wildlife R-S-65-89, Special Report 65.

Bergerud, A. T., W. Wyett, and J. B. Snider. 1988. The role of wolf predation in limiting a moose population. Journal of Wildlife Management 47:977–988.

Berris, C. R. 1987. Interactions of elk and residential development: Planning, design, and attitudinal considerations. Landscape Journal 6:31–41.

Boutin, S. 1992. Predation and moose population dynamics: A critique. Journal of Wildlife Management 56:116–127.

Bowden, D. C., and R. C. Kufeld. 1995. Generalized mark-sight population size estimation applied to Colorado moose. Journal of Wildlife Management 59:840–851.

Boyce, M. S. 1989. The Jackson elk herd: Intensive wildlife management in North America. Cambridge University Press. 306 pp.

Boyce, M. S., and E. M. Anderson. 1999. Evaluating the role of carnivores in the Greater Yellowstone ecosystem. Pages 265–283 *in* Carnivores in ecosystems: The Yellowstone experience. Yale University Press, New Haven.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer-Verlag, New York. 353 pp.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Pages 183–246 *in* T. H. Coaker, editor. Applied Biology. Volume I. Academic Press, New York, New York.

Choquenot, D. 1991. Density-dependent growth, body condition, and demography in feral donkeys: Testing the food hypothesis. Ecology 72:805–813.

Clutton-Brock, T. H., F. E. Guiness, and S. D. Albon. 1982. Red deer: The ecology and behavior of two sexes. University of Chicago Press, Chicago.

Cogan, R. D., and D. R. Diefenbach. 1998. Effect of undercounting and model selection on a sightability-adjustment estimation for elk. Journal of Wildlife Management 62:269–279.

Coughenour, M. B., and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications 6:573–593.

Cox, C. 1998. Delta method. Pages 1125–1127 *in* P. Armitage and T. Colton, editors. Encyclopedia of biostatistics. Volume 2. John Wiley & Sons. Chichester, United Kingdom.

Dennis, B., and M. L. Taper. 1994. Density dependence in time series observations of natural populations: Estimates and testing. Ecological Monographs 64:205–224.

Dublin, H. T., A. R. E. Sinclair, S. Boutin, E. Anderson, M. Jago, and P. Arcese. 1990. Does competition regulate ungulate populations? Oecologia 82:283–288.

Edge, W. D., C. L. Marcum, S. L. Olson, and J. F. Lehmkuhl. 1986. Nonmigratory cow elk herd ranges as management units. Journal of Wildlife Management 50:660–663.

Fryxell, J. M. 1987. Food limitation and demography of a migratory antelope, the white-eared kob. Oecologia 72:83–91.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monograph 20:1–59.

Gysel, L. W. 1959. An ecological study of the winter range of elk and mule deer in the Rocky Mountain National Park. Journal of Forestry 58:696–703.

Hobbs, N. T., D. L. Baker, J. E. Ellis, D. M. Swift, and R. A. Green. 1982. Energy- and nutrition-based estimates of elk winter range carrying capacity. Journal of Wildlife Management 46:12–21.

Houston, D. B. 1982. The Northern Yellowstone elk: Ecology and management. MacMillan Publishing, New York, New York.

Huff, D. E., and J. D. Varley. 1999. Natural regulation in Yellowstone National Park's northern range. Ecological Applications 9:17–29.

Kay, C. E., and F. H. Wagner. 1994. Historical condition of woody vegetation on Yellowstone's northern range. Pages 151–169 *in* D. G. Despain, editor. Plants and their environments. National Park Service, Technical Report 93, Denver, Colo.

Larkins, K. F. 1997. Patterns of elk movement and distribution in and adjacent to the eastern boundary of Rocky Mountain National Park. M.S. thesis, University of Northern Colorado, Greeley.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose and tree rings on Isle Royale. Science 266:1555–1558.

Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis. 227 pp.

Merrill, E., M. K. Bramble-Brodahl, R. W. Marrs, and M. S. Boyce. 1993. Estimation of green herbaceous phytomass from Landsat MSS data in Yellowstone National Park. Journal of Range Management 46:151–157.

Messier, F. 1991. The significance of limiting and regulation factors on the demography of moose and white-tailed deer. Journal of Animal Ecology 60:377–393.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75:478–488.

National Park Service. 2001. Management policies. U.S. Government Printing Office, Washington, D.C.

Olmsted, C. E. 1979. The ecology of aspen with reference to utilization by large herbivores in Rocky Mountain

National Park. Pages 89–97 *in* M. S. Boyce and L. Hayden, editors. North American elk. University of Wyoming Press, Laramie.

Packard, F. M. 1947. A study of the deer and elk herds of Rocky Mountain National Park, Colorado. Journal of Mammalogy 28:4–12.

Peterson, R. O. 1999. Wolf-moose interaction on Isle Royale: The end of natural regulation? Ecological Applications 9:10–16.

Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. 1992. Numerical recipes in C: The art of scientific computing. Cambridge University Press, UK. 994 pp.

Saether, B. E., R. Anderson, O. Hjeljord, and M. Heimer. 1996. Ecological correlates of regulation variation in life history of the moose (*Alces alces*). Ecology 77:1493–1500.

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–45.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys in north-central Idaho. Journal of Wildlife Management 51:622–630.

SAS Institute. 1989. SAS/IML software: usage and reference. Version 6. First edition. SAS Institute, Cary, North Carolina, USA.

SAS Institute. 1990. SAS/STAT user's guide, Version 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.

Sauer, J. R., and M. S. Boyce. 1983. Density dependence and survival of the elk in northwestern Wyoming. Journal of Wildlife Management 47:31–37.

Shenk, T. M., G. C. White, and K. P. Burnham. 1998. Sampling-variance effects on detecting density dependence from temporal trends in natural populations. Ecological Monographs 68:445–463.

Sims, P. L., and J. S. Singh. 1978. The structure and function of ten western North American grasslands. Journal of Ecology. 66:573–597.

Sinclair, A. R. E., and P. Arcese. 1995. Population consequences of predator-sensitive foraging: The Serengeti wildebeest. Ecology 76:164–173.

Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on calf mortality. Journal of Wildlife Management 61:12–25.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998. Thunder on the Yellowstone revisited: An assessment of management of native ungulates by natural regulation, 1968–93. Wildlife Society Bulletin 26:375–390.

Smith, B. L., and S. H. Anderson. 1998. Juvenile survival and population regulation of the Jackson elk herd. Journal of Wildlife Management 62:1036–1045.

Steinhorst, R. K., and M. D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 45:415–425.

Stevens, D. R. 1980. The deer and elk of Rocky Mountain National Park, a 10-year study. ROMO-N-13. Rocky Mountain National Park.

Theobold, D. M., J. R. Miller, and N. T. Hobbs. 1997. Estimating the cumulative effects of development on wildlife habitat. Landscape and Urban Planning 39:25–36.

Unsworth, J. W., F. A. Leban, D. J. Leptich, E. O. Garton, and P. Zager. 1994. Aerial survey: User's manual. Second edition. Idaho Department of Fish and Game, Boise. 84 pp.

Van Dyke, F. G., W. C. Klein, and S. T. Stewart. 1998. Long-term range fidelity in Rocky Mountain elk. Journal of Wildlife Management 62:1020–1035.

Wagner, F. H., R. Foresta, R. B. Gill, D. R. McCullough, M. R. Pelton, W. F. Porter, and H. Salwasser. 1995. Wildlife policies in the U.S. national parks. Island Press, Washington, D.C.

Webb, W. L., S. R. Szarek, W. Laurenroth, R. Kinerson, and M. Smith. 1978. Primary production and water use on native forest, grassland, and desert ecosystems. Ecology 59:1239–1247.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement:120–138.

White, G. C., and B. C. Lubow. 2002. Fitting population models to multiple sources of observed data. Journal of Wildlife Management 66(2):300–309.

Wong, C. 1996. Population size estimation using the modified Horvitz-Thompson estimator with estimated sighting probabilities. Ph.D. dissertation, Colorado State University.

Long-Term Changes in Willow Distribution on the Winter Range of Rocky Mountain National Park

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Abstract. We determined the extent and spatial pattern of changes in willow (*Salix* spp.) cover in the riparian areas of the eastern slope of Rocky Mountain National Park (RMNP), Colorado, between 1937 or 1946 and 1996, and related these changes to suspected causative factors. The study was conducted in two watersheds of the northeastern side of RMNP, which includes the Moraine Park area of the Big Thompson River watershed (2,481 m), and the Horseshoe Park area of the Fall River watershed (2,598 m). Changes in vegetation were inferred from digital maps generated from aerial photointerpretation and field surveys. Low-resolution digital maps were created based on old (1937 or 1946) and new (1996) aerial photos to determine the extent of willow decline. High-resolution digital maps of vegetation cover were created from a field survey conducted in the summer of 1998. In these maps, willow cover was described in terms of morphotypes (sapling, young short, old short, intermediate, and tall), density, and percentage of dead plants. Digital and attribute information were combined to produce maps.

The decrease in riparian shrub cover in Moraine Park was 21 ha (21%) and 17 ha (19%) in Horseshoe Park over the 50- or 59-year period. Reductions in the total length and surface water of the main river were 56% and 69% in Moraine Park and 44% and 47% in Horseshoe Park, respectively. Tall willow cover was found mainly in the upper areas of both valleys. Short old willow morphotypes were spatially distributed preferentially in areas affected by flooding in Horseshoe Park, and in areas where major river reductions were observed in Moraine Park. Both valleys had sites that were being colonized by willows, in wet meadows, and in the case of Horseshoe Park, open areas created by flood disturbance. The decline in tall willow cover corresponded to 54% and 65% in Moraine Park and Horseshoe Park, respectively, over 50–59 years.

Willow decline in Moraine Park was apparently the result of a reduction in water availability for growth. Over the last 50 years there has been a trend toward simplification of river spatial pattern, i.e., less complex branching and channelization, and a decrease in total water surface area in Moraine Park. The same trend in river morphology was documented in Horseshoe Park, but in that drainage, willow decline occurred mainly because of a large flood disturbance in 1982. In both valleys, surveys indicated a decline in beaver in excess of 90% since 1940. This has generated unfavorable conditions for willow growth. The causes of these fluvial changes were not determined, but were likely related to a decline in beaver populations and an increase in elk population (from approximately 700 to about 3,000 total elk, and from 500 to 1,000 elk within the park, during the study period). The elk increase has also placed increased browsing pressure on willow, which has led to a reduction in plant heights. Persistence of these riparian willow communities in their former abundance and extent may depend on the reestablishment of beaver.

Keywords: Beaver impoundments, elk browsing, hydrology, riparian areas, vegetation transitions, willow.

Introduction

Riparian vegetation comprises a small area of the landscape along river courses, in which the river has a major control on physical conditions (Tabacchi et al. 1990; Gregory et al. 1991). These areas are subject to periodic fluvial disturbances occurring because of flooding and/or migration of the active channel and meanders of the river (Bradley and Smith 1986; Gregory et al. 1991; Miller et al. 1995). Disturbance produces irregular patches of riparian vegetation types, arranged in a mosaic along the area of river influence (Miller et al. 1995). Non-fluvial disturbances are also common. These include fire, wind, plant disease, insect outbreaks (Gregory et al. 1991), herbivory by large mammals (Naiman 1988; Johnston and Naiman 1990a; Collins and Helm 1997), and beaver dams (Johnston and Naiman 1990b). Riparian areas have been extensively modified by human activities resulting in habitat degradation, which has affected both terrestrial and aquatic species composition (Décampus et al. 1988; Roth et al. 1996). Trends in cover and characteristics of riparian vegetation are often difficult to distinguish from the normal recurrent disturbance effects, so long-term analyses are required (Johnston and Naiman 1990c; Miller et al. 1995).

Documentation of temporal and spatial dynamics of landscape pattern has been greatly stimulated by the availability of new technological tools, in particular geographic information system (GIS) and remote sensing technology (Ustin et al. 1993; Johnson and Gage 1997). The comparison of historic and recent aerial photos at a medium level of resolution is a reliable, quantitative method for evaluating long-term vegetation changes, particularly when combined with GIS (Johnston and Naiman 1990c; Clemmer 1994). This approach was used here to analyze the temporal change of riparian shrub cover in two watersheds in Rocky Mountain National Park (RMNP), Colorado, and to make inferences about the factors that could drive vegetation change.

Willow (*Salix* spp.) dominates the riparian landscapes of the eastern slope of RMNP, forming a complex mosaic of patches of willow plants of different heights. A decline in willow abundance, distribution, and stature has apparently occurred on these areas. Three main hypotheses have been proposed for willow declines (Singer et al. 1998a): (1) higher grazing pressures on willow, caused by increases in the elk (*Cervus elaphus*) population; (2) warmer and drier climatic trends occurring during this last century; and (3) decline in beaver (*Castor canadensis*) population. Since humans extensively used this study area and drained some areas in the park, human impact should also be considered among the probable causative factors.

In this report, GIS maps of riparian vegetation and hydrology of two closed watersheds of RMNP were generated at two scales of resolution (high and low-resolution digital maps). The analysis procedure was designed to answer the following set of questions: Has the spatial distribution of willow vegetation been reduced at the landscape scale? If so, what is the spatial pattern of willow decline, and what factors could be associated with this pattern? Since vegetation changes are normally controlled by a complex interaction of factors, we hypothesized that multiple causative factors might explain the overall changes in vegetation cover. However, factors could be hierarchical, with some of them primary and others secondary. Primary factors might override the effects of secondary factors. Some of the proposed factors that could produce changes in willow cover, for example, drier climatic trend, elk population increase, and beaver decrease, were similar in both study watersheds. Consequently, these primary factors would produce similar changes in the patterns of willow cover in both watersheds. However, any differences between watersheds would indicate that more localized primary factors are driving these changes.

Methods

Study Sites

The study was conducted in two watersheds of the northeastern side of RMNP which includes the Moraine Park area of the Big Thompson River watershed (2,481 m), and the Horseshoe Park area of the Fall River watershed (2,598 m). Vegetation in these valleys is composed of communities of riparian shrubs dominated by willow (*Salix monticola*, *S. geyeriana*, and *S. planifolia*), and in some areas by birch (*Betula* spp.). Meadows occur in several parts of the valley farther from the river course. Wet meadows are dominated by *Poa* spp., and dry meadows by *Carex* spp. and *Artemisia* spp. Vegetation communities dominated by trees represent a minor proportion of the total cover, and include conifers (*Pinus contorta* and *Pinus ponderosa*) and aspen (*Populus tremuloides*) communities. The two watersheds are within 5 km of each other and have perennial alpine snowfields at their headwaters (Baron 1992). Mean annual precipitation for the sites is 41 cm (Singer et al. 1998a) and peak stream flow usually occurs in early to mid-June.

Historical Changes in Land Use, Elk, and Beaver

Native people camped and hunted in the valleys, mountains, and tundra of what is now known as RMNP since 3850 B.C. (Hess 1993). Trappers and explorers occasionally visited this area but it was not until 1859 that permanent settlement began (Hess 1993). The first record of settlers within current park boundaries was in 1875, when Abner Sprague built a cabin and grazed 200 cattle in Moraine Park, but in the 1880s and 1890s the Sprague Ranch expanded to 1,000 acres and shifted in focus from cattle to tourism (Buchholtz 1983). Moraine and Horseshoe Parks were not within the national park boundary when it was created in 1915. From the 1870s until the 1930s, ranches and resorts occupied much of Horseshoe and Moraine Parks (Buchholtz 1983). Horseshoe Park was incorporated into the national park boundaries in 1932. Stead's Ranch, the Moraine Park remnant of Abner Sprague's 1875 homestead, was purchased in 1962 by the National Park Service and returned to a natural meadow. This ranch at one time consisted of a 600-acre ranch, a lodge, barns, cabins, and a golf course (Buchholtz 1983).

Human activities have brought about important changes in the composition and characteristics of the vegetation. It is clear that drainage and irrigation ditches were built on Moraine Park, and remnants are still evident today. Ditches could have been used to drain overly wet areas and to irrigate hay fields and the golf course. The golf course was irrigated through at least 1961. An official Park Service report [1930] described conditions on the various ranges. In Moraine Park... "the whole area is grazed by domestic stock throughout the year and is badly overgrazed". This included the grassland areas. The meadow areas were again cut for hay and later used as pasture. "A heavy growth of willow" existed along the streams... Horseshoe Park was badly overgrazed [by livestock]". These comments indicate that grasses were being heavily used by livestock, but shrubs and trees were less affected" (D. Stevens, 1980, National Park Service, unpublished report). In Horseshoe Park, one of the main disturbances on riparian vegetation was the flood produced by the failure of the Lawn Lake Dam in 1982. Lawn Lake is located at treeline (3,350 m above sea level); downstream from Lawn Lake the Roaring River descends to join the Fall River in Horseshoe Park at an elevation of 2,605 m (Jarret and Costa 1993). Sediment from the Lawn Lake flood covered a willow carr community in Horseshoe Park, and in this area, some of the material transported by the flood was deposited as an alluvial fan (Keigley 1993).

Wildlife has been extensively hunted since the arrival of the first European settlers. The winter range for elk in RMNP encompasses about 10,000 ha. This includes the two study valleys, as well as other valleys and private and national forest lands outside the park in the town of Estes Park and the Estes Valley, Colorado (Singer et al. 1998a). The elk had been hunted to extinction by 1900, but in 1913 and 1914, 49 elk from Yellowstone were transplanted to the park (Hess 1993). By 1942, elk had increased to approximately 1,500 individuals. A program of elk control by shooting animals, begun in 1944, reduced the population to around 400 individuals (Hess 1993). Since 1968, under the natural regulation policy, the elk population has increased to 3,000 individuals (Singer et al. 1998b), 1,000 of which winter in RMNP (Lubow et al., this volume).

Beaver were abundant in the areas of RMNP prior to European settlement, but they started to be intensively trapped in the mid-1800s (Hess 1993). "Exactly how many beaver pelts may have been extracted from the streams of RMNP during the fur trade era is unknown .... signs of the lucrative trade dotted the nearby region, allowing us to assume that trappers worked every likely drainage. By 1830 small trading posts began to appear... But just as these posts were built, men's fashion in hats changed... demand for beaver pelts declined, and within a decade [the].. forts were deserted" (Buchholtz 1983). Pressure on beaver did not seem to decline, however, and "in 1890 beaver was virtually eliminated from the adjacent valley of Estes Park" (Hess 1993). However, beaver were abundant in the national park when it was established in 1915 (Hess 1993). The first detailed surveys of beaver on the major drainages of the park, including the study area, were done in 1939 and 1940 (Packard 1947). Other surveys were done in 1964 (Hickman 1964), 1980 (Stevens and Christianson 1980), and 1994 to 1998 (Zeigenfuss et al., this volume). In all surveys, beaver populations were estimated indirectly from signs of beaver activities that were registered by walking on the stream bank. Surveys are problematic to compare; however, the estimates clearly indicate a declining trend over time (Zeigenfuss et al., this volume). On the Big Thompson River, the estimated number of beavers was 315, 102, 18 and 12 in 1939, 1964, 1980 and 1994–1998, respectively. Most of these beavers were in Moraine Park. Values reported for the Fall River in Horseshoe Park were 96, 24 and 6 in 1939, 1980 and 1994–1998, respectively.

Digital Map Generation

Low-Resolution Digital Maps

Digital maps of Moraine and Horseshoe Parks were created from interpreted aerial photos obtained for different years (Table 1). Aerial photos were scanned, geo-registered, and interpreted, rectified and digitized on a high-resolution computer screen. Photos were scanned with a 600-dpi resolution and the generated image files were geo-registered based on x-y UTM coordinate points. UTM coordinates of prominent features such as trees or road intersections were registered with a global positioning system (GPS) (Trimble Pathfinder Professional) with an error lower than 2 m. For image geo-registration, 18 and 30 GPS points were used in Moraine and Horseshoe Parks, respectively. GPS locations were uniformly distributed throughout the area of interest. A 2-degree polynomial geometric correction procedure, available in ERDAS-IMAGINE Software (1998, Version 8.3), was used to geo-register the 1996 image files based on GPS locations. Aerial photos older than 1996 were registered using the corrected 1996 images as a reference. Vegetation and hydrological features were digitized using ARC/EDIT module of ARC/INFO Software (version 7.0; ESRI 1994) program, employing the digital photos as a background image. This procedure greatly increases the possibility of identifying features, allowing both margins of river channels to be digitized.

Vegetation was classified in five classes, namely: open, meadow, riparian shrub, aspen (*Populus tremuloides*), and forest (*Pinus* spp.). Areas with a high percentage of bare soil were included in the open class; areas dominated by grasses were considered meadows. Since willow and birch, the two shrubs that grow in these riparian areas, could not be separated in the photo-interpretation, they were included in the riparian shrub class. Hydrological features were also delineated from the aerial photos. Main river, temporary and old river channels, and ponds were digitized. All channels that contained water were considered main river. Branches or meanders of the river that did not contain water were classified as temporary or old if they were wet or dry, respectively.

High-Resolution Digital Maps

During the summer of 1998, we surveyed the same areas covered in the low-resolution maps in Moraine and Horseshoe Parks. Aerial photos of these valleys taken in 1996 (Table 1) were used as a guide to organize the survey. Homogeneous vegetation patches were identified in the field by visual observation, and a GPS unit was used to delimit its boundaries. The number, as well as the size, and shape of the patches were determined according to the vegetation characteristics, in order to minimize within patch heterogeneity. Hydrological features such as main river, lakes, or ponds were mapped following the same method. We walked along the

Table 1. Aerial photography used to map willow cover and river in the two study watersheds.

Year	Site	Map type	Scale	Film type	Commissioning agency
1937	Moraine Park	River	1:22,000	Black & White	U.S. Forest Service
	Horseshoe Park lower area of the valley	Vegetation-river	1:20,000		
1946	Moraine Park	Vegetation	1:20,000	Black & White	U.S. Forest Service
	Horseshoe Park, upper area of the valley	Vegetation-river	1:20,000		
1996	Both watersheds	Vegetation-river	1:28,000	Color	Rocky Mountain National Park

boundaries of every vegetation patch or hydrological feature with a GPS unit set to digitize lines. Since the focus of the studies was on willow cover, the boundaries of the survey area were defined by the extent of willow distribution. However, some patches without willow plants occurring between the extent of the willow distribution were also delimited. GPS digital data and the associated attribute information were incorporated in ARC-INFO Software (version 7.0; ESRI 1994) to generate polygon coverages. The final error of the GPS-generated lines was lower than 2 m after correcting the data for the distortions that are purposefully introduced by the satellite system.

As in the case of the low-resolution maps, vegetation patches were primarily classified according to the general characteristics of the vegetation. A more detailed classification system was created to identify vegetation classes and subclasses. Further, in those patches where willows were present, additional attributes were registered. Four groups of species were recognized in the woody strata, namely: willow (*Salix* spp.), birch (*Betula* spp.), conifers (*Pinus* spp.) and aspen (*Populus tremuloides*) (Fig. 1). Patches without woody strata or with few sparse woody individuals were included in the meadow class. Woody vegetation classes were distinguished based on the dominant and co-dominant species. The group that presented the highest density in a patch was considered dominant, without regard to the overall woody strata density. Other groups occurring in a patch were co-dominant. Groups comprised of isolated individuals in an overall high-density patch were not considered in the classification. Since visual observation was used to delimit and classify vegetation patches, there was no quantitative value for the minimum number of plants determining if a group should be classified as co-dominant, or not included. Nevertheless, ambiguous cases were rare, because no more than two groups occurred in most patches. Since the survey was targeted on willow areas, some vegetation classes such as meadow were only partially surveyed (particularly one large meadow in Horseshoe Park, and several meadow areas in Moraine Park). Forest and aspen vegetation classes were separated from the riparian vegetation. Consequently, they were seldom included in the survey. Only willow and birch were completely surveyed.

Additional attributes were used to describe the heterogeneity in willow cover in more detail. Four categories were defined to characterize the morphological characteristics of: (a) dominant, (b) co-dominant willow morphotypes, (c) density, and (d) percentage plants dead (Table 2). As previously described, this classification was based on visual estimations. A zero value was assigned in all of the four categories in the case of patches without willow plants. Density was estimated considering both live and dead willow plants. The morphotype that presented the highest density in a patch was considered dominant and the second most common morphotype was considered co-dominant. Only one morphotype was included in the co-dominant categories to make the classification simpler.

Height difference was the primary attribute used to discriminate willow morphotypes, but more detailed observations were made to differentiate between saplings and young short willow, and between young and old short willow. We considered saplings to be individuals that were recently established (4–5 years) from seeds or vegetative reproduction, but not from resprouting of old individuals. Areas with high density of willow saplings, and without woody strata, were classified in the meadow-willow vegetation subclass (Fig. 1). We identified willow saplings using several morphological characteristics such as height shorter than 50 cm, small basal diameter of the largest stem (around 5 mm), brownish stem without sign of lignification, and small crown size relative to the size of the plant. These latter characteristics indicated that plants were not sprouts from old individuals. Additionally, some of the largest stems were dated based on the ramification pattern, and were between 4 and 5 years old. The young willow category included plants that were similar in height to short willow morphotypes (approximately 1.5 m in the case of tallest plants). Mature plants were composed of several large stems and consequently had crowns several times larger than plants considered as saplings. The largest stem diameter in short young willows was on the order of 1.5 to 2.0 cm. These plants looked younger than other short willows, as indicated by the brownish color of the stem that contrasted with a white color typical of old stems of old willow plants. Additionally, no dead stems, in particular old dead stems, were found inside or between the canopies of young plants, as were commonly found in older short willow stands. This distinction was made to infer dynamics occurring within the short morphotypes.

Patches comprised of saplings or young short willows were interpreted differently if other morphotypes were or were not present in the patch. If patches with a high density of saplings or young short willows occurred together with other willow morphotypes, they were interpreted as areas originally covered by willow with high recruitment. Areas dominated by saplings or young short willow, in which no other dead or live willow morphotypes were present, were considered to be areas

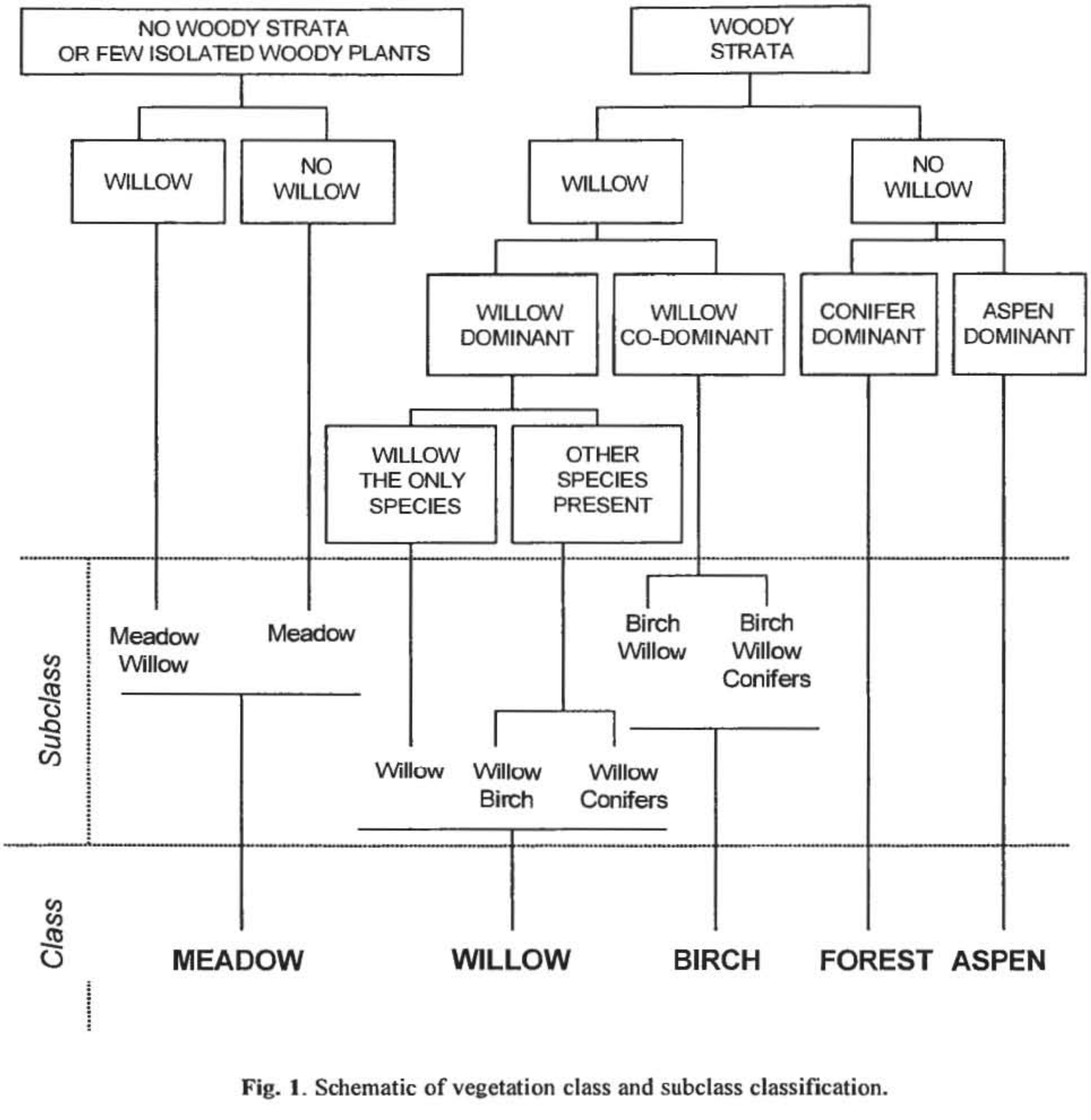

Fig. 1. Schematic of vegetation class and subclass classification.

Table 2. Description of categories used to classify patches that contain willow.

Category	Values	Description
Dominant willow	0. No willow	
Codominant willow	1. Sapling	Less than 0.5 m tall
	2. Short young	0.5 to 1.5 m tall, young stems
	3. Short old	0.5 to 1.5 m tall, old stems
	4. Intermediate	1.5 to 2.0 m tall
	5. Tall	Greater than 2.0 m tall
Willow density	0. No willow	
	1. Few willows	Sparse willows
	2. Low density	Distance between plants around 5 m
	3. Moderate density	Distance between plants around 3 m
	4. High density	Distance between plants less than 2 m
Dead willow	0. No willow	
	1. Less than 10%	
	2. 10 to 30%	
	3. 30 to 50%	
	4. 50 to 80%	
	5. Greater than 80%	

recently colonized by willows. These patches were classified as "new colonization" if only saplings were present and were interpreted to be areas that had been colonized less than or equal to 4 or 5 years ago. Similarly, patches that contained young short willows and saplings, but not other morphotypes, were interpreted as an older colonization (older than 5 years), and designated in the maps as "colonized several years ago".

Data Analysis

Changes in willow vegetation were interpreted relative to hydrological changes and historic events. GIS data from the low-resolution maps were used to examine the transitions in riparian shrub cover. Willow was the most common shrub in these watersheds, so we assumed that the riparian shrub class was mostly composed of willows. GIS data were derived from 1998 field surveys by aggregation of detailed vegetation attributes. Willow cover was estimated based on three criteria resulting from a combination of different attributes used to classify willow patches (Table 3). The first criterion considered willow cover to be patches in which willow plants were present. Since this was the least strict criterion, it gave the highest values of total willow cover and was used to calculate percent cover of the different willow types. The second criterion classified willow cover as areas where willow was the dominant vegetation type. A third and stricter criterion classified willow cover as woody areas dominated by willow with a high density of living individuals.

Cover areas of riparian shrub classes from maps created by the interpretation of old and new aerial photos were compared. The minimum resolution of the photo-interpretation was inferred by overlaying low and high-resolution maps. In this way, the minimum map resolution in the photo-interpretation was defined based on the characteristic of the vegetation in the high-resolution maps, namely dominant group, density, and percentage of dead plants. This procedure allowed us to determine characteristics of the low-resolution polygons based on the attributes recorded in the high-resolution maps.

Table 3. Total area (ha) covered by willows in the surveyed watersheds according to three different criteria. Values in parentheses indicate percent covered using criteria 1 (willows present).

	Classification			Area covered (ha)	
Criteria	Vegetation class	Vegetation subclasses	Willow category	Moraine Park	Horseshoe Park
1 Willows present	Not specified	Not specified	Dominant willow >0	104.5 (100)	88.3 (100)
2 Dominant vegetation	Willow	Not specified	Not specified	71.6 (68)	72.4 (82)
3 High density Low dead percentage	Willow	Not specified	Willow density = 3 or 4 Dead willows = 1 or 2	50.0 (48)	65.3 (74)

Results

Low-Resolution Digital Maps

Important hydrological changes, including reductions in the complexity of the river pattern and in total surface water, were found in both watersheds. Changes were more pervasive in Moraine Park, where the length and water surface area of the main channel were reduced by 56% and 69%, respectively (Table 4). Most changes in the river course occurred in the south main branch of the river (Fig. 2). By 1996, the river channel had almost no branching and most of the temporary river courses had disappeared. The complex pattern of the river observed in 1937 was most likely the result of beaver activities, but it was difficult to identify beaver ponds. All ponds that were identified in the 1937 and 1996 maps (Fig. 2) were not a result of beaver activities. Beaver created several dams that produced small impoundment areas, but the main impact of beaver appeared to be an increase in river ramification and meanders. Most of the 1937 river channels that had disappeared by 1996 could not be identified in the photos. Flooded areas on wet meadows were evident in the central part of the Moraine Park valley in both years, but were more extensive in 1996 (Table 4). In Horseshoe Park, the length and surface water of the main channel of the river in 1996 were reduced to 44% and 47%, respectively, of the values observed in 1937–1946 (Table 4). The main reduction in river complexity occurred in the upper reaches of the valley (Fig. 3). Several ponds created by beaver could be clearly identified on the old photos. These ponds disappeared by 1996. Important hydrological changes had also occurred in this valley, produced by a 1982 flood event. Changes in the lower part of the valley did not appear to be as important as in the upper areas, but the river pattern become less meandering by 1996.

Changes in spatial patterns and a decline in the total area covered by riparian shrubs were determined in both watersheds. The reduction was 21 ha (21%) in Moraine Park during the span of 50 years, and 17 ha (19%) in Horseshoe Park during the time spans of 50 and 59 years (1937 and 1946 aerial photos; Table 1). In Moraine Park, riparian shrubs covered 101 ha in 1937 and 80 ha in 1996. Changes in shrub cover occurred mostly in the wider part of the valley (Fig. 4). The two narrow valleys in the upper areas of Moraine Park (west) did not show any important change. Compared to the spatial pattern of willow cover delimited in the 1946 photos, willow in the northwest part of Moraine Park slightly increased over meadows, and the forest area also became larger. It is important to consider that in these two narrow valleys there is an ecotonal zone in which riparian areas dominated by willow are replaced by birch and forest. These transitions were difficult to delimit from the photos. Wider areas of the watershed in Moraine Park showed major changes in willow cover. Decreases in willow cover were spatially associated with reductions in river meanders and small impoundments. Some meadow areas identified in the 1996 map were previously covered by willow.

In Horseshoe Park, willow cover was reduced from 90 ha in 1937/1946 to 73 ha in 1996. The 1982 flood caused a remarkable change in vegetation cover in the middle of the watershed (Fig. 3). In the upper area of the watershed, where the flood had less effect, willow vegetation cover did not change noticeably, but there

Table 4. Length (km) and surface area (ha) of hydrological features in Moraine Park in 1937 and 1996 and Horseshoe Park in the combined years of 1937/1946 and 1996.

	Moraine Park				Horseshoe Park			
	Length		Surface area		Length		Surface area	
	1937	1996	1937	1996	1937/1946	1996	1937/1946	1996
Main river	30.2	13.3	23.8	7.5	16.8	9.4	9.7	5.1
Current meanders	12.1	6.9	10.1	2.6	0.5	1.8	0.2	1.0
Old meanders	3.0	0.3	2.5	0.1	2.2	2.3	0.8	1.6
Ponds	-	-	1.4	1.0	-	-	10.9	47.6
Flooded areas	-	-	4.6	21.4	-	-	-	-

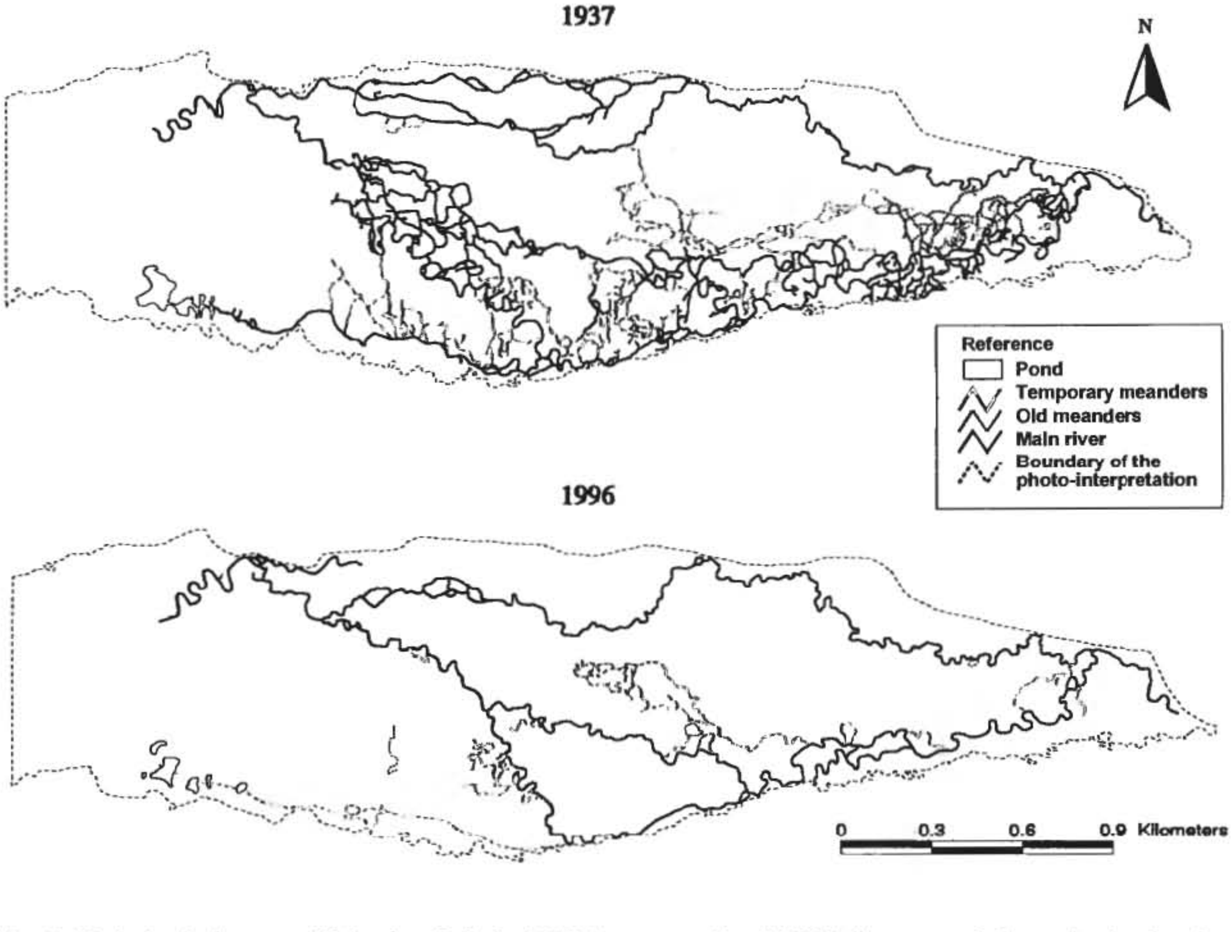

Fig. 2. Hydrological maps of Moraine Park in 1937 (upper map) and 1996 (lower map) determined using low resolution digital maps based on aerial photo interpretation.

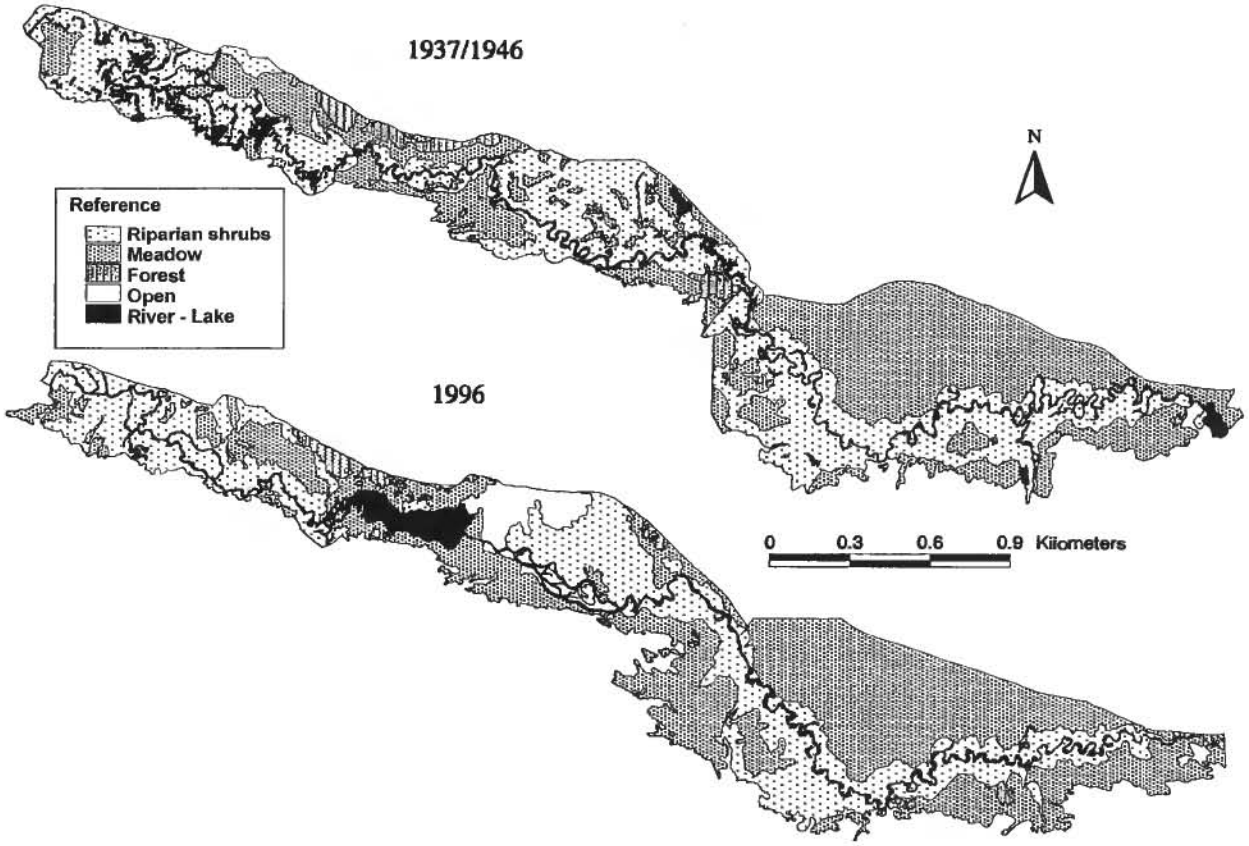

Fig. 3. Spatial distribution of vegetation classes and hydrology in Horseshoe Park in 1946, in the upper part of the valley and in 1937 in the lower part of the valley (upper map), and the same area in 1996 (lower map). Maps were created using low-resolution digital maps based on aerial photo interpretation.

was an important reduction in the total impoundment areas. Unlike Moraine Park, the reduction in surface water was not associated with a willow cover decline. Changes in willow cover in the lower part of the valley were not as spatially localized as in Moraine Park. Some willow stands were replaced by meadows, and a minor proportion was replaced by forest.

High-Resolution Digital Maps

Vegetation maps of Moraine and Horseshoe Parks produced by the ground-based GPS survey (Fig. 5) were similar to the 1996 low-resolution air photo maps (Figs. 3 and 4). Although, some meadow and forest patches were not delineated in the GPS based maps, more details in the riparian shrub cover were included. The shrub vegetation class was separated into areas dominated by birch and willow. The birch cover class was greater in Moraine Park than in Horseshoe Park (18 ha and 0.7 ha, respectively). Birch cover was mostly restricted to the south part of Moraine Park in the area where major changes in the river channel were documented. The three different methods used to classify willow cover produced markedly different estimates of willow in Moraine Park but not in Horseshoe Park (Table 3). This indicated that the spatial pattern of willow cover was more complex in Moraine Park than in Horseshoe Park.

Willow cover was very heterogeneous. Observed combinations of area types and willow categories ranged from areas in which willow were decreasing and had a high percentage of dead individuals, to meadows or open areas, that had been colonized by willow during the last few years (Table 5). Dead willow areas were more

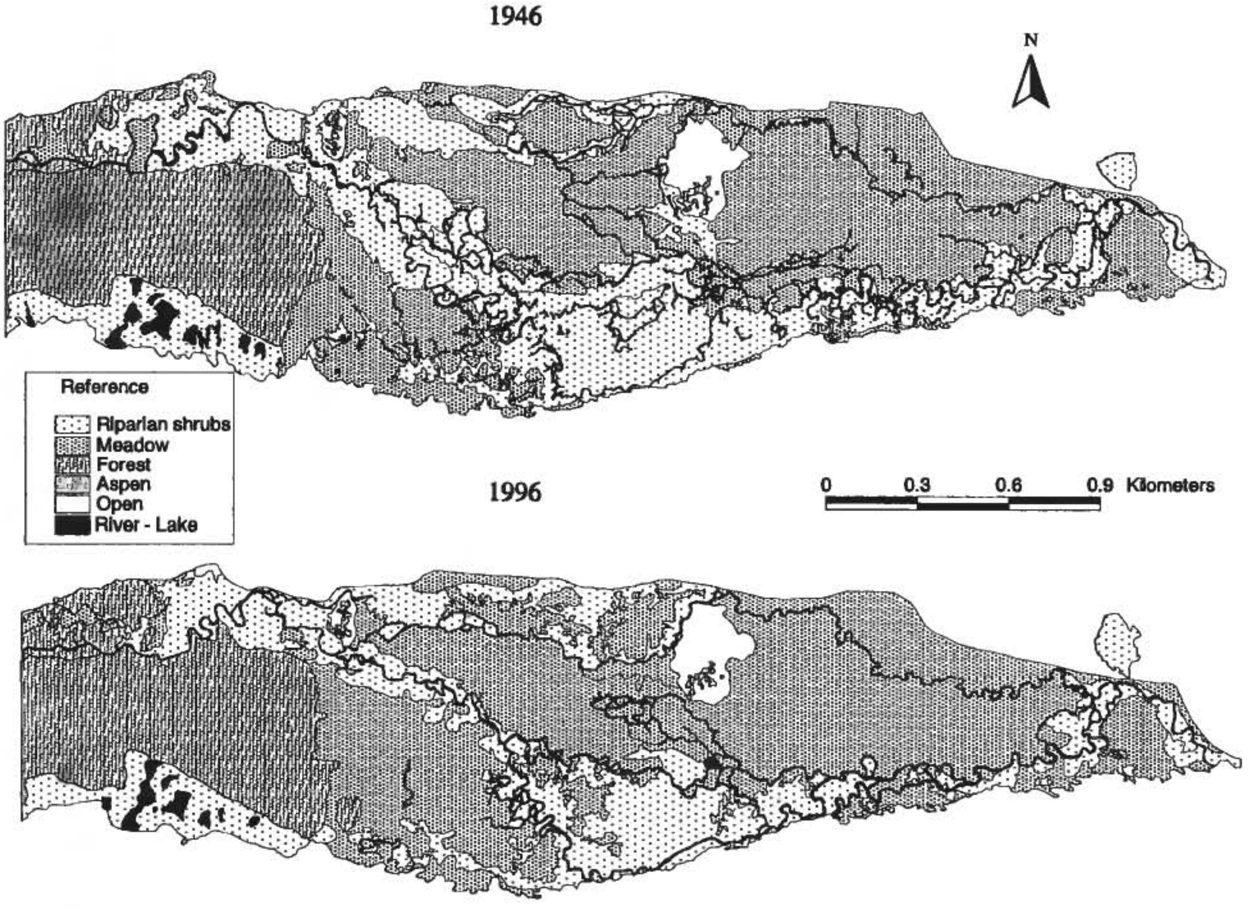

Fig. 4. Spatial distribution of vegetation classes and hydrology in Moraine Park in 1946 (upper map) and 1996 (lower map), determined using low resolution digital maps based on aerial photo interpretation.

extensive in Moraine Park than in Horseshoe Park (Table 5 and Fig. 6). In Moraine Park, these areas were dominated by tall willow as evidenced by the high number of dead willow with large crowns, and several tall stems that remained on the plant. Some of the live willows were also tall, but with several dead stems indicating stressful conditions for willow growth. Many old river channels and old signs of beaver activity were found in the two largest dead willow polygons. On the contrary, only a few patches dominated by dead willow were found in Horseshoe Park (Fig. 6). New and old willow colonization was found in both parks. These areas were more extensive in Horseshoe Park (34% and 12%, respectively), but some of them had a low density (Table 5). In Moraine Park, the major areas colonized by willow were on a meadow that received water diverted from the northeast branch of the river by beaver disturbances. These areas corresponded in part to some of the flooded areas identified in the low-resolution maps (Fig. 2). Flooding was produced by beaver activity. Beaver dams apparently reduced water flux in the main channel, resulting in a ramification of the river into several small channels. Although there was evidence of new beaver cuts on willows, beaver did not seem to maintain the dams. Under high water flow resulting from snowmelt (June and July), water moved out of the channel and into the meadow. This water was ultimately routed to the southern main branch of the river. Water flow through the meadow was gone by August in the summer of 1998. Several willow saplings were established in this area under conditions of soil water saturation. In Horseshoe Park, new willow colonization

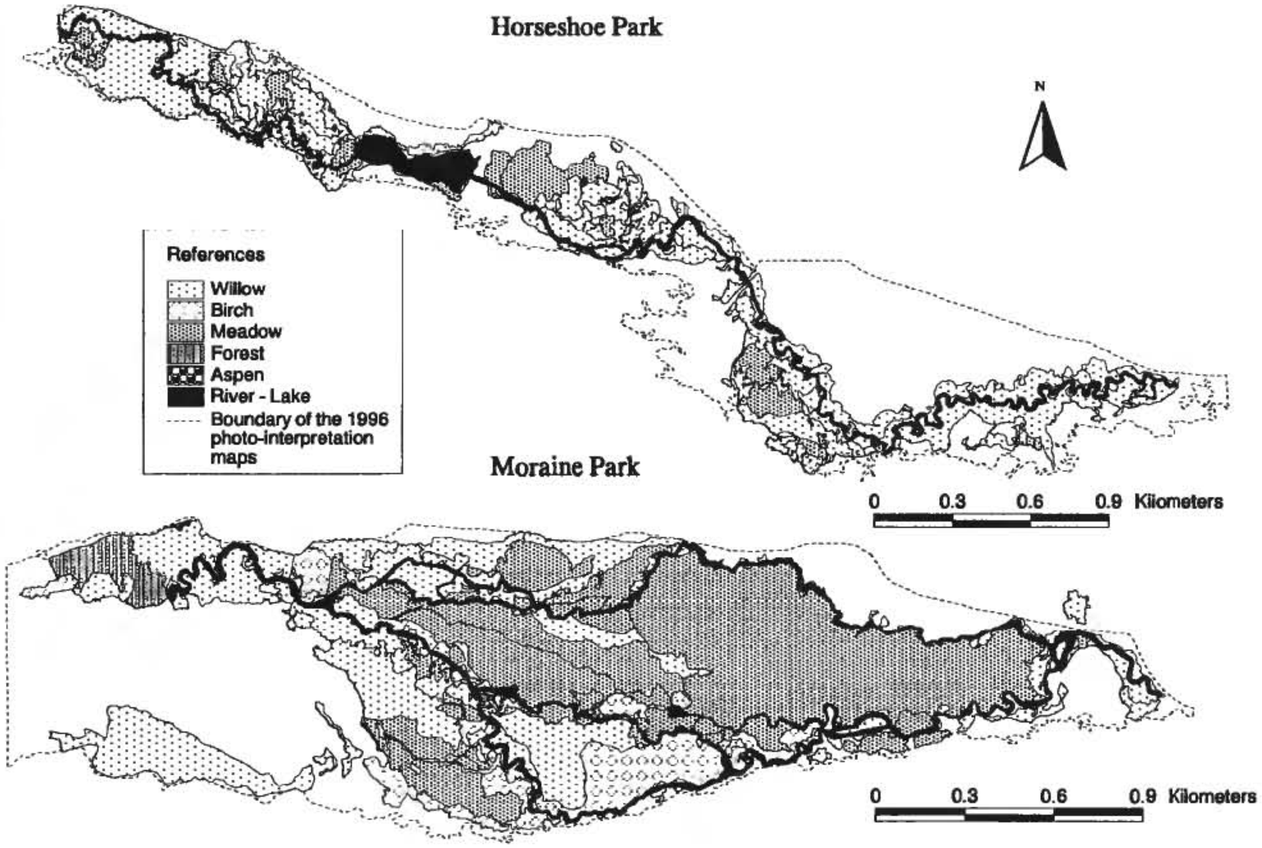

Fig. 5. Spatial distribution of vegetation classes in Horseshoe Park (upper map) and Moraine Park (lower map), determined using high resolution digital maps based on field mapping.

was found on the alluvial fan created by the 1982 flood (Fig. 6). Willows were also colonizing several meadows in the upper areas of the valley. Evidence of old colonization was also found in meadows of both the upper and lower parts of Horseshoe Park. Several small patches with high willow recruitment were found in areas temporarily flooded by the river in both watersheds.

Differences in willow morphotypes were the other source of heterogeneity in willow cover. Short old categories were abundant in Horseshoe Park (Table 5), but most of the short willows in Moraine Park occurred at low densities in the south-central part of the watershed. These areas were classified as areas covered by low willow density (Table 5). If low-density dead willow is included, the total cover of the short old morphotype increases considerably in Moraine Park but not in Horseshoe Park (Table 5). Short morphotypes were on the areas where major reductions in river channels were documented, indicating that these morphotypes occurred in areas of unfavorable growing conditions.

Tall willow was more abundant in the upper areas of the valley in both watersheds (Fig. 7). Changes in river course were probably less important in these upper areas because the river is constrained to a narrow valley. The tall willow polygon in the southwest part of the valley in Moraine Park has many ponds (not shown in the GPS maps) and saturated soils, which create favorable conditions for willow growth. Even though major changes in surface water were documented in the upper part of the valley in Horseshoe Park, no shift to lower willow cover or larger cover of short old morphotypes had occurred. In the lower valley of Horseshoe Park, tall morphotypes tended to be more abundant in areas farther from the river course.

Table 5. Total area covered by willow (ha) according to criteria 1 in Table 3, divided into different area types and willow categories. Percentage of total willow cover in parentheses.

		Willow categories				Area covered (ha)	
	Area type	Dominant	Codominant	Dead	Density	Moraine Park	Horseshoe Park
Colonization							
New	Saplings	Young	None	Low	Any	8.4 (8)	3.0 (3)
Old	Short young	Short Young	Young or none	Low	Low	0.02 (0)	12.2 (14)
					High	4.2 (4)	14.8 (17)
Areas originally covered by willow							
	Short old	Short old	Any	Low	High	10.1 (10)	18.7 (21)
	Intermediate	Intermediate	Any	Low	High	7.6 (7)	4.1 (5)
	Tall	Tall	Any	Low	High	28.3 (27)	30.4 (34)
	Dead willow	Any	Any	High	High	17.6 (17)	2.1 (2)
	Low density	Any	Any	Any	Low	28.3 (27)	3.2 (3)
Total						104.6 (100)	88.3 (100)

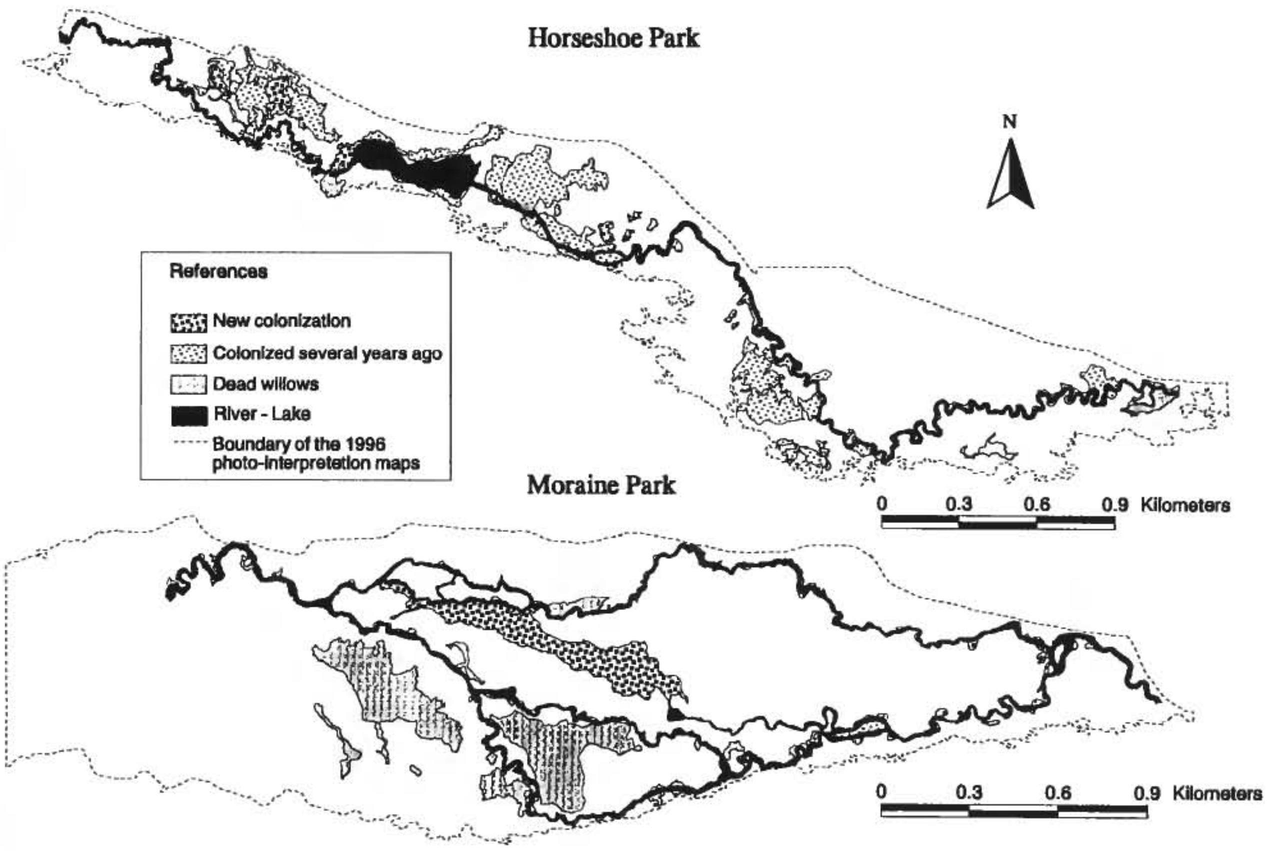

Fig. 6. Spatial distribution of areas dominated by dead willows and areas colonized by willows in Horseshoe Park (upper map) and Moraine Park (lower map), determined using high resolution maps based on field sampling.

Intermediate morphotypes were found in the wider areas of both valleys more spatially associated with short old willow morphotypes.

A more complicated pattern of river channels could be inferred from the extensive evidence of abandoned branches of the river and old meanders in Moraine Park. Old meanders were also found in Horseshoe Park, but they seemed to be less frequent than in Moraine Park. A great deal of evidence of old beaver activities was found in Moraine Park, but little was found in Horseshoe Park. Few signs of new beaver activities were observed in either watershed. Only one small beaver pond was found in the tall willow area of Horseshoe Park.

Comparison Between Low and High-Resolution Maps

In both valleys, willow cover based on criterion 2 (Table 3) was similar to the riparian shrub cover of low-resolution maps. In the case of Horseshoe Park, riparian shrub cover corresponded almost exactly to the value of willow cover estimated by using criterion 2 (723,676 m^2 and 727,389 m^2, respectively). In Moraine Park, riparian shrub cover overestimated willow cover obtained with criterion 2 by 83 ha (716,012 m^2 and 799,471 m^2, respectively). The riparian shrub class included areas dominated by birch, but excluded most of the dead willow

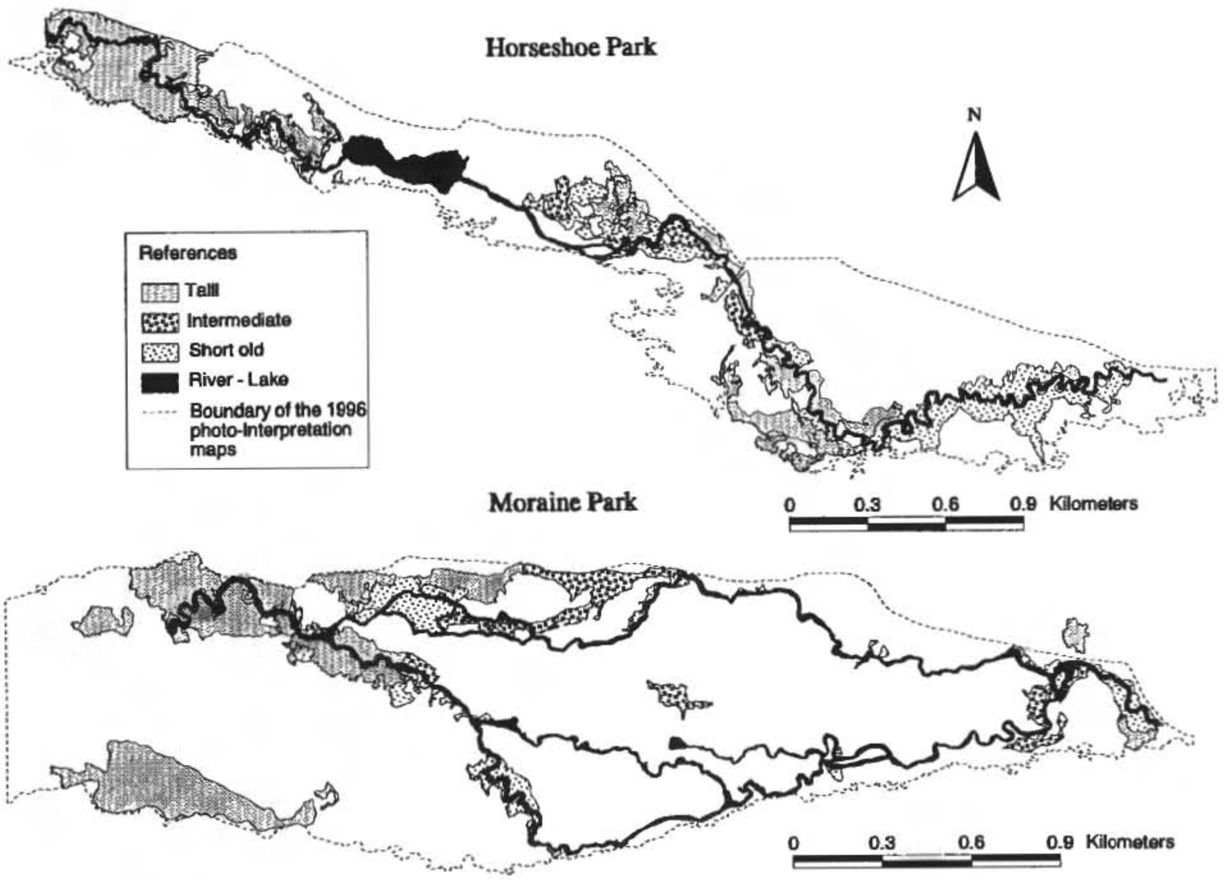

Fig. 7. Spatial distribution of willow morphotypes in Horseshoe Park (upper map) and Moraine Park (lower map), determined using high resolution maps based on field sampling.

areas. Since birch and dead willow covered a small portion of Horseshoe Park, cover values obtained from the different resolution maps were nearly the same. On the contrary, in Moraine Park, riparian cover was larger in the low-resolution map because dead willow areas could not be excluded, and cover of some of the shrub patches was overestimated.

Discussion

Geomorphological characteristics of drainage segments (reaches) have important effects on the development of riparian vegetation (Gregory et al. 1991). The upper areas of both study watersheds occurred in narrow valleys and had constrained reaches. Consequently, the position of the stream channel was relatively fixed. Riparian vegetation in the upper areas of both watersheds was dominated by tall willow and no important changes in riparian cover occurred in these areas. Lower areas of both study watersheds had unconstrained reaches, characterized by a lack of significant lateral constraint and low streamflow gradient. This allowed the stream to form braided channels. Importantly, short willow morphotypes were mostly restricted to these lower, unstable reaches, where there were major changes in hydrology between 1946 and 1996.

Decreases in willow cover as estimated from the change analysis only took into account areas where willows disappeared. Other changes in willow community characteristics, such as the proportion covered by different morphotypes, were not included. On the 1937/1946 aerial photos it was difficult to identify whether areas covered by riparian shrubs corresponded to tall willow, or a combination of different willow morphotypes and birches. In contrast, the GPS survey provided accurate estimates of the proportion of the areas covered by different morphotypes and birches, but only for 1996. The combination of information from the historical and recent cover maps allowed us to make two inferences about trends in willow cover over the study period. The first requires an assumption that in the old photos all of the areas classified as riparian shrubs were dominated by tall willows. From this we inferred that tall willow declines equaled 54% and 65% for Moraine and Horseshoe Park, respectively. If, in addition to the previous assumption, areas currently classified as birch are also considered to have been formerly dominated by tall willows, then the declines in tall willow become 72% and 66% on Moraine and Horseshoe Park, respectively. Changes in willow cover, such as reductions in willow density or shifts from tall to short morphotypes, could not be determined with this data. However, it is safe to say that this analysis of willow decline, based only on areas where willow disappeared, underestimated the total changes that actually occurred.

A comparison of estimates of willow decline using the two different methods (low and high-resolution) provides additional insight about the effects of disturbance. From the low-resolution maps, declines were determined based on the difference between old and recent air photos, assuming that willow were the dominant shrub species. From the GPS survey, declines were inferred based on the amount of area dominated by old dead willow plants. By comparing the two results, we found that the declines based on aerial extent of dead willow were 20% and 80% less than the estimates based on disappearance in Moraine and Horseshoe Park, respectively. This indicated that most dead willow plants remained in Moraine Park, but dead willows were removed in Horseshoe Park, probably by the 1982 flood event.

Even though changes to drier climatic conditions (Singer et al. 1998a), could have affected willow growth and productivity, lower precipitation did not seem to be the primary causative factor producing the observed willow decline. Both valleys experienced a drier climatic trend, but showed different willow cover dynamics. Water used for willow growth came mainly from groundwater rather than current precipitation (Alstad et al. 1999), and the level of the water table was mainly regulated by the hydrological characteristics of the river (Patten 1998). Willow growth would not be affected by decreased precipitation, as long as the water table level remained high. In this way, many willows could be buffered from a slightly lower precipitation. However, since the depth of the water table during the willow growing season is mostly determined by the winter snowpack accumulations and the spring-summer melting rate (Patten 1998), it is also possible that water tables were reduced, or of shorter duration, under climate change.

As expected, changes in hydrology were a critical factor in determining willow colonization and population persistence in both parks; however, hydrological changes were different between parks. In Moraine Park, willow disappeared from areas where major reductions in river complexity were documented. In 1996, the main channel of the river was simpler, and well delimited compared to 1937/1946. Although this could have been the result of reduced water flow, the previous high river complexity and impoundment areas were clearly the result of beaver activities. Well-defined beaver dams surrounded by riparian shrubs were found in the upper Horseshoe Park valley in 1937/1946. Almost all of these ponds disappeared by 1996, but no noticeable changes in riparian shrub vegetation were documented as was observed in Moraine Park.

These contrasting responses of the riparian shrub community to decline in beaver could have resulted from differences in interactions between basin geomorphology and beaver activities. Johnston and Naiman (1987) distinguished the characteristics of beaver dams in upland V-shaped valleys from wetlands with extensive floodplains. Beaver dams in upland streams produced small ponds with well-defined contours. In these ponds, there was little change in surface water level when stream water level fluctuated. In wetland floodplains, small beaver dams often inundated a large surface with shallower water depth and the pond boundary was diffuse. Beaver alterations seemed to have less impact on ecosystem level processes in wetlands than on uplands because soils in wetlands were under saturated conditions (Johnston and Naiman 1987). Well-defined beaver dams were found in the upper areas of Horseshoe Park, in the V-shaped part of the valley. There, the water table was probably not reduced by the decrease in beaver and their ponds, because the water table was controlled by geomorphology more than by beaver ponding. If this was the case, then hydrological conditions for shrub growth were little affected by the beaver decline.

Floodplains of both watersheds represented conditions that were intermediate between the two contrasting situations just described. On floodplains, geomorphic characteristics were similar to a valley with a low elevation gradient, but soil water saturation could occur only during a short period of time, in a restricted area close to the river. Water tables, in areas close to the river, fluctuated between 20 cm and 100 cm during the annual peak in stream flow (June) (Zeigenfuss et al., this volume). In this situation, beaver dams noticeably changed the hydrological conditions for vegetation growing around edges of ponds. Although ponds did not have a defined boundary as in the case of wetlands, they were not large. The gradient of the floodplain in Moraine Park was large enough to limit the size of the pond because further increases in pond surface area were limited by the formation of a new drainage channel. In this valley, well-defined beaver ponds were difficult to identify in 1946, but there were several small impoundment areas and many branches of the river.

This hydrological process ultimately increased the branching pattern of the river, and probably resulted in a larger area of water subsidization than would occur with a few large beaver ponds. Thus, decreases in beaver abundance caused a simplification of the river course and a reduction in the area of land surface influenced by the river and associated water tables. In areas where water tables were diminished, drier conditions prevailed, and riparian shrub communities were replaced by meadows.

Willow decreases in Horseshoe Park seemed to be, in large part, caused by the flood disturbance following the collapse of an earthen dam in 1982. Most of the reduction in riparian shrub cover occurred on downstream areas that were directly affected by the flood. In 1996, areas with bare soils created by the flooding were being colonized by willow. Periodic large flood disturbances that destroy vegetation and generate open patches for plant establishment have been considered to be important in models of riparian landscape structure (Miller et al. 1995). Some riparian species depend on these recurrent disturbance events for establishment. Thus, alterations of the flood regime have negatively affected many riparian ecosystems (Bradley and Smith 1986).

The flood event that occurred in Horseshoe Park produced a larger disturbance than normally expected in a recurrent flood regime in mountain valleys (Patten 1998). The hydrological characteristics of the river were not only altered downstream but also upstream, through a large mass of rocks and boulders that slid into the valley (Jarret and Costa 1993). Restriction of river flow in the area of the alluvial fan could have increased water tables in the upper areas of the valley. This is the area where major reductions in beaver ponds were found.

In addition, water table levels in the meadows that were colonized by willow in the upper areas of the valley (Figs. 3 and 6) could have increased since the flooding, producing favorable conditions for willow establishment. Willow seedlings rapidly colonized the sediments deposited in the alluvial fan in the summer of 1983 (Keigley 1993). Even though some patches contained a high density of seedlings, few of them survived to the following years (Keigley 1993). Most of the willow observed on the alluvial fan in 1998 came from the original establishment of 1983 (Keigley 1993). This area was classified in the GPS survey as being colonized several years ago because it was dominated by young short willows (Fig. 6). These willows were no older than 15 years.

Willow produces wind-dispersed seeds that have a limited viability and no willow seed bank ever develops (Raven 1992). In RMNP, tall willow normally produce a large number of seeds and seed availability does not limit willow establishment (Cottrell 1995). Willow saplings (younger than 4–5 years) were observed in meadows with high soil water content indicating that recruitment is not restricted to bare soil as occurs with other riparian species (Bradley and Smith 1986). However, wet sandbars are suitable sites for willow establishment, as indicated by high recruitment observed in areas affected by flooding.

The study areas have been intensively affected by human activities since the late 1800s. Important changes could have occurred in riparian communities before the area became part of the national park. Nevertheless, during the period covered by this study, the impacts of human activities on riparian communities decreased because the area became protected under national park policy. However, in the last 50 years, both watersheds have shown signs of deterioration in the riparian plant communities. These changes do not seem to have been caused by direct impacts on the ecosystem. However, humans may have generated conditions that led to increased elk population size, which could have affected the riparian ecosystem.

The large proportion of willows with short morphotypes in 1996 could be a result of increased elk browsing. Elk browse on willow mainly during the winter, on the new shoots developed during the previous growing season. An increase in elk browsing on willow leaders could produce suppressed willow morphotypes. In a similar way, high elk browsing pressure inhibits height elongation on young aspen stems, and suppressed plants are preferentially browsed by elk (Romme et al. 1995). Tall plants are protected from browsing because new meristems are beyond the reach of elk. Disturbances, such as flooding or beaver activities, facilitate elk access to willow shoots. Interestingly, in Horseshoe Park, short and intermediate willow morphotypes were primarily located in the downstream flooded area. Disturbances might open up the willow canopy, stimulating stem turnover. Elk could then access new stems causing an increase in the density of stems with a suppressed morphology. This process would ultimately lead to a short willow community. Additionally, young willows growing under heavy browsing levels will be kept in a short morphotype. It is expected that under heavy browsing, areas newly colonized by willow will be primarily comprised of short morphotypes, thus increasing the total area of short willow.

Elk browsing pressure on willow increased following reintroduction and cessation of artificial controls, but it is not clear how this could have affected the extent of willow cover. We hypothesize that increased elk browsing did not directly cause a long-term decrease in riparian shrub cover but may have indirectly contributed to the decline. All of the areas where willow disappeared suffered important hydrological changes. A willow cover decline was also found in Yellowstone National Park (Engstrom et al. 1991), where a similar interaction between elk and drier conditions had occurred (Singer et al. 1998a). During the 1988 drought in Yellowstone, willow in two stands located on dry marginal sites died. Willows in one stand were heavily browsed but willows in the other were not (Singer et al. 1994). Under a long-term trend of reduced water availability, other vegetation types will replace riparian shrubs, since they are not adapted to withstand water stress (Patten 1998). Under this scenario, differences in the level of elk browsing on willow would make little difference in the long-term vegetation trend. Thus, elk could have reduced willow canopy cover within a willow patch by suppressing plant growth, but the total area covered by willow in the valley would be primarily controlled by the amount of wet habitats suitable for riparian vegetation growth. However, elk could indirectly affect beaver by reducing the extent of tall willow morphotypes. Beaver decreases induced the reduction of river length and water subsidized surface area, causing drier conditions for willow growth. It is not clear why beavers have almost disappeared from these RMNP watersheds, but it is possible that the elk increase contributed to the beaver decline.

Direct species interactions (physical interaction) have been most commonly studied, but recently, indirect effects have been shown to be important in many studies (Wootton 1994; Schmitz et al. 1997; Olff and Ritchie 1998). Beaver have a direct effect on riparian shrubs by cutting stems that are used for food or building dams and lodges (Nolet et al. 1994). Additionally, beaver impoundments create favorable physical conditions for riparian vegetation growth (Naiman 1988; Johnston and Naiman 1990b,c). Shrub reinvasion has been observed in abandoned beaver ponds (Remillard et al. 1987). Fragmentation of willow plants and the movement of the cut stems by beaver could be an important factor in the asexual propagation of the species (Cottrell 1995). At the same time, a direct interaction occurred between elk and willow. Changes in willow communities induced by elk, such as increases in cover of suppressed morphotypes, will have indirect negative effects on beaver. One of the major challenges in ecology is the identification of the strength of species interactions (Wootton 1994; Bertness and Leonard 1997). The signs and intensities of the interactions are dynamic. They depend on the size of the beaver and elk population, as well as the characteristics of the riparian vegetation and environmental conditions. Plant biomass production responses to different levels of browsing (Bergström and Danell 1987), beaver cutting (Kindschy 1989), and biogeochemical changes induced by elk or beaver also need to be considered (Naiman and Melillo 1984; Pastor and Naiman 1992; Hobbs 1996). Species interactions, particularly between beaver and willow, seem to be an important source of stability in these riparian ecosystems, which are subject to continuous disturbance events. These ecosystems are largely dependent on beaver, which act as a keystone species (Bond 1994; Heywood 1995) generating favorable conditions for willow growth. Thus, persistence of these riparian communities will depend on the reestablishment of the biotic and abiotic conditions that support beaver populations.

Conclusions

Trends in willow cover were similar in both parks, but the characteristics of the decline and conditions of the current vegetation were different. In Moraine Park, riparian shrub declines were spatially associated with major reductions in river complexity. In Horseshoe Park, declines were mainly spatially associated with areas that were directly affected by the 1982 flood disturbance. Willow vegetation in Moraine Park was more heterogeneous than in Horseshoe Park. This heterogeneity was caused by a high proportion of short willow morphotypes that grew in low density in areas dominated by birch and dead willow cover. Willow colonization was found in both parks on wet meadows and also in areas affected by flooding in Horseshoe Park.

The potential causes of willow decline are many, but it is clear that beaver played a role in increasing riparian habitat cover by increasing stream channel complexity, creating impoundments of water, and thus increasing the area of land surface where there is an elevated water table. The decline in beaver between 1939 and 1969 is not well quantified, and the available data indicate that there were still many beaver present in 1969. It would be useful, therefore, to conduct an additional willow survey using 1969 aerial photography, to try and determine how much of the willow decline occurred before or after 1969.

Humans may have played a role in decreasing riparian habitat, through their activities between 1875–1961, including substantial alterations of the hydrology through ditching in Moraine Park. Despite these alterations, however, beavers were still present in abundance in 1939 and to a lesser extent in 1969. Horseshoe Park was not affected this way, yet there was still a decline in willow cover, and a shift to shorter morphotypes. There is a need to try to reconstruct human activities and their effects more precisely.

Elk wintering in RMNP increased in number from 0 in 1914, to at least 800 in 1943, were kept at 600 or below 1944–1968, and then increased to over 1,000 in the late 1980s. Yet, studies indicate that willows are well adapted to tolerate herbivory. Willows were still abundant in 1939–1946, when there were also abundant elk. There may also have been abundant elk prior to their extirpation through market hunting. Climate data suggest a slight warming and drying, but the impacts of such a climate shift on hydrology and riparian habitats have not been determined. In our opinion, decreases in the area of riparian, water-subsidized habitat resulting from beaver decline have probably been much more significant than either changes arising from elk herbivory alone, or from lower precipitation. The cause(s) of the beaver decline are still unknown. There is a need to evaluate alternative explanations which might include: disease outbreak; beaver overabundance and resultant crash due to loss of forage; competition with elk; and loss of habitat and forage due to human land use and hydrologic alterations.

Literature Cited

Alstad, K. P., J. M. Welker, S. Williams, and M. J. Trlica. 1999. Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: An isotopic study using $\delta^{13}C$ and $\delta^{18}O$. Oecologia 120:375–385.

Baron, J. 1992. Surface water. Pages 142–183 *in* J. Baron, editor. Biogeochemistry of a subalpine ecosystem: Loch Vale watershed. Springer-Verlag, Berlin.

Bergström, R., and K. Danell. 1987. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. Journal of Ecology 57:533–544.

Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: Lessons from intertidal habitats. Ecology 78:1990–2003.

Bond, W. J. 1994. Keystone species. Pages 237–253 *in* E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer-Verlag, Berlin.

Bradley, C. E., and D. G. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. Canadian Journal of Botany 64:1433–1442.

Buchholtz, C. W. 1983. Rocky Mountain National Park: A history. Colorado Associated University Press, Boulder.

Clemmer, P. 1994. Riparian area management: The use of aerial photography to manage riparian-wetland areas. Technical Reference 1737-10. U.S. Department of the Interior. Bureau of Land Management, Denver, Colorado.

Collins, W. B., and D. J. Helm. 1997. Moose, *Alces alces*, habitat relative to riparian succession in the boreal forest, Susitna River, Alaska. Canadian Field-Naturalist 111:567–574.

Cottrell, T. R. 1995. Willow colonization of Rocky Mountain mires. Canadian Journal of Forest Research 25:215–222.

Décampus, H., M. Fortune, F. Gazelle, and G. Patou. 1988. Historical influence of man on the riparian dynamics of a fluvial landscape. Landscape Ecology 1:163–173.

Engstrom, D. R., C. Whitlock, S. C. Fritz, and H. E. Wright. 1991. Recent environmental change inferred from the sediments of small lakes in Yellowstone's northern range. Journal of Paleolimnology 5:139–174.

ERDAS-IMAGINE. 1998. ERDAS, Inc., 2801 Buford Highway N.E., Suite 300, Atlanta, GA 30329-2137, USA.

ESRI. 1994. Environment Systems Research Institute, Inc., 380 New York Street, Redlands, CA 92373, USA.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540–551.

Hess, K. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot.

Heywood, V. H., editor. 1995. Global biodiversity assessment. Cambridge University Press, Cambridge, New York.

Hickman, S. D. 1964. A beaver census of Moraine Park, Rocky Mountain National Park. Unpublished report.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Jarret, R. D., and J. E. Costa. 1993. Hydrology and geomorphology of the 1982 Lawn Lake dam failure, Colorado. Pages 1–17 *in* H. E. McCutchen, R. Herrmann, and D. R. Stevens, editors. Ecological effects of the Lawn Lake flood of 1982, Rocky Mountain National Park. Scientific Monograph NPS/NRROMO/NRSM-93/21.

Johnson, L. B., and S. H. Gage. 1997. Landscape approaches to the analysis of aquatic ecosystems. Freshwater Biology 37:113–132.

Johnston, C. A., and R. J. Naiman 1987. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. Landscape Ecology 1:47–57.

Johnston, C. A., and R. J. Naiman. 1990a. Browse selection by beaver: Effects on riparian forest composition. Canadian Journal of Forest Research 20:1036–1043.

Johnston, C. A., and R. J. Naiman. 1990b. Aquatic patch creation in relation to beaver population trends. Ecology 71:1617–1621.

Johnston C. A., and R. J. Naiman 1990c. The use of geographic information systems to analyze long-term landscape alteration by beaver. Landscape Ecology 4:5–19.

Keigley, R. B. 1993. Observations of plant ecology on the Lawn Lake flood alluvial fan. Pages 93–214 *in* H. E. McCutchen, R. Herrmann, and D. R. Stevens, editors. Ecological effects of the Lawn Lake flood of 1982, Rocky Mountain National Park. Scientific Monograph NPS/NRROMO/NRSM-93/21.

Kindschy, R. R. 1989. Regrowth of willow following simulated beaver cutting. Wildlife Society Bulletin 17:290–294.

Miller, J. R., T. T. Schulz, N. T. Hobbs, K. R. Wilson, D. L. Schrupp, and W. L. Baker. 1995. Changes in the landscape structure of a southeastern Wyoming riparian zone following shifts in stream dynamics. Biological Conservation 72:371–379.

Naiman, R. J. 1988. Animal influences on ecosystem dynamics. BioScience 38:750–752.

Naiman, R. J., and J. M. Melillo. 1984. Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). Oecologia 62:150–155.

Nolet, B. A., A. Hoekstra, and M. M. Ottenheim. 1994. Selective foraging on woody species by the beaver *Castor fiber*, and its impact on a riparian willow forest. Biological Conservation 70:117–128.

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

Packard, R. M. 1947. A survey of the beaver population in Rocky Mountain National Park, Colorado. Journal of Mammalogy 28:219–227.

Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. The American Naturalist 139:690–705.

Patten, D. T. 1998. Riparian ecosystem of semi-arid North America: Diversity and human impacts. Wetlands 18:498–512.

Raven, J. A. 1992. The physiology of *Salix*. Proceedings of the Royal Society of Edinburgh 98B:49–62.

Remillard, M. M., G. K. Gruendling, and D. J. Bogucki. 1987. Disturbance by beaver (*Castor canadensis* Kuhl) and increased landscape heterogeneity. Pages 103–123 *in* M. G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York.

Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk, and fire in northern Yellowstone National Park. Ecology 76:2097–2106.

Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scale. Landscape Ecology 11:141–156.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. Ecology 78:1388–1399.

Singer, F. J., L. C. Mack, and R. G. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435–443.

Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. Barnett. 1998a. Elk, multiple factors, and persistence of willow in national parks. Wildlife Society Bulletin 26:419–428.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998b. Thunder on the Yellowstone revisited: An assessment of management of native ungulates by natural regulation, 1968–1993. Wildlife Society Bulletin 26:375–390.

Stevens, D. R., and S. Christianson. 1980. Beaver populations on the eastern slope of Rocky Mountain National Park. Unpublished report.

Tabacchi, E., A. M. Plantly-Tabacchi, and O. Décampus. 1990. Continuity and discontinuity of riparian vegetation along a fluvial corridor. Landscape Ecology 5:9–20.

Ustin, S. L., M. O. Smith, and J. B. Adams. 1993. Remote sensing of ecological processes: A strategy for developing and testing ecological models using spectral mixture analysis. Pages 339–358 *in* J. R. Ehleringer and C. B. Field, editors. Scaling physiological processes: Leaf to globe. Academic Press, Inc., San Diego.

Wootton, J. T. 1994. Predicting direct and indirect effects: An integrated approach using experiments and path analysis. Ecology 75:151–165.


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CHAPTER THREE

Vegetation Responses to Natural Regulation of Elk in Rocky Mountain National Park

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Abstract. Little experimental information is available on the relationship between herbivory by native ungulates and vegetation in relatively undisturbed environments. A quasi-experimental situation exists in Rocky Mountain National Park, where elk (*Cervus elaphus*) populations have increased about 3-fold since 1968, following their release from artificial controls within the park boundaries. We reviewed data collected on vegetation transects established and monitored over the 25-year period from 1968 through 1992. Data were subjected to rigorous statistical analysis to detect trends following the release of elk from artificial controls. Increases in elk habitat use and decreases in deer habitat use were observed on all transects over the 25-year period. Significant increases in moss and lichen cover occurred in three of four vegetation types. Percent cover of bare ground, forbs (particularly *Selaginella densa*), and *Carex* spp. increased on grassland transects. Increases in timothy (*Phleum pratense*) were observed on meadow transects. Graminoid and litter cover increased on sagebrush transects, and shrub and litter cover increased on bitterbrush transects.

We concluded the lack of control (fenced) plots in this sampling design, the types of measures, the small number of replicates, and nonrandom placement of plots limit the inferences and sensitivity from the work. Unique strengths of the work included the long time period (25 years), good distribution of samples, consistency of the observer (D. Stevens), and placement of the plots in the most heavily grazed sites.

Some grazing-induced responses were detected. Grazing-resistant species such as sedges (native), timothy (exotic), and club mosses increased and the amount of bare ground increased on some grazed sites. However, the changes within this sampling program alone were not alarming. The amount of bare ground increase was minor (4%), and grass and shrub cover increased in the shrub plots. The inferential power of this sample design was limited to the study plots only. Other factors (climate change, succession) were not controlled for using fenced plots and the sensitivity of the methods and plots to detect change were limited. For example, the low number of transects in willow was not adequate to monitor conditions on the entire winter range. Lacking controls, observed changes may have been due to other factors (climate trends, beaver dam abandonment, stream channel changes), not elk herbivory alone. We recommend using a new sampling design that would include controls, pretreatment data, random site selection, and much more replication.

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Keywords: Elk, herbivory, natural regulation, potential overgrazing, vegetation monitoring.

Introduction

Little experimental information is available on the relationship between herbivory by native ungulates and vegetation in relatively undisturbed environments. A quasi-experimental situation exists in Rocky Mountain National Park, where elk (*Cervus elaphus*) populations have increased about 3-fold since 1968, following their release from artificial controls within the park boundaries. Elk were native in the area, but were extirpated, or nearly so, by the late 1800s. Elk were reintroduced to the area in 1913–1914, and steadily increased until they numbered about 1,000 in 1944 (Packard 1947), but due to concerns over vegetation conditions, populations were reduced and then held below 500 from that time until 1968. Culling of the herd was discontinued in 1969 under the premise that elk within the park would regulate themselves if left alone, and following release from artificial controls, they subsequently increased. Ambitious efforts were made by the agencies involved to slow or control the elk densities on lands immediately outside the park through late season harvests of both sexes. Interagency goals were to harvest 500–600 elk per year, a number that was 15% to 17% of the estimated elk population — a level of harvest that might have limited or regulated the elk population, depending on the rate of other elk losses. The maximum rate of increase in a wild elk population where survival rates are high is about 33% per annum (Eberhardt et al. 1996). But it has proven impossible to obtain a harvest of 500–600 elk, and more recently, access to private lands and tolerance for sport hunting have declined in the area. Human developments such as subdivisions, town developments, and ranchettes with a few head of horses, have increased exponentially in the past 10–15 years. The human population of the Estes Valley in 1970 was 3,554. That number had reached 8,889 by 2000 (U.S. Census Bureau data). As a result of less access by sportsmen to private lands, elk harvests declined from 442 $\pm$ 78 ($\bar{x} \pm$ SD) before 1987 to 302 $\pm$ 36 since 1987, raising concerns that the elk population has further increased since 1987 (Fig. 1). Elk have habituated to people and the developments in town, and as a result, have recently gained access to rich food sources in the form of irrigated and fertilized golf courses, pastures, lawns, and ornamental shrubs. Access to these new food sources, combined with shallow snows in town, might have further fueled the elk increases. Concerns over possible further elk increases since 1987 have been expressed by agency managers and others (Hess 1993).

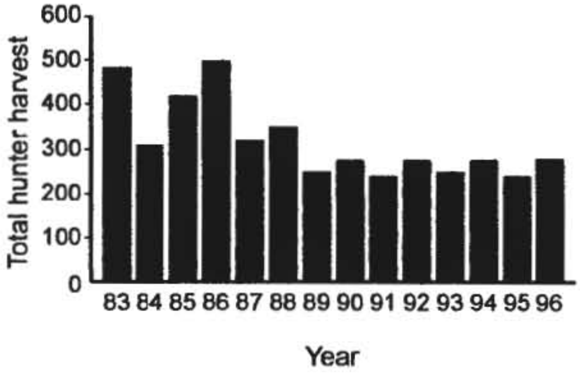

Fig. 1. Total hunter harvest of elk outside Rocky Mountain National Park from 1983–1996.

Elk were absent or held to low densities by human controls on the winter range for over half the century (late 1800s to 1969) and vegetation conditions and succession may have changed as a result of the underpopulation of a large native herbivore. Some vegetation changes observed since 1969 might be interpreted as a return to more natural conditions with the return of elk to a more significant role in the ecosystem. Vegetation conditions may not be declining beyond natural conditions to be expected from elk grazing (Stevens 1980,1992; Houston 1982).

National parks have a mission to preserve natural ecosystems and processes (U.S. Department of the Interior, National Park Service 1988). Large native ungulate herbivores can influence many aspects of plant structure, growth, and net primary productivity. Ungulates grazing and the action of their hooves can result in more bare ground, soil compaction, and higher sediment yields from grazed sites. Increases in bare ground could result in a warmer or drier soil microclimate. A warmer soil, if moisture is equivalent, could result in increased nitrogen mineralization on grazed sites. Ungulates can also influence the nitrogen cycle by changing litter quality, thereby affecting nitrogen mineralization rates, and by adding readily available nitrogen to the upper soil levels in the form of urine and feces (Hobbs 1996). Thus, the natural heterogeneity of nitrogen within the landscape can be influenced by ungulates.

Net primary productivity can either increase or decrease as a result of ungulates. Elk grazing increases nitrogen and other nutrient content and digestibility of forages in other study areas (Frank and McNaughton 1992; Singer and Harter 1996). Elk apparently return nutrients to the grasslands at a high rate (Frank and McNaughton 1992) and grazed plants may be less susceptible to drought effects. Intensely grazed grasses and shrubs had more optimal root:shoot ratios, longer growing seasons, higher water conductance, and higher survival than ungrazed counterparts (Georgiadis et al. 1989; Welker and Menke 1990). McNaughton (1979) and Holland and Detling (1991) observed that rates of photosynthesis and nitrogen uptake were higher on grazed sites. Ungulates can create spatial heterogeneity, modulate successional processes, and control the switching of ecosystems between alternative states (Hobbs 1996). Thus, we regard ungulate herbivory as a natural ecosystem process. Some effects of elk on vegetation, soil, and nutrient processes, whether positive or negative, should be considered normal and natural in a national park ecosystem where elk are a native species.

The challenge for land and resource managers is to determine what conditions are "natural" (a value-laden term) because so little information is available for the area prior to the influence of settlers in the mid-1800's. It is not clear at what point the effects of elk herbivory exceed those expected under natural conditions and become excessive effects, or overgrazing. National Park Service (NPS) policy states that ungulates in parks can be controlled when those concentrations are unnatural and due to the effects of modern man, but unnatural concentrations can also be hard to define operationally (U.S. Department of the Interior, National Park Service 1988). However, natural processes to control populations of native species should be relied upon to the greatest extent possible.

Definitions of Overgrazing

Overgrazing is also a value-laden term which can be defined in various ways (see review by Coughenour and Singer [1991]). Overgrazing is defined simply as any excess of herbivory that leads to degradation of plant and soil resources. The excess, which may be caused by humans, should be defined. By our definition, overgrazing could not occur in a pristine pre-Columbian ecosystem with intact predator fauna. Those grazing effects should all be considered natural and undisturbed.

One's perceptions might influence how overgrazing will be defined. A range manager might define overgrazing as any grazing in excess of that level which would result in maximum production of livestock animal tissues from the system. A wildlife manager might seek maximum sustained yield (MSY) for sport hunting purposes. In that context, overgrazing would be in excess of that for MSY. Typically, MSY for a wild herbivore like elk might be 53% to 60% of the ecological carrying capacity of the habitat (ECC or *K*). Ecological carrying capacity, or the ungulate-vegetation ceiling, is defined as the maximum dynamic capacity of the habitat, forage, and climate of the area to sustain the herbivore. Thus, if *K* of a certain area was estimated at 1,700 elk, MSY might occur at about 1,200 elk and any grazing in excess of that would be overgrazing. In the most liberal context, ungulates, whether native or nonnative, are predicted to obtain a new stable equilibrium with their vegetative forage base — the Caughley model (Caughley 1979, 1981). In the Caughley model, considerable mortality of some plants, major shifts in plant species to less palatable and more resistant species, and some reduction in plant productivity, are quite acceptable. Just let the animals and plants do their own thing and everything will be all right. That is what has happened time and time again in nature. For example, when elk and other ungulates crossed the Bering Land Bridge, they encountered systems that were not yet adapted to their herbivory and yet, eventually, the system adapted. Obviously, none of these definitions is appropriate for a national park.

Four hypothetical scenarios of elk density have been proposed for Yellowstone National Park, where this subject has been intensely investigated but where little agreement exists within the scientific community (Fig. 2). The first proposed density scenario, the natural regulation hypothesis of Cole (1971) and Houston (1971, 1976), predicts a food-limited elk density at or near ECC or *K* with little or no limitation by predators or Native Americans. This was the premise by which elk were released from artificial controls in both Yellowstone and Rocky Mountain National Parks in 1968. But in the ensuing decades it was determined that predators, especially where both bears and wolves were significant, could limit, and possibly regulate, ungulates in many situations (Bergerud et al. 1983; Boutin 1992; Gasaway et al. 1992). The second proposed scenario, based on predictions and extensive computer simulations, suggests wolves and bears would reduce elk 8% to 20% following full restoration of 75–100 wolves to the northern area — the predator-limited K_I of Garton et al. (1990), Boyce (1993), and Mack and Singer (1993). Third, based on

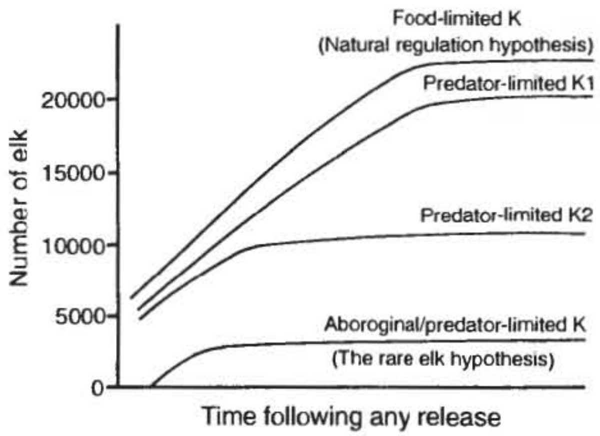

Fig. 2. Four hypothetical scenarios of elk density in Yellowstone National Park under different carrying capacity models (from Cole 1971; Boyce 1993; Lime et al. 1993; Kay 1994).

observations from the far north, other wolf experts predict 200 wolves will occupy the area and wolves and bears will limit elk to 40% to 50% of K — the predator-limited K_2 (Gasaway et al. 1992; Lime et al. 1993; Messier 1995). The fourth scenario, the rare elk hypothesis, is based on the premise that Native Americans were efficient at hunting and pursued elk to great lengths and reduced elk populations to <10% of K (Kay 1990, 1994; Wagner et al. 1995a,b).

For purposes of this paper, we define overgrazing in three contexts. We suggest all three might be considerations in a management decision. First, appropriate grazing may be defined in terms of the population density of elk that are suspected to have occurred on the park winter ranges at the time of pre-Columbian man, with natural migrations of elk in place and intact native predator fauna.

This, our preferred choice for a population density definition of overgrazing, is that wolves, bears, and other predators limited elk numbers in prehistoric times in Rocky Mountain National Park to about one-fourth less than the K for the area. We selected this scenario based on the greater consensus of experts and modelers who preferred this option (Garton et al. 1990; Boyce 1993; Lime et al. 1993; Mack and Singer 1993). We hasten to add, however, that a high degree of uncertainty and scientific debate surround these predictions.

Secondly, we propose another definition of overgrazing for Rocky Mountain National Park based on plant mortality, species composition, alterations to less palatable plants, or alterations to ecosystem processes beyond those effects expected from the system prior to arrival of modern man. There should be no reduction in plant cover, no increase in bare ground, no reduced input of organic matter, no increase in soil temperature or decrease in soil moisture, nor any increase in sediment or nutrient loss beyond levels expected from elk in a natural, undisturbed ecosystem. In other words, the effects of grazing of elk that occurred in prehistoric times with an intact native predator guild should be acceptable and grazing effects beyond that level should be unacceptable.

A third definition of overgrazing is any grazing beyond that level of elk grazing that is sustainable over long periods of time. In other words, there should not be a net loss of nitrogen, organic matter, or other nutrients of a magnitude that would not be sustainable over a long period of time. Elk herbivory in excess of that level would be overgrazing.

The objectives of this report are to review, analyze, and interpret the data collected on vegetation transects and plots established and monitored by former park biologist D. Stevens, from 1968, following the release of elk from artificial controls, to 1992. We subjected the data to statistical analysis to detect trends following the release of elk. We also comment on whether this sampling design is sensitive enough to detect changes on this range from 1968–1992 and we provide recommendations on improved experimental and sampling designs that are more robust.

Description of the Study Area and Elk Populations

Study Area

Description of the study area was taken from Gysel (1959), Stevens (1980), and Hobbs et al. (1981). The elk winter range on the east side of Rocky Mountain National Park encompasses about 10,000 ha on the eastern slope of the Continental Divide in the upper montane zone. Glacial moraines running east-west divide the body of this area into four major valleys: Horseshoe Park, Beaver Meadows, Moraine Park, and Hallowell Park. Elevations in the study area range from 2,400 m at the valley bottoms to 2,800 m on moraine ridgetops. Mean annual precipitation is 41 cm, most occurring as wet spring snows. North-facing slopes are dominated by dense stands of lodgepole pine (*Pinus contorta*) and Douglas fir (*Pseudotsuga menziesii*), while communities of ponderosa pine (*Pinus ponderosa*)/shrub (mainly *Purshia tridentata*) and big sagebrush (*Artemisia tridentata*) dominate south-facing slopes. The flat valley bottoms are covered with sedges (*Carex* spp.), grasses, and riparian shrubs (*Salix* spp., *Betula* spp.) in wetter areas, and grasses in drier areas.

Predominant vegetation types in the upper montane zone include ponderosa pine/shrub, ponderosa pine/Douglas fir, lodgepole pine, mesic montane forest, aspen (*Populus tremuloides*), willow, shrub/grassland, grassland, meadow, and wet meadow. Elk typically utilize the conifer forests mainly for resting during midday and move into meadows and grasslands in the morning and evening to feed (Stevens 1980; Green and Bear 1990). While the winter range extends beyond the park boundaries into the town and valley of Estes Park, this study was primarily limited to the areas within Rocky Mountain National Park (Fig. 3).

Elk Populations

Our analysis of elk use of plants and vegetation trends would be incomplete without concurrent knowledge on elk population densities. At the time elk were released from artificial controls in 1968, park managers estimated 500 elk occurred within the park (Stevens 1980, 1982). Some uncertainty surrounds this figure since it was based on ground counts. But the estimate was generated by biologist, Neil Guse, who knew the elk population and winter range well. Elk could be found and were regularly hunted outside of the park from 1942 to 1968, but at the time of the release of the park elk from controls, few elk inhabited the town of Estes Park (T. Hobbs, personal communication.). Following cessation of controls within the park, elk increased rapidly and in 1979–1982, Bear (1989) estimated there were 2,273 (range 1,627 to 3,075) elk in the entire (park and Estes Valley) population.

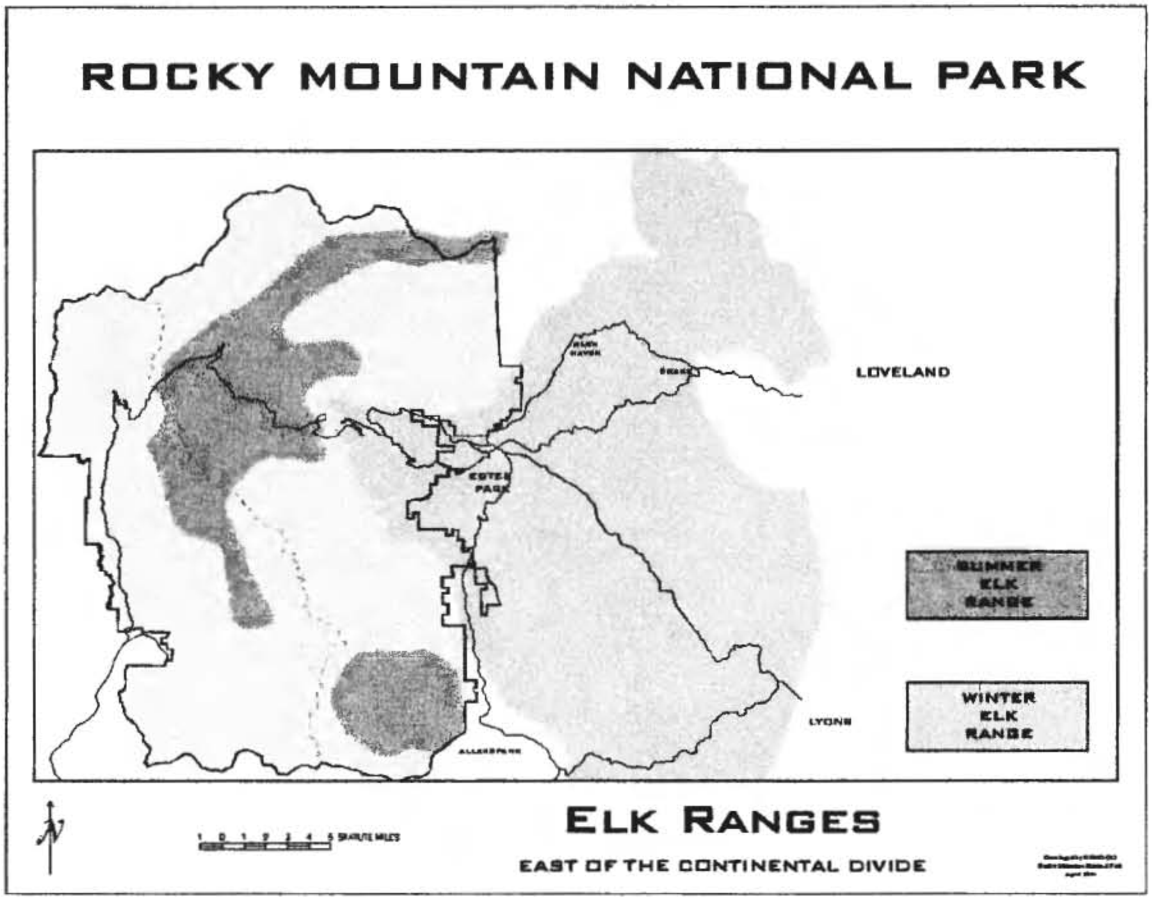

Fig. 3. Winter and summer elk ranges east of the Continental Divide in Rocky Mountain National Park.

Unfortunately, Bear (1989) did not report a separate estimate for the park alone, but it appears that elk increased 2- to 3-fold in the park. Additionally during this period, elk began to habituate to, and use, the town area more, where they gained access to rich food sources in irrigated and fertilized pastures and lawns. The town of Estes Park is approximately 250 m lower in elevation than park winter ranges, snow depths are shallower, and temperatures are warmer. Between 1968 and the present, elk increasingly invaded and took advantage of an unoccupied, but fertile, habitat in the town.

Calf:cow ratios (calves:100 cows) gathered in the area also provided evidence that elk were increasing after 1968. Calf:cow ratios averaged 48 ± 7 from 1979–1982, suggestive of an elk increase, but calf ratios declined to 36 ± 8 from 1991–1996, suggestive of a slowing of the elk increase (Fig. 4). Calf:cow ratios were also higher in the town than the park during 1990–1996, suggesting the rate of elk increase, at least in recent years, was higher in town.

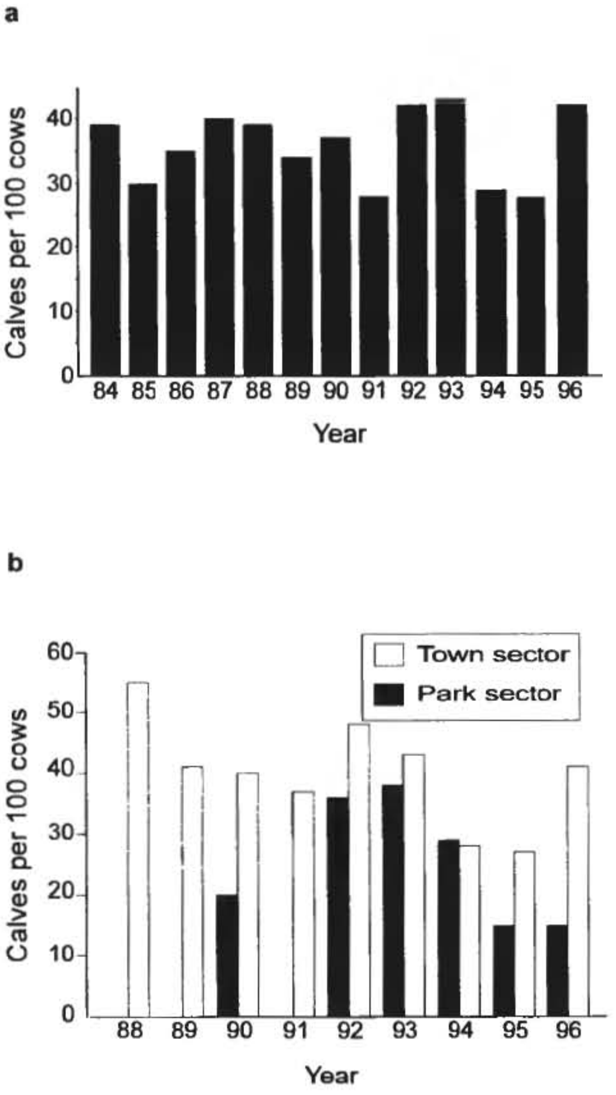

Fig. 4. Ratio of calves:100 cows on Rocky Mountain National Park winter range, 1984–1996 (a); and compared between the park (aerial classification) and town (ground classification), 1988–1996 (b).

