DISSERTATION

LABILE AND TOTAL CARBON AND NITROGEN DYNAMICS IN TWO GRASSLAND ECOSYSTEMS

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY DOUGLAS WALTER GRANT ENTITLED LABILE AND TOTAL CARBON AND NITROGEN DYNAMICS IN TWO GRASSLAND ECOSYSTEMS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

LABILE AND TOTAL CARBON AND NITROGEN DYNAMICS IN TWO GRASSLAND ECOSYSTEMS

Natural perennial grasslands are characterized by a high degree of spatial and temporal variability in total and labile soil organic matter (SOM). The objective of this research was to quantify the spatial distribution and relationships between total and labile carbon (C) and nitrogen (N) in two semi-arid grasslands, a shortgrass steppe (SGS) and a Northern mixed-grass prairie (NMP). Soil samples (0-5 and 5-10 cm depth) were collected from the two ecosystems in 2001. Analyses of water soluble organic carbon (WSOC) and water soluble nitrogen (WSN) were performed along with 21-day aerobic incubations for potentially mineralizable C and N to examine the relationships between these parameters and root biomass, total soil organic C (SOC), total N and inorganic N (iN). Results indicated that nitrogen immobilization processes dominate in NMP, which had greater microbial activity, root biomass and total SOM than SGS, but lower mass of field-moist WSOC ($WSOC_{FM}$) and iN, which represented labile C and N pools. Incubation results indicated that microbes from bare-ground microsites were more C-limited than microbes from grass-occupied soils.

Rhizoplane soil associated with coarse and fine roots accounted for approximately 28 % and 16 % of the total soluble C present in the 0-10 cm depth in NMP and SGS ecosystems, respectively. Concentration of WSOC in rhizoplane soil was one to two

orders of magnitude higher than bulk soil. Concentrations of WSOC in grass crown-associated soil were on average 4.2 fold higher than in bulk soil.

Additional data were collected in 2001, 2002, and 2003 in a NMP plant community. Continuous moderate grazing, along with two different lengths of rest from grazing treatments, were used to examine above- and below-ground ecosystem responses to a change in management. Bare microsites had lower root biomass in surface soils and higher temperatures on the soil surface and at 5 cm depth than grass-occupied microsites. Total pools of C and N were relatively unresponsive to changes in management, but did respond to year-to-year variations in precipitation. Results suggested that recovery from continuous grazing can occur rapidly, and rates of recovery are likely to be dependent on precipitation levels.

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I. Introduction

Historically, research on the effects of grazing on semi-arid rangeland has primarily focused on the impacts of different grazing management practices on plant community composition, plant density by species, and forage production (Kepner et al. 1993, Bedell & Buckhouse 1994). Generations of researchers have focused on the influence of leaf removal on aboveground growth, while little attention has been paid to belowground phenomena (Biswell & Weaver 1933, Trlica & Rittenhouse 1993). Belowground biogeochemical processes occupy a key position in controlling plant population dynamics and site stability (Burke et al. 1997). Therefore, an understanding of the belowground components and processes, and how these processes vary among different ecosystems, may lead to better management strategies that promote rangeland health and sustainability.

The foundation of understanding the belowground components of grazed ecosystems is an understanding of soil organic matter (SOM) dynamics and the effects of management on root biomass, exudation and turnover (Reeder et al. 2001). SOM is the primary source of nutrients for plant growth and is the largest reservoir of carbon (C) and nitrogen (N) in semiarid rangeland ecosystems (Follett 2001). In addition to its importance in nutrient cycling, SOM is a major energy source for soil microorganisms (Dormaar 1988, Lynch & Whipps 1990), as well as a critical determinant of soil water holding capacity and aggregate structure (Brady & Weil 1999). The quantity and quality of SOM are therefore major factors that determe forage production and quality, as well as ecosystem stability. Knowledge of how grazing affects C and N cycling between SOM and the plant community is likely to be beneficial for the development of sustainable

management strategies which promote a desirable species composition, without reductions in soil organic N.

Soil Organic Matter

In natural perennial grassland systems most of the SOM occurs in the surface layer of the soil deposited by plant roots and surface litter over millennia. Fibrous grass root systems produce soils high in SOM, which represents 90% of the total C in most temperate grassland ecosystems (Dormaar 1992, Burke et al. 1997, Reeder et al. 2001). SOM distribution is very heterogeneous in native rangelands, and is not distributed uniformly, either horizontally or vertically, in soils (Hook et al. 1991, Burke et al. 1998, Reeder et al. 2001, 2004, Bird et al. 2002). Landscape position and soil texture influence many soil properties such as C and N in natural grasslands (Schimel et al. 1985, Dodd & Lauenroth 1997). SOM content is influenced by such factors as temperature and moisture, resulting in variations from micro-topographic to regional scales (Schimel et al. 1985, Burke et al. 1989, 1998, 1999). Root decomposition also increases when temperature and moisture conditions are favorable. The long-term balance between decomposition and primary production relate directly to SOM content (Ihori et al. 1995).

Exposed surface soil (bare ground) tends to be warmer than plant-occupied soil, which stimulates a faster turnover rate of the microbial population and increases decomposition of SOM (McGill et al. 1986). Plant root biomass and SOM also decrease when comparing plant-occupied soil to bare ground (Hook et al. 1991, 1994, Burke et al. 1999). Plant species composition is important because root distribution and decomposability both vary by species (Weaver 1958, Caldwell 1979, Dormaar 1992).

Therefore, accurate measurements of aboveground plant species cover and bare ground abundance relative to soil type and topographic position, and their associated soil properties, are important to characterize plant and soil dynamics at a landscape scale. A landscape approach, i.e. one focused on variation and interaction among ecosystem units, is important for the evaluation of nutrient cycling processes, which vary strongly depending on site factors (Groffman et al. 1993). Moreover, using spatial variability of the various SOM pools in interpreting responses to change in management should make the data even more representative of ecological processes (Herrick et al. 2002, National Research Council 1994).

Grazing Management

Management has a significant influence on plants and soils of an ecosystem. Heavy grazing and mismanagement lead to C loss, which results in a decrease of overall productivity (Kimble et al. 2001). Bauer et al. (1987) found lower organic C content in grazed than in ungrazed soils regardless of texture. Grazing resulted in a 12% decrease of organic C in the top 7.6 cm of the medium-textured soil. Dormaar et al. (1997) also showed that grazed areas had soils that were lower in total C and N, but had higher NH_4^+ and NO_3^- than soils that had been protected from grazing for 5 years. Conversely, Smoliak et al. (1972) found higher total soil C and belowground plant biomass on heavily grazed areas compared with light or no grazing after 19 years of treatments. Species composition changed as a result of grazing, with decreased basal area of cool season grasses, while basal area of *Bouteloua gracilis* increased. Different amounts and kinds of roots associated with these species may explain differences in soil C (Smoliak et al.

1972). A mix of cool (C_3) and warm-season (C_4) species maximizes productivity and the length of the grazing season (Williams & Markley 1973, Coyne et al. 1995). Shifts in species composition may be undesirable, especially if the length of the growing season is reduced by a decrease in abundance of C_3 species.

Heavy grazing and historical cultivation both result in a reduction of root biomass (Dormaar et al. 1994). Under very heavy grazing, less forage is left as carryover and root growth is reduced leading to the return of fewer organic residues to the soil (Johnston et al. 1971). Multiple years of very heavy grazing can cause a transformation in soil characteristics to those of a more arid microclimate (Johnston et al. 1971). Xeric regions generally have lower microbial activity than more mesic environments. Lower levels of microbial biomass are found in cultivated compared with prairie soils (DeLuca & Keeney 1994). Therefore, a decrease in soil microbial biomass on heavily grazed pastures may indicate a shift in soil characteristics from that of healthy grassland towards that of a cultivated field, as soils warm and bare ground increases, causing SOM losses to occur.

In addition to effects on soil properties and species composition, grazing also removes aboveground plant material. Frequent and severe defoliation depletes total nonstructural carbohydrates (TNC) and reduces herbage yield (Buwai & Trlica 1977). Removal of leaf material causes immediate cessation of belowground growth, which may allow more net C to be used for reestablishing photosynthetic material (Richards 1984).

Inorganic Nitrogen

Recent findings indicate that responses of grasses to defoliation, a common occurrence in rangelands, in part consists of release of labile root exudates (Guitian &

Bardgett 2000, Hamilton & Frank 2001). Hamilton and Frank (2001) showed that release of exudates provides a readily available C source, which stimulates N-mineralization in the rhizosphere and results in a positive feedback to the plant in the form of plant-available inorganic N. Decomposition of SOM in general provides the majority of inorganic N for plant production, including ammonium (NH_4^+) and nitrate (NO_3^-) (Dormaar 1988, Cambardella & Elliot 1992). Decomposition of more humified particulate organic matter (POM) and SOM is enhanced by release of labile root exudates in the vicinity, which is an example of rhizosphere priming effects (Kuzyakov 2002). Modification of rhizosphere pH by roots also influences nutrient availability (Dakora & Phillips 2002).

Inorganic N rarely accumulates in healthy grasslands because of rapid reimmobilization (Woodmansee et al. 1981). Decreased root growth and reductions in photosynthate supply are likely to decrease a plant's ability to actively take NH_4^+ and NO_3^- ions from the soil (Coyne et al. 1995). Therefore, heavy grazing may decrease the ability of plants to take up inorganic N, causing it to accumulate in the soil (Reeder et al. 2004). Detection of changes in soil properties, including inorganic N, may occur shortly after grazing treatments change, or conversely may take many years. In addition, ratios of particular soil properties, such as soluble C to inorganic N, may help indicate shifts in soil characteristics that are related to nutrient cycling dynamics (DeLuca & Keeney 1993).

Water Soluble Organic Carbon

SOM consists of many components that vary in mass and rate of turnover including water soluble organic carbon (WSOC) (Gregorich et al. 2000). Soluble organic

C represents one of the most labile fractions of SOM, and has turnover times ranging from days to months (Cook & Allan 1992, Boyer & Groffman 1996). Dissolved organic carbon (DOC) is defined as the soluble organic compounds that pass a 0.45 um filter and represents the theoretical equivalent of *in situ* soil solution (Thurman 1985). In the study of soluble or DOC many different methods of extraction are employed, making comparisons of results from measurements of WSOC and DOC less interpretable. Forested system studies and laboratory incubations often refer to DOC, which leaches from litter and occurs in soil pores of the soil O and A horizons, percolates down to lower horizons, and may even ultimately reach subsurface water sources and streams (Boyer and Groffman 1996, Hagedorn et al. 2002). Concentrations of soluble C generally decrease as the water percolates down the soil profile from sorption by colloids and Al and Fe oxides of mineral subsoils (Jardine et al. 1989, Kaiser et al 1996, Zech et al. 1994, Moore 1998). This transport probably occurs infrequently in semiarid grasslands, and only after high intensity precipitation events. However, leached organics contribute to the soil structure of lower horizons (Hagedorn et al. 2002, Marschner & Kalbitz 2003), even if only moved down with infrequent large precipitation events. Additionally, temperature and wind conditions before and subsequent to specific precipitation events can affect soil properties, such as infiltration. Therefore, the influence of the specific precipitation event on plant productivity of the given system is dependent on temporal soil moisture dynamics.

In contrast to DOC, WSOC is usually obtained with a 5:1 (liquid:solid) extraction ratio that involves shaking, which breaks down aggregates and releases bound organics from colloidal surfaces that may become re-adsorbed from solution if left in the soil

matrix. However, during decomposition qualitative shifts in soluble C develop in parameters such as molecular size fractions (Magid et al. 1996, Smolander & Kitunen 2002), degree of hydrophobicity (Cook & Allan 1992, Andersson & Nilsson 2001), various types of spectroscopy (Kalbitz et al. 2003), and UV absorbance (Chin et al 1994, Dai et al. 2001, Smolander & Kitunen 2002, Kalbitz et al. 2003), which represent changes in bioavailability and are related to soluble organics in general (whether DOC or WSOC). Soluble C and DOC do not represent the exact same fraction of the SOM, but DOC is included in the WSOC fraction. Since WSOC is obtained through extraction, it is not the truly dissolved phase but rather it represents the potentially soluble phase (Marschner & Kalbitz 2003).

Root Exudation

Root exudates, sloughing and decomposition of root cells and litter leachates all contribute to soil soluble C (Qualls & Haines 1992, Dormaar 1988, Reeder et al. 2001). Lysis and decomposition of microbial cells that died can also contribute to the soluble organic pool. Soil microorganisms use root exudates and dead root cells as food sources (Minchin & McNaughton 1984, Dormaar 1988, Qualls et al. 1991, Brady & Weil 1999, Reeder et al. 2001, Hogberg & Hogberg 2002, Kuzyakov 2002). Exudation may be expected to increase as plants grow and root biomass increases (Bokhari & Singh 1974). High levels of soluble C may indicate either high levels of exudation by the plant roots occupying the soil, or a low level of microbial uptake because of a small microbial community or other edaphic factors that limit microbial activity. The pool of soluble C that arises from root exudates or decomposition products from roots is transient in nature

due to high lability (Sanchez & Bursey 2002). However, the concentration of soluble C rises with dessication and subsequent cell lysis as protoplasm is released from soil microorganisms (Sparling et al. 1998). Air-drying of the soil sample therefore leads to a change in both the magnitude and origin of the soluble organic compounds. Alternatively, soluble C extraction of moist soils contain little C derived from microbial cells and may be important in studies that relate microbial biomass with concentrations of available nutrients (van Ginkel et al. 1994), because this fraction of soluble C represents a good indicator of root exudation and sloughing (Cheng et al. 1993, Cheng et al. 1996). This method more accurately reflects what carbon resources may become available to microorganisms in soil solution after *in situ* precipitation events.

Over a decade ago Cheng et al. (1993) noted that we knew relatively little about exudation. All roots have the ability to secrete or loose both low- and high-molecular weight molecules, primarily carbonaceous compounds, into the rhizosphere in response to both biotic and abiotic stresses (Bertin et al. 2003). Root exudation, also known as rhizodeposition, is actually a combination of various mechanisms of release including diffusion, excretion, secretion, and root debris deposition (Pinton et al. 2001, Uren 2001, Bertin et al. 2003). Many of the compounds released are involved in primary or secondary metabolic processes or plant defense (Bertin et al. 2003). Organic compounds released by roots consist of a myriad of molecular weights and structures, including: mono- and polysaccharides, amino acids, organic acids, aromatic acids, fatty acids, lipids, phenolics, allelochemicals, nucleosides, steroids, carbohydrates, siderophores, mucilage, proteins, enzymes, and vitamins (Uren 2001, Kuzyakov 2002, Dakora & Phillips 2002, Bertin et al. 2003). Inorganic ions (H^+, OH^-, HCO_3^-) are also released by roots into the

rhizosphere (Dakora & Phillips 2002). Root exudation occurs primarily through a passive process via diffusion, and may be enhanced during stress (Bertin et al. 2003). Total C released through root exudates in the important rangeland grass species *Bouteloua gracilis* was estimated to be 15% of net C fixation (Biondini et al. 1988) and as much as 25-40% for other species (Coyne et al. 1995, Uren 2001). Quantification of WSOC in soils from rangelands may increase knowledge about exudation by important grasses and how exudation may be influenced by factors such as grazing and drought.

Research Objectives:

The objectives of this research were: 1) To measure total and labile pools of C and N in both shortgrass steppe and mixed-grass prairie ecosystems in relation to aspect and microtopographic position and compare these pools to C and N mineralization potentials during aerobic incubations; 2) to quantify the amount of WSOC associated with grass roots and crowns relative to bulk soil in both shortgrass steppe and mixed-grass prairie rangelands; and 3) to examine soil and plant response variables as potential early indicators of ecosystem response to change in grazing management by measuring the influence of different lengths of rest from grazing on these variables in a mixed-grass prairie plant community.

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II. Landscape Variability of Labile and Total C and N in Surface Soils Of Two Semi-arid Grassland Ecosystems

Abstract

Natural perennial grasslands are characterized by a high degree of spatial and temporal variability in total and labile soil organic matter (SOM). Biogeochemical processes that drive nutrient dynamics may be more closely related to quantity of labile SOM than to total SOM. The objective of this research was to quantify the spatial distribution and relationships between total and labile carbon (C) and nitrogen (N) in two semi-arid grasslands. The influence of microtopographic position and aspect were evaluated to characterize innate variability of soil properties associated with these characteristics. Soil samples (0-5 and 5-10 cm depth) were collected in the early growing season from shortgrass steppe and northern mixed-grass prairie ecosystems. Analyses of water soluble organic carbon (WSOC) and water soluble nitrogen (WSN) were performed along with 21-day aerobic incubations for potentially mineralizable C and N to examine the relationships between these parameters and root biomass, total soil organic C (SOC), total N and inorganic N (iN). Results indicated that northern mixed-grass prairie had greater microbial activity, root biomass and total SOM than shortgrass steppe, but lower mass of field-moist WSOC ($WSOC_{FM}$) and iN, which represented labile C and N pools. Incubation results indicated that microbes from bare-ground microsites were more C-limited than microbes from grass-occupied soils. Nitrogen immobilization processes are likely to occur more frequently in the northern mixed-grass prairie system, while net N mineralization may be more common in the shortgrass steppe ecosystem. In northern mixed-grass prairie a lack of plant available N may frequently limit plant growth.

Introduction

Native perennial grassland ecosystems are generally characterized by a high degree of spatial and temporal variability (Burke et al. 1999, Bird et al. 2002), and by the storage of approximately 90% of ecosystem C belowground in soil organic matter (SOM) (Burke et al. 1997, Reeder & Schuman 2002). SOM is a major determinant of ecosystem function and stability because it is the primary source of many nutrients for plant growth, provides much of the water-holding capacity of the soil and acts as a substrate for microbial activity (Brady & Weil 1999). An understanding of the biogeochemistry of grasslands and their response to management therefore requires an understanding of the quantity, quality, and heterogeneity of SOM.

In grassland ecosystems, the quantity of SOM is spatially variable not only horizontally across the landscape (Yonker et al. 1988, Hook et al. 1991, Burke et al. 1999, Reeder 2003), but also vertically within the soil profile, where SOM often correlates with root mass and distribution (Weaver et al. 1935, Reeder et al. 2001). The degree of spatial variability of SOM is controlled by both abiotic and biotic factors such as temperature and moisture, topographical position and aspect, plant community, and soil texture (Schimel et al. 1985, Dodd & Lauenroth 1997, Burke et al. 1989a, 1999). At the regional scale, patterns of SOM are related to regional patterns of precipitation and temperature, with SOM generally increasing with increasing precipitation and decreasing with increasing temperature (Burke et al. 1989a), and with heterogeneity generally higher in semi-arid and arid regions than in more mesic regions (Bird et al. 2002). At the landscape scale, spatial variation in SOM is influenced by topographic position and its influence on SOM redistribution by water and wind (Burke et al. 1999). Aspect affects

soil moisture dynamics and may also indirectly influence SOM distribution. At the micro-topographic scale, heterogeneity in SOM is strongly influenced by plant species and the amount of exposed soil surface (Hook et al. 1991, 1994, Burke et al. 1999, Reeder et al. 2004). SOM tends to be lower in bare ground areas than beneath plants because the soil is exposed to erosional and depositional processes (Martinez-Turanzas et al. 1997), and because exposed soil is generally warmer than plant-occupied soil, thereby stimulating microbial decomposition of SOM (McGill et al. 1986). Plant community composition also is an important factor in SOM heterogeneity at the micro-topographic scale since fibrous grass roots are the primary source of material for SOM formation in grasslands (Dormaar 1992, Reeder et al. 2001), and species vary in root mass, distribution and decomposability (Weaver 1958, Caldwell 1979, Dormaar 1992).

An assessment of quantity and spatial variability of total SOM is insufficient to understand how SOM affects ecosystem dynamics, because SOM consists of many organic components that vary in mass and rate of turnover (Gregorich et al. 1999). The majority of SOM is comprised of recalcitrant humic materials with slow rates of turnover; only a small fraction (1-2%) of SOM is readily decomposable, with turnover rates ranging from days to months (Parton et al. 1988, Burke et al. 1997). This labile pool is composed of living microorganisms and soluble organic compounds released from live and decaying microorganisms and plant roots (Cook & Allan 1992, Cheng et al. 1993). Evaluation of the size of the labile pool is important to understand SOM dynamics because the metabolic processes of the soil microbial biomass are responsible for the formation and decomposition of SOM, and thereby the cycling of C and many nutrients in the ecosystem (Reeder et al. 2001). In addition, changes in soluble C and the

light fraction of OM can correspond to changes in total SOM (Zak et al. 1990, Biederbeck et al. 1994).

Changes in soil parameters including labile organic matter may be useful as early indicators of soil ecological stress in some systems (Dick 1997, Garcia et al. 2002). Various procedures have been used to estimate the active or labile fraction of SOM. Aerobic incubations methods are often used to measure soil microbial biomass (Jenkinson & Powlson 1976, Wu et al. 1990) or potential microbial activity (Franzluebbers et al. 2000). The concentration of WSOC in field-moist soil provides a measure of C that is readily available for microbial use (Sikora and McCoy 1990, Cook and Allan 1992), as well as a measurement of root exudation (Cheng et al. 1993, 1996). WSOC extracted from field moist soils generally contains little C derived from microbial cells (van Ginkel et al. 1994, Davidson et al. 1987, DeLuca & Keeney 1994, Gregorich et al. 1999), whereas the concentration of WSOC in air-dry or low temperature oven-dry soils has been found to be correlated with microbial biomass (Burford & Bremner 1975), microbial activity (Davidson et al. 1987, DeLuca & Keeney 1994,), and total soil C (Burford & Bremner 1975, Sparling et al. 1998).

A field study was performed to evaluate the interactions of landscape and microtypic position on soil organic C and N transformations in two semi-arid grasslands, a shortgrass steppe, and a northern mixed-grass prairie. Sampling was conducted to characterize inherent heterogeneity of surface soil OM in relation to microsite conditions and topographic position, and to test the question of how total soil organic carbon (SOC), WSOC and C and N mineralization potentials were related and dependent on ecosystem type, aspect and microtypic position. Specifically, it was hypothesized that these soil

parameters would be higher in the Northern mixed-prairie (NMP) than shortgrass steppe (SGS), higher on north-facing than flat aspects, and higher in grass-occupied soil than bare-ground microsites (plant interspaces). This research quantified distribution patterns of SOM, C and N in the surface soils of the two grassland ecosystems to assess the relative importance of differences in dominant plant functional type on SOM dynamics and the relationship between total and labile soil C and N.

Materials and Methods

Site Descriptions

Soil samples were collected from two semi-arid grassland ecosystems, the shortgrass steppe (SGS) and the Northern mixed-grass prairie (NMP). The SGS site was located at the USDA-ARS Central Plains Experimental Range, on the western side of the Pawnee National Grasslands, about 60 km northeast of Fort Collins, Colorado (40°49'N, 107°47'W). Shortgrass steppe vegetation is characterized by C_4 grasses with a dominant component of blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths] (Milchunas et al. 1989, Lauenroth and Milchunas 1992). Some C_3 grasses also exist at SGS including needle-and-thread (*Stipa comata* Trin. and Rupr.) and western wheatgrass [*Pascopyrum smithii* (Rybd.) Love].

Samples were collected on the SGS from two pastures that had been moderately grazed by cattle for the past 70 years. In each pasture, samples were collected from *Boutleoua gracilis*-occupied soil and from small (8-20 cm diameter) plant interspaces (bare ground) on two landscape positions; a flat upland terrace (Olney fine sandy loam soil) and a north-facing slope (3-5%) (Cushman sandy loam soil). Both soils were

classified as fine-loamy, mixed, mesic Ustollic Haplargids, with an average A-horizon thickness of 10 cm (NRCS Soil Survey, 1991).

The mixed-grass prairie site was located at the USDA-ARS Fort Keogh Livestock and Range Research Laboratory, about 18 km southwest of Miles City, Montana (46°20'N, 105°50' W), hereafter referred to as northern mixed prairie (NMP). The two study pastures sampled were located on an Eapa silty loam soil type, classified as a fine-loamy, mixed, frigid aridic Argiboroll, with an average A-horizon thickness of 8 cm (NRCS Soil Survey 2000). The plant community is characterized by C_3 grasses which share dominance including, *Stipa comata, Pascopyrum smithii,* and a component of C_4 grasses, such as *Bouteloua gracilis* (Coupland 1992). Historically, the sites have been grazed by cattle at moderate intensities, with one of the two pastures having been rested from grazing for one season. Samples were collected from *Stipa comata*-occupied soil and bare ground, on both flat and north-facing (2-5% slope) landscape positions.

Soils and Sample Collection

A 50-m transect was established on each of the landscape positions within each pasture. Replicate surface cores (0-5, 5-10 cm x 3.18 cm diam.) from bare ground and *Stipa comata*- or *Bouteloua gracilis*-occupied soils were collected from 3 randomly selected sample locations per transect. Sample collection occurred in the late spring of 2001 during early season plant growth and before the onset of the stresses that accompany depressed soil moisture levels. Because the soil surface occupied by grasses such as *Bouteloua gracilis* is 2-3 cm higher than adjacent bare ground spaces (Hook et al. 1991), grass crowns were separated from the surface of mineral soil cores during

collection using a serrated knife. This allowed the 0-5 cm soil core to correspond to the same horizontal layer of soil under plants or bare ground.

Soil samples were placed in coolers immediately after collection and kept refrigerated (4° C) until processed. Field-moist samples were weighed before processing, and bulk densities (BD) of soil cores were calculated using the field weight, gravimetric water content and volume of each soil sample. Samples were processed by removing visible ("coarse") roots with forceps and passing the sample through a 2 mm screen. The < 2 mm field moist soil was sub-sampled for analyses of gravimetric water content and field moist water soluble organic C ($WSOC_{FM}$); the remaining soil was oven-dried at 60° C and stored in ziplock plastic bags at room temperature until further analyses. Equal weights of dried soil from each of the 3 replications of a given site and block were composited to obtain sufficient sample for aerobic incubation and extraction of $WSOC_{OD}$ and WSN_{OD} (n = 8 per system and depth).

Analysis for concentration of $WSOC_{FM}$ followed the procedure of Davidson et al. (1987) with slight modifications. Extractions consisted of 8 g of soil with 40 ml de-ionized water (5:1 ratio, rather than the 2:1 ratio of Davidson et al. 1987) placed in a 50 ml plastic vial. The soil solution was shaken on a wrist-arm shaker for 30 minutes and then centrifuged for 7 minutes (rather than 5 minutes) at 5760 rpm. After centrifugation the supernatant was decanted from the soil pellet into a funnel lined with a 12.5 cm Whatman GF/A glass microfiber filter. A vacuum extractor was then used to filter the solution through a 0.45 micron nylon acrodisc 25 mm diameter filter. Extracts were frozen and subsequently thawed in a warm water bath and mixed before soluble C analysis, which for the $WSOC_{FM}$ was performed using a Shimadzu TOC 5050A Total

Organic Carbon Analyzer (Shimadzu Intruments, Inc. Columbia, MD). Samples of the composited dried soil were extracted following the above-mentioned procedure and were analyzed on a different instrument, a Shimadzu TOC-V $_{CPH}$ (Shimadzu Instruments, Inc. Columbia, MD), which measures both WSOC and Water Soluble Nitrogen (WSN).

Aerobic incubations were performed using 25 g of dried soil weighed into a 90 ml wheaton snap-cap vial. BD was calculated and a syringe was used to add the correct amount of deionized H_2O to bring each sample to 50% water-filled pore space. Samples were incubated in 1 L mason jars at 25° C with 1 N NaOH used to trap respired CO_2. Base traps were replaced at 3, 10 and 21 days following initiation of the incubation and titrated after addition of 4 ml of barium chloride with 0.5 N HCl to pH of 8.3. Pre- and post-incubation soil NH_4^+ and NO_3^- contents were determined by extraction with 1 N KCl (4:1 extraction ratio) and analyzed with a Lachat Quikchem FIA+ 8000 Series Flow Injection Autoanalyzer (Quikchem, division of Lachat Chemicals, Mequon, WI).

Total C and N were determined on air-dry powder-ground soil samples with a Carlo Erba NA 1500 automatic carbon-nitrogen analyzer (Haake Buckler Instruments Inc., Saddle Brook N.J.), and inorganic C was measured by a modified pressure-calcimeter method (Sherrod et al. 2002).

Statistical Analyses

The experimental design consisted of a split-split plot with ecosystems representing the whole plot, north-facing and flat aspects representing the two subplots, and bare-ground and grass-occupied microsites representing the sub-subplots. The MIXED model procedure was used in SAS (1996 SAS Institute Inc.) for statistical analysis of variance (ANOVA). Two replicate sites were measured for each system.

Three randomly selected locations (experimental units) were sampled within each subplot. Therefore, the total number of observations was 48 (2 systems x 2 aspects x 2 microsites x 3 EUs x 2 replicate pastures), with 47 total degrees of freedom. The error term degrees of freedom were calculated using the Satterthwaite method (DDFM = SATTERTH). Independent random effect variables included site nested within system [site (system)], which was the error term used to test for main effect differences between systems. The other random effect was the site nested within system-by-aspect interaction, which was the error term used to test the system-by-aspect interaction. Estimates for these variance components were compared to the residual to determine which was greater. This was done with an F-ratio test (site (system) / residual) and residuals of the covariance parameter estimates with ratios of $p > 0.20$ were pooled with the error term. If the estimate was greater than the residual the component was left in the model, and if not the error terms were pooled (random effect removed from the model).

The full factorial design was used for analysis with main effects of system, aspect, and microsite and all appropriate interaction terms followed by backwards model selection to remove non-significant interaction terms. Interactions with a $p \leq 0.15$ were left in the model (G. Richardson personal communication) and interpretation of only comparisons identified *a priori* within the interaction were done using the appropriate p-values (comparisons of LS Means). This procedure is similar to redoing the analysis with one of the interaction terms considered as a "by variable" to analyze the interaction.

Statistical analysis initially consisted of comparison of dependent variables including BD, soil moisture and root biomass using least significant differences with alpha = 0.05. Afterwards $WSOC_{FM}$, total C and N of soil and other dependent variables

were analyzed with root biomass considered as an independent variable, along with the other independent variables, to test for the dependence of these parameters on root biomass. This allowed for proper interpretation of the data so that differences between systems represented true differences between systems external to the inherent differences in root biomass. Since root biomass was a continuous variable, the numerator df = 1. Respired CO_2 and net N mineralization from aerobic incubations, oven-dry WSOC ($WSOC_{OD}$) and water soluble nitrogen (WSN_{OD}) analyses were performed on composite samples consisting of equal weights from each of the 3 reps from a given site and block (n=16 per depth). Therefore, only the main-effect means and one-way interactions were compared for C and N mineralization potential and $WSOC_{OD}$ and WSN_{OD} data and associated ratios. All reported differences were significant at the alpha ≤ 0.05 level unless otherwise stated.

