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RESPONSE OF COLORADO TALLGRASS PRAIRIE TO FIRE, WINTER GRAZING, AND NITROGEN MANIPULATION

by

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ABSTRACT

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Response of Colorado Tallgrass Prairie to Fire, Winter Grazing, and Nitrogen Manipulation

Thesis directed by Professor Timothy R. Seastedt

Keywords: ecology, tallgrass prairie, fire, grazing, fertilization, reverse fertilization, nitrogen, biomass, conservation, plant species, land management

This study examined management alternatives for conservation of Colorado tallgrass prairie. Fire, winter grazing and nitrogen manipulation were compared in a three-way factorial design at two sites. Plots were treated and monitored from 1993 to 1996. Fire treatments were applied in April and May. Winter grazing allowed cattle between December and May. Nitrogen treatments included fertilization and reverse fertilization (carbon addition to immobilize nitrogen). Responses included changes in soil temperature, moisture and nitrogen; aboveground plant biomass, and plant species composition.

Nitrogen was expected to limit production and control vegetation responses to fire and winter grazing. Data suggested that moisture limited production and controlled vegetation responses to treatments. Plots that were irrigated, or winter -grazed, were cooler and wetter than other plots. Burned plots were warmer at the non-irrigated site.

Fire and reverse fertilization were both expected to reduce nitrogen and exotic cover. Reverse fertilization reduced ammonium and fire showed a similar trend. However, neither treatment affected native or exotic stem density or cover. Fire increased native species diversity. Reverse-fertilization reduced overall species diversity and forb stem density, but increased C_4 grass cover.

Productivity was related both to resource availablity, and cover frequency of the highly productive native C_4 grasses that dominate tallgrass prairie. Winter grazing increased production at the irrigated site by increasing cover of native C_4 grasses. Fertilization failed to stimulate production because it induced species shifts reducing native C_4 grass cover. Fire increased biomass only at the irrigated site in the wettest year. Typical treatment responses for Colorado tallgrass were consistent with drought year treatment responses in eastern tallgrass prairie. At the non-irrigated site, winter grazing, like chronic grazing, reduced production and forb stem density. At the irrigated site, however, winter grazing differed from chronic grazing, increasing production, native species diversity, native cover, and C_4 grass cover.

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CHAPTER 1

Introduction

COLORADO TALLGRASS PRAIRIE

Colorado tallgrass prairie is a relict of tallgrass prairies which extended across the great plains in the early Holocene 10,000 to 8,000 yBP. Axelrod (1985) suggests that an altithermal drying period between 9,000 and 7,000 yBP separated these relicts from the mainland tallgrass prairie. As the climate became drier, upland vegetation in the central and western great plains areas shifted to the short and mixed grass plains seen today from Canada to Texas.

The effects of this warming were likely ameliorated along the Front Range where the Pinedale Glacial period had just ended. Pollen evidence (Maher 1972) suggests that warming did not occur along the Front Range until 7,600 yBP, so this area could have become a refugia for mesic species during the altithermal. Conditions along the Front Range between 7,600 and 6,700 yBP were similar to those of the past 3,000 years (Maher 1972) and could have supported the present tallgrass prairie distribution. While high altitude areas experienced neoglacial conditions between 6,700 and 3,000 yBP Markgraf & Scot (1981) suggest that the Front Range may have been warm & dry with strong monsoonal rains. Those conditions would be ideal for tallgrass species, which may have expanded their range during that period.

Presently tallgrass species persist in mesic bottomlands and on sand hills throughout the Great Plains. Just east of Colorado's Front Range, tallgrass prairie relicts survive in rocky alluvium (Branson, et al. 1965) or seasonally wet areas fed by natural streams or modern irrigation (Chapter 2). However, most of the Colorado tallgrass prairie, like the mainland tallgrass prairie, was plowed, converted to exotic grasses, or lost to urban and suburban development. Only that used for grazing survived. Many relict tallgrass prairie sites continue to be threatened directly by development and invasion by exotic weeds, and indirectly by diversion of water resources.

OBJECTIVES

This study was motivated by the desire of the City of Boulder Open Space department to determine which land management strategies would best conserve existing tallgrass prairie sites. This study was conducted at three tallgrass prairie sites owned by the City of Boulder. Figure 1.1 shows the location of the study sites with relation to Boulder, Eldorado Springs, and nearby foothills of the Front Range. Study sites are further described in Chapter 4. Because previous studies have shown that wildlife use of tallgrass prairie is directly related to habitat quality (Marcot and Mannan 1992) , this effort concentrated on conserving plant structure and diversity. Conservation goals include increasing the cover and biomass of native plants relative to exotics; increasing native plant diversity; and promoting tall, dense stands of flowering stems.

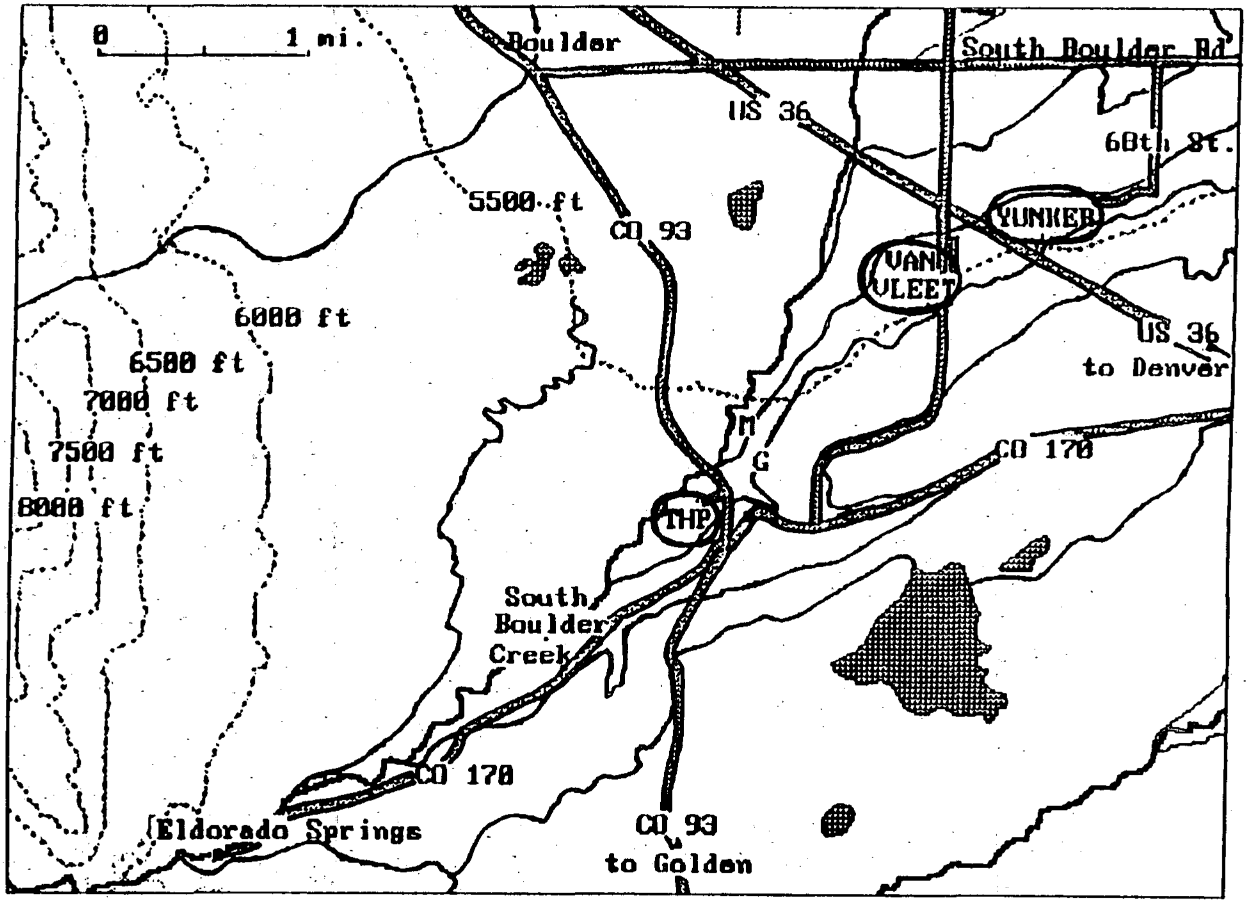

Figure 1.1 - Map of Study Sites.
Circled labels show study sites, THP, Van Vleet, and Yunker. M designates the Marshallville irrigation ditch and G indicates the Goodhue irrigation ditch. Foothills of the Front Range are shown in topographic contours in the western area of the map. Sites are desribed in detail in Chapter 4.

Pursuit of these goals entailed comparing various land management regimes and assessing their value as restoration/conservation treatments. Treatments compared included a full factorial comparison of the effects of three land management treatments: two periodic disturbance treatments, fire and winter grazing, and a nitrogen manipulation treatment. Both fire and winter grazing treatments had only two levels, treated and not treated. The nitrogen manipulation treatment had three levels: increased nitrogen availability (fertilization by nitrogen addition), no change in nitrogen availability (control), and decreased nitrogen availability (reverse fertilization by carbon addition).

Both fire and winter grazing treatments restore disturbances that occurred at these sites prior to the introduction of ranching in the 1870's. Fire probably occurred in the prairie along the Front Range every seven to ten years (Veblen and Lorentz 1991). Historical records indicate that bison, deer, elk and antelope periodically grazed the local area. Local grazing pressure was probably higher in the winter because bison and elk wintered in the area, but spent summers elsewhere (Willard, 1990). Deer still use all of these tallgrass sites periodically, but the winter grazing treatment was applied using domestic cattle. And the grazing exclosure only excluded domestic ungulates.

Both fire and winter grazing were expected to benefit tallgrass prairie by removing plant standing dead and litter and favoring the warm season C_4 grasses that dominate tallgrass prairies. Removing plant litter reduces the accumulation of litter or thatch which reduces production in mainland tallgrass prairies (Hayes and Seastedt

1989). Additionally, fire or grazing in April and May damaged cool season C_3 grasses active at that time, reducing their ability to compete with the warm season C_4 grasses.

Nitrogen availability was manipulated for two reasons: first, to examine the effectiveness of reverse fertilization to control invasions by exotic weeds; second, to examine the hypothesis that differences between fire and grazing effects are due to their different effects on nitrogen availability.

This study combined pursuit of applied conservation and restoration goals with examination of ecosystem theory. Previous studies suggest that while fire does release nitrogen previously immobilized in plant litter, losses of nitrogen to smoke actually decrease nitrogen availability in frequently burned systems. Repeated fire compounds nitrogen losses so that annually burned systems are very nitrogen limited (Eisele et al. 1989; Hobbs et al. 1991).

By contrast, chronic year round grazing has been shown to increase nitrogen availability. The continuous cycling of nitrogen from soil to plant growth to herbivore to soil increases nitrogen availability in continuously grazed systems (Holland and Detling).

However, the grazing regime for this study was not year-round grazing. Cattle were winter grazed from January through May. This seasonal grazing regime has been used to successfully maintain tallgrass pastures for over a century (Madson 1993) , and has been used at the study sites for at least the past 20-30 years. So it showed promise as a conservation management tool. Winter grazing is not equivalent to year round grazing and may produce very different effects both on plants and nitrogen availability.

The study assessed progress toward plant community conservation goals by measuring the response of plant physical structure, aboveground net primary production and community composition to the individual and combined effects of fire, winter grazing (January - May), and nitrogen manipulation (both addition and immobilization). Each of these three categories of plant community response examines a different aspect of ecosystem health. The physical structure determines the suitability of the area as wildlife habitat (Peterson, et al. 1985; Marcot and Mannan 1992). Aboveground net primary production is an overall index of ecosystem health (Seastedt, et al. 1991). Community composition indicates the extent of exotic invasion, and the extent of species historically associated with this plant community or other documented tallgrass prairie plant communities.

These three aspects of plant community response provide a basis for comparison with plant communities from the main body of tallgrass prairie. Soil response also provides a basis for comparison. Soil parameters including soil moisture, mineral and microbial nitrogen, and soil organic matter were used to examine the effects of nitrogen manipulations and the role of soil parameters in mediating fire and winter grazing effects.

Comparing tallgrass prairie plant communities from Colorado to similar plant communities from the more mesic areas of the eastern Great Plains provided insight into the relative influence of biotic (plant community) and abiotic (climate and soil) factors in response to disturbance and nitrogen availability.

RESEARCH QUESTIONS

Each of the three measures of ecosystem health (aboveground net primary production, physical structure, and plant community composition) was used to test these hypotheses about the response of tallgrass prairie to fire, winter grazing, and nitrogen manipulation.

Treatment Hypotheses

1. Both fire and winter grazing benefit Colorado tallgrass prairie by reducing accumulated litter, releasing light limitations and reducing woody species
2. Both fire and winter grazing may degrade Colorado tallgrass prairie by reducing available water and providing potential invasion sites
3. Fire also benefits Colorado tallgrass prairie by reducing available nitrogen, and providing a competitive advantage to native species.
4. Grazing also degrades Colorado tallgrass prairie by increasing nitrogen availability.
5. Immobilizing nitrogen by adding carbon (reverse fertilization) benefits Colorado tallgrass prairie by reducing available nitrogen and providing a competitive advantage to native species.
6. Increasing total nitrogen by adding nitrogen (fertilization) degrades Colorado tallgrass prairie by increasing available nitrogen and providing a competitive advantage to weedy species.

Ecosystem and Restoration Ecology Questions

1. How do soil responses to treatments mediate plant responses ?
2. Which treatment responses are consistent for both Colorado and mainland tallgrass prairie and which responses show regional differences?
3. How do fire and winter grazing effects differ ?
4. How effective is reverse fertilization in controlling exotic species in Colorado tallgrass prairie ?
5. Which land management regimes best conserve Colorado tallgrass prairie?

Answering these questions provided validation of certain ecological principles in this ecosystem, illustration of the role of nitrogen availability in mediating fire and grazing effects, and specific recommendations for future management of Colorado tallgrass prairie. To address question five, treatment responses were compared with conservation goals defined below.

DEVELOPING CONSERVATION GOALS

Conserving Colorado tallgrass prairie involves controlling the plant community composition and vegetation structure. Land management treatments alter conditions to favor certain species at the expense of others. Monitoring plant species cover and aboveground biomass detects these changes in community composition. Treatments also change the vegetation structure by promoting or suppressing flowering, monitoring flowering stem density and height detects these changes.

The exact species composition of pre-agriculture Colorado tallgrass prairie is unknown but may be assumed to possess the following characteristics. First, the plant species were native to North America. Second, they included the same tallgrass species present today, namely[1] *Andropogon gerardii* Vitm., *Panicum virgatum* L., *Sorghastrum avenaceum* (Michaux) Nash[2], and associated species *Schizachyrium scoparium* Nees[3], and *Sporobolus asper* (Michaux) Kunth. Third, these tallgrass species flowered with sufficient frequency for the system to be considered "tallgrass" or “true” prairie (Daniels 1911; Vestal 1913; Vestal 1914). Flowering is important to the physical structure of tallgrass prairie because it is the flower stems, not the leaves that grow one to two meters high, providing enough cover to conceal adult deer. When tallgrass species do not flower, the grass cover is 40cm or less. From these three assumptions I generated two conservation goals: first, to maintain or increase the cover of native plants relative to exotics, and second, to promote tall dense flower stems in tallgrass species.

The value of tallgrass as habitat for animals seeking cover (Peterson, et al. 1985) and the aesthetics of tallgrass prairie (Madson 1982; Madson 1993) depend on the physical structure of the tallgrass prairie, the density and height of the flowering stems. So promoting tall, dense flowering stems in the dominant grasses promotes a habitat for wildlife endemic to the tallgrass system. Diversity of stem heights is also important for wildlife habitat (Marcot and Mannan 1992), and to maintain the patch structure (Glenn and Collins 1990) characteristic of tallgrass prairie. One way to achieve diverse stem heights is to increase species diversity.

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[1] Nomenclature in the text follows *Colorado Flora, Eastern Slope* (Weber 1993). Synonyms from the Flora of the Great Plains (Association 1986) and archaic names relevant to historically documented flora of the area will be shown in footnotes when the name first appears in the text. Synonyms are shown in Appendix D, Table D.1.

[2] *Sorghastrum nutans* Michaux (Flora of the Great Plains) (Association 1986).

[3] *Andropogon scoparium* Michaux (archaic) (Daniels 1911; Vestal 1913).

Studies in mainland tallgrass prairie have shown that tallgrass prairies have high native diversity, but are dominated by a few warm season perennial grasses. Warm season grasses follow the photosynthetic pathway, and are often referred to as C_4 grasses, to distinguish them from cool season, or C_3 grasses and herbs that follow the C_3 photosynthetic pathway. Colorado tallgrass prairie probably had diversity and dominance characteristics similar to mainland prairie, so the third and fourth conservation goals are high native diversity and dominance by the perennial C_4 grasses that were important components of the historical flora. Fortunately the dominant elements of the Boulder tallgrass flora were described as early as 1906 (Daniels 1911) and in more detail by Vestal (1913, 1914).

Conservation goals

1. Maintain or increase native cover.
2. Promote flowering of tallgrass species.
3. Maintain or increase native plant species diversity.
4. Maintain or increase dominance of perennial C_4 grasses identified as important components of the historical flora.

ORGANIZATION OF THIS DOCUMENT

Introductory material is included in this chapter. Chapters two, three, and four contain information on the responses of soil resources, productivity, and plant species composition. Chapter five describes management recommendations based on the productivity and plant community responses. Data are included in appendices, and reference materials in a bibliography. Plant species nomenclature follows Weber's Colorado Flora: Eastern Slope (1993). Table D.1 shows synonyms from the Flora of the Great Plains (Great Plains Flora Association 1986), and archaic synonyms.

CHAPTER 2

Soil Response to Fire, Winter Grazing, and Nitrogen Manipulation

ABSTRACT

Tallgrass prairie in the eastern Great Plains has been shown to respond to fire and grazing with changes in soil parameters including temperature (Weaver 1954; Collins and Wallace 1986), inorganic and microbial N (Eisele et al. 1989; Hobbs et al. 1991), and soil moisture (Weaver 1954; Collins and Wallace 1986). Colorado tallgrass prairie receives approximately half the precipitation of eastern tallgrass sites so responses to fire, winter grazing, and direct nitrogen manipulation treatments appeared to differ from those of eastern tallgrass prairie. Response patterns differed with site and sometimes with local moisture variations within site. Treatments induced effects on soil temperature, moisture, and SOM, and had little or no effect on inorganic or microbial N.

Fire increased soil temperatures at the non-irrigated site and showed a trend toward reducing ammonium in reverse fertilized and control plots. Fire had no significant effect on inorganic nitrogen or field moisture. Winter grazing reduced soil temperatures at both sites and increased field moisture in reverse fertilized plots, especially at the non-irrigated site. Winter grazing had no effect on inorganic nitrogen.

INTRODUCTION

The response of soil parameters to fire, winter grazing and nitrogen manipulation provides long-term feedbacks for plant production, structure, and community composition responses (Seastedt 1995). Assumptions about soil responses, especially nitrogen responses, provided the rationale for considering these treatments as possible conservation management tools. Evaluation of these assumptions will provide information that facilitates the interpretation of the vegetation responses considered in upcoming chapters.

Plant community response to nitrogen manipulation is assumed to be due to changes in soil nitrogen availability. The mechanisms for fire and grazing effects are less obvious, but may involve changes in soil parameters including nitrogen (Hobbs et al. 1991), moisture (Weaver 1954; Knapp and Gilliam 1985), permeability (Magier and Ravina 1984; Beatty 1989) and soil organic matter (Christensen 1987; Seastedt and Ramundo 1990). Changes in these soil parameters involve changes in ecosystem processes including nitrogen and carbon cycling (Christensen 1987; Holland and Detling 1990; Hobbs et al. 1991), primary production (Sims and Singh 1978), decomposition (Seastedt and Ramundo 1990; Hossain et al. 1995), and the weathering, leaching and fixation of nutrients (Christensen 1987; Beatty 1989; Brady 1990).

Soil and surface temperatures have been related to plant growth rates via effects on soil moisture and microbes (French and Sauer 1974), and to evaporation rates of soil moisture (Thornthwaite 1954). Litter removal by either fire or winter grazing is expected to increase soil temperature. Both surface and soil temperatures of all plots were measured periodically over a period of 62 days after fire treatments and compared to determine how fire and winter grazing affected soil temperature, and how long the effects persisted.

Addition of ammonium nitrate will increase levels of nitrogen in the short term. Over the long term this nitrogen may be stored in the soil as organic N, taken up by plants or microbes, or removed by leaching or denitrification. This experiment tested whether four years of May and June nitrogen amendments (mean $15 gN/m^2/yr$) accumulate sufficiently to increase mid-season (July) KCl extractable nitrogen significantly. It further tested whether carbon amendments ($25gC/m^2/yr$) applied to other plots at the same times reduced mid-season KCl extractable nitrogen significantly. Carbon amendments consisted of materials with high carbon-nitrogen ratios (sawdust) or no nitrogen (sugar). Microbes decomposing this material respond to nitrogen deficiency by taking up soil nitrogen that would otherwise be available to plants (Hunt et al. 1988; McLendon and Redente 1992).

Comparing the effects of nitrogen manipulation with those of fire and grazing provided insights into whether differences between fire and grazing effects are due to their different effects on soil nitrogen. Both fire and grazing remove excess plant litter, increasing light, early season soil temperatures, and evaporation. Several investigators in the eastern Great Plains (Eisele et al. 1989; Blair 1997) have found that fire reduced inorganic (plant available) nitrogen in tallgrass prairie. Year-round grazing, on the other hand, caused higher inorganic nitrogen, due largely to the rapid redistribution of nitrogen via urine deposition (Hobbs et al. 1991). Fire may have a different effect in the more arid Colorado tallgrass prairie. The effects of the winter grazing practiced here are likely to differ from the effects of year-round grazing. The grazing comparison in this study examines whether excluding all grazing from 1987 through 1996 reduced KCl extractable nitrogen, compared to continued winter grazing in prairie that has been grazed since the 1870's.

Field moisture provided an estimate of plant available water. Moisture of the sieved soil provided the fresh weight to oven dry weight correction used to report nitrogen assay results on the basis of oven dry weight, but this measurement was not used to estimate plant available water because moisture may be lost during sieving.

Comparing SOM between different treatments tested whether fire and grazing reduce SOM and whether their effects on SOM are equivalent. Comparing SOM to the availability of different forms of nitrogen also tested whether cation exchange sites on SOM increased available mid-season nitrogen or whether SOM fixed ammonium, immobilizing it and reducing the amount of nitrogen actually available to plants.

Hypotheses

From the information above, I developed the following hypotheses for the response of surface and soil temperatures to treatments. First, fire will increase surface temperature, which will remain higher than that of non-fire plots until decreased by shading due to plant growth. Second, winter grazing will increase surface temperature, which will remain higher than that of ungrazed plots until decreased by shading due to plant growth.

From the information above, I also developed the following hypotheses for the response of KCl extractable inorganic nitrogen and K_2SO_4 extractable microbial nitrogen to treatments. First, fertilization (nitrogen addition) will increase inorganic nitrogen. Second, reverse fertilization (carbon addition) will increase microbial N reducing inorganic nitrogen. Third, fire will decrease both inorganic and total nitrogen. Fourth, winter grazing will increase inorganic and total nitrogen.

Lastly, from the information above, I developed these hypotheses on the response of soil moisture to treatments. First, fertilization (nitrogen addition) and reverse fertilization (carbon addition) will have no significant effect on soil moisture. Second, fire and winter grazing will decrease soil moisture, by removing plant litter increasing temperatures and stimulating production and plant uptake.

METHODS

Study Sites

The three study sites Figure 1.1 had tallgrass plant communities containing *Andropogon gerardii*, *Panicum virgatum*, *Sorghastrum avenaceum*[1], *Schizachyrium scoparium*, and *Sporobolus asper*. Two of these sites were parcels of the Colorado tallgrass natural area. Previous and concurrent floral and faunal studies of all three sites provided additional information about these sites. Table A.3 (Appendix A) shows the subject and investigators for several recent research projects at these three sites.

I selected sites with different soils and different irrigation regimes so that results would be general enough to apply to most local tallgrass sites. Sites included both moist and xeric tallgrass prairie. Moist tallgrass prairie supports species similar to lowland tallgrass prairie in the eastern Great Plains, while the xeric tallgrass prairie supports species similar to upland tallgrass prairie. Both the wettest and the driest sites are part of the Colorado tallgrass natural area.

The two natural area sites have ungrazed areas fenced to exclude domestic grazing since 1987. Each of these grazing exclosures contained twelve plots each for a total of twenty-four ungrazed plots. Winter grazed areas at all three sites have been grazed for the past century and contain twelve plots each for a total of thirty-six winter grazed plots, and sixty plots altogether.

The wettest site, on the Yunker II property (natural area parcel 6), is north of the Boulder turnpike and southwest of the Whaley drive cul de sac. The site is on Hargreave clay loam soil (50 - 100 cm deep) on Fox Hills-Laramie sandstone (a large and important aquifer). The site is both subirrigated and surface irrigated from the Goodhue ditch. Grazed areas are part of a 97 hectare area winter grazed by cows and calves from December to May. Plot locations and treatments in the ungrazed exclosure at this site are shown in Figure A.1 (Appendix A). Plot locations for the grazed area are shown in Figure A.2 (Appendix A).

The driest site, THP (natural area parcel 3), is west of the Sans Souci mobile home park on Nederland very cobbly loam soil (deeper than 2.5 m and 78-95% rock). A map showing plot locations and treatments for the ungrazed area at this site is shown in Figure A.3 and the grazed area is shown in Figure A.4.

This site is in the South Boulder Creek flood plain where it was probably flooded annually until water diversion out of South Boulder Creek began in the early

1870's. Numerous other ditches, both above and below this site were pulled from South Boulder Creek over the next twenty years. The southwestern part of the property is still subirrigated from the Goodhue ditch, but the study plots are north of that area and are very dry. Excavation at this site in 1994 revealed that the water table was more than 1.5 m below the surface.

The third site, Van Vleet, is also on Nederland very cobbly loam soil (more than 2.5m deep with 78-95% rock) on the plateau above the Marshallville ditch just South of the Boulder turnpike and west of Cherryvale road. The plots are on the flat area northwest of the well house and are surface irrigated. A map of these plots is shown in Figure A.5.

The Van Vleet site is not part of the designated tallgrass natural area. It also has no grazing exclosure so data from this site were excluded from analysis of winter grazing effects including the full factorial analysis. However, since the Yunker and THP sites differ in both soil and irrigation regime, Van Vleet is an important intermediate site. Van Vleet has the same soil as THP and the same irrigation regime as Yunker. Data from the Van Vleet site provided qualitative insight into the relative contributions of soil and irrigation to the site effects detected in the Yunker and THP data.

Land Management Treatments

Land management treatments included fire, winter grazing, fertilization, and reverse fertilization. Fire and winter grazing treatments mimic the probable historic disturbance regime. The reverse fertilization (carbon addition) nitrogen manipulation treatment was expected to reverse some of the effects of atmospheric nitrogen deposition. Treatments were applied to the 6m x 6m area extending 0.5m outside the boundaries of the 5m x 5m plot to provide uniform treatments within the area and reduce edge effects.

Fire treatments were applied in the late spring (late April or early May). All fire plots were burned the first year (1993). Thereafter two sites per year were burned so that all sites were burned three out of four years. Second year (1994) fire treatments were applied only at THP and Van Vleet; third year (1995) fire treatments were applied to Yunker and Van Vleet; and fourth year fire treatments were applied to Yunker and THP. Fire dates are shown in Table 2.1.

Table 2.1 Fire Treatments

Full Factorial Design Plots	1993	1994	1995	1996
Yunker II	April 26	not burned	May 10	May 8
THP	April 30	May 24	not burned	May 8
Additional All-Grazed Plot with same soil as THP and same irrigation as Yunker II				
Van Vleet	April 26	May 24	May 10	not burned

Domestic cattle grazed designated areas at the Yunker and THP sites from December to May. Domestic grazing has been excluded from the ungrazed areas since 1987. Grazing intensities calculated from stocking rates are shown in Table A.5.

Nitrogen manipulation treatments for this study included fertilization (N addition) and reverse fertilization (carbon addition to stimulate N immobilization by microbes). Fertilization and reverse fertilization treatments were applied in two equal applications each year, in May and June. Fertilization consisted of application of ammonium-nitrate to provide a total of 20gN/m^2 in 1993 and 1996 and 10gN/m^2 in 1994 and 1995. Reverse fertilization consisted of application of sawdust and sugar to provide 25gC/m^2.

