SPATIAL AND TEMPORAL VARIATION IN GREENHOUSE GAS FLUX AS AFFECTED BY MOWING ON GRASSLANDS OF HUMMOCKY TERRAIN IN SASKATCHEWAN

A Thesis Submitted to the College of

Graduate Studies and Research

In Partial Fulfillment of the Requirements

For the Degree of Master of Science

In the Department of Plant Sciences

University of Saskatchewan

Saskatoon

By

MATTHEW DAVID BRAUN

PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a Postgraduate degree from the University of Saskatchewan, I agree that the Libraries of this University may make it freely available for inspection. I further agree that permission for copying of this thesis in any manner, in whole or in part, for scholarly purposes may be granted by the professor or professors who supervised my thesis work or, in their absence, by the Head of the Department or the Dean of the College in which my thesis work was done. It is understood that any copying or publication or use of this thesis or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis.

Requests for permission to copy or to make other use of material in this thesis in whole or part should be addressed to:

Head of the Department of Plant Sciences
51 Campus Drive
University of Saskatchewan
Saskatoon, Saskatchewan S7N 5A8

ABSTRACT

Global climate change has been linked to the increase in greenhouse gas (GHG) emissions. Mixedgrass Prairie of hummocky terrain in Saskatchewan is an understudied landscape contributing an unknown quantity of greenhouse gases (GHGs) to global climate change. The objectives of this study were to determine the effects of topography and mowing on carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) flux and to correlate them with environmental and plant community characteristics. The study site was located in the Northern Mixedgrass Prairie of the Missouri Coteau near Macrorie, SK. April mowing and an unmowed control were imposed on six different landform elements. Carbon dioxide, CH_4 and N_2O were measured every 7-10 days from spring until fall for two years with closed, vented chambers. Soil physical characteristics, weather and plant community characteristics were measured. Landform element and mowing influenced the flux of all three gases in both sampling seasons. Soil CO_2 flux ranged from 3.1 to 23.3 kg CO_2-C ha^{-1} d^{-1} among the unmowed control plots and 3.6 to 26.4 kg CO_2-C ha^{-1} d^{-1} after mowing. Soils were a net sink for CH_4, consuming 1.4 to 4.4 g CH_4-C ha^{-1} d^{-1} among the unmowed control plots and 1.8 to 4.1 g CH_4-C ha^{-1} d^{-1} among the mowed plots. Nitrous oxide flux ranged from -0.25 to 1.17 g N_2O-N ha^{-1} d^{-1} among the unmowed control plots and -0.20 to 1.51 g N_2O-N ha^{-1} d^{-1} among the mowed plots. Greenhouse gas flux changed from year-to-year and within years. The greatest GHG flux rate occurred in the depression landform element. Mowing increased the positive flux of CO_2 and N_2O while increasing the negative flux of CH_4. Species composition was correlated with soil water, topography, percentage litter cover and GHG flux rate. Overall, the Mixedgrass Prairie of Saskatchewan likely contributes very little to GHGs. Properly managed, the Mixedgrass Prairie has a well-balanced nutrient cycle that includes various GHGs. The grassland ecosystem plays a role in mitigating climate change by retaining carbon that would be released to the atmosphere with poor grazing management or the conversion to arable agriculture. Government agencies and the ranching industries could best mitigate GHG emissions of Mixedgrass Prairie in Saskatchewan by promoting the retention of above-ground plant material, increasing below-ground carbon sequestration and the avoidance of conversion to cropland.

ACKNOWLEDGMENTS

I would like to thank my two co-supervisors, Drs. Y. Bai and B. McConkey for accepting me as a student and for their support during this process. I also appreciated the support and guidance shown by my advisory committee members, Drs. R. Farrell, G. Hughes, D. Pennock and J.T. Romo and my external examiner, Dr. R. Lemke. Financial assistance for this project was provided by the Biological Greenhouse Gas Sources and Sinks Program of the Canadian Agri-Food Research Council, the Centre for Studies in Agriculture, Law and the Environment, the Prairie Adaptation Research Collaborative Graduate Scholarship Program and the University of Saskatchewan Rene Vandeveld Postgraduate Scholarship. Family, friends, colleagues and some strangers provided extraordinary assistance during the completion of this project. Those people include Dick Braun, Kathy Braun, Eugene Penner, Shelley Penner, Jolene Braun, Jan Braun, Dale Gross, Bin Xu, Youming Qiao, Andrew Pantel, Amber Neumen, Dalei Chen, Jie Qiu, Frances Rodenburg, Tyler Colberg, Darin Richman, Darrell Hahn, Jeff Braidek, Tom Yates, Zhenyang Lu, Zhaohui Wei, Ron Dunning and several inhabitants of the Rural Municipality of Coteau who helped get my truck out of the mud… twice. I would like to give special thanks to my wonderful life-partner Julie Bergen. She was and is my out-standing stand-in technician who did a little bit of everything.

Finally I would like to acknowledge all the people who bus, bike or walk when they could drive. Random acts of "under-consumption" gave me a reason to finish this project and hope for the future.

QUOTATIONS

“Heterogeneity, at a variety of spatial scales, is all-pervasive in natural environments.”
-Stewart, A.J.A., E.A. John, and M.J. Hutchings. 2000

“The Kyoto conference did not achieve much with regard to limiting the buildup of greenhouse gases in the atmosphere. If no further steps are taken during the next 10 years, CO_2 will increase in the atmosphere during the first decade of the next century essentially as it has done during the past few decades. Only if the new cooperation among countries succeeds will the Kyoto conference represent a step toward the ultimate objective of the convention: " . . . to achieve . . . stabilization of greenhouse gas concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system."”
-Bolin, B. 1998.

“Landscape to an ecologist is the vegetation and associated faunal populations draped over the geomorphology that give it most of its colour and texture.”
-Miles, J., R.P. Cummins, D.D. French, S. Gardner, J.L. Orr, and M.C. Shewry. 2001.

“A useful approach for evaluating microbial processes at landscape scales is to establish relationships between these processes and ecosystem properties that are easily estimated at large scales.”
-Groffman, P.M. and C.L. Turner. 1995.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

Greenhouse gases (GHGs) are an important part of the earth's atmosphere, trapping heat by absorbing and then radiating long-wave radiation (Paltridge and Platt, 1976). Since the industrial age, atmospheric concentrations of GHGs such as carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) have increased beyond the previous range of variation (Prather et al., 1995) due to the human-induced burning of fossil fuels, deforestation and changes in land use (Shallcross et al., 2003). Increased greenhouse gas (GHG) emissions and decreased GHG sinks contribute to global climate change (Prather and Ehhalt, 2001). Over the last 100 years, Northern Hemisphere temperatures have increased, often exceeding historic trends in annual temperatures (Mann and Bradley, 1999). In Saskatchewan, the climate has changed in the past 50 years so that spring now begins earlier and winter arrives later (Cutforth et al., 1999).

Greenhouse gases can be investigated at various scales. Greenhouse gases are climate regulators studied at the global scale and over long periods (Wuebbles and Edmonds, 1991). At the national and provincial scale, reducing sources and increasing sinks of GHGs is the centre of an internationally recognized problem that the Canadian and Saskatchewan governments have agreed to confront (Grubb et al., 1999). At the rangeland ecosystem or landscape level, N_2O emissions are a loss of nutrients while CO_2 and CH_4 sinks store carbon (C) (Paul and Clark, 1996). Quantifying production and consumption of GHGs promotes a better understanding of ecosystem functioning and health (Parton et al., 1988; Smith et al., 1995), in turn enabling the mitigation of GHGs (Desjardins et al., 2001). Topography is defined in this study as a collection of landform elements. Landform element and defoliation of rangelands creates landscape scale differences in exposure to solar radiation (Buffo et al., 1972), water relations (Ellis, 1938) and nutrient cycles (Archer and Smeins, 1991; Thurow, 1991). Past landscape scale studies have indicated that variation in environmental and plant community attributes due to landform element and defoliation influence GHG flux. Plant community structure, function and composition influence GHG emissions by altering nutrient cycling (Hooper and Vitousek, 1997), modifying soil hydrology (Naeth et al., 1991) and hosting different microbial communities (Bolton et al., 1993; Wrage et al., 2001). Defoliation by grazing alters GHG flux patterns directly through feces and urine input (Vermoesen et al., 1997; Yamulki et al., 1998) and indirectly by altering the plant community, which influences the microbial environment and GHG flux (Franzluebbers and Stuedemann, 2003), soil temperature (Ruz-Jerez et al., 1994), and soil water (Thurow, 1991). At the individual soil pedon level, GHG flux is limited by O_2, C and (nitrogen) N availability (Paul and Clark, 1996). Few studies have attempted to correlate environmental and plant community attributes with biotic processes to develop landscape scale indicators of GHG flux (Bubier and Moore, 1995; Groffman et al., 2000; Mitchell et al., 2003).

The Missouri Coteau is a topographically complex landform stretching from central Saskatchewan to South Dakota. The defining geological characteristic of the Missouri Coteau is the knob and kettle terrain (Gravenor and Kupsch, 1958). Heterogeneous landscapes such as the Missouri Coteau provide a variety of microenvironments for organisms that influence GHG flux rates such as grazing vertebrates (Stuth, 1991), soil microbes (Metting, 1993) and plants (Ayyad and Dix, 1964). The flux of GHGs in Saskatchewan rangelands have not been adequately studied, leaving a knowledge gap in the national GHG sources and sinks budget. Study of the flux of GHGs in Saskatchewan rangelands is likely hampered by the difficulty of designing studies on non-level landscapes and smaller GHG flux rates in rangelands compared to croplands (Bowden, 1986). The objectives of this project were to determine; 1) the spatial variability and magnitude of GHG flux in complex terrain of the Northern Mixedgrass Prairie, and; 2) the interaction of landform element and mowing on GHG flux. Grazing management can then be used on this complex topography as a tool for controlling rangeland GHG flux (Howden et al., 1994), which may help the ranching industry meet obligations outlined by the Kyoto Accord. The null hypotheses were: 1) landform element and mowing have no effect on environmental attributes, 2) landform element and mowing have no effect on plant community characteristics, 3) landform element and mowing have no effect on greenhouse gas flux and 4) environmental attributes, plant community characteristics and GHG flux are not correlated.

2. LITERATURE REVIEW

2.1 Greenhouse Gases and Climate Change

Recent ratification of the Kyoto Accord compels many nations, including Canada, to detail total GHG flux over their different landscapes and understanding the influence of ecosystem processes (Mosier et al., 1998c). Greenhouse gases of concern for Canadian agriculture are CO_2, N_2O and CH_4 (Desjardins and Riznek, 2000; Olsen et al., 2003). Carbon dioxide, CH_4, N_2O and various halocarbons are responsible for 64, 20, 6 and 10%, respectively, of the increase in the greenhouse effect (Jain and Hayhoe, 2003). Greenhouse gas molecules absorb long-wave radiation emitted by the earth's surface (Coe and Webb, 2003), thereby heating the atmosphere (Paltridge and Platt, 1976). The global warming potential (GWP) of a GHG is based on the specific wavelengths a molecule absorbs plus the biogeochemical residence time of the GHG. The greenhouse effect maintains the planet at a mean annual temperature of 14°C. Without the greenhouse effect the average temperature would be -18°C (Wuebbles and Edmonds, 1991).

Concentrations of GHGs, and therefore the magnitude of the greenhouse effect have changed over time. The estimated concentrations of CO_2 and N_2 when the earth's atmosphere was first formed were 98% and 2%, respectively (Wayne, 2003). The evolution of photosynthetic organisms and the decline of volcanic activity decreased the concentration of CO_2 and increased the concentration of O_2 (Wayne, 2003). Presently, the earth's atmosphere is 78% N_2, 21% O_2 and less than 0.1% CO_2 (Ruddiman, 2001). Variation in GHG concentrations and global temperatures are closely correlated in geological history (Petit et al., 1999).

The industrial revolution marked the beginning of major anthropogenic changes in the concentrations of GHGs and the magnitude of the greenhouse effect. Burning fossil fuels, cutting forests and converting land to arable agriculture increase atmospheric GHG concentrations (Trenberth et al., 1996). Increases in GHGs have moved global temperatures out of their normal range of variation (Jain and Hayhoe, 2003). Average temperatures now exceed maximum temperatures from the past half-million years (Jain and Hayhoe, 2003).

Carbon dioxide has increased from a concentration of 280 ppm in the 1800s to a concentration of 367 ppm in 1999 (Prentice, 2001). The lifespan of CO_2 is approximately 120 years (Shallcross et al., 2003). Carbon dioxide is assigned a global warming potential (GWP) of 1 and is used as a base value for determining the GWP of other GHGs. The major anthropogenic contributors of CO_2 to the atmosphere include the overuse of fossil fuels, land use changes and cement manufacturing (Jain and Hayhoe, 2003). Abiotic sinks for anthropogenically produced CO_2 include absorption by ocean water and the atmosphere (Shallcross et al., 2003).

The atmospheric concentration of CH_4 increased by 150% to 1,745 ppb since pre-industrial times (Intergovernmental Panel on Climate Change, 2001). Methane has a life span of 9-15 years (Schimel et al., 1996) with a GWP 23 times greater than CO_2 (Intergovernmental Panel on Climate Change, 2001). The anthropogenic sources of CH_4 include enteric fermentation, fossil fuel related activities and rice paddies (Intergovernmental Panel on Climate Change, 2001). Methane is abiotically removed from the atmosphere by reacting with hydroxyl radicals (OH) to produce methyl radicals and water vapour and in the stratosphere with chlorine to produce methyl radicals and hydrochloric acid (Tyler, 1991).

Nitrous oxide has risen from a pre-industrial concentration of 275 ppb to the current concentration of 310 ppb (Shallcross et al., 2003). The average life span of N_2O is 120 years (Prather et al., 1995) and it has a GWP 296 times that of CO_2 (Intergovernmental Panel on Climate Change, 2001). An abiotic sink of N_2O is its reaction with atmospheric constituents like ozone (Wang et al., 1976), the resultant destruction of which increases the amount of UV-B and UV-C rays that reach the earth's surface.

2.2 Greenhouse Gas Flux and Grasslands

Native rangelands of the Canadian prairies are an important part of the economic, social and natural landscape in the region. Very little is known about GHG flux of uncultivated areas. Undisturbed landscapes are important because they occupy large areas of land and contribute significantly to global GHG emissions (Bowden, 1986; Shallcross et al., 2003). Variability of factors controlling GHGs is one of the obstacles to understanding GHG emissions from undisturbed landscapes (Clayton et al., 1994; Smith et al., 1994b).

2.2.1 Ecology of the Northern Mixedgrass Prairie

The Northern Mixedgrass Prairie region is the northern most portion of the Mixedgrass Prairie (Coupland, 1950) and occupies 390,000 km^2 (Coupland, 1961). Dominant grass species are *Hesperostipa comata* (Trin. & Rupr.) Barkworth (needle-and-thread), *Hesperostipa curtiseta* (A.S. Hitchc.) Barkworth (western porcupine grass), *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths (blue grama), *Elymus lanceolatus* (Scribn. & J.G. Sm.) Gould (northern wheatgrass) and *Pascopyrum smithii* (Rydb.) A. Löve (western wheatgrass) (Nomenclature follows the Integrated Taxonomic Information System, 2005) (Coupland, 1961). The Northern Mixedgrass Prairie covers the Brown and Dark Brown soil zones in Saskatchewan (Coupland, 1961). The climate is semiarid to dry subhumid (Sanderson, 1948). Annual precipitation is 310 mm in the southwest corner of Saskatchewan and increases in the northeast corner of the province, reaching 435 mm near the *Populus tremuloides* Michx. (aspen) - *Festuca hallii* (Vasey) Piper (plains rough fescue) ecotone (Coupland, 1961). Average annual air temperatures range from 3.6ºC in Swift Current, SK to 1.1ºC in the northeast portion of the Northern Mixedgrass Prairie (Coupland, 1950). The combination of low precipitation and cold temperatures make the climate and hydrology of the Northern Mixedgrass Prairie unique (Conly and van der Kamp, 2001). Within the Northern Mixedgrass Prairie portion of the province, precipitation differs little from the southwest to the northeast, but cooler temperatures in the northeast reduce potential evapotranspiration, thereby decreasing the moisture deficit in a gradient from southwest to northeast. Soils of the Mixedgrass Prairie of Saskatchewan are glacially derived (Christiansen, 1979) with 55% of glacial lacustrine or glacial fluvial origin and 40% of unsorted glacial till origin (Coupland, 1961). Nitrogen content of soils ranges from 0.10 to 0.24% in the Brown Soil Zone and 0.15 to 0.35% in the Dark Brown Soil Zone (Mitchell and Moss, 1948; Willms et al., 1990; Frank et al., 1995). Soil organic carbon content ranges from 1.6 to 4.6% (Willms et al., 1990; Slobodian et al., 2002; Willms et al., 2002). Glaciers and disintegration of glacial ice formed the topographic features of the Northern Mixedgrass Prairie (Gravenor and Kupsch, 1958).

Within the bounds of the climate, plant species composition and production are influenced, among other factors, by topography and grazing (Coupland et al., 1960; Biondini et al., 1998; Curtin, 2002). Graminoid production varies among the five faciations, or plant community assemblages, of the Northern Mixedgrass Prairie. The *Stipa-Agropyron* faciation produces 445 to 1,421 kg graminoid dry matter ha^{-1} y^{-1}, the *Stipa-Bouteloua-Agropyron* faciation 363 to 1,001 kg graminoid dry matter ha^{-1} y^{-1}, the *Stipa-Bouteloua* faciation 342 to 794 kg graminoid dry matter ha^{-1} y^{-1}, the *Bouteloua-Agropyron* faciation 272 to 596 kg graminoid dry matter ha^{-1} y^{-1}, and the *Agropyron-Koeleria* faciation 520 to 755 kg graminoid dry matter ha^{-1} y^{-1} (Coupland, 1961). Grass production depends on spring growth (Frank and Hofmann, 1989) and is water and N limited (Willms et al., 2002). Removing standing dead plant biomass increases evaporation and decreases water infiltration (Coupland et al., 1960), thereby decreasing annual net primary production compared to sites with greater standing dead plant materials (Willms et al., 2002).

The Missouri Coteau rises 50 to 150 m above the surrounding Mixedgrass Prairie landscape, stretching southeast from North Battleford, SK into South Dakota (Mitchell et al., 1944; Tatina, 1994). The Missouri Coteau is a glacially influenced escarpment of the Mixedgrass Prairie that separates the second and third prairie steppes (Mitchell et al., 1944). Glaciers have deposited unsorted material, rich in clay on and around the Missouri Coteau (Gravenor and Kupsch, 1958), creating a mosaic of soil types and range sites (Biondini et al., 1998). The resultant landscape is part of the prairie pothole region characterized by many bodies of water smaller than one hectare that flood in most springs and often dry during the course of a year (Conly and van der Kamp, 2001). Steep slopes make up the majority of the uncultivated native grassland in the Missouri Coteau (Acton et al., 1998). In Saskatchewan, 27% of the 23,000 km^2 of the Missouri Coteau remain as native grassland (Hammermeister et al., 2001; Environment Canada, 2005b).

2.2.2 Disturbances in the Northern Mixedgrass Prairie

The Northern Mixedgrass Prairie evolved under a combination of grazing and fire, therefore defoliation is a natural part of the ecosystem (Curtin, 2002). Rangeland plants of the Northern Mixedgrass Prairie generally stop or slow root growth when above-ground plant materials are removed (Crider, 1955; Jameson, 1963), decreasing carbohydrates in above-ground and below-ground plant tissue (Brown, 1995). Dominant species of the Northern Mixedgrass Prairie generally recover above-ground primary production lost due to defoliation after being left undisturbed for a minimum of two growing seasons (Kowalenko and Romo, 1998).

Livestock selectively graze specific plants or parts of plants (Coupland et al., 1960). Beebe and Hoffman (1968) noted that heavy grazing removes taller grasses and allows weedy species to dominate. Mowing can also contribute to the increase of less palatable species in the Mixedgrass Prairie ecosystems (Tatina, 1994).

Soil water is generally increased when dead plant materials are retained on the surface (Kowalenko and Romo, 1998). Grazing reduces the amount of dead plant materials, thereby decreasing soil water (Whitman, 1974). Plant growth is water limited in the Mixedgrass Prairie, and maintaining litter through grazing management increases plant production (Facelli and Picket, 1991; Willms, 1995). Removal of litter also increases forb productivity (Willms et al., 1986).

Soil water is influenced directly and indirectly by defoliation of vegetation. The wind speed at 15 cm above the surface of grazed and ungrazed Mixedgrass Prairie was 2.1 and 0.6 km hr^{-1}, respectively (Whitman, 1974). Surface roughness caused by vegetation is negatively correlated with snow transportation (Pomeroy and Gray, 1995). Areas with sparse vegetation lose more snow than areas with dense vegetation (van der Kamp et al., 2003; Essery and Pomeroy, 2004).

Defoliation increases soil temperature (Weaver and Rowland, 1952). Dead and living plant materials shield the soil surface, intercepting 95 to 99% of incoming sunlight (Weaver and Rowland, 1952; Facelli and Pickett, 1991). Removing above-ground biomass can increase soil temperatures by 2 to 5°C (Hulbert, 1969; Whitman, 1974).

Above-ground biomass and litter provides temporary storage of nutrients (Facelli and Pickett, 1991). Removing above-ground biomass decreases organic material inputs to the soil (Knapp and Seastedt, 1986), root biomass (Biondini et al., 1998) and litter inputs (Coupland and Johnson, 1965). Defoliation contributes to increased soil bulk density by decreasing inputs of organic matter necessary for creating the soil structure that decreases soil bulk density (Whitman, 1974). Carbon inputs to the soil decrease with biomass removal while soil temperature and soil respiration increase (Knapp and Seastedt, 1986). Above-ground biomass removal decreased total soil N 64 to 78% compared to ungrazed Mixedgrass Prairie (Frank et al., 1995). Heavy grazing in the Mixedgrass Prairie of North Dakota decreased root biomass, but did not decrease soil N (Biondini et al., 1998).

2.2.3 Impact of climate change on the Northern Mixedgrass Prairie

Increasing concentrations of GHGs are predicted to change the climate of the Northern Mixedgrass Prairie. McGinn and Shepherd (2003) predicted a 4 to 32% increase in precipitation in Saskatchewan and a 3.2 to 5.3ºC and 2.9 to 5.0ºC increase in minimum and maximum temperatures, respectively. Weather data for Swift Current, SK shows that annual precipitation is negatively correlated with mean minimum and maximum temperatures over time (Cutforth, 2000). Future increases in temperatures on the Northern Mixedgrass Prairie may be combined with decreased annual precipitation (Cutforth, 2000). Weather data from the last 100 years suggests no increase in precipitation at Indian Head, SK and only a marginal increase in temperature over that same period (Clark et al., 2000). Contrasting studies state that annual temperatures in the Northern Mixedgrass Prairie have increased over the past century (Skinner and Gullett, 1993; Bootsma, 1994). The moisture deficit can increase with increased annual temperature and no change in precipitation because evaporation also increases.

The distance from the moderating effects of temperature from oceans and positive feedback of changes in snow and ice make the Northern Mixedgrass Prairie more susceptible to changes in global climate (Skinner and Majorowicz, 1999). Changes in annual precipitation or precipitation effectiveness are a major concern for agriculture in the Northern Mixedgrass Prairie because available soil water is one of the main constraints of forage production in this area (Willms and Jefferson, 1993). Forage production is influenced by seasonal fluctuations in precipitation. Standing crop of grass was reduced by 27% when growing season precipitation was limited to 34% of the maximum historical high in the Northern Mixedgrass Prairie (Köchy and Wilson, 2004). Newbauer et al. (1980) stated that a 13-year period of above average precipitation increased forage yields in eastern Montana by 61 to 110%. Long-term changes in climate also influence biomass production at a regional scale (Williams and Wheaton, 1998). The potential production of rangelands decreases when climate change causes shifts in species composition to those that produce less biomass (Coupland, 1958; Willms and Jefferson, 1993).

2.3 Biogenic Production and Consumption of Greenhouse Gases

Metabolic processes of animals, plants and soil microbes are biogenic sources and sinks of GHGs (Davidson and Schimel, 1995; Paul and Clark, 1996). Organisms capture energy from the flow of electrons during respiration. Organic C provides the only source of electrons and O_2 is the only electron acceptor for many organisms. The production and consumption of a variety of GHGs requires diverse microbial communities using a variety of electron acceptors and donors (Metting, 1992).

Changes in the soil environment are important to GHG flux because GHG consumption and production are enzymatic processes with optimum temperature and pH, availability of electrons, water and O_2 (Smith et al., 1993). The environment dictates the rate of GHG consumption and production in plants and microbial communities. The environment also determines the type of GHG produced or consumed by microbes.

The complexity of the soil biotic community allows for the simultaneous production and consumption of several GHGs by different soil organisms (Rogers and Whitman, 1991). A positive flux of a gas indicates net production and an increase in its concentration in the atmosphere, while a negative flux indicates net consumption and a decrease in its concentration in the atmosphere. Production and consumption may occur at the same time in the same soil column, but only the net result is usually reported.

2.3.1 Carbon dioxide

Soil CO_2 respiration is greater on most arable lands than on rangelands (Smith et al., 1997; Schmidt et al., 2001) (Table 2.1). Results from the Mixedgrass Prairie show that peak summer respiration ranges from 13 kg C ha^{-1} d^{-1} in Saskatchewan to 69 kg C ha^{-1} d^{-1} in North Dakota. Respiration ranged from 1 to 15 kg C ha^{-1} d^{-1} in the Mixedgrass Prairie of Wyoming to 2 to 106 kg C ha^{-1} d^{-1} in the Tallgrass Prairie of Kansas.

Table 2.1 Above-canopy CO_2 flux rate data in grassland regions. Rates were recalculated for consistency of units.

Location	Land Use/ Vegetation Type	Condition/ Treatment	CO_2 Flux (kg C ha^{-1} d^{-1})	Reference
Colorado	Arable agriculture	Summary	50 to 200	Schmidt et al., 2001
Saskatchewan	Mixedgrass	Laboratory results	43	Redmann and Abouguendia, 1978
Saskatchewan	Mixedgrass	Peak summer respiration	13	Redmann, 1978
Saskatchewan	Mixedgrass	Summer	45 to 134	de Jong et al., 1974
Saskatchewan	Mixedgrass	Average across all landform positions at peak	47	de Jong, 1981
North Dakota	Mixedgrass	Peak respiration control	57	Frank et al., 2002
		Peak respiration grazed	69	
Wyoming	Mixedgrass	Control	3 to 6	Lecain et al., 2000
		Light grazing	1 to 9	
		Heavy grazing	1 to 15	
Kansas	Mixedgrass	Seasonal mean	10 to 30	McCulley et al., 2005
Kansas	Tallgrass	Ungrazed	2 to 106	Bremer et al., 1998

Terrestrial photosynthesis accounts for 70 to 80% of gross annual global CO_2 uptake (Paul and Clark, 1996). Photosynthetic organisms capture energy from light, splitting water molecules and CO_2 molecules to create various sugar compounds. Plant photosynthesis is a CO_2 sink when conditions are favourable for plant growth and plant respiration is a source of CO_2 when plant growth is slowed or stopped (Frank et al., 2002). Autotrophic bacteria require CO_2 as a carbon source for metabolism, but most soil microbes are heterotrophic and produce CO_2 rather than consume it (Paul and Clark, 1996). The below-ground environment is modified by plant roots and shared with microbes (Robinson et al., 2003). Root growth enriches grassland soils with organic carbon and ensures high microbial activity (Conant et al., 2001).

Soil CO_2 production is derived from the respiration of living organisms and includes the decomposition of organic materials under some conditions (Redmann and Abouguendia, 1978; Hanson et al., 2000). Root respiration of dominant grasses in the Northern Mixedgrass Prairie account for up to 20% of total above-ground and below-ground respiration (Warembourg and Paul, 1977). Decomposition of dead plant materials and respiration of living plants makes up the remaining 80% of total above-ground and below-ground CO_2 respiration.

Soil temperature and soil water influence the rate of CO_2 respiration of the Northern Mixedgrass Prairie. Sixty-six to 74% of the variation in soil CO_2 respiration was explained by soil temperature, soil water and precipitation (Redmann, 1978), among which soil temperature was the best indicator. Soil temperature can account for 44 to 81% of the variation in soil respiration (Frank et al., 2002). Water concentrations of above-ground dead plant materials modify above-ground and below-ground respiration by changing the environment (Redmann, 1978). The Mixedgrass Prairie was the most sensitive to interannual variation in precipitation among grasslands studied (McCulley et al., 2005). Year-to-year variation in precipitation is a determinant of annual CO_2 flux on the Mixedgrass Prairie of Saskatchewan (de Jong et al., 1974). Peak daytime soil respiration in the Mixedgrass Prairie at Matador, SK was in late June to early July (Redmann, 1978). Soil respiration increased from April to mid-June, declining with the onset of water stress in late June (de Jong, 1981). Topography affects soil water and may then influence soil respiration. In a landscape scale study dealing with CO_2 and the Northern Mixedgrass Prairie, CO_2 production increased from upper to lower slope positions (de Jong, 1981).

Grazing can decrease or increase soil respiration in prairie ecosystems through trampling of plants, compaction of soil and increased soil erosion (Carran et al., 1995; Oenema et al., 1997). Heavy grazing contributes to net CO_2 production in some ecosystems, possibly by increasing C inputs to the soil (Tiessen et al., 1998; Lecain et al., 2000). Biomass removal decreases soil respiration in the Tallgrass Prairie (Bremer et al., 1998) (Table 2.1). Soil respiration increases with increasing grazing intensity in the Mixedgrass Prairie (Frank et al., 2002).

Agricultural practices like intensive cultivation and overgrazing decrease the amount of plant materials returned to the soil, contributing up to 90% of C loss in Canadian agriculture (Smith et al., 1997). Respiration of arable agriculture soils can be as much as an order of magnitude greater than respiration from grassland ecosystems (Table 2.1). Best management practices and increasing the extent of rangelands could reduce Canada's contribution to global climate change by sequestering 50 to 75% of Canadian agriculture's CO_2 production over the next 30 years (Dumanski et al., 1998).

2.3.2 Methane

Methane production can occur in arable lands and natural ecosystems during some parts of the year (Wang and Bettany, 1995; Savage et al., 1997) (Table 2.2). Methane consumption by arable soils is typically small (Mosier et al., 1997; Schmidt et al., 2001) (Table 2.2). Boreal forest soils of Manitoba (Savage et al., 1997) are capable of CH_4 consumption and production, similar to the Mixedgrass Prairie of Iowa (Chan and Parkin, 2001). Pastures in Ontario (Lessard et al., 1997) consume less CH_4 than the Shortgrass Prairie of Colorado (Mosier et al., 1997) or the Mixedgrass Prairie in Iowa (Chan and Parkin, 2001). Arable agriculture or cultivation of tame grasses decreases CH_4 consumption in the Shortgrass Prairie of Colorado (Mosier et al., 1997). The Tallgrass Prairie of Kansas consumes more CH_4 when it is burned than when it is unburned or planted to annual crops (Tate and Striegl, 1993). Methane flux rates range from production of 312 g C ha^{-1} d^{-1} to consumption of 48 g C ha^{-1} d^{-1} in German pastures (Koschorreck and Conrad, 1993; Glatzel and Stahr, 2001).

The interaction between CH_4 production and consumption is complex (Dunfield et al., 1995; Mosier et al., 1998b). Methane is produced when soil is water saturated (Mancinelli, 1995). As water drains, mesoaerophilic methanotrophs begin functioning, consuming CH_4 produced in saturated areas of the soil profile as well as CH_4 entering the soil (Mancinelli, 1995). As the soil dries further, most CH_4 production ceases and the soil becomes a net CH_4 sink (Mancinelli, 1995). If the soil continues to dry, microbes become water stressed and CH_4 production and consumption cease (Schnell and King, 1996). When soil is moistened, the CH_4 sink effect decreases because CH_4 production increases or because the decreased diffusion rate of O_2 or CH_4 in water limits CH_4

Table 2.2 Methane flux rate data in grassland regions. Rates were recalculated for consistency of units.

Location	Land Use/ Vegetation Type	Condition/ Treatment	CH_4 Flux (g C ha^{-1} d^{-1})	Reference
Colorado	Arable agriculture	Survey	-5.8	Schmidt et al., 2001
Colorado	Shortgrass	Wet soil	-7.5	Mosier et al., 1997
Saskatchewan	Arable agriculture	Low landform positions	0.2 to 58	Wang and Bettany, 1995
Saskatchewan	Mixedgrass	Low landform positions	0.5 to 79	Wang and Bettany, 1995
Manitoba	Boreal Forest	Upland	-19 to 4.5	Savage et al., 1997
Ontario	Arable agriculture	Manure applied	-2.2 to 0.7	Lessard et al., 1997
Ontario	Pasture	Fall	-3.0 to -2.4	Dunfield et al., 1995
Colorado	Rocky Mountains	Moist meadow swale	-7.5	Torn and Harte, 1996
		Dry ridges	-11	
Colorado	Rocky Mountains	Subalpine meadow	-5.1 to -0.8	Mosier et al., 1993
Colorado	Shortgrass	Native	-4.8	Mosier et al., 1997
		Ploughed	-3.6	
		Planted to tame grass	-3.0	
Colorado	Shortgrass	Swale	-3.6	Mosier et al., 1991
		Midslope	-6.3	
Colorado	Shortgrass	Sandy soils, midslope position	-8.8	Mosier et al., 1996
		Swales	-5.1	
Kansas	Tallgrass	Burned	-7.6	Tate and Striegl, 1993
		Unburned	-4.7	
		Planted to annual grains	-6.4 to -3.4	
Iowa	Mixedgrass		-16 to 5.9	Chan and Parkin, 2001
Germany	Pasture	Fertilized	-48 to 240	Glatzel and Stahr, 2001
		Unfertilized	-48 to 312	
Germany	Meadow	Extensively managed	-7.1 to -5.9	Koschorreck and Conrad, 1993

oxidation (Mosier et al., 1998b).