Results

Root biomass, bulk density, and soil moisture

Northern mixed-grass prairie (NMP) root mass was greater than SGS root mass for all depth increments (Table 1). A strong interaction occurred between system and aspect for all depth increments, where NMP root mass was greater on flat terrain than the north-facing aspect while this was not the case for SGS (Figure 1). Root biomass on north-facing aspects at the SGS was similar to the north-facing aspects at the NMP, while on flat areas root biomass was higher on NMP than the SGS for all depth increments. Inclusion of both topographic positions shows that root biomass did not differ between microsites because of high variability. The trend in the 0-5 cm depth increment showed

that grass-occupied soil root biomass (398 g m^{-2}) was 37% higher than root biomass in bare-ground microsites ([290 g m^{-2}] ($p = 0.15$)).

Bulk density (BD) did not differ between systems for any depth increment. Average BD at the SGS was 1.35, 1.41 and 1.38 g cm^{-3} and at the NMP were 1.31, 1.39 and 1.35 g cm^{-3} for the 0-5, 5-10 and 0-10 cm depths, respectively. Microsite influenced BD in that bare soil was denser than grass-occupied soil for the 0-5 and 0-10 cm depth increments (Table 2).

Gravimetric soil water content did not differ between the two systems for any depth increment, but differed between microsites (Table 2). Bare ground had lower water content than grass-occupied soil for the 0-5 and 0-10 cm depths, but not the 5-10 cm depth. Aspect did not significantly influence soil water content at the time of sampling for any depth increment.

Total SOC and N

Total soil organic carbon (SOC) was higher at the NMP than the SGS in the 0-5 cm and 0-10 cm depths, but SOC did not differ between the two ecosystems in the 5-10 cm depth (Table 1). An interaction occurred between microsite and system in the 0 -10 cm depth; with higher SOC in grass-occupied (1137 g m^{-2}) than bare (979 g m^{-2}) SGS microsites, but comparable amounts of SOC between NMP microsites (grass = 1224 g m^{-2}, bare = 1216 g m^{-2}). No microsite-by-system interaction occurred in the 5-10 cm depth increment, but there was a trend, bare ground had 484 g m^{-2} and grass had 554 g m^{-2} ($p = 0.060$).

Total soil N (TN) was highly correlated with SOC ($r^2 = 0.864$), and was higher at the NMP than the SGS in the 0-5 cm and 0-10 cm depths (Table 1). In the 5-10cm depth, the two systems did not differ in TN, but grass-occupied soils were higher in TN (57 g m^{-2}) than bare microsites (51 g m^{-2}) ($p = 0.073$).

The ratios of SOC to TN were not significantly different between systems for any depth increment. Microsites differed in SOC:N ratio in the 0-5 cm depth, with grass-occupied soil having a higher C:N ratio (10.6) than bare soil (10.2).

Total inorganic N, ammonium and nitrate

Ammonium N (NH_4^+-N) was higher at the NMP than the SGS for the 0-5, but not the 5-10 cm depth (Table 1). Bare ground had higher amounts of NH_4^+-N (0.43 g m^{-2}) than grass-occupied areas (0.28 g m^{-2}) in the 0-5 cm depth. However, this trend was reversed for the 5-10 cm increment, with bare ground at 0.06 g m^{-2} and grass having 0.11 g m^{-2}.

Nitrate N (NO_3^--N) contrasted NH_4^+ in that it was noticeably higher at the SGS than at the NMP for all depth increments (Table 1). A system-by-aspect interaction occurred for the 0-10 cm depth because the NMP had similar amounts of NO_3^- for flat (0.35 g m^{-2}) and north-facing (0.34 g m^{-2}) aspects, while SGS flat terrain (2.62 g m^{-2}) had higher amounts of NO_3^- than north-facing aspects (2.18 g m^{-2}), most of which was attributable to differences in the surface 5 cm where aspects were similar at the NMP (0.15 g m^{-2}) but flat ground (1.51g m^{-2}) was higher than north-facing (1.22 g m^{-2}) at the SGS.

Total inorganic N (iN) was higher at the SGS than the NMP for all three depth increments (Table 1). A system-by-aspect interaction occurred for the 0-10 cm depth with the NMP having similar amounts of iN for flat (0.85g m^{-2}) and north-facing (0.89 g m^{-2}) blocks, while on flat ground at SGS (3.03 g m^{-2}) had higher amounts of iN than north-facing slopes (2.46 g m^{-2}). This interaction was largely caused by greater amounts of NO_3^- in SGS than NMP.

Water Soluble Organic Carbon (WSOC)

Bulk soil $WSOC_{FM}$ in the surface 10 cm was highly dependent on root biomass ($p = 0.007$) and was higher for the SGS (3.13 g m^{-2}) than for the NMP (2.79 g m^{-2}) (Table 1). In the surface 5 cm $WSOC_{FM}$ was dependent on both SOC and on root biomass and was higher for the SGS (1.80 g m^{-2}) than the NMP (1.40 g m^{-2}). $WSOC_{FM}$ tended to be higher for bare ground (1.75 g m^{-2}) than grass occupied (1.45 g m^{-2}) soil for the surface 5 cm ($p = 0.062$). $WSOC_{FM}$ was not dependent on root biomass in the 5-10 cm increment bulk soil, total soil C, or microtypic conditions. However, there was a system-by-aspect interaction, which showed that on flat aspects $WSOC_{FM}$ at SGS (1.18 g m^{-2}) was less than flat areas at NMP (1.44 g m^{-2}) and north-facing aspects (1.48 g m^{-2}) at the SGS.

Overall concentration of $WSOC_{FM}$ in bulk soil showed a mean value of 22.8 ug g^{-1} soil with a range from 12.7 to 55.1 at the SGS. At the NMP, mean concentration of $WSOC_{FM}$ in bulk soil was 20.7 ug g^{-1} soil with a range from 13.6 to 42.5. In contrast concentration of $WSOC_{OD}$ at SGS had a mean value of 88.3 ug g^{-1} soil with a range from 57.3 to 129.1 and at NMP the range was from 82.7 to 139.7 with a mean of 115.7 ug g^{-1} soil.

$WSOC_{FM}$ / SOC Percentage

The relationship between total SOC and bulk soil $WSOC_{FM}$ was also evaluated on a percentage basis (($WSOC_{FM}$ / SOC)*100). This value is a measure of relative lability since it reflects the percentage of SOM that becomes soluble upon extraction. The ratio was highly dependent on root biomass ($p = 0.0007$), which indicates that more SOM might be soluble in soils with higher root densities as a result of increased quantities of exudates such as organic acids. The percentage was different between the two ecosystems in the surface 10 cm, with 0.24 in NMP and 0.30 in SGS, but was in the surface 5 cm alone, with 0.21 and 0.32 for NMP and SGS, respectively (data not tabled).

Carbon and Nitrogen Mineralization Potential

Mineralization potential of soil organic C and N was determined with a 21-day aerobic incubation. The NMP system showed greater CO_2 evolution rates than SGS (ug CO_2-C g^{-1} day^{-1}) after 0-3, 3-10, 10-21 days and mean rate (cumulative ug CO_2-C $g^{-1}day^{-1}$ / 21) for both 0-5 and 5-10 cm depths (Table 3). Mean values for net N mineralization were 17.5 and 15.5 for NMP and 16.2 and 14.9 (cumulative ug N g^{-1} soil) at the SGS for 0-5 and 5-10 cm depths, respectively. Systems did not differ, nor did microsites. The ratio of cumulative CO_2-C evolved to net N mineralization (ug g^{-1} soil 21 $days^{-1}$) was higher for NMP (16.3) than SGS (12.3) for the 0-5 cm depth ($r^2 = 0.654$). This ratio also was higher for NMP (15.9) than SGS (12.1) for 5-10 cm depth ($r^2 = 0.649$), and was influenced by aspect with flat ground (14.7) higher than north-facing (13.3) slopes ($p = 0.051$) (data not tabled). Another interesting correlation was of the ratio of CO_2 evolved /

net N mineralization with the $WSOC_{OD}$ / WSN_{OD} ratio resulting in an $r^2 = 0.292$ (n=16) for the 0-5 cm depth and $r^2 = 0.654$ (n=16) for the 5-10 cm increment. The $WSOC_{OD}$ to WSN_{OD} ratio itself was higher for NMP than SGS for both depths (Table 3), and tended to be higher for grass-occupied soil than bare ground in the 0-5 cm depth ($p = 0.067$, Table 2).

Grass-occupied microsites tended to have higher CO_2 evolution than bare-ground for 0-3 day ($p = 0.052$) and mean CO_2 evolution rate ($p = 0.096$) for the 0-5 cm depth, as well as the 3-10 day rate for the 5-10 cm depth ($p = 0.089$, Table 2). $WSOC_{OD}$ and WSN_{OD} analyses on sub-samples of the same composite soils used for the incubations revealed that CO_2 evolution was positively correlated with $WSOC_{OD}$ after 3 days ($r^2 = 0.512$, Figure 2a) and with 21 day means ($r^2 = 0.473$, Figure 2b). WSN_{OD} was higher for SGS than NMP (Table 3) which is largely attributable to the higher levels of NO_3^- at the SGS (Table 1).

The difference between $WSOC_{OD}$ and $WSOC_{FM}$ was dependent on the system (Table 3) and microsite (Table 2) for the 0-5 cm depth ($r^2 = 0.565$). The 5-10 cm depth also was correlated with system and microsite with $r^2 = 0.729$, though microsites did not differ. When comparing CO_2 evolution rates, correlations with the difference between $WSOC_{OD}$ and $WSOC_{FM}$ agreement was strongest with the 3-day CO_2 evolved data (r^2 =.554, Figure 2c), than the 10 or 21-day data. This difference was correlated with mean CO_2 evolution rates as well ($r^2 = 0.458$, Figure 2d). Calculation of this difference as a ratio to compare systems (SGS/NMP) yielded values of 0.697 for the 0-5 cm depth and 0.682 for the 5-10 depth. These ratios were almost identical to the ratios for CO_2

evolution during incubations (SGS/NMP) with 0.696 and 0.717 for the 0-5 and 5-10 cm depths, respectively.

The $WSOC_{OD}$ to $WSOC_{FM}$ ratio also differed between systems in a manner similar to the difference between $WSOC_{OD}$ and $WSOC_{FM}$. The mean values for this ratio (0-10 cm) were 5.7 for NMP and 4.1 for SGS.

Discussion

Systems differences in total SOC, TN, and root biomass resulted from long-term plant shoot and root productivity and deposition in the systems as affected by climate variables, which is not surprising. This is corroborated by the higher root biomass at NMP for all surface depths and is consistent with findings by others that higher biomass is associated with more precipitation found in NMP than SGS (Lauenroth et al. 1999).

Although higher in total SOC, TN, and root biomass, the NMP had lower levels of labile forms of C and N. We hypothesized that higher levels of $WSOC_{FM}$ would occur at NMP because exudation may be expected to increase as root biomass increased (Bokhari & Singh 1974). Lower levels of $WSOC_{FM}$ likely resulted from higher microbial activity at NMP than SGS as suggested by higher CO_2 evolution rates and higher $WSOC_{OD}$ levels and hence more uptake of labile C. The difference between $WSOC_{OD}$ and $WSOC_{FM}$ also suggested a higher microbial biomass at NMP because drying of the soil sample causes a change in both the magnitude and origin of the soluble C as dessication and subsequent cell lysis lead to the release of organic compounds from the protoplasm of soil microorganisms. The mean values for the ratio of $WSOC_{OD}$ to $WSOC_{FM}$ soil (0-10 cm) were 5.7 for NMP and 4.1 for SGS, and were within the range reported by Davidson et al. (1987). However, different levels of $WSOC_{FM}$ may reflect a

difference in the amount of exudation between dominate grass species in the two systems and agrees with speculation by Frank et al. (1995) that *Bouteloua gracilis* has higher rates of exudation than other northern mixed-grass prairie species. Biondini et al. (1988) found that *Bouteloua gracilis* releases 15% of net fixed C in the form of root exudates. Field-moist WSOC values measured at any one moment in time are difficult to interpret because $WSOC_{FM}$ represents a net value of soluble organic matter from a variety of sources such as root exudates, sloughing and decomposition of root cells and litter leachates (Dormaar 1988, Qualls et al. 1991, Reeder et al. 2001) minus recent microbial uptake of labile C.

Higher mass of iN at SGS largely resulted from differences in NO_3^-, which was 7 times higher at SGS than NMP, while NH_4^+ was less than two-fold higher at NMP. This may have resulted from higher uptake rates of iN or lower mineralization rates associated with cooler spring temperatures in the NMP. Additionally, rainfall often occurs at SGS in smaller low intensity events (Lauenroth & Milchunas 1992), which are unlikely to leach nitrate from the surface soil.

Comparison of CO_2 evolution rates as a measure of microbial activity showed the strongest correlations with the 3-day CO_2 evolution data, which agrees with findings by Franzluebbers et al. (2000). Analysis of ratios indicated that the surface soil at SGS may support a more C limited microbial community compared to a more mineral N limited plant system in NMP. The CO_2 evolved: net N mineralization ratio and the $WSOC_{OD}$: WSN_{OD} ratios both indicate that microbial activity was more C limited in the SGS than the NMP under optimal incubation conditions. Additionally, the *in situ* microbial community in NMP may be more N limited leading to net immobilization and low plant

available N. In contrast, a relatively C limited microflora at SGS could lead to selective pressure favoring species that have greater rates of root exudation. Therefore, *Bouteloua gracilis* might have an adaptive advantage over cohabitant species which exude less, potentially contributing to its competitive superiority in the shortgrass ecosystem.

Aspect did not have a consistent influence on most soil properties measured. The system-by-aspect interaction that occurred for root biomass indicated that root biomass was positively influenced by a north-facing aspect in SGS, but flat ground had higher root biomass than north-facing aspects at NMP. This interaction in root biomass probably resulted from a slightly cooler microclimate on the north-facing slopes at NMP corresponding to a shorter growing season at higher latitudes, hence less biomass accumulation. The north-facing slopes at SGS may be positively influenced by the greater soil moisture content resulting from lower soil temperatures. Alternatively, topographic position may have a stronger influence on some properties other than aspect *per se.* Spatial variation in SOM is strongly influenced by topographic position and aspect, and their influences on soil water and SOM redistribution by wind and water (Burke et al. 1999). North-facing slopes sampled in the NMP would likely be classified as shoulder slope positions where run-off predominates, while in SGS the sample areas would likely fall into the side or toe-slope classification where run-on occurs. $WSOC_{FM}$ also showed that north-facing slopes at SGS (5-10 cm depth) had higher values than flat terrain, while this difference was reversed at NMP. Garcia et al. (1997) found that lower slope positions had higher masses of water soluble carbon because of migration of this fraction with run-off water. This likely explains the system-by-aspect interaction found in our study because north-facing slopes sampled at NMP may be run-off zones, while at

SGS these slopes may be run-on zones. However, findings by Hagedorn et al. (2002) from forested systems showed that the origins of dissolved organic carbon (DOC), which migrates with soil water, and WSOC are not the same. However, this may differ in pulse driven semiarid grassland soils.

Not all soil properties showed a system-by-aspect interaction. The ratio of cumulative CO_2-C evolved to net N mineralization (ug g^{-1} soil) was influenced by aspect (5-10 cm depth) with flat areas having higher ratios than north-facing slopes ($p = 0.0511$). Findings by others indicated that this ratio reflected relative C or N limitation during incubations (Schimel 1986, Burke et al. 1989b, Holland & Detling 1990, Reeder et al. 1998). This indicated that soil microbes in the 5-10 cm depth increment of flat areas may be more N limited than those occupying north-facing slopes.

In the surface 5 cm of soil $WSOC_{FM}$ was slightly higher for bare ground areas than grass-occupied soils independent of root biomass differences between microsites. This may indicate that roots occupying bare ground microtypes release more labile C into the soil per g root mass. Hamilton and Frank (2001) found that a commonly grazed perennial grass exuded C into the rhizosphere following defoliation. This release of exudates stimulated the release of a pulse of inorganic nitrogen from the soil microbial uptake of the labile C and the concurrent associated N mineralization. The $WSOC_{OD}$ to WSN_{OD} ratio from the surface 5 cm in our study implies that microbes from bare ground spaces may be more C limited than microbes from grass-occupied soils. Grasses exhibiting preferential exudation from roots occupying bare ground soils might facilitate uptake of mineral N as microbial populations in bare ground microtypes respond quickly to labile C source inputs which can be quickly mineralized.

Bare microsites in this analysis showed lower soil moisture levels than grass-occupied soil which probably reflects loss to greater evaporative demand from the surface of exposed mineral soil. BD was undoubtedly higher in bare ground spaces as a result of less plant material and SOC and possibly surface compaction. Hook et al. (1991) found that total SOC and the SOC: TN ratios of grass-occupied surface soil in SGS were greater than those of open microsites. Results from this study agree with these findings because an interaction occurred between microsite and system with higher SOC in grass-occupied than bare microsites in SGS, but comparable amounts of SOC between NMP microsites. Grass occupied microsites in both systems showed higher SOC:N ratios than bare ground spaces in the surface 5 cm. This difference may be attributable to warmer soil temperatures and thus more microbial breakdown of SOM in the bare mineral patches (soil temperature comparison data not shown). The higher SOC: TN ratio associated with plant occupancy of a microsite indicated that more SOC is deposited at the microsite as the plant grows. When a plant dies and a microsite is vacated the deposition of SOM decelerates while the decay rate is likely to increase.

Conclusions

Measures of labile C and N pools are important to understand biogeochemical processes in semi-arid soil systems since landscape variability of total C and N pools is high. Though no single soil property examined in this study revealed a strong conclusion unto itself, evaluation of a number of the variables together reveals differences between N cycling processes in these systems and differences between microsites. Since microsite conditions influenced a number of soil properties, monitoring of ecosystem

responses to changes in grazing management practices, which influence species composition and bare-ground abundance, is important. Microbes from bare ground spaces may be more C limited than microbes from grass-occupied soils. Preferential exudation from roots occupying bare ground soils might facilitate plant uptake of mineral N as the microbes there await a labile C source which can be quickly decomposed. Labile WSOC was dependent on root biomass, but systems also differed in a number of soil properties independent of differences in root biomass. Microbial activity in the top 10 cm was more likely limited by C availability at SGS and by N availability at NMP. If *Bouteloua gracilis* exudes relatively more labile C than other species, corresponding to more plant available N, this might render an adaptive advantage contributing to superior competitive ability under certain environmental conditions.

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Table 1. Means for root mass and soil total and labile C and N (g m^{-2}) in the soil profiles (0-10 cm) of Northern mixed prairie (NMP) and Shortgrass steppe (SGS).

Depth	Root Mass		SOC		TN		NH_4^+		NO_3^-		Total iN		$WSOC_{FM}$	
cm	(g m^{-2})		(g m^{-2})		(g m^{-2})		(g m^{-2})		(g m^{-2})		(g m^{-2})		(g m^{-2})	
	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS
0 – 5	440*	248	678*	564	66*	54	0.43*	0.28	0.15	1.37*	0.58	1.65*	1.40	1.80*
5 – 10	218*	145	542	496	55	53	0.10	0.07	0.19	1.03*	0.29	1.10*	1.39	1.33
0 - 10	658*	393	1220*	1060	121*	107	0.53*	0.35	0.34	2.40*	0.87	2.75*	2.79	3.13*

Note: *Indicates value is greater than the other system (LSD, alpha = 0.05). Compare means only within a paired column and depth increment.

Table 2. Comparisons of field soil properties and CO_2 evolution of grass-occupied (Grass) and interspace (Bare) microsites.

Depth (cm)	% H_2O (g/g)		BD		WSOC $_{OD}$ (ug g^{-1} soil)		WSOC $_{OD}$ / WSN $_{OD}$		WSOC $_{OD}$ - WSOC $_{FM}$ (ug g^{-1} soil difference)		ug CO_2-C g^{-1} soil day^{-1} 0-3 days		ug CO_2-C g^{-1} soil day^{-1} 3-10 days		ug CO_2-C g^{-1} soil day^{-1} 21 day mean	
	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass
0 – 5	9.2	10.5*	1.36*	1.29	88	105†	6.2	8.0†	63.4	81.9*	27.4	31.2†	11.1	12.3	10.9	12.0†
5 – 10	12.1	12.1	1.40	1.39	104	110	9.5	10.0	85.3	90.3	27.1	27.8	9.2	10.1**	9.6	10.4
0 - 10	10.6	11.3*	1.38*	1.34	96	108	7.9	9.0	74.4	86.1	-	-	-	-	-	-
p =					0.059		0.067				0.052		0.089		0.096	

Note: *Indicates value is greater than the other microsite (LSD, alpha = 0.05). † Indicates significantly greater at alpha = 0.10. Compare means between microsites only within a paired column and depth increment.

Table 3. Incubation and $WSOC_{OD}$ and WSN_{OD} data with ratios for composite soil samples (0-5 and 5-10 cm).

Depth	ug CO_2-C g^{-1} soil day^{-1} 0-3 days		ug CO_2-C g^{-1} soil day^{-1} 3-10 days		ug CO_2-C g^{-1} soil day^{-1} 21 day mean		$WSOC_{OD}$ (ug g^{-1} soil)		WSN_{OD} (ug g^{-1} soil)		$WSOC_{OD}$ / WSN_{OD}		$WSOC_{OD}$ / $WSOC_{FM}$		$WSOC_{OD}$ - $WSOC_{FM}$ (ug g^{-1} soil difference)	
cm	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS
0 – 5	36*	22	13*	10	13*	9	107*	86	10.8	16.6*	9.9*	5.2	5.0*	3.2	85.6*	59.7
5 – 10	33*	22	11*	9	12*	8	124*	90	8.8	13.2*	14.1*	6.8	6.2*	4.7	104.4*	71.2

Note: *Indicates value is greater than the other system (LSD, alpha = 0.05). Compare means only within a paired column and depth increment.

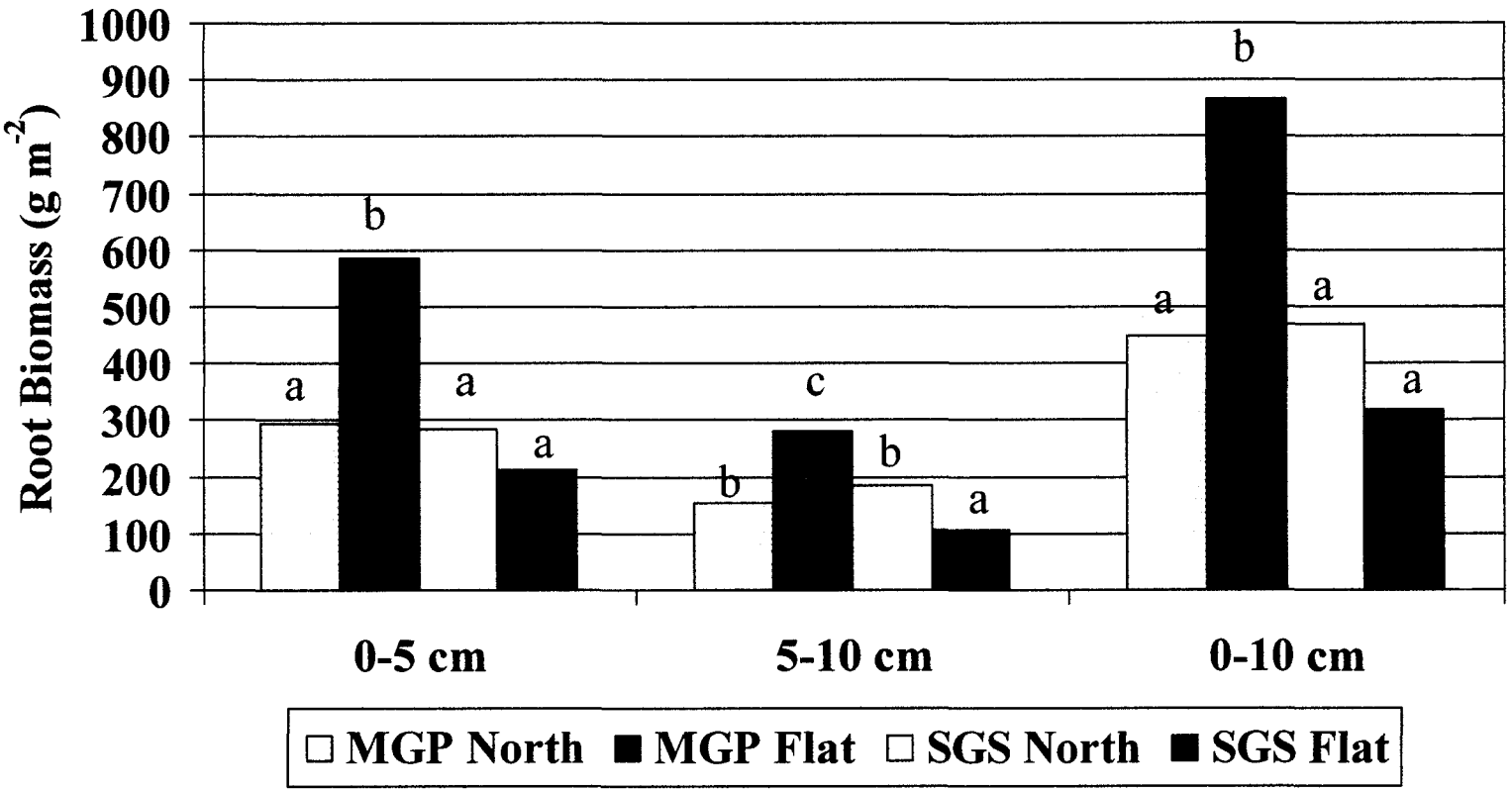

Fig. 1. Root Biomass (g m^{-2}) for Northern mixed prairie (NMP) and Shortgrass steppe (SGS) system-by-aspect interaction for 0-5, 5-10, and 0-10 cm. Means within a depth increment with the same letter do not differ (LSD, alpha = 0.05). Compare means only within a depth increment.

Figure 2 a

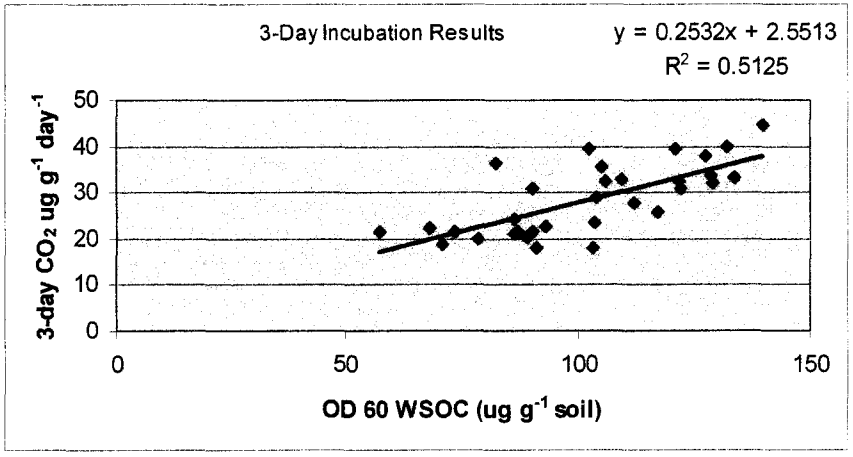

Figure 2 b

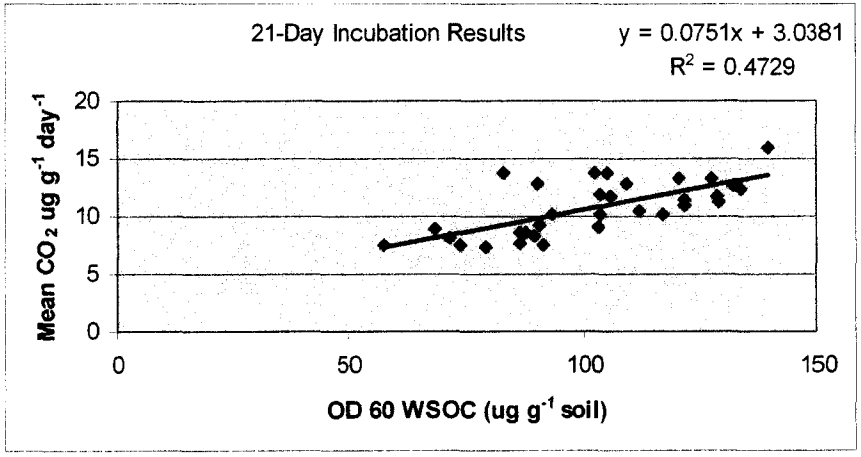

Figure 2 c

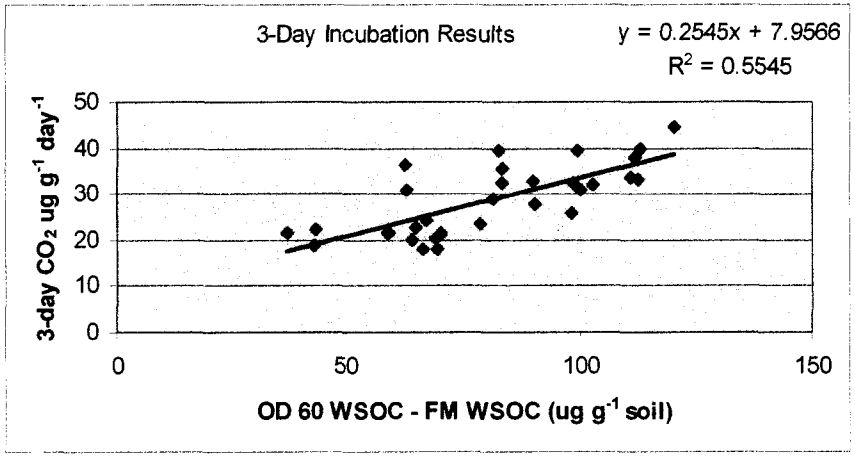

Figure 2 d

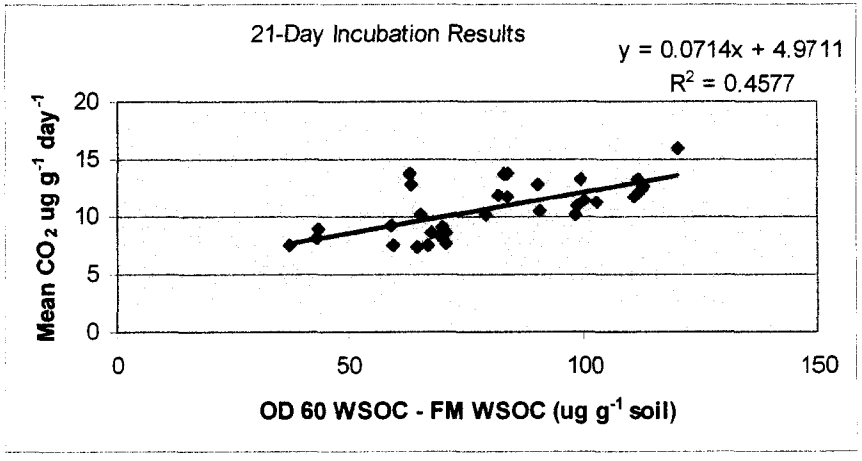

Fig. 2. Correlations of rate of CO_2 evolved (ug g^{-1} soil) per day with $WSOC_{OD}$ from soil oven-dried at 60° C (OD 60 WSOC) at 3 days (a) and 21 days (b). CO_2 evolution rate per day correlated with concentration of $WSOC_{OD} - WSOC_{FM}$ at 3 days (c) and 21 days (d). Note that the scales differ between 3-day (a,c) and 21-day (b,d) graphs.