Field Measurements

Soil temperatures were measured following fire treatment in 1993. Temperatures from 1993 were used because fire plots at both THP and Yunker were burned that year. Surface temperatures were measured with an IR thermometer on sunny days between the hours of noon and one PM. Soil temperatures were measured with a soil thermometer at 10 cm deep. Temperatures were measured approximately 10 days apart for 62 days after fire treatment. Significant treatment effects and differences between site, replicate plot, and depth of measurement were determined by repeated measure Analyses of Variance (ANOVA) comparing soil and surface temperatures at the THP and Yunker at a given time after fire treatment. This statistical method is described below.

Soil samples were taken from each plot in July 1996 (mid-season). Soil samples for each plot consisted of three cores 2.5 cm in diameter and 8 cm deep obtained with a standard soil corer. Obtaining cores of even this modest depth is difficult in the Nederland very cobbly sandy loam soils at the Van Vleet and THP sites because 78-95% of the volume of these soils is rock. The lack of available coring sites made repeated soil sampling impractical. To assure maximum confidence in this one-time mid-season data set, several procedures were used to establish confidence levels for the data. The use of composite soil samples composed of five cores, taken at least one meter apart and at least 0.5 meter from the edge of a plot helped average over spatial variation within the plot. Cores were stored in resealable plastic bags on ice until transport to the lab where they were refrigerated less than 48 hours before sieving and nitrogen extraction. Preparation and analysis of redundant extracts from the same soil sample established confidence levels for the extraction procedure. Redundant analyses of the same extract established confidence levels for the extract assay procedure.

Laboratory Analysis

Samples from each group of six plots were processed at the same time to assure consistency within the group. First, field moisture samples were separated and weighed. The rest of the sample was passed through a 2 mm sieve to homogenize and desegregate the sample. The fresh sieved material was divided into four samples of approximately 5-10g each: a sieved moisture sample, an KCl extractable inorganic nitrogen sample, and two samples for K_2SO_4 extractable microbial nitrogen. Sieved moisture samples were oven dried to determine the sieved moisture so extract data could be reported on an oven dry weight basis. These samples were then used to measure soil organic matter (SOM).

The KCl extractable nitrogen sample was assayed for both nitrate and ammonium using potassium chloride extraction and an alkaline phenol based method on a Lachat Quik-Chem system. Microbial nitrogen was calculated by subtracting the

K_2SO_4 extractable nitrogen from a fresh soil subsample from the total K_2SO_4 extractable nitrogen obtained from a subsample of the same soil that was fumigated with chloroform for five days to release the microbial nitrogen. Nitrogen from the K_2SO_4 extracts was also assayed using an alkaline phenol based method on a Lachat Quik-Chem system. Nitrogen data included both forms of KCl extractable nitrogen, ammonium (NH_4^+) and nitrate (NO_3^-); microbial nitrogen; and total K_2SO_4 extractable nitrogen.

Field moisture was measured by weighing a sample of fresh soil into a tared tin boat, drying for 48 hours at 35°C, and re-weighing. The difference between the fresh and 35°C weights was the field moisture of the sample. To report field moisture per gram of oven dried (108°C) soil, the sample was then oven dried at 108°C.

Field capacity, the amount of water that will be drawn up into the soil against gravity, was measured as follows. Soil samples were put into tared tins with screen bottoms, the tins were placed in a pan, and water added to the pan and left to absorb up into the soil samples for eighteen hours. Each tin was then removed from the pan, drained for fifteen minutes, weighed, air dried at 35°C for 48 hours, and reweighed. Field capacity was reported as the difference between the wet and dry weights, divided by the dry weight.

Soil organic matter (SOM) was measured by the loss on ignition method. Chemically bound water lost during the process was measured by rewetting the ashed sample and repeating the loss on ignition process. SOM values were then corrected to account for the loss of chemically bound water. This correction was necessary because the chemically bound water content differed between the two soils.

Experimental Design and Statistical Analysis

A randomized block three-way factorial experiment examined the response to fire, winter grazing, and nitrogen manipulation (both fertilization and reverse fertilization) at three sites over four years. Data were analyzed using the SPSS Advanced and Professional Statistics Package Version 6.1 for Windows (SPSS 1994). Data from replicate plots at the same site were treated as repeated measures, with pairs of replicates classified as wetter or drier by mean field moisture of the six plots in that replicate group. So significant effects of replicate indicate significant effects of local soil moisture.

Soil nutrient and moisture resources were represented by six closely related variables: ammonium, nitrate, microbial N, field moisture, field capacity, and SOM. Principal factor analysis was used to reduce these six variables to three principal factors, and varimax rotation was used to rotate the factors to facilitate categorization of the original variables into groups associated with each factor. Response of these factors to treatments was assessed by ANOVA as described below.

Analysis proceeded in two stages. Repeated measures analysis was used to increase the statistical power and reduce autocorrelation. First, the 48 plots at Yunker and THP were analyzed using multivariate analysis of variance on the full factorial treatment model shown in Table 4.8. Then, the 36 winter grazed plots from all three sites were analyzed to examine the role of soil and irrigation in treatment responses at winter grazed sites.

Nitrogen manipulation was coded into two dichotomous dummy variables: Nitrogen (linear) and Nitrogen (quadratic). Nitrogen (linear), tested whether the direction of reverse fertilization effects was opposite the direction of fertilization effects, for example the expected effect on nitrogen levels.

Nitrogen (quadratic) tested whether reverse fertilization and fertilization effects were in the same direction. For example, both treatments might increase soil moisture: reverse fertilization through reduced plant uptake and reduced transpiration and fertilization through increased shading. When both reverse fertilization and fertilization treatments affect a variable in the same way, the effect is quadratic, even when the mechanism for the effect is different for each of the two treatments.

Initial analyses of response data were blocked by Site to extract general response information. Unfortunately, the response to these treatments was strongly Site dependent. Blocking by site revealed little of the underlying data structure, so Site was used along with replicate as a repeated measure in the analysis.

The separate effects of fertilization (N addition) and reverse fertilization (C addition) were considered for those variables that showed significant nitrogen manipulation main effects or a trend ($p<0.1$) toward a nitrogen response. These analyses compared only one nitrogen treatment to the control. The model for these ANOVAs differs from the model of table 2.2 only in the deletion of all sources of variation involving the quadratic component of the nitrogen effect, and the reduction of the total degrees of freedom to 31.

Table 2.2 - Within and Between Management Regime ANOVA Model

n = the number of study plots per ANOVA cell for analysis of that source of variance

	Source of Variance	df	n
Between Management Regime Main and Two-Way Effects	Fire	1	24
	Winter Graze	1	24
	Nitrogen (quadratic)	1	16 :32
	Nitrogen (linear)	1	16
	Fire × Winter Graze	1	12
	Fire × Nitrogen (quadratic)	1	8 : 16
	Fire × Nitrogen (linear)	1	8
	Winter Graze × Nitrogen (quadratic)	1	8 16
	Winter Graze × Nitrogen (linear)	1	8
	error	2	
Within Management Regime Effects involving Site	Site	1	24
	Fire × Site	1	12
	Winter Graze × Site	1	12
	Nitrogen (quadratic) × Site	1	8 : 16
	Nitrogen (linear) × Site	1	8
	Fire × Winter Graze × Site	1	6
	Fire × Nitrogen (quadratic) × Site	1	4 : 8
	Fire × Nitrogen (linear) × Site	1	4
	Winter Graze × Nitrogen (quadratic) × Site	1	4 : 8
	Winter Graze × Nitrogen (linear) × Site	1	4
	error	2	
Within Management Regime Effects involving Replicate	Replicate	1	24
	Fire × Replicate	1	12
	Winter Graze × Replicate	1	12
	Nitrogen (quadratic) × Replicate	1	8 : 16
	Nitrogen (linear) × Replicate	1	8
	Fire × Winter Graze × Replicate	1	6
	Fire × Nitrogen (quadratic) × Replicate	1	4 : 8
	Fire × Nitrogen (linear) × Replicate	1	4
	Winter Graze × Nitrogen (quadratic) ×	1	4 : 8
	Winter Graze × Nitrogen (linear) ×	1	4
	error	2	
Within Management Regime Effects involving Replicate × Site	Replicate × Site	1	12
	Fire × Replicate × Site	1	6
	Winter Graze × Replicate × Site	1	6
	Nitrogen (quadratic) × Replicate × Site	1	4 : 8
	Nitrogen (linear) × Replicate × Site	1	4
	Fire × Winter Graze × Replicate	1	3
	Fire × Nitrogen (quadratic) × Replicate	1	2 : 4
	Fire × Nitrogen (linear) × Replicate	1	2
	Winter Graze × Nitrogen (quadratic) ×	1	2 : 4
	Winter Graze × Nitrogen (linear) ×	1	2
	error	2	
TOTAL DEGREES OF FREEDOM FOR MODEL		47	

Examining Soil and Irrigation Components of Site Effects

The grazed plots at Yunker and THP were compared to the plots from the all-grazed Van Vleet site to examine the separate effects of soil type and irrigation on various soil parameters. When repeated measures ANOVA using the model in Table 2.2 detected a significant effect involving site, the dependent variable was tested for Soil and Irrigation effects. Since the sites used for the full factorial model had different Soils and different Irrigation regimes, either or both of these might be responsible for the site effect. Comparison of both sites, Yunker and THP, to a third intermediate site, Van Vleet, decomposed the two components of the site effect. Repeated measures ANOVA, using the model shown in Table 2.3, detected Soil effects by comparing data from sites with the same irrigation regime, but different soil types: Yunker and Van Vleet. The same ANOVA model detected Irrigation effects by comparing data from sites with the same soil, but different irrigation regimes: THP and Van Vleet. Because the Van Vleet site had no ungrazed areas, comparisons were made only between grazed areas at the three sites. The analysis is only valid for grazed areas, and cannot detect the cause of site effects involving the winter grazing regime. Nevertheless, the analysis provided some insight into the source of interactions involving site.

Table 2.2 - Model to Separate Soil and Irrigation Components of Site Effect
n = the number of plots per ANOVA cell for analysis of that source of variance

	Source of Variance	df	n
Between Management Regime Main and Two-Way Effects	Fire	1	12
	Nitrogen (quadratic)	1	8 : 16
	Nitrogen (linear)	1	8
	Fire × Nitrogen (quadratic)	1	8 : 16
	Fire × Nitrogen (linear)	1	8
	error	2	
Within Management Regime Effects involving Site	Site	1	24
	Fire × Site	1	12
	Nitrogen (quadratic) × Site	1	8 : 16
	Nitrogen (linear) × Site	1	8
	Fire × Nitrogen (quadratic) × Site	1	4 : 8
	Fire × Nitrogen (linear) × Site	1	4
	error	2	
Within Management Regime Effects involving Replicate	Replicate	1	24
	Fire × Replicate	1	12
	Nitrogen (quadratic) × Replicate	1	8 : 16
	Nitrogen (linear) × Replicate	1	8
	Fire × Nitrogen (quadratic) × Replicate	1	4 : 8
	Fire × Nitrogen (linear) × Replicate	1	4
	error	2	
TOTAL DEGREES OF FREEDOM FOR MODEL		23	

SOIL RESPONSE RESULTS

Soil and Surface Temperatures

Surface temperatures immediately following fire treatment (1 hour after fire) at the THP site were higher than those in unburned plots (F=31.72; df=2,119; p=.030). Winter grazing had no significant effect on surface temperatures.

When temperatures at the surface and 10 cm deep were considered, both Fire and winter grazing were significant , and both interacted with site (Table 2.4). Both surface and soil temperature differences were compared in a repeated measures ANOVA using site, replicate, temperature depth, and sample, as repeated measures. Significant management induced temperature differences persisted at least 40 days after fire treatment at THP and 42 days after fire treatment at Yunker.

The main effects of fire and winter grazing on soil temperatures differed. Fire warmed the soil (Figure 2.1), while winter grazing cooled it (figure 2.2). However, both fire and winter grazing also interacted with site. Fire warmed plots at the non-irrigated THP site, but cooled them at the irrigated Yunker site (Figure 2.1). The direction of the winter grazing effect was consistent at both sites, but the magnitude of the effect was greater at the drier site

The irrigated site, Yunker, was cooler than the non-irrigated site, THP. Wetter replicates were cooler than drier replicates. Over both sites, surface temperatures were cooler overall than 10 cm deep temperatures. However, the effect of depth on temperature reversed with site.. Surface temperatures were cooler than soil temperatures at THP, but surface temperatures were warmer than soil temperatures at Yunker.

Winter grazing interacted with nitrogen manipulation and site as shown in Figure 2.2). Temperature variation over time is shown in Figure 2.3. Fertilization cooled irrigated or ungrazed plots, but warmed non-irrigated, grazed plots (Figures 2.4 and 2.5), while reverse fertilization had the opposite effect. Both winter grazing and the linear component of nitrogen manipulation interacted with site x replicate.

Table 2.4 - ANOVA of Treatment Effects on Soil and Surface Temperatures

Fire, Winter grazing, Depth, Site, and Replicate all had significant main effects on temperature, and fire, winter grazing, and depth all interacted with site. The only significant effects involving nitrogen were interactions between Nitrogen (linear) × Site and both winter grazing and Replicate. n = number of plots in ANOVA cell.

Source	df	p	Treatments	n	mean ± se
Between Treatment Regime Main and Two-Way Effects					
Fire	1	0.034	fire	240	23.89 ± 0.02
			no fire	240	22.84 ± 0.02
Winter Graze	1	0.014	winter grazed	240	21.95 ± 0.02
			cattle excluded	240	22.62 ± 0.01
error	2				
Within Treatment Regime Effects involving Depth					
Depth	1	0.016	surface	240	22.97 ± 0.02
			10 cm deep	240	23.91 ± 0.02
error	2				
Within Treatment Regime Effects involving Site					
Site	1	<0.000	THP	240	25.88 ± 0.02
			Yunker	240	21.01 ± 0.02
Fire × Site	1	0.002		see effect Figure 2.1	
Winter Graze × Site	1	0.008		see effect Figure 2.2	
Winter Graze × Nitrogen (linear) × Site	1	0.038		see effect Figure 2.2	
error	2				
Within Treatment Regime Effects involving Replicate					
Replicate	1	0.016	drier	240	24.09 ± 0.01
			wetter	240	22.80 ± 0.02
error	2				
Within Treatment Regime Effects involving Depth x Site					
Depth × Site	1	0.011		see effect Figure 2.3	
error	2				
Within Treatment Regime Effects involving Depth x Replicate					
Winter Graze × Depth × Replicate	1	0.049			
error	2				
Within Treatment Regime Effects involving Replicate × Site					
Winter Graze × Replicate × Site	1	0.012		see effect Figure 2.4	
Nitrogen (linear) × Replicate × Site	1	0.044		see effect Figure 2.5	
error	2				
Within Treatment Regime Effects involving Depth x Replicate × Site					
error	2				
TOTAL degrees of freedom	95				

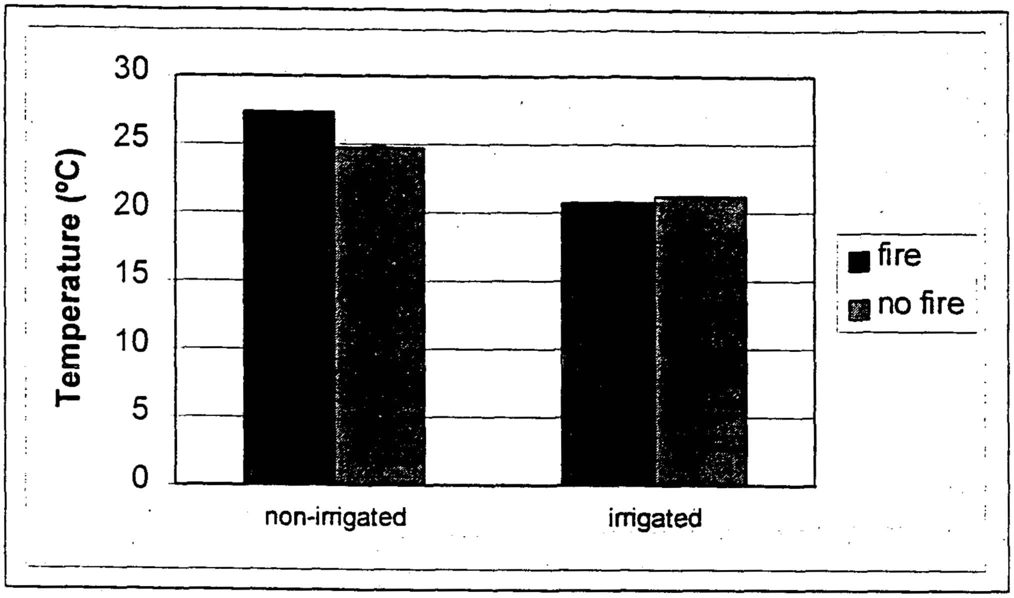


Figure 2.1 - Fire x Site Effects on Mean (Soil and Surface) Temperature
Temperatures 40 days (non-irrigated site) and 42 days (irrigated site) after fire treatment. At irrigated site fire plots were slightly cooler, probably due to increased shading from fire stimulated growth. At non-irrigated site fire plots warmer probably due to reduced shading and increased evaporation. Error bars are too small (SE max = 0.02) to be seen at this scale.

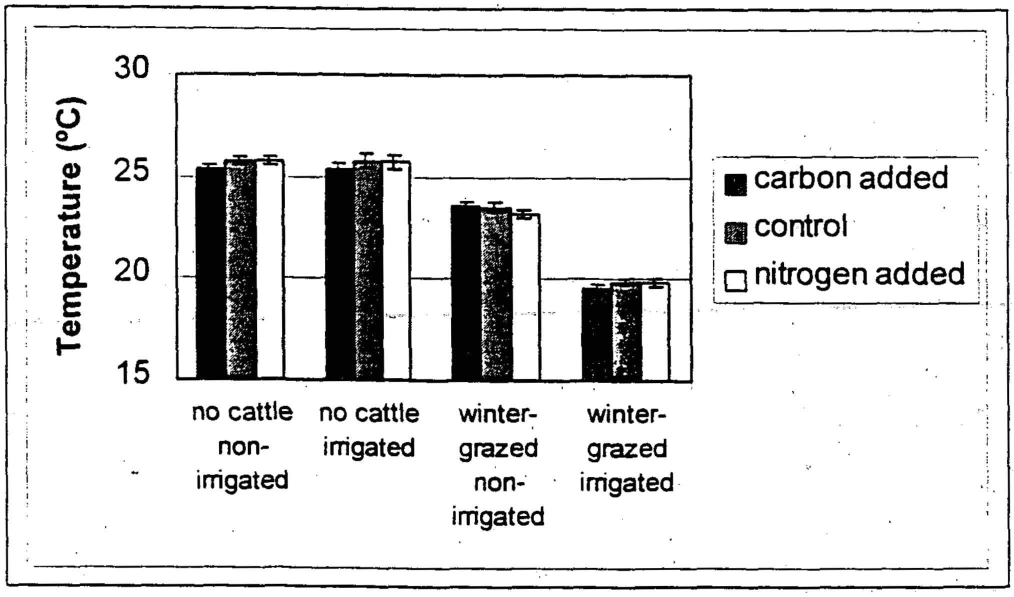
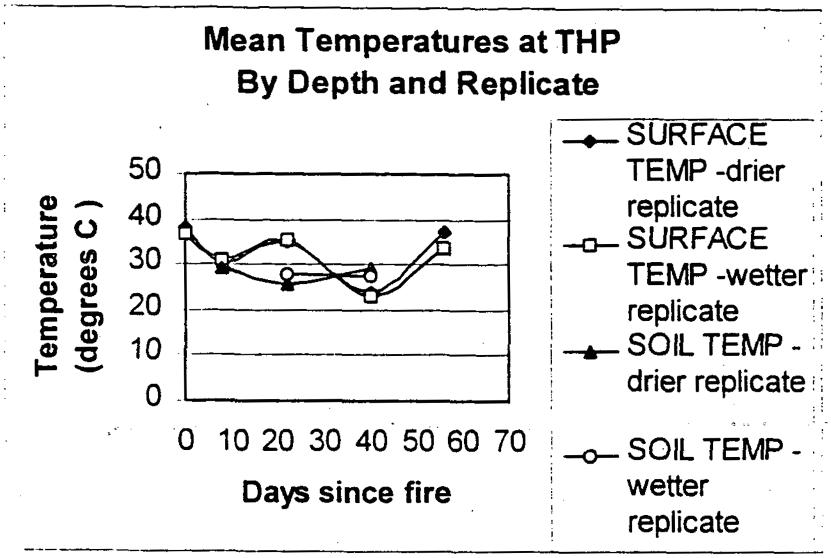


Figure 2.2 - Winter Graze x Nitrogen Manipulation (linear) x Site Effects on Mean (Soil and Surface) Temperature
Temperatures 40 days (non-irrigated site) and 42 days (irrigated site) after fire treatment. Winter grazing cools plots at both sites, more so at the irrigated site. Nitrogen addition cooled plots that were not irrigated. Error bars show standard errors for all data. **Note baseline shift, X axis is at 15°C.**

a. THP site



b. Yunker site

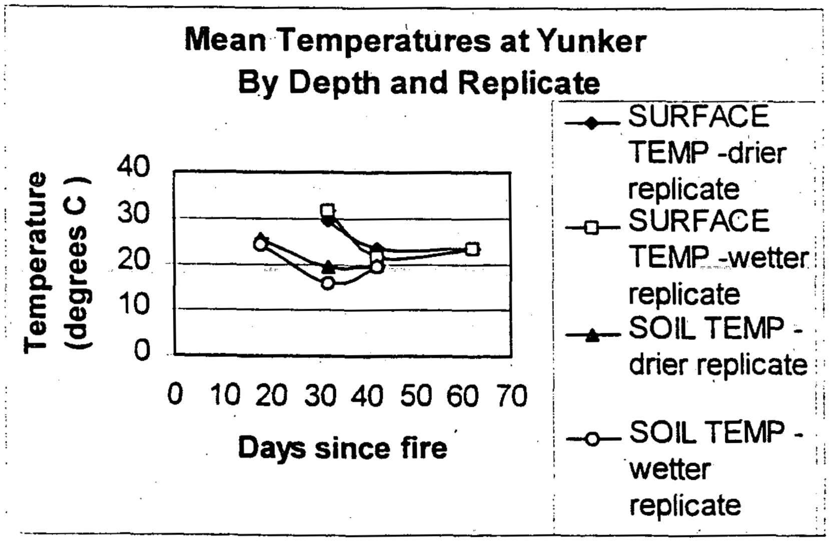
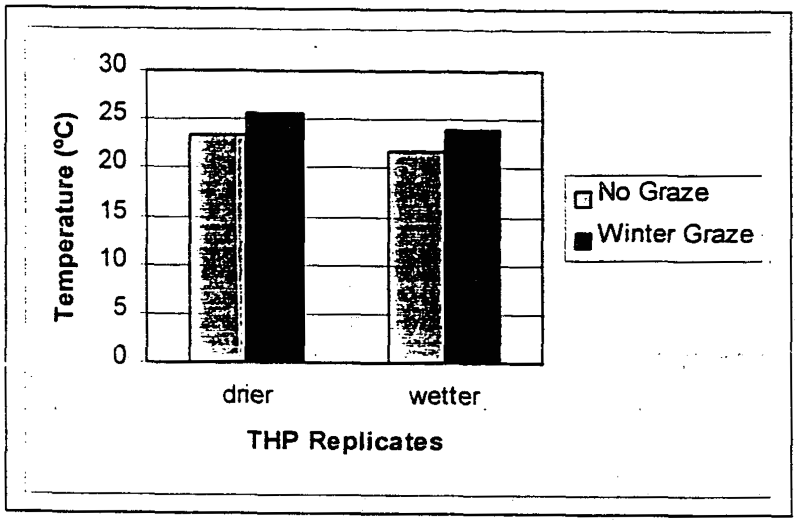


Figure 2.3 - Soil Temperatures by Depth and Replicate at a non-irrigated site, THP (a), and an irrigated site, Yunker (b).
Error bars are too small (max S.E. = 0.11) to be seen at this scale. Replicates follow similar patterns. Depth has stronger effect earlier in season. Significant depth × site effect (Table 2.3) 40-42 days after fire.

a. THP site



b. Yunker site

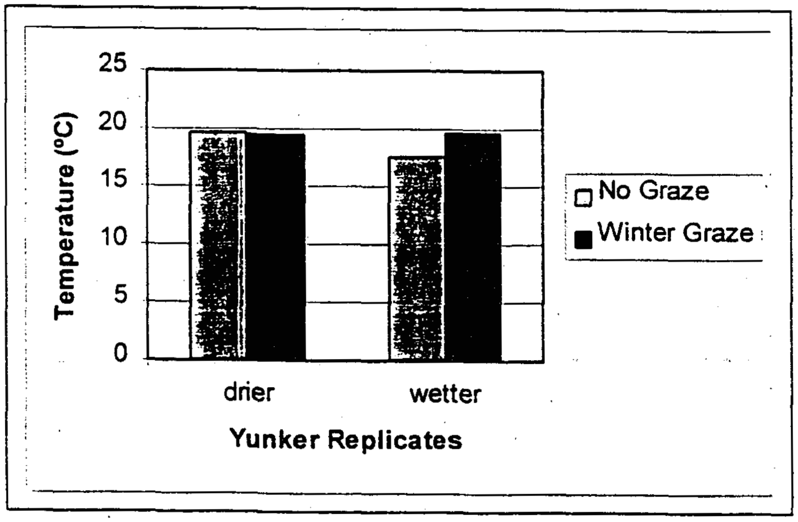
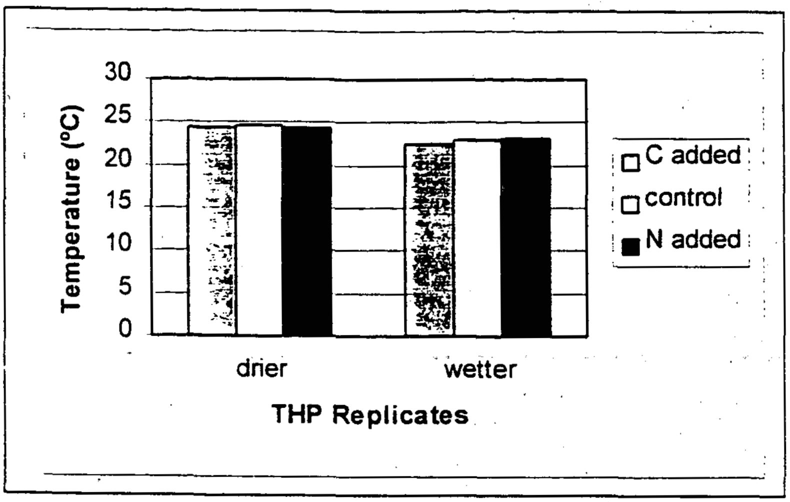


Figure 2.4 - Soil Temperatures by Grazing x Site x Replicate
(a) non-irrigated site, THP; (b) irrigated site, Yunker.
Temperatures 40-42 days after fire This effect significant ($p=0.012$; Table 2.3). Error bars are too small (max S.E. = 0.01) to be seen at this scale.

a. THP site



b. Yunker site

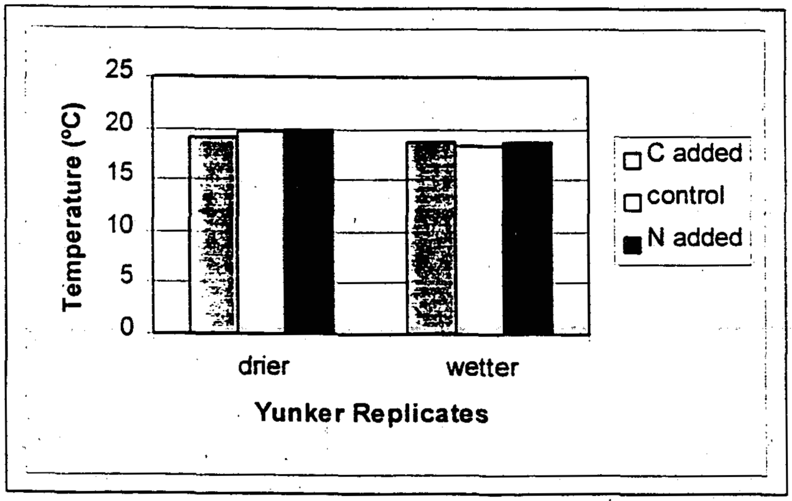


Figure 2.5 - Soil Temperatures by N (linear) x Replicate x Site
(a) non-irrigated site, THP; (b) irrigated site, Yunker.
Effect is linear with N addition in wetter replicates at non-irrigated site and drier plots at irrigated site, with higher temperatures in fertilized plots. This is probably due to increased moisture uptake in fertilized plots, and reduced uptake in reverse fertilized plots. Effect significant (p=0.044,Table 2.3). These temperatures 40-42 days after fire. Error bars are too small (max S.E. = 0.15) to be seen at this scale.

