RELATIONSHIPS BETWEEN PLANT COMMUNITIES AND SOIL CARBON IN THE PRAIRIE ECOZONE OF SASKATCHEWAN

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ABSTRACT

Accumulation of CO_2 in the atmosphere has triggered research on topics related to causes, effects, and solutions to potential problems associated with global warming. The present research was conducted to determine if grassland plant communities can be managed to promote sequestration of carbon in the soil, potentially mitigating the effects of increasing atmospheric CO_2. The effects of shrub invasion or heavy livestock grazing on peak standing crop of phytomass, root mass and soil organic carbon content were therefore studied. These studies were complimented by a study of the decomposition rates of leaves and roots of snowberry and grasses. The effects of snowberry encroachment on peak standing crop of aboveground phytomass, and soil organic carbon content (SOC) were also studied. Total aboveground phytomass in the snowberry community was more than triple that of the ecotone and was 6-times greater than that of the grassland community. Similarly, the mass of large roots was greatest in the snowberry community (1.2 kg m^{-2}, SE= 0.19), intermediate in the ecotone (0.5 kg m^{-2}, SE= 0.08), and least in the grassland (0.1 kg m^{-2}, SE= 0.04). Conversely, the mass of fine and medium roots was not different ($P>0.05$) among the three communities, averaging 0.7 kg m^{-2} in all communities (SE= 0.03, 0.07, 0.49 in snowberry, ecotone and grassland, respectively). Greater aboveground phytomass did not correspond with greater SOC in the snowberry community. Soil organic carbon in the upper 50 cm averaged 8.3 (SE= 0.7), 7.9 (SE= 1.0), and 7.9 (SE= 0.7) kg m^{-2} in snowberry, ecotone, and grassland communities, respectively. Peak standing crop of aboveground phytomass averaged 157 g m^{-2} (SE= 27) and 488 g m^{-2} (SE= 48) in grazed and ungrazed grassland, respectively. Conversely, grazing had no affect on root mass. The mass of fine roots averaged 0.9 kg m^{-2} (SE= 0.04) and 0.8 kg m^{-2} (SE= 0.06) in grazed and ungrazed grassland, respectively, while that of medium roots averaged 0.6 kg m^{-2} (SE= 0.07) in both grazing treatments. Total SOC in the upper 50 cm of soil was not affected ($P>0.05$) by livestock grazing, averaging 5.5 kg m^{-2} (SE= 0.7) in grazed and 6.8 kg m^{-2} (SE= 0.9) in ungrazed grassland. Livestock grazing also had no effect ($P>0.05$) on SOC at the 0-3, 3-10, 10-20, 20-30, and 30-40 cm depths. The SOC in fine- and coarse-textured soils averaged 7.6 kg m^{-2} (SE= 0.8) and 5.1 kg m^{-2} (SE=0.7), respectively. Differences existed

between decomposition of roots and leaves for graminoids and snowberry. On a monthly basis decomposition was 0.6 to 0.8 % greater in leaves than roots. The decomposition of roots and leaves ranged from 2.2 to 5.0 % $month^{-1}$. Decay rate constants for leaves ranged from 0.45 yr^{-1} (SE= 0.03) to 0.71 yr^{-1} (SE= 0.02) while those of roots ranged from 0.34 yr^{-1} (SE= 0.03) to 0.47 yr^{-1} (SE= 0.04). The decomposition of roots and leaves did not correspond with macroclimatic or regional climate data nor with initial C:N content of the plant material. In summary, invasion of snowberry into grassland does not appear to conflict with goals related to maintenance of SOC in Mixed Prairie. Current grazing management regimes also appear to be consistent with goals related to maintenance of existing SOC. Soil texture had a greater effect on SOC than management of the plant community. Decomposition of leaves and roots appeared to be controlled by many interacting factors such as plant organ type, collection year, study year (climate) and physical and/or chemical characteristics of the site.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

APPENDICES

1.0 INTRODUCTION

The acknowledgement of accumulating CO_2 in the atmosphere and understanding of its likely anthropogenic causes has triggered widespread research on topics related to causes, effects, and solutions to potential problems of global warming. One potential mitigation measure for the increasing release of CO_2 is the counteraction of this release by increasing C sequestration in soils (Lal 2002). Agricultural soils are targeted for C sequestration because they are extensive, their soil organic carbon content is below historic levels, and the potential for sequestration is expected to be relatively great. Grassland used for livestock grazing is an example of agricultural land that is recognized as having potential to sequester C in soils (Follett et al. 2001).

This research is consistent with the goals of the Kyoto Protocol (Conference of the Parties 1997) which signified widespread recognition of the need to mitigate effects of increasing levels of atmospheric CO_2. The Kyoto Protocol generally emphasizes the need to reduce emissions of human-caused greenhouse gases; however, the potential for mitigating environmental effects of excess atmospheric CO_2 may also play a role in addressing global warming. A strategy for mitigating the effects of excess atmospheric CO_2 is to increase the carbon content of soil; this research was intended to provide information on sequestration of carbon. Specifically, this research was intended to answer questions about how prairie vegetation may be manipulated to sequester carbon in soil.

Grasslands may have the potential for carbon sequestration because they are the most extensive major natural vegetation formation at a global scale (Gould 1968). They are present on most continents and the climate, flora, fauna, growth form, and physiognomy are similar (Carpenter 1940). This global formation is comprised of steppes in Russia, velds in South Africa, pampas in South America, puszta in Hungary,

and prairies in North America (Carpenter 1940). Collectively, the historical area of grasslands was 3.2 billion ha, or 24% of the global land area (Shantz 1954).

Grasslands are an extensive vegetation formation and once occupied 50 million ha in Canada (Rowe 1972). However, the area of native grassland in Canada also declined over the past 50 years leaving 1.1, 6.6, 5.3, and 1.7 million ha in Manitoba, Saskatchewan, Alberta, and British Columbia, respectively (Horton 1994). Samson and Knopf (1994) estimated that the historic range of Mixed Prairie in Alberta and Saskatchewan has been reduced from 8.7 and 13.4 million ha to 3.4 and 2.5 million ha in each province, respectively. The U.S. Forest Service estimated that 125 million ha remained in 1980 (U.S. Forest Service 1980).

Despite the reduction of natural grassland, it is important to understand the functioning of the carbon cycle in these areas because grasslands contain 10 to 30% of the global soil organic carbon (SOC) (Eswaran et al. 1993). Batjes (1999) estimated that grassland/steppe, extensive grasslands, and savannas collectively contain 230 to 246 Pg C in the upper 1 m of soil. It is therefore hypothesized that small increases in the amount of carbon sequestered in soil will be great because of the extensiveness of grasslands (Follett 2001).

Input from plants and decomposition by microorganisms are the drivers of the carbon cycle of the grassland ecosystem. Livestock grazing is the predominant agricultural activity on grasslands and has the potential to alter the quantity and quality of carbon input to the system by affecting the species composition, structure and functioning of grassland ecosystems. More information on the potential effects of livestock grazing on functioning of the carbon cycle in grassland is therefore required to assess the ability of these lands to sequester carbon.

Plant species composition, structure, and functioning of grasslands is also changed when shrubs invade native grassland. The effects of livestock grazing and snowberry invasion have been studied in various ecosystems and regions over the past several decades. Previous studies on the effects of snowberry expansion was conducted in Desert Grasslands in the southern United States (Barth and Klemmedson

1978, Hibbard et al. 2001, Jackson et al. 2002). These studies may not directly apply to the Northern Great Plains of Canada, however, because species composition, soils and climate are different in these regions of North America. Similarly, several studies on the effects of grazing on SOC in grassland have been conducted in Mixed Prairie and Shortgrass Prairie in the central and southern Great Plains (Manley et al. 1995, Schuman et al. 1999, Reeder and Schuman 2002). The current research focuses on Mixed Prairie in the Northern Great Plains, which occurs in Saskatchewan, Alberta, and the Northern United States, and adds to the work already completed in this area (Johnston et al. 1971, Smoliak et al. 1972, Dormaar et al. 1984, Dormaar and Willms 1990, Dormaar et al. 1997). Studies of the effects of snowberry invasion and livestock grazing on soil organic carbon in grassland were supplemented with a study of decomposition rates of leaves and roots of grasses and snowberry.

Commitments by the Canadian Government to keep emissions of greenhouse gas within specific targets and the realization that information on soil carbon sequestration is lacking serve as the impetus for this research. The primary objective of this research was to determine how SOC is affected by land management practices that directly or indirectly alter the species composition and plant community structure in Mixed Prairie. It was hypothesized that livestock grazing and snowberry invasion alter the SOC content of grassland communities. This research has three main purposes:

i. To determine if existing vegetation in grazed and ungrazed grassland corresponds with SOC.
ii. To determine if SOC corresponds with plant community characteristics in snowberry, ecotone, and grassland communities.
iii. To determine if decomposition varies among leaves and roots of grasses and snowberry.

This research was therefore designed to determine if land management activities also affect SOC. This information is required because managing plant communities to increase SOC sequestration may help Canada meet its goals as outlined in the Kyoto Protocol (Conference of the Parties 1997).

2.0 LITERATURE REVIEW

The terminology describing land that is predominantly used for grazing domestic livestock is inconsistent throughout the literature. Several terms are interchangeably used to describe vegetation that is comprised of perennial, herbaceous plants that may be native or introduced. Grazing land, pasture land, prairie, grassland, and rangeland are terms that are frequently used. Grazing land may be considered a collective term that refers to any land that is predominantly used for grazing by domestic livestock while pasture land is grazing land that is comprised of introduced or domesticated native forage species (USDA 1997). Grassland may therefore be defined as land on which the vegetation is dominated by grasses, grass-like plants, and/or forbs (USDA 1997). Similarly, grassland is land where the historic climax plant community is predominantly grasses, grass-like plants, forbs, or shrubs (USDA 1997). This definition may therefore apply to natural grasslands, savannas, shrublands, deserts, and a variety of other plant associations (USDA 1997). Grassland is the term used throughout this discussion and should be interpreted to include land that is naturally dominated by native grasses and was not disturbed by cultivation before completing this study.