Methods

Vegetation Trends

In 1968, then park biologist David Stevens, established a long-term monitoring program in key vegetation types used by elk. He selected representative sites in those vegetation communities and locales receiving the highest elk use (Stevens 1980, 1992). Transects were chosen nonrandomly and were well-distributed across the winter range in easily accessible areas of highest elk densities. Transects were not established in peripheral or low-use areas of the winter range.

Forty-two line transects were established in six key vegetation types on the elk winter range of Rocky Mountain National Park from 1968–1971 (Fig. 5). Primary transect lines were 100 ft (30.49 m) in length and established along the contour. Nine of these transects were in bitterbrush (*Purshia tridentata*); 4 in sagebrush (*A. tridentata*); 4 in aspen (*Populus tremuloides*); 6 in willow (*Salix* spp.); 8 in meadow; and 11 in upland grasslands. Elk diets on the eastern winter range of Rocky Mountain National Park consisted of a wide variety of species, mainly graminoids, 55%, followed by shrubs, 38%, and forbs, 6% (Table 1) (Stevens 1980; Hobbs et al. 1982).

Elk Use

Transects in bitterbrush, sagebrush, willow, and aspen were established to monitor browsing by elk and deer on the major shrub species on these transects. On

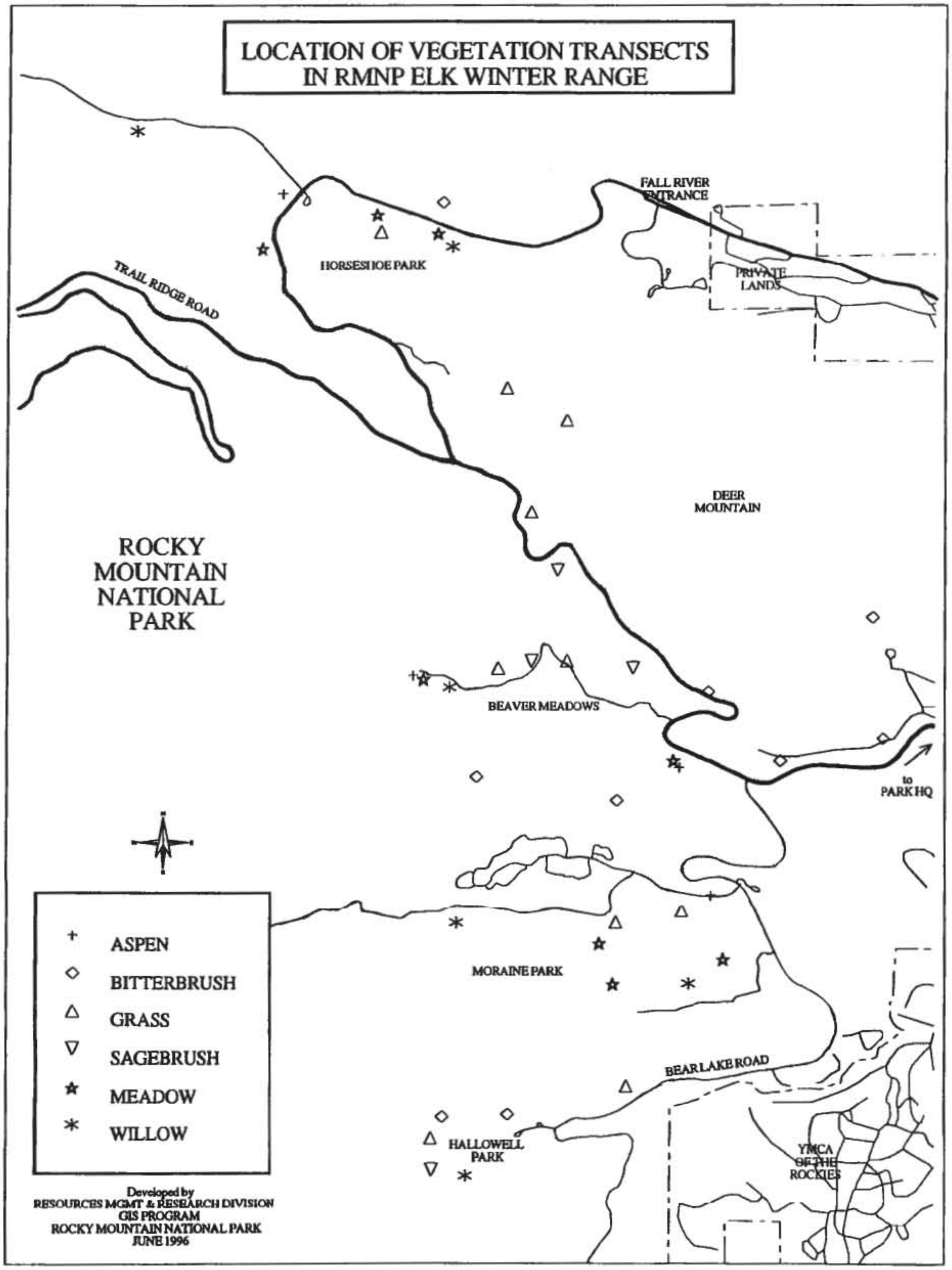

Fig. 5. Location of vegetation transects on Rocky Mountain National Park elk winter range used by D. Stevens from 1968–1992.

Table 1. Predominant components of elk winter diets in Rocky Mountain National Park from Hobbs et al. (1982) and Stevens (1980).

Graminoids	Forbs	Shrubs
Bromus inermis	*Eriogonum umbellatum*	*Salix* spp.
Bouteloua gracilis	*Potentilla* spp.	*Populus tremuloides*
Calamagrostis canadensis		*Purshia tridentata*
Carex spp.		*Potentilla fruticosa*
Juncus balticus		*Rosa woodsii*
Muhlenbergia montana		*Alnus tenuifolia*
Muhlenbergia richardsoni		*Prunus virginiana*
Phleum pratense		*Chrysothamnus viscidiflorus*
Stipa comata		*Betula* spp.
Poa spp.		*Ribes* spp.

each of these transects, 25 to 40 shrubs of the key species for that vegetation type were tagged along the transect line and assessed annually for percent leader use, form class, and decadence following the "key browse technique" of Cole (1963). Data on average height and percent cover of shrub species were collected approximately once every 5 years using the line intercept method (Canfield 1941), on bitterbrush, sagebrush, and willow transects. Data on height, basal area, and density were collected approximately once every 5 years using the point-centered quarter method (Phillips 1959; Mueller-Dombois and Ellenberg 1974), on aspen transects.

Plant utilization and use of the transects by elk and deer were measured annually on grassland and meadow transects. A variety of methods were used throughout the 25-year period to determine percent utilization on these transects, including clip-and-weigh, counts of grazed versus ungrazed plants, and ocular estimation. Use by deer and elk was monitored annually by counting the number of pellet groups of each species on 10 100-ft^2 (9.3 m^2) plots, located on a line parallel to the primary transect line, on all transects, except those in willow. Days use per acre by deer and elk were calculated following the methods described by Overton and Davis (1969), using the formula:

$$t = \frac{(1/a)\sum y_i}{13}$$

where t = days of use per acre by deer or elk, a = the total area sampled (in acres), and y_i = the total number of pellet groups per acre on the ith sample plot. A defecation rate of 13 groups per day was assumed for both deer and elk, thus:

$$43.55\sum y_i/13 = 3.35\sum y_i,$$

which is days use per acre we used.

A modified Daubenmire (1959) technique was used to determine occurrence and percent cover of herbaceous and small shrub species on bitterbrush, sagebrush, grassland, and meadow transects. These samples were collected approximately once every 5 years. This technique involved sampling 21 (20 x 50 cm) plots distributed at 5 ft (1.52 m) intervals along the 100 ft (30.5 m) transect line.

Statistical Methods

Both parametric and nonparametric methods of analysis were used. Because transect locations were subjectively selected, transects were treated as fixed effects using two-way analysis of variance with year as the other factor. Linear contrast methods were used to test for significant trends in the responses over time. Nonparametric analyses (rank transformations) were used for variables which otherwise might violate the distributional assumptions required for analysis of variance procedures (parametric analyses). In the nonparametric analysis, the data were ranked by transect, and then ranked data were analyzed using general linear models. Annual data were analyzed using general linear models (PROC GLM) to determine significant changes over the 25-year period in average percent leader use, average days of elk use per acre, and average days of deer use per acre year. Percent cover by species, height, density, and basal area data, from the Daubenmire, line intercept, and point-centered quarter plots were analyzed using PROC GLM and ranked by species. Percent change in variables which is reported in the **Results** section is based on regression models fitted to the data. Analyses were performed using SAS 6.08 statistical software.

We did not analyze utilization data from grassland and meadow transects because variation in sampling methods through the years may have affected the comparability of the data from one sampling period to the next. We performed no statistical analyses on decadence and form class data on browse transects due to the subjective and qualitative nature of these data, and because tag numbers were often reused when the original tagged plant died.

The entire data set for each vegetation type was broken into smaller subsets for analysis in those instances where the first sampling year differed among the transects. When significant trends over time were observed in all subsets for a vegetation type, we assumed that the trend was significant for the vegetation type as a whole. One willow transect and one aspen transect were dropped from the 25-year analysis because the original transects were destroyed in 1982 by the Lawn Lake flood.

Results

Trends in Elk Habitat Use

Increases in elk habitat use and declines in deer habitat use, as evidenced by pellet counts over the 25-year period, were observed on all transects which had pellet counts. There was no overall change in consumption (percent leader use) of browse species. Changes in cover of graminoids, forbs, shrubs, mosses/lichens, litter, and bare ground varied by vegetation type (Table 2). Significant ($P < 0.05$) trends are summarized by vegetation type below.

Grassland Transects

Elk habitat use, as indicated by density of fecal piles, on grassland transects increased by 48% over the period 1969–1993 (Fig. 6a). Deer habitat use, however, decreased from the period 1969–1984 and then increased from 1985–1993 (Fig. 6b). Overall, deer habitat use decreased by 48% on these transects over the entire sampling period. Significant increases in percent cover of bare ground (34%), forbs (30%), and lichens/mosses (1,200%) on these transects occurred from 1968–1988 (Fig. 7a,b,c). Most of the increase in forbs is attributable to the increase of *Selaginella densa*. Percent cover of *Carex* spp. more than doubled (136% increase). Little clubmoss (*S. densa*) and lichen species increased significantly (76% and 728%, respectively) throughout this period as well (Fig. 8a,b,c).

Meadow Transects

Elk habitat use on meadow transects doubled over the period 1971–1992 (Fig. 9). Percent cover of *Phleum pratense* showed a significant increase of 54% over the period 1978–1988 (Fig. 10).

Table 2. Statistically significant change of measured variables ($P < 0.05$) over 25-year period 1968–1992 (0 = no change, + = increase, – = decrease).

Vegetation type	Days use per acre		Percent leader use of shrubs	Percent cover by functional group					
	Elk	Deer		Graminoids	Forbs	Shrubs	Mosses/ lichens	Litter	Bare ground
Grassland	+	–		0	+	0	+	0	+
Meadow	+	0		0	0	0	0	0	0
Willow			0						
Aspen			0						
Sagebrush	+	–	0	+	0	0	+	+	0
Bitterbrush	+	–	0	0	0	+	+	+	0

Aspen Transects

No significant changes were found in basal area, density, or average height of aspen trees on these transects for the period 1968–1988. But the variance between transects was large and the number of sample plots (n = 3–4) was small.

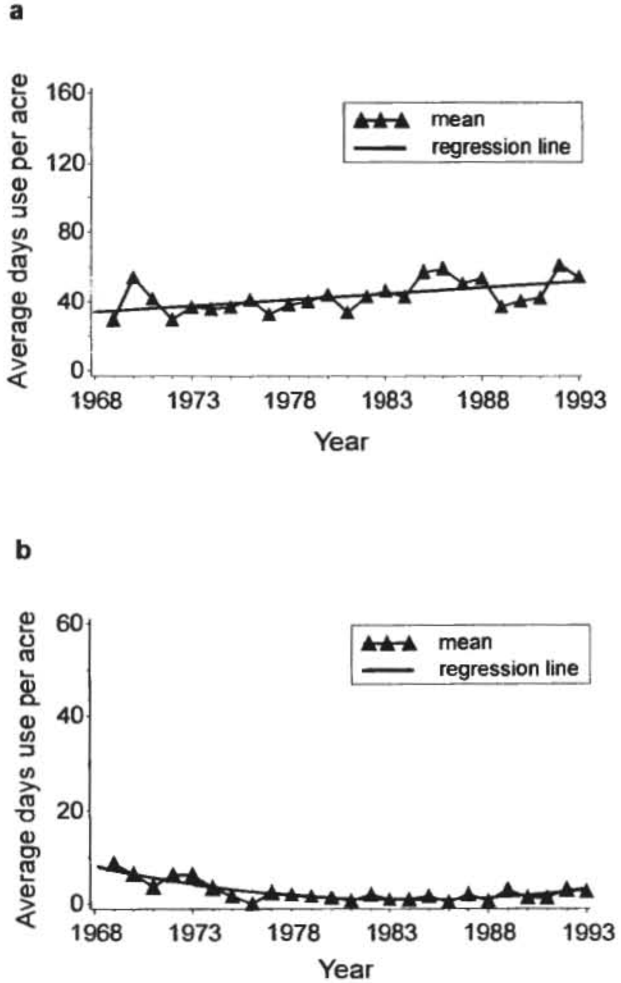

Fig. 6. Average days use per acre by elk (a), and mule deer (b) on grassland transects as determined by pellet count plots, 1968–1993.

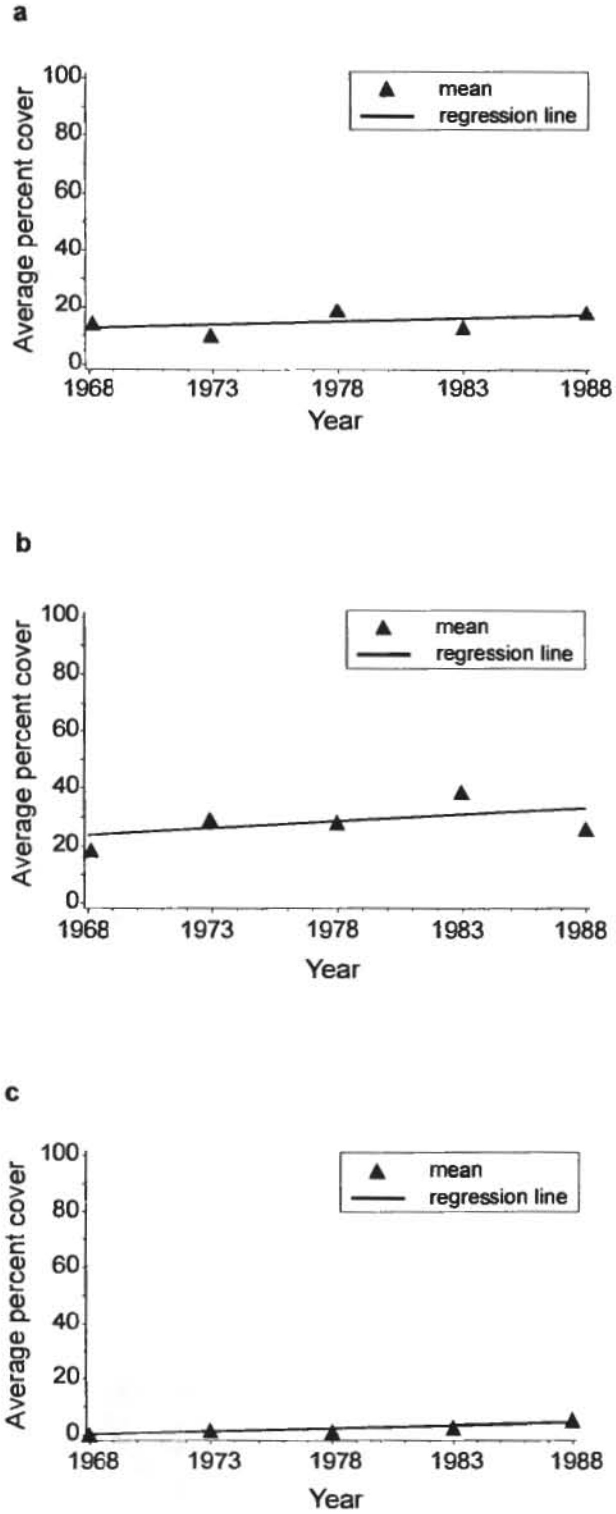

Fig. 7. Average percent cover of bare ground (a), forbs (b), and mosses and lichens (c) on grassland transects, 1968–1988.

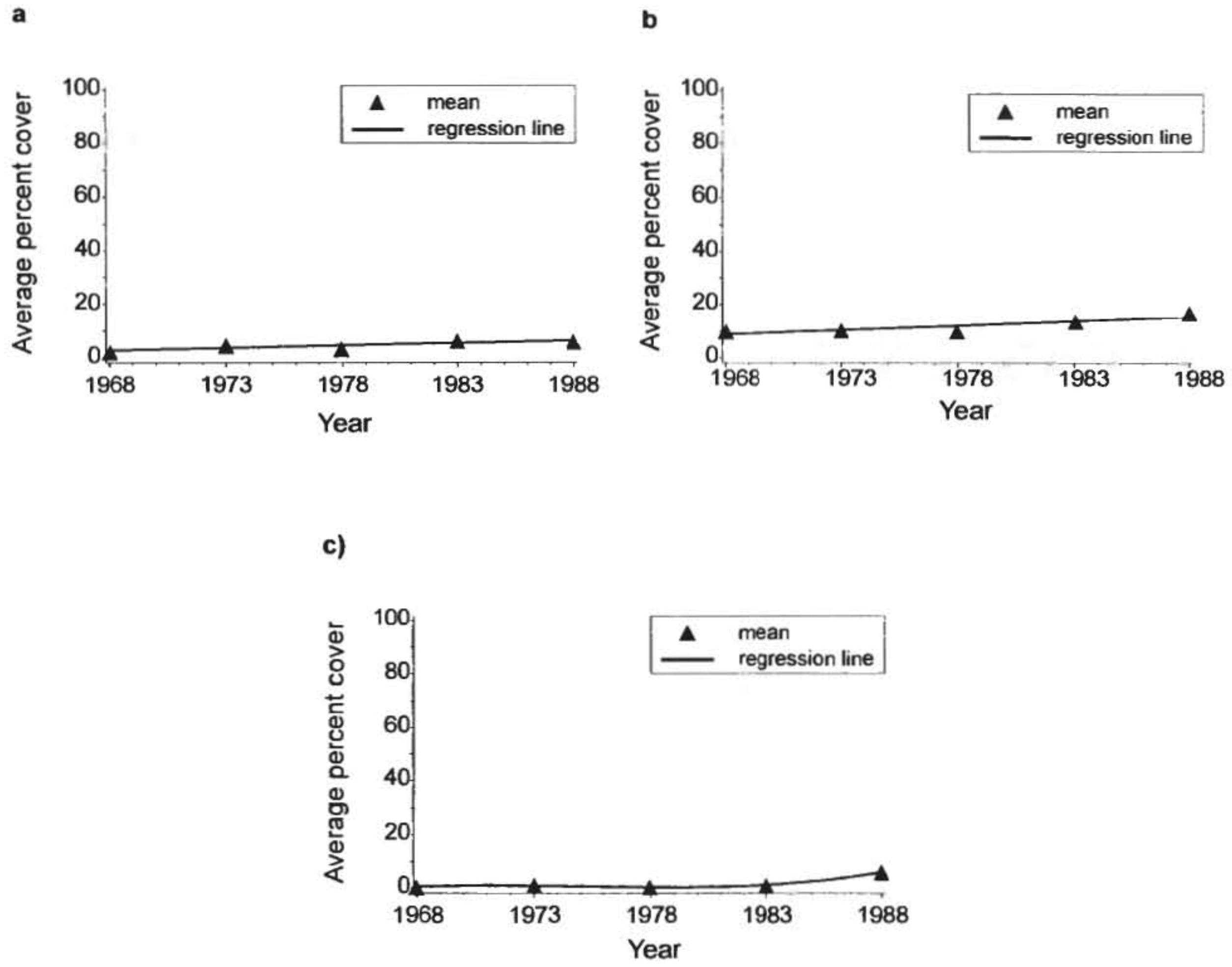

Fig. 8. Average percent cover of *Carex* spp. (a), *Selaginella densa* (b), and lichens (c) on grassland transects, 1968–1988.

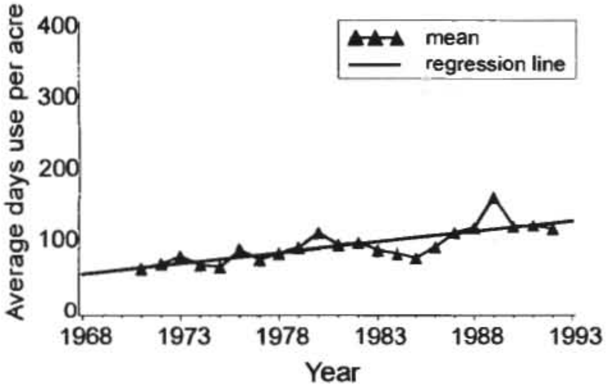

Fig. 9. Average days use per acre by elk on meadow transects, 1968–1992.

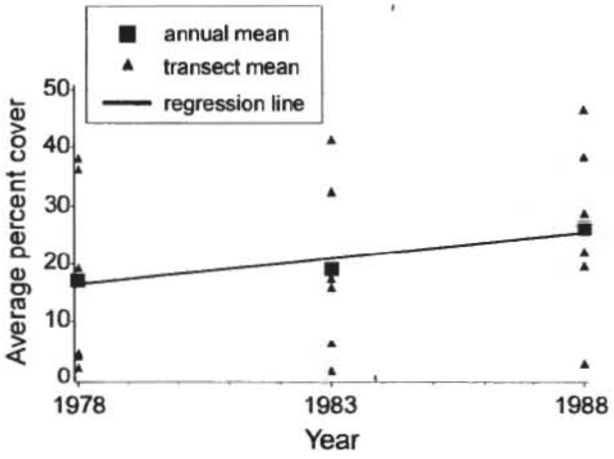

Fig. 10. Average percent cover of *Phleum pratense* on meadow transects, 1978–1988.

Willow Transects

Ungulate herbivory, documented by percent leader use on willow transects, did not change substantially during the period 1968–1992. There are indications of a slight decline from 1968–1983 (9%), followed by an increase (3%) through 1992 (Fig. 11). Overall, percent leader use declined by 6% from 1968–1992. Mean height of *Alnus tenufolia* increased 78% from 1973–1988 (Fig. 12).

Sagebrush Transects

No significant changes in consumption (percent leader use) on sagebrush transects occurred during the period 1968–1992. Elk habitat use (days use per acre) increased 112% on these transects throughout the period between 1968–1992 (Fig. 13a). Deer days use per acre declined from 1968–1983, then increased during 1984–1992 (Fig. 13b). Overall, deer use declined 48.7% over the entire period. Ranked data for mean height of *Purshia tridentata* showed a significant increase over the period 1968–1988. Mean height (unranked data) increased 56% over this period (Fig. 14). Percent cover of grasses, mosses/lichens, and litter increased by 32%, 1063%, and 62% respectively, on sagebrush transects between 1968–1988 (Fig. 15a,b,c).

Bitterbrush Transects

No significant trend in consumption (percent leader use) was apparent on bitterbrush transects from 1969–1992. Elk days use per acre increased 62% on bitterbrush transects from 1969–1992 (Fig. 16a). Deer days use per acre decreased 63.6% over this same period (Fig. 16b). Percent cover and mean height of *P. tridentata* increased, 36% and 14%, respectively, on bitterbrush transects over the period 1968–1988 (Fig. 17a,b). Percent cover of mosses/lichens, litter, and shrubs increased 123%, 50%, and 24%, respectively, over this period (Fig. 18a,b,c).

Discussion

Vegetation Trends

We were unable to determine whether or not overgrazing occurred based on the experimental design and limitations of the sample. We concluded there were no overwhelmingly obvious indications of any overgrazing based on the following evidence: (1) bare ground increased only in grassland type and this increase, while statistically significant, was relatively minor, only about 4% (Fig. 7a), and there was no evidence of any concomitant reduction of plant cover; (2) no obvious significant shifts toward less palatable species were indicated; (3) assuming changes in plant productivity can be reflected by increasing canopy coverage, no decline, and possibly an increase in plant production, may be inferred from the increases in canopy cover of grasses and sedges; and (4) significant shifts in species composition, as would be indicated by significant increase of weedy species and exotics coupled with decreases of native plants, were not evident with two exceptions. The first exception that we observed was an increase in cover in grassland of lichens and *S. densa*, which tend to grow on rock and gravel substrates (Nelson 1992). Their increase may be a response to the minor increase in bare ground. MacCracken et al. (1983) found that the lichen, *Parmelia chlorochroa*, was significantly associated with bare ground and drier sites in Montana grassland and sagebrush vegetation. This lichen decreased in the absence of grazing. Increases in mosses/lichens were also observed in sagebrush and bitterbrush types. Anderson et al. (1982) reported a 3-fold increase of lichen and moss cover in moderately to heavily grazed areas over areas with light grazing intensity. During and Willems (1986) found similar decreases in lichen and mosses with decreased grazing in Dutch chalk grasslands. Second, we documented an increase in timothy, an exotic grass, over the study period. Timothy is grazing-resistant, but is also a preferred elk forage. The changes documented are not suggestive of overgrazing. However, we were unable to investigate all of our stated criteria of overgrazing. In particular, the very limited data from controls (exclosed vegetation) did not permit us to determine which of these changes were due to elk herbivory alone. The very limited data from within the exclosures (statistical tests were not possible) indicated there were similar amounts of bare ground, and that *Carex* spp., *S. densa*, and lichens also increased in the controls. Thus, at this time, and based on this data set and sampling program, we found no overwhelmingly obvious indications of any severe overgrazing of the herbaceous species. We do suggest, however, that additional data be gathered.

Increases in height of bitterbrush may be due to decreasing days use per acre by deer in both bitterbrush and sagebrush plots. *P. tridentata* is a primary browse species for mule deer (*Odocoileus hemionus*) as well as elk in both sagebrush and bitterbrush types (Stevens 1980; Hobbs et al. 1981).

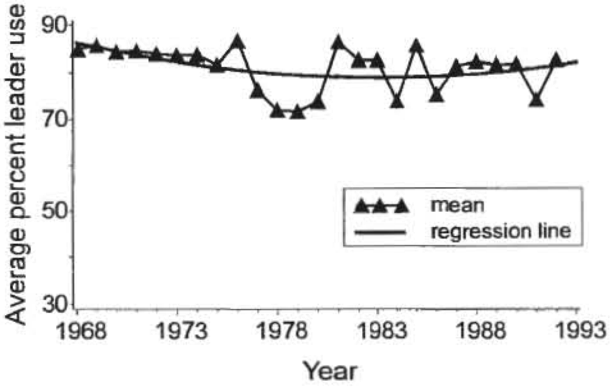

Fig. 11. Average percent leader use of *Salix* species, 1968–1992.

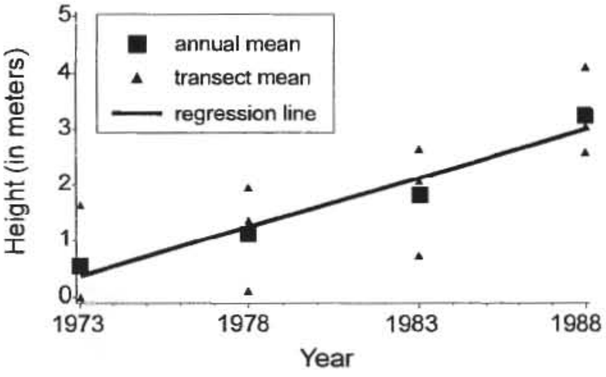

Fig. 12. Average height of *Alnus tenufolia* on willow transects, 1973–1988.

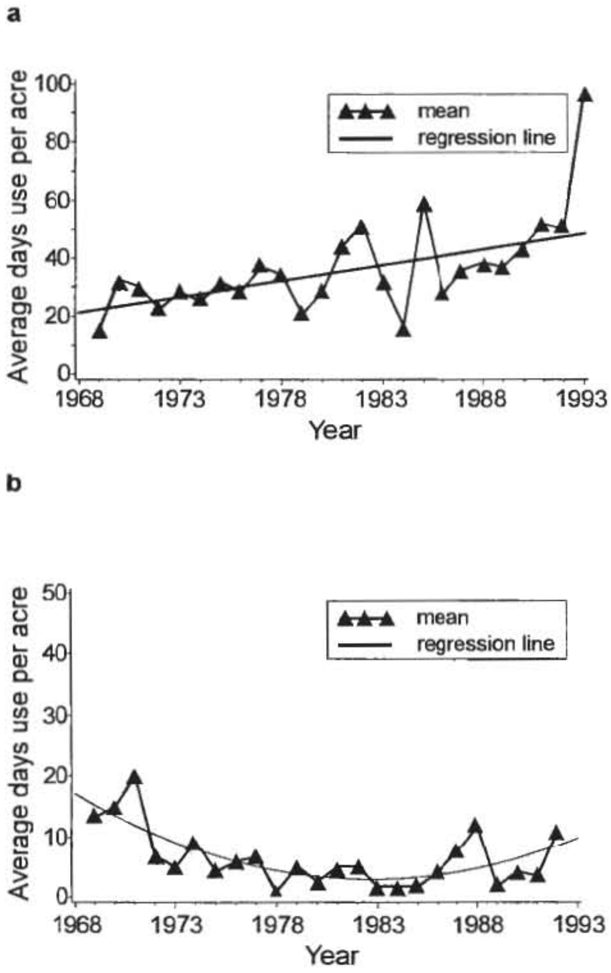

Fig. 13. Average days use per acre by elk (a), and mule deer (b) on sagebrush transects, 1968–1992.

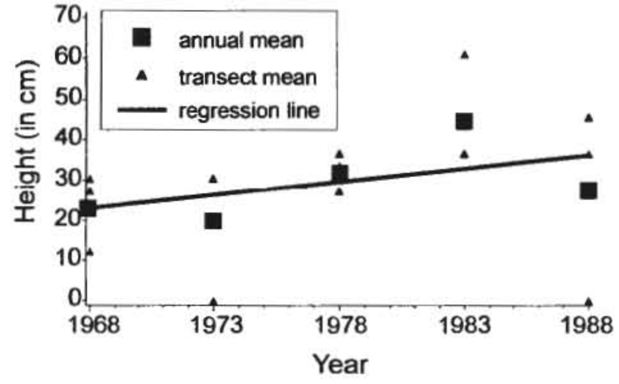

Fig. 14. Mean height of *Purshia tridentata* on sagebrush transects, 1968–1988.

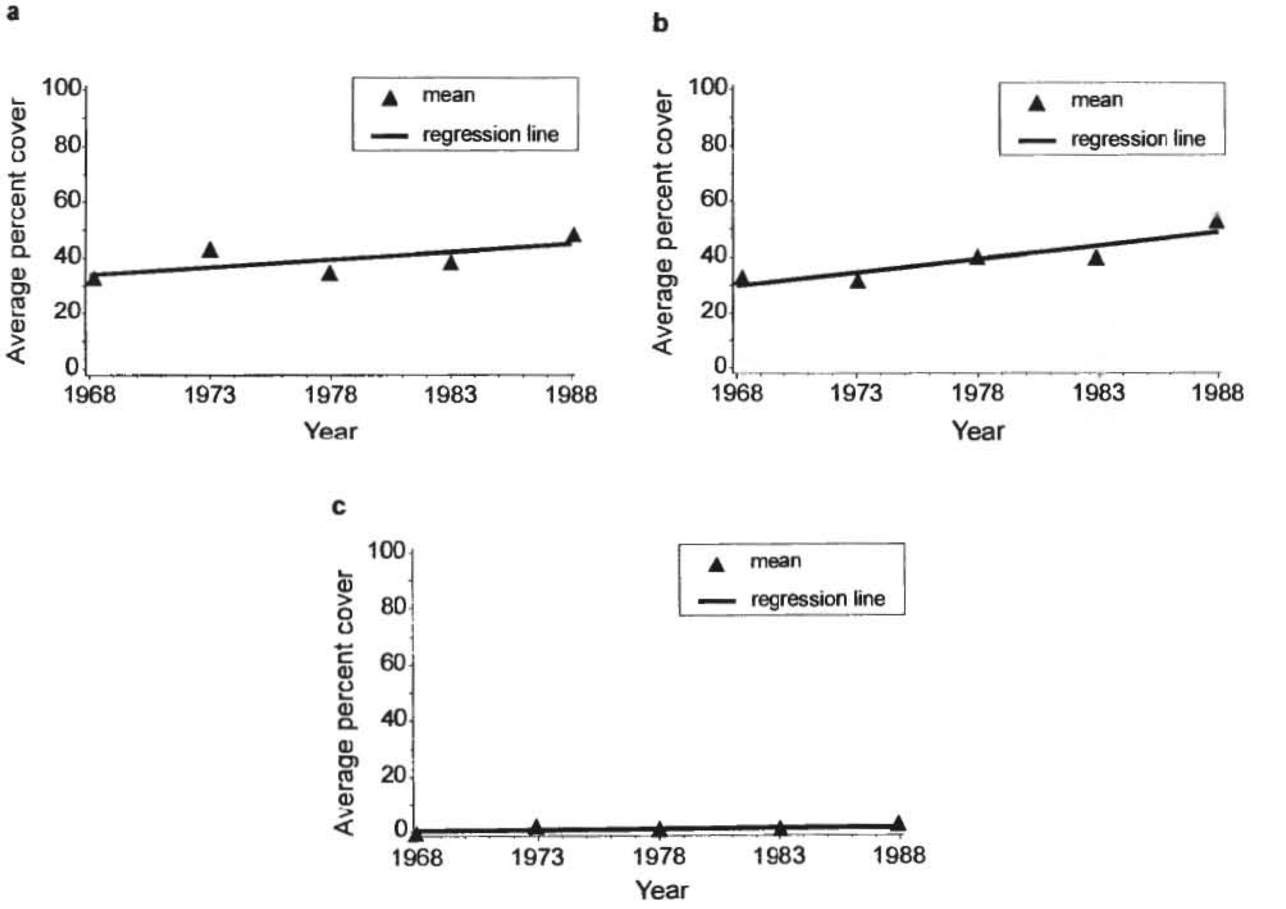

Fig. 15. Average percent cover of graminoids (a), litter (b), and mosses and lichens (c) on sagebrush transects, 1968–1988.

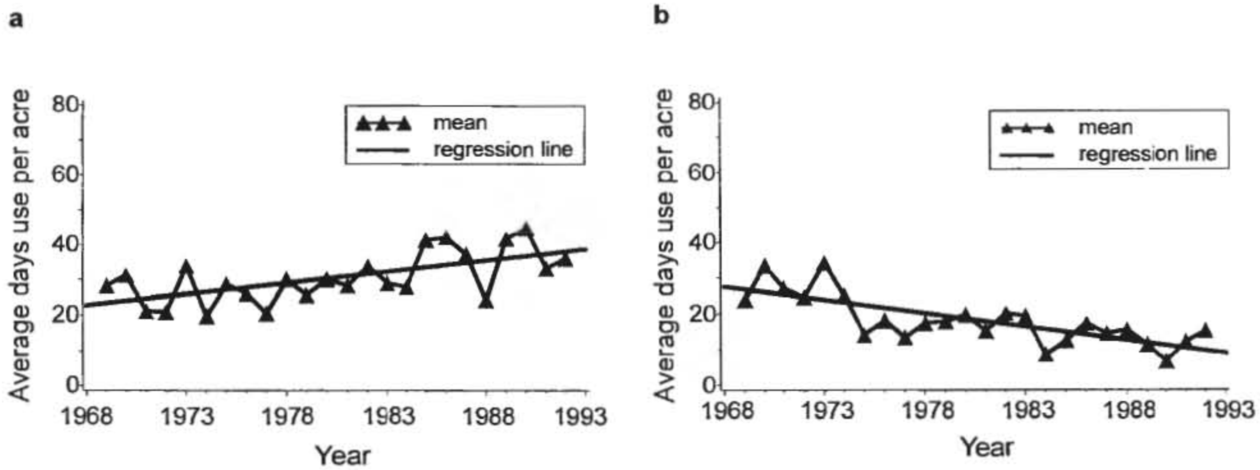

Fig. 16. Average days use per acre by elk (a), and mule deer (b) on bitterbrush transects as determined by pellet count plots, 1968–1992.

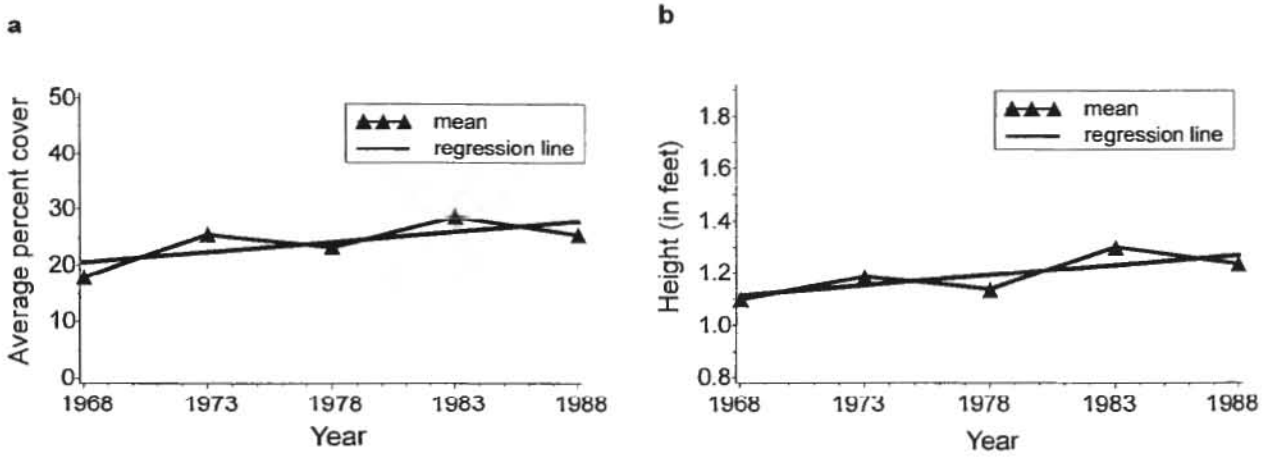

Fig. 17. Average percent cover (a), and mean height (b) of *Purshia tridentata* on bitterbrush transects, 1968–1988.

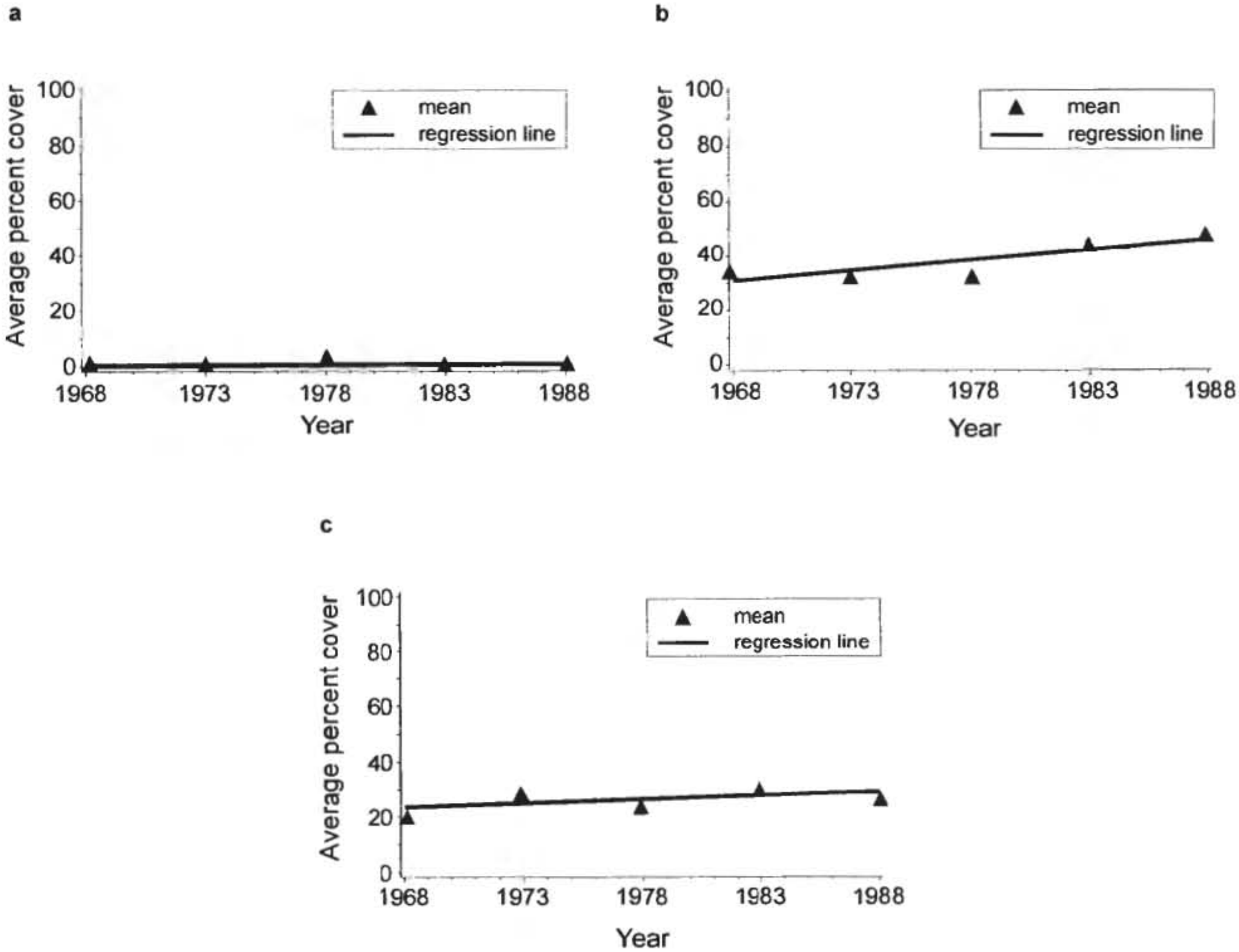

Fig. 18. Average percent cover of mosses and lichens (a), litter (b), and shrubs (c) on bitterbrush transects, 1968–1988.

Increasing height of alder may be an indication of changes in dominant species in willow sites. However, though significant, this increase was relatively minor (approximately 1 ft [30 cm] average height increase over 25 years). The increase was not paralleled by similar increasing cover of alder and decreasing cover of willow species. Increasing heights of alder may reflect the fact that alder is not as heavily browsed by elk as willow (personal observation) and could point to an eventual shift in species composition from willow to alder.

Stevens' annual reports (Stevens 1983–1992) indicate increases in decadence and decreases in reproduction of willows on willow transects — an observation which is not corroborated by our analysis of willow percent cover data on these transects. While it is true that percent cover of willows decreased on at least two of the transects, the other four transects remained stable or increased over the 25-year time span (Fig. 19). Also, we were not able to use data from transect 22 in our 25-year analysis because that transect was moved after the 1982 flood destroyed the original transect. Our analysis does indicate declines on transects 17 and 19, the same two transects that Stevens noted as declining; however, these declines are offset in our analysis by increases in cover on sites 16 and 20. In Stevens' reports, only the declines in transect 17 were attributed primarily to elk, while declines on transect 19 in Lower Moraine Park were attributed primarily to changes in hydrology and secondarily to elk herbivory. A larger sample size across all winter range willow communities would give

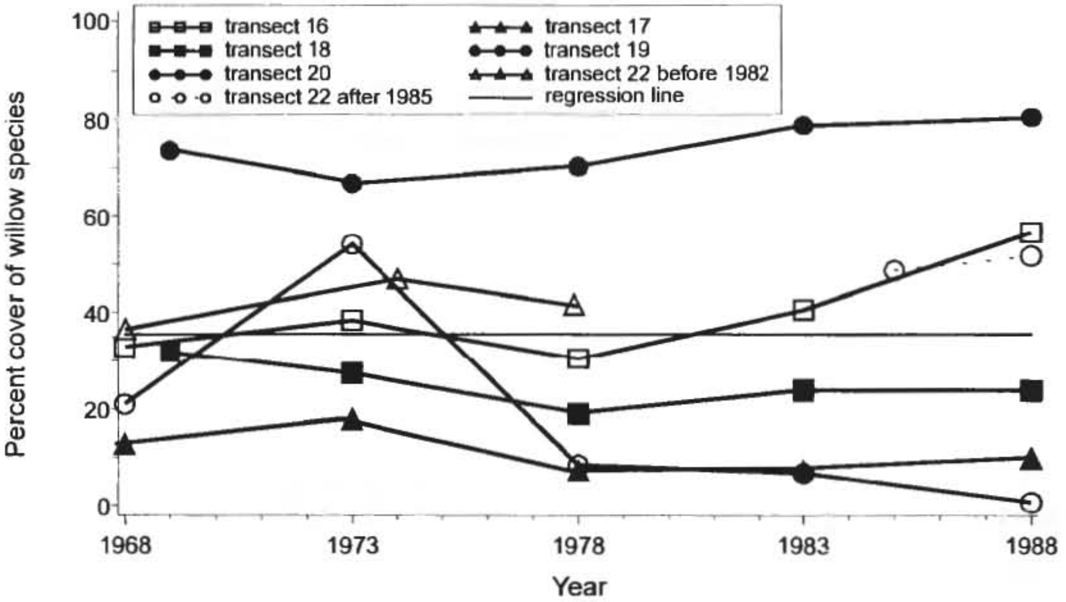

Fig. 19. Percent cover of *Salix* spp. by transect, 1968–1988.

a better picture of the direction of change in these willow communities. Larger sample size would also reduce the impact of loss of a few sample plots to events such as the 1982 flood.

This same case is even more exaggerated in the aspen transects. Stevens' annual reports specifically mention declines in aspen recruitment (Stevens 1969–1992). Slight increases in the density of mature trees (>8 ft tall) were observed on all three transects (Fig. 20a). While the density of young trees declined dramatically on one transect, it increased on another, while it initially decreased, then increased again over time on the third (Fig. 20b). When all transects are analyzed together, the impact of dramatic change in one plot is diminished. With only three transects to analyze, we have no way of knowing whether any of these plots is more representative of conditions on the range as a whole than any other. That the plots were not randomly selected makes conclusions about the entire winter range aspen community even less valid. Addition of data points from a fourth transect illustrates how additional points might or might not cause shifts in averages for a community type (Fig. 20c,d). It should be pointed out that many of the aspen sampling points actually violated one of the assumptions necessary to use the point-centered quarter method (Mueller-Dombois and Ellenberg 1974). The point-centered quarter method is limited by the need for each quarter at a sampling point to contain a plant. Many points contained one or two quarters which had no aspen plants. Thus, the aspen densities reported here are not entirely accurate, and more suitable methods should be considered in future monitoring programs.

Increases in graminoids and litter in grasslands on the study area suggest that with increased elk herbivory grazing "lawns" may be developing (McNaughton 1984). One species of exotic grass, timothy, increased in meadow sites and native sedges increased in grassland sites. Both of these graminoid groups are grazing-resistant and potential increasers under elk grazing (Smith 1960). Both timothy and sedges are readily consumed by elk (Hobbs et al. 1981, 1982), and are not considered unpalatable forages to elk. Are the increases in timothy and sedges resulting in declines in other native species? Our data did not verify any declines, but we hasten to add that such declines might have occurred and not been detected with this sampling program, due to inadequacy in the number or extent of sampling.

Changes in species cover may be poorly estimated using cover classes of unequal sizes as occurred here. Methods which use unequal cover classes tend to overestimate abundance of species with low average cover and underestimate abundance of species with high

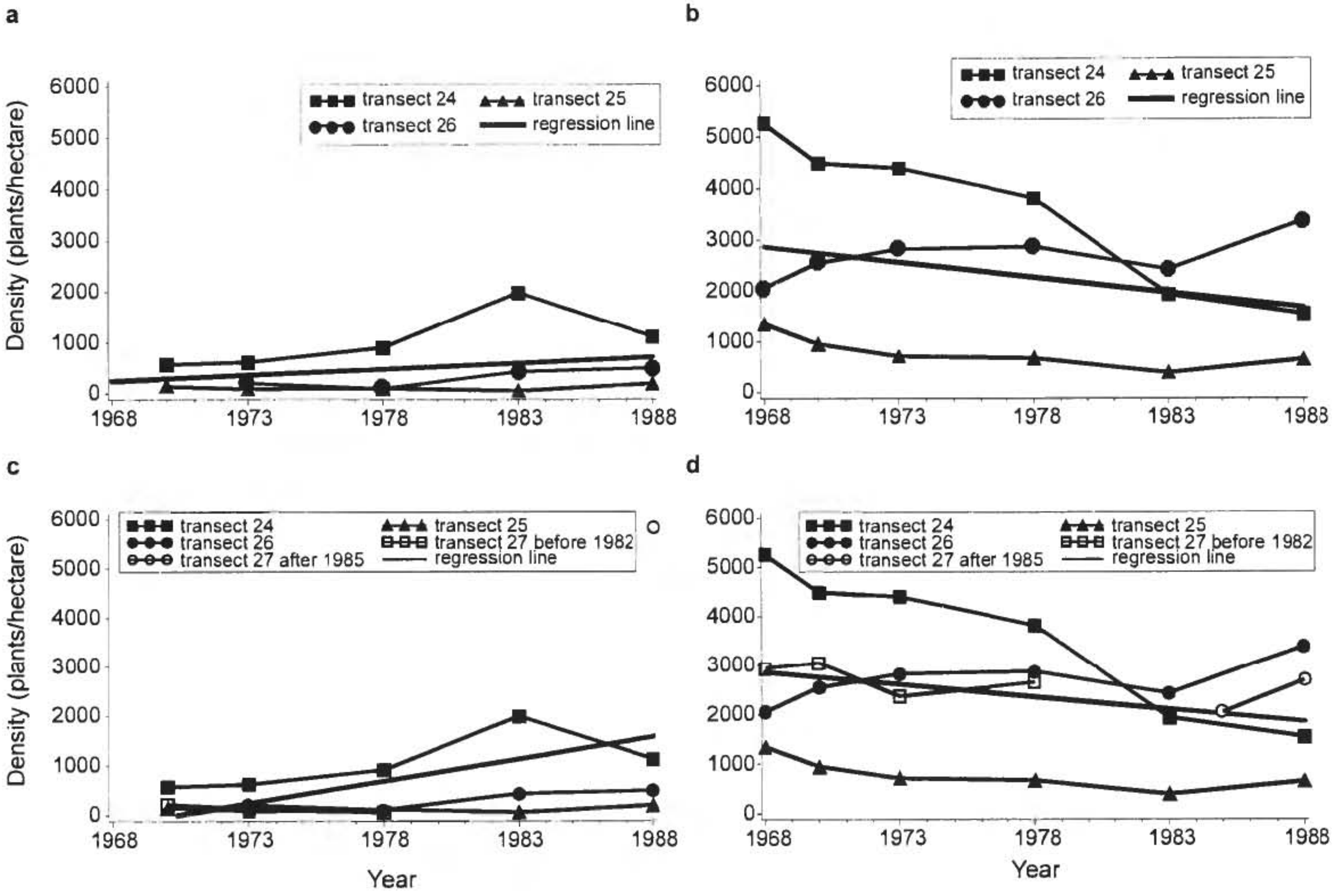

Fig. 20. Density of *Populus tremuloides* on aspen transects. Mature trees (over 2.44 m in height) with only three transects and regression line (a), and including transect destroyed by Lawn Lake flood (c). Young trees (less than 2.44 m in height) with three transects and regression line (b), and including transect destroyed by Lawn Lake flood (d).

average cover (Floyd and Anderson 1987; Mitchell et al. 1988). As a result, a minor change in canopy cover of a particular species may occur and be obscured since only the midpoint of the class is used in calculation of average canopy cover for the sites. For example, two coverage values, one of 52% and one of 74%, would both be assigned to the cover class 50%–75%, the midpoint of which is 62.5. Thus, the 22% increase in canopy cover of this species would not be evident. Canopy cover estimates may also be biased by size of individual plants of a species, plant density, or size of the plot being sampled (Hanley 1978; Floyd and Anderson 1987; Mitchell et al. 1988). Tests of statistical power to estimate the number of samples required to detect a treatment effect were not routinely done in 1968. Thus, either the degree of community stratification or the number of sample plots may have been inadequate to detect a significant trend even when one actually occurred.

Research and Monitoring Recommendations

A Clear Statement of Questions and Needs

No monitoring program can afford to sample everything, everywhere. Thus, research hypotheses need to be more clearly stated than in the past. The changes in vegetation and ecosystem parameters that will be acceptable need to be better defined. Any premise that a significant wintering population of elk will have no effect on vegetation or ecosystem processes is naive. Any human-caused concentrations of elk should be managed by the National Park Service (U.S. Department of the Interior, National Park Service 1988). At what point do elk concentrations become unnatural? At what point do vegetative conditions become unacceptable? These threshold points need to be unambiguously defined. Predictions need to be made as to what density of elk wintering in the park should be expected from a naturally functioning ecosystem. This will be a complex assignment because elk migrations are disrupted by human developments to some extent, and because so little information exists on prehistoric conditions. This subject is so complex that an advisory panel was asked to assist park staff in April 1997 on the development of vegetation management goals for elk range in the park.

In particular, park staff needs to decide which groups of plants or ecosystem processes to focus on. Should the focus be on plants which are most sensitive to changes in elk numbers? That would be most valuable if any control of elk numbers is proposed, or if there is an increase or decrease in elk numbers. This analysis suggests that timothy, sedges, lichens, *S. densa*, and bare ground are most sensitive to changes in elk numbers. Should rare or declining plants be emphasized? If so, the ongoing studies of Stohlgren et al. (1997) should tell the park what species to focus on. Changes in rare plants will be harder to detect and will require more sampling and dollars. Another option is to focus sampling on highly visible or high public profile plants, such as willow and aspen.

Monitoring of Ungulate Populations

Ultimately, elk population goals will be set as a way of achieving vegetation goals. Thus, any continued monitoring of vegetation under current elk management, or any change in elk management, will depend on a parallel effort to census the elk population. Predictive modeling might be useful in this context. What level of change in elk density will result in a specified vegetation response? A census technique(s) is needed by park management that will detect a ±15% change in elk numbers both in town and in the park sectors (Homer Rouse, Park Superintendent, 1993–1995, personal communication). One town census should be conducted per year. Census work in progress, employing the Idaho aerial sightability model (park sector) and mark-resight (town), meets these criteria. Detailed classifications (bulls, cows, spikes, calves) should be conducted each year to sample production and recruitment in the elk population. This should continue to be done both in town and the park. Any evaluation of density-dependence in the elk population will require annual counts and detailed classification to detect, for example, a decline in calf recruitment with increasing elk population size that might indicate density dependence. Since each year will provide only one data point in regression analyses, no annual counts/classifications should be missed.

Mule deer populations may have declined over the sample period. Additional monitoring of the mule deer population should occur.

Experimental Design

The single greatest strength of the 25-year sampling program and data set of Stevens (1980, 1992) was the high level of consistency in how and when the measures were taken (Stevens took every measure) and the impressive length of time of the study. Another strong point was that the samples were well-distributed over the entire winter range. Also, the transects were placed in areas of greatest elk use and densities. Thus, the sampling was most likely to detect any changes due to elk abundance. The sampling program was a tremendous accomplishment in its consistency and number of years, and we compliment Dave Stevens for the work.

Stevens' (1980, 1992) 25-year study provided an impressive data set which sampled a large number of variables and vegetation types. However, future experimental or monitoring programs would benefit from consideration of additional design features, including: random site selection stratified by vegetation type; larger numbers of independent sample sites; objective and quantitative measurement techniques; consistent data collection methods; and consistency of sampling dates within vegetation types (Table 3).

The single greatest weakness in the Stevens (1980, 1992) program was in the lack of adequate controls. Equal sampling effort should have been expended in control situations such as inside grazing exclosures or in similar sites with few elk. Otherwise, the treatment of elk grazing cannot be isolated from other potentially confounding influences such as effects of climate, fire suppression, natural succession, or others. For example, timothy might have increased both inside and outside of exclosures. We do not know that.

Only three large long-term exclosures exist and they were erected 6 years prior to the release of elk from controls and no canopy coverage data were collected within these exclosures at the time they were erected. These exclosures sample slightly different communities, only one of which is included in two different exclosures. The exclosures are inadequately replicated and all three are located within the Beaver Meadows area and therefore represent one small portion of the entire winter range. Sampling in these exclosures was inconsistent over the study period and not conducted in concert with the sampling of the unprotected vegetation transects. As a result, we were unable to do a trend analysis using these data. We did visually examine mean canopy coverage data for those species which showed significant changes on the unprotected vegetation transects, but the data were too limited for statistical tests (Appendix). Thus, our highest priority recommendation is that any new sampling program include the new network of exclosures that were established in 1994 and/or any additional exclosures added at a later date.

Additional limitations of the 25-year program were that the sample sites were originally selected to be representative and their selection was nonrandom. Greater inference can be made to the entire elk winter range if sample sites are located in a completely random fashion across the entire landscape. Representative site selection is the preferred option if the number of sample sites is very limited by funds. But when sites are selected nonrandomly in representative locales, statistical inferences are limited only to those plots themselves, and not to the general area, nor to the entire winter range. Nonrandom selection of sample sites limits conclusions about changes on larger scales.

Also, the 25-year program relied heavily on line transects. While use of line transects is a widely accepted and efficient means to sample plant communities, they have a high degree of spatial autocorrelation. As a result, individual samples along a transect are not independent from each other. Within-site variance is reduced, but at an expense of time and labor. We suggest that this time would be better used sampling a smaller number of plots/sites, but across more sites. A greater number of sites would provide a more accurate estimation of the

Table 3. Advantages and disadvantages of various experimental designs and sampling regimes.

Experimental design	Advantages	Disadvantages
Annual measurement	More data points in regressions	Greater monetary and labor cost
Less frequent measurements	Fewer data points	Lower monetary and labor cost
Greater replication at a site	Samples within-site variance Time efficient	Loss of landscape inference
Landscape replication	Greater inference	Time consuming
Random selection of sites	Greater inference	Greater monetary and labor cost
Representative site selection	Best when funds are limited	Less inference

true means of variables measured. The size and shape of plots used to count pellets (100 ft^2) and the plots used for sampling plant cover (20 x 50 cm) were adequate. Aerial plant cover, however, is a highly variable measure easily influenced by observer differences, wind at the time of sampling, and other variables. We suggest basal plant cover is less variable and a better measure. We also suggest that plant productivity, by species, is even better, since ultimately the productivity of the site is the final measure of the success of any elk management program.

The 25-year sampling program provides a unique and valuable long-term data set for assessing trends. The complete dropping of this program is a decision that must be weighed heavily and is beyond the purview of our research group. We have identified enough shortcomings in the program to recommend that the program no longer be conducted in its existing fashion. If portions of the existing program are to be maintained, power calculations need to be conducted, and, if necessary, additional sample sites need to be selected. An equivalent number of samples should be added inside of the new exclosures to provide adequate controls to the treatment of elk grazing. Only the most valid plots and measures should be continued. Any of the remaining measures or plots that are subjective should be dropped. All of the new sites should be randomly located. We suspect portions of the current program would need to be approximately tripled to meet these criteria. Park staff need to ask themselves if they are comfortable with the measures, the original selection of sites, and a significant increase in time and effort to stick with portions of the old program. Any dropping of the old program would have to be weighed against the loss of a unique, long-term sampling program.

Should the park management decide to develop an entirely new sampling program, we suggest the following steps. First, park staff needs to decide which plant groups to focus on: species most likely to change, rare species, or high profile-visible shrubs and trees (see Discussion above). Second, the specific treatments to be sampled need to be selected. Will fire, trend over time, changes in beaver abundance or water tables, climate, or other factors be incorporated into the design? What should the sensitivity to any change in elk density be? Will the program need to detect changes due to a 25%, 50%, or 100% change in elk numbers? Third, the study area of concern needs to be defined. Should the sampling focus only on the high elk use areas, to save time and money? Elk use may not be linear in habitats as numbers change, so perhaps less preferred types should also be sampled. Fourth, once these questions have been answered, the optimal sample plot size, shape, and sample measures can be selected, and tests of power conducted to determine adequate sample sizes to detect a treatment effect. Fifth, plot locations can then be located randomly using the park's geographic information system.

Plant recruitment and population turnover rates need to be sampled. In particular, concern exists for inadequate levels of seed production, seedling establishment, root sprouting, and recruitment or stand expansion in aspen and willows. Willow stands and aspen clones appear to be stationary or slowly declining. Greater consistency in tagging of browse plants in the future would allow measures of age-specific mortality. In Stevens' work, changes in individual plant identification made it difficult to follow decline of the plant population through time. This problem could be solved in the future by having stricter definitions of plant age categories and discontinuing tag numbers of plants which die, and assigning previously unused numbers to replacement plants which are added at later dates. Percent protein (N) should be measured, along with additional nutrient concentrations and fibrous constituents, if estimation of nutritional-based ecological carrying capacity is to be used in elk management. Nutrient measures could also provide information to evaluate the sustainability of elk grazing in the system. Belowground plant reserves have been ignored, and although difficult to measure, they are important to understanding the effects of elk on plant production. Therefore, we recommend the park consider looking not only at traditional vegetation species composition, but also at these ecosystem variables. Ultimately, managers may determine that a shift in species composition is acceptable, providing the productivity and sustainability of the system is maintained.

Acknowledgments

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Literature Cited

Anderson, D. C., K. T. Harper, and R. C. Homgren. 1982. Factors influencing development of cryptogamic soil crusts in Utah deserts. Journal of Range Management 35:180–185.

Bear, G. D. 1989. Seasonal distribution and population characteristics of elk in Estes Valley, Colorado. Special Report Number 65. Colorado Division of Wildlife R-S-65-89.

Bergerud, A. T., W. Wyett, and J. B. Snider. 1983. The role of wolf predation in limiting a moose population. Journal of Wildlife Management 47:977–988.

Boutin, S. 1992. Predation and moose population dynamics: A critique. Journal of Wildlife Management 56:116–127.

Boyce, M. S. 1993. Predicting the consequences of wolf recovery to ungulates in Yellowstone National Park. Pages 234–269 *in* R. S. Cook, editor. Ecological issues on reintroducing wolves into Yellowstone National Park. National Park Service Science Monograph NPS/NRYELL/NRSM-93/22. U.S. Government Printing Office, Washington, D.C.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388–394.

Caughley, G. 1979. What is this thing called carrying capacity? Pages 2–8 *in* M. S. Boyce and L. D. Hayden-Wing, editors. North American elk: Ecology, behavior and management. University of Wyoming, Laramie.

Caughley, G. 1981. Overpopulation. Pages 7–19 *in* P. A. Jewell and S. Holt, editors. Problems in management of locally abundant wild animals. Academic Press, N.Y.

Cole, G. F. 1963. Range survey guide. U.S. Department of the Interior, National Park Service. Grand Teton National History Association, Moose, Wyo.

Cole, G. F. 1971. An ecological rationale for the natural and artificial regulation of native ungulates in parks. Transactions of the North American Wildlife Conference 36:417–425.

Coughenour, M., and F. J. Singer. 1991. The concept of overgrazing on Yellowstone's northern range. Pages 209–232 *in* M. S. Boyce and R. Keiter, editors. Examining the Greater Yellowstone. Yale University Press, New Haven, Conn.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43–64.

During, H. J., and J. H. Willems. 1986. The impoverishment of the bryophyte and lichen flora of the Dutch chalk grasslands in the thirty years 1953–1983. Biological Conservation 36:143–158.

Eberhardt, L. E., L. L. Eberhardt, B. L. Tiller, and L. L. Cadwell. 1996. Growth of an isolated elk population. Journal of Wildlife Management 60:369–373.

Floyd, D. A., and J. E. Anderson. 1987. A comparison of three methods for estimating plant cover. Journal of Ecology 75:221–228.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73:2034–2058.

Garton, E. O., R. L. Crabtree, B. B. Ackerman, and G. Wright. 1990. The potential impact of a reintroduced wolf population on the northern Yellowstone elk population. Pages 359–391 *in* Wolves for Yellowstone? A report to the U.S. Congress, Volume II: Research and analysis. Yellowstone National Park, Wyo.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 20:1–59.

Georgiadis, N. J., R. W. Ruess, S. J. McNaughton, and D. Western. 1989. Ecological conditions that determine when grazing stimulates grass production. Oecologia 81:316–322.

Green, R. A., and G. D. Bear. 1990. Seasonal cycles and daily activity patterns of Rocky Mountain elk. Journal of Wildlife Management 54:272–279.

Gysel, L. W. 1959. An ecological study of the winter range of elk and mule deer in the Rocky Mountain National Park. Journal of Forestry 58:696–703.

Hanley, T. A. 1978. A comparison of the line-interception and quadrat estimation methods of determining shrub canopy coverage. Journal of Range Management 31:60–62.

Hess, K. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot. 167 pp.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Hobbs, N. T., D. Baker, J. E. Ellis, and D. M. Swift. 1981. Composition and quality of elk winter diets in Colorado. Journal of Wildlife Management 45:156–170.

Hobbs, N. T., D. L. Baker, J. E. Ellis, D. M. Swift, and R. A. Green. 1982. Energy and nitrogen based estimates of elk winter range carrying capacity. Journal of Wildlife Management 46:12–21.

Holland, E. A., and J. K. Detling. 1991. Plant responses to herbivory and belowground nitrogen cycling. Ecology 71:1040–1049.

Houston, D. B. 1971. Ecosystems of national parks. Science 172:648–651.

Houston, D. B. 1976. The status of research on ungulates in northern Yellowstone Park. Pages 11–27 *in* Research in the parks. Transactions of the National Parks Centennial Symposium, American Association for the Advancement of Science, U.S. Department of the Interior, National Park Service Symposium Series No. 1.

Houston, D. B. 1982. The Northern Yellowstone elk: Ecology and management. McMillan Publishing, N.Y. 474 pp.

Kay, C. E. 1990. Yellowstone's northern elk herd: A critical evaluation of the "natural regulation" paradigm. Ph.D. dissertation, Utah State University, Logan. 490 pp.

Kay, C. E. 1994. Aboriginal overkill, the role of Native Americans in structuring western ecosystems. Human Nature 5:359–398.

Lime, D. W., B. A. Koth, and J. C. Vlaming. 1993. Effects of restoring wolves on Yellowstone area big game and grizzly bears: Opinions of scientists. Pages 306–326 *in* R. S. Cook, editor. Ecological issues on reintroducing wolves into Yellowstone National Park. National Park Service Science Monographs 92/22. U.S. Government Printing Office, Washington, D.C.

MacCracken, J. G., L. E. Alexander, and D. W. Uresk. 1983. An important lichen of southeastern Montana rangelands. Journal of Range Management 36:35–37.

Mack, J. A., and F. J. Singer. 1993. Using Pop-II models to predict the effects of wolf predation and hunter harvests on elk, mule deer, and moose on the northern range. Pages 49–74 *in* R. S. Cook, editor. Ecological issues on reintroducing wolves into Yellowstone National Park. National Park Service Science Monograph NPS/NRYELL/NRSM-93/22. U.S. Government Printing Office, Washington, D.C.

McNaughton, S. J. 1979. Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. American Naturalist 113:691–703.

McNaughton, S. J. 1984. Grazing lawns: Animals in herds, plant form, and coevolution. American Naturalist 124:863–886.

Messier, F. 1995. Ungulate population models with predation: A case study with the North American moose. Ecology 75:478–488.

Mitchell, J. E., P. N. S. Bartling, and R. O'Brien. 1988. Comparing cover-class macroplot data with direct estimates from small plots. American Midland Naturalist 120:70–78.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, N.Y. 547 pp.

Nelson, R. A. 1992. Handbook of Rocky Mountain plants. Fourth edition. Roberts Rinehart, Niwot, Colo. 444 pp.

Overton, W. S., and D. E. Davis. 1969. Estimating the numbers of animals in wildlife populations. *In* R. H. Giles, editor. Wildlife management techniques. The Wildlife Society, Washington, D.C.

Packard, F. M. 1947. A study of the deer and elk herds of Rocky Mountain National Park, Colorado. Journal of Mammalogy 28:4–12.

Phillips, E. A. 1959. Methods of vegetation study. E. Holt and Co., Inc. New York, N.Y. 107 pp.

Singer, F. J., and M. K. Harter. 1996. Comparative effects of elk herbivory and the 1988 fires on Northern Yellowstone National Park grasslands. Ecological Applications 6:185–199.

Smith. D. R. 1960. Description and response to elk use of two mesic grassland and shrub communities in the Jackson Hole region of Wyoming. Northwest Science 34:26–36.

Stevens, D. R. 1969-1992. Ungu late winter habitat conditions and management. Annual reports to the National Park Service. ROMO-N-08a.

Stevens, D. R. 1980. The deer and elk of Rocky Mountain National Park. A 10 year study. ROMO-N-13.

Stohlgren, T. J., M. B. Coughenour, G. W. Chong, D. Binkley, M. Kalkhan, L. D. Schell, D. Buckley, and J. Berry. 1997. Landscape analysis of plant diversity. Landscape Ecology 12:155–170.

U.S. Department of the Interior, National Park Service. 1988. Management policies. U.S. Government Printing Office, Washington, D.C.

Wagner, F. H., R. Foresta, R. B. Gill, D. R. McCullough, M. R. Pelton, W. F. Porter, and H. Salwasser. 1995a. Wildlife policies in the U.S. national parks. Island Press, Washington, D.C. 242 pp.

Wagner, F. H., R. Keigley, and C. Wombalt. 1995b. Ungulate herbivory of willows on Yellowstone's northern winter range: Comment to Singer et al. (1994). Journal of Range Management 48:4 75–477.

Welker, J. M., and J. W. Menke. 1990. The influence of simulated browsing on tissue relations, growth and survival of *Quercus douglasii* seedlings under slow and rapid rates of soil drought. Functional Ecology 4:807–817.

Appendix. Percent canopy cover of selected species from within three exclosures erected in 1962. Means (and standard errors) are reported. Means with no reported standard error indicate only one data point available for that sampling period.

		Year				
Vegetation type	Species	1970	1971	1975	1984	1990
Grassland	Bare ground	12.00	23.20	9.60	8.20	10.70
		(6.00)	(0.30)	(3.60)	(1.90)	(5.55)
	Carex spp.	1.00	Trace	0.40	1.18	3.60
				(0.30)	(0.72)	(2.50)
	Selaginella densa			0.90	0.89	1.05
				(0.10)	(0.06)	(0.35)
	Lichen				2.14	1.25
					(0.95)	(0.75)
Meadow	Bare ground	1.55	36.25	12.50		
		(1.45)	(5.15)	(2.50)		
	Carex spp.	45.50	0.55	2.00	21.20	14.90
		(8.50)	(0.45)	(1.00)	(9.50)	(9.50)
	Selaginella densa			1.50		
				(0.50)		
Sagebrush	Bare ground	22.30	13.60	7.50	20.30	15.27
		(2.33)	(3.15)		(3.60)	(1.29)
	Carex spp.	14.00	3.63	6.50	13.08	12.73
		(6.03)	(0.88)		(2.34)	(1.65)
	Selaginella densa			7.00	0.88	0.90
					(0.78)	(0.20)
	Lichen				5.85	1.80
					(2.15)	(0.80)

CHAPTER FOUR

Factors Influencing Plant Productivity in Shrub Communities on Elk Winter Range of Rocky Mountain National Park: Experiments on Elk Herbivory, Water Availability, and Burning

By

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Abstract. Elimination of large predators and reduced hunter harvest has led to concerns that an increasing elk (*Cervus elaphus*) population may be adversely affecting vegetation on the low elevation elk winter range of Rocky Mountain National Park, Colorado. Vegetation production and nutrient responses to herbivory, water availability, and burning were studied over a 5-year period to determine the effects of these processes on willow (*Salix* spp.) and bitterbrush (*Purshia tridentata*) communities.

Elk herbivory suppressed willow heights, leader lengths, and annual production, as well as herbaceous productivity of willow sites. Water impoundment had a positive effect on herbaceous production ($P < 0.05$), but little effect on shrubs in willow sites. Water impoundments on drier sites increased graminoid production over sites that had naturally high water tables. Surveys conducted to evaluate current beaver numbers and distribution documented a 94% population decline on the elk winter range since 1940, indicating the potential for altered hydrologic regimes in the past 50 years.

Burning in upland bitterbrush communities decreased amounts of shrub cover and production, but had no apparent effects on herbaceous standing crop biomass, with the exception of *Stipa comata*, which had lower production after burning ($P < 0.001$) and the carbon content of summer grasses. Grazing resulted in decreased herbaceous standing crop biomass, increased nitrogen content of upland grasses, and increased dry matter digestibility of forbs and grasses.

Vegetation conditions in willow sites on the elk winter range appear to be affected by a number of factors, of which elk herbivory is only one. Elk herbivory appears to be the predominant force in determining vegetation productivity in willow sites, but its effects may be exacerbated by lowered water tables. Restoration of fire through prescribed burning to bitterbrush communities does not appear to be effective in increasing herbaceous forage production; however, the majority of burns took place in spring when there was little fuel to carry a fire. Fall burns may prove more effective.

Keywords: Beaver, *Cervus elaphus*, herbivory, hydrology, national park management, prescribed fire, *Salix*.

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Introduction

Native large mammalian herbivores significantly influence plant species abundances and ecosystem processes (McNaughton 1984; Hobbs 1996). However, human developments can concentrate animals onto smaller ranges, thus increasing population densities while diminishing forage availability, and may decrease movements between, and within, seasonal ranges, potentially changing the scope of herbivore influence. Additionally, human manipulations of landscapes, such as the draining of wetlands for agricultural purposes and planting of crop species, can alter the plant communities on which herbivores rely. These influences may combine to create situations where less common plant communities and associated animal species are altered due to increased herbivory, competition from non-native or grazing-resistant plant species, and changing environmental and climate conditions.

Ideally, national parks and other protected areas should be pristine areas where habitats are protected from "unnatural" influences. However, many of these areas have been subjected to extensive human alterations, either presently or in the past. Therefore, many of the ecosystems represented in these areas are missing important elements, including key predators and other animal species; an intact complement of native habitats, including healthy riparian areas; and plant communities unaltered by exotic species (Huff and Varley 1999; Wright 1999).

The impact of ungulate herbivory on plant production has been hotly debated. Several researchers have demonstrated "grazing optimization", where plant productivity increases in response to grazing through overcompensation of the plant for tissues lost to herbivores (McNaughton 1979, 1984; Dyer et al. 1991). However, application of this theory to U.S. western rangelands was questioned by Painter and Belsky (1993), Patten (1993), and Bartolome (1993). DeAngelis and Huston (1993) pointed out the importance of physiological characteristics and environmental conditions in response of individual plants to herbivory.

Broad-scale declines in willows (*Salix* spp.) have occurred at a number of locations in the Intermountain U.S. West where there are also dense ungulate populations (Boyce 1989; Singer et al. 1994). Elk (*Cervus elaphus*) are protected at some of these locations, such as in national parks and the National Elk Refuge, Wyoming. Predators were eliminated at some of these sites and considerable confusion exists over what effect predators and Native Americans might have had in regulating or limiting the abundance of elk (Kay 1990, 1994; Wagner et al. 1995a; McNaughton 1996; Singer et al. 1998a). Willow declines in the presence of high elk densities have been documented in Rocky Mountain National Park (RMNP) and Yellowstone National Park (YNP) (Singer et al. 1998b; Zeigenfuss et al. 1999) and the National Elk Refuge (Smith and Robbins 1994). All of these areas have similar histories of human alterations of the landscape and hydrologic conditions. The climate has become warmer and drier throughout the century, thus contributing to willow declines in YNP and RMNP (Balling et al. 1992; Singer et al. 1998b). Beaver declines have also been documented in both of the parks on their major elk winter ranges (Consolo-Murphy and Hanson 1993; D. Stevens and S. Christianson, Rocky Mountain National Park, unpublished report).

Willows typically become established on disturbed sites with abundant water. Willows are adapted to outgrow the reach of ungulates and to out-compete neighboring plants through rapid vertical growth rates and large belowground storage of nutrients and energy (Bryant et al. 1983). A more arid climate might reduce water availability to willows. Cooper et al. (1998) found that in a dry year in RMNP, water tables in a restored area previously drained by ditching dropped to a degree similar (40–70 cm) to pre-restoration levels. It could be assumed that this dry climate effect would be exacerbated in areas where natural flows had not been restored over longer periods of arid conditions. Beaver declines may also contribute to willow declines. Beaver populations play important roles in channel geomorphology, increasing water tables, retention of sediment and organic matter, modifying nutrient cycling and decomposition, and habitat modification, including community and species compositions (Naiman et al. 1986). Climate change, increasing elk numbers, and beaver declines varied this century (Singer and Cates 1995; Wagner et al. 1995b) and potentially interacted in their impacts on ecosystem processes. Thus, any research other than experiments planned to differentiate these effects are unlikely to shed further light on the factor(s) most responsible for willow declines.

Water stress may act to make plants more vulnerable to herbivory and reduce the ability of a plant to compensate for tissue losses. Physiologically stressed plants may produce less total resin and phenols compared to healthy plants (Kozlowski 1971; Singer et al. 1994, 1998b; Cates et al. 1999), and thus may be fed on preferentially by herbivores (Gurchinoff and Robinson 1972; White 1984; Halls et al. 1994; Swihart and Picone

1998). Herbivory may interact with water stress in a number of ways. Herbivory may lower shoot/root ratios, thus reducing the transpiration tissues (leaves, shoots) and improving the water status (i.e., reducing water stress) of the grazed plants (Wright et al. 1989). Where most of the plants are grazed, such as in the Serengeti grasslands, the reduction in overall transpiring plant tissues may serve to increase soil water and extend the growing season (Georgiadis et al. 1989). However, herbivory and water stress may also interact to reduce the long-term ability of the plant to recover. Browsed willows in RMNP apparently have less access to the ground water table than unbrowsed willows, suggesting that browsed willows have lost root structures that had access to the water table (Menezes et al., this volume).

Fire also plays an important role in plant production by releasing nutrients to the soil in a more accessible form for plant uptake, as well as introducing structural heterogeneity to the plant communities. Wildfires have been suppressed in RMNP for most of its history, and until recently, prescribed fire has not typically been used as a management tool.

Management of elk and vegetation in Rocky Mountain National Park, Colorado has been an issue since the 1930s. Elk populations were maintained at constant levels through removals by park management from the 1930s–1967, but have increased about 3-fold since the cessation of artificial controls within the park boundaries in 1968. Park managers are concerned that possible unnatural concentrations of elk may alter natural plant communities and ecosystem sustainability. Concerns over possible further elk increases and concurrent vegetation declines [particularly in willow (*Salix* spp.) and aspen (*Populus tremuloides*) communities on the winter range] have been expressed in recent years (Olmsted 1979, 1980; Hess 1993). Analysis of vegetation conditions on the winter range from 1968–1992 led former park biologist, David Stevens, to conclude that only willow and aspen stands on optimum habitat would survive under current browse pressure (D. Stevens, National Park Service, unpublished report).

Changing vegetation conditions may be a natural product of climate change, human-induced changes, hydrologic changes, fire suppression, or an expected result of recovery of elk to greater densities following cessation of artificial controls. All of the meadows that make up the significant proportion of elk feeding areas on the park winter range were altered throughout this century by extensive hydrologic changes. Direct human-induced alterations included: drainage and irrigation for cultivation; water removals to support homesteads, lodges, and National Park Service (NPS) administrative and visitor facilities; and water rights diversions. Beaver declines resulted in altered stream courses, dry channels, and drained ponds. Elk were absent, or their populations controlled at low densities, for over half a century (late 1800s to 1969). Vegetation conditions and succession may have changed because of underpopulation of a large native herbivore. Some vegetation changes observed since 1969 might be interpreted as a return to more natural conditions (pre-European settlement) with the return of elk to a more significant role in the ecosystem. Vegetation conditions may not be declining beyond natural conditions to be expected from elk grazing (Houston 1982).

Upland bitterbrush communities make up 50% of the feeding areas within the park's elk winter range. Elk utilize the understory grasses to a great extent in the winter, removing approximately 60% of growth annually (Singer et al., this volume). Previous studies have shown that since elk were released from artificial controls, percent of cover of bare ground on grasslands has increased (Zeigenfuss et al. 1999), and in bitterbrush areas, shrub cover is increasing. Stevens (unpublished report) observed that grasslands predominate with the disturbance of fire or heavy ungulate grazing. Grasslands may be decreasing and shrub cover increasing on xeric sites due to fire suppression policies that have prevailed in the park since its establishment. There has also been concern over the potential for shifts in species composition towards more palatable, grazing-resistant species, such as *Poa pratensis*, *Phleum pratense*, and *Koeleria macrantha* because of high levels of grazing.

We addressed the major issues of herbivory, water availability, and fire through a series of controlled experiments based on the following hypotheses:

(a) Plant productivity has declined due to elk. It will increase when elk are excluded and levels of herbivory that are higher than ambient levels will decrease plant productivity.

(b) Production in willow sites will respond positively to increased water availability. Willow sites with high water tables will better sustain elk herbivory as reflected by increased willow production, willow heights, and herbaceous production.

(c) Plant species composition has been altered by several years of elk herbivory. Excluding elk herbivory will result in shifts in plant species diversity.

(d) Beaver populations have continued to decline over the past 17 years.

(e) Plant production and shrub cover in bitterbrush sites will respond positively to prescribed burning. Initial increases in herbaceous plant production and eventual increases in cover of bitterbrush will follow burning. Quality of forage in burned sites will increase as reflected by increased nitrogen concentration and dry matter digestibility of forage.

Study Area and Treatments

Sixteen study sites were randomly selected in the elk winter range of the northeastern side of RMNP in the montane riparian and upland shrub communities. Vegetation communities were identified and random points generated in each vegetation type using a Geographic Information System (GIS).

Twelve study sites were located in riparian willow communities of: (1) the north and south sides of the Moraine Park area of the Big Thompson River drainage of the Big Thompson watershed (elevation 2,481 m); and (2) the Horseshoe Park area of Fall River drainage of the Big Thompson watershed (elevation 2,598 m). Predominant willow species throughout all areas were *Salix monticola*, *S. planifolia*, and *S. geyeriana* mixed with other mesic shrubs, such as *Potentilla fruticosa*, *Betula glandulosa*, *B. occidentalis*, and *Alnus tenuifolia*. Eight of these sites (four in Moraine Park and four in Horseshoe Park) were located in drier areas with little or no current beaver activity that supported short, heavily browsed willow. In all of these "short willow" sites, evidence from dead and decadent willows indicates that plants over 2 m tall were once present on all of these sites. The other four sites (two in Moraine Park and two in Horseshoe Park) were located in beaver-occupied areas (including areas of recent activity), or high water table areas, that supported taller willow plants subject to less severe hedging by the elk. These sites are referred to as "tall" willows.

Two 30.5 m x 45.7 m paired plots were chosen at each site. One randomly selected plot was fenced to exclude elk and deer and the other remained unfenced. Exclosures were erected in August–November 1994. In half of the sites with shorter willows (two in each drainage, n = 4), we attempted to raise the water table. This treatment, referred to as "short-watered" willows, was imposed in spring 1995. The treatments consisted of sheet metal check dams placed in both the grazed and ungrazed (exclosed) areas at each site. The dams were placed in existing ephemeral stream channels to impede the flow of rain and snowmelt runoff and raise the water levels locally. The rest of the shorter willow sites (two in each drainage, n = 4) were left to their normal hydrologic regimes and referred to as "short-control" willows. Throughout the growing season, water table levels at all the sites were monitored using wells and by measuring water levels on either side of check dams. Annual herbaceous consumption averaged 55% of annual production and shrub consumption averaged 33% of current annual growth throughout the study period (Singer et al., this volume). Elk were the primary ungulate herbivore in these systems.

Within each willow exclosure, simulated browsing treatments were conducted during winter (January–March) each year. At the outset, each exclosure was divided into sections that were randomly assigned to a "clipped" treatment or an "ungrazed" treatment. The clipped treatment, from fall 1995 onward, consisted of clipping 75% of the current year's growth from all forage shrubs and clipping 75% of the herbaceous layer in that section of the exclosure. This was intended to simulate greater herbivory that might occur with an increase in elk numbers or concentrations and to test the effects of these higher consumption levels. All clipped plant material was removed from the exclosure. Ungrazed treatments were unmanipulated areas within the exclosures. The grazed (unfenced) plots were left to unregulated elk grazing and browsing.

Four study sites were randomly located in upland communities. These sites were all located on southern exposures in the areas of Hallowell Park (elevation 2,652 m), Deer Ridge (elevation 2,591 m), Aspenglen Campground (elevation 2,500 m), and the Beaver Meadows Entrance Station (elevation 2,454 m). Primary vegetation cover consisted of antelope bitterbrush (*Purshia tridentata*) and mountain muhly (*Muhlenbergia montana*) associated with sparse ponderosa pine (*Pinus ponderosa*). These sites were established to study the effects of herbivory and prescribed burning on production and species composition in this vegetation type. Two 30.5 x 45.7 m paired plots were chosen at each site. One was randomly selected to be fenced to exclude elk and deer and the other was open to grazing and browsing. Exclosures were erected in March–May 1995. Half of the area inside and outside exclosures at each site was burned in late fall 1995 or late April/early May 1996. Annual herbaceous consumption averaged 60% and shrub consumption averaged 12% throughout the study period (Singer et al., this volume).

Methods

Hydrological Monitoring

Area snowpack (at the Willow Park SNOTEL site) data were obtained from the USDA Snow Survey Office and growing season precipitation data from Colorado Climate Center's Estes Park site. The Willow Park SNOTEL site is located 9.2 km east of Horseshoe Park, at the head of the Fall River drainage. During the 1997 growing season, rain gauges were maintained within Moraine Park and Horseshoe Park. Simple open-top gauges were placed in open, unobstructed areas and read at least once every 2 weeks, depending upon rainfall events. River levels were monitored during the 1997 growing season. Metal bars were placed in river channels at the study sites in both watersheds. The top ends of these bars were surveyed with reference to an arbitrary elevation plane. Measurements of river levels were made every 2 weeks.

In the summer of 1994, 81 shallow wells were installed in the two watersheds under investigation to monitor seasonal and annual changes in water levels, as well as those induced by our damming treatments. Fifty wells were placed in the Horseshoe Park willow study sites and 31 in the Moraine Park willow study sites. Wells at most sites were placed along site boundaries both parallel and perpendicular to the flow of water through the site. Wellheads were referenced to the same arbitrary plane of elevation as the river channel bars. Depth of penetration for the wells varied from less than 1 m to just over 2 m below the surface. Depth of wells was determined by the maximum depth that could be reached using a gas-powered auger, or 0.5 m past the first sign of the water table. Wells were constructed of 2-inch diameter PVC pipe slotted along the entire length that was underground. During the growing seasons from 1995 to 1998, groundwater levels were read at least once per month at all sites, usually coinciding with the reading of river levels. It was not possible to collect pre-treatment groundwater data prior to the installation of the check dams, so we compared them to undammed short willow sites nearby.

Beaver Surveys

Beaver surveys were conducted on 11 streams within the Big Thompson River watershed in the northeastern portion of the park. Field surveys were conducted from October 1994 through December 1998 repeating similar ground surveys conducted in 1939–1940 (Packard 1947), 1964, and 1980–1981 (Rocky Mountain National Park, unpublished data). We surveyed stream reaches in which beaver activity had been reported in the prior surveys, mapping the location of signs of current beaver activity, including fresh cuts on vegetation, food caches, and lodges and dams with fresh work or vegetation cuttings from the current year. Surveys were conducted during all months, but were concentrated between October and May when frozen stream channels facilitated walking.

We compared the number of lodges recorded for the most recent survey of each stream with the number recorded for the same areas in the earlier surveys. We estimated the population size for each stream based on an assumed colony of six beavers per lodge following prior surveys. Where current activity was evident but no lodge located, we assumed one active colony of six beavers. We compared the estimate based on our most recent survey to 1939–1940, 1964, and 1980–1981 estimates.

Shrub and Herbaceous Production

Three 9.3 m^2 randomly-selected circular plots were established in each treatment at each study site in 1994 for measuring shrub production. Data on shrub production were collected in the late summers of 1994–1996 and 1998 for willow sites and 1994–1997 for bitterbrush sites. Data collected on each plant included species; canopy diameters (widest and perpendicular to widest diameter); plant height; number of stems; and an estimate of percent of canopy dead. On every fourth individual of each shrub of each species, a subsample of the number of browsed and unbrowsed leaders; diameters at twig base, tip, and point of browse (grazed plots only); and leader lengths (1996–1998) were also collected. Several willows ($n = 2$–4) of the three predominant species in each treatment at each exclosure were also tagged for more intensive measurement throughout the course of the study. Catkin production was measured in June 1996 and 1998 on tagged plants. Annual aboveground production was estimated using log-log predictor regressions of total production (dependent variable) on canopy volume (independent variable) of willows and bitterbrush following Peek (1970). Plant material removed from the tagged plants during annual willow clipping treatments was collected for use in creating regression models. A number of willow and bitterbrush plants located outside the study sites, but within close proximity to them, were sampled for plant production in late summer 1995 and 1996. These samples included leaves and twigs and were spectroscopy). All dry matter digestibility, non-structural carbohydrate, and mineral analyses were performed at the Range Nutrition Laboratory at Colorado State University, Fort Collins.

Statistical Analyses

Statistical analyses were performed using SAS (version 6.12) statistical software. Shrub annual production, height, species-specific production, canopy area and volume, catkin production, and leader lengths were tested for differences between all treatments. Herbaceous standing crop biomass and species composition were also examined for treatment differences. Data from willow sites were analyzed for differences between all treatments using PROC MIXED in SAS, an analysis procedure that is a generalization of the standard linear model designed to analyze data generated from several sources of variation. This method allowed us to account for, and test for, the effects caused by the different watersheds (Moraine vs. Horseshoe), as well as random sites. Differences between individual means were determined using the probability associated with the *t*-statistic for pairwise comparisons between least square means. PROC GLM, the general linear model for data with only one source of variation, was used for analysis of data from bitterbrush sites since these sites were not grouped in watersheds, but randomly placed over the entire landscape of available bitterbrush. The F-protected least significant difference was used to determine significant differences between means. When the assumptions of equal variance were not met, variables were log transformed to stabilize variance. Comparisons between years were performed using only the ungrazed and grazed treatments. Due to the wide variability in sample means, differences between treatments were considered significant at the 90% confidence level ($P < 0.10$).

Because the water additions were limited in magnitude (12–37 cm) and duration (May and June only), we also investigated the response of willows to water through correlations of growth parameters to depth to the water table.

Results

Hydrological Monitoring

Above-average snowpack conditions existed at the beginning of the growing season for the first 3 years of the study (1995–1997). The water year 1998 snowpack was similar to the 30-year average in magnitude, time, and duration. Figure 1 compares the 4 years covered by this study with the 30-year average for 1961–1990 for the area.

May through mid-June of the 1995 growing season was a period of above-average precipitation. Total precipitation for these 2 months was 20 cm above the 30-year average. This precipitation, combined with the heavy runoff from the above-average late season snowpack (Fig. 1), led to very high water tables in our study sites. The resultant high river levels made data collection difficult at some sites and led to the late-June flooding of at least one site in Horseshoe Park. The growing season precipitation total (May–September) for 1995 was 14 cm greater than the 30-year average. Totals for the next three growing seasons (1996–1998) were within 3 cm of the 30-year average. Rain gauge measurements in the 1997 growing season indicated very similar rainfall patterns and totals for the two watersheds (27.4 cm for Horseshoe Park and 26.5 cm for Moraine Park).

Dates of peak river levels varied, from early June in 1998 to the end of June in 1995, as a function of snowpack characteristics of that year (L. Zeigenfuss, U.S. Geological Survey, personal observation). The amplitude of river level change in Horseshoe Park was approximately twice that of Moraine Park, perhaps due in part to differences in channel morphology. Fluctuations in groundwater peaks and lows from year to year were the result of variations in timing and volume of snowpack runoff (May–June), and variations in precipitation inputs throughout the season (Fig. 2). Even

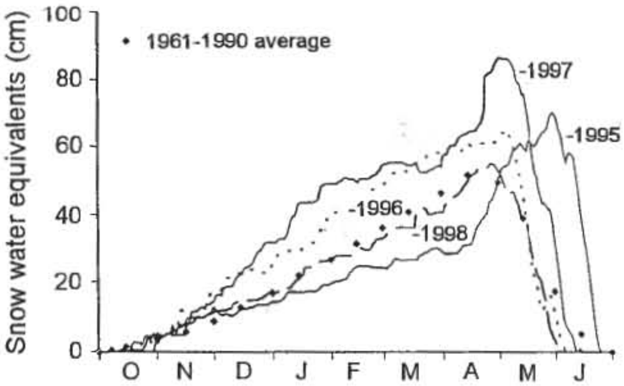


Fig. 1. Snowpack data for Willow Park, Rocky Mountain National Park, Colorado. Thirty-year average (1961–1990) compared to 1995–1998 Water Years. Source: USDA Snow Survey Office, Lakewood, Colorado.

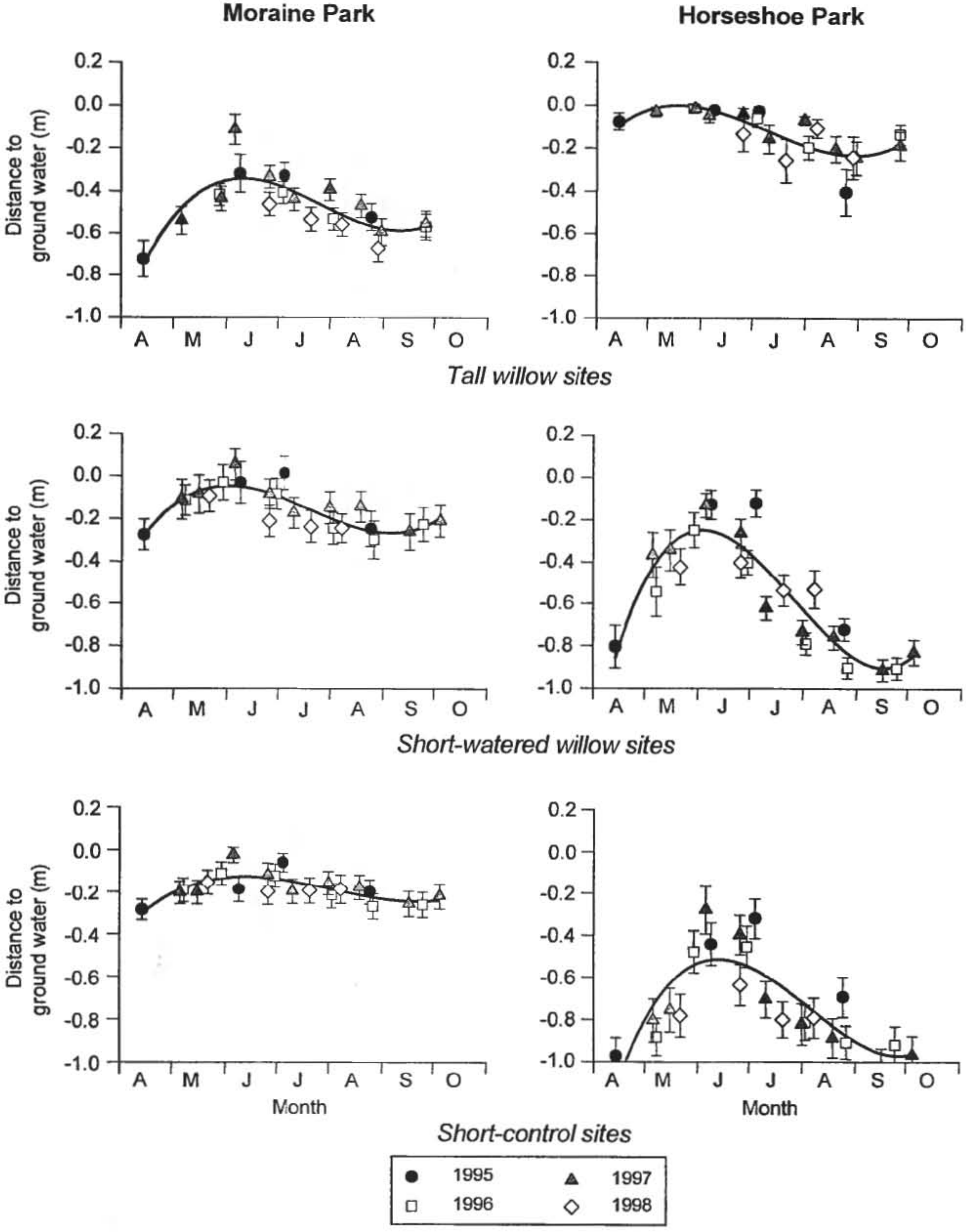
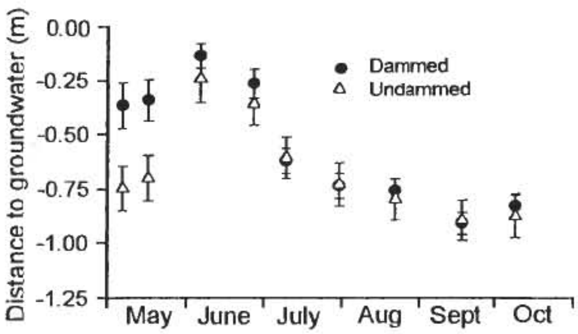


Fig. 2. Distance to groundwater in: (a) tall willow sites; (b) short-watered willow sites; and (c) short-control willow sites in Moraine and Horseshoe Parks, Rocky Mountain National Park, Colorado, 1995–1998.

when low rainfall conditions were experienced during July–September, groundwater levels never averaged more than 1 m below the surface. We hypothesized that tall willow sites would be wetter (i.e., that wetter conditions contributed to the presence of taller willows). Sites in Horseshoe Park followed the pattern we expected. Tall willow sites were the wettest, followed by short-watered sites, and short-control sites. However, this pattern was not present in Moraine Park where the short-control sites were wettest and the tall sites were the driest (Fig. 2). The check dams were successful in holding additional water at the sites during the early growing season. The mean difference between groundwater levels between dammed and undammed sites in May of 1997 was 37 cm for Horseshoe Park and 12 cm for Moraine Park (Fig. 3). Early season difference between water elevation in the channel behind the dam and that at the nearby intersection with the river was approximately 0.6 m. By early July, after spring run-off had subsided, water no longer backed up behind the check dams, and the difference in mean groundwater levels between short-watered and short-control willow sites had disappeared.

a. Horsetooth Park 1997



b. Moraine Park 1997

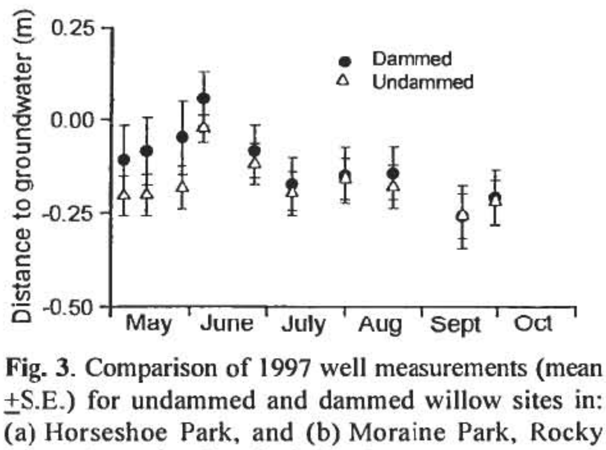


Fig. 3. Comparison of 1997 well measurements (mean ±S.E.) for undammed and dammed willow sites in: (a) Horseshoe Park, and (b) Moraine Park, Rocky Mountain National Park, Colorado.

Within each park, significant differences ($P = 0.058$ for Horseshoe Park and $P = 0.038$ for Moraine Park) between groundwater levels in short-watered and short-control willow sites occurred at the beginning of the growing season (May), before the rise in river levels (Fig. 3). At the time of high river levels and the resultant higher ground water levels throughout the system (early June) the difference between damming treatments lessened but still existed.

While each site in the study was unique in its surface water and groundwater characteristics, all sites exhibited high groundwater levels in the first half of the growing season. At all sites, even the lower late-season groundwater levels appeared to be high enough to be readily accessible for willows and other deep rooted plants in the sites all years (Alstad et al. 1999). At some sites in years of low precipitation (1994, 1998), *Carex* plants further away from watered channels (which have shallower roots than willows) may have experienced periods of water stress during the later half of the growing season (Alstad et al. 1999).

Beaver Populations

Beaver activity occurred on 8 of the 11 streams surveyed. Since 1981, one stream (Hidden Valley Creek) was abandoned and colonies established on one unoccupied stream (Mill Creek). Two streams that were abandoned between 1940 and 1981 (Wind River and Beaver Brook) remained unoccupied.

The total number of active lodges declined 83% between 1940 and 1981, and an additional 12% by 1994–1998, resulting in an overall decline of 95% since 1941 (Table 2). Similarly, the total estimated population size on surveyed drainages declined 79% between 1940 and 1981, and an additional 15% by 1994–1998, resulting in an overall decline of 94% since 1941 (Table 2). Estimated population sizes declined on all streams except the North Fork of the Big Thompson. The largest declines occurred on the Fall River, Big Thompson River, Glacier Creek, and Mill Creek.

Plant Production and Nutrient Responses to Water Manipulations and Herbivory Treatments in Willow Sites

Grazing resulted in significantly lower willow production ($P = 0.017$) than ungrazed and clipped treatments by 1998 (Fig. 4). This difference only became

Table 2. Active beaver lodges and estimated beaver population size in the Big Thompson River watershed on elk winter range in Rocky Mountain National Park, Colorado.

Location	Active lodges			Estimated population size		
	1939–1940	1980–1981	1994–1998[a]	1939–1940	1980–1981	1994–1998[a]
North Fork	1	1	0	6	6	6
Cow Creek	4	2	2	24	18	12
Fall River (Horseshoe Park)	13	10	0	96	24	6
Hidden Valley Creek	10	2	0	70	6	0
Beaver Brook	6	0	0	36	0	0
Big Thompson River (Moraine Park)	52	3	2	315	18	12
Cub Creek	7	1	1	60	6	6
Mill Creek	22	0	2	144	0	12
Glacier Creek/Boulder Brook	18	4	1	150	24	6
Wind River	3	0	0	18	0	0
Total	136	23	7	919	195	60

[a] Numbers reported are for most recent year surveyed in the period 1994–1998.

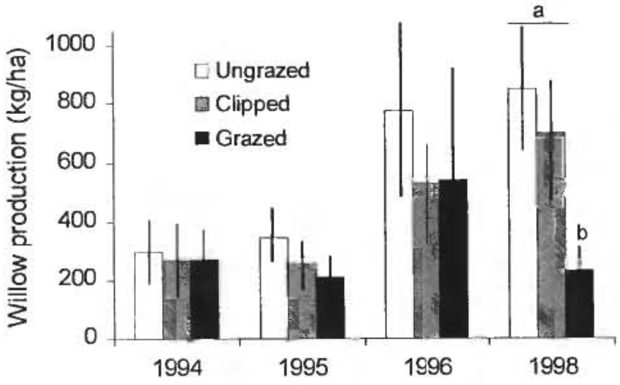


Fig. 4. Willow production (kg/ha) under different grazing treatments (different letters denote significant difference, $P < 0.02$) on elk winter range of Rocky Mountain National Park, Colorado.

evident 4 years post-treatment. There was an interaction effect between year and herbivory treatment for willow production ($P < 0.001$). After 4 years of rest from grazing, willow production had increased by 209% (Fig. 4). Willows browsed by elk were shorter than those protected or treated with clipping ($P < 0.002$) after only 2 years (Fig. 5). Willow leader lengths were shorter ($P = 0.033$) under grazed (17.5 ± 2.4 cm; $\bar{x}$ ± SE) and ungrazed (15.9 ± 2.4 cm) treatments than clipped treatments (23.1 ± 1.9 cm) in 1998. Overall leader lengths were greater ($P = 0.001$) in Moraine Park (23.2 ± 2.0 cm) than Horseshoe Park (14.9 ± 1.4 cm). In 1996, there was an interaction effect on leader length between herbivory treatment and location ($P = 0.021$) because all browsed leaders of willows under grazing were shorter in Moraine Park. All clipped willow leaders in Moraine Park were longer than clipped willow leaders in Horseshoe Park. Willow catkin production (catkins/m^3 of shrub canopy volume) was ~70% lower under clipped (21.2 ± 3.5) and grazed (16.8 ± 6.1) than the ungrazed (69.0 ± 13.6) treatment.

Herbaceous standing crop biomass (graminoids + forbs) in both grazed and clipped treatments was 18–29% lower than in the ungrazed treatment by the fourth year post-treatment ($P = 0.016$; Fig. 6). While we did detect a pre-treatment difference in herbaceous standing crop biomass in 1994 with higher biomass in grazed sites (mainly attributed to grazed sites in Horseshoe Park), this difference was no longer significant by 1996. Percent basal cover of grasses and bare ground were greater ($P < 0.001$ and $P = 0.036$, respectively) in grazed sites. Mean cover of bare ground was 7.72 ± 2.16% in grazed as opposed to 3.10 ± 1.62 % in ungrazed sites. Shrub cover ($P = 0.004$) and litter cover ($P < 0.001$) were lower under grazing. Less litter accumulated ($P < 0.009$) in grazed and clipped plots by 2 years post-treatment.