The biotic production of CH_4 from rangeland soils is an anaerobic process. Anaerobic soil conditions occur occasionally in depressions of Northern Mixedgrass Prairie (Barnes et al., 1983; Conly and van der Kamp, 2001). Aggregates in moist, but not water-saturated soils, can form anaerobic microsites where methanogens produce CH_4 (Conrad, 1996). During snow melt and after large precipitation events, the Northern Mixedgrass Prairie in a low landform position near Lanigan, SK produced more CH_4 than low landform positions on arable lands in the same area (Wang and Bettany, 1995). Electron acceptors with electrical potentials greater than that of CH_4 must be used up before CH_4 is produced (Paul and Clark, 1996). Methanogenic microbes use hydrogen gas, produced during the decomposition of organic materials, as an electron source. Hydrogen gas is combined with various C sources to produce CH_4 (Miller, 1991).

The oxidation of CH_4 by methanotrophic bacteria accounts for approximately 10% of the global CH_4 sink (Topp and Pattey, 1997). Methanotrophs can consume CH_4 produced in the soil or CH_4 entering the soil from the atmosphere (Moiser et al., 1997; Schmidt et al., 2001). Methanotrophs use three methods to consume CH_4, each beginning with the conversion of CH_4 to formaldehyde (Mancinelli, 1995). The dissimilatory method restricts bacteria to capturing energy from the oxidization of formaldehyde CO_2 and H_2O and does not allow the retention of any C (Paul and Clark, 1996). The ribulose monophosphate method allows methanotrophs to assimilate the formaldehyde, converting it to different C molecules for use as biomass (Mancinelli, 1995). Methanotrophs using the serine method assimilate the formaldehyde and convert it to carboxylic acids and amino acids used in biomass production (Mancinelli, 1995).

Ammonium limits CH_4 consumption because the enzyme responsible for CH_4 consumption, methane monooxygenases (MMO), oxidizes ammonium (NH_4^+) instead of CH_4, thus decreasing the CH_4 sink potential of the soil (Hütsch, 2001). The oxidation of NH_4^+ by MMO also produces toxic N compounds that inhibit the methanotrophic population (Hütsch, 2001) and therefore repeated NH_4^+ fertilisation decreases the methanotrophic microbial population and the soil consumption of CH_4 long after application of NH_4^+ ceases (Mancinelli, 1995; Mosier et al., 1996). Nitrate (NO_3^-)

fertiliser has no effect on CH_4 consumption or can stimulate it (Lessard et al., 1997; Hütsch, 2001).

Soil water status varies with time of year, thereby determining the CH_4 flux of a landscape. Consumption of CH_4 on pastures in Ottawa, ON was similar to that on the Shortgrass Prairie of Colorado during the fall; it increased with decreasing soil water content (Table 2.2) (Dunfield et al., 1995). Methane consumption increased from greater to lesser soil water content in the Rocky Mountains of Colorado (Torn and Harte, 1996). Soil water was the greatest influence in controlling CH_4 consumption in a subalpine portion of Colorado (Mosier et al., 1993). In the same area, peak CH_4 consumption occurred at 15% water-filled pore space (WFPS) on sandy soils compared to 20% WFPS on fine-textured soils (Mosier et al., 1996).

Soil structure is important to CH_4 flux because methanotrophs accumulate on the surface of coarse-textured soils and within soil aggregates (Conrad, 1996; Mosier et al., 1997). Tillage disturbs these structures and may reduce habitat necessary for methanotrophs (Willison et al., 1995). Undisturbed soils tend to consume CH_4 more often than they produce it (Wang and Bettany, 1995). Ploughing the Shortgrass Prairie of Colorado immediately reduced CH_4 consumption by 60% (Mosier et al., 1996).

The ideal temperature range of MMO is between 20 and 40ºC, but diurnal changes in temperature do not change CH_4 consumption (Topp and Pattey, 1997). Burning in the Tallgrass Prairie removes litter and modifies the microenvironment, influencing soil temperature and water; less than 20% of the variation in CH_4 consumption of burned and unburned Tallgrass Prairie was explained by soil moisture and soil temperature (Tate and Striegl, 1993). Methane flux is correlated with plant community and landform position, but the most influential factor seems to be soil water (Schmidt et al., 2001). On the other hand, soil organic matter and mean annual temperatures explained 69 to 82 % of the variation in CH_4 and CO_2 flux of upland boreal forest near Thompson, MB (Savage et al., 1997). In the Shortgrass Prairie of Colorado, mesic slope positions consumed less CH_4 than xeric landform positions presumably due to differences in soil water (Mosier et al., 1991).

2.3.3 Nitrous oxide

Arable soils in central Alberta (Nyborg et al., 1997) produce more N_2O than those near Swift Current, SK (Izaurralde et al., 2004) and a perennial grassland in South Dakota (Mummey et al., 1998), all of which produce several orders of magnitude more N_2O than pastures in central Saskatchewan (Corre et al., 1999) (Table 2.3). Mesic grasslands under intensive management (i.e. fertilization, high grazing frequency and high grazing intensity) produce more N_2O than semiarid arable soils (Carran et al., 1995; Velthof et al., 1996a; Velthof et al., 1996b). The Tallgrass Prairie of Kansas (Groffman and Turner, 1995) produces similar amounts of N_2O as intensively managed pastures in Scotland (Clayton et al., 1994; Dobbie et al., 1999), New Zealand (Carran et al., 1995) and the Netherlands (Velthof et al., 1996b).

Nitrous oxide is produced through nitrification, denitrification and nitrifier denitrification (Wrage et al., 2001; Bolan et al., 2004). Denitrification is the only biological process in which N_2O is consumed (Wrage et al., 2001). Different microbes and their enzymes uniquely regulate each step of the N conversion processes involving N_2O (Groffman, 1991). Nitrous oxide flux is sensitive to many soil factors, including pH, organic C content, N content, water, temperature and the size and type of microbial population (Groffman and Turner, 1995; Beauchamp, 1997; Cavigelli and Robertson, 2001). As these factors vary in space and time, the relative contribution of each process changes, influencing the magnitude and direction of N_2O flux (Müller et al., 2004).

Autotrophic nitrification is the oxidation of NH_4^+ or NH_3 to NO_2^- then NO_3^- by two groups of aerobic microbes (Davidson, 1991; Wrage et al., 2001). Nitrous oxide is directly released during the chemical decomposition of intermediates (NH_2OH or NO_2^-) and indirectly when other organisms denitrify the newly formed NO_3^- (Wrage et al., 2001). Heterotrophic nitrification, more common among fungi (Odu and Adeoye, 1970), releases N_2O and indirectly contributes to N_2O emissions by producing substrates for denitrification (Wrage et al., 2001). Under aerobic conditions, heterotrophic nitrification produces more N_2O than autotrophic nitrification (Anderson et al., 1993).

Table 2.3 Nitrous oxide flux rate data in grassland regions. Rates were recalculated for consistency of units.

Location	Land Use/ Vegetation Type	Condition/ Treatment	N_2O Flux ($g\ N\ ha^{-1}\ d^{-1}$)	Reference
Saskatchewan	Arable agriculture	Shoulder slope	0.4	Izaurralde et al., 2004
		Back slope	0.8	
		Foot slope	1.8	
Saskatchewan	Pasture	Shoulder to foot slope	0.005 to 0.16	Corre et al., 1999
Alberta	Arable agriculture	Unfertilized, spring thaw	41	Nyborg et al., 1997
		Fertilized, spring thaw	106	
Alberta	Parklands native and forage vegetation	Undisturbed upland	0.9	Izaurralde et al., 2004
		Undisturbed depression	11	
Quebec	Arable agriculture	Spring melt	47	van Bochove et al., 1996
	Forest		< 1	
Ontario	Pasture	Fertilized	7	Wagner-Riddle and Thurtell, 1998
South Dakota	Restored to grassland	Conversion to perennial grasses	5.8	Mummey et al., 1998
Kansas	Tallgrass	Unburned	6 to 27	Groffman and Turner, 1995
		Burned	-2.2 to 19	
		Burned and grazed	0.3 to 8.2	
Belgium	Forest	Undisturbed	-1.8	Goossens et al., 2001
New Zealand	Pasture	Low fertility hills	1.4	Carran et al., 1995
		Poorly drained hills	9.6	
New Zealand	Pasture	Ungrazed	4.3 to 54	Carran et al., 1995
		Grazed	22 to 92	
Netherlands	Intensively managed pasture	June grazing	257	Velthof et al., 1996b
		September grazing	53	
		November grazing	62	
UK	Pasture	Grazed	1360	Velthof et al., 1996a
Scotland	Pasture	Ungrazed	153	Clayton et al., 1994
		Grazed	557	
Scotland	Pasture	Intensively managed	5.2 to 50	Dobbie et al., 1999

Denitrification is the step-wise reduction of NO_3^- to N_2 via NO_2^- and NO carried out by several groups of predominately heterotrophic, facultative anaerobic microbes using different enzymes (Firestone, 1982). Each step requires a separate enzyme with different rates under different conditions (Cavigelli and Robertson, 2001). Nitrous oxide is released when NO reduction is faster than reduction of N_2O and N_2O escapes into the atmosphere. Of the four enzymes necessary for complete NO_3^- reduction, the enzyme controlling N_2O reduction (nitrous oxide reductase) is most sensitive to increased O_2 concentration, low C:N ratio and low pH (Tiedje, 1988; Wrage et al., 2001). Nitrous oxide reductase enzymes from different species have unique sensitivities to O_2, contributing to differences in N_2O production between arable and untilled land (Cavigelli and Robertson, 2000; Cavigelli and Robertson, 2001).

Nitrifier denitrification is the oxidation of NH_3 to NO_2^- followed by the reduction of NO_2^- to N_2 that is carried out by one group of autotrophic NH_3 oxidizers using the same enzymes used in the nitrification and denitrification processes (Wrage et al., 2001). This process is restricted by microbial population size and is most likely to occur at low O_2 concentrations, and possibly low pH, when NH_3 is available. Nitrifier denitrification decreases in wet, fine-textured soils, is limited by NO_2^- availability in grassland soils and is an important source of N_2O in drier soils (Webster and Hopkins, 1996; Wrage et al., 2004).

The ratio of nitrification production of N_2O to denitrification production of N_2O changes with environmental conditions like O_2 availability and soil temperature. Water saturated, anaerobic soils tend to release N_2O produced by denitrification, while nitrification is the predominant contributor of N_2O in moist, warm soils (Müller et al., 2004). The threshold between nitrification and denitrification is approximately 60% WFPS (Bouwman, 1998; Müller and Sherlock, 2004). Nitrification accounts for as little as 5% of total N_2O production in wet soils (Müller and Sherlock, 2004) and as much as 60% in dry soils (Mummey et al., 1994). Nitrifier denitrification accounted for 29% of N_2O produced on a dry sandy-loam site (Webster and Hopkins, 1996). Nitrification and nitrifier denitrification are important processes in uncultivated soils (Wrage et al., 2001).

Nitrous oxide reductase is the only enzyme capable of N_2O reduction and thus the step in denitrification involving this enzyme is the only biological sink for N_2O (Conrad, 1996). Nitrous oxide uptake by forest soils may be driven by NO_3^- limitations (Papen et al., 2001). Small N_2O sinks have been reported for several natural ecosystems, but often with no attempt to explain the process or its controls (Groffman and Turner, 1995; Regina et al., 1996; Goossens et al., 2001; Wrage et al., 2004).

The rate of N_2O production varies within year, but a short period in spring often accounts for the large majority of the total production (Müller et al., 2002). Nitrous oxide emissions during spring thaw accounted for 47 to 93% of the yearly total N_2O emissions from arable soils in the Canadian prairies (Nyborg et al., 1997; Corre et al., 1999; Lemke et al., 1999). Ammonium fixed on soil particles and C and N from leakage induced by cell death are made available by the freezing and thawing of soils (Groffman and Tiedje, 1989; Müller et al., 2002). Reduced microbial immobilization in spring may also increase NO_3^- availability (Izaurralde et al., 2004). Emissions in the summer may decrease due to lack of anaerobic conditions and water stress (Mummey et al., 1994).

The microbial environment, including pH (Yamulki et al., 1997), temperature, oxygen availability (Wrage et al., 2001), and substrate availability (Lemke et al., 1998), affects N_2O flux rate. The optimum soil temperature for N_2O production in Germany and New Zealand grasslands was between 10 and 15°C (Müller and Sherlock, 2004). Fertilised pastures in Scotland with 40 to 80 mg N kg dry soil^{-1} of NO_3^- and NH_4^+ emitted more N_2O than less intensively managed pastures (Dobbie et al., 1999). Tight N cycling and low soil NO_3^- concentrations typical of uncultivated soils such as forests and pastures limit N_2O production (Smith et al., 1994; Corre et al., 1996) and negate any relationship between WFPS and N_2O flux rate (Dobbie et al., 1999). A perennial grass field in Ontario (Wagner-Riddle and Thurtell, 1998) and Alberta arable lands (Lemke et al., 1998) with low soil NO_3^- concentrations also had low N_2O production. Nutrients from microbes killed by water stress can also contribute to an increase in N_2O emissions at the onset of precipitation events (Mummey et al., 1994). Soil water and soil NO_3^- contents accounted for 46 to 77% of variation in N_2O production (Velthof et al., 1996b; Izaurralde et al., 2004). These fine scale controls are in turn constrained by coarse scale attributes such as topography, climate and land use.

Topography controls hydrology and pedology of soils, which influences the microbial environment important for N_2O flux. Mineral N was randomly distributed, but denitrification formed a depression-centred pattern related to topographically induced anaerobic conditions on a field in southern Saskatchewan (Pennock et al., 1992), similar to N_2O emissions from a perennial grass pasture in the United Kingdom (Velthof et al., 2000). The spatial pattern of N_2O flux persisted in time, but the magnitude of the flux changed. Low and intermediate landform positions produced the majority of the N_2O in a study in the Alberta Parklands and near Swift Current, SK (Izaurralde et al., 2004). Cumulative N_2O emissions of grazed New Zealand pastures were 7 times greater on poorly drained landscapes than on low fertility hills (Carran et al., 1995).

Land use and plant community influence N_2O flux. Disturbing the function of natural ecosystems often increases N_2O production (van Bochove et al., 1996; Mummey et al., 1998). Grazing increased N_2O flux by 2 to 5 times compared to ungrazed areas on intensively managed pastures in Scotland and New Zealand (Clayton et al., 1994; Carran et al., 1995). Biomass removal has the opposite effect in the Tallgrass Prairie of Kansas where burning and grazing decrease N_2O emissions by up to 3 times (Groffman and Turner, 1995). Grazing influences the spatial variability of N_2O flux by distributing feces and urine patches that generate localized "hotspots" with very high emissions (Yamulki et al., 1998). Among natural plant communities within an ecosystem N_2O production can vary up to an order of magnitude (Izaurralde et al., 2004).

2.4 Landscape Scale Variability Related to GHG Production and Consumption

Topography creates variation in environmental conditions that control GHG flux, including physical environment and plant community characteristics. Linking topography with the physical environment and plant community aids in understanding GHG flux processes at the landscape level.

2.4.1 Variability in the physical environment among landform elements

Topographical redistribution of above-ground and below-ground water has long been recognised as a soil forming factor (Ellis, 1938). Precipitation applied evenly over an uneven landscape accumulates in areas with converging surfaces and drains from areas with diverging surfaces (Ellis, 1938). The accumulation of rainfall on different surfaces on a hill depends on the wind direction and the surface aspect, and may vary by 100 to 150% in high winds (Sharon, 1980; Lentz et al., 1995). Overland flow from rainfall events rarely contributes to topographic redistribution of water on hummocky landscapes in Saskatchewan (Hayashi et al., 1998). More than 25 mm of rain per day is required to generate overland flow on a hummocky field in Saskatchewan (Woo and Rowsell, 1993). Surface roughness and topographical depressions decrease wind speed and increase snow accumulation (Pomeroy et al., 1993; Hayashi et al., 1998). In open areas, wind can remove 85% of fallen snow (Pomeroy et al., 1993). Snow accumulation increases to a maximum on the lee side of hills and where vegetation density is the greatest (Essery and Pomeroy, 2004). Snowmelt is the most important contributor to depression flooding on hummocky fields in Saskatchewan (Hayashi et al., 1998). Soils of perennial grass fields allow infiltration into the frozen soils during snowmelt, decreasing the amount of runoff available to flood depressions (van der Kamp et al., 2003). The influence of water movement on soil erosion in native prairies is generally small compared to arable fields. Landform element did not influence soil redistribution on a Mixedgrass Prairie in Saskatchewan (Pennock et al., 1994). The topography of a site ensures that concave and depression landform elements consistently accumulate more water and eroded materials than other landform elements. The amount of water accumulated influences soil chemical processes, plant community composition, total plant production and WFPS.

The amount of solar radiation absorbed depends on the angle of the sun relative to the horizon and the angle of the surface relative to the horizon. At northern latitudes, potential direct incident radiation (PDIR) increases with increasing surface angle on southern slopes (Buffo et al., 1972). Surfaces with 0º angle receive intermittent amounts of PDIR, while PDIR on north-facing slopes decreases with increasing surface angles (McCune and Keon, 2002). Sun-facing north slopes in southern latitudes can receive 80% more radiation than south-facing slopes (Radcliffe and Lefever, 1981). Sun-exposed slopes are generally warmer than slopes not directly facing the sun.

Soil temperature on south-facing slopes was 2 to 4ºC greater than soil temperature on north-facing slopes on Mixedgrass Prairie in Saskatchewan (Ayyad and Dix, 1964). Soil temperatures were greater and soil dried sooner on north-facing slopes compared to south-facing slopes in New Zealand (Radcliffe and Lefever, 1981). The southern slopes of the Nebraska Sand Hills are drier and warmer than north-facing slopes (Pählsson, 1974). These two slope aspects also had different vegetation and microclimates. Consequently, south-facing slopes had one-half as much ignitable C as north-facing slopes. Landform position affects soil organic carbon (Oztas et al., 2003). North and lower slopes of a Mixedgrass Prairie had more soil N than south and upper slopes, respectively (Lieffers and Larkin-Lieffers, 1987).

2.4.2 Spatial variation in plant community characteristics

Plant community composition and productivity are most influenced by soil water availability (Coupland, 1961; Redmann, 1975) and to a lesser extent by temperature (Barnes et al., 1983). Therefore, topographic variation is vital in determining species composition, mainly through its affects on soil water (Cantlon, 1953; Dix, 1968) and to some extent solar radiation (Lieffers and Larkin-Lieffers, 1987). Each species has a specific optimum range of growing conditions (Ayyad and Dix, 1964). Species like *Muhlenbergia cuspidata* (Torr. ex Hook.) Rydb. (plains muhly) and blue grama are usually restricted to south-facing slopes in the Northern Mixedgrass Prairie (Ayyad and Dix, 1964; Barnes et al., 1983). Generally, cool season plants, like plains rough fescue and *Carex obtusata* Lilj. (blunt sedge), dominate north-facing slopes and lower landform positions (Ayyad and Dix, 1964). Northern wheatgrass, *Carex filifolia* Nutt. (threadleaf sedge) and needle-and-thread dominate south-facing slopes and upper positions (Ayyad and Dix, 1964).

Production increases when soil water is increased (Willms et al., 1986, Willms et al., 1993). Irrigation increased above-ground biomass of graminoids in the Mixedgrass Prairie of Saskatchewan by 40% compared to the control (Colberg and Romo, 2003). Biomass production of hummocky landforms mirrors the topographic pattern of water distribution (Pennock et al., 1987). For example, depressions are generally more productive than uplands in the Northern Mixedgrass Prairie (Kantrud et al., 1989). Plant growth in depressions is influenced by greater water availability and the salinity of the water (Walker and Coupland, 1968).

2.4.3 Using the hierarchical approach to study landscape scale greenhouse gas variability

Landscape ecology provides a foundation for the study of complex interactions between abiotic and biotic factors that control ecological processes such as GHG flux

(Risser, 1987). One of the goals of landscape-scale ecosystem studies is to predict the spatial and temporal patterns of ecosystem processes based on more easily observed factors (Groffman and Turner, 1995). Disturbances, biotic processes and environmental constraints functioning at different temporal and spatial scales form patterns across the landscape (Urban et al., 1987). Topography is a coarse scale environmental constraint in space and defoliation falls within the coarse scale of topography. These agents create patterns of plant growth and microbial processes by altering resource availability and growth conditions (Ayyad and Dix, 1964; Pennock et al., 1992).

Hierarchical examination of these agents of heterogeneity has led to their use in categorizing plant composition and structure (Turner et al., 1994). A similar arrangement of patterns may exist in relation to microbes responsible for GHG flux and their response to constraints (Turner et al., 1994). Therefore, the GHG flux pattern may mirror landscape scale plant patterns of structure, function and composition (Groffman and Turner, 1995; Corre et al., 1996).

The hierarchical approach divides GHG flux regulation factors into distal and proximal groups to explain variability brought about by a heterogeneous landscape (Corre et al., 1996; Bolan et al., 2004). Distal factors indirectly control GHG flux at a coarse scale. These factors change very slowly and over large areas. Examples of distal factors include climate, topography and land use. Proximal factors vary within the confines of the distal factors and directly control GHG flux at a fine scale. Proximal factors can change quickly with quick reactions from soil microbes. Examples of these include O_2 availability, pH, H_2O, N and C. Changes in proximal factors can vary GHG flux rates over 100 m or less (Velthof et al., 2000). Landscape derived differences in distal factors vary GHG flux rates from region to region (Bowden, 1986; Smith and Dobbie, 2001).

Topography refers to the combination of slope aspect and slope shape on a surface. Aspect is the compass direction the surface is facing and slope shape describes surface curvature. Divergent surfaces, called convex slope shape, shed water while convergent surfaces, called concave slope shape, collect water (Pennock, 2003). Aspect and slope shape describe different landform elements including, but not limited to, north-facing aspect, and concave shaped slope (NV), north-facing aspect, and convex shaped slope (NX), south-facing aspect, and concave shaped slope (SV), south-facing aspect, and convex shaped slope (SX), level upland (UP) and depression (DP).

Mowing is a distal factor operating at a smaller scale than topography and refers, in this study, to the removal of above-ground plant materials. Mowing is a disturbance that alters the structure, function and composition of a stand (Huntly, 1991). Mowing directly and indirectly influences the environment of plants and microbes responsible for GHG flux without adding nutrients or increasing bulk density of soil.

2.5 Management Issues for Greenhouse Gas Mitigation in the Northern Mixedgrass Prairie

Reducing disturbances as a form of land management may be the best management practice for GHG mitigation. Overall, drastic soil disturbance decreases CH_4 consumption and increases CO_2 and N_2O production. Conventional tillage systems converted to reduced tillage increase CO_2 sequestration (Mummey et al., 1998), while full season studies show that reduced tillage systems have lower N_2O emissions than conventional tillage systems in the Mixedgrass Prairie region (Lemke et al., 1999). Methane consumption by soil bacteria is increased by reduced tillage (Hütsch, 2001). Ammonium application, common to arable agriculture, inhibits CH_4 oxidation by bacteria (Topp and Pattey, 1997) and decreases the CH_4 oxidizing soil bacteria population (Hütsch, 2001). Perennial crops in an arable crop rotation can decrease GHG emissions. Greenhouse gas emissions from *Medicago sativa* L. (alfalfa) and *Poa pratensis* L. (Kentucky bluegrass) were lower than from annual crops (Wagner-Riddle et al., 1997). The conversion of 10.5 million hectares of the croplands in the USA to perennial cover would decrease N_2O emissions by an estimated 31 Gg-N yr^{-1} (Mummey et al., 1998). Converting some Saskatchewan pastures back to forests could increase ecosystem C by approximately 3 times because standing trees are a larger pool of C than pasture vegetation (Fitzsimmons et al., 2004).

Producers can change management to address GHG flux. Oenema et al. (1998) recommended that the effects of farm practices be considered in the long-term or strategic sense and medium-term or tactical sense instead of the day-to-day operational time frame. Strategic and tactical planning could involve determining yearly farm inputs and outputs of nutrients and grazing regimes that recognize the impact of biomass removal on soil processes. Cataloguing and managing for GHG sinks is a small step to addressing climate change. One of the core climate change problems is large-scale land conversion from uncultivated ecosystems to cultivated lands or the conversion of forested ecosystems to grazed grassland ecosystems. The next step for those working to slow or reverse anthropogenically induced climate change is to look for ways to reduce or reverse those conversions.

2.6 Summary

The concentration of GHGs directly determines the amount of heat the earth's atmosphere retains, thereby influencing the climate. Concentrations of CO_2, CH_4 and N_2O have all increased since the beginning of the industrial revolution. Evidence of present and future climate change is mounting. Determining the controls and magnitude of GHG flux helps Canada comply with internationally agreed upon emission reduction targets. Gathering this information is difficult due to the number and type of factors affecting GHG flux. The physical environmental and plant community influence GHG flux, which vary in time and space. Some of the variation can be explained by closely examining topography, land management and plant community characteristics. A hierarchical approach aids in classifying and understanding variation in the natural ecosystem. The best management practices for mitigating climate change may be the ones that best maintain ecosystem function.

3. MATERIALS AND METHODS

3.1 Site Description

The study site is approximately 20 km south of Macrorie, SK in the Mixed Grassland Ecoregion (Acton et al., 1998) of the Missouri Coteau. The legal land description is SW-20-26-9W3 (51°14'N, 107°15'W; 720 m elevation). The Calcareous Dark Brown and Orthic Regosol soils in this area originate from glacial till and are part of the Weyburn Soil Association (Ellis et al., 1970). The topography is hummocky with strongly sloping to moderately rolling surfaces and slopes of 10 to 15% (Ellis et al., 1970). Similar to Coupland's (1950) description of the Mixedgrass Prairie, dominant plant species at the study site are northern wheatgrass and western porcupine grass. Plains rough fescue is present and most abundant in the more protected, mesic areas (Coupland, 1961). Aspen and *Salix* spp. (willow) are common around depressions while *Symphoricarpos occidentalis* Hook. (snowberry) patches occur in mesic landform positions (Coupland, 1950). The site has not been grazed for at least 10 years before the study, but some depressions have been hayed in the past decade (Ron Dunning, personal communication).

3.2 Experimental Design and Treatment Design

A landscape-scale comparative mensurative experimental design was used to select blocks with the same topographical features (Eberhardt and Thomas, 1991; Pennock, 2004). There were five replicates of six different landform elements with two treatments imposed as randomized complete blocks on each landform element for a total of 60 experimental units. The six landform elements were north-facing aspect and concave shaped slope (NV), north-facing aspect and convex shaped slope (NX), south-facing aspect and concave shaped slope (SV), south-facing aspect and convex shaped slope (SX), level upland (UP) and depression (DP). Landform elements were chosen visually and confirmed with digital elevation maps. Mowing is an established simulation of grazing that has been used to test the effects of above-ground biomass removal on the structure, function and composition of range ecosystems without increasing bulk density, selectively removing species or adding urea and feces (Haferkamp and Karl, 1999; Eneboe et al., 2002). The control and mowing treatments were randomly assigned within each replicate. Each treatment plot measured 2×20 m with a 2×4 m sampling area established at the centre for gas, soil and vegetation sampling. A Jari sickle bar mower (Year-A-Round Corporation, Mankato, MN, USA) was used to cut vegetation to a height of 7.5 cm within the 2×20 m treatment plot. Mowing was completed on 18 April 2003 and mowed plant materials were removed from the plots. This experiment was repeated in 2004 on the same landform elements using the same control plots, but with mowing imposed on 22 April 2004 on previously unmowed plots. The 2003-2004 sampling season was from 30 April 2003 to 20 April 2004, while the 2004-2005 sampling season was from 3 May 2004 to 10 March 2005.

3.3 Data Collection

3.3.1 Environmental attributes

Points within the study area were catalogued with a global positioning system (GPS; TSC1 Asset Surveyor, Trimble Navigation Limited, Sunnyvale, CA, USA) and a laser-sited theodolite (Electronic Total Station, SET5, Sokkisha Co. LTD., Tokyo, Japan). Two horizontal coordinates were combined with the relative elevation to capture changes in topography within and around the blocks. The three coordinates were used to generate a digital Elevation Model (DEM) with Surfer (Surfer 7, Golden Software, Inc., Golden, CO, USA).

Soil temperature probes (Campbell Scientific 107B; Campbell Scientific Canada, Edmonton, AB) were buried to a depth of 5 cm within each 2×4 m sampling area in the spring of 2003. Hourly temperatures were recorded using two Campbell Scientific 21X data loggers. Only one block was monitored because of a lack of equipment. Temperature probes were removed in the fall of 2003 and reinstalled in the spring of 2004. A Sierra/ISCO model-2501 tipping bucket (Nova Lynx Corporation, Grass Valley, CA, USA) calibrated to 0.658 mm per tip, recorded precipitation on one of the data loggers. Weather data were also obtained from the Rock Point Environment Canada Weather Station located approximately 10 km away (51°9'N107°16'W; 725 m elevation) (Environment Canada, 2005a).

Two samples of soil bulk density were collected from 0 to 15 cm from each block of each landform element using a 15 × 8 cm metal cylinder (Blake and Hartge, 1984). Surface material was removed before sampling and samples were dried at 80°C for 48 hours and weighed. The average bulk density was reported for each landform element.

Five soil samples from 0 to 15 cm from each 2 × 4 m sampling area were collected and bulked for soil texture analysis using the Bouyoucos Hydrometer Procedure (Dodd et al., 2000). Samples were dried at 100°C for 24 hours, sifted and then ground through a 2-mm sieve (Bouyoucos, 1962). Fifty gram samples were saturated with distilled water and subjected to particle dispersal by adding a dispersal agent (0.02N sodium pyrophosphate $Na_4P_2O_7 \cdot 10H_2O$), shaking for 6 hours, resting for 24 hours, blending for 30 seconds and shaking by hand for approximately 30 seconds. Solution density was determined from hydrometer readings 40 seconds and 2 hours after final shaking, respectively. Density readings, corrected for water temperature at time of reading, were used to calculate final percentage of clay, silt and sand.

A snow survey was conducted on 1 March 2004 and 8 March 2005. Snow samples were taken from each 2 × 4 m sampling area using a snow sampling tube (7 cm i.d.). The tube was inserted into the snow pack and the depth of snow was recorded (Goodison et al., 1981). The intact snow core was placed in a labelled plastic bag and weighed. The mass of each snow sample was converted to water equivalent in millimetres of water.

Slope angle and aspect were measured for each plot to calculate potential direct incident radiation (PDIR, MJ m^{-2} yr^{-1}). The UP and DP landform elements have no slope angle and therefore no directional aspect. Slope angle and aspect were converted from degrees to radians for PDIR calculations (McCune and Keon, 2002).

Soil samples, from 0 to 15 cm, were collected from all 2 × 4 m sampling areas on each gas sampling date. One-half of each sample was used to determine soil water content (oven-dried for 24 h at 100°C) (Gardner, 1982). Percentage of water-filled pore space (WFPS) from 0 to 15 cm was determined (Peterson and Calvin, 1965) for each 2 × 4 m sampling area from gravimetric soil water, bulk density and particle density. The remaining one-half of each soil sample was frozen and one sample date from spring, summer, and fall of each year were selected for NH_4^+ and NO_3^- analysis. Soil samples used to determine N were dried, sifted and ground through a 2 mm sieve. Nitrogen was extracted from the soil using 2 M KCL. This solution was refrigerated at 4°C until it was analysed with a colorimetric analyser (Keeney and Nelson, 1982).

3.3.2 Plant community structure, species composition and biomass production

Four 0.25 m^2 quadrats were randomly placed within each 2 × 4 m sampling area in early August of 2003 and 2004. The percentage canopy covers of litter, bare soil, *Selaginella densa* Rydb. (club moss) and each vascular species were visually estimated. Species richness was calculated as the number of species in 0.25 m^2 and species evenness as the relative abundance of all of the species. The Shannon-Wiener Diversity Index is a measure of relative abundance and richness of a given area.

Four 0.25 m^2 quadrats were randomly placed within each plot and all standing crop was hand-clipped to ground level in mid-August of 2003 and 2004. Samples were sorted into wheatgrasses (western wheatgrass, northern wheatgrass and *E. trachycaulus* (Link) Gould ex Shinners (slender wheatgrass)), needle grasses (western porcupine grass, needle-and-thread and *Nassella viridula* (Trin.) Barkworth (green needle grass)), plains rough fescue, other graminoids and forbs (including shrubs and tree seedlings). Samples were dried for 48 h at 80°C and weighed.

In 2003, a representative portion of each grass and graminoid sample was sorted by colour (green = standing-live and brown = standing-dead) to determine the live and dead proportions of the entire sample. Samples of 10 g or less were sorted entirely. For samples between 10 and 100 g, 10 g were sorted. Approximately 10% to a maximum of 20 g was sorted for samples over 100 g. The double sample method was used to estimate standing-live verses standing-dead biomass in 2004 (Pieper, 1978; Anonymous, 1986). Each sample was weighed and the percentage standing-live biomass of the total was visually estimated based on the colour of leaves. Representative portions (as in 2003) of 8 randomly selected samples from each species and mowing treatment were sorted to determine actual percentage of standing-live biomass. Regression analysis of the actual live and estimated live percentage was used to calculate actual standing-live biomass for all samples. Between 73 and 75% of the variation in the estimated proportion of standing-live biomass to standing-dead biomass was accounted for by the sampler. The weight of the total sample was multiplied by the estimated proportion of standing-live biomass and the slope of the regression equation for that species to arrive at the estimated standing-live weight. Standing-dead weight was calculated as the weight of the total sample minus the estimated weight of the standing-live biomass.

3.3.3 Gas sample collection and analysis

Immediately following mowing in 2003 and 2004, a chamber base (50×50 cm angled aluminium) was inserted in the soil to a depth of 5 cm (Clayton et al., 1994) at the centre of each 2×4 m sampling area. Closed clear polymethylmethacrylate sheet (Plexiglas®; Arkema, Paris) chambers, as described by Hutchinson and Mosier (1981), were built following current guidelines (International Atomic Energy Agency, 1992; P. Rochette and G.L. Hutchinson, unpublished report). Chambers were built $55 \times 55 \times 20$ cm with a closed-cell foam gasket base (Blackmer and Bremner, 1980), an internal, horizontally mounted battery operated fan (Norman et al., 1997) and a 10 cm $\times$ 3 mm (i.d.) pressure vent tube covered with open-celled foam to shield it from the wind and prevent mass flow out of the chamber (Conen and Smith, 1998; Hutchinson and Livingston, 2001). Chambers were covered with reflective insulation to prevent temperature increase (Black and Bremner, 1980). A thermocouple wire and a rubber-stopped septum were installed.