Factor Analysis

Factor analysis of soil nitrate, soil ammonium, microbial nitrogen, field moisture, field capacity and soil organic matter, produced three factors that together explained 69.8% of the total observed variance among the six soil variables. Varimax rotation produced soil factors strongly associated with certain soil parameters. The first soil factor was strongly associated with the inorganic N variables, nitrate N and ammonium N, and explained 35.5% of the variance. The second soil factor was strongly associated with field moisture and microbial N, and explained 25.7% of the variance. The third soil factor was strongly associated with the two soil field capacity and soil organic matter, and explained 8.6% of the variance. The rotated factor matrix is shown in Table 2.4.

Table 2.4 - Varimax Rotated Soil Factors

	Soil Factor 1	Soil Factor 2	Soil Factor 3
Nitrate N	.98031	-.17266	-.07517
Ammonium N	.90736	.05605	-.05041
Microbial N	.01872	.93170	.04144
Field Moisture	-.06270	.70441	-.02382
Field Capacity	-.16908	.57490	.60470
SOM	-.01830	-.04227	.51586

Plant Available Nitrogen Variables (Nitrate N, Ammonium N, Soil Factor 1)

Nitrate showed no significant treatment effects. Though the linear component of Nitrogen Manipulation showed strong trends both as a main effect and interacting with site (Table 2.6). Neither ammonium nor soil factor 1 showed significant treatment effects. but soil factor1 showed trends similar to nitrate (Table 2.6).

Table 2.6 - Trends from ANOVA of Treatment Effects on mid-season Nitrate, Ammonium, and Soil Factor 1

Nitrate, and Soil Factor 1 both showed strong trends with the linear component of N manipulation. No significant treatment effects.

Source	df	p			Treatments	n	mean ± se (µgN/g OD soil)	
		Nitrate N	Ammonium N	Soil Factor 1			Nitrate N	Ammonium N
Between Treatment Regime Main and Two-Way Effects								
Nitrogen (linear)	1	NS 0.065	NS 0.106	NS 0.066	C added	16	1.27 ± 0.09	3.04 ± 0.13
					Control	16	2.19 ± 0.12	4.72 ± 0.18
					N added	16	29.55 ± 2.67	29.73 ± 2.97
error	2							
Within Treatment Regime Effects involving Site								
Nitrogen (linear) × Site	1	NS 0.063	NS 0.114	NS 0.070	C added - THP	8	1.73 ± 0.24	1.37 ± 0.16
					Control - THP	8	2.41 ± 0.07	3.07 ± 0.09
					N added - THP	8	57.26 ± 5.80	51.67 ± 7.64
					C added - Yunker	8	0.81 ± 0.08	4.71 ± 0.16
					Control - Yunker	8	1.96 ± 0.32	6.36 ± 0.42
					N added - Yunker	8	1.83 ± 0.14	7.79 ± 0.31
error	2							
Within Treatment Regime Effects involving Replicate								
error	2							
Within Treatment Regime Effects involving Replicate × Site								
error	2							
TOTAL degrees of freedom	47							

Separate ANOVAs comparing each of the nitrogen treatments to the control, revealed significant effects of reverse fertilization, but not of fertilization. Reverse fertilization to the control showed that reverse fertilization significantly reduced ammonium levels ($p_{1,31}$ =0.046; means Table 2.6) and showed a trend toward reducing nitrate levels ($p_{1,31}$ =0.075; means Table 2.6). Additionally, analysis of the reverse fertilized and control plots showed trends toward a fire induced reduction in ammonium ($p_{1,31}$ =0.065; means: fire (3.58 ± 0.16 μgN/g soil) no fire (4.73 ± 0.40 μgN/g soil)), and an interaction between fire and grazing ($p_{1,31}$ =0.077), that winter grazing tended to increase ammonium in burned plots. but tended to reduce it in unburned plots.

ANOVAs comparing fertilized and control plots, showed that fertilization had no significant effects on either mid-season nitrate or mid-season ammonium. In fact comparisons involving fertilized and control plots showed no significant treatment effects and no trends of any sort. Mid-season nitrogen levels of fertilized plots were the product of four years of fertilization and of differing levels of plant uptake. While nitrate and ammonium levels in the reverse fertilized and control plots varied over only one order of magnitude, levels in fertilized plots varied over four orders of magnitude (Table 2.6, and Appendix E, Table E.2). This enormous variation was not explained by the treatment and site factors in the ANOVA model. Inspection of the data showed low levels at the irrigated site and levels that varied from low to extremely high at the non-irrigated site.

Confidence levels for the nitrogen measurements were as follows. Assays of three different extracts per soil sample for three different samples (one for every twenty analyses) gave confidence levels for the extraction procedure of 8.22% for ammonium N and 14.42% for nitrate N. Three different assays of the same extract for three different extracts gave confidence levels for the assay procedure of 4.70% for ammonium N and 8.77% for nitrate. Total KCl extracted inorganic N was 6% higher than the total K_2SO_4 extractable N from the same sample with a linear relationship (r^2 of 0.968).

Field Moisture and Associated Variables (Microbial N, and Soil Factor 2)

Treatment effects on these three variables involve interaction with site or replicate (Table 2.7). Fire had no effect on field moisture, microbial N, or the soil factor associated with them, soil factor 2. Microbial nitrogen varied with replicate (local soil moisture) and with replicate x site (Table 2.7), but showed no significant treatment effects. As expected, field Moisture (Table 2.7) varied with site and replicate (local soil moisture). Field moisture was greatest at the irrigated site, Yunker, and in wetter replicates (recall that replicates were classified, wetter or drier, on the basis of mean field moisture). Effects of both winter grazing and nitrogen manipulation on field moisture varied with site (Figure 2.7). The effects of site on field moisture were similar, but not identical, to the effects of local moisture variation (Replicate) (Figure 2.8). Neither soil (p=.138) nor irrigation (p=.234) was clearly responsible for the site effect on field moisture, when comparing grazed areas. Soil Factor 2 varied with both site and replicate (Table 2.7). Both soil (p=.022) and irrigation (p=.034) contributed to the site effect on soil Factor 2 .

Table 2.7 - Significant Treatment Effects from ANOVAs of mid-season Field Moisture, Microbial N, and Soil Factor 2

ANOVA model for SOM and Soil Factor 3 given in Table 2.1. P values are given for significant effects and for trends with greater than 90% confidence.

Source	df	p			Treatments	n	mean	mean Microbial N
		Moisture	Microbial N	Soil Factor 2			Moist (%)	µgN/g OD soil
Between Treatment Regime Main and Two-Way Effects								
Winter Graze × Nitrogen (linear)	1	NS 0.090	NS	NS		8		
error	2							
Within Treatment Regime Effects involving Site								
Site	1	0.013	NS	0.041	THP	24	24.4 ± 1.2	51.2 ± 1.2
					Yunker	24	28.6 ± 0.7	56.8 ± 0.6
Winter Graze × Site	1	NS	NS 0.078	NS		12	see Figure 2.6	
Nitrogen (quadratic) × Site	1	0.025	NS	NS		8:16	see Figure 2.6	
Nitrogen (linear) × Site	1	0.010	NS	NS		8	see Figure 2.6	
Winter Graze × N (quadratic) × Site	1	0.020	NS	NS		8:16	see Figure 2.6	
Winter Graze × N (linear) × Site	1	0.010	NS	NS		8	see Figure 2.6	
error	2							
Within Treatment Regime Effects involving Replicate								
Replicate	1	0.006	0.045	0.015	drier	24	23.2 ± 1.0	42.4 ± 0.1
					wetter	24	43.6 ± 1.1	65.6 ± 0.8
Winter Graze × Replicate	1	NS	NS 0.096	NS		12	see Figure 2.7	
Nitrogen (quadratic) × Replicate	1	NS 0.083	NS	NS		8:16	see Figure 2.7	
Nitrogen (linear) × Replicate	1	NS 0.081	NS	NS		8	see Figure 2.7	
Winter Graze × N (linear) × Replicate	1	NS 0.064	NS	NS		8	see Figure 2.7	
error	2							
Within Treatment Regime Effects involving Replicate × Site								
Replicate × Site	1	NS	0.023	NS 0.059		12		
error	2							
TOTAL degrees of freedom	47							

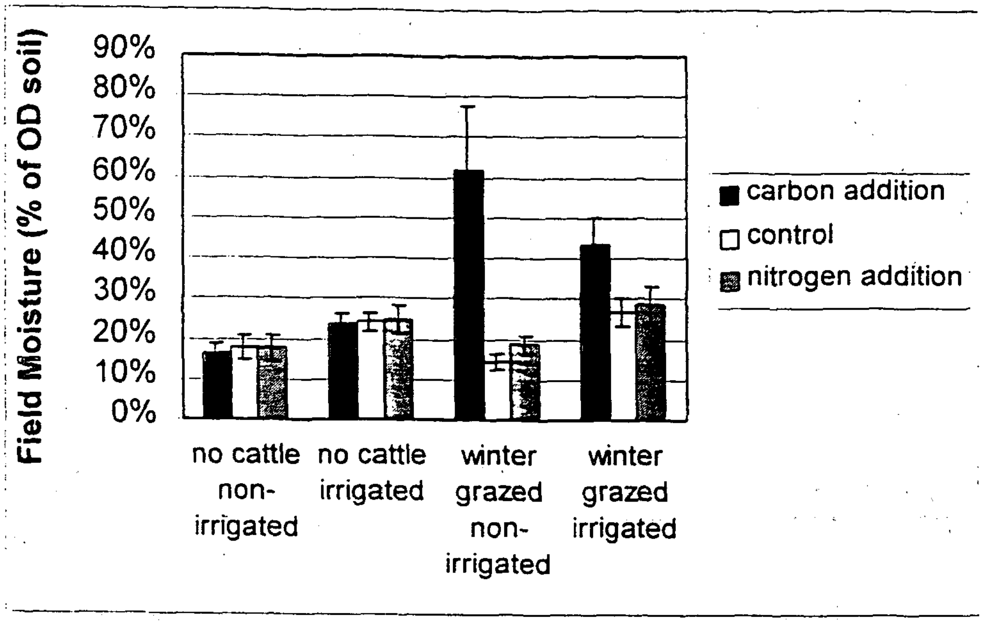


Figure 2.6 - Effects of Nitrogen Manipulation x Winter Graze x Site on Field Moisture

In ungrazed areas nitrogen manipulation has little effect on field moisture, but in Winter-Grazed areas carbon addition (reverse fertilization) increases field moisture. The effect is most dramatic in at the non-irrigated site. (means ± se).

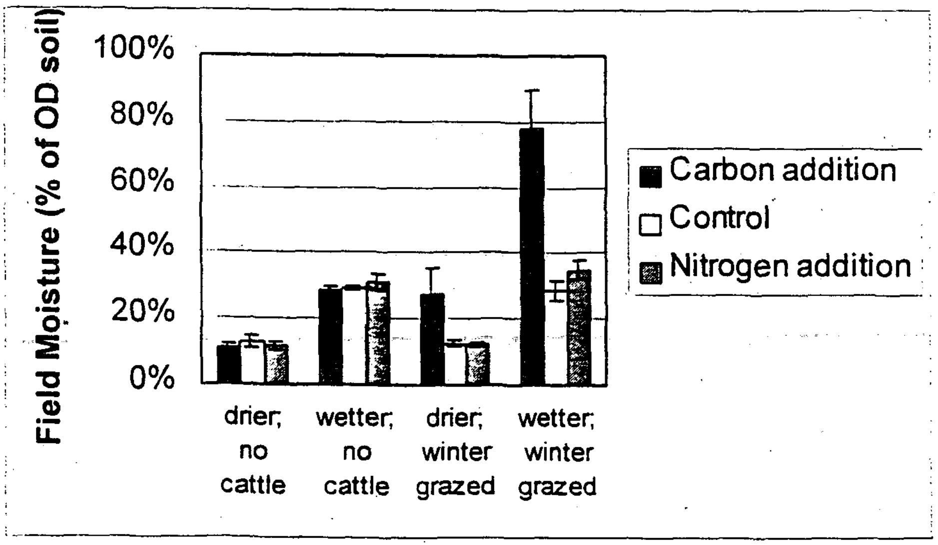


Figure 2.7 - Effects of Nitrogen Manipulation x Winter Graze x Replicate on Field Moisture

In ungrazed areas nitrogen manipulation has little effect on field moisture, but in Winter-Grazed areas carbon addition (reverse fertilization) increases field moisture. The effect is most dramatic in wetter replicates. Nitrogen addition slightly increased soil moisture in wetter replicates. (means ± se).

Soil Organic Matter and Associated Variables (Field Capacity, Soil Factor 3)

Soil organic matter (SOM) varied with replicate (local moisture) and the effect of these local moisture variations (replicate) varied with the winter grazing, and with site (Table 2.8). Winter grazing increased SOM in wet replicates. Site modified the SOM response to local moisture variation (replicate) so that drier replicates had greater SOM at the irrigated site, Yunker, but the wetter replicates ha greater SOM at the non-irrigated site, THP. Site modification of the effect of the local moisture variation (replicate) was due entirely to effects on the winter grazed replicates, reflecting the winter grazing x replicate x site effect (Table 2.8, Figure 2.8). ANOVAs using the model shown in Table 2.2 to examine the contributions of soil and irrigation to the observed site effect showed a significant (p=.017) irrigation effect on SOM, but no significant soil effect.

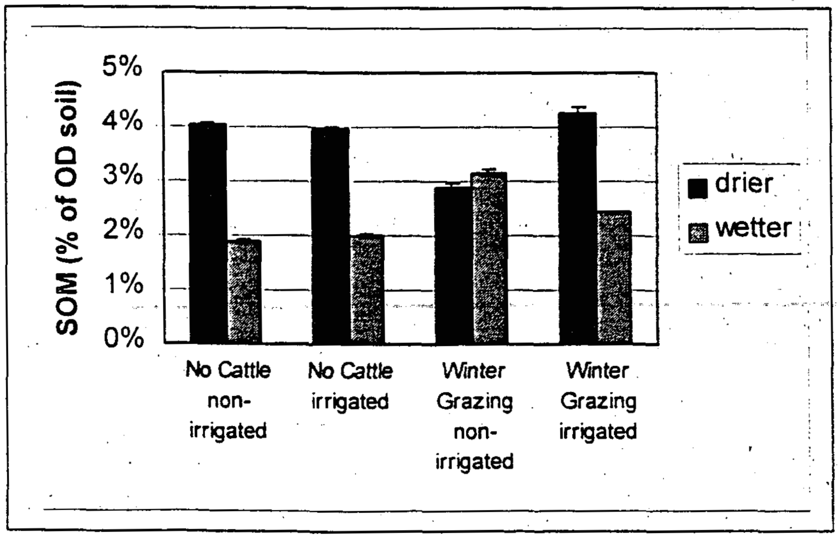


Figure 2.8 - Effects of Winter Grazing x Replicate x Site on Soil Organic Matter
Ungrazed plots at both sites and Winter-Grazed plots at the irrigated site show the same pattern, with greater SOM in drier replicates. This effect is probably due to slower decomposition in drier replicates. Winter Grazed plots at the non-irrigated site show the opposite pattern, with slightly higher SOM in the wetter replicates. This effect is probably due to more fine roots in the wetter replicate. Bars show mean SOM ± standard error.

Table 2.8 - Significant Treatment Effects from ANOVAs of mid-season SOM, Field Capacity, and Soil Factor 3

ANOVA model for SOM and Soil Factor 3 given in Table 2.1. Model for Field Capacity described in Text. P values shown when P<0.10.

Source	df	p SOM	p Soil Factor 3	df	p Field Capacity	Treatments	n	mean SOM (%)	n	mean Field Capacity (%)
Between Treatment Regime Main and Two-Way Effects										
Winter Graze	1	NS 0.076	NS	1	NS		24		8	
Nitrogen (linear)	1	NS	NS 0.086	0	not in model		16			
Fire × Winter Graze	1	NS 0.060	NS	0	not in model		12			
Fire × Nitrogen (quadratic)	1	NS 0.094	NS	0	not in model		12			
error	2			1						
Within Treatment Regime Effects involving Site										
Site	1	NS	0.004	1	0.017	THP	24	2.99 ± 0.04	8	95.5 ± 0.8
						Yunker	24	3.16 ± 0.02	8	124.1 ± 1.5
Winter Graze × Site	1	NS	NS 0.066	1	NS 0.064		12	see Fig. 2.9	4	
error	2			1						
Within Treatment Regime Effects involving Replicate										
Replicate	1	0.002	0.005	1	NS	drier	24	3.78 ± 0.03	8	110.3 ± 2.5
						wetter	24	2.37 ± 0.02	8	109.3 ± 2.0
Winter Graze × Replicate	1	0.011	0.013	1	NS		12	see Fig. 2.9	4	
Fire × Nitrogen (quadratic) × Replicate	1	NS 0.076	NS	0	not in model		4:8			
error	2			1						
Within Treatment Regime Effects involving Replicate × Site										
Replicate × Site	1	0.010	NS	0	not in model		12	see Fig. 2.9		
Winter Graze × Replicate × Site	1	0.006	NS	0	not in model		6	see Fig. 2.9		
Fire × Winter Graze × Replicate × Site	1	NS	NS 0.073	0	not in model		3			
Winter Graze × N (linear) × Replicate × Site	1	NS 0.093	NS	0	not in model		2			
error	2			1						
TOTAL degrees of freedom	47			11						

Field capacity varied only with site (p=.017; df=1,11), though a strong winter grazing x site trend (p=.064, df=1,11) was also seen. The principal factor associated with SOM and field capacity, soil factor 3, varied with site, replicate (local moisture variation), and Grazing x replicate (Table 2.8). Examining the contributions of soil and irrigation to the site effect showed a strong trend (p=.060) toward an irrigation effect and no significant soil effect. The ANOVA model used to examine field capacity data, excluded tests of nitrogen effects, which were not expected to affect field capacity.

DISCUSSION

Soil and Surface Temperatures

As expected both fire and winter grazing affected soil and surface temperatures. The main effects of fire and winter grazing on temperature were significant indicating that both soil and surface temperatures showed the same pattern, and that temperature effects extend at least 10 cm deep. Within treatment regimes, the main effects of depth, site and replicate (local moisture variation) were all significant. The depth effect indicated a significant difference between mean surface temperatures and mean soil temperature 10 cm deep. The site effect indicated significant difference between mean temperatures at the irrigated site, Yunker, and the non-irrigated site, THP.

Both of fire and winter grazing were expected to remove litter, increasing insolation, and warming the soil. This was expected to increase plant growth rates, stimulating production so that later in the season the increased biomass would shade the soil, reducing insolation and evaporation, and cooling the soil, reversing the temperature effect. Surface temperature measurements one hour after fire treatment at the non-irrigated site, THP, showed the expected significant increase in surface temperature of burned plots. At the non-irrigated site, THP, fire increased both soil and surface temperatures 40 days after fire treatments (Table 2.3, Figure 2.1). This supports the portion of the hypothesis that predicts that fire treatment will warm the soil, and indicates that the effect extends at least 10 cm deep. However, contrary to predictions the increased light did not stimulate growth. Production data from this site confirmed that fire reduced biomass at the non-irrigated site (Chapter 3). So the temperature effect did not reverse over time. Temperatures in burned plots at the non-irrigated site remained higher than unburned plots at least 60 days after fire treatment (Figure 2.3).

Contrary to predictions, winter grazing reduced temperatures (Table 2.4) and increased moisture (Table 2.7) in winter-grazed plots at both sites. And other research (Chapter 3) showed that despite similar effects on temperature (Table 2.4) and field moisture (Table 2.7), the effect of winter grazing on biomass differed with site.

Principal Soil Factors

Nearly 70% of the variance in nitrogen, moisture and soil parameters was explained by three principal factors, related to plant inorganic nitrogen, moisture, and soil characteristics. The first factor, soil factor 1, was related to KCl extractable nitrate and ammonium (Table 2.5), and explained 35.5% of the variance in soil parameters. But, soil factor 1 showed no response to treatment or site (Table 2.6). The second factor, soil factor 2 (Table 2.5), was related to both field moisture and microbial N, and explained 25.7% of the observed variance in soil parameters. Soil factor 2 showed no response to treatments, and depended only on site and local moisture variation (between replicate plots).

Only soil factor 3, related to SOM and field capacity, showed any treatment effect. Soil factor 3 explained only 8.6% of the variance in soil parameters and showed a response to winter grazing that varied with local moisture differences (between replicate plots). Significant site and replicate effects show that soil heterogeneity, particularly differences in soil moisture, at both large (site) and small (replicate) scales was responsible for most variation in soil variables and factors. Only a small part of the overall variance in soil parameters was affected by experimental treatment, and that treatment was winter grazing. Winter grazing exclusion had been applied since 1987, six years earlier than other treatments began.

Since both winter grazing treatments and replicate groups occurred in blocks, the winter grazing x replicate effect may reflect spatial heterogeneity. However, the lack of a significant winter grazing x site effect, and the remarkable similarity between the SOM patterns in ungrazed areas at both site (figure 2.8) suggest that the winter grazing treatment was, at least partially, responsible for the response of soil factor 3, soil characteristics. The pattern of SOM response to winter grazing x site x replicate (figure 2.8) is similar to the pattern of biomass response to winter grazing x site. The effect that winter grazing had on the SOM in different replicates, reversed with site. Similarly, the effect of winter grazing on biomass also reversed at the two sites. Indeed, biomass patterns determine how much material is produced to be converted into SOM. Changes in biomass production can be expected to feed back into SOM levels over time. However, these changes in biomass can also be expected to follow changes in soil resources. The lack of response to treatments in both the nitrogen and moisture factors showed that the nearly 70% of the variance in nitrogen and moisture resources could be explained by principal factors that were independent of treatment effects.

Inorganic Nitrogen

Nitrate levels were consistently lower than ammonium levels suggesting that nitrate is preferred by plants in this system or quickly leached or ammonium is fixed by SOM or, at the Yunker site, clays. The failure of nitrogen addition to provide a consistent and significant increase in soil inorganic nitrogen levels showed that mid-season soil nitrogen depended not only on nitrogen input and immobilization, but also on leaching and plant uptake.

Extremely high mid-season nitrogen levels in fertilized plots at the non-irrigated site, especially in burned plots, and the concomitant reduced biomass in those plots (Chapter 3), suggested that low plant uptake of N in these plots allowed fertilization treatments to accumulate in those plots. If low production in those plots reduced plant uptake of N, then plant uptake of moisture would be similarly reduced, increasing levels of residual moisture. Indeed, moisture data showed that, despite a significant increase in temperature, fire failed to reduce field moisture. Instead the combination of increased temperature (Table 2.4) and reduced plant uptake, due to reduced biomass (Chapter 3), maintained moisture levels.

The hypothesis that carbon addition (reverse fertilization) would reduce inorganic nitrogen was supported with significant reduction of ammonium and a trend toward reduction of nitrate. Differences between the ammonium response and the nitrate trend suggest that carbon addition may also stimulate nitrification. This might be an interesting topic for future research.

Neither fire nor winter grazing affected inorganic nitrogen. The hypothesis that fire would reduce inorganic nitrogen was not supported. However, ANOVA comparing only the reverse fertilized and control plots showed a trend toward fire reducing ammonium. The lack of a significant fire effect on nitrogen is not surprising. Seastedt and Ramundo (1990) found that the direct influence of fire on soil chemistry was "slight at best". In contrast to year-round grazing, winter grazing had no significant effect on either nitrate or ammonium. This contrasts with results of year-round grazing in tallgrass prairie (Hobbs, Thompson et al.1991) and other systems (McNaughton, 1985; Floate, 1981) where year-round grazing increased inorganic nitrogen.

Microbial Nitrogen

Microbial nitrogen showed no significant treatment effects (Table 2.7). It varied with replicate (local moisture variation) and with site x replicate. Wetter replicates had 155% the microbial activity of drier replicates only 5m away, indicating a high degree of spatial variability. And, since wetter replicates consistently had greater microbial N, a high degree of moisture dependence. The difference between replicates was largest at the non-irrigated site. However, the variation between sites was not significant. Mean microbial nitrogen (an estimate of microbial biomass) was equivalent at the two sites, but microbial N at the non-irrigated site was concentrated in wetter areas, while those at the irrigated site were evenly dispersed. result of the increased moisture availability in winter grazed plots.

Soil Moisture

Patterns of response to treatments differed with site (Table 2.7). Field moisture responses to treatments appear inversely related to temperature responses. In contrast to predictions, both nitrogen addition (fertilization) and carbon addition (reverse fertilization) interacted with winter grazing to increase soil moisture in winter grazed areas, but had no effect on plots in ungrazed areas. Fertilization and reverse fertilization also interacted with site and with winter graze x site. Since replicates were classified as wetter or drier based on the mean soil moisture of the replicate group, it was clear that wetter replicates would have higher moisture. However, I was surprised that the difference between replicates (only 5m apart) was large enough to be significant and to show trends toward interacting with treatment effects (Table 2.7 and Figure 2.8).

As expected, soil moisture was greatest in wetter plots and at the irrigated site, Yunker (Table 2.7). Given the different irrigation regimes the differences between sites are remarkably small (Figures 2.7 and 2.8). The non-irrigated site, THP, has a deep rocky soil that concentrates available moisture. In addition plant biomass is lower at the non-irrigated site (Chapter 3), reducing plant uptake and transpiration. The irrigated site, Yunker, has a shallow clayey soil over sandstone.

The hypothesis that winter grazing would increase evaporation and reduce soil moisture was not supported. In contrast to predictions, field moisture increased, and temperature decreased in grazed areas, especially at the non-irrigated site. This effect was due to the dramatic increase in field moisture of reverse fertilized plots in the grazed areas (Figure 2.7) probably due to reduced plant uptake. The hypothesis that fire would decrease soil moisture was not supported. High temperatures in fire plots (Table 2.3) would cause increased evaporation, but apparently reduced plant uptake compensated, so that mean soil moisture did not differ between burned and unburned plots.

Soil Organic Matter

Soil organic matter (SOM) varied with site, with local soil moisture (replicate), and these response patterns were modified by winter grazing. SOM values may differ between sites due to different soils, different management histories. They may differ with site or replicate due to moisture driven differences in fine root production or decomposition rates. Both SOM (Table 2.8) and mean biomass (Chapter 3) were greater at the irrigated site, Yunker, than at the non-irrigated site, THP. The increased SOM at the irrigated site may include differences in fine root production (roots smaller than 2mm) as well as differences in SOM.

SOM was also higher in drier replicates (Table 2.8, Figure2.8). Although decomposition rates were not measured directly in this study, microbial nitrogen in wetter replicates was 155% of that in drier replicates (Table 2.7). The increased microbial activity in wetter replicates supports a hypothesis of increased decomposition rates in wetter replicates, reducing SOM. Microbial N trends with winter graze x replicate may also provide insight into the winter graze x replicate effect on SOM (Table 2.8, Figure 2.8).

Summary

Fire increased soil temperatures at the non-irrigated site and showed a trend toward reducing ammonium in reverse fertilized and control plots. Fire had no significant effect on inorganic nitrogen or field moisture. Winter grazing reduced soil temperatures at both sites and increased field moisture in reverse fertilized plots, especially at the non-irrigated site. Winter grazing had no effect on inorganic nitrogen. Winter grazing was expected to have an effect similar to fire. Contrary to expectations, winter grazing reduced temperatures and increased soil moisture at both sites, and had no effect on litter (Chapter 3). Winter grazing increased biomass at the irrigated site, Yunker, but reduced it at the non-irrigated site, THP (Chapter 3).

Nearly 70% of the variance in nitrogen, moisture and soil parameters was explained by three principal factors, related to plant inorganic nitrogen, moisture, and soil characteristics. However, only soil factor 3, related to SOM and field capacity, showed any treatment response (to winter grazing), and explained only 8.6% of the variance in soil parameters. That treatment, winter grazing exclusion, had been applied since 1987, six years earlier than other treatments began.

Significant site and replicate effects showed that soil heterogeneity, particularly differences in soil moisture, at both large (site) and small (replicate) scales was responsible for most variation in soil variables and factors.

Reverse fertilization reduced ammonium compared to control plots. Fertilization had no consistent effect on inorganic N. Neither fire nor winter grazing affected inorganic N. Microbial nitrogen (an estimate of microbial biomass) showed no response to reverse fertilization; but appeared to be moisture limited rather than substrate limited. That pattern of response caused microbial nitrogen to be included with field moisture in the second soil factor. However, the lack of microbial response to the increased moisture in reverse fertilized plots suggested that microbial activity depends also on plant activity. Increased microbial N was related to reduced SOM.

Winter grazing increased field moisture, especially at the non-irrigated site. Fire had no effect on soil moisture, although it increased soil and surface temperatures at the non-irrigated site. Both fertilization and reverse fertilization interacted with winter grazing to increase field moisture in winter-grazed plots.