The descriptions for the types, or associations, of grasslands can also be ambiguous. Historically, six grassland associations were recognized in North America including Mixed Prairie, Shortgrass Prairie, Tallgrass Prairie, Desert Grasslands, Palouse Prairie, and Annual Grasslands. More recently, however, a variety of classifications were developed for these associations. Canada has a hierarchical, ecological classification system comprised of Ecozones, Ecoprovinces, Ecoregions, and Ecodistricts (Marshall and Schut 1999). The land units that pertain to the grassland described herein are classified as Mixed Prairie (Coupland 1950, Coupland 1961). The

boundaries of this association are similar to the boundaries of the Prairie Ecozone in Saskatchewan (Acton et al. 1998). The area where the present studies were completed is classified as the Moist Mixed Grassland Ecoregion within the Prairie Ecozone (Acton et al. 1998).

The terms heavily grazed and ungrazed grasslands are used in this document to describe the past use of grasslands by domestic livestock. For this research, ungrazed grassland refers to grassland that has not been grazed by livestock for more than 10 consecutive years. Conversely, heavily grazed grassland is defined as land where grazing removed most of the plant material annually, and the frequency of grazing is shorter than the time needed by plants to recover from grazing. Heavily grazed grasslands are therefore dominated by plant species that avoid or tolerate grazing while ungrazed grasslands are comprised of species that decrease in abundance as grazing intensity and frequency increases (c.f. Abouguendia 1990).

2.1 Estimates of Global and local carbon sequestration in the soil

Terrestrial ecosystems, oceans, atmosphere, and geological formations that contain fossil and mineral carbon are the four principle pools of global C (Schlesinger 1995). Carbon exchange among these pools is balanced because the amount of carbon fixed through photosynthesis is offset by the release of carbon through plant respiration and decomposition of organic residues (Schlesinger 1995). Known anthropogenic sources of carbon in this global exchange system include CO_2 released during fossil fuel combustion (5.4 Pg yr^{-1}) and deforestation (1.6 Pg C yr^{-1}) (Schlesinger 1995). Oceans and the atmosphere are known sinks for carbon from these anthropogenic sources and approximately 3.2 and 2.0 Pg C yr^{-1} , respectively, are sequestered (Schlesinger 1995). The remaining 1.8 Pg C yr^{-1} is largely unaccounted for and is believed to be absorbed by terrestrial ecosystems (Schlesinger 1995).

The missing C is assumed to be deposited in terrestrial ecosystems, but it has not been located or directly measured with certainty (Scholes et al. 1999). The global

distribution patterns (spatial and temporal) of atmospheric CO_2 and isotopic composition of atmospheric CO_2 provide evidence that suggests the missing C is in the terrestrial pool (Enting and Mansbridge 1991, Ciais et al. 1995). In addition, there is evidence that it is located in the northern hemisphere (Keeling et al. 1996).

Factors that could suggest missing C is in terrestrial vegetation include changes in the growth rate and extent of temperate forests, CO_2 fertilization effects on vegetation, and nitrogen fertilization (Scholes et al. 1999). However, the potential error associated with estimates of other pools in the global cycle is great enough to account for the missing C (Scholes et al. 1999).

The role of soil in the carbon balance of terrestrial ecosystems is not clear and a greater understanding of processes involved in carbon emission from soil and sequestration in soil are required (Schlesinger 1995). Soil is a key component of understanding the terrestrial C balance because it is the largest near-surface reservoir of C (Post et al. 1982). The global soil carbon reservoir is estimated to be 1500 Gt (1 Gt = 10^{12} kg of C) in the upper 1 m (Amundson 2001) with an additional 900 Gt in the 1-2 m depth (Kirschbaum 2000). The significance of soil carbon sequestration is demonstrated by estimates that indicate global soil carbon exceeds the total amount in vegetation and the atmosphere (Schlesinger 1995, Swift 2001). Other estimates further indicate that a 10% increase in organic soil carbon is equivalent to all of the anthropogenic CO_2 emitted over 30 years (Kirschbaum 2000). Some scientists, however, hypothesized that additional storage capacity of soils may not be significant (Schlesinger and Andrews 2000, Schimel et al. 2001, Gill et al. 2002) and others predicted that soil carbon sequestration may be offset by a warmer environment, greater decomposition of organic matter, and greater release of CO_2 back into the atmosphere (Kirschbaum 2000).

Soil organic matter is defined as recognizable plant and animal material that does not contain its original structural organization (Amundson 2001) or as the non-living component of organic matter in the soil (Trumbore 1997). Soil organic matter contributes to and regulates several important ecological functions including

sequestration of atmospheric CO_2 (Batjes 1998, Swift 2001), regulation of soil fertility through nutrient cycling and development and maintenance of soil structure (Swift 2001). In prairie ecosystems, for example, many biological processes are related to decomposition of organic residues that are predominantly derived from roots (Dormaar et al. 1984).

The plant-based source of SOM dictates that it consists largely of humic substances, lignin-derived substances, carbohydrates, and other organic compounds (Swift 2001). SOC can be affected by plant species composition, the amount of phytomass produced, anthropogenic perturbations, and environmental factors because it is comprised of plant-derived components. It is also hypothesized that factors such as grazing management, primary production, plant species composition and conversion of native grassland to snowberry-dominated communities will impact the form and amount of SOC.

2.2 Soil carbon quantities and properties and controlling factors

Carbon occurs in organic and inorganic forms in soils. Inorganic carbon in soil is in the form of calcium carbonate ($CaCO_3$) and about 1700 Pg of this form are present in the global soil pool (Post et al. 1982). Remaining soil carbon is organic in nature and is derived primarily from plants and soil organisms. The organic carbon compounds in soil may also be divided into five general categories (Beauchamp et al. 1989). These categories consist of cellulose (15 to 60 % of dry mass), hemicellulose (10 to 30 % of dry mass), lignin (5 to 30 % of dry mass), water soluble constituents (simple sugars, and acids), and ether and alcohol-soluble constituents (fats, oils, waxes and resins). Plants are therefore a primary source of SOC and CO_2 fixed during photosynthesis is transferred to soil through leaf litter, roots, and root exudates (van Veen et al. 1991, Trumbore 1997).

Based on information about sources and forms of SOC, it is likely that alteration of the composition, productivity, distribution, or health of plants in a

grassland community will affect the quality and quantity of carbon transferred to soil. For example, it is possible that the shift in species composition from a native graminoid-dominated sward to a snowberry-dominated community will affect the quality and/or quantity of carbon transferred to the soil and it may alter the carbon budget and SOC. Similarly, changes to species composition and structure of swards in response to grazing may alter the form, quality, and/or quantity of carbon transferred to soil and therefore the amount of SOC.

On a global scale, the soil carbon budget represents a steady state between the input of plant debris from net primary production and losses from respiration. About 55 Pg C yr^{-1} are input by vegetation and about 68 Pg C yr^{-1} are lost through herbivores and fire (Schlesinger 1995). Gross respiration is greater than input of material in this budget due to the portion of plant respiration that occurs below ground, but overall there is a net accumulation of about 0.4 Pg C yr^{-1} (Schlesinger 1990).

Translocation of carbon from aboveground plant parts and roots to soil represents the primary inputs of organic matter in soil and it is generally accepted that particulate organic matter is derived from plants (Six et al. 2001). However, primary production and the amount of SOC are not linearly correlated (van Veen et al. 1991). Sources of SOC are variable and many processes affect transfer and storage and different fractions of the SOC pool decompose at different rates. For example, simple sugars and proteins decompose within hours or days whereas lignins, cutans, and humic substance take much longer (Swift 2001). SOC is therefore grouped into active, intermediate (or slow), and passive carbon pools depending on residence time or turnover rate (Seastedt et al. 1994, Trumbore 1997).

Residence time of a particular pool or fraction is determined by ^{14}C dating and is derived from the ratio of ^{14}C:^{12}C (Swift 2001). On the other hand, turnover time is the amount of carbon in the pool or fraction divided by the annual rate of addition of carbon to that pool (Swift 2001). Turnover of carbon in soil is controlled by biological processes that are regulated by soil structure and availability of substrates to

decomposers which further depends on chemistry of the substrate and the mineral components of the soil (Christensen 2001, Six et al. 2001).

The primary physical fractions used in studies of SOC include uncomplexed organic matter and primary and secondary organomineral complexes (Christensen 2001). Uncomplexed organic matter is a transitory pool between litter and those fractions associated with minerals and it is abundant in cold and dry climates, acidic soil, and soils with permanent cover such as grassland. Uncomplexed organic matter is typically larger than 2 mm and is not readily recognized as litter nor is it incorporated into primary organomineral complexes. The dependence on litter for input into this fraction causes high seasonal variability in response to litter production. Turnover of uncomplexed organic matter is generally slower than litter, but faster than organic matter associated with clay or silt (Christensen 2001). This fraction is further subdivided into free or occluded organic matter in soil. Free organic matter is comprised of loose organic particles and particulate matter that adheres to secondary organomineral complexes. Occluded organic matter, on the other hand, is physically protected within aggregates and is therefore less available for decomposition than free organic matter (Christensen 2001).

The primary organomineral complexes are associated with clay, silt, and sand and range in size from less than 2 μm to 2000 μm (Christensen 2001). Organic matter in an organomineral complex is plant- and/or microorganism-derived and decomposition differs between the two sources depending on size of the complex (Christensen 2001). Decomposition of plant-derived material increases from sand to silt to clay-sized complexes and clay-sized fractions are therefore dominated by microbial organic matter while silt is associated with aromatic residue from plants (Christensen 2001). The secondary organomineral complexes, or aggregates, are typically classified as micro aggregates (less than 250 μm) or macroaggregates (greater than 250 μm) (Christensen 2001). These complexes are comprised of mineral-associated and uncomplexed organic matter, microorganisms, and fine roots and are therefore more complex than other fractions (Christensen 2001). Formation of these

fractions in soil depends largely on size distribution of primary complexes, soil properties such as clay mineralogy, on abiotic processes such as cycles of wetting and drying and freezing and thawing, and on biological factors such as faunal activity and plant roots (Christensen 2001).

The distribution of different fractions through the solum leads to spatial variability in turnover rate and turnover slows with depth. This turnover rate ranges from several years for litter near the surface to 15 to 40 years in the upper 10 cm, and over 100 years below 25 cm of soil (Batjes 1998). The fast-cycling, or active, carbon pool consists primarily of root exudates and rapidly decomposing components of fresh plant litter and hydrolyzable components associated with mineral surfaces. The residence time of carbon in the active pool is typically less than 1 year (Amundson 2001). Although this fraction is not the primary means of carbon sequestration in soil, organic matter in the fast-cycling pool is ecologically important. This importance stems from a process driven by microbes that transform root-derived compounds from the fast cycling pool during biosynthesis and energy production (van Veen et al. 1991) which in turn affects the nutrient balance of the site.