Gas samples were collected at approximately 10-day intervals for a total of 18 sample dates from late April to late October in 2003, 17 sample dates from late March to early October in 2004 and 1 sample date in March 2005. A sampling order of plots was randomly generated for each date. Chambers were placed on top of the chamber bases and secured with straps. Gas samples were drawn from chambers using a 20 cm^3 syringe at 0 (T0), 30 (T30), and 60 (T60) minutes after chamber placement. The chamber's internal fan was run for 30 seconds before T30 and T60 gas sampling. Samples were stored in labelled, evacuated 12 cm^3 vials at 4ºC until analysed. Chamber temperatures were recorded at the same intervals. Ambient air samples were taken at chamber height throughout the sampling period and across the site. When a base was obstructed by snow during spring sampling, chambers were placed on top of snow.

Gas samples were analysed for CO_2, N_2O, and CH_4 using gas chromatography (GC) (Farrell et al., 2002). Sample analyses were performed either at the Department of Soil Science, University of Saskatchewan, Saskatoon or the Semiarid Prairie Agricultural Research Centre, Agriculture and Agri-Food Canada, Swift Current. Although the two labs used slightly different GC systems, previous work has demonstrated that the results are consistent (R.E. Farrell, personal communication).

Carbon dioxide analyses at Saskatoon, SK were conducted using a Varian CP-2003 micro-GC (Varian Canada Inc., Mississauga, ON) equipped with a micro-thermal conductivity detector (TCD) and a Poraplot U column (10.0 m × 0.32 mm i.d. silica capillary column), both maintained at 44ºC. Gas samples were introduced using a 30-position, vacuum-activated valve system with injection temperature of 110°C, sample volume of 50 μL and ultra-high purity helium (UHP He) as the carrier gas. The system was calibrated using standard gases (CO_2 in air) obtained from Praxair (Mississauga, ON). Data was processed with Varian *Star Chromatography Workstation* software (ver. 5.51). Internal calibration curves were obtained by applying linear, least squares regression to the CO_2 concentration (ppmV) versus peak area data. Carbon dioxide concentrations in the headspace samples were then calculated automatically from the regression equation.

Methane and N_2O analyses were carried out sequentially using a Varian CP 3800 GC (Varian Canada Inc., Mississauga, ON) equipped with a flame ionization detector (FID) for CH_4 analyses and dual electron capture detectors (ECD) for N_2O analyses. For CH_4 analyses, the injector temperature was 70°C, the column temperature was 35°C and detector temperature was 200ºC. Separations were carried out using a Cpsil 5 CB column (15.0 m × 0.25 mm i.d. fused silica capillary column, DF = 0.25 µm) with UHP He (15 mL min^{-1}) as the carrier gas. Samples of 300 µl were introduced using a CombiPAL™ auto-sampler (CTC Analytics AG, Switzerland) with on-column injection and a split ratio of 3:1. The system was calibrated using standard gases (CH_4 in air) obtained from Praxair.

The N_2O system was analysed with injector temperature at 100°C, column temperature at 35°C and detector temperature at 370ºC. Separations were carried out using Poraplot Q columns (12.5-m $\times$ 0.32-mm i.d. fused silica capillary column, including a 2.5-m particle trap, DF = 8 µm) with UHP He (16 mL min^{-1}) as the carrier gas and P5 (95:5 Ar:CH_4 mix) as the make-up gas (11 mL min^{-1}). The auto-sampler injects 300 µl of gas sample on-column using a split injection system with a split ratio of 10:1 and P5 as the make-up gas and UHP He as the carrier gas. The system was calibrated using standard gases (N_2O in N_2) obtained from Praxair.

Data for the CH_4 and N_2O analyses was processed with Varian *Star Chromatography Workstation* software (ver. 6.2). Internal calibration curves were obtained by applying linear, least squares regression to the gas concentration (ppmV CH_4; ppbV N_2O) versus peak area data. Methane and N_2O concentrations in the headspace samples were then calculated automatically from the regression equations.

At Swift Current, SK the concentrations of all three gases were determined using a Varian CP 3800 equipped with a CombiPAL™ auto-sampler. The auto-sampler injects the gas sample into a 10 port sampling valve, which then transfers the sample to two, 0.5 mL sample loops. One loop introduces the sample onto an 80/100 mesh Porapak N pre-column (0.4572 m $\times$ 3.18 mm i.d.; injector temperature = 70°C) and the other introduces the sample onto an 80/100 mesh Porapak QS column (1.83 m $\times$ 3.18 mm i.d.; column temperature = 80°C) using UHP He as the carrier gas. Carbon dioxide is then determined using a TCD maintained at 130°C with a filament temperature of 220°C and CH_4 is determined using a FID maintained at 200°C. For N_2O analyses, the sample was introduced onto an 80/100 mesh Hayesep D column (1.83 m $\times$ 3.18 mm i.d.) using P10 (90:10 Ar:CH_4 mix, flow rate = 30 mL min^{-1}) and detected using a ^{63}Ni-ECD maintained at 380°C.

Peak areas were quantified by comparing sample peak areas with that of a commercial custom mixed standard (Praxair) composed of CO_2 385 µL L^{-1} (balance N_2), CH_4 1.46 µL L^{-1} and N_2O 1.11 µL L^{-1}. Peak areas for all three gases were quantified with Varian *Star Chromatography Workstation* software (ver. 6.2).

Minimum detectable concentration difference (MDCD) for a given sample date was calculated as two times the standard deviation of ambient samples for that sample date. Time zero minutes sample concentrations were deemed outliers and replaced by the average T0 sample concentration if they were greater than or less than 1.5 times the second quartile of all the T0 samples. Time thirty minutes sample concentrations were deemed outliers and replaced by the average of T0, T30 and T60 sample concentrations for that experimental unit on that sampling date if the T30 sample concentration was less than the T0 sample concentration and less than T60 sample concentration and the difference between the average of the T0 and T60 samples concentrations and the T0 sample concentration was greater than or less than 1.5 times the MCDC. Time sixty minutes sample concentrations were deemed outliers and replaced by the average of all T60 sample concentrations for that sampling date if the T60 sample concentration was greater than the T0 sample concentration and the T30 sample concentration was greater than the T0 sample concentration and if the T60 sample concentration was not equal to the T0 sample concentration or the T60 sample concentration was greater than the T0 sample concentration. Sample concentrations were adjusted for air temperature and atmospheric pressure. Chamber volume, chamber area and MDCD were used to determine flux rate. Differences between the T60 and T30 sample concentrations, the T30 and T0 sample concentrations and the T60 and T0 sample concentrations were compared to MDCD. If difference between the T30 and T0 sample concentrations was "FALSE" or if the difference between the T30 and T0 sample concentrations and the difference between the T60 and T0 sample concentrations were "FALSE" then the flux rate was set to zero. The least squares method was used to compare sample time intervals with adjusted sample concentrations from one experimental unit. The generated slope equalled the mass of a GHG released or consumed m^{-2} s^{-1}. Cumulative fluxes were calculated by interpolated flux rates generated for the 60 minute sampling period to the period half-way to the next sampling date and the period half-way to the previous sampling date (Pennock et al., 2005). For instance, CH_4 consumption rate was 5 ng CH_4 m^{-2} s^{-1} on 15 July 2004. The previous sampling date was 6 July 2004 and the next sampling date was 27 July 2004. The flux rate from 15 July 2004 was then used to calculate the flux for 4 days previous to 15 July 2004, 15 July 2004 and 5 ½ days after 15 July 2004. Cumulative flux of CO_2 was converted from μg CO_2 m^{-2} $season^{-1}$ to kg of CO_2-C ha^{-1} d^{-1}, CH_4 flux rates were converted from ng CH_4 m^{-2} $season^{-1}$ to g CH_4-C ha^{-1}

d^{-1} and N_2O flux rates were converted from ng N_2O m^{-2} $season^{-1}$ to g N_2O-N ha^{-1} d^{-1} to generate weighted daily average by dividing by the number of days that sample season covered. Cumulative flux data were also converted to kg CO_2 equivalent $season^{-1}$ by multiplying by the GWP of 23 for CH_4 and 296 for N_2O.

3.4 Data Analysis

A general linear model (PROC GLM) from SAS (ver. 8.0) (SAS Institute Inc., Cary, NC, USA) was used to determine the effects of landform element, mowing and sample date on GHG flux rates and WFPS. The effects of landform element and mowing on different measured factors including soil physical characteristics, soil temperature, snow accumulation, biomass (standing-live graminoid, standing-dead graminoid, forbs and shrubs and total above-ground biomass), species richness, species evenness and Shannon-Weiner diversity index were determined from an ANOVA generated with PROC GLM. Means separation was done using least significant difference test (LSD) (Zar, 1984). A significant level of P = 0.05 was used.

The relationship between landform element, mowing and species composition was plotted using Detrended Correspondence Analysis (DCA) in CANOCO (ver. 4.5) (Microcomputer Power, Ithaca, NY, USA) (ter Braak and Šmilauer, 2002). Detrended Canonical Correspondence Analysis (DCCA) from CANOCO was used to determine the standard deviation of the species gradients for each year (6.131, 2.304, 2.370 and 1.661 for Axes 1 to 4 in 2004 and 5.076, 2.160, 1.946, 1.390 for Axes 1 to 4 in 2003). Axis 1 had a standard deviation greater than 3 to 4, indicating a unimodal species response most appropriately analysed with Canonical Correspondence Analysis (CCA) from CANOCO using Hill's technique to scale species response (ter Braak, 1987; ter Braak and Šmilauer, 2002). This technique plots experimental units and environmental gradients using points and arrows, respectively, to generate a joint plot that can only be interpreted relatively (ter Braak, 1987; McCune and Grace, 2002). Canonical Correspondence Analysis uses multiple linear least-squares regression to determine weighted average experimental unit scores (Palmer, 1993). The joint plot is plotted using Linear Combination (LC) scores of dependent and independent variables. Canonical Correspondence Analysis shows how environmental gradients like soil water control species distribution and how environmental gradients like CO_2, CH_4 and N_2O flux change in relation to species composition. Therefore, species composition can be used to distinguish areas with high or low GHG flux (Bubier, 1995; Bubier and Moore, 1995). The length of an environmental variable arrow indicates its relative importance, the direction indicates its correlation with the species composition axis and the angle of one arrow relative to another indicates the relative correlation between the two variables (Palmer, 1993). Negative portions of environmental gradients are not displayed in CANOCO and need to be imagined as an arrow equal to the positive environmental gradient extending in the opposite direction, indicating, in the case of cumulative CH_4 flux, cumulative CH_4 consumption (ter Braak and Šmilauer, 2002).

Species recorded in less than 5% of experimental units were removed from the CCA matrix to limit the influence of rare species (McCune and Grace, 2002). Correlated variables that contained similar information were removed to aid clarity. Significance of remaining variables was determined using forward selection. This step-wise selection process uses a Monte Carlo test with 9,999 unrestricted permutations to determine the P value of each environmental variable (ter Braak and Šmilauer, 2002). Variables with a P > 0.01 were removed (Qian et al., 2003).

4. RESULTS

4.1 Variability in Environmental Attributes as Affected by Landform element and Mowing

4.1.1 Precipitation, air and soil temperatures, and solar radiation

During the 2003 sampling season, temperatures in the Macrorie area were hotter and precipitation was less than the 30-year average (Table 4.1). The average monthly air temperature at the Rock Point Environment Canada Weather Station in 2003 was equal to or warmer than the 30-year average in every month but February, March and November. The mean annual temperature in 2003 was 0.5ºC greater than the 30-year average. Total monthly precipitation during winter and early spring was mostly higher in 2003 than the 30-year average, but precipitation for the whole year was 71% of the 30-year average.

Temperature during the 2004 sampling season was lower than the 30-year average (Table 4.1). From April to October, only April and September were warmer than the 30-year average. The mean annual temperature was 0.1ºC warmer in 2004 than the 30-year average. Precipitation from April through October in 2004 was 120% of the 30-year average for the same period. Over the entire year, 2004 precipitation was 106% of the 30-year average.

Mowing in the previous year did not influence 2004 snow accumulation (displayed as mm snow water equivalent), but landform element did influence 2004 snow accumulation ($P < 0.001$) (Figure 4.1). Snow water equivalent was greatest on the DP landform element, the NV landform element had the second greatest and all other landform elements had less accumulated snow water equivalent. There was no snow accumulation on the site on the snow sampling date in the spring of 2005, but water had accumulated in the DP landform element at that time (personal observation).

Table 4.1 Mean monthly air temperatures (°C) and total monthly precipitation (mm) at Rock Point, SK.

Month	----- 30-Year Average -----		---------- 2003 ----------		---------- 2004 ----------	
	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation
January	-14.0	17.1	-12.9	21.4	-15.9	10.6
February	-10.4	10.3	-13.6	24.8	-7.5	5.0
March	-4.0	18.2	-6.2	2.6	-1.0	6.8
April	4.9	22.6	5.2	52.4	6.0	8.4
May	11.5	55.1	11.6	24.2	8.3	50.6
June	15.9	69.7	15.9	37.8	13.4	74.2
July	18.6	60.1	20.3	33.0	18.2	59.2
August	17.8	36.5	21.8	7.4	15.1	105.8
September	12.2	30.2	12.2	32.6	12.3	28.4
October	5.4	18.5	8.6	21.4	4.0	24.2
November	-4.8	17.9	-8.6	5.6	-0.6	0.6
December	-11.6	20.9	-6.6	4.8	-9.3	25.6
Average	3.5		4.0		3.6	
Total		366.9		268.0		399.4

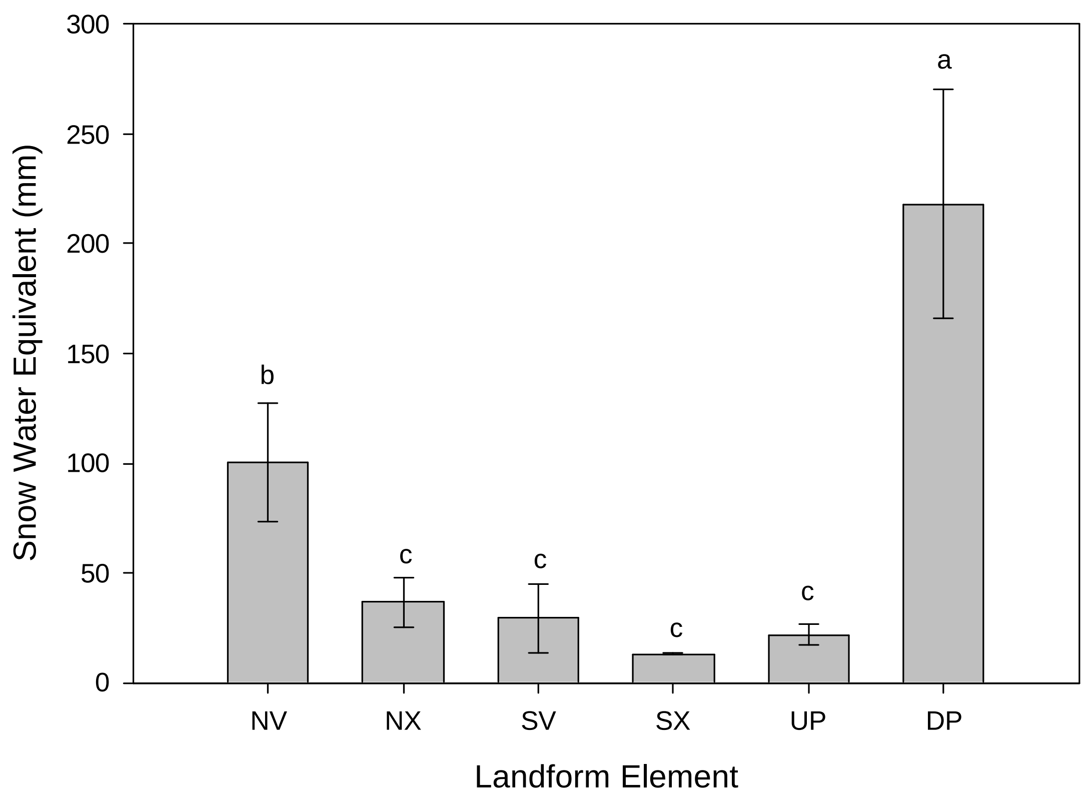

Figure 4.1 Snow accumulated (mean ± SE, mm water equivalent) as of 1 March 2004 on NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements at Macrorie, SK. Bars with the same letters are not significantly different (P = 0.05).

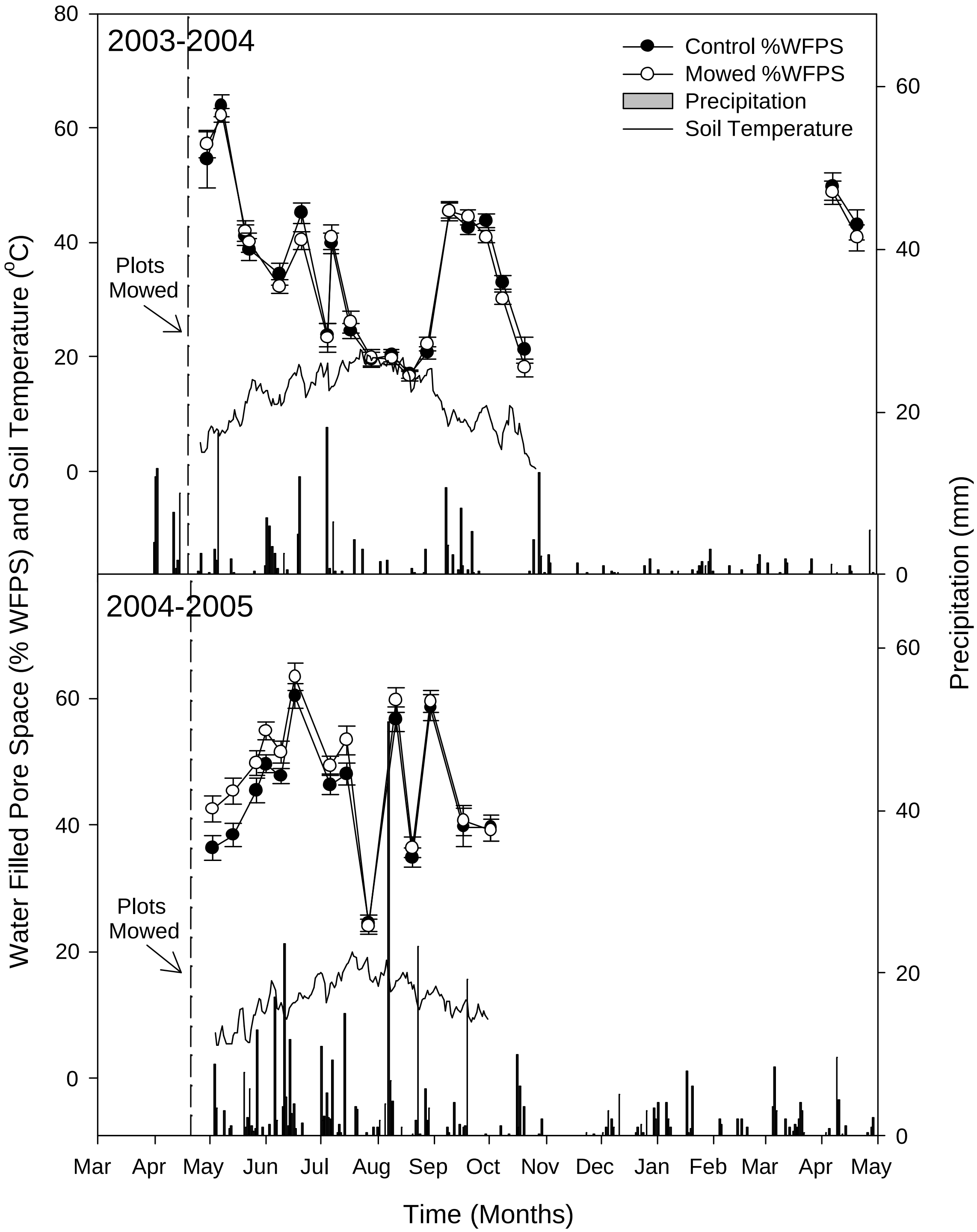

Figure 4.2 Mean water-filled pore space (mean ± SE, % WFPS) for control and April mowing averaged across six landform elements on sample dates and mean soil temperature (at 5 cm depth, °C) during 2003-2004 and 2004-2005 sampling season. Bars represent precipitation (mm) as recorded at Rock Point, SK.

Soil temperatures peaked in July and August (Figure 4.2). Mowing did not significantly change soil temperature. The difference in soil temperature among landform elements over the sampling season was as high as 6.4ºC in 2003 and 4.6ºC in 2004.

When years were considered a random variable, soil temperature was different among landform elements, but not between mowing treatments (Table 4.2). South-facing landform elements had the highest soil temperature, north-facing and DP landform elements had the lowest soil temperatures, and UP landform elements had intermediate soil temperatures. When surface shape and year were considered random variables, north-facing landform elements were 4.7ºC cooler than south-facing landform elements, but there was no difference between mowing treatments.

Table 4.2 Mean soil temperature (mean ± SE, ºC) at 5 cm depth on NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements with control and April mowing over 2003 and 2004 at Macrorie, SK. North and south landform elements represent combined temperatures from concave and convex shapes of respective north and south-facing aspects.

Landform Element	Soil Temperature (ºC)
NV	14.4 ± 0.6 c[1]
NX	13.9 ± 0.3 c
Combined north-facing landform elements	14.2 ± 0.3 B[2]
SV	18.0 ± 0.6 ab
SX	19.8 ± 1.1 a
Combined south-facing landform elements	18.9 ± 0.7 A
UP	16.0 ± 1.5 bc
DP	13.8 ± 0.6 c

[1] Means with the same lower case letters are not significantly different ($P = 0.05$).
[2] Means with the same upper case letters are not significantly different ($P = 0.05$).

Potential direct incident radiation, derived from aspect and slope (Table 4.3) differed significantly among landform elements (Figure 4.3). The NV and NX landform elements receive 91 and 89% less, respectively PDIR than the UP and DP landform elements. South-facing landform elements received similar PDIR as the UP landform element.

Table 4.3 Aspect (degree, north = 0, east = 90, south = 180, west = 270) and slope (degree) of NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements at Macrorie, SK.

Landform Element	Aspect (°)	Slope (°)
NV	15	8
NX	270	10
SV	162	13
SX	149	14
UP	na	0
DP	na	0

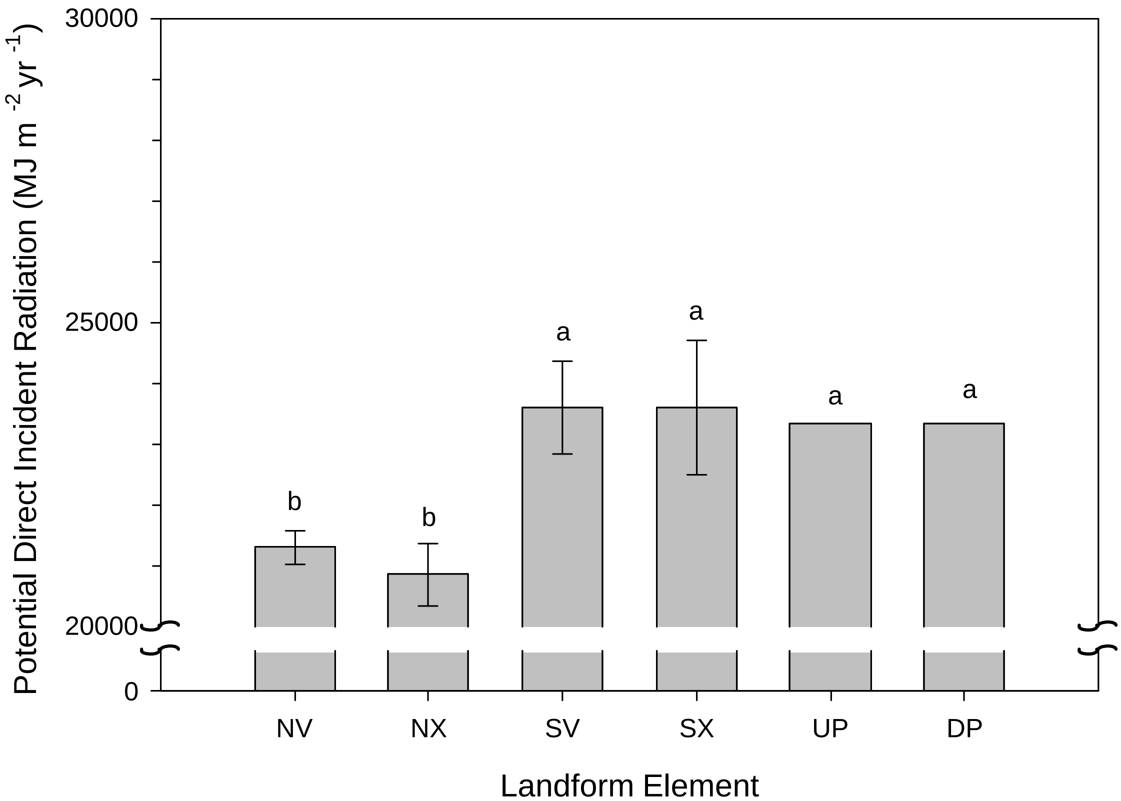

Figure 4.3 Average annual potential direct incident radiation (MJ m^{-2} yr^{-1}) calculated using the longitude, aspect and slope of NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements at Macrorie, SK.

4.1.2 Variation in physical characteristics of soil among landform elements

Soils had a sand content between 49 and 53% except soil from the DP landform element with 36% sand (Table 4.4). Clay content ranges from 9 to 15%. Sand and silt, but not clay, varied among landform elements. Soils of the DP landform element have less sand and more silt than soils of other landform elements. Soils of the north-facing and UP landform elements have a loam texture while soils of the south-facing landform elements are a sandy loam texture. Soils of the DP landform element have the greatest silt and clay content, giving them a silt loam soil texture. Bulk density varied with landform element and was greatest on the SX landform element and least on the DP landform element.

Table 4.4 Physical characteristics of soil[1] (mean ± SE) of NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements at Macrorie, SK.

Landform Element	Sand (%)	Silt (%)	Clay (%)	Soil Texture	Bulk Density ($g\ cm^{-3}$)
NV	50 ± 0.8 a[2]	39 ± 0.9 b	11 ± 1.0	Loam	1.10 ± 0.05 b
NX	51 ± 0.8 a	38 ± 0.3 b	11 ± 1.0	Loam	1.13 ± 0.01 ab
SV	53 ± 1.0 a	38 ± 1.1 b	9 ± 0.7	Sandy Loam	1.20 ± 0.02 ab
SX	53 ± 0.9 a	35 ± 0.6 b	12 ± 0.7	Sandy Loam	1.23 ± 0.01 a
UP	49 ± 1.3 a	37 ± 0.8 b	14 ± 1.3	Loam	1.22 ± 0.03 ab
DP	36 ± 3.0 b	49 ± 2.6 a	15 ± 2.4	Silty Loam	0.86 ± 0.12 c

[1] From 0 to 15 cm. Soil texture classes are based on The Canadian System of Soil Classification (Soil Classification Working Group, 1998).
[2] Means with the same letters within a column are not significantly different (P = 0.05).

4.1.3 Water-filled pore space of soils as affected by landform element, mowing and time

Water-filled pore space (WFPS), an indicator of soil water content and aeration, was high when precipitation occurred and soil temperature was low (Figure 4.2). Average WFPS for all landform elements and mowing treatments at the beginning of the sampling season was 56% for 2003-2004 and 39% for 2004-2005. A 20 to 25% fluctuation in WFPS between dry and wet periods was common. The highest average WFPS was in May 2003 (63%) and June 2004 (61%) and the lowest in August 2003 (17%) and July 2004 (24%). In the fall, average WFPS was 20% for 2003-2004 and 39% for 2004-2005.

Water-filled pore space was interactively affected by landform element and sample date ($P < 0.001$), mowing and sample date ($P = 0.028$), and mowing and landform element ($P < 0.001$) in 2003-2004 (Table 4.5). In 2004-2005, WFPS was interactively affected by landform element and sample date (P < 0.001), and by mowing and landform element (P < 0.001).

Table 4.5 Water-filled pore space (mean ± SE, % WFPS) for NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements with control and April mowing in 2003-2004 and 2004-2005 at Macrorie, SK.

Landform	-------------- 2003-2004 --------------			-------------- 2004-2005 --------------		
Element	Control	Mowing	Mean	Control	Mowing	Mean
NV	38.9 ± 1.7 A	36.2 ± 1.6 B	37.6 ± 1.1	49.0 ± 1.6 A	48.0 ± 1.5 A	48.5 ± 1.1
NX	35.1 ± 1.4 A	35.2 ± 1.4 A	35.2 ± 1.0	43.5 ± 1.2	48.1 ± 1.3	45.8 ± 0.9
SV	37.3 ± 1.6 A	34.7 ± 1.6 B	36.0 ± 1.1	44.9 ± 1.6 A	44.3 ± 1.7 A	44.6 ± 1.2
SX	27.9 ± 1.3 B	30.2 ± 1.3 A	29.1 ± 0.9	36.0 ± 1.4 B	41.3 ± 1.7 A	38.6 ± 1.1
UP	34.7 ± 1.5	34.4 ± 1.5	34.5 ± 1.1	42.5 ± 1.5 B	49.5 ± 1.7 A	46.0 ± 1.2
DP	38.4 ± 2.1 A	38.1 ± 2.2 A	38.3 ± 1.5	52.3 ± 1.9 B	55.5 ± 1.9 A	53.9 ± 1.3
Mean	35.2 ± 0.7	34.6 ± 0.6		44.7 ± 0.7	47.8 ± 0.7	

[1] Means followed by the same upper case letter within a row and a sampling season are not significantly different (P = 0.05).
[2] Treatment means with no letter showed interaction between mowing and sample date.

Within each landform element in 2003-2004, mowing decreased WFPS on the NV (P = 0.005) and SV landform elements (P = 0.002) and increased WFPS on the SX landform element (P < 0.001; Table 4.5). Water-filled pore space on the UP landform element was influenced by the interaction of mowing and sample date (P = 0.044). Mowing decreased WFPS on 8 May 2003 on the UP landform element and had no effect on all other sample dates.

Among landform elements during the 2004-2005 sampling season, mowing increased WFPS compared to control on the SX (P < 0.001), UP (P < 0.001) and DP (P = 0.021) landform elements (Table 4.5). Water-filled pore space was interactively influenced by mowing and sample date on the NX landform element (P = 0.024). Mowing increased WFPS compared to control on 3 May 2004, 27 May 2004 and 1 June 2004 for the NX landform element.

Differences in WFPS among landform elements depended on sample date in both years. Except on 10 September 2003 when WFPS was greatest on SV, UP and SX, WFPS was greatest on the DP landform element and least on the SX landform element (data not shown). Mowing decreased WFPS from 30 September 2003 to 21 October 2003 (Figure 4.2).

In 2004-2005, mowing increased WFPS compared to control between 14 May 2004 and 1 June 2004 (Figure 4.2). Except on 6 July 2004 when WFPS was greatest on the SX landform element, WFPS was greatest on the DP, NV, NX and sometimes the UP landform elements.

4.1.4 Nitrogen content of soil as affected by landform element, mowing and time

Soil NO_3^- varied among the three sample dates and landform elements in 2003 (Figure 4.4), but not among mowing treatments. Soils sampled on 30 April had the most NO_3^-, 9 September soil samples had 44% less than 30 April soil samples and soil samples from 5 July had 85% less than those from 30 April. Soils from UP and NV landform elements had more NO_3^- than soils from all other landform elements. Soils from DP landform element were not sampled in spring of 2003 due to the presence of water.

In 2004, landform element and sample date, but not mowing, influenced soil NO_3^- (both at $P < 0.001$) (Figure 4.4). Soil samples from 6 July had the most NO_3^- while soils sampled on 3 May had 34% less than those on 6 July and soils sampled on 19 September had 45% less than those on 6 July. The soils on the DP landform element had the most NO_3^-, soils on the NV, NX, SV and SX landform elements had the least NO_3^-, and soils on the UP landform element had intermediate amounts of NO_3^-.

Soil NH_4^+ was similar among the three sample dates in 2003 (Figure 4.5). Soils from DP landform element were not sampled in spring of 2003 due to the presence of water. Overall, NH_4^+ varied significantly among the soils of landform elements, decreasing from the DP, NX, UP, NV, SV to SX ($P = 0.045$). Mowing did not change NH_4^+ of soils; overall soil NH_4^+ in 2004 was affected by sample date and landform element. The 3 May soil samples had the most NH_4^+ while soil samples from 6 July had 40% less NH_4^+ than those from 3 May and soil samples from 19 September had 57% less NH_4^+ than those from 3 May ($P < 0.001$). Ammonium was greater in NV, DP and NX than other landform elements ($P = 0.002$).