SOM depended on large scale (site) and small scale (replicate) variations in moisture. Drier replicates at both sites had nearly double the SOM of wetter replicates, except at the non-irrigated site winter grazing reversed the pattern. Drier replicates also have lower microbial biomass, which may slow decomposition rates, increasing SOM. The irrigated site had higher SOM probably due to higher productivity.

Soil parameters varied more with site and local moisture than with treatments. Treatments affected temperature, moisture, and SOM. And SOM was inversely related to microbial N. Treatments had little effect on inorganic nitrogen. Response patterns showed that observed effects were related to variations in moisture with location (site or replicate), or treatments that affected moisture itself or moisture related variables, including temperature, microbial biomass, and SOM. These response patterns show that moisture availability is the primary limiting resource in this system. The lack of nitrogen related response patterns indicate that nitrogen showed little response to treatments and little relation to other soil parameters.

CHAPTER 3

Peak Biomass Response to Fire, Winter Grazing and Nitrogen Manipulation

ABSTRACT

Reoccurring fire and ungulate grazing has been shown to benefit the productivity of North American tallgrass prairie in the eastern Great Plains. Colorado tallgrass prairie has persisted with different climatic and fire regimes for much of the past 8,000 years. I used a factorial design using fire, grazing, and soil amendments to modify nitrogen, light and moisture availabilities, to examine the effects of these variables on the primary productivity (peak biomass) of Colorado tallgrass prairie.

Productivity of Colorado tallgrass prairie was limited by moisture, with N limitation providing a secondary control under moist conditions. This contrasts with eastern tallgrass where productivity is limited primarily by N availability and secondarily by moisture. Moist Colorado tallgrass prairie sites showed productivity responses to treatments similar to those reported for eastern tallgrass prairie. Drier Colorado sites showed productivity responses to treatments that differed from those of both eastern sites and moist Colorado sites. Contributions of climate, soil and irrigation to moisture availability appear to control the pattern of productivity in tallgrass prairies on both sides of the Great Plains.

INTRODUCTION

Management practices for tallgrass prairie, most notably the requirement for periodic fire, are based on ecological principles validated in studies of eastern tallgrass prairie, which occurs in the eastern Great Plains. These practices may not completely address the needs of Colorado tallgrass prairie, which receives less than half (Callahan 1987) the 83.5cm mean annual precipitation of the Konza prairie LTER site (Greenland 1987). Testing these practices in Colorado tallgrass prairie helps ecologists understand the breadth or limitations of general ecological principles and determine which ecosystem variables describe regional properties and which describe general properties of the tallgrass ecosystem.

Principles understood to be important for the maintenance of tallgrass flora include the need to remove accumulated litter (Knapp and Seastedt 1986) and to generate establishment sites for interstitial species (Glenn and Collins 1990) to maintain the characteristic patch structure. These processes are accomplished by large and small scale disturbances including periodic fire (Hulbert 1986; Collins and Wallace 1990); aboveground (Vinton et al. 1993; Gibson et al.1990) and below-ground (Seastedt et al. 1988) herbivory; wind (Hulbert 1930; Weaver 1954) and soil processing (Branson et al. 1965; James 1991; Vinton and Hartnett 1992).

Additionally, tallgrass prairie is prone to periodic drought (Weaver 1954). Periodic drought is not understood to be necessary for the maintenance of tallgrass prairie, though historically it probably is responsible for the maintenance of the Great Plains as a grassland system, and so provided habitat, at the edges of the plains for tallgrass prairie. Tallgrass prairie flora includes both drought tolerant and drought escaping species (Weaver 1954).

Above ground net primary peak biomass, plant biomass per unit area, provides an index of plant vigor (Seastedt, Briggs et al. 1991). When combined with plant community data, peak biomass data contribute to an assessment of ecosystem health.

Fire, winter grazing and nitrogen manipulation affect aboveground peak biomass by changing the availability of resources including nitrogen, water and light. Aboveground peak biomass increases when the amounts of available resources are maximized. In most terrestrial ecosystems, nitrogen is a limiting resource (Vitousek & Howarth 1991, Seastedt et al. 1991). Light may be limited in tallgrass prairie when disturbance has been excluded causing plant litter to accumulate (Daubenmire 1968; Hulbert 1973; Abrams et al. 1986; Knapp and Seastedt.1986; Seastedt et al. 1991). Increasing light through fire or winter grazing may increase peak biomass of some species; though this may not increase total peak biomass. Lack of water may also limit peak biomass in drier areas or years (Weaver 1954, Benning 1993).

Water limitation is believed to be the major factor controlling transitions between tallgrass, mixed grass and shortgrass prairies (Jenny 1980; Weaver 1954). Indeed tallgrass prairie presence along the Colorado Front Range invites examination of how this mesic plant community obtains sufficient moisture to survive in this arid climate. Vestal (1913) argued that topography provided areas of greater moisture. Branson et al. (1965) suggested that rocky soils provided increased available moisture. Comparison of soil characteristics of Boulder County soils showed that those soils supporting tallgrass were either deep rocky soils that functioned as unconsolidated aquifers, shallow soils laying over sandstone aquifers, or soils that were seasonally innundated (Hopkins, unpublished results). Release from water limitation by irrigation increases total peak biomass. It also favors mesic species that tend to be highly productive. However, more mesic species may be more vulnerable to drought.

Available nitrogen may be increased by fertilization or stimulating N cycling. In highly productive systems many nutrients are immobilized in plant biomass and detritus (Knapp and Seastedt 1986). In addition nutrients may be immobilized by soil components including clays and soil organic matter (SOM) (Brady 1990) or soil fauna (White et al. 1988; Hossain et al. 1995). Both fire (Hobbs et al. 1991) and grazing (McNaughton 1985) stimulate the return of nutrients from plants to soil, but they have different long term effects on available nitrogen. Frequent fire reduces total N creating a highly productive, but nitrogen limited system (Seastedt et al. 1991). Chronic grazing reduces root biomass limiting the ability of plants to exploit the nitrogen released (Jones 1985) and limiting peak biomass. Winter grazing may have different effects because herbivory occurs while the dominant tallgrass species are dormant.

Light limitation is caused by plant litter accumulation. Light is further limited by dominant tallgrasses during the summer growing season (Weaver, 1954). limiting cover of other species (Vinton and Hartnett 1992). Release of light limitation by fire or grazing benefits plants active at that time. to benefit dominant C_4 species fire and grazing disturbances were timed to release light limitation in late spring just before tallgrasses emerge.

This study examined resource controls on productivity of Colorado tallgrass prairie, by monitoring peak biomass of experimental plots for three years. Plots were treated with fire, winter grazing, nitrogen manipulation (both fertilization and reverse fertilization) in a three way factorial design at two sites with different soils, irrigation regimes, and management histories.

I tested the following hypotheses, derived from reports of productivity controls in eastern tallgrass. First, peak biomass will increase with litter removal; and both fire and winter grazing will remove litter, reducing soil moisture and increasing soil temperatures. Second, peak biomass will increase with inorganic nitrogen; and both fire and reverse fertilization will reduce inorganic nitrogen, while both winter grazing and fertilization will increase it. Third, peak biomass will increase with soil moisture; and irrigation will increase soil moisture, while both fire and winter grazing reduce it. Finally, climate and regional differences will cause controls on the productivity of Colorado tallgrass prairie to differ from those of eastern tallgrass prairie.

The first three of the hypotheses address how the effects of fire and winter grazing differ. The second and third address how soil differences between sites and soil responses to treatments mediate plant responses. The last addresses which treatment responses were consistent for both Colorado and mainland tallgrass prairie and which responses showed regional differences.

METHODS

Study Sites

The three study sites (Figure 1.1) had tallgrass plant communities containing *Andropogon gerardii*, *Panicum virgatum*, *Sorghastrum avenaceum*[1], *Schizachyrium scoparium*, and *Sporobolus asper*. Two of these sites were parcels of the Colorado Tallgrass Natural Area. Previous and concurrent floral and faunal studies of all three sites provided additional information about these sites. Table A.3 (Appendix A) shows the subject and investigators for several recent research projects at these three sites.

I selected sites with different soils and different irrigation regimes so that results would be general enough to apply to most local tallgrass sites. Sites included both moist and xeric tallgrass prairie. Moist tallgrass prairie supports species similar to lowland tallgrass prairie in the eastern Great Plains, while the xeric tallgrass prairie supports species similar to upland tallgrass prairie. Both the wettest and the driest sites are part of the Colorado tallgrass natural area.

The two natural area sites have ungrazed areas fenced to exclude domestic grazing since 1987. Each of these grazing exclosures contained twelve plots each for a total of twenty-four ungrazed plots. Winter grazed areas at all three sites have been grazed for the past century and contain twelve plots each for a total of thirty-six winter grazed plots, and sixty plots altogether.

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[1] Great Plains Flora name: *Sorghastrum nutans* (Great Plains Flora Association 1986)

Yunker Site

The wettest site, on the Yunker II property (natural area parcel 6), is north of the Boulder turnpike and southwest of the Whaley drive cul de sac. The site is on Hargreave clay loam soil (50 - 100 cm deep) on Fox Hills-Laramie sandstone (a large and important aquifer). The site is both subirrigated and surface irrigated from the Goodhue ditch. Winter grazed areas are part of a 97 hectare area winter grazed by cows and calves from December to May. Tallgrass stems at this site are 1.2-1.5m tall. Plot locations and treatments in the ungrazed exclosure at this site are shown in Figure A.1 (Appendix A). Plot locations for the grazed area are shown in Figure A.2 (Appendix A). Plant species found at this site include those typical of lowland tallgrass communities in the eastern Great Plains. Dominant grasses are big bluestem (*Andropogon gerardii)* and switchgrass (*Panicum virgatum*).

THP Site

The driest site, THP (natural area parcel 3), is west of the Sans Souci mobile home park on Nederland very cobbly loam soil (deeper than 2.5 m and 78-95% rock). A map showing plot locations and treatments for the ungrazed area at this site is shown in Figure A.3 and the grazed area is shown in Figure A.4.

This site is in the South Boulder Creek flood plain where it was probably flooded annually until water diversion out of South Boulder Creek began in the early 1870's. Numerous other ditches, both above and below this site were pulled from South Boulder Creek over the next twenty years. The southwestern part of the property is still subirrigated from the Goodhue ditch, but the study plots are north of that area and are very dry. Excavation at this site in 1994 revealed that the water table was more than 1.5 m below the surface. Tallgrass stems at this site average less than 1m high, but the plant community is similar to upland tallgrass prairie, and dominated by Indian grass (*Sorghastrum avenaceum*).

Van Vleet Site

The third site, Van Vleet, is also on Nederland very cobbly loam soil (more than 2.5m deep with 78-95% rock) on the plateau above the Marshallville ditch just South of the Boulder turnpike and west of Cherryvale road. The plots are on the flat area northwest of the well house and are surface irrigated. A map of these plots is shown in Figure A.5.

The Van Vleet site is not part of the designated tallgrass natural area. It also has no grazing exclosure so data from this site were excluded from analysis of winter grazing effects including the full factorial analysis. However, since the Yunker and THP sites differ in both soil and irrigation regime, Van Vleet is an important intermediate site. Van Vleet has the same soil as THP and the same irrigation regime as Yunker. Data from the Van Vleet site may provide insight into the relative contributions of soil and irrigation to observed site differences.

The Van Vleet site has higher plant species richness in tallgrass, shortgrass and weed species. Tallgrass species include Big Bluestem (*Andropogon gerardii*), Switchgrass (*Panicum virgatum*), Indian grass (*Sorghastrum avenaceum*).

Experimental Design & Analysis

A randomized block three-way factorial experiment examined the response to fire, winter grazing, and nitrogen manipulation (both fertilization and reverse fertilization) at three sites over three years. Climate data for 1993-1995 are shown in Table A.4 (Appendix A). Land management treatments included fire, winter grazing, fertilization, and reverse fertilization. Fire and winter grazing treatments mimic the probable historic disturbance regime. Nitrogen manipulation tests nitrogen limitations on peak biomass in this system. The reverse fertilization (carbon addition) nitrogen manipulation treatment was expected to reverse some of the effects of atmospheric nitrogen deposition. These treatments are believed to affect plant resources as shown in Table 3.1.

Fire treatments were applied in the late spring (late April or early May). All fire plots were burned the first year (1993). Thereafter two sites per year were burned so that all sites were burned three out of four years. Second year (1994) fire treatments were applied only at THP and Van Vleet; third year (1995) fire treatments were applied to Yunker and Van Vleet; and fourth year fire treatments were applied to Yunker and THP. Fire dates are shown in Table 2.1.

Table 3.1 Hypothetical Effects of Treatments on Three Plant Resources

Management		Plant Resources Affected		
Strategy	Treatments	Nitrogen	Light	Water
Fire	April or May Fire	less N	more light	less water
Winter Grazing	Jan-May cattle graze	more N	more light	less water
Nitrogen Manipulation	N addition	more N	-	-
	N immobilization	less N	-	-

Domestic cattle grazed designated areas at the Yunker and THP sites from December to May. Domestic grazing has been excluded from the ungrazed areas since 1987. Grazing intensities calculated from stocking rates are shown in Table A.5.

Nitrogen manipulation treatments for this study included N addition (fertilization) and N immobilization (reverse fertilization). Fertilization and reverse fertilization treatments were applied in two equal applications each year, in May and June. Fertilization consisted of application of ammonium-nitrate to provide a total of 20gN/m2 in 1993 and 1996 and 10gN/m^2 in 1994 and 1995. Reverse fertilization consisted of application of sawdust and sugar to provide 25gC/m^2.

Field Measurements

Temperatures at the soil surface and 10cm below the surface were measured as described in Chapter 2. Mid-season field moisture was measured and mid-season soil nitrate and ammonium extracted for composite soil samples taken in July 1996. Samples were collected, field moisture measured, and nitrogen extracted as described in Chapter 2. Temperature (Table 2.3), field moisture (Table 2.5) and nitrogen (Table 2.4) responses were evaluated using repeated measures ANOVA.

To examine the different effects of fire and winter grazing on litter removal, litter biomass from the 1993 field season was separated from live biomass in the peak biomass sample. Litter from a 0.9m^2 area was oven dried, weighed, and reported on a mass per unit area basis (Appendix B, Table B.2). Samples were harvested by the methods described in Chapter 7. Repeated measures ANOVA, with site as the repeated measure (Chapter 7, Table 7.1), detected significant site and treatment effects. Litter in ungrazed plots had accumulated over past six years. Comparisons between burned and unburned plots showed what fraction of accumulated litter was removed by fire. Comparisons between grazed and ungrazed plots showed what fraction of the accumulated litter was removed by annual grazing over the past six years.

Peak Biomass samples were harvested annually from 1993 to 1996. To compare with peak biomass data from Konza Prairie Long Term Ecological Research Site, peak biomass samples were harvested in late August or September in 1993 and 1996. To test hypotheses about senescent foliage and litter accumulation, senescent peak biomass samples were harvested in October of 1994 and 1995. Peak biomass samples consisted of all aboveground biomass in a 30cm x 30cm (1993 and 1994) or 20 x 50 cm (1995 and 1996) frame. Samples were clipped within 0.3 cm of ground level, dried and weighed. Data are reported as grams per square meter.

The number of forb stems and grass flower stems were counted within the 0.1m^2 area of the 1995 peak biomass sample immediately before harvest. These numbers were divided by the area to give stem densities per square meter. Species with less than ten stems over the thirty peak biomass samples were excluded from the analysis. Species were separated into functional groups including: native species, exotic species, monocots, dicots, C_4 grasses, C_3 grasses, C_3 forbs, and all C_3 species.

Analysis

Data from different years and different sites were treated as repeated measures. Repeated measures analysis was used to increase the statistical power and reduce autocorrelation. Analysis proceeded in two stages. First, the 48 plots at Yunker and THP were analyzed using multivariate analysis of variance on the full factorial treatment model shown in Table 3.1. Second, the 36 winter grazed plots from all three sites were analyzed to examine the role of soil and irrigation in treatment responses at winter grazed sites.

Nitrogen manipulation was coded into two dichotomous dummy variables: nitrogen (linear) and nitrogen (quadratic). Nitrogen (linear), tested whether the direction of reverse fertilization effects was opposite the direction of fertilization effects, for example the expected effect on nitrogen levels. Nitrogen (quadratic) tested whether reverse fertilization and fertilization effects are in the same direction. For example, a if both treatments increased soil moisture the effect would be quadratic, even if the mechanism for the effect were different for each of the two treatments.

Initial analyses of response data were blocked by site to extract general response information. However, the response to these treatments was strongly site dependent. Blocking by site revealed little of the underlying data structure, so site was used, with year, as a repeated measure in the analysis. Data were analyzed using the SPSS: Advanced and Professional Statistics Package Version 6.1 for Windows (SPSS 1994).

Table 3.1 - Repeated Measures ANOVA Model for Peak Biomass Data

n = the number of study plots per ANOVA cell. Sample date used as covariate in the analysis.

	Source of Variance	df	n
Between Management Regime Main and Two-Way Effects	Fire	1	36
	Winter Graze	1	36
	Nitrogen (quadratic)	1	32 :48
	Nitrogen (linear)	1	24
	Fire × Winter Graze	1	18
	Fire × Nitrogen (quadratic)	1	12 : 24
	Fire × Nitrogen (linear)	1	12
	Winter Graze × Nitrogen (quadratic)	1	12 : 24
	Winter Graze × Nitrogen (linear)	1	12
	error	2	
Within Management Regime Effects involving Site	Site	1	36
	Fire × Site	1	18
	Winter Graze × Site	1	18
	Nitrogen (quadratic) × Site	1	12 : 24
	Nitrogen (linear) × Site	1	12
	Fire × Winter Graze × Site	1	9
	Fire × Nitrogen (quadratic) × Site	1	6 : 12
	Fire × Nitrogen (linear) × Site	1	6
	Winter Graze × Nitrogen (quadratic) × Site	1	6 : 12
	Winter Graze × Nitrogen (linear) × Site	1	6
	error	2	
Within Management Regime Effects involving Year	Year	2	24
	Fire × Year	2	12
	Winter Graze × Year	2	12
	Nitrogen (quadratic) × Year	2	8:16
	Nitrogen (linear) × Year	2	8
	Fire × Winter Graze × Year	2	6
	Fire × Nitrogen (quadratic) × Year	2	4 : 8
	Fire × Nitrogen (linear) × Year	2	4
	Winter Graze × Nitrogen (quadratic) × Year	2	4 : 8
	Winter Graze × Nitrogen (linear) × Year	2	4
	regression with covariate (Sample date)	1	
	error	3	
Within Management Regime Effects involving Year × Site	Year × Site	2	12
	Fire × Year × Site	2	6
	Winter Graze × Year × Site	2	6
	Nitrogen (quadratic) × Year × Site	2	4 : 8
	Nitrogen (linear) × Year × Site	2	4
	Fire × Winter Graze × Year × Site	2	3
	Fire × Nitrogen (quadratic) × Year × Site	2	2 : 4
	Fire × Nitrogen (linear) × Year × Site	2	2
	Winter Graze × Nitrogen (quadratic) × Year × Site	2	2 : 4
	Winter Graze × Nitrogen (linear) × Year × Site	2	2
	regression with covariate (Sample date)	1	
	error	3	
TOTAL DEGREES OF FREEDOM FOR MODEL		71	

RESULTS

Litter Removal

Significant effects on litter biomass are shown in Table 3.2. Fire reduced litter. Fire also showed trends toward interactions with both site and winter graze x site. The fire x site trend suggests that fire was more effective at removing litter at the irrigated site, Yunker. This is consistent with field observations that the irrigated site, with its higher fuel load more effectively "carried the fire". At the non-irrigated site fuel sources were sometimes separated sufficiently to prevent ignition of some fuel sources.

Table 3.2 - Repeated Measures ANOVA Results for Litter

Only significant effects ($p<0.05$) and strong trends ($p<0.10$) are shown. The complete ANOVA model is shown in Table 7.1.

	Source of Variance	p	treatment	mean ± s.e.
Between Management Regime Main and Two-Way Effects	Fire	0.015	No Fire	248 ± 10
			Fire	199 ± 7
Within Management Regime Effects involving Site	Fire × Site*	0.057 NS		
	Fire × Winter Graze × Site*	0.095 NS		

* Site effect probably due to Irrigation (p=0.059); Soil effect not significant.

Physical and Chemical Responses

Fire increased soil temperatures (Chapter 2, Table 2.3, Figure 2.1), while winter grazing reduced them (Table 2.3, Figure 2.2). Fire had no significant effect on field moisture. Winter grazing increased soil moisture, especially in reverse fertilized plots at the non-irrigated site, THP, and in fertilized plots at the irrigated site, Yunker (Chapter 2, Table 2.7, Figure 2.7). Fire showed no significant effects on either nitrate or ammonium in the full factorial ANOVA model (Chapter 2, Table 2.1). However, when fertilized plots were omitted from the analysis, and only reverse fertilized and control plots considered, fire showed a trend toward reducing ammonium (p=0.065, Chapter 2). Winter grazing had no significant effects on ammonium for either the full factorial ANOVA model (Chapter 2, Table 2.1) or for models separating fertilization and reverse fertilization effects.

Peak Above Ground Biomass

Mean peak biomass by site and year is shown in Table 3.3. Mean peak biomass for these three years differed with weather. Weather patterns showing differences between the three years during the C_4 growing season are shown in Table 3.3. Weather data for all months of the study period (1993 - 1995) are shown in Appendix A, Table A.4.

The first year, 1993, was the 4th coldest and 19th wettest year over the past one hundred years (Callahan 1993), these conditions were quite favorable to the tallgrass prairie relicts in this study. The second year, 1994, was a drought year, the 36th driest and 30th warmest year of the past one hundred years (Callahan 1994); it was hot and dry in both spring and summer. Vegetation at all three study sites senesced early and extensive leaf rolling was observed in both *A. gerardii* (big bluestem) and *P. smithii* (western wheatgrass) at both cobbly loam sites (Van Vleet and THP). The third year, 1995, had an exceptionally wet and cool spring, but a hot summer (Callahan 1995).

Mean litter mass did not differ significantly between the three sites, however the two irrigated sites had greater live peak biomass than the non-irrigated site (Table 3.3). Mean peak biomass at the two sites responded differently to year (Figure 3.4). Peak Biomass at all three sites was greatest in 1993 and lower in 1994, but peak biomass at the non-irrigated site, THP, was lowest in the drought year 1994, while peak biomass at the irrigated site, Yunker remained near the 1993 level. However, fire plots at Yunker were not burned in 1994 (Table 3.4). Plots that were burned in the previous year had higher peak biomass than unburned plots or plots burned that year (Table 3.4).

Repeated measures analysis of variance, over three years, showed significant site and year effects and significant interactions between both treatments and these two factors (Table 3.5). None of the treatment main effects was significant. Significant effects includes site, year and their interactions with fire and winter grazing. The site effect is due entirely to Irrigation. The Soil effect was not significant.

Winter grazing reduced peak biomass at the non-irrigated site, THP, and increased it at the irrigated site, Yunker (Figure 3.2). Fire x site showed a similar

Table 3.3 *Mean Aboveground Peak Biomass by Site and Year*

Means with different letters are significantly different ($p<0.05$). 1994 was a drought year. Fire plots not burned at Yunker in 1994 and THP in 1995 increasing mean peak biomass. Data from sites where fire plots were not burned that year are underlined.

Year	Month	vegetation state when sampled	Peak Biomass: Mean ± Standard Error (g/m^2)			Climate Data **								
			Yunker	Van Vleet	THP	precipitation (cm)					mean high T (°C)			
			irrigated sandy clay loam	irrigated very cobbly loam	not irrigated very cobbly loam	Jan-April	May	June	July	Aug.	May	June	July	Aug.
1993	Sept	peak	1210 ± 98 a	1198 ± 58 a	835 ± 67 b	14.9	4.4	8.6	3.6	6.6	21.4	26.3	29.1	27.8
	- live fraction		967 ± 90 c	973 ± 40 c	631 ± 50 d									
	- litter fraction		243 ± 32 e	226 ± 29 e	204 ± 25 e									
1994	Nov	senescent	1170 ±105 a	472 ± 79 f	337 ± 37 g	18.5	3.4	2.4	0.9	6.5*	25.0	30.4	30.2	29.4
1995	Dec	senescent	551 ± 47 h	427 ±125 fgh	428±116 fgh	21.3	24.4	10.2	1.8	3.7	16.9	24.5	30.0	32.1
(1993-1995 mean)			977 ± 12 y	699 ± 23 y	533 ± 10 z									

*Total precipitation for August 1994 was received in a single afternoon and did not break the drought.

** Boulder climate data from Boulder Weather (Callahan 1993, Callahan 1994, Callahan 1995) - climate data for all months is shown in Chapter 4, Table 4.2.

trend (Figure 3.3). Mean peak biomass at the two sites responded differently to year (Figure 3.4). Peak Biomass at all three sites was greatest in 1993 and lower in 1994, but peak biomass at the non-irrigated site, THP, was lowest in the drought year 1994, while peak biomass at the irrigated site, Yunker remained near the 1993 level.

Relationship Between Drought and the Effect of Year on Peak Biomass

To examine whether the significant year effect over these three years was due to the 1994 drought, repeated measures ANOVAs using the model shown in Table 3.1 were used to compare productivity in each pair of years. Variations in peak biomass between the cool moist year, 1993, and the drought year, 1994, showed no significant effects. Variations in peak biomass between the drought year, 1994, and the following year, 1995, showed significant winter graze x site effects , but only a trend with year (p=0.073). No significant variations were seen between one year and the next. Variations in peak biomass between years was significant only when comparing the cool moist year 1993, with the post-drought year 1995 (p=0.029).

Table 3.4 Colorado Tallgrass Prairie Peak Biomass with Drought, Winter Grazing, Fire and Nitrogen Treatments

Konza Prairie N treatment was addition of 20g/m^2 annually, while Boulder N treatment was 20g/m^2 in 1993 and 10g/m^2 in 1994 and 1995.

Weather and Winter Grazing		Mean Peak Biomass (g/m^2)						Precipitation (cm)					
	Site	C alone	C + Fire	control	Fire alone	N alone	N + Fire	Year	April	May	June	July	Aug
normal years ungrazed	Yunker	1224	933	1048	1356	1365	1191	1993	6.5	4.4	8.6	3.6	6.6
	THP	920	1295	968	903	1001	702						
	Yunker	327	364	578	632	540	308	1995	12.6	24.4	10.2	1.8	3.7
	THP*	641	199*	1474	502*	870	156*						
normal years winter-grazed	Yunker	1253	1523	1262	1423	1518	1484	1993	6.5	4.4	8.6	3.6	6.6
	Van Vleet	1410	1057	1265	1004	1338	1338						
	THP	989	694	807	690	687	360						
	Yunker	557	759	628	434	708	777	1995	12.6	24.4	10.2	1.8	3.7
	Van Vleet	135	482	988	453	415	190						
	THP*	202	105*	266	109*	319	286*						
drought years ungrazed	Yunker*	935	886*	748	1055*	1083	593*	1994	8.8	3.4	2.4	0.9	6.5
	THP	238	174	400	287	380	230						
drought year winter-grazed	THP	238	174	400	287	380	230	1994	8.8	3.4	2.4	0.9	6.5
	Van Vleet	472	308	711	322	707	311						
	THP	325	190	500	346	621	354						

* These data show response to fire the PREVIOUS year, no fire treatment in that year

Table 3.5 - Repeated Measures ANOVA Results for Peak Biomass Data

Only significant effects ($p<0.05$) and strong trends ($p<0.10$) are shown. The complete ANOVA model is shown in Table 3.1. Sample date was used as covariate in the analysis.

	Source of Variance	p	Treatment	mean ± s.e.
Between Management Regime Main and Two-Way Effects	Winter Graze × Nitrogen (quadratic)	0.098 NS		
Within Management Regime Effects involving Site	Site*	0.028	THP	533 ± 10
			Yunker	977 ± 12
	Fire × Site*	0.077 NS	see Figure 3.2	
	Winter Graze × Site*	0.046	see Figure 3.1	
Within Management Regime Effects involving Year	Year	0.001	1993	1022 ± 14
			1994	753 ± 21
			1995	489 ± 13
	Fire × Year	0.027	see Figure 3.4	
	Winter Graze × Year	0.008	see Figure 3.5	
	Winter Graze × Nitrogen (quadratic) × Year	0.038		
Within Management Regime Effects involving Year × Site	Year × Site*	0.028	see Figure 3.3, Table 3.3	
	Nitrogen (linear) × Year × Site*	0.080 NS		
	Fire × Winter Graze × Year × Site*	0.076 NS		

*Site effect was due entirely to Irrigation ($p=0.020$; df=1,2); Soil effect was not significant.