III. Rhizoplane and Grass Crown Associated Soil Contribution to Total Water Soluble Organic Carbon in Surface Soils of Two Grasslands

Abstract

Distribution of soluble organic matter is heterogeneous in soils of native ecosystems and is composed of a small and ephemeral pool that becomes active after pulse precipitation events. Water soluble organic carbon (WSOC) measurements may be useful as indicators of change in total soil organic carbon levels. Root exudates and root decomposition products contribute heavily to WSOC concentrations in soil, and rhizosphere soil associated with the coarse root systems contain an important fraction of the total soil soluble C. A study was conducted to examine the relative contribution of rhizoplane soil to the total soluble C present in surface soils to 10 cm depth in two native grassland ecosystems. Roots were removed from field moist soil and immediately analyzed for concentration of WSOC and compared with WSOC measurements for bulk soil. Rhizoplane soil associated with coarse and fine roots accounted for approximately 28 % and 16 % of the total soluble C present in the 0-10 cm depth in Northern mixed-grass prairie (NMP) and shortgrass steppe (SGS) ecosystems, respectively. Concentration of WSOC in rhizoplane soil was one to two orders of magnitude higher than bulk soil. Concentration of WSOC in grass crown-associated soil were on average 4.5 and 3.8 fold higher than in bulk soil in the NMP and SGS, respectively. Differences in the contribution of rhizoplane soil to the total WSOC pool independent of root biomass indicated a clear difference between the two grasslands irrespective of inherent differences in root biomass. This emphasized the importance of not discarding roots from soil during processing unless reasonable estimates of rhizoplane WSOC have been

made. Measurement of total WSOC provided a clear indication of soil property differences corresponding to plant occupation of soil or lack thereof (plant interspaces).

Introduction

Organic matter (OM) distribution in grassland soils closely corresponds to proximity of recent and historic plant inputs, which arise primarily in the form of roots and litter deposition. Fibrous grass root systems produce soils high in soil organic matter (SOM), which represents about 90% of the total C in most temperate grassland ecosystems (Dormaar 1992, Burke et al. 1997, Reeder & Schuman 2002). Distribution of SOM is not uniform, either horizontally or vertically, in native rangeland soils (Yonker et al. 1988, Burke et al. 1998, 1999, Reeder et al. 2001, Reeder 2003). SOM consists of many components that vary in turnover rate (Parton et al 1988), including water soluble organic carbon (WSOC) (Gregorich et al. 2000). Soluble organic C represents one of the most labile fractions of SOM, which have turnover times ranging from days to months (Cook & Allan 1992, Burke et al. 1997, Reeder et al. 1998). Root exudates, sloughing and decomposition of root cells and litter leachates all contribute to soil soluble C (Dormaar 1988, Reeder et al. 2001, Qualls et al. 1991). Carbon (C) from dead root cells and exudates in the form of WSOC provide a readily-available source of energy for microbial growth and activity, and concentrations of WSOC in the soil are related to rates of biological decomposition and associated release of nutrients from SOM (Minchin & McNaughton 1984, Dormaar 1988, Cook & Allen 1992, Reeder et al. 2001, Kuzyakov 2002).

Almost two decades ago Ingham et al. (1985) speculated that herbage removal in range plant species would lead to distinct changes in microbial activities in the rhizosphere. Recent findings indicate that response of grasses to defoliation, a common occurrence in rangelands, in part consists of a release of labile root exudates (Guitian & Bardgett 2000, Hamilton & Frank 2002). Additionally, in soils a soluble state is a prerequisite for microbial uptake of organic compounds, since solid phase organic matter must undergo extra-cellular dissolution or hydrolysis before passing through the cell membrane (Marschner & Kalbitz 2003). Soluble organic matter plays a crucial role in the relationships among plants, total OM, soil microbial dynamics and resultant ecosystem function. Therefore, quantification of changes in labile fractions of SOM and how these changes relate to root biomass are important for understanding C storage and cycling in perennial grasslands.

Soluble organic C extracts from field moist soils ($WSOC_{FM}$) contain little C derived from microbial cells and may therefore be important in studies relating microbial biomass to concentrations of available nutrients (van Ginkel et al. 1994) because this fraction of soluble C represents a good indicator of root exudation and sloughing (Cheng et al. 1993, Cheng et al. 1996). WSOC concentration increases upon soil desiccation and consequential cell lysis, as protoplasm is released from soil microorganisms into the soil solution (Davidson et al 1987, DeLuca & Keeney 1994). Therefore, air-drying of the soil sample leads to a change in both the magnitude and origin of the soluble organic compounds.

Landscape position and soil texture influence soil properties such as C and N in natural grasslands (Schimel et al. 1985, Dodd & Lauenroth 1997). SOM content is

influenced by many factors, such as temperature and moisture, resulting in variations from micro-topographic to regional scales (Schimel et al. 1985, Burke et al. 1989, 1999). Like total SOM, WSOC may be influenced by topographic position (Garcia et al. 1997). Exposed surface soil (bare ground) tends to be warmer than plant occupied soil, which stimulates a faster turnover rate of the microbial population and increases decomposition of SOM (McGill et al. 1986). The presence or absence of a plant in a given microsite may be more closely related to soil resources than differences between plant species (Vinton & Burke 1995), and plant density can influence dynamics of labile SOM pools (Robles & Burke 1997). Both plant root biomass and SOM decrease when plant-occupied soil is compared with bare ground (Hook et al. 1991, 1994, Vinton & Burke 1995, Burke et al. 1999). The surface of soil occupied by crowns of grasses, such as *Bouteloua gracilis*, is 2-3 cm higher than adjacent bare ground microsites (Hook et al. 1991), and concentrations of WSOC may be expected to be higher in proximity to grass crown-associated soil. Plant species composition is also important because root distribution and decomposability both vary by species (Weaver 1958, Caldwell 1979, Dormaar 1992). Therefore, accurate measurements of soil properties from both bare ground and plant-occupied microsites among different soil types and topographic positions are important for characterizing root and soil dynamics at a landscape scale.

The pool of soluble carbon arising from root exudates or decomposition products from roots is transient in nature as a result of high lability (Sanchez & Bursey 2002). Soluble compounds that are either released by plant roots or are byproducts of root decomposition will occur in the highest concentration in proximity to the root of origin and decrease in concentration along a concentration gradient with increasing distance

away from the root surface, and as a result of microbial uptake, may decrease more rapidly than would be expected based on diffusion alone. Total C released through root exudates in *Bouteloua gracilis* was estimated to be 15% of net C fixation (Biondini et al. 1988). Together with other rhizodeposition products, released C accounts for as much as 40% of net C fixed for other species (Lynch & Whipps 1990, Coyne et al. 1995). Microbes effectively utilize labile exudates of *Bouteloua gracilis* because presence of microbes in the rhizosphere of this species results in lower levels of residual sugars in rhizosphere soil (Klien et al. 1988). Differences in microbial populations exist between bulk soil and rhizoplane soil (Rodriguez-Zaragoza & Garcia 1997). This may arise because plant induced variation in microbial biomass and activity result from variation in labile C inputs to soil (Groffman et al. 1996). A large amount of C present in the rhizosphere is not accounted for in budgets that fail to quantify root exudation and respiration (Cheng & Johnson 1998). Therefore, failure to include roots may lead to considerable underestimates of WSOC measurements in surface soils of grasslands where root densities are high.

This research effort was undertaken to quantify the contribution of various fractions of soil to the WSOC in surface soils and to relate these values to microtypic and landscape position of two perennial grassland ecosystems. Specific objectives were to: 1) quantify the fraction of WSOC in rhizoplane soil compared with bulk soil, 2) determine the amount of WSOC in the crown-associated soil fraction of dominant grassland species and 3) to relate these values to variations among different microsites and ecosystems.

Materials and Methods

Site Descriptions

Samples were collected from shortgrass steppe (SGS) and northern mixed-grass prairie (NMP) ecosystems. Two SGS pastures were sampled in May 2001 at the USDA-ARS Central Plains Experimental Range (CPER), located on the western side of the Pawnee National Grasslands, about 60 km northeast of Fort Collins, Colorado (40°49'N, 107°47'W). Dominated by the C_4 grass *Bouteloua gracilis,* [(H.B.K.) Lag. ex Griffiths], the area has been moderately grazed for the past 70 years, and has been described previously (Schimel 1985, Milchunas et al. 1989, Burke et al. 1999, Grant & Grant Chapter 2). Samples were collected from *Boutleoua gracilis* occupied spaces and plant interspaces (bare ground) from two soil types, which differed based upon topographic position. The soil on flat areas was an Olney sandy loam and on the north-facing slopes (2-5% slope) was a Cushman sandy loam. Both soil types are classified as fine-loamy, mixed, mesic Ustollic Haplargids (NRCS Soil Survey 1991).

The two NMP study areas sampled were located at the Radar Station range about 18 km southwest of Miles City, Montana (46°20'N, 105°50' W), which is part of the USDA-ARS Fort Keogh Livestock and Range Research Laboratory. Soil and root-rhizoplane data were collected in June 2001, while grass crown samples were collected in June 2002. The mixed-grass prairie plant community is characterized by co-dominant C_3 grasses such as needle-and-thread (*Stipa comata* Trin. and Rupr.) and western wheatgrass [*Pascopyrum smithii* (Rybd.) Love], as well as some C_4 grasses (*Bouteloua gracilis*), and has been described previously (Coupland 1992, Heithschmidt et al. 1995, Grant Chapter 2). Historically, the pastures were grazed at moderate intensities, with one of the two

pastures having been rested from grazing starting in 2000. Samples were collected from *Stipa comata*-occupied soil and bare ground, on both flat and north-facing (2-5% slope) landscape positions on Eapa silty loam soil, classified as a fine-loamy, mixed, frigid aridic Argiboroll (NRCS Soil Survey 2000).

Soil Collection

Surface soil cores (0-5, 5-10 cm x 3.18 cm diam.) from bare ground and grass-occupied soils were randomly collected with 3 replicates along 50 m transects. Soil surfaces from grass-occupied microsites are 2-3 cm higher than the bare ground spaces (Hook et al. 1991, Ihori et al. 1995), therefore grass crowns and associated soil were separated from the mineral soil during collection using a serrated knife. This allowed the same zero point to be used to correspond to the same horizontal layer of mineral soil consistently, whether under grass or bare ground (as described by Grant Chapter 2). In addition, separate collection of crowns and associated soil allowed this fraction to be analyzed separately and then compared to bulk mineral soil.

Field moist soil samples were processed by removing coarse roots and rhizoplane soil adhering to the roots with forceps and then passing the remaining bulk soil sample through a 2 mm screen. The < 2 mm fraction of soil, hereafter referred to as "bulk soil", was analyzed for soluble C and results are reported in Grant & Reeder, in prep. (Grant Chapter 2). A representative subsample of the bulk soil was oven dried at 105° C for determination of gravimetric water content. Crowns and associated soil were separated by passing the sample through a 2 mm screen. The < 2 mm fraction of the crown-associated soil (hereafter referred to as crown-soil) was analyzed for field moist water

soluble organic carbon ($WSOC_{FM}$) and air-dry WSOC ($WSOC_{AD}$) concentrations using a standard method (following the procedure of Davidson et al. (1987) with slight modifications) with 4 g of soil and 20 ml de-ionized water (5:1 ratio) placed in a 50 ml plastic vial. The suspension was shaken on a wrist arm shaker for 30 minutes and then placed on a centrifuge for 7 minutes at 5760 rpm. After centrifugation the supernatant was poured into a funnel lined with a 12.5 cm Whatman GF/A glass microfiber filter and then vacuum extracted through a 0.45 micron nylon acrodisc filter. A representative subsample of the crown-soil was oven dried at 105° C for determination of gravimetric water content.

Coarse root systems with their adhering rhizoplane soil were extracted using 30 milliliters of de-ionized H_2O per g field moist roots. Roots in water were gently shaken on a reciprocating shaker for 90 seconds to remove rhizoplane soluble C. Roots were not shaken for a longer period of time to minimize chances of release of soluble compounds from the roots during the shaking procedure. The solution was then passed through a glass microfiber filter and extracted following the same method previously described for extracting the crown-associated soil. Roots were recovered from the glass microfiber filter using forceps and dried at 60° C before weighing and ash correction (550° C) to obtain root biomass.

Soluble C analysis was performed using a Shimadzu TOC 5050A Total Organic Carbon Analyzer, which measured soluble total and inorganic C content (Shimadzu Instruments Inc., Columbia, MD). Total WSOC was obtained by subtraction.

An independent subset (n = 32) of processed soil samples from various depth increments was washed over a 0.147 mm screen to determine total root biomass and the

percentage of roots that was left in the soil after hand picking. Fine roots were collected, dried at 60° C, weighed and corrected for ash content. This was done to quantify the relationship between weight of roots picked by hand from soil during processing and the weight of roots remaining in the sample after removal of large roots.

Statistical Analyses

The GLM model procedure was used in SAS (1996 SAS Institute Inc.) for statistical analysis of variance (ANOVA). The experimental design consisted of a split-split plot with ecosystems representing the whole plot, north-facing and flat aspects representing the two subplots, and bare-ground and grass-occupied microsites representing the sub-subplots. Two replicate pastures were measured for each system. Three randomly selected locations (experimental units, EUs) were sampled within each subplot (50 m transect). The total number of observations was 48 (2 systems x 2 aspects x 2 microsites x 3 EUs x 2 replicate pastures), with 47 total degrees of freedom. Crown-associated soil comparisons between systems were performed by microsite (n = 24). Appropriate error terms were used in all comparisons and variance components were pooled whenever possible.

The full factorial design was used for analysis with main effects of system, aspect, and microsite and all appropriate interaction terms followed by backwards model selection to remove non-significant interaction terms. Significant interactions were left in the model and only comparisons identified *a priori* within the interaction were done using the appropriate p-values and comparisons of least squares estimates (LS Means). Statistical analysis initially considered the dependence of belowground variables

(Rhizoplane soil WSOC, Total WSOC, Belowground % from Rhizoplane and Total WSOC/SOC) on root biomass (continuous variable), and experimental treatments were considered as discrete independent variables for 0-5, 5-10 and 0-10 depths. This facilitated proper interpretation of belowground data so that differences between systems represented true differences between systems irrespective of inherent differences in root biomass. Crown-soil field moist WSOC ($WSOC_{FM}$) and air-dry WSOC ($WSOC_{AD}$) analyses were based only on grass-occupied soil. Percentages of $WSOC_{FM}$ in the entire plant-soil system were based on the 0-10 cm soil increment with crown-soil and soil from plant interspaces. Arithmetic means are reported with mean separations for least significant differences (LSD) based on LS means. Comparisons identified *a priori* were tested and differences are significant at the alpha = 0.05 level, unless otherwise noted.

Results

Rhizoplane Soil and Total $WSOC_{FM}$

In the 0-5 cm depth, $WSOC_{FM}$ in rhizoplane soil did not differ between the two ecosystems, although a system-by-microsite interaction occurred along with a dependence on root biomass (Table 1). The interaction revealed that mass of rhizoplane soil $WSOC_{FM}$ was higher in bare ground (0.33 g m^{-2}) than in grass-occupied (0.23 g m^{-2}) soil at NMP, while no differences between microsites were detected at SGS. Microsites did not differ (Table 2), but grassland systems did differ in the 5-10 cm depth and for the entire 0-10 cm soil increment (Table 1). A significant system-by-microsite interaction also appeared in the 0-10 cm depth, revealing that grass-occupied rhizoplane $WSOC_{FM}$

was similar for both systems, but bare ground rhizoplane $WSOC_{FM}$ was higher at NMP (0.48 g m^{-2}) than at SGS (0.28 g m^{-2}).

Rhizoplane soil $WSOC_{FM}$ accounted for a significant proportion of the total soil $WSOC_{FM}$ in both systems. The percentage of total $WSOC_{FM}$ from the rhizoplane soil differed between the shortgrass system (8.4%) and the mixed-grass system (14.1%) in the surface 10 cm of soil. The surface 5 cm accounted for this difference (Table 1). A significant microsite by system interaction occurred in the surface 5 cm, showing that bare ground (18.6%) had a greater percentage than grass-occupied soil at NMP (14.8%), while this difference was reversed at SGS with 7.3% for bare ground and 11.1% for grass-occupied soil. Systems differed in the 5-10 cm depth increment (Table 1). Surprisingly, rhizoplane $WSOC_{FM}$ as a percentage of total belowground $WSOC_{FM}$ was not dependent on root biomass for any depth.

Mean concentration of $WSOC_{FM}$ in bulk soil was 22.8 ug g^{-1} soil with a range from 12.7 to 55.1 ug g^{-1} at SGS. At NMP mean concentration of $WSOC_{FM}$ in bulk soil was 20.7 ug g^{-1} soil with a range from 13.6 to 42.5 ug g^{-1}. Oven dry root biomass of picked roots was highly correlated ($r^2 = 0.829$) with field moist root wt and accounted for 70% of the field moist weight. Assuming that the remainder of the field moist weight was all soil (not accounting for soil or root H_2O), a conservative estimate can be calculated for the concentration of $WSOC_{FM}$ in the rhizoplane soil. This analysis revealed that at SGS the rhizoplane soil mean concentration was 1883 ug $WSOC_{FM}$ g^{-1} soil with a range from 604 to 5373. Division of the concentration in rhizoplane soil by the concentration in bulk soil revealed that the concentration of $WSOC_{FM}$ on average 92 times higher in the rhizoplane soil than in bulk soil, with a range from 25 to 288 times as

high in the SGS. Mean concentration of rhizoplane soil at NMP was 803 ug g^{-1} soil with a range from 213 to 4759 ug g^{-1} soil. Concentration of $WSOC_{FM}$ in rhizoplane soil at NMP was on average 42 times higher than bulk soil with a range from 12 to 308 times higher than bulk soil.

Total belowground $WSOC_{FM}$ (bulk soil + rhizoplane) in the surface 10 cm showed a significant dependence on root biomass, though systems did not differ (p=.0650) (Table 1). However, in the surface 5 cm depth, total $WSOC_{FM}$ was dependent on system as well as root biomass. A microsite difference revealed that mass of total $WSOC_{FM}$ in bare ground soil (1.99 g m^{-2}) was greater at the p=.0561 level than grass-occupied soil (1.67 g m^{-2}) in the 0-5 cm depth. Total $WSOC_{FM}$ was dependent only on root biomass in the 5-10 cm increment (Table 1). While all total soil $WSOC_{FM}$ mass measurements were dependent upon root biomass, the percentage of total $WSOC_{FM}$ which was in the rhizoplane soil was not at all dependent on root biomass.

Total soil organic carbon (SOC) and total soil $WSOC_{FM}$ in the surface 10 cm were compared on a percentage basis ((WSOC/ SOC)*100). This value reflects the percentage of total soil organic matter (SOM) that may become soluble upon extraction and filtration. In the 0-10 cm depth this ratio was highly dependent on total soil C and on root biomass. The percentage that was soluble was dependent on the system for the surface 10 cm, and in the surface 5 cm alone (Table 1). Root biomass also significantly influenced this ratio in the 0-5 and 5-10 cm depths (Table 1). In the 5-10 cm depth increment value was dependent on total soil C with a significant interaction between system and microsite, revealing that grass-occupied soil was similar for both systems, but the percentage was higher for bare ground soil in NMP (0.34 %) than in SGS (0.26 %).

Coarse and Fine Roots

The analysis of picked roots compared to fine roots left after picking showed that on average for all microsites and depth increments only 52 % of the total root biomass was removed from the soil samples with forceps during processing. If we consider that large roots and fine roots contribute equal amounts of $WSOC_{FM}$ per unit root biomass we have a conservative estimate of the contribution of fine roots since there is undoubtedly a greater volume and surface area per gram of fine roots than coarse roots. Using this conservative estimate allows quantification of the approximate contribution of $WSOC_{FM}$ that was associated with rhizoplane soil, from coarse and fine roots together. This calculation resulted in an average of 28 % with a range from 6 to 71 % of the total $WSOC_{FM}$ at NMP and an average of 16 % with a range from 6 to 42 % for SGS. Therefore, a very significant proportion of the total $WSOC_{FM}$ in the surface soil is associated with roots.

$WSOC_{FM}$ and $WSOC_{AD}$ in Soil from Crown Locations

Percent gravimetric soil H_2O ($g\ g^{-1}$) in grass-crown associated soil was very low and similar between the two systems. Soil H_2O was 2.8 and 3.0 % in NMP and SGS, respectively. The weight of crown-associated soil was similar for the two systems, with 12.7 kg m^{-2} in NMP and 14.6 kg m^{-2} in SGS. However, a system by aspect interaction occurred revealing that flat areas at SGS (15.6 kg m^{-2}) had greater mass of crown-associated soil than similar areas at NMP (10.8 kg m^{-2}), though north-facing aspects were similar. Concentration of $WSOC_{FM}$ in crown associated soil was not different between

systems, with an average concentration of 88.2 ug g^{-1} soil in NMP and 78.9 ug g^{-1} in SGS. Aspect had a significant influence on concentration because flat areas (102 ug g^{-1} soil) was higher than north-facing slopes (64.9 ug g^{-1}). Systems did not differ, but a system-by-aspect interaction occurred showing that flat areas at NMP had higher concentrations than north-facing aspects at NMP or either landscape position at SGS. A comparison of concentration of $WSOC_{FM}$ in crown associated soil to that of grass-occupied bulk soil revealed that systems were similar in this regard, with concentrations 4.5 and 3.8 fold higher than bulk soil in NMP and SGS, respectively. However, flat areas (5.4 times greater) were higher than north-facing slopes (2.9 times greater). Mass of $WSOC_{FM}$ from crown-associated soil was 1.11 (g m^{-2}) at NMP and 1.15 (g m^{-2}) at SGS and systems were similar.

Concentration of $WSOC_{AD}$ was similar between the two systems and highly variable. Mean concentration in NMP was 148.3 ug g^{-1} soil, with a range from 61.4 to 265.6 ug g^{-1}, and at SGS was 124.4 ug g^{-1} soil, with a range from 65.6 to 210.5 ug g^{-1}. Mass of $WSOC_{AD}$ also did not differ between systems with 1.88 and 1.81 (g m^{-2}) at NMP and SGS, respectively.

Contribution of Different $WSOC_{FM}$ Fractions

The total $WSOC_{FM}$ in the plant-soil system, including crown and root associated soil along with bulk soil (0-10 cm), was evaluated to determine what percent of the total was attributable to each different fraction (Table 3). Within grass-occupied soil, the contribution from bulk soil was similar between the systems, though SGS was greater than NMP in bare ground microtypes. The average contribution from the bulk soil was

greater in bare areas than grass-occupied microsites (Table 3), which is at least partially attributable to a lack of crown-associated soil. The contribution from rhizoplane soil was greater for bare than grass-occupied microtypes on average for NMP. The percentage from rhizoplane soil also was higher for NMP than SGS for both microtypes (Table 3). Means from both microsites combined were likely artificially skewed because bare-ground was assumed to account for 50% of the ground surface area in these systems. However, this does highlight the importance of quantification of the proportion of the total plant community which is actually non-plant occupied soil surface. Overall total mass of $WSOC_{FM}$, including crown and root associated soil along with bulk soil (0-10 cm) reveals that the two systems are actually very similar for this soil property with a total of 3.79 g m^{-2} and 3.99 g m^{-2} in NMP and SGS, respectively ($p = 0.4199$). However, total mass of $WSOC_{FM}$ in the plant-soil system differs markedly between bare-ground (3.39 g m^{-2}) and grass-occupied (4.39 g m^{-2}) microsites ($p = 0.0002$).

Discussion

Rhizoplane soil $WSOC_{FM}$ was the one variable that noticeably differed between systems in the surface 10 cm of soil. Interestingly the mass of rhizoplane soil $WOSC_{FM}$ was higher in NMP than SGS, in opposition to the trend of $WSOC_{FM}$ in bulk soil. As a result, an additive measurement resulted in a different conclusion than would be reached when considering either bulk soil or rhizoplane soil alone. Characterization of WSOC in the bulk soil without inclusion of rhizoplane WSOC showed that the two systems were different in mass of WSOC, however when the rhizoplane fraction was included, the systems were similar at the alpha = 0.05 level, leading to a slightly different interpretation

of the results. This emphasizes the importance of quantifying roots from soil during processing so that reasonable estimates of rhizoplane WSOC can be made for systems in which rhizoplane WSOC accounts for a significant fraction of overall WSOC. A failure to include roots leads to considerable underestimation of WSOC as suggested by Cheng & Johnson (1998).

Bulk soil WSOC was related to a number of variables in the surface 5 cm including root biomass and total C. This indicated that the origin of the compounds extracted from the soil were soluble rhizodeposits and decomposition products of both roots and SOM, which supplied energy to the microbial community (Kuzyakov 2002, Reeder et al. 2001). Therefore, WSOC from a field moist soil does not represent the root exudates alone, but a variety of compounds that vary in origin and degree of recalcitrance. Microbial degradation of OM in the rhizoplane also contributes to WSOC, but the fraction associated with this process compared to exudation is unknown. When bulk soil WSOC was considered alone, the two systems were different for the 0-5 and 0-10 cm depths at the alpha = 0.05 level, with SGS having more WSOC than NMP (Grant Chapter 2).

Concentrations of $WSOC_{FM}$ were substantially higher in rhizoplane soil than bulk soil. High WSOC concentrations in the rhizoplane soil indicated that soluble OM resulted from processes that occurred in proximity to or at the root surface. This supported the notion that $WSOC_{FM}$ arises primarily from exudation of these grass species. In water-limited ecosystems, belowground biochemical and biological processes regulate production when soil moisture is adequate and the distribution of organic matter is influenced by plant species and cover (Noy-Meir 1973, Lauenroth & Coffin 1992,

Garcia et al. 1994). Dissolved organic matter (DOM) that infiltrates into and moves through soils after precipitation events is included within measurements $WSOC_{FM}$ (Chantigny 2003). In contrast to measurements of *in situ* DOM that would be highly variable in these pulse driven semiarid systems, $WSOC_{FM}$ levels may fluctuate less and therefore act as a better indicator of ecosystem response to change. WSOC from a semiarid environment represents potentially soluble OM that only occurs ephemerally *in situ* after pulse precipitation events, because the soil of semi-arid ecosystems is rarely at field capacity and therefore rarely has soluble OM in equilibrium with total OM. Between pulse precipitation events at extremely low soil moisture potentials WSOC becomes very small in the absence of soil solution. At that point the C in the soluble fraction becomes adsorbed to soil colloidal surfaces where it becomes either reversibly or irreversibly bound.

Soil analysis for soluble C using standard soil processing techniques underestimates total soil soluble C because the soluble C associated with the root system is unaccounted for. Measurements that use only bulk soil maybe as much as 14 % lower than true WSOC levels present in the 0-10 cm depth. In addition, differences between grassland systems in the contribution from rhizoplane soil WSOC may cause misleading conclusions about comparisons between systems if roots are not evaluated. The relative contribution of rhizoplane soil to the total soil C pool may vary depending on soil type, soil H_2O content, root density and plant species or plant community type. Estimated $WSOC_{FM}$ associated with coarse roots and fine roots together accounted for a substantial portion of total belowground $WSOC_{FM}$.

Microsite differences may be attributable to warmer soil temperatures and thus, more microbial decay of SOM in bare areas (McGill et al. 1986). The higher OC:N ratio associated with plant occupancy of a microsite indicates that more OC is being deposited at the microsite as the plant grows (Grant Chapter 2). When a plant dies, input rates of OM decline and decomposition rates increase causing bare ground to differ in biogeochemical dynamics from grass-occupied soil. Though differences in microsite were not significant for either bulk or rhizoplane WSOC alone, adding the two values together to get total WSOC revealed that bare ground has higher levels of WSOC than grass-occupied soil in the surface 5 cm. This difference would not be revealed without the additive analysis of roots and bulk soil together.

Crown-associated soil $WSOC_{FM}$ was similar between the two grasslands. However, the concentration in soil from the crown areas was higher for flat areas than north-facing slopes, which agrees with findings by Garcia et al. (1997) that WSOC may be influenced by topographic position like total SOM. Sloped landscape positions are more susceptible to run-off dynamics, which may explain why concentrations were lower there than in flat areas. This would constitute redistribution of WSOC, with grass-crowns acting as a source and A-horizon soils acting as a sink for WSOC. In turn, higher concentrations of WSOC in the 0-5 cm depth than the 5-10 cm depth and in the surface 10 cm depth (A-horizon) than in B-horizons show that surface soils act as a source of WSOC to subsurface horizons, which act as a sink. The process of soluble organic matter redistribution in grasslands is probably similar in many respects to the dynamics of litter throughfall acting as a source of soluble OM in forest soils (Neff & Asner 2001). The two semiarid grasslands evaluated in this study are pulse-driven systems, which have

infrequent precipitation events (Coupland 1992, Lauenroth & Milchunas 1992). Each significant precipitation event which results in water movement through litter leads to a flux of soluble OM (Neff & Asner 2001). Loss of labile nutrient-rich organics from surface horizons via leaching is important in controlling nutrient distribution in soil profiles (Schoenau & Bettany 1987). Therefore, soluble compounds released either by plant roots or as byproducts of root and plant-debris decomposition, will occur in the highest concentration in proximity to the source of origin and decrease in concentration along a concentration gradient with increasing distance away from the source. Inclusion of these sources is important for understanding soluble OM dynamics.

Higher quantities of WSOC in air-dry soil than field moist soil reflect the increase that occurs from release of intracellular contents upon microbial cell lysis, changing both the magnitude and origin of the WSOC. This high level of increase indicates that the grass-crown-associated soil represented a medium of high microbial activity, probably as a result of the proximity to the grass crown, which provided a relatively constant substrate source like plant litter and exudates.

Findings by Hamilton and Frank (2001) showed that release of exudates provided a readily available C source that stimulates N-mineralization in the rhizosphere, resulting in a positive feedback to the plant in the form of plant-available inorganic N. Higher levels of $WSOC_{FM}$ in bare microtypes in NMP may be a response to high plant demand for inorganic nitrogen in this system. Microbial activity in the top 10 cm may be more limited by C availability in SGS and by nitrogen availability in NMP (Grant Chapter 2). If mineralization rates are higher in bare ground microsites, then preferential exudation of roots occupying these microsites would be advantageous for plants growing in proximity.

However, if quantities of bare ground get too large the total amount of labile and total plant C inputs is likely to decrease, which may result in less microbial activity and translate to decreased ecosystem function.