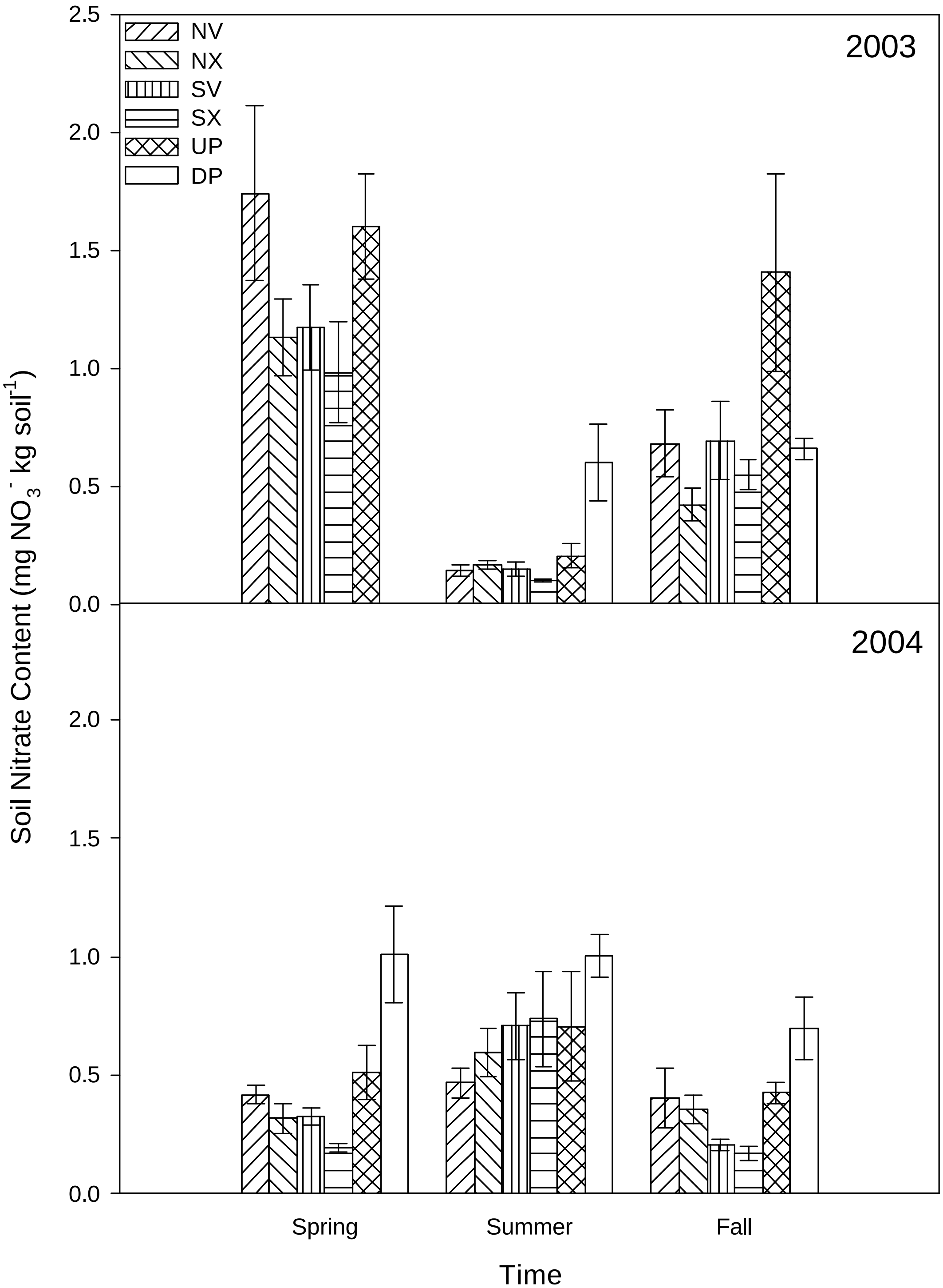

Figure 4.4 Soil nitrate content (mean ± SE, mg NO_3^- kg soil^{-1}, 0-15 cm) on NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression (data not available for 30 April 2003) landform elements during 2003 and 2004 at Macrorie, SK (Spring = 30 April 2003 and 3 May 2004, Summer = 5 July 2003 and 6 July 2004, Fall = 9 September 2003 and 19 September 2004).

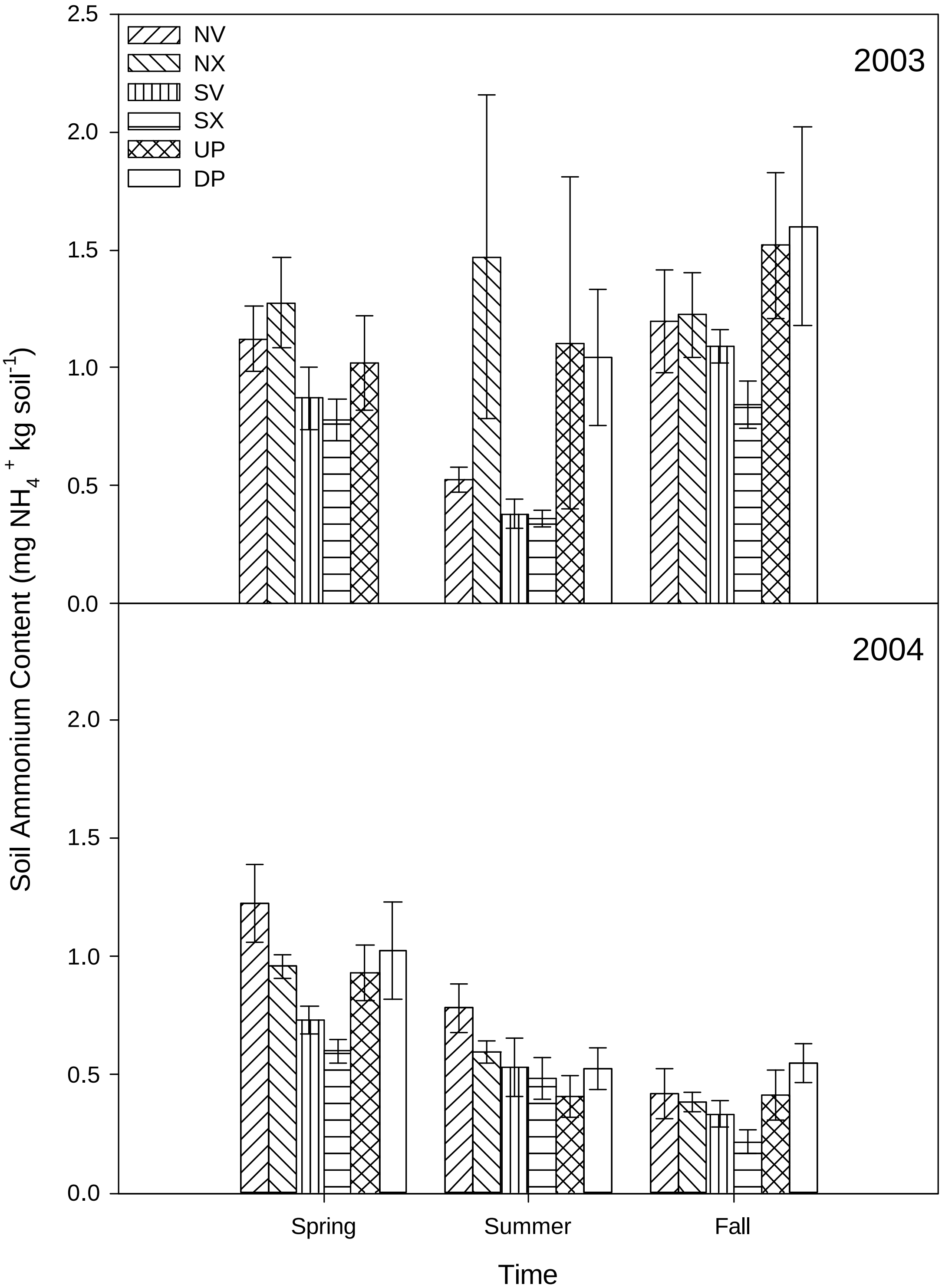

Figure 4.5 Soil ammonium content (mean ± SE, mg NH_4^+ kg soil^{-1}, 0-15 cm) NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression (data not available for 30 April 2003) landform elements during 2003 and 2004 at Macrorie, SK (Spring = 30 April 2003 and 3 May 2004, Summer = 5 July 2003 and 6 July 2004, Fall = 9 September 2003 and 19 September 2004).

4.2 Variability in Plant Community Characteristics and Biomass Production as Affected by Landform Element and Mowing

4.2.1 Plant community characteristics as affected by landform element and mowing

Species richness was lower on the UP landform element than other landform elements in both years ($P = 0.010$ for 2003 and $P = 0.015$ for 2004), but was similar between mowing treatments ($P > 0.05$), averaging 11 and 13 species per m^2 for 2003 and 2004, respectively (Table 4.6). Species evenness was greatest on the UP and DP landform elements, least on NX and NV, and intermediate on SX and SV landform elements in 2003 ($P < 0.001$). In 2004, species evenness was greatest on SX, SV, DP and UP and least on NX and NV landform elements ($P < 0.001$). Mowing increased species evenness in 2004, but not in 2003.

The Shannon-Wiener Diversity Index (H') differed significantly among landform elements in 2003 ($P < 0.001$) (Table 4.6). Diversity was greatest on the DP and SX landform elements and lowest on SV, NX and NV landform elements. The diversity index in 2004 was greatest on the SX and least on NV landform elements ($P = 0.003$). Mowing had no affect on the diversity index in either year ($P > 0.05$).

Detrended Correspondence Analysis (DCA) based on species composition produced similar separation of experimental units for both years (Figures 4.6 and 4.7). The DP landform element was separated from other landform elements along Axis 1. North-facing landform elements were spread along the lower portion of Axis 2, south-facing landform elements were spread along the upper portion of Axis 2 and the UP landform element overlapped with south-facing and north-facing landform elements. Except for variation in species composition among SX landform elements in 2004, which were closely grouped, variation within the north-facing landform elements tended to be less than in other landform elements. One NX and one NV experimental unit in 2003 and 2004, respectively, appeared to be outliers.

Table 4.6 Plant community characteristics (mean ± SE) per 0.25 m^2 (mean of 4, 0.25 m^2 quadrats) in August of 2003 and 2004 on NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements with control and April mowing at Macrorie, SK.

Landform	------------ Richness ------------			--------------- Evenness ---------------			Shannon-Wiener Diversity Index		
Element	Control	Mowing	Mean	Control	Mowing	Mean	Control	Mowing	Mean
------ 2003 ------									
NV	12 ± 2	11 ± 1	11.5 a[1,2]	0.40 ± 0.06	0.47 ± 0.05	0.44 c	0.99 ± 0.17	1.13 ± 0.15	1.06 d
NX	11 ± 1	11 ± 2	11.2 a	0.50 ± 0.05	0.51 ± 0.06	0.50 c	1.21 ± 0.17	1.23 ± 0.22	1.22 cd
SV	11 ± 1	10 ± 0	10.5 a	0.63 ± 0.08	0.63 ± 0.04	0.63 b	1.49 ± 0.20	1.49 ± 0.11	1.49 b
SX	9 ± 1	12 ± 1	10.6 a	0.62 ± 0.05	0.76 ± 0.03	0.69 ab	1.36 ± 0.09	1.85 ± 0.07	1.60 ab
UP	6 ± 1	9 ± 1	7.5 b	0.79 ± 0.06	0.69 ± 0.04	0.74 a	1.32 ± 0.13	1.49 ± 0.17	1.41 bc
DP	13 ± 2	11 ± 1	11.8 a	0.72 ± 0.05	0.74 ± 0.07	0.73 a	1.83 ± 0.20	1.73 ± 0.17	1.78 a
Mean	10.4	10.6		0.61	0.64		1.37	1.49	
------ 2004 ------									
NV	13 ± 2	13 ± 2	13.1 a[2]	0.52 ± 0.04	0.59 ± 0.05	0.56 c	1.31 ± 0.17	1.52 ± 0.18	1.42 c
NX	13 ± 1	15 ± 2	14.4 a	0.60 ± 0.05	0.69 ± 0.05	0.65 b	1.55 ± 0.11	1.87 ± 0.17	1.71 ab
SV	14 ± 1	12 ± 1	13.1 a	0.72 ± 0.05	0.74 ± 0.04	0.73 a	1.93 ± 0.15	1.82 ± 0.18	1.87 ab
SX	12 ± 1	13 ± 1	12.7 a	0.73 ± 0.03	0.80 ± 0.03	0.77 a	1.82 ± 0.08	2.07 ± 0.12	1.95 a
UP	11 ± 1	9 ± 1	9.9 b	0.75 ± 0.03	0.73 ± 0.03	0.74 a	1.79 ± 0.08	1.58 ± 0.16	1.68 b
DP	14 ± 3	13 ± 1	13.1 a	0.73 ± 0.04	0.76 ± 0.06	0.75 a	1.88 ± 0.19	1.92 ± 0.17	1.90 ab
Mean	12.9	12.5		0.68 B[3]	0.72 A		1.71	1.80	

[1] When interaction between landform element and mowing was not significant (P > 0.05), means of main effects were separated using LSD. When interaction between landform element and mowing was significant, data were analysed within each landform element and each mowing treatment. Means were then separated within each mowing treatment or landform element using LSD.

[2] Means followed by the same lower case letters within a column and a year are not significantly different (P = 0.05).

[3] Means followed by the same upper case letters within a row and a plant community characteristic are not significantly different (P = 0.05).

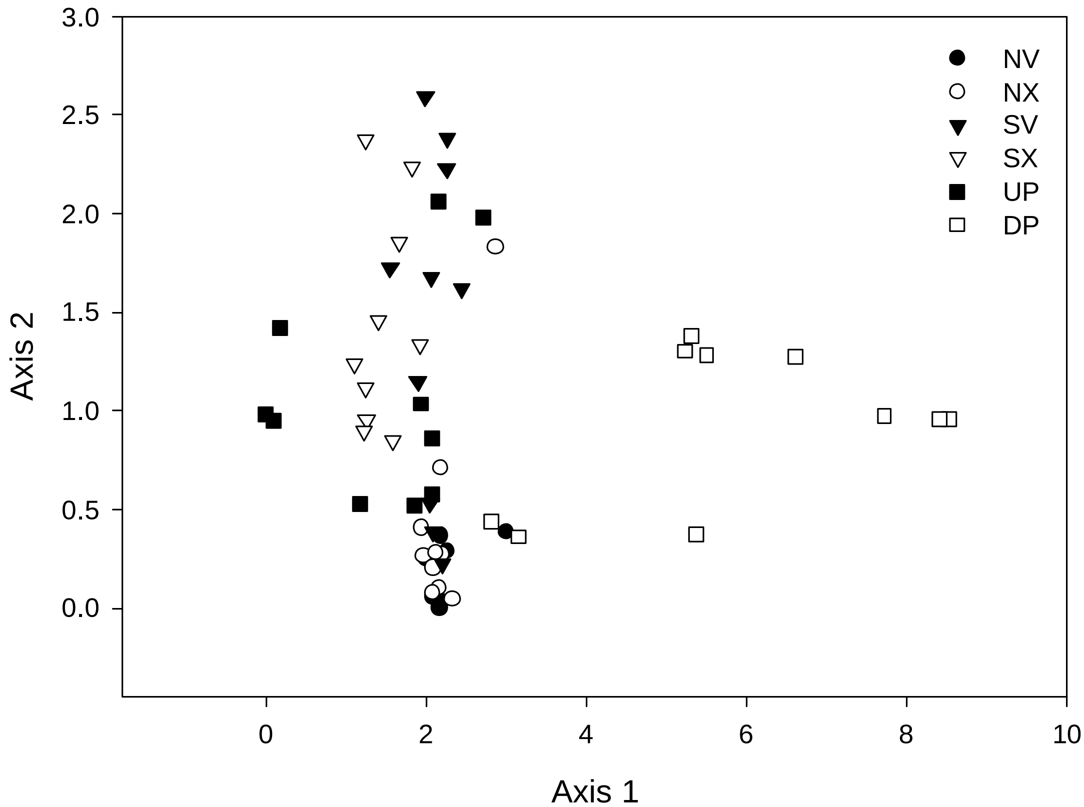

Figure 4.6 Scatterplot based on Axis 1 and Axis 2 of Detrended Correspondence Analysis for 2003 species composition on NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements at Macrorie, SK.

Forbs and shrubs with the greatest canopy cover in both years were *Pulsatilla patens* (L.) P. Mill. (prairie crocus), *Rosa arkansana* Porter (prairie rose), *Artemisia frigida* Willd. (fringed sage), and *Anemone canadensis* L. (Canada anemone) (Tables 4.7 and 4.8). Graminoids with the greatest canopy cover were plains rough fescue, western wheatgrass, needle-and-thread, western porcupine grass and *Carex pensylvanica* Lam. (sun-loving sedge). Canopy cover of plains rough fescue was greatest on the north-facing and SV landform elements in both years. Canopy cover of western wheatgrass was greatest on the SV and UP landform elements in both years. Canopy cover of needle-and-thread and western porcupine grass was greatest on the SX landform elements. Canopy cover of sun-loving sedge was greatest on the SV landform elements in both years.

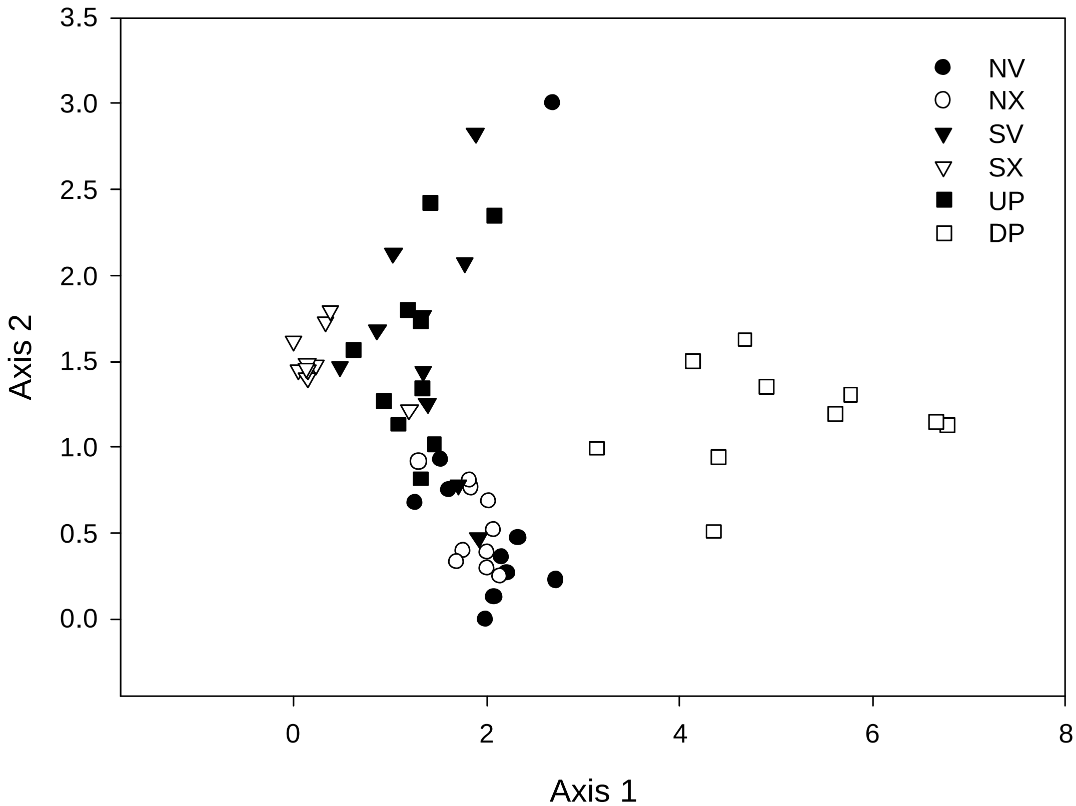

Figure 4.7 Scatterplot based on Axis 1 and Axis 2 of Detrended Correspondence Analysis for 2004 species composition on NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements at Macrorie, SK.

Litter cover was greater on the UP, SV and DP landform elements than all other landform elements in 2003 (Tables 4.7 and 4.8). Litter cover was greater on the NV, SV, NX and UP landform elements than all other landform elements in 2004. Bare soil cover and clubmoss cover were greater on the SX landform elements than all other landform elements in 2003 and 2004.

Table 4.7 Ground cover (%) and the cover of the five most common species on NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements in 2003 at Macrorie, SK.

Landform Element	-- Ground Cover -- Type	Cover	------------ Forbs/Shrubs ------------ Species	Cover	------------ Graminoids ------------ Species	Cover
NV	Litter	24 c[1]	*Pulsatilla patens*	4	*Festuca hallii*	56
	Bare soil	< 1 b	*Artemisia frigida*	2	*Carex pensylvanica*	1
	Selaginella densa	0 b	*Anemone canadensis*	2	*Hesperostipa curtiseta*	1
			Astragalus flexuosus	1	*Elymus trachycaulus*	1
			Rosa arkansana	1	*Pascopyrum smithii*	1
NX	Litter	25 bc	*Pulsatilla patens*	4	*Festuca hallii*	48
	Bare soil	1 b	*Artemisia frigida*	3	*Pascopyrum smithii*	5
	Selaginella densa	1 b	*Rosa arkansana*	2	*Hesperostipa curtiseta*	2
			Campanula rotudifolia	1	*Carex pensylvanica*	1
			Thermopsis rhombifolia	1	*Hesperostipa comata*	1
SV	Litter	32 ab	*Rosa arkansana*	3	*Festuca hallii*	20
	Bare soil	1 b	*Artemisia frigida*	2	*Carex pensylvanica*	9
	Selaginella densa	2 b	*Artemisia ludoviciana*	2	*Hesperostipa curtiseta*	9
			Pulsatilla patens	2	*Hesperostipa comata*	7
			Anemone canadensis	< 1	*Pascopyrum smithii*	6
SX	Litter	19 c	*Rosa arkansana*	6	*Hesperostipa comata*	27
	Bare soil	7 a	*Artemisia frigida*	3	*Hesperostipa curtiseta*	7
	Selaginella densa	8 a	*Pulsatilla patens*	3	*Carex filifolia*	6
			Phlox hoodii	1	*Carex pensylvanica*	5
			Pediomelum esculentum	1	*Festuca hallii*	4
UP	Litter	34 a	*Astragalus flexuosus*	3	*Festuca hallii*	16
	Bare soil	< 1 b	*Pulsatilla patens*	3	*Elymus lanceolatus*	12
	Selaginella densa	1 b	*Artemisia frigida*	1	*Pascopyrum smithii*	10
			Phlox hoodii	< 1	*Hesperostipa comata*	9
			Tragopogon dubius	< 1	*Hesperostipa curtiseta*	4
DP	Litter	27 abc	*Polygonum amphibium*	8	*Poa pratensis*	11
	Bare soil	0 b	*Anemone canadensis*	6	*Festuca hallii*	9
	Selaginella densa	< 1 b	*Artemisia ludoviciana*	2	*Carex rostrata*	8
			Thalictrum venulosum	2	*Poa compressa*	4
			Galium boreale	1	*Carex* spp.	4

[1] Means with the same letters within a cover type are not significantly different among landform elements (P = 0.05).

Table 4.8 Ground cover (%) and the cover of the five most common species on NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements in 2004 at Macrorie, SK.

Landform Element	-- Ground Cover --		------------ Forbs/Shrubs ------------		------------ Graminoids ------------	
	Type	Cover	Species	Cover	Species	Cover
NV	Litter	48 a	*Anemone canadensis*	4	*Festuca hallii*	39
	Bare soil	0 b	*Pulsatilla patens*	3	*Pascopyrum smithii*	6
	Selaginella densa	< 1 b	*Artemisia frigida*	3	*Elymus lanceolatus*	4
			Vicia americana	1	*Carex pensylvanica*	3
			Stellaria spp.	1	*Elymus trachycaulus*	2
NX	Litter	46 a	*Pulsatilla patens*	5	*Festuca hallii*	38
	Bare soil	0 b	*Rosa arkansana*	5	*Elymus lanceolatus*	4
	Selaginella densa	0 b	*Artemisia frigida*	4	*Carex pensylvanica*	4
			Thermopsis rhombifolia	2	*Elymus trachycaulus*	2
			Campanula rotudifolia	2	*Hesperostipa comata*	2
SV	Litter	48 a	*Rosa arkansana*	7	*Festuca hallii*	16
	Bare soil	1 b	*Pulsatilla patens*	2	*Carex pensylvanica*	12
	Selaginella densa	< 1 b	*Artemisia frigida*	2	*Hesperostipa comata*	10
			Vicia americana	1	*Hesperostipa curtiseta*	9
			Artemisia ludoviciana	1	*Pascopyrum smithii*	8
SX	Litter	27 b	*Rosa arkansana*	7	*Hesperostipa comata*	25
	Bare soil	6 a	*Pulsatilla patens*	3	*Carex filifolia*	13
	Selaginella densa	9 a	*Artemisia frigida*	3	*Hesperostipa curtiseta*	12
			Pediomelum esculentum	2	*Carex pensylvanica*	8
			Liatris punctata	1	*Festuca hallii*	2
UP	Litter	43 a	*Pulsatilla patens*	6	*Elymus lanceolatus*	15
	Bare soil	1 b	*Artemisia frigida*	2	*Festuca hallii*	15
	Selaginella densa	< 1 b	*Astragalus flexuosus*	1	*Hesperostipa comata*	13
			Vicia americana	1	*Carex pensylvanica*	9
			Erigeron caespitosus	1	*Pascopyrum smithii*	8
DP	Litter	33 b	*Anemone canadensis*	13	*Poa pratensis*	17
	Bare soil	0 b	*Taraxacum officinale*	7	*Carex rostrata*	10
	Selaginella densa	0 b	*Polygonum amphibium*	7	*Carex pensylvanica*	5
			Unknown1	3	*Pascopyrum smithii*	4
			Mentha arvensis	3	*Hordeum jubatum*	4

[1] Means with the same letters within a cover type are not significantly different among landform elements (P = 0.05).

4.2.2 Biomass production as affected by landform element and mowing

Forb and shrub biomass was greatest on the DP landform element in both years, lowest on the UP landform element in 2003 and the SV and UP landform elements in 2004, and intermediate on other landform elements (P < 0.001 in both years) (Table 4.9).

Table 4.9 Above-ground biomass (mean ± SE, g m^{-2}) recorded in August of 2003 and 2004 on NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements with control and April mowing at Macrorie, SK[1].

Landform Element	Forbs and Shrubs			Graminoids: Standing-Live			Graminoids: Standing-Dead		
	Control	Mowed	Mean	Control	Mowed	Mean	Control	Mowed	Mean
2003 Growing Season									
NV	16.7 ± 5.5	17.8 ± 4.4	17.2 b[3]	119.3 ± 14.2 A a	117.3 ± 16.8 A a	118.3	494.3 ± 96.0 a	58.1 ± 7.4 ab	276.2 ± 85.7
NX	22.3 ± 14.3	19.0 ± 7.9	20.7 b	110.0 ± 12.1 A a	93.1 ± 5.4 A ab	101.5	462.0 ± 100.4 a	71.5 ± 11.5 a	266.8 ± 80.7
SV	22.9 ± 6.2	13.0 ± 3.4	18.0 b	96.8 ± 12.3 A a	78.2 ± 8.6 B bc	87.5	232.6 ± 17.1 b	58.0 ± 9.6 ab	145.3 ± 30.5
SX	20.0 ± 4.6	10.8 ± 2.4	15.4 b	82.4 ± 10.2 A a	75.7 ± 10.8 A bc	79.1	172.5 ± 28.2 b	41.8 ± 5.6 bc	107.2 ± 25.7
UP	6.7 ± 3.9	6.8 ± 2.4	6.8 c	149.4 ± 34.7 A a	110.2 ± 14.1 A ab	129.8	350.9 ± 85.9 ab	65.5 ± 13.3 ab	208.2 ± 62.8
DP	87.9 ± 42.0	36.0 ± 24.5	62.0 a	140.7 ± 17.2 A a	44.6 ± 15.3 B c	92.6	167.8 ± 48.9 b	26.6 ± 3.0 c	97.2 ± 33.0
Mean	29.4 A[2]	17.2 B		116.4	86.5		313.4 ± 35.9 A	53.6 ± 4.4 B	
2004 Growing Season									
NV	18.0 ± 4.6	37.0 ± 10.6	27.5 bc	143.5 ± 17.6	100.8 ± 12.2	122.2 b	275.0 ± 63.8 a	41.9 ± 6.6 b	158.5 ± 49.2
NX	36.6 ± 14.6	50.5 ± 6.6	43.6 b	142.0 ± 25.1	96.7 ± 13.9	119.4 b	219.9 ± 26.7 ab	48.1 ± 5.1 b	134.0 ± 31.4
SV	26.1 ± 4.2	17.2 ± 2.3	21.7 c	108.7 ± 7.9	103.1 ± 8.7	105.9 bc	197.1 ± 40.8 ab	51.5 ± 4.1 b	124.3 ± 31.0
SX	28.2 ± 3.7	30.4 ± 1.2	29.3 bc	90.6 ± 10.8	81.0 ± 8.3	85.8 c	75.4 ± 14.0 c	27.3 ± 7.6 b	53.7 ± 10.0
UP	18.0 ± 5.6	29.4 ± 12.3	23.7 c	129.8 ± 9.6	95.8 ± 7.4	112.8 b	244.6 ± 12.1 ab	78.3 ± 14.1 a	161.5 ± 29.1
DP	71.4 ± 16.6	78.7 ± 26.4	75.1 a	165.2 ± 18.7	151.0 ± 34.7	158.1 a	163.7 ± 39.9 bc	53.4 ± 9.2 b	108.5 ± 26.6
Mean	33.1	40.5		130.0 A	104.7 B		195.9 ± 18.3 A	50.9 ± 4.0 B	

[1] Some data were from A. Pantel, unpublished data.
[2] Means with the same lower case letters within a column and a year are not significantly different (P = 0.05).
[3] Means with the same upper case letters within a row and a plant group (i.e. Forb and shrub, Standing-Live, Standing-Dead) are not significantly different (P = 0.05).

Mowing reduced forb and shrub biomass by 41% in 2003 ($P = 0.016$), but had no effect on forb and shrub biomass in 2004.

The effect of landform element on standing-live biomass of graminoids was inconsistent between the two years (Table 4.9). The effects of landform element and mowing interacted in 2003. Within the control treatment there was no difference among landform elements ($P > 0.05$), but within the mowing treatment, standing-live biomass of graminoids was greatest on the NV landform element and least on the DP landform element ($P = 0.005$). Mowing decreased standing-live biomass of graminoids in 2003 on the SV and DP landform element by 19% and 68%, respectively ($P = 0.036$ and 0.008, respectively), but not on other landform elements. The standing-live biomass of graminoids was greatest on the DP landform element and least on the SX landform element in 2004 ($P < 0.001$). Mowing reduced standing-live biomass of graminoids on all landform elements by 19% compared to control with a range from 5 to 32% depending on the landform element ($P < 0.001$).

Mowing reduced standing-dead biomass of graminoids by 82 and 74% compared to the control for 2003 and 2004, respectively ($P < 0.001$ for both years, Table 4.9). The effect of landform element on standing-dead biomass of graminoids was different in both years. The effects of landform element and mowing interacted in 2003 and 2004 ($P =$ 0.032 and 0.014, respectively). Standing-dead biomass of control plots was greatest on north-facing and UP landform elements in 2003 and least on the south-facing and DP landform elements. Of the mowed landform elements, the standing-dead biomass of graminoids was greatest on the NX, UP, NV and SV landform elements and least on the SX and DP landform elements. In 2004, standing-dead biomass of graminoids among control landform elements was greatest on the NV landform element and least on the SX landform element ($P < 0.001$). Within the mowed landform elements, standing-dead biomass of graminoids was greatest on the UP landform element and lower on all other landform elements. Depending on the landform element, the difference between control and mowing treatment was as great as 88% on the NV landform element in 2003 and as little as 63% on the SX landform element in 2004.

Total above-ground biomass varied among landform elements ($P = 0.010$) and mowing treatments ($P < 0.001$) in 2003 (Table 4.10). Total above-ground biomass was generally greatest on the NV and NX landform elements, while total above-ground biomass was least on the SX landform element. Mowing decreased total above-ground biomass by 67% compared to control. Landform element and mowing interactively influenced total above-ground biomass in 2004 ($P = 0.013$). Within the control treatment, total above-ground biomass was greatest on the NV landform element, intermediate on the DP, NX, UP and SV landform elements and least on the SX landform element ($P < 0.001$). Within the mowing treatment, total above-ground biomass was greatest on the DP landform element. Except on the SX and DP landform elements, mowing reduced total above-ground biomass on all landform elements.

Table 4.10 Total above-ground biomass (mean ± SE, g m^{-2}) recorded in August on NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements with control and April mowing in 2003 and 2004 at Macrorie, SK.

Landform Element	2003			2004		
	Control	Mowed	Mean	Control	Mowed	Mean
NV	630.2 ± 92.2	193.2 ± 18.3	411.7 ± 85.3 a[1]	436.4 ± 63.4 A a	179.8 ± 10.3 B b	308.1 ± 52.4
NX	594.3 ± 99.8	183.6 ± 13.6	389.0 ± 83.3 a	398.5 ± 29.6 A ab	195.3 ± 17.5 B b	296.9 ± 37.5
SV	352.4 ± 23.8	149.1 ± 12.3	250.7 ± 36.2 bc	331.9 ± 45.6 A b	171.8 ± 9.0 B b	251.9 ± 34.5
SX	275.0 ± 36.3	128.3 ± 15.1	201.7 ± 30.7 c	194.2 ± 26.8 A c	143.4 ± 11.2 A b	168.8 ± 16.1
UP	507.0 ± 105.2	182.5 ± 12.6	344.8 ± 73.6 ab	392.5 ± 19.7 A ab	203.5 ± 9.3 B b	298.0 ± 33.1
DP	396.4 ± 35.2	100.1 ± 38.0	248.2 ± 55.1 bc	400.3 ± 27.2 A ab	283.1 ± 48.7 A a	341.7 ± 32.8
Mean	459.2 ± 36.3 A[2]	156.1 ± 9.8 B		359.0 ± 20.6	196.1 ± 11.6	

[1] Means followed by the same lower case letters within a column are not significantly different ($P = 0.05$).
[2] Means followed by the same upper case letters within a row and a year are not significantly different ($P = 0.05$).

4.3 Variability in GHG Flux Rates as Affected by Landform Element and Mowing

4.3.1 Carbon dioxide

Carbon dioxide emissions from the soil surface were greater in 2004-2005 than in 2003-2004 (Figure 4.8). Carbon dioxide emissions were low before mid-May and after mid-September. Carbon dioxide flux rate peaked at 50 µg CO_2 m^{-2} s^{-1} in mid-May and was lowest in late October at 2 µg CO_2 m^{-2} s^{-1} in 2003-2004. In 2004-2005, CO_2 flux rates were highest in mid-July at 231 µg CO_2 m^{-2} s^{-1}. The lowest CO_2 flux at 3 µg CO_2 m^{-2} s^{-1} was measured on 10 March 2005.