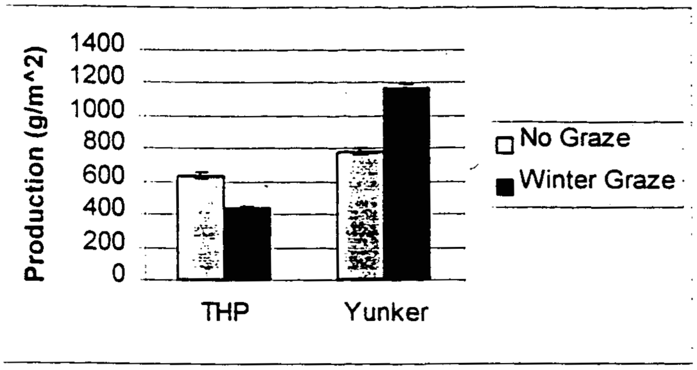

Figure 3.1 - Winter Grazed x Site Effects on Peak Biomass
Winter grazing increased peak biomass at irrigated Yunker site, but reduced it at the non-irrigated THP site. This effect is significant (p=0.046, Table 3.5) similar to the fire trend (Fig. 3.3).

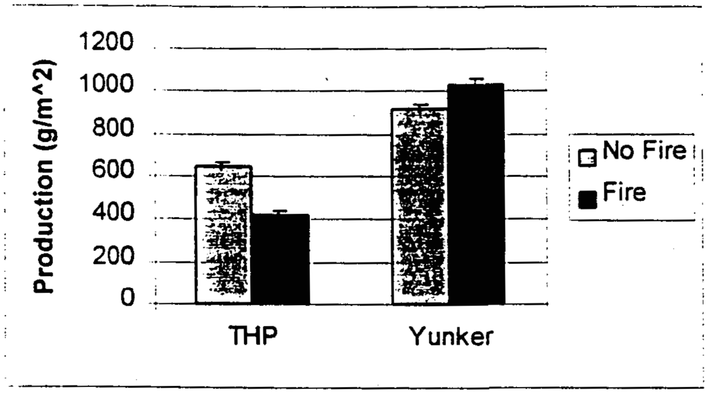

Figure 3.2 - Peak Biomass Trend with Fire x Site
In a trend similar to the winter grazing effect (Figure 3.3), fire tended to increase peak biomass at the irrigated Yunker site, but reduce it at the non-irrigated THP site. Trend with p=0.077 (Table 3.5).

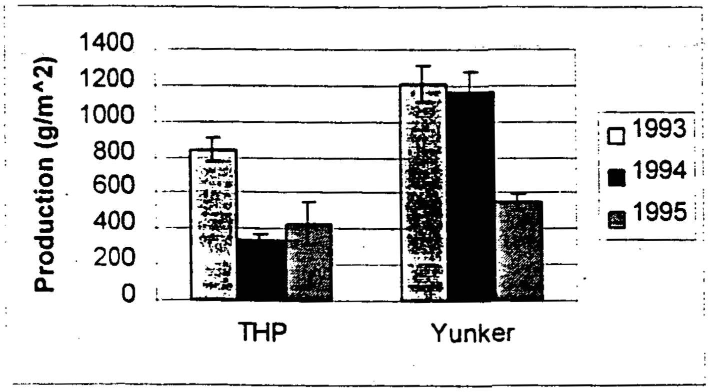

Figure 3.3 - Site x Year Effects on Peak Biomass
The 1994 drought year affected the two sites differently. Fire plots at the Yunker site were not burned in 1994 increasing mean peak biomass at that site. However the effects of drought were evident at both sites in 1995. Site x year effect was significant (p=0.028, Table 3.5).

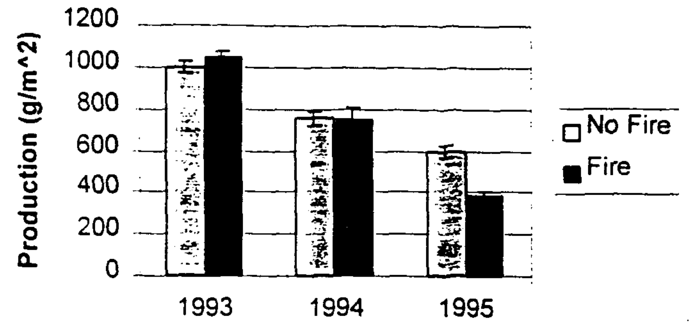

Figure 3.4 - Fire x Year Effects on Peak Biomass
Fire increased peak biomass the cool moist year, 1993. Fire had little effect in 1994, but fire plots at Yunker were not burned in 1994 increasing mean peak biomass of fire plots. Fire reduced peak biomass dramatically in 1995 at both sites. Fire reduced peak biomass most in the year following the drought. Effect is significant (p=0.027, Table 3.4).

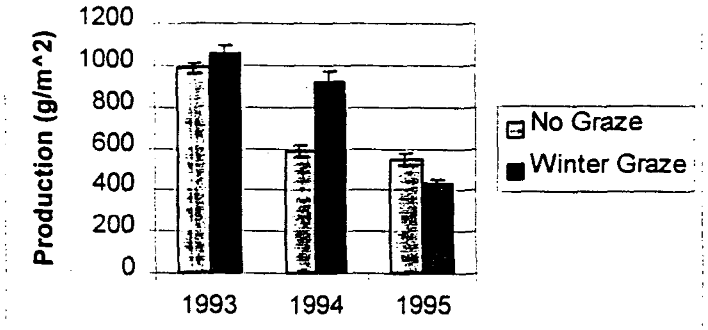

Figure 3.5 - Winter Grazing x Year Effects on Peak Biomass
Winter grazing increased peak biomass in both 1993 and 1994, but reduced it in 1995. Like fire, winter grazing reduced peak biomass in the year following the drought. Effect is significant (p=0.008, Table 3.4)

DISCUSSION

Peak biomass at both irrigated and non-irrigated Colorado tallgrass sites (Table 3.1) cover a range that includes peak biomass values from Konza prairie sites with similar fire and nitrogen treatments (Table 3.6).

Table 3.6 Konza Prairie Peak Biomass with Fire and Nitrogen Treatments

Compare to Colorado data (Table 3.4). Konza Prairie N treatment was addition of 20g/m² annually, all sites were ungrazed

Weather		Mean Peak Biomass (g/m²)					Precipitation (cm)				
	Site	control	Fire alone	N alone	N + Fire	Year	April	May	June	July	Aug
normal year	**Konza**	**380**	**470**	**420**	**580**	**1990**	**2.3**	**10.0**	**18.0**	**18.0**	**18.0**
drought year	**Konza**	**210**	**250**	**240**	**390**	**1989**	**1.2**	**6 .0**	**4 .0**	**4 .0**	**13.5**

Konza Prairie comparison data from Benning (1993). These data did no include C or C+ Fire responses.

Fire and Winter Grazing Control of Peak Biomass Through Litter Removal

First, I hypothesized that both fire and winter grazing would remove litter, increasing soil temperatures, and peak biomass, and reducing soil moisture. Knapp and Seastedt (1986) showed that removal of accumulated litter increased peak biomass in eastern tallgrass prairie, partly due to increased soil temperatures and reduced soil moisture. Fire reduced litter (Table 3.2) increased soil temperatures (Chapter 2) and reduced soil moisture (Chapter 2) as expected. However, fire had no significant effect on peak biomass. It showed a trend toward increasing biomass only in at the irrigated site in the wettest year (1993). Lack of fire response is consistent with reports from drought years and from drier upland sites in eastern tallgrass prairie (Benning 1993; Briggs and Knapp 1996)

Winter grazing had no effect on litter (Table 3.2), but increased soil moisture, reducing soil temperatures at both sites (Chapter 2). However, peak biomass response to winter grazing differed with both site and year (Table 3.5). Winter grazing increased peak biomass at the irrigated site and in both 1993 and 1994, but reduced it at the non-irrigated site and in the post-drought year (1995). This pattern shows that the biomass response to winter grazing depended on available moisture. Decomposition of the site effect into soil and irrigation effects lent further support to that conclusion, because only irrigation had a significant effect on peak biomass; soil did not (Table 3.5).

The effect of winter grazing differed with site. At the irrigated site, winter grazing stimulated production (Table 3.5) by increasing cover of high productivity C_4 grasses (Chapter 4). These grasses produce more shade than their C_3 competitors

(Weaver 1954) reducing evaporation and because of their C_4 photosynthesis transpire less than C_3 grasses and forbs, so they increased soil moisture and reduced soil temperatures (Chapter 2), compared to ungrazed areas. At the non-irrigated site, winter grazing reduced peak biomass (Table 3.5) which one assumes reduced plant uptake and transpiration increasing residual soil moisture in winter grazed areas at that (Chapter 2). The peak biomass response to winter grazing at the irrigated site, and in wet years, was similar to the typical response to chronic grazing in eastern tallgrass prairie, while the response at the non-irrigated site and in drier years was more consistent with reports of drought years and drier upland sites in eastern tallgrass prairie (Weaver 1954). This hypothesis must be modified as follows. Fire will remove litter, but will not affect productivity; winter grazing will not affect litter, but will increase productivity at irrigated sites and reduce it at non-irrigated sites.

Fire and Winter Grazing Control of Peak Biomass Through Nitrogen Resources

Second, I hypothesized differences between fire and winter grazing effects on peak biomass would be correlated with differences between their effects on inorganic nitrogen; and that fire would reduce inorganic nitrogen, while winter grazing increased it. Fire has been shown to reduce inorganic N in eastern tallgrass prairie (Eisele et al. 1989; Hobbs et al. 1991), and chronic grazing has been shown to increase available inorganic N in a variety of grasslands (McNaughton 1985; Holland and Detling 1991). In Colorado tallgrass prairie, this hypothesis also required modification.

Neither fire nor winter grazing had a consistent effect on inorganic nitrogen (Chapter 2). However, when fertilized plots were excluded from the analysis and only reverse fertilized plots compared to controls, fire did show a trend toward the expected reduction of ammonium (Chapter 2). Winter grazing, however, had no effect on inorganic N. Their different effects on inorganic N had no correlation with their effects on peak biomass. Contrary to expectations, their effects on peak biomass were similar; both fire and winter grazing increased production in the wet year; winter grazing also increased it at the irrigated site, while fire showed a similar trend. This hypothesis must also be modified as follows. Neither fire nor winter grazing affected inorganic nitrogen, so the different effects of fire and winter grazing on productivity were not due to their different effects on nitrogen.

Fertilization and Reverse Fertilization Control of Peak Biomass

Third, I hypothesized that fertilization would increase both inorganic nitrogen and peak biomass, while reverse fertilization would reduce them. Peak biomass would increase with fertilization, if N were the limiting resource, as it is in eastern tallgrass prairie (Seastedt et al. 1991). Apparently, in Colorado tallgrass prairie, N is not the primary limiting resource, so this hypothesis must also be modified. When all treatments were considered, neither fertilization nor reverse fertilization had consistent effects on inorganic N or peak biomass. Patterns of inorganic N distribution suggested that N accumulated in fertilized plots at the non-irrigated site, apparently because moisture limited production and plant uptake of the additional N. When fertilized plots were excluded from the analysis and only reverse fertilized plots compared to controls, the reverse fertilized plots had lower ammonium than controls (Chapter 2), but this had no effect on peak biomass.

Differences between Tallgrass Prairies in Colorado and the Eastern Plains

Finally, I hypothesized that climate differences would cause controls on the productivity of Colorado tallgrass prairie to differ from those of eastern tallgrass prairie. Controls of productivity in irrigated Colorado tallgrass prairie in a wet year (1993) were very similar to those typical of eastern tallgrass prairie. Fire reduced litter and increased peak biomass and winter grazing increased peak biomass. However, the lack of significant nitrogen response showed that the limiting resource in Colorado tallgrass prairie was not N, as it is in eastern tallgrass prairie. In Colorado, moisture availability appears to limit productivity.

The moisture limitation hypothesis is supported by the site and year effects on the Yunker and THP data (Table 3.5, Figure 3.3), by the irrigation effect on the Van Vleet and THP data (Table 3.5), by the absence of a soil effect on the Yunker and Van Vleet data (Table 3.5), and by the reduced biomass at the non-irrigated site compared to the irrigated sites (Table 3.3).

Moisture limitations in most years and at non-irrigated Colorado tallgrass prairie sites cause productivity patterns similar to those reported for drought years and drier sites (Weaver 1954; Benning 1993; Briggs and Knapp 1996) in eastern tallgrass prairie. Drought productivity patterns in eastern tallgrass prairie include reduction of biomass with fire (Table 3.6) or winter grazing. Colorado tallgrass prairie showed reduced production in fire plots at the non-irrigated site and in drier years, and in winter grazed plots at the drier site (Table 3.5).

Productivity patterns typical of non-drought eastern tallgrass prairie (Abrams et al. 1986; Seastedt et al. 1991; Briggs and Knapp 1996) include increased production with both fire and grazing. These patterns were only observed in Colorado tallgrass prairie at the irrigated site in a wet year. Winter grazing increased productivity at the irrigated site all three years, while fire only tended to increase production at the irrigated site in the wettest year. Fire, critical to the maintenance of eastern tallgrass prairie, played a less important role in controlling production of Colorado tallgrass prairie. Climate differences between Colorado and the eastern plains caused different patterns of productivity control, but consistencies between typical Colorado tallgrass prairie productivity and drought year eastern tallgrass prairie productivity show that moisture limits productivity on both sides of the Great Plains.

Summary

The responses of non-irrigated Colorado tallgrass prairie differed from those of irrigated Colorado tallgrass prairie. Conducting a similar treatment study at a drier eastern prairie site, and comparing those results to the non-irrigated Colorado site would provide more insight into regional differences.

Productivity of Colorado tallgrass prairie was limited primarily by moisture availability. Under moist conditions (wetter years and irrigated site) N limitation provided a secondary control. This pattern differs from that of eastern tallgrass prairie where productivity is limited primarily by N availability. Productivity patterns at moist Colorado tallgrass prairie sites were similar to those reported for eastern tallgrass prairie. In contrast, productivity patterns at drier Colorado sites differed from those of both moist Colorado sites and eastern plains sites. Contributions of climate, soil and irrigation to moisture availability appear to control the pattern of productivity in tallgrass prairies on both sides of the Great Plains.

CHAPTER 4

Plant Species Composition Response to Fire, Winter Grazing and Nitrogen Manipulation

ABSTRACT

The role of fire, ungulate grazing, and N availability in controlling plant species composition has been well documented for tallgrass prairie in the eastern plains of North America. Tallgrass relicts found along the Colorado Front Range, however, have experienced different intensities and frequencies of these disturbances over the last 8,000 years. I measured plant species diversity in a three way factorial experiment examining responses to three years of fire, winter grazing, and soil nitrogen manipulation.

Both fire and winter grazing increased the diversity of native species, and reduced evenness of all species. Winter grazing increased cover of the C_4 native grasses that dominate tallgrass prairie, and of all native species. Fire, however, reduced C_4 native grass cover in plots without nitrogen manipulation, and had no effect on C_4 native grass cover in either fertilized or reverse fertilized plots. Fertilization reduced C_4 native grass cover, while reverse fertilization increased C_4 native grass cover.

INTRODUCTION

The tallgrass prairie of North America has been the subject of numerous studiesof factors controlling plant species diversity (Collins 1996). At one level of resolution, the tallgrass prairie is fire derivd and fire maintained (Sauer 1950). Frequent fires at return intervals of 2-5 years prevented establishment of woody species in these areas (Hulbert 1982; Glenn and Collins 1986). This fire prone system generated an intense nitrogen limitation that led to the dominance of a few grasses. The plant species themselves contributed to N limitation by retranslocating N before senescence producing low N litter and root detritus that stimulate microbial immobilization of soil N (Wedin and Tilman 1990; Seastedt et al. 1991; Ojima et al. 1994).

Grazing by large ungulates can reduce N limitation (Holland and Detling 1990) by increasing the rate of N cycling (McNaughton 1985). Grazing enhanced N availability has been shown to increase prairie species diversity (Collins and Glen 1995; Collins et al. 1998). Nitrogen additions can also directly modify plant species composition and affect diversity (Wedin and Tilman 1990; Collins et al. 1998).

The above studies have all been conducted in the semi-humid grasslands of the eastern Great Plains. Relict tallgrass prairie can still be found on the western edge of the Great Plains, along the Front Range of Colorado. These Colorado tallgrass sites are dominated by the same four C_4 native grass species that dominate eastern tallgrass prairie. Managers of these sites need to know whether species composition of Colorado tallgrass prairie controlled by the same constraints as eastern tallgrass prairie.

Colorado tallgrass prairie has experienced a drier climate than eastern tallgrass prairie. Tallgrass prairie at the base of the Front Range of Colorado receives 41 cm mean annual precipitation (Callahan 1987), about half the 84 cm mean annual precipitation of the Konza prairie LTER site in the eastern Great Plains (Greenland, 1987).

Colorado tallgrass prairie also had a lower fire frequency than eastern tallgrass, with fire return times in Colorado prairie ranging from seven to ten years (Veblen and Lawrence 1990) in contrast to fire return times of two to five years for eastern tallgrass prairie (Hulbert 1988). Impacts of large ungulate grazing on Colorado tallgrass prairie may also have differed from those in eastern tallgrass. where bison herds were more common.

I therefore measured the effects of fire, winter grazing, and soil nitrogen manipulation on the plant community of a relict Colorado tallgrass prairie that supported a plant community similar to that of eastern tallgrass prairie.

I used findings from the eastern tallgrass prairie to propose the following hypotheses. First, fire will increase species diversity and the cover of both monocot and C_4 native grass species. Second, winter grazing will increase species diversity and monocot cover, but reduces native cover. Third, fertilization will increase overall cover and induce species shifts from perennial native grasses toward fast growing nitrogen limited annual exotic forbs. Fourth, reverse fertilization (carbon addition) will have the opposite effect: reversing some of the effects of atmospheric nitrogen deposition, reducing overall cover, and cover of exotic annual forbs. The reverse fertilization treatment is expected.

METHODS

Study Site

The Yunker study site (figure 2.1), established in 1993, supported tallgrass plant communities containing *Andropogon gerardii*, *Panicum virgatum*, *Sorghastrum* *avenaceum*[1], *Schizachyrium scoparium*, and *Sporobolus asper*. It is part of the Colorado tallgrass natural area. Previous and concurrent floral and faunal studies of this site Table 4.1 increased available information about this site. This site is moist tallgrass, similar to lowland tallgrass prairie on the eastern Great Plains.

Ungrazed areas have been fenced to exclude domestic grazing since 1987. Both winter grazed and ungrazed areas at this site had twelve plots each for a total of twenty-four plots. Because all winter grazed plots were on one side of the fence, while all ungrazed plots were on the other side, 30-45m distant, observed winter grazing effects may include effects related to that separation. However, assignment of fire and nitrogen manipulation treatments to these plots was done at random, so the effects of fire and nitrogen manipulation are statistically independent of spatial effects.

This site, on the Yunker II property of the City of Boulder Open Space (state natural area parcel 6), is north of the Boulder turnpike and southwest of the Whaley drive cul de sac. The site is on Hargreave clay loam soil (50 - 100 cm deep) on Fox Hills-Laramie sandstone (a large and important aquifer). The site is both subirrigated and surface irrigated from the Goodhue ditch. Winter grazed areas are part of a 97 hectare area grazed by cows and calves from December to May. Tallgrass stems at this site are 1.2-1.5m tall. Plot locations and treatments in the ungrazed exclosure at this site are shown in Figure A.1 (Appendix A). Plot locations for the grazed area are shown in Figure A.2 (Appendix A).

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[1] Great Plains Flora name: *Sorghastrum nutans* (Great Plains Flora Association 1986)

Plant species found at this site include those typical of lowland tallgrass communities in the eastern Great Plains. Dominant grasses are big bluestem (*Andropogon gerardii)* and switchgrass (*Panicum virgatum*). Other tallgrass prairie species found here include Little Bluestem (*Schizachyrium scoparium*), dropseed (*Sporobolus airoides*); and occasional sideoats grama (*Bouteloua curtipendula*). Weeds here include Canada thistle (*Cirsium arvense*), bindweed (*Convolvulus arvensis*), English plantain (*Plantago lanceolata*) and occasional curly dock (*Rumex crispus*). Native roses are present in both the grazed and ungrazed areas, but are cropped heavily in the grazed area. Milkweed (*Asclepius speciosa*) is common in the exclosure but is absent from the grazed area across the fence.

Land Management Treatments

Land management treatments included fire, winter grazing, fertilization, and reverse fertilization. Fire and winter grazing treatments mimic the probable historic disturbance regime. The reverse fertilization (carbon addition) nitrogen manipulation treatment was expected to reverse some of the effects of atmospheric nitrogen deposition and reduce exotic cover.

These treatments are believed to affect plant resources as shown in Table 3.1 (Chapter 3). Changing resource availability alters the competitive balance between different plant functional groups, favoring certain plant functional groups over others. Reintroducing pre-settlement disturbance regimes should favor pre-settlement vegetation. This in turn will provide habitat for pre-settlement wildlife.

Nitrogen addition (fertilization) and nitrogen immobilization (reverse fertilization) provide two directions of nitrogen variation from the controls. The three levels of nitrogen treatments allowed examination of nitrogen limitations on species composition. By reducing nitrogen availability, nitrogen immobilization was expected to reduce exotic plant cover favoring native species.

Fire and winter grazing treatments were timed to reduce biomass of and competition from cool season C_3 native grasses when warm season C_4 tallgrasses emerge. Typical phenology of these grasses and timing of treatments are shown in table 4.1. Treatments were applied to the 6m x 6m area extending 0.5m outside the boundaries of the 5m x 5m plot. This increased uniformity of treatments in the 5m x 5m monitored plot and reduced edge effects (edge:area ratio) by 21%.

Table 4.1 Phenology of Grasses and Timing of Treatments

Treatments timed to stress cool season grasses reducing competition as tallgrasses emerge. Fire and first applications of N and C occurred in late April or early May.

	Phenology		Timing of Treatments		
	Warm Season Tallgrass	Cool Season Grasses	Fire	Winter Grazing	N & C Addition
Jan	senescent	senescent*		Cattle	
Feb	senescent	senescent*		Cattle	
Mar	senescent	emerge		Cattle	
Apr	senescent	flower	Fire$^{1993\ only}$	Cattle	First application^{1993}
May	emerge	flower	Fire$^{1994-1996}$	Cattle	First application$^{1994-1996}$
June	veg	flower			Second application$^{all\ yrs}$
July	flower	vegetative			
Aug	flower	vegetative			
Sept	senescent	vegetative			
Oct	senescent	senescent*			
Nov	senescent	senescent*			
Dec	senescent	senescent*		Cattle	

* cool season grasses and forbs may be active during warm periods in winter.

Fire treatments were applied in the late spring (late April or early May). Flame was applied at the edges of the burn areas creating a slower burning backing fire. This method provides the most intense fire treatment (de Ronde, Goldammer et al. 1990). Even so, the fire burned unevenly within the plots leaving patches of green C_3 plants. This mimics the effects of natural fire and provided for development of patchiness critical to tallgrass prairie (Glenn and Collins 1990). Plots were burned April 26, 1993 and May 8, 1995.

Domestic cattle grazed designated areas at the Yunker and THP sites from December to May. Domestic grazing has been excluded from the ungrazed areas since 1987. Grazing intensities calculated from stocking rates are shown in Table A.5.

Nitrogen manipulation treatments for this study included N addition (fertilization) and N immobilization (reverse fertilization). Fertilization and reverse fertilization treatments were applied in two equal applications each year, in May and June. Fertilization consisted of application of ammonium-nitrate to provide a total of 20gN/m2 in 1993 and 1996 and 10gN/m^2 in 1994 and 1995. Reverse fertilization consisted of application of sawdust and sugar to provide 25gC/m^2.

Field Measurements

Species names follow Weber's (1993) Colorado Flora: Eastern Slope. Alternate names including common names, and species names used by the Great Plains Flora (1986) and archaic names used by writers of early floral accounts of this area (Coulter 1889; Daniels 1911; Vestal 1913, 1914) are shown in Appendix D, table D.1.

Cover Frequency

Cover frequency was measured by the point intercept method. Species at the center of a cross hair viewed with the ESSCO "Coverpoint" projector were identified. This system selects a clearly identifiable point for plant species identification reducing bias due to plant size, showiness, or recognizability. All plant species intercepting the point were included for cover estimation. This means that percent cover for understory species is accurately represented. However, when understory plants are of different species from overstory plants, the sum of percent cover frequencies for all species in a plot may be greater than 100.

The cover frequency for a given species was calculated from the number of points intercepting that species divided by the total number of points. Points were sampled around the circumference of four one meter diameter circles placed systematically within each plot.

When a point intercepted no vegetation the point contributed to the frequencies of litter (fallen dead plant material), bare rock, or bare soil. The ratio of rock frequency to the sum of the last two provided an estimate of the fraction of rock on the soil surface. This allowed comparison of mean surface rock fractions between sites. The ratio of the litter frequency to the sum of all three non-vegetative frequencies provided an estimate of the fraction of the soil surface covered by litter. This fraction was used to compare the litter removal effects of fire and winter grazing.

Presence and Absence

Every species observed in each 5 m x 5m plot was recorded as present. These lists include both species detected by the point intercept method and those not intercepting any of the sampling points. To calculate The Shannon-Weaver diversity index and the modified Hill ratio evenness index, cover frequency values for species that were present in the plot but not detected by the point intercept sample in that quadrant were estimated as follows.

For species not intercepting points in any of the four quadrants, the cover frequency was estimated at half the detection threshold. The detection threshold is a cover frequency of one divided by the number of points sampled, so for 108 sampling points, the cover estimate is 0.046 %.

For species that did not intercept points in a given quadrant, but did intercept points in one or more of the other quadrants in the plot, the cover estimate for a given quadrant was one fourth of the total cover estimated from the combined point intercept data for all four quadrants in the plot. That estimate is 0.25 multiplied by the sum of all points intercepted in all four quadrants of the plot divided by the sum of all points sampled in all four quadrants of the plot.

Experimental Design and Analysis

A randomized block three-way factorial experiment examined the response to fire, winter grazing, and nitrogen manipulation (both fertilization and reverse fertilization) at three sites over four years.

The Shannon-Weaver diversity index (Shannon and Weaver 1949) was calculated for each quadrant in the plots. The overall Shannon-Weaver diversity index was calculated for all species present in the plot. The native Shannon-Weaver diversity index was calculated using only the native species present; and the exotic Shannon-Weaver diversity index was calculated using only the exotic species.

The Shannon-Weaver diversity index (Shannon and Weaver 1949) is estimated from the measured and estimated cover values as follows (Ludwig and Reynolds 1988).

$$\widehat{H'} = -\Sigma\left[p_i \ln\left(p_i\right)\right] \qquad \text{eqn. 4.1}$$

where p_i is the proportional abundance, or cover frequency, of the ith species

The modified Hill index (Alatalo 1981) is a modification of Hill's original (Hill 1973) evenness index that is preferred (Ludwig and Reynolds 1988) because it approaches zero as the number of abundant species approaches one. It is calculated from the Shannon-Weaver diversity index, $\widehat{H'}$, and Simpson's number, λ, as follows:

$$E = \frac{(1/\lambda)-1}{e^{H'}-1} = \frac{N2-1}{N1-1} \qquad \text{eqn 4.2}$$

Where the values N1 and N2 are Hill's first and second order diversity numbers corresponding to the numbers of very abundant (N1) and abundant (N2) species. This index was chosen because it is less dependent on sample size than other evenness indices (Ludwig and Reynolds 1988).

Species were separated into functional groups to assess treatment effects on different functional groups. Characteristics used to assign a species to a particular functional group included origin (native vs. exotic), photosynthetic pathway (C_4 and C_3 functional groups), growth habit (grasses and sedges vs. herbaceous species vs. shrubs), and life history (perennial vs. annual). Cover frequencies for functional groups were computed as the sum of the cover frequencies for each species in the group.

Statistical Analysis

Data from replicate plots were treated as repeated measures using the model shown in Table 4.2. Repeated measures analysis was used to increase the statistical power and reduce autocorrelation. Nitrogen manipulation was coded into two dichotomous dummy variables: nitrogen (linear) and nitrogen (quadratic). Nitrogen (linear), tested whether the direction of reverse fertilization effects was opposite the direction of fertilization effects, for example the expected effect on nitrogen levels.

Nitrogen (quadratic) tested whether reverse fertilization and fertilization effects are in the same direction. For example, a if both treatments increased soil moisture: reverse fertilization through reduced plant uptake and transpiration and fertilization through increased shading. When both nitrogen and carbon addition treatments affect a variable in the same way, the effect is quadratic, even when the mechanism for the effect is different for each of the two treatments. Data were analyzed using the SPSS: Advanced and Professional Statistics Package Version 6.1 for Windows (SPSS 1994).

RESULTS

General Characteristics

Species present at the Yunker study site are shown in Appendix D, Table D.1. Forty-three plant species were present at this site. Table D.2 shows the cover frequencies for native plant species and non-vegetative cover. Table D.3 shows the cover frequencies for exotic plant species.