The water impoundments early in the growing season did not have any impact on willow production (Fig. 7). Willow production was greater in tall sites than either short-watered or short-control willow sites in 1994–1996 ($P < 0.001$); however, in 1998, this difference was not significant ($P = 0.118$). The height differences selected at the start of the study were maintained, despite water impoundment, and heights were greater ($P < 0.036$)

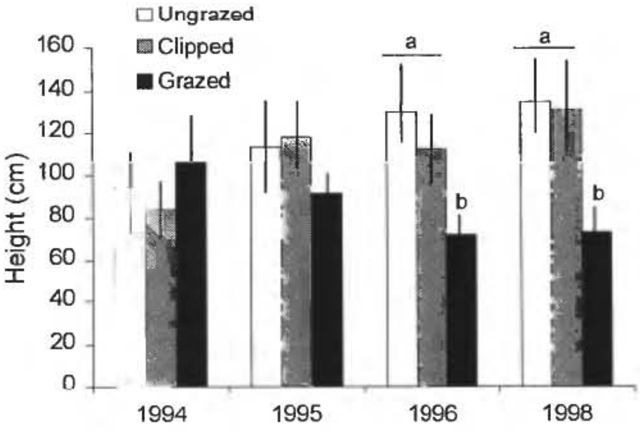


Fig. 5. Average heights of willows under different grazing treatments on elk winter range of Rocky Mountain National Park, Colorado.

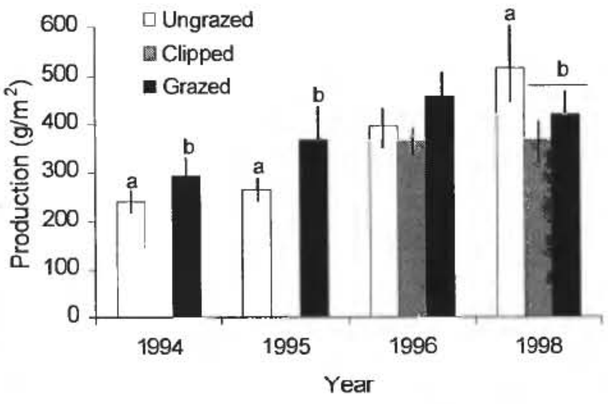


Fig. 6. Annual herbaceous production under different grazing treatments on elk winter range of Rocky Mountain National Park, Colorado (different letters denote significant difference, $P < 0.10$).

in tall sites than short-control or short-watered sites in all years.

Herbaceous standing crop biomass response to the water impoundment was difficult to interpret. At the onset of the study in 1994, herbaceous biomass was greater in short willow sites destined for water impoundments than other short willow sites. However, in 1995, the first year of damming, herbaceous biomass was, on average, 30% greater ($P = 0.006$) in tall willow sites, than both watered and control short willow sites. Following 2 and 4 years of water impoundment, in 1996 and 1998, biomass in short-watered sites was significantly greater than in short-control sites ($P = 0.051$ and $P = 0.036$), and exceeded tall sites (though not significantly so) both years (Fig. 8). This effect may have been due to *apriori* site differences between short-control and short-watered sites, or a response to water impoundment on the sites.

Shrub production and herbaceous standing crop biomass responded to total March–September precipitation, but this response fit a quadratic curve well in most cases (r^2 ranged from 0.44 to 0.94), implying that perhaps there is a threshold level of precipitation beyond which herbaceous production did not increase. However, the year of highest precipitation, 1995, also had a shortened growing season (L. Zeigenfuss, U.S. Geological Survey, personal observation) due to late warming. This may also have contributed to the lowered production during this year. In 1998, litter accumulations were also significantly greater in short-watered and tall sites than short-control sites, likely resulting from increased production in 1997.

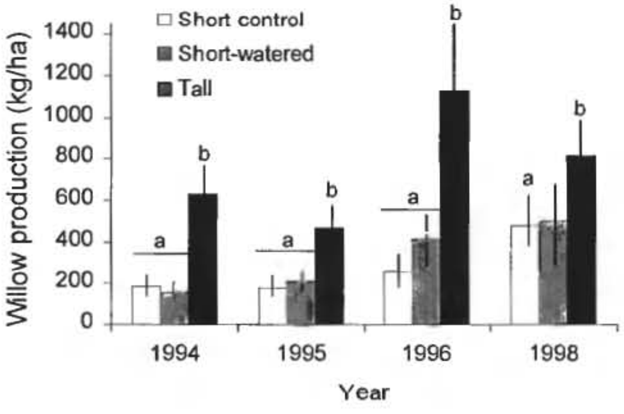


Fig. 7. Willow production (kg/ha) under different water treatments in willow communities on elk winter range of Rocky Mountain National Park, Colorado (different letters denote significant difference, $P \leq 0.05$).

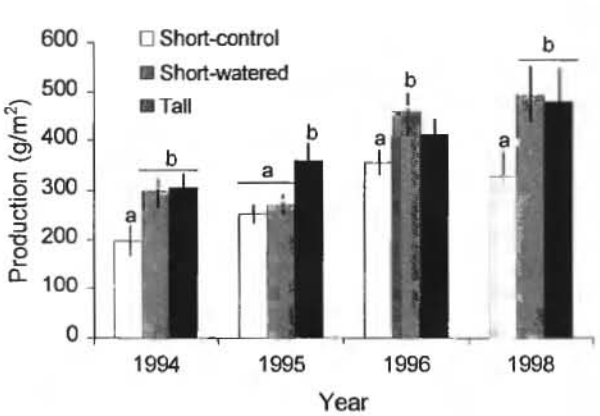


Fig. 8. Herbaceous production in willow sites with different water treatments on elk winter range of Rocky Mountain National Park, Colorado (different letters denote significant difference, $P \leq 0.05$).

Depth to water table in June and July was weakly correlated to herbaceous standing crop biomass and current annual growth of willows, but the percent of variation explained was very low (r^2 ranged from 0.04–0.06). For herbaceous plants, the association was positive, with consistently higher production with higher water tables (Fig. 9a). However, the influence of water on willow growth was difficult to interpret. While the highest production levels were achieved in sites with the highest water tables, overall, the association was slightly negative. When the data were separated by drainage, we found that most of this negative association was attributable to the Moraine Park sites, which had fewer wells, particularly in tall willow sites, and less variation in water table, with no dry sites, and few wet sites (Fig. 9b–c).

N content of graminoids and forbs was lower ($P = 0.007$ and $P = 0.080$, respectively) in clipped than grazed or ungrazed treatments (Table 3). Dry matter digestibility of graminoids was greater under grazing (Table 3). Graminoid N content increased and total nonstructural carbohydrates decreased when sites were dammed as well ($P = 0.053$; Table 4).

N content of *S. monticola* and *S. planifolia* was lower under grazing and clipping, but only significantly so in *S. monticola* ($P = 0.035$) and only in winter twigs (Table 5). Summer willow twigs and leaves did not vary in N content between treatments. Grazing led to lower percent dry matter digestibility of willows, but these values were only significantly lower ($P = 0.035$) in winter twigs of *S. planifolia* (Table 5). Calcium and potassium concentrations of *S. monticola* ($P < 0.02$; Table 5) were

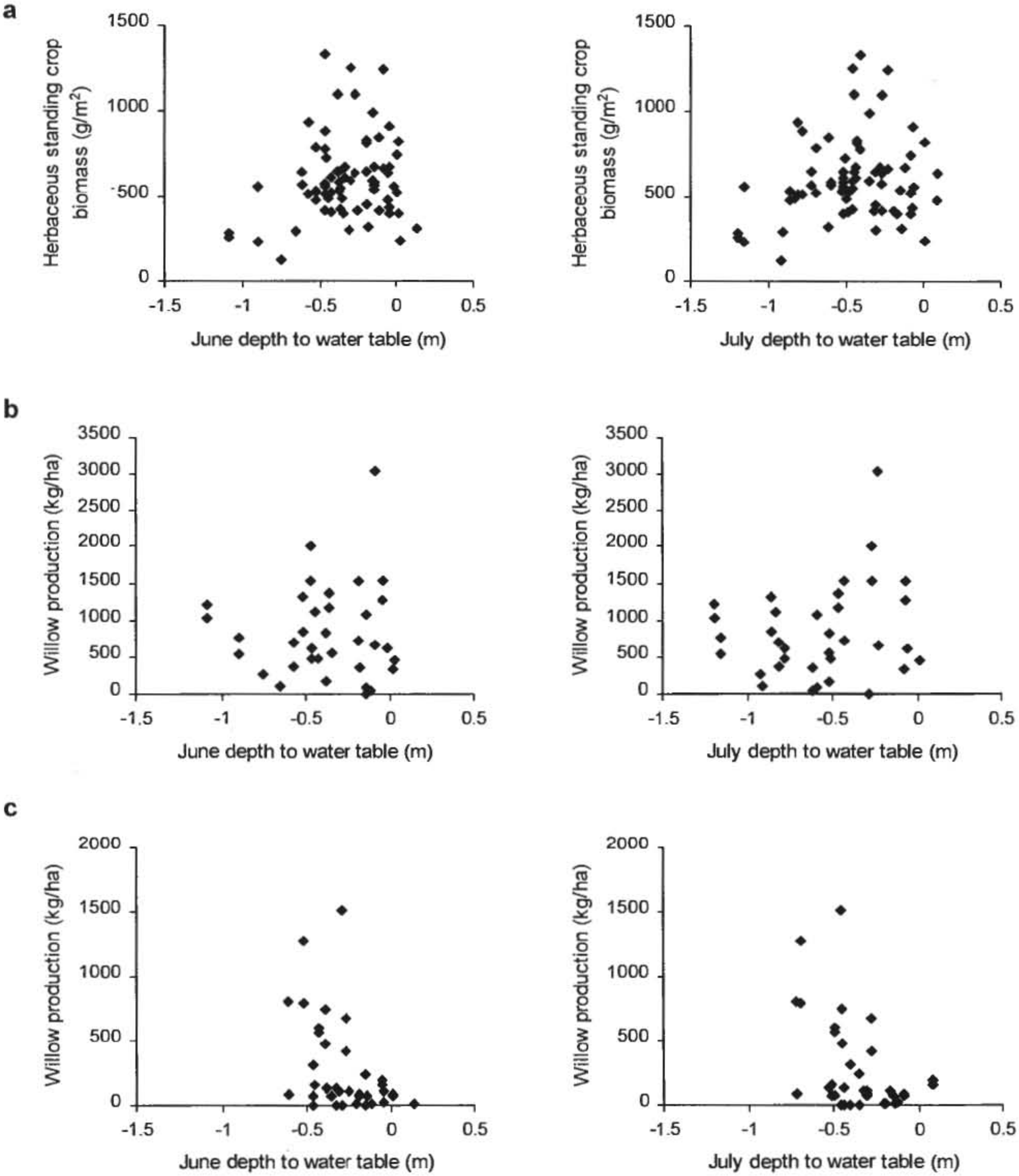


Fig. 9. Correlation of depth to water table with herbaceous biomass (a) and willow production in Horseshoe Park (b) and Moraine Park (c).

Table 3. Nutrient content of herbaceous plants under different herbivory treatments on willow sites on elk winter range of Rocky Mountain National Park, Colorado, 1998.

	Graminoids			Forbs		
	Ungrazed	Clipped	Grazed	Ungrazed	Clipped	Grazed
Carbon (%)	44.26	44.35	44.10	43.56	42.43	42.32
Nitrogen (%)	1.74	1.48[a]	2.00	2.48	2.03[a]	2.51
Dry matter digestibility (%)	54.72	55.29	57.16[a]	75.00	69.96	74.81
Total non-structural carbohydrates (%)	12.12	13.83	11.78	11.78	9.55	9.00

[a]Different from other treatments at $P \leq 0.10$.

greater under grazing. Phosphorus concentration was lower under both clipped and grazed for *S. monticola* and *S. planifolia* ($P < 0.10$; Table 5). N and C content of willows were not affected by water treatments. Concentrations of magnesium and potassium were higher in winter twigs of *S. monticola* and *S. planifolia* in tall sites ($P < 0.050$; Table 6). Phosphorus content of *S. monticola* was greater in both tall and short-watered sites ($P = 0.090$).

An interaction effect between herbivory and water treatments was noted for *S. geyeriana*. Willows of this species in tall sites that were subjected to grazing and clipping had higher potassium concentrations than did willows in short-control sites subjected to herbivory ($P = 0.030$). Iron concentrations were also higher in *S. geyeriana* plants subjected to elk grazing in short-control sites ($P = 0.048$).

Only a few significant differences in species composition were found due to herbivory in willow sites, and all were in forbs. Grazed sites had more *Solidago* spp. ($P = 0.048$), while ungrazed sites had more bluebell (*Mertensia ciliata*) ($P = 0.076$). Interestingly, one species, false Solomon's seal (*Maianthemum stellatum*), showed an increase ($P = 0.034$) under clipping.

Plant Production Responses to Burning and Herbivory in Bitterbrush Sites

Burning resulted in a reduction of total shrub canopy volume and area ($P < 0.013$; $P < 0.021$) in 1996 and 1997 (Fig. 10), as was expected from the initial consumptive effects of fire. However, resprouting from burned plants was evident in all sites. Production of *Purshia tridentata* was not different in 1996, but production was six times greater ($P = 0.006$) in unburned sites than burned sites by 1997, suggesting that plant mortality took place during the first year following the fires. Many dead bitterbrush plants were observed on the burned sites in 1997 as well. No other significant effects of grazing on upland shrub production variables were observed.

Burning had no significant impacts on total herbaceous production, graminoid production, or forb production ($P > 0.10$) in these bitterbrush sites (Fig. 11); however, production was greater ($P = 0.077$) in ungrazed sites (pooled over burning treatment) by 1997. Herbaceous litter had increased significantly ($P = 0.003$) in ungrazed treatments by 1997. Increases in graminoid production occurred in 1995–1997 when compared to 1994, but these differences were not linked to burning or grazing treatments and were most likely due to the low precipitation that year.

Needle-and-thread grass (*Stipa comata*) had significantly less ($P = 0.063$) production in 1997 in plots that were burned and was greatest in unburned, grazed treatments. Percent cover of *Artemisia ludoviciana* and *Eriogonum umbellatum* was greater in ungrazed than grazed sites; however, no other significant differences in percent cover or abundance of species were observed.

No differences in nitrogen content, dry matter digestibility, or total non-structural carbohydrates could be found to be attributable to burning. However, percent carbon content of grasses was greater in burned treatments (45.01 ± 0.25 vs. 44.43 ± 0.18%). Nitrogen content and dry matter digestibility were higher ($P = 0.090$ and $P = 0.087$ respectively) in grazed grasses (n = 1.24 ± 0.09%; DMD = 46.55 ± 1.73%) than ungrazed grasses (n = 0.98 ± 0.11%; DMD = 41.77 ± 94%) when pooled across burning treatments. Dry matter digestibility was also greater ($P = 0.032$) in grazed forbs (59.68 ± 2.49%) compared to ungrazed forbs (52.34 ± 1.73%).

Table 4. Nutrient content of herbaceous plants under different water treatments on willow sites on elk winter range of Rocky Mountain National Park, Colorado, 1998.

	Graminoids			Forbs		
	Short-control	Short-watered	Tall	Short-control	Short-watered	Tall
Carbon (%)	44.38	44.19	44.15	44.50[a]	42.43	41.34
Nitrogen (%)	1.53[a]	1.85	1.84	2.47	2.28	2.27
Dry matter digestibility (%)	56.54	54.20	54.43	70.96	73.00	75.80
Total non-structural carbohydrates	15.5[a]	11.21	11.02	9.95	10.66	9.90

[a] Significantly different from other treatments ($P \leq 0.10$).

Discussion

Elk populations in RMNP decreased plant productivity in willow communities. Elk herbivory is the primary factor driving productivity declines, in particular, the shorter stature of many willows. Although an interaction effect between herbivory and water table depth in our experimental manipulations was not found, this may have been due to our small samples size (n = 4) and high sample variance, incorrect assumptions as to site-specific water table differences, relatively short time frame (4 years post-treatment) for measurement of effects, and the relatively short-lived and localized nature of our water impoundments. Our inferences as to water dynamics were limited by the smaller number of wells in Moraine Park, particularly in tall willow sites, and the fact that our sampling did not include dry years (1995–1999 were years of average or above-average annual precipitation). This problem was further confounded by the positive correlation of elk density with water table height found in these sites (Singer et al., this volume). Higher densities of elk in locations with higher water tables may mean the negative effects of elk herbivory on plant production are overwhelming any positive influence of higher water tables in these areas. Comparing grazed sites in years of different growing season precipitation further emphasized the importance of the amount of available water to plant production. Production was much lower during 1994 in our study area – a year with lower than average precipitation.

Herbivory by ungulates, such as elk, can influence many aspects of plant structure, growth, and net primary productivity. Net primary productivity can either increase or decrease as a result of ungulate herbivory (McNaughton 1979; Painter and Belsky 1993). In RMNP, productivity increased when plants were protected from grazing. This trend was obvious starting in 1996 and the effect was significant by the fourth and final year of our study. Based on observation of exclosures in RMNP and YNP (this study; Singer et al. 1994, 1998b), we expect continued increases in canopy coverage and annual production within protected sites for some years. Herbaceous production may decline as increasing shrub canopy takes over areas or shades out understory herbs.

The effect of our clipping treatment on herbaceous biomass indicates that increased grazing pressure could further depress plant productivity in these communities. Willow production and average heights were lower in clipped than unclipped treatments, and lowest in sites grazed by elk. The timing of clipping vs. elk herbivory may explain the lesser negative response to clipping. By the end of the study, it became apparent that elk remove plant material during the spring, after the emergence of new shoots and leaves, as well as during winter dormancy, which was the period when the clipping treatments were conducted. This difference could account for the greater willow productivity, longer leaders, and greater heights observed under the clipping treatment compared to elk grazing. However, the decrease in catkin production was similar under clipping to the grazed treatment, leading us to conclude that winter clipping and browsing have equivalent effects on seed production.

Ungulate grazing and hoof action resulted in more bare ground and soil compaction on the study sites. There may possibly be higher sediment yields from the grazed sites. Any increase in bare ground could result in a warmer soil microclimate. Warmer soil, if moisture is equivalent, could result in increased N mineralization

Table 5. Nutrient content of willows under different herbivory treatments on willow sites on elk winter range of Rocky Mountain National Park, Colorado, 1998.

	Salix geyeriana			*Salix monticola*			*Salix planifolia*		
	Ungrazed	Clipped	Grazed	Ungrazed	Clipped	Grazed	Ungrazed	Clipped	Grazed
Winter									
Carbon (%)	52.04	51.84	51.83	51.24	51.49	50.81[a]	50.80	50.86	50.43
Nitrogen (%)	1.14	1.15	1.08	1.18[a]	1.10	1.08	1.25	1.19	1.10
Dry matter digestibility (%)	37.20	37.51	36.06	36.26	35.84	35.0	34.60	33.79	32.40[a]
Calcium (mg/L)	0.61	0.64	0.65	0.71	0.68	0.81[a]	0.62	0.68	0.65
Potassium (mg/L)	0.23	0.26	0.25	0.22	0.21	0.27[a]	0.28	0.24	0.30
Phosphorus (mgL)	0.13	0.14	0.13	0.13[a]	0.12	0.12	0.14[a]	0.13	0.13
Summer									
Carbon (%)	50.97	51.09	50.50[a]	48.95	48.93	48.73	49.77	49.68	49.43
Nitrogen (%)	1.68	1.72	1.71	1.73	1.78	1.74	1.70	1.72	1.79
Dry matter digestibility (%)	42.22	43.12	41.11	42.59	43.08	41.02	40.43	40.39	38.17

[a] Different from other treatments at $P < 0.10$.

Table 6. Nutrient content of willows under different water treatments on willow sites on elk winter range of Rocky Mountain National Park, Colorado, 1998.

	Salix geyeriana			*Salix monticola*			*Salix planifolia*		
	Short-control	Short-watered	Tall	Short-control	Short-watered	Tall	Short-control	Short-watered	Tall
Winter									
Dry matter digestibility (%)	36.46	38.14	36.16	35.88	35.48	35.73	34.20	32.49	34.10
Potassium (mg/L)	0.19	0.23	0.32	0.19	0.22	0.28[a]	0.25	0.24	0.34[a]
Phosphorus (mg/L)	0.12	0.13	0.15	0.11[a]	0.12	0.13	0.13	0.12	0.14
Magnesium (mg/L)	0.12	0.14	0.15	0.13	0.12	0.15[a]	0.12	0.11	0.15[b]
Summer									
Dry matter digestibility (%)	42.45	41.88	42.12	42.60	39.78[a]	44.30	39.76	39.54	39.68

[a] Different from other treatments ($P < 0.10$).

[b] Different only from short-watered ($P < 0.10$).

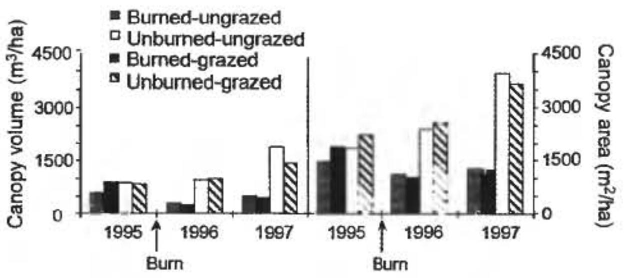


Fig. 10. Annual total shrub canopy volume (m^3/ha) and area (m^2/ha) responses to burning and grazing treatments in bitterbrush sites on elk winter range in Rocky Mountain National Park, Colorado.

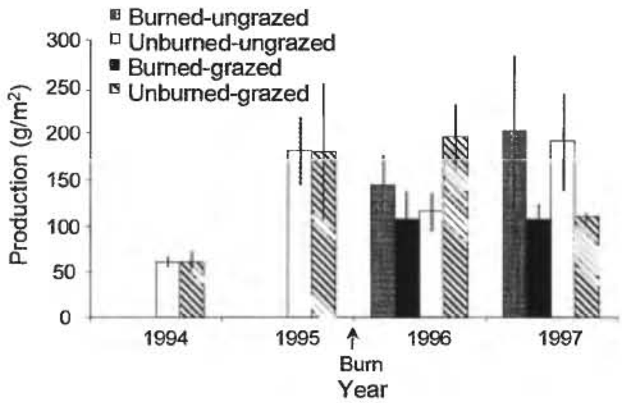


Fig. 11. Herbaceous production (g/m^2) in response to grazing and burning treatments in bitterbrush sites on elk winter range in Rocky Mountain National Park, Colorado.

on grazed sites. While we did find evidence of increased percent bare ground in grazed willow sites vs. protected areas, the mean bare ground was only 7.7%. Studies conducted in concert with ours found no increase in N mineralization on grazed sites compared to sites protected for either 4 years or 36 years (Binkley et al., this volume; Menezes et al. 2001). Percentage bare ground was significantly lower in one of two upland shrub communities protected from grazing for 36 years, but not in a wet meadow community (Schoenecker et al., this volume). Percentage spring soil moisture ranged from 1–10% greater in areas protected from grazing for 36 years (D. Binkley, Colorado State University, unpublished data), but no differences in soil moisture were found between 4-year-old exclosures and grazed areas (R. Menezes, Natural Resources Ecology Laboratory, unpublished data). Summer soil temperatures were 1–5 degrees cooler in the 36-year-old exclosures (D. Binkley, Natural Resources Ecology Laboratory, unpublished data).

Ungulates can influence the natural heterogeneity of N in the landscape by changing litter quality, thereby affecting N mineralization rates, and by adding readily available N to the upper soil levels in the form of urine and feces (Hobbs 1996). Elk grazing increased N and other nutrient content and digestibility of forages in other study areas (Frank and McNaughton 1992; Singer and Harter 1996). Increases in graminoid N concentration under grazing in willow and bitterbrush sites indicate that elk are having a positive influence, at least in the short-term, on N cycling in RMNP willow communities. N levels decreased in the clipped treatment, which seems counter-intuitive until the lack of additions of either urine and feces, or decomposing plant litter, is considered. The increased percent dry matter digestibility and concentration of important forage nutrients (such as calcium) under grazing may create heavily grazed patches, which attract continued use. Such "grazing lawns" have been argued to cause evolution of plants to withstand long-term heavy grazing (McNaughton 1986). In the short-term (i.e., less than an evolutionary time scale), the effects of heavy grazing may be reduced productivity or species shifts. However, some effects of elk on vegetation and soil and nutrient processes should be considered normal and natural in a national park ecosystem in which elk are a native species.

Hydrologic changes may be exacerbating the effects of elk herbivory in RMNP, despite our ability to determine significant response of plant production to water table dynamics. Hydrologic changes over the last 50 years include a 69% decrease in surface area of water in Moraine Park and a 47% decrease in Horseshoe Park (Peinetti et al., this volume). This decline has been attributed primarily to decreases in beaver activity and beaver dams. Concurrent declines in willow cover of 20% were observed during the same period. Decline in cover of tall willows ranged from 54–65% (Peinetti et al., this volume). Elk populations increased during the same period from ~700 to 3,000 (Lubow et al. 2002). Beaver activity on the surveyed streams has declined substantially over the past 17 years, contributing to a substantial decline since 1940. Actual beaver population sizes are unknown and comparisons of population estimates derived from different surveys are problematic; however, the estimates are likely a reasonable indication of the relative population trend over time. Low winter stream flow levels, plague, tularemia epidemic, poaching, predation, and competition with deer and elk over woody browse, were suggested as factors that may have contributed to beaver declines prior to 1980. There is evidence for each of these possible causes. In 1982, the Lawn Lake dam collapsed, causing a large flood on the Fall River downstream of the Roaring River, which contributed to the large beaver decline, recorded in that drainage since 1981 (4 of 10 lodges recorded in 1981 were in the path of the flood). Since 1994, three cases of tularemia were confirmed from beaver carcasses found along the Big Thompson and Fall Rivers. Overall declines have occurred in areas lightly-used (Glacier Creek) or moderately used (Hallowell Park, Cow Creek) by elk during winter, as well as elk winter concentration areas (Moraine Park, Horseshoe Park, and Beaver Meadows).

The decline in beaver populations may also be contributing to declining willow populations under heavy elk herbivory through reduced recruitment sites. Beaver cuttings from willow often root and become established along beaver ponds, dams, and flooded channels. Old beaver ponds often provide ideal substrate for establishment of willow seedlings. The loss of beavers and their consequent effects of raising the water table and stimulation of suckering in willow following beaver cutting (Kindschy 1989) are potentially leading to lowered regeneration in willow communities.

Other limiting factors may be hydrologic changes due to human water use or a change to a warmer, drier climate over the period of decline (Singer et al. 1998b). All of the meadows in the major elk feeding areas experienced water diversions for agriculture, resort and housing developments, and irrigation along the Colorado Front Range in the past. In recent decades, 95% of the diversions in Beaver Meadows, and 80% of those in Horseshoe Park have been eliminated. Only 50% of water diversions from Moraine Park have been restored (K. Czarnowski, National Park Service, personal communication). However, there is no way of knowing whether restoration of diverted water reverses changes to the ecosystem which may have occurred during years of lower water availability. The combination of climate change over the last century to drier conditions, in concert with heavy elk herbivory, may also contribute to willow decline. Analysis of climate records around Estes Park shows a temperature increase of 0.89°C and precipitation decreases of more than 1 cm over the last century (Singer et al. 1998b).

Whatever the cause of the decline, the decreasing numbers of beaver have altered hydrology on the elk winter range in the park. Areas formerly occupied by beaver are now merely dry channels that fill with water only during spring runoff or occasional heavy rain events. The reduction in length of streams on the winter range (44–56% less) due to channel straightening and simplification are attributed to the beaver decline (Peinetti et al., this volume). Several decades following beaver abandonment, water and/or nutrient-stressed willows may become less able to recover from tissue losses due to ungulate herbivory (Kozlowski 1971; Gurchinoff and Robinson 1972; Bryant and Kuropat 1980).

We did not detect any shifts in species composition to more palatable, grazing-resistant species due to elk herbivory. While it might be argued that our time frame was too short to detect shifts in species composition, other studies of long-term grazing near three exclosures of 36 years in the same areas of RMNP have found few species effects (Stohlgren et al. 1999). One species that increased under protection in our study, *Mertensia ciliata*, was also one of only 24 species found exclusively within 36-year old exclosures by Stohlgren and others (L. Schell, Natural Resources Ecology Laboratory, personal communication). A few significant differences in species composition that were found in willow sites were associated with location (Moraine Park vs. Horseshoe Park) or water treatment (short-control vs. short-watered or tall). Because many of these differences have more to do with plant population distributions, former agricultural practices, or suitable habitat (some plants naturally grow better in a wetter or drier habitat), we will not discuss them here, except to mention that increases in water tables due to reintroduction of beaver to some of these areas would likely have some consequent effects on species composition.

Management Recommendations

Reducing elk numbers and/or reducing elk concentrations, altering the timing of use of willows, or exclusion of elk from willow communities will likely result in increases in plant productivity. Fencing parts of these communities to encourage greater seed production and establishment, and to allow some individual willows to increase in size beyond the reach of elk, may help sustain willow communities over the long term. Our study showed increased height of willows within 2 years of protection from browsing and increased catkin production within 4 years.

Reintroduction or restoration of beaver populations to parts of this range, or artificial manipulations of hydrology in willow areas to simulate beaver ponds will allow these sites to sustain high levels of herbivory, and will hasten height recovery of any willows that are protected from herbivory for 5–10 years. While our study was inconclusive as to the contribution of the water table to production, hydromanipulations could be aimed at catching and holding runoff to provide more water earlier in the growing season. Simulated beaver cuttings (Kindschy 1989) to stimulate suckering, and plantings from cuttings, could be used within protected areas to increase willow establishment.

Protection from browsing and water enhancement for short periods (less than 10 years) alone would not necessarily lead to sustainable willow communities. Management to encourage elk movement away from willow communities would also be necessary. Elk tend to be concentrated in certain areas of the range, such as Moraine Park. Shrub consumption levels reflect these increased elk densities (Singer et al., this volume). Management of elk to decrease these concentrations could lead to lowered levels of consumption, and thus increased plant productivity and potentially a return to larger communities of tall, healthy willows.

Prescribed fire had little effect on forage production or quality in upland bitterbrush communities. This may have been because the majority of the fires were conducted in spring when there was little fuel left to carry a fire. However, a large natural fire in Yellowstone had few effects on upland grasslands, with biomass increases only evident 2 years post-fire, and little change in nutrient concentration or digestibility of forages (Singer and Harter 1996). As the park's prescribed fire program expands, further study of the interaction of elk herbivory and fire effects are recommended.

Literature Cited

Alstad, K. P., J. M. Welker, S. A. Williams, and M. J. Trlica. 1999. Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: An isotopic study using $\delta^{13}C$ & $\delta^{18}C$. Oecologia 120:375–385.

Balling, C. B., G. A. Meyer, and S. G. Wells. 1992. Climate change in Yellowstone National Park: Is the drought-related risk of wildfires increasing? Climatic Change 22:35–45.

Bartolome, J. W. 1993. Application of herbivore optimization theory to rangelands of the western United States. Ecological Applications 3:27–29.

Boyce, M. 1989. The Jackson elk herd: Intensive wildlife management in America. Cambridge University Press, United Kingdom.

Bryant, J. P., and P. Kuropat. 1980. Selection of winter forage by subarctic browsing vertebrates: The role of plant chemistry. Annual Review of Ecology and Systematics 11:261–285.

Bryant, J. P., F. S. Chapin III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate history. Oikos 40:357–368.

Cates, R. G., J. Zou, S. C. Wooley, F. J. Singer, L. C. Mack, and L. C. Zeigenfuss. 1999. Predisposition of willows to elk browsing due to willow interactions with abiotic factors. Pages 191–195 *in* D. McArthur, W. K. Ostler, and C. Wambolt, editors. Proceedings of the shrubland ecotones. RMRS-P-11. U.S. Department of Agriculture Forest Service. Rocky Mountain Research Station, Ogden, Utah. 299 pp.

Consolo-Murphy, S., and D. D. Hanson. 1993. Distribution of beaver in Yellowstone National Park, 1988–89. Pages 38–48 *in* R. S. Cook, editor. Ecological issues on reintroducing wolves into Yellowstone National Park. National Park Service Scientific Monographs No. 22. Denver, Colo.

Cooper, D., L. H. MacDonald, S. K. Wenger, and S. W. Woods. 1998. Hydrologic restoration of a fen in Rocky Mountain National Park, Colorado, USA. Wetlands 18:335–345.

DeAngelis, D. L., and M. A. Huston. 1993. Further considerations on the debate over herbivore optimization theory. Ecological Applications 3:30–31.

Dyer, M. I., C. L. Turner, and T. R. Seastedt. 1991. Mowing and fertilizing effects on productivity and spectral reflectance in *Bromus inermis* plots. Ecological Applications 1:443–452.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73:2034–2058.

Georgiadis, N. J., R. W. Ruess, S. J. McNaughton, and D. Western. 1989. Ecological conditions that determine when grazing stimulates grass production. Oecologia 81:316–322.

Gurchinoff, S., and W. L. Robinson. 1972. Chemical characteristics of jack pine needles selected by feeding spruce grouse. Journal of Wildlife Management 36:80–87.

Halls, S. C., D. R. Gang, and D. J. Weber. 1994. Seasonal variation in volatile secondary compounds of *Chrysothamnus nauseosus* (Pallas) Britt; *Asteraceae* spp. Hololeucus (Gray) Hall & Clem. influences herbivory. Journal of Chemical Ecology 20:2055–2063.

Hess, K. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot. 167 pp.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Houston, D. B. 1982. The Northern Yellowstone elk: Ecology and management. McMillan Publishing, N.Y. 474 pp.

Huff, D. E., and J. D. Varley. 1999. Natural regulation in Yellowstone National Park's northern range. Ecological Applications 9:17–29.

Kay, C. E. 1990. Yellowstone's northern elk herd: A critical evaluation of the "natural regulation" paradigm. Ph.D. dissertation, Utah State University, Logan. 490 pp.

Kay, C. E. 1994. Aboriginal overkill, the role of Native Americans in structuring western ecosystems. Human Nature 5:359–398.

Kindschy, R. R. 1989. Regrowth of willow following simulated beaver cutting. Wildlife Society Bulletin 17:290–294.

Kozlowski, T. T. 1971. Growth and development of trees. Academic press. Vol. I. 462 pp.

Lubow, B. C., F. J. Singer, T. L. Johnson, and D. C. Bowden. 2002. Dynamics of interacting elk populations within and adjacent to Rocky Mountain National Park. Journal of Wildlife Management. In press.

McNaughton, S. J. 1979. Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. American Naturalist 134:1–19.

McNaughton, S. J. 1984. Grazing lawns: Animals in herds, plant forms, and coevolution. American Naturalist 124:863–886.

McNaughton, S. J. 1986. Grazing lawns: On domesticated and wild grazers. American Naturalist 128:937–939.

McNaughton, S. J. 1996. Wildlife policies in the U.S. national parks (book review). Journal of Wildlife Management 60:685–687.

McQuarrie, A. D. R., and C. L. Tsai. 1998. Regression and time series model selection. World Scientific, Singapore. 455 pp.

Menezes, R. S. C., E. T. Elliott, D. W. Valentine, and S. A. Williams. 2001. Effects of herbivory and proximity to surface water on C and N dynamics of elk winter range. Journal of Range Management 54:400–408.

Naiman, R. J., J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67:1254–1269.

Olmsted, C. E. 1979. The ecology of aspen with reference to utilization of large herbivores in Rocky Mountain National Park. Pages 89–97 *in* M. S. Boyce and L. D. Hayden-Wing, editors. North American elk: Ecology, behavior and management. University of Wyoming, Laramie.

Olmsted, C. E. 1980. The effect of large herbivores on aspen in Rocky Mountain National Park. Ph.D. thesis. University of Colorado, Boulder. 141 pp.

Packard, F. M. 1947. A survey of the beaver population in Rocky Mountain National Park, Colorado. Journal of Mammalogy 28(3):219–227.

Painter, E. L., and A. J. Belsky. 1993. Application of herbivore optimization theory to rangelands of the western United States. Ecological Applications 3:2–9.

Patten, D. T. 1993. Herbivore optimization and overcompensation: Does native herbivory on western rangelands support these theories? Ecological Applications 3:35–36.

Peek, J. M. 1970. Relation of canopy area and volume to production of three woody species. Ecology 51:1098–1101.

Singer, F. J., and R. G. Cates. 1995. Response to comment: Ungulate herbivory on willows on Yellowstone's northern winter range. Journal of Range Management 48:563–565.

Singer, F. J., and M. K. Harter. 1996. Comparative effects of elk herbivory and the 1988 fires on northern Yellowstone National Park grasslands. Ecological Applications 6:185–199.

Singer, F. J., L. Mack, and R. G. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435–443.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998a. Thunder on the Yellowstone revisited: An assessment of management of native ungulates by natural regulation, 1968–93. Wildlife Society Bulletin 26:375–390.

Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998b. Elk, multiple factors, and persistence of willows in national parks. Wildlife Society Bulletin 26:419–428.

Smith, B. L., and R. L. Robbins. 1994. Migrations and management of the Jackson elk herd. Resource Publication, National Biological Survey, 1994, volume 199. 61 pp.

Swihart, R. K., and P. M. Picone. 1998. Selection of mature growth stages of coniferous browse in temperate forests by white-tailed deer (*Odocoileus virginianus*). American Midland Naturalist 139:269–274.

Stohlgren, T. J., L. D. Schell, and B. V. Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9:45–64.

Wagner, F., R. Foresta, R. B. Gill, D. R. McCullough, M. R. Pelton, W. Porter, and H. Salwasser. 1995a. Wildlife policies in the U.S. National Parks. Island Press. Washington, D.C. 242 pp.

Wagner, F. R., R. Keigley, and C. Wombalt. 1995b. Ungulate herbivory of willows on Yellowstone's northern winter range: Comment to Singer et al. (1994). Journal of Range Management 48:475–477.

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90–105.

Wright, R. G. 1999. Wildlife management in the national parks: Questions in search of answers. Ecological Applications 9:30–36.

Wright, S. L., R. W. Hall, and J. W. Peacock. 1989. Effects of simulated insect damage on growth and survival of red oak (*Quercus rubra*) seedlings. Environmental Entomology 18:235–239.

Zeigenfuss, L. C., F. J. Singer, and D. Bowden. 1999. Vegetation responses to natural regulation of elk in Rocky Mountain National Park. Biological Science Report USGS/BRD/BSR-1999-0003. U.S. Government Printing Office, Denver, Colo. 23 pp.

CHAPTER FIVE

Changes Induced by Elk Herbivory in the Aboveground Biomass Production and Distribution of Willow (*Salix monticola* Bebb): Their Relationship with Plant Water, Carbon, and Nitrogen Dynamics

By

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Abstract. Willows are dominant woody plants of many high-elevation riparian areas of the western USA, and constitute an important food resource for various ungulates, which tend to concentrate in riparian areas. The response of willow to grazing was analyzed in the elk winter range of Rocky Mountain National Park, by considering the effect of elk grazing on *Salix monticola* Bebb, one of the most common willow species in this area. Ungrazed and grazed treatments were established during the 1997 growing season (May to October), using eight long-term exclosures built in the fall of 1994. Plants in the grazed treatment were in areas open to grazing, but were protected from grazing by small exclosures during the experimental period. Winter grazing by elk induced the following measured responses in plant morphology and development: (1) higher shoot biomass production but similar leaf biomass and leaf area per plant, (2) a lower number of and bigger shoots, (3) a lower number of and bigger leaves, and (4) flower inhibition. In addition, we infer that grazing induces lower belowground allocation and a more negative nitrogen (N) balance but a higher soil N uptake. We conclude that elk grazing negatively affects willow even though willow compensate for aboveground biomass removal. Continuous grazing produces long-term changes in willow morphology that constrain plant growth and development. High plant utilization, as occurred in this experiment, could therefore reduce the competitive ability and survivorship of willow, in particular under drier environmental conditions.

Keywords: Cervus elaphus, grazing, plant-animal interactions, riparian ecosystem, Rocky Mountain National Park, *Salix monticola*.

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Introduction

Ungulate activities modify ecosystem structure and function (Naiman 1988). Large herbivores directly affect plants through tissue removal, but they can also induce long-term changes in nutrient cycling (Detling 1988; Huntly 1991; Pastor and Naiman 1992; Hobbs 1996), which can modify the competitive ability of a particular plant species or functional group (Bryant 1987; Pastor and Naiman 1992). At the plant level, removal of plant tissues by ungulates causes morphological and physiological changes in the plant over a broad range of temporal scales (Briske and Richards 1995). However, most of the information regarding plant responses to herbivory is based on studies conducted on grasses, and the literature on the response of woody plants to defoliation is limited. Several differences are expected between graminoid and woody plant responses, due to plant characteristics and different patterns of ungulate tissue removal. Woody plants have a juvenile and mature stage of development, with an age trend in aboveground annual woody biomass production. Tissue removal can induce changes in this development pattern (du Toit et al. 1990) determining long-term morphological changes (Bergström and Danell 1987). Strategies to prevent grazing differ from those of herbaceous plants (Rohner and Ward 1997), and involve physical responses such as the production of thorns (Gowda 1996; Cooper and Ginnett 1998), chemical defenses (Bergström 1992; Herms and Mattson 1992), and unique growth strategies (Bergström 1992). Many woody plants are grazed during the period of dormancy, with a lag phase between the occurrence of grazing and manifestation of a plant response (Danell et al. 1994). Finally, foraging selectivity of browsers of woody plants is higher than that of grazers of herbs (Hofman 1989; Bergström 1992), and plant responses depend on the type and time of tissue removal (du Toit et al. 1990; Bergström 1992). These characteristics can result in important differences between woody and graminoid plant responses to defoliation.

In this paper, we analyzed grazing-induced changes in various physiological and morphological characteristics of a riparian willow (*Salix monticola* Bebb). Willows are the dominant woody plants in the high-elevation riparian areas of the western United States (Patten 1998). Large ungulate herds regularly congregate in riparian areas and browse on willows. Thus, these willows have successfully evolved under grazing, and constitute a good model to evaluate woody plant responses to grazing. Additionally, grazing pressure on willows has increased in recent years in many montane riparian areas due to human interventions (Kay 1994; Patten 1998). These include livestock grazing, but also increases in the concentrations of wild ungulates in riparian areas. Many riparian areas are showing decreases or degradation of willow communities (Patten 1998). Prediction of the effect of ungulate pressure on riparian ecosystem processes is largely dependent on understanding the response of willow to tissue removal. Few studies have been conducted to analyze changes induced by grazing on these riparian willows. In particular, it is not clear how willow physiological processes altered by grazing are linked to plant productivity and survivorship (Singer et al. 1998; Alstad et al. 1999). Higher water potential and higher leaf carbon isotope discrimination was found in grazed *S. monticola* willows than in ungrazed controls, which can improve willow regeneration and survivorship (Alstad et al. 1999). We hypothesized that grazing on willow produces long-term effects in plant morphology determining changes in physiological processes and survivorship. Our study had the following primary objectives: (1) to determine aboveground biomass production and distribution in willows under grazing and non-grazing conditions; (2) to relate biomass production and morphological changes induced by grazing to plant performance; and (3) to infer how elk (*Cervus elaphus*) grazing affects plant survivorship.

Materials and Methods

The experiment was carried out during the 1997 growing season (May to October), on willows growing inside elk exclosures, and on paired plots adjacent to each exclosure and open to grazing. Four exclosures (30 x 46 m) were built in August and November 1994 in short willow (<1.5 m height) communities, at each of the following sites in Rocky Mountain National Park (RMNP), Colorado: the Moraine Park area in the Big Thompson River watershed (2,481 m altitude) and the Horseshoe Park area in the Fall River watershed (2,598 m altitude). Two treatments were established: the ungrazed treatment consisted of two plants inside each exclosure, and the grazed treatment comprised two plants of a paired plot open to grazing until May 1997. At this time, small exclosures were built around each selected plant to prevent removal of new tissues formed during the course of the experiment. To select plants, we identified in each plot (exclosure or paired grazed area) all *S. monticola* that represented the most frequent size type (canopy volume and height) within the plot. From this subset we randomly chose two plants per plot. *S. monticola* is one of the dominant willow species in these watersheds, and is a common willow in the lower-elevation riparian areas of the northern Colorado Rocky Mountains (Cottrell 1995). Mean winter consumption of willow by elk was estimated to be as much as 28% in both study valleys and for the entire willow cover (Singer et al., this volume). However, the utilization of short willow tends to be higher, though not significantly so, because elk tend to concentrate in the area of short-willow communities and in open meadows. During the winter, elk concentrate at densities as high as 66–110 elk km^{-2} in Moraine Park, and at lower densities in Horseshoe Park (15 to 30 elk km^{-2}; Singer et al., this volume). No other ungulates concentrate in such dense herds in these valleys, so willow grazing is almost entirely due to elk.

Soil moisture was monitored on a weekly basis in all plots with a time domain refractometer, Trace System model 6050 1. Due to soil depths, measurements were made between 0 and 28 cm in Moraine Park and 0 and 58 cm in Horseshoe Park. Measurements were taken under the canopy of the selected plants and in the adjacent area between willow canopies. Groundwater depths were monitored each month on wells installed inside the exclosures and in the grazed areas (Zeigenfuss et al., this volume). During the growing season, we determined the time periods of the phenological phases for a representative sample of stems of different sizes (six to eight target stems) in each of the selected plants. Plants were visited every 2 weeks from 10 May until the end of October. Bud break, flowering, seed dispersal, and leaf shedding were determined by visual observation of the target stems. The phenological phase was considered initiated when more than 50% of the marked stems were in this phase. The number of 1997 shoots in the target stem was counted approximately every 2 weeks, and one shoot at the top of the stem was selected for measurements of shoot length, leaf number, and the length of the longest leaf. On each sample date, several ungrazed 1997 shoots from adjacent *S. monticola* plants were collected to determine the morphological variables described above, and the total leaf area of each shoot. These data were used to create a multiple linear-regression model of leaf area per shoot using shoot morphological variables as predictors. For each shoot and date, morphological variables were transformed to leaf area and multiplied by the total number of 1997 shoots on the stem. Leaf area per stem was expressed as a ratio to the maximum leaf area value of all measurement dates within the stem.

Gas exchange measurements were performed on selected plants during the second week of June on leaves of the upper canopy of the 32 selected plants. A second set of gas exchange measurements was made on fully developed leaves in the upper portion of the canopy on the second week of July. Leaves were repeatedly measured throughout the day, on 2 days, on two plants growing in the same exclosure and two plants in the associated grazing plot. Between July 17–22, a third set of measurements was made on five plants per treatment on leaves located at different positions in the canopy. All gas measurements were made with a LI-COR LI-6200 portable photosynthesis system (LI-COR, Lincoln, Nebraska) equipped with a 0.25-l leaf chamber. We discarded gas exchange data from any run in which the standard error of the slope of the CO_2 concentration over time was greater than 10% of the value of the slope (LI-COR 1990). We also discarded data with an error higher than 20% between the estimation of transpiration using the relative-humidity method and the estimate using leaf energy balance (LI-COR 1992).

During the first week of September before leaf shedding started, we harvested eight plants per treatment (one per exclosure and paired plot) by cutting all stems at ground level. We measured the total dry weight of woody and leaf biomass of each stem of the harvested plants. In addition, leaf number and area were measured on all marked stems. A regression model of leaf area on leaf dry weight was constructed for each treatment with measurements performed on the target stems. These regression models were used to estimate total leaf area of the harvested plants. For each stem, shoots (segments of the stem produced each year) of different ages were separated. The age of each stem shoot was identified based on the position of the shoot according to the sympodial ramification pattern of willows, or the scar marks of the stems in the case of older shoots (Alliende and Harper 1989). Ring counts were also performed on some shoots to check the accuracy of the method. In all cases, the predicted age of the two methods gave the same result. Cohorts of shoots were formed by grouping all shoots of the same age within each harvested plant, and total dry weight determined for each shoot cohort.

Nitrogen dynamics were inferred from samples of leaves and 1996 and 1997 shoots taken from: (1) all of the selected plants at four times during the growing season, (2) the 16 plants harvested in the first week of September, (3) the 16 unharvested plants in October, and (4) leaves collected from the soil surface litter in litter traps in October 1997. Nitrogen was also determined in shoot cohorts from one of the largest target stems of each of the 16 harvested plants. Analyses were conducted with a LECO CHN analyzer and expressed as percent N. In addition, total N of different plant parts was calculated based on biomass and percent N measurements from the harvested plants. Total N in the aboveground woody biomass (PN) of each plant (m) was calculated as:

$$PN_m = \sum_n NS_{n,m} \times SB_{n,m} \qquad (1)$$

where NS and SB are the proportion of N and biomass, respectively, of each shoot cohort (n) within a plant. Total N in leaves and shoot cohorts of the harvested plants was calculated in a similar manner. Total N retranslocated back to the plant from the leaves during senescence (RN) and total N lost through litterfall (LiN) were estimated using the following equations:

$$RN_m = (NL1_m - NL2) \times LB_m \qquad (2)$$

$$LiN_m = NL2 \times LB_m \qquad (3)$$

where NL1 and NL2 represent the proportion of N in leaves prior to and after litterfall (September and October samples, respectively), and LB is the leaf biomass of each of the 16 harvested plants. Note that NL2 is not plant specific.

Statistical Analysis

A complete randomized-block design ANOVA for comparison of experiments was used to analyze most of the measured variables. The exclosure and paired grazed plot were considered as a block, and the ANOVA test was used to check for differences between sites (Moraine and Horseshoe Parks), treatments, or interactions. Treatments were also compared with a covariance (ANCOVA) analysis in the case of biomass variables to account for the effect of initial heterogeneity in plant size. ANCOVA was also used to analyze the relationship between different plant biomass compartments (leaves, 1996 and 1997 shoots). Gas exchange variables of the second set of measurements were analyzed using a nested mixed model, and in the case of the third set of measurements using a t-test of the difference between values taken in the upper and lower canopies. In the latter case, data of both treatments were pooled because of the small sample size. Finally, percent N of different shoot cohorts was compared considering the differences among all combinations of cohorts taken by pairs within the plant, because percent N values of different cohorts were not statistically independent.

Results

Hydrological Conditions for Willow Growth

Water tables followed a negative trend during the growing season but records were not deeper than 0.5 m during June and July, and not deeper than 1 m during the entire growing season. The volumetric soil moisture followed the same negative trend, except that it was more affected by a rain event that occurred at the end of July 1997. No differences were found in soil water content either between parks, or between versus under willow canopies. Soils were saturated at the beginning of the season and soil water decreased to 39% in the first 0–28 cm at the end July, when it rose to about 46% due to a rain event. Soil moisture steadily decreased in August but values were not lower than 37%. Thus, plants were not water limited during the entire growing season. The observed soil volumetric moisture values corresponded to high soil water potentials, as these are relatively coarse soils (Menezes 1999).

Phenology and Leaf Area Dynamics

The growth period lasted approximately 3 months, from June through August (Fig. 1). Leaves started to develop 2 weeks later in *S. monticola* than in *S. planifolia*, the co-dominant willow species in the study area. Additionally, ungrazed plants started growth a few days earlier than grazed plants. Catkins began to form from buds of previous-year shoots just prior to bud break, and seed dispersal occurred early in the growing season. No catkins were found on the grazed plants. This was not only the case for the selected plants but for all the short willow plants that we checked at different locations in both valleys. Most shoots were differentiated early in the growing season (Fig. 2a). Leaves were formed during the season at the same time as shoot growth, since all leaves developed on new shoots (Fig. 2b,c). In August, changes in the measured variables were minor, indicating that vegetative growth ended during this month. Grazed plants produced fewer shoots per stem than the ungrazed plants (Fig. 2a) but were significantly longer ($P < 0.01$; Fig. 2b). In addition, grazed plants produced fewer leaves than ungrazed plants (411 and 228 mean number of leaves/stem, $P = 0.035$), but leaves were bigger (3.7 and 5.1 cm^2 $leaf^{-1}$, $P = 0.015$).

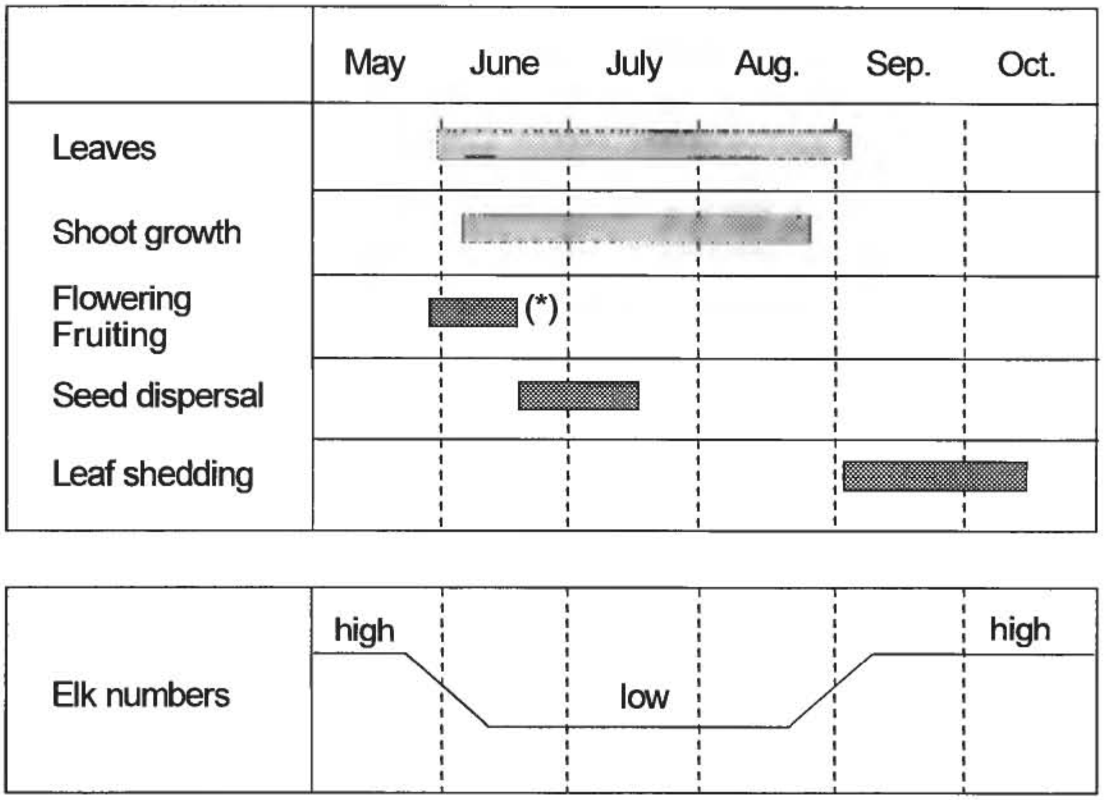

Fig. 1. Phenological phases of *Salix monticola* and relative number of elk on the study areas. (*) no flowers were found in grazed plants.

No differences between treatments were found in specific leaf area [77.1 and 74.2 cm^2 g^{-1} ($P = 0.83$) for ungrazed and grazed treatments, respectively]. Total plant leaf area steadily increased during the growing season in a similar manner in both treatments (Fig. 2d). Differences between treatments were significant only on the first date of measurement, probably because the ungrazed plants started growing earlier than grazed plants.

Plant Biomass

Similar ranges of total woody biomass were found in plants of the ungrazed (470–2,720 g) and grazed (380–3,110 g) treatments. Nevertheless, at the beginning of the experiment, plants in the ungrazed treatments were taller (1.71 m vs. 0.92 m; $P = 0.001$) and larger (3.19 m^3 vs. 1.36 m^3; $P = 0.03$). Ungrazed plants were also taller at the end of the experiment (1.97 vs. 1.20 m; $P = 0.0003$). Aside from initial differences in plant morphology, total dry weights of woody biomass, leaves, and 1997 shoots were not different at the end of the experiment (Fig. 3). Total plant leaf area was not different between treatments ($P = 0.4$). The range of variation was 1.7–9.4 m^2 for the ungrazed, and 1.3–6.9 m^2 for the grazed treatment. The ungrazed treatment had significantly more biomass than the grazed treatment in 1994 and 1995 shoot cohorts, but biomasses of the 1996 shoot cohort were similar. The biomass of shoots older than 1994 appeared to be greater in the grazed plants but the difference was not significant. Mean plant biomass at the end of the experiment was greater in Horseshoe Park than in Moraine Park (1,830 g and 830 g, respectively; $P = 0.05$); however, the interaction between parks and grazed treatments was not significant for any of the variables measured.

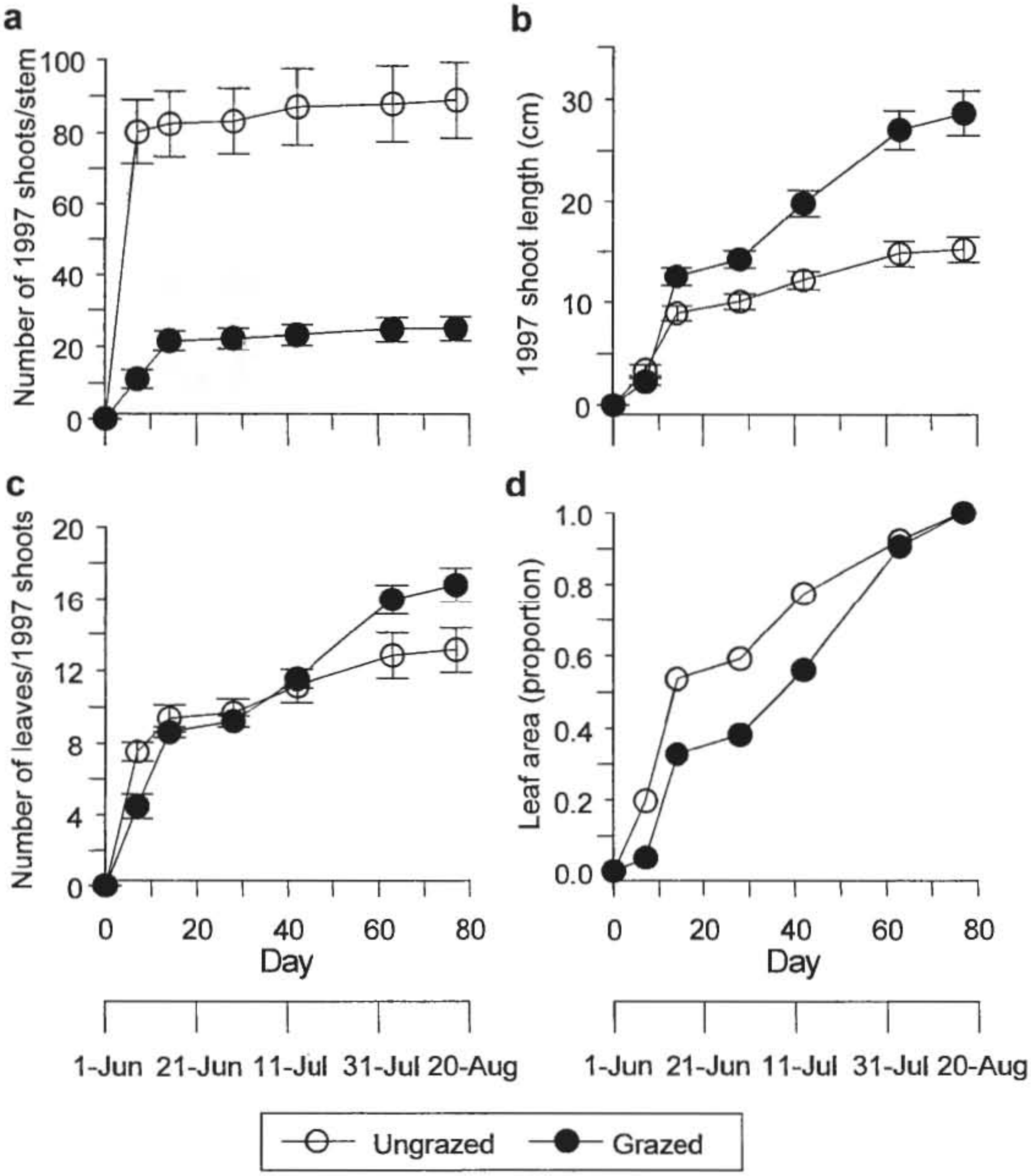

Fig. 2. Number of 1997 shoots per stem (a), 1997 shoot length (b), number of leaves per 1997 shoots (c), and proportion of total leaf area (d) through the growing season. Values indicate means of the ungrazed and grazed treatments, and vertical bars indicate standard errors.

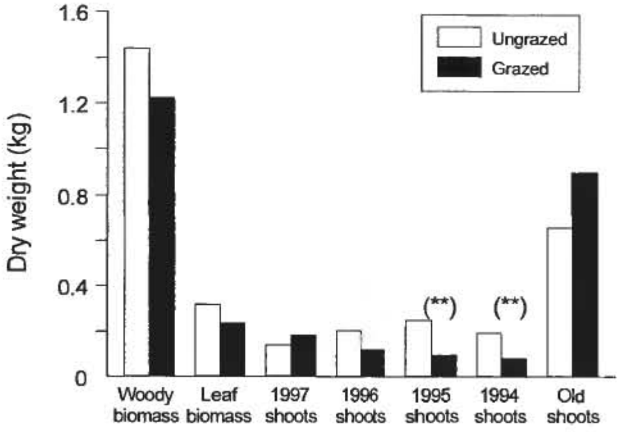

Fig. 3. Dry weight of total woody biomass and different plant components for the ungrazed and grazed treatments. References: (**) means are statistically different (P<0.01).

No differences between treatments were found in the rate of change of leaves, or 1996 and 1997 shoot biomass when total plant biomass was used as a covariate. But, as expected, all slopes were significant (P = 0.001). Treatment means corrected for plant size were different only in the case of 1997 shoot biomass (P = 0.05). When the 1997 shoot biomass was analyzed using leaf biomass or leaf area as a covariate, grazed plants showed a higher slope (P <0.001) and corrected mean (P <0.01). These results indicated that grazed plants produced more shoot biomass per unit of leaf biomass or leaf area. In addition, grazed plants produced more 1997 biomass when corrected by the 1996 shoot biomass (P = 0.009). This latter result is probably related to the observed difference in the branching pattern of plants of different treatments. Almost all shoots formed by the ungrazed plants were developed from previous-year shoots (1996), but in the grazed treatment, many 1997 shoots were developed from shoots older than 1 year (epicormic shoots). The number of epicormic shoots was as high as 30% in grazed willows, while few shoots (less than 3%) of the willows inside the exclosures were epicormic (Peinetti 2000).

Gas Exchange

Gas exchange variables obtained at the beginning of the season did not differ between treatments. The rate of photosynthesis was not correlated with light intensity (P = 0.2), but transpiration was positively correlated (P = 0.03) in the restricted range of light intensities over which measurements were performed (1,000–2,000 μmol m^{-2} s^{-1}). Water use efficiency (WUE) showed a linear decrease with higher light intensity in this range of radiation (r = 0.81; P = 0.004). In the second series of measurements, a wider range of microclimatic conditions was covered, but no treatment effects were found for any of the gas exchange variables. In this case, photosynthesis rates increased with increasing light intensity up to approximately 1,500 μmol m^{-2} s^{-1} (r = 0.59; P = 0.0001). Beyond this level, photosynthesis rates no longer correlated with light intensity (P = 0.31) (Fig. 4a). Photosynthesis rates tended to increase with increasing temperature, but the two variables are not well correlated (r = 0.25; P = 0.03) (Fig. 5a). Conversely, transpiration followed a linear increase with light intensity as in the first set of measurements, and an exponential increase with temperature (Figs. 4b and 5b). WUE tended to decrease with radiation but the

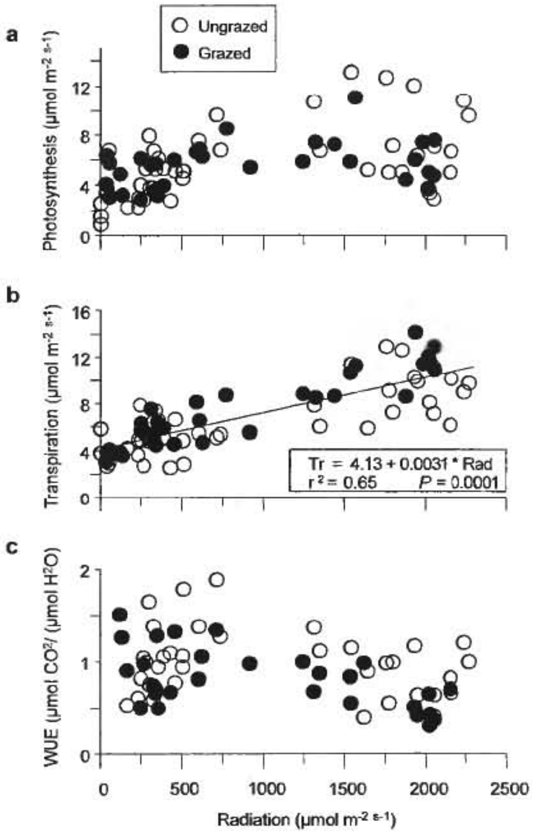

Fig. 4. Photosynthesis (a), transpiration (b), and water use efficiency (WUE) (c) as a function of light intensity in ungrazed and grazed treatments. WUE values at a light intensity lower than 100 μmol m^{-2} s^{-1} are not shown. The regression model was constructed with values of both treatments.

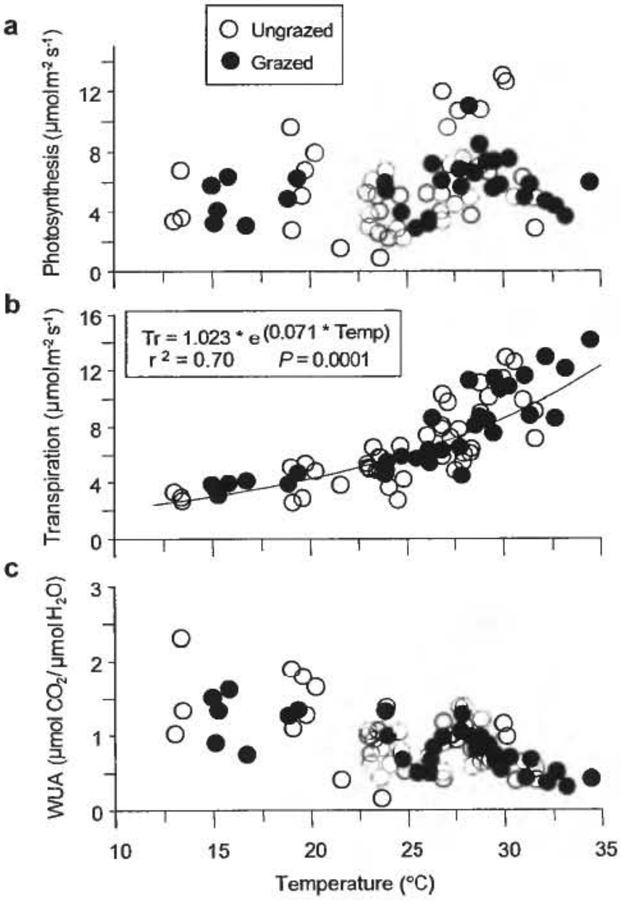

Fig. 5. Photosynthesis (a), transpiration (b), and water use efficiency (WUE) (c) as a function of temperature in the ungrazed and grazed treatments. The regression model was constructed with values of both treatments.

correlation between these two variables was low (r = -0.29; P = 0.01; Fig. 4c). WUE displayed a weak negative linear relationship with temperature (r = -0.33; P = 0.0001; Fig. 5c). At light intensities lower than 100 µmol m^{-2} s^{-1}, high values of WUE were found due to very low levels of transpiration (data are not shown in Fig. 4c).

Light intensity was the variable showing the highest variability within the canopy of plants of both treatments (P = 0.001). Plant canopies reduced the light intensity that had reached the upper canopy by 10%, although light reductions to less than 50% of the upper canopy were not uncommon. Temperatures tended to be lower in the lower part of the canopy (P = 0.001), with differences as high as 2°C. CO$_2$ concentrations tended to be higher in the lower canopy (P = 0.003). Changes in environmental correlation conditions affected gas exchange variables, with photosynthesis and transpiration consistently higher in the upper canopy (P <0.01), but with similar WUE (P = 0.09).

Plant Nitrogen

The percent N in 1996 shoots seemed to be higher at the beginning of the season, and decreased thereafter until the end of the growing season when values increased again, probably due to translocation of N from leaves (Fig. 6). Leaves had highest N concentrations at the beginning of the season when they were not fully developed, with concentrations decreasing thereafter. A significant amount of N was retranslocated at the time of leaf senescence, producing a decrease in the N concentration of the leaves prior to litterfall. Grazed plants showed a higher leaf N concentration than ungrazed plants on some sample dates (Fig. 6). The percent N in 1997 shoots did not differ between treatments. At the beginning of the season, 1997 shoot N was higher than 1996 shoot N, but percent N decreased thereafter with increasing shoot length until the end of August. At this time, N concentration increased. It is interesting to note that this increase in N concentration did not correspond with the translocation of N from the leaves that occurred in the following month, but was coincident with the decrease in shoot extension growth (Fig. 2b).

Percent N in shoot cohorts did not differ between treatments. One-year shoots exhibited the highest percent N in woody biomass (1.16%; P <0.001). In general, cohorts younger than 3 years showed higher percent N than older cohorts (P <0.01; mean percent N in cohorts 4–12 years old was 0.42 ± 0.04). Leaves were the most important N sinks in the plant, but an important proportion of the total aboveground N was also allocated to the new shoots (Fig. 7a). The estimated total aboveground plant N content, and the N content of different plant compartments did not differ between treatments. However, on a relative basis, total plant N allocated into new shoots was significantly higher in grazed than ungrazed plants (0.11 vs. 0.19 1997 shoot N/total woody N; P = 0.003). Elk grazing reduced 1996 shoot N proportion to lower values than in ungrazed plants (0.08 vs. 0.047 1996 shoot N/total woody N; P = 0.001). The amount of N allocated to leaves relative to total plant N was similar between treatments (P = 0.40). However, on a relative basis, ungrazed plants retained more of the N invested in leaves than did grazed plants (Fig. 7b). The estimated N translocated from

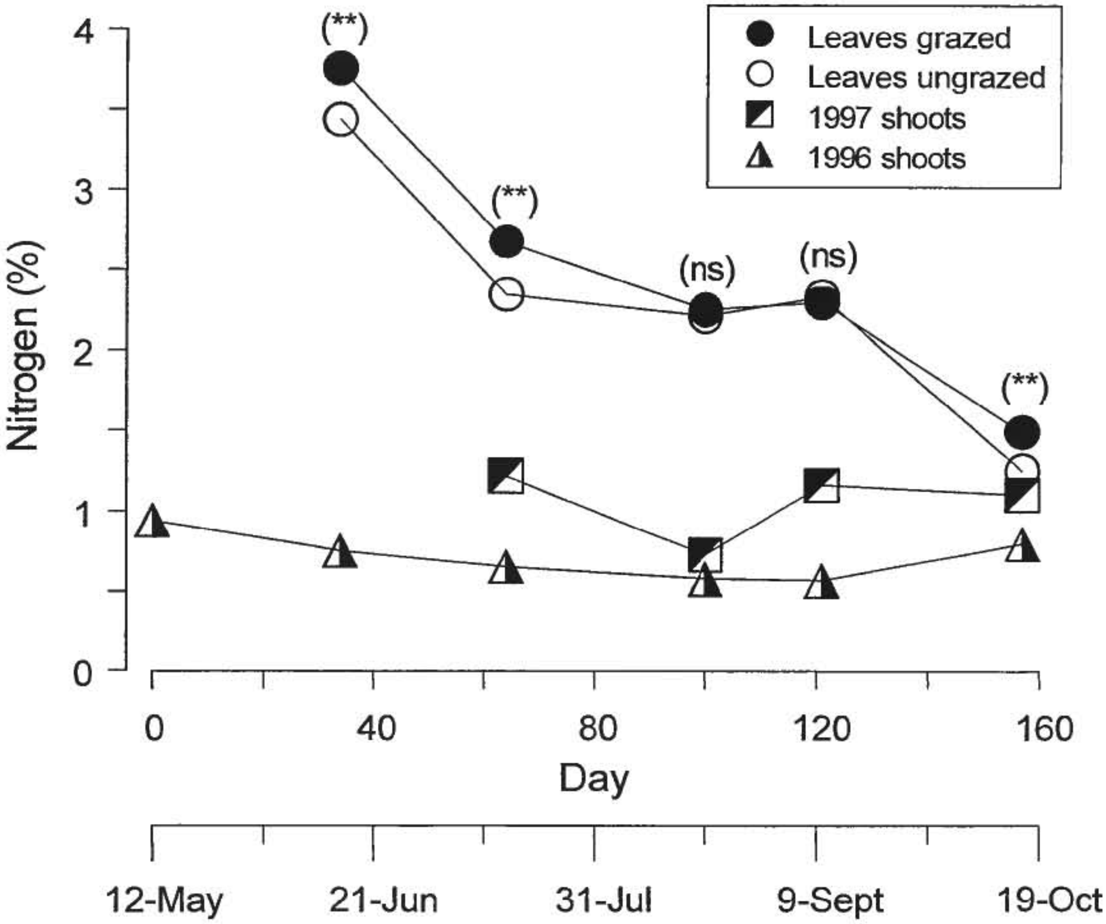

Fig. 6. Percentage of nitrogen in leaves, 1996 and 1997 shoots. Treatment means are represented only in the case of leaves. References: (**) means are significantly different ($P < 0.05$); (ns) means are not statistically different.

leaves was 3.9 g plant^{-1} in the ungrazed and 1.8 g plant^{-1} in the grazed treatment. These values were equivalent to the N allocated into the new shoot (1.6 and 2.1 g plant^{-1} for the ungrazed and grazed plants, respectively).

Discussion

Willows are grazed primarily during the winter and late summer, when most of the elk herd is on the winter range. Thus, the protection of grazed plants during the summer should not have produced any important changes in the natural pattern of willow utilization. Leaf stripping is the common form of elk grazing at the end of the summer, while during winter, elk select shoots that developed in the previous growing season. Grazing on willow, as well as aspen (*Populus tremuloides*), has increased greatly on the winter range of RMNP in the last 30 years or so, due to an increase in the elk population (Hess 1993; Baker et al. 1997; Singer et al. 1998). Despite high winter grazing intensity, shoot and leaf productivities of short willow were not reduced. This type of response is considered compensatory growth (McNaughton 1979, 1983). Compensatory and overcompensatory aboveground growth were documented in graminoids under moderate herbivory (Briske and Richards 1995), and in woody species (Wolff 1978; Danell et al. 1985; Bergström and Danell 1987; Edenius et al. 1993; Hjältén 1999). However, total plant aboveground productivity provides a limited view of the

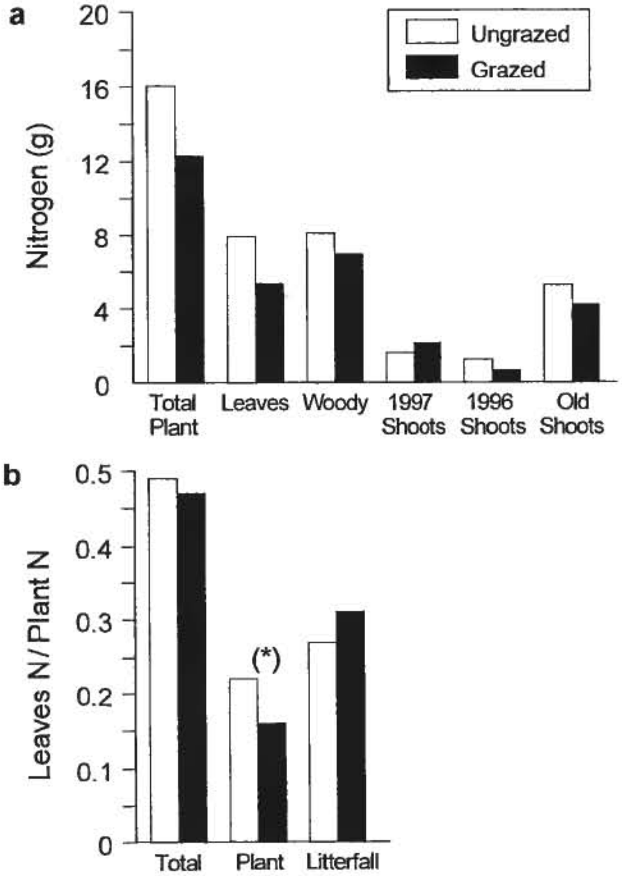

Fig. 7. Total nitrogen in the plant and in different plant components (a) and the ratio to total nitrogen of nitrogen recuperated by the plant and lost through litterfall (b). Bars represent mean values of ungrazed and grazed treatments (* means are statistically different at $P < 0.05$).

changes induced by grazing on woody plant performance. Other aspects need to be considered, in particular plant morphology (Jacobs 1969; Danell et al. 1985; Bergström and Danell 1987). Changes in plant morphology could, in turn, have different secondary effects. Elk grazing reduces the number of axillary meristems and constrains the number of buds available for new tissue development in the following growing season. Grazed willows seem to overcome this constraint by producing longer and thicker shoots, and increased branching by developing shoots from axillary meristems of shoots older than 1 year. Since leaves are produced only on new shoots, which were significantly reduced by grazing, the production of larger leaves was also a compensatory response. All of these morphological changes have been documented as induced responses to winter grazing in other woody plants (du Toit et al. 1990), and in particular under winter grazing (Danell et al. 1994). Despite compensatory growth, continuous grazing will ultimately reduce plant height and size compared with ungrazed controls (Wolff 1978; Bergström and Danell 1987). After many years, plants protected from grazing differ from continuously grazed plants to the extent that they can no longer be used as controls for measuring grazing effects (Wambolt et al. 1998; see also Fig. 3). Similarly, in our experiment, after 3 years of protection, willows inside the exclosure were taller and had larger canopies than grazed willows. Plant height suppression occurred because elk preferentially grazed on shoots developed in the upper canopy. Height increase is considered an important strategy of woody plants to avoid grazing (Romme et al. 1995; Rohner and Ward 1997). Thus, by stimulating thicker and longer shoots and a lower shoot position, grazers generate a positive feedback between present and future grazing (Danell et al. 1985; du Toit et al. 1990; Romme et al. 1995). Increased palatability or reduction in concentration of secondary metabolites in grazed plants could also favor the development of this positive feedback (Danell et al. 1985; du Toit et al. 1990).

Other woody plant-grazer interactions involve a negative feedback mediated by plant secondary metabolites (Bryant et al. 1985). Elk grazing also induced the development of shoots from the lower part of the plant (old buds). These shoots do not contribute significantly to overall plant height increase but will make the canopy more compact. A more compact canopy will probably increase leaf overlap and reduce plant carbon input by self-shading. A strong gradient in microclimatic and gas exchange variables was found within the willow canopy. However, our data did not allow us to determine how different canopy architectures affect carbon input. Elk grazing also inhibited willow catkin production. Grazing reduced the number of axillary buds that are potentially available to develop into flowers during the next growing season. Flowering is probably inhibited because plants tend to prioritize vegetative growth as constrained by the number of axillary buds (Bergström and Danell 1987). Alternatively, continuously intense grazing induces a more juvenile pattern of development (Willard and McKell 1978; Bryant et al. 1985). A reduction in flower production is commonly documented in woody plants under grazing (Willard and McKell 1978; Katsma and

Rusch 1980; Bergström and Danell 1987). Intense grazing would have a significant negative effect on willow population ecology and fitness, if seed abundance were limiting (Paige and Whitham 1987).

Most studies of the effect of herbivory on plants that have demonstrated compensatory growth have been limited to measurements on aboveground biomass (Painter and Belsky 1993). However, increased aboveground productivity could result from a reduction in belowground carbon allocation instead of higher plant productivity. Our results seem to indicate that the compensatory response observed on grazed willows was the result of a reduction in the amount of carbon allocated belowground. We assume that the carbon gain by willows during the entire growing season is distributed between different plant compartments as follows:

$$NCI = LC + SC + WC + RC \qquad (4)$$

where NCI = net carbon input, LC = leaf carbon, SC = new-shoot carbon, WC = carbon allocated in woody tissues older than 1 year, and RC = carbon allocated to roots. We found that grazed willows allocated more carbon in 1997 shoots than did plants of the ungrazed treatment:

$$SC_u < SC_b \qquad (5)$$

where the subscripts u and b represent ungrazed and grazed plants, respectively. From equation 4, and considering that leaf biomass did not differ between treatments ($LC_u = LC_b$), then:

$$NCI_u - WC_u - RC_u < NCI_b - WC_b - RC_b \qquad (6)$$

Assuming that the biomass derived from the growth of the cambium is a small proportion of total plant productivity and/or there was no difference between ungrazed and grazed plants in this biomass component, then:

$$NCI_u - RC_u < NCI_b - RC_b \qquad (7)$$

Equation 7 indicates that grazed plants need to have a higher NCI in order to maintain a root carbon allocation similar to that of the ungrazed plants. The data showed no evidence of a higher NCI in grazed plants, as indicated by similar photosynthesis rates, total leaf areas, and leaf area dynamics in plants of both treatments. Together, these results indicate that there is a lower allocation belowground in grazed compared to ungrazed plants. Woody plants probably tend to allocate more carbon aboveground in order to restore an allometric shoot/root ratio after grazing (Kramer and Kozlowski 1979). An increase in aboveground allocation is important for the plant to reestablish canopy photosynthesis capability (Briske and Richards 1995). Reduction of belowground biomass has been observed in grasses under herbivory (Coughenour 1985; Holland and Detling 1990), but no data are available for woody plants. If our inferences are correct, then persistent grazing will limit root growth, which will likely result in a shallower root system in grazed than in ungrazed plants. Since willows primarily use groundwater (Alstad et al. 1999), a shallow root system will reduce the ability of grazed willows to obtain water from a deeper water table. Consequently, reduction in the area influenced by the river and its associated water table, and changes in the river course that have occurred in this watershed have most likely increased willow mortality (Peinetti et al., this volume). Thus, this grazing intensity would probably reduce willow survival in those areas of the watershed where the water table has been deepened by shifts in stream channels.

Aboveground N concentrations in grazed plants are often higher than in ungrazed plants (Detling 1988; Briske and Richards 1995). Grazing also favors an increase in N concentration in woody plants (Danell et al. 1985; du Toit et al. 1990), but the response is variable, depending on the time that plants are grazed (Danell et al. 1994). Grazed willows showed higher percent N, but only in leaves. This pattern was not consistent throughout the entire growing season (see also Alstad et al. 1999). However, N concentrations in leaves and young shoots of willows varied due to growth and translocation, making the results difficult to interpret without considering the overall plant N balance. Grazed plants showed a more negative nitrogen balance than ungrazed plants because they recovered less N from leaves, and every winter they lost some nitrogen in the younger shoots to elk grazing. Nevertheless, percent N in the most active aboveground biomass (leaves and younger shoots) tended to be higher or similar to that of ungrazed plants. If the N pool is lower in the grazed willows at the start of the growing season, grazed plants will need to take up a higher proportion of N from the soil. In some deciduous species, a significant portion of the N that supports growth and reproduction comes largely from retranslocation out of senescing leaves (Chapin et al. 1990). A lower amount of stored N in grazed plants could be one reason for later growth initiation. Even though grazed plants compensate for lower N storage, late growth initiation could occur because the time lags between microbial N mineralization in the soil, soil N uptake, and mobilization to the growing tips are probably longer than the time needed for N translocation from storage reserves. Grazed plants could mobilize more N from the soil if grazing increased soil N availability. Elk could increase N availability by various mechanisms, such as fecal and urine deposition (Frank et al. 1994; Hobbs 1996), by inducing lower carbon allocation to roots, which reduces microbial growth and N immobilization (Holland and Detling 1990), or by redistributing nutrients within the landscape (Afzal and Adams 1992; Russele 1992). Accordingly, elk herbivory in these willow communities has likely increased N return and litter quality, thus increasing long-term N cycling and availability (Menezes 1999).

Willow compensated for aboveground tissue removal by elk by increasing aboveground productivity. Despite this compensatory response, we infer that continuous grazing reduces plant performance by reducing root growth, particularly under the drier conditions generated by an increase in groundwater depth. Additionally, elk grazing induced important changes in plant morphology that constrained plant growth and development and modified carbon and N dynamics.

Acknowledgments

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Literature Cited

Afzal, M., and W. A. Adams. 1992. Heterogeneity of soil mineral nitrogen in pasture grazed by cattle. Soil Science 56:1160–1166.

Alliende, M. C., and J. L. Harper. 1989. Demographic studies of a dioecious tree. I. Colonization, sex and age structure of a population of *Salix cinerea*. Journal of Ecology 77:1029–1047.

Alstad, K. P., J. M. Welker, S. A. Williams, and M. J. Trlica. 1999. Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: An isotopic study using 13 C and 18 O. Oecologia 120:375–385.

Baker, W. L., J. A. Munroe, and A. E. Hessl. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 20:155–165.

Bergström, R. 1992. Browse characteristics and impact of browsing on trees and shrubs in African savannas. Journal of Vegetation Science 3:315–324.

Bergström, R., and K. Danell. 1987. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. Journal of Ecology 57:533–544.

Briske, D. D., and J. H. Richards. 1995. Plant responses to defoliation: A physiological, morphological, and demographic evaluation. Pages 635–710 *in* D. J. Bedunah and R. E. Sosebee, editors. Wildland plants: Physiological ecology and developmental morphology. Society for Range Management, Denver, Colo.

Bryant, J. P. 1987. Feltleaf willow-snowshoe hare interactions: Plant carbon/nutrient balance and floodplain succession. Ecology 68:1319–1327.

Bryant, J. P., G. D. Wieland, T. Clausten, and P. Kuropat. 1985. Interactions of snowshoe hare and feltleaf willow in Alaska. Ecology 66:1564–1573.

Chapin, F. S., E. Schulze, and H. A. Mooney. 1990. The ecology and economics of storage in plants. Annual Review of Ecology and Systematics 21:423–447.

Cooper, S. M., and T. F. Ginnett. 1998. Spines protect plants against browsing by small climbing mammals. Oecologia 113:219–221.

Cottrell, T. R. 1995. Willow colonization of Rocky Mountain mires. Canadian Journal of Forest Research 25:215–222.

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.

Danell, K., R. Bergström, and E. Lars. 1994. Effects of large mammalian browsers on architecture, biomass and nutrients of woody plants. Journal of Mammalogy 75:833–844.

Danell, K., K. Huss-Danell, and R. Bergström. 1985. Interactions between browsing moose and two species of birch in Sweden. Ecology 66:1867–1878.

Detling, J. K. 1988. Grasslands and savannas: Regulation of energy flow and nutrient cycling by herbivores. Ecological Studies 67:131–148.

du Toit, J. T., J. P. Bryant, and K. Frisby 1990. Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. Ecology 71:149–154.

Edenius, L., K. Danell, and R. Bergström. 1993. Impact of herbivory and competition on compensatory growth in woody plants: Winter browsing by moose on Scots pine. Oikos 66:286–292.

Frank, D. A., R. S. Inouye, N. Huntly, G. W. Minshall, and J. E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: Nitrogen dynamics in Yellowstone National Park. Biogeochemistry 26:163–188.

Gowda, J. H. 1996. Spines of the *Acacia tortilis*: What do they defend and how? Oikos 77:279–284.

Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: To grow or defend. Quarterly Review of Biology 67:283–335.

Hess, K. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot.

Hjältén, J. 1999. Willow response to pruning: Effect on plant growth, survival and susceptibility to leafgallers. Ecoscience 6:62–67.

Hobbs, N. T. 1996. Modification of ecosystem by ungulates. Journal of Wildlife Management 60:695–713.

Hofman, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. Oecologia 78:443–457.

Holland, E. A., and J. K. Detling. 1990. Plant response to herbivory and belowground nitrogen cycling. Ecology 7:1040–1049.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annual Review of Ecology and Systematics 22:477–503.

Jacobs, R. D. 1969. Growth and development of deer-browsed sugar maple seedlings. Journal of Forestry 12:870–84.

Katsma, D. E., and D. H. Rusch. 1980. Effects of simulated deer browsing on branches of apple trees. Journal of Wildlife Management 44:603–612.

Kay, C. E. 1994. The impact of native ungulates and beaver on riparian communities in the Intermountain West. Natural Resource and Environmental Issues 1:23–44.

Kramer, P. J., and T. T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York.

LI-COR. 1990. The LI-6200 primer: An introduction to operating the LI-6200 portable photosynthesis system. LI-COR, Lincoln, Neb.

LI-COR. 1992. LI-6200 technical reference. LI-COR, Lincoln, Neb.

McNaughton, S. J. 1979. Grazing as an optimization process: Grass-ungulate relationship in the Serengeti. American Naturalist 113:691–703.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329–336.

Menezes, R. S. C. 1999. Soil-plant herbivore interactions and nutrient dynamics in semi-arid grazing systems in northeastern Brazil and western USA. Ph.D. thesis, Colorado State University, Fort Collins.

Naiman, R. J. 1988. Animal influences on ecosystem dynamics. BioScience 38:750–752.

Paige, K. N., and T. G. Whitham. 1987. Overcompensation in response to mammalian herbivory: The advantage of being eaten. American Naturalist 129:407–416.

Painter, E. L., and A. J. Belsky. 1993. Application of herbivore optimization theory to rangelands of the western United States. Ecological Applications 3:2–9.

Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist 139:690–705.

Patten, D. T. 1998. Riparian ecosystem of semi-arid North America: Diversity and human impacts. Wetlands 18:498–512.

Peinetti, H. R. 2000. Riparian willow dynamics and their interaction with environmental and biological factors in the elk winter range of Rocky Mountain National Park (Colorado) -- a multiscale analysis. Ph.D. dissertation, Colorado State University, Fort Collins.

Rohner, C., and D. Ward. 1997. Chemical and mechanical defense against herbivory in two sympatric species of desert *Acacia*. Journal of Vegetation Science 8:717–726.

Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk, and fire in northern Yellowstone National Park. Ecology 76:2097–2106.

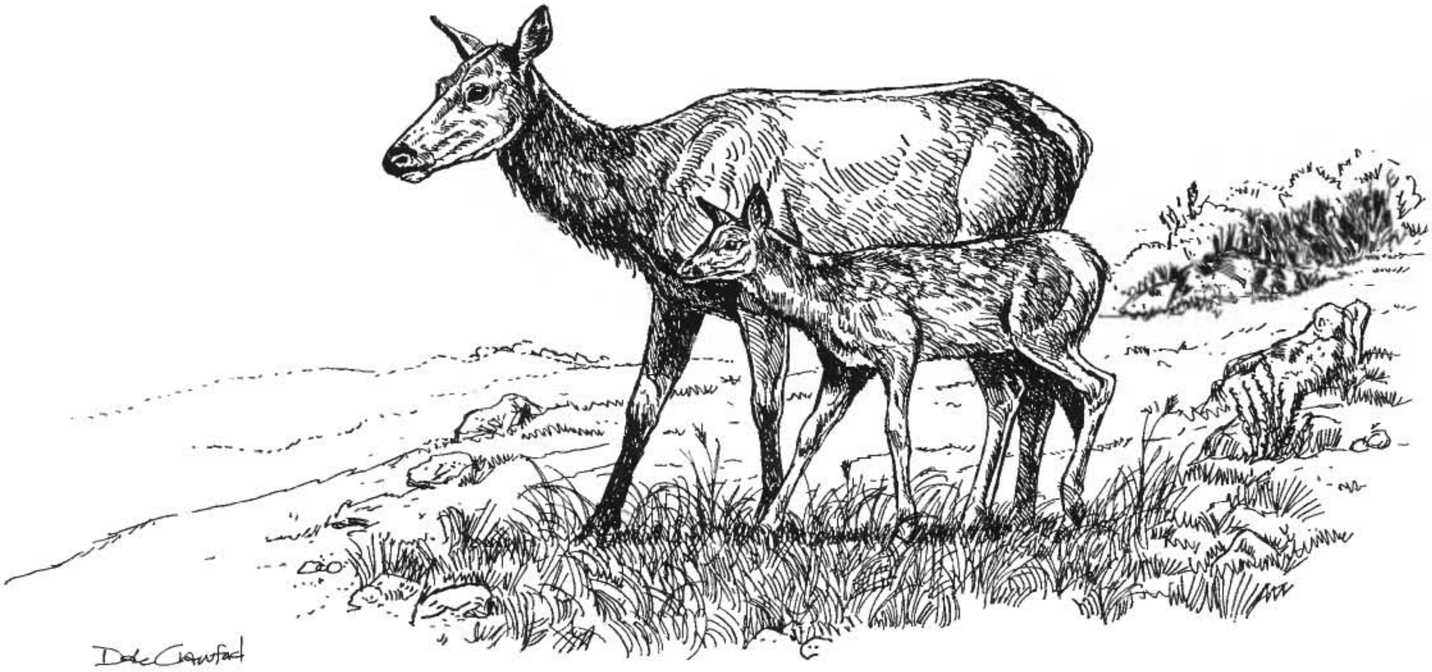
Russele, M. P. 1992. Nitrogen cycle in pasture and range. Journal of Production Agriculture 5:13–23.

Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. Barnett. 1998. Elk, multiple factors and persistence of willows in national parks. Wildlife Society Bulletin 26:419–428.

Wambolt, C. L., W. W. Fraas, and M. R. Frisina. 1998. Bitterbrush (*Purshia tridentata* Pursh) growth in relation to browsing. Great Basin Naturalist 58:28–37.

Willard, E. E., and C. M. McKell. 1978. Response of shrubs to simulated browsing. Journal of Wildlife Management 42:514–519.

Wolff, J. O. 1978. Burning and browsing effects on willow growth in Interior Alaska. Journal of Wildlife Management 42:135–140.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Effects of Herbivory and Proximity to Surface Water on C and N Dynamics on the Elk Winter Range in Rocky Mountain National Park

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Abstract. It has been suggested that recent increases in elk herbivory and changes in hydrology towards drier conditions have contributed to declines in willow (*Salix* spp.) communities in the winter ranges for elk in Rocky Mountain National Park (RMNP). During the fall of 1994, we constructed 12 large elk exclosures in two watersheds of the elk winter range in RMNP, and conducted field experiments during the growing seasons of 1995 to 1999 to investigate the effects of herbivory and proximity to surface water on the dynamics of carbon (C) and nitrogen (N). We found that elk herbivory led to increases ($P < 0.05$) in N concentration of willow litter and decreases in litterfall biomass, but herbivory did not affect losses of C and N from litter in any of the growing seasons. Soil moisture levels were higher in lower landscape positions, which probably led to higher ($P = 0.001$) C losses from litter, in comparison to upper landscape positions. In plots where N fertilizer was added, we observed an increase ($P < 0.05$) in willow shoot length, shoot biomass, and the average amount of N in the shoots, indicating that availability of N is limiting plant growth in our study sites. Elk herbivory had no effect on soil inorganic N availability and *in situ* net N mineralization rates, maybe because of the short time since treatment establishment (4 years). However, we estimated that the return of N to the soil in grazed plots could be as much as 265% of the N return in exclosed plots, due perhaps to N transfers from the summer range to the winter range. Our results demonstrate that elk herbivory and proximity to surface water have significant influences on the biogeochemical cycles of the winter ranges for elk in RMNP. Greater return of N to the soil, combined with increased litter quality in the grazed plots, indicate that elk could contribute to increases in N cycling rates and availability in the long-term, which could lead to changes in ecosystem structure and function in the winter range for elk in RMNP.

Keywords: Browsing, *Carex*, grazing, litter, nitrogen availability, *Salix*, willow.

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Introduction

Since 1968, elk (*Cervus elaphus*) numbers in Rocky Mountain National Park (RMNP), Colorado, have been managed under a policy of natural regulation, which rests on the assumption that density-dependent mechanisms would result in equilibrium between large ungulate herbivores and plant resources. During this period, elk numbers increased from approximately 700 to about 3,000 animals, and park managers are concerned about the effects these increases will have on the soils and vegetation of the elk winter range within the park (Singer et al. 1998a).

Willow (*Salix* spp.) communities have reportedly been declining on elk winter ranges of RMNP during the last few decades (Hess 1993; Singer et al. 1998b), and similar declines have also been reported for Yellowstone National Park (YNP) (Chadde and Kay 1991; Kay and Wagner 1994; Singer et al. 1998b). In addition to increased elk herbivory, two other factors have been proposed to explain these declines in willow communities: (1) climates are warmer and drier this century, possibly resulting in lowered stream flows and less water availability to plants (Singer et al. 1998b); and (2) beaver populations have declined on the eastern slope of RMNP (Stevens and Christianson 1980), which may further contribute to the drying of these ecosystems.

Large herbivores can significantly influence plant community structure and biogeochemical cycles within the soil-plant system (Frank et al. 1994; Frank and Groffman 1998; Hamilton et al. 1998; Schuman et al. 1999; Wijnen et al. 1999). Herbivores can influence nutrient cycling by removing plant biomass and returning more readily available nutrients to the soil (McNaughton et al. 1988; Frank et al. 1994; Hamilton et al. 1998), increasing soil nitrogen (N) mineralization rates and plant N uptake (Frank and Groffman 1998; Wijnen et al. 1999), and spatially redistributing nutrients within the landscape (McNaughton 1985; Afzal and Adams 1992; Russelle 1992). In some N-limited systems, herbivory may lead to slower rates of nutrient cycling due to increases in the dominance of non-browsed plant species, which may produce litter with low nutrient concentrations or with high concentrations of secondary compounds (Pastor et al. 1993; Ritchie et al. 1998). In addition, herbivory can influence plant growth and physiology (Toft et al. 1987; Welker and Briske 1992; Singer et al. 1998a,b; Fahnestock and Detling 1999) and alter carbon (C) and N allocation within plants (Welker et al. 1985, 1987; Holland and Detling 1990; Singer et al. 1998a; Alstad et al. 1999). Changes in the root:shoot ratio following browsing may lead to improvements in the water balance of plants (Welker and Menke 1990), while the removal of meristems (Briske 1986) or overgrazing (Pengelly 1963; Singer et al. 1998a) may reduce their future growth potential. Whether herbivory has a positive or negative influence on plants may depend in part on the specific characteristics of each system (Georgiadis et al. 1989; Hamilton et al. 1998; Mazancourt et al. 1998; Alstad et al. 1999).

Beaver (*Castor canadensis*) can also influence plant communities and biogeochemical cycles of ecosystems. By building dams, beavers contribute to the entrapment of sediment and organic matter and modify nutrient cycling and decomposition dynamics (Naiman et al. 1986). Active beaver ponds may increase N and phosphorus (P) inputs to the flooded systems (Naiman and Melillo 1984) and increase water availability to plants, which enhance the conditions for willow growth and reestablishment of shoots, sprouts, and seedlings (Naiman et al. 1986; Singer et al. 1998b). It has been suggested that the observed declines in beaver populations on the eastern slope of RMNP have contributed to a decrease in the surface area of water (ponds and streams) within the winter range of elk since the beginning of this century (Singer et al. 1998b). These reductions in surface water may alter the biogeochemical cycles of those ecosystems, and could further reduce the ability of willow to respond to elk herbivory.

Plant-available N is usually a limiting element for plant growth in terrestrial ecosystems (Power 1977; Kiehl et al. 1997; Wijnen et al. 1999). The cycling of N in these systems is linked to the C cycle by internal organic matter transfers and positive and negative feedback loops between decomposers, plants, and herbivores (Aber and Melillo 1991; Pastor and Naiman 1992). Therefore, the dynamics of C and N are of critical importance to primary productivity and overall ecosystem function (Power 1994; Schuman et al. 1999). There is no available information about the effects of elk herbivory or the reduction in surface water on the dynamics of C and N in the winter ranges of elk in RMNP. This information is necessary to help park managers formulate policies that will maintain elk and beaver populations at levels that are adequate for preserving the natural functioning of these ecosystems. Therefore, the objective of this study was to perform experimental field manipulations to investigate the effects of elk herbivory and proximity to surface water on the C and N cycles of the winter ranges of elk in RMNP.

Methods

Study Sites

The low elevation winter range for elk in RMNP encompasses about 17,000 ha, which includes land within the eastern side of the park and private and national forest lands outside the park in the town of Estes Park and Estes Valley, Colorado (Singer et al. 1998b). Our study sites were located in two riparian ecosystems on the northeastern side of RMNP: Moraine Park (Big Thompson River watershed, elevation 2,481 m) and Horseshoe Park (Fall River watershed, elevation 2,598 m). The two watersheds are within 5 km of each other and have perennial alpine snowfields at their headwaters. Mean annual precipitation for the sites is 41 cm (Singer et al. 1998b) and peak stream flow usually occurs in early to mid-June (USDA 1995, 1996, 1997). The 30-year average temperature for the adjacent Estes Valley ranges from 9°C to 17°C during the 5-month growing season of May through September (Alstad et al. 1999). The study area consists of wet meadows dominated by willow (*S. monticola*, *S. geyeriana*, and *S. planifolia*), other shrubs such as birch (*Betula* spp.), sedges (*Carex* spp.), rushes (*Juncus balticus*), and grasses (*Phleum* spp., *Calamagrostis* spp., *Bromus* spp., *Poa* spp.). The wintering elk population numbers about 3,000 animals, of which about one-third generally spends the winter within the park (Larkins 1997; Singer et al. 1998b).

Experimental Treatments

In the wet meadows of both parks, twelve 30 m x 46 m exclosures were erected within willow communities along the rivers between August and November of 1994. Next to each exclosure, 30 m x 46 m plots were chosen and marked off as paired plots open to grazing (grazed plots). Each site consisted of an exclosure and a grazed plot. Eight sites (four in Moraine Park and four in Horseshoe Park) were placed in areas with little or no current beaver activity, and contained heavily browsed willow (short willow). The other four sites (two in each park) were located in wetter areas, generally containing taller willow plants subjected to less severe browsing by elk (tall willow). In half of the short willow sites (two in each park), hydro-manipulation treatments were imposed by placing sheet metal check dams on ephemeral stream channels both inside the exclosures and in the grazed plots (short-watered willow). We expected these check dams to catch snowmelt and rain runoff through the spring and raise the water table at the sites. Twenty-five dams were installed in April and May 1995 and were relatively successful in holding additional water at these sites. The dams were intended to add water, but the treatment was unable to simulate water additions in the amounts accomplished by beaver dams on larger, permanent streams (Singer et al. 1997). The other four exclsoures in short willow sites were left to normal hydrologic regimes (short-control willow). In each exclosure and associated grazed plot, an average of five shallow (0.5 m to 2 m) wells were installed in the spring of 1995 for the purpose of monitoring groundwater levels. During early 1996 and 1997, three dams were constructed by beaver near two sites within the wetter area of Moraine Park, but these dams were washed out during the spring floods of 1996 and 1997.

The area within each exclosure was sub-divided in 15 x 23 m sub-plots and two treatments were imposed throughout the period of the study: (1) 75% current annual growth (CAG) removal (clipped plots); and (2) no clipping at all (ungrazed plots). Additionally, elk browsed willows outside the exclosures (grazed plots). The 75% CAG removal treatment was applied between January and April of 1995, 1996, 1997, and 1998, and consisted of clipping all forage shrubs and herbaceous plants in each sub-plot. All clipped plant biomass was removed from the exclosures.

Litterfall

Litter was collected in each experimental plot during the fall of 1995, 1996, and 1997, through the use of 15 greenhouse trays (totaling ~2.3 m^2) arranged in a 5 x 3 regularly spaced grid (9.1 x 15.9 m). The grids were established randomly within each sub-plot before willow senescence began, and each tray was anchored to the ground using two or more large spikes. Litter was collected weekly from early September to late October until litterfall was complete. The litter was then composited within each experimental replication, sorted by genus and litter type, air dried, and weighed. Oven-dry corrections were applied within each category by drying a subsample at 60°C. Litterfall biomass was calculated as oven dry mass per unit area. Total N and C content of litter was determined using a LECO CHN-1000 analyzer.

Litter Decomposition

During September and October of 1994, we collected litter material to generate a standard litter that was used in the decomposition experiments. Willow leaf litter was collected by locating greenhouse trays directly under willow canopies. Graminoid litter was collected by clipping and collecting dead biomass throughout the study area. We dried all litter in a 35°C forced air oven, and subsamples (2 g) from the two standard litter types (willow leaves and graminoid tissue) were enclosed in 1 mm nylon mesh bags. The bags were used in litter decomposition experiments to investigate the effects of herbivory, landscape position, and plant cover on the decomposition rates of willow and graminoid litter during the 1995, 1996, and 1997 growing seasons. In all experiments, the litterbags were left in the field during the entire length of the growing season (from late May until mid-September), and then collected, air-dried, weighed, ground to a fine powder, and stored until analysis. Carbon and N in the decomposed litter were analyzed using a LECO CHN-1000 analyzer, and C and N losses were calculated on an ash-free dry weight basis by subtracting the amounts in the pre-decomposition from the post-decomposition litter.

During the growing season of 1995, four bags of each litter type (willow leaves and graminoid tissue) were randomly placed within the exclosures in the ungrazed plots and outside the exclosures in the grazed plots for all 12 sites. In 1996 and 1997, in each of the ungrazed and grazed plots, we selected two willow shrubs located at two different landscape positions: (1) lower landscape positions, next to a stream or a pond; and (2) upper landscape positions, at least 10 m away from a stream or pond and 0.5 m higher in the landscape than lower landscape positions. Bags of both willow and graminoid litter were placed under the canopies of the selected willow and in open grass areas next (within 2 m) to the shrubs. Two bags of each litter type were placed within each treatment replication in order to reduce microsite variability.

Elk Dung Quantification

We estimated the amount of C and N returned to the soil in elk dung by counting the number of scat piles along 30 m transects within our experimental grazed plots, and measuring the concentrations of C and N in the dung. The survey was conducted after the elk herds left the winter range for the summer range during late spring 1997. We selected eight grazed plots (four in each park) and established four randomly placed transects per plot. In each transect, we measured the distance from the scat piles to the transect, and calculated the density of piles per area. Only scat piles that were visually identified as from the previous fall and winter were counted. In order to estimate dry matter and C and N content in each dung pile, we obtained 51 samples (26 from Horseshoe Park and 25 from Moraine Park) by collecting all dung from fresh piles during late fall of 1997. After collection, the samples were air-dried, weighed, ground to a fine powder, and sub-sampled for determination of moisture and ash content. The concentrations of C and N in the dung were determined using a LECO CHN-1000 analyzer and expressed on an ash-free dry weight basis.

Soil Characteristics and N Availability

Soil samples (0 to 15 cm) were collected in July 1997 from the grazed, ungrazed, and clipped plots. Within each treatment replication, 25 to 30 cores were randomly collected with a soil core sampler 2 cm in diameter and combined in a paper bag. After collection, the samples were taken to the laboratory, air-dried, and passed through a 2 mm sieve. Soil particle distribution was measured in each sample using the hydrometer method (Gee and Bauder 1986). Sub-samples (10 g) of each sample were ground to a fine powder with a ball mill. The sand fraction (>53 mm) of each sample was ground to a fine powder with a ball mill, for determination of particulate organic matter (POM) C and N (Cambardella and Elliott 1992). Total C and N in the total soil and sand fraction were determined with a LECO CHN-1000 analyzer. Soil pH was measured in a 2.5:1 (water:soil) suspension.