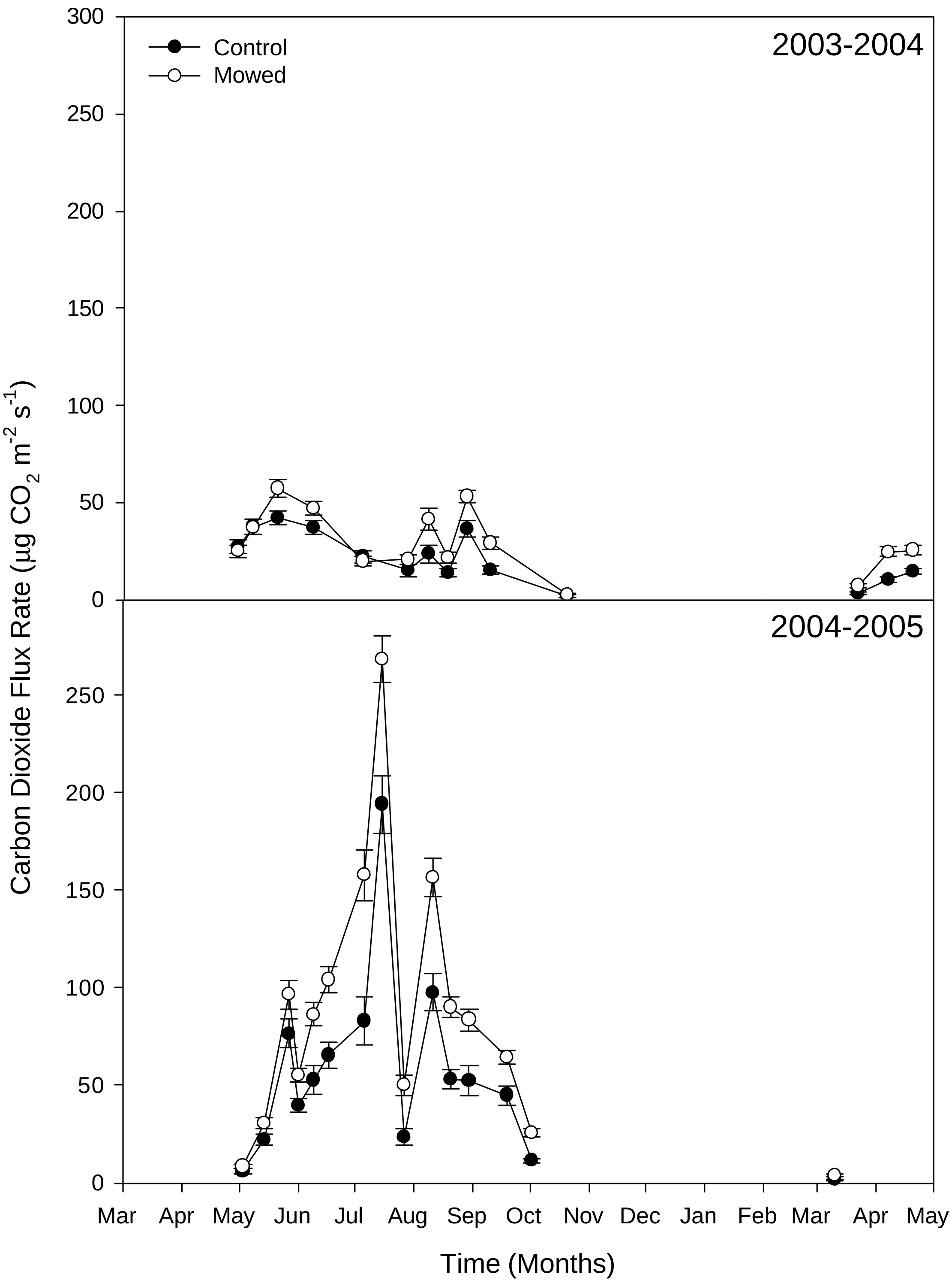

Figure 4.8 Carbon dioxide flux rate (mean ± SE, µg CO_2 m^{-2} s^{-1}) of control and April mowing averaged across six landform elements in 2003-2004 and 2004-2005 at Macrorie, SK.

Carbon dioxide emissions were affected by the three-way interaction of landform element, mowing and sample date in 2003-2004 ($P = 0.033$) and by the two-way interactions of landform element and sample date, mowing and sample date, and landform element and mowing in 2004-2005 ($P < 0.001$ for all three) (Figure 4.9). During spring and early summer of 2003, when the DP landform element was flooded and therefore inaccessible, CO_2 flux rates were greatest from the SV, UP and NV landform elements. Except on the final sampling day in 2003 when CO_2 flux rate was greatest on the SV landform element, the CO_2 flux rate was always greatest on the DP landform element after June. From September to October, the soils of the NV, NX and SX landform element usually emitted less CO_2 than the soils of other landform elements. In 2004-2005, the CO_2 flux rate was greatest from the DP landform element on every sample date that landform element was a significant factor in emissions rates. Carbon dioxide flux rates were greater in the mowing treatment than the control on most dates, ranging from 27 to 47% greater in 2003-2004 and 21 to 58% greater in 2004-2005.

4.3.2 Methane

Except on 7 April 2004 when CH_4 flux rates were positive, CH_4 flux rates from the soil were negative in both sampling seasons (Figure 4.10). In 2003-2004, mowing increased CH_4 uptake compared to control on 5 sample dates and 3 sample dates in 2004-2005. Differences in CH_4 consumption between mowing and control were as high as 58% on 29 July 2003 and 88% on 6 July 2004. Methane uptake was greater on control plots than on mowed plots only on 30 April 2003 ($P = 0.042$).

In 2003-2004, CH_4 flux was affected by the interaction between landform element and sample date ($P < 0.001$) (Table 4.11). In the 2004-2005, landform element and mowing ($P = 0.008$), landform element and sample date ($P = 0.023$), and mowing and sample date ($P < 0.001$) interactively affected CH_4 flux rates. During the spring and early summer in 2003, the CH_4 consumption rate was greatest on the south-facing landform elements and least on the NV and UP landform elements. During summer, the CH_4 consumption rate was greatest on the DP landform element, intermediate on the NX, SV and SX landform elements and least on the UP and NV landform elements.

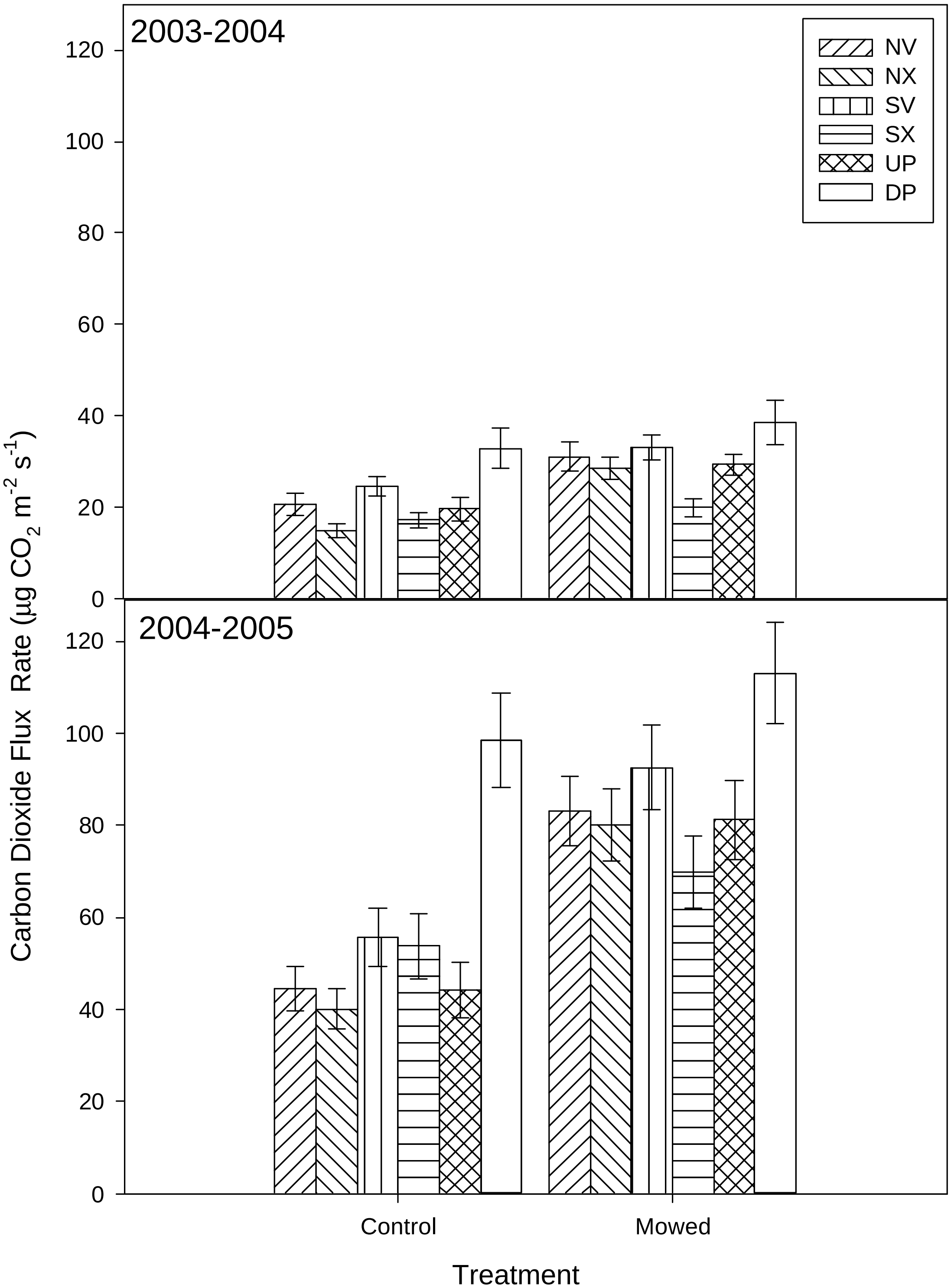

Figure 4.9 Average carbon dioxide flux rate (mean ± SE, µg CO_2 m^{-2} s^{-1}) of control and April mowing and NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements in 2003-2004 and 2004-2005 at Macrorie, SK.

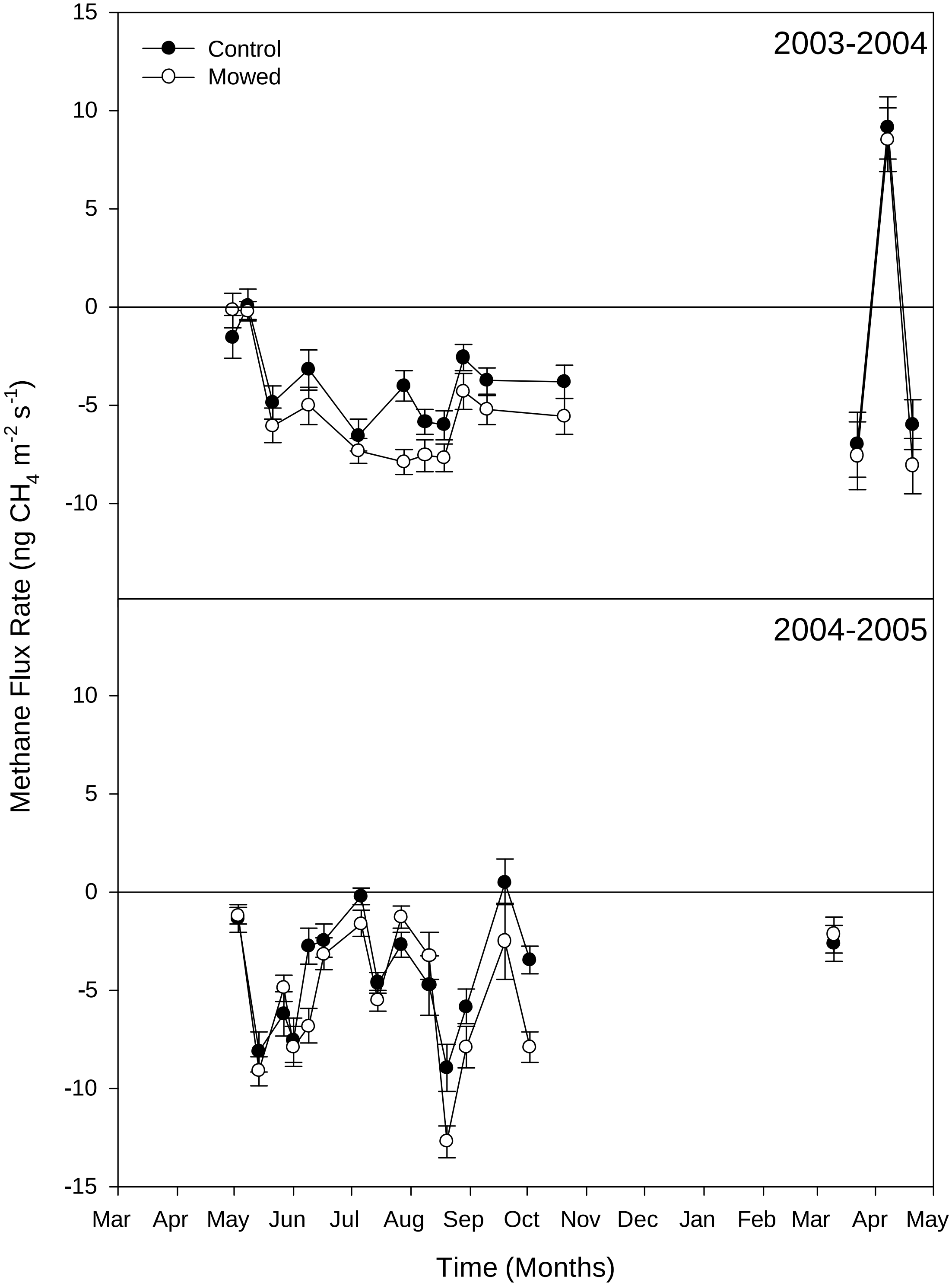

Figure 4.10 Methane flux rate (mean ± SE, ng CH_4 m^{-2} s^{-1}) of control and April mowing averaged across six landform elements in 2003-2004 and 2004-2005 at Macrorie, SK.

Within the control treatment, landform element and sample date interactively influenced CH_4 flux rate in 2004-2005 (P = 0.011) (Table 4.11). Within the mowing treatment, the CH_4 consumption rate was least on the UP landform element (P = 0.001). On sample dates when landform element was a significant determinant of CH_4 flux, soils on the SX landform element consumed the most and soils on the DP landform elements consumed the least.

Table 4.11 Average methane flux rate (mean ± SE, ng CH_4 m^{-2} s^{-1}) for NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements with control and April mowing in 2003-2004 and 2004-2005

Landform Element	-------- 2003-2004 --------			-------- 2004-2005 --------		
	Control	Mowed	Mean	Control	Mowed	Mean
NV	-1.55 ± 0.70 A[1]	-2.72 ± 0.70 B	-2.13 ± 0.50	-2.58 ± 0.52	-4.94 ± 0.54 b[2]	-3.76 ± 0.38
NX	-2.88 ± 0.66 A	-4.57 ± 0.69 B	-3.73 ± 0.48	-4.10 ± 0.67	-6.26 ± 0.65 b	-5.18 ± 0.48
SV	-3.61 ± 0.72 A	-4.43 ± 0.75 A	-4.02 ± 0.52	-4.29 ± 0.62	-5.58 ± 0.57 b	-4.93 ± 0.42
SX	-4.86 ± 0.88 A	-5.12 ± 0.79 A	-4.99 ± 0.59	-7.30 ± 0.91	-6.39 ± 1.01 b	-6.85 ± 0.68
UP	-1.86 ± 0.61 [3]	-4.34 ± 0.83	-3.10 ± 0.52	-2.77 ± 0.60	-3.22 ± 0.60 a	-3.00 ± 0.42
DP	-2.08 ± 1.02 A	-3.46 ± 1.14 B	-2.77 ± 0.76	-3.55 ± 0.57	-5.09 ± 0.67 b	-4.32 ± 0.44
Mean	-2.83 ± 0.32	-4.13 ± 0.34		-4.11 ± 0.28	-5.25 ± 0.29	

[1] Means followed by the same upper case letter within a row and a sampling season are not significantly different (P = 0.05).
[2] Means with the same lower case letter within a column and a sampling season are not significantly different (P = 0.05).
[3] Treatment means with no letter showed interaction between mowing and sample date.

4.3.3 Nitrous oxide

During 2003-2004, landform element and sample date interactively affected N_2O flux rate (P < 0.001). Nitrous oxide flux rate was significantly greater than zero in 2003-2004 on only 7 sample dates (Figure 4.11). Nitrous oxide flux differed among landform elements on 2 sample dates. On 22 March 2004, the DP landform element had greater flux rates than all other landform elements (P < 0.001). On 20 April 2004, N_2O flux rate was greatest on the UP and SX landform elements while N_2O flux rate on north-facing landform elements was the least (P = 0.004). Mowing affected N_2O flux rates only on 29 August 2003 when mowing increased N_2O emission rates compared to the control (P = 0.022).

During 2004-2005, sample date, landform element and mowing all significantly influenced N_2O flux rate. On 7 sample dates the average N_2O flux rate was greater than

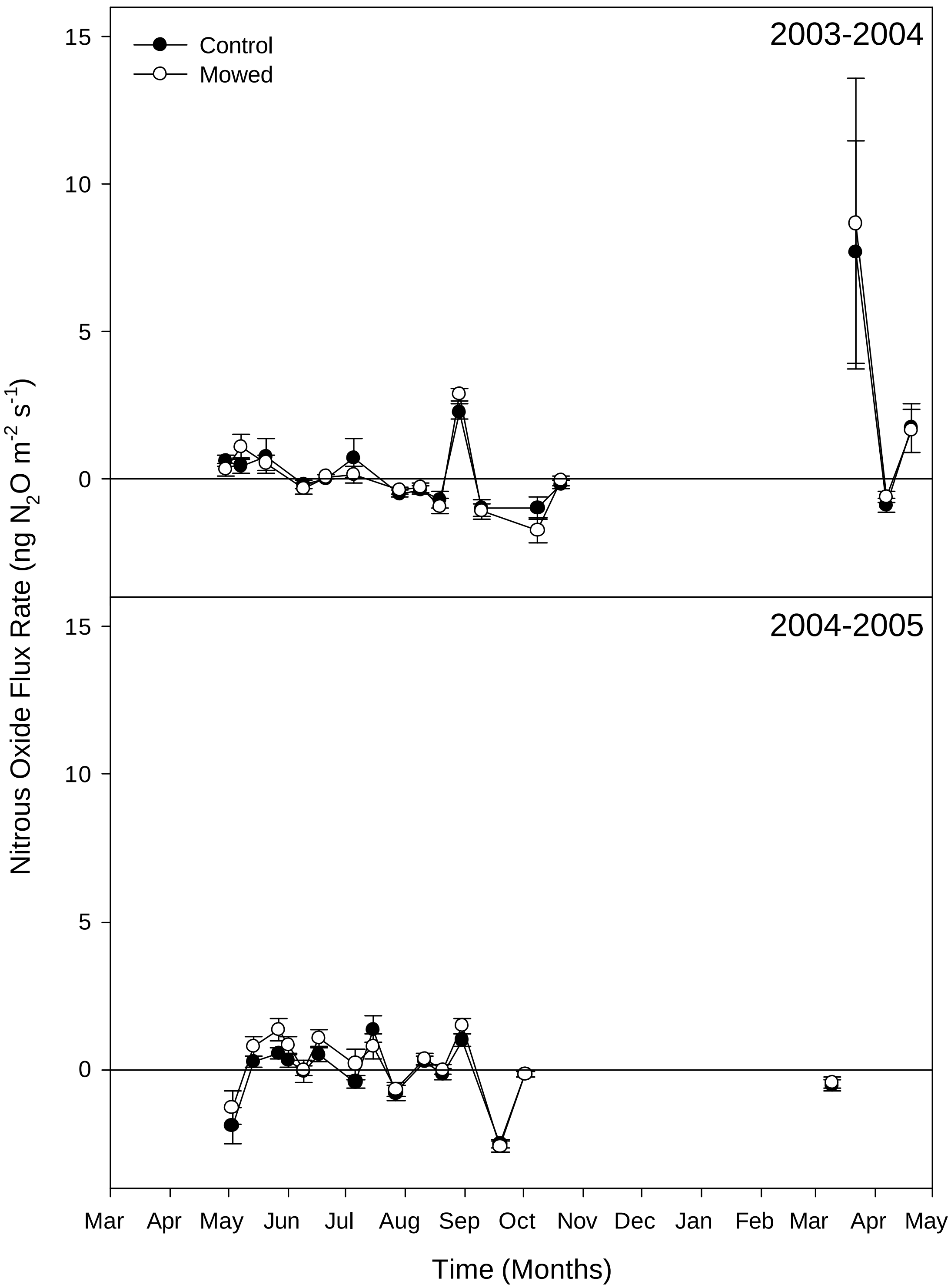

Figure 4.11 Nitrous oxide flux rate (mean ± SE, ng N_2O m^{-2} s^{-1}) of control and April mowing averaged across six landform elements in 2003-2004 and 2004-2005 at Macrorie, SK.

zero (Figure 4.11). Nitrous oxide flux differed among landform elements on 15 July 2004, 11 August 2004 and 30 August 2004. On 15 July 2004, the N_2O flux rate from the SV, DP and UP landform elements was greater than the N_2O flux rate on all other landform elements. On 11 August 2004, the N_2O flux rate on the DP and SV landform elements was greater than the N_2O flux rate from all other landform elements. On 30 August 2004, the N_2O flux rate from the DP landform element was again the greatest while the N_2O flux rates from all other landform elements were similar to each other. Mowing increased N_2O flux rates as a main effect ($P = 0.003$).

4.3.4 Weighted average, cumulative emissions and consumption, and carbon budget

Weighted daily average CO_2-C emissions were influenced by the main effects of landform element and mowing during 2003-2004 ($P = 0.006$ and $P = 0.022$ for landform element and mowing, respectively) and 2004-2005 ($P < 0.001$ for both landform element and mowing) (Table 4.12). Mowing increased weighted average daily CO_2-C flux by 21% in 2003-2004 and 55% in 2004-2005. In 2003-2004, the weighted average CO_2-C flux of control and mowing treatment ranged from 3.4 to 6.8 kg CO_2-C ha^{-1} d^{-1}, depending on landform element. Weighted daily average CO_2-C emissions were greatest on the DP landform element and least on the NX and SX landform elements. In 2004-2005, the range of weighted daily average CO_2-C emissions was 11.9 to 24.9 kg CO_2-C ha^{-1} d^{-1}. Weighted daily average CO_2-C emissions were greatest on the DP landform element.

Landform element was a significant determinant of weighted daily average CH_4-C uptake in both sampling seasons ($P = 0.027$ in 2003-2004 and $P = 0.039$ in 2004-2005) (Table 4.12). In 2003-2004, weighted daily average CH_4-C uptake was greatest on the SX, SV and NX landform elements, while weighted daily average CH_4-C uptake was least on the UP, DP and NV landform elements. In 2004-2005, weighted daily average CH_4-C uptake was greatest on the SX and NX landform elements and least on the NV and UP landform elements. Mowing tended to increase weighted daily average CH_4-C uptake by 0.5 g CH_4-C ha^{-1} d^{-1} in 2003-2004 and 0.7 g CH_4-C ha^{-1} d^{-1} in 2004-2005.

Weighted daily average N_2O-N flux was influenced by landform element in both sampling seasons ($P < 0.001$ and in 2003-2004 and $P = 0.028$ in 2004-2005) (Table 4.12).

Table 4.12 Weighted daily average carbon dioxide (CO_2) flux (mean ± SE, kg C ha^{-1} d^{-1}), methane (CH_4) flux (mean ± SE, g C ha^{-1} d^{-1}) and nitrous oxide (N_2O) flux (mean ± SE, g N ha^{-1} d^{-1}) from NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements with control and April mowing in 2003-2004 and 2004-2005 at Macrorie, SK.

Landform Element	CO_2			CH_4			N_2O		
	Control	Mowed	Mean	Control	Mowed	Mean	Control	Mowed	Mean
2003-2004									
NV	4.7 ± 0.5	6.2 ± 0.5	5.4 ± 0.5 ab	-1.5 ± 0.4	-2.5 ± 0.7	-2.0 ± 0.4 a	0.01 ± 0.16	0.09 ± 0.27	0.05 ± 0.14 b
NX	3.1 ± 0.4	5.5 ± 1.3	4.3 ± 0.8 bc	-2.9 ± 0.4	-3.1 ± 0.5	-3.0 ± 0.3 abc	0.20 ± 0.20	-0.04 ± 0.06	0.08 ± 0.11 b
SV	4.8 ± 0.2	6.5 ± 1.5	5.6 ± 0.8 ab	-3.1 ± 0.7	-3.6 ± 0.3	-3.3 ± 0.4 bc	0.09 ± 0.04	0.03 ± 0.08	0.06 ± 0.04 b
SX	3.3 ± 0.5	3.6 ± 0.0	3.4 ± 0.2 c	-4.4 ± 0.7	-4.1 ± 0.9	-4.2 ± 0.5 c	-0.06 ± 0.08	-0.12 ± 0.09	-0.09 ± 0.06 b
UP	4.5 ± 0.6	6.7 ± 0.3	5.6 ± 0.6 ab	-1.9 ± 0.6	-3.3 ± 0.8	-2.6 ± 0.5 ab	< 0.01 ± 0.07	0.30 ± 0.19	0.15 ± 0.11 b
DP	7.8 ± 0.5	5.8 ± 1.0	6.8 ± 0.7 a	-2.2 ± 0.3	-2.5 ± 0.5	-2.4 ± 0.3 a	1.17 ± 1.09	1.51 ± 1.20	1.34 ± 0.73 a
Mean	4.7 ± 0.4 B	5.7 ± 0.4 A		-2.7 ± 0.3	-3.2 ± 0.3		0.24 ± 0.19	0.29 ± 0.22	
2004-2005									
NV	8.6 ± 0.6	16.7 ± 0.8	12.7 ± 1.4 b	-1.8 ± 0.6	-2.9 ± 0.5	-2.3 ± 0.4 ab	-0.22 ± 0.08	-0.14 ± 0.06	-0.18 ± 0.05 b
NX	7.8 ± 0.6	16.0 ± 1.9	11.9 ± 1.7 b	-2.2 ± 0.6	-3.5 ± 0.6	-2.9 ± 0.5 bc	-0.25 ± 0.05	-0.14 ± 0.06	-0.19 ± 0.04 b
SV	11.1 ± 1.0	18.6 ± 1.8	14.9 ± 1.6 b	-2.4 ± 0.6	-3.1 ± 0.3	-2.8 ± 0.3 abc	-0.14 ± 0.15	0.30 ± 0.32	0.08 ± 0.18 a
SX	10.3 ± 1.2	14.0 ± 0.7	12.2 ± 0.9 b	-3.9 ± 0.9	-3.4 ± 0.9	-3.7 ± 0.6 c	-0.20 ± 0.05	-0.20 ± 0.07	-0.20 ± 0.04 b
UP	8.6 ± 0.6	16.1 ± 1.5	12.4 ± 1.5 b	-1.4 ± 0.3	-1.8 ± 0.7	-1.6 ± 0.4 a	-0.15 ± 0.11	-0.01 ± 0.04	-0.08 ± 0.06 ab
DP	23.3 ± 4.2	26.4 ± 3.2	24.9 ± 2.5 a	-2.3 ± 0.6	-3.1 ± 0.4	-2.7 ± 0.4 abc	0.15 ± 0.23	0.13 ± 0.15	0.14 ± 0.13 a
Mean	11.6 ± 1.2 B	18.0 ± 1.0 A		-2.3 ± 0.3	-3.0 ± 0.3		-0.13 ± 0.05	-0.01 ± 0.07	

[1] Means followed by the same upper case letters within a row and a gas type (i.e. CO_2, CH_4 or N_2O) are not significantly different (P = 0.05).
[2] Means followed by the same lower case letters within a column and a gas type are not significantly different (P = 0.05)

Weighted daily average N_2O-N flux was greatest on the DP landform element in 2003-2004. The only positive daily average N_2O-N flux came from the DP and SV landform elements while all other landform elements had negative weighted daily average N_2O-N fluxes. Mowing tended to increase the weighted daily average N_2O-N flux compared to control.

Landform element and mowing affected cumulative CO_2-C emissions in 2003-2004 ($P = 0.033$ and $P = 0.009$ for landform element and mowing, respectively) and in 2004-2005 ($P < 0.001$ for landform element and mowing) (Table 4.13). Cumulative CO_2-C emissions were greatest from the SV, UP, NV and DP landform elements in 2003-2004. Cumulative CO_2-C emissions were greatest from the DP and SV landform elements and cumulative CO_2-C emissions were least from the NX landform element in 2004-2005. Mowing increased CO_2-C flux by 28 and 58% compared to the control in 2003-2004 and 2004-2005, respectively. Net CO_2-C emissions ranged from 1,533 kg CO_2-C ha^{-1} on the UP landform element with mowing treatment to 699 kg CO_2-C ha^{-1} on the NX landform element with control treatment in 2003-2004 and 4,336 kg CO_2-C ha^{-1} from the DP landform element with mowing treatment to 1,616 kg CO_2-C ha^{-1} from the NX landform element with control treatment in 2004-2005.

Landform element had a significant impact on the net consumption of CH_4-$C0_2$ equivalent in both sampling seasons ($P = 0.013$ in 2003-2004 and $P = 0.023$ in 2004-2005) (Table 4.13). Net consumption of CH_4-$C0_2$ equivalent was greatest on south-facing landform elements and least on the NV and DP landform elements in 2003-2004. Net consumption of CH_4-$C0_2$ equivalent was greatest on the SX landform element and was least on the UP landform element in 2004-2005. Net consumption of CH_4-$C0_2$ equivalent on mowed landform elements was 2 and 3 kg CH_4-$C0_2$ equivalent ha^{-1} more than net consumption of CH_4-$C0_2$ equivalent from landform elements of the control treatment in 2003-2004 and 2004-2005, respectively. Net CH_4-$C0_2$ equivalent consumption ranged from 22 kg CH_4-$C0_2$ equivalent ha^{-1} on the SX landform element to 10 kg CH_4-$C0_2$ equivalent ha^{-1} on the DP landform element in 2003-2004 and from 18 kg CH_4-$C0_2$ equivalent ha^{-1} on the SX landform element and 8 kg CH_4-$C0_2$ equivalent ha^{-1} on the UP landform element in 2004-2005.

Landform element influenced cumulative N_2O-$C0_2$ equivalent flux in 2003-2004 ($P < 0.001$) while landform element and mowing influenced cumulative N_2O-$C0_2$ equivalent flux

Table 4.13 Cumulative carbon dioxide (kg CO_2-C ha^{-1} season $^{-1}$), methane (kg CH_4-CO_2 equivalent ha^{-1} season $^{-1}$) and nitrous oxide (kg N_2O - CO_2 equivalent ha^{-1} season $^{-1}$) flux rates from NV – north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression landform elements with control and April mowing in 2003-2004 and 2004-2005 at Macrorie, SK.

Landform Element	--------- kg CO_2-C ha^{-1} $season^{-1}$ ---------			-- kg CH_4-CO_2 equivalent ha^{-1} $season^{-1}$ --			----- kg N_2O-CO_2 equivalent ha^{-1} $season^{-1}$ -----		
	Control	Mowed	Mean	Control	Mowed	Mean	Control	Mowed	Mean
					2003-2004				
NV	1068 ± 101	1404 ± 123	1236 ± 104 a	-8 ± 2.2	-13 ± 3.6	-11 ± 2.2 a	1 ± 11	6 ± 18.1	3 ± 9.5 b
NX	699 ± 91	1254 ± 302	976 ± 188 ab	-15 ± 1.9	-16 ± 2.7	-16 ± 1.5 ab	14 ± 13.6	-3 ± 3.8	5 ± 7.4 b
SV	1095 ± 55	1471 ± 346	1283 ± 178 a	-16 ± 3.9	-19 ± 1.6	-18 ± 2.0 bc	6 ± 2.7	2 ± 5.0	4 ± 2.7 b
SX	754 ± 119	810 ± 6	782 ± 55 b	-23 ± 3.5	-21 ± 4.6	-22 ± 2.6 c	-4 ± 5.6	-8 ± 5.9	-6 ± 3.8 b
UP	1016 ± 131	1533 ± 72	1275 ± 134 a	-10 ± 2.9	-17 ± 4.1	-14 ± 2.8 ab	<1 ± 4.7	20 ± 12.7	10 ± 7.7 b
DP[3]	1322 ± 84	1147 ± 204	1234 ± 106 a	-9 ± 1.2	-11 ± 2.1	-10 ± 1.2 a	59 ± 54.5	88 ± 69.9	73 ± 40.0 a
Mean	992 ± 62 B	1270 ± 94 A		-14 ± 1.6	-16 ± 1.4		12 ± 9.5	17 ± 13.0	
					2004-2005				
NV	1794 ± 123	3463 ± 170	2628 ± 295 bc	-9 ± 2.9	-14 ± 2.5	-11 ± 2.0 ab	-13 ± 5.0	-9 ± 3.6	-11 ± 3.0 b
NX	1616 ± 123	3313 ± 393	2465 ± 343 c	-11 ± 3.1	-17 ± 2.6	-14 ± 2.2 bc	-15 ± 3.3	-9 ± 3.6	-12 ± 2.7 b
SV	2308 ± 215	3869 ± 373	3089 ± 330 b	-12 ± 2.9	-15 ± 1.3	-13 ± 1.6 bc	-8 ± 9.5	19 ± 19.8	5 ± 11.2 a
SX	2138 ± 255	2910 ± 142	2524 ± 188 bc	-19 ± 4.4	-16 ± 4.4	-18 ± 3.0 c	-12 ± 3.0	-12 ± 4.1	-12 ± 2.4 b
UP	1784 ± 130	3345 ± 317	2564 ± 306 bc	-7 ± 1.2	-9 ± 3.4	-8 ± 1.7 a	-9 ± 6.8	-1 ± 2.7	-5 ± 3.8 ab
DP	3816 ± 683	4336 ± 517	4076 ± 413 a	-9 ± 2.2	-12 ± 1.4	-10 ± 1.3 ab	7 ± 11.2	6 ± 7.4	7 ± 6.2 a
Mean	2243 ± 183 B	3539 ± 153 A		-11 ± 1.3	-14 ± 1.2		-9 ± 3.0 B	-1 ± 3.8 A	

[1] Means followed by the same upper case letters within a row and a gas type (i.e. CO_2, CH_4 or N_2O) are not significantly different ($P = 0.05$).
[2] Means followed by the same lower case letters within a column and a gas type are not significantly different ($P = 0.05$).
[3] Cumulative values for the DP landform element were calculated from 122 days in 2003.

in 2004-2005 (P = 0.017 and P = 00.48, respectively) (Table 4.13). The largest cumulative N_2O-$C0_2$ equivalent emission was recorded on the DP landform element in 2003-2004 while the largest cumulative N_2O-$C0_2$ equivalent emission was recorded on the DP and SV landform elements in 2004-2005. Mowing increased the N_2O-N flux by 8 kg N_2O-$C0_2$ equivalent ha^{-1} $season^{-1}$ in 2004-2005.