The non-vegetated area, including litter, rocks and bare ground covered 10.6% of the total area. So vegetation covered 89.4% of the total area. Points occupied by two or more species occurred over 21.2% of the total area. Of the non-vegetated area, 89.1% was litter, 6.3% was rock and the remaining 4.6% was bare ground.

Table 4.2 - Repeated Measures ANOVA Model for Species Cover Data

Source of Variance	Degrees of Freedom	plots per ANOVA cell
Main Effects		
Fire	1	12
Winter Graze	1	12
N manipulation(Quad)	1	8 or 12
N manipulation (Linear)	1	8
Two-Way Effects		
Fire x Winter Graze	1	6
Fire x N (Quad)	1	4 or 12
Winter Graze x N (Quad)	1	8 or 12
Fire x N (linear)	1	4
Winter Graze x N (linear)	1	4
Error	2	
Effects involving Quadrant		
Quadrant	3	6
Fire x Quadrant	3	3
Winter Graze x Quadrant	3	3
N manipulation(Quad) x Quadrant	3	2 or 4
N manipulation (Linear) x Quadrant	3	1
Fire x Winter Graze x Quadrant	3	1
Fire x N (Quad) x Quadrant	3	1
Winter Graze x N (Quad) x Quadrant	3	1
Fire x N (linear) x Quadrant	3	1
Winter Graze x N (linear) x Quadrant	3	1
Error	6	

Native warm season (C_4) perennial grasses dominate with over 70% cover. This group also contains the three most common species at the site: *Andropogon gerardii* (Big Bluestem), *Sporobolus airoides* (Prairie dropseed), and *Panicum virgatum* (Switchgrass). These three dominant native species together cover 69.5% of the area. The fourth dominant is an exotic grass, *Poa pratensis* (Kentucky Bluegrass)

Four perennial grass species cover 83.9% of the area. The other 39 species present in these plots include 22 native species collectively covering 11.7% of the area and 16 exotic species collectively covering 14.6% of the area. The exotic species include four dicotomous weeds: *Convolvulus arvensis* (field bindweed), *Plantago lanceolata* (English plantain), *Rosa arkansana* (an adventive rose) and *Cirsium incanum* (hoary thistle, a species similar to Canada thistle). Together these four species occupy a larger area (13.4% of the total) than all 22 subdominant native species combined.

Treatment Responses

Species Diversity

Response of overall species diversity to treatments was assessed using the Shannon-Weaver diversity index. The overall species diversity index was calculated using all species present in the plots. Overall species diversity (Appendix D, Table D.2) showed at most, a modest response to both fire and N manipulation (Table 4.3). Overall species diversity tended to increase with fire and nitrogen addition and to decrease with carbon addition.

Native Species diversity (Appendix D, Table D.3) , as measured by the Shannon-Weaver index computed with only native species, increased significantly with both fire and winter grazing (and spatial separation), and even more so with both (Table 4.3). Exotic species diversity (Appendix D, Table D.4), as measured by the Shannon-Weaver index computed with only exotic species, showed no significant treatment response. Data for the analysis are shown in Appendix D, Table D.4.

Table 4.3 - Treatment Response of Species Diversity

Source of Variance	p	Treatment	Mean	SE
Overall Species Diversity				
Main Effects				
Fire	0.070 NS	Fire	1.79	0.04
		No Fire	1.53	0.03
N manipulation (Linear)	0.062 NS	C addition	1.49	0.01
		Control	1.62	0.08
		N addition	1.88	0.06
Two-Way Effects	NS			
Effects involving Quadrant	NS			
Native Species Diversity				
Main Effects				
Fire	0.02	Fire	1.19	0.02
		No Fire	0.95	0.04
Winter Graze	0.01	Winter Graze	1.2	0.02
		No Graze	0.94	0.04
Two-Way Effects				
Fire x Winter Graze	0.04	+F +WG	1.24	0.05
		--F + WG	1.16	0.01
		+F --WG	1.14	0.03
		--F --WG	0.74	0.03
Effects involving Quadrant				
N manipulation (Linear) x Quadrant	0.091 NS			

Evenness

Winter grazing (and spatial separation) reduced plant species evenness, as measured by the modified Hill's index (Table 4.4). Fire also tended to reduce evenness. Data for the analysis are shown in Appendix D, Table D.5.

Table 4.4 - Treatment Response of Plant Species Evenness Index

Source of Variance	p	Treatment	Mean	SE
Main Effects				
Fire	0.050	Fire	0.36	0.02
		No Fire	0.70	0.06
Winter Graze	0.038	Winter Graze	0.34	0.02
		No Graze	0.72	0.06
Two-Wav Effects	NS			

Cover Frequency of Plant Functional Groups

Winter grazing (and spatial separation) increased native plant cover (Table 4.5) and C_4 native grass cover (Table 4.5). Reverse fertilization also increased C_4 native grass cover while fertilization reduced it. Fire reduced C_4 native grass cover in control plots, but increased grass cover in fertilized and reverse fertilized plots to the level of the unburned control. This effect is shown in Table 4.5 as an interaction between fire and the quadratic component of nitrogen manipulation.

The group of all monocots (including the C_4 native grasses described above and C_3 grasses, sedges and reeds) showed no significant treatment response. Although the nitrogen manipulation effects on C_4 native grasses appears to drive a similar trend (p=0.097) toward reduction of all monocots in fertilized plots. Perennial plant cover and litter cover showed no treatment response or trends.

DISCUSSION

Dominant functional groups and species

Three perennial C_4 native grasses : *Andropogon gerardii* (Big Bluestem), *Sporobolus airoides* (Prairie dropseed), and *Panicum virgatum* (Switchgrass), covered 69.5% of the area. This figures is consistent with descriptions of eastern tallgrass prairie (Weaver 1954).

Table 4.5 - Treatment Response of Cover of Plant Functional Groups

N manipulation treatments: +N= fertilization, +C = reverse fertilization

Source of Variance	p	Treatment	Mean	SE
Native Plant Cover				
Main Effects				
Winter Graze	0.046	Winter Graze	0.84	0.01
		No Graze	0.61	0.02
Two-Way Effects	NS			
C_4 Native Grass Cover				
Main Effects				
Winter Graze	0.006	Winter Graze	0.77	0.01
		No Graze	0.49	0.02
N manipulation (Linear)	0.034	C addition	0.70	0.04
		Control	0.62	0.04
		N addition	0.57	0.05
Two-Way Effects				
Fire x N (Quad)	0.045	+F +N or C	0.67	0.05
		+F control	0.56	0.07
		--F +N or C	0.60	0.05
		--F control	0.67	0.09

The remaining vegetated area 41.1% of the total, is covered by 40 interstitial species of which a little more than half the area (21.2% of the total area) represents understory species. The 22 native interstitial species cover slightly more than one quarter of the interstitial area, only 11.7% of the total area. The exotic grass *Poa pratensis* dominates the understory, covering over one third of the interstitial area (14.3% of the total). While this grass does contribute to the preservation of the system as a grassland, it also contributes to exotic dominance of the interstitial species.

Four exotic dicots together occupy a larger area (13.3% of the total area) than all 22 native interstitial species combined. The other eleven exotic interstitial species cover the remaining 1.8%. Exotic interstitial species cover nearly three times the area of native interstitial species. These exotics displace natives, and since prairie forbs occur naturally at low frequencies loss of nearly three quarters of the available interstitial area to exotic species may threaten rare native prairie forbs.

Species Diversity

Overall species diversity showed no significant response, but strong trends of increasing diversity in response to fire and to fertilization (Table 4.3) invited further examination. Native Species diversity increased significantly with fire and with winter grazing (and spatial separation), and even more so with both (Table 4.3). Responses to fire and winter grazing (and spatial separation) were similar in direction and magnitude. This suggests that a characteristic common both fire and winter grazing (and spatial separation), the removal of litter and live biomass, is responsible for the increases in native species diversity. Removal of litter and live biomass increases the area available for colonization by new species. Fortunately, new species colonizing these areas were native. Exotic species diversity showed no significant treatment response. The significantly greater native diversity in plots exposed to both fire and winter grazing (and spatial separation) suggests that fire adapted species colonized burned plots and that different grazing adapted species colonized winter grazed plots, so only plots exposed to both treatments were colonized by both sets of species. Future analysis will address identification of colonizing species within these groups.

Evenness

Plant species evenness, as measured by the modified Hill's index, was reduced by winter grazing (and spatial separation) and fire (Table 4.4), even though overall species diversity showed no significant effect. Like native species diversity, evenness responded similarly to fire and winter grazing (and spatial separation). Both treatments reduce evenness. This suggests that litter and biomass removal, common to both fire and winter grazing (and spatial separation), was responsible for the both the evenness and native diversity responses.

Patchy removal of litter and biomass by both fire and winter grazing (and spatial separation) may create colonization patches, reducing evenness. Observations of fire treatments showed uneven burning with efficient biomass removal in areas of contiguous senescent plant matter, and little or no biomass removal in areas with high levels of green plants or bare ground. Biomass removal by winter grazing (and spatial separation) was also uneven apparently due to herbivore preference for certain plants, whether due to species or phenology. Both high native diversity and low evenness are characteristic of healthy prairies suggesting that both fire and winter grazing treatments may be appropriate management for conserving these prairies.

Cover Frequency of Plant Functional Groups

Winter grazing (and spatial separation) increased native plant cover (Table 4.5) and C_4 native grass cover (Table 4.5). These changes were due to the colonization of winter grazed patches by the native species that increased native species diversity and to expansion of existing C_4 native grass clones.

Reverse fertilization, like winter grazing (and spatial separation), increased C_4 native grass cover while fertilization reduced it. The lack of nitrogen manipulation effect on total native plant cover and total monocot cover shows that nitrogen manipulation altered the balance between the C_4 native grasses that dominate healthy tallgrass prairie and their C_3 monocot competitors, without reducing native or monocot cover. While fertilization did not reduce native cover as observed in other systems (Marrs and Gough ; Vitousek), the reduction of C_4 grass cover may indicate a shift from C_4 dominated tallgrass prairie toward C_3 dominated grass or shrubland. Reverse fertilization, like winter grazing (and spatial separation), increased C_4 native grass cover, suggesting that reverse fertilization might be an appropriate management tool for ungrazed tallgrass prairie.

Fire reduced C_4 native grass cover in control plots, but increased C_4 native grass cover in fertilized and reverse fertilized plots to the level of the unburned control. This effect is shown in Table 4.5 as an interaction between fire and the quadratic component of nitrogen manipulation. Since fire had no effect on total native plant cover or total monocot cover, the fire induced reduction of C_4 native grass cover in control plots represents a shift from C_4 native grasses to C_3 native grasses. This type of species shift contrasts with the fire effects observed in eastern tallgrass prairie (Weaver 1954; Collin and Wallace 1986). Additionally, shifts from highly productive C_4 tallgrass species toward less productive C_3 species explains why fire failed to stimulate production in Colorado tallgrass prairie (Chapter 3), as it does in eastern tallgrass prairie (Collin and Wallace 1986).

The group of all monocots (including the C_4 native grasses described above and C_3 native grasses, sedges and reeds) showed no significant treatment response. Although the nitrogen manipulation effects on C_4 native grasses appears to drive a similar trend (p=0.097) toward reduced monocot cover in fertilized plots and increased monocot cover in reverse fertilized plots. Such a trend would be consistent with McLendon and Redente's (1986) observation that reverse fertilization reduced forb cover, and bears further study.

Lack of treatment effects on perennial plant cover showed that, despite treatment induced species shifts, this grassland continues to be dominated by perennial species. Litter cover showed no treatment response possibly due to low resolution due to the low frequency of exposed litter. Future data could record understory litter as well as the exposed litter recorded in this data set, to provide higher resolution of the litter cover frequency. If litter cover does not respond to treatment, as these data suggest, then the biomass removal effects attributed to both fire and winter grazing (and spatial separation) may have been due to removal of standing dead and live biomass rather than exposed plant litter.

Fire, winter grazing (and spatial separation) and nitrogen availability all play a role in controlling species composition of Colorado tallgrass prairie. As in eastern tallgrass prairie, fire increased species diversity and reduced evenness. In contrast to eastern tallgrass prairie, fire in Colorado tallgras prairie failed to increase either C_4 native grass cover and therefore failed to increase production (Chapter 3).

In contrast to observations in eastern tallgrass prairie nitrogen effects on species diversity were insignificant (Table 4.). In contrast to observations by

McLendon and Redente (1992), nitrogen manipulation did not affect forb cover. However, fertilization induced species shifts from C_4 native grasses to C_3 native monocots, and reverse fertilization had the opposite effect. Thus, as expected, nitrogen manipulation appeared to alter the competitive balance between the C_4 native grass that dominate tallgrass prairie and their C_3 competitors. And reverse fertilization (carbon addition) shows promise as a tool for maintaining C_4 dominance of tallgrass prairie.

CHAPTER 5

Management Recommendations for Colorado Tallgrass Prairie

HISTORICAL DESCRIPTIONS OF COLORADO TALLGRASS PRAIRIE

Nineteenth century Colorado botanists described tallgrass prairie which extended along the Front Range from Fort Collins to Pueblo with tallgrass "bottom lands" along rivers well into the Great Plains (Malin 1947). The existence of tallgrass prairie species in Wyoming and New Mexico suggests that these states once supported tallgrass prairie as well (Great Plains Flora Association 1977).

The dominant plant species of the pre-drought tallgrass prairie existing in Daniel's and Vestal's time was *Schizachyrium scoparium*, while the dominants of today's late twentieth century prairie, *Andropogon gerardii*, *Panicum virgatum*, and *Sorghastrum avenaceum*[1], were interstitial species in the pre-drought prairie. In the eastern Great Plains, Weaver (1954) observed that the great drought caused *A. gerardii* to replace *S. scoparium* as the dominant tallgrass prairie grass. Similar species replacements apparently also occurred in Colorado tallgrass prairie.

Decisions about "best management" strategies must consider whether management goals should favor reconstructing plant communities that existed here in the past (i.e. the *Schizachyrium scoparium* dominated prairie with tallgrasses as interstitial species), or constructing plant communities that exist elsewhere (i.e. the eastern Great

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[1] Synonym: *Sorghastrum nutans* (Great Plains Flora Association 1986)

Plains) and are more similar to those existing today (i.e. *Andropogon gerardii*, *Panicum virgatum*, and *Sorghastrum avenaceum* dominated tallgrass prairie). The fact that many *Schizachyrium scoparium* dominated "tallgrass" prairies of the eastern Great Plains were also taken over by either *A. gerardii* or *Pascopyrum smithii*[2] (western wheatgrass) after the great drought of the 1930's suggests that this species shift was widespread and may allow the community as a whole to better survive the present climatic conditions. Nevertheless, as conservationists we must consider whether we are conserving the plant community that occurred here naturally, or attempting to construct tallgrass prairie as it occurs in the eastern Great Plains.

HISTORICAL MANAGEMENT OF COLORADO TALLGRASS PRAIRIE

Most of the Colorado tallgrass prairie, like the eastern tallgrass prairie, was plowed or grazed. Most of today's agricultural land was grassland prior to settlement (Sims, 1988). Of the 300 million hectares of grasslands in what is presently the United States, only 125 million hectares remain (Kuchler, 1964). Twenty two percent of these (less than 23 million hectares) are tallgrass prairie (Sims, 1988). In Missouri, only 0.5% of the original tallgrass prairie remains (Risser, 1988).

As the urban corridor along the Front Range grows, we continue to lose examples of the Colorado tallgrass prairie to development. Those areas that do remain either surround government installations such as Rocky Mountain Arsenal or Rocky Flats or are used as pastures for domestic cattle, or both. Tallgrass pastures in the South Boulder Creek drainage have been grazed for over 100 years.

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[2] Synonym: *Agropyron smithii* (Great Plains Flora Association 1986)

In 1986 the Colorado Natural Areas Commission designated these examples of Colorado tallgrass prairie belonging to and managed by the City of Boulder Open Space as a Colorado Natural Area. The tallgrass management plan limits land use and management methods for land within the designated natural area. While parts of the natural area continue to be leased for spring cattle grazing, other parts have excluded cattle grazing since 1987. Annual monitoring of plant cover in both grazed and ungrazed parts of the natural area showed that cover of exotic weedy species such as Canada thistle (*Cirsium arvense* (L.) Scopolic) increased in areas where grazing was excluded. Prescribed fire controlled weed infestations successfully, but involved investment of staff time and resources. This study was planned to help the City of Boulder Open Space determine what combination of fire and grazing would be the best for the conservation of tallgrass prairie areas both in and out of the designated natural area, and whether nitrogen manipulation could achieve some of the conservation goals.

DEFINING CONSERVATION GOALS

Conserving Colorado tallgrass prairie involves controlling the plant community composition and vegetation structure. Land management treatments alter conditions to favor certain species at the expense of others. Monitoring plant species cover and aboveground biomass detected these changes in community composition. Treatments also change the vegetation structure by promoting or suppressing flowering. Monitoring flowering stem density and height detected these changes.

The exact species composition of pre-settlement Colorado tallgrass prairie is unknown but may be assumed to have had the following characteristics: First, the plant species were native to North America; Second, the species include those described in early Boulder area descriptions of "true" or relict tallgrass prairie (Daniels 1911; Vestal 1913, 1914); Third, the tallgrass species present were dense enough and flowered with sufficient frequency to have been described as "true prairie" or tallgrass prairie. Conservation goals following from these characteristics include dominance by native species present in early descriptions and occurring with sufficient density, height, and flowering frequency to provide tallgrass vegetation structure.

The dominant native plant species described by Daniels (1911) and Vestal (1913, 1914) included those present today: *Andropogon gerardii* Vitman *Panicum virgatum* L., *Sorghastrum avenaceum* (Michaux)Nash, and associated species *Schizachyrium scoparium* Nees, and *Sporobolus asper* (Michaux) Kunth. These tallgrass species flowered in sufficient numbers to prompt Daniel (1911) to classify these prairies as "true" or tallgrass prairie, and Vestal (1914) to consider it a relict of tallgrass prairies. However, the dominance of *Schizachyrium scoparium* prior to the 1930s (Daniels 1911; Vestal 1913) suggests that the composition of Colorado tallgrass prairie, like some of the *S. scoparium* dominated prairies of the eastern Great Plains (Weaver 1954), may have permanently changed during the great drought.

Research in the eastern Great Plains has shown that tallgrass prairie characteristics include tall and dense flowering stalks (Hulbert and Wilson 1983; Knapp and Hulbert 1986), spatial heterogeneity or "patchiness" (Glenn and Collins 1990), and dominance of a few perennial grass species that provide a framework for a diverse community of interstitial plants (Stieger 1930; Weaver 1954; Risser 1988). Additionally, "healthy" tallgrass prairie, dominated by tallgrass species has higher production than prairies where production is limited by litter accumulation (Knapp and Seastedt 1986), or where tallgrass species have been "grazed out" and replaced by lower production species (Weaver 1954; Phillips 1955).

Conserving the dominant plant species and recreating these characteristics provides a favorable climate for the conservation or reestablishment of the more diverse components of the plant community. Conservation or restoration of the plant community and vegetation structure provides suitable habitat for native wildlife as well (Peterson et al. 1985).

Historically Based Conservation Goals

1. increased native cover and diversity; reduced exotic cover and diversity
2. dominated by native species mentioned in historical descriptions
3. tall flowering stems (at least in patches) of native species

Conservation Goals Based on Tallgrass Prairie Research from the Eastern Great Plains

1. high production
2. dominated by perennial C_4 tallgrass species (high C_4/C_3 ratio)
3. high diversity
4. low evenness
5. high native C_4 stem density
6. tall flowering stems of tallgrass species

These conservation goals allow objective measurement of both tallgrass aesthetics and exotic plant presence. They acknowledge the impacts of exotic plants on native plant communities and include criteria for comparing the exotic plant control that each land management regime provides. Management recommendations include those treatment combinations that furthered these goals.

APPLICATION OF ECOLOGICAL PRINCIPLES

Plant community composition and aboveground primary production of Colorado tallgrass prairie changed in response to fire, winter grazing, and nitrogen manipulation treatments. Nitrogen availability also changed and may mediate some of the plant community composition and aboveground primary production responses. Fire treatments occurred in April or May. Winter grazing of cattle occurred from January through May. Nitrogen manipulation treatments included both fertilization (nitrogen addition) and reverse fertilization (carbon addition to immobilize nitrogen). Plant community, aboveground primary production, nitrogen, temperature and moisture responses indicated how fire, winter grazing and nitrogen manipulation treatments affected Colorado tallgrass prairie; whether Colorado tallgrass prairie followed ecological principles demonstrated in other native ecosystems; and progress toward conservation goals for Colorado tallgrass prairie.

Plant community composition follows ecological principles governing the maintenance of both grassland and native plant communities. Most grassland plant communities worldwide are maintained by periodic grazing or fire which prevents accumulation of plant litter (Knapp and Seastedt 1986) and succession to shrubland or forest (Archer 1989). However, the frequency and intensity of disturbance necessary to maintain the grassland depends on several variables including precipitation. Colorado tallgrass prairie may require less frequent fire than tallgrass prairie in the eastern Great Plains. Plant community composition was expected to respond to periodic fire and grazing with more grass. and fewer shrubs. These treatments were also expected to reduce litter.

Nitrogen availability depends on ecosystem processes. Nitrogen availability then affects both plant community composition and primary production. Native plant communities require sufficiently low nitrogen availability to allow native plants to outcompete exotic plants (Marrs and Gough 1989). Native plants are adapted to local nitrogen limitations (Crawley 1986). When nitrogen availability increases, exotics released from nitrogen limitation may outcompete natives.

In this study, nitrogen addition modeled processes that increase available nitrogen, and adding carbon modeled processes that reduce nitrogen availability. Adding carbon sources such as sugar or sawdust stimulates microbial processes that reduce available nitrogen. Microbes decomposing materials with more than ten carbon atoms for every nitrogen atom will immobilize soil nitrogen making it unavailable to plants (Hunt et al. 1988; Chapter 2). Fire may also reduce available nitrogen by volatilizing it (Hobbs et al. 1991; Chapter 2). Reduced nitrogen availability stresses fast growing forbs (McLendon and Redente 1992; Chapter 4), including many exotic weeds, while favoring native species (Marrs and Gough 1989; Chapter 4). Addition of carbon sources or periodic fire was expected to conserve native plant communities threatened by exotic weeds. Plant community composition was expected to respond to increased nitrogen with increased exotic plant cover and to reduced nitrogen with reduced exotic plant cover.

Aboveground primary production depends on both plant community composition and resource availability. Annual aboveground primary production determines the frequency of fire or winter grazing required to prevent plant litter accumulation from changing the plant community (Archer 1989) and reducing production (Seastedt et al. 1991). Thus, fire adapted plant communities have sufficient primary production to promote accumulation of flammable plant litter (fuel). This increases the probability that fire will occur maintaining the fire adapted community (Goldammer 1990). Aboveground primary production was expected to respond to periodic fire with reduced litter biomass and increased senescent biomass (fuel) as the plant community shifted to a fire adapted community. Grazing also removes both live biomass and standing dead, reducing litter. Aboveground primary production was expected to respond to winter grazing with reduced litter biomass and lower senescent biomass (fuel) than fire adapted communities.

Both fire and grazing adapted plant communities increase production in response to increased resources. The rapid growth response of grazing adapted grass species allows these species to exploit additional nitrogen resources quickly so grazing adapted grasses are likely to outcompete other grass and forb species in high nitrogen situations. Aboveground primary production was expected to increase with fertilization (nitrogen addition), especially in winter grazed areas.

This study examined whether the difference between fire and winter grazing effects on the plant community were mediated by available nitrogen. Previous research showed that fire reduces available nitrogen (Eisele et al. 1989), and that grazing creates areas with locally high concentrations through waste deposition (Power 1981). This study examined how fire and winter grazing affected available nitrogen and the plant community, and compared fire and winter grazing effects to nitrogen addition and immobilization effects. This comparison showed that effects of fire on both soil nitrogen and plant litter removal differ from those of winter grazing (Chapters 2 and 3), so both nitrogen and plant litter effects may contribute to the resulting plant species composition (Chapter 4).

MANAGEMENT RESULTS

Plant community composition

Plant community composition was expected to respond to periodic fire and winter grazing with more grass (monocots), and fewer shrubs. Neither fire nor winter grazing significantly affected either monocot cover (Chapter 4). Only two shrub species occurred in these plots, *Rosa woodsii* and *Rosa arkansana*. Rose stem densities were not distributed through the plots sufficiently to allow ANOVA analysis; although roses occurred in quite a few plots, only four plots had roses in the stem density samples (Appendix C, Table C.4). The two plots with the highest rose stem densities were both burned plots. Two of the rose plots were winter grazed, and one of them was both burned and grazed. Neither fire nor winter grazing eliminated these particular shrubs.

Fire and winter grazing were also expected to reduce litter. Fire reduced litter mass (Chapter 3). While winter grazing did appear to reduce litter slightly, the effect was not significant. Winter grazing's positive effect on production may have increased litter input enough to offset any litter reduction effects.

Reverse fertilization (carbon addition) and periodic fire were expected to conserve native plant communities threatened by exotic weeds, by reducing available nitrogen favoring low nitrogen adapted native plants. Reverse fertilization reduced available ammonium (Chapter 2), but had no effect on nitrate. Fire showed a trend toward reduction of ammonium (Chapter 2) supporting the idea that fire and reverse fertilization had similar effects on available nitrogen. However, both effects were observed only when reverse fertilization plots were compared to control plots and fertilization plots were omitted from the analysis. Neither fire nor reverse fertilization had significant effects on exotic stem density or exotic cover.

Plant community composition was expected to respond to increased nitrogen with increased exotic plant cover. Fertilization (nitrogen addition) had no effect on exotic plant cover or exotic stem density. In fact it did not significantly affect available nitrogen levels, because the variance in nitrogen levels in fertilized plots was so high (Appendix E, Table E.3). Results suggested that plots at THP were limited by moisture, rather than nitrogen, and that nitrogen accumulated in THP plots, especially burned THP plots.

Aboveground primary production

Aboveground primary production was expected to respond to periodic fire with reduced litter mass and increased production (fuel) as the plant community shifted to a fire adapted community. Fire reduced litter as described above (Chapter 3). Fire increased production in 1993, but reduced it in 1995. Fire showed a trend toward reducing production at the non-irrigated site, THP, but increasing it at the irrigated site, Yunker (Chapter 3). However, fire plots at Yunker also showed reduced production in 1995, the year following the drought. The effect of fire appears to depend on Site and Year so that fire increased production only at wetter sites, in wetter years. Fire reduced production at drier sites and in years that were dry or that followed dry years.

Aboveground primary production was expected to respond to winter grazing with reduced litter biomass and lower production (fuel) than fire adapted communities. Winter grazing had no significant effect on litter, but did increase production at the irrigated site, Yunker (Chapter 3). Since it had no effect on litter, winter grazing increased production by some other mechanism. Winter grazing had been expected, like year round grazing, to increase nitrogen availability, but it had no significant effect on nitrogen. Winter grazing did increase available moisture, although there is no evidence that moisture limited production at the irrigated site. By contrast, winter grazing reduced production at the non-irrigated site, THP (Chapter 3).

Aboveground primary production was expected to respond to reverse fertilization with reduced production and to fertilization with increased production.This was not observed.

Instead, the strongest effects on production are related to Site, Year, and the effects of fire and winter grazing. These factors all controlled soil moisture. Site effects on production were determined to depend on Irrigation differences. Year differences depended on temperature and moisture differences (Chapter 7). Fire controlled temperature (Table 5.3). And winter grazing controlled both temperature

(Table 5.3) and moisture (Table 5.7). The primacy of these temperature and moisture controlling factors, and the relative unimportance of both nitrogen treatments, shows that moisture, not nitrogen, limited production in these sites.

Stem height

Fire and winter grazing were expected to increase stem height of all species, by removing litter and stimulating production. Fire did increase the stem height of one species, *Andropogon gerardii* (big bluestem) (Table 6.1), but had no significant effect on the stem heights of the other four tallgrass species. Winter grazing reduced the stem height of *Schizachyrium scoparium* (little bluestem) (Table 6.1). Trends from the stem height path analysis model (Table 6.2) suggest that fire tended to increase stem heights in *S. scoparium*, and to reduce stem heights in *Panicum virgatum* (switchgrass) and *Sorghastrum avenaceum* (yellow Indian grass). Path analysis trends for winter grazing suggest it tended to increase stem height in *A. gerardii* and *S. avenaceum* and reduce it in *P. virgatum*. Neither fire nor winter grazing affected all species positively. Instead the mosaic of stem heights at a site may provide insight into the management history of that site. Certainly the strong stem height response of *A. gerardii* gives a clear indication that an area has been burned.