The intermediate or slow pool is composed of material with a turnover rate of 10 to 100 years (Amundson 2001). This pool is the largest fraction of SOC and is the most difficult to study because it is not well defined and it is comprised of fractions with variable turnover rates (Trumbore 1997). The very slow or passive pool consists of SOC fractions that have residence times greater than 100 years (Amundson 2001). Carbon in the passive pool resists decomposition for physical reasons such as occlusion with soil structures and attachment to clay and for chemical reasons such as formation of refractory organic compounds (Amundson 2001). Humification is a key process regulating the amount of carbon transferred to the passive pool in the form of humic substances which may be protected by the clay fraction in soil (Anderson 1979).

Humic substances are the category of naturally occurring materials found in, or extracted from, soil, sediment, and water (MacCarthy 2001) and are composed of humic acid, fluvic acid and humin (Rice 2001). Humic substances are found in

terrestrial and aquatic ecosystems and are an abundant form of organic matter on earth (MacCarthy 2001). Humin is insoluble in an aqueous solution and it is an important constituent of SOC because the humic fraction is the most resistant to decomposition (Rice 2001). Carbon-14 dating indicates that humin organic carbon is about 1000 years old (Rice 2001). The long-term storage of carbon in the passive pool may therefore be the key to increasing carbon sequestration because losses to respiration and decomposition likely offset storage in active and short-term pools. Long-term sequestration of carbon therefore requires transfer of some carbon to pools with slow turnover. Enhanced sequestration of atmospheric carbon in soil may be dependent on finding ways to promote storage in passive forms such as humus, rather than increasing total SOC in pools with short residence times (Batjes 1998). Promoting soil carbon storage therefore requires an understanding of the factors that regulate input, decomposition, and allocation to the three fractions.

Key factors that affect the carbon budget include soil water content, soil temperature, nutrient supply, soil texture, and mineralogy (Batjes 1998). Other factors that affect SOC may include oxygen supply rate (drainage), soil pH, plant cover, species composition, and soil bulk density. In theory, land management practices can also influence the carbon budget of a site by altering the composition and structure of vegetation. This theory is based on the premise that land management activities, such as livestock grazing can affect SOC by altering the species composition or by affecting the physical and chemical properties of that community.

Water can control the species composition and amount of vegetation in a community and affect input of material into the SOC pools. Although the amount of precipitation received has the greatest influence on the water balance, land management activities also play a role. For example, the way that livestock grazing is managed can affect the water cycle which could alter the species composition and amount of plants growing on the site (Willms and Jefferson 1993). These alterations could influence the quality and quantity of plant material in a community and, in turn, influence the rate of decomposition of soil organic matter. Water plays an important

role in regulation of soil processes such as heterotrophic respiration. Respiration in the soil by roots and microorganisms is the principle process through which carbon in the soil is returned to the atmosphere as CO_2. Consequently, change in the amount of SOC with time is the difference between inputs from plants and soil organisms and losses as CO_2 produced during heterotrophic respiration (Amundson 2001). Respiration therefore plays a key role in the carbon budget and respiration increases with increasing temperature while SOC decreases as temperature increases (Burke et al. 1989, Kirschubaum 2000, Schlesinger and Andrews 2000).

Ecosystem C models are based on an understanding of the effects of water and temperature on respiration. For example, the initial version of the Century model of the plant-soil ecosystem was developed based on the understanding that grassland productivity and SOC dynamics are positive functions of precipitation as constrained by temperature and nutrient availability (Seastedt et al. 1994). Subsequent versions of the model also included fire effects, root:shoot ratios, and C:N ratios (Seastedt et al. 1994). Temperature is therefore generally accepted to be an important factor that affects accumulation of SOC or loss thereof by influencing respiration. The effect of temperature on decomposition was demonstrated by laboratory studies that suggest increasing temperature by 1^{o} C could decrease SOC by 10 % in regions where annual mean temperature is 5^{o} C while 3 % of SOC could be lost from areas with a mean soil temperature of 30^{o} C (Kirschbaum 1995). Kirschbaum (1995) also predicted that the effect of raising temperature could be greater when absolute values of carbon are considered because soil in cool regions contain greater amounts of C.

Macroclimate is another factor that affects the carbon balance. Franzluebbers et al. (2001) concluded that thermic regions (relatively warm) cannot retain great proportions of organic inputs as SOC when compared to frigid regions (relatively cool) because decomposition rates are greater in thermic regions. However, they also noted that the biologically active C components in thermic regions were as great per unit mass of soil and 3.3 times greater per unit of SOC. Temperature and soil water are important factors affecting respiration and therefore SOC, but the interaction of

temperature and water content is likely more important for regulation of the carbon budget at a site. In soil of an arid shrub-steppe, the respiration rate approached maximum when soil water content was 6 to 10 %, depending on temperature, but was generally optimal at temperatures above 15^{o} C (Wildung et al. 1975).

Soil texture plays a role in SOC cycling by controlling factors such as the turnover of material released by roots (van Veen et al. 1991). Organic matter associated with clay typically includes enriched microbial parts, while silt is associated with aromatic material from plants, and sand is associated with uncomplexed fractions and enriched in plant polymers (Christensen 2001). Jenkinson (1977) concluded that retention of ^{14}C labeled C over a 10-year period increased as clay content increased. Although there is a concerted effort to increase SOC, each soil has a finite capacity to sequester carbon (Paustian et al. 2000). Clay and silt particles have greater capacity to adsorb carbon than sand (Ingram and Fernandes 2001) and the finite capacity will therefore vary among soil types. These statements are supported by several studies that indicate soil texture controls the formation and turnover rate of active and slow organic matter pools in Great Plains grassland (Merckx et al. 1985, Parton et al. 1987, van Veen et al. 1991). Hook and Burke (2000) also concluded that soil texture and topographic position explained much of the landscape-scale variation observed among carbon pools in shortgrass steppe. The size of a SOC pool decreased as sand content increased, varying by factors of 2 to 4.5 over the range of sand contents encountered.

Soil minerals also play a stabilizing role in the cycling of SOC and influence of mineralogy on the carbon budget may be similar to that of climate or vegetation (Batjes 1998). Torn et al. (1997) used radiocarbon analysis to explore interactions between mineralogy and SOC along two gradients of soil age and climate in a humid environment and concluded that non-crystalline minerals and organic carbon were positively correlated. They also concluded that accumulation and losses of SOC are largely driven by changes in the millennial scale cycling of mineral-stabilized carbon, rather than by changes in the amount of fast cycling organic matter or in net primary productivity.

Plant cover may also have an effect on the carbon budget. Jenkinson (1977) concluded that decomposition of labeled roots was slower in soil with growing grass than in the same soil kept bare. The soil with grass growing in it also contained 47% more of the labeled carbon than the soil kept bare. In addition, soil that supported live grass for the first 5 years of the 10 year study and was kept bare for the last 5 years lost labeled C twice as fast as the same soil that was kept bare over the 0-10 year period (Jenkinson 1977). Studies in cultivated landscapes also indicate that erosion can remove SOC (de Jong and Kachanoski 1988). Observed carbon loss from cultivated sites over a 20-year period varied from 0.2 to 0.42 kg m^{-2} in the upper 15 cm of a fine-textured Dark Brown Chernozem and from 0.30 to 1.8 kg m^{-2} in a medium-textured Brown Chernozem (de Jong and Kachanoski 1988). This effect of erosion on SOC redistribution is less of a factor in uncultivated land (de Jong et al. 1983).

Plant species composition and/or diversity may affect SOC by altering decomposition. Bardgett and Shine (1999) concluded that the addition of litter to microcosms increased microbial biomass and respiration in soil relative to the control. Plant species diversity also affected microbial biomass and accounted for 83 % of the observed variance. Dormaar (1975) concluded that species diversity affected SOC because Brown soils supporting needle-and-thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth) and western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Löve) contained more decomposable organic matter than soil supporting blue grama (*Bouteloua gracilis* (HBK) Lag.). These results are the primary premise behind the hypothesis that livestock grazing alters SOC content because livestock grazing can alter species composition of the Mixed Prairie (Coupland 1961).

2.3 Effects of shrub invasion on SOC

Shrub abundance has increased in arid and semiarid grasslands over the past 300 years and may continue to expand into grasslands in response to climate change (Archer 1989). These vegetation changes have been reported for grassland

ecosystems worldwide (Brown and Archer 1999), including the Canadian Prairies (Johnston and Smoliak 1968). The shift from grassland to shrubland is an issue because ecosystem functions may be affected (Biedenbender et al. 2004). For example, plant species composition, primary production, plant resource allocation, rooting depth, and soil faunal communities can be altered by shrub invasion, which may subsequently modify the carbon balance (Jackson et al. 2002). Connin et al. (1997) concluded that the replacement of semiarid grassland by shrubs affects the mass of roots, litter production, soil C cycling, nutrient availability and long-term soil carbon sequestration at the ecosystem scale. Soil organic carbon in the invaded grassland ecosystem may also be affected by altered nutrient cycles (Trumbore 1997, Jackson et al. 2002) and by modified availability, quality, and/or quantity of carbon sources (Amundson 2001, Jackson et al. 2002). These predictions are supported by studies that indicate shrub patches are islands of high fertility because they trap wind-blown sediment which leads to greater concentrations of materials and elements, such as soil carbon (Wezel et al. 2000). Greater concentration of SOC in shrub communities indicates that shrub invasion could have a positive effect in areas where carbon sequestration is a land management objective.

Predictions that shrub invasion in grassland will increase SOC are supported by Barth and Klemmedson (1978) whose study showed that SOC decreased as the distance from the centre of velvet mesquite (*Prosopis juliflora* (Sw.) DC) and palo verde (*Cercidium floridum* (Benth. ex Gray)) increased in the Upper Sonoran Desert. Soil organic carbon in subtropical savanna of Texas also increased following woody plant encroachment (Hibbard et al. 2001). Hibbard et al. (2001) concluded that mean annual sequestration in areas encroached by woody plants was variable, ranging from 8 to 23 g m^{-2} in the upper 10 cm of soil. These researchers therefore speculated that the extensive nature of vegetation change in grassland may have important implications for understanding how global carbon cycles have been altered since settlement of arid and semiarid regions in North America. On the other hand, Hudak

et al. (2003) concluded that SOC may initially increase with shrub encroachment but then decline when shrub density inhibits understory graminoids.