4.3.5 Relationships between environmental attributes, plant community characteristics and greenhouse gas flux

Significant environmental variables, as determined by the Monte Carlo permutation test, included in the CCA for 2003-2004 were mean gravimetric soil water, aspect, snow water equivalent, slope shape and cumulative CO_2 flux (Table 4.14). For the 2003-2004 sampling season, the first 4 axes of CCA explained a total of 28% of the variation in species composition (Table 4.15). Soil water and aspect were the two most important environmental factors controlling species composition. Soil water and snow water equivalent were strongly correlated with Axis 1 (correlation coefficient (r) = 0.904 and r = 0.742, respectively) (Table 4.16, Figure 4.12). Aspect and slope shape were both negatively correlated with Axis 2 (r = -0.842 and r = -0.359, respectively). Soil water was weakly correlated with aspect (r = -0.317) and with slope shape (r = 0.237) (Table 4.17, Figure 4.12). Snow water equivalent and soil water were also correlated (r = 0.563) while cumulative CO_2 flux was correlated with soil water (r = 0.145).

Species and environme ntal data from 2003 were spread widely along Axis 1 and much less along Axis 2 (Figure 4.12). The DP landform element was at the extreme high end of the soil water, snow, cumulative CO_2 and slope shape gradients. Cumulative CO_2 flux appears as a short gradient, indicating a weak effect on species composition.

Table 4.14 Additional variance explained (λ_A), F Value and P Value of each environmental variable derived from manual forward selection using Monte Carlo permutation test with 9,999 unrestricted permutations in 2003-2004.

Environmental Variable	λ_A	F Value	P Value
Soil H_2O	0.71	8.33	< 0.001
Aspect	0.35	4.38	< 0.001
Snow water equivalent	0.30	3.95	< 0.001
Slope shape	0.16	2.16	0.002
Cumulative CO_2 flux	0.17	2.30	0.001
---------------- P > 0.01 Cut off -----------------			
Cumulative N_2O flux	0.13	1.87	0.075
% Sand	0.17	2.37	0.001
% Litter	0.11	1.73	0.026
% Bare soil	0.11	1.62	0.062
Bulk density	0.11	1.50	0.075
% Water-filled pore space	0.14	2.12	0.004
Mowing treatment	0.09	1.49	0.081
NH_4^+	0.07	1.10	0.336
% Clay	0.06	0.82	0.683
Total biomass	0.04	0.70	0.799
Cumulative CH_4 flux	0.05	0.74	0.780
Potential direct incident radiation	0.05	0.70	0.786
NO_3^-	0.03	0.51	0.961

Table 4.15 Canonical Correspondence Analysis summary statistics from 2003-2004 species and environment data, including importance value of each axis (Eigenvalue: 0 = unimportant, 1 = very important), variance in species composition explained by each axis and cumulative variance explained.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.778	0.412	0.236	0.167
Variance in species data:				
% Explained	13.9	7.3	4.2	3.0
Cumulative % explained	13.9	21.2	25.4	28.4

Table 4.16 Correlation coefficients (r) from the Canonical Correspondence Analysis representing intra-set correlations between significant environmental variables and ordination axes in 2003-2004.

Environmental Variable	Axis 1	Axis 2	Axis 3	Axis 4
Soil H_2O	0.904	0.393	0.160	-0.055
Aspect	-0.079	-0.842	0.407	-0.298
Snow water equivalent	0.742	-0.043	-0.638	-0.195
Slope shape	0.447	-0.359	0.040	0.326
Cumulative CO_2 flux	0.415	-0.147	0.108	0.677

Table 4.17 Correlations (r) from the Canonical Correspondence Analysis of significant environmental variables in 2003-2004.

	Aspect	Slope shape	Snow water	Soil H_2O	Cumulative CO_2
Aspect	1				
Slope shape	0.057	1			
Snow water	-0.215	0.217	1		
Soil H_2O	-0.317	0.237	0.563	1	
Cumulative CO_2	0.034	0.027	0.145	0.308	1

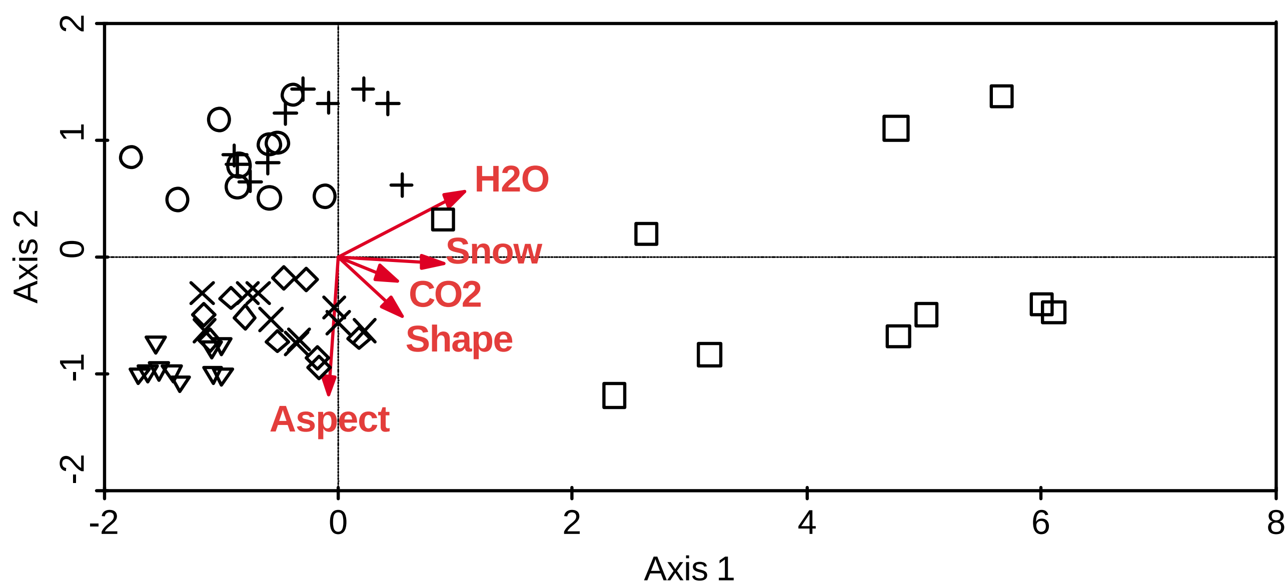

Figure 4.12 Joint plot of linear combinations of 2003-2004 environmental variables (average gravimetric soil water content, snow water equivalent in the spring, cumulative CO_2 flux, slope shape and aspect) and species composition from control and April mowing and + NV – north-facing aspect and concave shape, ? NX – north-facing aspect and convex shape, ? SV – south-facing aspect and concave shape, ▽ SX – south-facing aspect convex shape, X UP – level upland, ☒ DP – depression landform elements at Macrorie, SK.

Significant north-facing aspect and concave shaped slope, NX – north-facing aspect and convex shaped slope, SV – south-facing aspect and concave shaped slope, SX – south-facing aspect and convex shaped slope, UP – level upland and DP – depression environmental variables, as determined by the Monte Carlo permutation test, included in the CCA for 2004-2005 were mean gravimetric soil water, aspect, soil NO_3^- content, % litter cover, cumulative CO_2 flux, % sand content, cumulative CH_4 flux and slope shape (Table 4.18). The first 4 axes explained 31% of the variance in species composition

(Table 4.19). The strongest and most important variables for explaining species composition were soil water, aspect, % sand and litter cover. Soil water was positively correlated with Axis 1 ($r = 0.903$) and % sand was negatively correlated with Axis 1 ($r = -0.801$) (Table 4.20, Figure 4.13). Aspect was negatively correlated with Axis 2 ($r = -0.854$) and litter cover was positively correlated with Axis 2 ($r = 0.557$). Aspect was correlated with H_2O ($r = -0.442$), % sand was correlated with slope shape ($r = -0.526$) and soil water ($r = -0.711$), and cumulative CO_2 flux was weakly correlated with % sand ($r = -0.377$) (Table 4.21, Figure 4.13).

Table 4.18 Additional variance explained (l $_A$), F Value and P Value of each environmental variable derived from manual forward selection using Monte Carlo permutation test with 9,999 unrestricted permutations in 2004-2005.

Environmental Variable	λ_A	F Value	P Value
% Soil H_2O	0.70	8.80	< 0.001
Aspect	0.31	4.22	< 0.001
Soil NO_3^-	0.22	2.94	< 0.001
% Litter	0.18	2.59	< 0.001
Cumulative CO_2 flux	0.16	2.33	0.001
% Sand	0.15	2.26	0.002
Cumulative CH_4 flux	0.13	1.99	0.005
Slope shape	0.13	1.91	0.005
---------------- P > 0.01 Cut off ----------------			
Mowing treatment	0.09	1.52	0.052
% Clay	0.09	1.39	0.097
Total biomass	0.09	1.40	0.106
Bulk density	0.08	1.26	0.177
% Water-filled pore space	0.17	1.49	0.075
% Bare soil	0.07	1.08	0.357
Soil NH_4^+	0.06	1.09	0.336
Potential direct incident radiation	0.07	1.16	0.257
Cumulative N_2O flux	0.06	1.05	0.377

Table 4.19 Canonical Correspondence Analysis summary statistics from 2004-2005 species and environment data, including importance value of each axis (Eigenvalue: 0 = unimportant, 1 = very important), variance in species composition explained by each axis and cumulative variance explained.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.777	0.370	0.282	0.199
Variance in species data:				
% Explained	14.7	7.0	5.3	3.8
Cumulative % explained	14.7	21.7	27.0	30.8

Table 4.20 Correlation coefficients (r) from the Canonical Correspondence Analysis representing intra-set correlations between significant environmental variables and ordination axes in 2004-2005.

Environmental variable	Axis 1	Axis 2	Axis 3	Axis 4
% Soil H_2O	0.903	0.371	0.183	-0.080
Aspect	-0.145	-0.854	-0.160	-0.115
Soil NO_3^-	0.243	0.294	-0.593	-0.482
% Litter	-0.296	0.557	0.024	0.223
Cumulative CO_2 flux	0.614	-0.168	-0.037	0.361
% Sand	-0.801	-0.114	0.279	-0.170
Cumulative CH_4 flux	0.088	0.322	-0.106	0.524
Slope shape	0.502	-0.200	-0.042	0.303

Table 4.21 Correlations (r) from the Canonical Correspondence Analysis of significant environmental variables in 2004-2005.

	Aspect	Slope shape	% Soil H_2O	% Litter	Cumulative CH_4 flux	Cumulative CO_2 flux	% Sand	Soil NO_3^-
Aspect	1							
Slope shape	-0.047	1						
% Soil H_2O	-0.442	0.302	1					
% Litter	-0.243	-0.296	-0.027	1				
Cumulative CH_4 flux	-0.187	0.187	0.121	0.033	1			
Cumulative CO_2 flux	0.050	0.212	0.481	0.083	-0.110	1		
% Sand	0.203	-0.526	-0.711	0.088	-0.114	-0.377	1	
Soil NO_3^-	-0.076	0.225	0.253	0.173	-0.106	-0.012	-0.311	1

The CCA joint plot for 2004-2005 showed a similar spread of species composition along environmental gradients as observed in 2003-2004 (Figure 4.13). Extending the cumulative CH_4 flux gradient in the opposite direction, indicating cumulative CH_4 consumption, places south-facing landform elements on the high end of the cumulative CH_4 consumption gradient. The NO_3^- content of soil was positively correlated with cumulative CH_4 flux while cumulative CO_2 flux was positively correlated with slope shape. Aspect appeared to be negatively correlated with cumulative CH_4 flux gradients and uncorrelated with cumulative CO_2 flux. The DP landform element is at the high end of CO_2 flux.

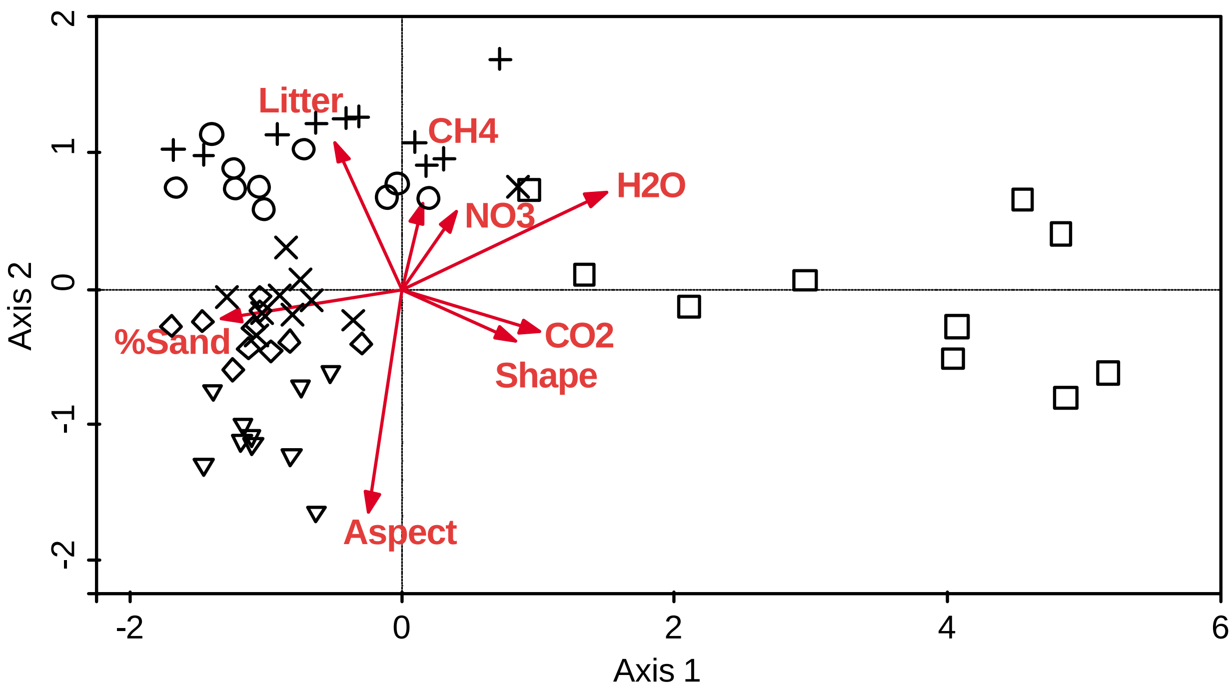

Figure 4.13 Joint plot of linear combinations of 2004-2005 environmental variables (% litter cover, cumulative CH_4 flux, average soil NO_3^-, average gravimetric soil water content, cumulative CO_2 flux, slope shape, slope aspect and % sand content of soil) and species composition from control and April mowing and + NV – north-facing aspect and concave shape, ? NX – north-facing aspect and convex shape, ? SV – south-facing aspect and concave shape, ▽ SX – south-facing aspect convex shape, ╳ UP – level upland, ☒ DP – depression landform elements at Macrorie, SK.

5. DISCUSSION

5.1 Plant Community Characteristics as Influenced by Landform Element and Mowing

Landform element and mowing influenced plant community composition. Species richness varied with landform element. There were fewer species on the UP landform element than all other landform elements in both years. Species richness decreases from upper to lower landform positions in the Missouri Coteau (Tatina, 1994) and increases from south-facing slopes to north-facing slopes in the Mixedgrass Prairie of southern Alberta (Lieffers and Larkin-Lieffers, 1987). Increased habitat diversity is thought to increase species richness at the landscape level (Burnett et al., 1998). Soil microbial diversity is therefore expected to be lower on the UP landform element because soil microbial diversity is positively correlated with plant species diversity (Metting, 1993).

Plant species evenness was influenced by landform elements. Decreased species evenness on the north-facing landform elements compared to south-facing landform elements are likely due to the dominance of plains rough fescue in those areas. Plains rough fescue produces large quantities of biomass, out-competing other species when temperature and soil water conditions are ideal (Looman, 1969). Species evenness was greatest on the north-facing slopes of coulees in the Mixedgrass Prairie possibly because other slopes had recently eroded (Lieffers and Larkin-Lieffers, 1987). In the current study, decreased species evenness on the north-facing landform elements compared to south-facing landform elements, was associated with lower soil temperatures and slightly greater WFPS (Chapter 4.1). Mowing increased species evenness in 2004, but not 2003. Canopy cover of forbs and shrubs increased relative to canopy cover of grasses with mowing (Willms et al., 1986). Drought conditions of 2003 may have limited the effect of mowing on species evenness.

The Shannon-Wiener Diversity Index was greatest on the DP and SX landform elements, likely due to growing conditions unique to those landform elements. Dix and Smiens (1967) stated that species diversity is greatest on mesic sites, but least on very wet parts of the landscape, but that was not true in the current study. The DP landform element can be flooded or remain dry, depending on the year, but increased soil water may support a more diverse plant community in that area. As well, flooding has a disturbance effect. Therefore, vegetation in the DP landform element must be adapted to live in water or start growing after the water has disappeared, which may make the growing season in the DP landform element shorter than in other landform elements. Barnes et al. (1983) stated that species diversity and species richness is greatest on well-drained upper slopes with low NO_3^- content. Soils on these landform elements warm sooner, therefore allowing earlier growth than on other landform elements in the spring and a longer growing season (Cantlon, 1953), which allows the growth of warm season plants and may favour greater species diversity on the SX landform element.

Plant species composition among landform elements was similar in 2003 and 2004 as shown by the DCA. The DP landform element can be separated from other landform elements by Axis 1, which most likely reflects a soil water gradient. The north-facing and south-facing landform elements were spread along Axis 2, which reflects aspect and/or temperature. Intuitively, the UP landform elements are intermediate between north-facing and south-facing landform elements along Axis 2. The DCA did not separate plots by treatment, indicating that mowing did not cause a significant change in species composition.

Forb and shrub biomass was greater in 2004 than in 2003, possibly due to increased precipitation in 2004; precipitation is a major determinant of year-to-year changes in forb growth in the Mixedgrass Prairie (Gillen and Sims, 2004). Landform element was an important factor affecting forb and shrub biomass in both years. Forb and shrub biomass was greatest in the DP landform element in both years and least on the south-facing landform elements. Forbs and shrubs made up a larger portion of the canopy cover in the DP landform element than in other landform elements (Chapter 4.2). Competition for N from grasses with extensive root systems may have reduced forb and shrub growth (Raynaud and Leadley, 2004). On the other hand, water availability and water use may be more important for competition between forbs and grasses than N in semiarid areas (Booth et al., 2003). Mowing decreased forb and shrub biomass in 2003, when precipitation was below the long-term average, but not in 2004.

Standing-live biomass of graminoids was influenced by year-to-year variation in precipitation. Standing-live biomass of graminoids was greater in 2004 when precipitation was greater compared to 2003. Standing-live biomass of graminoids is the first plant community characteristic to recover after drought (Coupland, 1958). Landform element also influenced standing-live biomass of graminoids. Sites that provide optimum growing conditions for plants have greater growth than areas that provide less than optimum growing conditions (Kormondy, 1996). The north-facing landform elements receive less solar radiation, often have greater WFPS and greater soil N (Chapter 4.1) and generally had greater standing-live biomass of graminoids than south-facing landform elements. Soil C may be greater on these landform elements because of the high plant production and C input to the soil.

April mowing decreased standing-live biomass of graminoids on the SV and DP landform elements in 2003 and on most landform elements in 2004. Mowing reduced standing-live biomass of graminoids even though most growth had not started. Among the months of mowing, April and May mowing had the least negative impact on plant growth in the Mixedgrass Prairie in Saskatchewan (Romo and Bai, 2005). Mowing reduces the photosynthetic capacity of plants, decreasing C input to the soil via the roots (Biondini et al., 1998). On the other hand, reduced growth decreases plant competition for N, increasing soil N available for microbes (Corre et al., 1996). Mowing can have opposing effects on soil water as well; decreasing transpiration of the leaf canopy (Willms and Jefferson, 1993), but increasing evaporation from the soil (Willms, 1995).

Standing-dead biomass of graminoids varied among landform elements. Standing-dead biomass of graminoids and soil N were greater on control plots of north-facing landform elements than on the control plots of south-facing landform elements (Chapter 4.1). Mowing decreased standing-dead biomass of graminoids, decreasing organic matter available for incorporation with the soil. If above-ground biomass removal is repeated for many years, soil N may decrease (Biondini et al., 1998). Mowing removes plant matter, including soluble C, an important source of C for microbes that is easily leached from plant materials (Shelp et al., 2000).

Total above-ground biomass was influenced by landform element and mowing in both years. Total above-ground biomass was similar to another study in the Mixedgrass Prairie (Ripley and Saugier, 1978), but nearly twice that reported from Mixedgrass Prairie in Alberta (Whysong and Bailey, 1975). Species that produce large amounts of forage, such as plains rough fescue, are present in most areas of the study site, but north-facing areas appear ideal for this species and a large quantity of plant materials accumulated. Over time, accumulation of total above-ground biomass builds up soil N on the north-facing and DP landform elements (Chapter 4.1). Above-ground biomass influences biotic processes by slowing root and soil microbial desiccation caused by the sun and the wind (Facelli and Pickett, 1991), making the soil environment more suitable for microbial activity. Total above-ground biomass retained on plots may have reduced the effects of landform element and mowing on evaporation, decreasing evaporation from soil and decreasing variation of WFPS across the landscape.

Mowing reduced total above-ground biomass and the relative reduction was most severe on the SX landform element in both years, possibly due to slower plant regrowth compared to north-facing landform elements (Romo and Bai, 2005). Reducing total above-ground biomass had no affect on measured soil temperature in the present study. Reducing above-ground biomass can decrease soil temperatures during the winter, increasing the plants' susceptibility to cold temperatures (Johnston et al., 1971; Kowalenko and Romo, 1998). Decreasing soil temperature can slow microbial activity during the spring and fall (Paul and Clark, 1996). Precipitation events = 5 mm constitute approximately 70% of the precipitation of the Mixedgrass Prairie of Saskatchewan (Colberg and Romo, 2003) and can be entirely absorbed by a litter layer (Couturier and Ripley, 1973; Facelli and Pickett, 1991). Litter can capture up to 200% of its oven-dried weight in water during precipitation events (Naeth et al., 1991), which is then exposed to evaporation and not added to the soil (Weaver and Rowland, 1952). Above-ground plant matter increases the infiltration of precipitation (Larson and Whitman, 1942; Hopkins, 1954), decreases run off (Willms, 1995) and maintains soil water (Willms et al., 1986). Therefore, above-ground plant material can change water dynamics that influence biotic processes (Willms et al., 1993). When water is severely limiting, increasing litter does not increase plant growth (Willms and Jefferson, 1993).

The differences in plant community characteristics as seen among landform elements were likely influenced by differences in growing conditions, like soil water, soil temperature and soil N. Mowing influenced some plant community characteristics by removing accumulated dead plant material and decreasing above-ground growth. The plant community influences the environment by extracting nutrients, storing nutrients, decreasing the soil temperature and modifying the soil water (Miles, 1987). Different environments associated with different plant communities may influence the microbial community important for GHG flux (Cavigelli and Robertson, 2001).

5.2 Greenhouse Gas Flux Rates as Influenced by Landform element and Mowing

Carbon dioxide flux rates in this study were positive, presumably because of respiration from soil microbes, roots and above-ground plant parts. Assimilation of CO_2 during the 60 minutes the chambers were in place was not measured and a balanced CO_2 budget could not be established. It should be noted that given above-ground and below-ground assimilation of CO_2, net CO_2 flux from the study site would have been much lower than the flux rates reported in the present study.

Carbon dioxide respiration from the soil may be responding to coarse scale increases in N deposition, atmospheric CO_2 concentrations and subsequent increases in available soil C (Köchy and Wilson, 2001; Flanagan et al., 2002). Over time, the release of CO_2 is expected to closely match the uptake of CO_2 across the Northern Great Plains (Frank and Dugas, 2001). Reeder and Schuman (2002) suggested that the Mixedgrass Prairie resists changes in total C by redistributing C within the soil profile.

Carbon dioxide flux rates are important for the measurement of soil activity, including microbial and root respiration. Carbon dioxide flux rates from the Mixedgrass Prairie of Wyoming were within the range from the current project (Lecain et al., 2000). Carbon dioxide flux rates were greater on the Mixedgrass Prairie of North Dakota completely denuded of vegetation, likely due to the extra exposure of the soil to solar radiation and death of plants (Frank et al., 2002). The weighted daily average flux rate in the current study is lower than that for arable agriculture systems (Schmidt et al., 2001).

Tillage increases decomposition of soil organic matter by breaking apart aggregates that protect organic matter from decomposition. Carbon dioxide emissions from a Mixedgrass Prairie soil in Saskatchewan indicated much greater soil respiration than the current study possibly due to soil disturbance during soil handling (Redmann and Abouguendia, 1978).

Carbon dioxide flux rates were greater in 2004-2005 than in 2003-2004. Year-to-year variation in precipitation and temperature are common in the Mixedgrass Prairie and are important for biotic and abiotic processes of the grassland ecosystem (Coupland, 1958; Bootsma, 1994). Standing-live biomass of graminoids also increased in 2004 compared to 2003. Increased precipitation directly increases CO_2 emissions by improving the growing conditions for plant roots and soil microbes (McCulley et al., 2005). Carbon dioxide flux is also indirectly increased by greater precipitation because increased plant growth during a wet year transports more photosynthate to the roots, which eventually benefits soil microbes (McCulley et al., 2005).

Within year fluctuations of CO_2 emissions are caused by changes in C availability, soil water and soil temperature (Bremer et al., 1998; Epstein et al., 1998; Frank and Dugas, 2001). Low soil temperatures can limit CO_2 flux (Bremer et al., 1998; Frank et al., 2002), as in the current study during the spring and fall. The peak of daily CO_2 flux in 2004 was similar in time to the peak of the soil temperatures. Periods of low CO_2 flux were similar in time to cold periods in the spring and fall, and hot and very dry periods during the summer for both years. Landform elements influence CO_2 emissions by changing soil water and soil temperature.

The influence of landform element on CO_2 flux rates, weighted average daily CO_2-C and cumulative CO_2-C emissions were similar to the influence of landform element on plant community characteristics (Chapter 4.2). Compared to other landform elements, soil temperature and soil water were less limiting to plant growth and CO_2 emissions in the DP landform element. On the other hand, even though CO_2 emissions were least on the SX landform element where soil temperature was adequate for plant growth, water usually limited plant growth and CO_2 emissions. Carbon dioxide emissions recorded from the SX landform element were less than CO_2 emissions recorded from the NX landform element. Carbon dioxide respiration appears more responsive to changes in soil water than to changes in soil temperature. Typical of northern wetlands, the bulk density and the ratio of standing-dead biomass of graminoids to standing-live biomass of graminoids were low on the DP landform element (Kantrud et al., 1989). Plant production increases in moist conditions compared to xeric conditions, but decomposition increases too (Kantrud et al., 1989). Past haying of DP landform elements may also have contributed to low standing-dead biomass of graminoids to standing-live biomass of graminoids ratio.

Mowing increased CO_2 flux rates, weighted average daily CO_2-C and cumulative CO_2-C emissions in both years. Grazing can increase CO_2 emissions by increasing plant photosynthesis and C transported to the roots (Lecain et al., 2000). Grazing, trampling associated with grazing and mowing also increases CO_2 emissions by increasing soil temperature, damaging roots and adding plant matter to the soil (Redmann, 1978; Bremer et al., 1998). Mowing decreased standing-dead biomass of graminoids while increasing CO_2 flux in the current study. Mowing often increases the absorption of solar radiation by the soil surface and could increase soil temperature thereby increasing soil respiration. In the current study, mowing did not increase soil temperature. Except on the SX and DP landform elements, differences in weighted daily average CO_2 flux between control and the mowing treatment were large in all landform elements.

Similar to other non-flooded soils, soils in the present study consumed CH_4 throughout the year (Topp and Pattey, 1997). The exception was 7 April 2004, when CH_4 production was likely favoured and emissions were above zero. The production of CH_4 is possible during the snowmelt in the Mixedgrass Prairie (Wang and Bettany, 1995) or after rain (Chan and Parkin, 2001). Methane is often simultaneously produced and consumed within the same soil column (Topp and Pattey, 1997). In soil that is not water saturated, methane production occurs in the anaerobic areas created by soil structure (Conrad, 1996). Clay content of soils was similar in all landform elements in the current study. As soils are wetted, decreased O_2 diffusion into the soil increases CH_4 production over its consumption (Mosier et al., 1998b). As soils dry, diffusion of O_2 into the soil increases, anaerobic conditions decrease and consumption can be greater than production. Methane consumption in the current study is similar to that on the Shortgrass Prairie of

Colorado (Mosier et al., 1991; Mosier et al., 1997) and pastures in Ontario (Dunfield et al., 1995).

Within-year fluctuation of CH_4 consumption in the present study may have been caused by the variation of temperature and soil water. Cold temperatures are thought to decrease CH_4 oxidation (Potter et al., 1996), but consumption was least during summer when the soil temperature was greatest. Drying the soil reduces anaerobic microsites and methanotrophic activity, while wetting the soil has the opposite effect (Schnell and King, 1996). Except in the fall of 2003 when soil water was limited, CH_4 consumption of soil was greatest at the beginning and the end of the sample season when soil water was also greatest.

Landform element influenced CH_4 flux rates, weighted daily average CH_4-C and cumulative CH_4 consumption (Mosier et al., 1996; Torn and Harte, 1996), but the influence of this factor on CH_4 flux rates was inconsistent over time. Methane uptake on the DP landform element was among the least in 2003-2004, but increased compared to other landform elements the following year. The DP landform element was flooded in the spring of 2003, and CH_4 was likely produced during this period. Measurements of GHG flux from the DP landform element only began in 2003 when water in the DP landform element had disappeared, but the CH_4 consumption to CH_4 production ratio at this point may have been lower than elsewhere in the landscape because of previous CH_4 production while water saturated. Despite accumulating more snow than all other landform elements, the DP landform elements did not flood in spring of 2004 and therefore the series of conditions that may have influenced CH_4 flux in the DP landform element in 2003 did not occur. The changing soil water of this landform element may have been responsible for the changing CH_4 flux rates during the two years. Methane consumption recorded on the SX landform element remained greater than CH_4 consumption recorded on other landform elements possibly due to the lack of soil NH_4^+, which can inhibit CH_4 oxidation (Hütsch, 2001). Nitrous oxide production, a soil process that is N-limited, can be inversely related to CH_4 oxidation (Mosier et al., 1991). No inverse relationship appeared to occur in the present study, though the CCA from 2004-2005 suggests that CH_4 consumption and NO_3^- may be negatively correlated. The consumptive flux of CH_4 is often determined by the ratio of CH_4 production to CH_4

consumption within the soil column (Mosier et al., 1998b). The CH_4 consumption on the SX landform element conditions may have been high because CH_4 production was rarely favoured by conditions on that landform element. The soil of the SX landform element was usually dry and wetting very dry soils can increase CH_4 consumption (Schnell and King, 1996). Therefore, precipitation may have increased CH_4 consumption on the SX landform element the most, because soil was driest there. Methane consumption rate was high on the SV landform element probably because soil temperature requirements for CH_4 consumption were met and soil water, needed to drive the consumption of CH_4, was often greater than on the SX landform element. Methane consumption rate was the least on the NV landform element because cool, moist condition, relative to south facing landform elements, may have decreased the CH_4 consumption to production ratio.

Mowing tended to increase CH_4 consumption. In soils where water impeded CH_4 consumption, mowing may have increased soil temperature and decreased soil water, which could also increase CH_4 consumption (Mosier et al., 1998b). Removal of above-ground biomass also increases CH_4 consumption in the Tallgrass Prairie because of changes in soil temperature and soil water (Tate and Striegl, 1993). The relationship between mowing and WFPS and mowing and CH_4 consumption, however, was not consistent in the present study. Mowing increased, decreased or did not change soil water and CH_4 depending on the time of year and the landform element.

Nitrous oxide emissions were near zero on most sample dates. Soil N was limited in the present study. Total mineral N (NH_4^+ and NO_3^-) in an area of Black Soil in Saskatchewan ranged from 3 to 7 mg N kg soil^{-1} in pastures to 20 mg N kg soil^{-1} on a fallow arable field (Corre et al., 1996), while total mineral N in the present study was below 2 mg N kg soil^{-1}. The combination of competition for N and dry soils decreases N_2O flux rates (Mummey et al., 1994). The rate of N_2O production in the current study was similar to pastures in Saskatchewan (Corre et al., 1999) and less than arable lands in Saskatchewan and Alberta (Izaurralde et al., 2004). The mean NO_3^- content of soil on all landform elements in the present study is below the 5 mg NO_3^- kg dry soil^{-1} threshold needed for denitrification to be the major source of N_2O (Lemke et al., 1998). There is no relationship between WFPS and N_2O production when denitrification occurs at low rates (Groffman and Tiedje, 1991). There is also no clear relationship between soil N and

N_2O when soil N is below the 5 mg threshold (Izaurralde et al., 2004). Water-filled pore space was likely well below the threshold necessary for major N_2O production in the current study. Therefore, when WFPS increased above the necessary threshold, the production of N_2O would still be constrained by low amounts of soil N. Nitrous oxide production was constrained by low amounts of soil N and low WFPS on all landform elements in this study.

Negative N_2O flux rates occurred on several sample dates, but consumption of N_2O was much less than that recorded from Tallgrass Prairie in Kansas or forest in Belgium (Groffman and Turner, 1995; Goossens et al., 2001). Nitrous oxide consumption occurs only during the denitrification process when microbial activities responsible for N_2O reductase are faster than that for NO (Beauchamp, 1997; Cavigelli and Robertson, 2001). Nitrous oxide uptake in a N-limited forest ecosystem was attributed to denitrifying bacteria consuming atmospheric N_2O as a source of electron acceptors instead of NO_3^- (Papen et al., 2001). Denitrification requires a WFPS of 60 to 90% (Bolan et al., 2004), a condition rarely met in the present study (Figure 4.2). Nitrifier denitrification does not have the same WFPS requirement as denitrification and occurs in unsaturated soils of natural ecosystems (Wrage et al., 2004). Nitrifier denitrification utilises the denitrification process and may also consume N_2O.