Quantification of $WSOC_{FM}$ in surface soils after removal of grass crowns and roots from soil samples will result in considerable underestimates of soluble OM. When all of these potential sources of soluble organic matter are quantified together the similarities between the NMP and SGS ecosystems become apparent, and the differences between bare ground and grass-occupied soil are revealed. Since differences between microsites are more substantial than differences between ecosystems, it is clear that determinations of bare-ground abundance are important for making landscape scale estimate of WSOC pools. In this sense our results agree strongly with findings by Vinton and Burke (1995) that quantification of plant cover patterns is critical for estimation of ecosystem function at large-scales in semi-arid grasslands because local plant-induced patterns in soil properties differ markedly from those of bare soil.

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Table 1. Means for total SOC, $WSOC_{FM}$ from bulk soil and rhizoplane soil, percentage from rhizoplane belowground (0-10 cm) and percentage of SOC that is soluble of Northern mixed prairie (NMP) and Shortgrass steppe (SGS). **Significant system-by-microsite interactions occurred for this variable in the 0-5 and 0-10 cm depth increments.

Depth	Root Biomass		SOC		Bulk $WSOC_{FM}$		**Rhizoplane - $WSOC_{FM}$		Total $WSOC_{FM}$		Belowground % from rhizoplane		Total $WSOC_{FM}$ / SOC (x100)	
	($g\ m^{-2}$)		($g\ m^{-2}$)		($g\ m^{-2}$)		($g\ m^{-2}$)		($g\ m^{-2}$)		(%)		(%)	
cm	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS
0 – 5	*440	248	*678	564	1.40	1.80*	0.28 †	0.18	1.68	1.98* †	*16.7	9.2	0.25	0.35* †
5 – 10	218	145	*542	496	1.39	1.33	*0.18	0.11	1.57	1.44 †	*11.6	7.6	0.30	0.31 †
0 - 10	*658	393	*1220	1060	2.79	3.13*	*0.46 †	0.29	3.25	3.42 †	*14.1	8.4	0.28	0.33* †

Note: *Indicates systems were significantly different within a depth increment; †Indicates comparison is dependent on root biomass (LSD, alpha = 0.05).

Table 2. Means for total SOC, $WSOC_{FM}$ from Bulk Soil and Rhizoplane Soil, Percentage from Rhizoplane Belowground (0-10 cm) and percentage of total SOC that was soluble of bare ground (Bare) and grass-occupied (Grass) microsites. *A significant system-by-microsite interaction occurred for this variable in the 0-5. **Significant system-by-microsite interactions occurred for this variable in the 0-5 and 0-10 cm depth increments.

Depth	SOC		Bulk $WSOC_{FM}$		**Rhizoplane - $WSOC_{FM}$		Total $WSOC_{FM}$		*Belowground % from rhizoplane		Total $WSOC_{FM}$ / SOC (x100)	
(cm)	($g\ m^{-2}$)		($g\ m^{-2}$)		($g\ m^{-2}$)		($g\ m^{-2}$)		(%)		(%)	
	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass
0 – 5	619	623	1.75	1.45	.25	.21	1.99	1.66	13.0	13.0	.32	.28
5 – 10	484	554	1.33	1.39	.13	.16	1.46	1.55	9.0	10.2	.32	.31
0 - 10	1103	1177	3.08	2.84	.38	.37	3.46	3.21	11.0	11.6	.32	.29

Table 3. Percent of Total $WSOC_{FM}$ in the plant-soil system in the surface 10 cm of soil of grass-occupied (Grass) and bare ground (Bare) microsites and mean values by system for Northern mixed prairie (NMP) and Shortgrass steppe (SGS).

	Grass			Bare			Mean		
Soil fraction	NMP	SGS	Ave	NMP	SGS	Ave	NMP	SGS	Ave
Bulk soil	65.5	67.4	66.5 a	85.3	92.8*	89.0 b	75.4	80.1*	77.7
Rhizoplane	10.4*a	7.3	8.8 a	14.7*b	7.2	11.0 b	12.5*	7.2	9.9
Crown	24.1	25.3	24.7	-	-	-	12.1	12.7	12.4

Note: *Indicates systems are significantly different within the given microsite; different letters indicate that bare and grass microsites within a system differed (LSD, alpha = 0.05).

IV. Response of Soil and Plant Variables to Differences in Microtopography and Rest from Grazing in a Northern Mixed-Grass Prairie

Abstract

While aboveground changes in relative plant species and bare ground abundance are commonly used to detect changes resulting from changes in grazing management, quantifiable belowground indicators are largely unknown for semi-arid rangelands. Continuous moderate grazing, along with two different lengths of rest from grazing treatments, were used to examine above- and below-ground ecosystem responses to a change in management. The influence of microtopographic position was also measured to evaluate differences between grass-occupied soil and bare ground microsites in a Northern mixed-grass prairie plant community. Bare ground microsites had lower root biomass in surface soils and higher temperatures on the soil surface and at 5 cm depth than grass-occupied microsites. Total pools of carbon (C) and nitrogen (N) were relatively unresponsive to changes in management, but did respond to year to year variations in precipitation. Water soluble organic carbon (WSOC) represents a pool of labile soil C which may be a useful indicator of changes in the nutrient cycling integrity associated with concurrent changes in plant species composition and bare ground abundance. WSOC concentrations in the wettest year of sampling (2003) indicated that rest from grazing for 4 years was similar to rest from grazing for 11 years and both differed from the continuously grazed treatment. These results suggested that recovery from continuous grazing could occur rapidly, and rates of recovery were likely to be dependent on precipitation levels.

Introduction

The goal of rangeland ecosystem management is to maintain or restore the health and sustainability of the ecosystem while supporting sustainable economies and communities (McGinty 1995). However, efforts to develop sustainable management systems that avoid irreversible damage and desertification of rangelands are restricted by the paucity of quantifiable indicators capable of detecting changes in ecosystem processes and function before a threshold of change is crossed to a less desirable state (Weltz et al. 2003). Quantifiable indicators of changes in aboveground ecosystem structure in response to changes in management have been developed, such as measuring changes in plant community composition and abundance of bare ground (Kepner et al. 1993, Bedell & Buckhouse 1994, West et al. 1994, Heitschmidt et al. 1999, Pellant et al. 2000), changes in litter cover or plant functional groups (Pellant et al. 2000), or changes in canopy cover, plant frequency, density and biomass by species (Kepner et al. 1993, Bedell & Buckhouse 1994, Heitschmidt et al. 1995). However, indicators of belowground ecosystem response to change in management are largely unknown for semi-natural rangelands. The National Research Council (1994) recognized the fundamental importance of nutrient cycling to ecosystem health, and recommended that indicators that evaluate the integrity of nutrient cycles be included in assessments of rangeland health or response to change in management. They suggested that the best indicator of rangeland nutrient cycling integrity is an assessment of changes in the spatial and temporal distributions of soil nutrients.

Semiarid rangelands are generally limited by scarcity of water resources (Noy-Meir 1973). Moisture in surface soil generally fluctuates as it increases after

precipitation and then decreases rapidly with high evaporative loss (McAuliffe 2003). In water limited systems, the distribution of organic matter is influenced by plant species cover, and belowground biochemical and biological processes that regulate production when soil moisture is adequate (Noy-Meir 1973, Lauenroth & Coffin 1992, Garcia et al. 1994). Soil organic matter (SOM) is the primary source of nutrients for plant growth and is the largest reservoir of carbon (C) and nitrogen (N) in rangeland ecosystems (Follett 2001). SOM content is influenced by many factors, such as moisture and temperature, resulting in variations from micro-topographic to regional scales (Burke et al. 1989, 1998, Schimel et al. 1985). In general, livestock grazing does not disturb the soil to the same extent as tillage, but it may influence soil C and other nutrients (Frank et al. 1995).

Belowground indicators of the response of perennial plant communities to management will differ to some degree from indicators used to detect changes in annual cropping systems where mixing of the surface soil by tillage alters soil properties, such as bulk density and infiltration, and may alter soil texture and nutrient supply (Doran & Parkin 1994). Response to grazing management in perennial grasslands may be quantified through changes in root biomass (Holland & Detling 1990, Holland et al. 1996, McNaughton et al. 1998), labile pools of C and N (Jezile 2001, Reeder et al. 2004), acceleration of the rate of N cycling (Bardgett et al. 1998, Frank & Evans 1997, McNaughton et al. 1997), and possible grazing-induced changes in root exudation (Bardgett et al. 1998). Grazing-induced increases in soil biological activity may feedback to the plants by stimulating net N mineralization, thus increasing N availability for plant uptake (Guitian & Bardgett 2000, Hamilton & Frank 2001). Alternatively, increased transformation of N from defecation of grazing animals could result in an overall net loss

of N from the ecosystem via NO_3 leaching, NH_3 volatilization, and denitrification (Frank & Evans 1997).

Indicators of ecosystem change may be useful in a state-and-transition model context. These indicators could be especially useful if they can be used to detect changes in the state of a system as it is in transition before crossing a threshold to another potentially less desirable state (Friedel 1991), which may require significant resource inputs to reverse the trend. Aboveground and belowground responses to change are likely to be linked because the components are implicitly dependent on each other, since plants provide a carbon source for the soil microbial community, which in turn decomposes organic matter and releases nutrients for plant growth (Porazinska et al. 2003). For example, belowground indicators including changes in water soluble organic carbon (WSOC) have been linked to declines in plant cover (Garcia et al. 2002, Jezile 2001). This may result from the fact that plant roots and root exudates contribute to soil WSOC (Dormaar 1988, Reeder et al. 2001). Soil microorganisms utilize dead root cells and root exudates that provide a carbon rich food source (Minchin & McNaughton 1984, McGill et al. 1986, Dormaar 1988, Lynch & Whipps 1990, Boyer & Groffman 1996). Specifically, exudates from important cool- (C_3) and warm-season (C_4) rangeland grasses provide a substrate for microbes (Klein et al. 1988, Biondini et al. 1988). Changes in soil parameters such as labile organic matter may be useful as early indicators of soil ecological stress in some systems (Dick 1997, Garcia et al. 2002). Therefore, changes in pools of labile C and N that can be linked to deterioration of ecosystem function may be useful in rangeland systems as part of rangeland monitoring programs.

We initiated a study to examine the influence of different periods of rest from grazing on plant and soil parameters over a three year period in Northern mixed-grass prairie rangeland. Fine-scale measurements were made at the microsite level to make better landscape-scale estimates of system response to change in grazing management. The objectives of the study were 1) to measure the response of different variables to rest from grazing, including: (a) aboveground plant community composition and bare ground abundance, (b) belowground plant biomass and C and N content, and (c) labile pools of C and N, including water-soluble organic C, and inorganic N (NH_4 and NO_3) contents; 2) to determine how these variables were related to one another and what differences exist among these variables for bare ground and grass-occupied microsites; and 3) to determine whether changes in belowground variables could serve as sensitive indicators of changes in above-ground plant community variables.

Materials and Methods

Site Description

Soil samples were collected from a semi-arid Northern mixed-grass prairie plant community. The site was located at the USDA-ARS Fort Keogh Livestock and Range Research Laboratory, about 18 km southwest of Miles City, Montana (46°20'N, 105°50' W). The soil type at the research site was an Eapa silty loam (fine-loamy, mixed, frigid Aridic Argiboroll) with an average A-horizon thickness of 8 cm (NRCS Soil Survey 2000). Mixed-grass prairie plant communities consist of a mixture of shortgrass and mid-grass species (Coupland 1992). The plant community at the research site was dominated

by cool-season (C_3) grasses including important species, *Stipa comata, Pascopyrum smithii,* and other co-dominants.

Historically, the area has been grazed at heavy to moderate intensities and the Eapa loam soil site has been described by others (Heitschmidt et al. 1995, Grings et al. 1996). Grazing treatments consisted of continuous moderate grazing, rest from cattle grazing since 2000 and rest from cattle grazing since 1993. For each grazing treatment samples were collected from two blocks consisting of flat and slightly north-facing portions of the site. A 50-m transect was established on each of the landscape positions within each treatment. Cores were collected from 3 random locations per block. Rest-from-grazing treatments were not replicated in space resulting in data that consisted of pseudoreplicates for the grazing treatments.

Sample Collection

Surface soil cores (0-5, 5-10 cm x 3.18 cm diam.) were collected in September 2001 and June 2002 and 2003 using a step probe. Cores were collected from *Stipa comata*-occupied soil in addition to plant interspaces (bare ground). Grass crowns were removed from the top of each core using a serrated knife and analyzed separately to make sure that comparisons between grass-occupied and bare ground soils were based on the exact same horizontal depth increment. Cores were separated into 0-5 and 5-10 cm depth increments. Extremely low soil moisture levels in 2001 and 2002 caused most plants to senesce by the time of collection. Plants were actively growing at the time of sample collection in 2003 since soil moisture conditions were more favorable than in the two previous years.

Ocular cover estimates for bare ground and litter abundance as well as plant foliar cover were done using a 0.25 m^2 frame (50 x 50 cm) with a method made popular by Daubenmire (1959). Only exposed mineral soil was considered to be bare ground; soil underneath a plant canopy or within a crown was not considered to be effective bare ground. Plant species were grouped together by functional type including: cool-season (C_3) grasses, warm-season (C_4) grasses, C_3 *Carex* species, forbs, shrubs, cacti, and lichen/moss. All cover measurements were made by the same person over the duration of the study to avoid any subjective differences between observations. No baseline cover data were collected prior to the implementation of experimental grazing treatments.

Surface soil cores were collected in June 2003 as they were in 2001 and 2002, except that only the 0-5 cm depth increment was analyzed in 2003. This was done because previous analyses revealed few differences between grazing treatments in the 5-10 cm depth increment. Soil NH_4^+, NO_3^- and root biomass data were not collected for samples taken in 2003. Soil temperature data were collected in 2002 using a Hanna Pronto Plus 2-in-1 infrared (IR) and probe digital thermometer* with an accuracy of $\pm 1^o$ C. IR was used for measuring surface temperatures at a height of 15 cm above the soil surface with a 3-to-1 distance to spot ratio, yielding a temperature value for a 5 cm diameter area on the soil surface. The probe was used to measure soil temperature at 5 cm and 10 cm below the soil surface. Temperatures were measured in both *Stipa comata*-occupied soil and bare ground for all three experimental treatments.

Sample Processing and Analyses

Soil samples were placed in coolers immediately after collection and kept

refrigerated (4° C) until processed. Field-moist samples were analyzed for determination of gravimetric water content of each soil sample (g g^{-1}). Samples were processed by removing visible coarse roots with forceps and passing the sample through a 2 mm screen. The less than 2 mm field moist soil was sub-sampled for analysis of field-moist water soluble organic C ($WSOC_{FM}$); sub-samples of field-moist soils were dried at 60° C for oven-dry water soluble organic C ($WSOC_{OD}$) determinations. The remaining soil was air-dried and stored in plastic bags at room temperature for other analyses.

Analysis for WSOC concentration followed the procedure of Davidson et al. (1987) with slight modifications. Extractions consisted of 8 g of soil with 40 ml of de-ionized water (5:1 ratio, rather than the 2:1 ratio of Davidson et al. 1987) placed in a 50 ml plastic vial. The soil solution was shaken on a wrist-arm shaker for 30 minutes and then centrifuged for 7 minutes (rather than 5 minutes) at 5760 rpm. After centrifugation the supernatant was poured into a funnel lined with a 12.5 cm Whatman GF/A glass microfiber filter. A vacuum extractor was then used to filter the solution through a 0.45 micron nylon acrodisc filter. Extracts were then frozen, subsequently thawed, and mixed prior to soluble C analysis, which was performed using a Shimadzu TOC 5050A Total Organic Carbon Analyzer for samples from 2001 and 2002. The instrument measured total and inorganic water soluble C content and soluble organic carbon was obtained by subtraction. Extracts of samples collected in 2003 were analyzed on a Shimadzu TOC-V_{CPH} (Shimadzu Instruments, Inc. Columbia, MD).

Total C and N were determined on oven-dry (60° C) powder-ground soil samples with a Carlo Erba NA 1500 automatic carbon-nitrogen analyzer (Haake Buckler Instruments Inc., Saddle Brook N.J.), while inorganic C was measured by a modified

pressure-calcimeter method (Sherrod et al. 2002). Inorganic N (NH_4^+ and NO_3^-) concentrations were determined using 1 N KCl with a 10:1 extraction ratio (air-dry soil). NH_4^+ and NO_3^- extracts were measured with a Lachat Quikchem FIA+ 8000 Series Flow Injection Autoanalyzer (Quikchem, division of Lachat Chemicals, Mequon, WI).

Statistical Analyses

The MIXED model procedure was used in SAS (1996 SAS Institute Inc.) for a repeated measures analysis of variance (ANOVA). Repeated measures analyses were performed with two different covariance matrix types, including compound symmetry (CS) and first-order autoregressive (AR 1). Compound symmetry was determined to be the best variance-covariance matrix; reported differences are therefore based on repeated measures analysis with compound symmetry. The experimental design consisted of a split-split plot, with north-facing and flat aspects representing the two subplots, and bare ground and grass-occupied microsites representing the sub-subplots. Three randomly selected locations were sampled within each subplot. For soil variables the total number of observations was 36 (3 experimental treatments x 2 aspects x 2 microsites x 3 EUs), with 35 total degrees of freedom. For plant cover estimates ten randomly located replicate frames (0.25 m^2) were sampled per subplot. The error term degrees of freedom were calculated using the Satterthwaite method (DDFM = SATTERTH).

The full factorial design was used for analysis with main effects of date, treatment, aspect, and microsite and all appropriate interaction terms followed by backwards model selection to remove non-significant interaction terms. Significant interactions were left in the model. Only comparisons identified *a priori* within the

interactions were interpreted using the appropriate p-values (comparisons of LS Means). Comparisons between treatments were made by year when strong date effects occurred in the model. Arithmetic means are reported with differences based on least significant differences and all reported differences are significant at the alpha = 0.05 level.

Results

Most cover variables (litter, bare ground, total plant cover) showed strong treatment-by-date interactions. Therefore, comparisons between treatments were made by collection date (Table 1). Bare ground abundance was greater and litter abundance was lower in the continuously grazed treatment than the rest since 1993 treatment for all three sampling dates. Cool-season graminaceous plants (cool-season grasses + *Carex* spp.) had lower levels of cover in the continuously grazed treatment than the two rest treatments for all sampling dates (Table 1). Cool-season grasses alone showed the same response as cool-season grasses + *Carex* species, with lower levels in the grazed treatment than the two rest from grazing treatments, which had similar values. Warm-season (C_4) grasses showed the opposite response with greater abundance in the grazed treatment (22.5 %) than in the rest-since-2000 treatment (17.1 %) and the rest-since-1993 treatment (8.8 %).

Soil moisture, total soil C and total soil N were influenced by collection date, but the main effects of experimental treatment were not significant (Table 2). However, a treatment-by-microsite interaction occurred for total soil C and N (Table 3). A microsite-by-year interaction occurred for soil moisture revealing that bare ground (4.7 %) had

lower soil moisture than grass-occupied soil (5.4 %) in 2002, while microsites did not differ in 2001 or 2003.

Root C and N did not differ between grazing or rest treatments, but did differ between years (Table 2). Root N was influenced by microsite with higher levels in bare ground (0.64 %) than grass-occupied (0.56 %) microsites. The C-to-N ratio of roots was influenced by grazing treatment, revealing that the rest from grazing since 2000 treatment (40) had higher values than the rest since 1993 treatment (35) or the continuously grazed treatment (34), which were similar (treatment data not shown in table). Root biomass (g m^{-2}) was not influenced by treatment, but was influenced by main effects of date and microsite (Table 4). Bare ground microsites had less root biomass than grass-occupied sites in both the 0-5 and 5-10 cm depth increments.

Both NH_4^+ and NO_3^- along with total inorganic nitrogen (NH_4^+ and NO_3^-) were strongly influenced by collection date for both the 0-5 and 5-10 cm depth increments (Table 5). Grazing treatment also influenced total inorganic N, with the majority of the difference arising from differences in NH_4^+. In the 0-5 cm depth increment the rest since 2000 treatment had lower levels of inorganic N (4.5 ug g^{-1} soil) than the continuously grazed (5.0 ug g^{-1} soil) and rest since 1993 (5.2 ug g^{-1} soil) treatments, which were similar.

Water soluble organic carbon from field-moist ($WSOC_{FM}$) and oven-dry (60° C) soils ($WSOC_{OD}$) were influenced primarily by collection date (Table 5). Both variables had the lowest values in the year when collection occurred with favorable soil moisture content (2003). Differences between $WSOC_{OD}$ and $WSOC_{FM}$ and the $WSOC_{OD}$ to $WSOC_{FM}$ ratio were influenced by the main effect of date as well as a treatment-by-date

interaction (Table 6). For both of these variables and $WSOC_{OD}$ the grazed treatment had lower values than the two rest from grazing treatments in 2003 (Table 6).

WSOC was considered as a fraction of total soil C (WSOC/Total C) x100)) and analyzed separately (Table 7). This analysis revealed that no significant interactions occurred for WSOC as a percentage of total soil C. Main effects of date and microsite were significant for both $WSOC_{FM}$ and $WSOC_{OD}$, with bare ground having lower levels of WSOC than grass-occupied soil. Grazing treatment differences were not significant for $WSOC_{FM}$, but $WSOC_{OD}$ levels were greater for the rest since 2000 treatment than the other two treatments (Table 7).

C and N concentration of grass crowns was strongly influenced by collection date with the highest values occurring in 2001 (data not shown). A treatment-by-date interaction for both C and N occurred for the < 2 mm fraction of crown-associated soil. This interaction revealed that grazing treatments did not differ from one another in 2001 and 2002, but in 2003 C and N concentrations were higher in the rest since 1993 treatment than the other two treatments, which were similar.

Soil temperature (^{o} C) data were measured at the time of sample collection in 2002. Temperatures at 10 cm were not influenced by microtypic conditions at all, but the rest since 1993 treatment (24.7 ^{o}) had lower temperatures than the rest since 2000 treatment (26.6 ^{o}) and the grazed treatment (27.9 ^{o}), which were similar. At the 5 cm depth, microsite conditions affected temperatures; bare ground (32.7 ^{o}) had higher temperatures than grass-occupied soil (30.6 ^{o}). Treatment influenced temperature at 5 cm as well. The rest since 1993 treatment (29.9 ^{o}) had lower temperatures than the rest since 2000 treatment (32.1 ^{o}) and the grazed treatment (32.9 ^{o}), which were similar. Soil

surface temperatures were instantaneously affected by cloud cover at the time of sampling. Therefore, only differences between microsite pairs were analyzed (bare ground vs. grass-occupied) and experimental treatments were not compared for this variable. Surface soil temperatures were very strongly influenced by microtypic conditions ($p < 0.0001$) with bare ground temperatures (42.6 °) which were much higher than grass-occupied soil temperatures (31.6 °). Aspect did not consistently influence soil temperature or any other response variable.

Precipitation data were examined because soil water is such an important driver for ecosystem processes which are likely to influence many of the measured soil parameters. These data revealed that precipitation prior to collection of soil samples was responsible for observed differences in soil moisture, and that the amount of precipitation in the previous 2 months, and especially in the 10 days before collection had the strongest influence on soil moisture levels (data not shown).

Discussion

Water is the limiting factor for plant and microbial activity in mixed-grass prairie ecosystems and therefore drives aboveground and belowground processes (Biondini & Manske 1996, Heitchmidt & Haferkamp 2003, Grant 2004 (Chapter 2)). In this ecosystem year-to-year variability in precipitation is great, which is reflected in changes in ANPP (Biondini & Manske 1996, Heitchmidt & Haferkamp 2003). This variability causes organic matter deposition and decomposition dynamics to fluctuate greatly, making it difficult to detect differences in soil properties between experimental treatments. A high degree of spatial heterogeneity in soil properties of semi-natural

perennial plant communities also makes detection of differences in relatively large pools of total C and N problematic (Bird et al. 2002, Reeder 2003, Reeder et al. 2004). For example total soil C changed between 2001 and 2002 by 800 ppm, while differences between the continuously grazed treatment and the rest from grazing since 1993 treatment were only in the range of 360 ppm. Therefore, within treatment variability was so high that finding statistical differences between treatments for total pools of C and N becomes less likely. Measurement of labile pools may therefore be better than measurement of total pools for determining differences resulting from changes in management. Because labile forms of SOM turn over rapidly (from days to months) they are more sensitive to alteration by management practices than total pools of soil C (Burke et al. 1997, Reeder et al. 1998).

In the present study increases in abundance of C_3 species and decreases in abundance of C_4 species occurred with rest from grazing. This agrees with finding by others that C_4 grasses (mainly *Bouteloua gracilis*) decline when grazing is removed from areas that have been historically grazed (Frank et al. 1995, Biondini & Manske 1996). This implies that *Bouteloua gracilis* is less competitive with cool-season species in the absence of grazing pressure, and more competitive when large herbivores are present.

The aboveground plant response to rest from grazing may occur rapidly if the plant community is healthy and the rest occurs during periods of normal or above-normal precipitation. In the present study, total plant cover increased with removal of grazing compared to the continuously grazed treatments which agrees with findings by Biondini & Manske (1996). This response was evident even after only two growing-seasons of rest and the rapidity of the response was probably because of good spring moisture in

2000 and 2001. Plant response during drought years is likely to be less dramatic as plants use dormancy as a drought avoidance mechanism, which leads to minimal growth. Aboveground and belowground components are implicitly dependent on each other since plants provide a carbon source for the soil microbial community, which in turn mineralize nutrients for plant growth (Porazinska et al. 2003). Some belowground properties that are directly related to plant roots, such as $WSOC_{FM}$ (Cheng et al. 1993, van Ginkel et al. 1994, Cheng et al. 1996, Gregorich et al. 2000), may respond to changes in management concurrently with the aboveground changes since the above- and belowground response of a given plant are inevitably linked. However, in this study $WSOC_{FM}$ as a single variable did not respond to differences in management, but did reflect differences between microsites and collection date.

$WSOC_{OD}$ is a measurement of the WSOC which was present *in situ* along with the intracellular contents of the microbial population which are released upon cell lysis during desiccation (Davidson et al. 1987, DeLuca & Keeney 1994). Therefore, subtraction of the inherently variable WSOC (field-moist) from the $WSOC_{OD}$ may be a better indicator of microbial activity than either of these variables alone. Findings by Grant (2004, Chapter 2) showed that subtraction of $WSOC_{FM}$ from $WSOC_{OD}$ provides a parameter that is correlated with CO_2 evolution during aerobic incubations, which is a measure of microbial activity. Use of this analysis revealed that experimental treatments did not differ in a drought year (2002), but in a year with favorable soil moisture conditions (2003) the two rest treatments had higher values of CO_2 evolution than the continuously grazed treatment. This may reflect higher microbial activity resulting from increased belowground C inputs by plants as a result of a C surplus that is present

because aboveground losses of C (defoliation) are reduced compared with the continuously grazed treatment.

Microsite differences were evident despite high year to year variability. Root biomass was almost 40% lower in the surface 5 cm of soil of bare ground microsites than grass-occupied microsites. Soil temperatures were higher at the 5 cm depth and on the surface for exposed mineral soil (bare ground) than plant-occupied soil, which agrees with findings by McGill et al. (1986). Higher soil temperatures support the hypothesis that decomposition rates may be higher for bare microsites than grass-occupied microsites. However, no differences between microsites occurred for inorganic N concentrations meaning that differences in *in situ* net nitrogen mineralization between microsites were not detected. Lower root biomass in bare ground microsites than grass-occupied microsites in rangelands agrees with findings by others (Hook et al. 1991, Hook et al. 1994, Vinton & Burke 1995, Burke et al. 1998). Root biomass could be lower as a result of more decomposition in bare microsites. However, soil moisture values were lower for bare ground microsites than grass-occupied microsites in 2002. In mixed-grass prairie soil moisture may generally be lower in bare ground microsites than grass-occupied microsites (Grant et al. 2003). Therefore, moisture conditions in bare microtypes may be less consistent and on average lower than conditions in grass-occupied microtypes, causing roots to be less likely to grow into bare microtypes. This would probably lead to lower quantities of root exudates in bare microtypes, as indicated by the lower $WSOC_{FM}$ /Total C values observed in this study. Fewer plant inputs from roots and exudates, which act as substrates for microbial activity, could result in smaller

microbial populations, which may be reflected by the lower $WSOC_{OD}$/Total C values observed in this study.

Stable states probably occur during sustained periods of grazing or rest from grazing in this semiarid ecosystem. However, after a change in management the system may be in flux for a few years before reaching a new stable state. This may be why some variables, such as inorganic N and root C:N ratios, showed a similar response for the grazed treatment and the rest from grazing since 1993 treatment, while values for the rest since 2000 treatment were dissimilar. This makes collection of data over a number of years critical when trying to detect differences resulting from changes in management. Additionally, changes in soil properties arising from a change in management probably accumulate or deteriorate subtly, making multi-year studies to measure responses essential.

In northern mixed-grass prairie communities, rest from grazing in a system which has been continuously grazed for decades is likely to result in more litter deposition on the soil surface (Biondini & Manske 1996). This along with a greater abundance of cool-season grasses probably resulted in the decrease in bare ground abundance observed in this study. Belowground indicators that reflect a change in grazing management may occur concurrently with changes in the aboveground plant community as a result of the inherent link between aboveground and belowground processes, but the specific indicators used in this study are more likely to be lagging indicators than leading indicators.

The findings from this study suggest that precipitation or lack thereof (drought) is the primary factor influencing ecosystem processes in this community, while grazing is

of secondary importance, as noted by others (Biondini & Manske, Biondini et al. 1998, Heitschmidt & Haferkamp 2003). Rest from grazing during periods of drought may be beneficial for system recovery following drought, but prolonged rest is probably not necessary to maintain ecosystem health and may actually be detrimental to plant communities that have evolved with a history of grazing by large ungulates. However, periodic episodes of rest may be beneficial for plant reproductive dynamics and maintenance of a desirable composition of plant species.

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Table 1. Cover abundance of bare ground, litter, total plant cover and total C_3 species. Treatment-by-date interactions were significant for most variables. *Only main effect treatment differences were significant for this variable.

	Bare Ground			Litter			Total Plant Cover			*C_3 Species (grasses + caresis)		
Date	Rest (1993)	Rest (2000)	Grazed	Rest (1993)	Rest (2000)	Grazed	Rest (1993)	Rest (2000)	Grazed	Rest (1993)	Rest (2000)	Grazed
2001	8.4 a	15.2 b	31.6 c	23.2 c	18.6 b	12.4 a	68.5 b	66.2 b	56.0 a	41.0 b	38.9 b	26.2 a
2002	6.2 a	14.0 b	19.3 b	23.1 b	11.7 a	8.6 a	70.8 a	74.3 a	72.1 a	48.0 b	46.3 b	33.1 a
2003	7.9 a	17.8 b	26.3 c	29.6 b	24.1 ab	17.2 a	58.1 a	58.0 a	51.3 a	41.0 b	37.1 b	21.4 a

Note: means in a column followed by different letters differ (alpha = 0.05). Compare means only within a year.

Table 2. Soil and root properties from 2001, 2002, 2003 in the 0-5 cm depth and 2001, 2002 in the 5-10 cm depth.