A study conducted along a precipitation gradient in New Mexico, Colorado, and Texas revealed that drier sites gained and wetter sites lost SOC following invasion by woody species such as mesquite (*Prosopsis* sp.), creosote (*Larrea* sp.), and juniper (*Juniperus* sp.) (Jackson et al. 2002). In addition, losses of soil carbon at the wetter sites were substantial enough to offset greater C in aboveground phytomass. Jackson et al. (2002) therefore concluded the estimates of carbon sequestration that rely on greater aboveground carbon storage in woody species to compensate reduced storage in other fractions may be incorrect.

2.4 Effects of livestock grazing on SOC

Livestock grazing has the potential to indirectly alter the soil carbon balance by impacting the physical, chemical, and biological processes that control it. For example, herbivores influence grassland soil functions by accelerating nutrient cycling in patches where wastes are deposited (Day and Delting 1990, Jaramillo and Delting 1992). Herbivores also increase decomposition rates by reducing C:N ratios of plant shoots (Holland et al. 1992) and roots (Risser and Parton 1982, Seastedt 1985) and by affecting mineralization (Holland and Delting 1990, Frank and Groffman 1998). Grazing may also affect the soil food-web, and therefore SOC, by influencing the type and amount of root exudates which in turn affects soil organisms (Bardgett et al. 1998). Longer term effects on soil organisms may be triggered by herbivory if belowground net primary production is altered, if plant litter quality changes, or if plant species composition changes (Bardgett et al. 1998). Grazing management may therefore affect factors that control the quality and quantity of SOC in grasslands.

Grazing management strategies that maintain grassland species composition and structure that is comparable to ungrazed grassland are predicted to increase SOC

(Schuman et al. 2002). Conversely, overgrazing may reduce C input from litter, increase soil temperature, and alter microbial activity and decomposition (Abril and Bucher 2001). Abril and Bucher (2001) concluded that overgrazing subtropical woodland decreased SOC and that SOC accumulated when cattle were removed. Conant et al. (2001) conducted a literature review on the effect of management on soil carbon and also concluded that soil C in overgrazed sites decreased relative to moderately grazed sites. However, the effects of grazing management on SOC are variable and Conant et al. (2001) noted that the majority of studies concluded grazing increased soil C most in warm dry regions. They also concluded that the average annual rate of SOC increase was 7.7 % in areas with a long history of grazing while sites with a relatively short grazing history lost an average of 1.8%. Following this literature review, Conant et al. (2003) conducted a study on the effect of management-intensive grazing (short rotation grazing) or mowing on soil carbon fractions and concluded that total soil C in the top 10 cm was greater in management-intensive grazing systems than the control at three of the four study sites. They also concluded that total soil C in the 10 to 20 cm depth increment was greater in management-intensive grazing systems at one study site and greater in the 20 to 50 cm increment at another. On average, however, 50 % of the total soil C difference between these grazing systems was accounted for in the top 10 cm while 30 % of the difference was accounted for in the 10 to 20 cm depth (Conant et al. 2003). This study also indicated that particulate organic matter was different in the top 10 cm at two of the study sites and that root carbon was greater at two of the four sites.

Conclusions of research on grazing management effects on SOC are inconsistent (Bauer et al. 1987, Milchunas and Lauenroth 1993, Mathews et al. 1994, and Manley et al. 1995). For example, Bauer et al. (1987) concluded that ungrazed grassland contained greater SOC than grazed grassland while Manley et. al (1995) concluded that there was less SOC in exclosures than in all grazing treatments. Conversely, Frank et al. (1995) concluded that heavy grazing had no effect on SOC relative to an exclosure and that grazing at moderate stocking rates reduced SOC

relative to ungrazed grassland. They speculated that carbon removal by grazing animals may be the cause of this response while an increase in the dense shallow roots of blue grama (*Bouteloua gracilis* (HBK) Lag.) in the heavily grazed treatment likely accounted for maintenance of SOC relative to the control.

Results reported by Frank et al. (1995) are supported by a study conducted in Alberta in which Smoliak et al. (1972) concluded that total carbon, alcohol/benzene extractable carbon, and alkaline-soluble carbon increased following 19 years of heavy grazing by sheep relative to light or no grazing. They also speculated that the change in amount and kind of roots that accompanied a shift in species composition in heavily grazed areas is the reason for the greater amounts of carbon. Dormaar and Willms (1990), and Dormaar et al. (1984) also reported that total carbon and concentration of carbon increased following grazing due to replacement of species such as needle-and-thread by blue grama. Alternatively, Schuman et al. (1999) concluded that 12 years of heavy grazing on previously ungrazed Mixed Prairie in Wyoming did not alter the amount of SOC in the 0-60 cm soil depth relative to light grazing. They also concluded that this lack of effect on SOC occurred despite decreased peak standing crop and increased cover of blue grama in heavily grazed sites relative to lightly grazed sites. Similarly, Henderson et al. (2004) concluded that grazing does not affect SOC despite greater vegetation and litter mass in ungrazed areas than in grazed areas. They therefore concluded that management practices that maintain range in good to poor condition may be consistent with the goal of maintaining SOC in Northern Great Plains. These studies indicate that grazing intensity and plant species composition affect the relationships between SOC and grazing. Soil texture is another factor that could affect this relationship. Potter et al. (2001) studied the effect of stocking rate on SOC in two soil types and concluded SOC decreased as stocking rate increased in relatively sandy soil while SOC was similar in grazed and ungrazed treatments in relatively fine-textured soil. Soil where SOC decreased with increasing stocking rate had greater sand content and less initial SOC in the control relative to the second soil type in which grazing effects were not

detected. It therefore appears that SOC response to grazing is dependent on site factors such as soil texture and the initial SOC content. Spatial and temporal variability of climate, soil characteristics, past disturbance history, and other site and environmental conditions may also influence the response of SOC to grazing. This variability may therefore explain why reports are contradictory as a whole, despite conclusive site-specific findings about the correlation between SOC and grazing.

2.5 Decomposition of plant material

Energy flow and nutrient cycling are major ecosystem processes that lead to fixation of CO_2 and production of organic compounds that store energy (Mason 1977). Much of the energy stored in plants is used by herbivores while the remainder senesces and enters the decomposer system (Mason 1977). Energy and nutrients from plants are redistributed and eventually recycled through decomposition. During decomposition, dead organisms are reduced to large particles, then to smaller particles, and eventually into molecules that are further broken down into carbon dioxide, water, and mineral components (Mason 1977). Decomposition is also defined as the process through which physical, chemical, and biological mechanisms transform organic matter into increasingly stable forms (Berg and McClaugherty 2003). The physical processes referred to in this definition include fragmentation by wet-dry and shrink-swell, hot-cold cycles, and by animals, wind, leaching, and transport in water. The chemical transformation of organic material includes oxidation and condensation while biological mechanisms of decomposition are ingestion, digestion, and extracellular enzyme activity (Berg and McClaugherty 2003). Mason (1977) also noted that decomposition and breakdown are not synonymous. The decomposition measured by litterbag studies is mostly caused by the breakdown of tissue from large to small particles which is the initial phase of the decomposition process. This distinction is important because litterbag studies do not distinguish between what is respired as CO_2,

and what is leached out of the litter or lost due to fragmentation (Berg and McClaugherty 2003).

The process of decomposition is initiated when an organism dies and rapid leaching of soluble constituents occurs and causes the number of microorganisms surrounding the material to increase (Mason 1977). Enzymatic action around the decomposing plant material continues to fragment it and causes the nitrogen concentration to increase as C is consumed and released as CO_2 by decomposers. Animals continue to invade the area of the decomposing particles and they further fragment the material by ingesting it or by ingesting the bacteria and fungi in the area around it. Feces from animals around the organic matter are subsequently colonized by microorganisms and the size and mass of the organic particle decreases while the chemical structure changes (Mason 1977). A simple expression of decomposition is therefore described as a decrease in mass of organic material. A more detailed expression includes loss of matter, change in chemical composition of the remainder, and possibly fragmentation of the material (Swift et al. 1979). These physical and chemical changes of decomposition may be further attributed to the processes of leaching, catabolism, and comminution (Swift et al. 1979).

Leaching is a physical process that removes water-soluble matter from organic material. Removal of water-soluble matter decreases the mass and changes the chemical composition of an organic particle (Swift et al. 1979). Catabolism is the energy-yielding enzymatic reaction, or reactions, through which complex organic compounds are transformed into smaller and relatively simple molecules (Swift et al. 1979). Comminution, on the other hand, occurs when the size of an organic particle is reduced. Comminution differs from catabolism in that it is primarily a physical process that occurs when animals feed on an organic particle while catabolism is a chemical process (Swift 1979). In reality, however, these three processes occur concurrently and the effects of an individual process may be indistinguishable (Swift et al. 1979).

The primary factors that control the rate of decomposition are the decomposer organisms, the physico-chemical environment, and the quality of the organic material

(Swift et al. 1979). The effect of decomposers is related to their functional ecology and distribution pattern while the physico-chemical environment is related to water availability, aeration, oxygen availability, pH, and temperature (Swift et al. 1979). The quality of the organic matter, on the other hand, is related to its value as a food source for other organisms. High quality organic matter decomposes more rapidly than poor-quality material quality because of how material quality influences decomposers.

The decomposition of organic matter may also be correlated with palatability to herbivores. Moretto et al. (2001) and Moretto and Distel (2003) concluded that leaf litter of palatable grasses decomposed faster than that of unpalatable species. Grime et al. (1996) concluded that leaf palatability and litter decomposition rate are positively correlated. The content of nitrogen, lignin, and phosphorus in plant material influences the rate of decomposition of that material (Mun and Whitford 1998, Hendrickson et al. 2001, Moretto and Distel 2003). Plants with a greater C:N ratio and a relatively great concentration of lignin, typically decompose more slowly and species with these characteristics are often referred to as poor-quality. Moretto and Distel (2003) concluded that high-quality plant litter decomposed more rapidly because the initial N and P concentration are greater, lignin concentration is lower, and the C:N, lignin:N, and lignin:P ratios in leaf litter and roots are lower. Similarly, Taylor et al. (1989b) concluded that N content and the C:N ratio were better indicators of the rate of decomposition for leaf litter than the lignin:N ratio. Mun and Whitford (1998) also concluded that decomposition of roots was negatively correlated with initial lignin concentration. Lignin content was positively correlated with the decomposition rate while the C:N ratio was negatively correlated (Hendrickson et al. 2001). Studies of relationships between leaf litter quality, decomposability of leaf litter, and plant response to herbivory were conducted by Wardle et al. (2002) and they concluded that there is a positive correlation between litter decomposition rate and the reduction of vegetation density caused by browsing mammals.