Nitrous oxide flux rates were greater in 2003-2004 than in 2004-2005 because spring sampling in the 2003-2004 included days in the spring of 2004 with large production while spring sampling in 2004-2005 was low. Nitrous oxide production is often greater following a dry year because NO_3^- builds up in the soil during dry years (Mummey et al., 1994), but in the current study, the year following drought did not have greater N_2O production.

Within year variation of N_2O flux rates is due to fluctuations in weather, soil water, availability of NO_3^- and rate of nitrification (Mummey et al., 1994; Bolan et al., 2004). The timing of the large positive flux that occurred 22 March 2004 is consistent of large N_2O emissions in the spring of other years (Lemke et al., 1999). Dead microbes and NH_4^+ fixed on soil particles add to available sources of N_2O substrate when soils thaw in spring (Müller et al., 2002) because N_2O producing microbes benefit from C and

N leaked from microbes or roots damaged by the freeze thaw cycle (Wagner-Riddle and Thurtell, 1998; Bolan et al., 2004).

Landform element and mowing induced differences in soil temperature and soil water, both contributing to differences in N_2O flux (Corre et al., 1996; Izaurralde et al., 2004) in 2004. On 22 March 2004, the majority of N_2O emissions were recorded on the DP and south-facing landform elements. Plants cannot compete for soil N while dormant in March. Decreased snow cover, earlier warming and earlier microbial activity in spring on south-facing landform elements compared to north-facing landform elements may increase the production of N_2O by south-facing landform elements compared to north-facing landform elements. Upper slope positions produce more N_2O than lower slope positions in spring (Corre et al., 1996). For the rest of the sampling season, production of N_2O from the DP landform element constitutes most of the total N_2O budget because of greater soil water and soil N than in other landform elements. Nitrous oxide flux rates in spring of 2005 were low, probably because the soil was still too cold for microbial activity. In soils with low denitrification rates where nitrification is the main source of N_2O, WFPS is not a good indicator of N_2O (Groffman and Tiedje, 1991), but gravimetric soil water may be used to predict N_2O emissions (Izaurralde et al., 2004). Nitrous oxide production is positively correlated with biomass production in the Tallgrass Prairie (Groffman and Turner, 1995), but not in the current study (Chapter 4.3). Cooler and usually wetter north-facing landform elements were expected to have greater N_2O flux, but competition for soil N between microbes and plants may have favoured plant growth given the large amount of plant biomass in this area. Plant growth and N_2O production may have been limited by low amounts of soil N or soil water.

Mowing increased N_2O production the most on the south-facing and UP landform elements. Mowing decreased standing-live biomass of graminoids and may have therefore decreased the uptake of soil N, allowing more of it to be transformed into N_2O. Grazing increases N_2O emissions, but usually because of animal deposited N and trampling action (Ryden, 1985; De Klein et al., 2001). In fact, grazing increases denitrification more than mowing (Ryden 1986; Oenema et al., 1997).

The CCA joint plot for 2003-2004 shows that during a dry year the correlations between species composition and GHG flux rates was weak. Greenhouse gas flux from all landform elements was low in 2003-2004, therefore the correlation between GHG flux and species composition was weak. Species composition, even though varying with landform element, cannot be used to explain variations in GHG emissions in 2003-2004.

The 2004-2005 CCA joint plot shows the importance of the DP landform element in determining landscape scale variation in GHG flux. The DP landform element was at the high end of both CO_2 and CH_4 flux gradient arrows. The joint plot also showed that soil water content was correlated to GHG flux. Soil water content was a significant environmental variable in determining species distribution, while WFPS, an indicator of anaerobic conditions, was not significant. Anaerobic conditions are important for high N_2O emission rates, but these conditions did not occur in the present study. Therefore, most GHG flux occurred in aerobic conditions and soil water content was probably more important than WFPS because soil water controls general microbial activity and not just the activity of obligate anaerobic microbes. The chosen environmental variables only account for 28 to 31% of the variation in species composition. The environmental conditions measured during the sampling season attempted to explained the rate of plant growth and microbial activity associated with GHG flux, but not the survival or death rates of plants. Environmental attributes that influence plant germination and survival, like cold stress days, winter soil temperature and germination conditions may have a greater influence on the distribution of species. If the variables measured were not the same ones that determine survival and death of plants, then the variance in species distribution explained by the environmental variables would be low.

Topography and vegetation can be related to landscape scale GHG flux (Beauchamp, 1997; Reay et al., 2005). The return of plant materials to the soil can influence the rate of soil processes (Miles, 1985; Miles, 1987), possibly changing GHG flux. Differences in N uptake and soil water use among plant communities can also change GHG flux rates (Epstein et al., 1998). Using plant communities as indicators of GHG flux assumes that plant distribution and production are distinctive and predictable throughout the landscape. However, plant growth and GHG flux do not appear to be equally constrained across the landscape. Plant growth on the DP and north-facing landform elements is less water limited than on the south-facing landform elements. Plant growth may mute differences in the characteristics of the physical environment that should create landscape patterns of GHG flux. Factors controlling plants and GHG flux rates are similar, but plant growth may be limited at different rates of these factors than GHG flux rates or plant distribution may be controlled by unmeasured factors, making the use of plants as indicators of fine scale GHG variations difficult.

The soil CO_2 flux rate may be good indicator of biological activity rather than a calculation of net contribution to global climate change. Consumption of CH_4 amounts to several hundred g C ha^{-1} $season^{-1}$, which nearly balances the N_2O produced when comparing the GWP of each gas. Nitrous oxide flux varies between production and consumption.

6. SUMMARY AND PRACTICAL IMPLICATIONS

The flux of GHGs by living organisms in soil is controlled by the environment (Rogers and Whitman, 1991). The environment is influenced by abiotic factors such as climate (Metting, 1993), soils (Ladd et al., 1993) and topography (Ellis, 1938), and biotic factors such as soil organisms (Paul and Clark, 1996), vegetation structure (Epstein et al., 1998), composition (Robinson et al., 2003) and grazing (Daniel et al., 2002). These factors interact to influence the spatial and temporal variability of GHGs (van Kessel et al., 1993; Velthof et al., 1996a).

Similar patterns in plant community characteristics occurred across the landscape in both sampling seasons. Species richness, species evenness and species diversity were all affected by landform element while only species evenness was affected by mowing in 2004. Landform element was important in determining the distribution of species at a landscape level in both sampling seasons. Precipitation and mowing appeared to be important determinants of forb, shrub and graminoid biomass production. Forb, shrub and standing-live biomass of graminoids were greater in 2004 than in 2003, possibly responding to increased precipitation. Standing-dead biomass of graminoids was less in 2004 compared to 2003, reflecting decreased standing-live biomass in 2003 needed to add to standing-dead biomass in 2004. Water-filled pore space was generally greatest on the DP and NX landform elements and these landform elements had more total biomass than drier landform elements. Mowing removed biomass thereby slowing plant growth and changing the soil environment.

Gas flux was affected by landform element, mowing and sample date. The flux rates of CO_2, CH_4, and N_2O fluctuated in response to changes in soil water and soil temperature across time and across the landscape. Landform element significantly affected the flux of CO_2, CH_4, and N_2O. The largest production of CO_2 and N_2O were recorded on the DP landform element, while the largest consumption of CH_4 was recorded on the SX landform element. Mowing increased CO_2 emissions, CH_4

consumption and N_2O production. Interpretation of multivariate analysis of species composition and environmental gradients was difficult in a dry year. In a wet year, like 2004-2005, aspect was negatively correlated with CH_4 flux, while slope shape was positively correlated with CO_2 flux. Carbon dioxide emissions appear similar to emissions from studies from the Mixedgrass Prairie of Saskatchewan (Redmann, 1978). The soils in the present study consume similar amounts of CH_4 to soils of pastures in Ontario (Dunfield et al., 1995). Nitrous oxide production appears less than N_2O production from arable land in Saskatchewan (Izaurralde et al., 2004), but similar to N_2O production of pastures in Saskatchewan (Corre et al., 1999).

Characteristics of the physical environment, plant community characteristics and GHGs were all influenced by landform element and mowing. Therefore, the null hypotheses that: 1) landform element and mowing have no effect on environmental attributes, 2) landform element and mowing have no effect on plant community characteristics, 3) landform element and mowing have no effect on greenhouse gas flux and 4) environmental attributes, plant community characteristics and GHG flux are not correlated are all rejected, but with reservations as to the application of these conclusions. Landform element and mowing contributed to differences in the characteristics of the physical environment, plant community characteristics and GHG flux. Differences in PDIR among landform elements, accumulated snow water equivalent and soil temperature suggests that patterns in plant community characteristics may be similar to patterns in GHG flux rates. The current study shows, however, that differences in the characteristics of the physical environment like soil N, WFPS and GHG flux rates were not consistent through time. Mowing modified plant community characteristics, especially species evenness. Mowing also increased CO_2 flux and, to a lesser extent, increased CH_4 consumption and N_2O production. Soil water and soil temperature were also correlated with GHG flux, but changes in all of these factors over time make interpretation of results difficult.

It is important to determine when a landform element was sampled for the accurate development of a net GHG budget for a landscape scale study. The DP landform element can be flooded in spring and dry later in the season. This landform element has the potential to be a source of anaerobically produced CH_4 and N_2O, a sink for CH_4, and a source for CO_2 depending on when water is present. The SX landform element is generally the driest portion of the landscape, but may be the first to produce N_2O during the spring following a wet fall or heavy snowfall because it is the first landform element to warm. It is therefore imperative that the influence of the combination of various landform elements on hydrological processes over time be stressed when studying landscape scale GHG flux because studies recommend frequent sampling in spring to capture the majority of N_2O emissions (Corre et al., 1999).

Canadian agriculture contributes 8.3% of Canada's total GHG emissions (Olsen et al., 2003). The Canadian government plans to mitigate agricultural GHGs by identifying best management practices that change the production and consumption of GHGs to positively influence climate change (Agriculture and Agri-Food Canada, 2003). The starting point for proposed best management practices for the Mixedgrass Prairie of Saskatchewan is to recognize the relative source and sink that rangelands represent compared to arable lands. The net emissions of GHGs from Saskatchewan rangeland are relatively low (de Jong, 1981; Corre et al., 1999), but the potential for increased emissions from rangeland is high if improperly managed (Mosier et al., 1998a; Mosier et al., 1998b). For instance, cultivated soils of Saskatchewan have lost 21% of stored C from 1910 to 1990 (Smith et al., 1997).

Management for GHG flux on the Mixedgrass Prairie of Saskatchewan needs to be addressed at several scales. At the fine scale it should be noted that mowing increased CO_2 and N_2O emissions production. Therefore, grazing management that retains plant material will reduce CO_2 and N_2O emissions and benefit rangeland production (Willms et al., 2002). Range health assessments suggest changes in grazing management that promote ecosystem functions like soil development, water retention, biodiversity maintenance and nutrient cycling (Adams et al., 2005). Because the functions high-lighted in range health assessments also control GHG flux, range health assessments could easily be modified to inform range managers of the impact of grazing on GHG flux so that producers can reduce CO_2 and N_2O production. Healthy range could also include the most beneficial GHG flux. Other suggestions include preventing increases in the bulk density of the soil. Any increase in the bulk density would increase the WFPS and increase N_2O production.

At a medium scale, such as the Missouri Coteau, the DP landform element stands out as an important contributor to the GHG flux of the entire landscape. The Missouri Coteau has a distinctive vegetation type, landform, climate and land use with very little flux of GHGs except in the DP landform element, which has distinctive vegetation associated with periodic, high water availability. Therefore, any correlation between the characteristics of the physical environment, the plant community and GHG flux may be better reflected at this medium scale rather than the fine scale.

Management that leads to vegetative cover change on the Mixedgrass Prairie is an important contributor to climate change at the coarse scale (Skinner and Majorowicz, 1999). A policy of preventing the conversion of the Mixedgrass Prairie to arable agriculture and encouraging the conversion of croplands to perennial grasses would benefit Canadian attempts to mitigate GHGs by retaining, or increasing important CO_2 storage, CH_4 sinks as well as not adding to N_2O production. The role of rangelands in mitigating climate change may be heightened in light of increased atmospheric CO_2 concentration and N deposition, both of which could increase productivity and increase the sink ability of Saskatchewan rangelands. The retention and restoration of rangelands may also provide a stable source of agriculture production in the light of global climate change and the potential of increasing periods of drought. Grazing policy initiatives that promote the sustainable use of rangelands could benefit the climate as well as the people.

7. LITERATURE CITED

Acton, D.F, G.A. Padbury, and C.T. Stushnoff. 1998. The ecoregions of Saskatchewan. Canadian Plains Research Center, University of Regina, Regina, SK, Canada.

Adams, B.W., G. Ehlert, C. Stone, D. Lawrence, M. Alexander, M. Willoughby, C. Hincz, D. Moisey, A. Burkinshaw and J. Carlson. 2005. Rangeland health assessment for grassland, forest and tame pasture. 2nd edition. Publication Number T/044. Alberta Sustainable Resource Development, Public Lands and Forests Division, Rangeland Management Branch, Lethbridge, AB, Canada.

Agriculture and Agri-Food Canada. 2003. The greenhouse gas mitigation program for Canadian agriculture. Agriculture and Agri-Food Canada, Ottawa, ON, Canada.

Anderson, I.C., M. Poth, J. Homstead, and D. Burdige. 1993. A comparison of NO and N_2O production by the autotrophic nitrifier *Nitrosomonas europaea* and the heterotrophic nitrifier *Alcaligenes faecalis*. Applied and Environmental Microbiology 59:3525-3533.

Anonymous. 1986. Sampling methods with special reference to range management. Pages 215-250 *in* C.W Cook and J. Stubbendieck, editors. Range research: basic problems and techniques. Society for Range Management, Denver, CO, USA.

Archer, S., and F.E. Smeins. 1991. Ecosystem-level processes. Pages 109-139 *in* R.K. Heitschmidt and J.W. Stuth, editors. Grazing management: an ecological perspective. Timber Press, Portland, OR, USA.

Ayyad, M.A., and R.L. Dix. 1964. An analysis of a vegetation-microenvironmental complex on prairie slopes in Saskatchewan. Ecological Monographs 34:421-442.

Barnes, P.W., L.L. Tieszen, and D.J. Ode. 1983. Distribution, production, and diversity of C_3- and C_4- dominated communities in a mixed prairie. Canadian Journal of Botany 61:741-751.

Beauchamp, E.G. 1997. Nitrous oxide emission from agricultural soils. Canadian Journal of Soil Science 77:113-123.

Beebe, J.D., and G.R. Hoffman. 1968. Effects of grazing on vegetation and soils in southeastern South Dakota. American Midland Naturalist 80:96-110.

Biondini, M.E., B.D. Patton, and P.E. Nyren. 1998. Grazing intensity and ecosystem processes in a Northern Mixed-Grass Prairie, USA. Ecological Applications 8:469-479.

Blackmer, A.M., and J.M. Bremner. 1980. A simple chamber technique for field measurements of emissions of nitrous oxide from soils. Journal of Environmental Quality 9:251-256.

Blake, G.R., and K.H. Hartge. 1984. Bulk density. Pages 363-375 *in* A. Klute, editor. Methods of soil analysis. Part 1. Physical and mineralogical methods. 2nd edition. American Society of Agronomy, Inc. and Soil Science Society of America, Inc., Madison, WI, USA.

Bolan, N.S., S. Saggar, J. Luo, R. Bhandral, and J. Singh. 2004. Gaseous emissions of nitrogen from grazed pastures: processes, measurements and modelling, environmental implications, and mitigation. Pages 37-120 *in* D.L. Sparks, editor. Advances in agronomy, Volume 84. Elsevier Academic Press, Amsterdam, The Netherlands.

Bolton, Jr., H., J.K. Fredrickson, and L.F. Elliott. 1993. Microbial ecology of the rhizosphere. Pages 27-64 *in* F.B. Metting, Jr., editor. Soil microbial ecology. Marcel Dekker, Inc., New York, NY, USA.

Booth, M.S., M.M. Caldwell, and J.M. Stark. 2003. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. Journal of Ecology 91:36-48.

Bootsma, A. 1994. Long term (100 yr) climatic trends for agriculture at selected locations in Canada. Climatic Change 26:65-88.

Bouwman, A.F. 1998. Nitrogen oxides and tropical agriculture. Nature 392:866-867.

Bouyoucos, G.J. 1962. Hydrometer method improved for making particle size analysis of soils. Agronomy Journal 43:434-438.

Bowden, W.B. 1986. Gaseous nitrogen emissions from undisturbed terrestrial ecosystems: an assessment of their impacts on local and global nitrogen budgets. Biogeochemistry 2:249-279.

Bremer, D., J.M. Ham, C.E. Owensby, and A.K. Knapp. 1998. Responses of soil respiration to clipping and grazing in a tallgrass prairie. Journal of Environmental Quality 27:1539-1548.

Brown, R.W. 1995. The water relations of range plants: adaptations to water deficits. Pages 291-413 *in* D.J. Bedunah and R.E. Sosebee, editors. Wildland plants: physiological ecology and developmental morphology. Society for Range Management. Denver, CO, USA.

Bubier, J.L. 1995. The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. Journal of Ecology 83:403-420.

Bubier, J.L., and T.R. Moore. 1995. Predicting methane emission from bryophyte distribution in northern Canadian peatlands. Ecology 76:677-693.

Buffo, J., L. Fritschen, and J. Murphy. 1972. Direct solar radiation on various slopes from 0 to 60 north latitude. USDA Forest Service Research Paper PNW-142. PNW Forest and Range Experiment Station, Portland, OR, USA.

Burnett, M.R., P.V. August, J.H. Brown, Jr., and K.T. Killingbeck. 1998. The influence of geomorphological heterogeneity on biodiversity. I. A patch-scale perspective. Conservation Biology 12:363-370.

Cantlon, J.E. 1953. Vegetation and microclimates on north and south slopes of Cushetunk Mountain, New Jersey. Ecological Monographs 23:241-270.

Carran, R.A., P.W. Theobald, and J.P. Evans. 1995. Emission of nitrous oxide from some grazed pasture soils in New Zealand. Australian Journal of Soil Research 33:341-352.

Cavigelli, M.A., and G.P. Robertson. 2000. The functional significance of denitrifier community composition in a terrestrial ecosystem. Ecology 81:229-241.

Cavigelli, M.A., and G.P. Robertson. 2001. Role of denitrifier diversity in rates of nitrous oxide consumption in a terrestrial ecosystem. Soil Biology and Biochemistry 33:297-310.

Chan, A.S.K., and T.B. Parkin. 2001. Effect of land use on methane flux from soil. Journal of Environmental Quality 30:786-797.

Chapin, F.S., III, F.S., A.J. Bloom, C.B. Field, and R.H. Waring. 1987. Plant responses to multiple environmental factors. BioScience 37:49-57.

Christiansen, E.A. 1979. The Wisconsinan deglaciation of southern Saskatchewan and adjacent areas. Canadian Journal of Earth Sciences 16:913-938.

Clark, J.S., E.K. Yiridoe, N.D. Burns, and T. Astatkie. 2000. Regional climate change: trend analysis of temperature and precipitation series at selected Canadian sites. Canadian Journal of Agricultural Economics 48:27-38.

Clayton, H., J.R.M. Arah, and K.A. Smith. 1994. Measurement of nitrous oxide emissions from fertilized grassland using closed chambers. Journal of Geophysical Research 99:16599-16607.

Coe, H., and A.R. Webb. 2003. Atmospheric energy and the structure of the atmosphere. Pages 35-58 *in* C.N. Hewitt and A.V. Jackson, editors. Handbook of atmospheric science: principles and applications. Blackwell Publishing, Malden, MA, USA.

Colberg, T.J., and J.T. Romo. 2003. Clubmoss effects on plant water status and standing crop. Journal of Range Management 56:489-495.

Conant, R.T., K. Paustian, and E.T. Elliott. 2001. Grassland management and conversion into grassland: effects on soil carbon. Ecological Applications 11:343-355.

Conen, F., and K.A. Smith. 1998. A re-examination of closed flux chamber methods for the measurement of trace gas emissions from soils to the atmosphere. European Journal of Soil Science 49:701-707.

Conly, F.M., and G. van der Kamp. 2001. Monitoring the hydrology of Canadian prairie wetlands to detect the effects of climate change and land use change. Environmental Monitoring and Assessment 67:195-215.

Conrad, R. 1996. Soil microorganisms as controllers of atmospheric trace gases (H_2, CO, CH_4, OCS, N_2O, and NO). Microbiological Reviews 60:609-640.

Corre, M.D., D.J. Pennock, C. van Kessel, and D.K. Elliott. 1999. Estimation of annual nitrous oxide emissions from a transitional grassland-forest region in Saskatchewan, Canada. Biogeochemistry 44:29-49.

Corre, M.D., C. van Kessel, and D.J. Pennock. 1996. Landscape and seasonal patterns of nitrous oxide emissions in a semiarid region. Soil Science Society of America Journal 60:1806-1815.

Coupland, R.T. 1950. Ecology of the Mixed Prairie in Canada. Ecological Monographs 20:271-315.

Coupland, R.T. 1958. The effects of fluctuations in weather upon the grasslands of the Great Plains. The Botanical Review 24:274-317.

Coupland, R.T. 1961. A reconsideration of grassland classification in the Northern Great Plains of North America. Journal of Ecology 49:134-167.

Coupland, R.T., and R.E. Johnson. 1965. Rooting characteristics of native grassland species in Saskatchewan. Journal of Ecology 53:475-507.

Coupland, R.T., N.A. Skoglund, and A.J. Heard. 1960. Effects of grazing in the Canadian Mixed Prairie. Pages 212-215 *in* Proceedings of the Eighth International Grassland Congress, Great Britain.

Couturier, D.E., and E.A. Ripley. 1973. Rainfall interception in Mixed Grass Prairie. Canadian Journal of Plant Science 53:659-663.

Crider, FJ. 1955. Root-growth stoppage resulting from defoliation of grass. USDA-SCS Technical Bulletin Number 1102. Washington, DC, USA.

Curtin, C.G. 2002. Livestock grazing, rest, and restoration in arid landscapes. Conservation Biology 16:840-842.

Cutforth, H.W. 2000. Climate change in the semiarid prairie of southwestern Saskatchewan: temperature, precipitation, wind, and incoming solar energy. Canadian Journal of Soil Science 80:375-385.

Cutforth, H.W., B.G. McConkey, R.J. Woodvine, D.G. Smith, P.G. Jefferson, and O.O. Akinremi. 1999. Climate change in the semiarid prairie of southwestern Saskatchewan: late winter–early spring. Canadian Journal of Plant Science 79:343-350.

Daniel, J.A., K. Potter, W. Altom, H. Aljoe, and R. Stevens. 2002. Long-term grazing density impacts on soil compaction. Transactions of the American Society of Agricultural Engineers 45:1911-1915.

Davidson, E. 1991. Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems. Pages 219-235 *in* J.E. Rogers and W.B. Whitman, editors. Microbial production and consumption of greenhouse gases: methane, nitrogen oxides, and halomethanes. American Society for Microbiology, Washington, DC, USA.

Davidson, E.A., and J.P. Schimel. 1995. Microbial processes of production and consumption of nitric oxide, nitrous oxide and methane. Pages 327-357 *in* P.A. Matson and R.C. Harris, editors. Biogenic trace gases: measuring emissions from soil and water. Blackwell Science Ltd., Oxford, England.

de Jong, E. 1981. Soil aeration as affected by slope position and vegetative cover. Soil Science 131:34-43.

de Jong, E., H.J.V. Schappert, and K.B. MacDonald. 1974. Carbon dioxide evolution from virgin and cultivated soil as affected by management practices and climate. Canadian Journal of Soil Science 54:299-307.

de Klein, C.A.M., R.R. Sherlock, K.C. Cameron, and T.J. van der Weerden. 2001. Nitrous oxide emissions from agricultural soils in New Zealand – A review of current knowledge and directions for future research. Journal of the Royal Society of New Zealand 31:543-574.

Desjardins, R.L., S.N. Kulshreshtha, B. Junkins, W. Smith, B. Grant, and M. Boehm. 2001. Canadian greenhouse gas mitigation options in agriculture. Nutrient Cycling in Agroecosystems 60:317-326.

Desjardins, R.L., and R. Riznek. 2000. Agriculture greenhouse gas budget. Pages 133-140 *in* T. McRae, C.A.S. Smith and L.J. Gregorich, editors. Environmental sustainability of Canadian agriculture: report of the agri-environmental indicator project. Agriculture and Agri-Food Canada, Ottawa, ON, Canada.

Dix, R.L. 1968. Some slope-plant relationships in the grasslands of the Little Missouri Badlands of North Dakota. Journal of Range Management 11:88-92.

Dix, R.L., and F.E. Smiens. 1967. The vegetation of Nelson County, North Dakota. Canadian Journal of Botany 45:21-58.

Dobbie, K.E., I.P. McTaggart, and K.A. Smith. 1999. Nitrous oxide emissions from intensive agricultural systems: variations between crops and seasons, key driving variables, and mean emission factors. Journal of Geophysical Research 104:26891-26899.

Dodd, M.B., W.K. Lauenroth, and I.C. Burke. 2000. Nitrogen availability through a coarse-textured soil profile in the Shortgrass Steppe. Soil Science Society of America Journal 64:391-398.

Dumanski, J., R.L. Desjardins, C. Tarnocai, C. Monreal, E.G. Gregorich, V. Kirkwood, and C.A. Campbell. 1998. Possibilities for future carbon sequestration in Canadian agriculture in relation to land use changes. Climate Change 40:81-103.

Dunfield, P.F., E. Topp, C. Archambault, and R. Knowles. 1995. Effect of nitrogen fertilizers and moisture content on CH_4 and N_2O fluxes in a humisol: measurements in the field and intact soil cores. Biogeochemistry 29:199-222.

Eberhardt, L.L, and J.M. Thomas. 1991. Designing environmental field studies. Ecological Monographs 61:53-73.

Ellis, J.H. 1938. The Soils of Manitoba. Manitoba Economic Survey Board, Winnipeg, MB, Canada.

Ellis, J.G., D.F. Acton, and H.C. Moss. 1970. The soils of the Rosetown map area (720). Saskatchewan. Publication 202. Saskatchewan Institute of Pedology, University of Saskatchewan, Saskatoon, SK, Canada.

Eneboe, E.J., B.F. Sowell, R.K. Heitschmidt, M.G. Karl, and M.R. Haferkamp. 2002. Drought and grazing. IV. Blue grama and western wheatgrass. Journal of Range Management 55:73-79.

Environment Canada. 2005a. http://www.climate.weatheroffice.ec.gc.ca/advanceSearch/searchHistoricDataStations _e.html; accessed on 1 June 2005.

Environment Canada. 2005b. http://www.pnr-rpn.ec.gc.ca /info/news/cc00s61.en.html; accessed on 20 March 2005.

Epstein, H.E., I.C. Burke, A.R. Mosier, and G.L. Hutchinson. 1998. Plant functional type effects on trace gas fluxes in the shortgrass steppe. Biogeochemistry 42:145-168.

Essery, R., and J. Pomeroy. 2004. Vegetation and topographic control of wind-blown snow distributions in disturbed and aggregated simulations for an Arctic tundra basin. Journal of Hydrometeorology 5:735-744.

Facelli, J.M., and Pickett, S.T.A. 1991. Plant litter–its dynamics and effects on plant community structure. Botanical Review 57:1- 32.

Farrell, R.E., E. de Jong, and J.A. Elliott. 2002. Gas Sampling and Analysis. Pages 1076-1111 *in* J. Dane and C. Topp, editors. Methods of soil analysis. Part 4. Physical methods. Soil Science Society of America, Madison, WI, USA.

Firestone, M.K. 1982. Biological denitrification. Pages 289-326 *in* F.J. Stevenson, editor. Nitrogen in agricultural soils. American Society of Agronomy. Madison, WI, USA.

Fitzsimmons, M.J., D.J. Pennock, and J. Thorpe. 2004. Effects of deforestation on ecosystem carbon densities in central Saskatchewan, Canada. Forest Ecology and Management 188:349-361.

Flanagan, L.B., L.A. Wever, and P.J. Carlson. 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. Global Change Biology 8:599-615.

Frank, A.B., and W.A. Dugas. 2001. Carbon dioxide fluxes over a northern, semiarid, mixed-grass prairie. Agricultural and Forest Meteorology 108:317-326.

Frank, A.B., and L. Hofmann. 1989. Relationship among grazing management, growing degree days, and morphological development for native grasses on the Northern Great Plains. Journal of Range Management 42:199-202.

Frank, A.B., M.A. Liebig, and J.D. Hanson. 2002. Soil carbon dioxide fluxes in northern semiarid grasslands. Soil Biology and Biochemistry 34:1235-1241.

Frank, A.B., D.L. Tanaka, L. Hofmann, and R.F. Follett. 1995. Soil carbon and nitrogen of Northern Great Plains grasslands as influenced by long-term grazing. Journal of Range Management 48:470-474.

Franzluebbers, A.J., and J.A. Stuedemann. 2003. Bermudagrass management in the Southern Piedmont, USA. III. Particulate and biologically active soil carbon. Soil Science Society of America Journal 67:132-138.

Gardner, W.H. 1982. Water content. Pages 493-544 *in* A.L. Page, R.H. Miller and D.R. Keeney, editors. Methods of soil analysis. Part 2. Chemical and microbiological properties, 2nd edition. American Society of Agronomy, Inc., Madison, WI, USA.

Gillen R.L., and P.L. Sims. 2004. Stocking rate, precipitation, and herbage production on sand sagebrush-grassland. Journal of Range Management 57:148-152.

Glatzel, S., and K. Stahr. 2001. Methane and nitrous oxide exchange in differently fertilised grassland in southern Germany. Plant and Soil 231:21-35.

Goodison, B.E., H.L. Ferguson, and G.A. McKay. 1981. Measurement and data analysis. Pages 191-274 *in* D.M. Gray and D.H. Male, editors. Handbook of snow principles, processes, management and use. Pergamon Press, Toronto, ON, Canada.

Goossens, A., A. de Visscher, P. Boeckx, and O. van Cleemput. 2001. Two-year field study on the emission of N_2O from coarse and middle-textured Belgian soils with different land use. Nutrient Cycling in Agroecosystems 60:23-34.

Gravenor, C.P., and W.O. Kupsch. 1958. Ice-disintegration features in western Canada. Journal of Geology 67:48-64.

Groffman, P.M., R. Brumme, K. Butterbach-Bahl, K.E. Dobbie, A.R. Mosier, D. Ojima, H. Papen, W.J. Parton, K.A. Smith, and C. Wagner-Riddle. 2000. Evaluating annual nitrous oxide fluxes at the ecosystem scale. Global Biogeochemical Cycles 14:1061-1070.

Groffman, P.M., and J.M. Tiedje. 1989. Denitrification in north temperate forest soils: spatial and temporal patterns at the landscape and seasonal scales. Soil Biology and Biochemistry 21:613-620.

Groffman, P., and J.M. Tiedje. 1991. Relationships between denitrification, CO_2 production and air-filled porosity in soils of different texture and drainage. Soil Biology and Biochemistry 23:229-302.

Groffman, P.M., and C.L. Turner. 1995. Plant productivity and nitrogen gas fluxes in a tallgrass prairie landscape. Landscape Ecology 10:255-266.

Grubb M., C. Vrolijk, and D. Brack. 1999. The Kyoto Protocol: a guide and assessment. Royal Institute of International Affairs and Earthscan Publications Limited, London, UK.

Haferkamp, M.R., and M.G. Karl. 1999. Clipping effects on growth dynamics of Japanese brome. Journal Range Management 52:339-345.

Hammermeister, A.M., D. Gauthier, and K. McGovern. 2001. Saskatchewan's native prairie: statistics of a vanishing ecosystem and dwindling resource. Native Plant Society of Saskatchewan Inc., Saskatoon, SK, Canada.

Hanson, P.J., N.T. Edwards, C.T. Garten, and J.A. Andrews. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48:115-146.

Hayashi, M., G. van der Kamp, and D.L. Rudolph. 1998. Water and solute transfer between a prairie wetland and adjacent uplands, 1. Water balance. Journal of Hydrology 207:42-55.

Hooper, D.U., and P.M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. Science 277:1302-1305.

Hopkins, H.H. 1954. Effects of mulch upon certain factors of the grassland environment. Journal of Range Management 7:255-258.

Howden, S.M., D.H. White, G.M. McKeon, J.C. Scanlan, and J.O. Carter. 1994. Methods for exploring management options to reduce greenhouse gas emissions from tropical grazing systems. Climate Change 27:49-70.

Hulbert, L.C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. Ecology 50:874-877.

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

Hutchinson, G.L., and G.P. Livingston. 2001. Vents and seals in non-steady-state chambers used for measuring gas exchange between soil and the atmosphere. European Journal of Soil Science 52:675-682.

Hutchinson, G.L., and A.R. Mosier. 1981. Improved soil cover method for field measurement of nitrous oxide fluxes. Soil Science Society of America Journal 45:311-316.

Hütsch, B.W. 2001. Methane oxidation in non-flooded soils as affected by crop production. European Journal of Agronomy 14:237-260.

Integrated Taxonomic Information System. 2005. http://www.itis.usda.gov/index.html; accessed on 11 June 2005.

International Atomic Energy Agency. 1992. Manual on measurement of methane and nitrous oxide emissions from agriculture. IAEA, Vienna, Austria.

Intergovernmental Panel on Climate Change. 2001. Climate change 2001: the scientific basis. Contribution of Working Group 1 to the third assessment report of the

Intergovernmental Panel on Climate Change. J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell and C.A. Johnson, editors. Cambridge University Press, Cambridge, UK.

Izaurralde, R.C., R.L. Lemke, T.W. Goddard, B. McConkey, and Z. Zhang. 2004. Nitrous oxide emissions from agricultural toposequences in Alberta and Saskatchewan. Soil Science Society of America Journal 68:1285-1294.

Jain, A.K., and K.A.S. Hayhoe. 2003. Global air pollution problems. Pages 339-375 *in* C.N. Hewitt and A.V. Jackson, editors. Handbook of atmospheric science: principles and applications. Blackwell Publishing, Malden, MA, USA.

Jameson, Donald A. 1963. Responses of individual plants to harvesting. The Botanical Review 29:532-594.