In addition, during the summer of 1996, we collected soil samples (0 to 20 cm) under willow trees and in associated open grass areas within 2 m to the trees. A total of 35 pairs of samples (shrub canopy plus open grass) were taken from the 12 ungrazed plots within the exclosures of Moraine Park and Horseshoe Park. The samples were air-dried and sieved through a 2 mm screen. Sub-samples (10 g) of each sample were ground to a fine powder with a ball mill, and total soil C and N were determined using a LECO CHN -1000 analyzer.

Soil moisture (0 to 14 cm) measurements were performed weekly in eight sites in Moraine Park and Horseshoe Park (four in each watershed) by Time Domain Reflectometry (TDR) (Ledieu et al. 1986) with a Trase System model 6050x1 during the 1997 growing season. Within each site and grazing treatment, soil moisture was measured under willow canopies and in associated graminoid plots next to the willow shrubs in both upper and lower landscape positions.

Within three ungrazed plots in each park, soil temperature was measured using HOBO® temperature data loggers during the 1997 growing season. The data loggers were wrapped with a thin plastic film to avoid damage by soil moisture, and buried in a vertical position from 1 to 6 cm depth. In each of the sites, we performed comparisons of soil temperature between: (1) willow canopies and graminoid plots; and (2) streamside (lower) and upper landscape positions. The temperature measurements were performed every 15 minutes for periods of 7 to 14 days.

In 1995, 1996, and 1998 soil *in situ* N availability in the experimental plots was assessed using ion-exchange resin bags. Paired cation and anion resin bags made from nylon stockings and containing about 15 cm^3 of exchange resins were placed 5 cm beneath the soil surface (Binkley 1984). In 1995 and 1996, 15 pairs of resin bags were placed in a regularly spaced grid (9.1 m x 15.9 m) within each treatment (grazed, ungrazed, clipped) in the 12 sites. In order to analyze the temporal variability of N availability, two sets of bags were placed in each treatment during the 1995 and 1996 growing seasons. The first set was left in place from mid-June to mid-July, and the second set from mid-July to mid-August. A different experimental procedure was utilized in 1998, in which six pairs of resin bags were randomly placed within each of the 12 ungrazed and grazed plots, and left in the field from May to October. For all 3 years, after removal of the bags, the N adsorbed in the resins was extracted with 50 ml of 2 M KCl, and the extracts frozen until analysis on an Alpkem automated spectrometer.

In 1997 and 1998, *in situ* measurements of net N mineralization were performed by conducting field soil incubations as described in Kolberg et al. (1997) using aluminum cores 15 cm long and 5 cm in diameter. During the 1997 growing season, cores were placed in upper and lower landscape positions within the 12 ungrazed and grazed plots of the two watersheds. Within each landscape position and grazing treatment, cores were placed under willow shrubs and in associated graminoid patches within 2 m of the willow plants. Four cores were placed inside each treatment replicate in order to reduce micro-site variability. Cation and anion resin bags were placed in the bottom of each core to capture the inorganic N leached from the core. During the 1998 growing season, six open-top field soil incubation cores were placed within the ungrazed and grazed plots in three different 6-week incubation periods (June to July, July to August, and August to October). Net soil N mineralized during the incubation periods was calculated by subtracting the initial amount of inorganic N in the soil from the final amount of inorganic N after the incubations, and the results were expressed in g N m^{-2}.

Nitrogen Fertilization

In each ungrazed and grazed plot in the 12 sites, we placed two paired circular subplots (each with 2 m radius) around willow plants at the end of the 1998-growing season. Within each pair of circular subplots, we applied two fertilization treatments: (1) no fertilization, and (2) 10 g N m^{-2} as ammonium nitrate. During late July 1999, willow shoots (CAG) were collected from the plants inside the subplots, dried at 60°C, weighed, and ground to a fine powder. Concentrations of C and N in shoots were determined using a LECO CHN -1000 analyzer.

Statistical Analyses

Statistical analyses were performed using the SAS Statistical Package (SAS, Version 6.12, SAS Institute Inc., Cary, NC, 1995). There were no significant interactions at any level including watershed, willow height, and hydro-manipulations. Therefore, the data from the experiments on litterfall, litter nutrient content, soil characteristics, and elk dung deposition were analyzed for the effect of elk herbivory using a randomized complete block design. The data from the experiments on litter decomposition and soil N availability were analyzed using a split-plot design with herbivory manipulations as the main treatment and landscape position or canopy position as sub-plots.

Results and Discussion

Litterfall

Litterfall biomass in the ungrazed and clipped plots was greater ($P < 0.05$) than in the grazed plots for the three growing seasons (Table 1). Across all growing seasons, litterfall biomass averaged 65.6 and 33.0 g m^{-2} inside and outside the exclosures, respectively. On average, willow leaves accounted for 58% of the litterfall biomass followed by herbs (20%), other shrub leaves

Table 1. Litterfall biomass in ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park during 1995, 1996, and 1997. Values represent means (n = 12) with standard errors in parentheses. Means within the same group followed by different letters are significantly different at P <0.05.

	Litterfall (g m^{-2})					
Treatment	Willow (*Salix* spp.) leaves	Other shrub leaves[1]	Herbs[2]	Wood	Unidentified material	All litter
1995						
Ungrazed	32.9 (9.8)^{a}	5.9 (2.7)^{a,b}	10.1 (2.4)	3.0 (1.0)	0.6 (0.2)	52.5 (10.2)^{a}
Clipped	34.1 (8.5)^{a}	13.2 (6.3)^{a}	8.0 (1.0)	4.4 (1.4)	0.3 (0.1)	60.0 (8.9)^{a}
Grazed	19.1 (7.1)^{b}	1.7 (0.6)^{b}	6.4 (0.9)	3.1 (1.4)	0.5 (0.2)	30.9 (8.5)^{b}
1996						
Ungrazed	55.0 (13.6)^{a}	9.1 (3.9)^{a,b}	3.1 (0.6)	3.1 (1.1)	1.4 (0.4)	71.6 (12.6)^{a}
Clipped	47.1 (10.6)^{a,b}	18.3 (8.6)^{a}	2.6 (0.5)	1.6 (0.4)	0.8 (0.2)	70.2 (9.7)^{a}
Grazed	26.6 (8.1)^{b}	3.7 (0.8)^{b}	3.4 (0.5)	5.1 (2.2)	0.7 (0.3)	39.4 (9.1)^{b}
1997						
Ungrazed	45.3 (12.3)^{a}	8.7 (4.0)^{a,b}	14.3 (3.3)	3.1 (1.0)	-	71.5 (11.1)^{a}
Clipped	41.6 (10.4)^{a}	15.5 (6.3)^{a}	7.2 (0.7)	2.2 (0.7)	-	66.4 (10.1)^{a}
Grazed	15.9 (6.0)^{b}	3.0 (0.9)^{b}	7.5 (1.0)	2.4 (1.1)	-	28.8 (7.1)^{b}

[a,b,c] Denote significant differences (P <0.05).

[1] Mostly birch (*Betula* spp.) leaves.

[2] Litter material from forbs and graminoid combined.

(16%), wood (5%), and unidentified material (1%). However, the use of trays for collecting litterfall may underestimate the amount of grass litterfall, since a significant portion of the senescent tillers still remain attached to the plant and were not collected and counted as litter. Willow leaf litterfall in the ungrazed and clipped plots was greater (P <0.05) than in the grazed plots during the 1995 and 1997 seasons, but in 1996 there were no significant differences between clipped and grazed plots (Table 1). Leaf litter from other shrubs, mostly birch (*Betula* spp.), was significantly lower in the grazed plots when compared to the clipping treatment inside the exclosures, but there were no differences between grazed and ungrazed plots. No grazing treatment differences were observed for the amounts of herb or wood litter during the three growing seasons.

Litterfall biomass was lower in the grazed plots, in comparison to the clipped and ungrazed plots, due to elk browsing during early fall before leaf senescence. However, inside the exclosures, even the removal of 75% of CAG in the clipped plots did not result in significant differences between the ungrazed and clipped plots during the three growing seasons. We suggest this lack of difference between clipped and ungrazed plots occurred in part because the artificial clipping of willow did not satisfactorily simulate elk browsing. Other studies have demonstrated the limitations of clipping experiments to reflect accurately the natural patterns of herbivory (Paige 1999). Visual observations in our field plots suggested that clipped plants inside the exclosures were morphologically similar to the plants in the ungrazed treatment, regarding height and canopy structure, while the grazed plants were apparently more suppressed and shorter than the plants in the two treatments inside the exclosures. These patterns probably resulted from the additional damage to willow leaders caused by elk when striping off leaves from the plants, as compared to artificial clipping. On average, elk may browse on more than 70% of the leaders in each plant in our study sites, and may remove nearly 40% of the length of each leader (Singer et al. 1998b). Additional field observations from our experiments demonstrate that an average of 20% of the length of browsed willow leaders may die after elk browsing due to bark damage, while only 2% of the length of the leader may die in the case of artificially clipped plants (R. Peinetti, Natural Resources Ecology Laboratory, personal communication). We suggest that the differences in growth and litterfall observed between grazed and clipped treatments in our study may result from: (1) greater leader damage during elk browsing, in comparison to artificial clipping; and/or (2) greater increases in plant height in clipped plants, in comparison to grazed plants, due to differences in the patterns of tissue removal during elk browsing or artificial clipping, which may influence canopy architecture. Overall, we suggest that the clipped plants in our study were able to overcompensate for the biomass removal and achieve greater fitness, in comparison to browsed plants, but additional studies are needed to test this hypothesis.

Willow leaf litter in the ungrazed and clipped plots had lower ($P < 0.05$) N content and higher ($P < 0.05$) C to N ratio than willow leaf litter in the grazed plots, but no significant treatment differences were found in litter from other shrubs, graminoids, or forbs (Table 2). Similar to our findings, Alstad et al. (1999) reported that early season willow tissue N concentration in plants under elk herbivory in our sites was significantly higher than in plants protected from herbivory. Often, grazing leads to increases in plant tissue N (McNaughton 1985; Holland and Detling 1990; Coughenour 1991; Hamilton et al. 1998) due to faster nutrient cycling and uptake by plants or a reduction in tissue biomass for allocation of N. Higher N concentration and lower C to N ratios in litter may lead to faster litter decomposition and greater nutrient availability (Irons et al. 1991; Ritchie et al. 1998). In our study site, the effects of elk herbivory on willow litter N concentration could lead to increases in the rate of litter decomposition and nutrient cycling, which could lead to changes in species composition and ecosystem functioning (Aber and Melillo 1991; Holland et al. 1992; Ritchie et al. 1998; Stohlgren et al. 1999).

Litter Decomposition

Grazing had no effect on the decomposition of willow and gramoinoid litter in any of our experiments, but C and N losses between willow and graminoid litterbags were significantly different. In the three growing seasons, C losses from willow litterbags were higher ($P < 0.05$) than from graminoid litterbags (Table 3). Interestingly, N losses from willow litter were lower than from graminoid litter (Table 3), perhaps because willow litter has a higher content of secondary compounds or promotes greater N immobilization during decomposition, when compared to graminoid litter. Browsed willow plants may increase the concentration of secondary defense compounds, such as tannins, as a response to prevent further herbivory (Singer et al. 1994). The standard litter utilized in our decomposition studies had a relatively high concentration of tannins, averaging 70.7 mg g^{-1} dry $matter^{-1}$ (Cates, et al., this volume). Our findings indicate that, even though willow litter has a lower C to N ratio when compared to graminoid litter, the presence of secondary compounds in willow litter may have caused a significant reduction in the losses of litter N when compared to graminoid litter.

In 1996, C losses from litterbags were higher ($P = 0.001$) in streamside positions than in upper landscape positions, but no significant differences were observed for N losses during 1996 or C and N losses during 1997 (Table 4). Soil moisture is usually an important factor contributing to decomposition and, in general, litter decomposition increases with increasing soil moisture in semi-arid ecosystems (Schlesinger 1997). Higher C losses observed in streamside positions in our study are likely due to higher soil water availability (Fig. 1). However, no significant differences in willow or graminoid litter decomposition were observed between streamside and upper landscape positions around the two beaver ponds in 1996. Average C and N losses from litterbags of the two litter types placed around the ponds were 36.4% and 2.9%, respectively. The lack of consistent differences in litter decomposition between different landscape positions in our experiments may have occurred because 1996 and 1997 had higher rainfall levels than the long-term average for those sites (Alstad et al. 1999). For these reasons, the differences in soil moisture may not have been as pronounced between landscape positions as they would have been in drier years, especially towards the end of the growing season, as indicated by the increases in soil moisture in July 1997 (Fig. 1).

Litterbags placed under willow canopies lost significantly more C and N than bags placed in graminoid plots (Table 5), even though soil moisture levels were slightly lower under willow canopies, compared to graminoid plots, especially in Horseshoe Park (Fig. 1). Average maximum soil temperatures from 1 to 6 cm in depth during the 1997 growing season were significantly lower under willow canopies than in graminoid plots in both Moraine and Horseshoe Parks (Fig. 2). These results indicate that the presence of willow shrubs has a significant influence on microclimatic conditions in our

Table 2. Nitrogen content and carbon to nitrogen ratio of different litter types in ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park in 1997. Values represent means (n = 12) with standard errors in parentheses. Means within the same group followed by different letters are significantly different at $P < 0.05$.

Treatment	Willow (*Salix* spp.) leaves	Other shrub leaves[1]	Graminoids	Forbs
Nitrogen (%)				
Ungrazed	1.25 (0.10)[b]	1.23 (0.15)	1.40 (0.11)	1.79 (0.13)
Clipped	1.27 (0.09)[b]	1.11 (0.13)	1.22 (0.08)	1.71 (0.15)
Grazed	1.49 (0.08)[a]	1.09 (0.11)	1.23 (0.09)	1.82 (0.12)
Carbon to nitrogen ratio				
Ungrazed	45.8 (3.2)[a]	48.5 (12.0)	37.2 (2.9)	31.0 (3.0)
Clipped	43.0 (4.2)[a]	53.4 (11.6)	42.1 (2.8)	32.6 (2.9)
Grazed	37.7 (3.1)[b]	49.9 (14.3)	43.5 (3.1)	31.4 (2.6)

[1] Mostly birch (*Betula* spp.) leaves.

[a,b] Different letters denote statistical differences at $P < 0.05$.

Table 3. Carbon and nitrogen losses from willow (*Salix* spp.) and graminoid leaf litter bags in Moraine Park and Horseshoe Park during the growing seasons of 1995, 1996, and 1997. Values represent means (n = 12) with standard errors in parentheses.

Litter type	% C loss	% N loss
1995		
Willow	30.2 (2.7)	6.3 (2.0)
Graminoid	22.9 (2.6)	10.3 (2.1)
P-value	n.s.[a]	0.026
1996		
Willow	29.0 (1.9)	3.4 (5.1)
Graminoid	22.9 (2.4)	15.2 (4.7)
P-value	0.046	0.005
1997		
Willow	22.1 (1.4)	2.7 (2.4)
Graminoid	16.4 (1.8)	16.4 (4.3)
P-value	0.013	0.005

[a] Not significantly different at $P < 0.05$.

Table 4. Carbon and nitrogen losses from litter bags placed in upper and lower landscape positions of Moraine Park and Horseshoe Park during the growing seasons of 1996 and 1997. Values represent means (n = 12) with standard errors in parentheses.

Landscape position	% C loss	% N loss
1996		
Streamside	31.7 (2.3)	5.7 (6.1)
Upper landscape	20.3 (1.9)	12.8 (6.0)
P-value	0.001	n.s.[a]
1997		
Streamside	18.1 (1.9)	6.5 (4.2)
Upper landscape	20.4 (1.3)	12.9 (2.7)
P-value	n.s.	n.s.

[a] Not significantly different at $P < 0.05$.

sites, contributing to reductions in soil temperature and soil moisture. We suggest that the rate of nutrient loss from litterbags was higher under willow canopies because: (1) shading by willow canopies may decrease soil temperature and increase soil moisture at the top few centimeters of the litter layer and soil. This may enhance litter decomposition, and/or (2) graminoid plants may have supported litterbags off of soil in open sites, which may have let them dry out more and decompose less than bags placed under willow canopies.

Return of N to the Soil

Based on the biomass and N content of aboveground litter in our sites (Tables 2 and 3), we calculated that the N return to the soil in litterfall during the 1997 growing season was greater ($P < 0.05$) in the ungrazed and clipped plots (0.83 and 0.82 g N m^{-2}, respectively) than in the grazed plots (0.42 g N m^{-2}), excluding the contribution of N in wood litter in all treatments. Similar to our findings, Pastor et al. (1993) found that moose browsing led to decreases in the amount of litterfall and nutrient return to the soil in litter. In our site, litter from willow, other shrubs, and herbs contributed to 62%, 17%, and 21% of the N returned to the soil inside the exclosures, and 51%, 16%, and 33% of the N returned to the soil in grazed plots, respectively. Elk dung biomass deposited on the soil during the 1997–1998 season averaged 42.2 ± 6.2 g m^{-2} across all sites. This value is similar to those reported by Frank and McNaughton (1992), who found that average herbivore dung deposition during the 5-month season in the winter range of YNP was 76.9 ± 30.1 g N m^{-2}. In our sites, average elk dung N concentration in the samples collected in late fall of 1997 was 2.0%. Based on our results, we estimated that approximately 0.87 ± 0.12 g N m^{-2} was returned to the soil in elk dung during the 1997–1998 winter season in our study site. Therefore, the amount of N returned to the soil as elk dung plus plant litter averaged 1.3 g m^{-2} in the grazed plots. The estimated amount of N returned to the soil in elk urine in our sites, based on the diet and specific characteristics of the herd, could be approximately 98% of the N returned to the soil in dung (Schoenecker et al., this volume). Based on these estimates, after including the potential N inputs from urine, the total amount of N returned to the soil in the grazed plots could be as high as 2.2 g N m^{-2}, which corresponds to 265% of the N returned as aboveground litter in the exclosed plots. Our results are consistent with the findings of Frank and McNaughton (1992), who found that elk and bison populations in YNP excreted 0.81 to 4.60 g N m^{-2} yr^{-1}, an amount that corresponded to roughly four times the amount of N returned in litterfall. In addition, those authors concluded that the intensity of herbivory was positively associated with both aboveground net primary production and the return of nutrients to the soil.

Ungulates usually accelerate nutrient cycling by modifying the amount and quality of residues returned to the soil (Hobbs 1996). Similar to the findings of Frank

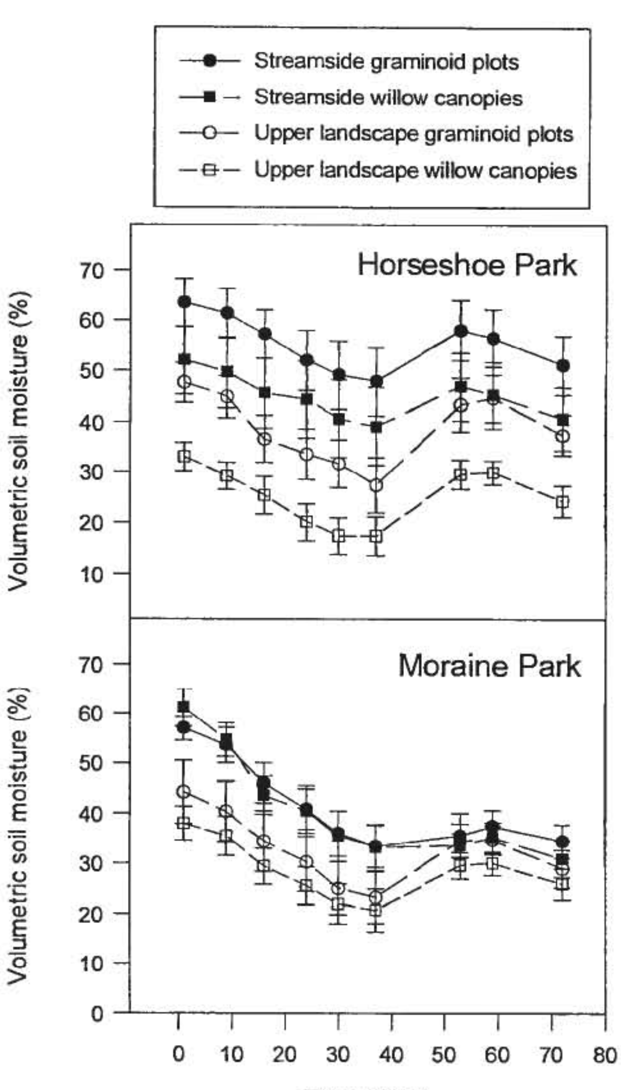

Fig. 1. Soil moisture (0 to 14 cm) under willow canopies and in graminoid plots in upper and lower landscape positions of Horseshoe Park and Moraine Park from early June to late August of 1997. Error bars represent standard errors of the means (n = 8).

Table 5. Carbon and nitrogen losses from litter bags placed under willow (*Salix* spp.) canopies and in graminoid plots in Moraine Park and Horseshoe Park during the growing seasons of 1996 and 1997. Values represent means (n = 8) with standard errors in parentheses.

1996	% C loss	% N loss
Willow canopies	35.7 (1.7)	24.2 (1.8)
Graminoid plots	7.7 (2.9)	-1.6 (2.4)
P-value	0.001	0.022
1997		
Willow canopies	23.1 (1.5)	15.5 (1.7)
Graminoid plots	16.0 (3.5)	3.4 (3.5)
P-value	0.00	0.012

et al. (1994) in Yellowstone, a portion of the excess N returned to the soil by elk in our study sites may correspond to transfers from the summer range. During winter, elk migrate from the summer range to the winter range at lower elevations to avoid snow and usually lose weight and N (F. Singer, U.S. Geological Survey, personal communication). Our results indicate that elk may be promoting a net transfer of N from the summer range to the winter range, and the extent of these transfers are likely related to the number of elk in this system. In the long-term, these N transfers could increase N availability, which in turn may affect ecosystem structure and functioning (Aber and Melillo 1991; Holland et al. 1992; Ritchie et al. 1998; Stohlgren et al. 1999).

Soil Characteristics and N Availability

There were no significant differences ($P < 0.05$) in total soil C and N, POM C and N, soil texture, and soil pH between grazing treatments in our sites within the 4 years after the establishment of the exclosures (Table 6). Similar to our findings, Frank and Groffman (1998) found no differences in soil total C and N between grazed plots and exclosed plots that had been protected from herbivory for 33 to 37 years in YNP. However, Frank and Groffman (1998) found that herbivores improved the quality of soil organic matter, increasing the labile fractions and decreasing the recalcitrant fractions. In our study, the relatively short time (4 years) since the establishment of the exclosures may not have allowed for the development of significant differences in the organic matter fractions between herbivory treatments. In addition, we found no differences in total soil C and N (0 to 30 cm) between soil samples taken in graminoid plots or under willow canopies. Total soil C and N

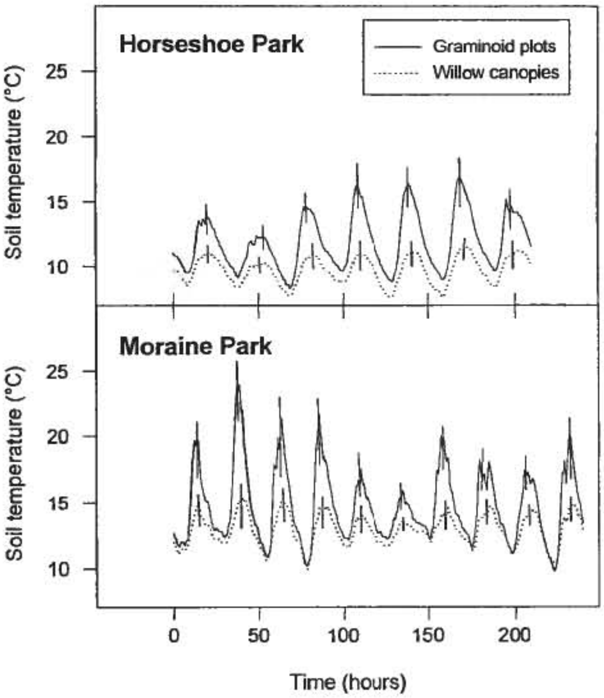

Fig. 2. Soil temperature (1 to 6 cm) under willow canopies and in graminoid plots in Horseshoe Park and Moraine Park during July 1997. Vertical lines represent the range of the 95% confidence interval for the means of maximum temperatures (n = 3).

averaged 6.2 and 0.44 g kg^{-1} in graminoid plots and 5.8 and 0.40 g kg^{-1} under willow canopies, respectively.

In all experiments with both ion-exchange resin bags and field soil core incubations, there were no significant differences in soil N availability between grazing treatments during the 4 years of the study. Several studies have reported increases in the rates of soil N mineralization with herbivory (McNaughton 1985; McNaughton et al. 1988; Holland and Detling 1990; Frank and Evans 1997). Frank and Groffman (1998) reported that N availability in plots grazed by elk was 100% higher than exclosed plots. Again, we suggest that the time since the establishment of the exclosures in our study did not allow for the development of detectable differences in soil N mineralization and availability between grazing treatments.

The assessment of N availability with ion-exchange resin bags during 1995 and 1996 indicated that, in general, both NH_4^+-N and NO_3^--N availability were higher ($P < 0.05$) during early to mid-season and declined afterwards (Table 7). In 1998, there was only one resin bag incubation period, and the total amount of N adsorbed to the bags was slightly higher than the sum of both periods of either 1995 or 1996, probably because the incubation period in 1998 was a few weeks longer. On average, the amount of NH_4^+-N adsorbed to the resin bags was 137 to 412% higher than NO_3^--N during the three growing seasons. The higher proportions of soil NH_4^+-N could benefit plant productivity in our sites, since plants with an evolutionary history of grazing show elevated growth responses to ammonium relative to other

Table 6. Soil characteristics (0–15 cm) of ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park in July 1997. Values represent means (n = 12) with standard errors in parentheses.

	Total C	Total N	POM C	POM N	Sand	Silt	Clay	
Treatment				g kg soil^{-1}				pH[a]
Ungrazed	50.3	3.38	15.9	0.81	523	209	152	4.64
	(9.0)	(0.63)	(3.5)	(0.19)	(59)	(40)	(19)	(0.10)
Clipped	47.7	3.27	13.3	0.63	494	235	161	4.67
	(7.1)	(0.54)	(2.0)	(0.09)	(55)	(47)	(25)	(0.12)
Grazed	42.7	2.82	11.3	0.53	549	234	118	4.60
	(6.2)	(0.44)	(2.0)	(0.12)	(37)	(29)	(19)	(0.11)

[a] Measured in water (2:1, water:soil)

Table 7. Inorganic nitrogen adsorbed to ion exchange resin bags during different incubation periods during 1995 and 1996, and one incubation period during 1998. Values represent means (n = 12) with standard errors within parentheses.

	Inorganic nitrogen (mg bag $^{-1}$)		
Incubation period	NO_3^- -N	NH_4^+ -N	NO_3^- N and NH_4^+ -N
1995			
June to July	1.08 (0.23)	4.45 (0.63)	5.53 (1.45)
July to August	0.64 (0.32)	2.12 (0.44)	2.78 (1.29)
P-value[a]	0.015	0.001	0.001
1996			
June to July	0.95 (0.52)	3.39 (0.81)	4.34 (1.14)
July to August	1.05 (0.55)	1.44 (0.53)	2.49 (0.87)
P-value	n.s.[b]	0.001	0.001
1998			
July to October	3.01 (0.55)	7.29 (1.98)	10.30 (2.43)

[a] *P*-value of comparisons between means of incubation periods.

[b] Not significantly different at $P < 0.05$.

Table 8. Inorganic nitrogen mineralized during field soil incubations (0 to 15 cm) using aluminum cores during 1997 and 1998. Values represent means for all treatments (n = 12) with standard errors within parentheses.

	Mineralized nitrogen (g m^{-2})		
Incubation period[a]	NO_3-	NH_4+	NO_3- + NH_4+
1997			
June to July	0.11 (0.04)	0.55 (0.15)	0.66 (0.16)
1998			
June to July	0.71 (0.44)	0.81 (0.80)	1.51 (0.77)
July to August	1.13 (0.38)	1.33 (0.95)	2.46 (1.17)
August to October	0.51 (0.23)	0.34 (0.52)	0.85 (0.59)

[a] Length of incubation period: 1997 = 4 weeks; 1998 = 6 weeks each period.

Table 9. Inorganic nitrogen adsorbed to ion exchange resin bags under willow (*Salix* spp.) canopies and in graminoid plots during different incubation periods of the 1995 and 1996 growing seasons. Values represent means (n = 12) with standard errors within parentheses.

Position	Inorganic N (mg bag^{-1})	
	June to July	July to August
1995		
Willow canopies	5.69 (2.13)	2.87 (1.20)
Graminoid plots	5.80 (1.92)	2.87 (1.11)
P-value	n.s.[a]	n.s.[a]
1996		
Willow canopies	4.98 (0.77)	3.07 (0.55)
Graminoid plots	4.01 (0.68)	2.42 (0.37)
P-value	0.018	n.s.[a]

[a] Not significantly different at $P < 0.05$.

Table 10. Effects of nitrogen fertilization on willow (*Salix* spp.) growth and N assimilation during the growing season of 1999. Values represent means (n = 12) followed by standard errors between parentheses.

Treatment	Shoot length (cm)	Shoot biomass (g)	Shoot N concentration (%)	Amount of N per shoot (g)
N fertilizer (10 g N m^{-2})	28.6 (1.4)[a,1]	27.3 (2.5)[a]	2.25 (0.05)	0.62 (0.06)[a]
No fertilization	22.5 (1.1)[b]	20.2 (2.4)[b]	2.14 (0.06)	0.43 (0.05)[b]

[a,b] Different letters denote statistical difference at $P < 0.05$.

[1] Means followed by different letters are significantly different at $P < 0.05$.

inorganic forms of N, particularly when subject to defoliation (Ruess 1984; Ruess and McNaughton 1987; Hobbs 1996). Similarly to the results from the experiments with ion-exchange resin bags, the amounts of net NH_4^+-N mineralized in the soil cores were usually higher than NO_3^--N (Table 8). In addition, total inorganic N in the soil was higher during early to mid-season during the 1998 growing season (Table 8). If plant uptake is higher during early to mid-season when plant growth and nutrient requirements are probably greater, the higher availability of nutrients during that period may contribute to the synchronization of nutrient supply and demand and enhance primary production and nutrient retention within the system (Myers et al. 1994). Interestingly, the presence of willow had a significant effect on N availability in our experiments with ion-exchange resin bags. During both incubation periods of 1996, the amounts of inorganic N adsorbed to resin bags located under willow canopies was higher ($P < 0.05$) than in bags placed in graminoid plots (Table 9), but no significant differences were observed during 1995. The higher N availability may be a consequence of higher amounts of litter N inputs and higher rates of N loss from litter under willow canopies, as indicated by our findings in 1996.

The data from the N fertilization experiment demonstrated that willow growth in the winter ranges for elk is limited by N availability, independently of grazing treatment. Both inside and outside the exclosures, N fertilizer additions increased ($P < 0.05$) willow shoot length, shoot biomass, and the amount of N in the shoots (Table 10). We suggest that elk herbivory could lead to long-term increases in N availability in our sites, because of induced increases in both litter quality and return of N to the soil. Increases in N availability could lead to changes in plant species composition and significantly alter ecosystem functioning because of shifts in the competitive interactions between plant species (Tilman 1982, 1988; Holland et al. 1992; Sterner 1994; Ritchie et al. 1998). Stohlgren et al. (1999) reported that exotic species were more likely to invade landscape patches with higher soil N and moisture, which could lead to a decline in native plant species and ecosystem diversity (Billings 1990; D'Antonio and Vitousek 1992).

Conclusions

Herbivory by elk significantly influenced the biogeochemical cycles of the winter ranges for elk in RMNP. Losses of C from litter and soil moisture were greater in streamside positions, when compared to upper landscape patches, indicating that reductions in surface water may lead to lower decomposition rates in our site. Elk grazing reduced the amount of litterfall biomass and the amount of N returned to the soil in litter. However, we estimated that the return of N to the soil through elk excretions plus aboveground litter in the grazed plots could be as much as 265% greater than inside the exclosures, maybe due to transfers of N from the summer range to the winter range. Willow litter contributed to 51% to 62% of the N returned to the soil in litterfall, and grazing by elk significantly increased the N concentration and reduced the C to N ratio of willow litter. We found no differences in soil total C and N, POM C and N, and N availability between grazed and ungrazed plots during the period of our study, maybe because there was not enough time (4 years) to develop significant differences between herbivory treatments. Nitrogen fertilization significantly increased willow shoot length, shoot biomass, and the average amount of N in the shoots, indicating that availability of N is a limiting factor for willow growth in our study sites. Greater return of N to the soil combined with increased litter quality in the grazed plots indicate that elk could contribute to increases in N cycling rates and availability in the long-term in our sites. Increased N availability could lead to changes in plant species composition and ecosystem functioning.

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Literature Cited

Aber, J. D., and J. M. Melillo. 1991. Terrestrial ecosystems. Saunders College Publications, Philadelphia, Pa.

Afzal, M., and W. A. Adams. 1992. Heterogeneity of soil mineral nitrogen in pasture grazed by cattle. Soil Science 56:1160–1166.

Alstad, K. P., J. M. Welker, S. Williams, and M. J. Trlica. 1999. Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: An isotopic study using $\delta^{13}C$ and $\delta^{18}0$. Oecologia 120:375–385.

Billings, W. D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. Pages 301–322 *in* G. M. Woodwell, editor. The earth in transition: Patterns and processes of biotic impoverishment. Cambridge University Press, Cambridge, UK.

Binkley, D. 1984. Ion exchange bags: Factors affecting estimates of nitrogen availability. Soil Science Society of America Journal 48:1181–1184.

Briske, D. D. 1986. Plant responses to defoliation: Morphological considerations and allocation priorities. Pages 425–427 *in* P. J. Joss, P. W. Lynch, and O. B. William, editors. Rangelands: A resource under siege. Proceedings of the Second International Rangeland Congress, Australian Academy of Sciences, Canberra, Australia.

Cambardella, C. A., and E. T. Elliott. 1992. Particulate soil organic-matter changes across a grassland cultivation sequence. Soil Science Society of America Journal 56:777–783.

Chadde, S. W., and C. E. Kay. 1991. Tall willow communities in Yellowstone's northern range: A test of the "natural regulation" paradigm. Pages 231–261 *in* R. B. Keiter and M. S. Boyce, editors. The greater Yellowstone ecosystem: Redefining America's wilderness heritage. Yale University Press, New York, New York.

Coughenour, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone northern winter range. Journal of Applied Ecology 28:71–82.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

Fahnestock, J. T., and J. K. Detling. 1999. Plant responses to defoliation and resource supplementation in the Pryor Mountains. Journal of Range Management 52:263–270.

Frank, D. A., and R. D. Evans. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology 78:2238 2248.

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.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73:2043–2058.

Frank, D. A., R. S. Inouye, N. Huntly, G. W. Minshall, and J. E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: Nitrogen dynamics in Yellowstone National Park. Biogeochemistry 26:163–188.

Gee, G. W., and J. W. Bauder. 1986. Particle-size analysis. Pages 383–411 *in* A. Klute, editor. Methods of soil analysis. Part 1. Second edition. Agronomy No. 9, ASA and SSSA, Madison, Wisc.

Georgiadis, N. J., R. W. Ruess, S. J. McNaughton, and D. Western. 1989. Ecological conditions that determine when grazing stimulates grass production. Oecologia 81:316–322.

Hamilton III, E. W., M. S. Giovannini, S. A. Moses, J. S. Coleman, and S. J. McNaughton. 1998. Biomass and mineral element responses of a Serengeti shortgrass species to nitrogen supply and defoliation: Compensation requires a critical [N]. Oecologia 116:407–418.

Hess, K. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

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

Holland, E. A., W. J. Parton, J. K. Detling, and L. Coppock. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. American Naturalist 140:685–706.

Irons, J. G., M. W. Oswood, R. J. Stout, and C. M. Pringle. 1991. Latitudinal patterns in leaf-litter breakdown – is temperature really important? Freshwater Biology 32:401–411.

Kay, C. E., and F. H. Wagner. 1994. Historical condition of woody vegetation on Yellowstone's northern range. Pages 151–169 *in* D. G. Despain, editor. Plants and their environments. National Park Service, Technical Report 93.

Kiehl, K, P. Esselink, and J. P. Baker. 1997. Nutrient limitation and plant-species composition in temperate salt marshes. Oecologia 111:325–330.

Kolberg, R. L., B. Rouppet, D. G. Westfall, and G. A. Peterson. 1997. Evaluation of an *in situ* net soil nitrogen mineralization method in dryland agroecosystems. Soil Science Society of America Journal 61:504–508.

Larkins, K. F. 1997. Patterns of elk movement and distribution in and adjacent to the eastern boundary of Rocky Mountain National Park. Thesis, University of Northern Colorado, Greeley.

Ledieu, J., P. de Ridder, P. de Clerk, and S. Dautrebande. 1986. A method of measuring soil moisture by time-domain reflectometry. Journal of Hydrology 88:319–328.

Mazancourt, C., M. Loreau, and L. Abbadie. 1998. Grazing optimization and nutrient cycling: When do herbivores enhance plant production. Ecology 79:2242–2252.

McNaughton, S. J. 1985. The ecology of a grazing system: The Serengeti. Ecological Monographs 55:259–294.

McNaughton, S. J., R. W. Reuss, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. Bioscience 38:794–800.

Myers, R. J. K., C. A. Palm, E. Cuevas, I. U. N. Gunatilleke, and M. Brossard. 1994. The synchronization of nutrient mineralization and plant nutrient demand. Pages 81–116 *in* P. L. Woomer and M. J. Swift, editors. The biological management of tropical soil fertility. TSBF and Sayce Publishing, UK.

Naiman, R. J., and J. M. Melillo. 1984. Nitrogen budget of a sub-arctic stream altered by beaver (*Castor canadensis*). Oecologia 62:150–155.

Naiman, R. J., J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest stream by beaver (*Castor canadensis*). Ecology 67:1254–1269.

Paige, K. N. 1999. Regrowth following ungulate herbivory in *Ipomopsis aggregata*: Geographic evidence for overcompensation. Oecologia 118:316–323.

Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist 139:690–705.

Pastor, J., B. Dewey, R. J. Naiman, P. F. McInnis, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74:467–480.

Pengelly, W. L. 1963. Thunder on the Yellowstone. Naturalist 14:18–25.

Power, J. F. 1977. Nitrogen transformations in the grassland ecosystem. Pages 195–204 *in* J. K. Marshall, editor. The belowground ecosystem: A synthesis of plant-associated processes. Range Science Department, Science Series No. 26, Colorado State University, Fort Collins.

Power, J. F. 1994. Understanding the nutrient cycling process. Journal of Soil and Water Conservation 49(2/supplemental):16–23.

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. 1984. Nutrient movement and grazing - experimental effects of clipping and nitrogen source on nutrient uptake in *Kyllinga nervosa*. Oikos 43:183–188.

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.

Russelle, M. P. 1992. Nitrogen cycle in pasture and range. Journal of Production Agriculture 5:13–23.

SAS Institute. 1995. SAS User's Guide. Release 6.12. SAS Institute Inc., Cary, NC.

Schlesinger, W. H. 1997. Biogeochemistry: An analysis of global change. Academic Press, San Diego, Calif.

Schuman, G. E., J. D. Reeder, J. T. Manley, R. H. Hart, and W. A. Manley. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecological Applications 9:65–71.

Singer, F. J., L. Mack, and R. G. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435–443.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998a. Thunder on the Yellowstone revisited: An assessment of management of native ungulates by natural regulation, 1968–1993. Wildlife Society Bulletin 26:375–390.

Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998b. Elk, multiple factors, and persistence of willows in national parks. Wildlife Society Bulletin 26:419–428.

Singer, F. J., E. T. Elliott, M. B: Coughenour, J. M. Welker, D. W. Valentine, S. A. Williams, L. C. Zeigenfuss, K. P. Alstad, and R. S. C. Menezes. 1997. Large mammalian herbivores, plant interactions and ecosystem processes in five national parks. Second annual report to Biological Resources Division, U.S. Geological Survey, 4512 McMurry Avenue, Fort Collins, Colo.

Sterner, R. W. 1994. Elemental stoichiometry of species in ecosystems. Pages 240–252 *in* C. G. Jones and J. H. Lawton, editors. Linking species and ecosystems. Chapman and Hall, New York, New York.

Stevens, D. R., and S. Christianson. 1980. Beaver populations on the east slope of Rocky Mountain National Park. Special Report to Rocky Mountain National Park, Estes Park, Colo.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki,

G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69:25–46.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, New Jersey.

Tilman, D. 1988. Plant strategies and the dynamic and structure of plant communities. Princeton University Press, New Jersey.

Toft, N. L., S. J. McNaughton, and N. J. Georgiadis. 1987. Effects of water stress and simulated grazing on leaf elongation and water relations of an East African grass, *Eustachys paspaloides*. Australian Journal of Plant Physiology 14:211–226.

U.S. Department of Agriculture Snow Survey Office 1995, 1996, 1997. Snowpack data for Rocky Mountain National Park. National Resources Conservation Service. Lakewood, Colo.

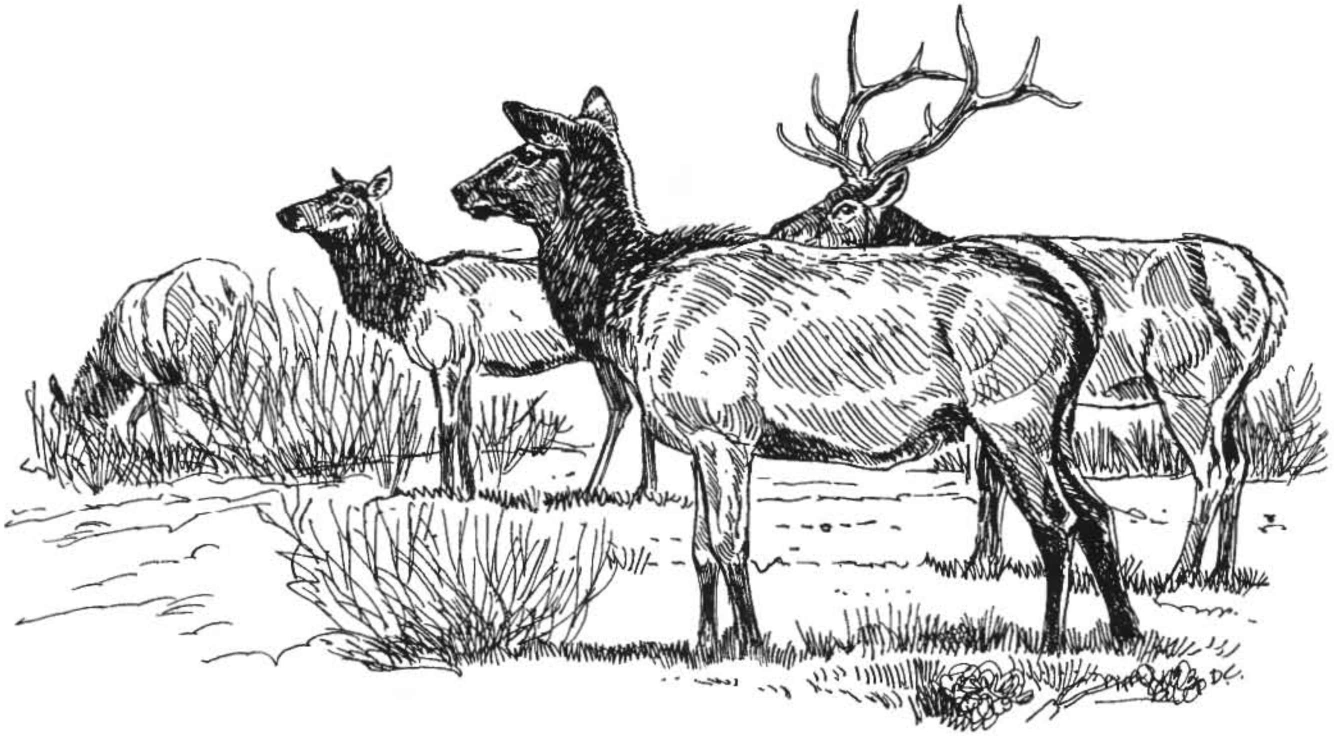
Welker, J. M., and D. D. Briske. 1992. Clonal biology of the temperate caespitose graminoid *Schizachyrium scoparium*: A synthesis with reference to climate change. Oikos 56:357–363.

Welker, J. M., and J. W. Menke. 1990. The influence of simulated browsing on tissue water relations, growth and survival of *Quercus douglasii* (Hook and Arn.) seedlings under slow and rapid rates of soil drought. Functional Ecology 4:807–817.

Welker, J. M., E. J. Rykiel, D. D. Briske, and J. D. Goeschl. 1985. Carbon import among vegetative tillers within two bunchgrasses: Assessment with carbon-11 labeling. Oecologia 67:209–212.

Welker, J. M., D. D. Briske, and R. W. Weaver. 1987. Nitrogen-15 partitioning within a three-generation tiller sequence of the bunchgrass *Schizachyrium scoparium*: Response to selective defoliation. Oecologia 24:330–334.

Wijnen, H. J., R. van der Wal, and J. P. Bakker. 1999. The impact of herbivores on nitrogen mineralization rate: Consequences for salt-marsh succession. Oecologia 18:225–231.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CHAPTER SEVEN

Carbon and Water Relations of *Salix monticola* in Response to Winter Browsing and Changes in Surface Water Hydrology: An Isotopic Study Using $\delta^{13}C$ and $\delta^{18}O$

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Abstract. To ascertain whether browsing or hydrologic conditions influence the physiological performance of willow (*Salix* spp.) and whether willows and graminoids (*Carex*) use and possibly compete for similar water resources, we quantified the *in situ* seasonal patterns of plant water and carbon relations over three growing seasons. Our studies were designed to address the physiological factors which may be responsible for poor woody plant regeneration in montane riparian habitats of Rocky Mountain National Park, Colorado. As these systems act to insure the delivery of fresh water to downstream users, the maintenance of their integrity is critical. We quantified plant water potentials, instantaneous rates of carbon fixation, leaf carbon isotope discrimination (Δ), leaf nitrogen content, and water sources using stable isotopes of water ($\delta^{18}O$). The carbon and water relations of willow were significantly affected by winter grazing by elk and in some cases, by landscape position with regards to proximity to active streams. Winter grazing of willow by elk significantly increased summer plant water potentials and integrative measures of gas exchange (Δ), though grazing did not consistently affect instantaneous rates of photosynthesis, leaf nitrogen nor the sources of water used by willow. No effect of experimental manipulations of surface water conditions on willow physiology was observed, likely due to the mesic nature of our study period. Using a two-member linear mixing model from $\delta^{18}O$ values, we calculated that willow appears to rely on streams for approximately 80% of its water. In contrast, sedges derive almost 50% of water from rainfall, indicating divergent water source use by these two life forms.

Based on these findings, winter grazing by elk improved willow water balance by possibly altering the shoot to root ratio which in turn leads to higher water potentials and higher degrees of season-long gas exchange while experimental damming had in general no effect on the physiological performance of willow plants. In addition, as the water sources of willow and sedge were significantly different, competition for water may not influence the growth, development and regeneration of willow. Thus, under the conditions of our study, herbivory had a positive effect on the physiological performance of willow, but it is still unclear whether these changes in physiology transcend into improved willow regeneration and survivorship. However, under drier environmental conditions such as lower snow packs and lower stream flows, grazing resistance of willow and ecosystem regeneration may be greatly hindered as willow's reliance on stream water indicates its vulnerability to changes in surface water and hydrological conditions.

Keywords: Plant-animal interactions, riparian ecosystems, Rocky Mountain National Park, stable isotopes, ungulates.

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Introduction

The carbon and water relations of native plants in riparian ecosystems are currently receiving attention because their physiology may influence community and ecosystem sustainability (Dawson and Ehleringer 1991; Busch and Smith 1995; Svejcar and Trent 1995; Dawson and Pate 1996; Kolb et al. 1997; Pimentel et al. 1997; Gleick 1998). Adequate regeneration of these ecosystems is essential to maintaining acceptable levels of biodiversity and the structural and functional aspects of habitats that deliver ecosystem services such as clean water (Naiman et al. 1995, 1998; Gleick 1998). There are, however, a host of woody dominated systems, which apparently are not regenerating adequately (Gordon et al. 1989; Singer et al. 1994, 1997; Kolb et al. 1997). The extent to which herbivores, changes in surface water conditions due to beaver (Naiman et al. 1988, 1994), and competition for water with herbaceous neighbors may all be influencing the physiology, growth, reproduction, and regeneration of woody species in riparian systems is, however, unclear.

Herbivory can influence growth and the physiological performance of plants (Coughenour et al. 1985; Toft et al. 1987; Welker and Menke 1990; Welker and Briske 1992; Busso and Richards 1995; Fahnestock and Detling 1999). For instance, herbivory may alter carbon and nitrogen allocation (Welker et al. 1985, 1987), rates of carbon assimilation (Caldwell et al. 1981; Detling and Painter 1983; Wallace et al. 1984) as well as plant water balance (Welker and Menke 1990; Day and Detling 1994). Whether herbivory and browsing have a positive or negative effect on plants may depend in part on environmental condition (Georgiadis et al. 1989) as changes in root to shoot ratio following browsing may be beneficial to the water balance of plants (Welker and Menke 1990) while the removal of meristems may reduce their future growth potential (Briske 1986).

Beaver (*Castor canadensis*) clearly impact the distribution of surface water across riparian ecosystems and greatly influence the biogeochemical cycles of these habitats (Naiman et al. 1988, 1994). Beaver impact woody species in these systems in both direct and indirect manners; directly by harvesting mature individuals for dam construction and indirectly as dams act to slow river or stream flows causing ponding and the dispersal of water across the floodplain (Naiman et al. 1994, 1995). This flooding may be an important component of willow (*Salix* spp.) plant survival (Singer et al. 1994) by maintaining high water potentials, which may enhance carbon gain improving the resistance of these plants to periodic browsing by ungulates (Svejcar and Trent 1995). Consequently, in regions where beaver have been trapped-out and harvested, willow plant water and carbon relations may be hindered, grazing resistance may be lower, and willow plant survivorship and ecosystem regeneration possibly threatened.

Herbaceous neighbors may compete with woody plants for belowground resources (Gordon et al. 1989; Callaway and Walker 1997) extracting water or nutrients at rates or to degrees which hinder woody plant resource acquisition, growth and possibly ecosystem regeneration (Gordon et al. 1989; Welker et al. 1991). These measures of competitive interactions between divergent life forms in montane riparian habitats have seldom, however, been demonstrated using stable isotope techniques (Dawson and Ehleringer 1991; Dawson 1993) which provide direct evidence for common use of groundwater as opposed to rainfall (Busch and Smith 1995; Dawson and Pate 1996; Dodd et al. 1998). One would anticipate that both herbaceous and woody plants in riparian ecosystems would have access to and utilize common water resources as grasses often have deep root systems which overlap with shrubs (Dodd et al. 1998). If these life forms utilize common resources, it is possible that herbaceous neighbors may extract resources that are necessary for woody plant growth and development which could hinder juvenile or mature woody plant regeneration (Gordon et al. 1989; Callaway and Walker 1997).

To study how browsing and surface water conditions affect willow physiology, and whether willow and herbaceous vegetation use similar water sources, we have quantified seasonal patterns of plant water and carbon relations *in situ* over 3 years where elk were present and excluded, and where surface water was artificially dammed and left undisturbed. We have used a host of approaches, at a multitude of temporal scales, from instantaneous rates of carbon fixation to integrative measures of leaf gas exchange ($^{13}C/^{12}C$ ratios) plus an examination of water sources using stable isotopes of water ($\delta^{18}O$), for both woody and herbaceous species (Ehleringer 1991; Ehleringer and Dawson 1992; Welker et al. 1995; Dodd et al. 1998) because we recognize that field measurements of instantaneous physiological performance can be limited in scope, especially where sampling occurs over several days, and that accurate interpretation of plant responses often requires a host of parameters (Caldwell et al. 1981; Chapin et al. 1987; Welker et al. 1997). We had three primary objectives: (1) to determine whether the carbon and water relations of willow are influenced by elk browsing and modifications of surface water hydrology; (2) to quantify whether the carbon and water relations of riparian vegetation is influenced by landscape position (adjacent to or distant from active steam channels); and (3) to quantify and compare the water sources of willow and herbaceous neighbors (*Carex* spp.) and their carbon relations as indicators of potential competition for similar water sources.

Materials and Methods

Study Sites

Our study sites were in riparian ecosystems on the northeast side of Rocky Mountain National Park. Two willow-dominated communities in the winter range of a migratory elk (*Cervus elaphus*) herd were selected within Moraine Park in the Big Thompson River watershed (elevation 2,481 m) and in Horseshoe Park of the Fall River watershed (elevation 2,598 m). The two watersheds are within 5 km of each other and have perennial alpine snowfields at their headwaters (Baron 1992). Willow species, primarily *Salix monticola*, *Salix geyeriana*, and *Salix planifolia*, are dominant in both watersheds with *Salix monticola* being the primary target species used in our study. The understory of these riparian areas was predominantly *Potentilla* shrubs and graminoids dominated by sedge species which form a continuous cover within the willow plant matrix. The 30-year average temperature in the Estes Valley ranges from 9° to 17°C during the 5-month growing season of May through September. The average total precipitation during the growing season averages 37 cm with >70% occurring in May and June (Colorado Climate Center 1995, 1996). Average peak snowpack level is 51 cm (snow water equivalent), and occurs in mid-April while peak stream flow typically occurs in early to mid-June (USDA 1995 and 1996).

Experimental Treatments

The study was designed as a randomized complete block experiment with a factorial arrangement of treatments, which included four replications (blocks) across both watersheds with two levels of grazing, grazed and ungrazed. The ungrazed treatments were established within four exclosures (46 m x 30 m) that were erected within each watershed between August and November of 1994 (eight exclosures total). An area surrounding each exclosure (approximately 100 m radius) was used as the corresponding grazed area used by elk during winter. We attempted to manipulate increases in the water table of several sites, as might occur if beaver dams were present in the area, by installing small check dams (1 cm thick sheet metal) in ephemeral stream channels in two of the study sites in Moraine Park and two sites in Horseshoe Park. This affected the surface water conditions for both an ungrazed and adjacent grazed area. Treatments with water additions will be referred to as short-watered willow sites. Sites with no water table manipulations will be referred to as short-control willow sites.

Field Measurements of Carbon and Water Relations

Salix monticola shrubs of medium height (0.75 to 2.0 m) were selected in close proximity to streams ("streamside") and in areas distant from streams ("upland" at least 10 m in a horizontal direction from streams and usually <0.5 m higher than streamside plants). Within 2 m of target willow plants, portions of sedge plants (10 cm diameter area) were excavated to 5 cm, which allowed us to retrieve nonphotosynthetic crown material for water extraction and photosynthetically active leaves for nutrient and $\delta^{13}C$ analysis (Ehleringer and Cooper 1988; Ehleringer 1991). Sedge material was collected three times in 1997, mid-June, mid-August and mid-September in both streamside and upland locations.

Willow physiological measures were carried out during 2-week periods each month throughout the summer from full leaf expansion to leaf senescence beginning in June and continuing through September of 1995 and 1996. In 1997, willow physiological measures were taken less frequently. In 1995 and 1996, midday willow leaf gas exchange measures were made between 1000 and 1300 hours, once during each 2-week period. A LICOR 6200 portable photosynthesis system (LI-COR, Inc., Lincoln, Nebraska) equipped with 0.25-L leaf chamber was used to determine instantaneous photosynthetic rates while recording photosynthetically active radiation (PAR). Air temperatures were also recorded at this time from the leaf chamber thermocouple when the fan was running and the chamber was open before gas exchange measurements. Area-specific photosynthesis results were calculated using the single leaf surface enclosed in the chamber. Willow leaves used for photosynthetic measurements were dried, ground, and analyzed for nitrogen content and carbon isotope ratios ($\delta^{13}C$) (Ehleringer 1991).

Willow total water potentials were measured on the same day as photosynthesis measures between 1100–1400 hr using the pressure chamber technique (Welker and Menke 1990). Representative leaders from the upper canopy of target shrubs were severed, immediately placed in the pressure chamber and total water potential was determined. The stems were then stripped of leaves, sealed in glass vials, placed on ice, and transported back to the lab and stored frozen until the xylem water was extracted and analyzed for $\delta^{18}O$ (Ehleringer and Osmond 1989; Dawson and Ehleringer 1991).

Monthly water samples for source water evaluation ($\delta^{18}O$) were collected from snow, groundwater wells which had a maximum depth of 2 m, stream surface water, and rain (Ehleringer and Dawson 1992; Dodd et al. 1998). Snow was collected in the two main watersheds in April by coring using a 5 cm x 30 cm tube. Each core was homogenized in a zip lock bag and a subsample placed into a 250 ml Nalgene bottle (acid washed and dried). The bottles were capped, sealed with Parafilm, placed into a cooler, transported to the laboratory and kept frozen until isotopic analysis for $\delta^{18}O$. Five representative cores were collected between our grazing exclosures. Stream water was collected at midday by placing a 250 ml Nalgene bottle just below the water surface in mid-stream, capping the bottle with little headspace, and sealing the cap with Parafilm. The sample was then placed in a cooler which was then transported back to the laboratory and the water samples frozen until $\delta^{18}O$ analysis. Well water was collected by inserting a Teflon tube down to the water level, and with the use of a hand pump, water was collected into a 250 ml Nalgene bottle, capped, sealed and transported in a similar manner as were the stream water and snow samples. Rain was collected in plastic gauges that contained oil to prevent evaporative enrichment (Dodd et al. 1998). Water samples were sealed, placed on ice, transported from the field and stored frozen until analysis. Snowpack data was derived from the SNOTEL data center for the Willow Park collection station approximately 10 km upstream of the Horseshoe Park study site.

Isotopic ($\delta^{13}C$) and Nitrogen Analyses

For the analysis of leaf tissue $\delta^{13}C$ abundance, leaves of willow and sedge were dried at 60°C for 72 hrs, and then ground in a ball mill to a fine powder and subsamples (<0.01 g) were combusted at 800°C in a Carlo-Erba NA 1500 Series 2 Carbon and Nitrogen analyzer attached to a VG-Optima® mass spectrometer. The mass spectrometer was initially calibrated against the NBS 22 primary standard while vacuum pump oil with a $\delta^{13}C$ value of -27.00 + - 0.20 relative to Pee Dee Belemnite (PDB) used as a secondary standard in each batch of samples. The sample $\delta^{13}C$ values are expressed relative to the standard for carbon, PDB (Craig 1957) using the equation:

$$\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1{,}000$$

where $\delta^{13}C$ is the carbon isotope ratio of the sample in parts per mil (%), R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratios of sample and standards, respectively. The precision of each isotope measurement is 0.03%. The $\delta^{13}C$ values were then converted to the discrimination (Δ) value where:

$$\Delta = \delta^{13}C_{sample} - \delta^{13}C_{standard}/\delta^{13}C_{air} - \delta^{13}C_{standard}$$

(O'Leary 1981; Farquhar et al. 1982). The $\delta^{13}C$ of the air was assumed to be -85% (Farquhar et al. 1989). The Δ values are integrative indicators of intercellular CO_2 concentration, which is affected by the balance between the leaf photosynthetic capacity and stomatal conductance (Farquhar et al. 1982). Willow leaves used for instantaneous gas-exchange measurements were also subsampled and used for analysis of foliar nitrogen concentration using a LECO CHN analyzer (LECO 1993). Since leaf photosynthate comprises more than 75% of total leaf N, these concentrations give an estimate of leaf Ribulose activity and complement information for analysis of photosynthesis activity. Both total nitrogen concentration and instantaneous gas-exchange measures were related to the carbon discrimination values to determine whether increases in leaf carbon isotope discrimination values were caused by increased carbon assimilation rates or increased stomatal conductance (Evans et al. 1986).

Plant Water Extraction and $\delta^{18}O$ Analysis

We extracted xylem water from plant stem tissue for willow and from nonphotosynthetic crown tissue of sedge (Dodd et al. 1998) using a vacuum distillation extraction line (Ehleringer and Osmond 1989). Plant tissue was placed into a glass vial that was subsequently evacuated to 10^{-3} mbar. The vial was then heated by immersion in boiling water for 3 hours to evaporate the free water. The evaporated water was collected in a cold finger by freezing with an ethanol-dry ice slurry. We then took 0.2 ml subsamples of the extracted water and transferred them to 1.0 ml glass vials, thoroughly aspirated the vials with CO_2 in a glove bag and equilibrated each batch for 10 hours at 40°C. The isotopic composition of the CO_2 in the headspace was measured using a multiprep sampler connected to a dual inlet VG-Optima® mass spectrometer (Epstein and Mayeda 1953; Ehleringer and Osmond 1989).

The sample $\delta^{18}O$ values are expressed relative to the standard for oxygen, V-SMOW (Vienna Standard Mean Ocean Water) using the equation:

$$\delta^{18}O = (R_{sample}/R_{standard} - 1) \times 1{,}000$$

where $\delta^{18}O$ is the oxygen isotope ratio of the sample in parts per mil (%), R_{sample} and $R_{standard}$ are the $^{18}O/^{16}O$ ratios of sample and standards, respectively. The precision of each isotope measurement is 0.2%.

The usual primary standard for oxygen is V-SMOW, although the δ values of the samples and three secondary standards were calculated using a linear calibration of the mass spectrometer against three primary standards of known δ values: V-SMOW, GISP, and SLAP (Gat 1980). The standard V-SMOW replaced the original primary oxygen standard SMOW, which was subject to characterization problems, and which has since been exhausted (Ehleringer and Dawson 1992). The three secondary standards we used were deionized tap water (DI); "cooked" deionized water (DI boiled for 12 hours); and snowmelt collected from Cameron Pass, Colorado, and all three were used in each batch of samples. We calculated the $\delta^{18}O$ abundance values of the water samples relative to V-SMOW by adjusting for any shift in the secondary standard occurring in separate batches, and applying the original linear calibration equation, as follows:

$$\text{actual } \delta^{18}O = 0.98 \times \text{observed } \delta^{18}O - 6.211,\ r^2 = 0.98.$$

The use of the calibration equation takes account of the fractionation coefficient of the H_2O-CO_2 equilibrium, and the contribution of O from the tank CO_2 used to aspirate the samples. In any case, the latter factor can be considered negligible, based on a 125:1 ratio of O in H_2O vs. CO_2 in the vials.

Comparisons of the $\delta^{18}O$ values of the source waters against the $\delta^{18}O$ values of the willow and sedge xylem water were made to evaluate the water sources used by riparian vegetation (Dawson and Pate 1996; Feild and Dawson 1998) and a simple two-end-member linear mixing model was used to calculate the proportion of rain water and subsequently groundwater in willow and sedge stem tissue (Feild and Dawson 1998). The two-end-members were defined by the average of stream and groundwater (-16.1%) and the average in summer rainfall (-7.0%). We calculated the rainwater proportion (P_r) in our plants by the ratio of the distances between groundwater $\delta^{18}O$ ($\delta^{18}O_{gw}$) and rain $\delta^{18}O$ ($\delta^{18}O_r$) and rainwater $\delta^{18}O$ ($\delta^{18}O_r$) and plant xylem water $\delta^{18}O$ ($\delta^{18}O_p$) (willow and sedge) (adapted from Feild and Dawson 1998), as:

$$P_r = (\delta^{18}O_{gw} - \delta^{18}O_p)/(\delta^{18}O_{gw} - \delta^{18}O_r).$$

We were assured that the xylem water we extracted was unfractionated source water by measuring the $\delta^{18}O$ values of willow stem bases, current and previous years growth, which we found to be similar (Singer et al. 1997, 1998).

Statistical Analysis

Leaf CO_2 assimilation rates, N concentrations, stem water potential, leaf carbon isotope discrimination, and stem water $\delta^{18}O$ values were analyzed using a split-plot factorial design where watershed was considered a random effect (Ott 1993; SAS Institute Inc. 1995). Watersheds were not significantly different ($P < 0.05$), therefore the data values from both Moraine Park and Horseshoe Park were pooled in the analysis to determine the effects of browsing, surface water hydrology, and proximity to streams. Analysis of variance (mixed procedure) (SAS Institute Inc. 1995) was used to test for significance at $P < 0.05$. Under our set of circumstances, we chose to use ANOVA as opposed to MANOVA as our response variables were limited and the scale of the response variables was appreciably different as in the case of instantaneous rates of photosynthesis compared to leaf carbon isotope discrimination (Potvin et al. 1990). A MANOVA may have improved the power of our statistical test, but the ANOVA results represent the most conservative findings and thus those are presented here. For source-water utilization differences between willow and sedge, we used a student's t-test ($P < 0.05$).

Results

Precipitation

Snowfall and Runoff

Over the course of our 3-year study, peak snowpack levels were above the long-term averages for Rocky Mountain National Park (Fig. 1) though their accumulation and dissipation patterns were different. Snowpack peaked in mid- to late-May in 1995, which was almost 30 days later than the long-term average (Fig. 1). In 1996, peak snowpack occurred close to that of the long-term average date in early May, which was similar to 1997, though the snow water equivalent at peak snowpack in 1997 was 30% greater than the long-term average. These snowpack characteristics transcended into some year-to-year variation in peak river levels; peak river levels in 1997 reaching 1 m in early June, 0.7 m in mid-June in 1996 and peak river levels of >1 m in late June in 1995 (Singer et al. 1997, 1998). In all years, once peak river depths had been reached, river levels gradually declined over the summer reaching their lowest levels in September, though precipitation events of 1 cm did slightly increase river levels for up to 1 week by up to 0.1 m (Singer et al. 1998).

Summer Rainfall

Summer precipitation is sporadic in the Rocky Mountain region. In general, summer rainfall begins in May with individual events being usually less than 1 cm though large showers can occur (Niwot Ridge LTER database; Alstad 1998). During our 3-year study period, the average daily precipitation was slightly higher in 1995, averaging 0.3 cm or approximately 47 cm for the summer period (150 days), while in 1996 summer rainfall was lower averaging 0.2 cm per day (30.5 cm total) (Fig. 2). Summer rainfall in 1996 was substantially less

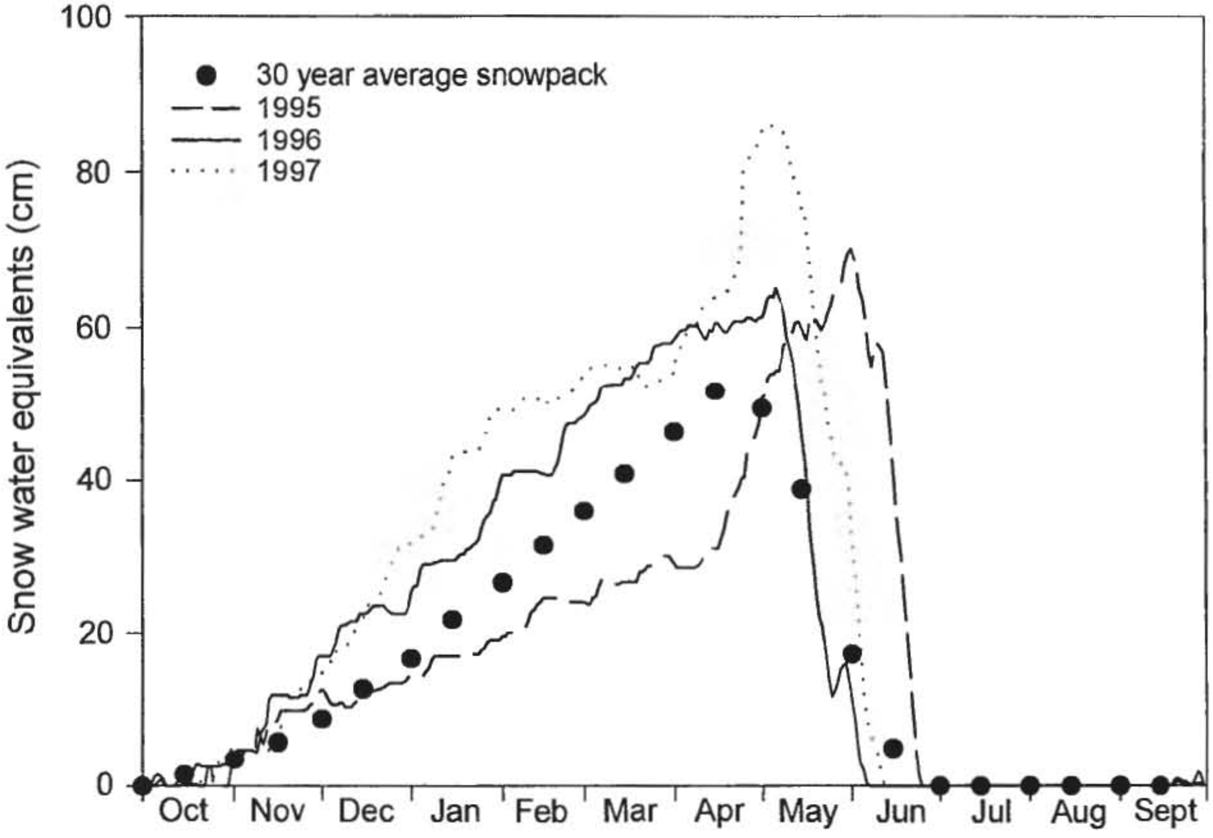

Fig. 1. Snowpack above Willow Park, Rocky Mountain National Park. Long-term (1961–1990) average versus 1995, 1996, 1997 water years. (Data from USDA Snow Survey Office Lakewood, Colorado, 1995, 1996, 1997.)

than in 1995 and 1997, especially in the months of June, July and August.

Total Plant Water Potentials

Stem water potentials of willow were significantly higher ($P < 0.01$) in 1995 as compared to 1996, averaging -0.6 MPa (n = 55) in 1995 and -0.9 MPa (n = 68) in 1996. In 1995, stem water potentials of willow decreased significantly from June (-0.54 MPa) to early September (-1.1 MPa) (Fig. 3a). There were no significant differences in plant water potentials between ungrazed and grazed plants, between plants in the short-watered willow sites and short-control willow sites, or between plants from different landscape positions in 1995. The total water potentials of willow plants decreased significantly ($P < 0.05$) over the course of the 1996 growing season, as well, (Fig. 3b) with grazed willow plants having higher water potentials than ungrazed plants ($P < 0.05$). Consequently, willow water potential exhibits a significant ($P < 0.02$) 2-way interaction where during the drier year; herbivory resulted in significant increases in plant water potentials. Water table manipulation (short-watered treatment) did not affect willow water potentials in either year, nor were there significant differences in the total water potentials between plants that were streamside as opposed to those in upland positions.

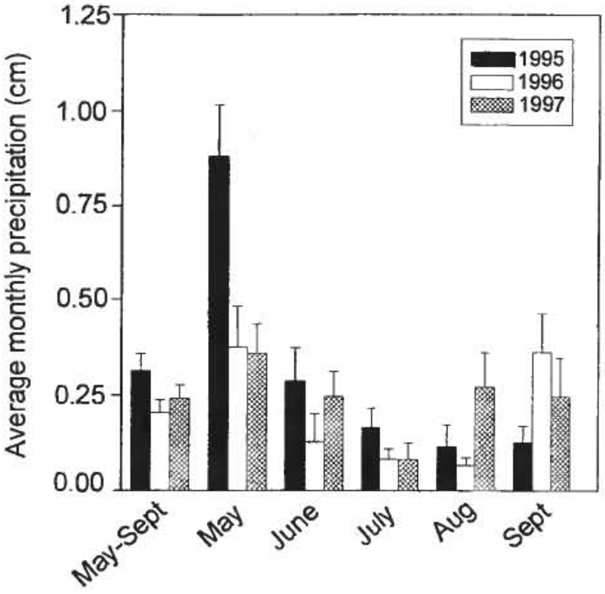

Fig. 2. Average monthly precipitation (cm) for the 1995, 1996, and 1997 growing seasons, Willow Park Climate Station, Rocky Mountain National Park. (Data from the USDA Snow Survey Office Lakewood, Colorado, 1995, 1996, 1997.)

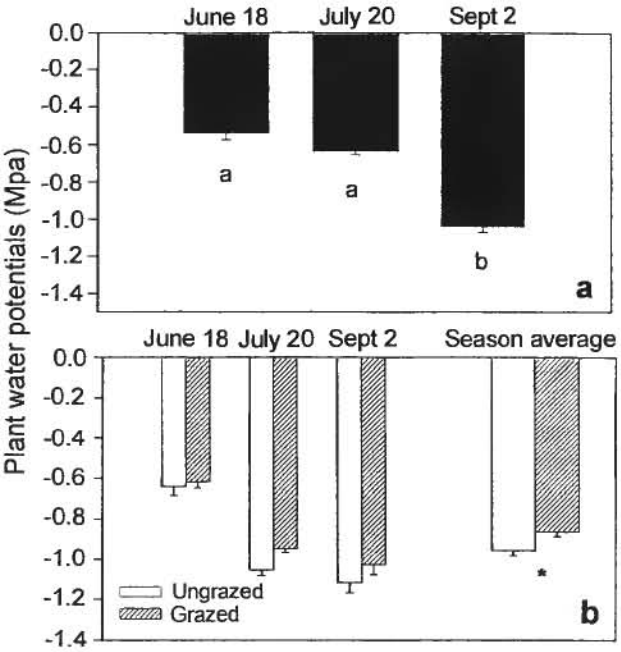

Fig. 3. *Salix monticola* plant water potentials for three sampling dates in 1995 (a) and 1996 (b) growing season and the yearly average water potentials for the grazed versus ungrazed (control) plants in 1996 (mean and S.E.). Different letters indicate significant ($P < 0.05$) differences between sampling dates. Significant differences between grazed and ungrazed (control) plants are noted with a * at $P < 0.05$.

Instantaneous Photosynthetic Rates

Instantaneous CO_2 assimilation rates of willow plants were not significantly ($P > 0.05$) different between 1995 and 1996, averaging 12.3-μmol m^{-2} s^{-1}. The rates of leaf CO_2 assimilation did not differ significantly between the June, July and September, though higher rates of assimilation in grazed willow plants were observed but only in July ($P < 0.05$) (Fig. 4a). Higher rates of carbon assimilation were also observed in plants that were streamside, though only where check dams had been installed and this only occurred in July ($P < 0.05$) (Fig. 4b).

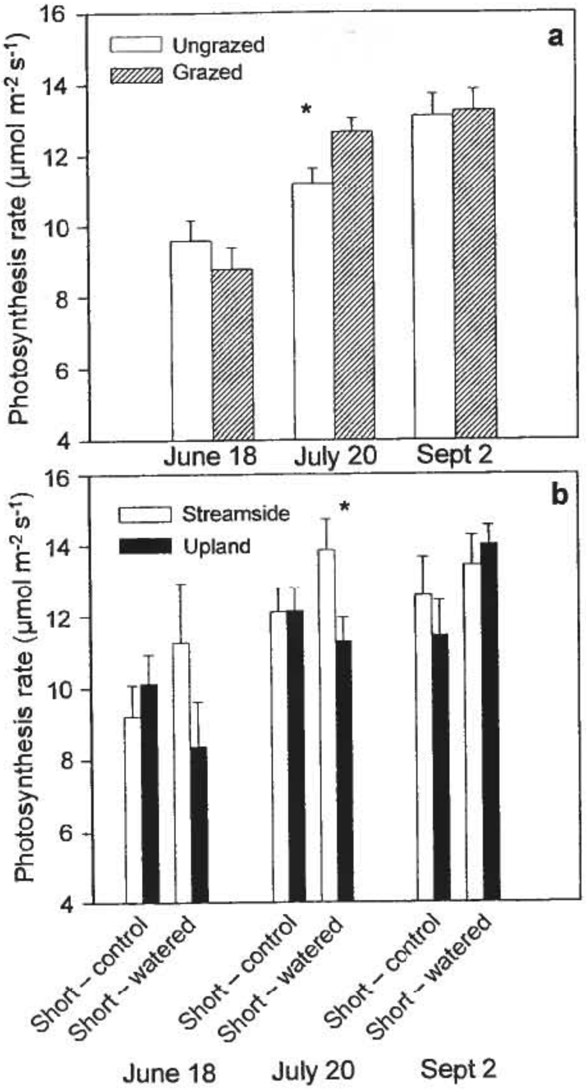

Fig. 4. *Salix monticola* photosynthetic rates for 1995 and 1996 growing seasons combined for grazed versus ungrazed (control) plants (a) and for plants that were streamside as opposed to located in upland positions where streams were either undammed or artificially dammed (mean and S.E.). An * indicates significant differences at $P < 0.05$ for grazed or ungrazed plants or plants that were located adjacent to streams or in upland positions.

Leaf Nitrogen

Leaf nitrogen content of willow plants decreased significantly ($P < 0.05$) between June and September (Fig. 5) while no significant differences between years were found. Leaf nitrogen contents were initially 3.2%, remained near this level through July, and decreased to 2.1% in September before leaf senescence. Grazed willow plants exhibited significantly ($P < 0.05$) higher leaf N contents in June compared to ungrazed plants though these differences were diminished by September. Leaf nitrogen content was not affected by damming nor were the leaf N contents different between streamside plants and those in upland locations.

Leaf Carbon Isotope Discrimination

Overall, the leaf carbon isotope discrimination (LCID) was significantly ($P > 0.001$) higher for willow

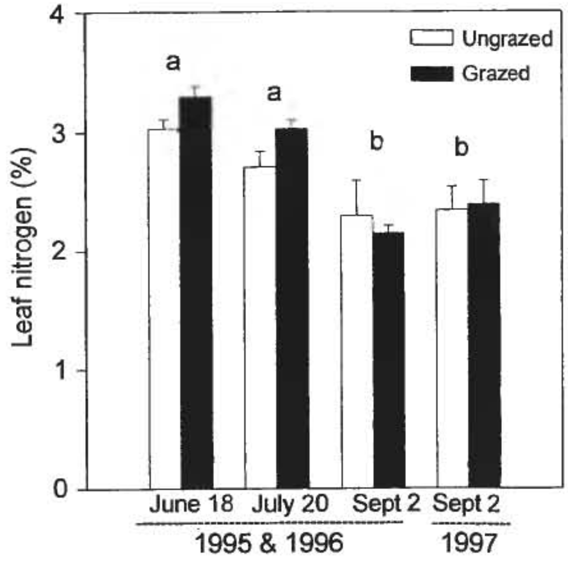

Fig. 5. Leaf nitrogen content (%) of ungrazed (control) and grazed plants for three sampling dates in 1995 and 1996 combined and for September in 1997 (means and S.E.). Different letters indicate significant differences, $P < 0.05$, between sample dates.

(20.5%) as opposed to that for the graminoid sedge that averaged 19.6% (data not shown). These differences were about 1%, representing a difference of approximately 30-ppm internal CO_2 concentrations (Donovan and Ehleringer 1994), which could be the result of species-specific differences in gas exchange, differences in leaf temperatures (Ehleringer et al. 1992) or possible differences in CO_2 sources (atmospheric vs. soil respired).

The LCID of willow plants harvested at the end of the growing season were found to be significantly (P <0.05) different between years for ungrazed plants (Fig. 6a). Carbon isotope discrimination was significantly (P <0.05) lower in 1996 compared to 1995 and 1997, by up to 1%. Grazing, too, significantly (P <0.003) affected the LCID of willow, with grazed plants having higher overall discrimination values compared to plants that were ungrazed in all years (Fig. 6b). Proximity to stream channel also affected the LCID of willow plants whereby plants adjacent to active stream channels had higher Δ values than plants away from stream channels, though this response was only significant (P <0.05) in year two (Fig. 6c). The Δ values of sedge were unaffected by proximity to stream channels.

$\delta^{18}O$ of Precipitation, Stream Water, and Plant Xylem Water

The average $\delta^{18}O$ values of the snow collected in late May in the riparian zone was -16.4%, while the $\delta^{18}O$ values of summer rain collected near the study sites averaged almost -8% (Fig. 7a). Over the course of the summer, stream water was depleted in $\delta^{18}O$ compared to summer rain, which became progressively enriched between May and October (Fig. 7b). Both stream water and groundwater collected from wells within the experimental sites, had $\delta^{18}O$ values almost identical to that of snow, averaging -16.1%. The $\delta^{18}O$ values of snow, stream and groundwater (well water) were very similar and were not significantly different, though on average willow $\delta^{18}O$ values were enriched compared to stream water while sedge xylem water $\delta^{18}O$ values were significantly (P <0.001) enriched compared to stream water. Willow and sedge $\delta^{18}O$ values were significantly different (P <0.001; Fig. 7a).

The $\delta^{18}O$ values of willow xylem water was not significantly different between plants that were streamside or in upland positions. In addition, the $\delta^{18}O$ values of xylem water in willow plants that were grazed by elk were not significantly different than those that were not grazed (Table 1) nor were there significant changes in the $\delta^{18}O$ values of xylem water in willow plants over the course of the summer (Singer et al. 1998). Sedge plants exhibited a seasonal enrichment and plants located adjacent to streams had $\delta^{18}O$ values of xylem water that were significantly (P <0.01) depleted compared with plants in upland locations in June and September (Fig. 8).

Our mixing model analyses showed that three-quarters (mean = 77%; se = 4.5%) of willow plant water

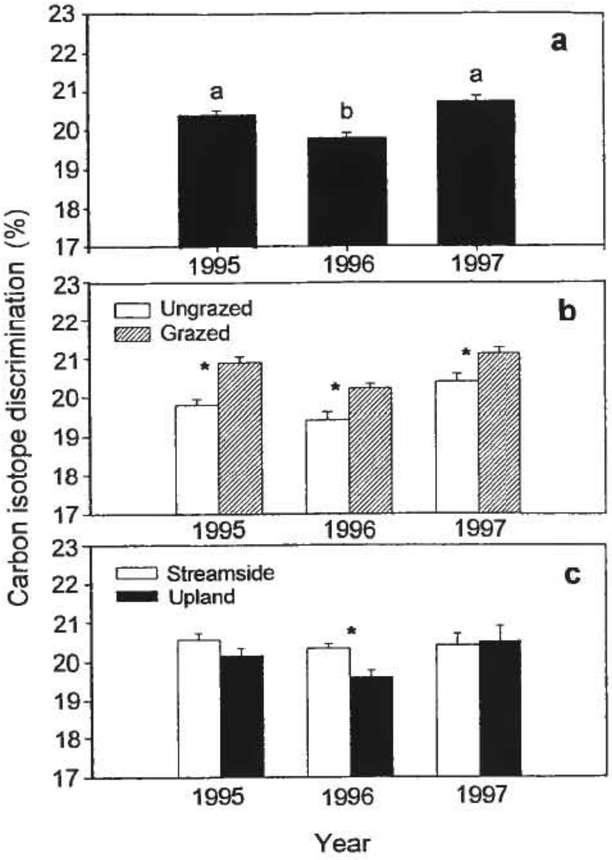

Fig. 6. *Salix monticola* leaf carbon isotope discrimination (LCID) values (mean and S.E.) based on plant collections late in the growing season (September) for 1995, 1996, and 1997 (a); late season LCID in ungrazed and grazed plants in 1995, 1996, 1997 (b); and late season LCID for plants located either streamside or in upland positions for 1995, 1996, and 1997 (c). Different letters indicate significant differences, P <0.05, between years and an * indicates significant differences between ungrazed or grazed plants or between plants located streamside or in upland positions.

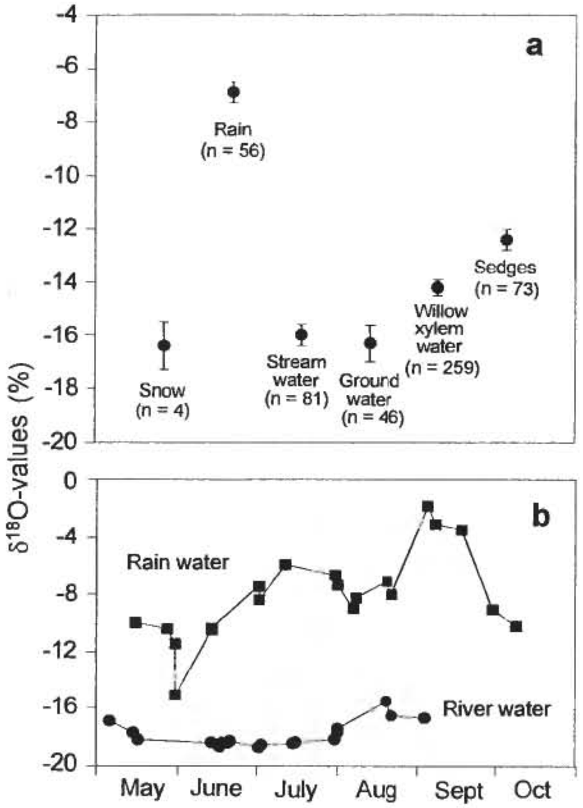

Fig. 7. δ^{18}O-values of *Salix monticola*, and *Carex* spp. xylem water, snow, rain, stream, and groundwater in Moraine Park, (1995, 1996, and 1997 combined) (a) and summer rain δ^{18}O-values versus stream water δ^{18}O-values during the 1997 growing season (b).

was derived from stream water/groundwater in these systems and only one-fourth (mean = 23%; se = 3%) of their water came from summer rain. In contrast, sedge reliance was significantly ($P < 0.01$) greater on summer rain (45%; se = 4%) while obtaining the other one-half of their water from groundwater (55%; se = 3%).

Discussion

We initially anticipated that winter grazing by elk would be detrimental to the physiological performance of willow, reducing rates of gas exchange, for example. We also anticipated that increases in stream water levels in short-watered willow sites would have a positive effect on willow carbon and water relations and that both willow and associated graminoid species would be competing for similar water resources in these riparian habitats. However, we found that in general, most of our measures of willow physiological performance were enhanced by winter grazing by elk and that the improvements in gas exchange (Δ) were most likely due to increases in stomatal conductance as opposed to an increase in photosynthetic rates. Under the mesic conditions of our study (snowfall and precipitation similar to the 30 year average in all years) the changes in surface water that we experimentally induced were not of a magnitude to elicit a consistent shift in willow carbon and water relations, though we would anticipate in years when snowpack and runoff are low, damming would have significant effect on the carbon and water relations of willow, especially late in the summer. In addition, our water source (δ^{18}O) data indicates that willow and the surrounding graminoids (sedge) do not use an identical mix of water sources and thus, competition for water may not be a factor which is curtailing the growth, development and regeneration of willow in these montane riparian habitats.

Generally, willow stem water potentials were high (-0.8 MPa) for both 1995 and 1996, reflecting the mesic nature of these ecosystems in contrast to woody plant water potentials in more arid regions (Gordon et al. 1989; Welker and Menke 1990; Momen et al. 1992), though we did observe higher stem water potentials in grazed willow plants relative to ungrazed plants in 1996 which is consistent with earlier studies of woody species (Welker and Menke 1990) and graminoid responses to grazing (Toft et al. 1987; Day and Detling 1994). The proposed mechanism by which grazed plants have higher water potentials is an increase in the root to shoot ratio of grazed plants whereby canopies are fairly smaller relative to their root biomass (McNaughton 1983; Wright et al. 1989). The effect of grazing on willow water potentials was, however, not consistent between 1995 and 1996 due possibly to the variation in snowfall timing and dissipation and surface water run-off patterns (Fig. 1). The significant increase in stem water potentials of the grazed willow plants in the second year may have resulted from the dependence of this response on a drier overall annual hydrologic regime, especially the diminished stream flows late in the summer (Singer et al. 1997, 1998).

The nitrogen content of willow leaves ranged between 3.2% and 2.2% over the entire growing season (Fig. 5), and were generally higher than other N values reported for willow leaves from other montane ecosystems (Singer et al. 1994; Dernburg 1997; Phillips 1997), though they were within the range reported by Phillips (1997). Winter grazing by elk did, however, cause an

Table 1. δ^{18}O-values (mean and SE) for *Salix monticola* stem water from riparian areas of the elk winter range in Rocky Mountain National Park, 1995 and 1996.^{a}

Source water	1995		1996		1995 and 1996 combined	
Streamside	-14.4	(0.6)	-14.4	(0.3)	-14.4^{a,b}	(0.4)
Upland	-12.5	(0.9)	-14.6	(0.3)	-13.6	(0.3)
Grazed	-12.2	(1.1)	-15.2	(0.5)	-13.7	(0.4)
Ungrazed	-13.8	(0.5)	-15.0	(0.4)	-15.0	(0.4)
Average	-12.9	(0.5)	-14.8	(0.2)	-14.2	(0.3)

[a] Values are relative to Standard Mean Oceanic Water (SMOW).

[b] Means were not significantly different (P <05).

increase in the N content of leaves, though the effects were not consistent over the entire growing season. Only in June was leaf N of grazed plants significantly higher than for ungrazed plants (Fig. 5). This lack of a consistent effect was not surprising as the ungrazed treatment actually represented the removal of grazing of willow plants by elk in our exclosure, just one year before our physiological measurements. The inconsistency of a short-term response of changes in leaf N associated with herbivory does not, however, preclude a long-term change in leaf mineral nutrition and associated processes. In grazed grasslands, grasses consumed by herbivores consistently have higher leaf nitrogen than ungrazed plants (Ruess et al. 1983; Ruess and McNaughton 1984; Jaramillo and Detling 1992), resulting from a more juvenile nature of leaf tissue in grazed grasses that had higher N content (Ruess et al. 1983; Wallace et al. 1984; McNaughton et al. 1988) and from herbivore inputs of urea and feces which may increase the soil N content and thus increase the availability of N for plants (Floate 1981; Ruess and McNaughton 1984; Wallace et al. 1984; Jaramillo and Detling 1992).

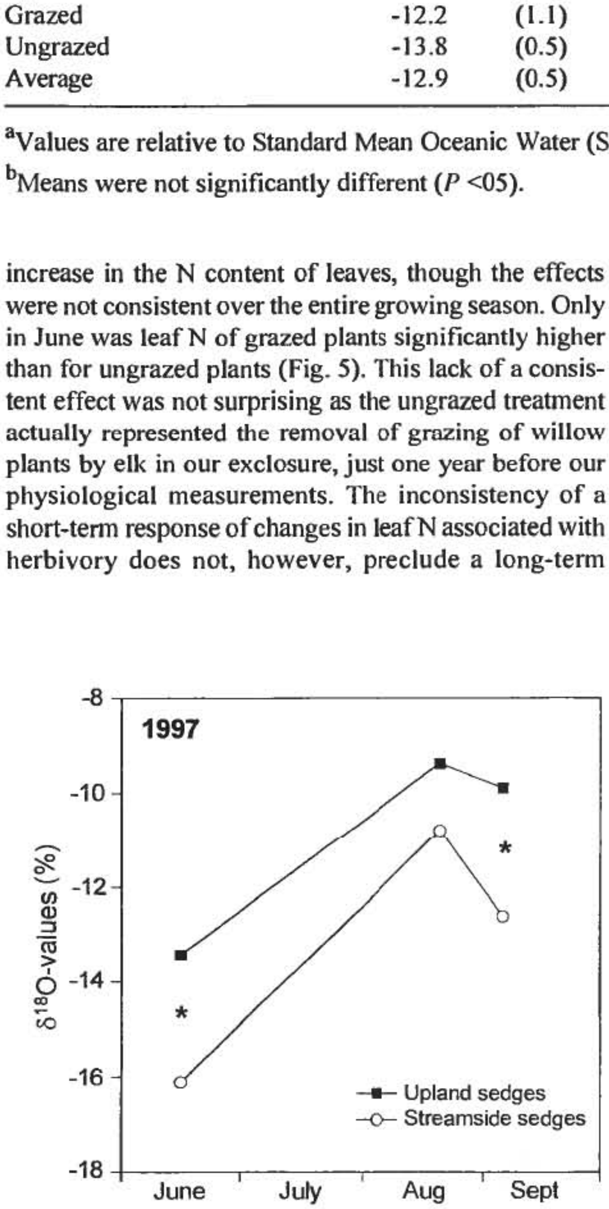

Fig. 8. δ^{18}O-values of sedge plants over the summer (1997) that were either streamside or in upland positions (mean and S.E.). An * indicates significant differences between landscape positions (P <0.05).

Willow leaf carbon isotope discrimination (Δ) was significantly higher for grazed as opposed to ungrazed plants in all years, contrary to our instantaneous gas exchange measures (Fig. 6). These increases in integrative leaf gas exchange indicate that over the course of the entire growing season, grazed plants may have had consistently higher intercellular CO_2 concentrations (Ehleringer et al. 1992). These differences in apparent carbon gain attributes induced by grazing may or may not correspond to differences in growth and reproduction, though higher LCID values were associated with higher water potentials in grazed as compared to ungrazed plants.

Higher rates of LCID values and associated higher rates of stomatal conductance could be due to reductions in leaf area associated with grazing without reductions in root biomass (McNaughton 1983). This could result in a shift in the root to shoot ratio, whereby acquisition of soil water and nutrients were distributed over a smaller canopy volume, altering gas exchange. This improvement in both the intrinsic and extrinsic conditions of grazed plants had been reported for graminoid species (Caldwell et al. 1981; McNaughton

1983) and less frequently for woody plants (Heichel and Turner 1983; Welker and Menke 1990; Houle and Simard 1996). Landscape position of willow plants across our valley floodplains also significantly influences LCID with streamside plants having higher Δ values than those plants that are in upland positions away from active stream channels (Fig. 6c). The higher rates of carbon isotope discrimination in streamside plants is likely due to greater access to streamwater which resulted in greater rates of stomatal conductance and higher C_i/C_a ratios (Ehleringer and Cooper 1988; Farquhar et al. 1989). Higher leaf carbon isotope discrimination of streamside plants as opposed to upland willow plants indicated that plants from streamside positions should have had either lower rates of photosynthesis or higher rates of stomatal conductance relative to the upland plants. However, photosynthesis was not different between streamside and upland plants. Thus, greater carbon isotope discrimination for streamside plants was probably caused by higher rates of stomatal conductance.

One would assume that higher rates of conductance would be associated with higher total plant water potentials in streamside plants. However, no significant differences were found in water potentials for plants from the two locations, suggesting that there existed a decoupling of total plant water status and stomatal conductance. Alternatively, plants near the streams may experience higher atmospheric humidity and thus lower vapor pressure deficits that should enhance stomatal conductance and subsequent carbon isotope discrimination (Schulze et al. 1987).

The mean xylem water $\delta^{18}O$ values of willow plants shifted very little over the course of the growing season, and were consistently close to that of streamwater averaging -14%. The slight enrichment from -16% to -14% for willow plants indicated the use of summer rain, but only to a small extent (~25%) indicating that streamwater was the dominant source of water used by willow. In contrast, sedge $\delta^{18}O$ values were much closer to that of summer rain on average (Fig. 7). However, sedge plants do exhibit a seasonal enrichment as their reliance on summer rain progressively increases and sedge plants close to stream channels make greater use of streamwater than plants in upland locations, which utilize summer rain to a greater degree (Fig. 8).

These differences in source water utilization between the graminoid and woody life forms in our riparian ecosystem are likely based in part on rooting characteristics, including root form and distribution. Grasses typically have fibrous root systems concentrated in part close to the soil surface providing a mechanism whereby they may utilize light summer showers (Sala and Lauenroth 1982; Dodd et al. 1998). Woody plants, including willow and cottonwood species, often have roots at depths providing access to deeper water sources, typically untapped by surrounding herbaceous vegetation, resulting in the spatial partitioning of soil resources (Walter 1979). Soil resource partitioning is typically hypothesized to occur only in semi-arid settings (Gordon et al. 1989; Dodd et al. 1998), though our study suggests that even in mesic habitats, different life forms may utilize different water source combinations.

Landscape position appeared not to influence the water source used by willow (Table 1). In general, the stream water is infiltrating the vadose zone across the entire riparian floodplain and the small difference in microtopography (<1.0 m) associated with streamside and upland plants was not enough to significantly affect the water source, especially in wet years. Ground water use, regardless of proximity to existing stream channels, was consistent with the findings of Dawson and Ehleringer (1991) in a riparian plant water-use study that showed that streamside trees used ground water throughout the season. This observation was also seen with boxelder (*Acer negundo* L.) trees in a montane riparian system in Arizona (Kolb et al. 1997). Deep root systems in these cases supplied the majority of the water regardless of proximity to stream channels.

In summary, the carbon and water relations of willow were significantly affected by winter grazing by elk and in some cases by landscape position with regards to proximity to active steam channels. Grazing of willow by elk increases plant water potentials and integrative measures of gas exchange (Δ), though grazing did not consistently affect instantaneous rates of photosynthesis or the sources of water used by willow as measured by the $\delta^{18}O$ values of xylem water. It appears that under the mesic conditions of our study, grazing may have a positive effect on carbon and water relations of willow, and that competition for water sources with surrounding graminoids may not be severe and may not hinder willow water acquisition or carbon fixation. Under drier conditions (low snowpack and low stream flow), however, willow plants will likely experience water stress and increased competition for water with herbaceous neighbors, leading to reductions in willow carbon fixation. Decreases in carbon gain may in turn lead to reductions in grazing resistance which would threaten the regeneration of *S. monticola* in these ecosystems.

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Literature Cited

Alstad, K. P. 1998. Seasonal patterns of *Salix* carbon and water relations: Effects of browsing and hydrologic conditions. Masters thesis, Department of Rangeland Ecosystem Science. Colorado State University, Fort Collins.

Baron, J. 1992. Chapter 8. Surface waters. Pages 142–182 *in* J. Baron, editor. Biogeochemistry of a subalpine ecosystem: Loch Vale Watershed. Volume 70. Springer-Verlag, New York.

Briske, D. D. 1986. Plant responses to defoliation: morphological considerations and allocation priorities. Pages 425–427 *in* P. J. Joss, P. W. Lynch, and O. B. Williams, editors. Rangelands: A resource under siege. Proceedings of the second international rangeland congress, Australian Academy of Sciences, Canberra, Australia.

Busch, D. E., and S. D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. Ecological Monographs 65:347–370.

Busso, C. A., and J. H. Richards. 1995. Drought and clipping effects on tiller demography and growth of two tussock grasses in Utah. Journal of Arid Environment 29:239–251.

Caldwell, M. M., J. H. Richards, D. A. Johnson, R. S. Nowak, and R. S. Dzurec. 1981. Coping with herbivory: Photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. Oecologia 50:14–24.

Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78:1958–1965.

Chapin III, S. F., A. J. Bloom, C. B. Field, and R. H. Waring. 1987. Plant responses to multiple environmental factors. Bioscience 37:49–56.

Coughenour, M. B., S. J. McNaughton, and L. L. Wallace. 1985. Responses of an African tall-grass (*Hyparrhenia filipendula* staph.) to defoliation and limitations of water and nitrogen. Oecologia 68:80–86.

Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide. Geochemica Et Cosmochimica Acta 12:133–149.

Dawson, T. E. 1993. Water sources of plants as determined from xylem water isotopic composition: Perspectives on plant competition, distribution, and water relations. Pages 465–496 *in* J. R. Ehleringer, A. E. Hall, and G. D. Farquhar, editors. Stable isotopes and plant carbon-water relations. Academic Press, San Diego, Calif.

Dawson, T. E., and J. R. Ehleringer. 1991. Streamside trees that do not use stream water. Nature 350:335–337.

Dawson, T. E., and J. S. Pate. 1996. Seasonal water uptake and movement in root systems of Australian phreatrophytic plants of dimorphic root morphology: A stable isotope investigation. Oecologia 107:13–20.

Day, T. A., and J. K. Detling. 1994. Water relations of *Agropyron smithii* and *Bouteloua gracilis* and community evapotranspiration following long-term grazing by prairie dogs. American Midland Naturalist 132:381–392.

Dernburg, A. R. 1997. Cattle preferences for willow (*Salicaceae*) in a montane riparian site. Ph.D. Colorado State University, Ft. Collins.

Detling, J. K., and E. Painter. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. Oecologia 41:127–134.

Dodd, M. B., W. K. Lauenroth, and J. M. Welker. 1998. Differential water resource use by herbaceous and woody plants in a shortgrass steppe community. Oecologia 117(4):504–512.

Donovan, L. A., and J. R. Ehleringer. 1994. Carbon isotope discrimination, water-use efficiency, growth, and mortality in a natural shrub population. Oecologia 100:347–354.

Ehleringer, J. R. 1991. $^{13}C/^{12}C$ fractionation and its utility in terrestrial plant studies. Pages 187–200 *in* carbon isotope techniques. Academic Press Inc., San Diego.

Ehleringer, J. R., and T. A. Cooper. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia 76:562–566.

Ehleringer, J. R., and T. E. Dawson. 1992. Water uptake by plants: Perspectives from stable isotope composition. Plant, Cell and Environment 15:1073–1082.

Ehleringer, J. R., and C. B. Osmond. 1989. Stable isotopes. Pages 281–300 *in* R. W. Pearcy, J. R. Ehleringer, H. A. Mooney, and P. W. Rundel, editors. Plant physiological ecology. Field methods and instrumentation. Chapman and Hall, London.

Ehleringer, J. R., S. L. Phillips, and J. P. Comstock. 1992. Seasonal variation in the carbon isotope composition of desert plants. Functional Ecology 6:396–404.

Epstein, S., and T. Mayeda. 1953. Variations of ^{18}O content of water from natural sources. Geochemica Et Cosmochimica Acta 42:213–224.

Evans, J. R., T. D. Sharkey, J. A. Berry, and G. D. Farquhar. 1986. Carbon isotope discrimination measured concurrently with gas exchange to investigate CO_2 diffusion in leaves of higher plants. Australian Journal of Plant Physiology 13:281–292.

Fahnestock, J. T., and J. K. Detling. 1999. Plant responses to defoliation and resource supplementation in the Pryor Mountains. Journal of Range Management 52(3):263–270.

Farquhar, G. D., M. C. Ball, S. von Caemmerer, and Z. Roksandic. 1982. Effect of salinity and humidity on δ^{13}C value of halophyte - Evidence for diffusional isotope fractionation determined by the ratio of intercellular/atmospheric partial pressure of CO_2 under different environmental conditions. Oecologia 52:121–124.

Farquhar, G. D., J. R. Ehleringer, and K. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40:503–537.

Feild, T. S., and T. E. Dawson. 1998. Water sources used by *Didymopanax pittieri* at different life stages in a tropical cloud forest. Ecology 1448–1452.

Floate, M. J. S. 1981. Effects of grazing by large herbivores in agricultural ecosystems. Pages 585–601 *in* F. E. Clark and T. Rosswall, editors. Terrestrial nitrogen cycles: Process, ecosystem strategies and management impacts. Volume 33. Ecological Bulletin, Swedish Natural Science Research Council, Stockholm.

Gat, J. R. 1980. The isotopes of hydrogen and oxygen in precipitation. Page 21 *in* P. Fritz and J. Ch. Fontes, editors. Handbook of environmental isotope geochemistry. Elsevier Scientific Publishing Company, New York.

Georgiadis, N. J., R. W. Ruess, S. J. McNaughton, and D. Western. 1989. Ecological conditions that determine when grazing stimulates grass production. Oecologia 81:316–322.

Gleick, P. H. 1998. Water in crisis: Paths to sustainable water use. Ecological Applications 8:571–579.

Gordon, D. R., J. M. Welker, K. J. Rice, and J. W. Menke. 1989. Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. Oecologia 79:533–541.

Heichel, G. H., and N. C. Turner. 1983. CO_2 assimilation of primary and regrowth foliage of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.): Response to defoliation. Oecologia 57:14–19.

Houle, G., and G. Simard. 1996. Additive effects of genotype, nutrient availability and type of tissue damage on the compensatory response of *Salix planifolia* spp. to simulated herbivory. Oecologia 107:373–378.

Jaramillo, V. J., and J. K. Detling. 1992. Small scale heterogeneity in a semi-arid North American grassland. I. Tillering, N uptake and retranslocation in simulated urine patches. Journal of Applied Ecology 29:1–8.

Kolb, T. E., S. C. Hart, and R. Amundson. 1997. Boxelder water sources and physiology at perennial and ephemeral stream sites in Arizona. Tree Physiology 17:151–160.

LECO. 1993. CHN-1000 Elemental Analyzer Instruction Manual Version 1.4. LECO Corp., St. Joseph, Missouri.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329–336.

McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. Bioscience 38:794-800.

Momen, B., J. W. Menke, and J. M. Welker. 1992. Tissue water relations *Quercus wislizenii* seedlings: Drought resistance in a California evergreen oak. Acta Ecologica 13:127–136.

Naiman, R. J., C. A. Johnston, and J. C. Kelly. 1988. Alteration of North American streams by beaver. Bioscience 38:753–762.

Naiman, R. J., G. Pinay, C. Johnston, and J. Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75:905–921.

Naiman, R. J., J. Magnuson, D. McKnight, J. Stanford, and J. Karr. 1995. Freshwater ecosystems and their management: A national initiative. Science 270:584–585.

Naiman, R. J., J. J. Manuson, and P. L. Firth. 1998. Integrating cultural, economic and environmental requirements for fresh water. Ecological Applications 8:569–570.

O'Leary, M. H. 1981. Carbon isotope fractionation in plants. Phytochemistry 20:553–567.

Ott, L. 1993. An introduction to statistical methods and data analysis. Fourth edition. Duxbury Press, Belmont, Calif.

Pimentel, D., J. Houser, E. Preiss, O. White, H. Fang, L. Mesnick, T. Barsky, S. Tariche, J. Schreck, and S. Alperr. 1997. Water resources: Agriculture, the environment, and society. Bioscience 47:97–106.

Potvin, C., M. J. Lechowicz, and S. Tardif. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. Ecology 71:1389–1400.

Phillips, R. 1997. Forage quality as affected by previous cattle use in a montane riparian ecosystem. M.S. thesis, Colorado State University, Ft. Collins.

Ruess, R. W., and S. J. McNaughton. 1984. Urea as a primitive coupler of plant-herbivore interactions. Oecologia 63:331–337.

Ruess, R. W., S. J. McNaughton, and M. B. Coughenour. 1983. The effects of clipping, nitrogen source and nitrogen concentration on the growth responses and nitrogen uptake of an East African sedge. Oecologia 59:253–261.

Sala, O. E., and W. K. Lauenroth. 1982. Small rainfall events, an ecological role in semi arid regions. Oecologia 53:301–304.

SAS Institute, Inc. 1995. SAS user's guide. Release 6.11. SAS Institute Inc., Cary, NC.

Schulze, E. D., R. H. Robichauz, J. Grace, P. W. Rundel, and J. R. Ehleringer. 1987. Plant water balance. Bioscience 37:30–37.

Singer, F. J., L. C. Mack, and R. G. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435–443.

Singer, F., T. Elliot, M. Coughenour, J. Welker, S. Williams, R. Peinetti, R. Menezes, L. Zeigenfuss, K. Alstad, D. Barnett, D. Valentine, R. Cates, and J. Zou. 1997. Large mammalian herbivores, plant interactions and ecosystem processes in five national parks – second annual report. Cooperative Agreement 1445-0009-94-1074, Subagreement 2. U.S. Geological Survey, Biological Resources Division. Ft. Collins, Colo.