The effect of chemical properties of plant material on decomposition is an indication that different species and different plant organs (roots, leaves, culms) are

likely to decompose at different rates. This assertion is supported by studies that indicate the rate of leaf decomposition is generally greater than that of stems (Koukoura et al. 2003). Greater decomposition of leaves than stems was attributed to the differences in allocation of metabolic products among plant parts and to environmental differences among growing seasons. The effect of environment, plant species, and plant material on decomposition was demonstrated by other studies. For example, leaves of grasses and forbs decreased at different rates under snow (Bleak 1970) while leaf litter of two shrub species decomposed more rapidly than root litter in another study (Kemp et al. 2003). Kemp et al. (2003) also concluded that drought did not affect the rate of decay for leaf litter of these species during the first 18 months, but decreased the rate of decomposition by about 25% during the latter part of the study. These authors therefore concluded that relatively large changes in precipitation produced comparatively small changes in decay rates of root and leaf litter.

The dominant effect of plant composition on decomposition is supported by Swift (1979). Swift (1979) concluded that litter quality may be the most important factor affecting microbial and meso-invertebrates while environmental conditions are secondary within sites. Conversely, Couteaux et al. (1995) concluded that there is a shift in the dominant processes regulating decomposition from biotic in temperate areas to abiotic in arid regions. Aridity creates unfavorable conditions for decomposition at the soil surface and discontinuous litter cover may hinder development of the decomposer community at the soil surface. Comparatively, Couteaux et al. (1995) observed that temperature and water are less constraining in wet tropical climates and decomposition rate is predominantly determined by soil type and humus and litter quality.

Specific factors that affect decomposition are temperature, water, soil texture, and plant species composition (Oades 1988, Taylor and Parkinson 1988b, Kochy and Wilson 1997). However, lignin content may affect decomposition differently across climatic regions, because litter quality and environmental conditions interact (Meentemeyer 1978). Couteaux et al. (1995) supported this conclusion by suggesting

that decomposition is more constrained by litter quality in areas where temperature and water are less constraining, such as in tropical environments. Understanding decomposition becomes more complicated when physical factors of the site are considered. Soil texture can influence decomposition rate by protecting soil organic matter (Oades 1988, Hassink et al. 1997). Oades (1988) concluded that clay content of soil and soil base status can affect mineralization of organic carbon. This effect on decomposition is related to the formation of organomineral complexes that protect and stabilize C compounds. Similarly, Hassink et al. (1997) concluded that soil texture and clay type may affect the capacity of soils to physically protect organic carbon.

Measuring decomposition rate is made more complicated by the interaction of abiotic and biotic conditions controlling this process. For example, species composition of the decomposer community can affect the rate of decomposition (Swift et al. 1979) and the microbial community can be altered by factors such as elevated soil CO_2 (Sowerby et al. 2000). Similarly, factors such as season can affect the decomposer community (Vossbrinck et al. 1979). The effect of plants, or the species composition of the plant community adds to the complexity of the decomposition process. For example, litterbag experiments indicated that decomposition was enhanced by including more than one plant species in the sample (Hector et al. 2000). Species effects on decomposition are supported by studies conducted on aspen (*Populus tremuloides* Michx.) green alder (*Alnus crispa* (Ait.) Pursh) and a mixture of the two species (Taylor et al. 1989a). Aspen, a nutrient-poor species, decomposed slowly, while alder is nutrient-rich and decomposed more rapidly. However, decomposition rate of the combined material was similar to that of alder, not aspen. Conversely, decay rate of mixed species samples was not different than rates predicted from red maple (*Acer rubrum* L.), flowering dogwood (*Cornus floribunda* L.) or chestnut oak (*Quercus prinus* L.) (Blair et al. 1990). Wardle et al. (1997) and Hector et al. (2000) also concluded that species richness was not a factor that controlled decomposition. Similarly, changes in species evenness of litter or in the dominant species did not affect decomposition (King et al. 2002). The response of

decomposition to species evenness and richness may be attributed to functional characteristics of plants. Several plants with similar functional characteristics decompose at similar rates because the composition of those materials is comparable. Cornelissen and Thompson (1997) concluded that graminoids with physically tough leaves and relatively high silicon content have reduced decomposition rates when compared to herbaceous dicot leaves. Cornelissen et al. (1999) also concluded that there is evidence of a link between defenses of photosynthetically functional leaves and litter resistance to decomposition. Based on the discussion in the previous paragraphs, it may be expected that high-quality, or palatable plant material, will decomposes more quickly than poor-quality, or unpalatable, material.

3.0 SOIL ORGANIC CARBON, ROOT MASS, AND ABOVEGROUND PHYTOMASS IN SNOWBERRY, ECOTONE, AND GRASSLAND COMMUNITIES

3.1 Introduction

The historic disturbance regime of grasslands includes grazing and fire and it created an environment that favored persistence of graminoids while hindering trees and shrubs. Settlement of the Canadian Prairies over the past 130 years changed the disturbance regime, specifically because fires are suppressed and the frequency and intensity of grazing has been modified. This altered disturbance regime in grasslands led to the expansion of trees and shrubs in some regions.

Other forms of environmental change may also affect the ability of shrubs to invade grassland. Shrub abundance has increased in arid and semiarid grasslands and leading Archer (1989) to hypothesize that shrubs may continue to expand into grasslands as climate changes. Increases in shrubs has been reported for grassland ecosystems worldwide (Brown and Archer 1999), including the Canadian Prairies (Johnston and Smoliak 1968). The shift from grassland to shrubland is an issue in semiarid grasslands because of the potential impacts on plant community functions such as livestock production, wildlife habitats, and watershed protection (Biedenbender et al. 2004). The invasion of shrubs into grassland could also change the ecosystem carbon balance. Plant species composition, primary production, plant resource allocation, rooting depth, and soil faunal communities can be altered by shrub invasion and may subsequently modify the carbon balance (Jackson et al. 2002).

Grasslands occupy about 3.4 million ha in Alberta and 2.5 million ha in Saskatchewan, but the area that is susceptible to shrub invasion is not currently

known. Understanding the effect of shrub invasion on SOC remains important, however, because of the expansiveness of grasslands and because they contain 10 to 30% of the global soil organic carbon (SOC) (Eswaran et al. 1993). Batjes (1999) estimated that grassland/steppe, extensive grasslands, and savannas collectively contain 230 to 246 Pg C in the upper 1 m of soil. It is therefore possible that small proportional increases in the amount of carbon sequestered in grassland soil will be significant for managing the global carbon balance (Follett 2001).

The effect of shrub invasion on SOC has not been widely studied and studies have not been conducted in Mixed Prairie. The effects of snowberry (*Symphoricarpos occidentalis* Hook.) invasion on SOC in the Prairie Ecozone was the focus of this study. The objective of the study was to determine the relative contribution of plants in snowberry, ecotone, and grassland communities to organic carbon, root mass, and aboveground phytomass. The hypothesis that SOC is greater on sites with greater phytomass was tested. A second hypotheses that soil texture effects the response of SOC, root mass, and aboveground phytomass to these communities was also tested.

3.2 Materials and methods

3.2.1 Site selection and description

Climate, soils, topography, plant species composition, and disturbance regimes vary throughout Saskatchewan. There is also variability in the distribution of carbon in soils, including variability with depth and spatially with the position of soils in a landscape (Eswaran et al. 1995). This variability prohibits a study of soil carbon sequestration at a large scale such as the province of Saskatchewan. Consequently, the Mixed Grassland and the Moist Mixed Grassland Ecoregions (Acton et al. 1998) were targeted for this investigation because the climate is relatively uniform. In addition, consistency in soil types, topographic positions, and plant communities can be

identified and replicated throughout the area for testing hypotheses about soil carbon sequestration.

Study sites used for this research were located in the Mixed Grassland and Moist Mixed Grassland Ecoregions of the Prairie Ecozone in central and southern Saskatchewan (Table 3.1). Snowberry patches used in this study ranged from 10 to 25 m in diameter, snowberry was the only shrub species, and canopy cover was greater than 40%. The age of the patches and rate of spread were indeterminate. All snowberry patches were located in grasslands dominated by native plants. Snowberry patches located near facilities such as water, salt or mineral supplies were also avoided during site selection as were sites where cattle were fed. None of the study sites had signs of recent fires, such as the presence of charred snowberry stems. The fire exclusion period for these study sites is not known.

3.2.2 Experimental design

The nine study sites were used as replicates. A transect that originated near the centre of the snowberry patch and extended into the grassland community was established at each site. Six, 2 x 2 m plots were positioned along the transect at each study site (Figure 3.1). The first plot was located in the snowberry patch where the snowberry was tallest and most dense. Two additional plots were positioned in the snowberry patch interior while one was located near the midpoint of the snowberry-grassland ecotone, and two were located in the grassland community (Figure 3.1). Distance between plots varied from about 3 to 5 m, depending on the size of the snowberry patch. More plots were located in the snowberry patch because the SOC was expected to be more variable in this community. Three subsamples within each of these plots were collected to increase the precision of the measurements and data from plots were averaged within snowberry patches, ecotones, and grasslands.

Table 3.1. Descriptions of nine study sites in central and southern Saskatchewan for the snowberry invasion study.