Date	% H_2O (g g^{-1})	Soil C (%)	Soil N (%)	Soil C: N Ratio	Root C (%)	Root N (%)	Root C: N Ratio
				0-5 cm			
2001	2.1 a	1.11 a	.113 a	9.8 b	19.3 a	.752 b	25.9 a
2002	5.1 b	1.19 b	.116 a	10.2 c	17.2 a	.511 a	34.3 b
2003	16.2 c	1.13 ab	.126 b	8.9 a	25.4 b	.533 a	48.5 c
				5–10 cm			
2001	3.9 a	0.82 a	.092 a	8.9 a	21.7 a	.698 b	32.1 a
2002	5.5 a	1.00 b	.100 b	10.0 a	19.7 a	.408 a	48.2 b

Means followed by the same letter do not differ (alpha = 0.05). Compare means only within a column and depth increment.

Table 3. Treatment-by-microsite interaction (Bare = bare ground, Grass = *Stipa comata*) for the 0-5 cm depth increment.

Depth	Soil C (%)		Soil N (%)		Soil C: N Ratio	
cm	Bare	Grass	Bare	Grass	Bare	Grass
Rest (1993)	1.26 b	1.09 a	.126 b	.114 a	10.0	9.6
Rest (2000)	1.11	1.13	.116	.116	9.6	9.8
Grazed	1.13	1.15	.119	.119	9.5	9.7

Note: means followed by different letters differ (alpha = 0.05).

Table 4. Root biomass (g m^{-2}) for each depth increment, by Date and by Microsite averaged over 2001 and 2002. Compare means only within a column and independent variable category. Root biomass data were unavailable for 2003.

	0-5 cm depth	5-10 cm depth	0-10 cm depth
Date		root biomass (g)	
2001	509.9 a	278.3 a	788.2 a
2002	807.1 b	313.5 a	1120.6 b
Microsite			
Bare	498.6 a	255.6 a	754.2 a
Grass	818.4 b	336.2 a	1154.6 b

Means followed by the same letter do not differ (alpha = 0.05).

Table 5. Inorganic nitrogen pools (NH_4^+, NO_3^-, and NH_4^+ plus NO_3^-) and labile water soluble organic carbon (WSOC) concentrations from field-moist (FM) and oven-dry (60° C) soil (OD). *A significant date-by-treatment interaction occurred for these variables as shown on Table 6. **$WSOC_{FM}$ in the 0-5 cm depth is also dependent on percent soil H_20 (g g^{-1} soil) p = 0.0007.

Date	NH_4^+ (ug g^{-1} soil)	NO_3^- (ug g^{-1} soil)	$NH_4^+ + NO_3^-$ (ug g^{-1} soil)	**$WSOC_{FM}$ (ug g^{-1} soil)	$WSOC_{OD}$ (ug g^{-1} soil)	*$WSOC_{OD}$ - $WSOC_{FM}$	*$WSOC_{OD}$ / $WSOC_{FM}$
depth				0-5 cm			
2001	4.62 b	0.63 a	5.24 b	35.9 b	132.0 b	96.1 b	3.7 a
2002	3.30 a	1.26 b	4.56 a	24.3 a	138.1 b	113.8 c	5.9 c
2003	-	-	-	22.8 a	96.2 a	73.4 a	4.4 b
depth				5–10 cm			
2001	4.80 b	0.71 b	5.51 b	25.1			
2002	3.25 a	0.48 a	3.73 a	28.3	-	-	-

Means followed by the same letter do not differ (alpha = 0.05). Compare means between years within a dependent variable.

Table 6. Treatment-by-date interactions for $WSOC_{OD}$, $WSOC_{FM}$, $WSOC_{OD}$-$WSOC_{FM}$, $WSOC_{OD}/WSOC_{FM}$ for 0-5 cm depth. *Only main effect date and microsite differences were significant for $WSOC_{FM}$ (no treatment-by-date interaction occurred). Main effect mean separations for differences between years are shown on Table 5.

	$WSOC_{OD}$ (ug C g^{-1} soil)			* $WSOC_{FM}$ (ug C g^{-1} soil)			$WSOC_{OD}$ - $WSOC_{FM}$ (ug g^{-1} soil)			$WSOC_{OD}$ / $WSOC_{FM}$ (ug g^{-1} soil)		
Date	Rest (1993)	Rest (2000)	Grazed	Rest (1993)	Rest (2000)	Grazed	Rest (1993)	Rest (2000)	Grazed	Rest (1993)	Rest (2000)	Grazed
2001	127.1 a	154.4 b	114.6 a	35.9 a	35.3 a	36.6 a	91.2 a	119.1 b	78.0 a	3.6 a	4.4 b	3.2 a
2002	135.7 a	135.4 a	143.2 a	24.2 a	23.4 a	25.3 a	111.5 a	112.0 a	117.9 a	5.9 a	6.1 a	5.8 a
2003	102.9 b	101.3 b	84.4 a	21.7 a	21.8 a	24.9 a	81.2 b	79.5 b	59.5 a	4.8 b	4.7 b	3.7 a

Means followed by the same letter do not differ (alpha = 0.05). Compare means only within a year.

Table 7. WSOC as a percentage of Total soil C ((WSOC/Total C) x 100). Date, microsite, and treatment all influenced $WSOC_{OD}$. Only main effect Date and Microsite differences were significant for $WSOC_{FM}$ (along with percent soil H_20 ($g\ g^{-1}$) $p = 0.0007$). *This comparison presents LS Means for the analysis which includes soil water (%) as a quantitative independent variable. Means followed by different letters differ (alpha = 0.05).

	*$(WSOC_{FM}$ / Total C) x 100	($WSOC_{FM}$ / Total C) x 100	($WSCOC_{OD}$ / Total C) x 100
		(0-5 cm depth)	
Date	LS Means		
2001	.16 a	.33 b	1.24 b
2002	.13 a	.20 a	1.17 b
2003	.45 b	.21 a	0.89 a
Microsite			
Bare	.23 a	.23 a	1.00 a
Grass	.27 b	.26 a	1.19 b
Treatment			
Rest (1993)	.24 a	.24 a	1.06 a
Rest (2000)	.24 a	.24 a	1.23 b
Grazed	.26 a	.26 a	1.02 a

V. Conclusions

Differences between a shortgrass and a mixed-grass ecosystem were relatively minor for a number of soil properties. Properties that differed between systems, such as differences in inorganic nitrogen, provided evidence of differences in nutrient cycling dynamics between these two grasslands. Many of the differences can be easily explained by long-term productivity dynamics that are a direct result of differences in climatic and edaphic conditions. Higher root biomass and microbial activity in the mixed-grass prairie suggest that the system is not limited by soil water to the same extent as the shortgrass steppe, and therefore nitrogen limitations are likely to occur more commonly in the mixed-grass communities.

Root exudates are an important source of soluble organic matter because concentrations of WSOC are orders of magnitude higher in rhizosphere-soil than in bulk-soil. Soil associated with grass crowns also contributes significantly to the overall pool of WSOC in surface soils. Therefore differences between bare microtypes and grass-occupied sites were even more pronounced when crown and rhizoplane soil contributions are accounted for along with bulk-soil fractions of WSOC. A greater percentage of total WSOC came from rhizoplane soil in the mixed-grass prairie than from the shortgrass prairie, which may be the result of inherent site differences in soil type, plant community composition, or climatic conditions. However, inclusion of bulk soil, rhizoplane soil, and crown associated soil fractions of WSOC indicated that the shortgrass steppe and mixed-grass prairie did not differ in overall quantities of $WSOC_{FM}$ in the surface 10 cm of soil. This highlights the importance of quantifying the amount of WSOC present in the root-

associated soil before removing and discarding roots, which has been a standard practice during soil processing for generations of soil scientists.

Examination of WSOC dynamics collected over multiple years in the mixed-grass prairie revealed that most soil response variables were more sensitive to year-to-year variations in precipitation than to changes in grazing management. Aboveground plant response to rest from grazing was evident before belowground indications of changes were detected. This may be a result of drought masking the response to rest from grazing. Additionally, systems may be in flux for some time before reaching an alternate stable state after a change in management. Since $WSOC_{FM}$ was clearly not simply a measure of root exudation rates *per se*, and it did not respond detectably to changes in grazing management, this measurement alone did not represent a good indicator of response to changes in management. Changes in quantities and qualities of soluble pools of C and N may nonetheless be the best indicators of ecosystem response to change in management. Specifically, the measure of the difference between $WSOC_{OD}$ and $WSOC_{FM}$ has biological relevance in that it was directly related to microbial activity, and may therefore be a good indicator of changes in nutrient cycling integrity.

In addition to the importance of understanding and managing SOM to optimize ecosystem health, recent concerns over rising atmospheric CO_2 levels have intensified interest in carbon cycling and the importance of soil C (IGBP TCWG 1998, Schimel 1998, 2000). Alteration of management practices, such as grazing intensity, may allow greater C sequestration from the atmosphere helping offset fossil fuel emissions (Kimble et al. 2001). Grass-dominated grazing lands in temperate latitudes may act as part of a terrestrial C sink, but there continue to be questions about the actual C sequestration

potential of these lands (Reeder et al. 2001). Monitoring changes in the total quantity of soil C resulting from changes in grazing management is difficult because grazing-induced changes are often small relative to the overall size of the SOM pool, and changes in the total pool are likely to be more responsive to changes in climate than changes in management. Therefore, an ability to detect relatively small changes in SOM may allow land mangers to quantify carbon actually being sequestered or lost with a given management regime. This could be particularly useful as the idea of "carbon credits" becomes a reality.

Bare ground and grass microsites differed in a variety of properties. These results agree with previous findings that soil and plant variables generally decline when unoccupied soil is compared with plant-occupied soil (Hook et al. 1991, Hook et al. 1994, Vinton & Burke 1995, Burke et al. 1998, 1999). Differences between microsites can be more substantial than differences between somewhat similar grassland ecosystems. Therefore, determination of bare ground abundance is important for making landscape scale estimates of soil carbon pools, including labile soluble organic fractions. These findings substantiated the importance of quantification of plant cover patterns, which are critical for estimation of ecosystem function at large-scales in semi-arid grasslands because local plant-induced patterns in soil properties differ markedly from those of bare soil (Vinton & Burke 1995).

Measurement of labile and total C and N pools over a period of multiple years in the mixed-grass ecosystem confirmed that field-moist WSOC concentration does fluctuate with *in situ* soil water content. Changes in differences between $WSOC_{OD}$ and $WSOC_{FM}$ may indicate ecosystem response to rest from grazing for a sufficient time as

to allow the system to reach a new stable state. However, more years of data would be needed to confirm this as a response to change in management. Belowground indicators that reflect a change in grazing management may occur concurrently with changes in the aboveground plant community as a result of the inherent link between aboveground and belowground processes. Results from this study suggested that precipitation, or lack thereof (drought) was the primary factor influencing ecosystem processes in this community, while grazing was of secondary importance, as noted by others (Biondini & Manske 1996, Biondini et al. 1998, Heitschmidt & Haferkamp 2003). Rest from grazing during periods of drought may be beneficial for system recovery following drought, but prolonged rest is probably not necessary to maintain ecosystem health. As noted by Biondini and Manske (1996), Klipple and Bement (1961) and Holechek et al. (1989), most of the recovery of range condition with change in grazing management occurs in the first 5-10 years in the Great Plains, with little added improvement thereafter.

The research accomplished to date has led to a number of new questions and interesting related experiments. One objective for the future is to measure qualities of WSOC from grasslands, such as UV absorbance, that provide a measure of bioavailability of organic constituents. Measures of water soluble nitrogen (WSN) can also be improved by quantifying the organic and inorganic fractions of the WSN extracts. If both WSOC and WSN are measured in this way we could be able to make more accurate determinations of overall lability of soluble organic matter from grasslands. Additional data collected in related experiments may be useful for interpretation of results from this dissertation. A related experiment carried out in the shortgrass steppe ecosystem where seasonal response of soil and plant community properties to drought

and topographic position was measured (Appendix A). *Atriplex canescens*-occupied soil C and N dynamics were also measured seasonally, with specific attention to duff layer characteristics, so comparisons can be made between shrub and grass microtype properties (Appendix B). A greenhouse experiment was conducted to look at *Bouteloua gracilis*-occupied soil WSOC response to soil moisture conditions at the time of harvest compared to prolonged drought response (Appendix C). Bi-weekly measurement of deep soil water dynamics across a topo-sequence have been made since April 2002 in the shortgrass steppe on the permanent transects established for this dissertation research (Appendix D). Simulation modeling work is planned for the near future to use CENTURY (DAYCENT) to examine response of SOM to drought and recovery from drought with and without grazing in shortgrass and mixed-grass ecosystems (Appendix E). Hopefully, the results from this research will provide a catalyst for further research in soluble organic matter dynamics in grasslands and determination of potential response variables that could be used to provide an indication of a shift in ecosystem state that result from changes in management. Overall the research done on this project from 2001 through 2004 may have generated more questions than it answered, but measurable progress is always good and generally good research is only accomplished through perseverance.

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Appendix A

Seasonal Measurement of Labile C and N in Shortgrass Steppe during Drought

Methods

An experiment was performed to assess seasonal dynamics of soil and plant carbon and nitrogen interactions in the shortgrass steppe. Transects were established on mid-slope positions of both north- and south-facing aspects and flat terrain at CPER. Three pastures which had been grazed at moderate intensities prior to 2001 were randomly designated with one of three experimental treatments, which consisted of continuation of moderate grazing, exclosure from cattle grazing, and increased stocking rates to a heavy grazing intensity. Sample collection occurred seasonally, with seven sampling dates from Spring 2001 to Fall 2002, including the winter of 2001-02. This period was markedly drier than "normal" years, with little measurable precipitation during the growing seasons following a relatively wet spring in 2001. Samples were collected repeatedly along the same permanent transects so that data could be statistically analyzed using repeated measures analysis.

The experimental design consisted of a split-split plot, with north-facing, south-facing and flat aspects representing the subplots, and bare ground and grass-occupied microsites representing the sub-subplots. Soil samples were collected from 0-5 and 5-10 cm depth increments at three randomly selected locations along each transect. The total number of observations for soil variables was 48 (3 experimental treatments x 3 aspects x 2 microsites x 3 EUs). Plant cover estimates were made on randomly selected 1 m^2 plots and separately on the southern most ¼ of the frame (0.25 m^2), which was subsequently

clipped for aboveground plant biomass by functional type. Soil and plant samples were collected from the same area so relationships between above- and belowground carbon and nitrogen dynamics could be quantified. In addition to total C and N soil samples were also analyzed for field-moist and air-dry WSOC and inorganic N content. Drought conditions during the sampling period may have masked differences between grazing treatments and topographic positions. As a result statistical analysis may be more powerful if different grazing treatments are considered as blocks so that differences between aspect, microsite, seasonal effects, and associated interactions may be examined. Interpretation of experimental results will be focused on biological and biochemical processes occurring during drought periods, which are likely to differ from dynamics during "normal" or wet years.

Appendix B

Soluble Organic Matter in Litter and Soil under *Atriplex Canescens* Canopies

Methods

Sampling of shrubs was performed along with measurement of quantities of shrub cover on different landscape positions so that landscape estimates of total and water soluble C may be made based on reasonable plant cover measurements. *Atriplex canescens* abundance is relatively low on flat terrain, but increases noticeably on south-facing slopes at CPER. Measurements of soil WSOC and total soil C were made seasonally on south-facing transects at the same time bare and grass microsites were sampled using the same methods (*Appendix A*). Litter samples (duff layer) were also collected and extracted for WSOC to evaluate the potential of shrub litter as a source of WSOC to microbes in the surface mineral soil horizons. Global positioning systems (GPS) data were collected on 3 pastures at CPER (Figure 1) to delineate areas with higher densities of salt-bush (*A. canescens*). Three large plots (100 m^2) were also sampled for shrub abundance within each high shrub density polygon. Height and diameter (cm) of each shrub was measured too. Geographic information systems (GIS) were used to assess the proportion of the total landscape occupied by *A. canescens* so that C inputs from woody plants may be ascertained in this predominately herbaceous grassland. The objective of the research was to compare landscape scale estimates of soil C pools made with and without inclusion of the shrub component.

CPER NASA Study Area

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Brigid Baldwin &
Doug Grant
06/06/2001

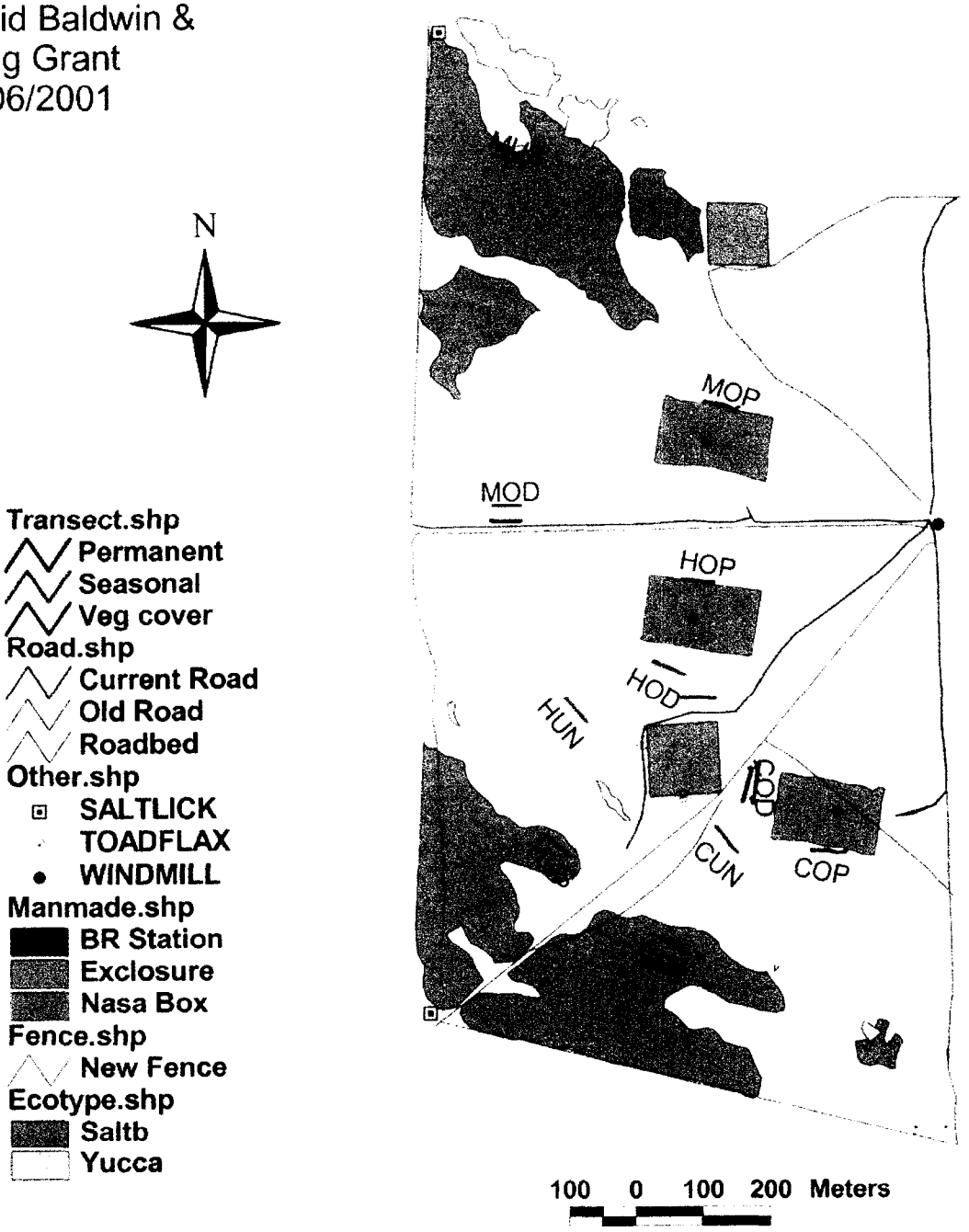


Figure 1. Polygons shaded grey-blue represent areas on south-facing slopes with high densities of Saltbrush (*Atriplex canescens*) in three pastures at CPER.

Appendix C

Influence of Short-term Soil Moisture and Prolonged Water Stress on WSOC in *Bouteloua gracilis* Occupied-soil

Methods

A greenhouse experiment was performed to examine the response of soil WSOC to soil moisture conditions in a controlled environment. Data from the experiment may be helpful for interpretation of field-experimental results from the seasonal soil sampling of *Bouteloua gracilis* occupied-soil (*Appendix A*). Each pot was filled with either fine or coarse textured native topsoil before a 10 cm diameter by 10 cm long cylindrical core, collected during plant dormancy from the Shortgrass steppe, was inserted into each pot. A total of 40 pots were used per soil texture. After watering the pots at 300 ml twice a week for 6 weeks half of the pots were randomly selected as the drought treatment, which had water reduced to 150 ml per week (Photograph 1), while the remainder received 300 ml per week (Photograph 2). Imposition of watering treatments continued for 12 weeks before harvesting of pots began.

Harvesting was done at 1, 5, 10, 15, and 20 days after the final watering so that soil moisture was very low by the final harvest date. Four pots of each soil texture by watering treatment were harvested per harvest date. After clipping aboveground plant material by functional type, the entire pot of soil was placed in a washtub and the intact root system was manually pulled away from "bulk" soil. The root systems then were placed over a piece of butcher paper to separate the "rhizosphere" soil from the roots and associated "rhizoplane" soil.

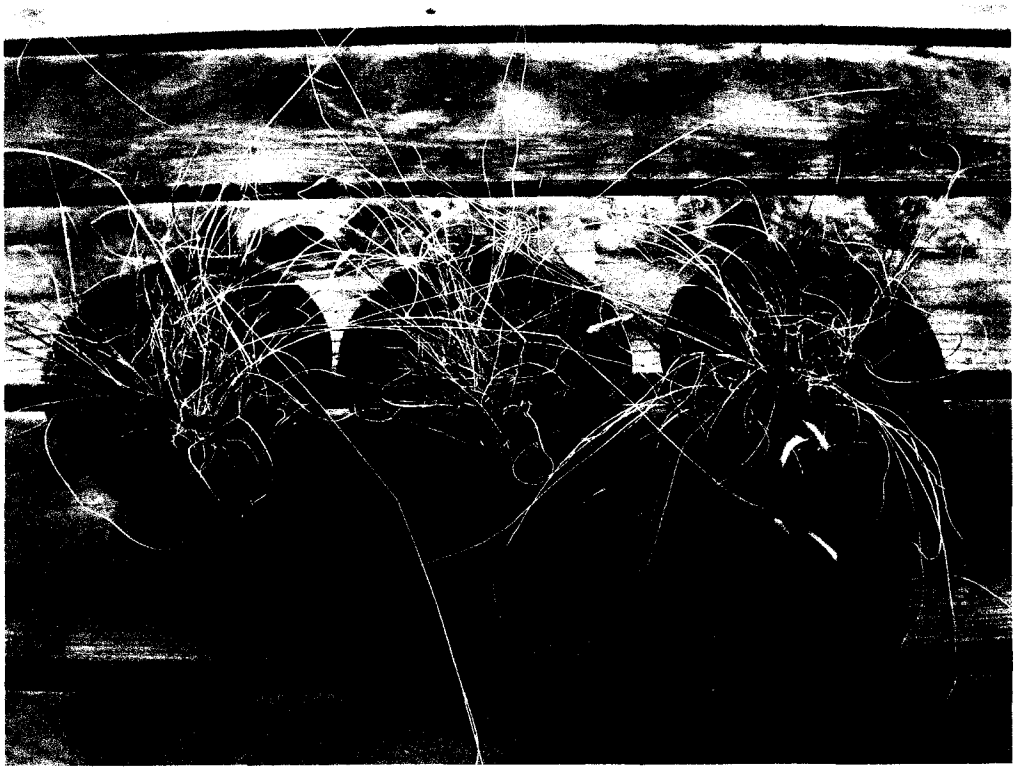
Root systems were extracted for WSOC using 350 ml of de-ionized water and gently shaking on a reciprocal shaker for 210 seconds. Root systems were then removed and dried at 60° C for weighing and analysis for total C and N content. Gravimetric water content (g/g) was determined by drying 10 g of field-moist soil at 105° C for bulk and rhizosphere soil fractions. Normal field-moist extractions of soil for WSOC (8 g in 40 ml) were performed. The remaining soil was air-dried, followed by another WSOC extraction on an air-dry portion of the sample (8 g in 40 ml).

The objectives of this experiment were to: 1) compare field-moist and air-dry soil samples for WSOC levels in a greenhouse environment, 2) look at relative importance of long-term water stress compared to soil water content at the point of sample collection and 3) to look at the relative magnitude of WSOC concentration in proximity to grass roots (rhizoplane, rhizosphere, and bulk-soil fractions). Hopefully the result will be helpful in answering the following questions:

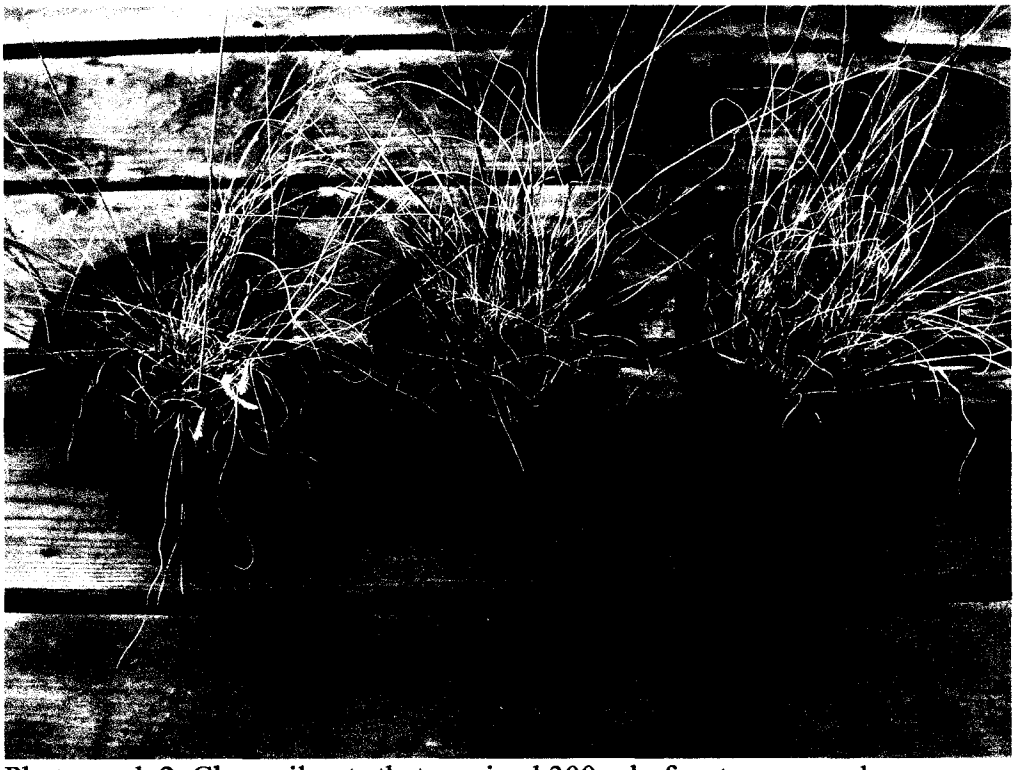
1) What happens to WSOC concentrations as soils dry out?

2) How does soil texture influence these dynamics?

3) Does a certain level of soil moisture correspond to a specific soil water potential where microbial cell lysis occurs, rendering field-moist soil WSOC comparable to air-dry soil WSOC?



Photograph 1. Clay soil pots that received 150 ml of water per week.



Photograph 2. Clay soil pots that received 300 ml of water per week.

Appendix D

Measurement of Landscape Soil Water Fluctuations through Time in Shortgrass Rangelands

Methods

Ongoing research at CPER is being performed to look at the influence of different grazing intensities and topographic positions on soil water dynamics from surface layers to deep soil horizons. Sentek* access tubes were installed in April 2002 on north- and south-facing slopes, as well as flat terrain and ridge-tops, to monitor the influence of aspect, topographic position and grazing intensity on soil moisture levels. Tubes are installed using a hand auger (Photograph 1) and a sledge hammer. A stabilizing tripod is used to hold the access tube in place, ensuring that it goes straight into the ground (Photograph 2). After the access tube is installed a cap is glued on to the tube so the Sentek* probe can be screwed on so that soil moisture readings can be made.

The Sentek* access tubes allow soil moisture content to be measured at 10 cm increments to a depth of 70 cm (or to 110 cm on flat terrain). Measurements of soil moisture are taken every 2 weeks during the growing season, and monthly during dormancy, on 27 access tubes distributed across landscape positions so that seasonal dynamics may be examined.

Soil cores were collected in 10 cm increments to 70 cm depth using a hydraulic soil probe (Giddings Machine Co.*), at the same time Sentek* soil moisture values were obtained in order to calibrate the Sentek* readings. The soil samples (n = 38) were weighed then dried at 105° C, and weighed again to determine the gravimetric (%) soil water content. The regression of Sentek* moisture values with gravimetric (%) moisture

values shows a strong correlation, with $r^2 = 0.81$ and a correlation coefficient of 2.99 (Figure 1). This means the Sentek* moisture values were approximately 3 times higher than the gravimetric (%) soil moisture (g/g). Because readings from the Sentek* are given in volumetric (%) soil moisture (cm^3/cm^3) values, and if it is assumed that the soil bulk density could be as high as 1.5, the Sentek* readings are about 2-fold higher than the actual empirical soil moisture values.

*Trade names are included only for the benefit of the reader and do not constitute preferential endorsement by the USDA over similar products on the market.

Photograph 1. Use of a hand auger to install access tubes at CPER (Shortgrass).

Photograph 2. Stabilizing tripod and sledge hammer used to install access tubes at CPER.

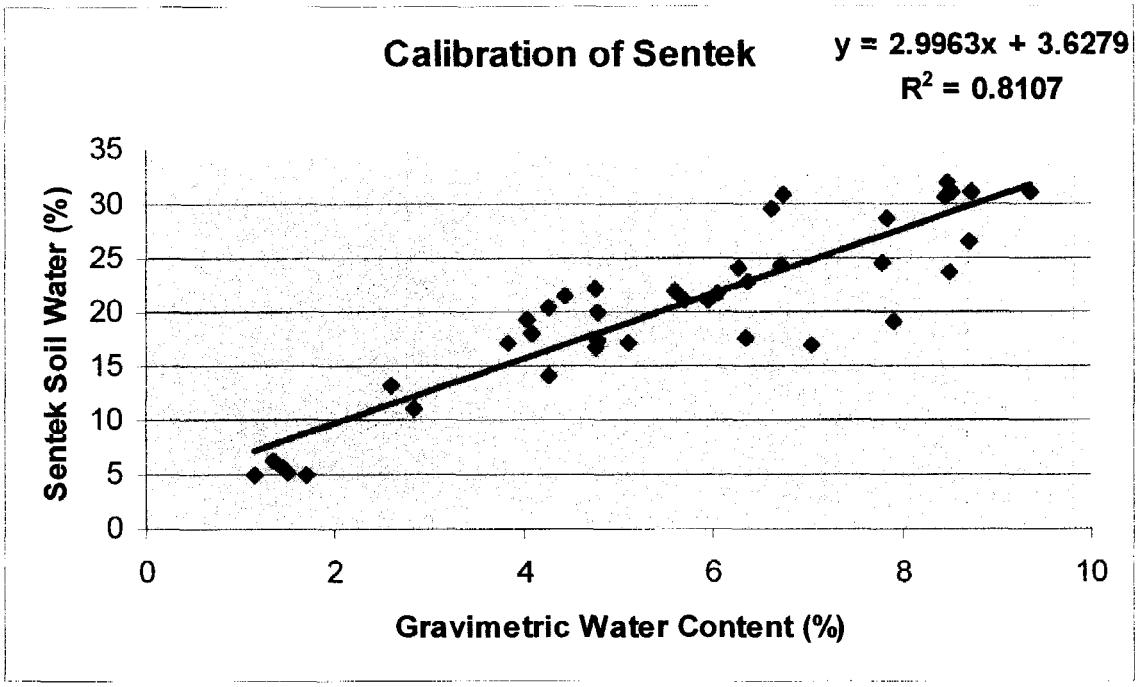


Figure 1. Regression equation used for calibrating Sentek* soil moisture readings (n = 38). Deep soil cores were collected along with Sentek* measurements to calibrate the instrument.