Singer, F., T. Elliot, M. Coughenour, J. Welker, S. Williams, R. Peinetti, R. Menezes, L. Zeigenfuss, K. Alstad, D. Barnett, D. Valentine, R. Cates, and J. Zou. 1998. Large mammalian herbivores, plant interactions and ecosystem processes in five national parks – third annual report. Cooperative Agreement 1445-0009-94-1074, Subagreement 3. U.S. Geological Survey, Biological Resources Division. Ft. Collins, Colo.

Svejcar, T. J., and J. D. Trent. 1995. Gas exchange and water relations of Lemmon's willow and Nebraska sedge. Journal of Range Management 48:121–125.

Toft, N. L., S. J. McNaughton, N. J. Georgiadis. 1987. Effects of water stress and simulated grazing on leaf elongation and water relations of an East African grass, *Eustachys paspaloides*. Australian Journal of Plant Physiology 14:211–226.

U.S. Department of Agriculture, Snow Survey Office. 1995, 1996, 1997. Snowpack data for Rocky Mountain National Park. National Resources Conservation Service. Lakewood, Colo.

Wallace, L. L., S. J. McNaughton, and M. B. Coughenour. 1984. Compensatory photosynthesis responses of three African graminoids to different fertilization, watering, and clipping regimes. Botanical Gazette 145:151–156.

Walter, H. 1979. Vegetation of the earth. Springer-Verlag, New York.

Welker, J. M., and D. D. Briske. 1992. Clonal biology of the temperate caespitose graminoid *Schizachyrium scoparium*: A synthesis with reference to climate change. Oikos 56:357–365.

Welker, J. M., and J. W. Menke. 1990. The influence of simulated browsing on tissue water relations, growth and survival of *Quercus douglasii* (Hook and Arn.) seedlings under slow and rapid rates of soil drought. Functional Ecology 4:807–817.

Welker, J. M., D. R. Gordon, and K. J. Rice. 1991. Capture and allocation of nitrogen by *Quercus douglassi* seedlings in competition with annual and perennial grasses. Oecologia 87:459–466.

Welker, J. M., D. D. Briske, and R. W. Weaver. 1987. Nitrogen-15 partitioning within a three-generation tiller sequence of the bunchgrass *Schizachyrium scoparium*: Response to selective defoliation. Oecologia 24:330–334.

Welker, J. M., E. J. Rykiel, D. D. Briske, and J. D. Goeschl. 1985. Carbon import among vegetative tillers within two bunchgrasses: Assessment with carbon-11 labeling. Oecologia 67:209–212.

Welker, J. M., T. H. E. Heaton, B. Spiro, and T. V. Callaghan. 1995. Indirect effects of winter climate on the delta $\delta^{13}C$ and the delta dD characteristics of annual growth segments in the long-lived, arctic plant *Cassitope tetragona*: A preliminary analysis. Paleoclimatology Research 15:105–120.

Welker, J. M., U. Molau, A. N. Parsons, C. H. Robinson, and P. A. Wookey. 1997. Responses of *Dryas octopetala* to ITEX environmental manipulations: A synthesis with circumpolar comparisons. Global Change Biology 3(1):61–73.

Wright, S. L., R. W. Hall, and J. W. Peasock. 1989. Effect of simulated insect damage on growth and survival of northern red oak (*Quercus rubra* L.) seedlings. Environmental Entomology 18:235–239.

CHAPTER EIGHT

Isotopic Evidence of the Effects of Herbivory and Landscape Position on Plant Nitrogen Sources in a Riparian Ecosystem

By

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Abstract. During the last few decades, changes in ungulate grazing and surface water hydrology have occurred in elk winter ranges in Rocky Mountain National Park (RMNP). These changes may be influencing the biogeochemistry and vegetation structure of these habitats, as evidenced by the decline in willow (*Salix* spp.) communities. Previous studies in riparian areas of RMNP demonstrated that sedges (*Carex* spp.) and willow utilize different proportions of groundwater vs. rainwater across different landscape positions in those habitats. However, whether these two plant growth forms differ in their sources of N has remained unknown. We conducted field studies in elk winter ranges in RMNP during the growing seasons of 1997 and 1998. In these studies, we utilized ^{15}N natural abundance and non-isotopic techniques to identify the N sources of willow and sedge under different herbivory treatments and landscape positions. Based on the isotopic evidence, we found that sedge plants seemed to acquire smaller proportions of groundwater N in upper landscape positions in comparison to the woody willow species, suggesting that the deeper rooting characteristics of willow may allow these plants to access more groundwater N. However, grazed willow plants in upper landscape positions seemed to acquire less groundwater N as compared to willow plants protected from herbivory. Therefore, it appears that herbivory by elk and the shifts in landscape hydrology, caused by reductions in beaver activity and a warming and drying trend, could have an interacting effect on willow by increasing the frequency of drought stress and possibly reducing the availability of nitrogen. The combination of these factors could explain, in part, the decline of willow communities across riparian habitats in Rocky Mountain National Park.

Keywords: ^{15}N natural abundance, beaver, *Carex*, elk, Rocky Mountain National Park, *Salix*, willow.

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Introduction

Changes in ungulate grazing and hydrology have occurred in the winter ranges of elk in Rocky Mountain National Park (RMNP) during the last few decades. These changes may be influencing the biogeochemistry and vegetation structure of these systems as evidenced by reductions in willow (*Salix* spp.) growth (Singer et al. 1998). Elk numbers have increased 3-fold (Singer et al. 1998) over the last 30 years, and currently a high density of elk (*Cervus elaphus*) graze these systems in winter. Changes in the hydrology of these systems are evident from aerial photographs between 1937 and 1996, which indicate that rivers are now less braided and there is less surface water than in the beginning of this century (Peinetti et al., this volume). These changes in hydrology are probably a result of the observed declines in beaver (*Castor canadensis*) activity (Stevens and Christianson 1980), which may change the biogeochemical cycles by altering the availability of stream and groundwater (Naiman et al. 1994; Terwilliger and Pastor 1999).

Based on $\delta^{18}O$ measurements, Alstad et al. (1999) found that sedge (*Carex* spp.) and willow in the elk winter ranges of RMNP utilize water from different sources. Willow appears to rely on groundwater (80% of total water uptake), which is recharged by streamwater throughout the floodplains. In addition, water sources of willow seemed to be independent of landscape position and consistent throughout the growing season. In contrast, sedges utilized mostly groundwater early in the season but seemed to take up increasing amounts of rainwater (up to 50%) towards the end of the season, especially when located in upper landscape positions. These differences in water source between the two plant functional groups may result from differences in rooting characteristics, but whether these two plant growth forms differ in their sources of nitrogen (N) is unknown. Based on the $\delta^{18}O$ measurements of Alstad et al. (1999), we anticipated that willows may be relying more strongly on groundwater N in comparison to sedges, especially in the case of plants located in upper landscape positions.

The mineral nutrition of plants in native habitats influences a suite of physiological and ecological processes such as carbon exchange, stress resistance, and competitive interactions (Chapin 1980; Welker et al. 1987, 1991; Nadelhoffer et al. 1999). Of the nutrients that may influence and limit plant growth, nitrogen is usually the most limiting element in terrestrial ecosystems (Aber et al. 1989; Nadelhoffer et al. 1999). Identifying the sources of plant nitrogen in terrestrial ecosystems cannot be easily done, but stable isotope techniques can be employed (Garten 1993; Michelsen et al. 1996; Nadelhoffer et al. 1996) especially under controlled experimentation and in combination with non-isotopic techniques (Handley and Scrimgeour 1997). Plants may acquire two forms of nitrogen mineralized from soil organic matter (NH_4^+ and NO_3^-) that may have different $\delta^{15}N$ values due to kinetic effects on isotope discrimination during organic matter decomposition (Shearer and Kohl 1986; Evans et al. 1996). In addition, a few studies have reported the uptake of organic forms of N from soil by some plants in arctic ecosystems (Chapin et al. 1993; Kielland 1994; Nasholm et al. 1998), but the relevance of the uptake of soil organic N forms by plants in other systems, including our study sites, is unknown, and still needs further investigation. In riparian habitats, soil inorganic N is not the only N source, as ground and stream water may contain inorganic N. Therefore, in riparian ecosystems, if the $\delta^{15}N$ signature of soil and water N sources differ, stable isotope techniques could be useful in combination with other approaches to characterize the patterns of plant N uptake (Handley and Raven 1992).

The primary questions asked by this study were: (1) Are there differences in the N uptake patterns of willow and sedge in different landscape positions? (2) How does winter elk herbivory affect the patterns of N uptake by willow and sedge in different landscape positions? Based on these questions, we hypothesized that: (a) sedge relies mostly on soil inorganic N in upper landscape positions, and on both soil inorganic N and groundwater N in lower landscape positions, following the patterns of water uptake; (b) regardless of landscape position, willow plants protected from grazing utilize a mixture of both groundwater and soil inorganic N because these plants, independently of landscape position, have access to the groundwater table; and (c) willow plants under elk grazing in upper landscape positions take up less groundwater N because grazing by elk may lead to a reduction in belowground carbon (C) allocation and limit the ability of these plants to reach the groundwater.

In order to test our hypotheses, we conducted field studies on the elk winter ranges in RMNP during the 1997 and 1998 growing seasons. In these studies, we utilized both ^{15}N natural abundance and non-isotopic biogeochemical techniques to identify the nitrogen sources of willow and sedge plants under herbivory treatments and different landscape positions.

Methods

Study Sites

Our study sites were located in two riparian ecosystems on the northeastern side of Rocky Mountain National Park: Moraine Park (Big Thompson River watershed, elevation 2,481 m) and Horseshoe Park (Fall River watershed, elevation 2,598 m). The two watersheds are within 5 km of each other and have perennial alpine snowfields at their headwaters (Baron 1992). Mean annual precipitation for the sites is 41 cm (Singer et al. 1998) and peak stream flow usually occurs in early to mid-June (USDA 1995, 1996). The 30-year average temperature for the adjacent Estes Valley ranges from 9 to 17°C during the 5-month growing season of May through September (Alstad et al. 1999). The study area consists of open grasslands and wet meadows dominated by sedges (*Carex* spp.) and willow (*Salix monticola*, *S. geyeriana*, and *S. planifolia*), with some birch (*Betula* spp.) (Singer et al. 1998). Among the *Salix* species, *S. monticola* is dominant in most areas and, for this reason, was selected as the target species for this study.

Grazing Treatments

Twelve 30 m x 46 m exclosures were erected to eliminate elk browsing (ungrazed plots) at randomly chosen sites within both riparian zones (six sites each in Horseshoe Park and Moraine Park) between August and November of 1994. Near each exclosure, a 30 m x 46 m plot area was marked off as a paired plot that was grazed by elk in winter (grazed plots). In each exclosure and associated grazed plot, an average of five shallow (0.5 m to 2 m) wells were installed using PVC pipes in the fall of 1994 to monitor groundwater levels and chemistry.

Design of Preliminary Experiment in 1997

Eight of the 12 sites in Moraine and Horseshoe Parks were selected (four sites in each park), and two willow plants were selected within each grazing treatment (grazed and ungrazed) for physiological and biogeochemical measurements. One representative plant was chosen in close proximity to streams (streamside) and another in areas distant from streams (upper landscape, which were at least 10 m in a horizontal direction from streams and approximately 0.4 to 0.6 m higher in elevation than streamside plants), resulting in a total of 32 selected plants and four experimental replications in each park. Sedge plots (1 m x 1 m) were marked next to each selected willow plant (within 2 m of distance). During August 1997, samples from non-photosynthetic tissue were collected from current year growth of willow and sedge plants, dried at 60°C for 72 hours, ground in a ball mill to pass a 0.5 mm sieve, and stored until analysis. Concentrations of carbon and nitrogen in plant tissue were determined using a LECO CHN Analyzer.

Surface water samples were collected with plastic vials from the Big Thompson and Fall Rivers in June, July, and August. Samples were collected at different dates from each river, combined in a single sample, and kept frozen until isotopic and chemical analyses.

In July 1997, 4-week in situ field soil incubations using aluminum cores (5 cm in diameter, 15 cm in length) were conducted according to the methodology described by Kolberg et al. (1997). Incubation cores (n = 5) were placed next to plants located at both streamside and upper landscape positions. At the end of the incubation period, the soil cores were collected, placed in plastic bags, kept refrigerated in coolers, taken to the laboratory, and kept refrigerated. Within two days of collection, the total soil weight of each sample was recorded, sub-samples (25 g) were extracted with 50 ml of 2 M KCl for 1 hour, filtered, and the extracts kept frozen until analysis. The total inorganic N (NH_4^+ plus NO_3^-) in river water samples and soil KCl extracts were diffused into 5 mm acidified filter paper disks according to the methodology described by Khan et al. (1998).

Experimental Design and Sampling in 1998

After observing a sharp contrast in the isotopic signatures of N sources and plants during the growing season of 1997, we established a different experimental design and conducted a more detailed study during the growing season of 1998. In this study, a total of 50 willow plants (23 and 27 in grazed and ungrazed plots, respectively) were selected from the 12 research sites of Moraine Park and Horseshoe Park. All the selected plants were located within 3 m from a well, in order to allow groundwater sampling and the determination of the exact water table depth next to each selected plant. Plants selected within the same site and grazing treatment were located at positions with different water table depths. Next to each willow plant (within 1 m), an associated sedge plot (0.5 m x 0.5 m) was marked for the purpose of collecting sedge tissue samples. Willow and sedge tissue samples (current annual growth [CAG]) were collected in both early July and early September, dried at 60°C for 72 hours, and then ground in a ball mill to pass a 0.5 mm sieve. Concentrations of carbon and nitrogen in plant tissue were determined using a LECO CHN Analyzer.

River water samples were collected from both the Big Thompson and Fall Rivers in mid-July, mid-August, and mid-September by immersing a 3.8 L container at different points along the river surface in the area of the experimental plots. The water samples were kept refrigerated in coolers until the inorganic N was diffused into 5 mm acidified filter paper disks as described by Khan et al. (1998).

Groundwater depth was monitored throughout the season by measuring the water levels in the wells associated with the plants. Groundwater samples (3.8 L) were collected in early August in each well using a small manual pump. A sub-sample (20 ml) from each groundwater and river water sample was placed into scintillation vials and frozen for the determination of groundwater N concentration using an Alpkem automated spectrophotometer. The remaining volume of each groundwater and river water sample was passed through a plastic column (20 cm long, 2 cm in diameter) filled with equal amounts of cation and anion exchange resins (US Filter, Pittsburgh, Pennsylvania). After all the water had gone through the column, the resin within each column was placed in a 250 ml Erlenmeyer flask and sequentially shaken for 15 minutes with five 30-ml aliquots of 2 M KCl as recommended by Kolberg et al. (1997). After each extraction, the extract was drained from the flask by placing a patch of nylon cloth at the mouth of the flask, and the five 30 ml aliquots from each sample were poured into a 200 ml plastic container and kept frozen until analysis. Before isotopic analysis, the N in river water and groundwater samples was diffused into 5 mm acidified filter paper disks, according to the methodology described by Khan et al. (1998).

In early August, next to each willow plant and sedge plot, three soil cores were collected (2.5 cm in diameter) to the depth of the groundwater. Each core was subdivided in 15 cm intervals up to a depth of 60 cm and 30 cm intervals up to a depth of 120 cm, depending on the depth of the water table. The soil from all three cores was combined by depth, placed in plastic bags, transported to the laboratory, air-dried, passed through a 2 mm sieve, and ground in a ball mill to pass a 0.25 mm sieve. Concentrations of total soil C and N were determined using a LECO CHN Analyzer.

Within and adjacent to the 12 exclosures, field soil incubations using aluminum cores (5 cm in diameter, 15 cm deep) were installed next to 19 willow plants and within the sedge plots, following the same procedure as described above for the 1997 growing season (Kolberg et al. 1997). For isotopic analysis, the inorganic N in the KCl extracts was diffused into 5 mm acidified filter paper disks as described by Khan et al. (1998).

Isotopic Analyses

The isotopic signatures of plant tissue, total soil N, and diffusion disks from water samples and extracts were determined using a Carlo-Erba NA 1500 Series 2 Carbon and Nitrogen Analyzer attached to a VG-Optima mass spectrometer at the Natural Resources Ecology Laboratory, Colorado State University. Natural ^{15}N abundance is expressed as delta units (*d*), which denotes parts per thousand deviations (%), from the ratio $^{15}N:^{14}N$ in atmospheric N_2,

$$\delta^{15}N = [(^{15/14}R_{sample} - {}^{15/14}R_{standard})/^{15/14}R_{standard}] \times 10^3$$

where R is the isotopic ratio and the standard is N_2 of air, which has a δ value of 0% (Handley and Scrimgeour 1997; Hogberg 1997).

Statistical Analyses

Statistical analyses were performed using the SAS Statistical Package (SAS 1995, Version 6.12, SAS Institute Inc., Cary, NC). During the 1997 growing season, plant tissue $\delta^{15}N$ was analyzed using a split-plot design with grazing treatments as the main factor and landscape positions as sub-plots. During the 1998 growing season, correlation and regression analyses were used to test our *apriori* hypotheses regarding the relationships between the $\delta^{15}N$ values of plant, soil or water, and landscape position.

Results

Preliminary Experiment – 1997 Growing Season

The $\delta^{15}N$ values of soil inorganic N in the experimental plots of Moraine and Horseshoe Parks averaged -6.14% (±0.51) and were significantly ($P = 0.003$) more depleted than river water $\delta^{15}N$ values from Big Thompson and Fall Rivers, which averaged -1.00% (±0.52). The sharp contrast between $\delta^{15}N$ values of potential plant N sources in our sites is very relevant, as it corresponds to the differences in plant tissue δ^{15}N values in different landscape positions.

Tissue δ^{15}N values of sedge plants ranged from -0.6 to +3.2%, while for willow plants these values ranged from -4.3 to +2.2%. There were no significant effects of elk herbivory on plant tissue δ^{15}N values, but landscape position had a significant effect on sedge tissue δ^{15}N (Table 1). Sedge plants located in upper landscape positions had δ^{15}N values similar to the δ^{15}N values of soil inorganic N, while the δ^{15}N values of sedge plants located adjacent to streams were significantly ($P < 0.05$) more enriched. To the contrary, willow tissue δ^{15}N was not affected by landscape position and was consistently near the value of stream water δ^{15}N.

1998 Growing Season

The patterns of δ^{15}N values of willow and sedge leaf tissue in 1998 were similar to 1997. Sedge tissue δ^{15}N was significantly influenced by landscape position (shallow water table depth is associated with streamside locations and deeper water table depth is associated with upland locations), during both July and September (Fig. 1). In contrast, willow δ^{15}N was not significantly affected by landscape position (water table depth), with the exception of grazed plants in July (Fig. 1). For both sedge and willow, there were no significant differences between the regression lines of the two grazing treatments in both sampling dates.

The data from our non-isotopic measurements yielded no significant differences between treatments. Throughout the growing season, there were no significant correlations between plant tissue total nitrogen content and water table depth or total soil N. Willow tissue nitrogen concentration (% dry weight) was significantly higher ($P < 0.05$) in grazed than in ungrazed plots in both sampling dates, averaging 2.72% and 2.27% in July, and decreasing to 2.23% and 2.06% in September, in grazed and ungrazed plots, respectively. Sedge tissue total nitrogen content was not significantly affected by elk grazing in the two sampling dates, and averaged 1.91% and 1.87% in July and 1.61% and 1.48% in September for grazed and ungrazed plants, respectively.

Total soil δ^{15}N (0 to 15 cm) ranged from -2.8% to +8.0%, and was significantly more depleted in upper landscape positions (Fig. 2a). Soil inorganic nitrogen δ^{15}N (0 to 15 cm) ranged from -10.4% to +5.4%, and also presented a significant positive correlation with water table depth, being significantly more depleted in upper landscape positions (Fig. 2b). A significant correlation ($P < 0.001$; $r = 0.73$) was observed between δ^{15}N values of inorganic N and that of total soil N in the upper soil horizon and, on average, δ^{15}N of inorganic soil N was 2.7% more depleted in relation to total soil δ^{15}N. Because field soil incubations were performed only in ungrazed plots, values of δ^{15}N of inorganic soil N in grazed plots were estimated with a linear equation, $Y = -3.71 + 1.77 X$; $r^2 = 0.53$), where Y is estimated δ^{15}N of inorganic soil N and X is δ^{15}N of total soil N. Groundwater δ^{15}N correlated negatively to water table depth in ungrazed plots (Fig. 2c), but no significant correlation ($P = 0.164$) was observed in the grazed plots. River water δ^{15}N ranged from +0.58% to +2.93%, and averaged +1.68% (±0.94).

Table 1. δ^{15}N values of willow and sedge tissue in upper landscape and streamside positions of Horseshoe Park and Moraine Park during August 1997. Values represent means ($n = 8$) followed by the standard error between parentheses. Means followed by different letters are significantly different at $P < 0.05$.

	Plant tissue δ^{15}N (%)	
Landscape position	Sedge	Willow
Horseshoe Park		
Upper landscape	-6.10 (2.34)[a]	-1.87 (0.44)[a]
Streamside	-0.74 (0.68)[b]	-1.82 (0.27)[a]
Moraine Park		
Upper landscape	-10.84 (1.45)[a]	0.03 (0.41)[a]
Streamside	-2.28 (3.10)[b]	-0.41 (0.65)[a]

[a,b]Different letters denote statistical differences at $P < 0.05$.

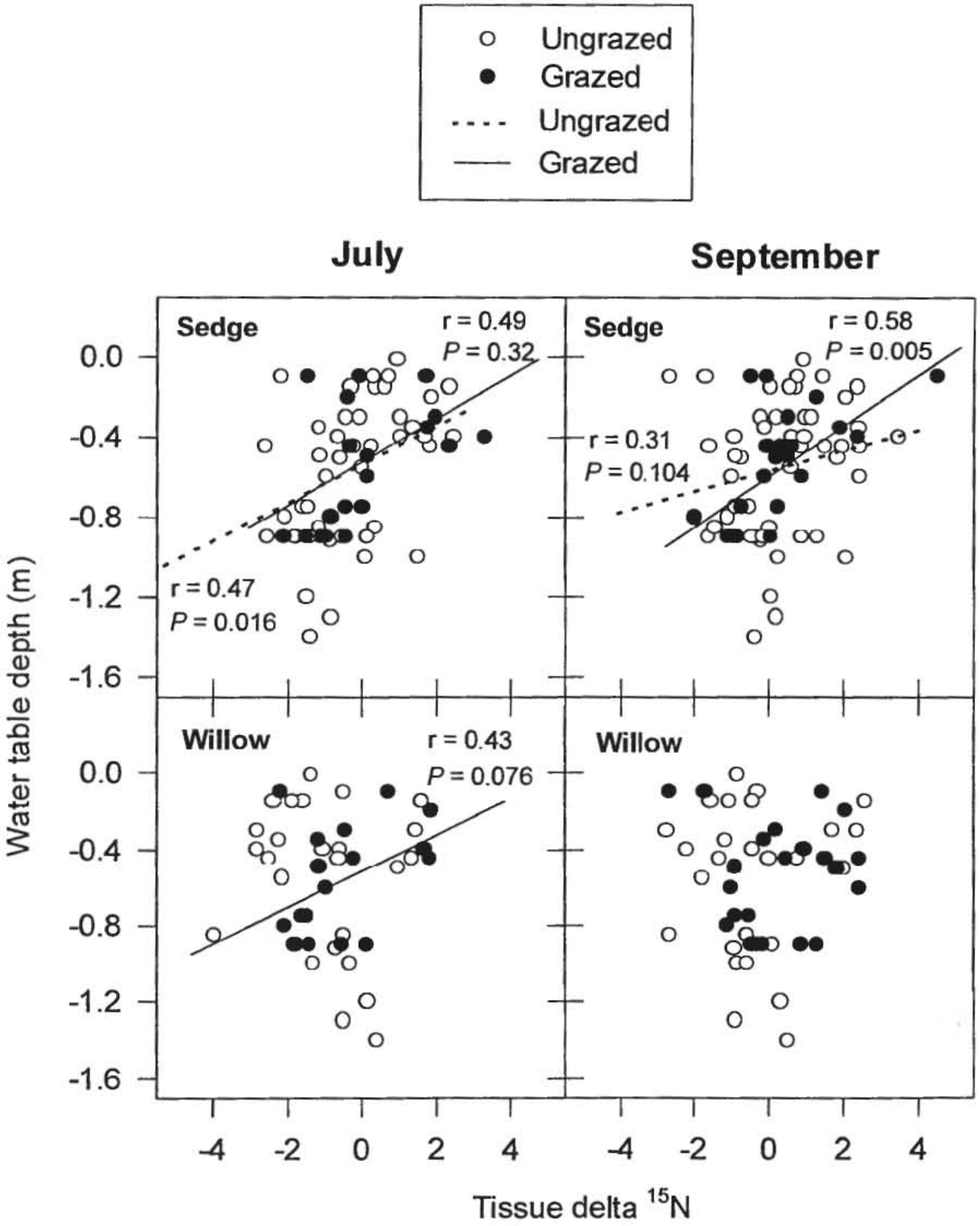

Fig. 1. Patterns of $\delta^{15}N$ values of grazed and ungrazed willow and sedge leaf tissue as related to water table depth (m) in willow communities on elk winter range of Rocky Mountain National Park, Colorado, 1998.

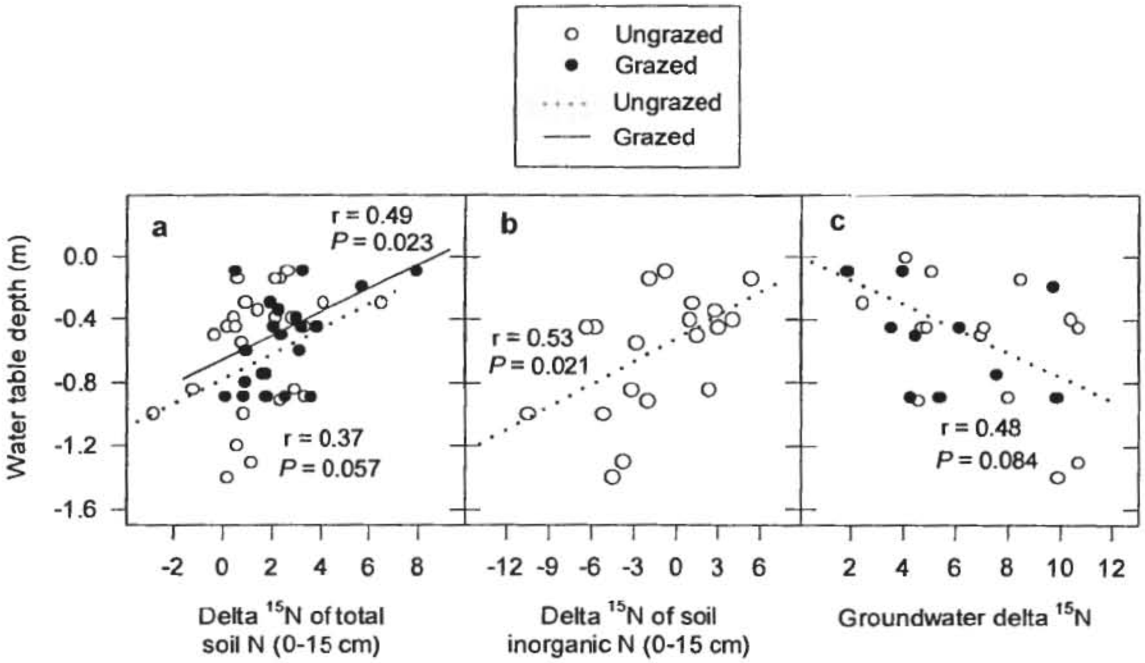

Fig. 2. Water table depth as related to δ^{15}N values of soil N (a), soil inorganic N (b), and groundwater (c) in willow communities on elk winter range of Rocky Mountain National Park, Colorado, 1998.

Sedge tissue δ^{15}N was significantly correlated to total soil δ^{15}N only in the case of grazed plants collected in September, but willow tissue δ^{15}N values of grazed and ungrazed plants were correlated to total soil δ^{15}N in both sampling dates (Fig. 3). The regression lines of the relationships between total soil δ^{15}N and tissue δ^{15}N from grazed and ungrazed sedge plants were significantly different ($P < 0.05$) in September, which suggests that grazed sedge plants may rely relatively more on soil N than groundwater N in comparison to ungrazed sedge plants and that the reliance on soil N may increase over the course of the summer (Fig. 3).

No significant correlations were observed between sedge tissue δ^{15}N and groundwater δ^{15}N, regardless of grazing regime or sampling date (Fig. 4). In contrast, there were significant correlations between groundwater δ^{15}N and tissue δ^{15}N of ungrazed willow plants in both July and September (Fig. 4). Interestingly, no significant correlations were observed in the case of grazed willow plants (Fig. 4), which suggests grazed willow plants may use less groundwater N. Tissue δ^{15}N values of sedge plants ranged from -2.6 to +4.53%, while for willow plants these values ranged from -4.0 to +2.6%. On average, δ^{15}N values of willow tissue were 2.4 and 6.9% more depleted than soil δ^{15}N and groundwater δ^{15}N, respectively. Similarly, δ^{15}N values of sedge tissue were 1.8% and 6.7% more depleted than soil δ^{15}N and groundwater δ^{15}N, respectively.

Discussion

The two potential inorganic N sources for riparian plants, being either from soil or from groundwater, differed in their δ^{15}N values by an average of 5% during the growing season of 1997. This difference is an important part of our study as it corresponds to the differences in the δ^{15}N values of plant tissue under divergent experimental treatments. The range of plant tissue δ^{15}N values observed in our study is consistent with values reported for plant tissue in terrestrial ecosystems, which usually vary between -5 to +2%, but

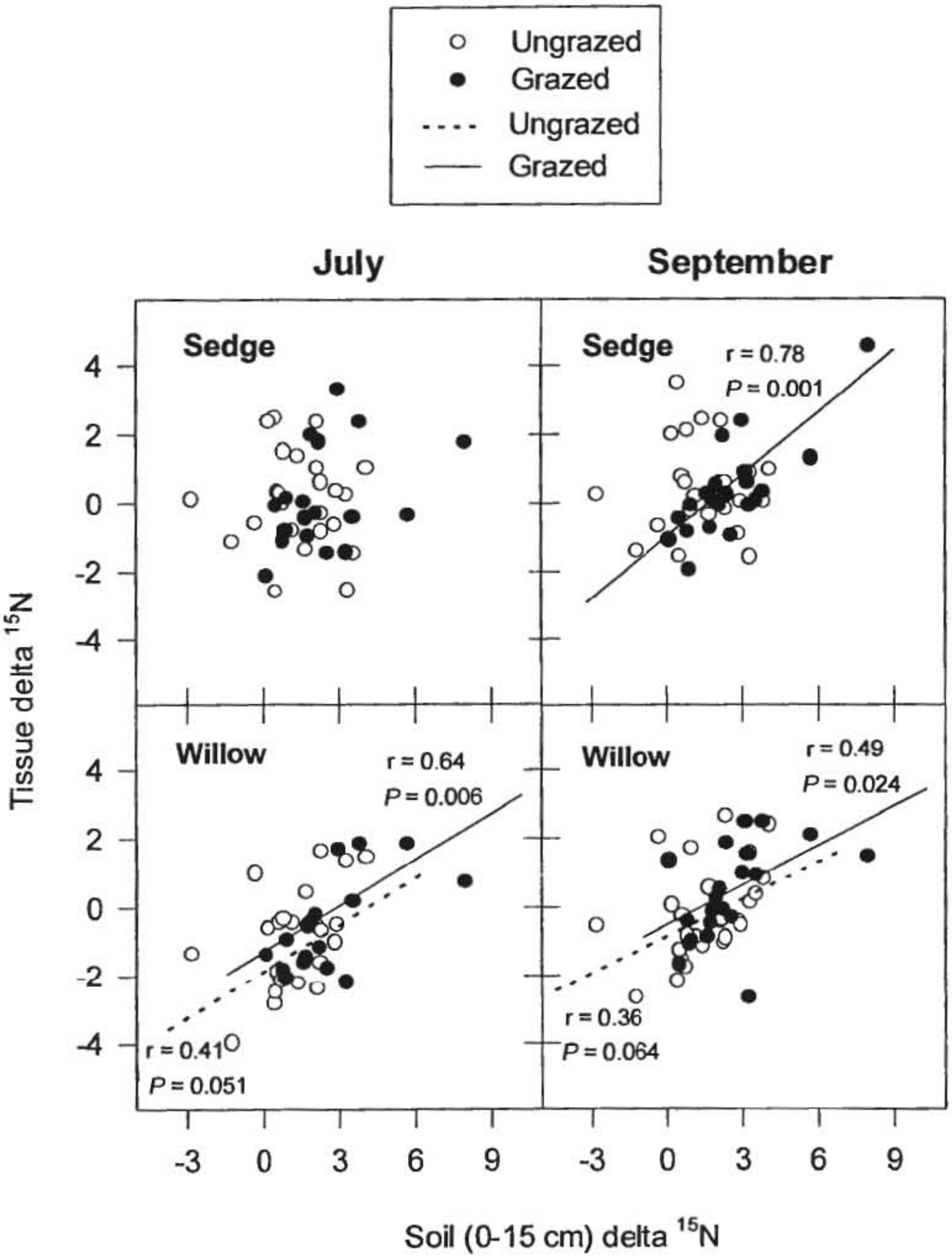

Fig. 3. Correlations between delta ^{15}N values of total soil N (0–15 cm) and sedge (a and b) and willow (c and d) tissue in July and September of 1998 in grazed and ungrazed plots of Moraine and Horseshoe Parks.

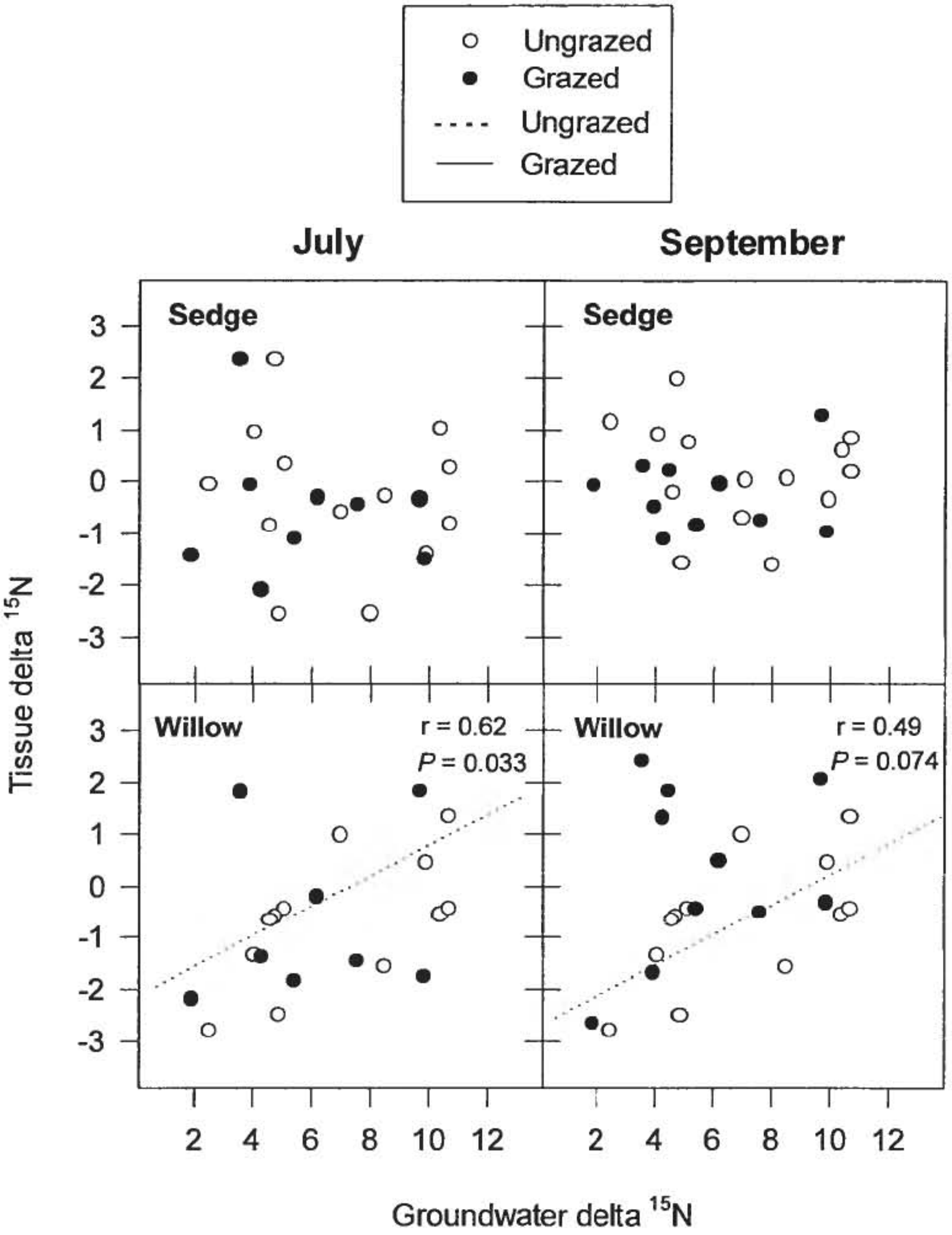

Fig. 4. Correlations between delta ^{15}N values of groundwater and sedge and willow tissue in July and September of 1998 in grazed and ungrazed plots of Moraine and Horseshoe Parks.

in some cases could range between -10 and +10% (Virginia and Delwiche 1982; Vitousek et al. 1989; Nadelhoffer and Fry 1994; Frank and Evans 1997). In general, the differences between plant tissue δ^{15}N and groundwater δ^{15}N in our study were consistently higher (c. 7%) than the differences between plant tissue δ^{15}N and total soil δ^{15}N (c. 2%), which suggests that both willow and sedge plants in our sites may rely mostly on uptake of soil N as opposed to groundwater N.

Effect of Landscape Position on N Sources

During 1997, we found that sedge tissue in lower landscape positions consistently exhibited enriched δ^{15}N values when compared to sedge plants growing in upland positions in the landscape (Table 1). In contrast, δ^{15}N values of willow tissue were not significantly different between landscape positions (Table 1). This evidence suggests that the shallow-rooted graminoid may be relying more on soil N and acquiring smaller proportions of river-groundwater N in upper landscape positions in comparison to the woody willow species. This general interpretation is supported by our additional finding during 1998, in which a significant correlation was observed for sedge tissue δ^{15}N and water table depth (Fig. 1), indicating that the lower the water table (i.e., less access to groundwater N), the more depleted the δ^{15}N values of sedge tissue. To the contrary, willow leaf δ^{15}N values were not associated with water table depth (Fig. 1) with the exception of grazed plants in July. These findings suggest that the deeper rooting characteristics of willow may allow these plants to tap groundwater N independent of landscape position, but grazing may limit the access to groundwater in upper landscape sites. Similar to our results, previous studies have reported higher tissue δ^{15}N values in plants growing in lower landscape positions in comparison to plants in upper landscape positions (Garten 1993; Sutherland et al. 1993).

The observations presented here that landscape position influences facets of mineral nutrition of riparian vegetation are corroborated by a previous study conducted by Alstad et al. (1999) addressing water sources of these same species in the same experiment. Measurements of δ^{18}O showed that sedge plants in upper landscape positions relied strongly on rainwater acquired from upper soil layers, while sedge plants located adjacent to streams and willow plants in both landscape positions, primarily use streamwater. The agreement between the patterns of δ^{18}O and δ^{15}N values in plant tissue strongly supports our hypotheses regarding the patterns of N uptake by willow and sedge in our study sites. These findings further demonstrate the usefulness of stable isotopes in ecological studies, since we were not able to detect any influence of landscape position or herbivory on plant N sources based solely on the non-isotopic data we collected.

Effect of Herbivory on N Sources

Our findings also suggest that elk herbivory may have a significant effect on the patterns of N uptake by willow plants. As indicated by the correlations between groundwater δ^{15}N and willow tissue δ^{15}N (Fig. 4), grazed willow plants may have a more limited access to groundwater N than willow plants protected from herbivory. These findings were corroborated by a parallel investigation, based on non-isotopic techniques, of the N balance of willow plants conducted in our study site, which indicated that grazed willow plants may not have as much access to groundwater N when compared to ungrazed willow plants. The findings from this parallel study demonstrated that ungrazed willow plants could take up at least 7% of the annual requirements of N from the groundwater, which was higher ($P < 0.001$) than that of grazed plants, which averaged only 4% (Peinetti et al. 2001).

We suggest that grazed willow plants may have less access to groundwater N due to a less developed rooting system. A carbon-balance study conducted in our site indicated that grazed willow plants might allocate less carbon to the rooting system, in comparison to willow plants protected from herbivory (R. Peinetti, Natural Ecology Resources Laboratory, personal communication). In addition, several previous studies have reported that heavily grazed plants often allocate a smaller proportion of their photosynthetically fixed carbon to belowground structures than do ungrazed or lightly grazed plants (Detling 1987; Briske and Richards 1995; Detling 1998).

In nitrogen-limited systems, competition for soil N by coexisting plants may cause plants to resort to different sources of N in order to meet their physiological requirements (Welker et al. 1991; Schulze et al. 1994; Michelsen et al. 1996). Menezes et al. (2001) conducted fertilization experiments in our study sites and found that N availability significantly limits growth and uptake of N by willow plants. Therefore, the ability of plants to use more than one source may be of significant importance for plant growth, development, and survival.

A reduced ability by grazed willow plants to access different sources of N could significantly reduce the ability of willow plants to respond to herbivory.

Summary and Conclusions

We summarize our findings in Fig. 5, which illustrates the suggested patterns of N uptake by grazed and ungrazed willow and sedge plants in different landscape positions, and shows the average $\delta^{15}N$ values of N sources and plant tissue under those treatments during the growing season of 1998. In conclusion, we suggest that shifts in landscape hydrology, due to reductions in beaver activity and a warming and drying trend, combined with intense elk herbivory, may have a compounding effect on willow by increasing the frequency of drought stress and possibly reducing the availability of nitrogen. Since willow growth and uptake of N is limited by N availability in our sites, reductions in stream water N sources could increase the limitation of N to these plants and lead to lower rates of photosynthesis and growth. We suggest that these effects explain in part the sensitivity of willow communities to elk grazing and their decline across elk winter ranges in Rocky Mountain National Park.

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Literature Cited

Aber, J. D., K. J. Nadelhoffer, P. Studler, and J. M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. Bioscience 39:378–385.

Alstad, K. P., J. M. Welker, S. A. Williams, and M. J. Trlica. 1999. Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: An isotopic study using $\delta^{13}C$ and $\delta^{18}C$. Oecologia 120:375–385.

Baron, J. 1992. Surface waters. Pages 142–183 *in* J. Baron, editor. Biogeochemistry of a subalpine ecosystem: Loch Vale Watershed. Volume 70. Springer-Verlag, New York.

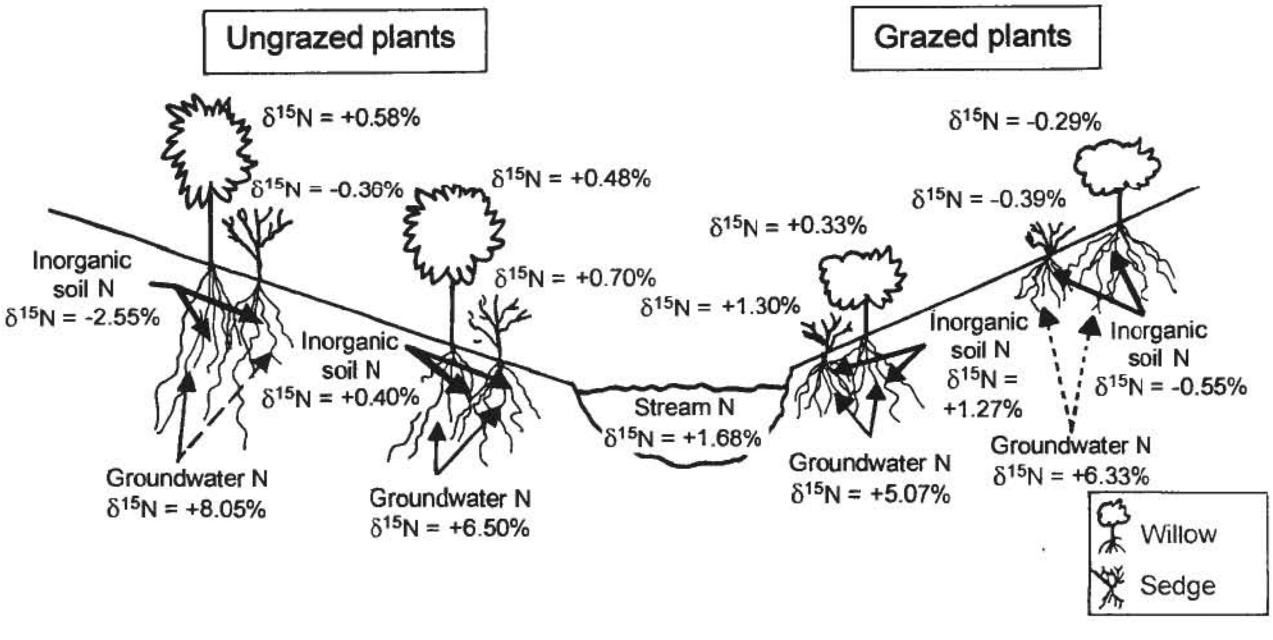

Fig. 5. Hypothetical patterns of N uptake by grazed and ungrazed willow and sedge plants in upper and lower landscape positions of Moraine and Horseshoe Parks.

Briske, D. D., and J. H. Richards. 1995. Plant responses to defoliation: A physiologic, morphologic, and demographic evaluation. Pages 635–710 *in* J. Bedunah and R. E. Sosebee, editors. Wildland plants: Physiological ecology and developmental morphology. Society for Range Management. Denver, Colo.

Chapin, F. S. 1980. Mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11:233–260.

Chapin, F. S., L. Moilanen, and K. Kielland. 1993. Preferential use of organic nitrogen for growth by a nonmycorrhizal arctic sedge. Nature 361:150–153.

Detling, J. K. 1987. Grass response to herbivory. Pages 56–68 *in* J. L. Capinera, editor. Integrated pest management on rangeland: A short grass prairie perspective. Westview Press, Boulder, Colo.

Detling, J. K. 1998. Mammalian herbivores: Ecosystem-level effects in two grassland national parks. Wildlife Society Bulletin 26:438–448.

Evans, R. D., A. J. Bloom, S. S. Sukrapanna, and J. R. Ehleringer. 1996. Nitrogen isotope composition of tomato (*Lycopersicom esculentum* Mill. Cv. T-5) growth under ammonium or nitrate nutrition. Plant, Cell, and Environment 19:1317–1323.

Frank, D. A., and R. D. Evans. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology 78:2238–2248.

Garten, Jr., C. T. 1993. Variation in foliar ^{15}N abundance and the availability of soil nitrogen on Walker Branch Watershed. Ecology 74:2098–2113.

Handley, L. L., and J. A. Raven. 1992. The use of natural abundance of nitrogen isotope in plant physiology and ecology. Plant, Cell, and Environment 15:965–985.

Handley, L. L., and C. M. Scrimgeour. 1997. Terrestrial plant ecology and ^{15}N natural abundance: The present limits to interpretation for uncultivated systems with original data from a Scottish old field. Advances in Ecological Research 27:133–212.

Hogberg, P. 1997. ^{15}N natural abundance in soil-plant systems. New Phytologist 137:179–203.

Khan, S. A., R. L. Mulvaney, and P. D. Brooks. 1998. Diffusion methods for automated nitrogen-15 analysis using acidified disks. Soil Science Society of America Journal 62:406–412.

Kielland, K. 1994. Amino acid absorption by arctic plants: Implications for plant nutrition and nitrogen cycling. Ecology 75:2373–2383.

Kolberg, R. L., B. Rouppet, D. G. Westfall, and G. A. Peterson. 1997. Evaluation of an in situ net soil nitrogen mineralization method in dryland agroecosystems. Soil Science Society of America Journal 61:504–508.

Menezes, R. S. C., E. T. Elliott, D. W. Valentine, and S. A. Williams. 2001. Effects of herbivory and proximity to surface water on C and N dynamics on elk winter range. Journal of Range Management 54:400–408.

Michelsen, A., I. K. Schmidt, S. Jonasson, C. Quarmby, and D. Sleep. 1996. Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia 105:53–63.

Nadelhoffer, K. J., and B. Fry. 1994. Nitrogen isotope studies in forest ecosystems. Pages 22–24 *in* K. Lajtha and R. H. Michener, editors. Stable isotopes in ecology and environmental science. Blackwell Scientific Publications, London.

Nadelhoffer, K. J., G. Shaver, B. Fry, A. Giblin, L. Johnson, and R. McKane. 1996. ^{15}N natural abundance and N use by tundra plants. Oecologia 107:386–394.

Nadelhoffer, K. J., B. A. Emmett, P. Gundersen, O. J. Kjonaas, C. J. Koopmans, P. Scheleppi, A. Tietema, and R. F. Wright. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature 398:145–148.

Naiman, R. J., G. Pinay, C. Johnston, and J. Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75:905–921.

Nasholm, T., A. Ekblad, A. Nordin, R. Giesler, M. Hogberg, and P. Hogberg. 1998. Boreal forest plants take up organic nitrogen. Nature 392:914–916.

Peinetti, H. R., R. S. C. Menezes, and M. B. Coughenour. 2001. Changes induced by elk browsing in the aboveground biomass production and distribution of willow (*Salix monticola* Bebb): Their relationships with plant water, carbon, and nitrogen dynamics. Oecologia 127:334–342.

SAS Institute. 1995. SAS User's Guide. Release 6.12. SAS Institute Inc. Cary, NC.

Schulze, E. D., F. S. Chapin III, and G. Gebauer. 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. Oecologia 100:406–412.

Shearer, G., and D. H. Kohl. 1986. N_2-fixation in field settings: Estimations based on natural ^{15}N abundance. Australian Journal of Plant Physiology 13:699–756.

Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998. Elk, multiple factors, and persistence of willow in national parks. Wildlife Society Bulletin 26:419–428.

Stevens, D. R., and S. Christianson. 1980. Beaver populations on the East slope of Rocky Mountain National Park. Special report to Rocky Mountain National Park, Estes Park, Colo.

Sutherland, R. A., C. van Kessel, R. E. Farrel, and D. J. Pennock. 1993. Landscape-scale variations in plant and soil nitrogen-15 natural abundance. Soil Science Society of America Journal 57:169–178.

Terwilliger, J., and J. Pastor. 1999. Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. Oikos 85:83–94.

USDA Snow Survey Office. 1995, 1996. Snowpack data for Rocky Mountain National Park. National Resources Conservation Service. Lakewood, Colo.

Virginia, R. A., and C. C. Delwiche. 1982. Natural N-15 abundance of presumed N-fixing and non-N-fixing plants from selected ecosystems. Oecologia 54:317–325.

Vitousek, P. M., G. Shearer, and D. H. Kohl. 1989. Foliar ^{15}N abundance in Hawaiian rainforest: Patterns and possible mechanisms. Oecologia 78:383–388.

Welker, J. M., D. D. Briske, and R. W. Weaver. 1987. Nitrogen-15 partitioning within a three-generation tiller sequence of the bunchgrass *Schizachyrium scoparium*: Response to selective defoliation. Oecologia 24:330–334.

Welker, J. M., D. R. Gordon, and K. J. Rice. 1991. Capture and allocation of nitrogen by *Quercus douglasii* seedlings in competition with annual and perennial grasses. Oecologia 87:459–466.

Response of Tannins and Phenolics of Willows to Simulated Herbivory, Water Dynamics, and Ambient Elk Herbivory on the Elk Winter Range of Rocky Mountain National Park

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Abstract. Plant secondary metabolites, including phenolics and tannins, function as defenses against natural enemies, and link several ecosystem processes through diverse mechanisms. We reviewed and summarized literature regarding the response of natural product chemistry in willows (*Salix* spp.) to grazing on sites that vary in their ability to support willow growth. This summary provided a conceptual model that was used to develop hypotheses regarding the effects that different site conditions might have on the ability of willows to respond to grazing by elk and mechanical clipping. Willow dynamics in response to elk herbivory on the elk winter range of Rocky Mountain National Park (RMNP), Colorado has been a topic of concern for most of this century. We examined the secondary metabolite responses of three willow species on the RMNP winter range under a number of different site conditions and grazing treatments. Sites were characterized alternatively as either: (1) wet or dry, based on depth to water table; (2) tall, short-watered, or short-control based on willow growth, presence of beaver activity, and water amendments made through installation of check dams; and (3) grazed, clipped, or ungrazed based on imposed herbivory treatments. Studies were conducted from 1995–1999 in exclosures erected in 1994. Additionally, we examined responses of willows protected for 30–35 years to varying levels of mechanical clipping (4) [0%, 50%, 100%] and compared to willows exposed to ambient elk herbivory for 30–35 years.

Willow species differed in phenolic and tannin production in most comparisons with phenolic production highest in summer leaves and twigs for *S. planifolia* followed by *S. monticola* and then *S. geyeriana*. *S. monticola* had higher tannin concentration than *S. planifolia*, with *S. geyeriana* producing the least. Phenolic production in twigs with leaves was significantly greater than that of twigs collected in the winter. Tannin production in willows at the tall sites in 1995 was higher compared to the short-control and short-watered sites. Tall willows from *S. geyeriana* and *S. monticola* in January 1999 had higher tannin concentrations compared to willows on the short-control sites, but tall willows did not differ from those at the short-watered sites.

We expected that willows growing on favorable habitats would respond to clipping and elk grazing by increasing their phenolic and tannin concentration. Few patterns were found that were consistent with the predicted results. However, willows growing on sites that were delineated by the presence of standing water and beaver activity did

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However, willows growing on sites that were delineated by the presence of standing water and beaver activity did have higher concentrations of phenolics and tannins compared to willows on sites with no standing water or recent beaver activity. Additionally, few significant increases in phenolic and tannin concentration were noted in the clipping and grazing treatments. These data, along with the lack of response in willows subjected to natural grazing levels, suggest that elk grazing has adversely affected the ability of willows to respond to grazing.

Tannins and phenolics tended to increase in the 50% clipped treatment in the 35-year-old exclosure. This suggests that the heavier 75% clipping level may have prevented willow response in the 4-year-old exclosure experiments. It was expected that willows grazed at ambient levels by elk outside the exclosure would also respond to elk grazing by increasing their secondary metabolite production such as that observed for the 50% clipping (ambient level of removal was 33% of current annual growth). Since grazed willows did not respond similarly, this suggests that elk have adversely affected willow physiology. Overall, the pattern noted among treatments in the 35-year-old exclosure represents the expected response of willows that are growing in a favorable environment. The lack of response in terms of increased secondary metabolites of heavily grazed willows could lead to greater palatability, and thus evermore increased grazing pressure on these plants.

Keywords: Elk, herbivory, phenolics, secondary metabolites, tannins, willow.

Introduction

At one time, secondary metabolites--which include the phenolics and tannins of willow (*Salix* spp.)--were thought to be waste products that might confer advantage to plants as antiherbivore and antimicrobial agents. Now they are known to function as defenses against natural enemies, and to link several ecosystem processes through diverse mechanisms (Cates 1996; Schimel et al. 1996). Tannins affect nutritional quality by binding with several primary metabolites (e.g., nitrogen-containing compounds like proteins, amino acids, DNA, RNA) often making them difficult to digest. Low molecular weight phenolics have been suggested to be toxic and/or act as feeding deterrents (Robbins 1993). Of these two, low molecular weight phenolics may play the major role in deterring ungulate grazing since some large animal herbivores may have evolved mechanisms that make tannins less effective as defenses (Robbins et al. 1987). For willows inhabiting sites favorable for growth, the challenge from tissue removal by herbivores and infection from pathogens normally results in an induced increase in these chemicals in remaining and new leaf and stem tissues (Karban and Baldwin 1997). In willows, where conditions for growth are unfavorable, plants may not be able to respond by increasing their production of defensive chemicals when exposed to natural enemies and simulated herbivory (Table 1). Comparing the response of tall willows versus short willows and willows growing on wetter sites with those on drier sites may aid in understanding the effects of abiotic conditions and grazing on willow physiology and growth (Johnston et al. 1993).

Because secondary metabolites are known to influence soil, litter, nutrient, and microbial processes, any change in the ability of willows to produce these chemicals may affect plant community dynamics. Low molecular weight phenolics serve as carbon sources for carbon-limited soil microbes, enhance immobilization of nutrients (Schimel et al. 1996), and act as inducers of microbial-higher plant interactions (Phillips 1992). Tannins, low molecular weight phenolics, and terpenes in litter have been shown to inhibit nitrification (Thibault et al. 1982; Baldwin et al. 1983; White 1986; Schimel et al. 1996). Tannins also inhibit microbial activity (Field and Lettinga 1992) and affect mineralization rates (Benoit et al. 1968; Schimel et al. 1996), but the mechanisms of action are unclear. Tannins bind to proteins that may make soil nitrogen (N) less available to microbes and higher plants; they may also bind to microbial exoenzymes leading to inhibition in the breakdown of tannin polymers (Benoit and Starkey 1968). Terpenes can act as toxic agents (White 1986) or as carbon sources for microbial growth, thereby tying up N through immobilization (Bremner and McCarty 1988). Based on these complex interactions, we have taken a broad conceptual approach in our studies of the effects of herbivory on willow secondary chemicals in litter and nutrient cycling (Table 1).

Table 1. Verified and predicted parameters describing sites favorable and unfavorable for willow growth, and willow and habitat responses on these sites, in the northern winter range of Yellowstone National Park, Wyoming. Taken from Cates et al. (1999).

	Site	
Parameter/Response	Unfavorable	Favorable
	Parameters	
Precipitation[1-4, 8]	Less, drier winters	Higher, wetter
Temperature[1-4, 8]	Warmer	Cooler
Water tables[1-3]	Lower	Perennially higher
Streambanks[1-3]	Prevalent downcutting	Less downcutting, vegetated
Flooding[1-3]	Common, extensive	Infrequent, reduced intensity
Streams[6, 7]	Single or few streams, narrow streams; increased flow	Network of braided, expounded streams, ponds; impounded water, high sediment organic matter
Beaver[3, 5, 6]	Few to none; loss of food supply	Common; food supply abundant (aspen, willow)
	Willow Response	
Production[1-3]	Reduced; negative gain in CAG	Net increase, vigorous gain in CAG
Recruitment[1-3]	Reduced to nonexistent	Seed productivity high, asexual
Leader length and weight[1-3]	Short, lighter	Longer, heavier
Plant height[1-3]	Reduced in stature	Able to grow beyond reach of elk
Browsing effect on growth form[2]	Morphological juvenility response; reduced physiological response	Morphological and physiological juvenility
Defense response	Reduced or none	Induced response vigorous
	Habitat	
Nutrients[6, 9]	Reduced input of N	Enhanced N availability
Aquatic invertebrates[6, 7]	Shredders, scrapers; biomass less	Collectors, predators; greater biomass
Carbon[6, 7]	Low carbon input	High carbon input and processing
Litter	More recalcitrant; slower processing	More rapidly processed
Plant community[2, 7, 8]	Grass, sedges, conifer encroachment, dryland shrubs	Mosaic of riparian vegetation; willow, aspen maintained

[1] Singer et al. (1998)
[2] Singer et al. (1994)
[3] Singer and Cates (1995)
[4] Balling et al. (1992a,b)
[5] Consolo-Murphy and Hanson (1993)
[6] Naiman et al. (1988)
[7] Naiman and Melillo (1984)
[8] Houston (1982)
[9] Jonas (1955)

Willow and aspen dynamics on the elk winter range of Rocky Mountain National Park (RMNP), Colorado has been a topic of concern and discussion during most of this century (Hess 1993). Over a 25-year period (1968–1992) after elk were released from human controls and when elk increased dramatically in the park, park biologist David Stevens concluded that increased grazing may be the most important cause of willow decline in some areas of the winter range (D. Stevens, National Park Service, unpublished annual reports 1969–1992). Stevens suggested that under current high levels of elk herbivory, willow survival might occur only in habitats capable of sustaining sufficient growth. Changes in willow cover over the 25-year period from 1968 to 1992 on six sites containing marked willows, were inconclusive, with one-third of the sites showing willow decline, one-third showing stable cover, and one-third showing increasing willow cover (Zeigenfuss et al. 1999). Zeigenfuss et al. (1999) noted that this sample size of willow plots was very small (n = 6) and inference was limited in this study. However, analysis of willow cover across the entire winter range landscape using aerial photo interpretation indicates that the willow decline on the entire winter range since 1946 has been about 19–21% (Peinetti et al., this volume).

Stevens (National Park Service, unpublished annual report [1991]) also suggested that beaver eliminated willow at pond sites and then abandoned these sites on the winter range. He noted that the loss of beaver might be related to a drop in the water table such that many sites on the winter range may not be able to support heavily grazed willow. Beaver populations have declined 94% over the last 60 years on the winter range (Zeigenfuss et al., this volume). Consequently, elk herbivory, hydrological considerations, and beaver may be important and interactive factors that affect willow dynamics in various ways. With these scenarios in mind, we reviewed the literature in an effort to develop a conceptual model delineating the response of natural product chemistry of willows to grazing on sites that may vary in growing conditions (Table 1).

Willows growing under favorable abiotic conditions appear to be able to withstand moderate levels of grazing by ungulates (Table 1, references therein). Under these conditions willows add new tissues, reproduce, and respond to grazing with induced defenses while rapid vertical growth rates allow at least a portion of the plant to grow beyond the reach of ungulates. Sites characterized by high water tables and favorable nutrient dynamics appear to be favorable to the vigorous growth of willows (Table 1). These dynamics appear to be greatly facilitated by the presence of beaver. Alternatively, sites characterized by lower water tables, relatively narrow, fast moving streams, lack of suitable litter and nutrient dynamics to sustain willow growth, and fewer beaver, seem to result in conditions unfavorable to healthy riparian willow communities (Table 1).

Based on these considerations, the following predictions were developed. For sites at RMNP that appear to have more favorable growing conditions for willows (e.g., tall willow sites, or sites with higher water table levels), the expectation was that willows inside exclosures that were clipped at levels similar to that for elk grazing would respond by increasing their phenolic and tannin concentration. On sites less favorable to willow growth (e.g., short willow sites, or sites with lower water tables), the expectation was that willows would not respond to clipping when compared to the unclipped, ungrazed control. Tall willow were predicted to respond differently than short willows in that the tall structure was demonstrated on this winter range to be largely a function of not only lower levels of ambient herbivory (Singer et al., this volume), but also good growing conditions. Tall willows on good sites were suspected to have deeper rooting zones than heavily browsed willows in locations further from streams, based on different isotopic signatures (Menezes et al., this volume). In other words, even though height of tall browsed willow was a product of several multiplicative factors including level of elk herbivory and site conditions, we expected tall willows to respond to the herbivory treatments differently than short, browsed willows.

Protection from grazing for long periods was also predicted to result in greater ability to respond with an increase in these natural products to moderate clipping. However, willows would not be able to respond by increasing phenolic and tannin concentration when subjected to either clipping 100% of new growth, or the high level of elk grazing observed on short willows on some parts of the winter range. For willows that were not protected from grazing prior to clipping treatments, it is difficult to predict if they would be able to respond to either protection or high clipping levels.

Study Area and Treatments

Details concerning site selection and description of experiments are found in Zeigenfuss et al. (1999, this volume), and are only slightly modified here. To reduce confusion, names of sites and types of treatment follow Zeigenfuss et al. (1999, this volume). Willow communities in elk winter range of the northeast side of

RMNP were identified and random locations for potential sites were generated using a Geographic Information System (GIS). Twelve study sites were selected from these points in riparian willow communities of: (1) the north and south sides of the Moraine Park area of the Big Thompson River watershed (elevation 2,481 m), and (2) the Horseshoe Park area of Fall River watershed (elevation 2,598 m). Predominant willow species throughout all areas were *Salix monticola*, *S. planifolia*, and *S. geyeriana* mixed with other mesic shrubs, such as *Potentilla fruticosa*, *Betula glandulosa*, *B. occidentalis*, and *Alnus tenuifolia*. Eight of these sites (four in Moraine Park and four in Horseshoe Park) were located in generally drier areas (i.e., side channels, abandoned beaver dams) with little or no current beaver activity (i.e., beaver-abandoned sites) that supported short, heavily grazed willow. Evidence from dead and decadent willows on these sites indicated that plants over 2 m tall were once present and each of these sites had an abundance of evidence of prior beaver pondings (old dams, old lodges that were now abandoned). The other four sites (two in Moraine Park and two in Horseshoe Park) were located in beaver-occupied areas (including areas of recent activity) that supported taller willow plants with less severe hedging by elk, referred to as "tall willow" sites.[1] Two 30.5 m x 45.7 m paired plots were chosen at each site. One randomly selected plot was fenced to exclude elk and deer and the other remained unfenced. Exclosures were erected in August–November 1994.

In half of the sites with shorter willows (two in each drainage, n = 4 total), we attempted to raise the water table. This treatment, referred to as "short-watered willows" (sites 3, 4, 8, 9), was imposed in spring 1995. The treatments consisted of sheet metal check dams placed in both the grazed and exclosed areas at each site. The dams were placed in existing ephemeral stream channels to impede the flow of rain and snowmelt runoff and raise the water levels locally. The rest of the shorter willow sites (two in each drainage, n = 4 total) were left to their normal hydrologic regimes and are referred to as "short-control willows" (sites 5, 6, 7, 10). Sites were also classified as "wet or dry" sites based on measurements of depth to water table. "Wet" sites were the six sites with the highest average water table levels (1, 2, 4, 7, 8, 10), while those designated as "dry" sites were the six sites with the lowest water table levels (3, 5, 6, 9, 11, 12). In the results, these effects are referred to as "water table" while those designated as "tall, short-control, and short-watered" are referred to as "height/water amended" treatments.

Throughout the growing season, water table levels at all the sites were monitored using wells and by measuring water levels on either side of check dams. Annual herbaceous consumption averaged 55% of annual production and shrub consumption averaged 33% of current annual growth (27% in winter alone) throughout the study period (Singer et al., this volume). Elk were the primary ungulate herbivore in these systems.

Within each willow exclosure, simulated grazing treatments were conducted during winter (January–March) each year 1995–1998. At the outset, each exclosure was divided into sections that were randomly assigned to a "clipped" treatment or an "ungrazed" treatment. The clipped treatment, from fall 1995 onward, consisted of clipping 75% of the current year's growth from all forage shrubs and clipping 75% of the herbaceous layer in that section of the exclosure. This was intended to simulate greater herbivory that might occur with an increase in elk numbers or concentrations, and to test the effects of these higher consumption levels. All clipped plant material was removed from the exclosure. Ungrazed treatments were unmanipulated areas located within the exclosures. The unfenced plots were left to the ambient level of elk grazing of herbaceous vegetation and browsing of shrubs characteristic of that site. Elk densities and thus herbivory levels, varied greatly across these winter range sites (Singer et al., this volume). In the results, these clipping and grazing treatments are referred to as "herbivory" treatments. Twig and leaf (summer) or twig only (winter) samples were collected from the current annual growth (CAG) of the same tagged willow plants in July 1995, July 1998, and January 1999.

One 0.4 ha exclosure was established in 1963 in a willow/wet meadow community in the Beaver Meadows area of the elk winter range. Few willows were available, so we selected 15 plants from a mix of species and randomly assigned each to a clipping treatment of 0%, 50%, or 100%. During winter (prior to spring budbreak), we removed all CAG from plants clipped at the 100% level, and we systematically clipped every second CAG shoot from plants clipped at the 50% level. The 0% treatment willow plants were completely protected

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[1] Two of the "short willow" sites that were beaver-abandoned in Moraine Park had high water tables. Best model selection suggested that high levels of elk herbivory at these sites were a more important factor to the willow growth parameters than was depth to the water table (Singer et al., this volume; Zeigenfuss et al., this volume).

from ungulate herbivory and clipping. We clipped willows from spring 1993 and through winter 1995–1996. All willow plants inside the exclosure had been protected from ungulate herbivory for 30 years prior to the beginning of the current study. Samples were collected in July 1996 from all 15 plants inside the exclosure, as well as from several willows (n = 10) exposed to ambient elk grazing (~33%) outside the exclosure.

Total tannins and phenolics from the current year's growth were analyzed to determine if there were differences in their production due to clipping or elk grazing, or due to artificial water amendment, or differences in water table levels. Leaf litter was collected from plants inside exclosures and those grazed by elk outside, but adjacent to the exclosures, in 1995. This was done by collecting senesced leaf material directly from willow plants prior to leaf abscission. Leaf litter that was exposed to decomposition in the field for six months was also collected as part of another study (Menezes et al. 2001) and analyzed for tannin and phenolic concentration.

Isolation and Quantification of Tannins

Shoots from each plant were analyzed for total tannins by the butanol-HCl method keeping willow species separate. Approximately 200 mg of freeze dried leaf and twig tissue (July 1995 and July 1998 samples) or twig tissue (January 1999) were extracted in 70% aqueous acetone in a test tube by sonication for 5 minutes at room temperature, and then centrifuged (4,500 rpm) for 10 minutes. The supernatant was taken to dryness, and 7 ml distilled water was added and sonicated for 5 minutes to dissolve the extract. From the solution, 0.2 ml was pipetted out of the solution into a test tube containing 4.8 ml MEOH. This was thoroughly mixed. One ml was removed and added to 6 ml butanol-HCl and 0.2 ml ferric ammonium sulfate solution. All was well shaken and heated to 95°C for 40 minutes. The sample was cooled and analyzed at 520 nm wavelengths using a spectrophotometer. From each willow species, tannins were extracted, purified, and used to formulate the reference standard for that species. Data were expressed as mg/g dry wt. Litter that was collected represented a combination of three willow species that were common at each site (*S. geyeriana*, *S. planifolia*, and *S. monticola*).

Isolation and Quantification of Phenolics

Freeze dried leaf and twig tissue (200 mg), or twig tissue (200 mg) for the winter sample, were extracted three times each with 3 ml $MeOH/CH_2Cl_2$ (50/50). The three extracts were combined. This solution was filtered and injected into a high-pressure liquid chromatograph (HPLC; Hewlett Packard 1090). HPLC solvents were: solvent A = water-acetic acid (98:2), solvent B = acetronitrile-acetic acid (98:2). Temperature was 50°C, flow was 1 ml/min, and wavelength detection was at 280 nm. The column was a Phenomenex Ultracarb 20, C_{18} reverse-phase 5-m column 25 cm x 4.6 mm, and fitted with a matching guard column. Total phenolics for both fresh and litter tissues were determined by summing the peak heights for compounds that consistently appeared each year in the chromatograms. These were generally the major peaks in the chromatograms. Data were expressed as relative peak height divided by 10,000 on a dry weight basis.

Statistical Analysis

All analysis was performed using SAS (ver. 6.12) statistical software. Total phenolics and tannins were tested for differences between species, water table, height/water amended, and herbivory treatments, and their interactions. Total phenolics and tannin data were analyzed for differences using the PROC MIXED program in SAS. This is a procedure that is a generalization of the standard linear model designed to analyze data generated from several sources of variation (SAS Institute 1995). Outliers were noted and eliminated from the sets according to the criteria found in the SAS univariate procedure. The number of samples analyzed for the July 1995, July 1998, and January 1999 data sets for each set of water table-height/water amended-herbivory-species combination ranged from three to five. Total sample number analyzed for July 1995 was 264, July 1998 was 235, and for January 1999, 273 samples.

The responses of willow phenolics and tannins among species, water table, and grazing and water amendment treatments were examined. Some investigators (Alstad et al. 1999; Zeigenfuss et al., this volume) found few or no differences in several willow measurements (height, annual production, rates of photosynthesis, total plant water potential) in the short willow sites due to water amendment. However, phenolics and tannins may respond differently in willows as compared to responses in willow elongation growth rates, current annual biomass production, or N dynamics. Consequently, we analyzed phenolic and tannin data in the context of the tall, short-control, and short-watered sites as well.

One of the objectives of this study was to determine if a different effect of clipping would occur on phenolic and tannin concentration of willows that had been isolated from grazing for about 30 years, in comparison to willows that had been removed from grazing for only four years or had clipping imposed upon them consequent with protection from elk grazing. Two sources of variation that had not been addressed previously were of concern; one due to chance variation in the aliquot of sample taken from the bulk sample for analysis, and the other due to species differences. These are especially important because the sample size is small due to the limitations of only one long-term exclosure and few individuals of each species being available. The variation within an individual willow was addressed by determining the phenolic and tannin concentration on three subsamples taken from each sample. An average across the subsamples was used in the statistical analysis. The tannin data were combined across species at this long-term exclosure. However, qualitative and quantitative differences in phenolics among willow species indicated that total phenolics could not be combined across species. Thus, we reduced the samples available for the analysis of the treatment effect on phenolics to only *S. monticola*.

Additionally, a colinearity test between the ambient elk consumption rates of willows at each site and phenolic and tannin concentrations was conducted using a SAS PROC GLM program. This linear regression analysis was carried out to determine if any relationship existed between consumption rates at each site and natural product concentration. The specific pairwise comparisons were elk consumption vs. 1995 summer willow tannin and phenolic concentration, 1998 summer tannin and phenolic concentration, and 1999 winter tannin and phenolic concentration. No significant ($P < 0.05$) correlations were noted in these analyses for any year or season.

Results

Tannin Responses to Treatments in 4-Year Exclosures

July 1995 represents the first year of sampling of willows for phenolics and tannins after installation of treatments. Ungrazed and clipped willows produced more tannin than did grazed willows when species and sites were combined (Table 2b). *S. monticola* tannin production in leaves and twigs was not significantly different from *S. planifolia*, but both species had higher tannin production than *S. geyeriana* (Table 2c,d,e). As expected, willows from the tall sites produced significantly more tannin than those at the short-control and short-watered sites (Table 2c). *S. monticola* produced more tannin at the wet sites, while *S. planifolia* willows produced more tannin at the dry sites (Table 2d).

After 4 years of treatments (July 1998), ungrazed willows produced more tannin than did clipped willows, but neither of these were significantly different in tannin production compared to grazed willows (Table 3b). All species were significantly different from the other species in their tannin production with *S. monticola* producing the highest level and *S. geyeriana* the lowest (Table 3c,d). Overall, there was no significant difference in tannin production between wet and dry sites (Table 3c). However, *S. planifolia* produced more tannins in willow leaves and stems at the dry sites compared to wet sites (Table 3c).

No differences in tannin production were found between grazed, ungrazed, and clipped willows when pooled across species in January 1999 (Table 4a). There were significant differences between all species with *S. planifolia* twigs containing the highest amount of tannin and *S. geyeriana* the lowest (Table 4b,c,e). No overall differences among tall, short-control, or short-watered sites were observed, but *S. geyeriana* and *S. monticola* produced more tannin at the tall sites than at the short-control sites (Table 4b). Alternatively, *S. planifolia* willows at the short-control sites produced more tannin than did willows at the short-watered sites (Table 4b). No overall differences were observed in tannin production between wet and dry sites (Table 4c); however, *S. planifolia* produced more tannin in willows at the dry sites compared to those at the wet sites (Table 4c). Finally, ungrazed and clipped willows at the dry sites produced more tannin than did grazed willows, but no differences among grazing treatments occurred at the wet sites (Table 4d).

Phenolic Responses to Treatments in 4-Year Exclosures

The phenolic data for 1995 did not meet the criterion of homogeneity for the statistical analysis; consequently, no statistical analysis was performed on these data. Unexpectedly, more phenolic was produced by willows at the dry sites in July 1998 compared to those growing on sites with a higher water table (Table 5b). No overall differences were observed among willows at tall, short-watered, and short-control sites (Table 5c). For individual species, no differences in phenolic production across sites was noted for *S. geyeriana* and *S. planifolia* (Table 5c),

Table 2. Tannin production (mg/g dry wt) in willow on elk winter range of Rocky Mountain National Park, Colorado, July 1995. (a) Test statistics for tannin production among species, water table, height/water amended and herbivory treatments, and their interactions; (b) mean tannin production ($\bar{x} \pm$ se) among herbivory treatments when sites and species are combined; (c) mean tannin production ($\bar{x} \pm$ se) among species across tall, short-control and short-watered sites, and for species when sites are combined and sites when species are combined; (d) mean tannin production ($\bar{x} \pm$ se) among species across wet and dry site; and (e) for species when sites are combined.

(a)	Source	F	*P*
	Species	6.0	0.003
	Height/water amended	4.6	0.010
	Herbivory	2.7	0.066
	Water table	0.6	0.425
	Species x Height/water amended	3.0	0.018
	Species x Herbivory	1.7	0.139
	Water table x Species	9.6	0.000

(b)	Herbivory	Ungrazed	Clipped	Grazed
		68.8 ± 2.2^{a}	69.7 ± 2.0^{a}	63.7 ± 2.0^{b}

(c)[1]	Species x Height/water amended	Tall	Short-control	Short-watered
	S. geyeriana	67.8 ± 3.2^{a}	52.8 ± 3.2^{b}	66.4 ± 3.7^{a}
	S. monticola	75.6 ± 3.0^{a}	72.3 ± 3.1^{a}	65.3 ± 2.8^{b}
	S. planifolia	73.4 ± 3.4^{a}	73.0 ± 7.9^{a,b}	62.6 ± 3.1^{b}
	Height/water amended	72.2 ± 1.9^{a}	65.3 ± 2.9^{b}	64.7 ± 2.5^{b}

(d)[1]	Species x Water table	Wet	Dry
	S. geyeriana	60.1 ± 2.9^{a}	63.9 ± 2.7^{a}
	S. monticola	76.9 ± 3.0^{a}	65.4 ± 2.0^{b}
	S. planifolia	63.3 ± 3.5^{a}	76.2 ± 4.0^{b}

(e)	Species	*S. geyeriana*	*S. monticola*	*S. planifolia*
		62.0 ± 1.9^{a}	70.9 ± 1.7^{b}	69.5 ± 2.9^{b}

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[1] Horizontal means, se followed by different letters significantly different ($P \leq 0.10$) between sites within a species.

Table 3. Tannin production (mg/g dry wt) in willow on elk winter range of Rocky Mountain National Park, Colorado, July 1998. (a) Test statistics for tannin production among species, water table, height/water amended and herbivory treatments, and their interactions; (b) mean tannin production ($\bar{x}$ ± se) among herbivory treatments when sites and species are combined; and (c) mean tannin production ($\bar{x}$ ± se) among species across wet and dry sites; and (d) for species when sites are combined.

(a) Source	F	*P*
Species	76.8	0.000
Water table	2.4	0.159
Height/water amended	0.3	0.746
Herbivory	3.1	0.045
Species x Water table	2.4	0.095

(b) Herbivory	Ungrazed	Clipped	Grazed
	67.4 ± 1.6^{a}	62.4 ± 1.5^{b}	65.0 ± 1.5^{a,b}

(c)[1] Species x water table	Wet	Dry
S. geyeriana	52.5 ± 1.9^{a}	53.1 ± 1.8^{a}
S. monticola	77.3 ± 2.6^{a}	77.4 ± 2.0^{a}
S. planifolia	62.6 ± 2.5^{a}	71.5 ± 2.5^{b}
Water table	63.4 ± 1.5^{a}	66.5 ± 1.3^{a}

(d) Species	*S. geyeriana*	*S. monticola*	*S. planifolia*
	52.8 ± 1.3^{a}	77.4 ± 1.6^{b}	66.9 ± 1.8^{c}

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[1] Horizontal means, se followed by different letters significantly different ($P \leq 0.10$) between sites within a species.

Table 4. Tannin production (mg/g dry wt) in willow on elk winter range of Rocky Mountain National Park, Colorado, January 1999. (a) Test statistics for tannin production among species, water table, height/water amended and herbivory treatments, and their interactions; (b) mean tannin production ($\bar{x}$ ± se) among height/water amended among species; (c) mean tannin production ($\bar{x}$ ± se) between water table among species; (d) mean tannin production ($\bar{x}$ ± se) between water table herbivory treatments; and (e) for species when sites are combined.

(a) Source	F	*P*
Species	97.9	0.000
Height/water amended	1.3	0.321
Herbivory	1.4	0.247
Water table	0.2	0.657
Species x Height/water amended	2.0	0.101
Species x water table	3.4	0.035
Water table x Herbivory	2.5	0.083

(b)[1] Species x Height/water amended	Tall	Short-control	Short-watered
S. geyeriana	54.8 ± 2.0^{a}	49.5 ± 2.2^{b}	50.2 ± 2.2^{a,b}
S. monticola	64.1 ± 2.2^{a}	58.4 ± 2.2^{b}	60.9 ± 2.1^{a,b}
S. planifolia	81.4 ± 3.1^{a}	91.7 ± 6.4^{a,b}	78.0 ± 3.1^{a,c}

(c)[1] Species x Water table	Wet	Dry
S. geyeriana	53.3 ± 1.9^{a}	49.6 ± 1.7^{a}
S. monticola	60.2 ± 2.0^{a}	62.0 ± 1.6^{a}
S. planifolia	79.8 ± 3.5^{a}	87.4 ± 3.1^{b}

(d)[2] Water table x Herbivory	Ungrazed	Clipped	Grazed
Wet	64.8 ± 2.3^{a}	62.1 ± 2.1^{a}	63.6 ± 2.6^{a}
Dry	65.4 ± 2.0^{a}	67.4 ± 2.1^{a}	60.9 ± 1.7^{b}

(e) Species	*S. geyeriana*	*S. monticola*	*S. planifolia*
	51.4 ± 1.2^{a}	61.1 ± 1.2^{b}	83.5 ± 2.5^{c}

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[1] Horizontal means, se followed by different letters significantly different ($P \leq 0.10$) between sites within a species.

[2] Horizontal means, se followed by different letters significantly different ($P \leq 0.10$) between herbivory treatments within a site designated by water table.

Table 5. Phenolic production (expressed as peak height divided by 10,000, dry weight) in willow on elk winter range of Rocky Mountain National Park, Colorado, July 1998. (a) *t*-test statistics for phenolic production among species, water table, height/water amended and herbivory treatments, and their interactions; (b) mean phenolic production ($\bar{x}$ ± se) between water table; (c) mean phenolic production ($\bar{x}$ ± se) species x height/water amended interaction; and (d) for species when all sites are combined.

(a) Source	F	*P*
Species	6,072.2	0.000
Water table	6.8	0.044
Height/water amended	0.5	0.639
Herbivory	1.7	0.177
Species x Height/water amended	0.2	0.051

(b) Water table	Wet	Dry
	1,583.8 ± 70.5^{a}	1,833.7 ± 67.0^{b}

(c)[1] Species x height/water amended	Tall	Short-control	Short-watered
S. geyeriana	72.9 ± 4.3^{a}	70.4 ± 5.5^{a}	83.9 ± 5.8^{a}
S. monticola	3,221.4 ± 175.1^{a}	2,720.8 ± 170.2^{b}	2,850.6 ± 166.9^{a,b}
S. planifolia	23,495.6 ± 1438.9^{a}	23,148.1 ± 2,784.7^{a}	20,685.1 ± 362.3^{a}

(d) Species	*S. geyeriana*	*S. monticola*	*S. planifolia*
	75.5 ± 3.0^{a}	2,923.0 ± 98.8^{b}	22,414.7 ± 1121.2^{c}

[1] Horizontal means, se followed by different letters significantly different ($P \leq 0.10$) between sites within a species.

but *S. monticola* produced more phenolic compounds at the tall site compared to willows at the short-control site.

Phenolic production in 1999 winter willow twigs differed between species with *S. geyeriana* producing significantly more phenolics in twigs than either of the other two species (Table 6b). *S. planifolia* produced the least quantity of phenolic compounds (Table 6b). Clipped willows produced significantly more phenolic than did ungrazed or grazed willows (Table 6c). Phenolic production among willows at the dry sites, when species and treatments were combined, was higher than that for willow at the wet sites (Table 6d).

Phenolic and Tannin Production in Willows Protected from Grazing for 35 Years

For the 35 year-old exclosure, tannins were significantly higher in the 50% clipped treatment than the 0% clipped, 100% clipped, or elk herbivory treatments (Table 7). Tannins from willows subjected to the 100% clipping level inside the exclosure were lower than the tannin concentration in ungrazed (0% clipped), lower than in the 50% clipped treatment, and lower than in willows outside the exclosure grazed by elk. Total phenolics increased in the 50% clipped treatment ($P = 0.155$; Table 7). Response of willow height and growth paralleled the responses for tannins and phenolics. Clipping willows at the 50% level resulted in no reductions of rate of height growth or rate of CAG production of willows (F = 0.21, F = 0.93 respectively; $P = 0.81$, $P = 0.4$ respectively; Singer et al. [1998]).

Willow Litter Phenolics and Tannins

Decomposed litter collected from tall, short-control, and short-watered sites contained only a minor amount of phenolic, and no measurable tannin, when compared to fresh litter (Table 8). Fresh litter contained higher tannin and phenolic concentrations than decomposed litter at all sites ($P < 0.05$). However, no differences were found between treatments within a site.

Table 6. Phenolic production (expressed as peak height divided by 10,000, dry weight) in willow on elk winter range of Rocky Mountain National Park, Colorado, January 1999. (a) Test statistics for phenolic production among species, water table, height/water amended and herbivory treatments, and their interactions; (b) mean phenolic production ($\bar{x}$ ± se) among species when all treatments combined; and, (c) mean phenolic production ($\bar{x}$ ± se) among herbivory when species and water table and height/water amended are combined; and (d) mean phenolic production ($\bar{x}$ ± se) for water table when species and treatments are combined.

(a) Source	F	*P*
Species	215.1	0.000
Height/water amended	0.8	0.493
Herbivory	2.5	0.090
Water table	8.3	0.025
Species x Water table	1.9	0.154

(b)[1] Species	*S. geyeriana*	*S. monticola*	*S. planifolia*
	140.3 ± 4.7^a	130.9 ± 3.7^b	57.4 ± 2.1^c

(c)[1] Herbivory	Ungrazed	Clipped	Grazed
	100.0 ± 3.3^a	107.3 ± 3.4^b	98.3 ± 3.2^a

(d)[1] Water table	Wet	Dry
	95.8 ± 3.1^a	108.2 ± 2.9^b

[1] Horizontal means, se followed by different letters significantly different ($P \leq 0.10$).

Discussion

Species Differences

Species differed in phenolic and tannin production in practically every comparison regardless of treatment or how sites were divided. In particular, tannin production in summer twigs and leaves among species was highest for *S. monticola* followed by *S. planifolia* and then *S. geyeriana*, but occasionally *S. planifolia* had higher tannin concentration than *S. monticola*. Tannin production in the winter was generally highest for *S. planifolia* followed by *S. monticola* and then *S. geyeriana*. A similar pattern was observed for phenolic production in summer twigs and leaves among species with *S. planifolia* highest followed by *S. monticola* and then *S. geyeriana*. For winter twig samples, phenolic production was highest in *S. geyeriana* followed by *S. monticola*. Phenolic production in samples of summer twigs and leaves combined was significantly greater than that of twigs collected in the winter.

A high level of variation in total phenolic production was shown among the three species tested. This variation is primarily due to each willow species differing in their qualitative and quantitative production of phenolics. Interaction between variables was apparently species driven (Table 6). This source of variation in itself may have masked water table, height/water amended, and herbivory effects. In addition, *S. monticola* and *S. planifolia* did not respond to water table and herbivory effects in the same way. For example, tannin production in 1995 was higher for willows of *S. monticola* at the wet sites, but for *S. planifolia* tannin, concentration was always higher in willows of this species growing on drier sites (Tables 2d, 3c, 4c).

Phenolic and Tannin Production in Willows as Related to Water Table and Treatments

It is unclear as to why a lack of homogeneity occurred in the July 1995 phenolic data set. No other data set had a similar problem. This collection immediately

Table 7. Total tannin (mg/g dry weight) response [$\bar{x}$ (sd)] and phenolic (expressed as peak height divided by 10,000, dry weight) in willow species subjected to clipping levels inside and outside of 35-year old exclosures on elk winter range in Rocky Mountain National Park, Colorado, July 1996.

	Simulated herbivory			Elk herbivory
Species	0%	50%	100%	
All species Tannins*	60.9(10)^{a}	80.1(17)^{b}	48.7(2)^{c}	63.1(22.5)^{a}
S. monticola Phenolics**	297(35)^{d}	411(87)^{e}	307(17)$^{\#}$	337(81)

*Means followed by different letters are significantly different, $P < 0.10$.

** Phenolics for *S. monticola* only; means followed by the letters d,e; $P = 0.155$ (n = 2 or 3).

[#] sd is the $\bar{x}$ of three runs of the same sample for the only individual in this category (not used in statistical analysis).

Table 8. Tannin (mg/g dry weight) and phenolic (expressed as peak height divided by 10,000, dry weight) concentration of fresh willow litter versus decomposing willow litter among herbivory and height/water amended treatments [$\bar{x}$, (sd*)] on elk winter range in Rocky Mountain National Park, Colorado, 1995. No significant differences between treatments were found.

Height/water amended treatment		Ungrazed	Clipped	Grazed
Tall				
Phenolics	F	424 (162)	555 (38)	412 (206)
	D	2,011 (501)	3,326 (538)	2,913 (2,693)
Tannin	F	64.1 (21)	67.7 (10)	65.1 (19)
Short-control				
Phenolics	F	189 (33)	372 (283)	325 (269)
	D	50 (42)	29 (98)	21 (9)
Tannin	F	77.2 (8)	70.7 (2)	72.0 (4)
Short-watered				
Phenolics	F	NA	NA	NA
	D	40 (26)	22 (9)	22 (8)

*All comparisons between fresh and decomposed litter significantly different, $P < 0.05$.

NA = data not available; F = fresh litter; D = decomposed litter.

followed the beginning of the clipping treatment and perhaps the initial clippings disrupted natural product metabolism such as was noted for Douglas-fir phenolic and tannin metabolism (Horner et al. 1993). In addition, the weather in spring 1995 was unusually cold and wet. Standing water from spring runoff was present on many sites into July, and cold temperatures delayed both spring runoff and leaf emergence 3–4 weeks (Zeigenfuss et al., this volume; L. Zeigenfuss, personal observation).

With regard to site quality, the expectation was that tall willow growing on sites with some beaver activity would produce the highest levels of phenolics and tannins. The data supported this expectation. Tannin production in willows at the tall sites in 1995 was higher compared to the short-control and short-watered sites. Tall willows from *S. geyeriana* and *S. monticola* in January 1999 also had generally higher tannin concentration compared to willows on the short-control sites, but tall willows did not differ significantly from those at the short-watered sites.

The tall willow with some beaver activity category represented the accumulated product of multiple factors in Rocky Mountain NP. The height of the willows was primarily influenced by elk densities and rates of elk herbivory (Singer et al., this volume). Multiple factor models and information criteria suggested that elk herbivory was the factor of overriding importance on eight parameters of willow growth and thus on observed willow heights, and that depth to the water table had a significant, but lesser, influence (Singer et al., this volume). Elk rate of consumption of CAG of 37% had a negative, suppressing influence on willow growth and biomass production peaked at consumption levels of about 21% (Singer et al., this volume). In other words, the tall willow patches were tall primarily due to elk herbivory levels, which were lower than for the short (beaver-abandoned) willow patches, but shallower depth to the water table and beaver dams also contributed to larger, more optimal sizes of willows. Other associated factors also contributed to the large size and higher densities of willow stems in this type. A portion of the willow plants were above the reach of elk and thus unbrowsed each year, the dense jungle of willow clumps also protected part of the patch from access by elk, and any active beaver dams and ponds made some of the willows less accessible to elk. Beaver dams increased the height of the water table and ponds neglected for a few years by beaver still retained some water. Also, depth of the rooting zone of short browsed willows on sites away from streamsides were apparently more shallow, further contributing to less-than-ideal water relations of the short-control willow category. Although depth to the water tables was shallow for a few of the short control patches, this type was generally characterized by long-term beaver abandonment of the site. There were no active dams, and streamside channels, meanders, oxbows, and braided channels were all dry, except for brief periods in the spring during peak run-off.

The short willows (beaver-abandoned sites) produced less secondary metabolites in RMNP (and also in Yellowstone NP; Singer et al. [1994], Singer and Cates [1995]) and these lower levels were near or below levels (e.g., 5% for tannins) that have been identified as thresholds where ungulates will browse more on shrubs (Cooper and Owen-Smith 1985). The lower growth rates, poorer growing conditions, and possible greater palatability to ungulates place the short willows in a downward spiral, particularly if elk populations continue to increase on the winter range. Apparently, long-term responses of heavily browsed willows led them to be more vulnerable to ungulate herbivory. This vulnerability includes the entire willow plant becoming within accessible reach of ungulates through shorter stature and smaller canopies with more perimeter accessible to browsers, lower growth rates, and lower secondary metabolites leading to greater palatability.

When sites were designated as wet or dry sites based on water table levels, mixed results occurred. In some cases, phenolics or tannins were higher in willows on the wet sites, but in other cases, these compounds were higher in concentration in willows on dry sites. Overall, the tall-short willow designation appeared to represent site quality better compared to the designation by water table depth (wet vs. dry).

We expected that willows would respond to both clipping and grazing through an increase in willow phenolic and tannin. The January 1999 clipped willows showed a significant increase in phenolics compared to ungrazed willows. However, in the majority of samplings, no difference in response in either phenolics or tannins occurred between the clipping and grazing treatments. Either the willows in general were not growing on sites favorable for supporting vigorous growth and hence were unable to respond to clipping or grazing, or the clipping and grazing levels were too severe. Data from willows in the 35-year-old exclosure and other studies on the willows at the study sites (Singer et al., this volume), suggest that the latter was likely and that ambient levels of elk herbivory not only negatively influence a wide spectrum of willow growth parameters (total CAG, twig CAG, mean height, maximum height stem density, plant density, canopy volume and area, catkin production; Singer et al., this volume; Zeigenfuss et al., this volume), but also production of secondary metabolites. The data from the 35-year exclosure also may indicate that 30 years relief from grazing allowed willows to recover enough to respond chemically to moderate levels of clipping.

Response of Tannins and Phenolics to Treatment in the 35-Year-Old Exclosure Compared to the 4-Year-Old Exclosure

The expected response was that the 50% clipping would result in an induced increased production in tannins and phenolics. Our observations in the 35-year-old exclosure support this expectation--tannins increased under 50% clipping and decreased significantly in the 100% clipping level compared to the no clipping treatment. With regard to elk grazing, the decreased response in tannins in willows grazed by elk outside the long-term exclosure suggests that elk have affected the ability of willows to respond to grazing. The significant increase in tannins at the 50%, but not at the 100% simulated herbivory level is also consistent with the literature (Karban and Baldwin 1997), and suggests that growing conditions inside this exclosure were sufficient to allow willows to respond positively in terms of secondary metabolites to this moderate clipping level.

The responses in the 4-year exclosures suggested that the 75% clipping was too high to permit an induced reaction in willows. Total phenolic production was lower in the older exclosure than observed for *S. monticola* in the 4-year-old exclosure possibly because willows inside the older exclosure had not been grazed for an extended time. The evidence also suggests that the 75% clipping level was too severe for a willow response in the 4-year-old exclosure, particularly with no recovery period from grazing.

It was expected that willows outside the exclosure would also respond to elk grazing by increasing their secondary metabolite production such as that observed for the 50% clipping. But we observed that elk grazed willows did not respond by increasing secondary metabolite production suggesting that elk herbivory levels had an adverse, long-term, accumulated, negative effect on not only willow size, structure, depth to the rooting zone, physiology, and growth rates (Alstad et al. 1999; Menezes et al., this volume; Singer et al., this volume; Zeigenfuss et al., this volume), but also a negative effect on the ability of willow to respond to herbivory with increased production of secondary metabolites. Overall, the pattern noted among treatments inside the 35-year-old exclosure represents the expected response of willows that are growing in a favorable environment.

Information from Yellowstone NP (YNP) tends to corroborate these conclusions. Apparently, most willows are growing on poor sites on Yellowstone's northern winter range (Singer et al. 1994) and the growing conditions are less favorable than in RMNP (Singer et al. 1998). Similar clipping experiments in YNP revealed no response in tannin or phenolic production at the 50% clipping level, and significant decreases in heights (22% decline) and CAG (250% decline) at the 100% clipping level (Singer et al. 1998). Similarly, height-suppressed, ungulate-browsed willows in YNP produced 41–64% less phenolics and 15–17% less tannins than ungrazed controls (Singer et al. 1994; Singer and Cates 1995), declines due to ungulate herbivory that are unprecedented in the ecological literature. The evidence from both parks suggests that poor site growing conditions and a long history of heavy browsing with associated reductions in plant sizes (and possibly also root biomass and depths) reduces the ability of willows to respond to ungulate herbivory by increasing production of secondary metabolites. Declines in nitrogen concentrations and content also occurred at the heaviest clipping levels (100%) and in ungulate-browsed willows compared to controls in YNP (Singer et al. 1998). Tannin production may be linked to the availability of nitrogen.

Summary

Based on our conceptual review of prior research of the effects of growing conditions and grazing on willow chemistry, the expected results were that willows growing on favorable habitats would respond to clipping and elk grazing by increasing their phenolic and tannin concentration. Patterns across the three years of sampling of the current year's growth in a series of 12 exclosures in place for only 4 years were not consistent with these predicted results probably because the clipping treatment of 75% was too severe to permit an increase in phenolic and tannin concentration. However, results at an exclosure in place for 30 years were consistent with the expectations, and willows clipped at moderate levels (50%) responded by increasing phenolic and tannin

content, while willows clipped at high levels (100%) and unclipped willows (0%) did not. Tall willow sites with less negative effects of elk herbivory on size and growth of willow, and with beaver activity (cuttings, some active dams) and the presence of standing water in channels, followed our original expectation and possessed higher concentrations of phenolics and tannins compared to short, hedged willows growing on beaver-abandoned sites (dry channels, abandoned dams). Few significant increases in phenolic and tannin concentration were noted in the clipping and grazing treatments, apparently because there has been a long-term (elk have been at high densities at the study sties for about 20 years) negative effect of the ambient levels of elk herbivory (average 33% removal of CAG) on willow response, and apparently because the 75% clipping treatment was too severe to permit an increased response by the willows. The lack of response in willows subjected to natural grazing levels, suggest that elk grazing has adversely affected the ability of willows to respond chemically to grazing and these lower levels of secondary metabolites can lead to greater palatability of grazed willows. Increased grazing pressure from increasing populations or concentrations of elk could further adversely affect willow growth and nutrient dynamics in these communities.

Literature Cited

Alstad, K. P., J. M. Welker, S. Williams, and M. J. Trlica. 1999. Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: An isotopic study using ^{13}C & ^{18}O. Oecologia 120:375–385.

Baldwin I. T., R. K. Olson, and W. A. Reiners. 1983. Protein binding phenolics and the inhibition of nitrification in subalpine balsam fir soils. Soil Biology and Biochemistry 15:419–423.

Balling, R. C., G. A. Meyer, and S. G. Wells. 1992a. Relation of surface climate and burned area in Yellowstone National Park. Agricultural and Forest Meteorology 60:285–293.

Balling, R. C., G. A. Meyer, and S. G. Wells. 1992b. Climate change in Yellowstone National Park: Is the drought-related risk of wildfires increasing? Climate Change 22:35–45.

Benoit, R. E., and R. L. Starkey. 1968. Enzyme inactivation as a factor in the inhibition of decomposition of organic matter by tannins. Soil Science 105:203–208.

Benoit, R. E., R. L. Starkey, and J. Basaraba. 1968. Effects of purified plant tannin on decomposition of some organic compounds and plant materials. Soil Science 105:153–158.

Bremner, J. M., and G. W. McCarty. 1988. Effects of terpenoids on nitrification in soil. Soil Science Society of America Journal 52:1630–1633.

Cates, R. G. 1996. The role of mixtures and variations in the production of terpenoids in conifer-insect-pathogen interactions. Recent Advances in Phytochemistry 30:179–216.

Cates, R G., J. Zou, S. C. Wooley, F. J. Singer, L. C. Mack, and L. C. Zeigenfuss. 1999. Predisposition of willows to elk browsing due to willow interactions with abiotic factors. Pages 191–195 *in* D. McArthur, W. K. Ostler, and C. Wambolt, compilers. Proceedings: Shrubland ecotones. RMRS-P-11. Ogden, Utah, U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station. 299 pp.

Consolo-Murphy, S., and D. D. Hanson. 1993. Distribution of beaver in Yellowstone National Park, 1988–1989. Pages 38–48 *in* R. S. Cook, editor. Ecological issues on reintroducing wolves into Yellowstone National Park. National Park Service Science Monograph. No. 22. Denver, Colo.

Cooper, S. M., and N. Owen-Smith. 1985. Condensed tannins deter feeding by browsing ruminant in a South African savanna. Oecologia 67:142–146.

Field, J. A., and G. Lettinga. 1992. Toxicity of tannin compounds to microorganisms. Pages 673–692 *in* R. W. Hemingway and P. E. Laks, editors. Plant polyphenols. Plenum Press, New York.

Hess, K. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot. 167 pp.

Horner, J. D., R. G. Cates, and J. R. Gosz. 1993. Effects of resource manipulation on the correlation between total phenolics and astringency in Douglas-fir. Journal of Chemical Ecology 19:1429–1437.

Houston, D. B. 1982. The Northern Yellowstone elk: Ecology and management. New York, New York. MacMillan Publishing Co. 473 pp.

Johnston, C. A., J. Pastor, and R. J. Naiman. 1993. Effects of beaver and moose on boreal forest landscapes. Pages 237–254 *in* R. Haines-Young, D. R. Green, and S. H. Cousins, editors. Landscape ecology and geographic information systems. Taylor and Francis, London.

Jonas, R. J. 1955. A population and ecological study of the beaver (*Castor canadensis*) of Yellowstone National Park. M.S. thesis. University of Idaho, Moscow.

Karban, R., and I. Baldwin. 1997. Induced response to herbivory. University of Chicago Press. 319 pp.

Menezes, R. S. C., E. T. Elliott, D. W. Valentine, and S. A. Williams. 2001. Effects of herbivory and proximity to surface water on C and N dynamics of elk winter range. Journal of Range Management 54:400–408.

Naiman, R. J., and J. M. Melillo. 1984. Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). Oecologia 62:150–155.

Naiman, R. J., C. Johnston, and J. Kelly. 1988. Alteration of North American streams by beaver. Bioscience 38:753–762.

Phillips, D. A. 1992. Flavonoids: Plant signals to soil microbes. Pages 201–231 *in* H. A Stafford and R. K Ibrahim, editors. Phenolic metabolism in plants. Plenum Press, New York.

Robbins, C. T. 1993. Wildlife feeding and nutrition. Academic Press, San Diego, California. 351 pp.

Robbins, C. T., S. Mole, A. E. Hagerman, and T. A. Hanley. 1987. Role of tannins in defending plants against ruminants: Reduction in dry matter digestion. Ecology 68:1606–1615.

Schimel, J. P., K. Van Cleve, R. G. Cates, T. P. Clausen and P. B. Reichardt. 1996. Effects of balsam poplar (*Populus balsamifera*) tannins and low molecular weight phenolics on microbial activity in taiga floodplain soil: Implications for changes in N cycling during succession. Canadian Journal of Botany 74:84–90.

Singer, F. J., and R. G. Cates. 1995. Response to comment: Ungulate herbivory on willows on Yellowstone's northern winter range. Journal of Range Management 48:563–565.

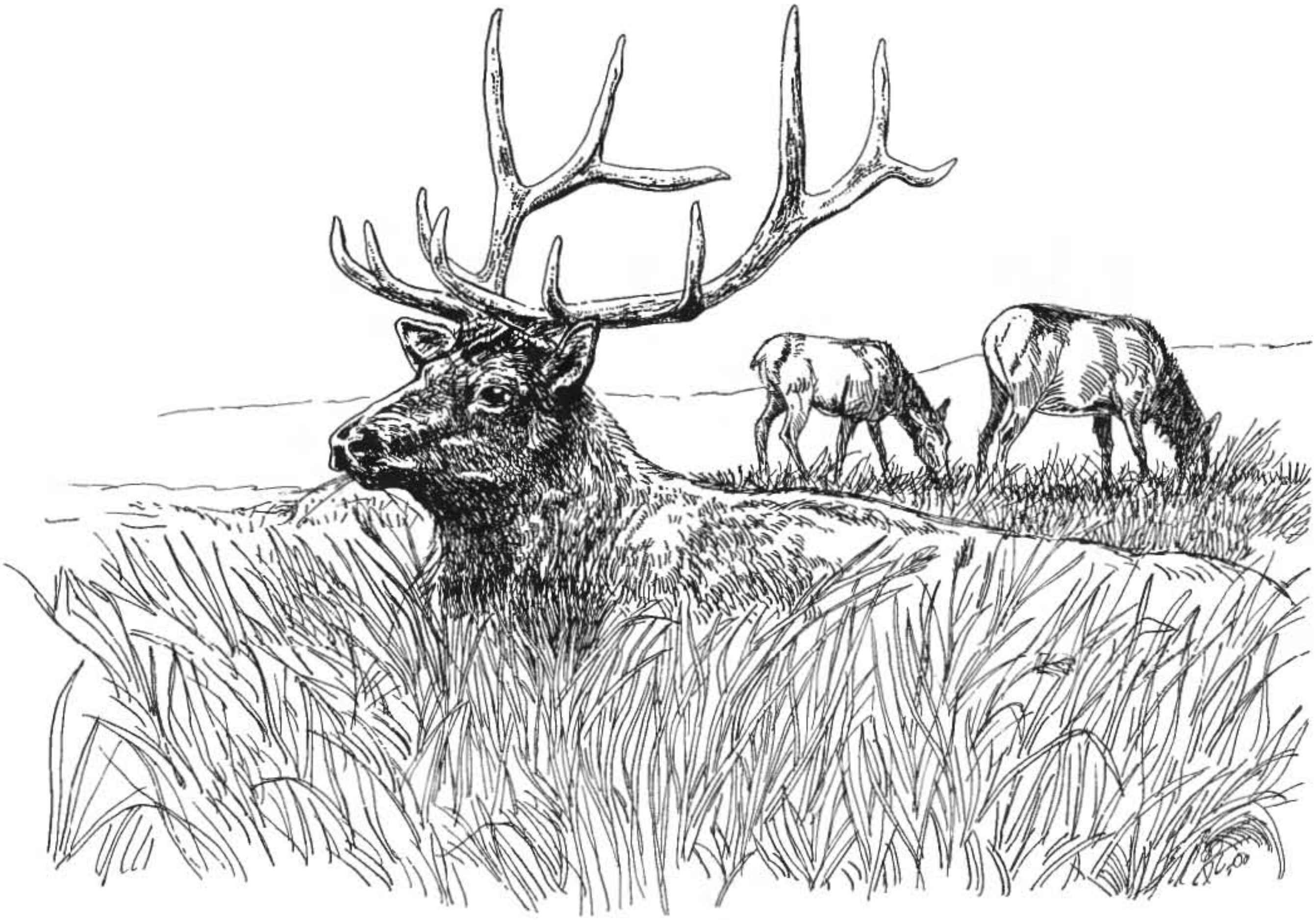
Singer, F. J., L. Mack, and R. G. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435–443.

Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998. Elk, multiple factors, and persistence of willows in national parks. Wildlife Society Bulletin 26:419–428.

Thibault, J. R., J. A. Fortin, and W. A. Smirnoff. 1982. *In vitro* allelopathic inhibition of nitrification by balsam poplar and balsam fir. American Journal of Botany 69:676–679.

White, C. S. 1986. Volatile and water-soluble inhibitors of nitrogen mineralization and nitrification in a ponderosa pine ecosystem. Biology and Fertility of Soils 2:97–104.

Zeigenfuss, L. C., F. J. Singer, and D. Bowden. 1999. Vegetation responses to natural regulation of elk in Rocky Mountain National Park. Biological Science Report USGS/BRD/BSR-1999-0003. U.S. Government Printing Office, Denver, Colo. 23 pp.



CHAPTER TEN

Influence of Elk Grazing on Soil and Nutrients in Rocky Mountain National Park

By

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Abstract. We used three 35-year exclosures to examine the effects of high elk populations on a variety of soil properties in three vegetation types: upland sagebrush, aspen, and meadow. Grazing and hoof action by elk significantly increased bulk density (from 0.87 kg/L ungrazed to 0.94 kg/L grazed), with greater effects on soils with fewer rocks. Grazing substantially reduced extractable calcium, magnesium, potassium, and phosphorus in the upland sagebrush type, but not in the aspen or meadow types. The only grazing effect on pH came in aspen vegetation types, where grazing prevented aspen establishment, and kept soil pH about 0.7 units higher than under aspen inside the exclosures. Grazing had no overall effect on total soil C and N across all exclosures and vegetation types, but soils from grazed portions of upland shrub areas had lower concentrations of extractable cations and phosphorus. The availability of soil nitrogen, indexed by in-field resin bags and net mineralization in soil cores, showed little overall effect of grazing. Limited data on soil leaching indicated a possibility of strong increases in nitrate leaching with grazing for an aspen vegetation type at one exclosure. Although we found little effect of grazing on soil N supply, we note that N fertilization doubled the production of grasses and shrubs; if grazing eventually led to changes in soil N supply, species composition and growth would likely change.

Keywords: Cervus elaphus, ecosystem processes, elk, grazing, mineralization, nitrogen, soil nutrients.

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Introduction

The population of elk (*Cervus elaphus*) has varied dramatically in the Front Range of the Rocky Mountains in Colorado. Intensive hunting extirpated elk in the late 1800s, but populations rose quickly following reintroduction in the early 1900s. Across the park, elk use varies by location and season. Areas of heavy grazing (particularly winter range for elk) show a lack of regeneration of aspen (Baker et al. 1997; Suzuki et al. 1999). The increases in elk populations, and concentrated areas of elk use, resulted from the elimination of all large predators (other than cougars), elimination or abbreviation of migration routes, and habituation of elk to humans and managed pastures, hay stacks, lawns, and golf courses.

Problems caused by overabundance of large mammals have concerned wildlife managers and scientists for decades (Caughley 1981). Traditionally, species were considered to be excessively abundant if high population densities reduced harvested yields, or if they caused unacceptable changes in the structure and composition of plant communities (Caughley 1981). For several reasons, these traditional approaches have been problematic. Approaches that define acceptable abundance in terms of harvestable yield focus narrowly on one species, and ignore effects of that species on other plants and animals. Defining desirable levels of abundance in terms of structural changes in plant communities may allow populations to reach undesirable levels before such changes can be detected (Caughley and Lawton 1981). Challenges in defining "harm" have prevented consensus [see reviews in Wagner et al. (1995) and Coughenour and Singer (1995)]. Basic ideas about density-dependent regulation of animal populations at equilibrium levels have also been questioned (Ellis and Swift 1988). These issues provide a problematic context for the discussion of "natural regulation" of herbivore populations by food supply, as currently practiced by the National Park Service in Yellowstone, Rocky Mountain, Grand Teton, and several other large western national parks (Wagner et al. 1995).

Grazing by domestic livestock typically alters soil organic matter, pools and turnover of nitrogen, and soil erosion, but these effects vary widely among locations (Risser and Parton 1982; Milchunas and Lauenroth 1993; Burke et al. 1997). Livestock impacts may be concentrated in some areas by fences, salt blocks, and supplemental water sources. Heavy livestock grazing compacts soil, reduces soil moisture up to 60%, lowers infiltration rates, creates a drier microclimate, and accumulates less litter (Knapp and Seastedt 1986; Fuls 1992).

The effects of wild, migratory ungulates on ecosystems may differ from those of domestic livestock. Wild populations of ungulates typically vary spatially and temporally in response to seasonal migrations and long-term population trends. In many cases, ideas and expectations about the nature and magnitude of grazing effects go far beyond the experimental tests available. Some sites are grazed only during the winter period when plants are dormant or for periods of only a few weeks during the growing season (McNaughton 1983; Frank and McNaughton 1992). Native ungulates may increase plant productivity, at least in the short term, by increasing nitrogen in forms that are more available to plants. Grazing may reduce root biomass and thus decrease the microbial biomass, thus reducing C:N ratios and making nitrogen more available to plants (Holland and Detling 1990; Seagle and McNaughton 1992). Herbivore feces and urine also provide large inputs of soluble nitrogen to plants (Risser and Parton 1982; Bazely and Jefferies 1985; McNaughton 1990). As a result of increased availability of nitrogen in a readily usable form on grazed sites, plant uptake of nitrogen is higher, leading to higher plant tissue concentrations of nitrogen (Moss et al. 1981; McNaughton 1983; Coughenour 1991; Singer 1995; Singer and Harter 1996). Tissue concentrations of nitrogen might be elevated above levels critical for overwinter survival of ungulates (Mould and Robbins 1981). Ungulates prefer to graze on regrowth from previously grazed sites, which leads to improved body condition and higher reproductive success (Moss et al. 1981; Iason et al. 1986; Gordon 1988; McNaughton 1988).

How substantial are the effects of elk on soils in the Rocky Mountains? Frank and Groffman (1998) examined soil properties inside and outside seven 2-ha exclosures that were in place for about 30 years, all in grass-dominated ecosystems in Yellowstone National Park. The net mineralization of soil nitrogen (N) was higher outside all seven exclosures than inside, with an average difference of about 2-fold. Four of the exclosures had substantial shrub cover, and no simple pattern of grazing impact was found. Shrubs at two exclosures showed no differences with respect to grazing, one had higher N mineralization under shrubs outside the fence, and the other higher N mineralization under shrubs inside the fence.

We assessed the impacts of heavy elk use on N using three large elk exclosures that have excluded elk and deer (but not small herbivores) for 35 years. We examined soil bulk density, total carbon (C) and N, as well as the minerals calcium (Ca), magnesium (Mg), phosphorus (P), and potassium (K), soil pH, available N, N-limitation on plant growth, and N leaching losses from the soil. The complete absence of ungulate grazing inside the exclosures is an artificial condition, given the long-term presence of ungulates in the region, so the gradient in grazing impacts between inside and outside the exclosures may be larger than would be found between typical ungulate populations and the current high-density situation.

Site Description and Methods

The three long-term elk exclosures are located in the Beaver Meadows area of Rocky Mountain National Park at an elevation of about 2,500 m. The climate is dominated by long, cold winters (average January temperature, -1° C), and sunny summers with frequent storms (July average temperature, 17° C). Precipitation averages about 41 cm/yr, distributed fairly evenly throughout the year with about half falling as snow.

The Estes Valley elk population was about 3,000 in the late 1990s (Lubow et al., this volume). In winter, about 70% of the elk stay within the town of Estes Park, and 25% to 30% reside inside the park. Grazing impacts are heavy in the lower valleys over winter and during spring and fall migrations to and from high-elevation summer range.

Exclosure 1 (0.4 ha) contains an upland sagebrush (*Artemisia tridentata*) community with scattered gooseberry (*Ribes inerme*), ponderosa pine (*Pinus ponderosa*), and grasses (*Bouteloua gracilis, Koeleria macrantha,* and *Muhlenbergia montana*). Exclosure 2 (1.2 ha) encompasses three vegetation types: upland sagebrush, mid-slope aspen (*Populus tremuloides*) with some scattered willows (*Salix monticola, S. geyeriana*, and *S. planifolia*), and lower-slope wet meadows dominated by sedge (*Carex* spp.) and grass (*Calamagrostis canadensis*). Exclosure 3 (0.4 ha) has two vegetation types: aspen and a mesic meadow (*Poa pratensis, Bromus inermis*, and *Phleum pratense*).

We stratified each exclosure into major vegetation types and sampled inside and outside the exclosures to determine the effects of elk grazing. Ten soil samples (6.2 cm diameter by 30 cm length, divided into two 15-cm intervals) were collected (in April 1999) at 2-m intervals along transects within each vegetation type and exclosure, and along paired transects that ran parallel to the fence lines. The transect locations were chosen 5–10 m away from the fence, in areas with matching microtopography. These samples were analyzed (by methods in USDA Natural Resources Conservation Service 1996) for bulk density (oven-dry basis), pH (2:1 water:soil paste), extractable phosphorus (Bray-1), and 1 M ammonium acetate-extractable calcium, magnesium, and potassium.

Available N was assessed by two methods, using the same sampling design as the soil samples. Net N mineralization was estimated with the closed-top-core technique (Adams and Attiwill 1986). Plastic tubes were pounded 15 cm into the mineral soil and capped for incubation periods ranging from 4 weeks (summer 1998) to 6 weeks (autumn 1998) to 6 months (winter 1998–1999). After the incubation period, soils were collected, mixed, and 10-g subsamples were extracted for 24 hours with 100 mL of 2 M KCl; ammonium-N and nitrate-N were determined on a Perstorp automated colorimeter. Net N mineralization was calculated as the post-incubation concentrations of ammonium and nitrate minus the concentrations from paired cores taken at the beginning of each incubation period. About one-third of the net mineralization rates were negative, and these values were set to 0 (representing no N available to plants for that sample location and period). The net N mineralization rates were summed across periods to give an annual estimate.

Ion exchange resin bags (Binkley and Hart 1989) were also used to estimate the availability of ammonium-N and nitrate-N. Resin bags were constructed with two sections: one with anion resin (14 mL of Sybron IONAC ASB-IPOH), and one with cation resin (14 mL of Sybron IONAC c-251 H^+). Each section of the resin bag was about 4 x 4 cm, with a band of heat-applied glue separating the pouches. In each vegetation type in each exclosure, 10 bags were placed 2 cm below the mineral soil surface, at 2-m intervals along a transect in May 1998, and retrieved in October 1998. A second set of resin bags was installed in October 1998 and retrieved in May 1999. In the laboratory, the anion and cation resin pouches were combined and extracted with 100 mL of 2 M KCl. Concentrations of ammonium and nitrate were determined colorimetrically on a Perstorp autoanalyzer.

We assessed the nitrogen limitation on plant growth by fertilizing small 2-m radius plots (12.5 m^2) with 10 g N/m^2 as urea, in March 1999. Two plots were fertilized in each vegetation type, inside and outside each exclosure. The extent of N limitation was evaluated by the length, mass, and N content of the 25 largest new shoots per shrub in July 1999 and by clipping herbaceous biomass from 0.25 m^2 plots.

The losses of N from the soil were estimated with porous cup lysimeters (2-cm diameter cups at 30–35 cm depth) in the wet meadow vegetation type for exclosure 2 and for the aspen vegetation type in exclosure 3. All the other exclosure and vegetation types were too rocky to insert lysimeters. Ten lysimeters were installed inside and outside at each site. The soils were too dry or frozen for sampling soil leachate except in the spring following snowmelt and major storms. On May 3, 13, 24, and June 22, 1999, water samples were collected from the lysimeters by applying a suction (-1 MPa), and returning several hours later to collect the accumulated water. Samples were stored in a cooler (2–4° C) for up to 5 hours before freezing for later analysis by automated colorimetry. Nitrogen concentrations were averaged across three sampling periods for each site. The variances of the soil solution concentrations were not normally distributed, so we used a non-parametric Kruskal-Wallis comparison to test for the effect of grazing.

We analyzed the effects of grazing three ways. We used *t*-tests to compare all samples within each exclosure with all samples outside that exclosure. We also used *t*-tests to compare individual vegetation types at each exclosure. These *t*-tests compared values inside and outside the exclosures, but given the lack of replication of sites, the *t*-tests could not separate true grazing effects from any other site difference that may have covaried with the location of the exclosure fences. No site differences were obvious, so we expect the *t*-tests represent primarily the grazing effects. Each vegetation type happened to be present at two exclosure sites, so we were able to test for the effect of grazing among sites with a split plot ANOVA approach (grazing treatment within exclosure site). We also tested for the overall effect of grazing by a split plot ANOVA (split-plot effect for grazing replicated at three sites).

Results

Across all vegetation types in all exclosures, the bulk density of the 0–15 cm depth mineral soil was higher in grazed units (0.94 kg/L; Table 1) than in ungrazed units (0.86 kg/L; $P = 0.04$). The pattern of greater bulk density on grazed units was strongest at exclosure 3, where the bulk density in the outside (grazed) area was 0.96 kg L, compared with 0.77 kg/L inside the exclosure. The mesic meadow vegetation type showed a greater difference in bulk density at exclosure 3 than did the aspen type. Despite the overall effect of higher bulk density in grazed units, the rocky upland sagebrush type showed no trend (Table 1).

No overall effect of grazing on pH was apparent across the exclosures and vegetation types, but grazing significantly affected soil pH in the aspen vegetation types (Table 1). This effect was consistent in both exclosures with aspen and was strongest at exclosure 3, where the 0–15 cm depth soil was 0.7 units lower inside the exclosure.

Grazing had no overall effect on total soil C and N across all exclosures and vegetation types (Table 2). The only significant effect among the vegetation types and exclosures was the mid-slope aspen type in exclosure 2, where the grazed area had 2.11 kg C/m^2 more C (to 30 cm) and 0.17 kg/m^2 more N than inside the exclosure. The effect of grazing in the aspen vegetation type at exclosure 3 was not significant (and was near 0), so we expect the large difference at exclosure 2 may result from site factors other than the effect of grazing.

The effects of grazing on soil cations and phosphorus were mixed. Grazing substantially reduced the quantities of extractable calcium, magnesium, potassium and phosphorus in the upland sagebrush type (Table 3), with average reductions of about one-third. The only other significant effect of grazing was higher extractable potassium in grazed aspen types.

Resin bags showed no overall effect of grazing through the growing season across all exclosures and vegetation types. The only significant effect was in exclosure 1, where net nitrification was three times higher with grazing than without (Table 4). Net N mineralization showed no significant effects of grazing treatments for individual communities within or across sites (Table 4). The resin estimates of N supply were generally higher for aspen than for upland sage or meadow, and net N mineralization also appeared higher for aspen.

No effects of grazing were evident in the soil solution concentrations in the wet meadow at exclosure 2 (Fig. 1), with both grazed and ungrazed units showing an average of about 0.10 mg N/L in springtime soil leachate. The effect of grazing appeared to be extremely large for the aspen vegetation type at exclosure 3, where the ungrazed unit with aspen trees averaged well under 1 mg N/L, compared with an average of nearly 5 mg N/L (mostly as nitrate) for the adjacent area where elk grazing has removed most of the aspen.

Table 1. Soil bulk density and pH by depth (means with standard deviations in parentheses).

Site #	Soil property by depth (cm)		Upland sagebrush		Mid-slope aspen		Lower-slope meadow		Site average	
			Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
1	Bulk density	0–15	1.19 (0.10)	1.17 (0.13)					1.19 (0.10)	1.17 (0.13)
	(kg/L)	15–30	1.10 (0.21)	1.21 (0.25)					1.10 (0.21)	1.21 (0.25)
	pH	15	6.6 (0.2)	6.6 (0.3)					6.6 (0.2)	6.6 (0.3)
		15–30	6.7 (0.1)	6.7 (0.1)					6.7 (0.1)	6.7 (0.1)
2	Bulk density	0–15	1.02 (0.14)	1.04 (0.18)	0.82 (0.14)	0.90 (0.14)	0.68 (0.23)	0.64 (0.33)	0.84 (0.22)	0.86 (0.29)
	(kg/L)	15–30	1.03 (0.19)	1.10 (0.27)	0.99 (0.16)	1.02 (0.19)	0.82 (0.16)	0.92 (0.11)	0.95 (0.19)	1.02 (0.21)
	pH	0–15	6.3 (0.2)	6.4 (0.2)	6.1 (0.2)	6.2 (0.6)	5.9 (0.3)	5.6 (0.3)	6.1 (0.3)	6.1 (0.5)
		15–30	6.4 (0.3)	6.4 (0.4)	6.1 (0.2)	6.4 (0.4)	5.8 (0.3)	5.6 (0.4)	6.1 (0.4)	6.1 (0.5)
3	Bulk density	0–15			0.83 (0.17)[a]	0.94 (0.12)[a]	0.70 (0.26)[a]	0.98 (0.15)[a]	0.77 (0.22)[a]	0.96 (0.14)[a]
	(kg/L)	15–30			1.00 (0.18)	0.96 (0.14)	0.88 (0.33)	0.96 (0.28)	0.94 (0.27)	0.96 (0.22)
	pH	0–15			5.4 (0.1)[a]	6.1 (0.3)[a]	6.3 (0.2)[a]	6.5 (0.0)[a]	5.8 (0.5)[a]	6.3 (0.3)[a]
		15–30			5.2 (0.2)[a]	6.2 (0.3)[a]	6.3 (0.1)[a]	6.5 (0.1)[a]	5.7 (0.6)[a]	6.3 (0.3)[a]
Vegetation type average										
	Bulk density	0–15	1.11 (0.15)	1.10 (0.17)	0.82 (0.15)	0.92 (0.15)	0.69 (0.24)[a]	0.81 (0.31)[a]	0.86 (0.25)[a]	0.94 (0.25)[a]
	(kg/L)	15–30	1.06 (0.20)	1.15 (0.26)	1.00 (0.17)	0.99 (0.16)	0.86 (0.26)	0.94 (0.26)	0.97 (0.22)	1.03 (0.23)
	pH	0–15	6.5 (0.2)	6.5 (0.3)	5.7 (0.4)[a]	6.2 (0.5)[a]	6.1 (0.3)	6.0 (0.5)	6.1 (0.4)	6.2 (0.5)
		15–30	6.6 (0.3)	6.5 (0.4)	5.6 (0.5)[a]	6.3 (0.3)[a]	6.1 (0.3)	6.1 (0.6)	6.1 (0.5)	6.3 (0.5)

[a] $P < 0.1$.

Table 2. Total soil C and N (kg/m^2) by depth (means with standard deviations in parentheses).

Site #	Element, soil depth (cm)	Upland sagebrush		Mid-slope aspen		Lower-slope meadow		Site average	
		Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
1	C 0–15	1.81 (0.84)	1.78 (0.63)					1.81 (0.84)	1.78 (0.63)
	15–30	3.60 (1.00)	3.11 (0.88)					3.60 (1.00)	3.11 (0.88)
	0–30	5.41 (1.53)	4.90 (1.47)					5.41 (1.53)	4.90 (1.47)
	N 0–15	0.14 (0.06)	0.14 (0.05)					0.14 (0.06)	0.14 (0.05)
	15–30	0.30 (0.09)	0.27 (0.08)					0.30 (0.09)	0.27 (0.08)
	0–30	0.44 (0.13)	0.41 (0.12)					0.44 (0.13)	0.41 (0.12)
2	C 0–15	1.71 (0.39)	1.62 (0.58)	5.08 (1.94)[a]	6.48 (1.38)[a]	6.18 (2.06)	6.51 (1.12)	4.69 (2.17)	5.28 (2.06)
	15–30	2.81 (0.79)	2.86 (0.83)	3.85 (1.35)	4.56 (0.86)	4.04 (1.01)[a]	4.98 (1.30)[a]	3.20 (1.44)	3.72 (1.78)
	0–30	4.53 (0.84)	4.48 (1.10)	8.93 (2.83)[a]	11.04 (1.67)	10.22 (1.87)	11.49 (1.86)	7.89 (3.15)	9.00 (3.60)
	N 0–15	0.14 (0.04)	0.12 (0.04)	0.40 (0.15)[a]	0.51 (0.12)[a]	0.52 (0.17)	0.52 (0.11)	0.38 (0.18)	0.42 (0.17)
	15–30	0.23 (0.06)	0.24 (0.09)	0.31 (0.13)	0.37 (0.06)	0.37 (0.12)	0.48 (0.18)	0.28 (0.14)	0.32 (0.18)
	0–30	0.36 (0.06)	0.36 (0.11)	0.71 (0.23)[a]	0.88 (0.14)[a]	0.89 (0.17)	1.00 (0.18)	0.65 (0.27)	0.75 (0.32)
3	C 0–15			6.84 (1.24)	6.39 (1.33)	3.96 (1.78)	4.34 (0.97)	5.40 (2.10)	5.37 (1.54)
	15–30			3.44 (1.22)	3.94 (1.53)	3.15 (1.90)	2.38 (0.94)	3.30 (1.56)	3.16 (1.47)
	0–30			10.28 (1.36)	10.33 (2.77)	7.12 (3.45)	6.72 (1.62)	8.70 (3.02)	8.52 (2.88)
	N 0–15			0.54 (0.10)	0.48 (0.09)	0.32 (0.13)	0.33 (0.08)	0.43 (0.16)	0.41 (0.11)
	15–30			0.25 (0.10)	0.31 (0.12)	0.25 (0.16)	0.16 (0.07)	0.25 (0.13)	0.23 (0.12)
	0–30			0.80 (0.13)	0.79 (0.20)	0.57 (0.27)	0.50 (0.13)	0.68 (0.24)	0.64 (0.22)
Vegetation type average									
	C 0–15	3.21 (0.96)	2.99 (0.84)	5.96 (1.82)	6.43 (1.32)	5.07 (2.19)	5.43 (1.51)	4.75 (2.06)	4.95 (1.91)
	15–30	1.76 (0.64)	1.71 (0.60)	3.64 (1.27)	4.25 (1.25)	3.60 (1.55)	3.68 (1.73)	3.00 (1.48)	3.21 (1.67)
	0–30	4.97 (1.28)	4.69 (1.28)	9.60 (2.27)	10.68 (2.26)	8.67 (3.13)	9.10 (2.98)	7.75 (3.07)	8.16 (3.40)
	N 0–15	0.26 (0.09)	0.25 (0.08)	0.47 (0.14)	0.49 (0.10)	0.42 (0.18)	0.43 (0.14)	0.39 (0.16)	0.39 (0.15)
	15–30	0.14 (0.05)	0.13 (0.05)	0.28 (0.12)	0.34 (0.10)	0.31 (0.15)	0.32 (0.21)	0.24 (0.13)	0.26 (0.16)
	0–30	0.40 (0.11)	0.39 (0.11)	0.75 (0.19)	0.83 (0.18)	0.73 (0.28)	0.75 (0.30)	0.63 (0.26)	0.66 (0.29)

[a] P <0.1.

Table 3. Extractable calcium, magnesium, potassium, and phosphorus (means with standard deviations in parentheses).

Site #	Cations (mmol/$_c$/m^2) and Bray-1 P (g/m^2)	Upland sagebrush Ungrazed	Upland sagebrush Grazed	Mid-slope aspen Ungrazed	Mid-slope aspen Grazed	Lower-slope meadow Ungrazed	Lower-slope meadow Grazed	Site average Ungrazed	Site average Grazed
1	Calcium	6.3 (2.5)	4.6 (2.4)					6.3 (2.5)	4.6 (2.4)
	Magnesium	1.1 (0.4)	0.7 (0.4)					1.1 (0.4)	0.7 (0.4)
	Potassium	0.57 (0.16)	0.36 (0.21)					0.57 (0.16)	0.36 (0.21)
	Phosphorus	3.4 (2.2)[a]	1.9 (1.2)[a]					3.4 (2.2)[a]	1.9 (1.2)[a]
2	Calcium	6.5 (1.3)[a]	2.8 (2.2)[a]	13.4 (8.1)	11.3 (8.3)	13.0 (8.1)	16.1 (6.4)	10.9 (7.2)	10.4 (7.9)
	Magnesium	1.4 (0.2)[a]	0.7 (0.4)[a]	5.0 (3.5)	3.4 (2.5)	3.7 (2.3)	3.8 (1.5)	3.3 (2.8)	2.7 (2.2)
	Potassium	0.4 (0.1)	0.3 (0.2)	0.61 (0.30)	0.71 (0.36)	0.71 (0.33)	0.92 (0.40)	0.58 (0.29)	0.65 (0.41)
	Phosphorus	1.3 (1.4)[a]	0.1 (0.3)[a]	0.04 (0.13)	0.54 (1.46)	<0.01	<0.01	0.45 (0.97)	0.24 (0.86)
3	Calcium			12.5 (3.9)	13.8 (3.6)	11.4 (2.6)	11.5 (4.1)	12.0 (3.3)	12.6 (4.0)
	Magnesium			3.8 (1.3)	3.1 (1.0)	2.2 (0.8)	2.0 (0.7)	3.1 (1.3)	2.5 (1.0)
	Potassium			0.85 (0.27)[a]	1.34 (0.51)[a]	1.18 (0.51)	0.90 (0.49)	1.01 (0.42)	1.12 (0.54)
	Phosphorus			0.03 (0.08)	0.45 (1.42)	3.1 (2.9)	4.7 (4.1)	1.56 (2.53)	2.59 (3.72)
Landscape average									
	Calcium	6.4[a]	4.2[a]	13.0	12.6	12.2	13.8	10.5	10.2
	Magnesium	1.2[a]	0.7[a]	4.4	3.2	3.0	2.9	2.9	2.3
	Potassium	0.50[a]	0.33[a]	0.73[a]	1.04[a]	0.95	0.91	0.72	0.76
	Phosphorus	2.4[a]	1.0[a]	0.03	0.50	1.55	2.37	1.31	1.29

[a] $P < 0.01$.

Table 4. Annual resin-bag N and net N mineralizations (means with standard deviations in parentheses).

Site #	Resin-N (mg/bag), or net mineralization (g N/m^2)	Upland sagebrush		Mid-slope aspen		Lower-slope meadow		Site average	
		Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
1	Resin NH_4-N	7.3 (9.0)	7.8 (7.5)					7.3 (9.0)	7.8 (7.5)
	Resin NO_3-N	3.2 (2.8)[a]	10.5 (7.3)[a]					3.2 (2.8)[a]	10.5 (7.3)[a]
	Resin sum	10.5 (10.2)	18.3 (13.5)					10.5 (10.2)	18.3 (13.5)
	Net N min.	3.8 (5.0)	3.8 (2.4)					3.8 (5.0)	3.8 (2.4)
2	Resin NH_4-N	5.2 (2.8)	4.1 (0.8)	10.0 (19.6)	5.8 (4.2)	5.0 (2.8)	2.8 (2.5)	6.7 (11.4)	4.5 (3.2)
	Resin NO_3-N	4.5 (4.3)	4.3 (2.6)	13.2 (29.4)	7.6 (5.5)	3.1 (0.7)	4.6 (2.6)	6.9 (17.1)	6.2 (5.2)
	Resin sum	9.7 (5.2)	8.4 (2.9)	23.2 (48.6)	13.3 (7.2)	8.0 (2.6)	7.4 (2.4)	13.7 (28.0)	10.6 (6.7)
	Net N min.	2.5 (1.0)	3.0 (1.6)	5.9 (4.2)	7.2 (8.2)	2.9 (1.8)	6.0 (7.8)	3.8 (3.0)	4.6 (5.2)
3	Resin NH_4-N			11.7 (15.9)	9.1 (9.1)	2.7 (1.6)	2.7 (1.6)	5.2 (6.3)	7.2 (11.9)
	Resin NO_3-N			6.7 (4.5)	6.8 (3.8)	4.8 (2.3)	3.5 (2.2)	4.8 (3.2)	5.7 (3.6)
	Resin sum			18.4 (18.6)	16.0 (12.7)	7.6 (2.7)	6.2 (1.9)	10.0 (9.0)	13.0 (14.1)
	Net N min.			6.1 (5.9)	7.9 (5.0)	6.2 (5.3)	3.7 (1.5)	6.2 (5.4)	5.6 (4.1)
Landscape average									
	Resin NH_4-N	6.2	5.9	10.9	7.1	3.8	2.8	7.0	5.1
	Resin NO_3-N	3.9	7.4	9.9	7.3	4.0	4.0	6.0	6.2
	Resin sum	10.1	13.4	20.8	14.4	7.8	6.8	13.0	11.3
	Net N min.	3.1	3.4	6.0	7.5	4.6	4.9	4.3	5.0

[a] $P < 0.01$.

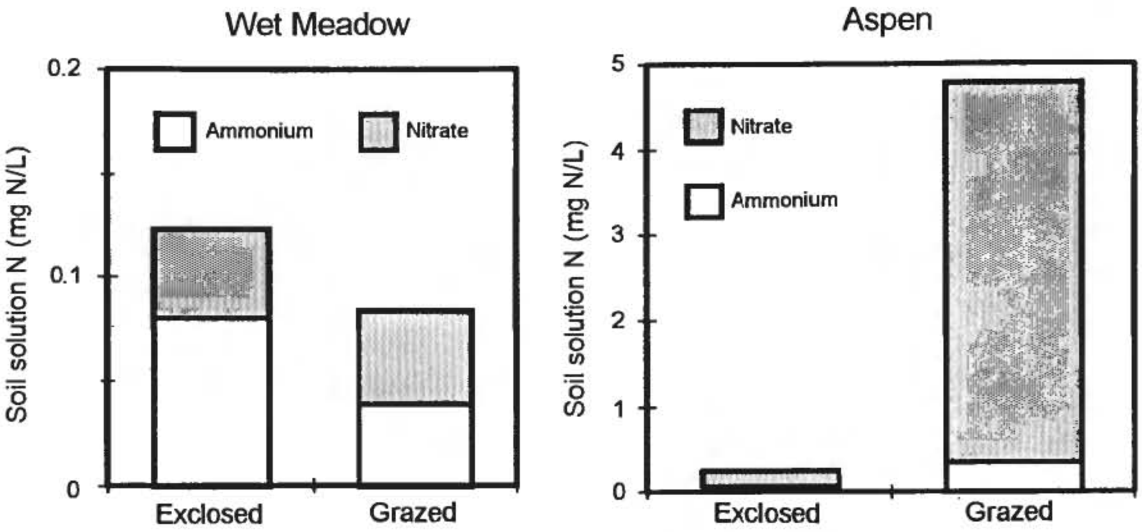

Fig. 1. Average (4 sampling periods at 2-week intervals in spring 1999) concentrations of ammonium-N and nitrate N in soil solutions sampled at 30–35 cm depth with ceramic cup tension lysimeters. No effect of grazing was apparent for the wet meadow site, but at the aspen site grazing substantially increased nitrate leaching ($P < 0.03$) and ammonium+nitrate leaching ($P < 0.02$).

Fertilization with N doubled the production of grasses (Fig. 2) and shrubs (Fig. 3), indicating that current productivity in these ecosystems are strongly N limited. The fertilization treatments showed no interaction with grazing ($P < 0.5$), so the N limitation on growth was not alleviated or exacerbated by grazing.

Discussion

The major effects of high elk populations in our study sites appear to be an increase in soil bulk density with grazing (except for the rocky upland sagebrush type), and an increase in soil pH with grazing of aspen vegetation types. We did not assess the direct cause of the lower pH under aspen, but given similar soil C and extractable cation concentrations, we expect the difference likely results from the accumulation of more-strongly acidic organic matter under aspen (Binkley et al. 1989). The total quantity of C and N stored in soils did not differ across the exclosures and vegetation types, with one exception (exclosure 2 aspen type), so we conclude there was no evidence of substantial effects of elk grazing on soil C and N. Grazing lowered the extractable quantities of base cations and phosphorus in the upland sagebrush soils, but not in the other soils. The resin bags and net N mineralization assays showed no strong effects of grazing.

These findings contrast somewhat with those of Frank and Groffman (1998) for seven exclosures in grassland sites in Yellowstone National Park. They found no effect of grazing on 0–10 cm depth soil bulk density, soil C, or soil N, but a consistently higher rate of net N mineralization from grazed areas. Lane and Montagne (1996) also examined these exclosures, and concluded that grazing increased the bulk density of the 0–5 cm depth soil by 30%. In Rocky Mountain National Park, elk grazing and hoof action compacted soils at two of the three sites, particularly in the grass type. Our single case of significant differences in soil C and N came from an aspen-dominated vegetation type, which was not represented in the Yellowstone study. Interestingly, the annual rates of net N mineralization were similar between the studies, ranging from 2.5 to 7.2 gN m^{-2} yr^{-1} for Rocky Mountain (average 4.7 gN m^{-2} yr^{-1}), and between 0.9 and 8.1 gN m^{-2} yr^{-1} for Yellowstone (average 3.0 gN m^{-2} yr^{-1}). The biggest difference between the two studies was in the rates of net N mineralization. The incubation methods differed slightly with the Yellowstone study using soils in plastic bags rather than tubes, but this should not introduce any major artifact. Our Rocky Mountain

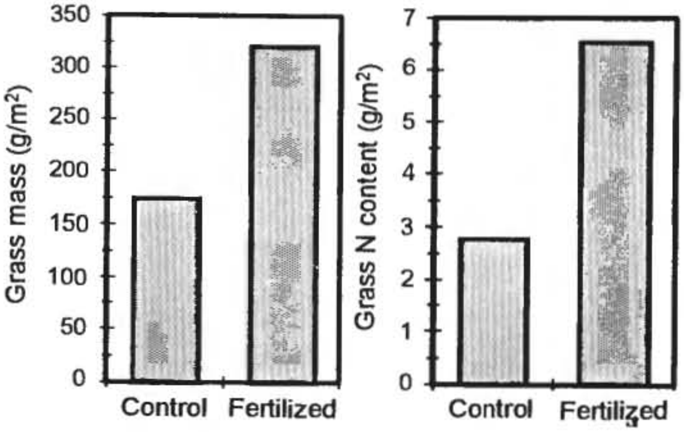

Fig. 2. Average mass and N content of grasses (with some herbs) in 0.25 m^2 plots with and without N fertilization ($P < 0.1$ for mass, $P < 0.05$ for N content; effect of grazing not significant).

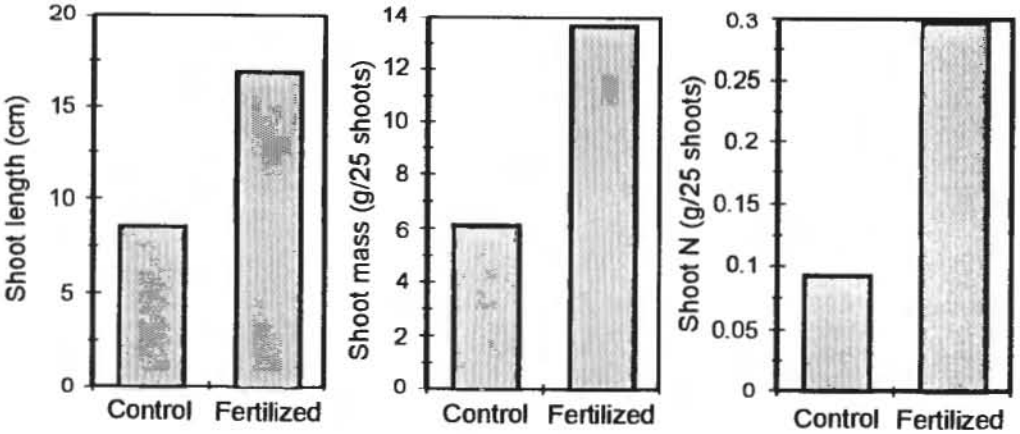

Fig. 3. Average shoot length, shoot mass and N content (total of 25 shoots/shrub) with and without N fertilization ($P < 0.02$ for length, $P < 0.05$ for mass, $P < 0.1$ for N content; effect of grazing not significant).

study used longer cores (0–15 cm, rather than 0–10 cm), which might increase the Rocky Mountain values relative to Yellowstone. The effect of grazing on net N mineralization was clear for the Yellowstone study, but no substantial effect was evident in our Rocky Mountain study. Given the similarity of approaches, we expect this difference in pattern between the two national parks probably represents a real difference in the effect of grazing rather than artifacts of the methods.

Why should the effects of elk grazing differ among vegetation types in Rocky Mountain National Park and between this park and Yellowstone National Park? No simple answers are available, and given that the much larger literature on livestock grazing shows the same inconsistent stories (Milchunas and Lauenroth 1993; Burke et al. 1997), we expect the real effects of grazing have real differences across vegetation types and locations. Important factors that influence the effect of grazing on a particular location might include the actual intensity of grazing (across years), the particular species present, any changes in vegetation composition, and the properties and dynamics of the soil.

The apparent effect of grazing on soil N leaching at exclosure 2 in the aspen vegetation type was surprisingly large. The differences in soil solution concentrations were consistent among lysimeters and across sampling dates, so we are confident the pattern was real. However, without replication of the exclosures, these real differences could result either from grazing or from site factors. Unfortunately, other studies have not examined soil leachates with respect to grazing exclosures, so we cannot say if our findings are representative or unusual.

Overall, the only clear effects of high elk populations in our study were: (1) higher soil bulk density (except for rockier, upland sage communities); and (2) lower extractable base cations and phosphorus in upland sagebrush sites, and higher soil pH where elk grazing prevented aspen growth. Grazing also appeared to have a large effect on nitrate leaching losses for the aspen type at exclosure 3, but without replication of sites we remain unsure about the contribution of grazing or site effects. We found no other clear evidence of major impacts of heavy elk grazing on soil N supply or overall accumulation of total N and C in the soil, and without such changes, we conclude there is no evidence of a substantial effect of elk on sustainability of soil fertility. We found no reason to speculate that any major decrease in elk populations would have major effects on soils. Any potential effect of large increases in elk populations would be difficult to predict, and we would not be confident in concluding that no soil changes would result. Our fertilization treatments clearly showed that the availability of N strongly limits plant growth, so we expect that any future development of grazing effects on N supply would have important implications for plant species composition and growth.

We stress that three large exclosures may not be enough to identify any effects except very large ones, and that more subtle effects might be apparent over longer time periods, or with stronger experimental designs (such as more replicate exclosures). A new suite of 16 exclosures was established in 1994; if these are maintained for several decades, they may provide a strong enough design to identify the effects of elk grazing on soils and nutrient cycling more definitively.

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Literature Cited

Adams, M. A., and P. M. Attiwill. 1986. Nutrient cycling and nitrogen mineralization in eucalypt forests of southeastern Australia. II. Indices of nitrogen mineralization. Plant and Soil 92:341–362.

Baker, W. L., J. A. Munroe, and A. E. Hessl. 1997. The effect of elk on aspen in the winter range of Rocky Mountain National Park, Colorado, USA. Ecography 20:155–165.

Bazely, D. R., and R. L. Jefferies. 1985. Goose feces: A source of nitrogen for plant growth in a grazed salt marsh. Journal of Applied Ecology 22:693–703.

Binkley, D., and S. C. Hart. 1989. The components of nitrogen availability assessments in forest soils. Advances in Soil Science 10:57–116.

Binkley, D., C. T. Driscoll, H. L. Allen, P. Schoeneberger, and D. McAvoy. 1989. Acidic deposition and forest soils. Springer-Verlag, New York.

Burke, I. C., W. K. Lauenroth, and D. G. Milchunas. 1997. Biogeochemistry of managed grasslands in central North America. Pages 85–102 *in* E. Paul, K. Paustian, E. Elliott, and C. Cole, editors. Soil organic matter in temperate agroecosystems. CRC Press, Boca Raton, Fla.

Caughley, G. 1981. Pages 6–9 *in* P. A. Jewell and S. Holt, editors. Problems in management of locally abundant wild mammals. Academic Press, Orlando, Fla.

Caughley, G., and J. H. Lawton 1981. Plant-herbivore systems. Pages 132–166 *in* R. M. May, editor. Theoretical ecology. 2e. Blackwell Scientific, Oxford.

Coughenour, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. Journal of Applied Ecology 28:71–82.

Coughenour, M. B., and F. J. Singer. 1995. Yellowstone elk population responses to fire: Landscape carrying capacity and spatial ecosystem modeling. Pages 169–180 *in* J. M. Greenlee, editor. Ecological implications of fire in Greater Yellowstone. International Association of Wildland Fire, Fairfield, Wash.

Ellis, J. E., and D. M. Swift. 1988. Stability of African pastoral ecosystems: Alternative paradigms and implications for development. Journal of Range Management 41:450–459.

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.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73:2043–2058.

Fuls, E. R. 1992. Ecosystem modification created by patch-overgrazing in semi-arid grassland. Journal of Arid Environments 23:59–69.

Gordon, I. J. 1988. Facilitation of red deer grazing by cattle and its impact on red deer performance. Journal of Applied Ecology 25:1–10.

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

Iason, G. R., D. C. Duck, and T. H. Clutton-Brock. 1986. Grazing and reproductive success of red deer: The effects of local enrichment by gull colonies. Journal of Animal Ecology 55:507–515.

Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits production of tallgrass prairie. BioScience 36:662–668.

Lane, J. R., and C. Montagne. 1996. Characterization of soils from grazing exclosures and adjacent areas in northern Yellowstone National Park. Pages 63–71 *in* F. Singer, editor. Effects of grazing by wild ungulates in Yellowstone National Park. U.S. Department of the Interior, National Park Service Technical Report NPS/96-01.

McNaughton, S. J. 1983. Grazing lawns: Animals in herds, plant form, and coevolution. American Naturalist 124:863–886.

McNaughton, S. J. 1988. Mineral nutrition and spatial concentration of African ungulates. Nature 334:343–345.

McNaughton, S. J. 1990. Mineral nutrition and seasonal movement of African ungulates. Nature 345:613–615.

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.

Moss, R., D. Welch, and P. Rothery. 1981. Effects of grazing by mountain hares and red deer on the production and chemical composition of heather. Journal of Applied Ecology 18:487–496.

Mould, E. D., and C. T. Robbins. 1981. Nitrogen metabolism in elk. Journal of Wildlife Management 45:323–334.

Risser, P. G., and W. J. Parton. 1982. Ecosystem analysis of the tallgrass prairie: Nitrogen cycle. Ecology 63:1342–1351.

Seagle, S. W., and S. J. McNaughton. 1992. Simulated effects of grazing on soil nitrogen and mineralization in contrasting Serengeti grassland. Ecology 73:1105–1111.

Singer, F. J. 1995. Effects of grazing by ungulates on upland bunchgrass communities of the northern range of Yellowstone National Park. Northwest Science 69:191–203.

Singer, F. J., and M. K. Harter. 1996. Comparative effects of elk herbivory and fires of 1988 on grasslands in northern Yellowstone National Park. Ecological Applications 6:185–199.

Suzuki, K., H. Suzuki, D. Binkley, and T. Stohlgren. 1999. Aspen regeneration in the Colorado Front Range: Differences at local and landscape scales. Landscape Ecology 14:231–237.

U.S. Department of Agriculture, Natural Resources Conservation Service. 1996. Pages 327–331 *in* Soil Survey Laboratory Methods Manual. Soil Survey Investigations Report No. 42, Version 3.0.

Wagner, F. H., R. Foresta, R. B. Gill, D. R. McCullough, R. R. Pelton, W. F. Porter, and H. Salwasser. 1995. Wildlife policies in the U.S. national parks. Island Press, Washington D.C. 242 pp.

Sustainability of Vegetation Communities Grazed by Elk in Rocky Mountain National Park

By

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Abstract. Current management of much of the worlds' grazing lands is either based on changes in plant species composition or on other management evaluation programs that emphasize changes in net aboveground production. Management based solely on changes in aboveground production has been criticized as too limited in view, because it ignores root production, nitrogen pools, nutrient processes, and the long-term sustainability of the ecosystem. The purpose of this study was to compare the effects of elk (*Cervus elaphus*) grazing on aboveground production, internal nitrogen (N) fluxes, N pools and inputs, and elk nutrient transfers across the landscape in different vegetation types in Rocky Mountain National Park (RMNP), Colorado. Nitrogen processes and possibly N pools were significantly reduced in the willow community, but not in the upland grass/shrub community. Nitrogen mineralization rates were lower in grazed versus ungrazed short willow sites ($P = 0.07$; n = 4 sites), as were nitrate (NO_3) pools ($P = 0.10$), but not in tall willow sites ($P > 0.10$; n = 4 sites) after 4 years. There was about half the annual N inputs to the soil surface in grazed willow sites (5.79g $N/m^2/yr$ = annual herbaceous biomass – offtake + litterfall + elk urine and feces) compared to ungrazed sites (9.66 g $N/m^2/yr$ = annual herbaceous biomass + litterfall), suggesting elk herbivory and movement led to a net loss of N in the willow vegetation type. Elk substantially reduced the annual growth of willows (*Salix* spp.) by 98% after 35 years and 66% after 4 years of treatment. Thus, height and canopy size of willows were reduced as well as willow litter biomass (65 $g/m^2/yr$ in ungrazed versus 33 $g/m^2/yr$ in grazed), and N yield of willows was 64% less in grazed plots. Elk grazing had no significant effect on other soil N pools (NH_4) or litter decomposition rates in either of the two willow types, nor on any nitrogen process rates or pools in the upland grass/shrub type ($P > 0.10$). Nitrogen concentrations in plant tissue were not influenced for the most part by elk grazing (increased N concentration found in only 4 of 13 species). Elk apparently also transported N away from aspen at an even higher rate (N inputs were 1.65 g $N/m^2/yr$ in grazed sites vs. 3.79 g $N/m^2/yr$ in ungrazed sites). Elk grazing reduced shrub biomass at 35-year treatments in upland grass/shrub communities, but led to more N inputs to the soil surface in this vegetation type (2.28 g $N/m^2/yr$ grazed versus 0.59 g $N/m^2/yr$ ungrazed). CENTURY modeling supported these observations. This soil N model predicted almost no change (0.5–2% less) in N or carbon (C) pools in 50 years in the upland grass/shrub vegetation type, but greater losses in the willow type. If elk population levels were increased to carrying capacity in the ecosystem (about 25% more consumption) projected losses after 50 years were greater, but still <4% for soil C and 1% for soil N in the upland type, and 6% for soil C and 2% for soil N in the willow type. Total shrub C was projected to decline 10% in 50 years in the willow type at current elk densities. We recommend conservative management of elk numbers and grazing until additional years of measures are gathered on the lower mineralization rates in the short willow type and until the projected declines in N pools can be verified.

Keywords: *Cervus elaphus*, elk, mineralization, nitrogen, overabundance, overgrazing, Rocky Mountain National Park, sustainability, willows.

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Current management of much of the world's grazing lands emphasizes changes in plant species composition (Dyksterhuis 1949; Lauenroth and Laycock 1989). One common example of current grazing management limits for western U.S. rangelands is the "increaser-decreaser-invader species" concept of Sampson (1919). Change in aboveground production of plants (Westoby et al. 1989; McNaughton 1993) is another common criteria for setting grazing limits. Milchunas and Lauenroth (1992) rated the long-term ability of the system to sustain productivity under the level of grazing as the highest priority for rangeland management. Change in net aboveground production due to grazing is also currently used to evaluate and manage many western U.S. rangelands, both in national parks, national wildlife refuges, and other public lands (Milchunas and Lauenroth 1992; Biondini et al. 1998). But emphasizing net aboveground production has been criticized as an incomplete view, in that changes in aboveground production might be short-lived and at the expense of root biomass (Belsky 1986) or long-term N pools and soil organic matter (Risser and Parton 1982; Burke et al. 1989). We selected elk grazing in RMNP, Colorado as a study situation where we could sample and compare both effects of elk on aboveground plant production and also effects of elk herbivory on longer-term ecosystem variables such as belowground root biomass, N pools, N inputs, soil organic matter, and N cycling.

Elk have become increasingly abundant in Rocky Mountain ecosystems in the U.S. and Canada. The elimination of large predators, disruption and loss of migration routes, and the creation of artificial forage sources in towns and developed areas have contributed to possible overconcentrations of elk (Wagner et al. 1995). Density-dependent regulation of elk in national parks has been questioned as to its ability to produce the expected equilibria behavior in animal populations (Ellis and Swift 1989), although net aboveground production has been maintained or even increased under natural regulation (Frank and McNaughton 1992, 1993; Singer et al. 1998a; Huff and Varley 1999). In this study, we explore an alternative approach to evaluating the appropriate numbers of ungulates based on the premise that alterations in ecosystem nutrient pools and flows will alter sustainable plant production and can also drive plant species composition changes.

Nitrogen is an essential nutrient that determines ecosystem production in most temperate ecosystems. Ecosystem N pools may take centuries to accumulate and turnover rates may be slow. In ecosystems with a high availability of N, plant species typically have a higher requirement for N and cycle N more rapidly. Organic matter content of the soil is also closely tied to N availability and ability of the soil to hold moisture. Depletion of N and soil organic matter by ungulates could reduce long-term plant productivity and alter plant species composition since many plants have specific N requirements.

Ungulates may be more than just consumers of plants and products of ecosystems. Ungulates may also be regulators of ecosystem processes (Frank and McNaughton 1992; McNaughton 1993; Hobbs 1996). The indirect effects that ungulates may have on ecosystem processes may exceed their direct effects of consuming plants. These indirect effects may include changes in N and defense chemical concentrations in plants, changes in the quality and quantity of litter, and changes to decomposition and mineralization rates (Fig. 1). Grazing may result in increased N availability to plants by reducing root biomass and thus microbial biomass, which reduces C:N ratios (Schimel et al. 1985; Holland and Detling 1990; Seagle et al. 1992). Ungulate feces and urine provide large inputs of soluble N that is readily available to plants (Risser and Parton 1982; Bazely and Jeffries 1985; McNaughton 1990), and the excretions promote decomposition rates (Seagle et al. 1992; Pastor et al. 1993). Nitrogen is more available to plants on grazed sites (Holland and Detling 1990; Seagle et al. 1992), especially near the soil surface where it is more accessible to plants (Archer and Smeins 1991). As a result, uptake rates of N by plants, plant tissue concentrations of N, N mineralization, and aboveground production of plant biomass may be increased on grazed sites (Moss et al. 1981; McNaughton 1984; Coughenour 1991; Frank and McNaughton 1992; Singer and Harter 1996; Frank and Groffman 1998). Ungulates may preferentially graze on plant regrowth from previously grazed sites leading to improved body condition and higher reproductive success (Moss et al. 1981; Iason et al. 1986; Gordon 1988) in a positive feedback loop that maintains grazing "hot spots" (McNaughton 1988).

Alternatively, ungulate grazing may result in reduced N pools and reduced N mineralization rates (Risser and Parton 1982; McInnes et al. 1992; Ritchie et al. 1998). Ritchie et al. (1998) reported that the resource limiting plant growth might dictate whether ungulates accelerate or decelerate N cycling and plant responses. If the plants are N limited and ungulates select N-rich plants and thus increase the dominance of plants with low tissue N, then litter quality, decomposition, and N

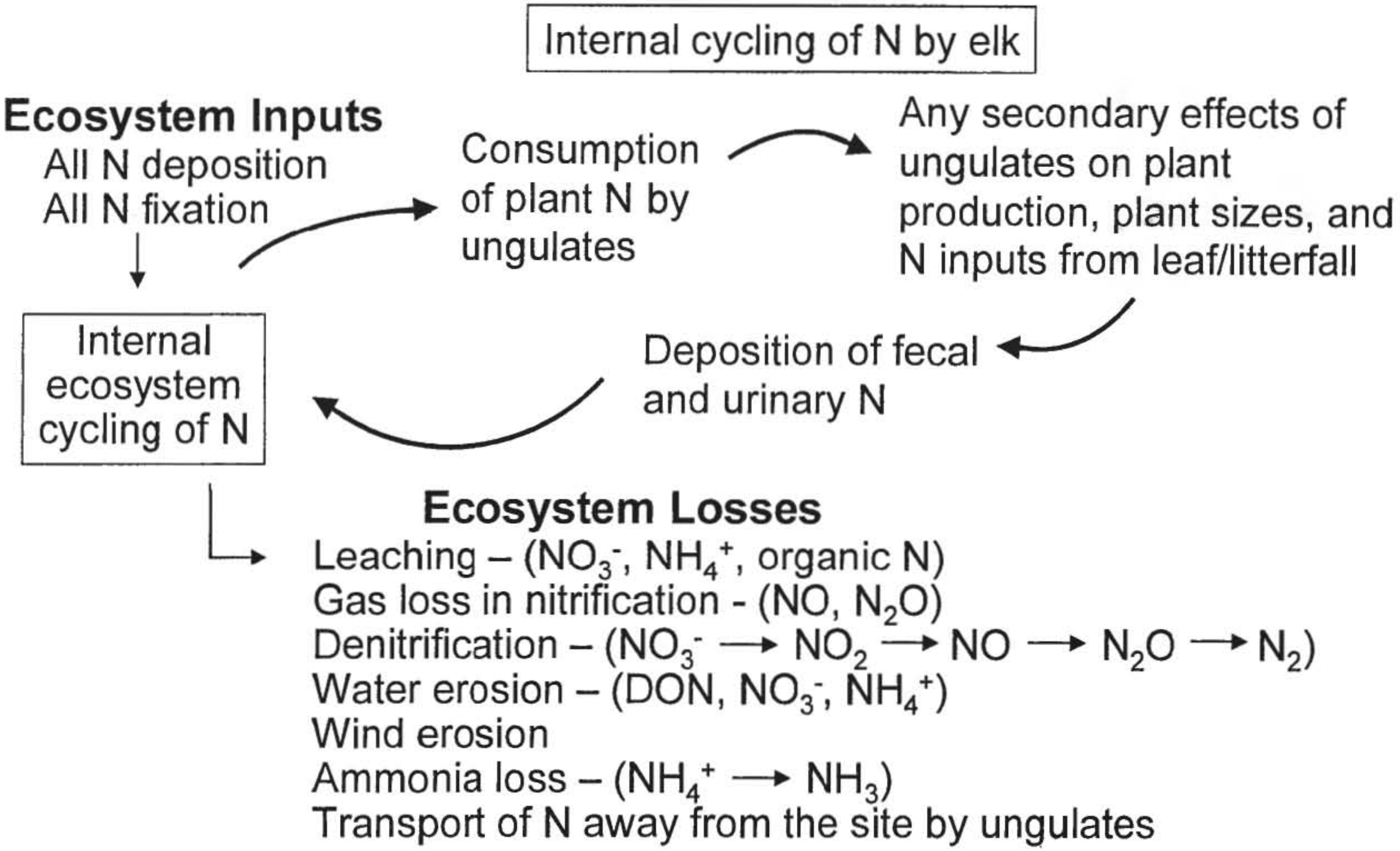

Fig. 1. Schematic diagram of N flows and fluxes demonstrating internal cycling of N by elk and ecosystem, or external inputs and outputs. Nitric oxide is represented by NO and DON represents dissolved organic nitrogen.

mineralization is lowered. However, if the dominant plants have high tissue N and/or tolerate herbivory, then herbivory will likely accelerate N cycling.

We conducted this study to determine whether: (1) elk herbivory results in a net gain or net loss of N inputs to the soil surface of the elk winter range; (2) there is a net transfer of N between vegetation types on the winter range or between seasonal ranges; (3) there are any secondary effects of elk on N pools or inputs through structural changes to the plant communities; (4) elk influence ecosystem processes such as mineralization rates or decomposition rates; and (5) there are long-term projections for N losses or N gains due to elk.

Study Area

The elk winter range in RMNP is located in the upper montane zone on the eastern slope of the Continental Divide and includes four major valleys: Beaver Meadows, Horseshoe Park, Moraine Park, and Hallowell Park (Gysel 1959; Stevens 1980; Hobbs et al. 1981; Zeigenfuss et al. 1999). The area is about 10,000 ha in size and ranges from 2,400 to 2,800 m in elevation. Valley bottom vegetation includes sedges (*Carex* spp.), grasses, and riparian shrubs [willow (*Salix* spp.), birch (*Betula* spp.)]. Slopes are vegetated by ponderosa pine (*Pinus ponderosa*)/shrub, mixed conifer (ponderosa pine/ Douglas fir (*Pseudotsuga menziesii*)), lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), and upland grass/shrub [predominantly bitterbrush (*Purshia tridentata*)] vegetation types.

35-Year Exclosure Sites

National Park Service staff established three exclosures in Beaver Meadows in 1963. Exclosure 1 (0.4 ha) supports primarily upland grass/shrub type; exclosure 2 (1.2 ha) supports aspen, upland grass/shrub, and willow type; and exclosure 3 (0.4 ha) supports aspen and mesic meadow. The upland grass/shrub type is primarily big sagebrush (*Artemisia tridentata*), with sparse bitterbrush and rabbitbrush (*Chrysothamnus viscidiflorus*). Predominant grasses include junegrass (*Koeleria macrantha)*, blue grama (*Bouteloua gracilis)*, and mountain muhly (*Muhlenbergia montana*). The willow type supports mountain willow (*Salix monticola)*, planeleaf willow (*S. planifolia)*, and Geyer willow (*S. geyeriana*). Canadian reed grass (*Calamagrostis canadensis*) and sedges (*Carex* spp.) predominate in the understory, as well as cow parsnip (*Heracleum sphondylium*), a forb species. Major grasses in the mesic meadow include smooth brome (*Bromus inermis)*, Kentucky bluegrass (*Poa pratensis*), and timothy (*Phleum pratense*), while the predominant forb is golden banner (*Thermopsis divaricarpa*) (Table 1).

4-Year Exclosure Sites

Sixteen exclosures were established in 1994 on the park's elk winter range in montane riparian and upland shrub communities. These sites were randomly located within strata using GIS procedures. Exclosures prevented large ungulate (deer and elk) herbivory, but did not exclude smaller herbivores. Areas inside the exclosures were considered the "ungrazed" treatment. "Grazed" treatment areas were located adjacent to these exclosures in the same vegetation community types, but beyond the area of any influence of the exclosure fence line (at least 5–7 m distant).

We focused on four of the exclosures that were established in short willow communities, four in tall willow communities, and four in upland grass/shrub communities, which were predominated by bitterbrush (Table 1). Short willow sites make up the largest part of the willow communities in the park (short willows, including dead, saplings, intermediate and low density willows make up 70% of all the willow communities, while tall willows make up the remaining 30%; Peinetti et al., this volume). Willow communities (both short and tall) make up only 4% of the elk winter range, although willows comprise a larger percent (30%) of the core winter range (Singer et al. 1998b) and about 11.7% of elk winter diets (Singer et al., this volume). Elk densities and consumption rates are higher in short willow communities than tall willow communities (30 ± 6 elk/km^2 vs. 24 ± 10 elk/km^2).

Methods

Nitrogen Pools

Aboveground N Pools

Herbaceous standing crop biomass was sampled by clipping three to five randomly placed 0.25-m^2 circular quadrats at each ungrazed and grazed site at 35-year and 4-year exclosures. All graminoids and forbs within the quadrat were clipped to measure annual peak production. Vegetation was oven dried at 55°C for 48

Table 1. Sampling locations for all ecosystem parameters showing in which treatment and vegetation type they were measured.

	4-year exclosures (n = 12)		35-year exclosures (n = 3)		
Parameter measured	Willow	Upland grass/shrub	Willow	Upland grass/shrub	Aspen
Litterfall	x	-	-	x	x
Herbaceous production	x	x	x	x	x
Shrub production	x	x	x	x	-
Nutrient concentration	x	x	x	x	x
Consumption by elk	x	x	x	x	x
Decomposition	x	-	-	-	-
N mineralization	x	x	x	x	x
Soil N availability	x	-	x	x	x
Soil N concentration	x	-	x	x	x
Root production and N concentration	x	x	x	x	x
Elk feces deposition (grazed plots only)	x	-	-	x	x

hours and then weighed. Visual estimates of percentage bare ground, moss, lichen, cacti, and shrubs were also recorded. Shrub current annual growth (CAG) was sampled from three to five 9.3-m^2 circular plots at ungrazed and grazed sites following Singer et al. (1994). Regression equations were developed for prediction of willow production for the three major willow species and bitterbrush (Peek 1970). R^2 values for these equations were high and ranged from 0.75 to 0.92 (Zeigenfuss et al., this volume). Shrub production values for sagebrush were estimated based on average twig weights and average twig counts per plant.

Nutrient concentration (% N) was measured at 35- and 4-year exclosures on composite graminoid and forb samples and shrub CAG twigs in ungrazed and grazed sites in August 1998. Samples were analyzed for concentrations of C, N, lignin, acid detergent fiber (ADF), cellulose, dry matter digestibility, calcium, manganese, magnesium, phosphorus (P), potassium, copper, zinc, and iron. Nutrient analyses were performed at the Range Nutrition Laboratory at Colorado State University, Fort Collins, Colorado.

Belowground N Pools

Total C and N in soil and sand fraction were determined at all 4-year exclosures as described in Menezes et al. (2001). In 35-year exclosures, 10 soil samples (6.2 cm diameter, 30 cm depth) were collected at 2 m intervals along transects in each vegetation type and exclosure, and along paired transects 5–10 m outside exclosures. Samples were analyzed by methods in USDA Natural Resources Conservation Service (1996) for N and C content.

Root samples in 4-year exclosures were collected in the fall of 1996 and the fall of 1998 in 35-year exclosures. We removed three root cores (6.35 cm in diameter, 20 cm deep each) from ungrazed and grazed plots for each vegetation type at the 35-year and 4-year exclosures. Cores were washed to remove soil, oven-dried, brushed to remove large particles of soil, sorted to coarse (>2 mm) and fine (<2 mm) components, and analyzed for biomass differences and N content. A subsample of roots was weighed, combusted at 550°C for 6 hours, then weighed to determine percent organic matter based on the ash sample. Actual root biomass was determined by multiplying % organic matter by the weight of the entire dried root sample.

Nitrogen Fluxes

N Inputs and Transfers

Litterfall was collected as part of a companion study (Menezes et al. 2001) at 4-year exclosure sites during the falls of 1995, 1996, and 1997, and at 35-year sites during the fall of 2000 in upland grass/shrub and aspen vegetation types (Table 1). Litter was collected using plastic greenhouse trays (15 trays, $2.3m^2$ total area 4-yr and 20 trays, $3.1m^2$ total area in 35-yr) placed in grids or linear transects in both ungrazed and grazed treatments at each site. In upland grass/shrub, we alternated the position of trays under and between shrubs. Litter was collected weekly to bi-weekly from September to October until litterfall was complete. The litter was then composited within each experimental replication, sorted by litter type, dried, and weighed. Litterfall biomass was calculated as oven dry mass per unit area. Total N and C content of litter was determined using a LECO CHN-1000 analyzer.

We measured elk fecal and urinary deposition from plots to determine the amount of N input by elk. We established three line transects in each of the main valleys, and placed eight 1-m^2 randomly located plots along each transect (9 transects, 72 plots total). Transects were sampled in the winters of 1997–1998 and 1998–1999. Plots were cleared and new fecal piles/plot recorded at the end of each season. We collected 22 piles of fresh elk feces to determine average N content/pile and average mass/pile. Samples were oven dried, and N and C content/pile determined using a LECO CHN analyzer. Fecal N added to sites during winter was calculated by multiplying fecal mass by % N of feces.

We estimated urinary input from elk with a ratio of urinary N to fecal N (U_{ratio}) using the formula: $U_{ratio} = 2.66 - 1.1DN$, derived from studies by Mould and Robbins (1981) assuming an average mass of elk of 200 kg, where DN = digestible N. Total input from urine and feces was calculated from: $N_{total} = FN + U_{ratio}FN$, where FN = fecal N. Estimates for volatilization loss from urine patches were taken from Schimel et al. (1986) and Jarvis et al. (1989).

To determine potential rates of transfer by elk between different vegetation types, (e.g., between willow, aspen, mixed conifer, mesic meadow, upland grass/shrub, and Ponderosa pine/shrub), we observed groups of radio-collared elk for 24-hour periods, one to two times per month during the winters of 1997–1998 and 1998–1999. We recorded behavior, location, vegetation type, group size, and movements of one to five groups for 24-hour periods. We pooled locations by time of day: morning (0600–0959 hr), midday (1000–1559 hr), evening (1600–1759 hr), and night (1800–0559 hr).

To estimate N transferred by elk during seasonal migrations, we calculated elk body mass losses and gains on summer and winter ranges using data from Cassier (1990) and Murie (1951). We followed Hobbs et al. (1982) for converting body mass lost to N and used population estimates from Lubow et al. (this volume).

Decomposition, Mineralization, and Soil N Availability

Decomposition was sampled as part of a companion study (Menezes et al. 2001). Net N mineralization was estimated with the closed top-core technique (Adams and Attiwill 1986). Plastic tubes were pounded 15 cm into the mineral soil and capped for incubation periods ranging from 4 weeks (summer) to 6 weeks (autumn) to 6 months (winter). After the incubation period, soils were collected, mixed, and 10-g subsamples extracted for 24 hours with 100 mL of 2 M KCl. Ammonium-N and nitrate-N were determined with Perstorp automated colorimetry. Net N mineralization was calculated as the post-incubation concentrations of ammonium and nitrate minus the concentrations from paired cores taken at the beginning of each incubation period. About half of the net mineralization rates were negative, so these values were set to 0 (representing no N available to plants for that sample location and period). The net N mineralization rates were summed across periods to give an annual estimate.

Soil N availability was assessed using ion-exchange resin bags (Binkley and Hart 1989) in 1995, 1996, and 1998 in 4-year exclosures (Menezes et al. 2001). Resin bags were also used at 35-year exclosures to estimate availability of ammonium-N and nitrate-N. In each vegetation type, 10 bags were placed 2 cm below the mineral soil surface, at 2 m intervals along a transect from May 1998 to October 1998, and again from October 1998 to May 1999. The two-section (anion and cation) resin pouches were combined and extracted with 100 mL of 2M KCl. Concentrations of ammonium and nitrate were determined colorimetrically on a Perstorp autoanalyzer.

Elk Consumption

To measure winter herbaceous consumption by elk, six 1-m^2 grazing cages were randomly located at grazed plots of 4- and 35-year exclosures. Paired $0.25m^2$ quadrats inside and outside cages were clipped in spring prior to greenup. Cages were randomly replaced after spring sampling to measure early summer consumption that occurs while elk migrate to summer ranges. Clipped vegetation was dried at 55°C in a forced air oven for 48 hours, and then weighed. Percent consumption was determined by the difference method:

$$\% \text{ consumption} = 100 \times (B_i - B_o)/B_i$$

where B_i = dry weight of biomass inside grazing cage, and B_o = dry weight of biomass outside cage.

Statistical Analysis

Non-normal data was transformed using arcsine square root transformations and SAS statistical software. Satterthwaite's *t*-test for unequal variances was conducted, unless otherwise noted. The F-protected least significant difference was used to determine significant differences between grazing treatment means in willow sites. Differences were determined at the 90% level ($P \leq 0.10$).

Biogeochemical Modeling

We simulated long-term responses of soil C, N, net N mineralization, total shrub C, shrub C production, shrub coarse root C, shrub fine root C, and aboveground live grass C using the CENTURY model (U.S. National Science Foundation Ecosystem Studies Research Project 1983). CENTURY simulates the long-term dynamics of C, N, P, and sulfur (S) for grassland, crop, forest, and savanna systems. The soil organic (NELEM) submodel simulates the flow of C and N through plant litter and the inorganic and organic pools in the soil. We entered major input variables using our empirical data whenever possible including: (a) monthly average maximum and minimum air temperatures (from Estes Park weather station); (b) monthly precipitation (from Estes Park weather station); (c) lignin content of plant material (this study); (d) plant, N, P, and S content (this study); (e) soil texture (R. Menezes, unpublished data); (f) atmospheric N inputs (from Baron et al. 2000); (g) N recycling from elk (this study); (h) initial soil C and N levels (this study); and (i) N and C removals by elk (this study). The model includes three soil organic matter pools (active, slow, passive) with different potential decomposition rates, above and belowground litter pools, and a surface decomposing litter pool. Decomposition rate is a function of precipitation, monthly temperature, and monthly potential evapotranspiration. The N associated with C lost in respiration was assumed to be mineralized. For total litter inputs with C:N ratios similar to this study, the model assumes decomposition results in net N mineralization, and decomposition of the structural component of the litter results in N immobilization (Parton et al. 1987; Metherell et al. 1993).

We simulated three scenarios of elk density and elk offtake: (a) no change from current density or offtake levels; (b) a 25% increase over current offtake levels on willow to simulate a possible further increase in elk numbers in the entire town-park population, increased willow use as elk numbers increase, and/or invasion of the winter range by moose (*Alces alces*) that currently inhabit the west side of the park (moose prefer willow as a key forage and even a few moose that enter the area would raise herbivory levels on the willow); and (c) a 40% less offtake by elk to simulate suspected offtake in the absence of human-altered forages in town, and if wolves (*Canis lupus*) and brown bears (*Ursus arctos*) were still present (Singer et al. 2002). The model was run for the previous 10 years to equalize the model and then 50 and 100 years into the future. We simulated only the upland grass/shrub and the willow vegetation types where our empirical data were most complete. We calculated weighted means for vegetation input variables to the CENTURY model by multiplying grams of biomass in the system by proportion of total biomass for the two vegetation types modeled.

Results

Nitrogen Pools

Aboveground N Pools

Elk herbivory reduced the structure (height, canopy volume, stem density) of willows and CAG produced by willows by 66% after 4 years ($P = 0.05$) and 98% after 35 years ($P = 0.10$) compared to protected willows (Table 2). Elk herbivory also reduced herbaceous production in the willow type by 22% after 4 years, but this difference was not significant (Table 2). Elk herbivory similarly reduced mean height and annual biomass production of several shrubs in the upland grass/shrub type (67% reduction in CAG after 35 years; $P = 0.01$). Annual herbaceous biomass produced in upland grass/shrub was not substantially altered by ungulate herbivory after 4 years, but decreased 32% after 35 years ($P = 0.10$) of protection. This was most likely due to the large increase in shrub cover of *A. tridentata* after 35 years of protection.

Concentrations of N were not greatly altered by elk herbivory (Table 2). We found increased N concentrations in only 4 of 13 grazed plant species (*A. tridentata*, $P = 0.10$; *Bouteloua gracilis*, $P = 0.01$; *Heracleum sphondylium*, $P = 0.09$; and *Koeleria macrantha*, $P = 0.01$) after 35 years of treatment. Higher N concentrations were also found in grazed forb species in the willow type after 35 years ($P = 0.01$), and in grazed upland shrubs after 35 years ($P = 0.02$; Table 2).

Elk herbivory reduced annual N yield (N produced/m^2/yr) of willows by 64% after 4 years ($P = 0.05$) and 98% after 35 years ($P = 0.10$), and N yield of upland

Table 2. Mean production and nitrogen values (and standard errors) of vegetation grazed by elk and protected from grazing for 4 years and 35 years. Root values are in grams/m^2 at 0–20 cm soil depth. * indicates significant difference ($P < 0.10$).

	Production (g/m^2/yr)				Nitrogen concentration (%)				Nitrogen yield (g/m^2/yr)			
	4-yr treatment		35-yr treatment		4-yr treatment		35-yr treatment		4-yr treatment		35-yr treatment	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Willow (tall and short pooled)												
Total herbaceous (g/m^2)	496±90	385±52	391±41	415±91	1.78±0.15	2.00±0.19	1.50±0.14	1.64±0.17	9.09±2.35	7.40±0.92	6.09±0.64	6.78±1.48
Forb (g/m^2)	101±29	69±22	78±18	22+14*	2.43±0.22	2.50±0.22	2.31±0.07	2.62±0.06*	2.81±0.72	2.13±0.53	1.79±0.40	0.58±0.35*
Graminoid(g/m^2)	406±78	319±45	299±52	393+144	1.72±0.18	1.88±0.21	1.34±.10	1.42±0.11	7.31±2.04	5.93±1.02	4.07±0.83	5.76±2.09
Shrub (g/m^2)	82±22	28±8*	229±103	5.0±1.4*	1.71±0.07	1.71±0.05	1.63±0.05	1.82±0.08	1.32±0.31	0.48±0.14*	3.74±1.68	0.09±0.03*
Coarse roots (g/m^3)	1,168±470	414±125	44±3	160±24*	0.64±0.11	0.73+0.10	0.69+0.17	1.10+0.48	7.74+3.21	2.60±0.57	0.31±0.09	1.98±1.14
Fine roots (g/m^3)	2033±384	3,055±1206	857±61	2,676±714*	0.97±0.06	0.93±0.11	0.72±0.04	1.09±0.01*	20.6±4.81	37.2±21.9	6.19±0.60	29.2±7.87*
Litterfall (g/m^2)	65±11	33±8*	-	-	1.25±0.1	1.49±0.1*	-	-	0.57	0.24	-	-
Upland grass/shrub												
Total herbaceous (g/m^2)	193+55	111+4	48±8	71±2*	1.22±0.10	1.38±0.07	1.11±0.01	1.22±0.06	2.36±0.72	1.53±0.09	0.54±0.09	0.87±0.02*
Forb (g/m^2)	101±55	42±15	12±3	14±6	1.47±0.17	1.69±0.20	1.47±0.17	1.69±0.20	1.56±0.94	0.72±0.23	0.18±0.04	0.24±0.09
Graminoid (g/m^2)	92±39	69±13	36±13	58±2	0.97±0.14	1.21±0.05	1.11±0.01	1.22±0.06	0.89±0.41	0.82±0.14	0.40±0.15	0.70±0.01
Shrub (g/m^2)	18±9	16±7	159±2	53±15*	-	1.19±0.1[a]	1.24±0.04	1.58±0.13*	-	0.20±0.04	1.98±0.08	0.59±0.05*
Coarse roots (g/m^3)	10±5	95±29*	53±21	69±55	0.59±0.09[b]	0.87±0.13	0.59±0.09	1.59±0.99	0.06±0.03	0.83±0.25*	0.30±0.07	1.65±1.56
Fine roots (g/m^3)	364±99	345±101	208±56	162±5	0.85±0.17	1.07±0.21	0.76±0.03	0.79±0.11	2.14±0.58	3.00±0.88	1.62±0.51	1.27±0.15
Litterfall (g/m^2)	-	-	8±2	12±3	-	-	0.74±0.06	0.74±0.07	-	-	0.05±0.02	0.10±0.01
Aspen												
Total herbaceous (g/m^2)	-	-	123±20	121±37	-	-	1.90±0.12	1.68±0.07	-	-	2.37±0.52	2.06±0.71
Forb (g/m^2)	-	-	43±11	36±16	-	-	2.99±0.03	2.82±0.14	-	-	1.29±0.32	1.05±0.49
Graminoid (g/m^2)	-	-	80±9	85±21	-	-	1.35±0.09	1.15±0.12	-	-	1.09±0.18	0.94±0.14
Shrub (g/m^2)	-	-	-	-	-	-	-	-	-	-	-	-
Coarse roots (g/m^3)	-	-	418±248	310±232	-	-	0.91±0.37	0.94±0.32	-	-	2.83±0.65	4.19±3.71
Fine roots (g/m^3)	-	-	358±53	406±202	-	-	1.18±0.22	1.03±0.04	-	-	4.16±0.22	3.70±1.37
Litterfall (g/m^2)	-	-	203±22	36±8*	-	-	0.70±0.01	0.50±0.01*	-	-	1.42±0.49	0.19±0.11

[a] Value from Hobbs et al. (1981).

[b] Value from 35 year data, since no coarse roots available during sampling year for nutrients. Production numbers for these coarse roots were derived from averaging 1995 and 1996 estimates.

shrubs by 70% ($P < 0.0001$; Table 2). Nitrogen yield of herbaceous vegetation in upland grass/shrub type was reduced after 35 years of protection from grazing ($P = 0.07$; Table 2).

Belowground N Pools

We found no effect of grazing treatment on soil N concentration in either 4- or 35-year exclosures, with the exception of a single sample site at mid-slope aspen type at 35-year exclosure 2, which had significantly higher N in grazed than ungrazed plots at depths of 0–15 cm and 0–30 cm ($P < 0.10$).

After 35 years of treatment in willow type, we found differences in fine root biomass ($P = 0.0009$), fine root N concentration ($P = 0.003$) and N yield ($P = 0.10$), but not in upland grass/shrub communities (Table 2). Coarse root biomass was nearly four times greater in grazed than ungrazed sites ($P = 0.03$; Table 2). Coarse root production was higher in grazed plots of upland grass/shrub communities ($P = 0.02$) after 4 years, but no differences were found in 35-year treatments (Table 2).

Nitrogen Fluxes

N Inputs and Transfers

Elk herbivory greatly reduced the sizes (height, diameter, volume) of some shrubs (*Salix* spp., *A. tridentata*) and thus reduced the amount of shrub leaf litterfall. After 4 years, biomass of litterfall in willow type was significantly higher in ungrazed than grazed plots ($P < 0.05$; data combined for 1995, 1996, and 1997; Table 2). No significant grazing treatment differences were detected for herb or wood litterfall in willow sites. Willow leaf litter N content was significantly higher in grazed than ungrazed plots ($P < 0.05$). At 35-year treatments, aspen litterfall biomass was four times higher in ungrazed than grazed plots ($P < 0.0001$; Table 2). At ungrazed sites in upland grass/shrub communities, litter biomass was higher specifically in leaf ($P = 0.005$), and wood ($P = 0.04$) litterfall, but not for overall litter biomass. Litterfall N content was higher in ungrazed than grazed plots in aspen type ($P < 0.0001$), but no difference in N concentration was found in upland grass/shrub litter (Table 2).

Elk deposited substantial amounts of fecal and urinary N on the winter range (Fig. 2). Fecal-N deposited averaged 0.71 $g/m^2/yr$ in grazed sites in all the valleys (Table 3). The highest deposition was at Moraine Park ($P = 0.115$) compared to Horseshoe Park and Beaver Meadows. Nitrogen concentration was 1.53% of fecal pile mass and the average mass was 138 g/pile (n = 22 piles); thus average N content/pile was 2.1 g N. The highest amount of fecal-N deposited was in willow vegetation (Table 3). We calculated an urinary-N:fecal-N ratio of 0.9768 and thus estimated the average urinary-N input from elk was 0.69 $g/m^2/yr$. We estimated the total combined N input from both fecal- and urinary-N as 1.41 $g/m^2/yr$ in grazed sites (Table 3) versus 0 $g/m^2/yr$ in ungrazed sites.

During eleven 24-hour observation periods, elk were observed 49% of the time bedded and 51% grazing. They were observed more often grazing in morning and evening ($P = 0.0001$), and more often bedded at night ($P = 0.0001$) than other times of the day (Table 4). Overall, elk were observed more often in mesic meadow vegetation (58%; $P = 0.0005$) than all other vegetation types, including Ponderosa pine/shrub (16%), upland grass/shrub vegetation (10%), willow (7%), mixed conifer (7%), and aspen (2%). There were no differences in use of vegetation types in the morning, but elk were observed significantly more in mesic meadow vegetation in midday and evenings ($P < 0.05$; Table 5). Elk were seen in mixed conifer and mesic meadow vegetation at night, and mesic meadow, aspen, willow, and upland grass/shrub vegetation in the evenings between 4 and 6 p.m. Elk appeared to be grazing in all vegetation types in mornings, in primarily mesic meadow during midday and evenings, and in willow, mixed conifer, and mesic meadow vegetation types at night. Elk transported N from the aspen, mesic meadow, and willow types where they spent more time feeding, to the conifer types where they spent less time feeding. The net movement of N away from aspen type was 0.60 g $N/m^2/yr$ (1.13 g $N/m^2/yr$ removed by elk grazing minus 0.53 added by feces and urine; Table 6). Similarly, the net movement of N away from the willow vegetation type was 2.01 g $N/m^2/yr$ (4.23 g $N/m^2/yr$ removed by elk minus 2.22 g $N/m^2/yr$ added by feces and urine; Fig. 2). Seasonal estimates of elk body mass gained on the summer range and lost on the winter range suggest a net transfer by elk of 0.016 g $N/m^2/yr$ from summer to winter range.

Decomposition, Mineralization, and Soil N Availability

We documented lower N mineralization in grazed versus ungrazed plots of short willow sites after 4 years of protection (0.39 grazed versus 1.83 ungrazed, $P = 0.07$, n = 4 sites, versus 3.25 grazed and 2.11 ungrazed, $P > 0.10$, n = 4, in tall willow sites). Nitrate pools were also lower in grazed than ungrazed plots of short willow

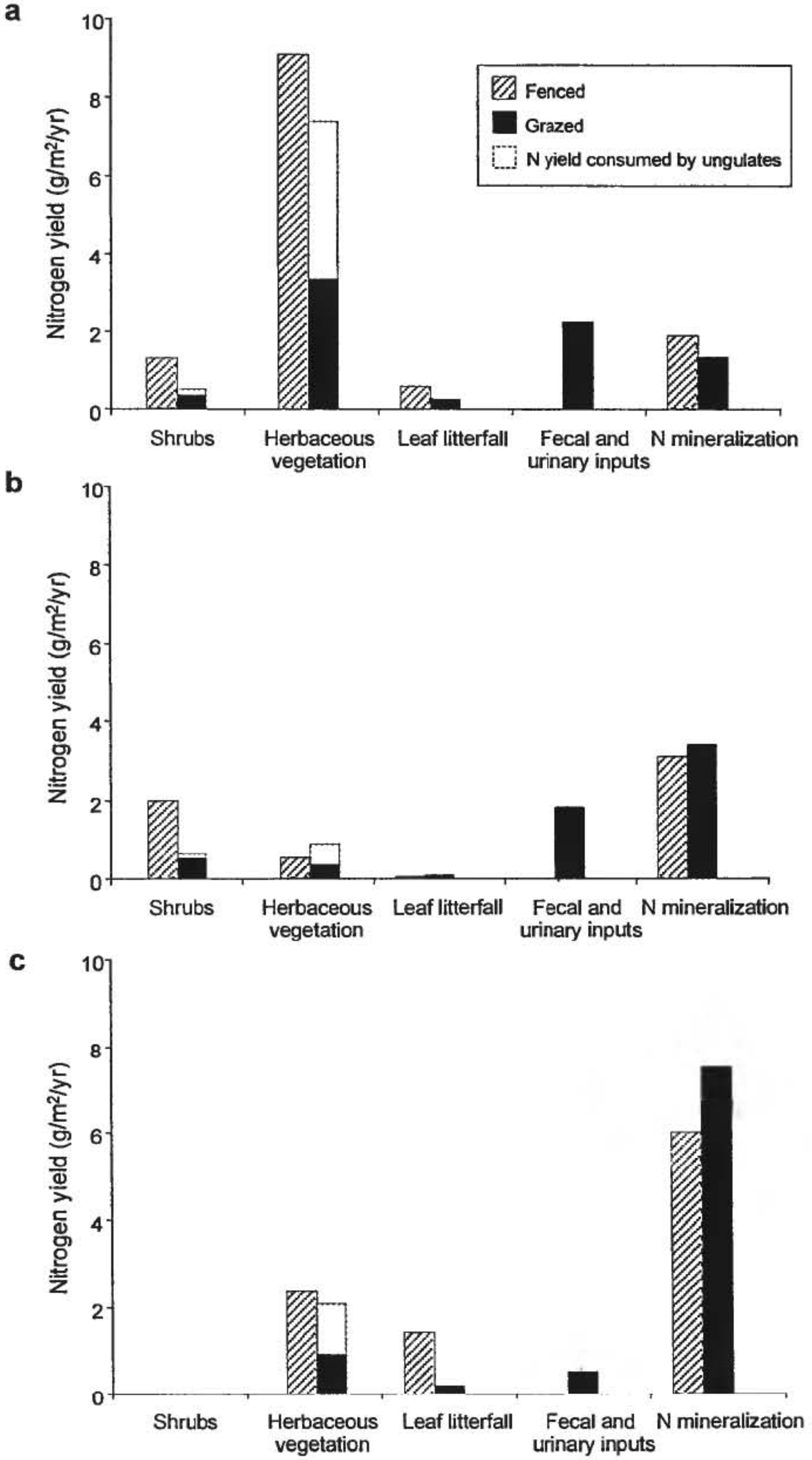

Fig. 2. Annual nitrogen produced by vegetation, removed by elk herbivory, fecal/urinary inputs by elk, and mineralization rates on the elk winter range, Rocky Mountain National Park, Colorado, in (a) tall and short willows pooled (4-year treatment data); (b) upland grass/shrub (35-year data), and (c) aspen (35-year data).

Table 3. Average fecal biomass, fecal-N, urinary-N, and total N deposited in different vegetation types on elk winter range in Rocky Mountain National Park, Colorado, winters 1997–1998 and 1998–1999.

Vegetation type	Number of transects	Average mass deposited (g/m²/yr)	Average fecal-N deposited (g/m²/yr)	Average urinary-N deposited (g/m²/yr)	Average total N deposited (g/m²/yr)
Meadow	10	34.6 ± 15.0	0.53 ± 0.23	0.52 ± 0.22	1.05
Upland grass/shrub	2	60.5 ± 8.6	0.93 ± 0.13	0.90 ± 0.13	1.83
Willow	4	73.4 ± 29.4	1.12 ± 0.45	1.09 ± 0.44	2.22
Aspen	2	17.3	0.26	0.26	0.53
Total average	18	46.44	0.71	0.69	1.41

sites (0.31 grazed versus 1.44 ungrazed, $P = 0.10$), but no differences for these N variables were detected in tall willows. Short willow sites are apparently a browsing induced conversion from the tall willow type (Peinetti et al., this volume), and the two types are structurally and functionally different from each other. Short willow grazed sites had 33% lower herbaceous production, 27% less CAG, and 38% shorter mean willow height than tall willow sites, while tall willow sites had more ground shade.

Elk herbivory had few effects on the structure, function, and N processes in the upland grass/shrub type (Fig. 2). We found no other grazing effect on total soil N availability, with the exception of upland grass/shrub type at 35-year exclosure 1, where NO_3 was three times higher in soil from grazed versus ungrazed plots ($P < 0.10$; n = 1 site). We found no grazing treatment effect on decomposition of willow or sedge litter, but nitrogen losses from litterbags were significantly higher in sedge than willow litter ($P = 0.012$).

Elk Consumption

Annual percent consumption of herbaceous biomass by elk in grazed plots was considerable (Table 6). In short willow sites, herbaceous consumption by elk averaged 67 ± 11% and 41 ± 7% in tall willow sites. Shrub CAG consumption (primarily bitterbrush) averaged 12 ± 3% in upland grass/shrub, and 33 ± 2% in pooled willow vegetation types during winter.

Biogeochemical Modeling

Upland Grass/Shrub

If elk herbivory was reduced 40% relative to current levels, CENTURY predicted elk grazing was sustainable. Total soil C, total soil N, net N mineralized, total shrub C, and coarse and fine root C would be roughly stable over periods of 50 and 100 years into the future. However, current levels of consumption by elk might decrease nutrients slightly. CENTURY predicted

Table 4. Average percent of time elk were observed bedded or grazing at different times of day during eleven 24-hour observation periods on the elk winter range, Rocky Mountain National Park, Colorado, winter of 1997–1998 and 1998–1999 (± SE).

Time of day	n	Average % of time bedded	Average % of time grazing
Morning	40	21 ± 5	79 ± 5
Midday	68	54 ± 4	46 ± 4
Evening	26	10 ± 2	90 ± 2
Night	123	63 ± 3	37 ± 3

Table 5. Average percent of time at different times of day that elk were observed in each vegetation type during eleven 24-hour observation periods on the elk winter range, Rocky Mountain National Park, Colorado, winters 1997–1998 and 1998–1999 (± SE).

Time of day	Mesic meadow	Upland grass/shrub	Willow	Aspen	Mixed conifer	Ponderosa pine/shrub
Morning	23 ± 4	12 ± 3	18 ± 4	14 ± 4	17 ± 5	16 ± 6
Midday	35 ± 4	11 ± 2[a]	9 ± 2[a]	9 ± 3[a]	20 ± 5[a]	16 ± 3[a]
Evening	36 ± 4	22 ± 4[a]	16 ± 2[a]	11[a]	No observation	15 ± 2[a]
Night	26 ± 4	11 ± 4[a]	15 ± 6	6 ± 3[a]	28 ± 17	14 ± 4[a]

[a] Denotes significant difference ($P \leq 0.05$) to mesic meadow vegetation type, the most used type.

total soil C would decrease 2% in 50 years, and 2.5% in 100 years, total soil N would decrease 0.5% in 50 years and 1% in 100 years, net N mineralized would decrease 0.7% in 50 years and 1.5% in 100 years, total shrub C (below and aboveground) would decrease 4% in 50 years and 7% in 100 years, and aboveground live grass C would decrease 0.4% in 50 years and 0.7% by 100 years (Fig. 3).

If levels of consumption increased 25% due to elk population increases and/or moose expansion into the area, larger nutrient losses were projected. Soil C would decrease 4% in 50 years and 5% in 100 years; total soil N would decrease 1% in 50 years and 2% in 100 years; net N mineralized would decrease 2% in 50 years and 3.5% in 100 years, while aboveground live grass C would increase 0.01% in 50 years (Fig. 3). The largest projected declines were in total shrub C, which decreased 15% in 50 years and 26% in 100 years. These projected nutrient declines were due to both consumption of vegetation by elk and to the secondary effects of elk herbivory, such as large reductions in sizes of several shrub species and the subsequent reduction in high quality and decomposable shrub leaf litter.

Willow

The model projected slightly larger decreases in C and N in willow vegetation type at current and higher elk consumption scenarios than for the upland grass/shrub type, except for total shrub C (Fig. 3). These larger predicted decreases were due to a combination of higher offtake levels by elk in willow vegetation and the reduction in sizes of shrubs (willow and birch) and subsequent lower shrub leaf litter inputs. Movement of N away from vegetation types where preferential feeding by elk occurred (aspen, willow) also contributed to a loss of nitrogen.

Discussion

Elk herbivory had a potentially large negative effect on N and C dynamics in willow and aspen types. We concluded elk herbivory and activity resulted in a net transfer and loss of N from these vegetation types. Elk reductions in willow shrub size, aboveground N pools, shrub litter, willow annual N yield, and elk consumption was not compensated for by elk inputs of fecal and urinary N [and N mineralization and N pools (NO_3) were lower after 4 years in short willow sites]. Elk consumption was also not compensated for by elk inputs in the aspen type. Long-term projections from the CENTURY model tended to support these conclusions. Nevertheless, we concluded that elk herbivory and activity resulted in almost no net change in N in the upland grass/shrub type. Elk apparently returned approximately as much N to the system to compensate for N removals from grazing and changes to N yield due to reductions in canopy size of shrubs. Long-term projections from the CENTURY model also tended to support this conclusion. The model projected only a 0.5% decline in soil N in 50 years at current high elk densities – a decline that would likely be difficult to detect using standard sampling techniques. More time may be needed to detect any additional changes, especially any effects on slower changing N pools.

Table 6. Estimated nitrogen inputs and outputs based on herbaceous offtake in four vegetation types on elk winter range, Rocky Mountain National Park, Colorado, 1998–1999.

Vegetation type	% of elk group observed feeding	% of time in vegetation type	N added by elk (g/m^2/yr)[a]	% herbaceous/ shrub offtake	N removed by elk based on % offtake (g/m^2/yr)	Net gain or loss of N due solely to elk inputs (feces, urine) and offtake (g/m^2/yr)	CENTURY modeled effects on soil N (g/m^2/yr)[b]
Aspen	92	7	0.53	55[c]	1.13[c]	-0.60	n.d.
Mesic meadow	51	39	1.05	56/NA	2.69	-1.64	n.d.
Upland grass/shrub	65	17	1.83	60/12	0.59	+1.24	-0.03
Willow	74	13	2.22	55/33	4.23	-2.01	-0.08

[a] Based on fecal plots sampled 1997–1999.

[b] Annual effects on soil N due to all effects of elk inlcuding secondary effects on plant morphology.

[c] Winter offtake only; no summer or shrub data available.

NA = not applicable.

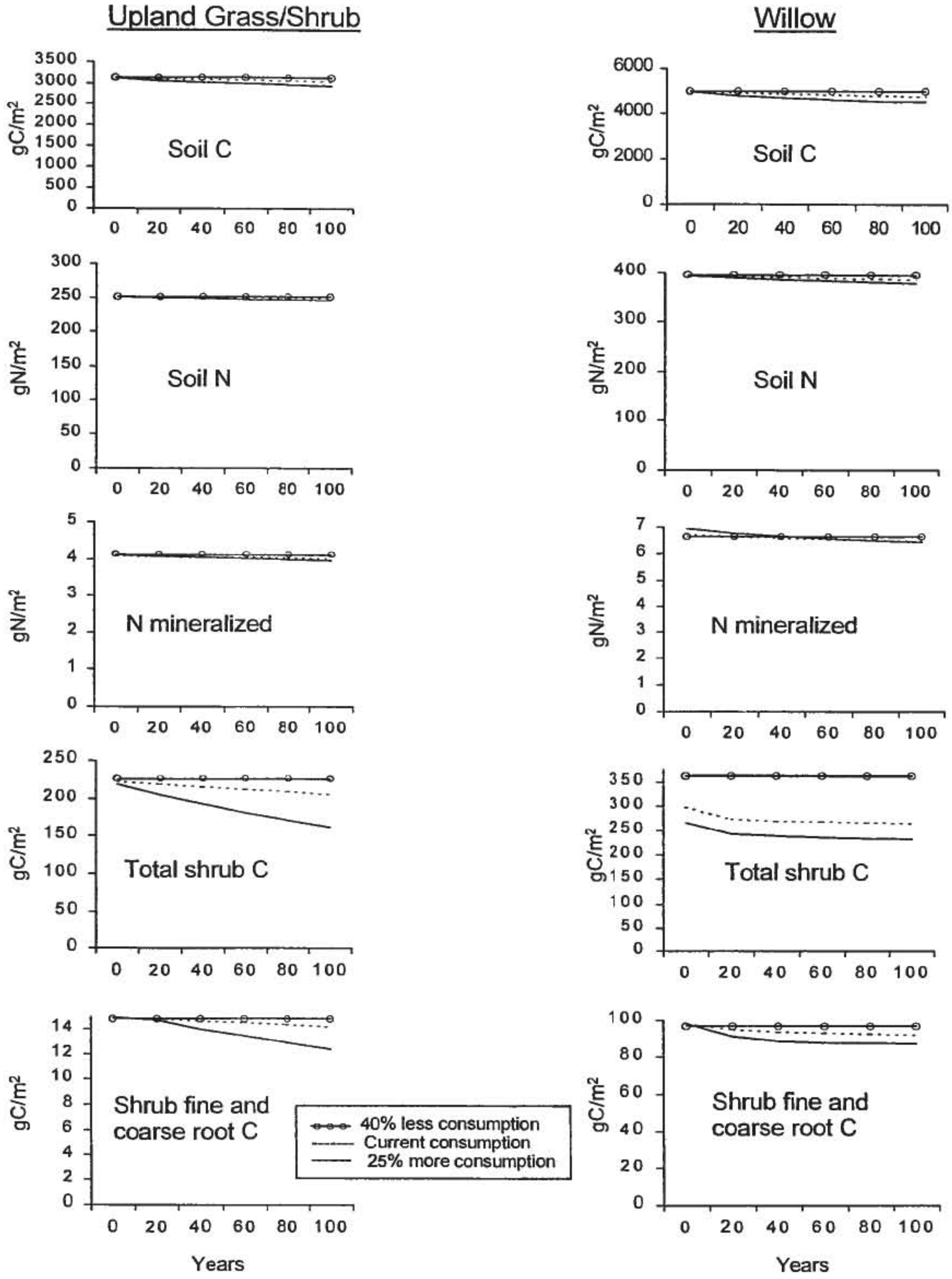

Fig. 3. Results of CENTURY model simulations on carbon and nitrogen in upland grass/shrub and willow vegetation types predicting effects of elk grazing up to 100 years into the future under different consumption levels in Rocky Mountain National Park, Colorado.

In contrast to our findings of lower N mineralization and N pools in the short willow type, other authors have reported increases in N mineralization due to grazing (Ruess 1984; Ruess and McNaughton 1987) and increases in the rate of N recycling as a result of fecal and urinary deposition. Soil mineral N levels were highest at moderate grazing levels in grasslands, but other model efforts have suggested overgrazing would deplete N. As in our study, Seagle et al. (1992) found a decrease in net soil N mineralization with heavy grazing. There is evidence that elk herbivory may be high enough in the short willow type to reduce N processes.

We found higher N concentrations in only one-third of the grazed plant species we sampled and in willow litter on grazed sites. This is consistent with many studies, which report higher N concentrations in plant tissues due to native ungulate herbivory (McNaughton 1984; Coughenour 1991; Singer 1995; Singer and Harter 1996). Typically, higher N concentration in grazed plants is associated with higher N mineralization on grazed sites (Frank and Groffman 1998; Ritchie et al. 1998). We do not know why mineralization rates were not higher due to grazing in RMNP grasslands. Our findings generally fit the criteria for decelerated N cycling predicted by Ritchie et al. (1998), at least in short willow sites.

We caution that we did not sample or quantify the entire N cycle in this ecosystem and that several unknowns exist. For example, volatilization from urine was not measured, but other research suggests these losses would be minor [10–15% of urinary N; Vallis et al. (1982); Schimel et al. (1986)]. In either case, the losses of N from urine might be less than the volatile losses from ungrazed plants, and thus ungulates might even reduce total volatile losses of N (Ruess and McNaughton 1987; Detling 1988). No effects of elk on leaching of N from soil were reported by a companion study (Binkley et al., this volume). Water erosion losses were unknown.

We concluded elk were transferring N between vegetation types and winter and summer ranges. In agreement with Frank et al. (1994) for Yellowstone National Park, our calculations for body mass lost on the winter range combined with winter elk consumption measurements, suggest there is a net movement of N over the year from summer to winter range by elk. Elk appeared to be preferentially feeding in aspen type in RMNP, as opposed to other types, and were transporting N away from aspen to surrounding vegetation types. In addition, our aspen offtake rates are for winter only, suggesting that elk may be having an even greater effect than we report here, if we were able to include summer offtake as well. Aspen type comprises a small part of the elk winter range (2%), thus elk may be having a significant effect in this type but relatively less impact on N dynamics across the entire winter range. McNaughton (1993) reported that African ungulates seek shade when they rest and deposit more feces and urine under trees than in the open. A redistribution of N means bedding areas in conifer forests might be enriched, while willow and aspen types would be depleted. At some point, the depletion might result in the slowing of plant growth rates and changes in plant species composition (McInnes et al. 1992; Ritchie et al. 1998).

Management Implications

Our findings concerning the effect of elk herbivory on nitrogen cycling and plant growth responses were somewhat conflicting. On one hand we documented substantial declines due to elk in the amount of N deposited to the soil in both willow and aspen vegetation types, but on the other hand we documented little effect of elk in the upland grass/shrub type. Observational studies of elk verified that elk were transporting N from willow and aspen types, their preferred feeding types, primarily to the conifer types, their favored bedding habitat. We predict declines in N in the willow and aspen types, a prediction also generally supported by CENTURY soil modeling, although the CENTURY model predicted smaller declines.

In support of these predictions, we found a decline in the NO_3 pool and N mineralization due to elk herbivory in the short willow type, but not in the upland grass/shrub type. Perhaps not enough time has passed to document other altered N pools or N mineralization rates. Therefore, we recommend conservative management of elk numbers and grazing effects, since: (1) all modeling scenarios of increased elk density resulted in projections of decreases in N and C; (2) scenarios of reduced elk density were more optimistic; and (3) a decline in N processes was found in one vegetation type. Conservative management of elk numbers would be appropriate until more time has passed to study the slow changing N pools and until further research is conducted on the effects on plant communities of observed differences in N processes and pools.

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Literature Cited

Adams, M. A., and P. M. Attiwill. 1986. Nutrient cycling and nitrogen mineralization in eucalypt forests of southeastern Australia. II. Indices of nitrogen mineralization. Plant and Soil 92:341–362.

Archer, S., and F. E. Smeins. 1991. Ecosystem-level processes. Pages 109–139 *in* R. K. Heitschmidt and J. W. Struth, editors. Grazing management: An ecological perspective. Timber Press, Portland, Oreg.

Baron, J. S., H. M. Rueth, A. M. Wolfe, K. R. Nydick, E. J. Allstott, J. T. Minear, and B. Moraska. 2000. Ecosystem responses to nitrogen deposition in the Colorado Front Range. Ecosystems 3:352–368.

Bazely, D. R., and R. L. Jeffries. 1985. Goose feces: A source of nitrogen for plant growth in a grazed salt marsh. Journal of Applied Ecology 22:693–703.

Belsky, A. J. 1986. Does herbivory benefit plants – a review of the evidence. American Naturalist 127(6):870–892.

Binkley, D., and S. C. Hart. 1989. The components of nitrogen availability assessments in forest soils. Advances in Soil Science 10:57–116.

Biondini, M. E., B. D. Patton, and P. E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. Ecological Applications 8(2):469–479.

Burke, I. C., W. A. Reiners, and D. Schimel. 1989. Organic matter turnover in a sagebrush steppe landscape. Biogeochemistry 7:11–31.

Cassier, E. F. 1990. Effects of disturbance by cross-country skiers on elk in Northern Yellowstone National Park. Final report to the National Park Service, Cooperative Agreement No. CA-9000-3-0002.

Coughenour, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. Journal of Applied Ecology 28:71–82.

Detling, J. K. 1988. Grasslands and savannas: Regulation of energy flow and nutrient cycling by herbivores. Ecological Studies 67:131–148.

Dyksterhuis, E. J. 1949. Condition and management of rangeland based on quantitative ecology. Journal of Range Management 2:104–115.

Ellis, J. E., and D. M. Swift. 1989. Stability of African pastoral ecosystems: Alternative paradigms and implications for development. Journal of Range Management 41:450–459.

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

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73:2043–2058.

Frank, D. A., and S. J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Ecology 73:2043–2058.

Frank, D. A., R. S. Inouye, N. Huntly, G. W. Minshall, and J. E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: Nitrogen dynamics in Yellowstone National Park. Biogeochemistry 26:163–188.

Gordon, I. J. 1988. Facilitation of red deer grazing by cattle and its impact on red deer performance. Journal of Applied Ecology 25:1–10.

Gysel, L. W. 1959. An ecological study of the winter range of elk and mule deer in the Rocky Mountain National Park. Journal of Forestry 58:696–703.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:19–31.

Hobbs, N. T., D. Baker, J. E. Ellis, and D. M. Swift. 1981. Composition and quality of elk winter diets in Colorado. Journal of Wildlife Management 45:156–170.

Hobbs, N. T., D. Baker, J. E. Ellis, D. M. Swift, and R. A. Green. 1982. Energy and nitrogen based estimates of elk winter range carrying capacity. Journal of Wildlife Management 46(1):12–21.

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

Huff, D. E., and J. D. Varley. 1999. Natural regulation in Yellowstone National Park's northern range. Ecological Applications 9:17–29.

Iason, G. R., D. C. Duck, and T. H. Clutton-Brock. 1986. Grazing and reproductive success of red deer: The effects of local enrichment by gull colonies. Journal of Animal Ecology 55:507–515.

Jarvis, S. C., D. J. Hatch, and D. H. Roberts. 1989. The effects of grassland management on nitrogen losses from grazed swards through ammonia volatilization: The relationship to excretal nitrogen returns from cattle. Journal of Agricultural Science (Cambridge) 112:205–216.

Lauenroth, W. K. and W. A. Laycock. 1989. Secondary succession and the evaluation of rangeland condition. Westview Press, Boulder, Colo.

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73(6):2059–2075.

McNaughton, S. J. 1984. Grazing lawns: Animals in herds, plant form, and coevolution. American Naturalist 124:863–886.

McNaughton, S. J. 1988. Mineral nutrition and spatial concentration of African ungulates. Nature 334:343–345.

McNaughton, S. J. 1990. Mineral nutrition and seasonal movement of African ungulates. Nature 345:613–615.

McNaughton, S. J. 1993. Grasses and grazers, science and management. Ecological Applications 3(1):17–20.

Menezes, R. S. C., E. T. Elliott, D. W. Valentine, and S. A. Williams. 2001. Effects of herbivory and proximity to surface water on C and N dynamics of elk winter range. Journal of Range Management 54:400–408.

Metherell, A. K., L. A. Harding, C. V. Cole, and W. J. Parton. 1993. CENTURY soil organic matter model environment, technical documentation agroecosystem version 4.0. GPSR Technical Report No. 4. U.S. Department of Agriculture, Agricultural Research Service, Great Plains Systems Research Unit.

Milchunas, D. G., and W. K. Lauenroth. 1992. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327–366.

Moss, R., D. Welch, and P. Rothery. 1981. Effects of grazing by mountain hares and red deer on the production and chemical composition of heather. Journal of Applied Ecology 18:487–496.

Mould, E. D., and C. T. Robbins. 1981. Nitrogen metabolism in elk. Journal of Wildlife Management 45:323–334.

Murie, O. J. 1951. The elk of North America. The Stackpole Company, Harrisburg, Pennsylvania, and Wildlife Management Institute, Washington, D.C., USA.

Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. Analysis factors controlling soil organic levels of grasslands in the Great Plains. Soil Science Society of America Journal 51:1173–1179.

Pastor, J., B. Dewey, and R. J. Naiman. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74(2):467–476.

Peek, J. M. 1970. Relation of canopy area and volume to production of three woody species. Ecology 51:1098–1101.

Risser, P. G., and W. J. Parton. 1982. Ecosystem analysis of the tallgrass prairie: Nitrogen cycle. Ecology 63:1342–1351.

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

Ruess, R. W. 1984. Nutrient movement and grazing: Experimental effects of clipping and nitrogen source in nutrient uptake in *Kyllinga nervosa*. Oikos 43:183–188.

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.

Sampson, A. W. 1919. Plant succession in relation to range management. U.S. Department of Agriculture Bulletin No. 791. U.S. Government Printing Office, Washington, D.C

Schimel, D. S., M. S. Stillwell, and R. G. Woodmansee. 1985. Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. Ecology 66(1):276–282.

Schimel, D. S., W. J. Parton, F. J. Adamsen, R. G. Woodmansee, R. L. Senft, and M. A. Stillwell. 1986. The role of cattle in the volatile loss of nitrogen from a shortgrass steppe. Biogeochemistry 2:39–52.

Seagle, S. W., S. J. McNaughton, and R. W. Ruess. 1992. Simulated effects of grazing on soil nitrogen and mineralization in contrasting Serengeti grasslands. Ecology 73:1105–1123.

Singer, F. J. 1995. Effects of grazing by ungulates on upland bunchgrass communities of the northern winter range of Yellowstone National Park. Northwest Science 69:191–203.

Singer, F. J., and M. K. Harter. 1996. Comparative effects of elk herbivory and fires of 1988 on grasslands in northern Yellowstone National Park. Ecological Applications 6:185–199.