MANAGEMENT RECOMMENDATIONS

Fire

Fire had several positive effects. Fire increased native species diversity and reduced evenness at the irrigated site (Chapter 4). Fire increased stem heights of

Andropogon gerardii (big bluestem) at both sites (Chapter 3) and may be used to stimulate the growth of this species in some areas. However, fire tended to reduce the height of the other three tallgrass species (Chapter 3), and reduced production in drier years and at drier sites. To promote a diversity of tallgrass species, fire management might be used in patches within a larger area. Fire management appears best suited to moist areas.

Fire management in arid climates and arid sites should include consideration of local hydrology and of weather over the past year. Fire may be used infrequently (not annually) to stimulate production in years following a normal or wet year. Fire should be used less frequently at drier sites. Fire should not be used at any site in a year when drought is expected or in the year following a drought.

Modern fire management requires considerable advance planning, requiring management agencies to prepare months or years ahead of the time they plan to burn, however administrative windows of opportunity may not coincide with ecological windows of opportunity. In these cases it is recommended that prescribed fires be postponed. Burn prescriptions should include not only weather conditions on the day of the burn, but also climatic conditions in the preceding year. Burning in the year after a drought may further reduce native populations and create establishment sites for drought adapted exotics, such as cheatgrass.

Winter Grazing

Winter grazing, like fire, also had several positive effects. Winter grazing increased native diversity and reduced evenness at the Yunker site (Chapter 4). Additionally, unlike fire, it increased the cover of native species and of C_4 grasses at the Yunker site. This may have been related to its positive effect on soil moisture. The effects of winter grazing on production differed with site. At the irrigated site, winter grazing increased both production (Chapter 3) and field moisture (Chapter 2). However, at the non-irrigated site, winter grazing reduced production (Chapter 3). Winter grazing increased production in years following normal or wet years, but reduced production following a drought year (Chapter 3, Figure 7.6).

The only significant effect of winter grazing on stem height was to reduce the stem height of *Schizachyrium scoparium* (Chapter 3). That effect suggests that winter grazing may have played a role in reducing the importance of this former dominant.

Winter grazing management in arid climates should include consideration of local hydrology and of weather over the past year. Winter grazing appears to be detrimental at the non-irrigated site, THP. This effect is even more dramatic when we consider that the mean dry weight removed at the THP site was less than the mean dry weight removed at the Yunker site (Table 4.6). It is recommended that the intensity of winter grazing be reduced or phased out at the THP site and at dry sites like it. If grazing continues, it is recommended that annual production continue to be monitored, and that grazing intensities be adjusted in response to information gained from that monitoring effort. If winter grazing were phased out at this site and others like it, those sites might be used in attempts to restore the *S. scoparium* dominated grasslands described by Daniels (1911) and Vestal (1913).

By contrast winter grazing appears to be beneficial at the irrigated site, Yunker. At the Yunker site, winter grazing had the same positive effects as fire, increasing native diversity and reducing evenness, but in addition winter grazing increased both native and C_4 cover. At the Yunker site winter grazing appears to be a better management tool than fire. Certainly fire might be used there, in patches, to stimulate growth of A. gerardii as described above. However, management of the Yunker site with winter grazing alone appears to provide healthy tallgrass prairie with high native diversity and cover.

Fertilization

Fertilization should not be continued at the dry site. Nitrate and ammonium levels at the dry site were extremely elevated in fertilized plots. These levels indicate that nitrogen accumulated at the dry site. Nitrogen addition at the dry site should be discontinued to avoid raising nitrogen levels further.

Fertilization at the wet site might be continued if further research into nitrogen effects were desired, however in the absence of such research nitrogen addition should stop. Even though mid-season nitrogen levels showed no significant pattern, fertilized plots at the THP site had extremely high levels of extractable inorganic nitrogen. Natural nitrogen cycling processes will keep the nitrogen levels in these plots elevated for some time. Power (1981) showed that nitrogen levels were elevated for years after deposition.

Reverse Fertilization

Reverse fertilization may be used with fire or at dry sites to reduce forb stem densities in areas where difficult weedy forbs persist. However, the use of reverse Fertilization without fire in wet or irrigated areas may increase forb stem densities above the control level (Figure 12.3). Additionally, it must be understood that the effects of reverse fertilization are not limited to exotic species. The target species appear to be fast growing annuals (McLendon and Redente 1992), but these are not always exotic. Further, reverse fertilization increases soil moisture with the potential to benefit moisture limited weedy species (Chapter 2).

Flexible Management in the Year Following a Drought

Reduced production in both winter grazed and fire treated plots in the year following the 1994 drought suggests that management in the year following a drought should be modified to reduce disturbance, even when that disturbance is beneficial in a normal year

I hope that these suggestions will be incorporated into the tallgrass management plan for the Colorado natural areas managed by the City of Boulder Open Space and other parcels of Colorado tallgrass prairie.

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APPENDIX A

Plot ID and Treatment Data

DATA DESCRIPTION

Appendix A contains descriptions and data for plot identification and treatment codes. Plot identification codes used follow the property names used by the City of Boulder Open Space. Location of the plots is described in Chapter 4. Chapter 4 also contains maps of each site with the location of each plot labeled. Treatment codes shown here were used as factors in the statistical analysis of all plant and soil response data.

Table A.1 Plot Identification and Treatment Variable Descriptions

Variable Name	Variable Label	Category Values	
PLOT_ID	Site, Grazing treatment, Fire treatment, N treatment, Replicate		
	Site:	(Y=Yunker,V=VanVleet,T=THP)	
	Grazing treatment:	(G=winter graze, X=cattle excluded)	
	Fire treatment:	(F=fire, O= no fire)	
	N treatment:	(C=Carbon added, O=control, N=Nitrogen added)	
	Replicate:	(0=drier, 1=moister)	
REPDIST	distance to replicate plot	meters center to center	
SOIL	Soil Series	Value	Label
	Yunker site	0	Hargreaves sandy clay loam
	THP & Van Vleet sites	1	Nederland very cobbly loam
IRRIG	Irrigation	Value	Label
	THP site	0	not irrigated
	Yunker & Van Vleet sites	1	irrigated
GRAZE	Grazing Treatment	Value	Label
		0	No Cattle
		1	Spring Grazing
FIRE	Fire Treatment	Value	Label
		0	No Fire
		1	Spring Fire
N_ADD	Nitrogen Addition	Value	Label
		0	no nitrogen added
		1	Nitrogen added
C_ADD	Carbon Addition	Value	Label
		0	no carbon added
		1	Carbon added
CONTROL	N manip treatments CONTROL = N_ADD + C_ADD	Value	Label
		0	control
		1	treated (C or N)
REP	replicate	Value	Label
		0	drier
		1	wetter

Table A.2 Plot Identification, Categorization and Treatment Data (n = 60)

PLOT ID	SOIL	IRRIG	GRAZE	FIRE	N ADD	C ADD	CONTROL	REP
YXOC0	0	1	0	0	0	1	1	0
YXOC1	0	1	0	0	0	1	1	1
YXOO0	0	1	0	0	0	0	0	0
YXOO1	0	1	0	0	0	0	0	1
YXON0	0	1	0	0	1	0	1	0
YXON1	0	1	0	0	1	0	1	1
YXFC0	0	1	0	1	0	1	1	0
YXFC1	0	1	0	1	0	1	1	1
YXFO0	0	1	0	1	0	0	0	0
YXFO1	0	1	0	1	0	0	0	1
YXFN0	0	1	0	1	1	0	1	0
YXFN1	0	1	0	1	1	0	1	1
YGOC0	0	1	1	0	0	1	1	0
YGOC1	0	1	1	0	0	1	1	1
YGOO0	0	1	1	0	0	0	0	0
YGOO1	0	1	1	0	0	0	0	1
YGON0	0	1	1	0	1	0	1	0
YGON1	0	1	1	0	1	0	1	1
YGFC0	0	1	1	1	0	1	1	0
YGFC1	0	1	1	1	0	1	1	1
YGFO0	0	1	1	1	0	0	0	0
YGFO1	0	1	1	1	0	0	0	1
YGFN0	0	1	1	1	1	0	1	0
YGFN1	0	1	1	1	1	0	1	1
TXOC0	1	0	0	0	0	1	1	0

Table A.4 - Weather During Study Period

NOAA Station - 50848 Latitude - 40.01° Longitude - 105.16° Elevation - 1645m (5400ft)

	Mean Max T (°C)			Mean Min T (°C)			Precipitation (cm)			Snowfall (cm)		
	1993	1994	1995	1993	1994	1995	1993	1994	1995	1993	1994	1995
Jan	3.89	8.56	8.28	-8	-4.67	-5.94	0.64	2.18	1.63	14.73	29.21	30.48
Feb	5	7.33	11.06	-6.56	-7.44	-3.94	2.29	3.48	3.89	23.62	39.12	41.4
March	12.22	14.17	12.89	-0.72	-1.06	-1.67	5.46	4.09	3.07	30.23	37.85	41.66
April	15.67	16.39	14	1.61	0.94	0.56	6.5	8.79	12.57	11.94	57.91	61.21
May	21.39	25	16.89	6.94	7	4.11	4.39	3.43	24.36	0.03	0	2.03
June	26.28	30.44	24.5	9.83	11.5	9.22	8.59	2.36	10.24	0	0	0
July	29.06	30.17	30	12.56	13.11	12.78	3.56	0.89	1.83	0	0	0
Aug	27.86	29.44	32.11	11.25	13.72	14.5	6.59	6.5	3.68	0	0	0
Sept	23.11	26.5	23.17	6.61	9.61	8.39	8.43	1.37	7.52	33.27	1.02	21.84
Oct	16.44	17.39	19.22	2.06	3.39	2.44	6.15	2.59	1.5	26.67	Trace	7.87
Nov	8.94	8.83	14.33	-4.94	-3.61	-4.56	5.51	5.72	3.84	68.58	60.2	45.21
Dec	8.33	9.11	9.11	-4.61	-4.56	-4.33	1.4	1.24	0.63	22.86	26.16	*
Annual Mean	26.08	28.33	26.58	9.58	11.36	10.58	59.5	42.65	74.12	231.93	251.46	251.71

Data from Callahan (1993,1994,1995)

Table A.3 - Recent Research Projects at These Study Sites

The present study is shown in bold type.

Open Space Name	Yunker II (U & G)	THP (U & G)	Van Vleet (G only)
Natural Area Parcel #	6	3	none
Grassland Biodiversity Transect #s	46 (U) 47 (U) 48 (G)	58 (U)* 59 (U)*	45 (G)
Plant Study			
Natural Area Monitoring	Nat. Area (1986-1989)	Nat. Area (1986-89)	
..Nat. Area Monitoring (continued)	Buckner (1990-1997..)	Buckner (1990-1996..)	
Land Management Effects	**Hopkins(1993-1996)**	**Hopkins(1993-96)**	**Hopkins(1993-96)**
Grassland Biodiversity	Bennett et al. (1994-96)	Bennett et al. (1994-1996)	Bennett et al. (1994-1997)
genetics of *A. gerardii*		Keeler (1995-1996)	Keeler (95-96)
Bird Study			
Wildlife Transects			Open Space
Grassland Biodiversity	Bock et al. (94-96..)	Bock et al. (1994-1996..)	Bock et al. (1994-1996..)
Small Mammal Study			
Inventory	Open Space (88)	Open Space (88)	Open Space (88)
Grassland Biodiversity	Bock et al. (1994-1996..)	Bock et al. (94-96..)	Bock et al. (1994-1996..)
Grasshopper Study			
Grassland Biodiversity	Bock et al. (1994-1996..)	Bock et al. (1994-1996..)	Bock et al. (1994-1996..)
Soil Study			
Land Management Effects	**Hopkins(1996)**	**Hopkins(1996)**	**Hopkins(1996)**
Grassland Biodiversity	Sinton (1997)	Sinton (1997)	Sinton (1997)

U = Ungrazed transect, G = winter grazed transect

* These transects in seasonally inundated area with very mesic flora, different from Hopkins plots. Natural Area transects cover both areas.

Sources: (City of Boulder Open Space 1986; Buckner (1990-1996); Bennett, 1997; Sinton, 1997)

Table A.2 (continued) Plot Identification, Categorization and Treatment Data (n = 60)

PLOT ID	SOIL	IRRIG	GRAZE	FIRE	N ADD	C ADD	CONTROL	REP
TXOC1	1	0	0	0	0	1	1	1
TXOO0	1	0	0	0	0	0	0	0
TXOO1	1	0	0	0	0	0	0	1
TXON0	1	0	0	0	1	0	1	0
TXON1	1	0	0	0	1	0	1	1
TXFC0	1	0	0	1	0	1	1	0
TXFC1	1	0	0	1	0	1	1	1
TXFO0	1	0	0	1	0	0	0	0
TXFO1	1	0	0	1	0	0	0	1
TXFN0	1	0	0	1	1	0	1	0
TXFN1	1	0	0	1	1	0	1	1
TGOC0	1	0	1	0	0	1	1	0
TGOC1	1	0	1	0	0	1	1	1
TGOO0	1	0	1	0	0	0	0	0
TGOO1	1	0	1	0	0	0	0	1
TGON0	1	0	1	0	1	0	1	0
TGON1	1	0	1	0	1	0	1	1
TGFC0	1	0	1	1	0	1	1	0
TGFC1	1	0	1	1	0	1	1	1
TGFO0	1	0	1	1	0	0	0	0
TGFO1	1	0	1	1	0	0	0	1
TGFN0	1	0	1	1	1	0	1	0
TGFN1	1	0	1	1	1	0	1	1
VGOC0	1	1	1	0	0	1	1	0
VGOC1	1	1	1	0	0	1	1	1

Table A.2 (continued) Plot Identification, Categorization and Treatment Data (n = 60)

PLOT ID	SOIL	IRRIG	GRAZE	FIRE	N ADD	C ADD	CONTROL	REP
VGOO0	1	1	1	0	0	0	0	0
VGOO1	1	1	1	0	0	0	0	1
VGON0	1	1	1	0	1	0	1	0
VGON1	1	1	1	0	1	0	1	1
VGFC0	1	1	1	1	0	1	1	0
VGFC1	1	1	1	1	0	1	1	1
VGFO0	1	1	1	1	0	0	0	0
VGFO1	1	1	1	1	0	0	0	1
VGFN0	1	1	1	1	1	0	1	0
VGFN1	1	1	1	1	1	0	1	1

Table A.5 - Winter Grazing Treatments

		prior to 1993 season		prior to 1994 season		prior to 1995 season		prior to 1996 season	
Site	grazed area (ha)	dates	dry wt. removed (g/m²)*	dates	dry wt. removed (g/m²)*	dates	dry wt. removed (g/m²)*	dates	dry wt. removed (g/m²)*
Full Factorial Design Plots									
Yunker	97	6 Feb- 1 May	63.5	10 Feb- 20 April	42.6	1 Feb- 5 May	83.9	13 Feb- 25 April	49.3
THP	11	21 Mar- 15 May	47.9	19 Feb- 3 May	44.2	1 Jan- 20 May	66.3	5 May- 1 July	40.5
Additional All-Grazed Plot with same soil as THP and same irrigation as Yunker II									
Van Vleet	91	15 Dec- 1 June	138**	15 Jan - 27May	58.1	1 Feb- 23 May	76.6	13 Feb- 1 May	94.5

Data calculated from stocking rates provided by Mark Grundy, Grazing Coordinator for the City of Boulder Open Space

* Calculated using standard 405kg vegetation dry wt /AUM where 1AUM =Animal Unit Month is 30 days grazed by 1 Animal Unit = 1 cow + 1 calf = 1 steer = 0.9 bull [Grundy, 1994 #286]

** this datum calculated from figures of [Grundy, 1994 #261], all other data calculated from figures from [Grundy, 1997 #262]

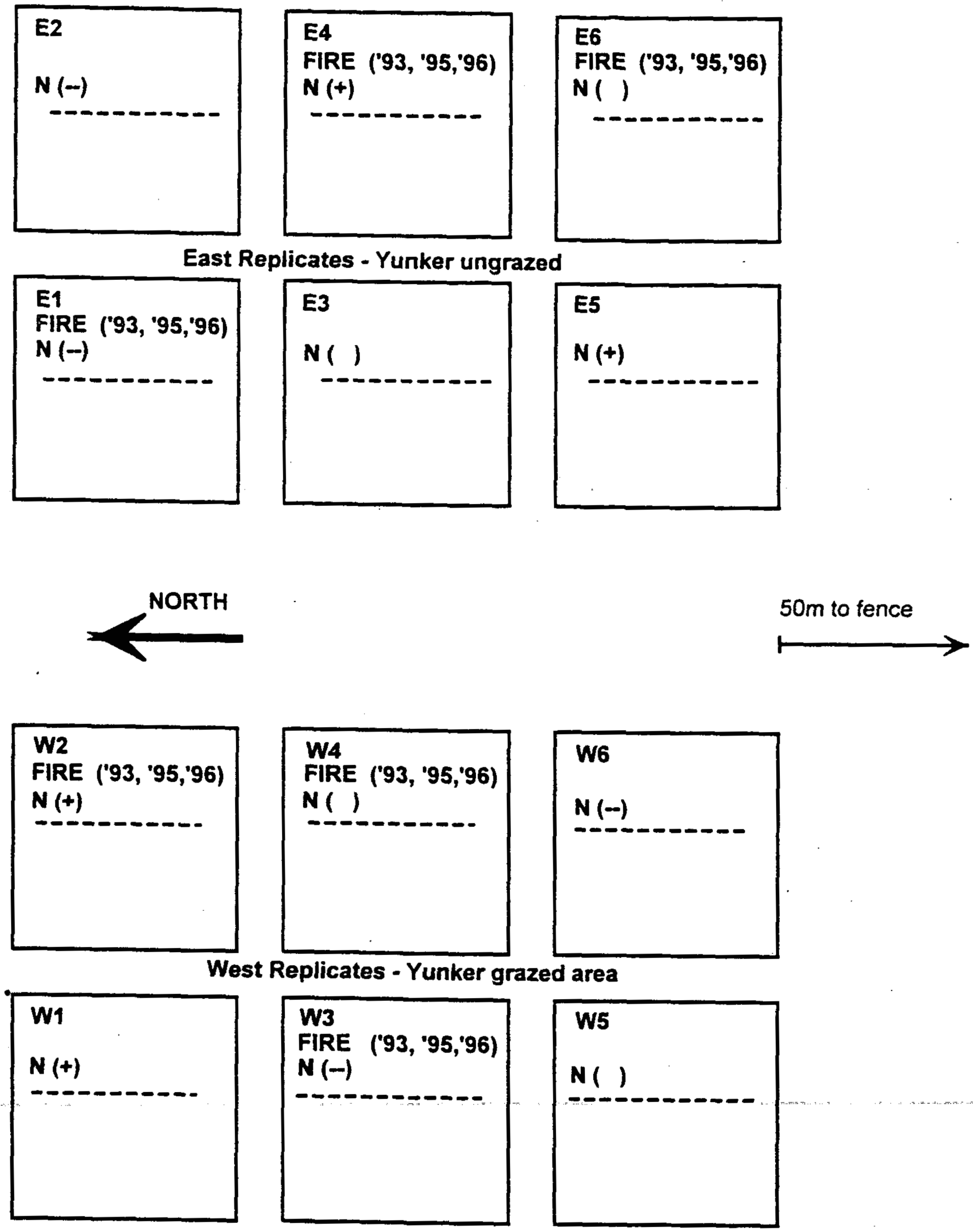

Figure A.1 - Map of ungrazed plots at Yunker site (north of fence)
Yunker Property (Colorado Natural Area parcel 3) north of grazed area. Subirrigated and sometimes surface irrigated from Goodhue ditch ~150m SE of plots. Soil is Hargreave sandy clay loam (50-100cm deep) over Fox Hills-Laramie sandstone.

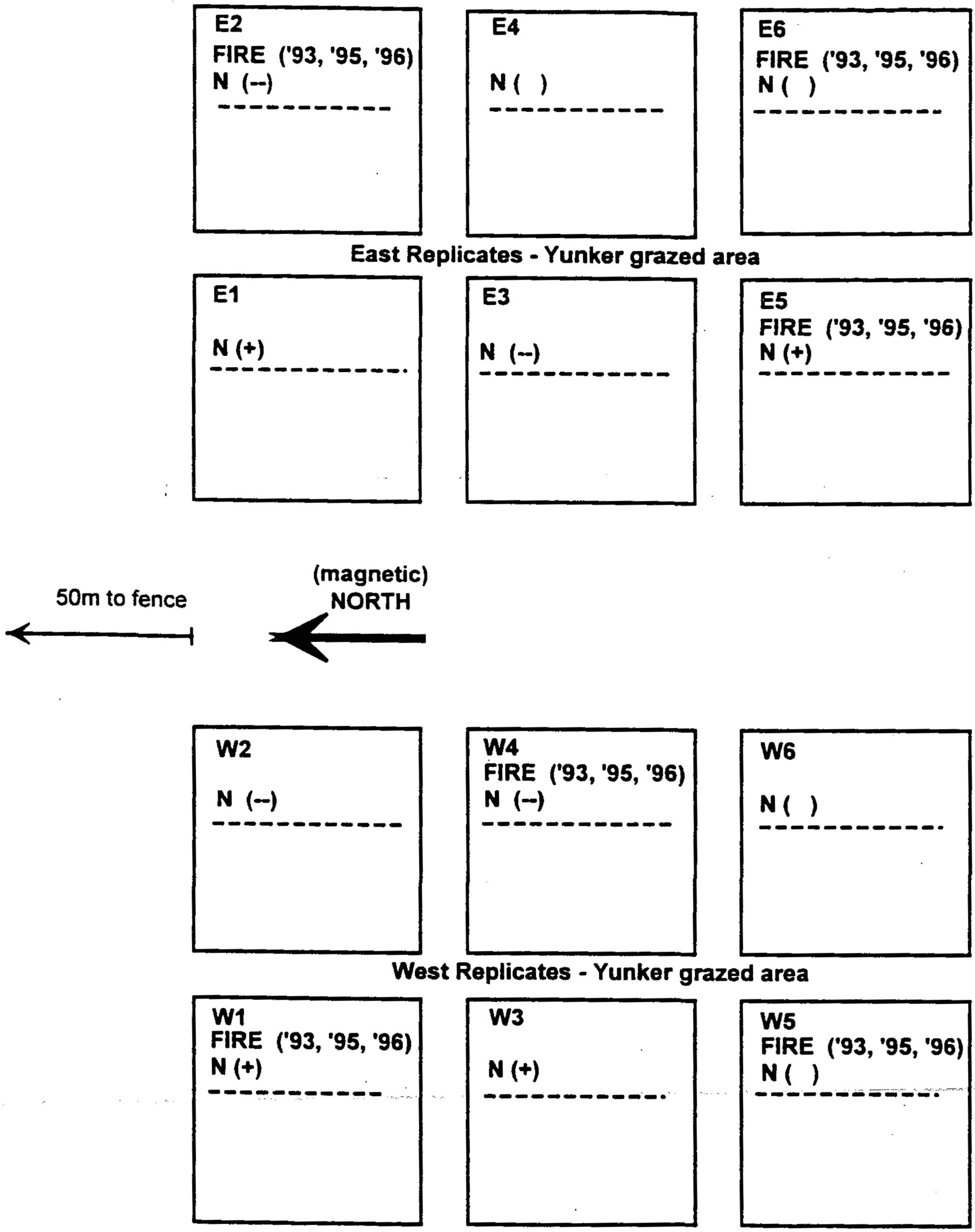

Figure A.2 - Map of grazed plots at Yunker site (south of fence)
Yunker Property (Colorado Natural Area parcel 3) grazed by cows & calves between Dec. and May. Subirrigated and sometimes surface irrigated from Goodhue ditch approximately 50m to the SE. Soil is Hargreave sandy clay loam (50-100cm deep) over Fox Hills-Laramie sandstone.

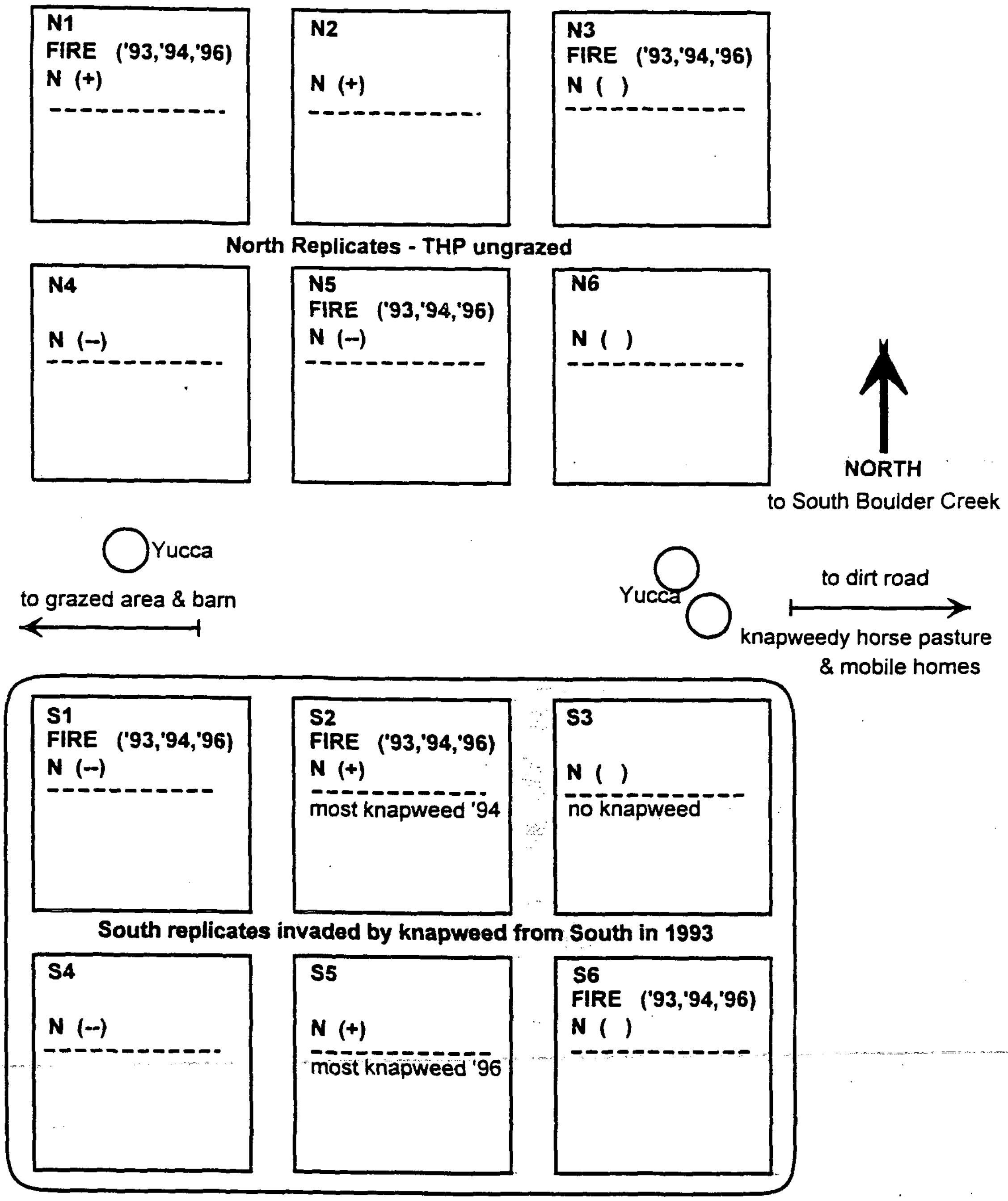

Figure A.3 Map of ungrazed plots at THP site (east of fence)
THP Property, (Natural Area parcel 6) with no domestic grazing.
No surface irrigation, these plots drier than grazed plots across fence.
Soil is Nederland very cobbly loam with 78-95% rock more than 2.5m deep.