Appendix E

CENTURY Analysis of Drought and Grazing Interaction and Recovery in Shortgrass and Mixed-grass Ecosystems

Background

Recent field research conducted at Central Plains Experimental Range (CPER), CO and near Miles City, MT has produced valuable empirical data sets during drought years that could be useful for modeling. Data collected during recent drought years may be indicative of grassland drought response in the future, especially if climate change leads to warmer drier environmental conditions in mid-latitudes. Few studies provide complete quantitative measurements of total grassland net primary productivity (NPP), including above-ground and below-ground components (Gill et al. 2002). However, changes in below-ground net primary productivity (BGNPP) and associated changes in SOM are relatable to environmental variables such as soil moisture and temperature. A combination of drought and heavy cattle grazing could lead to warmer soil temperatures. Soil warming accelerates SOM decay and CO_2 flux to the atmosphere (Melillo et al. 2002). As drought conditions reduce OM inputs from grasses semi-arid systems are likely to experience declines in SOM as mineralization continues to some extent at low soil water potentials. CO_2 flux measurements from CPER during 2002 indicate that heavy grazing during drought leads to net loss of system C (Morgan et al. 2003 – Poster). After multiple years of drought and heavy grazing decomposition may slow down as labile resources become less abundant due to lack of plant inputs during dormancy. Soil moisture levels may also become so low that microbes go dormant as well, becoming active only as pulses of infrequent moisture wet the surface soil horizon.

Rest from cattle grazing allows accumulation of surface litter. Build up of surface litter can affect soil temperature (LeCain et al. 2000). Reduced soil temperatures would decrease decomposition rates of SOM and along with increased plant inputs lead to net ecosystem carbon gain. Abundance of bare ground can also decrease with rest from grazing (Grant, Chapter 4). Research in mixed-grass prairie indicates that bare ground microsites have lower soil moisture levels in the surface 5 cm than grass-occupied soils (Grant et al. 2003). Therefore, long-term rest from grazing could lead to higher soil moisture levels.

In years of drought many ranchers may sell their herds due to lack of available forage on rangelands. Prices are lower when many are selling and prices may be higher when it comes time to buy a replacement herd. Therefore, some ranchers may choose to leave animals in a pasture despite inadequate forage supplies, putting stress on the plant community and degrading the resource base. At this point a change in grazing management could allow the resource base and SOM levels to recover. Increased sequestration rates of C have been linked to improved grazing management in grasslands and tend to be greatest in the 0-10 cm soil increment (Conant et al. 2001). Complete rest from grazing in "normal" or wet years may provide optimum conditions for ecosystem recovery from drought.

Proposed CENTURY Modeling Analysis

Shortgrass and Mixed-grass ecosystems would be evaluated using a daily timestep (DAYCENT) for temperature, precipitation and evapotranspiration variables to simulate drought conditions. Grazing treatments would consist of 3 treatments: very heavy

grazing, moderate grazing, and rest from cattle grazing. Following simulation of the above grazing treatments coinciding with 20 yrs of continuous drought or 20 years of intermittent drought (alternating 5 years of drought and 5 years of "normal" precipitation), recovery from the drought by grazing interaction would be simulated. This would be done by using temperature and precipitation data from "normal" years because substantial recovery is unlikely during drought years.

In addition to evaluating the recovery if the grazing treatments stay the same, the very heavy and moderate grazing treatments would be changed to rest from cattle grazing to reflect a change in management. This would allow examination of potential carbon sequestration of previously degraded ecosystems under optimum recovery conditions.

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Appendix F

Raw Data, Means, and P-values Tables for Chapters II and III

Appendix F. Table 1. Chp. II Soil Water, Bulk Density, Organic C, Root Biomass, Total N, and C:N Ratio of soil (0-5 cm) in Northern mixed prairie (NMP). *Ecosystem mean assumes 50 % grass and 50 % bare ground cover.

Microsite	Aspect	Site	Rep	Soil Water % (g/g)	Bulk Density	Organic C (g C m^{-2})	Root biomass (gm^{-2})	Total N (g N m^{-2})	C : N Ratio Org C/ Total N
Bare	Flat	E	1	7.8	1.44	752	339	75	10.0
			2	9.8	1.28	746	1789	69	10.8
			3	8.8	1.29	590	172	59	9.9
			Mean	8.8	1.34	696	766	68	10.2
		W	1	8.4	1.30	678	289	64	10.5
			2	8.4	1.46	575	651	52	11.1
			3	9.8	1.39	722	198	73	9.9
			Mean	8.9	1.38	658	379	63	10.5
	North	E	1	9.7	1.35	722	253	68	10.6
			2	9.4	1.27	595	204	64	9.3
			3	11.5	1.27	860	113	84	10.2
			Mean	10.2	1.30	726	190	72	10.0
		W	1	9.2	1.31	707	276	68	10.4
			2	8.3	1.39	608	188	60	10.1
			3	7.4	1.41	706	461	73	9.6
			Mean	8.3	1.37	674	309	67	10.0
		Category Mean		9.0	1.35	688	411	68	10.2
Grass	Flat	E	1	9.7	1.33	734	1172	65	11.4
			2	10.8	1.25	689	602	67	10.2
			3	9.4	1.23	703	367	65	10.8
			Mean	9.9	1.27	708	714	66	10.8
		W	1	13.9	1.23	710	449	65	11.0
			2	9.7	1.26	495	744	45	10.9
			3	11.3	1.23	673	270	62	10.8
			Mean	11.6	1.24	626	488	57	10.9
	North	E	1	10.4	1.32	521	197	51	10.1
			2	10.4	1.34	641	350	65	9.9
			3	13.1	1.09	788	206	77	10.2
			Mean	11.3	1.25	650	251	65	10.1
		W	1	10.9	1.43	748	353	72	10.4
			2	10.8	1.25	735	541	72	10.3
			3	11.4	1.24	577	383	57	10.1
			Mean	11.0	1.31	687	425	67	10.2
		Category Mean		11.0	1.27	668	470	64	10.5
		***Ecosystem Mean**		**10.0**	**1.31**	**678**	**440**	**66**	**10.4**

Appendix F. Table 2. Chp. II Soil Water, Bulk Density, Organic C, Root Biomass, Total N, and C:N Ratio of soil (0-5 cm) in Shortgrass steppe (SGS). *Ecosystem mean assumes 50 % grass and 50 % bare ground cover.

Microsite	Aspect	Site	Rep	Soil Water % (g/g)	Bulk Density	Organic C (g C m^{-2})	Root biomass (gm^{-2})	Total N (g N m^{-2})	C : N Ratio Org C/ Total N
Bare	Flat	E	1	8.3	1.39	404	67	42	9.6
			2	8.7	1.38	868	206	78	11.1
			3	9.5	1.39	546	73	54	10.1
			Mean	8.8	1.38	606	115	58	10.3
		W	1	8.8	1.39	509	145	49	10.5
			2	11.0	1.35	639	174	62	10.3
			3	9.1	1.37	458	149	49	9.3
			Mean	9.6	1.37	535	156	53	10.0
	North	E	1	8.9	1.28	533	153	51	10.4
			2	9.8	1.36	496	180	51	9.7
			3	10.6	1.38	571	288	56	10.2
			Mean	9.8	1.34	533	207	53	10.1
		W	1	9.9	1.40	551	180	57	9.7
			2	8.8	1.46	539	212	54	10.0
			3	8.6	1.46	485	206	47	10.4
			Mean	9.1	1.44	525	199	52	10.0
		Category Mean		9.3	1.38	550	170	54	10.1
Grass	Flat	E	1	9.8	1.35	583	321	52	11.2
			2	11.0	1.28	406	210	40	10.1
			3	10.5	1.28	580	194	55	10.5
			Mean	10.4	1.31	523	242	49	10.6
		W	1	8.1	1.40	471	206	44	10.7
			2	12.4	1.24	517	326	51	10.2
			3	9.3	1.32	572	474	52	10.9
			Mean	10.0	1.32	520	335	49	10.6
	North	E	1	11.8	1.31	706	329	70	10.0
			2	11.4	1.32	490	309	46	10.6
			3	9.6	1.31	683	372	60	11.3
			Mean	10.9	1.31	626	336	59	10.7
		W	1	8.6	1.42	648	565	61	10.7
			2	8.5	1.27	591	347	51	11.5
			3	9.1	1.31	695	271	61	11.4
			Mean	8.7	1.34	645	394	58	11.2
		Category Mean		10.0	1.32	578	327	54	10.8
		***Ecosystem Mean**		**9.7**	**1.35**	**564**	**248**	**54**	**10.4**

Appendix F. Table 3. Chp. II Soil Water, Bulk Density, Organic C, Root Biomass, Total N, and C:N Ratio of soil (5-10 cm) in NMP. *Ecosystem mean assumes 50 % grass and 50 % bare ground cover.

Microsite	Aspect	Site	Rep	Soil Water % (g/g)	Bulk Density	Organic C (g C m^{-2})	Root biomass (gm^{-2})	Total N (g N m^{-2})	C : N Ratio Org C/ Total N
Bare	Flat	E	1	12.6	1.36	456	341	48	9.6
			2	12.8	1.35	200	287	49	4.1
			3	12.8	1.40	678	210	64	10.7
			Mean	12.7	1.37	445	279	53	8.1
		W	1	12.4	1.50	642	300	58	11.1
			2	12.8	1.52	554	318	55	10.1
			3	11.7	1.36	577	111	60	9.7
			Mean	12.3	1.46	591	243	57	10.3
	North	E	1	12.8	1.28	451	59	48	9.5
			2	13.1	1.41	614	268	51	12.0
			3	12.8	1.37	598	71	68	8.7
			Mean	12.9	1.35	554	132	56	10.1
		W	1	13.5	1.39	560	209	58	9.7
			2	12.6	1.34	466	123	48	9.7
			3	12.9	1.41	535	260	35	15.2
			Mean	13.0	1.38	520	197	47	11.5
			Category Mean	12.7	1.39	528	213	53	10.0
Grass	Flat	E	1	12.3	1.36	555	459	53	10.6
			2	13.5	1.34	568	265	55	10.4
			3	11.6	1.28	534	244	53	10.1
			Mean	12.5	1.33	552	323	53	10.4
		W	1	10.6	1.47	608	258	63	9.6
			2	11.6	1.39	548	474	51	10.6
			3	14.1	1.41	593	97	59	10.0
			Mean	12.1	1.42	583	276	58	10.1
	North	E	1	12.7	1.43	464	146	50	9.3
			2	12.9	1.38	702	90	67	10.4
			3	12.9	1.27	632	121	66	9.6
			Mean	12.9	1.36	599	119	61	9.8
		W	1	14.4	1.51	459	114	53	8.6
			2	12.4	1.29	462	215	48	9.6
			3	12.1	1.52	546	180	52	10.5
			Mean	13.0	1.44	489	170	51	9.6
			Category Mean	12.6	1.39	556	222	56	9.9
			***Ecosystem Mean**	**12.7**	**1.39**	**542**	**217**	**55**	**10.0**

Appendix F. Table 4. Chp. II Soil Water, Bulk Density, Organic C, Root Biomass, Total N, and C:N Ratio of soil (5-10 cm) in SGS. *Ecosystem mean assumes 50 % grass and 50 % bare ground cover.

Microsite	Aspect	Site	Rep	Soil Water % (g/g)	Bulk Density	Organic C (gm^{-2})	Root biomass (gm^{-2})	Total N (gm^{-2})	C : N Ratio Org C/ Total N
Bare	Flat	E	1	8.9	1.41	310	133	30	10.2
			2	13.1	1.38	507	286	55	9.3
			3	12.1	1.47	528	67	56	9.4
			Mean	11.4	1.42	448	162	47	9.6
		W	1	9.8	1.40	385	71	44	8.7
			2	9.5	1.45	455	34	49	9.4
			3	10.7	1.42	399	94	45	8.8
			Mean	10.0	1.42	413	66	46	9.0
	North	E	1	10.3	1.39	514	274	54	9.6
			2	9.5	1.42	353	175	38	9.4
			3	8.6	1.53	413	166	48	8.6
			Mean	9.5	1.45	426	205	46	9.2
		W	1	14.5	1.37	423	92	48	8.8
			2	14.0	1.37	555	131	64	8.7
			3	16.6	1.34	446	57	50	9.0
			Mean	15.0	1.36	475	93	54	8.8
			Category Mean	11.5	1.41	441	132	48	9.2
Grass	Flat	E	1	9.6	1.45	317	119	33	9.7
			2	12.4	1.40	590	116	60	9.9
			3	11.5	1.45	591	139	63	9.4
			Mean	11.2	1.43	499	125	52	9.7
		W	1	10.3	1.46	909	65	81	11.2
			2	10.6	1.48	312	106	36	8.6
			3	10.5	1.30	385	36	43	9.0
			Mean	10.4	1.41	535	69	53	9.6
	North	E	1	10.5	1.42	509	392	53	9.7
			2	8.9	1.44	400	183	44	9.1
			3	8.7	1.37	491	161	51	9.7
			Mean	9.4	1.41	467	245	49	9.5
		W	1	16.2	1.32	684	244	72	9.5
			2	15.6	1.36	678	197	70	9.7
			3	13.3	1.37	740	148	79	9.4
			Mean	15.0	1.35	701	196	73	9.5
			Category Mean	11.5	1.40	551	159	57	9.6
			***Ecosystem Mean**	**11.5**	**1.41**	**496**	**145**	**53**	**9.4**

Appendix F. Table 5. Chps. II & III NH_4^+, NO_3^-, Total inorganic N (iN), and $WSOC_{FM}$ from Bulk soil, Root soil, and Total (0-5 cm) in NMP. *Ecosystem mean assumes 50 % grass and 50 % bare ground cover.

Microsite	Aspect	Site	Rep	NH_4^+ (g N m^{-2})	NO_3^- (g N m^{-2})	Total iN (g N m^{-2})	Bulk $WSOC_{FM}$ (g C m^{-2})	Root $WSOC_{FM}$ (g C m^{-2})	Total $WSOC_{FM}$ (g C m^{-2})
Bare	Flat	E	1	0.8	0.2	1.0	1.4	0.3	1.7
			2	0.5	0.1	0.6	2.7	0.6	3.4
			3	0.3	0.1	0.4	1.3	0.3	1.5
			Mean	0.5	0.1	0.7	1.8	0.4	2.2
		W	1	1.1	0.2	1.3	1.3	0.4	1.6
			2	0.2	0.2	0.4	1.3	0.2	1.5
			3	0.6	0.2	0.7	1.4	0.2	1.7
			Mean	0.6	0.2	0.8	1.3	0.3	1.6
	North	E	1	0.5	0.2	0.6	1.5	0.4	1.9
			2	0.5	0.1	0.6	1.2	0.1	1.4
			3	1.4	0.1	1.5	1.2	0.3	1.5
			Mean	0.8	0.1	0.9	1.3	0.3	1.6
		W	1	0.3	0.2	0.5	1.1	0.5	1.6
			2	0.2	0.2	0.3	1.5	0.2	1.7
			3	0.1	0.2	0.3	1.4	0.4	1.9
			Mean	0.2	0.2	0.4	1.3	0.4	1.7
			Category Mean	0.5	0.2	0.7	1.4	0.3	1.8
Grass	Flat	E	1	0.3	0.1	0.4	1.8	0.4	2.1
			2	0.4	0.2	0.6	1.5	0.2	1.6
			3	0.6	0.1	0.7	1.0	0.2	1.2
			Mean	0.4	0.1	0.5	1.4	0.2	1.6
		W	1	0.3	0.2	0.5	1.3	0.4	1.7
			2	0.1	0.1	0.2	1.6	0.3	1.9
			3	0.4	0.2	0.5	1.1	0.2	1.2
			Mean	0.3	0.2	0.4	1.3	0.3	1.6
	North	E	1	0.3	0.1	0.4	1.4	0.2	1.6
			2	0.3	0.1	0.4	1.8	0.2	2.0
			3	0.7	0.1	0.8	1.0	0.2	1.2
			Mean	0.4	0.1	0.5	1.4	0.2	1.6
		W	1	0.3	0.2	0.5	1.2	0.2	1.5
			2	0.2	0.2	0.4	1.5	0.2	1.7
			3	0.1	0.2	0.3	1.0	0.2	1.2
			Mean	0.2	0.2	0.4	1.3	0.2	1.5
			Category Mean	0.3	0.1	0.5	1.4	0.2	1.6
			***Ecosystem Mean**	**0.4**	**0.2**	**0.6**	**1.4**	**0.3**	**1.7**

Appendix F. Table 6. Chps. II & III NH_4^+, NO_3^-, Total inorganic N (iN), and $WSOC_{FM}$ from Bulk soil, Root soil, and Total (0-5 cm) in SGS. *Ecosystem mean assumes 50 % grass and 50 % bare ground cover.

Microsite	Aspect	Site	Rep	NH_4^+ (g N m^{-2})	NO_3^- (g N m^{-2})	Total iN (g N m^{-2})	Bulk $WSOC_{FM}$ (g C m^{-2})	Root $WSOC_{FM}$ (g C m^{-2})	Total $WSOC_{FM}$ (g C m^{-2})
Bare	Flat	E	1	0.5	1.2	1.7	1.7	0.1	1.8
			2	0.7	1.6	2.4	3.8	0.2	4.0
			3	0.6	1.6	2.2	1.4	0.2	1.6
			Mean	0.6	1.5	2.1	2.3	0.2	2.5
		W	1	0.1	1.7	1.8	1.2	0.1	1.3
			2	0.6	2.5	3.1	1.9	0.2	2.1
			3	0.1	0.8	0.9	1.0	0.1	1.0
			Mean	0.2	1.7	1.9	1.4	0.1	1.5
	North	E	1	0.4	1.3	1.7	1.2	0.1	1.4
			2	0.1	0.8	0.9	1.4	0.1	1.6
			3	0.6	1.1	1.7	3.7	0.2	3.9
			Mean	0.4	1.1	1.4	2.1	0.1	2.3
		W	1	0.1	1.4	1.6	3.0	0.1	3.1
			2	0.3	1.3	1.7	1.5	0.1	1.6
			3	0.1	1.0	1.1	1.6	0.1	1.7
			Mean	0.2	1.3	1.4	2.0	0.1	2.1
			Category Mean	0.4	1.4	1.7	2.0	0.1	2.1
Grass	Flat	E	1	0.2	1.8	2.0	1.0	0.2	1.2
			2	0.2	1.1	1.3	1.7	0.1	1.8
			3	0.1	1.7	1.7	1.6	0.2	1.8
			Mean	0.2	1.5	1.7	1.4	0.2	1.6
		W	1	0.9	1.1	2.0	1.7	0.2	1.8
			2	0.1	1.9	1.9	0.9	0.1	1.1
			3	0.2	1.0	1.2	2.4	0.7	3.0
			Mean	0.4	1.3	1.7	1.7	0.3	2.0
	North	E	1	0.1	0.8	0.9	1.3	0.1	1.4
			2	0.1	0.7	0.8	1.5	0.1	1.6
			3	0.5	1.1	1.5	2.1	0.2	2.3
			Mean	0.2	0.9	1.1	1.6	0.1	1.8
		W	1	0.1	1.0	1.2	2.1	0.2	2.3
			2	0.1	2.6	2.7	2.1	0.4	2.6
			3	0.1	1.4	1.5	1.4	0.1	1.5
			Mean	0.1	1.7	1.8	1.9	0.3	2.1
			Category Mean	0.2	1.4	1.6	1.6	0.2	1.9
			***Ecosystem Mean**	**0.3**	**1.4**	**1.6**	**1.8**	**0.2**	**2.0**

Appendix F. Table 7. Chps. II & III NH_4^+, NO_3^-, Total inorganic N (iN), and $WSOC_{FM}$ from Bulk soil, Root soil, and Total (5-10 cm) in NMP. *Ecosystem mean assumes 50 % grass and 50 % bare ground cover.

Microsite	Aspect	Site	Rep	NH_4^+ (g N m^{-2})	NO_3^- (g N m^{-2})	Total iN (g N m^{-2})	Bulk $WSOC_{FM}$ (g C m^{-2})	Root $WSOC_{FM}$ (g C m^{-2})	Total $WSOC_{FM}$ (g C m^{-2})
Bare	Flat	E	1	0.0	0.3	0.3	1.9	0.2	2.0
			2	0.0	0.2	0.2	1.4	0.2	1.6
			3	0.1	0.2	0.3	1.2	0.1	1.3
			Mean	0.0	0.2	0.2	1.5	0.2	1.6
		W	1	0.0	0.2	0.3	1.6	0.2	1.8
			2	0.0	0.2	0.2	1.5	0.2	1.7
			3	0.1	0.2	0.2	1.2	0.1	1.3
			Mean	0.0	0.2	0.2	1.4	0.2	1.6
	North	E	1	0.2	0.2	0.4	1.2	0.1	1.3
			2	0.1	0.2	0.3	1.1	0.1	1.2
			3	0.2	0.2	0.5	1.2	0.0	1.3
			Mean	0.2	0.2	0.4	1.2	0.1	1.3
		W	1	0.0	0.2	0.2	1.6	0.3	1.9
			2	0.0	0.2	0.2	1.7	0.2	2.0
			3	0.1	0.2	0.2	1.4	0.2	1.6
			Mean	0.0	0.2	0.2	1.6	0.2	1.8
			Category Mean	0.1	0.2	0.3	1.4	0.2	1.6
Grass	Flat	E	1	0.1	0.2	0.3	1.2	0.2	1.5
			2	0.0	0.2	0.2	1.7	0.2	1.9
			3	0.1	0.2	0.3	0.9	0.1	1.0
			Mean	0.1	0.2	0.3	1.3	0.2	1.5
		W	1	0.1	0.2	0.3	1.5	0.2	1.7
			2	0.1	0.1	0.2	1.6	0.2	1.9
			3	0.1	0.2	0.2	1.5	0.2	1.6
			Mean	0.1	0.2	0.2	1.5	0.2	1.7
	North	E	1	0.1	0.2	0.3	1.1	0.2	1.3
			2	0.1	0.3	0.4	1.1	0.6	1.7
			3	0.4	0.2	0.6	1.1	0.1	1.2
			Mean	0.2	0.2	0.4	1.1	0.3	1.4
		W	1	0.1	0.2	0.4	1.5	0.1	1.6
			2	0.1	0.1	0.3	1.6	0.1	1.8
			3	0.3	0.2	0.5	1.4	0.1	1.5
			Mean	0.2	0.2	0.4	1.5	0.1	1.6
			Category Mean	0.1	0.2	0.3	1.4	0.2	1.6
		***Ecosystem Mean**		**0.1**	**0.2**	**0.3**	**1.4**	**0.2**	**1.6**

Appendix F. Table 8. Chps. II & III NH_4^+, NO_3^-, Total inorganic N (iN), and $WSOC_{FM}$ from Bulk soil, Root soil, and Total (5-10 cm) in SGS. *Ecosystem mean assumes 50 % grass and 50 % bare ground cover.

Microsite	Aspect	Site	Rep	NH_4^+ (g N m^{-2})	NO_3^- (g N m^{-2})	Total iN (g N m^{-2})	Bulk $WSOC_{FM}$ (g C m^{-2})	Root $WSOC_{FM}$ (g C m^{-2})	Total $WSOC_{FM}$ (g C m^{-2})
Bare	Flat	E	1	0.0	1.1	1.1	1.2	0.2	1.4
			2	0.1	1.3	1.3	0.9	0.1	1.0
			3	0.1	1.0	1.1	1.0	0.1	1.0
			Mean	0.1	1.1	1.2	1.0	0.1	1.1
		W	1	0.0	0.7	0.8	1.0	0.1	1.1
			2	0.0	0.9	1.0	1.3	0.1	1.4
			3	0.0	1.4	1.5	1.1	0.2	1.2
			Mean	0.0	1.0	1.1	1.1	0.1	1.2
	North	E	1	0.0	1.0	1.0	1.3	0.1	1.3
			2	0.0	1.0	1.1	0.9	0.1	1.0
			3	0.0	0.6	0.6	1.0	0.1	1.1
			Mean	0.0	0.9	0.9	1.1	0.1	1.1
		W	1	0.0	0.7	0.8	1.4	0.1	1.5
			2	0.1	0.8	0.9	1.3	0.1	1.3
			3	0.1	0.8	0.9	2.3	0.1	2.4
			Mean	0.1	0.8	0.8	1.7	0.1	1.8
			Category Mean	0.1	0.9	1.0	1.2	0.1	1.3
Grass	Flat	E	1	0.2	0.7	0.9	1.2	0.1	1.2
			2	0.1	0.9	1.0	0.9	0.1	1.0
			3	0.0	1.1	1.2	2.1	0.1	2.2
			Mean	0.1	0.9	1.0	1.4	0.1	1.5
		W	1	0.0	0.8	0.9	1.2	0.1	1.3
			2	0.1	2.5	2.5	1.1	0.1	1.2
			3	0.0	0.9	1.0	1.2	0.2	1.4
			Mean	0.0	1.4	1.5	1.2	0.1	1.3
	North	E	1	0.1	2.6	2.7	1.3	0.1	1.4
			2	0.0	0.6	0.6	1.2	0.1	1.3
			3	0.0	1.0	1.1	1.7	0.1	1.8
			Mean	0.1	1.4	1.5	1.4	0.1	1.5
		W	1	0.1	0.5	0.6	1.6	0.1	1.7
			2	0.1	0.7	0.8	2.2	0.2	2.4
			3	0.1	1.1	1.2	1.5	0.1	1.6
			Mean	0.1	0.8	0.9	1.8	0.1	1.9
			Category Mean	0.1	1.1	1.2	1.4	0.1	1.6
			***Ecosystem Mean**	**0.1**	**1.0**	**1.1**	**1.3**	**0.1**	**1.4**

Appendix F. Table 9. Chp. II Concentrations of $WSOC_{FM}$, $WSOC_{OD}$, WSN_{OD}, and Net N Mineralization from 21-day aerobic incubation of composite samples (reps 1-3) from bulk soil (0-5 cm) in Northern mixed prairie (NMP) and Shortgrass steppe (SGS) Ecosystems. *Ecosystem mean assumes that ground cover is 50% bare ground and 50% grass.

Ecosystem	Microsite	Aspect	Site	$WSOC_{FM}$ (ug C g^{-1} soil)	$WSOC_{OD}$ (ug C g^{-1} soil)	WSN_{OD} (ug N g^{-1} soil)	Net N Mineralization (ug N g^{-1} soil 21 $days^{-1}$)
NMP	Bare	Flat	E	27.2	90.2	9.6	17
			W	19.4	102.3	12.6	16
			Mean	23.3	96.2	11.1	17
		North	E	20.1	82.7	13.9	15
			W	19.2	109.4	9.0	17
			Mean	19.6	96.0	11.5	16
		Category Mean		21.5	96.1	11.3	17
	Grass	Flat	E	21.8	105.2	9.8	19
			W	21.6	120.8	9.8	16
			Mean	21.7	113.0	9.8	17
		North	E	22.3	105.9	11.3	17
			W	19.5	139.7	10.3	22
			Mean	20.9	122.8	10.8	20
		Category Mean		21.3	117.9	10.3	18
		***Ecosystem Mean**		**21.4**	**107.0**	**10.8**	**18**
SGS	Bare	Flat	E	20.0	57.3	21.7	15
			W	33.5	103.2	17.9	14
			Mean	26.7	80.2	19.8	14
		North	E	28.0	71.1	13.8	14
			W	31.5	90.3	15.4	19
			Mean	29.7	80.7	14.6	16
		Category Mean		28.2	80.5	17.2	15
	Grass	Flat	E	24.8	68.2	13.7	13
			W	22.3	103.7	21.2	22
			Mean	23.5	86.0	17.5	17
		North	E	28.0	93.0	14.0	17
			W	24.7	103.7	14.8	17
			Mean	26.3	98.3	14.4	17
		Category Mean		24.9	92.2	15.9	17
		***Ecosystem Mean**		**26.6**	**86.3**	**16.6**	**16**

Appendix F. Table 10. Chp. II Concentrations of $WSOC_{FM}$, $WSOC_{OD}$, WSN_{OD}, and Net N Mineralization from 21-day aerobic incubation of composite samples (reps 1-3) from bulk soil (5-10 cm) in Northern mixed prairie (NMP) and Shortgrass steppe (SGS) Ecosystems. *Ecosystem mean assumes that ground cover is 50% bare ground and 50% grass.

Ecosystem	Microsite	Aspect	Site	$WSOC_{FM}$ (ug C g^{-1} soil)	$WSOC_{OD}$ (ug C g^{-1} soil)	WSN_{OD} (ug N g^{-1} soil)	Net N Mineralization (ug N g^{-1} soil 21 $days^{-1}$)
NMP	Bare	Flat	E	21.8	121.9	8.5	15
			W	19.6	132.4	8.3	15
			Mean	20.7	127.1	8.4	15
		North	E	17.5	128.6	10.6	17
			W	23.2	121.7	8.3	14
			Mean	20.4	125.1	9.4	16
		Category Mean		20.5	126.1	8.9	15
	Grass	Flat	E	19.1	117.1	7.8	13
			W	21.7	112.1	7.4	14
			Mean	20.4	114.6	7.6	13
		North	E	15.9	127.6	9.7	20
			W	21.1	133.7	9.5	15
			Mean	18.5	130.6	9.6	18
		Category Mean		19.5	122.6	8.6	15
		***Ecosystem Mean**		**20.7**	**124.7**	**8.6**	**15**
SGS	Bare	Flat	E	14.6	73.6	12.0	12
			W	16.0	86.3	12.0	15
			Mean	15.3	79.9	12.0	14
		North	E	14.7	78.8	12.3	15
			W	24.7	91.3	15.6	12
			Mean	19.7	85.0	14.0	13
		Category Mean		17.5	82.5	13.0	13
	Grass	Flat	E	19.1	86.3	11.6	12
			W	17.1	87.4	13.9	14
			Mean	18.1	86.8	12.7	13
		North	E	20.0	89.3	13.4	16
			W	26.2	129.1	14.6	23
			Mean	23.1	109.2	14.0	19
		Category Mean		20.6	98.0	13.4	16
		***Ecosystem Mean**		**19.0**	**90.2**	**13.2**	**15**

Appendix F. Table 11. Chp. II CO_2-C Evolution Rates from 21-day aerobic incubation of composite samples (reps 1-3) From bulk soil (0-5 cm) in Northern mixed prairie (NMP) and Shortgrass steppe (SGS) Ecosystems. *Ecosystem mean assumes that ground cover is 50% bare ground and 50% grass.