Singer, F. J., L. Mack, and R. G. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435–443.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998a. Thunder on the Yellowstone revisited:

An assessment of management of native ungulates by natural regulation, 1968–1993. Wildlife Society Bulletin 26(3):375–390.

Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998b. Elk, multiple factors, and persistence of willows in national parks. Wildlife Society Bulletin 26:419–428.

Singer, F. J., G. Wang, and N. T. Hobbs. 2002. The role of grazing ungulates and large, keystone predators on plants, community structure, and ecosystem processes in mixed grassland-coniferous landscapes in the western United States. *In* R. G. Anthony and C. Zabel, editors. Large mammal communities in U.S. western coniferous forests. Cambridge University Press.

Stevens, D. R. 1980. The deer and elk of Rocky Mountain National Park, a 10-year study. National Park Service Report No. ROMO-N-13.

USDA Natural Resources Conservation Service. 1996. Soil survey laboratory methods. Soil Survey Investigations Report No. 42, Version 3.0, Washington, D.C., USA.

U.S. National Science Foundation Ecosystem Studies Research Project. 1983. Organic matter and nutrient cycling in semiarid agroecosystems. Report DEB-7911988.

Vallis, I., L. A. Harper, V. R. Catchpole, and K. L. Weier. 1982. Volatilization of ammonia from urine patches in a sub-tropical pasture. Australian Journal of Agricultural Research 33:97–101.

Wagner, F. H., R. Foresta, R. B. Gill, D. R. McCullough, R. R. Pelton, W. F. Porter, and H. Salwasser. 1995. Wildlife policies in the U.S. national parks. Island Press, Washington, D.C.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42(4):266–278.

Zeigenfuss, L. C., F. J. Singer, and D. Bowden. 1999. Vegetation responses to natural regulation of elk in Rocky Mountain National Park. Biological Science Report USGS/BRD/BSR-1999-0003. U.S. Government Printing Office, Denver, Colo.

CHAPTER TWELVE

Ecological Evaluation of Potential Overabundance of Ungulates in U.S. National Parks: A Case Study

By

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Abstract. We conducted a study into the possibility of overabundance or overconcentration of elk (*Cervus elaphus*) and human alterations of elk habitat in Rocky Mountain National Park and the adjacent town of Estes Park, Colorado. National Park Service (NPS) policy is clear that an overabundance and unnatural concentration of ungulates can be managed, but ambiguities and vagueness exist in the ecological literature as to what constitutes an overabundance of ungulates. We reviewed the utility of applying five different ecological views or approaches--the ungulate population-predator limitation, biodiversity, sustainability/grazing optimization, overgrazing, and allowable use approaches--to a case study of a potential overabundance of elk. Unfortunately, most of the approaches available to ecologists were developed with goals in mind that were very different from goals for a national park. For example, the sustainability, overgrazing, and allowable use approaches were all originally developed with maximum secondary production by ungulates as the primary goal in mind. Our goal was to search these common views and methods for those approaches that were the most clear, easiest to apply, unambiguous, and most closely allied to National Park Service policy and guidelines. Elk within Rocky Mountain National Park increased to levels approximating food-limited carrying capacity (*K*) following release from human controls (live capture and removals) within the park in 1968. Estimates of the food-limited *K* using forage/nutritional-based methodology in the park averaged 1,154 ± 163 elk ($\bar{x} \pm$ se), while independent density-dependent population-based estimates of *K* were similar at 1,069 ± 55. Elk populations in the park stabilized approximately at these numbers over the previous 10 years (2001 population estimate = 1,074 ± 39 elk). However, elk numbers in the town sector averaged 1,975 ± 150 in 2001, and elk in town were still increasing. Our estimates of food-limited *K* that elk could eventually grow to in the town sector were 2,869 ± 415 elk, based on population analyses and ranged from 3,082 ± 103 to 3,391 ± 113 elk, based on forage estimates for an average year (based on 50–55% consumption rate). In a dry year, the forage-based estimate of the potential for elk the area could support was lower, ranging from 2,330 ± 78 to 2,563 ± 85 elk. The forage base for elk in town was artificially enhanced in a few locales due to fertilization and irrigation of human-altered grassland types such as pastures, lawns, and golf courses. The habituation of elk toward humans in the town sector allow them to use these rich forages and other grassland habitats in an area that is lower in elevation, has less snow cover, and also likely has fewer predators due to the human developments than does the park sector. However, these human increases to the elk forage base in town were more than balanced by losses to human activities such as housing developments and water impoundments on former usable riparian winter range. We estimated the town could support about 169 fewer elk following the human modifications than before the human developments took

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place. Elk negatively influenced seven different willow growth parameters in the park ($P < 0.001$) when elk numbers reached approximate densities of 32 ± 1 elk/km^2 and when consumption exceeded about 37%. Consumption rates of willow by elk averaged 30 ± 2% of the current annual shrub growth across the winter range, but grazing optimization, i.e., greater peak production of grazed willows compared to ungrazed willows, occurred at levels lower than this where moderate consumption rates of about 21% occurred on willows. On grazed grassland sites, there was a minor increase in bare ground. Also, the cover or production of three forb species decreased when compared to similar paired nearby plots that were ungrazed for 4 years. Herbaceous biomass production was 22% less ($P < 0.05$) in grazed willow sites compared to these paired ungrazed sites. There was no grazing treatment effect on plant species diversity in upland grass/shrub or willow. There also was no overall decline in nitrogen (N) and few changes in other macronutrient concentrations in plant tissues and few effects on root biomass or root N attributed to ungulate herbivory, except some increases in coarse root biomass occurred on grazed herbaceous communities. But in willow communities grazed for 35 years in the park, a decline in fine root biomass, root N concentrations, and aboveground N yield were observed compared to ungrazed sites ($P < 0.10$). We also found 79% lower N mineralization ($P = 0.07$) and 78% lower NO_3^- pools ($P = 0.01$) in grazed short willows compared to willows that were ungrazed for 4 years.

We concluded that the ungulate population-predator limitation and forage-based estimates of food-limited *K* approaches, and the overgrazing approach, were the most specific and readily measurable approaches to apply to the question of a possible overabundance of elk. However, population-based limitation estimates required many years of data and considerable cost and effort. National Park Service policy calls for preservation of natural processes, and predation effects were a major natural process potentially limiting ungulates. Restoration of all large capable predators, or in cases such as in RMNP where that may no longer be feasible, management intervention to duplicate this predator limitation, appears to be the approach that is closely aligned to NPS policy and guidelines. Recent information following the wolf (*Canis lupus*) restoration into Yellowstone National Park (YNP) suggests that the same multiple predators in RMNP (grizzly bears [*Ursus arctos*], coyotes [*Canis latrans*], in concert with wolves) might limit elk populations moderately (15–30%) below food-limited *K*. The overgrazing approach is simple to apply and this simple approach is the fastest to apply to clear-cut cases of severe overgrazing, or of no overgrazing. However, for those more ambiguous cases of intermediate effects that are more often the case, the approach can be over-simplistic for complex ecological systems. We concluded the allowable use approach could be readily applied to a park ecosystem, but only if park staff conducted considerable sampling of the effects on plants of different ungulate use levels. Our review of the published literature indicated no generalized guidelines for appropriate use levels, but instead plant responses to a specific level of consumption varied considerably by the evolutionary history of grazing in the area, climate, pre-adaptations of the plants to grazing (e.g., plants with prostrate growth and larger belowground root reserves are less sensitive to grazing), and season of the herbivore use. We concluded that application of the biodiversity and sustainability approaches were not as readily applicable to park managers, since those views were dependent on knowledge of complex ecosystem responses to ungulates and judgments as to the level of ungulate effects and plant changes considered acceptable in light of NPS mandates and policies. However, these approaches were also closely aligned to NPS policy and guidelines. Thus, their application is encouraged in those park ecosystems with extensive knowledge of ecological processes and conditions, such as is the case for RMNP. All of the approaches could potentially be useful to apply to a national park situation, providing there is adequate ecological information available.

Keywords: Allowable use, *Cervus elaphus*, elk, grazing, national park management, natural regulation, sustainability, ungulates.

Introduction

National Park Service (NPS) policy states that natural processes should be permitted to maintain wildlife populations in national parks to the largest extent possible (National Park Service 2001). Human activities have greatly altered some national park ecosystems from their pre-existing, natural state. Native predators have been eliminated in many national parks, migrations of ungulates have been altered by developments and activities outside of parks, keystone predator species may have been lost or their populations altered, and climate change may have altered ecosystems (Wagner et al. 1995a; Wright 1996; Singer et al. 1998a).

Many national parks manage ungulates according to natural regulation, or "hands-off", management within the parks. While natural regulation is largely consistent with the enabling legislation for U.S. national parks (NPS Organic Act of 1916; Leopold et al. 1963; Keiter 1988), the policy has been criticized for being based on inadequately tested scientific hypotheses (Wagner et al. 1995a). The natural regulation policy has been alternatively supported (Houston 1971, 1982; Yellowstone National Park 1997) and criticized (Kay and Wagner 1994; Wagner et al. 1995a) in the ecological literature. The criticisms of natural regulation point out the lack of limitation of ungulates due to extirpation of large wild mammalian predators in many parks (Lime et al. 1993; Peterson 1999), the absence of Aboriginal human control of ungulates (Kay 1994), and major alterations of ungulate migrations (Skinner 1928; Pengelly 1963; Chase 1986). Natural regulation management may also be operationally vague. The policy has been applied alternatively to park ecosystems with extirpated large predators and altered migrations (Cole 1971; Houston 1971, 1982), or to systems with migrations and large predators intact (Wright 1996; Yellowstone National Park 1997). NPS policy clearly states that unnaturally high populations of wildlife that are due to modern human activities may be controlled (NPS 2001). But the definition of an overconcentration or overabundance of ungulates may be vague and ambiguous in the ecological literature (Caughley 1976; McNab 1985; Keiter 1988; Wagner et al. 1995a; McShea et al. 1997; Boyce 1998).

Several commonly used approaches and their criteria exist in the ecological literature that may help guide managers during the evaluation of the appropriate numbers of ungulates in national parks. Our purpose was to review these approaches and apply them to a case study of the potential overabundance of elk (*Cervus elaphus*) in Rocky Mountain National Park (hereafter RMNP) and the adjacent town of Estes Park, Colorado. Our goal was to select an approach where both the key measures, and the logic of the paradigm or approach, were unambiguous, easy to apply, and closely aligned to NPS policy and guidelines.

Ungulate Population-Predator Limitation Approach

The analysis of ungulate populations could be the central focus of a park manager's assessment of ungulate abundance. For example, the estimation of food-limited ecological carrying capacity (hereafter food-limited K) is central to all population-based analyses. Food-limited K can be determined from: (a) linear and nonlinear density feedback relationships (Caughley 1976; Houston 1982; Boyce 1989); or (b) nutritional, GIS-assisted forage-based methods (Hobbs et al. 1982; Coughenour and Singer 1996). Populations at food-limited K are assumed to be regulated within some range by density-dependent processes caused by animal per capita restrictions in food availability (Caughley 1976; Dublin et al. 1990). The process of forage restriction in ungulates near food-limited K may also result in reductions in plant cover and production, plant species alterations, reduced body condition of ungulates, reduced survival rate of ungulates, and subsequently, a new and lower equilibrium between ungulates and forage conditions (Caughley 1976; Sinclair et al. 1985).

Predator limitation of ungulates below food-limited K may occur under natural conditions. Predators may limit ungulates either slightly below (7%–30%) food-limited K (Boutin 1992; Boyce 1993; Mack and Singer 1993), well below (40%–60%) food-limited K (Gasaway et al. 1992; Lime et al. 1993; Messier 1994), or the limitation may be highly variable over time (Fig. 1a). For example, a highly variable, predator-sensitive scenario was identified where predators remove vulnerable individuals and may periodically limit ungulates only during severe weather when there are more vulnerable individuals (McLaren and Peterson 1994; Sinclair and Arcese 1995; Mech et al. 1998). Limitation is more likely where there are multiple predators. Orians et al. (1997) and Peterson (1999) concluded that where both wolves and bears (*U. arctos*, *U. americanus*) coexist, ungulates are limited to lower densities than in cases where only bears or wolves occur. Additionally, a fourth alternative potential form of limitation, the Aboriginal overkill hypothesis of Kay

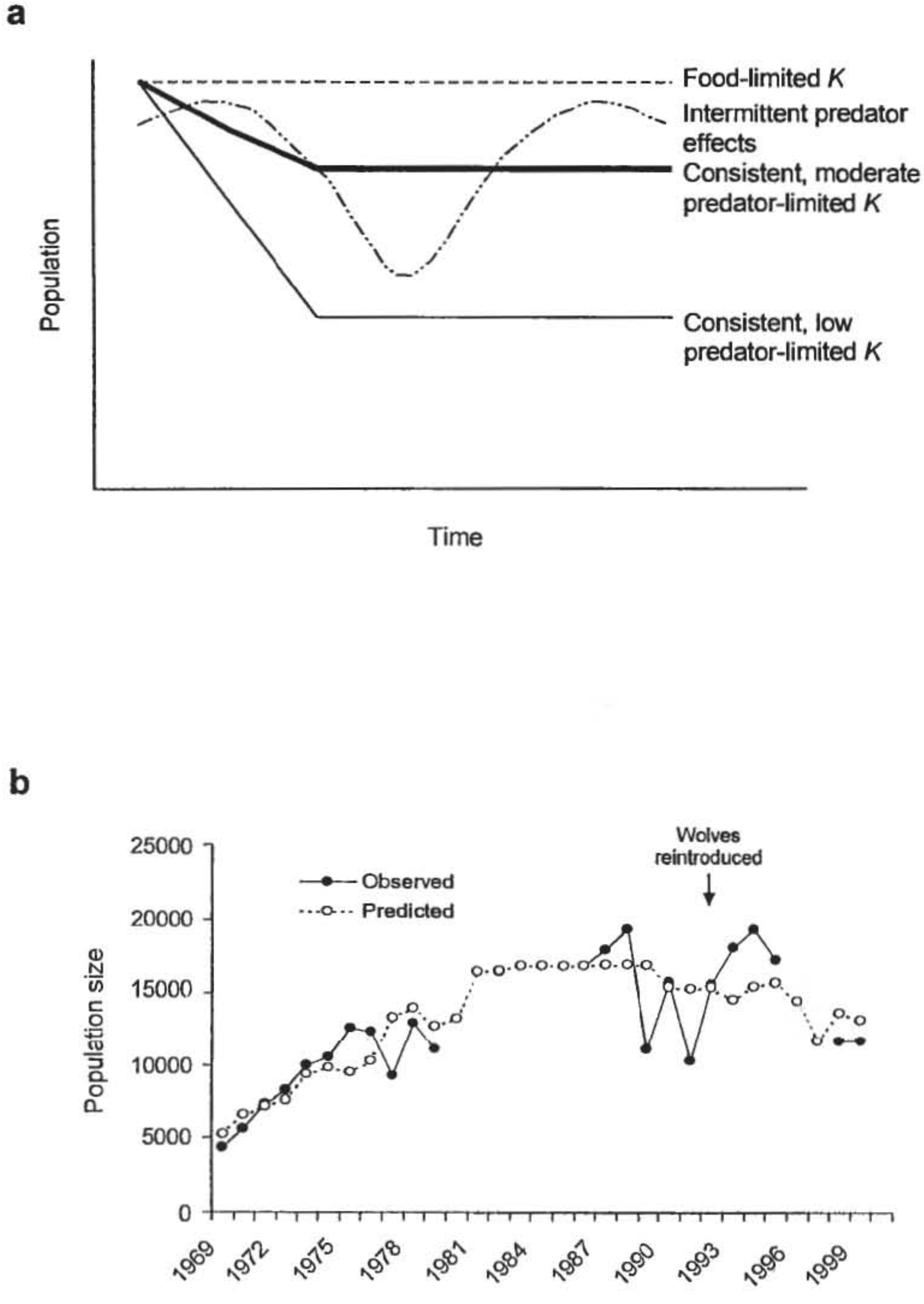


Fig. 1. Schematic representation of *K*, the ecological or food-limited carrying capacity for an ungulate released from human controls, such as elk were in both Rocky Mountain and Yellowstone National Parks. Also represented are several examples from the literature of moderate (Lime et al. 1993), large (Gasaway et al. 1983; Messier 1995), and very large (Kay 1994) limitations of ungulates. Most ungulate -vegetation or ungulate-predator limited systems regularly fluctuate 15% or more over short time scale, while longer term, large fluctuations, or shifts between these scenarios are also possible (a). The expected and observed elk population size in Yellowstone National Park before and after wolf reintroduction (Singer et al. 2002) (b).

(1994, 1998) states that Native Americans reduced ungulates, such as elk, by as much as 90–95% or more below food-limited *K*, although evidence for this view is limited (Boyce 1998; Yochim 2001). Also, ungulates might not necessarily be overpopulated, but alterations in movements and migrations might cause an overconcentration.

Population-based approaches may be useful in that the population analyses, their evaluation, and the subsequent management responses can be immediate. In addition, there is an ever-growing body of evidence in the scientific literature for suggesting predator-limitation of ungulates occurs in natural systems (Gasaway et al. 1992; Mech et al. 1998; Singer et al. 1998a). The approach also lends itself well to adaptive management, since the management goal is a specific population size, but the vegetation expectations of that goal can be periodically evaluated and modified, if necessary. Unfortunately for managers, a large degree of uncertainty continues to exist over the precise extent of predator limitation of ungulates and the variability of predator limitation in undisturbed, pre-European herbivore-predator systems (Boutin 1992; Singer et al. 1997). Further constraining application to the RMNP case, nearly all the evidence of limitation comes from studies of moose (*Alces alces*) and caribou (*Rangifer tarandus*), and little research has been conducted on potential limitation of elk (Jedrzejewska and Jedrzejewski 1998; Singer et al. 2002).

The most applicable example comes from the recent reintroduction of gray wolves into Yellowstone National Park (YNP). Potential limitation of this elk population by wolves was recently modeled by Singer et al. (2002). The dynamics of this elk population are some of the best understood. Density dependence, harvest, and weather relations are well established from prior quantitative analyses (Houston 1982; Boyce 1991; Coughenour and Singer 1996; Boyce and Merrill 1996; Cheville et al. 1998; Singer and Mack 1999). This information was used to predict an "expected" elk population's size and recruitment rate from 1995 to 1998 in the absence of wolves (Singer et al. 2002). The actual "observed" elk population following wolf restoration in 1995 was about 15% smaller and recruitment was lower (especially after 1997), strongly suggesting multiple predator limitation following the recent restoration of wolves (Singer et al. 2002; Fig. 1b), in concert with already existing predation on elk by coyotes, bears, and humans in the system (Singer et al. 1997).

The Biodiversity Approach

Alternatively, a park manager's measures in assessing ungulate abundance might focus on plant species, plant community, or other, diversity measures. Management of much of the world's grazing land is based primarily on changes in plant species composition (Milchunas and Lauenroth 1992). In particular, dominant individual species have been used as indicators of range condition under the increaser-decreaser-invader concept. It has been suggested that ungulates in national parks should not be allowed to exceed levels that impact these diversity values (Wagner et al. 1995a; Berry et al. 1997). NPS (2001) policy also states that the natural abundance and diversity of plants and animals should be maintained within the bounds of natural processes.

In the biodiversity view, the trend in the relative amount of both plant community and plant species (i.e., richness, evenness) diversity is the measured variable. Disadvantages to applying this view are that responses of plant diversity to protection from ungulates (exclosures) or to new ungulate management programs may be long-term, on the order of one to many decades. Other confounding variables to ungulate herbivory, such as fluctuating beaver populations, climate change, succession, or hydrologic change, may also affect plant diversity and, thus, confuse the interpretations of any effects due exclusively to the ungulates. In addition, ungulates in pristine, natural ecosystems are known to alter plant species diversity in highly variable ways (McNaughton 1979; Pastor et al. 1993; Stohlgren et al. 1999). Research has demonstrated that ungulate grazing can alternatively decrease plant diversity (Rummell 1951; Chew 1982), result in no difference (Gough and Grace 1998; Stohlgren et al. 1999), or increase plant diversity (Grime 1973; Mueggler 1984). Ungulate effects on plant diversity may be variable in natural systems depending on environmental conditions, evolutionary history of grazing, and predator limitation (Collins and Barber 1985; Stohlgren et al. 1999). The basic tenet by some researchers that there should be no measurable effects of ungulates on plant diversity (Wagner et al. 1995a,b) has been questioned by others (McNaughton 1993, 1996). Management for maximum plant species diversity may, in some instances, include management for moderate, or even high, densities of ungulates. Thus, the grazing system and these major ecological relationships need to be well understood before managers can set goals for plant diversity.

The Grazing Optimization and Sustainability Approaches

Measures to assess potential overabundance of ungulates might focus on their effects on plant production, sustainability and fertility of the ecosystem, and effects on ecosystem processes. These views assume that plants can respond to removal of aboveground tissues by ungulates through a number of compensatory responses and processes. In grassland grazing systems with native ungulates, less N is typically immobilized in litter and standing dead biomass (McNaughton 1983; Seagle et al. 1992), soil microbial biomass is likely decreased and, thus, net soil N mineralization is increased (Ruess and McNaughton 1987; Holland and Detling 1990; Frank and Groffman 1998). As a result, increased root uptake of N, increased N concentration in shoots, and increased N yield/unit tissue is often observed in herbaceous grassland plants grazed by native ungulates (Ruess 1984; Jaramillo and Detling 1988; Coughenour et al. 1990). The grazing optimization hypothesis has been observed at some moderate or low level of herbivory, where net primary production (NPP) is maximized and stimulated over ungrazed controls (McNaughton 1979, 1983, 1993; Dyer et al. 1993; Frank and McNaughton 1993; Turner et al. 1993; Green and Detling 2000). Compensatory responses in grasses enabled moderate levels of herbivory to be sustained (Biondini et al. 1998; Mazancourt et al. 1998). Several authors found no evidence for grazing optimization in grasslands (Verkaar 1992; Painter and Belsky 1993). Woody browse species may compensate for herbivory removals through increased number of branched shoots, increased size of regrowth shoots, and increased number of buds and number of long shoots (Bergström and Danell 1987). The central issue of this view is that providing plant production and soil fertility are maintained under grazing (McNaughton 1979, 1993; Frank and Groffman 1998), shifts in abundance of individual plant species or changes in biodiversity are of less concern. This view is useful to managers in that the end product, aboveground net primary production (ANPP), is a relatively straightforward and immediate measure to gather. Additionally, long-term productivity and sustainability is of paramount importance to ecosystem management. But sustained aboveground production under grazing may come at the expense of reduced root biomass, reduced seed production, or altered plant species abundance. These measures should also be sampled (Belsky 1986; Verkaar 1992; Painter and Belsky 1993) and thus is an expensive and complex approach to apply. Managers must also decide how much effects due to ungulates on production, soil, and ecosystem processes are acceptable in a natural functioning system (see McInnes et al. 1992; Pastor et al. 1993), and that is a complex question to ask.

The Overgrazing Approach

The overgrazing approach is the simplest approach that might be applied to a question of overabundance of an ungulate. Overgrazing is a value-laden term, but a term that is very simply defined as any excess of herbivory that leads to degradation of plant and soil resources. The challenge lies in defining what constitutes excess grazing since that definition is based on one's goals in managing an ecosystem. For example, a range manager, wildlife manager, or park manager might each define overgrazing differently (Coughenour and Singer 1991). In spite of these differences in opinion, there is some general agreement on what constitutes overgrazing of western rangelands. It is widely held, for example, that overgrazing results in reduced plant cover, increased bare ground, increased soil temperatures, drier soil, increased soil erosion, reduced organic inputs to the soil, and/or decreased plant productivity (Pengelly 1963; Westoby et al. 1989; Fuls 1992). Overgrazing also results in an increase in less palatable native plants, reduced size and vigor of plants, increased mortality of plants, invasion of perennial weeds, and eventually, invasion of annual weeds (Daubenmire 1940; Pengelly 1963; Westoby et al. 1989). These general criteria for overgrazing are relatively unambiguous. Thus, we feel the variables used in this view are relatively rapid and straightforward to sample, but the findings may be difficult to interpret. The challenge to the park manager is in deciding what constitutes "too much" of a grazing effect.

The Allowable Use Approach

Perhaps the most commonly used approach in the western United States for evaluation of the appropriate number of ungulates focuses on allowable use levels on forages. First, aboveground net primary production (ANPP) is measured. A judgment is then made as to what level of use, or consumption, is allowable in that system and then the consumption level is sampled and monitored. For example, a level of 50% allowable use is often applied to livestock forage on western rangelands.

But effects on plants and processes of these proposed levels of allowable use have only rarely been quantitatively evaluated (see Biondini et al. 1998).

This approach is useful to managers since the measures needed to apply it reflect current conditions. The measure of interest, consumption rate, is an unambiguous measure of the direct interaction between a plant species and the ungulate herbivore. The view also lends itself well to adaptive management programs since new goals for consumption levels may then be set if expectations are not met.

Disadvantages of applying this approach are that measures of production and consumption are labor- and cost-intensive, and plant responses are highly variable to any specific level of use depending on the life form of the plant. Grazing system responses are influenced by the relative amount of underground root reserves, evolutionary history of grazing in a particular system, environmental conditions, and season of herbivore use (Milchunas et al. 1988; Frank and McNaughton 1992, 1993; Hamilton et al. 1998; Mazancourt et al. 1998).

We concluded from our review of a number of papers that reported consumption rates and effects on plants, that any allowable use values would be highly variable between ecosystems (Fig. 2a,b). We calculated a mean and variance level of use that appeared to be either: (a) sustainable, i.e., allowable; or (b) not sustainable, i.e., detrimental to plant production, fitness components, and continued abundance of the plant(s). Herbs and shrubs that grow in forest understories were the most sensitive to ungulate herbivory, followed by plants in grasslands with less evolutionary history of grazing (e.g., South American grasslands, Great Basin grasslands). Less sensitive ecosystems (e.g., the short-grass prairie or Serengeti grasslands) were those pre-adapted to herbivory through a longer evolution with ungulates, more prostrate growth forms of plants, and larger underground root reserves (McNaughton 1979, 1983; Milchunas et al. 1988). Shrubs were generally less tolerant of herbivory than grasses, probably due to few reserve meristems, nonintegrated modules, and slow, determinant growth (Whitham et al. 1991). Understory shrubs and trees that grow under shade in mature forests were less tolerant than seral shrubs that grow in strong sunlight that were characterized by rapid annual vertical growth rates (Fig. 2b).

Study Objectives

The purpose of this investigation was to present a broad spectrum of data available from our research on elk abundance and effects in RMNP and the adjacent town of Estes Park, Colorado, and compare this information to the criteria stated for each of the five different approaches. Elk were eliminated from the park in the late 1800's, reintroduced in 1913–1914, and artificially controlled by trapping in the park ecosystem by managers until 1968. Since 1969, the elk population has continued to grow and concerns over their possible overabundance have been expressed (Hess 1993; Berry et al. 1997). Our primary goal was to determine which of the stated criteria of the five approaches were the least ambiguous to sample, the easiest to apply to this case study, and the most closely aligned to NPS management policies and guidelines. We compared the operational clarity (i.e., the features of the approach that were specific, quantifiable, and readily measurable) and the time, cost, and potential management consequences of applying a particular approach to the case example.

Study Area

The low elevation elk winter range of RMNP encompasses approximately 17,000 ha in the upper montane zone along the eastern boundary of the park and the adjacent Estes Valley. Elk are free to move between protected national park land and the mix of public and private land in the Estes Valley. Glacial moraines running east-west divide the body of the park area into four major valleys, while the town of Estes Park lies in the middle of a broad park-like valley. Elevations in the study area range from 2,300 m at the lower end of the Estes Valley to 2,800 m on moraine ridge tops. Mean annual precipitation is 41 cm, most of it occurring as wet spring snows. An additional 2,000 ha of high elevation alpine tundra support a wintering population of approximately 125 animals.

Methods

Population Analyses and Elk Concentrations

Seventy-three elk were radiocollared in January 1995 and monitored by ground and aircraft until 1998 (Larkins 1997; T. L. Johnson, RMNP, unpublished data). We divided the winter range into four logical sectors based on movements of radiocollared elk (Fig. 3). We estimated the total size of each sector and the area of each vegetation cover type in each sector (Appendix A) using geographic information systems (GIS). All elk

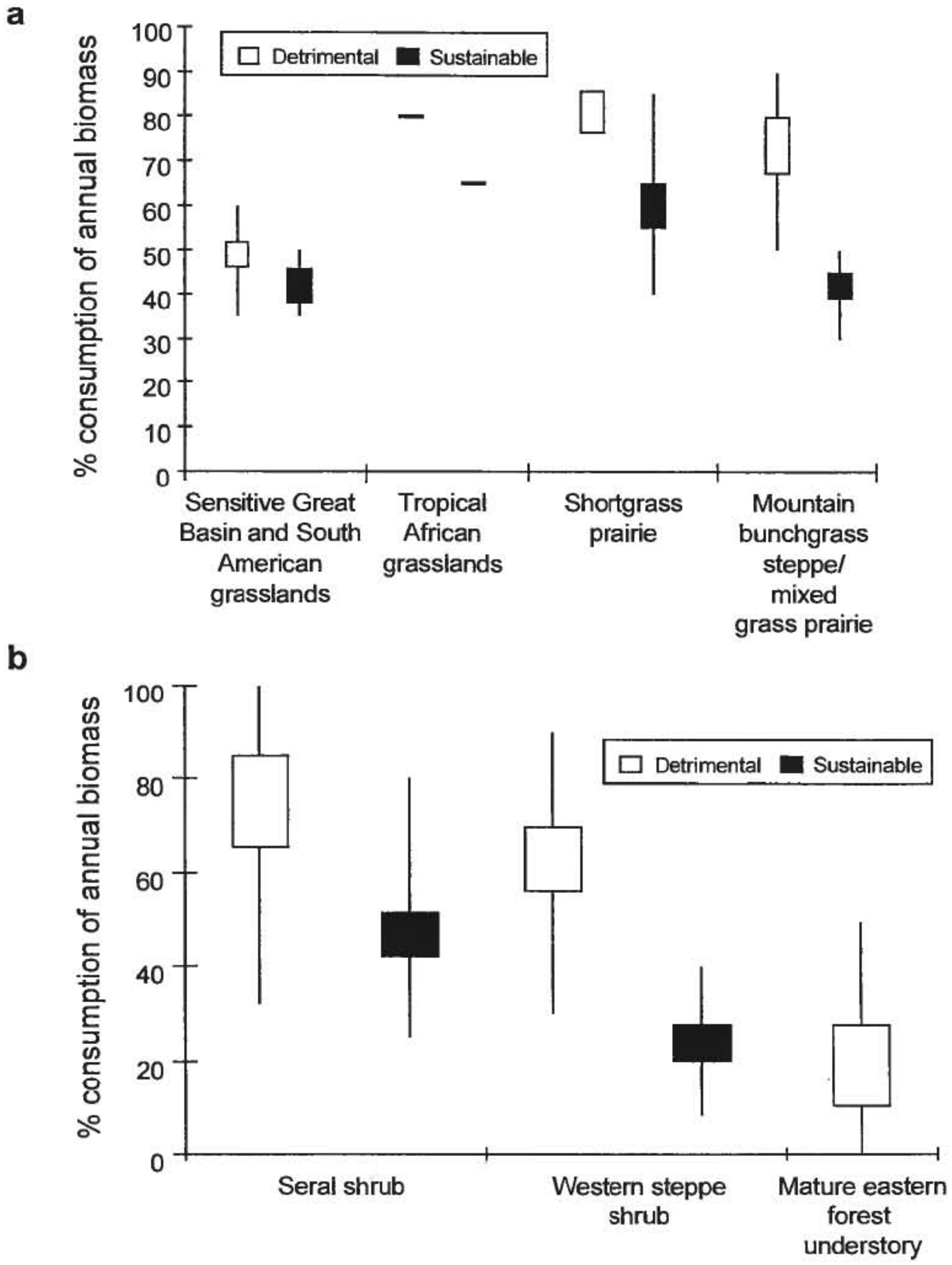


Fig. 2. Schematic of percent consumption of herbaceous (a) and shrub (b) species by ungulates that were reported in the literature to be sustainable or detrimental to growth, production, vigor or fitness components. Grassland Sources (a) include: Daubenmire (1940); Rummell (1951); Klippe and Costello (1960); McNaughton (1979, 1983); Hilbert et al. (1981); Mack (1981); Sneva et al. (1984); McLean and Wikeem (1985); Rickard (1985); Sala et al. (1986); Jaramillo and Detling (1988); Milchunas et al. (1988); Polley and Detling (1988); Frank and McNaughton (1992); Fuls (1992); Seagle et al. (1992); Singer and Harter (1996); Olson and Wallander (1997); Biondini et al. (1998); Frank and Groffman (1998); and Pucheta et al. (1998). Shrub Sources (b) include: Aldous (1952); Krefting et al. (1966); Willard and McKell (1978); Wolff and Zasada (1979); Oldemeyer (1981); Wolfe et al. (1983); Danell and Bergtröm (1985); Bergström and Danell (1987); Wagstaff and Welch (1991); McInnes et al. (1992); Pastor et al. (1993); Singer and Renkin (1995); Singer et al. (1994); and Ritchie et al. (1998).

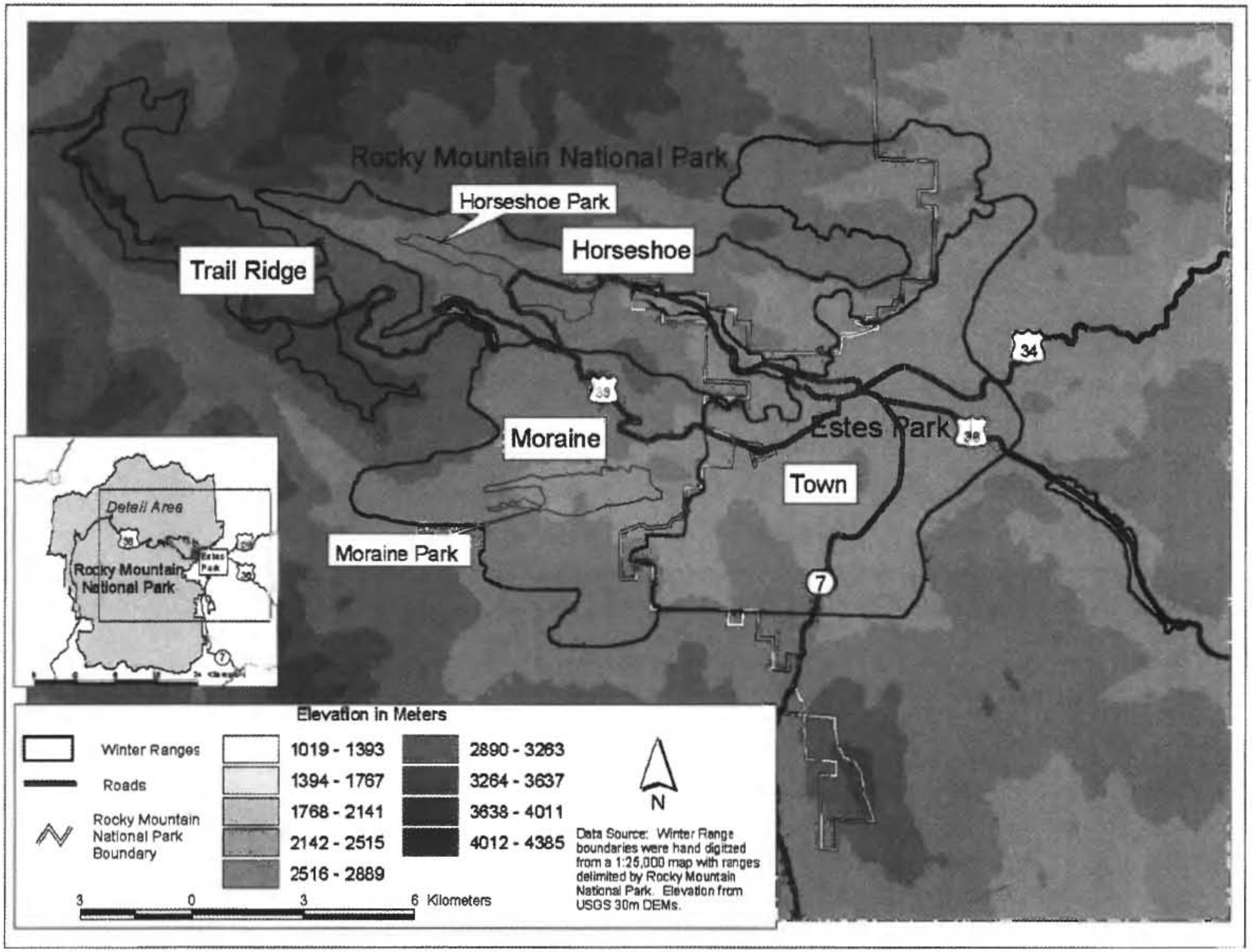


Fig. 3. Map of witner ranges of elk in Rocky Mountain National Park, Colorado.

radiolocations were plotted and digitized and each radiocollared elk was classified as to the sector in which it spent each season (town, Moraine, Horseshoe, Trail Ridge ranges). Winter elk density was calculated using data from 6 years of annual aerial surveys (F. J. Singer, unpublished data). The surveys concentrated on Horseshoe and Moraine Parks, and were not flown over the town of Estes Park or Trail Ridge Range. The surveys were flown seven times during the 6 years on March 9, 1994; February 14, 1995; December 15, 1995; February 11, 1996; February 19, 1997; March 12, 1998; and February 13, 1999. Elk density was calculated for each survey based on a grid with 100 m cell size and a 3,000 m search radius using the ArcView 3.1 GIS density calculation function. We used a kernel density method, which distributes the group size information from the observed group location and, therefore, results in a smoother density gradient. The total number of elk within 3,000 m of each cell was calculated and divided by the search area to find the density of the cell. All density grids were then summed and divided by the number of surveys to get an average density. The results were then mathematically smoothed. Elk distributions varied little between the study years (Larkins 1997), probably because snow depths were typically shallow across most of the winter range in the study winters and depths did not vary greatly, at least during the study years. Thus, we feel these values accurately represent annual average elk activity and elk grazing influences.

We estimated the elk population size in the park by recording sighting variables for each group of elk observed during systematic helicopter surveys of the primary winter range. The effect of these variables on sightability of elk was tested using radiocollared elk and the sightability corrections were used to estimate the number of animals missed following the methodology of Samuel et al. (1987), Unsworth et al. (1994) and this study. Elk in town were estimated from mark-resight estimates developed from repeat surveys each winter. We compared the potential of the town and park sectors to support elk using three methods: (1) population-based estimates of food-limited *K* (Houston 1982; Boyce 1993; Coughenour and Singer 1996); (2) forage-biomass based estimates (Holzgang 1997); and (3) forage and nutritional estimates of food-limited *K* (Hobbs et al. 1982). We assumed elk would reach food-limited *K* in the sectors due to the lack of evidence for any substantial predator or weather limitation. We compared these potential capabilities to the current estimates of elk that exist in the sectors using the aerial sightability estimates in the park and ground mark-resight estimates in town.

Data to estimate population size, age and sex composition, and survival rates were intermittently available for elk populations in RMNP from 1965 to 2001. Similar data were available for elk outside the park, in the Estes Valley, from 1979 to 2001. A population-projection model incorporating density dependence and weather covariates was developed and fit to the available population data in both the park and the town sectors. Model fitting was accomplished by minimizing the sum of squared errors between model estimates and direct estimates weighted by the inverse variances of each direct estimate, following Lubow et al. (this volume).

In the population model, both calf survival, S_c, and recruitment (similar relationship, not shown) for each population is related to density and four weather statistics through a logistic model:

$$S_c = \mathrm{LOGIT}(\beta_0 + \beta_1 N_T + \beta_2 \bar{T}_S + \beta_3 \bar{T}_W + \beta_4 \bar{P}_S + \beta_5 \bar{P}_W$$

where N_T is the total population size, $\bar{T}_S$ and $\bar{T}_w$ are average summer (April–August) and winter (September–February) temperature deviates, $\bar{P}_s$ and $\bar{P}_W$ represent average summer and winter precipitation deviates, and the β values are estimated parameters. LOGIT represents the logistic function:

$$\mathrm{LOGIT}[f(x)] = \frac{1}{1-e^{-f(x)}}$$

Alternative population models were considered and the best one selected using Akaike's Information Criteria (AIC_c). The smallest AIC_c values represent best biological models since the AIC_c statistic corrects for additions to the number of parameters (Burnham and Anderson 1992).

A second, independent food-based estimate of *K* in town was calculated following the methods used in the Swiss National Park (Holzgang 1997). This method involves using calculations of available forage, offtake, and forage requirements to estimate ungulate numbers. We used a 1996 Spot satellite image, with 10 m panchromatic and 20 m multispectral resolution to classify vegetation types for the elk winter range in the town of Estes Park, Colorado (Appendix B). Vegetation was stratified into open grasslands, pine grasslands, wet meadows, irrigated and slightly sub-irrigated grasslands, golf courses, disturbed grasslands, and forested types. A food-based estimate of *K* in the park sector was previously calculated by Hobbs et al. (1982). Total forage biomass was sampled (see "Allowable Use Measures" below) and corrected for available forage using a GIS with vegetation data (Appendices A and B). The total available forage biomass for elk was adjusted for sampled offtake values and divided by the forage required per elk for the 7-month winter use of the town range to arrive at *K* for the town. We predicted forage use would average 50–55% over the landscape based on observed use of forages by elk near *K* in the park (57% offtake) and near Maybell, Colorado (60% offtake, Hobbs 1996). We estimated average forage use across the landscape in town would be less than the park or Maybell examples due to some elk-proof fences, other human structures that blocked elk, and avoidance of some core subdivision lawns where elk use was restricted. We did not calculate how much of these town areas were inaccessible to elk, but we feel this lower range of use levels approximates the maximum average use level that might occur in town. We assumed the average elk consumption was 5 kg dried forage per day (Hobbs 1979). We calculated the average number of days elk spent in the town winter range ($\bar{x}$ = 210 ± 7 days) from 30 radiocollared elk over four winters to arrive at a mean of 1,050 kg forage consumed per elk per winter in town.

We also inspected the extent of any possible artificial concentrations of forages for elk in town by calculating the N yield in the fertilized and irrigated grassland types in town sampled in 1997–1998 and comparing that to the N yield from undisturbed grasslands in the town sector. Nitrogen yield was estimated as the concentration of N in forages multiplied by the peak standing crop biomass of forages. We also used GIS to estimate the areas of grasslands lost to human modifications (impoundments, buildings, and pavement) and GIS combined with groundtruthing to estimate the grassland areas that were improved due to human modifications (golf courses, irrigated pastures). From this, we projected an elk *K* for the town sector under pristine conditions. We present carrying capacity estimates for dry years, since those are years of critical minimums, and for average years, since the elk population will be most likely to track average forage conditions.

Vegetation Sampling Locations

Sixteen study sites were randomly selected in 1994 for placement of grazing exclosures (46 x 30.5 m) and paired grazed plots, in the elk winter range in the montane riparian and upland shrub communities of northeastern RMNP. Vegetation communities were identified and random points generated in the appropriate vegetation type using GIS. Twelve exclosure study sites were located in riparian willow communities of the Moraine Park area of the Big Thompson River drainage (elevation 2,481 m) and the Horseshoe Park area of the Fall River drainage (elevation 2,598 m). An additional 25 willow study locations in grazed sites throughout the park winter range were randomly selected using GIS and sampled in 1996. Four study sites were located in upland shrub/grassland sites. These sites were all located on southern exposures in the areas of Hallowell Park, Deer Ridge, Aspenglen Campground, and the Beaver Meadows Entrance Station.

Predominant willow species throughout willow areas were *Salix monticola, S. planifolia*, and *S. geyeriana* mixed with other wet site shrubs such as *Potentilla fruticosa, Betula glandulosa, B. occidentalis*, and *Alnus tenuifolia*. We selected willow communities for intense study because willow (*Salix* spp.) was suspected to be a significant diet component for elk (D. Stevens, personal communication; Hobbs et al. [1981]) and willows are not rare--willow communities comprise about 4% of the total winter range and 30% of the core elk winter range. We did not want to monitor a rare vegetation type, since rare plants or rare plant communities may not respond in linear fashion to elk densities and there may be no feedback. We also recognized a short willow type that constituted about 70% of the willow communities and a tall willow type that constituted 30% (Peinetti et al., this volume). Both types were sampled proportionately. Eight of the willow exclosure sites (four in Moraine Park and four in Horseshoe Park) were located in areas that had previously held beaver dams but had little or no current beaver activity, that had dewatered channels, and that supported short, heavily browsed willow. In all of these "short willow" sites, evidence from dead and decadent willows indicated that plants over 2 m tall were once present. The other four willow exclosures sites (two in Moraine Park and two in Horseshoe Park) were located in beaver-occupied areas (including areas of recent activity), that supported taller willow plants subject to less severe hedging by the elk that we referred to as "tall" willows.

Primary vegetation cover of the upland shrub/grassland type consisted of antelope bitterbrush (*Purshia tridentata*) and mountain muhly (*Muhlenbergia montana*) associated with sparse ponderosa pine (*Pinus ponderosa*).

Three pre-existing, longer-term exclosures were placed in a mixture of big sagebrush (*Artemisia tridentata*), wet meadow, and aspen (*Populus tremuloides*) vegetation types in 1963 in the Beaver Meadows drainage. These sites had not been randomly located. Grazed and ungrazed sites were also sampled at these exclosures.

Vegetation sampling in the town sector consisted of 14 sampling sites within six vegetation types sampled in 1997 through 1998. The vegetation/habitat types chosen reflect areas where elk are most often observed grazing in winter. Six sites in three additional vegetation types were chosen and sampled in summer 2000.

Elk Density Correlates to Willow Growth--Grazing Optimization

To test our assumption concerning the relative importance of willow in elk diets, 55 fresh elk fecal samples were collected on low elevation winter ranges in November 1994 and 1995; February 1995; and April/May 1995–1997. Samples were also taken on alpine summer range in the spring of 1995 and the summers of 1995–1997. Each sample was a composite of 8–10 fecal pellets from 8–10 individual elk in a group. Samples were frozen until immediately before processing, and then dried at 55°C for 48 hours before shipping to the Composition Analysis Laboratory in Fort Collins, Colorado. Samples were ground together and three subsamples taken from each sample for analysis. The dietary components in each subsample were identified to genus. Then the subsamples were pooled to determine average percentage contribution to total diet for that sample.

Twenty-five willow sample sites were randomly selected from within all mapped willow types on the winter range using GIS procedures and sampled in 1996. The following variables were measured on three to five circular subsample plots, each 9.3 m^2 in size, at each willow sample site: average shrub height (cm), maximum shrub height (cm), stem density (stems/ha), shrub density (shrubs/ha), twig production (kg/ha), total new shoot production or current annual growth (CAG; kg/ha), canopy volume (m^3/ha), and canopy cover (m^2/ha). The data were recorded for 3 willow species *(Salix monticola, S. planifolia*, and *S. geyeriana*) from the 25 plots as well as the 12 grazed plots paired to the willow exclosures in Moraine and Horseshoe Parks. The variables from the subsample plots at each location were averaged and pooled across willow species. Only this single mean was entered, since the subsamples of plots at a location were not independent of each other. Of these willow sample sites, 31 had enough information to be assigned to a category of average 1994–1999 elk density from the mapping effort. At the grazed plots paired to the 12 exclosure sites, consumption rates were calculated for 3 years (1995, 1996, and 1998). A single mean depth to the water table for the month of June, the time of most of the annual growth of willows, was also averaged from three water wells at each of these 12 sites for 3 years.

The effects of elk density, elk consumption of willows, and depth to the water table on the eight willow size and growth variables were inspected using linear regression. The CAG, stem density, plant density, twig production, shrub volume, and shrub area measures were log-transformed. Akaike's Information Criteria corrected for small sample size (AIC_c) was used to evaluate the best, or most parsimonious models:

$$AIC_c = \frac{\ln(SSE)}{n} + \frac{n+K}{n-K-2}$$

where SSE = sum of squares error and K = number of parameters (Burnham and Anderson 1992; McQuarrie and Tsai 1998). The AIC_c process provides a quantitative measure for the trade-off between the increased precision achieved by adding additional variables to the statistical models versus the "cost" to the parameter estimation of adding a variable. The lowest AIC_c values for a well-designed biological model indicate the "best" and most parsimonious model of the choices tested (Burnham and Anderson 1992).

Any threshold values in elk density or elk consumption rates that influenced willow size and growth variables were also inspected. The approximate threshold of elk density at which the willow growth variables were reduced 40% from peak values and to levels below ungrazed values, were identified using a line fit to the points using Friedman's smoothing method (S-plus 2000). A judgment was made that this threshold constituted a biologically important decline in willow growth. Any potential grazing optimization, or peak aboveground production that might be observed at moderate levels of ungulate consumption rates, was identified.

Effects of Elk on Plant Species Diversity

The Shannon-Weaver diversity index (Shannon and Weaver 1962) and species richness index (R) were calculated for 0.25-m^2 herbaceous plots sampled in the park, and then averaged across plots at each site to determine the average index value for species diversity and richness for each treatment (Appendix C). We tested for differences in diversity indices between grazed and ungrazed sites using non-parametric statistical analysis.

An analysis of variance of ranked data for each index in each vegetation type was conducted, as well as a Wilcoxon rank test. These indices were computed using all plant species without regard to whether plants were exotic or native. ANOVA tests of abundance of each individual species between grazed and ungrazed treatments were also conducted. We categorized plants into native and exotic species and then compared total production of natives and exotics between grazed and ungrazed sites with PROC MIXED, an analysis procedure that is a generalization of the standard linear model design using SAS (statistical analysis software) v6.12. PROC GLM, the general linear model for data with only one source of variation, was used for data analysis from upland grass/shrub sites and the F-protected least significant difference was used to determine significant differences between means.

Grazing Sustainability or Optimization Measures

Three 9.3 m² circular plots were established in each exclosure and grazed site to measure shrub production. Data on shrub production were collected in late summer of 1994–1996 and 1998 for willow sites and 1994–1997 for bitterbrush sites (Zeigenfuss et al., this volume). Data collected on each plant included species, canopy diameters (widest and perpendicular to widest diameter), plant height, number of stems, and estimate of percent of canopy that was dead. Regression equations were developed for prediction of production for the three major willow species and bitterbrush. Equations were developed separately for Moraine and Horseshoe Parks for 1995 and 1996. Then a pooled equation was developed and used to predict total willow production for 1994 and 1998. R^2 values for these equations were high and ranged from 0.75 to 0.92. Samples were taken from the 35-year exclosures following the same methods in 1998 and 2000.

Herbaceous standing crop biomass data were collected by clipping three to five randomly located 0.25 m² circular quadrats in late summer 1994 at each exclosed and grazed site. All graminoids and forbs within the quadrat were clipped and sorted by species to measure annual peak standing crop. Litter was also collected from within each quadrat. Vegetation was oven dried at 55°C for 48 hours and then weighed. Visual estimates of percentage bare ground, moss, lichen, cacti, and shrubs were also recorded. Town sample sites in subirrigated wet meadow, slightly subirrigated wet meadow, cattle grazed, ponderosa pine/grasslands, upland grasslands, and disturbed grasslands were sampled in July 1997 and 1998 (average precipitation years). Golf course sites were sampled in late November 1997 after mowing ceased. The wet meadow sites and disturbed grasslands were also sampled in July 2000 (a dry year). Subirrigated wet meadow sites were compared between average and dry years to determine a scale factor for biomass production between different precipitation years. This scaling factor was applied to the forage-based model used for estimating elk *K* in town. Methods follow those listed above with the exception that samples were grouped into graminoids and forbs. Predominant species were noted for purposes of comparison of sites. All vegetation types at the 35-year exclosures were similarly sampled in August 1998.

Several willow individuals (n = 2–4) of the three predominant species (*Salix monticola, S. planifolia*, and *S. geyeriana*) in each treatment at each exclosure were also tagged for more intensive measurement throughout the course of the study. Samples for nutrient analyses were obtained from these tagged willows in August 1998 and January 1999. Composite graminoid and forb samples from the previous growing season were collected from plots subjected to elk herbivory in April 1998 (all sites). Composite samples from current graminoid and forb growth were collected in July 1997 (bitterbrush sites) and 1998 (willow) from all treatments. Samples were analyzed for carbon (C) and N content using a LECO CHN-1000 Carbon Hydrogen and Nitrogen Analyzer. Dried and ground plant samples were combusted in a chamber and resultant gases passed through infrared cells to determine C and through a thermal conductivity cell to determine N.

Root samples were collected using a 6.35 cm diameter root corer driven 20 cm into the soil inside and outside of all 4-year exclosures in 1996 and 1999 and 35-year exclosures in 1999. Roots were refrigerated (~4° C) until they were processed. Processing of samples consisted of washing to remove soil from roots then drying them in a forced air oven at 55°C for at least 48 hours. Dried root samples were brushed to remove any remaining large particles of soil and then sorted into coarse (>2 mm) and fine (<2 mm) components. Dried root samples were then weighed to the nearest 0.0001 g and analyzed for percent total N as described above. A subsample of the roots was weighed, combusted in a muffle furnace at 550° C for 6 hours, then weighed again to determine the percent organic matter, based on the ash sample. The actual root biomass weight was then determined by multiplying the percent organic matter by the weight of the entire dried root sample.

Allowable Use Measures

Five 9.3 m^2 circular plots were measured in areas subjected to elk herbivory at each exclosure site to estimate shrub consumption by ungulates following the general methods described above. Winter use was measured before leaf bud break in May, and summer use was measured in August, 1994–1998. On every fourth individual of each species, a subsample of the number of browsed and unbrowsed leaders, and twig basal, tip, and browse diameters were also collected. Percent leader use was determined using the equation:

$$\%\ \text{leaderuse} = \frac{a}{a + b}$$

where a = number of browsed leaders and b = number of unbrowsed leaders. Average percent twig removed was determined using the method of Jensen and Urness (1981) and Pitt and Schwab (1990) following the formula:

$$\%\ \text{twig use} = \frac{100(D_p - D_t)}{D_b - D_t}$$

where D_p = twig diameter at point of browsing, D_t = diameter of a representative sample of twig tips, and D_b = basal diameter of current year's twig growth. Total consumption was determined by multiplying % leader use by % twig use.

Six grazing cages were randomly placed at each grazed plot for measurement of winter herbaceous consumption. Paired 0.25 m^2 plots inside and outside these cages were clipped in spring, prior to greenup. Cages were randomly relocated after the spring sampling to capture the early summer consumption that occurs during elk migration to summer ranges. Vegetation collected inside and outside these grazing cages was dried at 55°C in a forced air oven for 48 hours and then weighed. Percent consumption was calculated using the following formula:

$$\%\ \text{consumption} = \frac{100 * (B_i - B_o)}{B_i}$$

where B_i = dry weight of biomass inside grazing cage, and B_o = dry weight of biomass outside of the grazing cage.

Town sites, except the golf course, were sampled for winter offtake in March and April 1998, and spring-summer offtake in July 1998. Methods follow those listed above. Percent biomass consumed was compared between vegetation/habitat types for each sample period using analysis of variance methods.

All analyses of plant measures were performed using SAS (version 6.12) statistical software. Shrub and herbaceous production and consumption data from willow sites were analyzed for differences between grazed and ungrazed treatments using PROC MIXED. PROC GLM was used for analysis of data from upland grass/shrub sites and the F-protected least significant difference was used to determine significant differences between means. The variables of willow growth were log-transformed to stabilize variance.

Potential Overgrazing Measures

We sampled percent bare ground in 30 grazed and ungrazed plots at five paired locations at the 35-year exclosures in 1998 and at the 4-year exclosures. Bulk density and percent organic matter for the paired plots were sampled by Binkley et al. (this volume) and Menezes et al. (2001). Cover and biomass of herbaceous plants were sampled on three 0.25 m^2 plots at each grazed and ungrazed site. The effects of grazing on individual plant species and all plant species pooled were compared using ANOVA methods.

Results

Elk Population Analyses and Potential Overconcentrations

The radiocollared elk were classified as either town or park animals based on criteria of >65% of winter locations in one sector or the other. Sixty-two radiocollared elk spent the winter in either: (a) town, (b) the Horseshoe Park area, or (c) the Moraine Park and Beaver Meadows complex, and rarely moved among these three sectors. Eleven other radiocollared animals were classified as wanderers and moved freely among the town and park sectors. The Trail Ridge winter range only supports 100–125 animals and was not included in the plant studies, although the area is also a significant summer range for migratory elk.

Population-based estimate of food-limited *K* for the park sector of the elk population was 1,069 ± 55 ($\bar{x}$ ± se) animals (Table 1). The park sector of the elk population was at or near this level for about the last 10–13 years prior to the analysis (during which time λ, or population growth, leveled off and approximated 1.0). Colder winter temperatures were correlated with reduced calf recruitment (calves:cow at age 0.5 yrs) and with reduced calf survival (between age 0.5 to 1.5 years) in town. Recruitment of town elk also increased with warmer summer temperatures and greater summer precipitation. No weather covariates were significantly correlated with calf recruitment or survival in the park. Declining calf recruitment has been nearly linear and similar in both the park and town. However, density response of calf survival in the park was abrupt near carrying capacity and has not yet been detected in town, suggesting that this mechanism of density dependence is difficult to detect until the population is near carrying capacity. Forage-based food-limited *K* for the park sector was estimated by Hobbs et al. (1982) as 991 ± 102 in a dry year and 1,481 ± 261 in a wet year. Since Hobbs et al. (1982) only had estimates for years 40% wetter and 20% drier than average, we calculated an average precipitation year estimate by weighting the dry year estimate by twice that of the wet year (because it was twice as close to average). The resulting average precipitation year estimate of forage-based *K* in the park for elk was 1,154 ± 163 elk.

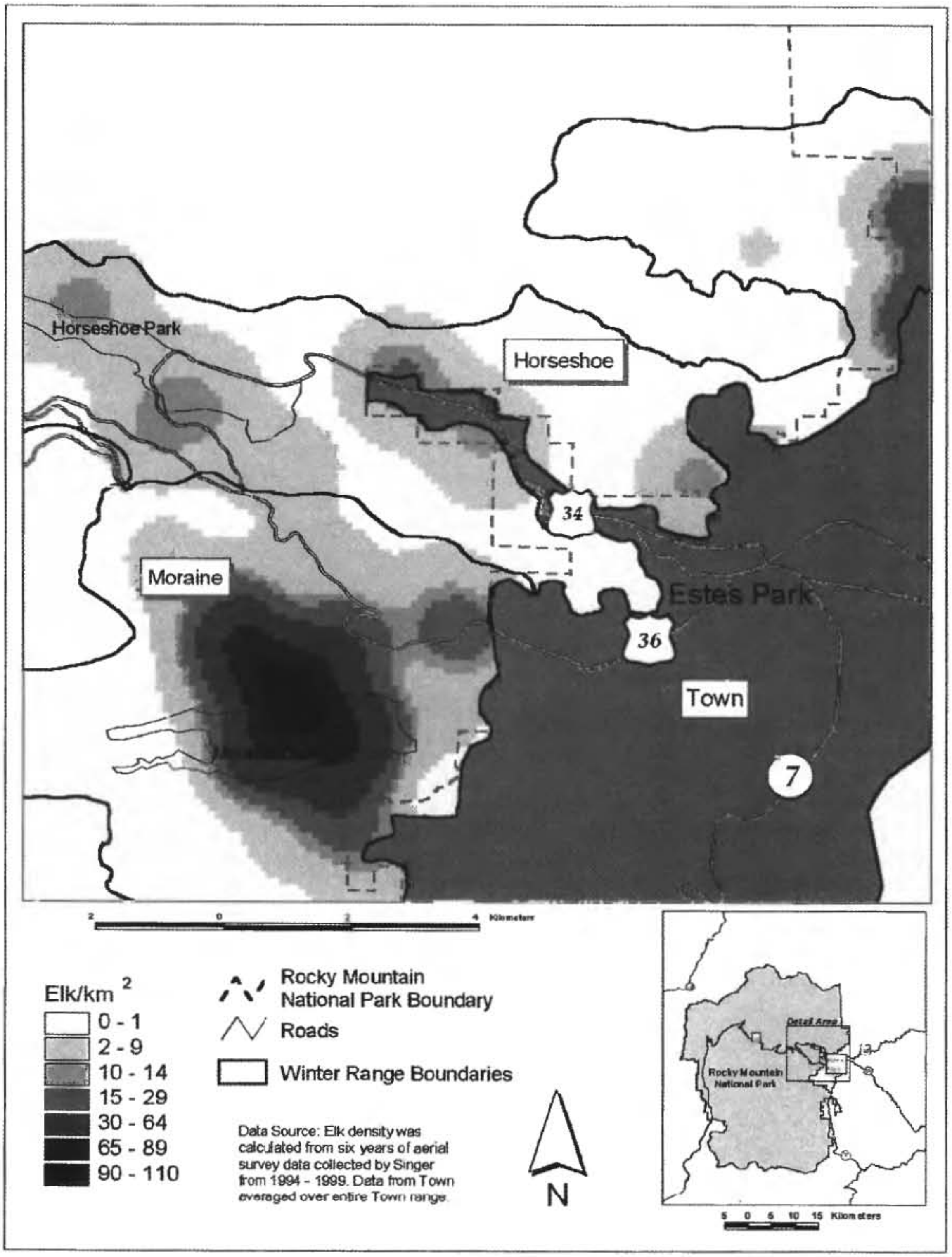
Population-based estimate for potential food-limited *K* for elk in the town sector was estimated at about 2,869 ± 415 elk, or well above the current (2001) average numbers of about 1,975 ± 150 elk estimated in the town sector. This sector of the population has recently grown as rapidly as 11.0% per year, and is most recently growing at 5.2% per year (1991–2001). Under average precipitation, the forage-based estimate of food-limited *K* for elk in the town sector ranged from 3,082 ± 103 to 3,391 ± 113 elk if consumption rates were 50–55%. This level of consumption was close to the average level measured in upland and willow areas in the park where elk exist at food-limited *K*. However, due to lowered plant production in dry years, forage-based estimate of food-limited *K* for elk in town dropped to 2,330 ± 78 to 2,563 ± 85 during a dry year. Population-based estimate of food-limited *K* for the entire elk population (both town and park) was estimated at 3,938 ± 419 elk (2,869 ± 415 in town, 1,069 ± 55 in the park).

Elk densities were variable in the park and were observed to be high (30–65 elk/km^2) to very high (66–110 elk/km^2) on about 7% of the park's winter range. The high elk concentration areas were almost exclusively in Moraine Park (Fig. 4). Elk densities were much lower, <10 elk/km^2, on the remaining 82% of the park primary winter range. Average elk density in the entire town sector was higher than overall density in the park sector (Fig. 4). Density of elk in town averaged approximately 28.5 elk/km^2. This is, no doubt, due to the larger total

Table 1. Comparison of three different estimates (x ± s.e.) of potential food-limited *K* and current population estimates for elk in Rocky Mountain National Park (park sector) and the adjacent town of Estes Park (town sector), Colorado.

	Elk population sector	
	Park	Town
Food-limited K: the potential to support elk Population-based, from growth trajectories park 1965–1999, town 1988–1999	1,069 ± 55	2,869 ± 415
Forage biomass or nutrition-based (1997–2000)	1,154 ± 163	3,082 ± 103
Population estimates (2001)	1,074 ± 39[a]	1,975 ± 150[b]

[a] Based on aerial sightability (1995–2001).
[b] Based on ground mark-resight (1995–2001).



Data Source: Elk density was calculated from six years of aerial survey data collected by Singer from 1994 - 1999. Data from Town averaged over entire Town range.

Fig. 4. Elk densities (elk/km^2) on winter range in Rocky Mountain National Park, Colorado, 1994–1999.

amount of grassland types in town (28.4 km^2) compared to total grasslands in the park sector (15.0 km^2). In addition, the town sector is about 100 m lower in elevation and has less snow in winter than the park sector. Biomass production and N yield on some irrigated and fertilized grasslands in the town sector also provide an unnaturally higher concentration of forage on those sites (Fig. 5).

The human improvements to the managed golf course and pasturelands (fertilization, irrigation) resulted in increased nitrogen yield in forages on those sites and nearly compensated for the complete loss of 0.47 km^2 of elk winter range to the Estes Lake impoundment and 1.05 km^2 to buildings and pavement. At 50% consumption rates, we estimated that 3,251 $\pm$ 109 elk could have been supported under average precipitation conditions in the town sector under pristine conditions, and that 3,082 $\pm$ 103, or about 5% fewer, elk can potentially be supported under these current human-altered conditions in the town sector. Under lower forage production during dry years, we estimated that 2,330 $\pm$ 77 elk could be supported under current modified conditions, and 2,424 $\pm$ 81 elk under pristine conditions.

Correlation of Elk Density to Willow Growth

Graminoids were the most important diet component (71%) during winter and spring, when elk made significant use of the park's winter range. All trees and shrubs combined comprised 22% of fall-winter-spring diets on the winter range. Willows (*Salix* spp.) comprised 11.7% of the elk diets during all three seasons when elk spent some time on the winter range (Appendix D).

Average winter elk density, 1994–1999, was negatively, but weakly, correlated to willow size, density, and production measures ($P < 0.10$; Table 2). For the 12 willow sites sampled during all 3 years, and where depth to the water table was also included as a covariate with elk density, there was also a significant negative correlation between elk density and willow size, stem density, and production measures, but not to total shrub density ($P = 0.87$). AIC$_c$ values indicated the best model included both elk density and depth to water (Table 2; Fig. 6). We found elk density to be positively correlated with higher water tables on some of our study sites (those in Moraine Park; $R = 0.44$, $P = 0.01$). Moraine Park was also the location where a negative relationship between water table levels and willow production and height was found. This indicates that any positive effects of higher water tables on willow production may be offset by the suppressing effects of high elk density on willow growth. In Horseshoe Park, where elk densities were lower overall, the water table level was positively correlated (though not significantly) with willow production and height, as well as herbaceous production. We concluded from these models that elk density had a much greater influence on willow growth in this study area than did depth to the water table. We also noted there were higher, although not significant, average elk densities in the short willow (30 $\pm$ 6 elk/km^2) versus the tall willow type (24 $\pm$ 10 elk/km^2; $P = 0.68$).

Elk consumption rates of willow were positively correlated with elk density ($P = 0.003$; $r^2 = 0.495$). The best fit (r^2 values) for the relation of elk consumption rates of CAG of willows to willow sizes and growth was slightly greater using a second order model that included the independent variable of consumption, consumption^2, and depth to the water table (Table 2). The lowest AIC$_c$ values, however, suggested the best model included a second order model with consumption only and not depth to the water table (although the AIC$_c$ differences between the two models were small and biologically insignificant--only two AIC$_c$ points--indicating water was potentially important). This curvilinear relationship to rates of consumption strongly suggested grazing optimization and a peak in willow growth at moderate levels of elk consumption ($\bar{x} = 21 \pm 0.4\%$ annual consumption of willow CAG), but a subsequent negative influence on willow growth at higher rates of consumption ($\geq 37\%$ consumption; Fig. 7). The smoothed relationship identified the approximate elk density of $\geq 32 \pm 1$ elk/km^2 and elk consumption rate of $\geq 37 \pm 3\%$ removal of willow as the threshold levels where our criteria of a 40% decline in most components of willow growth from maximum growth levels occurred (Figs. 6 and 7).

Shrub CAG, willow canopy volume and area, and annual shoot growth of willows were all best explained (i.e., the lowest AIC$_c$ values) by the second order model of elk consumption rates, while average willow height, maximum height, and stem and shrub densities were best explained by models that included both elk density and depth to the water table (Table 2).

Effects of Elk on Plant Species Diversity

Elk herbivory did not have a consistent effect on plant species diversity across vegetation types. However, species richness was greater in ungrazed plots in short willow sites in 1995 than grazed plots in the same year, but this difference was not quite significant ($P = 0.15$;

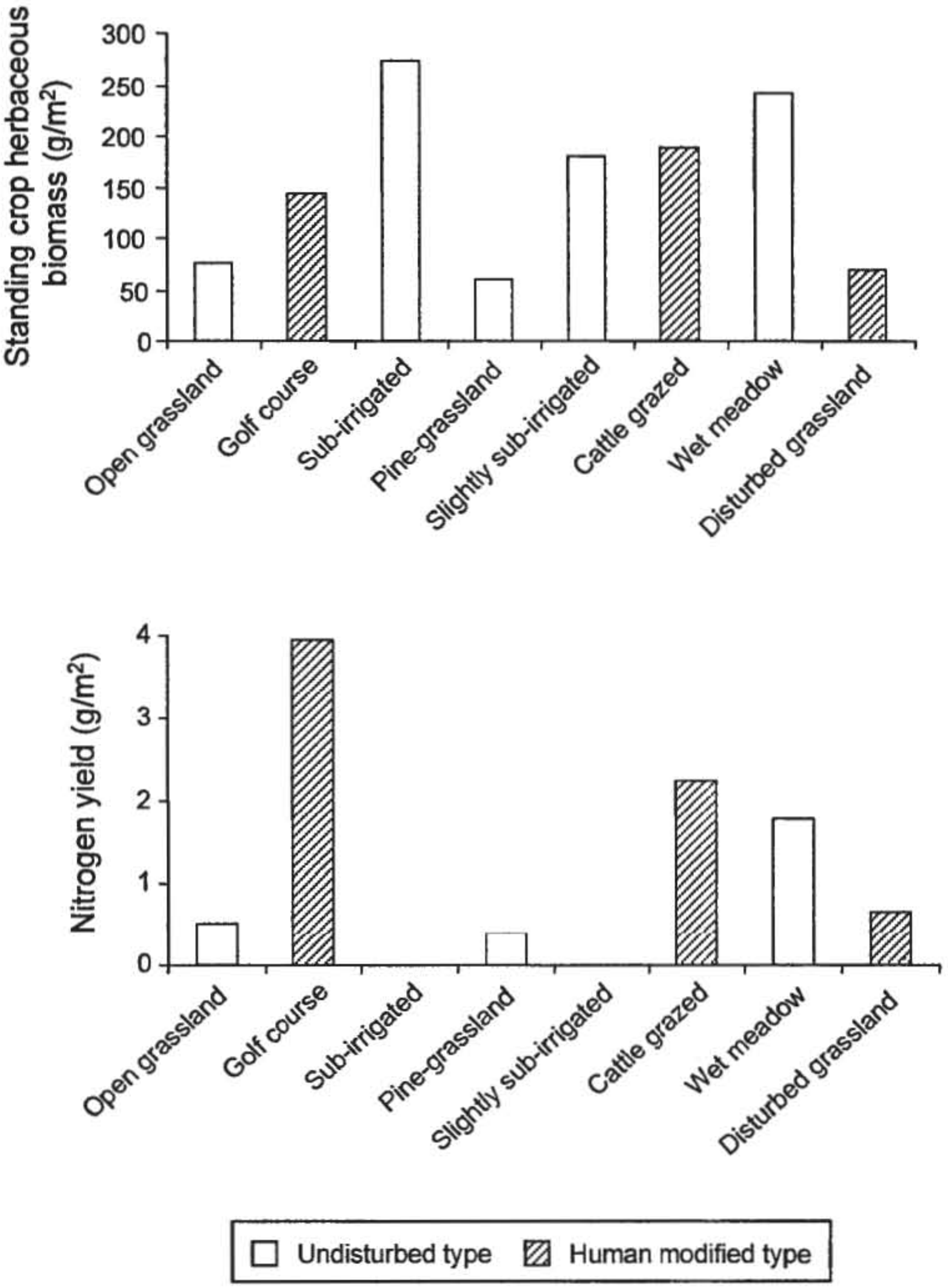


Fig. 5. Production and N yield (g/m^2) of herbaceous forage of select common human disturbed and undisturbed vegetation types in the town of Estes Park, and inside Rocky Mountain National Park, Colorado. Some values for N were not available.

Table 2. Model of independent elk density and consumption variables on willow size, density, and growth (dependent) variables in Rocky Mountain National Park, 1994–1998.

Dependent variables	Elk density, 1994–1999 vs. landscape sites sampled in 1996 (n = 31)	Elk density alone 1994–1999 (n = 35)	Elk density and depth to the water table (n = 35)	Elk consumption, consumption^2 (n = 35)	Elk consumption, consumption^2, and depth to the water table (n = 35)
Total current annual growth (CAG)					
r^2 =	0.111	0.409	0.46	0.466	0.467
F =	3.62	7.14	6.34	13.98	9.08
P =	0.07	0.0009	0.0008	0.0001	0.0002
AIC_c =	1.95	1.30	1.26	1.27	1.35
d.f. =	30	34	34	34	34
Average willow height					
r^2 =	0.0005	0.495	0.548	2.656	0.274
F =	0.02	10.12	9.08	5.79	3.98
P =	0.90	0.0001	0.0001	0.007	0.018
AICc =	9.86	7.13	7.09	7.57	7.67
d.f. =	30	34	34	34	34
Maximum willow height in plot					
r^2 =	0.007	0.511	0.604	0.25	0.257
F =	0.21	10.79	11.44	5.37	3.57
P =	0.65	0.0001	0.001	0.010	0.025
AIC_c =	10.63	8.40	8.25	8.89	8.96
d.f. =	30	34	34	34	34
Willow stem density/plot					
r^2 =	0.277	0.266	0.376	0.25	0.26
F =	11.13	3.74	4.53	5.35	3.64
P =	0.002	0.021	0.006	0.010	0.023
AIC_c =	0.58	0.21	0.12	0.29	0.37
d.f. =	30	34	34	34	34

Table 2. Concluded.

Dependent variables	Elk density, 1994–1999 vs. landscape sites sampled in 1996 (n = 31)	Elk density alone 1994–1999 (n = 35)	Elk density and depth to the water table (n = 35)	Elk consumption, consumption^2 (n = 35)	Elk consumption, consumption^2, and depth to the water table (n = 35)
Willow plant density/plot					
r^2 =	0.101	0.037	0.039	0.009	0.049
F =	3.28	0.40	0.30	0.14	0.54
P =	0.081	0.753	0.87	0.87	0.66
AIC_c =	0.94	0.54	0.61	0.62	0.67
d.f. =	30	34	34	34	34
Twig production					
r^2 =	0.11	0.406	0.455	0.467	0.468
F =	3.67	7.08	6.27	14.01	9.10
P =	0.06	0.0009	0.0009	0.0001	0.002
AIC_c =	1.94	1.30	1.26	1.27	1.34
d.f. =	30	34	34	34	34
Willow canopy volume/plot					
r^2 =	0.083	0.427	0.483	0.51	0.51
F =	2.62	7.71	7.00	16.69	10.79
P =	0.117	0.0005	0.0004	0.37	0.0001
AIC_c =	2.01	1.70	1.67	1.61	1.69
d.f. =	30	34	34	34	34
Willow canopy area/plot					
r^2 =	0.07	0.304	0.337	0.386	0.387
F =	2.23	4.51	4.54	10.06	6.51
P =	0.146	0.010	0.0004	0.0004	0.002
AIC_c =	1.17	1.12	1.07	1.06	1.14
d.f. =	30	34	34	34	34

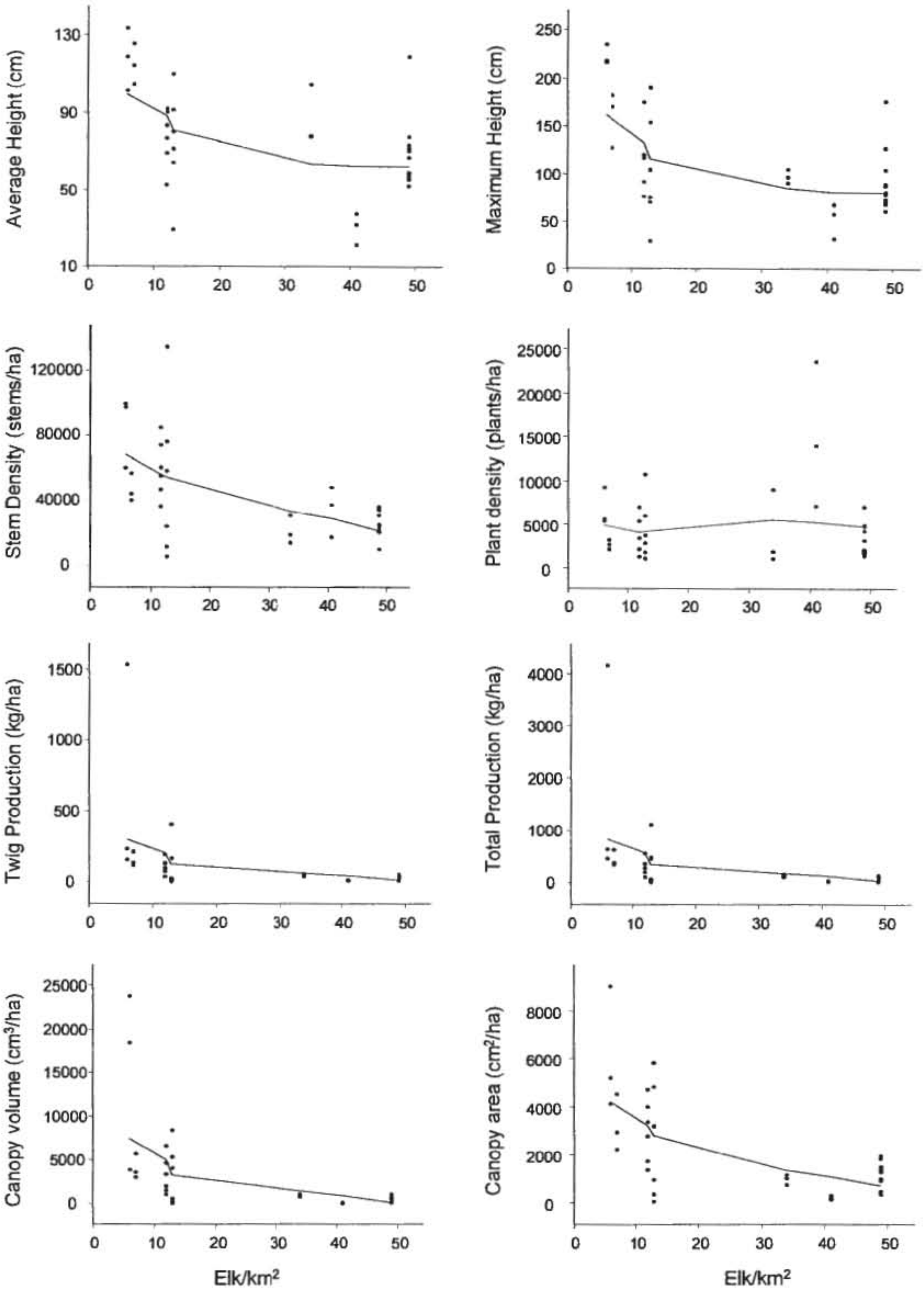


Fig. 6. Elk density (elk/km^2) compared to eight willow growth parameters for Rocky Mountain National Park, Colorado 1995, 1996, and 1998.

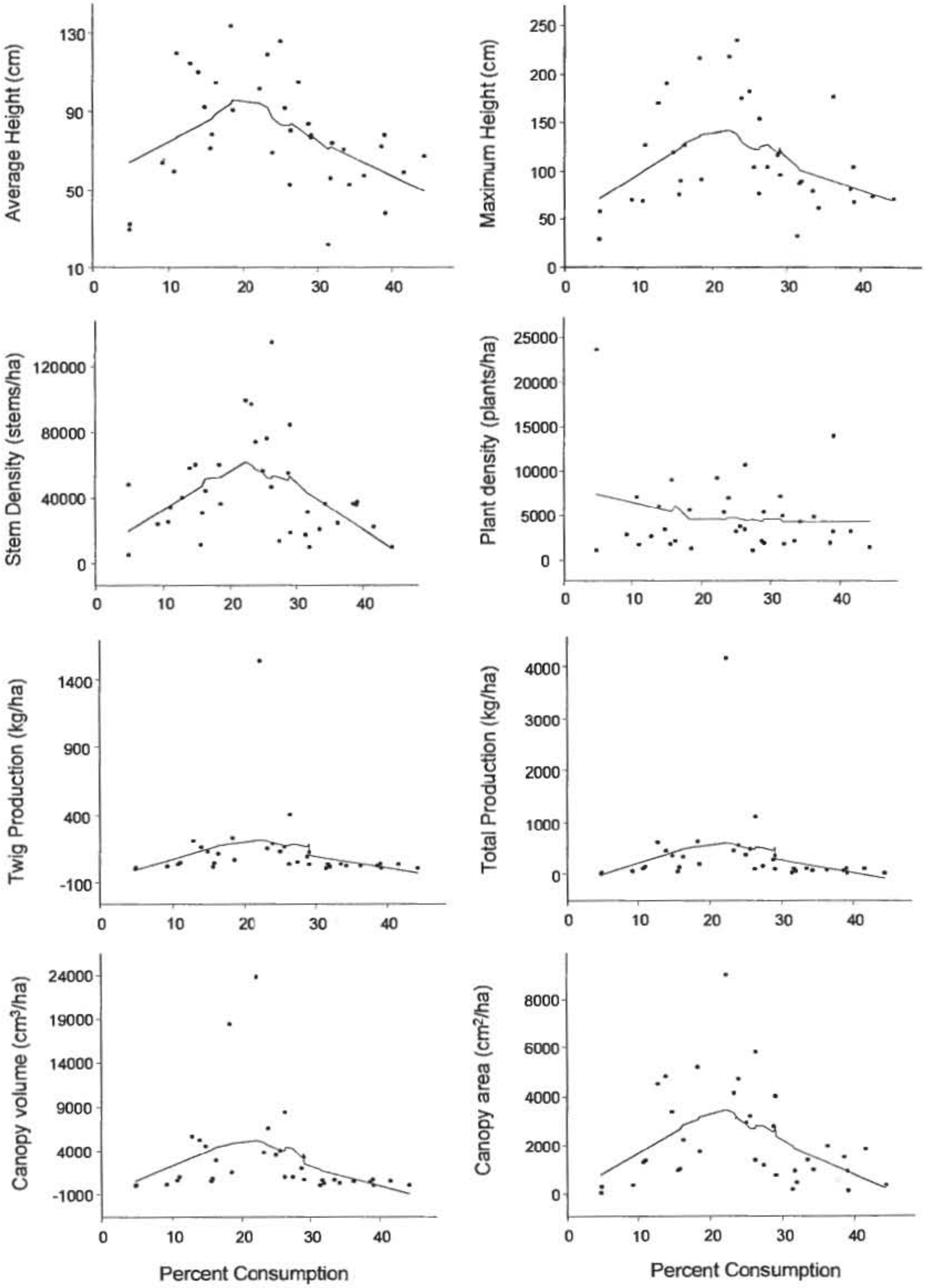


Fig. 7. Elk consumption rate (% offtake) compared to eight willow growth parameters for Rocky Mountain National Park, Colorado 1995, 1996, and 1998.

Table 3). No significant differences in plant diversity indices were evident in upland bitterbrush sites (Table 3). No differences in productivity of native or exotic species were observed between grazed willow and upland sites and sites that were ungrazed for 4 years ($P > 0.20$).

Any Evidence for Potential Overgrazing

A number of alterations to plant cover, soil, and plant abundance were observed that might meet the stated criteria for overgrazing. For example, willow production, willow height, and willow catkin production were lower on grazed sites compared to sites ungrazed for 4 years (Fig. 8). These willow responses were even more dramatic following 35 years of exclosure protection. There was more willow canopy area ($P = 0.07$), more willow canopy volume ($P = 0.08$), 265% higher stem density of willows ($P = 0.19$), and 244% taller willow heights ($P = 0.10$) in ungrazed plots. Shrub volume and shrub canopy area were also greater ($P < 0.001$) in ungrazed plots following 35 years of protection for big sagebrush, *A. tridentata*, (300% and 178% higher, respectively). These changes were accompanied by increases in *P. tridentata*, *Chrysothamnus viscidiflorus*, and *Ribes* spp. on the grazed plots (824% more total shrub volume and 665% more shrub canopy cover for these three species pooled). There were also some minor changes in the soil surface due to elk herbivory that would promote erosion. Soil bulk densities were slightly (1.7%) higher on grazed sites, there was 4.6% more bare ground on grazed sites following 4 years of protection ($P = 0.03$), and 6.4% more following 35 years, although this latter difference only approached statistical significance ($P = 0.14$).

A number of other samplings provided little evidence for any of the stated criteria for overgrazing. There were very minor alterations to macronutrients in plants, and no general trend towards depletion of macronutrients as predicted under overgrazing (aboveground N availability is presented in Schoenecker et al., this volume). The only differences noted in macronutrients in 171 plants sampled were increases in calcium and potassium on grazed sites for one willow species (*S. monticola*), but lower phosphorous for some willows on grazed sites (Table 4). There were very few, and almost no consistent, differences in the abundance of herbaceous species following 4 years of protection. Biomass of *Solidago* spp. was more abundant on grazed sites, while *Mertensia ciliata* was less abundant. Two species were altered more dramatically following 4 years of protection. Live cover of *Artemisia ludoviciana* was 62% less, cover of *Eriogonum umbellatum* was 50% less, and cover of accumulated herbaceous litter was 56% less on grazed sites. We found no differences in biomass of fine (mostly herbaceous) roots or N concentration in roots following 4 years of protection. But there was 850% greater biomass of coarse roots (still mostly herbaceous roots) in grazed upland sites compared to sites protected for 4 years ($P = 0.02$), and there was 364% more biomass of coarse roots in grazed willow sites compared to sites protected for 35 years ($P = 0.03$). After 35 years of treatment in willow type, we found differences in fine root biomass ($P < 0.001$), fine root N concentration ($P = 0.003$) and N yield ($P = 0.10$), but not in upland grass/shrub communities.

Elk Consumption Rates

Consumption of willow species averaged 27 ± 2% in winter (Table 5). Willow consumption was greater in short willow (34 ± 4%) than tall willow sites (26 ± 3%, $P = 0.04$) and in Moraine Park (31 ± 3%) than Horseshoe Park (22 ± 2%, $P = 0.01$). Shrub consumption in willow communities was lower in summer, when it averaged 6 ± 0.4% (Table 5).

Leader use (percent of all leaders browsed) of upland shrubs averaged 39 ± 5% and was lower than in willow sites ($P \leq 0.08$). Percent annual consumption of the CAG of upland shrubs was consistent between years ($P \geq 0.17$), averaging 12 ± 2% (range 8%–16%). Percent consumption of upland shrub CAG in summer was minimal, <1%.

Percent consumption of herbaceous vegetation during winter was higher (53 ± 9%) in bitterbrush sites than in willow sites (28 ± 1%). Percent consumption of herbaceous biomass during summer averaged 6 ± 0.6% in bitterbrush sites and 28 ± 9% in willows. Average annual herbaceous consumption was 60% for upland bitterbrush communities and 55% for willow communities over the 4-year study period.

Overall percent consumption of herbaceous biomass in town in winter was 30 ± 8% and did not differ ($P = 0.91$) between vegetation/habitat types. Summer herbaceous consumption averaged 29 ± 7% and did not differ greatly between types with the exception that consumption was lower ($P = 0.06$) in pine-grasslands. Total annual herbaceous consumption on the study plots in town averaged 57%.

Table 3. Annual values for diversity indices of sampled vegetation type on elk winter range of Rocky Mountain National Park, Colorado.

		Diversity (H)				Richness (R)			
		Grazed		Ungrazed		Grazed		Ungrazed	
Vegetation type	Year	Mean	95% c.i	Mean	95% c.i.	Mean	95% c.i.	Mean	95% c.i.
Short willow	1994	1.33	0.93–1.74	1.49	1.07–1.92	3.59	2.50–4.68	3.70	1.78–5.62
	1995	1.38	0.42–2.35	1.66	1.14–2.19	1.08	1.07–7.10	5.87	4.15–7.60
	1996	1.32	0.61–2.03	1.41	0.63–2.20	5.50	3.45–7.55	6.33	4.08–8.58
	1998	1.31	0.45–2.17	1.48	0.89–2.06	8.12	3.04–13.21	8.88	6.50–11.25
Tall willow	1994	1.02	0.45–1.59	0.83	0.06–1.61	2.91	0.44–5.38	2.30	0.13–4.47
	1995	0.92	-0.02–1.87	1.15	0.22–2.07	4.33	0.79–7.88	4.79	0.60–8.99
	1996	1.26	0.48–2.04	1.25	0.36–2.15	4.75	2.24–7.26	5.33	0.83–9.83
	1998	1.17	0.69–1.64	1.00	0.12–1.88	6.50	1.86–11.14	6.25	0.72–11.78
Upland bitterbrush	1994	1.39	0.89–1.88	1.24	0.75–1.72	3.36	2.39–4.33	2.95	1.72–4.18
	1995	1.64	0.51–2.78	1.71	1.03–2.40	4.17	1.81–6.52	3.17	1.76–4.57
	1996	1.48	0.81–2.16	1.46	1.05–1.87	5.17	3.58–6.76	4.25	3.07–5.43
	1997	1.57	1.05–2.08	1.59	1.28–1.90	5.21	4.48–5.94	5.08	3.99–6.18

c.i. = confidence interval.

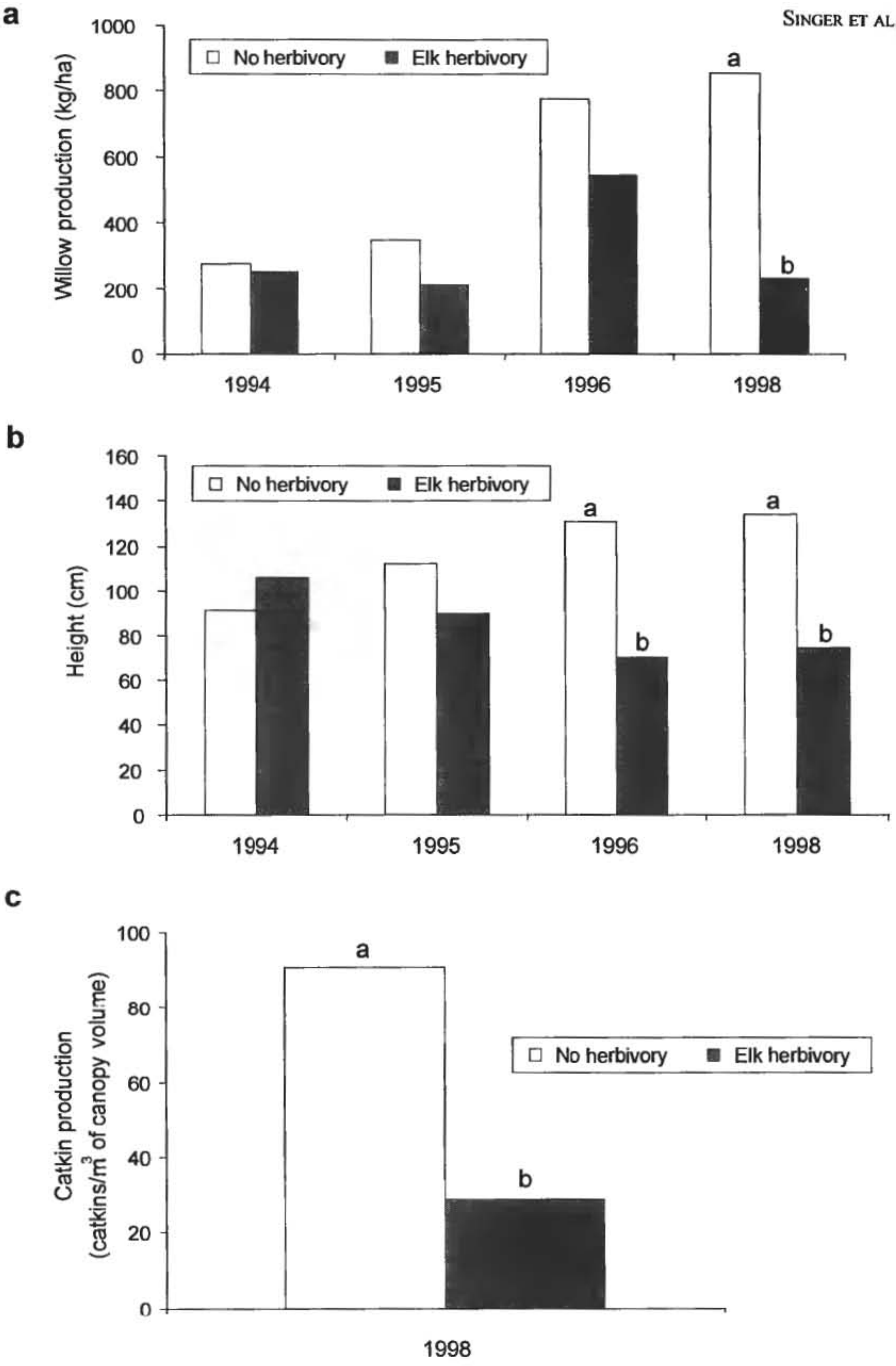


Fig. 8. Willow production (a); heights (b); and catkin production (c) for elk grazed vs. ungrazed sites (different letters denote significant difference, $P < 0.02$) on the elk winter range of Rocky Mountain National Park, Colorado.

Table 4. Nutrient content of willows and herbs under different herbivory treatments on willow sites on elk winter range of Rocky Mountain National Park, Colorado, 1998.

	Graminoids		Forbs		*Salix geyeriana*		*Salix monticola*		*Salix planifolia*	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Nitrogen (%)	1.74	2.00	2.48	2.51	1.14	1.08	1.18[a]	1.08	1.25	1.10
Dry matter digestibility (%)	54.72	57.16[a]	75.00	74.81	37.20	36.06	36.26	35.0	34.60	32.40[a]
Calcium (mg/L)					0.61	0.65	0.71	0.81[a]	0.62	0.65
Potassium (mg/L)					0.23	0.25	0.22	0.27[a]	0.28	0.30
Phosphorus (mg/L)					0.13	0.13	0.13	0.12	0.14[a]	0.13

[a] $P \leq 0.10$.

Table 5. Percent current annual growth of shrubs consumed by elk in willow communities in Rocky Mountain National Park, Colorado.

	1994[a]		1995		1996		1997		1998	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
Willow										
% of total leaders which have been browsed (A)	62.91	N/A	64.45	25.44	57.48	32.51			48.60	23.48
Average % of leader removed from browsed shoots (B)	58.43	N/A	32.13	35.56	46.52	19.33			32.98	28.25
% current annual growth removed (A*B)	37.14	N/A	21.61	5.76	28.08	6.91			17.09	6.93
Upland bitterbrush										
% of total leaders which have been browsed (A)			39.0	2.76	29.3	1.0	47.6	<1.0	33.2	
Average % of leader removed from browsed shoots (B)			25.8	N/A	28.6	28.6	33.8	9.5	31.4	
% current annual growth removed (A*B)			10.1	N/A	8.4	<1.0	16.1	<1.0	11.4	

[a] Winter values may be higher than other years due to variation in sampling methods.

Effects of Elk on Ecosystem Sustainability

Concentrations of N in live plant tissues were not greatly altered by elk herbivory. We found increased N concentrations in only 4 of 13 grazed plants (*A. tridentata*, $P = 0.10$; *Bouteloua gracilis*, $P = 0.01$; *Heracleum sphondylium*, $P = 0.09$; *Koeleria macrantha*, $P = 0.01$). N yield (N produced/m^2/year) was reduced in willow 64% following 4 years of protection ($P = 0.05$). N inputs from litterfall were also reduced from 0.57 g/m^2/year to 0.24 g/m^2/year ($P < 0.05$), although elk fecal and urinary inputs compensated for some of these losses in N inputs.

N mineralization rates were lower in grazed versus ungrazed plots of short willow sites after 4 years of protection (0.39 grazed versus 1.83 ungrazed, $P = 0.07$, $n = 4$ sites, versus 3.25 grazed and 2.11 ungrazed, $P > 0.10$, $n = 4$, in tall willow sites; Schoenecker et al., this volume). Nitrate pools were also lower in grazed than ungrazed plots of short willow sites (0.31 grazed versus 1.44 ungrazed, $P = 0.10$), but no differences for these N variables were detected in tall willows (Schoenecker et al., this volume).

From the same study plots, Schoenecker et al. (this volume) calculated that annual N inputs to the soil surface on grazed sites were only 60% (5.79g N/m^2/year) from a combination of herbaceous biomass left after grazing + shrub leaf litterfall + elk urine and feces compared to ungrazed sites (9.66g N/m^2/year; herbaceous biomass + litterfall). Similarly, annual N inputs to the aspen type on grazed sites were only 44% (1.65g N/m^2/year) that of ungrazed sites (3.79g N/m^2/year; Schoenecker et al., this volume).

Discussion

Population-Based Predator Limitation Approach

Our population-based estimates of food-limited *K* for elk in the park were strikingly similar to the nutritionally based, or food-limited, estimates of *K* made by Hobbs et al. (1982) (1,069 ± 55 versus 991 ± 102 dry year or 1,481 ± 261 wet year). The similarity of the approximation of current elk numbers in the park to the theoretical nutrition-based estimate and the observed equilibrium population size support the hypothesis that the park sub-population is currently limited through density-dependent processes by food resources, rather than by any other factors such as predators or weather. The population-based estimate of potential food-limited *K* for winter in town of 2,869 ± 415 elk was also similar to the forage-based estimate of food-limited *K* in town of 3,082 ± 103 to 3,391 ± 113 (average precipitation year), suggesting that *K* might be fairly well approximated in the town. However, we caution these estimates may be subject to errors, since elk in the town sector have not yet reached their *K* for winter and we selected an arbitrary value for average herbaceous forage use (50–55%) for our calculations. Thus, these town estimates should by viewed as provisional estimates.

Considerable published information from undisturbed systems with wolves and bears suggests that in pristine times, when natural densities of predators existed, elk in the RMNP system would likely have been limited below food-limited *K* most of the time by the large capable predators present at that time--grizzly bears, black bears, wolves, mountain lions (*Felis concolor*), and coyotes (Gasaway et al. 1992; Boyce 1993; Messier 1994). We concluded from the modeling of the northern Yellowstone elk population that limitation of the elk, on the order of about 15% fewer elk, has occurred since wolf restoration to the area, especially since 1997 (Singer et al. 2002). The northern Yellowstone elk population is similar in historic conditions to what the RMNP ecosystem must have represented. Elk are the dominant ungulate in both ecosystems, and their major predators were the same in both systems--gray wolves, grizzly bears, black bears, and coyotes. There is little additional empirical basis upon which to predict if the ultimate level of limitation of the northern Yellowstone elk population will be higher, or how consistent the limitation will be through the years, although computer models have predicted 25% or even higher levels of limitation of elk (Boyce 1993), particularly if harvests of antlerless elk by humans north of the park are not reduced (Singer and Mack 1999). Predators can act to hold ungulates at low densities for long periods (Gasaway et al. 1992; Messier 1995), especially in concert with periodic severe winters (McLaren and Peterson 1994; Mech et al. 1998). Wolf predation may act to increase the decline phase of ungulates following a peak density (since ungulates in poor condition are more vulnerable). But long-term stability under predator limitation should not always be expected by park managers. For example, predator-ungulate systems may shift between multiple equilibria (Messier 1994) due to predator-sensitive limitation and periodic weather fluctuations (McLaren and Peterson 1994; Mech et al. 1998).

We concluded that rich forage resources in human-disturbed grass types in the Estes Valley presently compensate for the negative effects of humans on habitat and forage losses due to developments. Preliminary estimates suggest that the town sector supports only about 169 (5%) fewer elk due to these human modifications, after subtracting all the losses (the area of Estes Lake impoundment and urban areas) and adding the increases (golf courses, irrigated grasslands) to the forage biomass for elk. Nitrogen concentrations, biomass production, and N yield were higher in these human-modified grass types in town (golf courses, irrigated pastures) compared to unmodified native grasslands. Those elk that selectively feed on these human-enriched sites (e.g., elk regularly forage on the golf course) should exhibit increased foraging efficiency, increased daily energy balance, decreased winter weight losses, and improved survival (Robbins 1983; Wickstrom et al. 1984; Iason et al. 1986).

Other factors also contribute to the attractiveness of the town to elk. The developments and human activity undoubtedly contribute to less predator activity. The town is lower in elevation than park winter range and snow depths are lower. There is no sport hunting within the Estes Park town limits whereas there is limited hunting on U.S. Forest Service and private land on the edge of town. The artificially maintained forage resources in town due to annual fertilization and irrigation contribute to unnatural stability in elk numbers, since these human-managed grasslands tend to dampen natural forage fluctuations due to drought and fire. Additionally, elk using the area will be less influenced by severe winters or predators (McLaren and Peterson 1994; Mech et al. 1998; Singer et al. 1998a). Large, stochastic fluctuations in ungulate numbers are a natural process that may permit events, such as episodic recruitment in some plant groups, and these fluctuations will be less in the altered town environment. The increased number of elk in town contribute to higher overall consumption rates on the park winter ranges since town elk migrate slowly through the park winter ranges and consume vegetation during their migrations. Most radiocollared elk that wintered in town spent an additional 64 ± 7 days on park winter range annually during their migration to the park's higher alpine summer range. Elk also demonstrated a high degree of habituation and willingness to graze rich forages in lawns, golf courses, and ornamental shrubs. There are almost no fences in town that obstruct elk. We predict that, in the absence of any human controls, elk populations will continue to increase up to 47% (921 more elk over the 2001 population estimate, assuming a 50–55% use of forage) to food-limited *K* in the town sector, and that these additional elk will further influence the park's winter ranges during their annual migrations to the park's summer range. However, in the long-term, the *K* for elk in town is predicted to eventually decline as human developments continue at a rapid pace in the area.

Effects of Elk on Plant Community and Plant Species Diversity

No indications of any large species shifts or declines in herbaceous plant species diversity due to elk herbivory after 4 years of protection from elk were found. These observations were in agreement with the independent findings of Stohlgren et al. (1999) for the same area. The abundance of only four herbaceous plant species was altered by elk herbivory. But we concluded that high densities of elk contributed to a large decline in willow size, structure, and growth at both the 4-year and 35-year exclosures. High levels of elk herbivory (above a threshold of 37% consumption of willow CAG) suppressed the maximal willow height, densities, volume, and CAG, although there was compelling evidence for grazing optimization at lower levels of about 21% use of willow CAG. These suppressing effects of high elk herbivory on willow growth likely have already resulted in declines in the recruitment and abundance of willow communities and further declines are also likely. Using aerial photos, GIS, and groundtruthing, Peinetti et al. (this volume) found that tall willows declined 22% in Moraine Park and 19% in Horseshoe Park from 1946–1996.

Our data suggested elk had a much larger effect than did depth to the water table on willow growth and abundance, at least under the limited range of depths of water tables and relatively high water tables in our study (average water tables varied from 0–1 m from ground surface at our sample sites and no water table ever fell below 1 m even during July or August). Thus, willows likely root to the water table at all study sites. We studied few of the most watered sites (i.e., we did not study beaver ponds) and also no dry willow sites with deep water tables (e.g., no sites of 2 m or lower were sampled). Also, depth to water table and elk density were positively correlated at some of the study sites, i.e. the highest elk densities were found at some sites that also had very high water tables, and elk effects overwhelmed any potential positive effects of high water at these sites. But we caution against concluding that depth to the water table was of little importance. For example, long-term climate change over the past 90 years to a warmer and drier climate may have contributed to a willow decline (although more recent conditions since 1995 have been wet and cool, Singer et al. [1998b]; Stohlgren et al. [1998]). It is not known, however, if this minor climate trend could have influenced depth to water tables. Greater precipitation and higher winter snow packs resulted in higher early growing season stream flows and higher measured water tables on the study sites (Zeigenfuss et al., this volume). Beaver declined 80%–90% on the elk winter range in the park from the 1940s through the mid-1990s (Zeigenfuss et al., this volume). As a result, stream channels are currently straighter and less complex in the lower reaches of the park's streams. There are presently fewer side channels, fewer oxbows, and fewer braided channels than was the case in 1946 aerial photos. Willow cover decreased ~20% over this same time period (Peinetti et al., this volume). Thus, this large beaver decline dewatered many areas, likely increased depth to water table at many sites, and likely contributed to the willow declines. The sites of greatest alteration and simplification of the stream channels (apparently due to the decline in beaver and the effects of their dams) corresponded tightly with the locales where willows also declined the most (Peinetti et al., this volume). We suggest the return of beaver to the entire winter range would improve growth conditions for willows and would assist willows in sustaining elk herbivory.

The Sustainability Approach Applied to Rocky Mountain National Park

Elk herbivory dramatically reduced sizes of four shrub species (3 willows and 1 upland shrub), and there was a 22% decrease in herbaceous production in willow communities. However, there was no measurable effect of elk herbivory on herbaceous production in any other vegetation community. Thus, we concluded the current level of elk herbivory was sustainable for 3 shrubs, but not a fourth shrub species, and most herbaceous vegetation in two vegetation types, but not sustainable for the willows and the herbaceous production in the willow type.

A key criterion to apply the sustainability approach is whether or not soil fertility, especially N and C abundances, are sustained under the level of ungulate grazing and actions of ungulates. We concluded that N and C abundances were apparently being maintained in the upland grass/shrub type, but that N processes and N pools were being reduced by elk grazing in the willow and aspen types. Annual inputs of N under elk herbivory were only about 60% in the willow type and about 44% in aspen type compared to ungrazed sites, and N mineralization rates were 79% lower in grazed willow sites (Schoenecker et al., this volume). Most authors report an increase in N cycling rates (Risser and Parton 1982) and increased N mineralization (Ruess and McNaughton 1987; Frank and Groffman 1998) with grazing by native ungulates due to the transfer of litter to more usable fecal and urinary inputs. But several other authors have also reported a decline in N mineralization and N availability due to ungulate herbivory (McInnes et al. 1992; Ritchie et al. 1998), attributed in some cases to heavy grazing levels (Seagle et al. 1992; Biondini et al. 1998). Although feedbacks to the elk population may eventually slow or stabilize the declines in soil fertility, we caution managers that at some point, the depletions might result in declines in plant growth and changes in species composition (McInnes et al. 1992; Ritchie et al. 1998).

We found an increase in N concentrations in only one-third of the plant species we sampled. A number of studies documented higher N concentrations in grazed plants, especially grasses, apparently due to higher N uptake rate by roots of grazed plants, and greater availability of N to plants due to higher net N mineralization on grazed sites (Coughenour et al. 1990; Holland and Detling 1990; Singer and Harter 1996; Frank and Groffman 1998).

Nitrate (NO_3^-) pools were 78% lower in grazed short willow sites in RMNP (Schoenecker et al., this volume). Variable results have been reported for effects of native ungulate grazing on N and C pools. Some authors reported no overall effect of ungulates on soil N and C pools (Frank and Groffman 1998; Ritchie et al. 1998), or even a decrease in these pools (McInnes et al. 1992; Pastor et al. 1993).