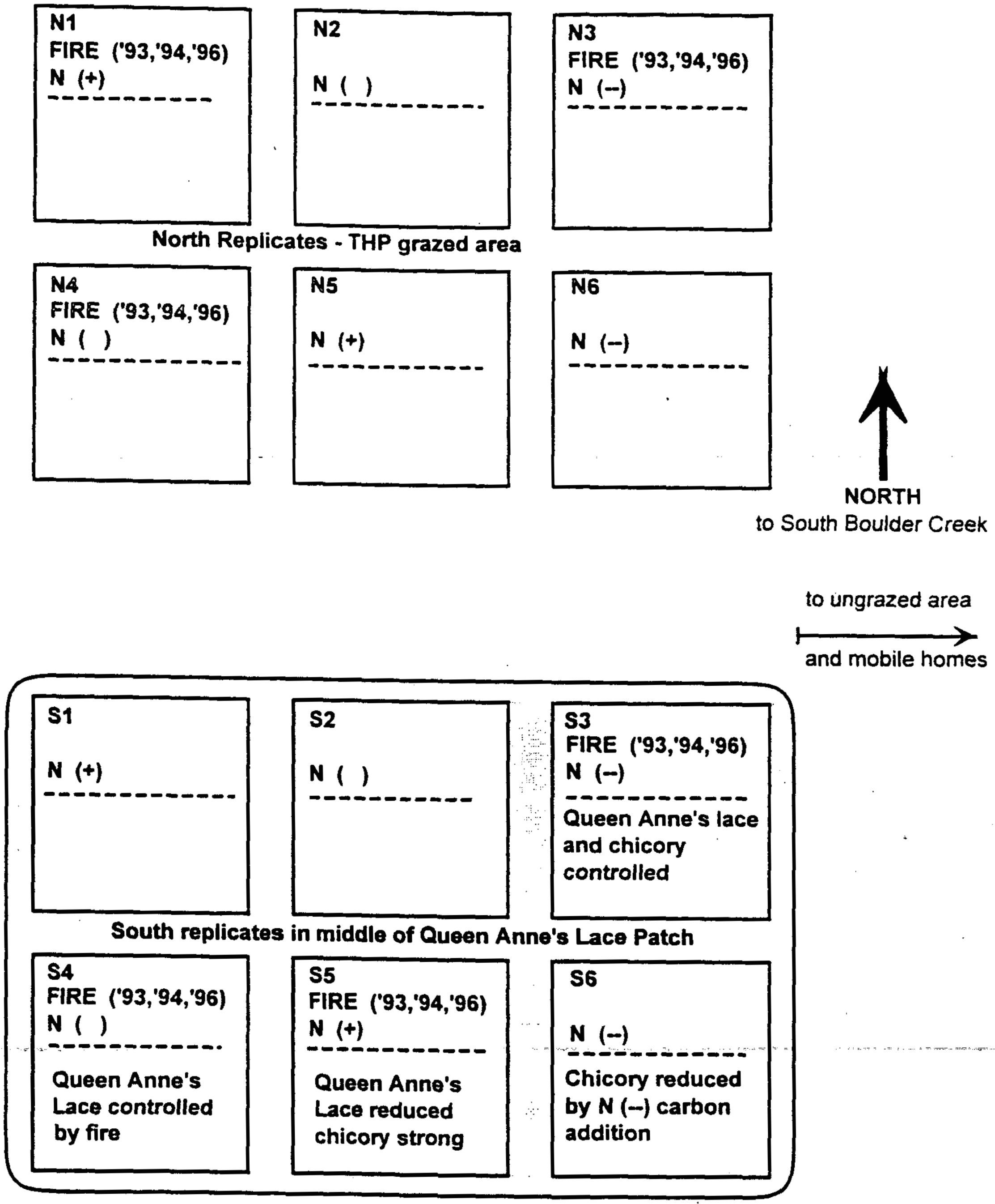

Figure A.4 Map of grazed plots at THP site (west of fence)
THP Property (Natural Area parcel 6) grazed between December and May by 3-6 Bulls. These plots may receive some subirrigation from the Goodhue ditch 100m south and South Boulder Creek 200m northwest. These plots are moister than the ungrazed plots at this site. Soil is Nederland very cobbly loam with 78-95% rock more than 150 cm deep.

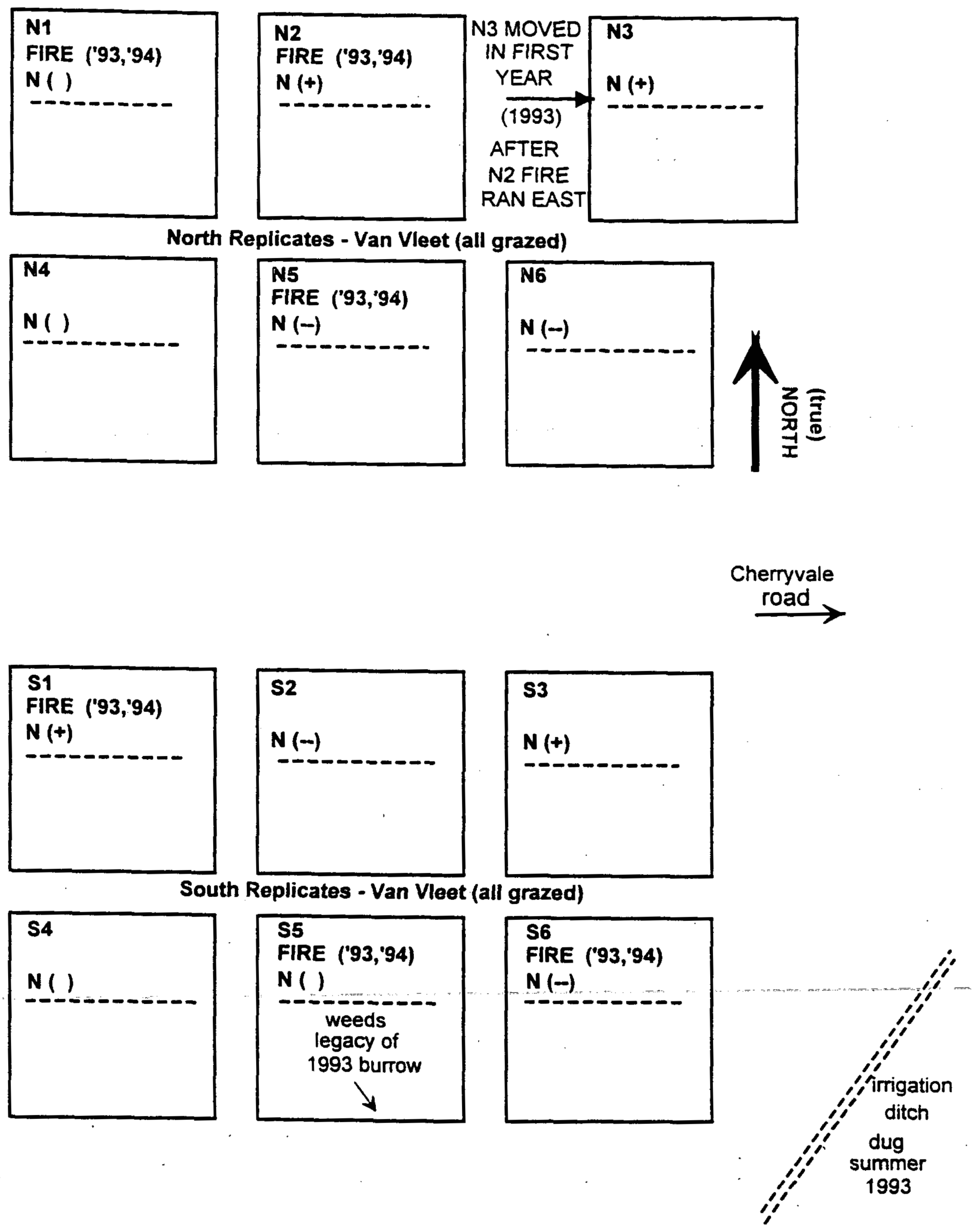

Figure A.5 Map of plots at Van Vleet site (all winter grazed)
Winter grazed (by cows & calves) Jan-May all years, also summer grazed 1993
Surface irrigated from Goodhue ditch via small ditch SE of plots, since 1993.
Soil is Nederland very cobbly loam more than 150cm deep with 78-95% rock volume.

APPENDIX B

Aboveground Net Primary Production Data

DATA DESCRIPTION

Appendix B contains aboveground net primary production (ANPP) data sets for four years (1993-1995).

Table B.1 Aboveground Net Primary Production (ANPP) Variables
Table B.2 Aboveground Net Primary Production Data g/m2 (n = 60)

Table B.1 Aboveground Net Primary Production (ANPP) Variables

Name	Label	Units of Measurement
HMON93	harvest month for 1993 ANPP	month + (day/31)
PROD_93	ANPP 1993	g/m^2
LITTER93	litter 1993	g/m^2
TPROD_93	total peak ANPP 1993	g/m^2
HMON94	harvest month 1994 ANPP	month + (day/31)
TSPROD94	total senescent ANPP 1994	g/m^2
HMON95	harvest month 1995 ANPP	month + (day/31)
TSPROD95	total senescent ANPP 1994	g/m^2
MEANPRO	mean total ANPP[1]	g/m^2

---

[1] MEANPRO = (TPROD_93 + TSPROD94 + TSPROD95) / 3

Table B.2 Aboveground Net Primary Production Data g/m^2 (n = 60)

PLOT ID	HMON93	PROD 93	LITTER93	TPROD93	HMON94	TPROD94	HMON95	TPROD95	MEANPRO
TXOC1	9.94	920	791.33	128.67	12.97	238.2	13	640.88	599.7
TXOO1	9.94	968	748.44	219.56	12.97	399.54	12.48	1,473.67	947.07
TXON1	9.81	1,001.11	709.67	291.44	12.97	379.87	12.68	869.98	750.32
TXFC1	9.94	1,295.22	909.11	386.11	12.97	173.87	12.97	199.33	556.14
TXFO1	9.95	907.33	657.86	249.47	12.97	286.87	13	502.08	565.43
TXFN1	9.81	702.11	578	124.11	12.97	229.98	13	156.48	362.86
TGOC1	9.77	989.44	714.78	274.67	12.97	324.65	12.81	202.38	505.49
TGOO1	9.81	807	635.78	171.22	12.97	499.65	12.68	266.18	524.28
TGON1	8.42	687	565.44	121.56	12.97	621.09	12.81	319.48	542.53
TGFC1	9.81	694.33	560.67	133.67	12.97	189.65	12.68	105.38	329.79
TGFO1	9.81	689.68	460.34	229.33	12.97	345.98	12.81	109.18	381.61

Table B.2 (continued) Aboveground Net Primary Production Data g/m² (*n* = 60)

PLOT ID	HMON93	PROD 93	LITTER93	TPROD93	HMON94	TPROD94	HMON95	TPROD95	MEANPRO
TGFN1	9	359.56	241.45	118.11	12.97	354.31	12.68	285.88	333.25
YXOC1	9.32	1,224.33	704.44	519.89	10.84	934.65	12.68	327.38	828.79
YXOO1	9.32	1,048.44	747.78	300.67	10.84	748.2	12.68	578.28	791.64
YXON1	9.32	307.24	209.44	97.8	10.84	1,083.2	12.68	540.38	643.61
YXFC1	9.32	933.22	806.56	126.67	10.84	886.43	12.68	364.18	727.94
YXFO1	9.32	1,356	1,212.56	143.44	10.84	1,054.76	12.68	631.68	1,014.15
YXFN1	9.32	1,191.22	1,002.44	188.78	10.84	593.09	12.68	307.98	697.43
YGOC1	8.42	1,252.78	989	263.78	11.06	1,218.76	12.68	557.08	1,009.54
YGOO1	9	1,262.33	988.56	273.78	11.06	1,229.98	12.68	628.08	1,040.13
YGON1	8.39	1,518.22	1,204.22	314	11.06	1,373.09	10.71	708.54	1,199.95
YGFC1	8.42	1,522.67	1,317.11	205.56	11.06	1,827.2	10.71	759.24	1,369.7

Table B.2 (continued) Aboveground Net Primary Production Data g/m² (n = 60)

PLOT ID	HMON93	PROD 93	LITTER93	TPROD93	HMON94	TPROD94	HMON95	TPROD95	MEANPRO
YGFO1	9.32	1,423.33	1,172.67	250.67	11.06	1,429.76	12.68	434.38	1,095.83
YGFN1	9.32	1,483.78	1,248.33	235.44	11.06	1,659.98	12.68	777.08	1,306.95
VGOC1	9.19	1,188.55	919.44	269.11	11.06	471.87	12.48	134.78	598.4
VGOO1	9.16	1,265.11	974.33	290.78	11.06	710.87	12.48	988.08	988.02
VGON1	9.16	1,338.56	1,040.11	298.44	11.06	707.2	12.48	414.48	820.08
VGFC1	9.48	1,057	906.56	150.44	11.06	308.43	12.48	481.88	615.77
VGFO1	9.16	1,003.67	865.33	138.33	11.06	322.43	12.48	352.88	559.66
VGFN1	9.19	1,338.11	1,130.89	207.22	11.06	311.2	12.48	189.38	612.9

APPENDIX C

Physical Structure Data

DATA DESCRIPTION

Appendix C contains plant physical structure data sets for all the grasses commonly found in these plots. This includes a list of species measured and the data sets that include that species (Table C.1), and membership in functional groups and species categories (Tables C.2 and C.3). Plant physical structure data sets include, flower stem density (1995) (Table C.4) and flower stem height (1993). Data from 1994 was not used because the Yunker site was not burned in 1994. Flower stem heights were greatest in 1993 (a wet year), increasing the chance of detecting treatment effects. Stem density was first measured in 1995.

Table C.1 - Species Cover, Presence, Height and Stem Density Variables
Table C.2 - Species Functional Groups and Stem Density Factors
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Table C.1. - Species Cover, Presence, Height and Stem Density Variables

		Data Sets In which Species Appears		
Variable Name	Species Name (Weber. 1993)	cover %	stem density stem/m^2	stem height cm
ABORTPV	Aborted *P. virgatum* inflorescences		x	
ABORTAG	Aborted *A. gerardii* inflorescences		x	
AGRGIG	*Agrostis gigantea*	x	x	x*
ALLGRAZ	Winter Grazing Adapted Group†		x	
ALLFIRE	Fire Adapted Group†		x	
ANDGER	*Andropogon gerardii*	x	x	x
BROJAP	*Bromus japonicus*	x	x	
CHOGRA	*Chondrosum gracile*[1]		x	x
CICINT	*Cichorium intybus*	x	x	
DICOLI	*Dichantheleum oligosanthes*	x	x	
JUNSPP	*Juncus spp.*	x	x	x*
NODIST	No Disturbance Adapted Group†		x	
PANVIR	*Panicum virgatum*	x	x	x
PLALAN	*Plantago lanceolata*	x	x	
POAAGA	*Poa agasizensis/pratensis*	x	x	x
POACOM	*Poa compressa*	x	x	x*
ROSWOO	*Rosa woodsii*	x		
ROSSPP	*Rosa spp.*	x		
SCHSCO	*Schizachyrium scoparium*[2]	x		x
SORAVE	*Sorghastrum avenaceum*[3]	x	x	x
SPOAIR	*Sporobolus airoides*	x	x	x
TALL	Tallgrass group† †		x	

* not measured in 1993

† species in these groups listed in table C.2

†† species in tallgrass group are: *Andropogon gerardii, Panicum virgatum, Schizachyrium scoparium*[2], *Sporobolus airoides,* and *Sorghastrum avenaceum*[3].

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[1] Great Plains Flora name *Bouteloua gracilis* (Great Plains Flora Assoc. 1986).

[2] Archaic name: *Andropogon scoparius* (Great Plains Flora Assoc. 1986).

[3] Great Plains Flora name *Sorghastrum nutans*.(Great Plains Flora Assoc. 1986).

Table C.2 - Species Functional Groups and Stem Density Factors
Factor matrix shown in Table C.3. Stem density factors tend to group species with the same photosynthetic pathway (all 5 groups); and origin (Stem Density Factors 1, 2, 4, and 5). Groups based on 1995 stem densities of species occuring in ten or more plots, tall grasses shown in **bold**.

	Species functional Group		
	C_4 Grasses	C_3 Monocots	C_3 Forbs
Stem Density Factor 1	***Andropogon gerardii*** ***Panicum virgatum***		
Stem Density Factor 2		*Agrostis gigantea* * *Bromus japonicus**	
Stem Density Factor 3		*Juncus spp.* *Poa compressa***	*Cichorium intybus* *
Stem Density Factor 4	***Sorghastrum avenaceum***[1] *Chondrosum gracile*[2]		
Stem Density Factor 5		*Poa pratensis/agasizensis***	*Plantago lanceolata* *

* introduced (exotic) species (Weber, 1993)
** identity and origin controversial: *Poa compressa* may not be native to this part of North America; *Poa pratensis/agasizensis* is probably the exotic *Poa pratensis* introduced before 1906 (Daniels, 1909), but it may be a native strain: *Poa agasizensis* (Boivin and Löve, 1960)

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[1] Great Plains Flora name is *Sorghastrum nutans* (Great Plains Flora Assoc. 1986).
[2] Great Plains Flora name is *Bouteloua gracilis* (Great Plains Flora Assoc. 1986).

Table C.3 - Varimax Rotated Stem Density Principal Factors

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Panicum virgatum	**0.90174**	-0.00340	0.09363	-0.02358	0.05581
Andropogon gerardii	**0.71231**	-0.05030	-0.33203	-0.09609	-0.25640
Bromus japonicus	-0.13046	**0.91055**	-0.02939	-0.09841	-0.04091
Agrostis gigantea	0.13513	**0.88675**	-0.16053	0.15264	-0.06020
Juncus spp.	0.05955	0.02005	**0.82347**	0.02971	0.01172
Poa compressa	-0.23289	-0.16844	**0.74058**	0.17044	-0.19851
Cichorium intybus	-0.02318	-0.08320	**0.49969**	-0.19765	-0.09375
Sorghastrum avenaceum	-0.13312	-0.00927	-0.01653	**0.95639**	-0.00861
Chondrosum gracile	0.65906	0.11298	-0.05144	**0.68826**	0.04808
Plantago lanceolata	-0.04007	-0.07265	-0.15076	-0.19230	**0.81545**
Poa pratensis	-0.04144	-0.02693	-0.06694	0.19642	**0.81534**

Table C.4 - Stem Density Data (stem/m²) (1995)

Stems were counted within the production harvest sample, so these values correspond exactly to the 1995 production sample.

PLOT_ID	PAN vir	abort Pv	SPO air	AND ger	abort Ag	POA com	JUN spp	AGR gig	PLA lan	ROS woo	SOR ave	CIC int	CHO gra	POA aga	DIC oli	BRO jap
TXOC1	20	10	0	10	60	1300	200	0	0	0	0	0	0	0	0	0
TXOO1	0	0	10	0	0	1220	0	0	0	0	70	0	0	0	0	0
TXON1	20	40	0	0	0	1220	20	0	0	0	0	0	0	0	0	0
TXFC1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TXFO1	20	0	0	0	0	330	0	0	0	0	20	0	0	0	220	0
TXFN1	30	170	40	0	0	620	0	0	0	0	0	0	0	0	0	0
TGOC1	20	0	0	0	0	350	0	0	0	0	0	30	0	0	0	0
TGOO1	0	0	30	0	0	800	0	0	0	0	0	20	0	0	0	0
TGON1	100	0	50	0	0	0	50	0	0	0	0	10	0	0	0	0
TGFC1	30	0	10	0	0	600	200	0	0	0	0	10	0	0	0	0
TGFO1	40	0	0	0	0	30	0	0	0	0	10	0	0	0	0	0
TGFN1	60	0	0	0	0	300	0	0	0	0	0	0	0	0	0	0
YXOC1	0	0	10	0	0	0	0	0	30	10	0	0	0	0	0	0
YXOO1	20	0	30	0	0	0	0	0	40	0	0	0	0	40	0	0
YXON1	30	0	10	10	0	0	0	0	10	0	0	0	0	10	0	0

Table C.4 - (continue) Stem Density Data (stem/m²) (1995)

PLOT_ID	PAN vir	abort Pv	SPO air	AND ger	abort Ag	POA com	JUN spp	AGR gig	PLA lan	ROS woo	SOR ave	CIC int	CHO gra	POA aga	DIC oli	BRO jap
YXFC1	0	0	60	100	0	0	0	0	0	0	0	0	0	0	80	0
YXFO1	0	0	50	70	0	0	0	50	20	100	0	0	0	0	0	0
YXFN1	50	0	20	0	0	0	0	0	70	0	0	0	0	0	0	0
YGOC1	20	0	80	30	0	0	10	110	0	10	0	0	0	0	0	0
YGOO1	100	0	20	50	0	0	0	0	0	0	0	0	0	0	0	0
YGON1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
YGFC1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
YGFO1	0	0	20	120	0	0	0	0	0	0	0	0	0	0	0	0
YGFN1	10	0	20	80	0	0	10	0	0	100	0	0	0	0	0	0
VGOC1	0	0	0	20	0	0	0	50	0	0	0	0	0	0	0	0
VGOO1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
VGON1	0	0	0	0	0	0	30	50	0	0	110	0	10	10	0	0
VGFC1	0	0	0	240	0	0	0	0	0	0	0	0	0	0	0	0
VGFO1	280	0	0	230	0	0	0	50	0	0	0	0	10	0	0	0
VGFN1	0	0	0	10	0	0	0	130	0	0	0	0	0	0	0	110

Table C.5 - Stem Heights for *Andropogon gerardii* (1993)

Treatments are shown at left, and data from different sites and replicates are listed in separate columns

	Yunker Site										THP Site									
	wetter replicatee (1)					drier replicate (0)					wetter replicate (1)					drier replicate (0)				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
GFC	138	150	133	143	155	100	90	95	84	74	0	0	0	0	0	99	114	108	111	119
GFN	115	110	115	94	115	95	90	94	77	100	0	0	0	0	0	82	84	93	73	89
GFO	132	120	125	138	115	105	105	110	105	100	97	105	76	73	92	94	91	101	107	89
GOC	132	134	115	120	130	0	0	0	0	0	0	0	0	0	0	94	102	93	93	100
GCN	140	139	124	136	142	0	0	0	0	0	0	0	0	0	0	100	106	100	106	109
GOO	147	138	136	148	139	0	0	0	0	0	0	0	0	0	0	105	105	110	115	107
XFC	123	100	91	89	91	125	123	120	131	128	0	0	0	0	0	108	114	115	113	112
XFN	153	115	105	100	110	94	90	88	92	90	53	60	50	53	55	119	110	121	139	112
XFO	119	115	110	115	98	134	138	110	115	123	0	0	0	0	0	124	123	115	133	126
XOC	110	65	105	95	100	0	0	0	0	0	0	0	0	0	0	69	102	84	92	93
XON	104	102	104	102	104	0	0	0	0	0	0	0	0	0	0	105	112	101	75	79
XOO	81	81	76	76	81	0	0	0	0	0	0	0	0	0	0	95	97	77	99	107

Table C.6 - Stem Heights for *Panicum virgatum* (1993)
Treatments are shown at left, and data from different sites and replicates are listed in separate columns

	Yunker Site										THP Site									
	wetter replicatee (1)					drier replicate (0)					wetter replicate (1)					drier replicate (0)				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
GFC	115	120	125	105	110	76	70	74	77	100	0	0	0	0	0	82	91	101	82	85
GFN	110	105	105	96	99	80	80	74	73	70	70	77	72	80	86	79	80	85	75	76
GFO	95	107	110	120	99	60	62	55	60	70	90	63	60	72	82	68	81	89	93	76
GOC	130	115	110	105	120	52	60	75	60	57	99	70	92	75	75	93	88	89	82	92
GCN	115	120	97	115	120	70	80	82	75	90	72	79	84	70	71	82	91	79	89	92
GOO	130	128	120	105	110	62	59	53	75	77	79	96	83	70	60	93	97	97	82	85
XFC	127	107	112	116	112	57	56	45	70	70	82	88	97	82	90	67	57	56	60	60
XFN	110	97	95	91	85	76	52	72	55	62	95	89	83	70	77	133	136	128	130	123
XFO	119	110	150	100	100	77	82	72	80	79	57	45	56	50	52	93	87	76	65	71
XOC	110	93	96	93	90	60	67	50	55	70	87	70	80	67	72	70	84	66	81	72
XON	97	94	114	84	107	86	82	80	75	87	84	82	88	80	75	92	90	79	82	102
XOO	99	102	109	104	97	57	50	70	66	55	72	62	77	65	64	0	0	0	0	0
GFC	115	120	125	105	110															

Table C.7 - Stem Heights for *Sorghastrum avenaceum (Sorghastrum nutans)* (1993)

Treatments are shown at left, and data from different sites and replicates are listed in separate columns

	Yunker Site										THP Site									
	wetter replicatee (1)					drier replicate (0)					wetter replicate (1)					drier replicate (0)				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
GFC	0	0	0	0	0	115	100	95	120	105	83	92	110	115	107	0	0	0	0	0
GFN	0	0	0	0	0	120	84	93	90	78	115	94	110	115	105	0	0	0	0	0
GFO	0	0	0	0	0	90	100	82	105	100	94	96	105	105	107	0	0	0	0	0
GOC	0	0	0	0	0	105	70	90	95	96	80	86	87	80	92	0	0	0	0	0
GCN	0	0	0	0	0	87	95	96	85	90	87	97	96	105	93	0	0	0	0	0
GOO	0	0	0	0	0	88	105	95	80	70	86	80	104	93	100	0	0	0	0	0
XFC	0	0	0	0	0	84	70	72	76	66	124	115	100	132	108	0	0	0	0	0
XFN	0	0	0	0	0	101	100	95	88	110	90	60	56	89	70	0	0	0	0	0
XFO	0	0	0	0	0	105	122	128	110	115	60	56	62	70	71	0	0	0	0	0
XOC	0	0	0	0	0	105	84	95	98	88	103	92	93	100	82	0	0	0	0	0
XON	0	0	0	0	0	82	99	98	105	115	118	100	90	100	87	0	0	0	0	0
XOO	0	0	0	0	0	95	87	82	85	91	0	0	0	0	0	0	0	0	0	0
GFC	0	0	0	0	0															

Table C.8 - Stem Heights for *Schizachyrium scoparium* (1993)

Treatments are shown at left, and data from different sites and replicates are listed in separate columns

	Yunker Site										THP Site									
	wetter replicatee (1)					drier replicate (0)					wetter replicate (1)					drier replicate (0)				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
GFC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GFN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GFO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GOC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GCN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GOO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	63	72	76	71	66
XFC	0	0	0	0	0	0	0	0	0	0	80	82	70	74	75	54	67	57	47	0
XFN	0	0	0	0	0	55	46	42	50	38	0	0	0	0	0	63	61	62	53	69
XFO	0	0	0	0	0	45	65	44	42	50	0	0	0	0	0	63	44	62	61	42
XOC	0	0	0	0	0	0	0	0	0	0	80	72	84	78	67	69	62	64	63	57
XON	0	0	0	0	0	0	0	0	0	0	72	66	70	71	69	54	66	57	55	49
XOO	0	0	0	0	0	72	66	70	67	69	0	0	0	0	0	0	0	0	0	0
GFC	0	0	0	0	0															

Table C.9 - Stem Heights for *Sporobolus airoides* (1993)

Treatments are shown at left, and data from different sites and replicates are listed in separate columns

	Yunker Site										THP Site									
	wetter replicatee (1)					drier replicate (0)					wetter replicate (1)					drier replicate (0)				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
GFC	0	0	0	0	0	55	70	66	54	54	32	57	51	43	53	0	0	0	0	0
GFN	0	0	0	0	0	40	52	52	36	52	63	52	55	61	51	0	0	0	0	0
GFO	0	0	0	0	0	55	57	62	42	54	47	52	50	63	43	0	0	0	0	0
GOC	0	0	0	0	0	0	0	0	0	0	46	52	61	67	40	0	0	0	0	0
GCN	0	0	0	0	0	42	45	35	56	37	62	53	56	50	54	0	0	0	0	0
GOO	0	0	0	0	0	50	45	52	53	47	66	46	50	40	40	0	0	0	0	0
XFC	55	66	70	64	52	45	40	42	44	50	0	0	0	0	0	0	0	0	0	0
XFN	60	55	56	66	64	55	42	56	50	46	35	24	30	40	47	0	0	0	0	0
XFO	66	70	62	65	55	51	56	62	55	45	47	37	46	47	50	0	0	0	0	0
XOC	50	40	44	52	46	0	0	0	0	0	52	46	53	50	51	0	0	0	0	0
XON	62	59	50	52	47	40	42	55	55	42	53	56	52	45	34	0	0	0	0	0
XOO	46	52	55	62	50	0	0	0	0	0	45	34	29	35	28	0	0	0	0	0
GFC	0	0	0	0	0															

APPENDIX D

Plant Community Data

DATA DESCRIPTION

Appendix D contains plant community data. To facilitate interpretation of this data by researchers using different taxonomic nomenclature, table D.1 shows synonyms from the Flora of the Great Plains (Great Plains Flora Association 1977) and archaic synonyms used in historical floral accounts (Coulter 1885; Daniels 1911; Vestal 1913; Vestal 1914; Malin, 1947). Table D.1 also shows which species are present at each of the three sites.

Plant community composition data includes cover frequency and presence-absence data for the 1995 field season. For the Yunker Site, overall, native and exotic species diversity indices and overall species evenness were calculated for each quadrant and these values used as repeated measures in ANOVA to detect treatment effects on diversity and plant community composition. For diversity and evenness calculations, point intercept cover values were used for all species detected by that method and estimated cover values were used for species present, but not detected, in the point intercept sample. Details of the estimation method are given in Chapter 9.

Table D.1. Plant Species Found at Study Sites
Table D.2 Overall Species Diversity
Table D.3 Native Species Diversity
Table D.4 - Exotic Species Diversity
Table D.5 - Species Evenness
Table D.6 - Litter Surface Abundance