				CO_2 Evolution Rates			
Ecosystem	Microsite	Aspect	Site	0-3 day mean (ug C g^{-1} soil day^{-1})	3-10 day mean (ug C g^{-1} soil day^{-1})	21 day mean (ug C g^{-1} soil day^{-1})	Cummulative (ug C g^{-1} soil 21 $days^{-1}$)
NMP	Bare	Flat	E	30.8	12.8	12.8	268
			W	39.5	13.6	13.8	290
			Mean	35.2	13.2	13.3	279
		North	E	36.2	12.9	13.8	289
			W	32.9	13.3	12.8	269
			Mean	34.5	13.1	13.3	279
		Category Mean		34.8	13.2	13.3	279
	Grass	Flat	E	35.6	13.7	13.7	288
			W	39.3	12.3	13.2	278
			Mean	37.4	13.0	13.5	283
		North	E	32.6	11.2	11.7	246
			W	44.5	16.2	15.9	334
			Mean	38.6	13.7	13.8	290
		Category Mean		38.0	13.3	13.6	286
		***Ecosystem Mean**		**36.4**	**13.3**	**13.5**	**283**
SGS	Bare	Flat	E	21.6	7.6	7.6	159
			W	18.0	8.9	9.0	189
			Mean	19.8	8.3	8.3	174
		North	E	18.6	9.2	8.1	170
			W	21.6	10.5	9.2	194
			Mean	20.1	9.9	8.7	182
		Category Mean		19.9	9.1	8.5	178
	Grass	Flat	E	22.4	9.1	8.9	187
			W	28.8	12.8	11.9	249
			Mean	25.6	11.0	10.4	218
		North	E	22.7	11.8	10.2	213
			W	23.4	11.1	10.1	213
			Mean	23.1	11.4	10.1	213
		Category Mean		24.3	11.2	10.3	216
		***Ecosystem Mean**		**22.1**	**10.1**	**9.4**	**197**

Appendix F. Table 12. Chp. II CO_2-C Evolution Rates from 21-day aerobic incubations of composite samples (reps 1-3) From bulk soil (5-10 cm) in Northern mixed prairie (NMP) and Shortgrass steppe (SGS) Ecosystems. *Ecosystem mean assumes that ground cover is 50% bare ground and 50% grass.

				CO_2 Evolution Rates			
Ecosystem	Microsite	Aspect	Site	0-3 day mean (ug C g^{-1} soil day^{-1})	3-10 day mean (ug C g^{-1} soil day^{-1})	21 day mean (ug C g^{-1} soil day^{-1})	Cummulative (ug C g^{-1} soil 21 $days^{-1}$)
NMP	Bare	Flat	E	30.9	11.1	11.4	239
			W	39.7	10.6	12.6	265
			Mean	35.3	10.9	12.0	252
		North	E	33.7	10.9	11.7	247
			W	32.3	10.0	11.0	231
			Mean	33.0	10.4	11.4	239
		Category Mean		34.2	10.6	11.7	245
	Grass	Flat	E	25.9	9.3	10.1	212
			W	27.8	9.7	10.5	220
			Mean	26.9	9.5	10.3	216
		North	E	37.8	12.4	13.3	280
			W	33.1	12.2	12.4	261
			Mean	35.5	12.3	12.9	270
		Category Mean		31.2	10.9	11.6	243
		***Ecosystem Mean**		**33.0**	**10.7**	**11.6**	**244**
SGS	Bare	Flat	E	21.5	7.6	7.6	159
			W	21.2	7.8	7.7	162
			Mean	21.3	7.7	7.6	160
		North	E	19.8	8.0	7.4	156
			W	18.0	8.0	7.5	158
			Mean	18.9	8.0	7.5	157
		Category Mean		20.1	7.8	7.6	159
	Grass	Flat	E	24.1	9.0	8.5	180
			W	21.6	10.0	8.5	179
			Mean	22.8	9.5	8.5	179
		North	E	20.1	9.3	8.2	173
			W	32.1	8.6	11.2	235
			Mean	26.1	9.0	9.7	204
		Category Mean		24.5	9.2	9.1	192
		***Ecosystem Mean**		**22.3**	**8.5**	**8.3**	**175**

Appendix F. Table 13. Percentage of total WSOC $_{FM}$ (0-10 cm) from Bulk soil, Roots (rhizoplane soil), Crowns and concentration in crown-associated soil (0-10 cm) in Northern mixed prairie (NMP). *Ecosystem mean assumes that ground cover is 50% bare ground and 50% grass.

Microsite	Aspect	Site	Rep	WSOC $_{FM}$ from Bulk (%)	WSOC $_{FM}$ from Roots (%)	WSOC $_{FM}$ from Crown (%)	Crown WSOC $_{FM}$ (ug C g^{-1} soil)
Bare	Flat	E	1	87	13	-	-
			2	84	16	-	-
			3	86	14	-	-
			Mean	86	14	-	-
		W	1	83	17	-	-
			2	88	12	-	-
			3	89	11	-	-
			Mean	86	14	-	-
	North	E	1	84	16	-	-
			2	90	10	-	-
			3	87	13	-	-
			Mean	87	13	-	-
		W	1	77	23	-	-
			2	89	11	-	-
			3	81	19	-	-
			Mean	83	17	-	-
		Category Mean		85	15	-	-
Grass	Flat	E	1	65	13	22	113
			2	80	9	11	60
			3	32	6	62	193
			Mean	59	9	32	122
		W	1	66	13	21	75
			2	62	11	28	137
			3	63	9	29	167
			Mean	64	11	26	126
	North	E	1	66	10	24	52
			2	69	19	12	31
			3	68	10	22	72
			Mean	68	13	19	52
		W	1	74	9	17	47
			2	75	9	16	64
			3	66	8	26	46
			Mean	72	9	19	52
		Category Mean		66	10	24	88
		***Ecosystem Mean**		**75**	**13**	**12**	-

Appendix F. Table 14. Percentage of total $WSOC_{FM}$ (0-10 cm) from Bulk soil, Roots (rhizoplane soil), Crowns and concentration in crown-associated soil (0-10 cm) in Shortgrass steppe (SGS). * Ecosystem mean assumes that ground cover is 50% bare ground and 50% grass.

Microsite	Aspect	Site	Rep	$WSOC_{FM}$ from Bulk (%)	$WSOC_{FM}$ from Root (%)	$WSOC_{FM}$ from Crown (%)	Crown $WSOC_{FM}$ (ug C g^{-1} soil)
Bare	Flat	E	1	90	10	-	-
			2	91	9	-	-
			3	93	7	-	-
			Mean	92	8	-	-
		W	1	93	7	-	-
			2	95	5	-	-
			3	88	12	-	-
			Mean	92	8	-	-
	North	E	1	96	4	-	-
			2	91	9	-	-
			3	93	7	-	-
			Mean	93	7	-	-
		W	1	93	7	-	-
			2	93	7	-	-
			3	96	4	-	-
			Mean	94	6	-	-
		Category Mean		93	7	-	-
Grass	Flat	E	1	69	6	25	68
			2	43	6	51	149
			3	75	13	12	56
			Mean	62	8	29	91
		W	1	72	8	20	50
			2	57	4	39	82
			3	66	8	26	75
			Mean	65	7	28	69
	North	E	1	73	8	19	73
			2	64	10	26	90
			3	69	6	25	88
			Mean	69	8	24	83
		W	1	76	7	17	44
			2	77	6	16	54
			3	68	5	27	119
			Mean	74	6	20	72
		Category Mean		67	7	25	79
		***Ecosystem Mean**		**80**	**7**	**13**	-

Appendix F. Table 15. P-values for Chapter II Table 1 ANOVA comparison of root mass, total C and N, and labile C and N (g m^{-2}) in the soil profiles (0-10 cm) of Northern mixed prairie (NMP) and Shortgrass steppe (SGS).

Depth (cm)	Root Mass (g m^{-2})		SOC (g C m^{-2})		TN (g N m^{-2})		NH_4^+ (g N m^{-2})		NO_3^- (g N m^{-2})		Total iN (g N m^{-2})		$WSOC_{FM}$ (g C m^{-2})	
	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS
0 – 5	.0122		.0002		.0001		.0295		.0001		.0001		.0011	
5 – 10	.0066		.2049		.4357		.0922		.0001		.0001		.5434	
0 - 10	.0039		.0018		.0053		.0114		.0001		.0001		.0131	

Appendix F. Table 16. P-values for Chapter II Table 2 ANOVA comparisons of field soil properties and CO_2 evolution of grass-occupied (Grass) and bare-ground (Bare) microsites during 21-day aerobic incubations.

Depth (cm)	% H_2O (g/g)		BD		$WSOC_{OD}$ (ug g^{-1} soil)		$WSOC_{OD}$ / WSN_{OD}		$WSOC_{OD}$ - $WSOC_{FM}$ (ug g^{-1} soil difference)		ug CO_2-C g^{-1} soil day^{-1} 0-3 days		ug CO_2-C g^{-1} soil day^{-1} 3-10 days		ug CO_2-C g^{-1} soil day^{-1} 21 day mean	
	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass
0 – 5	.0004		.0004		.0591		.0676		.0330		.0524		.1505		.0962	
5 – 10	.4806		.1852		.3424		.3713		.3927		.7691		.0894		.2215	
0-10	.0187		.0083		.1144		.1658		.1505		-		-		-	

Appendix F. Table 17. P-values for Chapter II Table 3 incubation and $WSOC_{OD}$ and WSN_{OD} data with ratios for composite soil samples (0-5 and 5-10 cm).

Depth (cm)	ug CO_2-C g^{-1} soil day^{-1} 0-3 days		ug CO_2-C g^{-1} soil day^{-1} 3-10 days		ug CO_2-C g^{-1} soil day^{-1} 21 day mean		$WSOC_{OD}$ (ug g^{-1} soil)		WSN_{OD} (ug g^{-1} soil)		$WSOC_{OD}$ / WSN_{OD}		$WSOC_{OD}$ / $WSOC_{FM}$		$WSOC_{OD}$ - $WSOC_{FM}$ (ug g^{-1} soil difference)	
	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS	NMP	SGS
0 – 5	.0001		.0012		.0001		.0275		.0008		.0001		.0011		.0053	
5 – 10	.0006		.0002		.0001		.0001		.0001		.0001		.0036		.0001	

Appendix F. Table 18. P-values for Chapter III Table 1 ANOVA comparisons of $WSOC_{FM}$ from rhizoplane soil (roots), Total $WSOC_{FM}$ belowground, percentage from rhizoplane (Roots) belowground (0-10 cm) and percentage of SOC which is soluble of Northern mixed prairie (NMP) and Shortgrass steppe (SGS).

Depth (cm)	Rhizoplane -$WSOC_{FM}$	Total $WSOC_{FM}$	Belowground % from rhizoplane	Total $WSOC_{FM}$ / SOC (x100)
	($g\ C\ m^{-2}$)	($g\ C\ m^{-2}$)	(%)	(%)
	NMP SGS	NMP SGS	NMP SGS	NMP SGS
0 – 5	.0682	.0043	.0001	.0001
5 – 10	.0056	.1739	.0250	.2890
0 - 10	.0035	.0650	.0001	.0004

Appendix F. Table 19. P-values for Chapter III Table 2 ANOVA comparisons of microsites for Total SOC, $WSOC_{FM}$ from rhizoplane soil, percentage from rhizoplane (roots) belowground (0-10 cm) and percentage of SOC which is soluble in Northern mixed prairie (NMP) and Shortgrass steppe (SGS) .

Depth (cm)	SOC ($g\ m^{-2}$)		Bulk $WSOC_{FM}$ ($g\ m^{-2}$)		**Rhizoplane - $WSOC_{FM}$ ($g\ m^{-2}$)		Total $WSOC_{FM}$ ($g\ m^{-2}$)		*Belowground % from rhizoplane (%)		Total $WSOC_{FM}$ / SOC (x100) (%)	
	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass	Bare	Grass
0 – 5	.7785		.0683		.2916		.0548		.9955		.1135	
5 – 10	.0603		.5586		.2793		.3439		.3678		.6000	
0 - 10	.1111		.2575		.8690		.2805		.5067		.0561	

Appendix F. Table 20. P-values and means for Chapter III Table 3 ANOVA comparisons of the percentage of total $WSOC_{FM}$ in the plant-soil system (0- 10 cm) of soil of grass-occupied (Grass) and bare-ground (Bare) microsites by system for Northern mixed prairie (NMP) and Shortgrass steppe (SGS).

Microsite	Grass			Bare			Mean		
Soil fraction	NMP	SGS	Ave	NMP	SGS	Ave	NMP	SGS	Ave
Bulk soil	65.5	67.4	66.5	85.3	92.8	89.0	75.4	80.1	77.7
System p-value	**.6587**			**.0295**			**.0423**		
Microsite p-value						.0001			
Rhizoplane	10.4	7.3	8.8	14.7	7.2	11.0	12.5	7.2	9.9
System p-value	**.0168**			**.0001**			**.0001**		
Microsite p-value				.0001		.0164			
Crowns	24.1	25.3		-	-	-	-	-	-
System p-value	**.8031**								

Note: System comparisons in bold indicate system differences within the given microsite; Microsite p-values indicate that Bare and Grass microsites differ within the system (NMP) or on average (Ave). No Microsite comparison exists for Crowns.

Appendix G

Raw Data, Means, and P-values Tables for Chapter IV

Appendix G. Table 1. Chp. IV 2001 Abundance (% Cover) of C_3 Grass, C_4 Grass, Sedge (C_3), Shrub, Litter, Bare Ground, and Total Plant Cover by Treatment.

			(%)						
Treatment	Aspect	Rep	C_3 Grass	C_4 Grass	Sedge (C_3)	Shrub	Litter	Bare Ground	Total Plant Cover
Rest (1993)	Flat	1	22	27	4	8	26	8	66
		2	29	20	3	5	24	9	68
		3	30	4	2	18	25	5	71
		4	30	5	24	5	22	6	73
		5	32	7	8	4	24	12	65
		Mean	29	13	8	8	24	8	68
	North	1	32	3	21	0	20	10	71
		2	29	5	16	20	18	5	78
		3	28	10	19	0	20	11	69
		4	19	9	28	3	27	9	65
		5	32	13	5	1	28	11	62
		Mean	28	8	18	5	22	9	69
	Treatment Mean		**28**	**10**	**13**	**6**	**23**	**8**	**68**
Rest (2000)	Flat	1	26	27	3	4	19	20	62
		2	18	9	22	5	14	26	61
		3	22	26	10	3	16	16	68
		4	26	13	19	1	19	13	69
		5	21	20	13	9	19	13	69
		Mean	22	19	13	4	17	17	66
	North	1	25	24	9	2	20	15	66
		2	28	10	25	0	23	13	65
		3	31	26	10	2	15	14	72
		4	32	11	18	5	23	11	67
		5	33	21	1	5	22	15	64
		Mean	30	18	12	2	20	13	67
	Treatment Mean		**26**	**19**	**13**	**3**	**19**	**15**	**66**
Grazed	Flat	1	16	15	6	4	11	47	43
		2	14	25	9	12	15	25	61
		3	12	14	18	7	12	37	52
		4	24	33	1	1	12	30	59
		5	16	30	4	8	15	27	59
		Mean	16	23	7	6	13	33	54
	North	1	23	25	8	5	16	24	60
		2	12	23	13	6	12	31	58
		3	17	26	15	4	10	27	64
		4	25	14	13	3	15	30	56
		5	20	17	0	12	10	40	51
		Mean	19	21	10	6	12	30	58
	Treatment Mean		**18**	**22**	**8**	**6**	**12**	**32**	**56**

Appendix G. Table 2. Chp. IV 2002 Abundance (% Cover) of C_3 Grass, C_4 Grass, Sedge (C_3), Shrub, Litter, Bare Ground, and Total Plant Cover by Treatment.

			(%)						
Treatment	Aspect	Rep	C_3 Grass	C_4 Grass	Sedge (C_3)	Shrub	Litter	Bare Ground	Total Plant Cover
Rest (1993)	Flat	1	31	30	9	1	17	11	73
		2	46	12	2	16	11	2	87
		3	45	15	4	1	21	6	74
		4	42	10	5	4	19	5	76
		5	34	4	15	17	22	6	73
		Mean	39	14	7	8	18	6	76
	North	1	46	8	3	3	31	4	66
		2	42	4	16	1	27	4	70
		3	36	6	9	2	29	15	56
		4	29	4	24	9	29	3	69
		5	36	13	11	2	27	8	66
		Mean	38	7	12	3	28	7	65
	Treatment Mean		**38**	**10**	**10**	**5**	**23**	**6**	**71**
Rest (2000)	Flat	1	48	23	6	3	11	9	81
		2	13	32	10	13	10	22	69
		3	37	12	8	14	15	9	77
		4	43	28	1	3	15	8	78
		5	39	19	8	2	14	16	71
		Mean	36	23	6	7	13	12	75
	North	1	36	25	4	2	12	18	70
		2	31	7	10	15	11	25	65
		3	42	8	19	5	11	12	78
		4	42	7	16	7	8	15	78
		5	52	4	3	18	11	9	80
		Mean	40	10	10	9	11	16	74
	Treatment Mean		**38**	**16**	**8**	**8**	**12**	**14**	**74**
Grazed	Flat	1	20	35	6	11	7	22	72
		2	20	25	13	11	7	19	75
		3	23	15	22	7	6	26	68
		4	16	24	2	21	16	13	72
		5	20	21	8	13	17	18	66
		Mean	20	24	10	12	10	19	70
	North	1	14	40	19	10	5	11	85
		2	23	26	21	5	9	17	74
		3	26	15	7	1	5	40	56
		4	24	31	21	0	7	16	78
		5	25	40	5	7	8	14	79
		Mean	22	30	14	4	7	19	74
	Treatment Mean		**21**	**27**	**12**	**8**	**9**	**19**	**72**

Appendix G. Table 3. Chp. IV 2003 Abundance (% Cover) of C_3 Grass, C_4 Grass, Sedge (C_3), Shrub, Litter, Bare Ground, and Total Plant Cover by Treatment.

			(%)						
Treatment	Aspect	Rep	C_3 Grass	C_4 Grass	Sedge (C_3)	Shrub	Litter	Bare Ground	Total Plant Cover
Rest (1993)	Flat	1	33	17	0	12	30	5	64
		2	35	22	0	9	28	3	69
		3	40	12	2	5	21	5	60
		4	28	18	1	8	28	4	60
		5	23	3	7	0	52	5	35
		Mean	32	14	2	7	32	4	58
	North	1	18	2	19	5	15	32	46
		2	33	5	10	2	36	8	51
		3	44	6	5	0	33	1	62
		4	40	7	16	0	20	12	64
		5	48	1	8	0	33	4	58
		Mean	37	4	12	1	27	11	56
	Treatment Mean		**34**	**9**	**7**	**4**	**30**	**8**	**58**
Rest (2000)	Flat	1	29	12	8	0	30	18	50
		2	28	7	13	3	23	13	63
		3	30	8	12	19	24	11	70
		4	28	10	12	6	23	18	57
		5	21	6	7	27	34	2	63
		Mean	27	9	10	11	27	12	61
	North	1	43	5	0	10	17	19	59
		2	15	8	6	9	18	50	39
		3	25	20	11	5	21	10	62
		4	27	13	11	0	28	11	52
		5	35	8	0	11	13	26	56
		Mean	29	11	6	7	19	23	54
	Treatment Mean		**28**	**10**	**8**	**9**	**24**	**18**	**58**
Grazed	Flat	1	9	26	9	1	13	41	46
		2	7	33	10	12	8	29	63
		3	12	31	9	6	21	16	51
		4	7	42	7	1	16	23	49
		5	6	18	25	4	3	42	54
		Mean	8	30	12	5	12	30	53
	North	1	8	21	15	0	24	30	46
		2	10	30	2	22	21	21	67
		3	4	53	0	4	26	11	47
		4	9	40	0	17	11	20	52
		5	13	18	2	4	29	30	39
		Mean	9	32	4	9	22	22	50
	Treatment Mean		**9**	**31**	**8**	**7**	**17**	**26**	**51**

Appendix G. Table 4. Chp. IV Soil Water, Root Biomass, Organic C, Total N, and C:N Ratio of soil (0-5 cm depth) by Treatment in 2001.

Treatment	Microsite	Aspect	Rep	Soil Water % (g/g)	Root biomass (gm^{-2})	Organic C (%)	Total N (%)	C : N Ratio Org C/ Total N
Rest (1993)	Bare	Flat	1	1.7	249	1.31	0.13	9.8
			2	1.5	336	1.19	0.12	9.7
			3	1.2	859	1.24	0.11	11.1
			Mean	1.5	481	1.25	0.12	10.2
		North	1	1.6	316	1.04	0.11	9.2
			2	1.5	562	1.29	0.13	9.9
			3	1.7	443	1.32	0.13	10.5
			Mean	1.6	440	1.21	0.12	9.8
	Grass	Flat	1	1.6	621	1.07	0.11	9.7
			2	2.1	573	1.35	0.12	11.1
			3	1.9	729	1.04	0.11	9.9
			Mean	1.9	641	1.16	0.11	10.2
		North	1	2.1	825	1.18	0.12	9.8
			2	2.3	1331	1.00	0.11	9.2
			3	2.7	1000	0.93	0.10	9.8
			Mean	2.4	1052	1.04	0.11	9.6
		Treatment mean		**1.8**	**653**	**1.16**	**0.12**	**10.0**
Rest (2000)	Bare	Flat	1	1.5	344	0.90	0.09	9.6
			2	1.8	779	1.17	0.11	10.3
			3	2.0	323	0.94	0.09	10.1
			Mean	1.8	482	1.00	0.10	10.0
		North	1	1.6	176	1.15	0.11	10.2
			2	1.7	128	1.13	0.11	10.2
			3	2.4	256	1.15	0.12	10.0
			Mean	1.9	187	1.14	0.11	10.1
	Grass	Flat	1	2.0	672	1.02	0.10	10.2
			2	1.9	396	1.11	0.11	10.3
			3	1.7	650	1.03	0.10	10.0
			Mean	1.9	573	1.05	0.10	10.2
		North	1	2.3	395	0.99	0.11	8.8
			2	2.8	855	0.95	0.10	9.6
			3	2.0	384	1.19	0.12	10.2
			Mean	2.4	545	1.04	0.11	9.5
		Treatment mean		**2.0**	**447**	**1.06**	**0.11**	**9.9**
Grazed	Bare	Flat	1	2.0	281	1.16	0.12	9.5
			2	1.9	618	0.94	0.10	9.0
			3	2.2	434	1.11	0.12	9.5
			Mean	2.0	444	1.07	0.11	9.3
		North	1	2.1	200	1.22	0.12	10.0
			2	1.8	277	1.31	0.11	11.8
			3	2.1	135	1.08	0.12	8.8
			Mean	2.0	204	1.20	0.12	10.2
	Grass	Flat	1	2.0	678	1.04	0.11	9.3
			2	2.9	745	1.00	0.11	9.0
			3	2.6	758	1.20	0.12	10.3
			Mean	2.5	727	1.08	0.11	9.5
		North	1	2.5	257	1.13	0.12	9.8
			2	2.2	484	1.06	0.11	9.7
			3	2.6	285	0.94	0.11	8.8
			Mean	2.4	342	1.04	0.11	9.4
		Treatment mean		**2.2**	**429**	**1.10**	**0.11**	**9.6**

Appendix G. Table 5. Chp. IV Soil Water, Root Biomass, Organic C, Total N, and C:N Ratio of soil (0-5 cm depth) by Treatment in 2002.

Treatment	Microsite	Aspect	Rep	Soil Water % (g/g)	Root biomass (gm^{-2})	Organic C (%)	Total N (%)	C : N Ratio Org C/ Total N
Rest (1993)	Bare	Flat	1	4.2	404	0.98	0.10	10.2
			2	5.6	355	1.29	0.12	10.6
			3	4.6	439	1.25	0.12	10.5
			Mean	4.8	400	1.17	0.11	10.4
		North	1	4.1	520	1.25	0.13	10.0
			2	5.1	517	1.26	0.13	10.1
			3	4.5	308	1.19	0.12	9.7
			Mean	4.5	448	1.23	0.12	9.9
	Grass	Flat	1	5.5	1051	1.06	0.11	9.9
			2	5.4	1670	1.22	0.12	10.3
			3	4.8	1023	1.27	0.12	10.8
			Mean	5.2	1248	1.18	0.11	10.3
		North	1	6.2	917	1.35	0.13	10.4
			2	5.2	660	1.04	0.11	9.5
			3	5.1	630	1.22	0.11	10.9
			Mean	5.5	736	1.20	0.12	10.2
		Treatment mean		**5.0**	**708**	**1.20**	**0.12**	**10.2**
Rest (2000)	Bare	Flat	1	4.8	409	0.93	0.10	9.1
			2	3.9	1032	1.28	0.12	10.7
			3	5.8	457	1.09	0.12	9.5
			Mean	4.8	633	1.10	0.11	9.8
		North	1	5.0	1398	0.96	0.10	9.7
			2	5.4	379	1.20	0.12	10.2
			3	4.5	438	1.11	0.11	10.2
			Mean	5.0	738	1.09	0.11	10.0
	Grass	Flat	1	4.4	372	1.15	0.11	10.6
			2	4.6	1878	1.56	0.14	11.6
			3	5.7	977	1.22	0.12	10.2
			Mean	4.9	1075	1.31	0.12	10.8
		North	1	5.6	871	1.17	0.11	10.5
			2	6.5	668	1.28	0.12	10.5
			3	5.2	908	1.25	0.12	10.6
			Mean	5.8	816	1.23	0.12	10.5
		Treatment mean		**5.1**	**816**	**1.18**	**0.11**	**10.3**
Grazed	Bare	Flat	1	4.9	264	1.14	0.11	10.5
			2	4.8	825	1.17	0.12	9.7
			3	4.9	521	0.91	0.10	9.6
			Mean	4.8	536	1.07	0.11	9.9
		North	1	4.7	856	1.16	0.11	10.5
			2	3.9	864	1.35	0.13	10.2
			3	4.0	1157	1.26	0.12	10.2
			Mean	4.2	959	1.26	0.12	10.3
	Grass	Flat	1	6.2	1408	1.07	0.11	9.6
			2	6.1	1386	1.15	0.11	10.6
			3	4.9	732	1.31	0.13	10.3
			Mean	5.7	1175	1.17	0.12	10.2
		North	1	5.5	1280	1.06	0.10	10.5
			2	5.7	470	1.34	0.13	10.3
			3	5.0	1020	1.42	0.14	10.4
			Mean	5.4	923	1.27	0.12	10.4
		Treatment mean		**5.0**	**899**	**1.19**	**0.12**	**10.2**

Appendix G. Table 6. Chp. IV Soil Water, Organic C, Total N, and C:N Ratio of soil (0-5 cm depth) by Treatment in 2003. No Root Biomass data were available for this collection date.

Treatment	Microsite	Aspect	Rep	Soil Water % (g/g)	Organic C (%)	Total N (%)	C : N Ratio Org C/ Total N
Rest (1993)	Bare	Flat	1	16.4	1.06	0.12	8.8
			2	18.3	1.20	0.13	9.3
			3	14.7	1.07	0.11	9.5
			Mean	16.5	1.11	0.12	9.2
		North	1	18.2	1.34	0.14	9.9
			2	14.3	1.16	0.14	8.3
			3	17.9	1.22	0.15	8.4
			Mean	16.8	1.24	0.14	8.9
	Grass	Flat	1	16.4	1.33	0.13	10.4
			2	16.3	1.35	0.12	11.1
			3	15.7	0.97	0.11	8.8
			Mean	16.1	1.22	0.12	10.1
		North	1	16.2	1.05	0.12	8.5
			2	17.4	0.78	0.12	6.5
			3	16.7	0.93	0.12	7.9
			Mean	16.8	0.92	0.12	7.6
		Treatment mean		**16.5**	**1.12**	**0.13**	**8.9**
Rest (2000)	Bare	Flat	1	17.5	1.62	0.16	10.3
			2	15.3	0.98	0.11	9.1
			3	15.7	0.99	0.11	8.9
			Mean	16.2	1.20	0.13	9.4
		North	1	17.5	0.82	0.10	7.9
			2	15.8	0.69	0.12	5.6
			3	13.7	1.36	0.15	9.1
			Mean	15.7	0.96	0.13	7.5
	Grass	Flat	1	17.3	1.01	0.12	8.4
			2	16.3	1.04	0.12	9.0
			3	14.9	1.33	0.13	10.5
			Mean	16.2	1.13	0.12	9.3
		North	1	17.2	1.18	0.13	9.4
			2	15.6	1.44	0.16	9.1
			3	17.0	0.92	0.11	8.3
			Mean	16.6	1.18	0.13	8.9
		Treatment mean		**16.1**	**1.12**	**0.13**	**8.8**
Grazed	Bare	Flat	1	17.1	1.50	0.16	9.3
			2	15.0	1.63	0.14	11.9
			3	16.0	1.07	0.12	8.8
			Mean	16.0	1.40	0.14	10.0
		North	1	17.3	1.21	0.13	9.3
			2	16.7	1.19	0.13	9.4
			3	17.1	1.42	0.15	9.4
			Mean	17.0	1.27	0.14	9.4
	Grass	Flat	1	16.1	1.20	0.13	9.0
			2	15.0	0.95	0.10	9.6
			3	14.5	0.98	0.12	8.5
			Mean	15.2	1.04	0.12	9.0
		North	1	15.5	0.85	0.10	8.2
			2	16.6	0.92	0.11	8.1
			3	13.0	0.93	0.13	7.4
			Mean	15.0	0.90	0.11	7.9
		Treatment mean		**15.8**	**1.15**	**0.13**	**9.1**

Appendix G. Table 7. Chp. IV Soil Water, Root Biomass, Organic C, Total N, and C:N Ratio of soil (5-10 cm depth) by Treatment in 2001.