Convincing evidence for browsing optimization in willows at moderate consumption rates was found (higher willow production occurred at 21% consumption of CAG than with no consumption). Danell et al. (1985) and Oldemeyer (1981) also reported browsing optimization at moderate consumption rates for birches (*Betula* spp.). But we found no evidence for grazing optimization in herbaceous plants, in agreement with Biondini et al. (1998) and Mazancourt et al. (1998) who found no optimization, although others found evidence for herbaceous grazing optimization by ungulates in Africa (McNaughton 1979, 1983, 1993) and in the western U.S. (Frank and McNaughton 1993).

Aboveground production might be (temporarily) maintained at the expense of belowground biomass (Belsky 1986; Verkaar 1992), and thus any assessment of grazing sustainability should include root responses (Verkaar 1992). We concluded that grazing generally resulted in no reduction of root biomass. The majority of studies report a decline in root biomass due to ungulate herbivory (Detling 1988; Coughenour et al. 1990; Holland and Detling 1990), but in support of our findings, a recent study of 11 locations in the Serengeti, Africa (McNaughton et al. 1998) found no evidence for decreases in root biomass even under intense herbivory by large numbers of wild ungulates, nor did Coughenour (1991) or Merrill et al. (1993) find any effect of ungulates on herbaceous root biomass in YNP.

Evidence for Overgrazing

A key criterion of the overgrazing approach is that excess grazing leads to more bare ground and accelerated sediment yields and erosion (Pengelly 1963; Westoby et al. 1989; Fuls 1992). Elk grazing in RMNP slightly increased upper soil bulk densities (1.7%) and slightly increased the percent of bare ground (4.6%). Accelerated sediment yield is a product of not only bulk density and bare ground, but also percent plant cover, infiltration rates, and slope. For the steep slopes of an elk winter range along the Gallatin River, Montana, Packer (1963) recommended that soil surface bulk densities be below 1.04 g/cm^3 and percent bare ground be less than 30% to protect soil surfaces from accelerated erosion. If Packer's (1963) data can be generalized, sediment yield should not be a concern on most of the RMNP winter range since the area consists of mostly flat sites and very gentle slopes. But the percent bare ground on wet meadow and upland grass/shrub ($\bar{x} = 28\%$ wet meadows, $\bar{x} = 38\%$ upland grass) approached or exceeded Packer's (1963) thresholds of concern as did observed bulk densities on grazed sites in three vegetation types (0.81 g/cm^3 in meadow, 0.92 g/cm^3 in aspen, 1.10 g/cm^3 in upland grass/shrub). These values suggest there might be some concern for accelerated erosion on steeper slopes on the winter range in the upland grass/shrub type, but specific research into measures of sediment yield would be required.

Another stated criterion of overgrazing is that shifts in plant species composition will occur, and in particular, less palatable forage species will increase (Pengelly 1963; Westoby et al. 1989; Fuls 1992). We observed little evidence for any significant increase in less palatable plant species due to elk herbivory in the willow or upland types. Stohlgren et al. (1999) also found no consistent effect of elk herbivory on plant diversity at the landscape scale in these same types. Several less palatable species (*Phleum pratense*, *Carex* spp., *Selaginella densa*) increased during 25 years on open range plots (grazed sites only with no controls) in the upland grass and meadow types on the winter range (Zeigenfuss et al. 1999). We interpret the increases in herbaceous root biomass in the grazed willow and upland type as an underground response to the declines in shrubs (*Salix* spp. and *Artemisia tridentata*) due to grazing. We did not excavate or sample shrub root systems, but we suspect these declined on the grazed sites.

The Allowable Use Approach Applied to National Parks

No magic golden rule exists in the literature for allowable use that could be unambiguously applied to a number of national parks. In contrast to any general rules, the published literature we reviewed suggests plant response to ungulate herbivory varied greatly between different ecoareas (Coughenour 1985; Milchunas et al. 1988; see review in Fig. 2). Our review indicated that, in general, plants growing in sites with higher N and water availability seemingly tolerated higher rates of herbivory (Hamilton et al. 1998; Mazancourt et al. 1998) and plants with a larger proportion of their biomass in roots, such as occurs in the shortgrass prairie and some other grasslands, also tolerated herbivory better. The timing of the herbivory also influenced plant responses (Mueggler 1975; Frank and McNaughton 1992) with fewer effects predicted from winter herbivory than from herbivory during the growing season. Herbivory during winter only is better sustained since the plants are in senescence, the ground is frozen, and the plants' reserves are shunted to the root systems and the ground is frozen and/or protected by snow cover to some extent from hoof action of ungulates (Frank and McNaughton 1992; Singer and Harter 1996; Singer et al. 1998b).

Consumption rates in those grassland types most similar to RMNP (e.g., mountain bunchgrass, mixed grass prairie; Fig. 2) that evolved with at least moderate herds of grazing ungulates (40–45%) appeared to be sustainable in most instances, but consumption rates of 60–80% were not. Exceptions were the more grazing resilient short grass prairie and the Serengeti grasslands, where higher consumption rates of 60–65% by ungulates were apparently sustainable. The RMNP grasslands will not be quite as resilient as the short grass prairie or the Serengeti grasslands, since both of those areas adapted to, and evolved with, grazing by large herds of ungulates (e.g., Serengeti: African buffalo, wildebeest, zebra; short-grass prairie: American bison). The current high consumption rate of 60% (averaged over 4 years) in upland grass/bitterbrush type, in the RMNP case example might be a concern to management based on the published literature. These high consumption rates have probably been limited to the previous 8–12 years. We suspect that, if maintained, these high consumptions could possibly result in future vegetation changes in the park, especially if elk in the town sector are allowed to further increase to their estimated potential and if consumption rates of plants in the park increase due to more town elk migrating through the park's winter range.

Our review indicated that, in general, productive, seral shrub communities (i.e., willow, aspen, birch, mountain maple) could typically sustain consumption rates of 42–50%, but consumption rates of 65–85% are not sustainable (Fig. 2). These published findings, many that are based on artificial clipping studies, predict the range of willow consumption rates we observed in RMNP should have no negative influences on willows (Aldous 1952; Krefting et al. 1966; Wolff and Zasada 1979; Wolfe et al. 1983; Bergström and Danell 1987). Yet, we observed substantial reductions in willow heights, volumes, and production at 37% consumption rates by elk. This discrepancy is apparently due to the fact that much of the information on shrubs is based on clipping studies to simulate herbivory. These studies assume artificial clipping mimics ungulate herbivory, but we conclude it does not. The effects of ungulate herbivory on willows in this study were roughly two-and-a-half times greater than equivalent CAG removal by clipping (Zeigenfuss et al., this volume). The physical damage from elk (rough breakage, stripping of bark) has a greater effect on willows than the clean, mechanical clipping of shoots. For example, an average of 20% of the adjacent length of a browsed leader died after winter browsing by elk in our study area, but only 2% of the leader died after mechanical clipping (Menezes et al. 2001).

Our review suggests upland shrubs of the Intermountain West generally sustained ungulate consumption rates of 24–28% CAG, while higher studied consumption rates of 55–68% were not sustainable. In the case example of RMNP, we found big sagebrush was more sensitive to removals than suggested by the literature. Although we found no effect on any upland shrubs due to grazing by elk at levels of 12% consumption of CAG following 4 years of protection, we found large size reduction in grazed sagebrush following longer periods (35 years) of grazing compared to ungrazed plants. However, three other upland shrub species actually increased slightly on these same grazed areas compared to ungrazed areas following 35 years of protection.

Conclusions

The Overgrazing Approach

The criteria for overgrazing are the most clearly stated and most simply and readily measured of any of the approaches, and thus we recommend this view be applied as the first choice in clear cut cases where, clearly, there is either overgrazing (i.e., many of the criteria for overgrazing can be documented), or in those cases where there is no evidence of overgrazing (i.e., when none or almost none of the criteria for overgrazing can be documented).

Unfortunately, most cases will fall into an intermediate category of observed criteria for overgrazing, as did the RMNP case example. Here we found the overgrazing approach to be less than adequate. Considerable judgments as to the severity of evidence will be required in these instances. In the RMNP data set, we investigated 20 exclosure comparisons that might constitute evidence of overgrazing, and only four of these comparisons met the criteria for overgrazing (less big sagebrush production, less willow production, less herbaceous production, more bare ground). For a fifth criteria, that of possible accelerated erosion, our measures indicated a concern in only one vegetation type. Does this mix of evidence for RMNP data constitute evidence for overgrazing or not? Another concern over this approach is that it was developed for agricultural systems. But, natural ungulate grazing might result in some increase in bare ground and some effects on plants, and many of their other actions (dusting, rubbing trees and shrubs, hoof action on soil compaction) must be viewed as natural effects. The variables measured for overgrazing criteria (e.g., percent bare ground, sediment yield, percent plant cover, trampling) may represent a very simplistic view of ecosystem dynamics and plant-herbivore relations as Westoby et al. (1989), Coughenour and Singer (1991), and McNaughton (1993) have pointed out.

The Allowable Use Approach

We recommend the application of allowable use criteria to national parks as another highly useful approach to managers, but only in cases where considerable empirical data are available for that area on effects of different levels of use. The principal disadvantages of this approach for widespread use are that, as our literature review suggested, there are few general rules that could be readily applied to a new study area with little background data (see Fig. 2). The response of plants to a specific use level will vary depending on the ecosystem type, the structure and growth form of the plants, and the extent of evolution with ungulate grazing (Fig. 2; McNaughton 1979, 1983; Milchunas et al. 1988). In the case example, of RMNP, a large amount of ecological information gathered by us and other researchers is available to apply the allowable use approach.

The advantage of this approach is that it provides a straightforward, quantitative measure of the direct interaction between herbivores and their plant forages, providing that specific information is available for the park. The approach provides the opportunity to set very specific vegetation goals. For example, should NPS managers decide, based on historical conditions and natural processes, that the current decline in willows in RMNP is a departure from natural conditions, the allowable use information we gathered suggest the current average rate of consumption of willows in the park winter range should be lowered from 27% to less than 21% (an approximate 22% decrease in average use). This would apparently protect most willow patches from overuse. This goal might be achieved by reducing the elk population in the park by roughly 22% to 838 elk, (1,074 elk * 0.78). This reduction is also roughly similar to the reduction (20–30%) suggested by the predator limitation estimates for YNP (Singer et al. 2002). We do caution, however, that this assumes a linear reduction in willow consumption and that elk distributions remain constant, neither of which might hold true. Management decisions still must be made as to the natural conditions and processes that prevailed in the park area and, thus, what effects of a specific use level by ungulates on plants will be acceptable and what effects are excessive.

The Biodiversity and Sustainability Approaches

We concluded that both the diversity and grazing optimization/sustainability approaches would be ambiguous and complex for most park managers to apply to a new assignment to an ecosystem question, although the approaches could be useful in well-studied and well-understood ecosystems. In human-altered systems, it is challenging to determine what influences of ungulates might be natural and acceptable. For example, ungulates in pristine, natural systems may alternatively increase, cause no change, or decrease plant diversity (McNaughton 1979, 1993; Stohlgren et al. 1999) or plant production (McNaughton 1983, 1993; Frank and McNaughton 1993; Biondini et al. 1998). Which response is the most appropriate in the particular natural system under observation? There may be no one single answer. Application of these approaches requires an understanding of the complex ecological relationships of that ecosystem. A sound scientific appreciation for which observed plant changes are due to factors other than ungulates (such as succession, climate change, fire suppression, or beaver declines) needs to be isolated from changes in the system that are due to ungulates alone. Use of these two approaches should not be ruled out by managers to evaluate ungulate effects, but a commitment of many years and much effort will likely be required to understand the ecosystem dynamics sufficiently to apply the views.

These two approaches, however, could be readily applied to a park such as the RMNP case example where there is extensive information on plant species and vegetation community diversity responses to ecosystem processes, such as succession, herbivory, fire, and fluvial processes (Olmstead 1979; Stohlgren et al. 1999; Zeigenfuss et al., this volume). One advantage of applying these approaches is that both are closely aligned to the NPS mandates to manage for diversity and maintain natural ecosystem processes (NPS 2001).

The Population-Based Predator Limitation Approaches

As our first choice for the most useful and most general approach for use by NPS managers, we selected the population-based or forage-based estimates of food-limited *K* applied in concert with actual observations of the extent of predator limitation of ungulates below food-limited *K* in that, or in similar, ecosystems. This approach is the most central and closely aligned to NPS policy, which calls for preservation of natural processes. One of, if not the most important natural process, includes the effects of large, capable predators on ungulates.

The population-based and forage-based estimates of food-limited *K* were also operationally clear, i.e., the methods were specific, quantifiable, and measurable (Table 6). Population-based estimates of *K* compared favorably (only ~7% different) to independent nutritionally-based estimates of *K*, lending credence to the accuracy of both independent estimates. Any possible management intervention would most readily be based on elk population size goals; thus, population-based analyses will be central to those goals. We concluded multiple natural predators in the RMNP ecosystem would have likely limited ungulates below density-dependent or food-limited *K* for elk during most years (Gasaway et al. 1992; Messier 1994; Sinclair and Pech 1996; Orians et al. 1997; Mech et al. 1998). The challenge to applying this approach is that the magnitude and duration of predator-limitation may not always be sufficiently understood and may be difficult to predict for a specific park area (Boutin 1992; Sinclair and Pech 1996; Crete 1998). Also, these approaches may require long-term data sets. For example, the detection of density dependence may require reduction of the ungulate population to less than or equal to one-fourth of *K* prior to any release (Shenk et al. 1998). Detection of density dependence, which is necessary to estimate food-limited *K* from the population growth trajectory, is often detected only after large (≥75%) reductions in animals, subsequent release of the population, and, finally, observation of the population growth trajectory for 12–18 years following release (Coughenour and Singer 1996; Shenk et al. 1998; McCullough 1999; this study in RMNP). This kind of unique information may not be available for many parks, but the information was available for our case study in RMNP.

The evidence for multiple predator limitation of elk in Yellowstone National Park, Wyoming following wolf restoration in 1995 should provide a useful starting number for the likely limitation of elk by multiple predators in a continental Rocky Mountain ecosystem. Computer modeling projected that the limitation of elk by wolves, in concert with other predators, in YNP is currently about 15% less than food- and weather-limited *K*, and additional limitation is possible (Singer et al. 2002). Wolves may also be altering the distributions of elk in Yellowstone National Park and their foraging patterns across the landscape (Ripple and Larsen 2000). Where there is specific information on the effects of predators, this approach requires more straight-forward interpretation of natural conditions.

Literature Cited

Aldous, S. D. 1952. Deer browse clipping in the Lake States region. Journal of Wildlife Management 16:401–409.

Belsky, A. J. 1986. Does herbivory benefit plants? A review of the evidence. American Naturalist 127:870–892.

Bergström, R., and K. Danell. 1987. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. Journal of Ecology 75:533–544.

Berry, J., D. Decker, J. Gordon, R. Heitschmidt, D. Huff, D. Knight, W. Romme, and D. Swift. 1997. Science-based assessment of vegetation management goals of elk winter range--Rocky Mountain National Park. Environment and Natural Resources Policy Institute, Colorado State University, Fort Collins. 16 pp.

Biondini, M., B. D. Patton, and P. E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. Ecological Applications 8:469–479.

Boutin, S. 1992. Predation and moose population dynamics: A critique. Journal of Wildlife Management 56:116–127.

Boyce, M. S. 1989. The Jackson elk herd: Intensive wildlife management in America. Cambridge University Press, United Kingdom.

Boyce, M. S. 1991. Natural regulation or the control of nature? Pages 183–208 *in* R. B. Keiter and M. S. Boyce, editors. The Greater Yellowstone ecosystem: Redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut.

Boyce, M. S. 1993. Predicting the consequences of wolf recovery in Yellowstone National Park. Pages 234–269 *in* R. S. Cook, editor. National Park Service Science Monograph No. 22.

Boyce, M. S. 1998. Ecological-process management and ungulates: Yellowstone's conservation paradigm. Wildlife Society Bulletin 26:391–398.

Boyce, M. S., and E. Merrill. 1996. Predicting effects of 1988 fires on ungulates in Yellowstone National Park. Pages 361–368 *in* F. J. Singer, editor. Effects of grazing by wild ungulates in Yellowstone National Park. Technical Report NPS/NRYELL/NRTR/96-01, NPS, Natural Resource Information Division, Denver, Colo.

Burnham, K. P., and D. R. Anderson. 1992. Data-based selections of an appropriate biological model: The key to modern data analysis. Pages 16–30 *in* D. R.

Table 6. Summary of the consequences for the application of five approaches for evaluating overabundance of ungulates in national parks.

	Approach to Evaluate Ungulate Abundance				
	Population-based	Biodiversity	Grazing optimization/ sustainability	Overgrazing	Allowable use
Operational clarity: Specific, quantifiable, and readily measurable	Moderate to high. Population parameters and *K* are measurable. Pristine conditions may not be known.	Low. Controls and other confounding variables may not be available.	High. ANPP and consumption readily measurable.	High. Only exclosures are needed.	Low, excessive and sustainable levels are rarely tested.
Relative time and costs	High. Large population perturbation or manipulation is necessary. 20–30 years of response may be needed.	Moderate. Sufficient time for grazing responses may require many years.	High. Sampling of nutrients and processes can be intensive and expensive.	Low to moderate. A number of years response may be needed, but measures are rapid and some evaluations will be immediately obvious.	Moderate. 4 years of plant data are required and costs for intensive plot sampling are moderate.
Elk management consequences	(a) Food-limited *K*. None to little management of the ungulate. (b) Simulate predator limitation. High. Frequent removal of animals will be necessary. Possible removals of animals or actions such as translocations or brief harassment hunts to alter distribution.	Possible reductions in elk may be necessary.	Depends on findings, can be minimal to a high level of management necessary.	Depends on findings.	Elk population is managed to obtain appropriate allowable use level.
Plant management consequences	Plant responses are predicted to follow the population goals of the ungulate.	Possible plantings, temporary exclosures or burnings to mitigate any ungulate overabundance.	Depends on findings.	Depends on findings.	Depends on findings.
Time required for a measurable feedback	Immediate.	Slow, possibly >20 years.	Rapid, a few years.	Slow.	Rapid.

McCullough and R. H. Barrett, editors. Wildlife 2001: Populations. Elsevier Applied Science Publications, New York. 1163 pp.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Pages 183–246 *in* T. H. Coaker, editor. Applied Biology. Volume I. Academic Press, New York, New York.

Chase, A. 1986. Playing God in Yellowstone: The destruction of America's first national park. Atlantic Monthly Press, Boston, Mass, USA. 446 pp.

Cheville, N. F., D. R. McCullough, and L. R. Paulson. 1998. Brucellosis in the Greater Yellowstone area. National Resource Council. Washington, D.C.

Chew, R. M. 1982. Changes in herbaceous and suffrutescent perennials in grazed and ungrazed desertified grassland in southeastern Arizona. 1958–78. American Midland Naturalist 108:159–169.

Cole, G. C. 1971. An ecological rationale for the natural and artificial regulation of native ungulates in parks. Transactions of the North American Wildlife Conference 36:417–425.

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

Coughenour, M. B. 1985. Graminoid responses to grazing by large herbivores: Adaptation, exaptations, and interacting processes. Annuals of Missouri Botanical Gardens 72:852–863.

Coughenour, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. Journal of Applied Ecology 28:71–82.

Coughenour, M. B., and F. J. Singer. 1991. The concept of overgrazing and its application to Yellowstone's northern winter range. Pages 209–230 *in* R. B. Keiter and M. S. Boyce, editors. The Greater Yellowstone ecosystem: Redefining America's wilderness heritage. Yale University Press, New Haven, Conn.

Coughenour, M. B., and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications 6:573–593.

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 83:546–552.

Crete, M. 1998. Ecological correlates of regional variation in the life history of the moose, *Alces alces*. Ecology 79:1836–1838.

Danell, K., and R. Bergström. 1985. Winter browsing by moose on two birch species: Impact on food resources. Oikos 54:11–18.

Danell, K., K. Huss-Danell, and R. Bergström. 1985. Interactions between browsing moose and two species of birch in Sweden. Ecology 66:1867–1878.

Daubenmire, R. 1940. Plant succession due to overgrazing in the *Agropyron* bunchgrass prairie of southeastern Washington. Ecology 21:55–64.

Detling, J. K. 1988. Grasslands and savannas: Regulation of energy flow and nutrient cycling by herbivores. Ecological Studies 67:131–148.

Dublin, H. T., A. R. E. Sinclair, S. Boutin, E. Anderson, M. Jago, and P. Arcese. 1990. Does competition regulate ungulate populations? Oecologia 82:283–288.

Dyer, M. I., C. L. Turner, and T. R. Seastedt. 1993. Herbivory and its consequences. Ecological Applications 3:10–16.

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

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73:2034–2058.

Frank, D. A., and S. J. McNaughton. 1993. Evidence for promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96:157–161.

Fuls, E. R. 1992. Ecosystem modification created by patch-overgrazing in semi-arid grassland. Journal of Arid Environments 23:59–69.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84:1–50.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 20:1–59.

Gough, L., and J. B. Grace. 1998. Herbivore effects on plant species diversity at varying productivity levels. Ecology 79:1586–1594.

Green, R. A., and J. K. Detling. 2000. Defoliation-induced enhancement of total aboveground nitrogen yield of grasses. Oikos 91:280–284.

Grime, J. P. 1973. Control of species density in herbaceous vegetation. Journal of Environmental Management 1:151–167.

Hamilton III, E. W., M. S. Giovannini, S. A. Moses, J. S. Coleman, and S. J. McNaughton. 1998. Biomass and mineral element responses of a Serengeti short-grass species to nitrogen supply and defoliation: Compensation requires a critical N. Oecologia 116:407–418.

Hess, K. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot. 167 pp.

Hilbert, D. W., D. M. Swift, J. K. Detling, and M. I. Dyer. 1981. Relative growth rates and the grazing optimization hypothesis. Oecologia 51:14–18.

Hobbs, N. T. 1979. Winter diet quality and nutritional status of elk in the upper montane zone, Colorado. Ph.D. dissertation, Colorado State University, Fort Collins.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60:695–713.

Hobbs, N. T., D. Baker, J. E. Ellis, and D. M. Swift. 1981. Composition and quality of elk winter diets in Colorado. Journal of Wildlife Management 45:156–170.

Hobbs, N. T., D. L. Baker, J. E. Ellis, D. M. Swift, and R. A. Green. 1982. Energy and nitrogen based estimates of elk winter range carrying capacity. Journal of Wildlife Management 46:12–21.

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

Holzgang, O. 1997. Herbivore-carrying capacity of grasslands in the Swiss National Park. Thesis. Swiss Federal Institute of Technology, Zurich.

Houston, D. B. 1971. Ecosystems of national parks. Science 172:648–651.

Houston, D. B. 1982. The Northern Yellowstone elk: Ecology and management. MacMillan Publishing, New York, New York.

Iason, G. R., C. D. Duck, and T. H. Clutton-Brock. 1986. Grazing and reproductive success of red deer: The effects of local enrichment by gull colonies. Journal of Animal Ecology 55:507–515.

Jaramillo, V. J., and J. K. Detling. 1988. Grazing history, defoliation, and competition: Effects on shortgrass production and nitrogen accumulation. Ecology 69:1599–1608.

Jedrzejewska, B., and W. Jedrzejewski. 1998. Predation in vertebrate communities: The Bailowieza Primeval Forest as a case study. Springer-Verlag, New York, New York.

Jensen, C. H., and P. J. Urness. 1981. Establishing browse utilization from twig diameters. Journal of Range Management 34:113–116.

Kay, C. E. 1994. Aboriginal overkill, the role of Native Americans in structuring western ecosystems. Human Nature 5:359–398.

Kay, C. E. 1998. Are ecosystems structured from the top down or bottom up: A new look at an old debate. Wildlife Society Bulletin 26:484–498.

Kay, C. E., and F. H. Wagner. 1994. Historical condition of woody vegetation on Yellowstone's northern range. Pages 151–169 *in* D. G. Despain, editor. Plants and their environments. National Park Service, Technical Report 93. Denver, Colo.

Keiter, R. B. 1988. Natural ecosystem management in park and wilderness areas: Looking at the law. Pages 15–40 *in* J. K. Agee and D. R. Johnson, editors. Ecosystem management for parks and wilderness. University of Washington Institute of Forest Resources, No. 65.

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

Krefting, L. W., M. H. Stenlund, and R. K. Seemel. 1966. Effects of simulated and natural browsing on mountain maple. Journal of Wildlife Management 30:481–488.

Larkins, K. F. 1997. Patterns of elk movement and distribution in and adjacent to the eastern boundary of Rocky Mountain National Park. Masters thesis, University of Northern Colorado, Greeley.

Leopold, A. S., S. A. Cain, C. M. Cottam, I. N. Garbielson, and T. L. Kimball. 1963. Wildlife management in the national parks. Transactions of the North American Wildlife Conference 24:28–45.

Lime, D. W., B. A. D. W., B. A. Koth, and J. C. Vlaming. 1993. Effects of restoring wolves on Yellowstone area big game and grizzly bears: Opinions of scientists. Pages 306–326 *in* R. S. Cook, editor. Ecological issues on reintroducing wolves into Yellowstone National Park. National Park Service Science Monographs 92/22.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: An ecological chronicle. Agro-ecosystems 7:145–165.

Mack, J. A., and F. J. Singer. 1993. Predicted effects of wolf predation on northern range elk using Pop-II models. Pages 234–269 *in* R. S. Cook, editor. Ecological issues on reintroducing wolves into Yellowstone National Park. National Park Service Science Monograph 92/22.

Mazancourt, G. de, M. Loreau, and L. Abbadie. 1998. Grazing optimization and nutrient cycling: When do herbivores enhance plant production? Ecology 79:2242–2252.

McCullough, D. R. 1999. Density dependence and life-history strategies of ungulates. Journal of Mammalogy 80:1130–1146.

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73:2059–2075.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266:1555–1558.

McLean, A., and S. J. Wikeem. 1985. Influence of season and intensity of defoliation on bluebunch wheatgrass survival and vigor in southern British Columbia. Journal of Range Management 36:694–700.

McNab, J. 1985. Carrying capacity and related slippery shibboleths. Wildlife Society Bulletin 13:403–410.

McNaughton, S. J. 1979. Grazing as an optimization process: Grass-ungulate relationships in the Serengeti. American Naturalist 11:691–703.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40:329–336.

McNaughton, S. J. 1993. Grasses and grazers, science and management. Ecological Applications 3:17–20.

McNaughton, S. J. 1996. Wildlife policies in U.S. national parks. Journal of Wildlife Management 60:685–687.

McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1998. Root biomass and productivity in a grazing ecosystem: The Serengeti. Ecology 79:587–592.

McQuarrie, A. D. R., and C. L. Tsai. 1998. Regression and time series model selection. World Scientific, Singapore. 455 pp.

McShea, W. J., H. B. Underwood, and J. H. Rappole. 1997. Deer management and the concept of overabundance. Pages 1–7 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance, deer ecology, and population management. Smithsonian University Press, Washington, D.C.

Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis. 227 pp.

Menezes, R. S. C., E. T. Elliott, D. W. Valentine, and S. A. Williams. 2001. Effects of herbivory and proximity to surface water on C and N dynamics of elk winter range. Journal of Range Management 54:400–408.

Merrill, E., M. K. Bramble-Brodahl, R. W. Marrs, and M. S. Boyce. 1993. Estimation of green herbaceous phytomass from Landsat MSS data in Yellowstone National Park. Journal of Range Management 46:151–157.

Messier, F. 1994. Ungulate population models with predation: A case study with the North American moose. Ecology 75:478–488.

Messier, F. 1995. On the functional and numerical responses of wolves to changing prey density. Pages 187–198 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton.

Milchunas, D. G., and W. K. Lauenroth. 1992. 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. American Naturalist 132:87–106.

Mueggler, W. F. 1975. Rate and patterns of vigor recovery in Idaho fescue and bluebunch wheatgrass. Journal of Range Management 28:193–204.

Mueggler, W. F. 1984. Diversity of western rangelands. Pages 211–217 *in* J. L. Cooley and J. H. Cooley, editors. Natural Diversity in Forest Ecosystems Proceedings Workshop. University of Georgia, Athens.

National Park Service. 2001. Management policies. U.S. Government Printing Office, Washington, D.C.

Oldemeyer, J. L. 1981. Estimation of paper birch production, utilization, and an evaluation of its response to browsing. Dissertation, Pennsylvania State University, Pittsburgh.

Olmstead, C. E. 1979. The ecology of aspen with reference to utilization by large herbivores in Rocky Mountain National Park. Pages 89–97 *in* M. S. Boyce and L. D. Hayden-Wing, editors. North American elk: Ecology, behavior, and management. University of Wyoming, Laramie.

Olson, B. E., and R. T. Wallander. 1997. Biomass and carbohydrates of spotted knapweed and Idaho fescue after repeated grazing. Journal of Range Management 50:409–412.

Orians, G., D. A. Cochran, J. W. Duffield, T. K. Fulla, R. J. Gutierrez, W. M. Hanemann, F. C. James, P. Karieva, S. R. Kellert, D. Klein, B. N. McLellan, P. D. Olson, and G. Yaska. 1997. Wolves, bears and their prey in Alaska. National Academy of Press, Washington, D.C.

Packer, P. E. 1963. Soil, stability requirements for the Gallatin elk winter range. Journal of Wildlife Management 27:401–410.

Painter, E. L., and A. J. Belsky. 1993. Application of herbivore optimization theory to rangelands of the western United States. Ecological Applications 3:2–9.

Pastor, J., B. Dewey, R. J. Naiman, P. F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74:467–480.

Pengelly, W. L. 1963. Thunder on the Yellowstone. Naturalist 14:18–25.

Peterson, R. O. 1999. Wolf-moose interaction on Isle Royale: The end of natural regulation. Ecological Applications 9:10–15.

Pitt, M. D., and F. E. Schwab. 1990. Assessment of a nondestructive method for estimating browse use. Journal of Wildlife Management 54:175–179.

Polley, H. W., and J. K. Detling. 1989. Defoliation, nitrogen and competition: Effects on plant growth and nitrogen nutrition. Ecology 70:721–727.

Pucheta, E., M. Cabido, S. Diaz, and G. Funes. 1998. Floristic composition, biomass and aboveground net plant production in grazed and protected sites in the mountain grassland of central Argentina. Acta Oecologia 19:97–105.

Rickard, W. H. 1985. Experimental cattle grazing in a relatively undisturbed shrub-steppe community. Northwest Science 59:66–72.

Ripple, W. J., and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biological Conservation 95:361–370.

Risser, P. G., and W. J. Parton. 1982. Ecosystem analysis of the tallgrass prairie: Nitrogen cycle. Ecology 63:1342–1351.

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.

Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, Inc. New York. 343 pp.

Ruess, R. W. 1984. Nutrient movement and grazing: Experimental effects of clipping and nitrogen source in nutrient uptake in *Kyllinga nervosa*. Oikos 43:183–188.

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.

Rummell, R. S. 1951. Some effects of grazing on ponderosa pine forest and range in central Washington. Ecology 32:594–607.

Sala, O. E., M. Osterheld, R. J. C. Leon, and A. Soriano. 1986. Grazing effects upon plant community structure in subhumid grasslands in Argentina. Vegetatio 67:27–32.

Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys in north central Idaho. Journal of Wildlife Management 51:622–630.

Seagle, S. W., S. J. McNaughton, and R. W. Ruess. 1992. Simulated effects of grazing on soil nitrogen and mineralization in contrasting Serengeti grasslands. Ecology 73:1105–1123.

Shannon, C. E., and W. Weaver. 1962. The mathematical theory of communication. University of Illinois Press, Urbana.

Shenk, T. M., G. C. White, and K. P. Burnham. 1998. Sampling variance effects on detecting density dependence from temporal trends in natural populations. Ecological Monographs 68:445–463.

Sinclair, A. R. E., and P. Arcese. 1995. Population consequences of predator-sensitive foraging: The Serengeti wildebeest. Ecology 76:882–891.

Sinclair, A. R. E., and R. P. Pech. 1996. Density dependence, stochasticity, compensation and predator regulation. Oikos 75:164–173.

Sinclair, A. R. E., H. Dublin, and M. Borner. 1985. Population regulation of Serengeti wildebeest: A test of the food hypothesis. Oecologia 65:266–268.

Singer, F. J., and M. K. Harter. 1996. Comparative effects of elk herbivory and the 1988 fires on northern Yellowstone National Park grasslands. Ecological Applications 6:185–199.

Singer, F. J., and J. A. Mack. 1999. Predicting the effects of wildfire and carnivore predation on ungulates. Pages 189–238 *in* T. W. Clark, editor. Carnivores in ecosystems: The Yellowstone experience. Yale University Press, New Haven, Conn.

Singer, F. J., and R. A. Renkin. 1995. Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park. Great Basin Naturalist 55:201–212.

Singer, F. J., L. Mack, and R. G. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435–443.

Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on calf mortality. Journal of Wildlife Management 61:12–25.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998a. Thunder on the Yellowstone revisited: An assessment of management of native ungulates by natural regulation, 1968–93. Wildlife Society Bulletin 26:375–390.

Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998b. Elk, multiple factors, and persistence of willows in national parks. Wildlife Society Bulletin 26:419–428.

Singer, F. J., G. Wang, and N. T. Hobbs. 2002. The role of grazing ungulates and large, keystone predators on plants, community structure, and ecosystem processes in mixed grassland-coniferous landscapes in the western United States. *In* R. G. Anthony and C. Zabel, editors. Large mammal communities in U.S. western coniferous forests. Cambridge University Press.

Skinner, M. P. 1928. The elk situation. Journal of Mammalogy 9:309–317.

Sneva, F. A., P. T. Rittenhouse, P. T. Tueller, and P. Reece. 1984. Changes in protected and grazed sagebrush-grass in eastern Oregon, 1937 to 1974. Oregon State University Agricultural Experiment Station, Corvallis.

S-Plus. 2000. Guide to Statistics, Volume I. Data Analysis Products Division, Mathsoft, Seattle, Washington.

Stohlgren, T. J., T. N. Chase, R. A. Pielke, Sr., T. G. F. Kittel, and J. S. Baron. 1998. Evidence that local land use practices influence regional climate, vegetation, and stream flow patterns in adjacent natural areas. Global Change Biology 4:495–504.

Stohlgren, T. J., L. D. Schell, and B. V. Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9:45–64.

Turner, C. L., T. R. Seastedt, and M. I. Dyer. 1993. Maximization of above ground grassland production: The role of defoliation frequency, intensity, and history. Ecological Applications 3:175–186.

Unsworth, J. W., F. A. Leban, D. J. Leptich, E. O. Garton, and P. Zager. 1994. Aerial survey: User's manual. Idaho Fish and Game Department, Boise.

Verkaar, H. J. 1992. When does grazing benefit plants? Trends in Ecology and Evolution 1:168–169.

Wagner, F. H., R. Foresta, R. B. Gill, D. R. McCullough, M. R. Pelton, W. F. Porter, and H. Salwasser. 1995a. Wildlife policies in the U.S. National Parks. Island Press, Washington, D.C.

Wagner, F. H., R. Keigley, and C. Wombalt. 1995b. Ungulate herbivory of willows on Yellowstone's northern winter range: Comment to Singer et al. (1994). Journal of Range Management 48:475–477.

Wagstaff, F. J., and B. L. Welch. 1991. Seedstalk production of mountain big sagebrush enhanced through short-term protection from heavy browsing. Journal of Range Management 44:72–74.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at an equilibrium. Journal of Range Management 42:265–273.

Whitham, T. G., T. Maschinski, K. C. Larson, and K. N. Paige. 1991. Plant responses to herbivory: The continuum from negative to positive and underlying physiological mechanisms. *In* P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, editors. Plant-animal interaction: Evolutionary ecology in tropical and temperate regions. John Wiley and Son, Inc.

Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. Journal of Wildlife Management 48:1285–1301.

Willard, E. E., and C. M. McKell. 1978. Responses of shrubs to simulated browsing. Journal of Wildlife Management 42:514–519.

Wolfe, M. L., W. H. Babcock, and R. M. Welch. 1983. Effects of simulated browsing on Drummond's willow. Alces 19:14–35.

Wolff, J. O., and J. C. Zasada. 1979. Moose habitat and forest succession on the Tanana River floodplain and Yukon upland. Alces 15:213–244.

Wright, R. G. 1996. National parks and protected areas: Their role in environmental protection. Blackwell Science, Cambridge, Mass. 470 pp.

Yellowstone National Park. 1997. Yellowstone's northern range: Complexity and change in a wildland ecosystem. National Park Service, Mammoth Hot Springs, Wyoming. 148 pp.

Yochim, M. J. 2001. Aboriginal overkill overstated. Human Nature 12:141-167.

Zeigenfuss, L. C., F. J. Singer, and D. Bowden. 1999. Vegetation responses to natural regulation of elk in Rocky Mountain National Park. Biological Science Report USGS/BRD/BSR-1999-0003. U.S. Government Printing Office, Denver, Colo. 23 pp.

Appendix A. Vegetation coverage of major elk winter ranges in eastern Rocky Mountain National Park, Colorado.

	Horseshoe Range		Moraine Range		Trail Ridge Range	
Cover class	Area (km^2)	Percent	Area (km^2)	Percent	Area (km^2)	Percent
Water	0.30	1	0.39	1	0.16	1
Willow	5.59	9	5.06	11	1.93	9
Grassland	3.57	6	4.14	10	2.55	12
Shrubland	2.57	4	2.23	5	0.80	4
Unvegetated	0.16	0	0.15	0	2.58	12
Aspen	0.23	0	0.22	1	0.03	0
Conifer	46.36	75	29.55	68	0.00	0
Pine grasslands	3.28	5	1.51	4	0.00	0
Subalpine forest	0.06	0	0.00	0	2.25	10
Tundra	0.00	0	0.00	0	0.137	1
Alpine range	0.00	0	0.00	0	11.07	51
Total	62.08	100	43.14	100	21.50	100

Appendix B. Vegetation coverage for the town winter elk range, Estes Park, Colorado.

Cover class	Area (km^2)	Percent
Shrubland	4.87	8.0
Grassland	13.83	22.8
Aspen	0.09	<1
Ponderosa pine	22.46	37.0
Douglas fir	0.36	<1
Lodgepole pine	7.08	11.7
Unvegetated	0.72	1.2
Water	0.80	1.3
Disturbed grasslands	2.91	4.8
Slightly irrigated grasslands	2.82	4.5
Subirrigated grasslands	0.52	<1
Golf course	0.62	1.0
Willow	3.60	5.9
Total	60.68	100

Appendix C. Indices used to measure herbaceous species diversity in grazed and ungrazed plots on elk winter range in Rocky Mountain National Park, Colorado.

Index	Formula	Source
Diversity	$H = -\sum_{k=1}^{s} (P_k) \ln(P_k)$	Shannon and Weaver (1962)
Richness	R = s/total number of plots	

P_k = the proportion of total biomass contributed by species K.

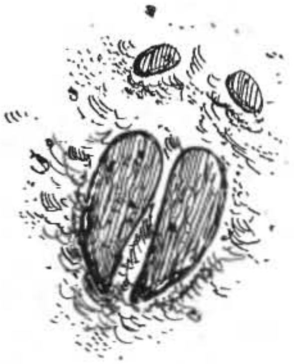
S = the number of species observed in a plot.

Appendix D. Primary components (>5%) of elk diets in Rocky Mountain National Park, 1994–1997.

		Percent of total diet by season			
Seasonal range	Genus	Spring	Summer	Winter	Fall
Alpine	*Salix*	6.9	57.0		
	Pinus	42.3			
	Carex	20.0	17.6		
	Stipa	7.6	4.3		
	Pseudotsuga	6.6			
	Artemisia tridentata		9.1		
	Other graminoids	9.4	4.2		
	Other forbs	4.8	6.0		
	Other woody browse	2.1	1.5		
Low elevation winter	*Salix*	9.7		10.2	15.2
	Pinus	6.0		12.6	8.1
	Carex	26.8		9.3	8.2
	Stipa	27.4		28.0	26.5
	Poa			8.2	8.6
	Agropyron			8.3	
	Juncus	8.6		8.7	6.9
	Phleum				5.3
	Other graminoids	13.8		8.1	9.7
	Other forbs	5.7		4.5	9.7
	Other woody browse	1.8		1.8	1.4

PART II

MODELING




DC.

Executive Summary of Model-Based Assessment of Elk in the Rocky Mountain National Park Ecosystem

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Rocky Mountain National Park (RMNP) was established after a period of substantial resource extraction by early settlers, including trappers, hunters, miners, loggers, and ranchers. A once abundant large herbivore, elk (*Cervus elaphus*) had by that time been extirpated from the region by a period of intensive market hunting in the 1860s and 1870s (Guse 1966). Mule deer (*Odocoileus hemionus*) were also much reduced. Elk were reintroduced in 1913–1914, and the population grew in size to approximately 900 animals in 1938–1939 (Packard 1947a). Elk were intensively managed from 1944–1968, due to early concerns that they were overabundant, and damaging the winter range. The herd was reduced by culling operations in 1944–1945 and 1949–1950, and generally kept in the 300–600 range through 1968. Public disapproval of elk culling in Yellowstone led to an experimental approach to management often referred to as natural regulation. The hypothesis was that elk would reach a natural food-limited carrying capacity, and population growth would be self-regulated through density-dependent competition for food. Since 1968, the elk herd in RMNP has been managed only by sport hunting outside of the park boundary, which has not controlled elk population growth. Furthermore, elk have been increasingly wintering outside the park boundaries in the town of Estes Park, where they also largely escape hunting.

Concerns about elk impacts on plants and other components of the ecosystem have heightened considerably during the last two decades (Olmsted 1977, 1979, 1997; Hess 1993; Wagner et al. 1995; Baker et al. 1997; Berry et al. 1997; Keigley and Wagner 1998). In particular, it has been suggested that elk are overabundant and present in unnatural densities due to lack of natural predators and Native American hunting. These authors felt that in pre-settlement times, elk were present at much lower densities, and they may not have wintered in the areas that now comprise RMNP. However, there appears to be no evidence that elk did not winter on the eastern slope of the park in historic times.

An effort was made to review the literature for prehistoric and historic elk presence. Prehistoric game drive systems discovered at high elevations within the park were most likely used to hunt elk (Benedict 1992, 1999). There was a considerable amount of historical evidence of elk presence prior to settlement (Sage 1846; Loring 1893; Sprague 1925; Fryxell 1928; Estes 1939).

Human impacts on the elk winter range prior to the creation of the national park provided an unnatural starting point for the elk reintroduction program, and likely exacerbated elk impacts on the range. Livestock grazing was widespread and apparently intense enough to cause significant changes in herbaceous vegetation cover (Mills 1924; McLaughlin 1931; Ratcliff 1941). Land had also been drained and willows cut to support haying operations (Gysel 1960).

A deer eruption in the 1930s, along with increased numbers of elk, brought about declines in upland shrubs (Ratcliff 1941), willow cover (Dixon 1939; Gysel 1960), and barking and suppression of regeneration in aspen (McLaughlin 1931; Ratcliff 1941; Packard 1942). Following the elk reduction programs of the 1940s, Buttery (1955) concluded that range condition had improved to fair condition, and was stable. After the cessation of elk reductions, Stevens (1980) found stable sagebrush grasslands, but increases in bare ground in grasslands between 1968–1979. Stohlgren et al. (1999) found grazing reduced herbaceous cover slightly, and increased diversity.

A greater level of concern has been recently expressed about elk impacts on riparian willow communities, beaver, and aspen. Aspen stands on the winter range have exhibited little or no regeneration, heavy bark scarring, and mortality (Olmsted 1979, 1997; Stevens 1980; Baker et al. 1997), all attributable to elk browsing. A recent analysis of historical aerial photography showed that over the last 50–59 years willow cover has declined by 19–21% (Peinetti 2000; Peinetti et al., this volume). These decreases were associated with 44–56% decreases in total stream channel density, which was believed to be a consequence of reduced beaver activity. Beaver have declined both on and off the winter range from high levels in 1925–1947 (Warren 1926; Packard 1947b) to current densities which are apparently 90% less than in 1940 (Hickman 1964; Stevens and Christianson 1980; Gense 1997; Zeigenfuss et al., this volume). Some authors have attributed the decline to elk, particularly their negative impacts on willow (Packard 1947b; Gysel 1960; Hess 1993). However, beaver numbers first declined when elk were being controlled below their food-limited carrying capacity.

These concerns led to the inception of several new studies of the elk winter range, including the present study. A 3-year study of elk impacts on upland grasslands and shrublands has shown little impact of herbivory (Zeigenfuss et al., this volume). Few effects have been noted of elk on soil carbon and nitrogen or herbaceous root biomass (Binkley et al., this volume; Schoenecker et al., this volume); however, in willow communities Schoenecker et al. (this volume) found markedly (5x) lower N mineralization outside short-term exclosures located in portions of the winter range judged to have high elk densities. All of the sites were in browsing-suppressed short willow communities. A 5-year study of elk browsing impacts on willow (Peinetti 2000; Singer et al., this volume; Zeigenfuss et al., this volume) has shown large increases in willow growth when protected from elk herbivory. Zeigenfuss et al. (1999) found a continuation of some of the negative vegetation trends observed earlier by Stevens (1980). Olmsted (1997) found further evidence that aspen stands were degrading. Berry et al. (1997) examined whether vegetation on the elk winter range has deviated from pre-Columbian conditions due to elk overabundance. They concluded elk were responsible for aspen and willow declines and decreases in upland range condition, and suggested that the vegetation be protected from herbivory to facilitate recovery from past damage.

The present modeling study was initiated with the specific aims of estimating elk carrying capacity and elk impacts on riparian willow. The more general purpose of this research was to assess the role of elk in the RMNP ecosystem. Ecosystem modeling was used to assess the role of elk in the ecosystem, and the way that ecosystem dynamics have been altered by interactions between elk, climate, and humans. Ecosystem modeling is a comprehensive approach to carrying capacity assessment. It simultaneously addresses different concepts of carrying capacity by explaining ecosystem dynamics in terms of underlying ecosystem processes. The model was used to represent plant and soil responses to herbivory, food limitation of the herbivore population, and predation. It was used to project ecosystem dynamics under past, present, and future management scenarios.

Model Description and Data Inputs

SAVANNA is a spatially explicit, process-oriented model of grassland, shrubland, savanna, and forested ecosystems developed originally for studies in East Africa (Coughenour 1992, 1993). The model has been applied to Elk Island National Park in Alberta (Buckley et al. 1995), the Pryor Mountain Wild Horse Range, Montana (Coughenour 2000), northern Australia (Ludwig et al. 1999), South Africa (Kiker 1998), and Tanzania (Boone et al. 2001). SAVANNA simulates processes at landscape through regional spatial scales over annual to decadal time scales. The model is composed of site water balance, plant biomass production, plant population dynamics, litter decomposition and nitrogen cycling, ungulate herbivory, ungulate spatial distribution, ungulate energy balance, and ungulate population dynamics submodels. Wolf predation and wolf population dynamics submodels are derived from a model used to assess wolf reintroduction into Yellowstone National Park (Boyce and Gaillard 1992; Boyce 1993).

The model was driven by weather data from weather stations in and surrounding the study area. Monthly precipitation and temperature maps were generated from spatial interpolation on elevation corrected data. Historical weather data since 1949 were readily available. Data for 1931–1948 were sparse, however there were key stations with data, including Estes Park, Grand Lake, and Fraser. Data for the period 1910–1930 were reconstructed based upon deviations from normal observed in the data from Fraser, Colorado, which had the most reliable and longest record. Data for the period 1775–1909 were reconstructed from the tree-ring database of Fritts (1991a,b).

SAVANNA requires a vegetation map for the initialization of plant biomass and population variables.

A single-source vegetation map for the entire elk range did not exist, primarily because the elk range extends outside the park boundaries, and includes land from three administrative agencies, the U.S. National Park Service, the U.S. Forest Service (USFS), and the Town of Estes Park. Consequently, a vegetation map was constructed from multiple sources. Vegetation cover maps from RMNP and the Arapahoe-Roosevelt National Forest (ARNF) were combined into a single coverage (Ron Thomas, RMNP GIS lab). Vegetation outside RMNP and ARNF, i.e., on private landholdings, was derived from a vegetation map of Larimer County, Colorado that was developed at Colorado State University from a Landsat-TM scene (McCool 1995; Todd 1995). Disturbed areas, human land uses and areas subsidized by water, were delimited with the aid of satellite data of the normalized difference vegetation index (NDVI). An "undisturbed" vegetation map was created to represent the vegetation cover prior to the settlement of the Estes Valley. Vegetation and land covers of anthropogenic origin on the Larimer County vegetation map were restored to undisturbed conditions. All areas classified as disturbed, urban, golf course, etc., were reclassified as grassland. The Big Thompson river course was markedly altered by development, including the construction of a dam and lake. Historical photographs of the valley before town and dam construction showed the former extent of the river course and riparian floodplain. These features were incorporated into the "undisturbed" vegetation map.

The model was configured to represent ten plant functional groups: upland grasses and forbs, riparian graminoids and forbs, upland shrubs, willow, aspen, ponderosa pine/Douglas fir, lodgepole pine, and subalpine conifers (spruce-fir). The area that was simulated was defined by the combined winter and summer ranges of the elk that winter on the east slope of RMNP, and in the town of Estes Park. Two subherds of elk were simulated, a park subherd and a town subherd, based on information that animals from these subherds exhibit fidelity to these ranges (Lubow et al., this volume). Mule deer were also simulated, primarily to represent their impacts on plants. Their range was assumed to be the elk-defined study area, but with different habitat preferences.

The plant growth model was parameterized from numerous data sources in the literature, and from recent field studies in RMNP. Then it was verified by comparing model outputs to observed biomass data from Hobbs (1979), Fisk et al. (1998), Singer et al. (this volume), and Zeigenfuss et al. (this volume). Comparisons were made for several major vegetation types including: dry grasslands, mesic riparian herbaceous, upland shrubs, willow, low elevation woodlands dominated by ponderosa pine (montane woodland), high elevation woodland and forest dominated by lodgepole pine, Engelmann spruce and subalpine fir, and alpine tundra. Comparisons were made under grazed and ungrazed conditions. The comparisons proved to be generally favorable.

Model Verification: The Control Run for 1949–1998

A simulation was conducted to represent observed ecosystem dynamics for the period 1949–1998. This was referred to as the control run because it represented a set of standard conditions to which results from other model experiments could be compared. Control run output provided additional information for verifying the model's behavior by comparing simulation results to observations. The control run was a calibration run for animal submodels, because key model parameters for diet selection, forage intake, energy use, and population dynamics were calibrated so that model outputs most closely matched observed values.

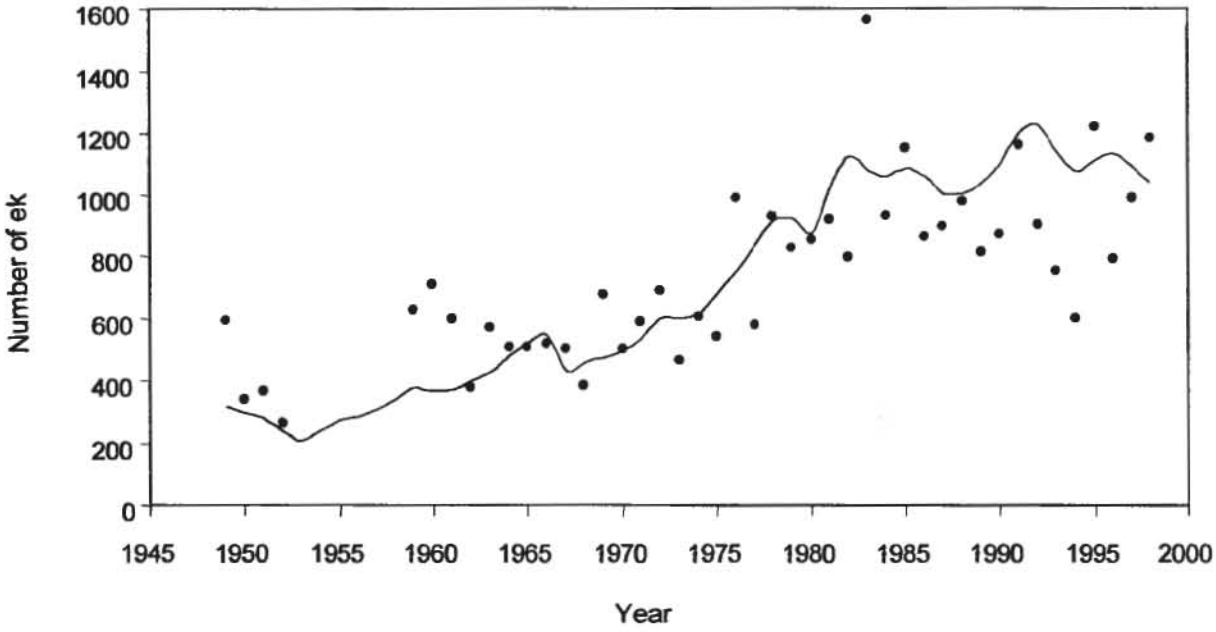
The simulated elk population was reduced using observed rates of elk offtake by hunter harvest and management removals. The deer population was maintained within a range of 400–600 animals throughout the simulation by removals as necessary.

The snow submodel was verified by comparisons between observed and predicted data at seven SNOTEL stations 1979–1998. The snow model performed satisfactorily at most of the sites.

Water table depths in riparian willow stands (Singer et al. 1999; Zeigenfuss et al., this volume) were used to parameterize model relationships between water table depth and streamflow in the watershed. These relationships were then used in the model to estimate water table depths for different willow sites within each watershed.

The elk population model was calibrated to observed, sightability-corrected count data 1959–1998 (Lubow et al., this volume). The model was calibrated to pass through the higher of the reasonable data points, on the assumption that lower values were undercounts. The model simulated the correct rate of population increase, and most importantly, represented the leveling-off of the park population during 1980–1998 (Fig. 1). This indicates that the model was representing density dependent competition for food, and thus food-limited carrying capacity, correctly. There was a clear decline in the ratio of calves to cows over the period 1949–1998.

a. The park elk subherd



b. The town elk subherd

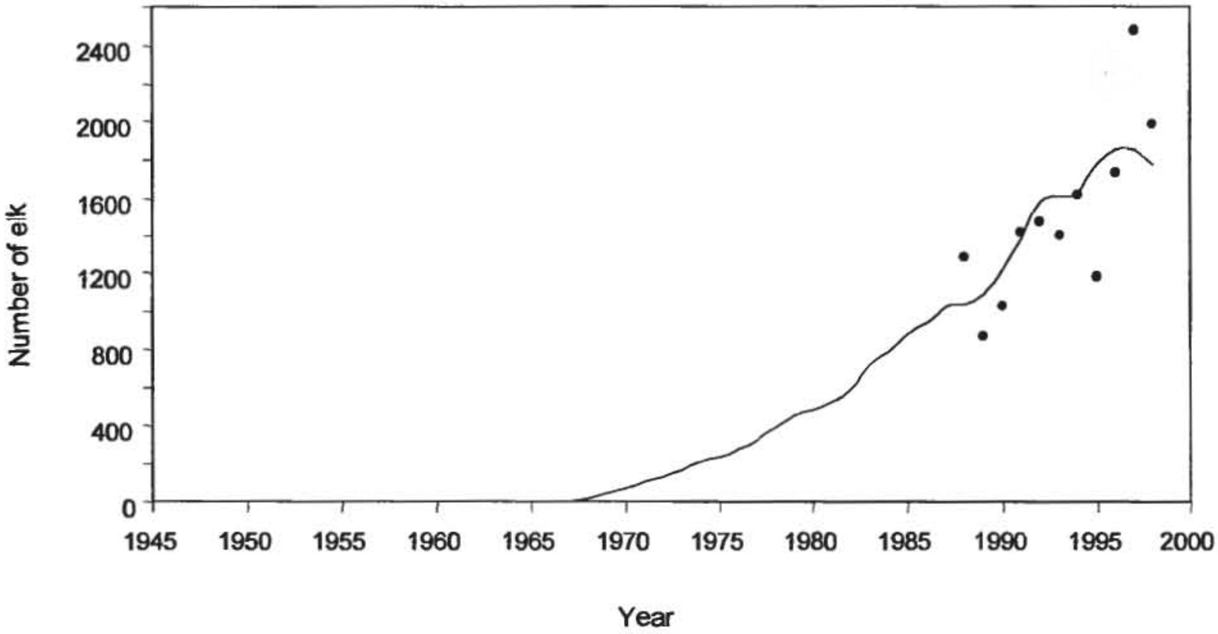


Fig. 1. Simulated (lines) and observed (points) population dynamics for (a) the park elk subherd; and (b) the town elk subherd of the eastern side of Rocky Mountain National Park and the town of Estes Park, Colorado.

This was consistent with data, and with the hypothesis that the elk population was exhibiting a density-dependent limitation on recruitment (Lubow et al., this volume).

Simulated spatial distributions of elk were in agreement with observed data. High densities of up to 90 elk/km^2 were simulated in the Moraine Park area. High densities were also simulated in certain areas of Horseshoe Park, but overall density was less than in Moraine Park. These densities are consistent with the contour maps generated from aerial survey data (Singer et al., this volume), which show density contours of 12–16 elk/km^2 in Horseshoe Park and >90 elk/km^2 in Moraine Park.

Simulated elk diets were consistent with data of Riorden (1948), Hobbs (1979), Stevens (1980), Baker and Hobbs (1982), and Singer et al. (2002).

The model predicted a reasonable spatial distribution of herbaceous biomass over the winter and summer ranges. Peak biomass generally ranged 40–150 g/m^2 on the winter range on grassland, shrubland, and ponderosa pine woodlands. Low production was simulated in the subalpine forests (20–40 g/m^2). Higher biomass levels were simulated on the alpine tundra and subalpine meadows. Aboveground net primary production was not much higher than peak standing crop.

Condition indices of elk reached maximum values each summer. End of winter minima declined over the period in response to increasing density and competition for limited forage. There was considerable variability among winters, reflecting differences in winter severity, and foraging conditions. Condition indices of the town population showed a similar pattern, but when densities were extremely low, winter minima were much higher than observed in the park population. As the town population increased, winter minima decreased markedly.

Model Experiments

Model experiments were conducted for three different time periods: 1775–1910, 1911–1948, and 1949–1998.

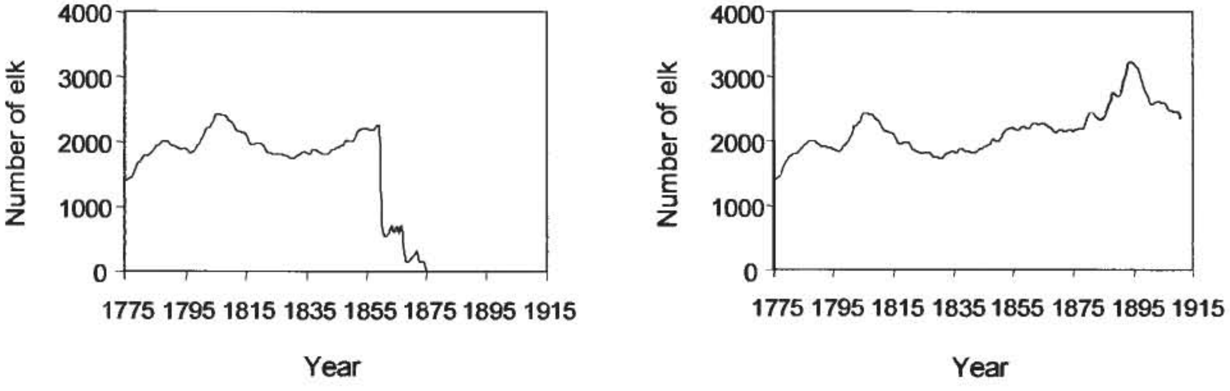
The Period Before Reintroduction of Elk (1775–1910)

The period before the reintroduction of elk (1775–1910) included transitions from an ecosystem undisturbed by Euro-American colonists but possibly affected by Native Americans, to an ecosystem that was heavily exploited by early settlers. Beaver trapping occurred prior to 1850, market hunting and extirpation of elk occurred in the 1870s, followed by logging, and heavy livestock grazing throughout the Estes Valley and the elk winter range inside the current park boundaries. Wolves were still present in 1894, but were extirpated well before 1917 (Stevens 1980). Simulation studies of this period were designed to examine the pre-settlement ecosystem, and the impacts of these initial disturbances.

The reconstructed undisturbed vegetation map was used in all of the 1775–1910 runs. Human impacts on ungulates were represented in the model through the imposition of prescribed hunting reductions. To reduce confounding effects, deer were kept at or below 600–700 throughout the entire simulation. Beaver on the elk winter range inside the park were held at 450 throughout. The control run for this period (a run to simulate actual conditions) examined the effects of the extirpation of elk by market hunting. Experimental runs were conducted to examine undisturbed conditions assuming one elk herd, undisturbed conditions assuming two elk subherds limited to the ranges now occupied by park and town subherds, respectively, and the effects of wolves.

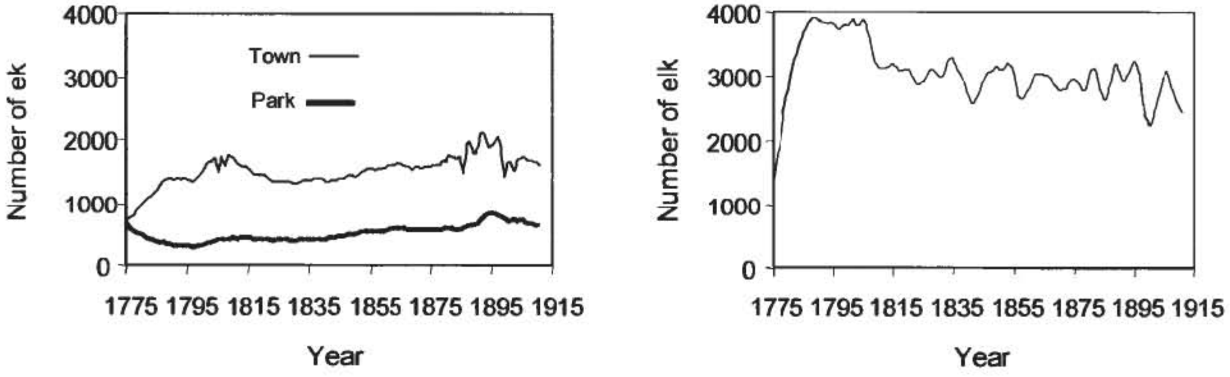
When the historic pattern of hunting was imposed, elk were extirpated as specified (Fig. 2a), and in response deer numbers increased and wolves were eliminated due to lack of prey. With no elk hunting, and with wolves (undisturbed conditions), total elk numbers varied between 1,500–3,500 and gradually increased throughout the simulation (Fig. 2b). Distinguishing two subherds indicated the relative sizes of subherds that would be expected in the two ranges. The park subherd varied between 300–800 elk, while the town subherd varied between 1,400–1,500 elk at first, increasing to approximately 1,600–2,000 elk in later years (Fig. 2c). Deer numbers were kept to <200 by wolf predation. Without wolves, total elk numbers increased at first to about 3,800, then numbers exhibited a dynamic equilibrium at approximately 2,800 elk, but with a declining long-term trend due to deteriorating range conditions (Fig. 2d). Elk numbers ended at a similar point with or without wolves, but elk and vegetation conditions were substantially improved in the presence of wolves. Elk condition indices remained higher in winter when wolves were limiting the population compared to when food was limiting the population. Elk mortalities due to starvation were therefore likely to be far less with wolves present.

When elk were hunted to historic levels, dryland herbaceous biomass, i.e., herbaceous layer biomass everywhere on the park elk winter range except in



a. Control (market hunting, wolves present)

b. Undisturbed conditions (no market hunting, wolves present), one elk subherd



c. Undisturbed conditions (no market hunting, wolves present), two elk herds

d. Hypothetical conditions (no market hunting, wolves absent)

Fig. 2. Elk populations of the eastern elk winter range of Rocky Mountain National Park and the Estes Valley, Colorado, in simulations of the period 1775–1910. All simulations were conducted with undisturbed vegetation and water table conditions and initialized at 1,200 elk (when two subherds were present, 600 in the park and town each).

riparian willow and wet meadows, increased. In undisturbed conditions (no market hunting and wolves present), dryland herbaceous biomass increased and then decreased slightly when elk were limited by wolves. Without wolves, dryland biomass declined gradually throughout the period. With historic elk hunting, willow cover increased to the maximum level (Fig. 3a), while with undisturbed conditions willow cover increased to near-maximal levels (Fig. 3b,c). In contrast, without wolves, willow cover declined (Fig. 3d). Aspen increased markedly following the extirpation of elk (Fig. 3a). With undisturbed conditions, aspen cover decreased even when wolves were present (Fig. 3b,c). The aspen decline was not accelerated by lack of wolves (Fig. 3d). This suggests that aspen cover at the inception of the park and elk reintroduction, could have been higher than if there were no elk extirpations.

To summarize the assessment of 1775–1910, it is very plausible for wolves and other predators to have maintained elk numbers below food-limited carrying capacity, but still at moderately high numbers, maintained by increased productivity of the vegetation compared to current conditions. Increased cover of willow could be supported, but beaver activities would be critical to maintenance of high water tables. Aspen would have had a difficult time becoming established or surviving the predator-limited densities of elk and mule deer on the core, lower elevation portions of the winter range. Purported evidence for aspen in those locations prior to 1870 should be carefully examined. Elk extirpation could have been a primary cause for the emergence of aspen stands in those locations. Effects of elk on beaver populations, or of bison impacts on elk winter forage were not considered.

Establishment of the Park and Reintroduction of Elk (1911–1948)

The period 1911–1948 included the inception of the park, the reintroduction of elk, and early conservation efforts. For most of the period, elk hunting was absent, or minimal. Hunting offtake was insignificant until 1941, and was 90–122 elk per year during the period 1941–1945 (Stevens 1980). The first significant management reduction did not occur until 1945, when 301 elk were removed (Stevens 1980). There were no reductions between 1946–1948, and hunting offtake was reduced to 20–80 per year. Thus, this was mainly a period of elk protection, with the first efforts of elk management occurring at the end of the period. Much of the elk winter range within the current park boundary was affected by human settlement, livestock grazing, haying, and resorts. Willow habitats were drained, and willow was removed to create pastures or hayfields. I assumed that between 1911–1931, the elk herd was mainly restricted to the area east of the current park boundary due to lack of access to the core grasslands in Moraine Park and Horseshoe Park, as these were grazed by domestic stock or hayed. Elk were introduced into the model in 1913 and 1914. Deer were kept at the 600–700 level until the period 1927–1942, when the population increased to 1,000–1,200 animals (Stevens 1980).

In the control run for this period, elk increased to about 800 animals by 1934, and then kept within a similar range to the estimated values. The undisturbed simulation began with the elk numbers simulated at the end of the undisturbed 1775–1910 run, and with wolves present. In this run, elk also had access to the full winter range, as opposed to being precluded from the core winter range inside the park. Wolves held the park subherd to 500–1,000 elk, while the town subherd increased to 2,500 and then declined to 1,200. Without wolves, the park subherd increased to 1,500, and the town subherd increased to about 2,700 before declining markedly to approximately 1,500.

There were few differences among dryland herbaceous biomass amounts in the different scenarios during this period. Willow cover increased to high levels in all runs where elk started out at zero, even with no elk reductions. The initial period when elk were absent or present at low numbers was sufficient for willow to reach tall stature. Once willow reached tall stature, it for the most part escaped herbivory. Subsequent conversion to short willow depended on the gradual mortality of old plants, and suppression of replacement plants. With the observed number of elk, and high water tables, the model did not simulate a decrease in willow during 1911–1948. In particular, the model could not explain willow declines under the number of elk present up until 1930. If water tables were high, the model only simulated willow declines during 1911–1930 if elk were assumed to be in the 500–1,000 range for the entire period, which was unrealistic. Willow declines were simulated during this period only when hydrology was altered. Humans likely played a significant role in these alterations.

In the control run, aspen increased at first but in about 1925–1930 began to decrease. In hypothetical runs with no elk or beaver present, the decrease did not occur. The results suggested that the combination of elk and beaver was responsible for the decline. In the undisturbed

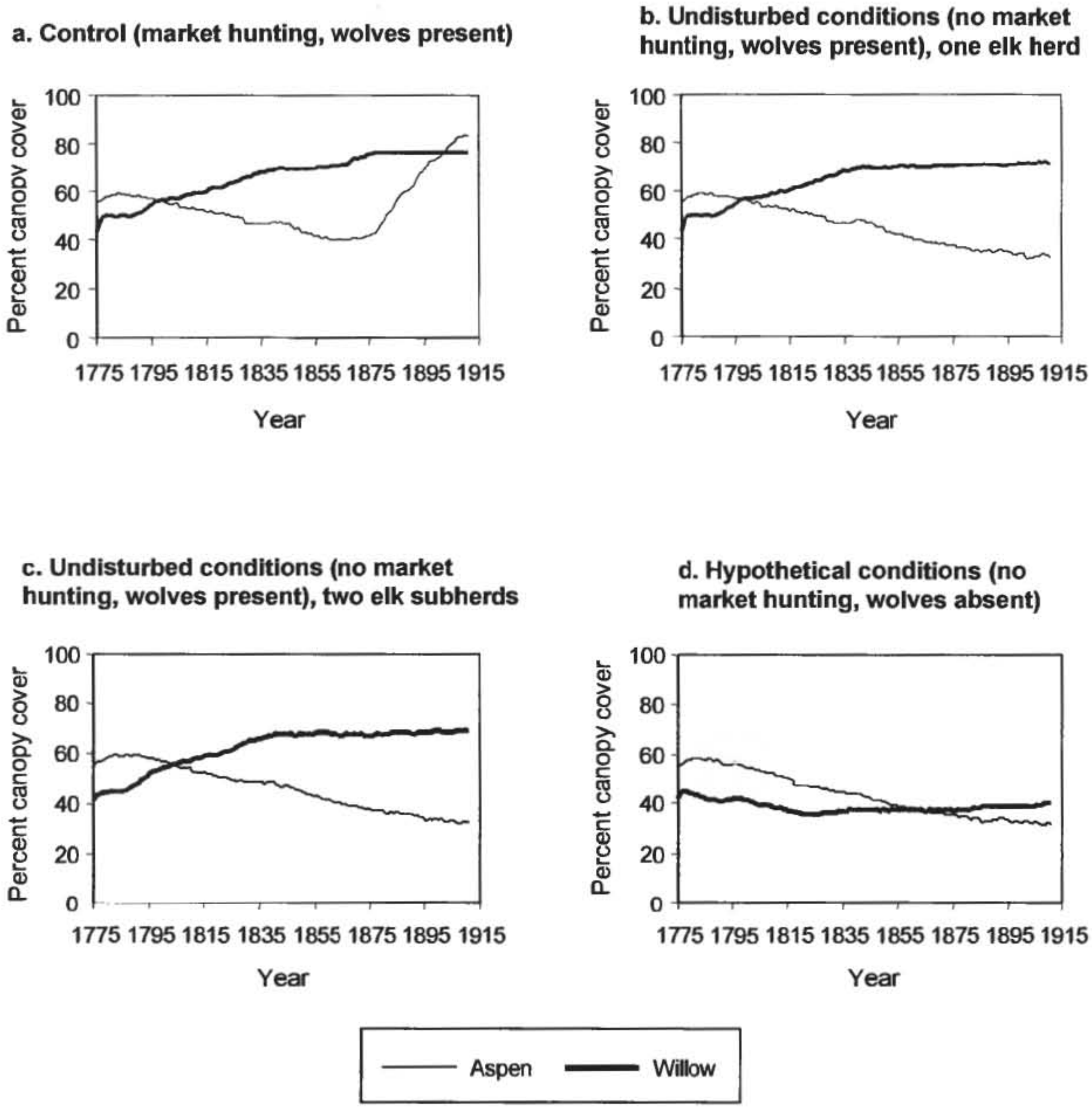


Fig. 3. Willow and aspen cover of the elk winter range of Rocky Mountain National Park and Estes Valley, Colorado, in simulations of the period 1775–1910. Cover reported as mean canopy cover within the grid-cells having those vegetation types. All simulations were conducted with undisturbed vegetation and water table conditions.

run with wolves, aspen remained steady at the low initial value, suggesting that aspen would be present at lower abundances in some locations on the core winter range.

The assessment of 1911–1948 revealed the importance of human disturbances both before and after 1911, in moving the system into what could be considered to be an alternate stable state. Livestock grazing, draining of wetlands, removal of elk and wolves, and compression of elevated numbers of beaver into reduced willow cover, all combined to reduce willow cover in Moraine and Horseshoe Parks further. Aspen declined as well, due to the combined effects of elk and beaver, but the initial presence of some of the aspen that declined in this period could have been a product of earlier elk extirpation.

Effects of Elk, Elk Management, and Simulated Wolf Predation (1948–1998)

Simulation experiments for 1949–1998 were intended to investigate the effects of elk, elk management, and wolves. In these runs, two elk populations and ranges were simulated, the park and the town populations. The first experiment was to allow elk populations to grow unchecked. The park population grew to a food-limited carrying capacity earlier than in the control run, and food-limited population sizes were slightly higher in the 1960s and 1970s than in the 1980s and 1990s. Food-limited carrying capacity of the park subherd appeared to be in the range of 1,000–1,300 elk. The town population increased to a slightly higher level than in the control run (1,900 vs. 1,800) before declining. In the undisturbed run with wolves, the park elk population was held to 300–500. The town population increased from 1,000 to 1,800, but then predation decreased the population to about 1,200. Wolf numbers varied between 14–17 throughout. Elk body condition in the run with no elk reductions was lower in winter than in the control run, throughout the simulation. In the undisturbed run, body condition was maintained at a higher level, with the exception of several severe winters.

When elk and deer were not reduced, there was about 10% less grass and 30% less forb biomass on drylands than in the control run by the end of the period. These results are consistent with Buttery's (1955) observations of modest increases in range conditions in some areas due to elk removals. In the undisturbed run, there was about 8% more grass and 5% more forb biomass than in the control run. Willow cover decreased with no elk reductions, while it remained constant in the control. In the undisturbed run, willow cover increased. All willow locations in the undisturbed run attained cover >60%. Reducing water tables had a negative effect on willow cover at three of the locations, but cover at those locations declined to lower values with elk than without elk. In additional experiments conducted to further examine the effects of water table levels, using undisturbed water tables led to an increase in willow compared to the control run which used current water table conditions. Conversely, switching to current water table conditions in the otherwise undisturbed run led to markedly lower willow covers. In the control simulation, aspen cover declined about 15%. With no elk reductions, the decline occurred earlier. In the undisturbed run with wolves, aspen cover also declined due to elk herbivory. In a hypothetical simulation with no elk present, aspen increased.

It seems likely, therefore, that the elk reductions in the 1940s–1950s brought about modest range improvement, and protected some, but not all willows and aspen. The reductions did not appear to have led to a restoration of willow to its former range, primarily because elk reductions do not address the problem of lowered water tables. While the elk reductions would have created opportunities for aspen recruitment in some areas, it seems unlikely that they would have promoted aspen regeneration on the primary elk concentration areas. While there is some evidence that elk reductions promoted aspen regeneration (Olmsted 1979; Baker et al. 1997), the spatial locations of such regeneration are critical to this interpretation. For example Stevens (1980) suggested that regeneration occurred in places where elk were shot and thus avoided using, and Olmsted (1979) showed that aspen only regenerated in areas with <50% utilization by elk.

Experiments with Elk and Beaver Densities

A factorially designed experiment was conducted in which elk and beaver densities were varied in all possible combinations, to assess their relative effects on plants. A response surface of willow cover generated from the results showed that elk and beaver can both have negative effects, but beaver effects are negligible at low elk densities. Increasing beaver had little impact on willow below 400 elk. In the range of predator-limited elk carrying capacity (400–800 elk), less than 450 beaver had little impact on willow.

Alternative Elk Management and Vegetation Fencing Scenarios

Alternative elk management and vegetation fencing scenarios were simulated by running the model for 50 years, starting in 1994, using weather randomly selected from data for the period 1949–1998. All runs began with current conditions, including current herbivore numbers, willow sizes and densities, and soil water table depths. There were three elk reduction scenarios. The park elk subherd was either never reduced, reduced to 600–800, or reduced to 200–400. In all elk reduction scenarios, the town population was reduced to 1,000–1,200. Beaver were assumed to start at current levels, and then gradually be restored to historic levels (450) over a 25-year period. Aspen and willow within the park boundary were either unfenced, or fenced to exclude elk and deer, but not beaver herbivory.

With no reductions of the park or town elk subherds, the park elk population fluctuated between 800–1,100 animals, consistent with the range previously estimated to be the food-limited carrying capacity (Fig. 4a). The town population increased at first to 2,400, then varied between 1,400–2,000. Fencing all of the willow and aspen inside the park reduced the food-limited carrying capacity of the park population by approximately 30–40% (Fig. 4b). Elk body condition in the winter was low when elk were not reduced. Reducing elk to 600–800 raised winter body conditions moderately, while reductions to 200–400 raised body conditions markedly.

Dryland herbaceous biomass remained essentially constant when elk were not reduced. However, when elk were reduced to 600–800, biomass increased slowly, over the entire period. Reducing elk to 200–400 caused a faster rate of biomass increase, and biomass was still increasing after 50 years. Fencing had no discernable effects on dryland herbaceous biomass. Without fencing, aspen declined to similar levels irrespective of elk reductions (Fig. 5a,c,e). During the years when aspen were protected by fencing, cover increased markedly (Fig. 5b,d,f). However, when the fence was removed, aspen began to decline once again, in all elk reduction treatments. Willow continued to decline when elk were not reduced (Fig. 5a), increased slightly when elk were reduced to 600–800 (Fig. 5c), and markedly increased when elk were reduced to 200–400 (Fig. 5e). Fencing resulted in a large increase in willow cover irrespective of reductions (Fig. 5b,d,f). After the fence was removed, willow began to decline when elk were not reduced and when reduced to 600–800 (Fig. 5d). In contrast, when elk were reduced to 200–400, willow cover remained at a high level after the fence was removed (Fig. 5f).

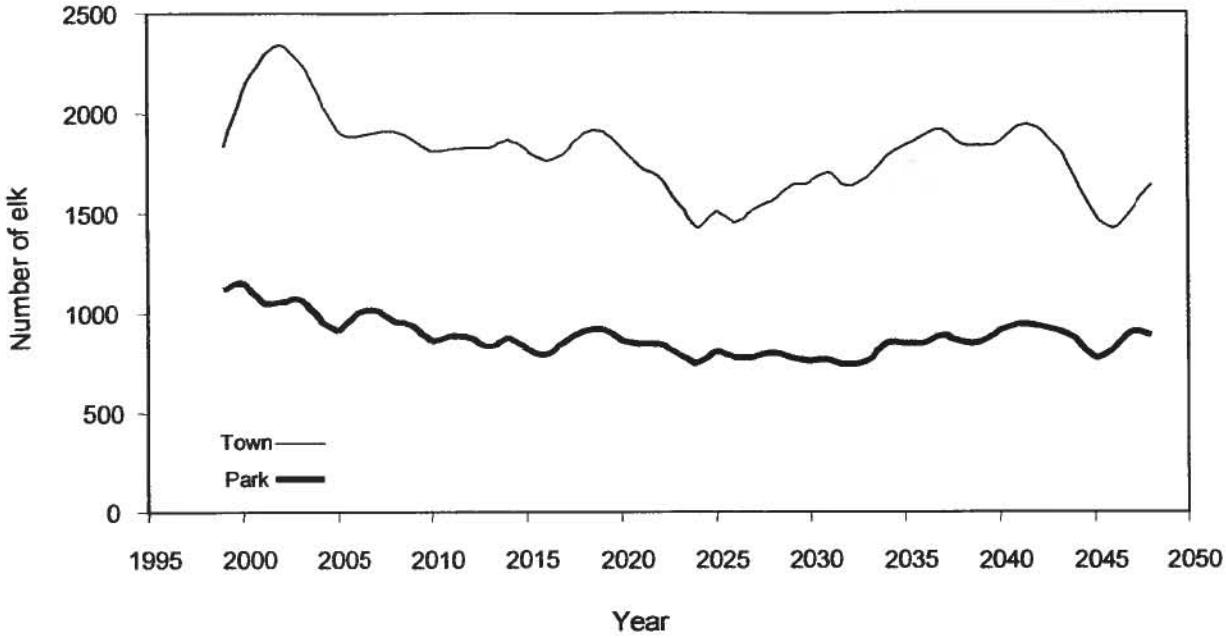
Increasing water table heights had little positive benefit when elk were not reduced and willow were unprotected by fencing (Fig. 6a). With fencing, the added water supported higher willow cover during the fenced period, which was sustained after the fences were removed, even with no elk reductions (Fig. 6b). With no fencing, higher water tables led to small increases in willow cover when elk were reduced to 600–800, and larger increases in willow cover when elk were reduced to 200–400 (Fig. 6c,e). With fencing, high water tables led to further increases in willow cover when fences were removed, and elk were reduced (Fig. 6d,f). Increased water table depth had no effect on aspen, because it was assumed that elevated water tables only occurred in riparian willow and wet meadow habitats, and not in aspen habitats.

Beginning with current vegetation, soil water table depths, and elk numbers, a hypothesized wolf reintroduction quickly reduced elk numbers in both the town and park subherds. After 15 years, the system stabilized at 14 wolves, about 200 elk in the park population, and about 1,000 elk in the town population. Wolves held elk to lower levels in future vs. historic runs because of deteriorated range conditions. Deer were held to 200.

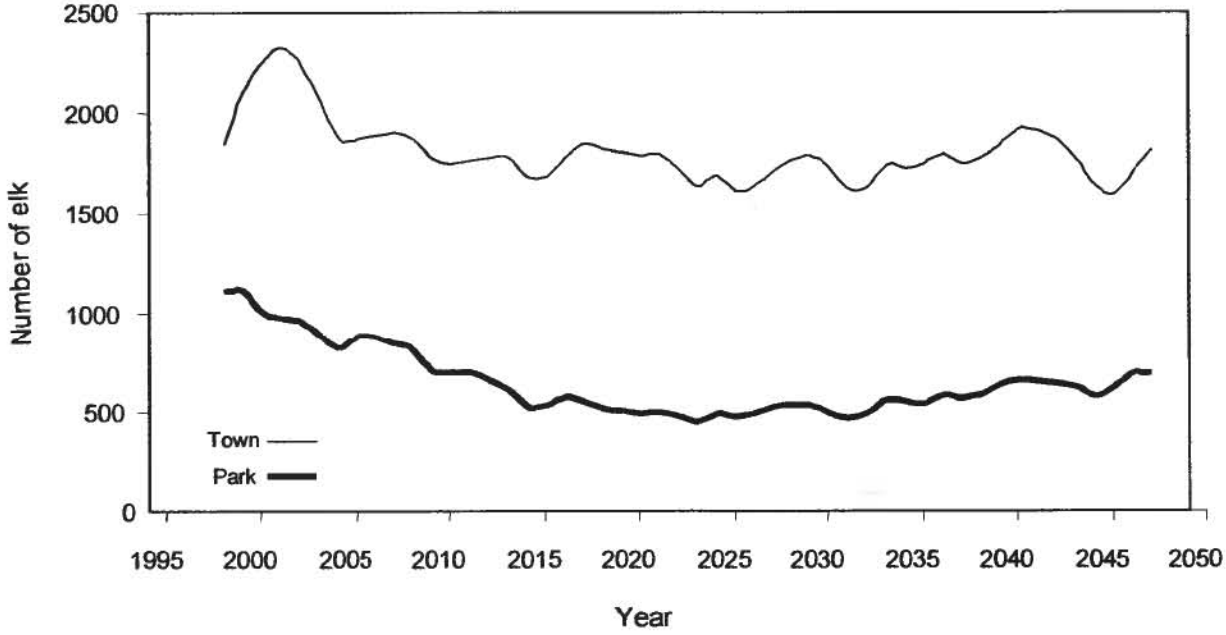
The assessment of alternative management scenarios showed that a marked elk reduction to levels which may be lower than those present in pre-settlement times, or fencing, would achieve a recovery of willow, but only in locations where water tables are still elevated. Reintroduction of beaver or other manipulations to raise water tables would be required to achieve a complete recovery. Aspen cover could be increased by fencing or severe elk reductions, however, elk numbers would have to be maintained very low, or once fences are taken down, aspen cover on the core winter range would again decline.

Sensitivity to Wolf Submodel Parameters

Simulations were performed to examine sensitivity to the wolf submodel parameters. The model was particularly sensitive to the parameter that represents how wolves control their own density through territoriality, the fraction of prey mortality that is compensatory vs. additive, and the way predation is distributed among age/sex classes. It was possible to find plausible parameter values that resulted in diminished or no effects of predation on elk population size, as well as values that resulted in lower elk numbers than noted above.

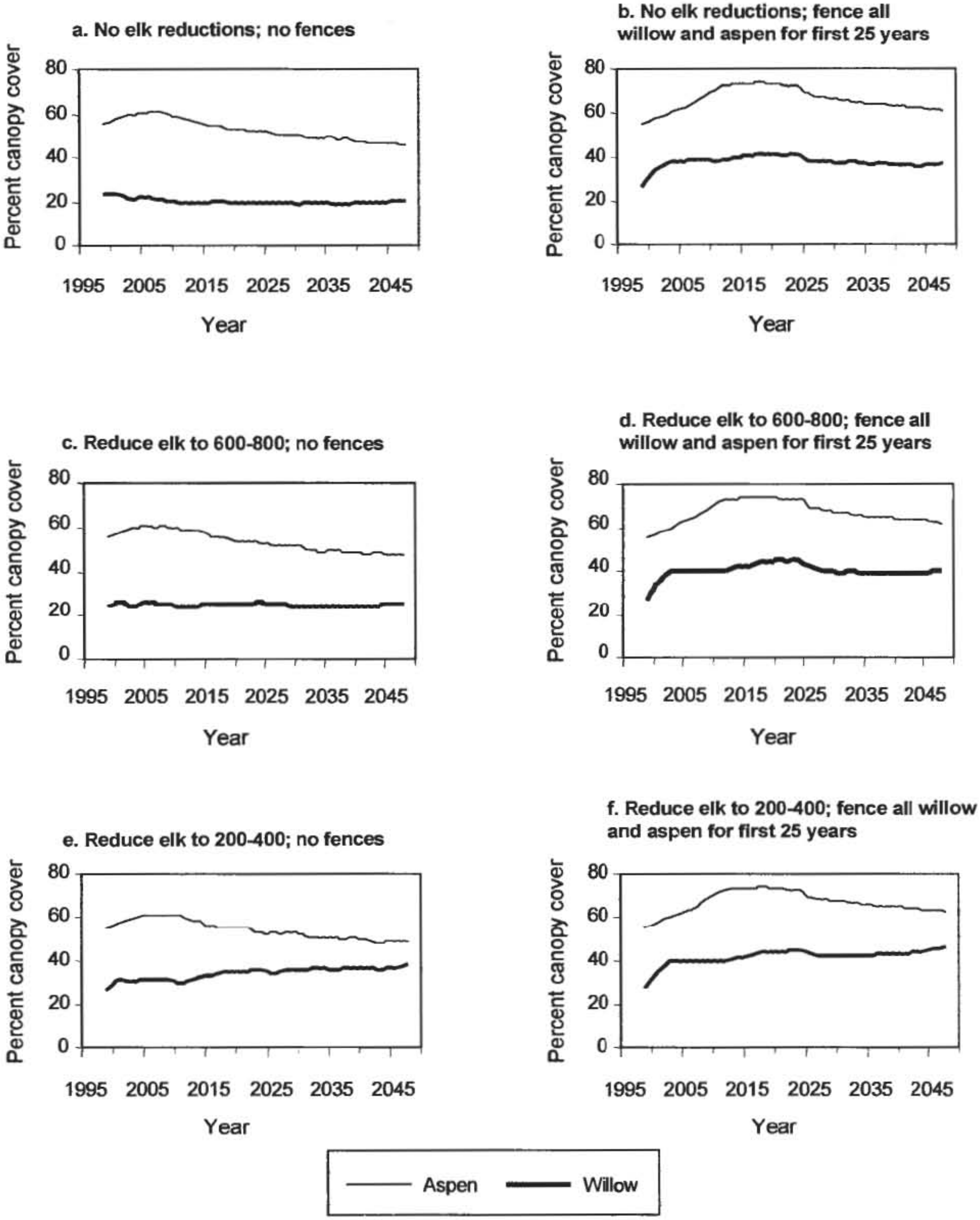


a. No elk reductions; no fences



b. No elk reductions; fence all willow and aspen inside the park for first 25 years

Fig. 4. Elk population dynamics under different future management scenarios for the elk winter range population of Rocky Mountain National Park and the Estes Valley, Colorado. Beaver population dynamics are prescribed, and are gradually restored to natural levels by 2030. (a) No elk reductions, no fencing; and (b) no elk reductions, fence all willow and aspen inside the park for the first 25 years. Elk reduction scenarios are not shown because elk populations in the park were held at either 600–800 or 200–400 animals (depending on the scenario) and the town population was held between 1,000–1,200.



a. No elk reductions; no fences

b. No elk reductions; fence all willow and aspen for first 25 years

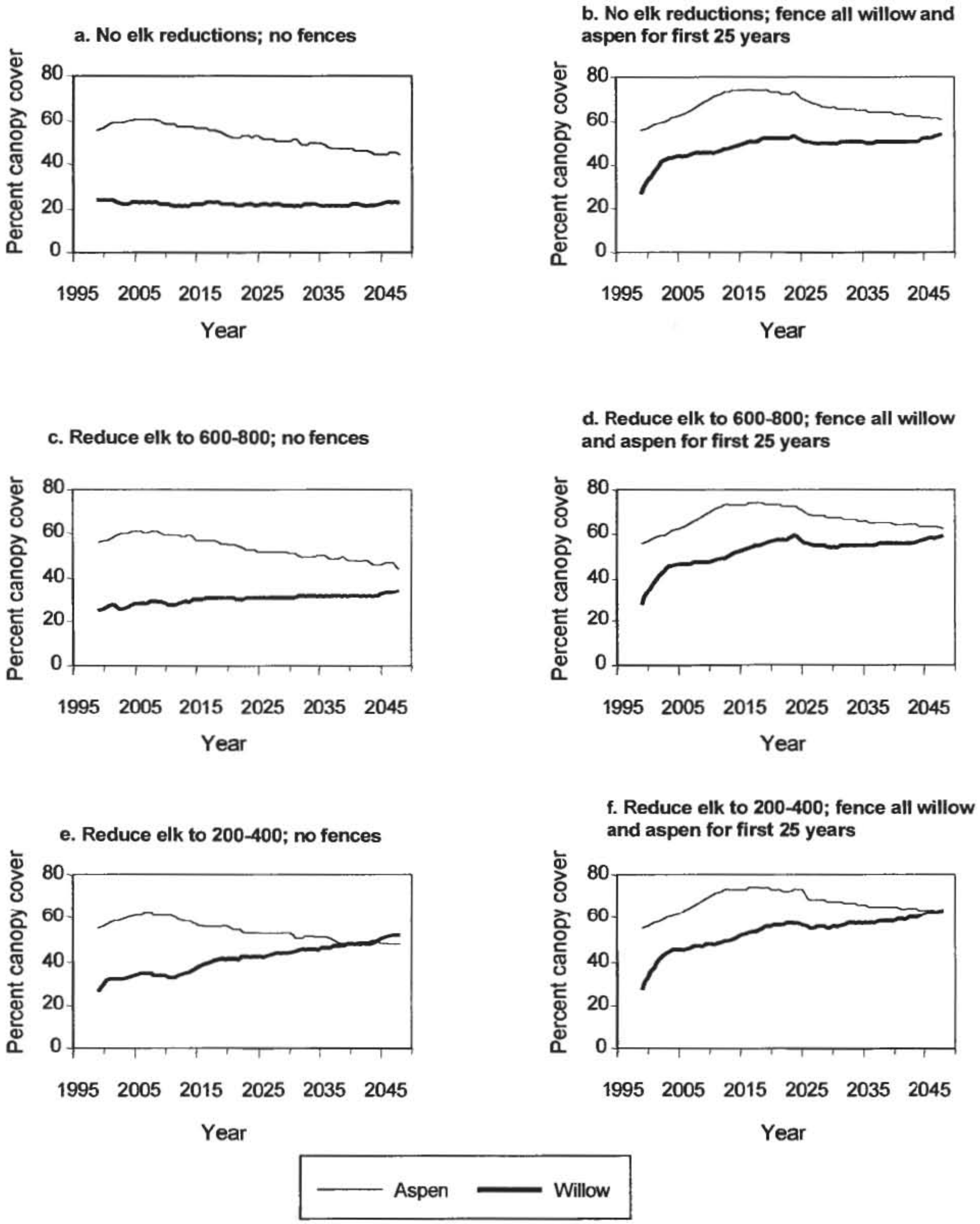
c. Reduce elk to 600-800; no fences

d. Reduce elk to 600-800; fence all willow and aspen for first 25 years

e. Reduce elk to 200-400; no fences

f. Reduce elk to 200-400; fence all willow and aspen for first 25 years

Fig. 5. Responses of willow and aspen to management scenarios for the elk winter range population of Rocky Mountain National Park and the Estes Valley, Colorado, using randomly selected weather from 1949–1998 and current water tables, for 50 years expressed as mean canopy cover within grid-cells of that vegetation type. See Fig. 6 for the same model scenarios with increased water tables.



a. No elk reductions; no fences

b. No elk reductions; fence all willow and aspen for first 25 years

c. Reduce elk to 600-800; no fences

d. Reduce elk to 600-800; fence all willow and aspen for first 25 years

e. Reduce elk to 200-400; no fences

f. Reduce elk to 200-400; fence all willow and aspen for first 25 years

Fig. 6. Responses of willow and aspen to management scenarios for the elk winter range population of Rocky Mountain National Park and the Estes Valley, Colorado, using randomly selected weather from 1949–1998 and increased water tables, for 50 years expressed as mean canopy cover within grid-cells of that vegetation type. See Fig. 5 for the same model scenarios with current water tables.

The model showed that the situation in RMNP is more complex than the simple plant-herbivore equilibrium predicted by natural regulation theory. While the elk-grassland subsystem may reach an equilibrium, that equilibrium would probably not have developed in the presence of wolves and other predators. Instead, a different dynamic equilibrium would be expected, involving interactions among three trophic levels. It would not be totally accurate to refer to this as a predator-limited number of elk, because the productivity of the forage base also has an influence. In a more productive system, there would be more herbivores and more predators alike, up until a limit on predator and possible herbivore numbers imposed by other factors aside from food, such as behavioral spacing. Because the tri-trophic equilibrium involves fewer elk than the bi-trophic equilibrium, there could be ramifications for plant species that are not necessarily limiting the elk population in a bi-trophic system, in particular aspen and willow.

Management Implications

Management of ungulates in U.S. National Parks is directed by the enabling legislation of the U.S. Congress (the Organic Act of 1916) which states that National Parks are "to conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such a manner and by such means as will leave them unimpaired for future generations." In this view, managers must conserve the vegetation structure that was a product of pre-settlement climate, soils, and ungulate herbivory. In Yellowstone and RMNP, this vegetation structure is thought to be characterized by greater abundances of aspen and willow than are present at the food-limited carrying capacities of their elk populations. Another view places more emphasis on the conservation of natural processes, and recognizes that ecosystems are dynamic, not static entities (Houston 1982; McNaughton 1996; Boyce 1998; Sinclair 1998; Huff and Varley 1999). National Park Service Management Policies (NPS 2001) state that the Service will try to maintain all the components and processes of naturally evolving park ecosystems, and will rely on natural processes to maintain native species and natural fluctuations in populations whenever possible. Natural processes are those which characterize ecosystems in general, rather than a specific ecosystem at a certain point in time. Thus, there is a fundamental policy discord, between a strict reading of the NPS Organic Act, and what many believe is a more modern and scientifically informed view about ecosystem dynamics in nature.

Ultimately the choice of elk management tactics reduces to a decision between trying to reconstruct, and then maintain, the vegetation structure which is believed to have been characteristic of the pre-settlement ecosystem, or allowing ecosystem processes to unfold with a minimal amount of human intervention so long as indigenous species are conserved. The question of which would be more natural or desirable cannot be answered here. The model provided insight into how a pre-settlement ecosystem might have looked and functioned, but it did not consider whether or not such an ecosystem is natural in the present time, most appropriate to NPS policies, or desirable to the American people who are the true owners of RMNP.

Literature Cited

Baker, D. L., and N. T. Hobbs. 1982. Composition and quality of elk summer diets in Colorado. Journal of Wildlife Management 46:694–703.

Baker, W. L., J. A. Munroe, and A. E. Hessl. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 290:155–165.

Benedict, J. B. 1992. Footprints in the snow: High-altitude cultural ecology of the Colorado Front Range, USA. Arctic and Alpine Research 24:1–16.

Benedict, J. B. 1999. Effects of changing climate on game-animal and human use of the Colorado high country (USA) since 1000 BC. Arctic, Antarctic, and Alpine Research 31:1–15.

Berry, J., D. Decker, J. Gordon, R. Heitschmidt, D. Huff, D. Knight, W. Romme, and D. Swift. 1997. Science-based assessment of vegetation management goals for elk winter range. Environment and Natural Resources Policy Institute, Colorado State University, Ft. Collins.

Boone, R., M. B. Coughenour, K. A. Galvin, and J. E. Ellis. 2001. Addressing management questions for Ngorongoro Conservation Area, Tanzania, using the Savanna modeling system. African Journal of Ecology. In press.

Boyce, M. S. 1993. Predicting the consequences of wolf recovery in Yellowstone National Park. Pages 234–269 *in* R. S. Cook, editor. National Park Service Science Monograph No. 22.

Boyce, M. S. 1998. Ecological-process management and ungulates: Yellowstone's conservation paradigm. Wildlife Society Bulletin 26:391–398.

Boyce, M. S., and J. M. Gaillard. 1992. Wolves in Yellowstone, Jackson Hole, and the North Fork of the Shoshone River: Simulating ungulate consequences of wolf recovery. Pages 4.75–4.115 *in* J. Varley and W. G. Brewster, editors. Wolves for Yellowstone? A report to the U.S. Congress. Vol. IV, Research and Analysis. National Park Service, Yellowstone National Park.

Buckley, D. J., F. Schreiner, M. Coughenour, and C. Blyth. 1995. The ecosystem management model: Integrating ecosystem simulation modeling and Arc/Info in Parks Canada. *In* GIS and environmental modeling: Progress and research issues. Proceedings of the Second International Conference on Integrating GIS and Ecological Modeling, Breckenridge, Colo.

Buttery, R. F. 1955. Range conditions and trends resulting from winter concentrating of elk in Rocky Mountain National Park. M.S. Thesis. Colorado State University, Ft. Collins.

Coughenour, M. B. 1992. Spatial modeling and landscape characterization of an African pastoral ecosystem: A prototype model and its potential use for monitoring drought. Pages 787–810 *in* D. H. McKenzie, D. E. Hyatt, and V. McDonald, editors. Ecological Indicators, Volume 1. Elsevier Applied Science, London and New York.

Coughenour, M. B. 1993. The SAVANNA landscape model – documentation and user's guide. Natural Resource Ecology Laboratory, Colorado State University, Ft. Collins.

Coughenour, M. B. 2000. Ecosystem modeling of the Pryor Mountain Wild Horse Range. Report to USGS, Biological Resources Division, National Park Service, and Bureau of Land Management. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins. 55 pp + 100 figs.

Dixon, J. S. 1939. The elk problem at Rocky Mountain National Park. Typewritten. Files at Rocky Mountain National Park.

Estes, M. 1939. The memoirs of Estes Park. Colorado State College Library, Library Bulletin No. 6. Fort Collins, Colo. (Reprinted in: Colorado Magazine 16[4]:121–132).

Fisk, M. C., S. K. Schmidt, and T. R. Seastedt. 1998. Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. Ecology 79:2253–2266.

Fritts, H. C. 199la. Reconstructing large-scale climatic patterns from tree-ring data: A diagnostic analysis. University of Arizona Press, Tucson.

Fritts, H. C. 1991b. Large scale climate reconstructions from tree-rings. International Tree-Ring Data Bank. IGBP PAGES/World Data Center-A for Paleoclimatology Data Contributions Series #91-011. NOAA/NGDC Paleoclimatology Program. Boulder, Colo.

Fryxell, F. M. 1928. The former range of the bison in the Rocky Mountains. Journal of Mammalogy 9:129–139.

Gense, J. 1997. Unpublished data. Files, Rocky Mountain National Park.

Guse, N. G., Jr. 1966. Administrative history of an elk herd. M.S. thesis. Colorado State University, Ft. Collins.

Gysel, L. W. 1960. An ecological study of the winter range of elk and mule deer in the Rocky Mountain National Park. Journal of Forestry 58:696–703.

Hess, K. Jr. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot.

Hickman, S. D. 1964. A beaver census of Moraine Park, Rocky Mountain National Park. Unpublished, Colorado State University. 15 pp.

Hobbs, N. T. 1979. Winter diet quality and nutritional status of elk in the upper montane zone, Colorado. PhD. dissertation, Colorado State University, Ft. Collins.

Houston, D. B. 1982. The northern Yellowstone elk: Ecology and management. MacMillan Press.

Huff, D. E., and J. D. Varley. 1999. Natural regulation in Yellowstone National Park's northern range. Ecological Applications 9:17–29.

Keigley, R. B., and F. H. Wagner. 1998. What is natural? Yellowstone elk population, a case study. Integrated Biology 1:133–148.

Kiker, G. A. 1998. Development and comparison of Savanna ecosystem models to explore the concept of carrying capacity. PhD. thesis, Cornell University, Ithaca, New York.

Loring, J. A. 1893. Field notes on a trip to Estes Park, May 28 to June 3, 1893. U.S. Biological Survey.

Ludwig, J. A., M. B. Coughenour, A. C. Liedloff, and R. Dyer. 1999. Modeling the resilience of Australian savanna systems to grazing impacts. Pages 771–776 *in* L. Oxley, F. Scrimgeour, and A. Jakeman, editors. MODSIM 99, International Congress on Modeling and Simulation Proceedings. Vol. 3. Modeling Society of Australia and New Zealand, Inc.

McCool, M. J. 1995. Classification of the Cache La Poudre watershed using Landsat thematic mapper data and ancillary spatial data. M.S. thesis. Colorado State University, Ft. Collins.

McLaughlin, J. S. 1931. First annual spring wildlife report. Typewritten files. Rocky Mountain National Park.

McNaughton, S. J. 1996. Book review – Wildlife policies in the U.S. National Parks. Journal of Wildlife Management 60:685–687.

Mills, E. A. 1924. The Rocky Mountain National Park: A history. Colorado Associated University Press, Boulder.

National Park Service. 2001. Management policies. U.S. Government Printing Office. Washington, D.C.

Olmsted, C. E. 1977. The effect of large herbivores on aspen in Rocky Mountain National Park. M.S. thesis. University of Colorado, Boulder.

Olmsted, C. E. 1979. The ecology of aspen with reference to utilization by large herbivores in Rocky Mountain National Park. Pages 89–97 *in* M. S. Boyce and L. Hayden-Wing, editors. North American elk. University of Wyoming Press.

Olmsted, C. E. 1997. Twenty years of change in Rocky Mountain National Park elk winter range aspen. Report to U.S. National Park Service, Rocky Mountain National Park.

Packard, F. M. 1942. Wildlife and aspen in Rocky Mountain National Park, Colorado. Ecology 23:478–482.

Packard, F. M. 1947a. A study of the deer and elk herds of Rocky Mountain National Park, Colorado. Journal of Mammalogy 28:4–12.

Packard, F. M. 1947b. A survey of the beaver population of Rocky Mountain National Park, Colorado. Journal of Mammalogy 28:219–227.

Peinetti, H. R. 2000. Riparian willow dynamics and their interaction with environmental and biological factors in the elk winter range of Rocky Mountain National Park (Colorado) – a multiscale analysis. PhD. dissertation. Colorado State University, Ft. Collins.

Ratcliff, H. M. 1941. Winter range conditions in Rocky Mountain National Park. Transactions of the North American Wildlife and Natural Resources Conference 6:132–139.

Riordan, L. E. 1948. Deer-elk survey. Colorado Game and Fish, Federal Aid Quarterly Report, pp 14–30.

Sage, R. 1846. Scenes in the Rocky Mountains, and in Oregon, California, New Mexico, Texas, and the grand prairies; or, Notes by the way, during an excursion of three years, with a description of the countries passed through, including their geography, geology, resources, present condition, and the different nations inhabiting them. By a New Englander. Carey & Hart, Philadelphia.

Sinclair, A. R. E. 1998. Natural regulation of ecosystems in protected areas as ecological baselines. Wildlife Society Bulletin 26:399–409.

Singer, F. J., T. Elliot, M. Coughenour, J. Welker, D. Binkley, D. Valentine, S. Williams, L. Zeigenfuss, K. Alstad, M. Kaye, R. Menezes, R. Peinetti, and R. Rochelle. 1999. Large mammalian herbivores, plant interactions, and ecosystem processes in Rocky Mountain National Park. Fourth Annual Report. U.S. Geological Service, Biological Resources Division, Ft. Collins, Colo.

Singer, F. J., G. Wang, and N. T. Hobbs. 2002. The role of grazing ungulates and large, keystone predators on plants, community structure, and ecosystem processes. *In* R. G. Anthony and C. Zabel, editors. Large mammal communities in U.S. western coniferous forests. Cambridge University Press.

Sprague, A. E. 1925. Game more plentiful now than 50 years ago in Estes Park region. Estes Park Trail. June 5, 1925.

Stevens, D. R. 1980. The deer and elk of Rocky Mountain National Park: A 10-year study. ROMO-13. Report to National Park Service, Rocky Mountain National Park.

Stevens, D. R., and S. Christianson. 1980. Beaver populations on east slope of Rocky Mountain National Park. Special report. U.S. National Park Service. Rocky Mountain National Park.

Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9:45–64.

Todd, S. W. 1995. Classification of the Laramie and Big Thompson watersheds using Landsat 5 TM imagery and ancillary GIS digital data. Colorado Division of Wildlife.

Wagner, F., R. Foresta, R. B. Gill, D. R. McCullough, M. R. Pelton, W. F. Porter, and H. Salwasser. 1995. Wildlife policies in the U.S. national parks. Island Press, Washington, D.C.

Warren, G. A. 1926. Notes on the beaver in Estes Park, Colorado. Roosevelt Wildlife Annals 1:193–234.

Zeigenfuss, L. C., F. J. Singer, and D. Bowden. 1999. Vegetation responses to natural regulation of elk in Rocky Mountain National Park. Biological Science Report USGS/BRD/BSR1999-0003. U.S. Government Printing Office, Denver, Colo.

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A research initiative was conducted 1994 to 1999 in Rocky Mountain National Park, Colorado by the U.S. Geological Survey and Natural Resources Ecology Laboratory (of Colorado State University) to evaluate the number, trends, and ecological effects of elk (*Cervus elaphus*) in the park and adjacent Estes Valley. This report consists of two sections (Empirical Findings and Modeling) and 12 chapters that detail the findings of this large and comprehensive research initiative.

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