Site	Soil Association, Landscape class, and Ecoregion	Dominant graminoids	Township[1]	Grazing history
Abbott	Blaine Lake Shallow lacustrine plain, Moist Mixed Grassland	*Festuca hallii* (Vasey) Piper *Poa pratensis* (L.)	S1T39 R3 W3	Protected from livestock for over 15 years
Kernen	Weyburn Lacustrine plain, Moist Mixed Grassland	*Festuca hallii* *Elymus lanceolatus* ((Scribn. & J.G. Sm.) Gould)) *Hesperostipa curtiseta* ((A.S. Hitchc.) Barkworth)	S9 T37 R4 W3	Protected from livestock for over 15 years
Montrose North	Dune Sand Hummocky dunes, Mixed grassland	*Hesperostipa comata* (Trin. & Rupr.) Barkworth *Koeleria macrantha* (Ledeb.) J.A. Schultes *Bouteloua gracilis* (HBK)Lag. *Carex* spp.	S3 T33 R7 W3	Moderately to heavily grazed for over 15 years
Montrose South	Dune Sand Hummocky dunes, Moist Mixed Grassland	*Pascopyrum smithii* (Rydb.) A. Löve *Carex* spp.	S34 T33 R7 W3	Moderately to heavily grazed for over 15 years
Biddulph	Dune Sand Hummocky dunes, Moist Mixed Grassland	*Hesperostipa comata* *Koeleria macrantha*	S12 T34 R5 W3	Protected from livestock grazing for over 15 years
Rudy	Dune Sand Hummocky dunes, Moist Mixed Grassland	*Bouteloua gracilis* *Koeleria macrantha*	S8 T32 R5 W3	Moderately to heavily grazed for over 15 years
Wilner	Weyburn Kettled till plain, Mixed grassland	*Hesperostipa comata* *Carex* spp.	S33 T26 R2 W3	Moderately to heavily grazed for over 15 years
Coop	Haverhill Shallow lacustrine plain, Mixed grassland	*Hesperostipa comata* *Carex* spp.	S20 T21 R15 W3	Moderately to heavily grazed for over 15 years
Matador	Sceptre Lacustrine plain, Mixed grassland	*Elymus lanceolatus* *Koeleria macrantha*	S15 T20 R14 W3	Protected from livestock grazing for over 25 years

[1] S= section, T= township, R=range and W= west of the 3rd meridian.

Figure 3.1. Diagram of plot locations in the snowberry, ecotone and grassland communities at one study site.

3.2.3 Biophysical data

Dependent variables, measured or estimated, included aboveground phytomass, species composition, percent cover of vascular plants, soil organic carbon, soil bulk density, mass of roots, and soil texture. Aboveground phytomass was measured in a 1x1 m subplot of each plot in August 2003. Litter was collected from the soil surface within this 1 x 1 m subplot by raking it and collecting it in paper bags. Snowberry within the subplot was clipped at ground level and stored in paper bags. Live and recently senesced forb and graminoid plant material was also clipped at ground level and placed in paper bags. All plant samples were dried at 85^{o} C to a constant mass.

Species composition and percent canopy cover was determined by identifying and recording all species within eight, 0.5 x 0.5 m subplots per plot in July 2003. The eight subplots were positioned within each 2 x 2 m plot. Canopy cover was visually estimated for all species present in each subplot (Bonham 1989). Snowberry canopy cover was estimated separately from the understory cover of forbs, graminoids and juvenile snowberry ramets. Species occupying less than 2.5% were scored at 1%. Mean percent cover per plot was calculated by summing the estimated cover of each species and dividing by eight (the number of subplots). Percent ground cover in each subplot was also estimated. Categories used for ground cover were snowberry leaf plus twig litter, graminoid and forb litter, bare ground, and rock. Ground cover was also averaged over the eight subplots for each 2 x 2 m plot.

Soil samples for measuring root mass were collected in July 2003 at each site. A hydraulic-powered punch with a 6.5 cm diameter core was used to collect soil samples (3 soil cores (subsamples) from the upper 50 cm of soil in each 2 x 2 m plot). Plant litter was removed from the soil surface before collecting the soil sample. Soil cores were divided into 0-3, 3-10, 10-20, 20-30, 30-40, and 40-50 cm depth increments and the three subsamples for each soil depth increment were pooled. The pooled subsamples for each depth were stored in paper bags, labeled, and stored at room temperature for more than 2 months before the mass of roots was determined.

Root mass was determined by placing the pooled soil sample from one plot on a 3 x 3 mm mesh screen that was placed over a 20 L pail. A second screen with 1 x 1 mm mesh was draped inside the pail and underneath the 3 x 3 mm screen. Warm water was sprayed onto the soil and root sample and large and medium roots were collected from the 3 x 3 mm screen after the soil was removed. Roots remaining on top of the 3 x 3 mm screen were sorted by hand into large (greater than 3 mm diameter) and medium (less than 3 mm diameter) size classes. Roots that remained on the 1 x 1 mm screen were also collected and combined with the medium roots from the 3 x 3 mm screen. Plant materials floating in the water after the 1 x 1 mm screen was removed were collected with a hand-held sieve with an approximate mesh size of 0.5 x 0.5 mm. Roots collected from the water were categorized as fine.

Roots in the large and medium categories were easily identifiable as roots. However, the small plant fragments that comprise the fine samples were unidentifiable, and consisted of small roots, fractions of roots, sloughed root epidermis, and fragmented and partly decomposed leaves and stems. All root samples for each depth increment were stored in tin cans, oven dried at 85^{o} C to a constant mass and weighed using a closed microbalance. Root material was stored at room temperature in labeled paper envelopes.

Soil bulk density was determined using the core method (Blake and Hartge 1986). Soil samples for measuring bulk density were collected at the 0-3, 3-10, 10-20, 20-30, 30-40, and 40-50 cm depths. The soil samples were collected by digging a hole

in each plot with a spade and inserting a bulk density tube into the soil at the midpoint of each depth increment. Soil tubes were pushed into the coarse-textured soil by hand or pounded into fine-textured soils. Bulk density tubes were extracted from soil by digging out a section of soil in front of the tubes. Soil was then shaved off the openings of the tubes using a knife. Soil samples from the cores at each depth increment for all plots were placed in tin cans and transported to the laboratory. Soil samples were dried at 85^{o} C to a constant mass and weighed.

Soil for measuring SOC was collected in June 2003 using a hydraulic punch as described for root collection. Three soil cores (subsamples) were collected from each plot and within several cm of the locations of soil cores used for roots. Each soil core was divided into 0-3, 3-10, 10-20, 20-30, 30-40, and 40-50 cm depth increments. The three subsamples for each depth increment at each plot were pooled, placed in paper bags, labeled, and air dried at room temperature for more than 2 months before being processed. Air dried soil samples were mechanically ground and recognizable plant materials were removed from soil samples before grinding by sieving or hand-picking, however, some plant materials could not be removed from soil aggregates. Approximately 50 g of dried soil was placed in a ball grinder for 2 to 3 minutes, or until the sample was a fine powdery texture (fine-textured soil) or until the sample was comprised exclusively of individual soil particles (coarse-textured soil). The ground soil samples were stored in plastic drum vials at room temperature after grinding. Approximately 0.15 g of the finely-ground soil was placed into A Leco CR-12 Carbon Analyzer to measure SOC which was set at 840^{o} C (Wang and Anderson 1998). Organic carbon in each sample was completely oxidized within 2 minutes. The carbon analyzer measured concentration of organic carbon in the soil sample.

The percent sand, silt, and clay in the A horizon of samples collected from each plot were determined using a hydrometer method similar to that described by Gee and Bauder (1979) and based on that of Bouyoucos (1962). Samples from the 3 to 10 cm depth were oven-dried at 85^{o} C to a constant mass. Samples of 100 g (coarse soil) or 50 g (fine soil) were placed in a plastic bottle and combined with 100 mL of distilled

water. The soil and water mixtures were combined with 20 mL of sodium pyrophosphate ($Na_4P_2O_710H_2O$) to improve dispersion of soil particles in the solution (Brewer and McCann 1982, Kettler et al. 2001). The bottles containing the soil solution were placed in an electric reciprocating machine for 3 hours, left idle for 24 hours, and shaken for 3 additional hours. After completing the shaking treatment, individual samples were placed in a blender and the suspension was mixed for 30 seconds. Each sample was placed in a separate sedimentation cylinder after blending and distilled water was added to the solution until the total contents of the cylinder measured 1130 mL (50 g soil samples) or 1205 mL (100 g soil samples). The cylinders were shook for 10 seconds and hydrometer readings were taken at 40 seconds and 120 minutes thereafter. Percent sand (0.05 to 2.0 mm in diameter), clay (less than 0.002 mm in diameter), and silt (0.002 to 0.05 mm in diameter) were calculated by Equations 1 to 3 based on Gee and Bauder (1979) and Bouyoucos (1962).

% sand = 100-(100*hydrometer at 40 seconds/dry mass of soil sample) (Equation 1)
% clay = 100* (hydrometer at 120 minutes/dry mass of soil sample) (Equation 2)
% silt = 100-(% sand + % clay) (Equation 3)

Soil particle data were used to determine the soil texture class for all six plots at each study site (Appendix 3.1). Soil texture class was determined from percent sand and clay for a sample (Agriculture Canada Expert Committee on Soil Survey 1987). For all analyses and discussions, coarse-textured soils were comprised of greater than 50% sand while fine-textured soils were comprised of less than 50% sand.

3.2.4 Data analysis

The snowberry, ecotone, and grassland communities were studied at each site in a random study design. Data from three plots in the snowberry community were averaged and compared to data from the single ecotone plot and to the average of the

two plots located in the grassland (Figure 3.1). Each replicate site was classified as coarse- or fine-texture for the analysis. The main effects of plant community and soil texture and their interaction were analyzed using a General Linear Model (GLM) analysis of variance (ANOVA) (Zar 1999). A Tukey multiple comparison test was conducted on all pairwise means. A critical value of $P \leq 0.05$ was used for evaluating significance of differences.

The potential correlation among species composition, environmental variables, and study sites was explored using ordination techniques available in CANACO (version 4.5) (ter Braak and Šmilauer 2002). The initial ordination analysis performed was a detrended canonical correspondence analysis (DCCA). The DCCA was conducted to determine the standard deviation of the plant species gradients for each ordination axis. This analysis indicated that the standard deviation of the first axis was greater than 3, indicating that the model is non-linear and that canonical correlation analysis (CCA) is the most appropriate technique for exploring the relationship among plant species and biophysical variables (ter Braak and Šmilauer 2002). The CCA was conducted using Hill's scaling technique to scale species response, which equalizes the average niche breadth for all axes, allows for relatively long gradients and is suitable for a unimodal response (ter Braak and Šmilauer 2002). Species that occurred in fewer than 5% of the study plots were omitted from the analysis to reduce the influence of rare species (McCune and Grace 2002). Correlated environmental variables were also removed from the model using manual forward selection (ter Braak and Šmilauer 2002). Forward selection is a step-wise process that uses a Monte Carlo test with 9999 unrestricted permutations to calculate the significance of each environmental variable (ter Braak and Šmilauer 2002). Variables with $P > 0.05$ were omitted from the CCA model. The Pearson product moment correlation coefficient was used to measure the degree of linear relationship between pairs of variables that were included in the CCA model.