Treatment	Microsite	Aspect	Rep	Soil Water % (g/g)	Root biomass (gm^{-2})	Organic C (%)	Total N (%)	C : N Ratio Org C/ Total N
Rest (1993)	Bare	Flat	1	2.7	66	0.83	0.10	8.6
			2	3.3	198	0.79	0.10	8.0
			3	3.5	602	0.69	0.08	8.5
			Mean	3.2	289	0.77	0.09	8.4
		North	1	3.3	347	0.79	0.08	9.6
			2	3.2	438	0.91	0.10	9.1
			3	3.8	212	0.70	0.09	8.1
			Mean	3.4	332	0.80	0.09	8.9
	Grass	Flat	1	3.0	79	0.75	0.09	8.3
			2	3.8	219	0.88	0.10	8.7
			3	4.0	428	0.80	0.09	9.2
			Mean	3.6	242	0.81	0.09	8.7
		North	1	3.7	364	0.99	0.11	9.1
			2	4.4	319	0.85	0.09	9.4
			3	4.4	395	0.89	0.10	9.1
			Mean	4.2	359	0.91	0.10	9.2
		Treatment mean		**3.6**	**306**	**0.82**	**0.09**	**8.8**
Rest (2000)	Bare	Flat	1	3.6	141	0.72	0.08	8.7
			2	4.8	270	0.97	0.10	9.8
			3	3.8	136	0.74	0.09	8.1
			Mean	4.1	182	0.81	0.09	8.9
		North	1	3.8	233	0.84	0.10	8.8
			2	3.6	531	0.73	0.08	8.8
			3	4.6	91	0.74	0.09	8.5
			Mean	4.0	285	0.77	0.09	8.7
	Grass	Flat	1	3.3	96	0.77	0.09	8.8
			2	4.8	109	0.94	0.10	9.6
			3	2.9	221	0.81	0.09	9.1
			Mean	3.7	142	0.84	0.09	9.2
		North	1	3.9	1821	0.78	0.09	8.4
			2	4.4	359	0.69	0.07	9.4
			3	4.6	184	0.64	0.07	9.2
			Mean	4.3	788	0.71	0.08	9.0
		Treatment mean		**4.0**	**349**	**0.78**	**0.09**	**8.9**
Grazed	Bare	Flat	1	4.11	161	0.83	0.09	9.07
			2	4.52	289	0.89	0.10	8.94
			3	3.68	196	0.61	0.07	8.30
			Mean	4.1	215	0.78	0.09	8.8
		North	1	3.70	104	0.90	0.10	8.65
			2	3.76	184	0.85	0.09	9.36
			3	3.50	210	0.93	0.10	9.69
			Mean	3.7	166	0.89	0.10	9.2
	Grass	Flat	1	4.49	206	0.81	0.09	9.18
			2	4.80	91	0.77	0.08	9.23
			3	3.56	325	0.90	0.10	9.13
			Mean	4.3	207	0.83	0.09	9.2
		North	1	4.06	126	0.87	0.09	9.24
			2	3.91	116	1.14	0.12	9.61
			3	4.61	169	0.87	0.10	8.91
			Mean	4.2	137	0.96	0.10	9.3
		Treatment mean		**4.1**	**182**	**0.86**	**0.09**	**9.1**

Appendix G. Table 8. Chp. IV Soil Water, Root Biomass, Organic C, Total N, and C:N Ratio of soil (5-10 cm depth) by Treatment in 2002.

Treatment	Microsite	Aspect	Rep	Soil Water % (g/g)	Root biomass (gm^{-2})	Organic C (%)	Total N (%)	C : N Ratio Org C/ Total N
Rest (1993)	Bare	Flat	1	5.6	174	0.91	0.10	9.5
			2	5.9	190	1.05	0.10	10.5
			3	6.0	202	0.99	0.10	9.7
			Mean	5.8	189	0.98	0.10	9.9
		North	1	5.5	381	1.21	0.12	10.0
			2	5.6	355	0.96	0.10	9.6
			3	6.7	369	1.10	0.12	9.3
			Mean	5.9	368	1.09	0.11	9.6
	Grass	Flat	1	5.9	254	0.91	0.09	10.1
			2	6.6	547	0.92	0.10	9.7
			3	5.8	415	1.15	0.12	9.8
			Mean	6.1	406	0.99	0.10	9.9
		North	1	6.3	368	1.16	0.12	9.7
			2	5.9	205	0.87	0.09	9.6
			3	5.7	416	0.89	0.09	10.0
			Mean	6.0	330	0.98	0.10	9.8
		Treatment mean		**6.0**	**323**	**1.01**	**0.10**	**9.8**
Rest (2000)	Bare	Flat	1	5.3	158	0.86	0.09	9.3
			2	4.5	476	1.12	0.12	9.7
			3	6.2	317	1.04	0.11	9.5
			Mean	5.3	317	1.01	0.11	9.5
		North	1	4.8	403	0.83	0.09	9.4
			2	5.8	331	1.02	0.07	14.6
			3	5.6	425	1.05	0.11	9.4
			Mean	5.4	386	0.96	0.09	11.1
	Grass	Flat	1	3.6	138	0.99	0.10	10.1
			2	6.1	324	1.04	0.11	9.7
			3	5.3	331	1.07	0.11	9.5
			Mean	5.0	264	1.03	0.11	9.7
		North	1	4.8	246	0.99	0.10	10.1
			2	6.0	278	0.96	0.10	10.0
			3	5.6	474	0.96	0.09	10.4
			Mean	5.5	333	0.97	0.10	10.2
		Treatment mean		**5.3**	**326**	**0.99**	**0.10**	**10.1**
Grazed	Bare	Flat	1	5.8	319	1.04	0.11	9.7
			2	4.8	317	1.02	0.11	9.6
			3	4.3	179	0.96	0.10	9.7
			Mean	5.0	272	1.01	0.10	9.7
		North	1	5.6	230	0.84	0.09	9.8
			2	4.7	286	1.10	0.11	9.8
			3	4.3	314	1.11	0.11	10.1
			Mean	4.8	277	1.02	0.10	9.9
	Grass	Flat	1	5.8	395	0.98	0.11	9.3
			2	4.7	650	0.96	0.10	9.8
			3	5.7	157	0.99	0.10	9.7
			Mean	5.4	401	0.98	0.10	9.6
		North	1	6.0	209	0.87	0.08	10.3
			2	5.6	197	1.11	0.11	9.8
			3	4.2	255	1.13	0.12	9.8
			Mean	5.3	220	1.03	0.10	10.0
		Treatment mean		**5.1**	**292**	**1.01**	**0.10**	**9.8**

Appendix G. Table 8. Chp. IV Soil Water, Root Biomass, Organic C, Total N, and C:N Ratio of soil (5-10 cm depth) by Treatment in 2002.

Treatment	Microsite	Aspect	Rep	Soil Water % (g/g)	Root biomass (gm^{-2})	Organic C (%)	Total N (%)	C : N Ratio Org C/ Total N
Rest (1993)	Bare	Flat	1	5.6	174	0.91	0.10	9.5
			2	5.9	190	1.05	0.10	10.5
			3	6.0	202	0.99	0.10	9.7
			Mean	5.8	189	0.98	0.10	9.9
		North	1	5.5	381	1.21	0.12	10.0
			2	5.6	355	0.96	0.10	9.6
			3	6.7	369	1.10	0.12	9.3
			Mean	5.9	368	1.09	0.11	9.6
	Grass	Flat	1	5.9	254	0.91	0.09	10.1
			2	6.6	547	0.92	0.10	9.7
			3	5.8	415	1.15	0.12	9.8
			Mean	6.1	406	0.99	0.10	9.9
		North	1	6.3	368	1.16	0.12	9.7
			2	5.9	205	0.87	0.09	9.6
			3	5.7	416	0.89	0.09	10.0
			Mean	6.0	330	0.98	0.10	9.8
		Treatment mean		**6.0**	**323**	**1.01**	**0.10**	**9.8**
Rest (2000)	Bare	Flat	1	5.3	158	0.86	0.09	9.3
			2	4.5	476	1.12	0.12	9.7
			3	6.2	317	1.04	0.11	9.5
			Mean	5.3	317	1.01	0.11	9.5
		North	1	4.8	403	0.83	0.09	9.4
			2	5.8	331	1.02	0.07	14.6
			3	5.6	425	1.05	0.11	9.4
			Mean	5.4	386	0.96	0.09	11.1
	Grass	Flat	1	3.6	138	0.99	0.10	10.1
			2	6.1	324	1.04	0.11	9.7
			3	5.3	331	1.07	0.11	9.5
			Mean	5.0	264	1.03	0.11	9.7
		North	1	4.8	246	0.99	0.10	10.1
			2	6.0	278	0.96	0.10	10.0
			3	5.6	474	0.96	0.09	10.4
			Mean	5.5	333	0.97	0.10	10.2
		Treatment mean		**5.3**	**325**	**0.99**	**0.10**	**10.1**
Grazed	Bare	Flat	1	5.8	319	1.04	0.11	9.7
			2	4.8	317	1.02	0.11	9.6
			3	4.3	179	0.96	0.10	9.7
			Mean	5.0	272	1.01	0.10	9.7
		North	1	5.6	230	0.84	0.09	9.8
			2	4.7	286	1.10	0.11	9.8
			3	4.3	314	1.11	0.11	10.1
			Mean	4.8	277	1.02	0.10	9.9
	Grass	Flat	1	5.8	395	0.98	0.11	9.3
			2	4.7	650	0.96	0.10	9.8
			3	5.7	157	0.99	0.10	9.7
			Mean	5.4	401	0.98	0.10	9.6
		North	1	6.0	209	0.87	0.08	10.3
			2	5.6	197	1.11	0.11	9.8
			3	4.2	255	1.13	0.12	9.8
			Mean	5.3	220	1.03	0.10	10.0
		Treatment mean		**5.1**	**292**	**1.01**	**0.10**	**9.8**

Appendix G. Table 10. Concentrations of labile C and N pools in soil (0-5 cm) NH_4^+, NO_3^-, $WSOC_{FM}$, $WSOC_{OD}$, and WSOC pools as a percentage of total Organic soil C in Northern mixed prairie (NMP) by Treatment in 2002.

Treatment	Microsite	Aspect	Rep	NH_4^+ (ug g^{-1} soil)	NO_3^- (ug g^{-1} soil)	$WSOC_{FM}$ (ug g^{-1} soil)	$WSOC_{OD}$ (ug g^{-1} soil)	$WSOC_{FM}$ / Org C (%)	$WSOC_{OD}$ / Org C (%)
Rest (1993)	Bare	Flat	1	3.3	0.7	16.4	111.9	0.17	1.14
			2	3.0	1.0	31.0	150.2	0.24	1.17
			3	2.9	1.1	35.9	128.1	0.29	1.03
			Mean	3.0	0.9	27.8	130.1	0.23	1.11
		North	1	3.2	0.9	33.5	156.2	0.27	1.25
			2	3.4	1.2	25.1	131.7	0.20	1.04
			3	3.1	1.6	16.9	110.9	0.14	0.93
			Mean	3.3	1.2	25.2	132.9	0.20	1.08
	Grass	Flat	1	3.4	1.0	20.7	148.9	0.19	1.40
			2	3.6	2.0	25.7	149.8	0.21	1.23
			3	2.7	1.5	23.6	144.0	0.19	1.14
			Mean	3.2	1.5	23.3	147.6	0.20	1.26
		North	1	2.7	2.6	27.0	146.4	0.20	1.08
			2	6.2	1.0	16.5	111.4	0.16	1.07
			3	2.7	1.0	18.5	138.5	0.15	1.14
			Mean	3.9	1.5	20.7	132.1	0.17	1.10
		Treatment mean		**3.3**	**1.3**	**24.2**	**135.7**	**0.20**	**1.14**
Rest (2000)	Bare	Flat	1	2.2	0.9	14.6	105.5	0.16	1.14
			2	2.5	1.3	30.6	121.7	0.24	0.95
			3	2.8	1.4	20.5	145.7	0.19	1.33
			Mean	2.5	1.2	21.9	124.3	0.19	1.14
		North	1	2.6	0.7	21.5	113.4	0.22	1.19
			2	2.6	1.0	15.5	119.9	0.13	1.00
			3	3.2	0.9	19.3	116.8	0.17	1.05
			Mean	2.8	0.8	18.8	116.7	0.18	1.08
	Grass	Flat	1	5.0	0.9	32.1	138.4	0.28	1.20
			2	2.5	0.8	40.3	169.7	0.26	1.09
			3	3.7	1.0	23.1	160.2	0.19	1.32
			Mean	3.7	0.9	31.8	156.1	0.24	1.20
		North	1	3.4	1.5	19.0	132.2	0.16	1.13
			2	3.7	1.6	23.4	159.1	0.18	1.24
			3	2.6	0.4	21.1	142.6	0.17	1.15
			Mean	3.2	1.2	21.2	144.6	0.17	1.17
		Treatment mean		**3.1**	**1.0**	**23.4**	**135.4**	**0.20**	**1.15**
Grazed	Bare	Flat	1	4.0	1.7	25.6	112.8	0.22	0.99
			2	6.5	1.1	22.9	117.2	0.20	1.00
			3	2.4	1.4	18.6	115.2	0.20	1.26
			Mean	4.3	1.4	22.4	115.1	0.21	1.08
		North	1	2.8	0.6	23.3	165.5	0.20	1.43
			2	3.4	1.1	27.8	126.6	0.21	0.94
			3	3.2	0.7	24.3	140.7	0.19	1.12
			Mean	3.1	0.8	25.1	144.3	0.20	1.16
	Grass	Flat	1	3.0	3.2	21.4	133.5	0.20	1.25
			2	3.4	1.4	18.1	126.7	0.16	1.10
			3	3.4	1.8	38.0	183.3	0.29	1.40
			Mean	3.3	2.1	25.8	147.8	0.22	1.25
		North	1	3.7	1.5	32.3	192.6	0.31	1.82
			2	3.0	1.2	24.1	154.7	0.18	1.16
			3	3.1	1.8	27.7	149.0	0.20	1.05
			Mean	3.3	1.5	28.0	165.5	0.23	1.34
		Treatment mean		**3.5**	**1.5**	**25.3**	**143.2**	**0.21**	**1.21**

Appendix G. Table 11. Chp. IV Concentrations of labile C pools in soil (0-5 cm) $WSOC_{FM}$, $WSOC_{OD}$, and as a percentage of total Organic soil C in 2003. NH_4^+ and NO_3^- data were unavailable for this collection date.

Treatment	Microsite	Aspect	Rep	$WSOC_{FM}$ (ug C g^{-1} soil)	$WSOC_{OD}$ (ug C g^{-1} soil)	$WSOC_{FM}$ / Org C (%)	$WSOC_{OD}$ / Org C (%)
Rest (1993)	Bare	Flat	1	26.5	109.8	0.25	1.04
			2	27.7	122.6	0.23	1.02
			3	20.4	83.6	0.19	0.78
			Mean	24.9	105.3	0.22	0.95
		North	1	14.0	72.1	0.10	0.54
			2	24.5	109.8	0.21	0.95
			3	18.5	82.0	0.15	0.67
			Mean	19.0	87.9	0.16	0.72
	Grass	Flat	1	23.6	140.9	0.18	1.06
			2	24.5	143.5	0.18	1.06
			3	22.6	90.3	0.23	0.93
			Mean	23.5	124.9	0.20	1.02
		North	1	21.0	89.5	0.20	0.85
			2	23.0	96.7	0.29	1.24
			3	13.9	94.0	0.15	1.01
			Mean	19.3	93.4	0.21	1.03
		Treatment mean		**21.7**	**102.9**	**0.20**	**0.93**
Rest (2000)	Bare	Flat	1	20.2	74.7	0.12	0.46
			2	21.9	92.8	0.22	0.95
			3	20.3	90.6	0.21	0.91
			Mean	20.8	86.0	0.18	0.77
		North	1	19.5	92.3	0.24	1.13
			2	18.2	99.7	0.26	1.44
			3	32.8	94.9	0.24	0.70
			Mean	23.5	95.6	0.25	1.09
	Grass	Flat	1	23.4	112.8	0.23	1.12
			2	25.0	109.4	0.24	1.05
			3	14.5	74.0	0.11	0.56
			Mean	21.0	98.7	0.19	0.91
		North	1	27.2	177.0	0.23	1.50
			2	21.1	92.3	0.15	0.64
			3	17.3	104.5	0.19	1.14
			Mean	21.9	124.6	0.19	1.09
		Treatment mean		**21.8**	**101.3**	**0.20**	**0.97**
Grazed	Bare	Flat	1	23.8	80.5	0.16	0.54
			2	14.7	57.4	0.09	0.35
			3	20.1	53.1	0.19	0.50
			Mean	19.5	63.7	0.15	0.46
		North	1	17.7	67.1	0.15	0.55
			2	15.3	65.9	0.13	0.55
			3	18.1	83.8	0.13	0.59
			Mean	17.0	72.3	0.13	0.57
	Grass	Flat	1	20.1	88.9	0.17	0.74
			2	23.0	87.2	0.24	0.92
			3	21.2	77.7	0.22	0.79
			Mean	21.5	84.6	0.21	0.82
		North	1	55.5	114.4	0.65	1.35
			2	15.0	72.6	0.16	0.79
			3	54.2	164.1	0.58	1.76
			Mean	41.6	117.0	0.47	1.30
		Treatment mean		**24.9**	**84.4**	**0.24**	**0.79**

Appendix G. Table 12. Chp. IV Concentrations of labile N and C pools in soil (5-10 cm) NH_4^+, NO_3^-, $NH_4^+ + NO_3^-$, and $WSOC_{FM}$, in Northern mixed prairie (NMP) by Treatment in 2001.

Treatment	Microsite	Aspect	Rep	NH_4^+ (ug N g^{-1} soil)	NO_3^- (ug N g^{-1} soil)	$NH_4^+ + NO_3^-$ (ug N g^{-1} soil)	$WSOC_{FM}$ (ug C g^{-1} soil)
Rest (1993)	Bare	Flat	1	4.0	0.7	4.7	27.0
			2	5.1	0.4	5.5	21.5
			3	5.2	0.4	5.5	35.9
			Mean	4.7	0.5	5.2	28.1
		North	1	5.1	0.4	5.6	24.3
			2	4.5	0.4	4.9	25.4
			3	5.3	0.4	5.7	21.9
			Mean	5.0	0.4	5.4	23.9
	Grass	Flat	1	4.3	0.7	5.0	22.3
			2	4.5	0.7	5.1	29.2
			3	5.8	0.4	6.2	22.7
			Mean	4.9	0.6	5.5	24.7
		North	1	5.0	0.7	5.7	30.0
			2	4.7	0.5	5.2	33.8
			3	5.2	0.6	5.8	26.5
			Mean	5.0	0.6	5.6	30.1
			Treatment mean	**4.9**	**0.5**	**5.4**	**26.7**
Rest (2000)	Bare	Flat	1	3.5	0.8	4.4	16.3
			2	4.9	1.0	5.9	25.2
			3	4.1	1.0	5.2	19.7
			Mean	4.2	1.0	5.1	20.4
		North	1	4.2	1.3	5.5	22.3
			2	4.4	1.0	5.3	24.8
			3	4.6	1.1	5.7	17.8
			Mean	4.4	1.1	5.5	21.6
	Grass	Flat	1	4.1	0.7	4.8	16.6
			2	4.9	1.3	6.3	44.3
			3	3.6	0.1	3.7	19.4
			Mean	4.2	0.7	4.9	26.7
		North	1	4.2	1.4	5.6	23.6
			2	4.0	1.1	5.1	28.5
			3	4.1	1.0	5.1	22.8
			Mean	4.1	1.1	5.3	25.0
			Treatment mean	**4.2**	**1.0**	**5.2**	**23.4**
Grazed	Bare	Flat	1	7.9	0.4	8.3	18.2
			2	5.2	0.5	5.7	30.8
			3	4.1	0.5	4.6	29.2
			Mean	5.7	0.5	6.2	26.1
		North	1	4.6	0.9	5.5	26.0
			2	4.7	0.6	5.3	21.5
			3	4.7	0.5	5.2	24.1
			Mean	4.7	0.7	5.3	23.9
	Grass	Flat	1	7.8	0.5	8.3	20.9
			2	5.2	0.5	5.7	20.5
			3	4.9	1.0	5.9	28.0
			Mean	6.0	0.6	6.6	23.1
		North	1	5.1	0.9	6.0	29.9
			2	5.2	0.8	6.0	29.1
			3	4.5	0.6	5.0	23.6
			Mean	4.9	0.7	5.7	27.6
			Treatment mean	**5.3**	**0.6**	**6.0**	**25.2**

Appendix G. Table 13. Chp. IV Concentrations of labile C and N pools in soil (5-10 cm) NH_4^+, NO_3^-, $NH_4^+ + NO_3^-$, and $WSOC_{FM}$, in Northern mixed prairie (NMP) by Treatment in 2002.

Treatment	Microsite	Aspect	Rep	NH_4^+ (ug N g^{-1} soil)	NO_3^- (ug N g^{-1} soil)	$NH_4^+ + NO_3^-$ (ug N g^{-1} soil)	$WSOC_{FM}$ (ug C g^{-1} soil)
Rest (1993)	Bare	Flat	1	2.9	0.3	3.2	23.3
			2	2.8	0.4	3.3	39.3
			3	3.1	0.4	3.6	33.0
			Mean	2.9	0.4	3.3	31.9
		North	1	2.8	0.5	3.3	33.1
			2	3.8	0.5	4.3	25.3
			3	3.6	0.8	4.4	28.6
			Mean	3.4	0.6	4.0	29.0
	Grass	Flat	1	3.1	0.5	3.6	22.1
			2	3.5	0.5	4.0	31.0
			3	3.3	0.9	4.2	34.1
			Mean	3.3	0.6	3.9	29.0
		North	1	2.8	0.6	3.3	32.5
			2	3.9	0.4	4.4	20.5
			3	3.3	0.6	3.9	23.4
			Mean	3.3	0.5	3.9	25.5
			Treatment mean	**3.2**	**0.5**	**3.8**	**28.8**
Rest (2000)	Bare	Flat	1	2.7	0.3	3.0	18.4
			2	2.2	0.5	2.7	27.0
			3	3.0	0.4	3.5	24.8
			Mean	2.6	0.4	3.1	23.4
		North	1	2.2	0.4	2.6	20.7
			2	3.5	0.3	3.8	21.4
			3	3.5	0.4	3.9	26.7
			Mean	3.1	0.3	3.4	22.9
	Grass	Flat	1	7.1	0.5	7.6	34.4
			2	2.8	0.6	3.4	48.1
			3	3.2	0.8	4.0	35.7
			Mean	4.4	0.6	5.0	39.4
		North	1	2.7	0.4	3.1	30.7
			2	2.8	0.3	3.1	30.6
			3	2.8	0.4	3.2	23.6
			Mean	2.8	0.3	3.1	28.3
			Treatment mean	**3.2**	**0.4**	**3.6**	**28.5**
Grazed	Bare	Flat	1	7.7	0.5	8.2	24.8
			2	3.1	0.4	3.6	24.8
			3	2.8	0.5	3.3	28.5
			Mean	4.6	0.5	5.0	26.0
		North	1	2.9	0.4	3.3	32.3
			2	2.9	0.5	3.4	27.4
			3	2.5	0.4	2.9	26.3
			Mean	2.8	0.4	3.2	28.7
	Grass	Flat	1	4.4	0.5	4.8	24.9
			2	2.8	0.4	3.2	26.5
			3	2.7	0.5	3.2	35.8
			Mean	3.3	0.4	3.7	29.1
		North	1	2.6	0.6	3.2	30.2
			2	2.4	0.4	2.8	25.8
			3	2.8	0.7	3.5	24.6
			Mean	2.6	0.6	3.2	26.9
			Treatment mean	**3.3**	**0.5**	**3.8**	**27.7**

Appendix G. Table 14. Chp. IV Soil Temperature by Treatment and Microsite at the soil surface, 5 cm depth, and 10 cm depth in 2002.

				Temperature (°C)		
Treatment	Microsite	Aspect	Rep	Surface Temp	5 cm	10 cm
Rest (1993)	Bare	Flat	1	53.0	30.4	23.9
			2	37.0	27.9	23.7
			3	48.0	31.4	25.7
			Mean	46.0	29.9	24.4
		North	1	47.0	30.8	24.8
			2	47.0	32.3	25.4
			3	43.0	31.9	25.6
			Mean	45.7	31.7	25.3
	Grass	Flat	1	44.0	31.2	23.5
			2	30.0	26.9	23.6
			3	35.0	27.7	24.6
			Mean	36.3	28.6	23.9
		North	1	31.0	30.1	24.7
			2	41.0	28.1	24.5
			3	34.0	30.8	27.1
			Mean	35.3	29.7	25.4
Rest (2000)	Bare	Flat	1	50.0	33.1	26.1
			2	44.0	33.7	26.6
			3	37.0	32.4	26.4
			Mean	43.7	33.1	26.4
		North	1	42.0	34.1	27.4
			2	39.0	33.5	26.8
			3	37.0	35.9	28.3
			Mean	39.3	34.5	27.5
	Grass	Flat	1	39.0	33.2	28.3
			2	31.0	31.8	27.0
			3	28.0	28.3	25.5
			Mean	32.7	31.1	26.9
		North	1	29.0	31.0	26.4
			2	25.0	27.7	24.3
			3	24.0	30.5	26.4
			Mean	26.0	29.7	25.7
Grazed	Bare	Flat	1	46.0	34.0	27.9
			2	45.0	32.9	26.9
			3	34.0	31.6	26.8
			Mean	41.7	32.8	27.2
		North	1	43.0	35.6	28.2
			2	36.0	33.2	28.0
			3	38.0	33.2	27.2
			Mean	39.0	34.0	27.8
	Grass	Flat	1	35.0	33.0	28.4
			2	33.0	34.2	29.8
			3	27.0	31.0	27.6
			Mean	31.7	32.7	28.6
		North	1	28.0	33.2	29.2
			2	26.0	32.9	28.4
			3	29.0	29.8	26.0
			Mean	27.7	32.0	27.9
	Bare Ground Mean			**42.6**	**32.7**	**26.4**
	Grass Occupied Mean			**31.6**	**30.6**	**26.4**

Appendix G. Table 15. P-values for Chapter 4 Table 1 ANOVA comparisons between treatments for cover abundance Of Bare Ground and Litter by collection year (2001-2003).

		Bare Ground			Litter		
Date		Rest (1993)	Rest (2000)	Grazed	Rest (1993)	Rest (2000)	Grazed
2001	Grazed	.0001	.0001	-	.0001	.0072	-
	Rest (2000)	.0076	-	.0001	.0469	-	.0072
	Rest (1993)	-	.0076	.0001	-	.0469	.0001
2002	Grazed	.0002	.0874	-	.0001	.1737	-
	Rest (2000)	.0144	-	.0874	.0002	-	.1737
	Rest (1993)	-	.0144	.0002	-	.0002	.0001
2003	Grazed	.0001	.0397	-	.0019	.1094	-
	Rest (2000)	.0026	-	.0397	.0795	-	.1094
	Rest (1993)	-	.0026	.0001	-	.0795	.0019

Appendix G. Table 16. P-values for Chapter 4 Table 1 ANOVA comparisons between treatments for Total Plant Cover and C_3 Species cover (C3 grasses + Caresis) by collection date (2001-2003).

		Total Plant Cover			**C_3 Species**		
Date		Rest (1993)	Rest (2000)	Grazed	Rest (1993)	Rest (2000)	Grazed
2001	Grazed	.0001	.0007	-	.0001	.0006	-
	Rest (2000)	.4280	-	.0007	.5774	-	.0006
	Rest (1993)	-	.4280	.0001	-	.5774	.0001
2002	Grazed	.6292	.4483	-	.0001	.0003	-
	Rest (2000)	.2158	-	.0007	.6357	-	.0006
	Rest (1993)	-	.2158	.6292	-	.6357	.0001
2003	Grazed	.1850	.1701	-	.0001	.0001	-
	Rest (2000)	.9609	-	.1701	.6387	-	.0001
	Rest (1993)	-	.9609	.1850	.	.6387	.0001

Appendix G. Table 17. P-values for Chapter 4 Table 2 ANOVA comparisons of Soil % H20, total C, and total N from 2001, 2002, and 2003 in the 0-5 cm depth and the 5-10 cm depth for 2001 to 2002.

				0-5 cm					
	$\%H_2O$ ($g\ g^{-1}$)			Soil C (%)			Soil N (%)		
Date	2003	2002	2001	2003	2002	2001	2003	2002	2001
2001	.0001	.0001	-	.5581	.0341	-	.0001	.2046	-
2002	.0001	-	.0001	.1202	-	.0341	.0015	-	.2046
2003	-	.0001	.0001	-	.1202	.5581	-	.0015	.0001

	5-10 cm		
	$\%H_2O$ ($g\ g^{-1}$)	Soil C (%)	Soil N (%)
Date	2002	2002	2002
2001	.1650	.0001	.0084

Appendix G. Table 18. P-values for Chapter 4 Table 4 ANOVA comparisons of Root Biomass by date and microsite for 2001 and 2002 in 0-5 cm, 5-10 cm, and 0-10 cm total depths.

	Root Biomass ($g\ m^{-2}$)		
	0-5 cm	5-10 cm	0-10 Total
Date	2002	2002	2002
2001	.0001	.4705	.0004
Microsite	Grass	Grass	Grass
Bare	.0002	.3424	.0012

Appendix G. Table 19. P-values for Chapter 4 Table 5 ANOVA comparisons of NH_4^+, NO_3^-, and $NH_4^+ + NO_3^-$ for 2001 and 2002 in 0-5 cm and 5-10 cm depths.

Depth	**0-5 cm**		
	NH_4^+	NO_3^-	$NH_4^+ + NO_3^-$
Date	2002	2002	2002
2001	.0001	.0001	.0026

	5-10 cm		
	2002	2002	2002
2001	.0001	.0001	.0001

Appendix G. Table 20. P-values for Chapter 4 Table 5 ANOVA comparisons of $WSOC_{FM}$, $WSOC_{OD}$, and $WSOC_{OD} - WSOC_{FM}$ in the 0-5 cm depth for 2001 to 2002.

	$WSOC_{FM}$ ($ug\ g^{-1}$ C soil)			$WSOC_{OD}$ ($ug\ g^{-1}$ C soil)			$WSOC_{FM}$ - $WSOC_{OD}$		
Date	2003	2002	2001	2003	2002	2001	2003	2002	2001
2001	.0098	.0003	-	.0001	.6546	-	.0001	.0015	-
2002	.2144	-	.0003	.0001	-	.6546	.0001	-	.0015
2003	-	.2144	.0098	-	.0001	.0001	-	.0001	.0001

Appendix G. Table 21. P-values for Chapter 4 Table 7 ANOVA comparisons of WSOC as a percentage of Total C from 2001, 2002, 2003 in the 0-5 cm depth. * This comparison in based on LS Means for the analysis which includes soil water (%) as an independent variable.

	*(WSOC $_{FM}$ / Total C) x 100			(WSOC $_{FM}$ / Total C) x 100			(WSOC $_{FM}$ / Total C) x 100		
Date	2003	2002	2001	2003	2002	2001	2003	2002	2001
2001	.0098	.2144	-	.0001	.0001	-	.0001	.2134	-
2002	.0003	-	.2144	.5228	-	.0001	.0001	-	.2134
2003	-	.0003	.0098	-	.5228	.0001	-	.0001	.0001

Microsite	Grass	Grass	Grass
Bare	.0185	.0622	.0001