Johnston, A., J.F. Dormaar, and S. Smoliak. 1971. Long-term grazing effects on fescue grassland soils. Journal of Range Management 24:185-188.

Kantrud, H.A., J.B. Millar, and A.G. van der Valk. 1989. Vegetation of wetlands of the prairie pothole region. Pages 132-187 *in* A. van der Valk, editor. Northern prairie wetlands. Iowa State University Press, Ames, IA, USA.

Keeney, D.R., and D.W. Nelson. 1982. Nitrogen-inorganic form. Pages 643-698 *in* A.L. Page, R.H. Miller and D.R. Keeney, editors. Methods of soil analysis. Part 2. Chemical and microbiological properties, 2nd edition. American Society of Agronomy, Inc. and Soil Science Society of Agronomy, Inc., Madison, WI, USA.

Knapp, A.K., and T.R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. BioScience 36:662-668.

Köchy, M., and S.D. Wilson. 2001. Nitrogen deposition and forest expansion in the Northern Great Plains. Journal of Ecology 89:807-817.

Köchy, M., and S.D. Wilson. 2004. Semiarid grassland responses to short-term variation in water availability. Plant Ecology 174:197-203.

Kormondy, E.J. 1996. Minimums, tolerances, and the medium. Pages 19-30 *in* S.L. Snavely, editor. Concepts of ecology, 4th edition. Prentice-Hall, Inc. Upper Saddle River, NJ, USA.

Koschorreck, M., and R. Conrad. 1993. Oxidation of atmospheric methane in soil: measurements in the field, in soil cores and in soil samples. Global Biogeochemical Cycles 7:109-121.

Kowalenko, B.L, and J.T. Romo. 1998. Defoliation and cold-hardiness of northern wheatgrass. Journal of Range Management 51:63-68.

Kowalenko, B.L, and J.T. Romo. 1998. Regrowth and rest requirements of northern wheatgrass following defoliation. Journal of Range Management 51:73-78.

Ladd, J.N., R.C. Foster, and J.O. Skjemstad. 1993. Soil structure: carbon and nitrogen metabolism. Geoderma 56:401-434.

Larson, F., and W. Whitman. 1942. A comparison of used and unused grassland mesas in the badlands of South Dakota. Ecology 23:438-445.

Lecain, D.R., J.A. Morgan, G.E. Schuman, J.D. Reeder, and R.H. Hart. 2000. Carbon exchange rates in grazed and ungrazed pastures of Wyoming. Journal of Range Management 53:199-206.

Lee, J.J., and R. Dodson. 1996. Potential carbon sequestration by afforestation of pasture in the south-central United States. Agronomy Journal 88:381-384.

Lemke, R.L., R.C. Izaurralde, S.S. Mahli, M.A. Arshad, and M. Nyborg. 1998. Nitrous oxide emissions from agricultural soils of the Boreal and Parkland regions of Alberta. Soil Science Society of America Journal 62:1096-1102.

Lemke, R.L., R.C. Izaurralde, M. Nyborg, and E.D. Solberg. 1999. Tillage and N source influence soil-emitted nitrous oxide in the Alberta Parkland region. Canadian Journal of Soil Science 79:15-24.

Lentz, R.D., R.H. Dowdy, and R.H. Rust. 1995. Measuring wind and low-relief topographic effects on rainfall distribution. Applied Engineering in Agriculture 11:241-248.

Lessard, R., P. Rochette, E.G. Gregorich, R.L. Desjardios, and E. Pattey. 1997. CH_4 fluxes from soil amended with dairy cattle manure and ammonium nitrate. Canadian Journal of Soil Science 77:179-186.

Lieffers, V.J., and P.A. Larkin-Lieffers. 1987. Slope, aspect, and slope position as factors controlling grassland communities in the coulees of the Oldman River, Alberta. Canadian Journal of Botany 65:1371-1378.

Looman, J. 1969. The Fescue Grasslands of western Canada. Vegetatio 19:128-145.

Mancinelli, R.L. 1995. The regulation of methane oxidation in soil. Annual Review Microbiology 49:581-605.

Mann, M.E., and R.S. Bradley. 1999. Northern Hemisphere temperatures during the past millennium: inferences, uncertainties, and limitations. Geophysical Research Letters 26:759-762.

McCulley, R.L., I.C. Burke, J.A. Nelson, W.K. Lauenroth, A.K. Knapp, and E.F. Kelly. 2005. Regional patterns in carbon cycling across the Great Plains of North America. Ecosystems 8:106-121.

McCune, B. and J.B. Grace. 2002. Analysis of ecological communities. MJM Software, Gleneden Beach, OR, USA.

McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13:603-606.

McGinn, S.M., and A. Shepherd. 2003. Impact of climate change scenarios on the agroclimate of the Canadian prairies. Canadian Journal of Soil Science 83:623-630.

Metting, Jr., F.B. 1993. Structure and physiological ecology of soil microbial communities. Pages 3-26 *in* F.B. Metting, Jr., editor. Soil microbial ecology. Marcel Dekker, Inc., New York, NY, USA.

Miles, J. 1985. The pedogenic effects of different species and vegetation types and the implications of succession. Journal of Soil Science 36:571-584.

Miles, J. 1987. Soil variation caused by plants: a mechanism of floristic change in grassland? Pages 37-49 *in* J. van Andel, J.P. Bakker and R.W. Snaydon, editors. Disturbance in grasslands. Causes, effects and processes. Kluwer Academic Publishers, Hingham, MA, USA.

Miller, T.L. 1991. Biogenic sources of methane. Pages 175-199 *in* J.E. Rogers and W.B. Whitman, editors. Microbial production and consumption of greenhouse gases: methane, nitrogen oxides, and halomethanes. American Society for Microbiology, Washington, DC, USA.

Mitchell, E.A.D., D. Gilbert, A. Buttler, C. Amblard, P. Grosvernier, and J.-M. Gobat. 2003. Structure of microbial communities in *Sphagnum* peatlands and effect of atmospheric carbon dioxide enrichment. Microbial Ecology 46:187-199.

Mitchell, J. and H.C. Moss. 1948. The soils of the Canadian section of the Great Plains. Soil Science Society of America Proceedings 13:431-437.

Mitchell, J., H.C. Moss, J.S Clayton, and F.H. Edmunds. 1944. Soil survey of southern Saskatchewan from township 1 to 48 inclusive. Soil Survey Report No. 12. University of Saskatchewan, Saskatoon, SK, Canada.

Mosier, A.R., J.M. Duxbury, J.R. Freney, O. Heinemeyer, and K. Minami. 1998a. Assessing and mitigating N_2O emissions from agricultural soils. Climatic Change 40:7-38.

Mosier, A.R., J.M. Duxbury, J.R. Freney, O. Heinemeyer, K. Minami, and D.E. Johnson. 1998b. Mitigating agricultural emissions of methane. Climatic Change 40:39-80.

Mosier, A.R., L.K. Klemedtsson, R.A. Sommerfeld, and R.C. Musselman. 1993. Methane and nitrous oxide flux in a Wyoming subalpine meadow. Global Biogeochemical Cycles 7:771-784.

Mosier, A.R., C. Kroeze, C. Nevison, O. Oenema, S. Seitzinger, and O. van Cleemput. 1998c. Closing the global N_2O budget: nitrous oxide emissions though the agricultural nitrogen cycle. Nutrient Cycling in Agroecosystems 52:225-248.

Mosier, A.R., W.J. Parton, D.W. Valentine, D.S. Ojima, D.S Schimel, and J.A. Delgado. 1996. CH_4 and N_2O fluxes in the Colorado shortgrass steppe 1. Impact of landscape and nitrogen addition. Global Biogeochemical Cycles 10:387-399.

Mosier, A.R., W.J. Parton, D.W. Valentine, D.S. Ojima, D.S Schimel, and O. Heinemeyer. 1997. CH_4 and N_2O fluxes in the Colorado shortgrass steppe 2. Long-term impact of land use change. Global Biogeochemical Cycles 11:29-42.

Mosier, A.R., D. Schimel, D. Valentine, K. Bronson, and W.J. Parton. 1991. Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands. Nature 350:330-332.

Müller, C., M. Martin, R.J. Stevens, R.J. Laughlin, C. Kammann, J.C.G. Ottow, and H.-J. Jäger. 2002. Processes leading to N_2O emissions in grassland soil during freezing and thawing. Soil Biology and Biochemistry 34:1325-1331.

Müller, C., and R.R. Sherlock. 2004. Nitrous oxide emissions from temperate grassland ecosystems in the Northern and Southern Hemispheres. Global Biogeochemical Cycles 18: Article Number GB1045, DOI:10.1029/2003GB002175.

Müller, C., R.J. Stevens, R.J. Laughlin, and H.-J. Jäger. 2004. Microbial processes and the site of N_2O production in a temperate grassland soil. Soil Biology and Biochemistry 36:453-461.

Mummey, D.L., J.L. Smith, and G. Bluhm. 1998. Assessment of alternative soil management practices on N_2O emissions from US agriculture. Agriculture Ecosystems and Environment 70:79-87.

Mummey, D.L., J.L. Smith, and H. Bolton, Jr. 1994. Nitrous oxide flux from a shrub-steppe ecosystem: source and regulation. Soil, Biology and Biochemistry 26:279-286.

Naeth, M.A., A.W. Bailey, D.S. Chanasyk, and D.J. Pluth. 1991. Water holding capacity of litter and soil organic matter in Mixed Prairie and Fescue Grassland ecosystems of Alberta. Journal of Range Management 44:13-17.

Naeth, M.A., A.W. Bailey, D.J. Pluth, D.S. Chanasyk, and R.T. Hardin. 1991. Grazing impacts on litter and soil organic matter in Mixed Prairie and Fescue Grassland ecosystems of Alberta. Journal of Range Management 44:7-12.

Newbauer, J.J. III, L.M. White, R.M. Moy, and D.A. Perry. 1980. Effects of increased rainfall on native forage production in eastern Montana. Journal of Range Management 33:246-250.

Norman, J.M., C.J. Kucharik, S.T. Gower, D.D. Baldocchi, P.M. Crill, M.B. Rayment, K. Savage, and R.G. Striegl. 1997. A comparison of six methods for measuring soil-surface carbon dioxide fluxes. Journal of Geophysical Research 102:28771-28777.

Nyborg, M., J.W. Laidlaw, E.D. Solberg, and S.S Malhi. 1997. Denitrification and nitrous oxide emissions from a Black Chernozemic soil during spring thaw in Alberta. Canadian Journal of Soil Science 77:153-160.

Odu, C.T.I., and K.B. Adeoye. 1970. Heterotrophic nitrification in soils – preliminary investigation. Soil Biology and Biogeochemistry 2:41-45.

Oenema, O., G. Gebauer, M. Rodriguez, A. Sapek, S.C. Jarvis, W.J. Corré, and S. Yamulki. 1998. Controlling nitrous oxide emissions from grassland livestock production systems. Nutrient Cycling in Agroecosystems 52:141-149.

Oenema, O., G.L. Velthof, S. Yamulki, and S.C. Jarvis. 1997. Nitrous oxide emissions from grazed grassland. Soil Use and Management 13:288-295.

Olsen, K., M. Wellisch, P. Boileau, D. Blain, C. Ha, L. Henderson, C. Liang, J. McCarthy, and S. McKibbon. 2003. Canada's greenhouse gas inventory. 1990-2001. Environment Canada, Ottawa, ON, Canada.

Pählsson, L. 1974. Relationship of soil, microclimate, and vegetation on a sandy hill. Oikos 25:21-34.

Palmer, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74:2215-2230.

Paltridge, G.W., and C.M.R. Platt. 1976. Radiative processes in meteorology and climatology. Elsevier Scientific Publishing Company, New York, NY, USA.

Papen, H., M. Daum, R. Steinkamp, and K. Butterbach-Bahl. 2001. N_2O and CH_4-fluxes from soils of a N-limited and N-fertilized spruce forest ecosystem of the temperate zone. Journal of Applied Botany-Angewandte Botanik 75:159-163.

Parton, W.J., J.W.B. Stewart, and C.V. Cole. 1988. Dynamics of C, N, P and S in grassland soils: a model. Biogeochemistry 5:109-131.

Paul, E.A., and F.E. Clark. 1996. Soil microbiology and biochemistry, 2nd edition. Academic Press, Toronto, ON, Canada.

Pennock, D.J. 2003. Terrain attributes, landform segmentation, and soil redistribution. Soil and Tillage Research 69:15-26.

Pennock, D.J. 2004. Designing field studies in soil science. Canadian Journal of Soil Science 84:1-10.

Pennock, D.J., D.W. Anderson, and E. de Jong. 1994. Distribution of cesium-137 in uncultivated black chernozemic landscapes. Canadian Journal of Soil Science 74:115-117.

Pennock, D.J., R.E. Farrell, R. Desjardins, E. Pattey, and J.I. MacPherson. 2005. Upscaling chamber-based measurements of N_2O emissions at snowmelt. Canadian Journal of Soil Science 85:113-125.

Pennock, D.J., C. van Kessel, R.E. Farrell, and R.A Sutherland. 1992. Landscape-scale variations in denitrification. Soil Science Society of America Journal 46:770-

776.

Pennock, D.J., B.J. Zebarth, and E. de Jong. 1987. Landform classification and soil distribution in hummocky terrain, Saskatchewan, Canada. Geoderma 40:297-315.

Peterson, R.G., and L.D. Calvin. 1965. Sampling. Pages 54-72 *in* C.A. Black, D.D. Evans, L.E. Ensminger, J.L. White, F.E. Clark and R.C. Dinauer, editors. Methods of soil analysis. Part 1. Physical and mineralogical properties including statistics of measurements and sampling. American Society of Agronomy, Inc., Madison, WI, USA.

Petit, J.R., J. Jouzel, D. Raynaud, N.I. Barkov, J.-M. Barnola, I. Basile, M. Bender, J. Chappellaz, M. Davis, G. Delayque, M. Delmotte, V.M. Kotlyakov, M. Legrand, V.Y. Lipenkov, C. Lorius, L. Pépin, C. Ritz, E. Saltzman, and M. Stievenard. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. Nature 399:429-436.

Pieper, R.D. 1978. Measurement techniques for herbaceous and shrubby vegetation. Department of Animal and Range Sciences. New Mexico State University, Las Cruces, NM, USA.

Pomeroy, J.W., and D.M. Gray. 1995. Snowcover accumulation, relocation and management. National Hydrology Research Institute Science Report No.7, Saskatoon, SK, Canada.

Pomeroy, J.W., D.M. Gray, and P.G. Landine. 1993. The prairie blowing snow model: characteristics, validation, operation. Journal of Hydrology 144:165-192.

Potter, C.S., E.A. Davidson, and L.V. Verchot. 1996. Estimation of global biogeochemical controls and seasonality in soil methane consumption. Chemosphere 32:2219-2246.

Prather, M.J., R. Derwent, D. Ehhalt, P. Fraser, E. Sanhueza, and X. Zhou. 1995. Other trace gases and atmospheric chemistry. Pages 73-126 *in* J.T. Houghton, L.G. Meira Filho, J. Bruce, Hoesung Lee, B.A. Callander, E. Haites, N. Harris and K. Maskell, editors. Climate Change 1994: radiative forcing of climate change and an evaluation of the Intergovernmental Panel on Climate Change IS92 emissions scenarios. Cambridge University Press, Cambridge, UK.

Prather, M., and D. Ehhalt. 2001. Atmospheric chemistry and greenhouse gases.

Pages 239-288 *in* J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell and C.A. Johnson, editors. Climate change 2001: the scientific basis. Contribution of Working Group 1 to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Prentice, I.C. 2001. The carbon cycle and atmospheric carbon dioxide. Pages 183-238 *in* J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell and C.A. Johnson, editors. Climate change 2001: the scientific basis. Contribution of Working Group 1 to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Qian, H., K. Klinka, R.H. Økland, P. Krestov, and G.J. Kayahara. 2003. Understorey vegetation in boreal *Picea mariana* and *Populus tremuloides* stands in British Columbia. Journal of Vegetation Science 14:173-184.

Radcliffe, J.E., and K.R. Lefever. 1981. Aspect influences on pasture microclimate at Coopers Creek, North-Canterbury. New Zealand Journal of Agricultural Research 24:55-66.

Raynaud, X., and P.W. Leadley. 2004. Soil characteristics play a key role in modeling nutrient competition in plant communities. Ecology 85:2200-2214.

Reay, D.S., D.B. Nedwell, N. McNamara, and P. Ineson. 2005. Effect of tree species on methane and ammonium oxidation capacity in forest soils. Soil Biology and Biochemistry 37:719-730.

Redmann, R. E. 1975. Production ecology of grassland plant communities in western North Dakota. Ecological Monographs 45:83-106.

Redmann, R.E. 1978. Soil respiration in a mixed grassland ecosystem. Canadian Journal of Soil Science 58:119-124.

Redmann, R.E., and Z.M. Abouguendia. 1978. Partitioning of respiration from soil, litter and plants in a mixed-grassland ecosystem. Oecologia 36:69-79.

Reeder, J.D., and G.E. Schuman. 2002. Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. Environmental Pollution 116:457-463.

Regina, K., H. Nykanen, J. Silvola, and P.J. Martikainen. 1996. Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity. Biogeochemistry 35:401-418.

Ripley, E.A., and B. Saugier. 1978. Biophysics of a natural grassland: evaporation. Journal of Applied Ecology 15:459-479.

Risser, P.F. 1987. Toward a holistic management perspective. BioScience 35:414-418.

Robinson, D., A. Hodge, and A. Fitter. 2003. Constraints on the form and function of root systems. Pages 1-31 *in* H. de Kroon and E.J.W. Visser, editors. Root ecology. Springer, Berlin, Germany.

Rogers, J.E., and W.B. Whitman. 1991. Introduction. Pages 1-6 *in* J.E. Rogers, and W.B. Whitman, editors. Microbial production and consumption of greenhouse gases: methane, nitrogen oxides and halomethanes. American Society for Microbiology, Washington, DC, USA.

Romo, J.T., and Y. Bai. 2005. Landscape level variation in recovery of production of native rangeland after grazing. Saskatchewan Agriculture Development Fund Project-20000272, Saskatoon, SK, Canada.

Ruddiman, W.F. 2001. Earth's climate: past and future. W.H. Freeman and Company, New York, NY, USA.

Ruz-Jerez, B.E., R.E. White, and P.R. Ball. 1994. Long-term measurement of denitrification in three contrasting pastures grazed by sheep. Soil Biology and Biochemistry 26:29-39.

Ryden, J.C. 1985. Denitrification losses from managed grassland. Pages 121-134 *in* H.L. Golterman, editor. Denitrification in the nitrogen cycle. Plenum Press, New York, NY, USA.

Ryden, J.C. 1986. Gaseous losses of N from grassland. Pages 59-73 *in* H.G. van Meer, J.C. Ryden and G.C. Ennik, editors. Nitrogen fluxes in intensive grassland systems. Martinus Nijhoff, Dordrecht, Germany.

Sanderson, M. 1948. The climates of Canada according to the new Thornthwaite classification. Scientific Agriculture 28:501-517.

Savage, K., T.R. Moore, and P.M. Crill. 1997. Methane and carbon dioxide exchanges between the atmosphere and northern boreal forest soils. Journal of Geophysical

Research-Atmospheres 102:29279-29288.

Schimel, D., D. Alves, I. Enting, M. Heimann, F. Joos, D. Raynaud, T. Wigley, M. Prather, R. Derwent, D. Ehhalt, P. Fraser, E. Sanhueza, X. Zhou, P. Jonas, R. Charlson, H. Rodhe, S. Sadasivan, K.P. Shine, Y. Fouquart, V. Ramaswamy, S. Solomon, J. Srinivasan, D. Albritton, I. Isaksen, M. Lal, and D. Wuebbles. 1996. Radiative forcing of climate change. Pages 65-132 *in* J.T. Houghton, L.G. Meira Filho, B.A. Callender, N. Harris, A. Kattenberg and K. Maskell, editors. Climate change 1995: the science of climate change. Contribution of Working Group 1 to the second assessment of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Schmidt, S.K., A.E. West, P.D. Brooks, L.K. Smith, C.H. Jaeger, M.C. Fisk, and E.A. Holland. 2001. Soil-atmosphere gas exchange. Pages 254-265 *in* W.D. Bowman and T.R. Seastedt, editors. Structure and function of an alpine ecosystem: Niwot Ridge, Colorado. Oxford University Press, Oxford, UK.

Schnell, S., and G.M. King. 1996. Responses of methanotrophic activity in soils and cultures to water stress. Applied and Environmental Microbiology 62:3203-3209.

Schuman, G.E., J.D Reeder, J.T Manley, R.H. Hart, and W.A. Manley. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecological Applications 9:65–71.

Shallcross, D.E., K. Wang, and C.H. Dimmer. 2003. Biogeochemical cycles and residence times. Pages 90-123 *in* C.N. Hewitt and A.V. Jackson, editors. Handbook of atmospheric science: principles and applications. Blackwell Publishing, Malden, MA, USA.

Sharon, D. 1980. The distribution of hydrologically effective rainfall incident on sloping ground. Journal of Hydrology 46:165-188.

Shelp, M.L., E.G. Beauchamp, and G.W. Thurtell. 2000. Nitrous oxide emissions from soil amended with glucose, alfalfa, or corn residues. Communications in Soil Science and Plant Analysis 31:877-892.

Sims, P.L., and R.T. Coupland. 1979. Producers. Pages 49-72 *in* R.T. Coupland, editor. Grassland ecosystems of the world: analysis of grasslands and their uses. Cambridge University Press, Cambridge, UK.

Skinner, W.R., and D.W. Gullett. 1993. Trends of daily maximum and minimum temperature in Canada during the past century. Climatological Bulletin 27:63-77.

Skinner, W.R., and J.A. Majorowicz. 1999. Regional climatic warming and associated twentieth century land-cover changes in north-western North America. Climate Research 12:39-52.

Smith, E.L., P.S. Johnson, G. Ruyle, F. Smeins, D. Loper, D. Whetsell, D. Child, P. Sims, R. Smith, L. Volland, M. Hemstrom, E. Bainter, A. Mendenhall, K. Wadman, D. Franzen, M. Suthers, J. Willoughby, N. Habich, T. Gaven, and J. Haley. 1995. New concepts for assessment of rangeland condition. Journal of Range Management 48:271-282.

Smith, K.A., and K.E. Dobbie. 2001. The impact of sampling frequency and sampling times on chamber-based measurements of N_2O emissions from fertilized soils. Global Change Biology 7:933-945.

Smith, J.L., J.J. Halvorson, and H. Bolton, Jr. 1994. Spatial relationships of soil microbial biomass and C and N mineralization in a semi-arid shrub-steppe ecosystem. Soil Biology and Biochemistry 26:1151-1159.

Smith, J.L., R.I. Papendick, D.F. Bezdicek, and J.M. Lynch. 1993. Soil organic matter dynamics and crop residue management. Pages 65-94 *in* F.B. Metting, Jr., editor. Soil microbial ecology: applications in agricultural and environmental management. Marcel Dekker, Inc., New York, NY, USA.

Smith, W.N., P. Rochette, C. Monreal, R.L. Desjardins, E. Pattey, and A. Jaques. 1997. The rate of carbon change in agricultural soils in Canada at the landscape level. Canadian Journal of Soil Science 77:219-229.

Soil Classification Working Group. 1998. The Canadian system of soil classification. 3rd edition. Publication 1646. Research Branch, Agriculture and Agri-Food Canada. Ottawa, ON, Canada.

Stein, V.B., and J.P.A. Hettiaratchi. 2001. Methane oxidation in three Alberta soilS: influence of soil parameters and methane flux rates. Environmental Technology 22:101-111.

Stewart, A.J.A., E.A. John, and M.J. Hutchings. 2000. The world is heterogeneous: ecological consequences of living in a patchy environment. Pages 1-8 *in* M.J.

Hutchings, E.A. John and A.J.A. Stewart, editors. The ecological consequences of environmental heterogeneity. Blackwell Science, Oxford, UK.

Stuth, J.W. 1991. Foraging behavior. Pages 65-84 *in* R.K. Heitschmidt and J.W. Stuth, editors. Grazing management: an ecological perspective. Timber Press, Inc., Portland, OR, USA.

Tate, C.M., and R.G. Striegl. 1993. Methane consumption and carbon dioxide emissions in tallgrass prairie: effects of biomass burning and conversion to agriculture. Global Biogeochemical Cycles 7:735-748.

Tatina, R. 1994. Ordination and description of prairie plant communities from the southern Missouri Coteau in South Dakota. Great Plains Research 4:147-162.

ter Braak, C.J.F. 1987. Ordination. Pages 91-173 *in* R.H.G. Jongman, C.J.F. ter Braak and O.F. R. van Tongeren, editors. Data analysis in community and landscape ecology. Pudoc, Wageingen, the Netherlands.

ter Braak, C.J.F., and P. Šmilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, NY, USA.

Thurow, T.L. 1991. Hydrology and erosion. Pages 141-159 *in* R.K. Heitschmidt, and J.W. Stuth, editors. Grazing management: an ecological perspective. Timber Press, Inc., Portland, OR, USA.

Tiedje, J.M. 1988. Ecology of denitrification and dissimilatory nitrate reduction to ammonium. Pages 179-244 *in* A.J.B. Zehnder, editor. Environmental microbiology of anaerobes. John Wiley and Sons, New York, NY, USA.

Tiessen, H., C. Feller, E.V.S.B. Sampaio, and P. Garin. 1998. Carbon sequestration and turnover in semiarid savannas and dry forest. Climatic Change 40:105-117.

Topp, E., and E. Pattey. 1997. Soils as sources and sinks for atmospheric methane. Canadian Journal of Soil Science 77:167-178.

Torn, M.S., and J. Harte. 1996. Methane consumption by montane soils: implications for positive and negative feedback with climatic change. Biogeochemistry 32:53-67.

Trenberth, K.E., J.T. Houghton, and L.G. Meira Filho. 1996. The climate system: an overview. Pages 51-64 *in* J.T. Houghton, L.G. Meira Filho, B.A. Callender, N. Harris, A. Kattenberg and K. Maskell, editors. Climate change 1995: the science of climate change. Contribution of Working Group 1 to the second assessment of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Turner, M.G., R.H. Gardner, R.V. O'Neill, and S.M. Pearson. 1994. Multiscale organization of landscape heterogeneity. Pages 73-79 *in* M.E. Jensen and P.S. Bourgeron, editors. Volume 2. Ecosystem management: principles and applications. USDA Forest Service General Technical Report PNAAW-GTR-318. Missoula, MT, USA.

Tyler, S.C. 1991. The global methane budget. Pages 7-38 *in* J.E. Rogers and W.B. Whitman, editors. Microbial production and consumption of greenhouse gases: methane, nitrogen oxides, and halomethanes. American Society for Microbiology, Washington, DC, USA.

Urban, D.L., R.V. O'Neill, and H.H. Shugart, Jr. 1987. Landscape ecology – A hierarchical perspective can help scientists understand spatial patterns. BioScience 37:119-127.

van Bochove, E., H.G. Jones, F. Pelletier, and D. Prévost. 1996. Emission of N_2O from agricultural soil under snow cover: a significant part of N budget. Hydrological Processes 10:1545-1549.

van der Kamp, G., M. Hayashi, and D. Gallen. 2003. Comparing the hydrology of grassed and cultivated catchments in the semi-arid Canadian prairies. Hydrological Processes 17:559-575.

van Kessel, C., D.J. Pennock, and R.E. Farrell. 1993. Seasonal variations in denitrification and nitrous oxide evolution at the landscape scale. Soil Science Society of America Journal 57:988-995.

Velthof, G.L., S.C. Jarvis, and O. Oenema. 1997. Spatial variability of nitrous oxide fluxes from grasslands: differences between soil types. Pages 173-179 *in* S.C. Jarvis and B.F. Pain, editors. Gaseous nitrogen emissions from grasslands. CAB International, New York, NY, USA.

Velthof, G.L., S.C. Jarvis, A. Stein, A.G. Allen, and O. Oenema. 1996a. Spatial variability of nitrous oxide fluxes in mown and grazed grasslands on a poorly drained clay soil. Soil Biology and Biochemistry 28:1215-1225.

Velthof, G.L., J.G. Koops, J.H. Duyzer, and O. Oenema. 1996b. Prediction of nitrous oxide fluxes from managed grassland on peat soil using a simple empirical model. Netherlands Journal of Agricultural Science 44:339-356.

Velthof, G.L., J.W. van Groenigen, G. Gebauer, S. Piertzak, S.C. Jarvis, M. Pinto, W. Corré, and O. Oenema. 2000. Temporal stability of spatial patterns of nitrous oxide fluxes from sloping grasslands. Journal of Environmental Quality 29:1397-1407.

Vermoesen, A., O. Van Cleemput, and G. Hofman. 1997. Contribution of urine patches to the emission of nitrous oxide. Pages 189-194 *in* S.C. Jarvis and B.F. Pain, editors. Gaseous nitrogen emissions from grasslands. CAB International, New York, NY, USA.

Wagner-Riddle, C., and G.W. Thurtell. 1998. Nitrous oxide emissions from agricultural fields during winter and spring thaw as affected by management practices. Nutrient Cycling in Agroecosystems 52:151-163.

Wagner-Riddle, C., G.W. Thurtell, G.K. Kidd, E.G. Beauchamp, and R. Sweetman. 1997. Estimates of nitrous oxide emissions from agricultural fields over 28 months. Canadian Journal of Soil Science 77:135-144.

Walker, B.H., and R.T. Coupland. 1967. An analysis of vegetation-environment relationships in Saskatchewan sloughs. Canadian Journal of Botany 46:509-522.

Wang, F.L., and J.R. Bettany. 1995. Methane emissions from a usually well-drained prairie soil after snowmelt and precipitation. Canadian Journal of Soil Science 75:239-241.

Wang, W.C., Y.L. Yung, A.A Lacis, T. Mo, and J.E. Hansen. 1976. Greenhouse effects due to man-made perturbations of trace gases. Science 194:685-690.

Warembourg, F.R., and E.A Paul. 1977. Seasonal transfers of assimilate ^{14}C in grassland: plant production and turnover, soil and plant respiration. Soil Biology and Biochemistry 9:295-301.

Wayne, R.P. 2003. Chemical evolution of the atmosphere. Pages 3-34 *in* C.N. Hewitt and A.V. Jackson, editors. Handbook of atmospheric science: principles and applications. Blackwell Science Ltd., Malden, MA, USA.

Weaver, J.E., and N.W. Rowland. 1952. Effects of excessive natural mulch on development, yield, and structure of native grassland. Botanical Gazette 114:1-19.

Webster, E.A., and D.W. Hopkins. 1996. Contributions from different microbial processes to N_2O emission from soil under different moisture regimes. Biology and Fertility of Soils 22:331-335.

Whitman, W.C. 1974. Influence of grazing on the microclimate of mixed grass prairie. Pages 207-218 *in* K.W. Kreitlow and R.H. Hart, editors. Plant morphogenesis as the basis for scientific management of range resources: proceedings of the workshop of the United States-Australia Rangelands Panel, Berkeley, CA, 29 March – 5 April 1971. USDA Miscellaneous Publication Number 1271, Berkeley, CA, USA.

Whysong, G.L., and Bailey, A.W. 1975. Production and nitrogen content of herbage in a silverberry (*Elaeagnus commutata*) community compared to adjacent grassland and forest communities. Canadian Journal of Plant Science 55:801-808.

Williams, G.D.V., and E.E. Wheaton. 1998. Estimating biomass and wind erosion impacts for several climatic scenarios: a Saskatchewan case study. Prairie Forum 23:49-66.

Willison, T.W., C.P. Webster, K.W.T Goulding, and D.S. Powlson. 1995. Methane oxidation in temperate soils: effects of land use and the chemical form of nitrogen fertilizer. Chemosphere 30:539-546.

Willms, W.D. 1995. Grazing management – A balancing act? Pages 39-42 *in* Z. Abouguendia, editor. Proceedings of the conference on total ranch management in the Northern Great Plains, Swift Current, SK. Grazing and Pasture Technology Program Saskatchewan Agriculture and Food, Swift Current, SK, Canada.

Willms, W.D., B.W. Adams, and J.F. Dormaar. 1996. Seasonal changes of herbage biomass on the Fescue Prairie. Journal of Range Management 49:100-104.

Willms, W.D., J.F. Dormaar, B.W. Adams, and H.E. Douwes. 2002. Response of the Mixed Prairie to protection from grazing. Journal of Range Management 55:210-216.

Willms, W.D., and P.G. Jefferson. 1993. Production characteristics of the Mixed Prairie: constraints and potential. Canadian Journal of Animal Science 73:765-778.

Willms, W.D., S.M. McGinn, and J.F. Dormaar. 1993. Influence of litter on herbage production in the Mixed Prairie. Journal of Range Management 46:320-324.

Willms, W.D., S. Smoliak, and A.W. Bailey. 1986. Herbage production following litter removal on Alberta native grasslands. Journal of Range Management 39:536-540.

Willms, W.D., S. Smoliak, and J.F. Dormaar. 1990. Vegetation response to time-controlled grazing on Mixed and Fescue Prairie. Journal of Range Management 43:513-517.

Woo, M.-K., and R.D. Rowsell. 1993. Hydrology of a prairie slough. Journal of Hydrology 146:175-207.

Wrage, N., G.L. Velthof, H.J. Laanbroek, and O. Oenema. 2004. Nitrous oxide production in grassland soils: assessing the contribution of nitrifier denitrification. Soil Biology and Biochemistry 36:229-236.

Wrage, N., G.L. Velthof, M.L. van Beusichem, and O. Oenema. 2001. Role of nitrifier denitrification in the production of nitrous oxide. Soil Biology and Biochemistry 33:1723-1732.

Wuebbles, D.J., and J. Edmonds. 1991. Primer on greenhouse gases. Lewis Publishers, Inc., Chelsea, MI, USA.

Yamulki, S., R.M. Harrison, K.W.T. Goulding, and C.P. Webster. 1997. N_2O, NO and NO_2 fluxes from a grassland: effect of soil pH. Soil Biology and Biochemistry 29:1199-1208.

Yamulki, S., S.C. Jarvis, and P. Owen. 1998. Nitrous oxide emissions from excreta applied in a stimulated grazing pattern. Soil Biology and Biochemistry 30:491

Zar. Jerrold H. 1984. Biostatistical analysis. 2nd edition. Prentice Hall, Inc., Englewood Cliffs, NJ, USA.