3.3 Results

3.3.1 Plant community and other biophysical characteristics in grassland, ecotone and snowberry communities

Canopy cover of snowberry in the snowberry community averaged 59% (SE= 4) while snowberry cover in the ecotone averaged 23% (SE= 4) (Figure 3.2, Appendix 3.2). Snowberry was not present in the grassland community. Canopy cover of herbaceous plants varied among communities averaging 40% (SE= 7), 61% (SE= 5), and 74% (SE= 6) in the snowberry, ecotone and grassland communities, respectively (Figure 3.2).

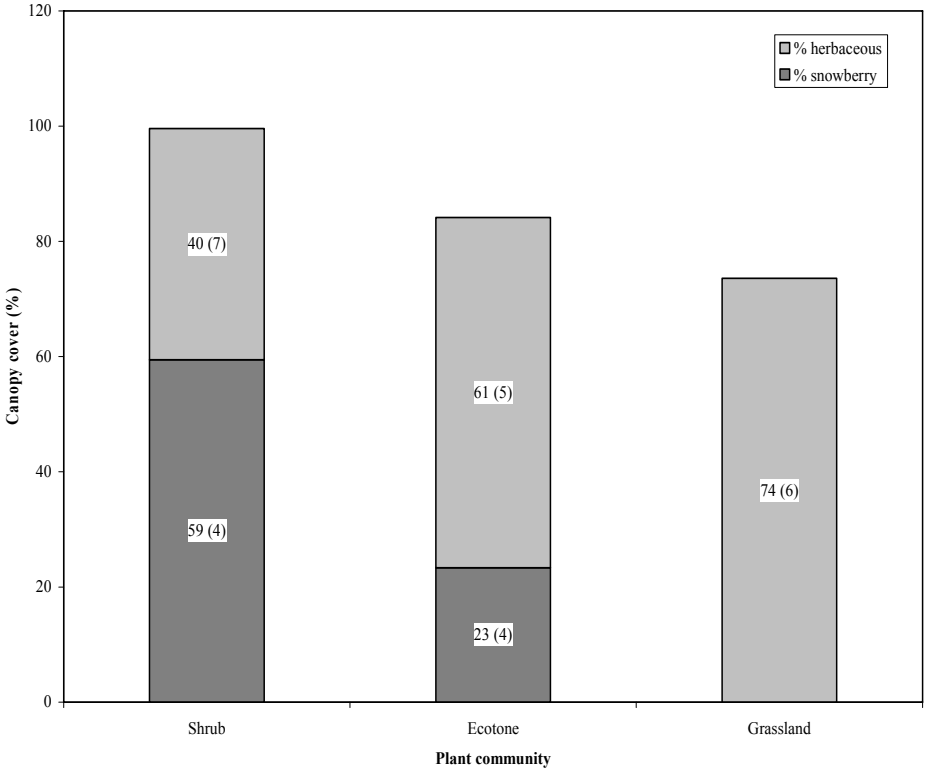

Figure 3.2 Average percent canopy cover of snowberry and herbaceous vegetation in snowberry, ecotone, and grassland communities at nine study sites. Values within % herbaceous and % snowberry for each plant community are means of the nine study sites. The SE for means are in parentheses.

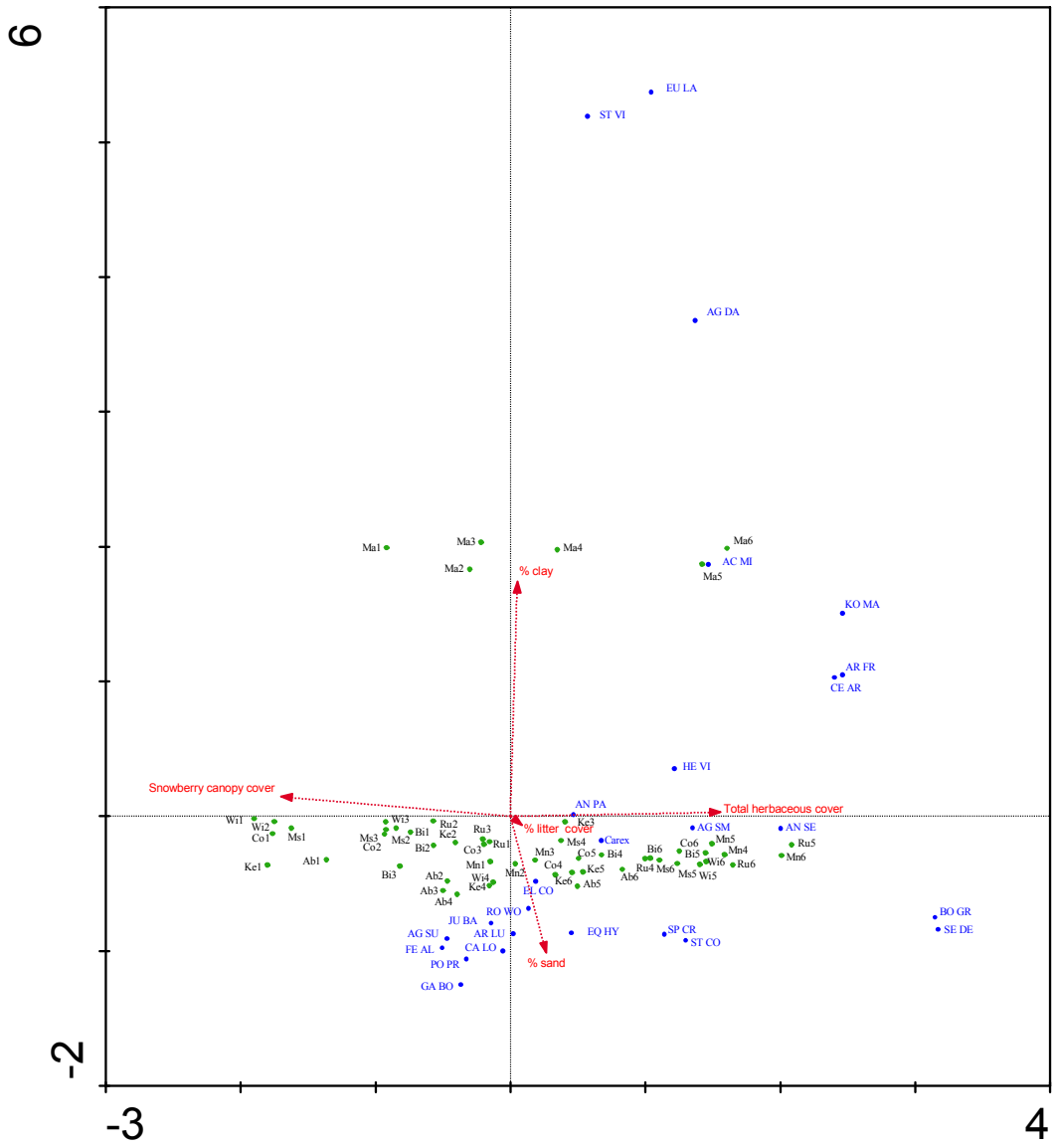

Figure 3.3. Canonical correlation analysis joint plot of linear combinations of species and biophysical variables at nine snowberry study sites (Wi = Wilner, Ru = Rudy, Co = Coop, Bi = Biddulph, Mn= Montrose North, Ms= Montrose south, Ab= Abott, Ke= Kernen, and Ma= Matador). Number 1, 2, and 3 after the site name indicate snowberry community, 4 is the ecotone, and 5 and 6 are grassland community. Species codes are derived from the first two letters of the genus name followed by the first two letters of the species name. Complete genus and species names are provided in Appendix 3.2.

Table 3.2. Canonical correlation analysis results showing additional variance explained (λ_A), and P-value of each biophysical variable measured in grassland, ecotone, and snowberry communities. The correlation model was derived by manual forward selection using Monte Carlo permutation tests with 9999 unrestricted permutations at $P \leq 0.05$.

Biophysical variable	λ_A	P-value
Snowberry canopy cover	0.48	**0.00**
% clay	0.35	**0.00**
% sand	0.19	**0.00**
% litter cover	0.14	**0.00**
Total herbaceous cover	0.08	**0.01**
Bare ground cover	0.06	0.09
0-3 cm soil C	0.05	0.17
Herbaceous phytomass	0.06	0.10
40-50 fine roots	0.05	0.16
10-20 cm soil C	0.05	0.17
Snowberry canopy cover	0.04	0.25
0-50 cm soil C	0.04	0.28
Snowberry litter cover	0.04	0.37
Snowberry phytomass	0.04	0.31
10-20 fine root mass	0.04	0.30
Total litter cover	0.04	0.40
20-30 cm soil C	0.04	0.30
40-50 cm soil C	0.04	0.39
3-10 medium root mass	0.03	0.54
0-3 fine root mass	0.03	0.47
40-50 large root mass	0.03	0.52
30-40 medium root mass	0.03	0.55
40-50 medium root mass	0.03	0.54
30-40 total root mass	0.03	0.55
40-50 total root mass	0.03	0.68
3-10 cm soil C	0.03	0.45
0-50 fine root mass	0.03	0.58
30-40 fine root mass	0.03	0.58
0-50 medium root mass	0.03	0.63
20-30 fine root mass	0.03	0.50
0-3 total root mass	0.03	0.56
0-50 mean root mass	0.03	0.68
20-30 mean root mass	0.02	0.75
0-3 large root mass	0.03	0.66
0-3 medium root mass	0.02	0.81
3-10 fine root mass	0.02	0.85
30-40 large root mass	0.02	0.87
30-40 cm soil C	0.02	0.84
20-30 large root mass	0.02	0.89
20-30 total root mass	0.02	0.90
0-50 large root mass	0.02	0.91
10-20 medium root mass	0.01	0.95
10-20 large root mass	0.01	0.98
10-20 total root mass	0.01	0.99
3-10 large root mass	0.01	0.99
3-10 total root mass	0.01	0.99
Litter mass	0.01	0.97
Total above ground phytomass	0.01	0.98

An ordination joint plot of the CCA also indicated that species composition varied among the three plant communities. Snowberry cover corresponded with Axis 1, which separated snowberry, ecotone, and grassland communities. Snowberry cover corresponded negatively with total herbaceous cover and % litter cover (Figure 3.3, Table 3.4). Soil texture, however, corresponded with Axis two (Figure 3.3). The first four axes of the RDA explained 40 % of the variance in species composition and 95 % of the variance in the species-environment relationship (Table 3.3).

Table 3.3. Canonical correlation analysis summary statistics from species and biophysical data, including importance value of each axis (eigenvalue: 0= unimportant, 1= very important), variance of species composition explained by each axis, cumulative variance explained, and the sum of all canonical eigenvalues. Species and other biophysical data were from grassland, ecotone, and snowberry communities at nine study sites.

	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalues	0.53	0.36	0.20	0.11	2.96
Species-environment correlations	0.93	0.90	0.77	0.58	
Cumulative percentage variance:					
of species data	18.0	30.0	36.7	40.3	
of species-environment relationship	40.5	70.9	86.8	95.2	
Sum of all eigenvalues					2.96
Sum of all canonical eigenvalues					1.25

Table 3.4. Correlations of biophysical variables used in the canonical correlation analysis. Biophysical data were from grassland, ecotone, and snowberry communities at nine study sites.

	Snowberry canopy cover	% litter cover	Total herbaceous cover	% sand	% clay
Snowberry canopy cover	1.00				
% litter cover	-0.34*	1.00			
Total herbaceous cover	-0.74*	0.18	1.00		
% sand	-0.01	-0.29*	-0.03	1.00	
% clay	0.01	0.10	0.09	-0.68*	1.00

* The correlation is significant ($P \leq 0.05$)

3.3.2 Soil organic carbon, N, C:N, and bulk density in grassland, ecotone, and snowberry communities

The CCA analysis supports the ANOVA for SOC because SOC was not a significant factor in the CCA model and interactions between snowberry community and soil texture were not significant (P>0.27) for SOC nor was SOC different (P>0.28) in the snowberry, ecotone, or grassland community. Soil organic carbon in the snowberry, ecotone and grassland communities, averaged 8.3 kg m^{-2} (SE= 0.7), 7.9 kg m^{-2} (SE= 1.0) and 7.9 kg m^{-2} (SE= 0.7), respectively (Table 3.5). Conversely, soil organic carbon was greater (P<0.01) in fine-textured soil (10.4 kg m^{-2}, SE= 0.6) than coarse-textured soil (6.2 kg m^{-2}, SE= 0.4) in the 0-50 cm depth. Average SOC in fine-textured soil was also greater than (P<0.01) fine textured soil at the 0-3, 3-10, 20-30, 30-40, and 40-50 cm depths (Table 3.5). The greatest differences occurred in the 0-3 cm and 3-10 cm depths where SOC in fine soil averaged 8.8% (SE= 0.97) and 4.1% (SE=0.39), respectively, compared to 4.2% (SE= 0.52) and 1.8% (SE= 0.21), respectively, in coarse soil (Table 3.5).

Table 3.5. Average soil organic carbon in grassland, ecotone, and snowberry communities. Plant community values are means of nine study sites and soil texture values are means of five coarse-textured soils or four fine-textured soils. The SE of means are in parentheses.

	Soil depth (cm)						
Plant community/ soil texture	0-50[1]	0-3	3-10	10-20	20-30	30-40	40-50
	Soil organic carbon (kg m^{-2})	Soil organic carbon (%)					
Snowberry	8.3 **a** (0.7)	5.7 **a** (1.26)	2.8 **a** (0.55)	1.6 **a** (0.25)	0.9 **a** (0.14)	0.7 **a** (0.17)	0.5 **a** (0.14)
Ecotone	7.9 **a** (1.0)	6.3 **a** (1.10)	2.7 **a** (0.49)	1.5 **a** (0.31)	0.9 **a** (0.20)	0.7 **a** (0.12)	0.5 **a** (0.09)
Grassland	7.9 **a** (0.7)	6.7 **a** (1.28)	3.0 **a** (0.62)	1.7 **a** (0.35)	1.2 **a** (0.28)	0.8 **a** (0.19)	0.6 **a** (0.15)
Fine texture	10.4 **a** (0.6)	8.8 **a** (0.97)	4.1 **a** (0.39)	2.2 **a** (0.26)	1.4 **a** (0.20)	1.2 **a** (0.11)	0.9 **a** (0.10)
Coarse texture	6.2 **b** (0.4)	4.2 **b** (0.52)	1.8 **b** (0.21)	1.1 **a** (0.11)	0.6 **b** (0.05)	0.4 **b** (0.03)	0.3 **b** (0.03)

[1] Means within soil depth and plant community or soil depth and soil texture classes that are followed by the same letters are not statistically different (P>0.05).

Average % N in soil was not different (P=0.36) in the grassland and snowberry communities, nor was the C:N ratio (P=0.30) (Table 3.6). However, average % N in soil was more than double in fine soil when compared to coarse soil (P<0.01). The C:N ratios were also greater (P<0.01) in the fine-textured soil than in the coarse-textured soil (Table 3.6).

Table 3.6. Average nitrogen content and C:N ratios from three soil depths in grassland and snowberry communities. Plant community values are means of nine study sites and soil texture values are means of five coarse-textured soils or four fine-textured soils. The SE of means are in parentheses.

Depth (cm)	Plant community/ soil texture	% N[1]	C:N
3-10	Grassland	0.24 **a** (0.05)	11.0 **a** (0.3)
	Snowberry	0.28 **a** (0.06)	11.6 **a** (0.2)
10-20	Grassland	0.16 **a** (0.02)	11.4 **a** (0.2)
	Snowberry	0.18 **a** (0.04)	11.8 **a** (0.3)
20-30	Grassland	0.10 **a** (0.02)	12.0 **a** (0.4)
	Snowberry	0.13 **a** (0.03)	11.9 **a** (0.4)
Texture	Coarse	0.12 **b** (0.01)	12.0 **a** (0.2)
	Fine	0.26 **a** (0.03)	11.2 **b** (0.1)

[1] Means within a column and soil depth, or within a column and soil texture class that are followed by the same letters are not statistically different (P>0.05).

Average bulk density of the soil was not different (P>0.15) in snowberry, ecotone, and grassland communities at all soil depths, except the 10-20 cm depth where bulk density was 0.16 g cm^{-3} greater (P=0.02) in grassland than in snowberry community (Table 3.7). As expected, bulk density of coarse soil was greater than (P≤0.05) that of fine soil at all depths. Differences in bulk density ranged from 0.14 g cm^{-3} in the 30-40 cm depth to 0.18 g cm^{-3} in the 3-10 cm depth (Table 3.7).

Table 3.7. Average bulk density at six soil depths in grassland, ecotone, and snowberry communities. Values for plant communities are means of nine study sites and those for soil texture classes are means of five coarse-textured soils or four fine-textured soils. The SE for means are in parentheses.

Plant community/ soil texture	Soil depth (cm) 0-3[1]	3-10	10-20	20-30	30-40	40-50
	Bulk density (g cm^{-3})					
Snowberry	0.76 **a** (0.07)	1.06 **a** (0.08)	1.16 **b** (0.07)	1.27 **a** (0.07)	1.29 **a** (0.07)	1.27 **a** (0.08)
Ecotone	0.86 **a** (0.08)	1.15 **a** (0.08)	1.24 **ab** (0.07)	1.32 **a** (0.07)	1.32 **a** (0.07)	1.35 **a** (0.06)
Grassland	0.90 **a** (0.08)	1.14 **a** (0.07)	1.32 **a** (0.06)	1.33 **a** (0.05)	1.35 **a** (0.05)	1.32 **a** (0.06)
Coarse texture	0.99 **a** (0.04)	1.30 **a** (0.03)	1.38 **a** (0.03)	1.46 **a** (0.02)	1.46 **a** (0.02)	1.48 **a** (0.03)
Fine texture	0.84 **b** (0.05)	1.12 **b** (0.03)	1.24 **b** (0.04)	1.31 **b** (0.04)	1.32 **b** (0.04)	1.31 **b** (0.03)

[1] Means within soil depth and plant community or within soil depth and soil texture class that are followed by the same letters are not statistically different (P>0.05).

3.3.3 Changes in mass, C, N, and C:N composition of roots in grassland, ecotone, and snowberry communities

Mass of fine roots was not different (P>0.14) in the snowberry, ecotone, and grassland communities. Conversely, the mass of fine roots was greater in fine- and coarse-textured soil at the 20-30, 30-40, and 40-50 cm depths (P<0.02)where the mass of fine roots was 0.3, 0.2, and 0.1 mg cm^{-3} greater in fine-textured than coarse-textured soils, respectively (Tables 3.8). The mass of fine roots was similar (P=0.56) in the 0-50 cm depth in fine- and coarse-textured soils.

The interaction between plant community and soil texture was not statistically significant for the mass of medium-size roots in the 0-50 cm depth (P=0.74). However, the mass of medium roots was 6.0 mg cm^{-3} greater (P=0.04) in the 0-3 cm depth of the ecotone than in the snowberry community (Table 3.9). Mass of medium roots was not different in snowberry, ecotone, and grassland communities in all other depth increments. With one exception, mass of medium roots was not affected by soil texture (P>0.12). The only difference observed in the mass of medium roots in coarse- and

fine-textured soils was at the 30-40 cm depth where mass of medium roots was 0.2 g cm^{-3} greater in fine-textured soil than in the coarse-textured soil (P=0.01) (Table 3.9).

Table 3.8. Average mass of fine roots in grassland, ecotone and snowberry communities. Values for plant communities are means of nine study sites and those for soil texture classes are means of five coarse-textured soils or four fine-textured soils. The SE for means are in parentheses.

	Soil depth (cm)						
Plant community/ soil texture	0-50[1]	0-3	3-10	10-20	20-30	30-40	40-50
	FRM[2] ($kg\ m^{-2}$)	Fine root mass ($mg\ cm^{-3}$)					
Snowberry	0.7 **a** (0.03)	11.3 **a** (1.32)	2.3 **a** (0.16)	0.9 **a** (0.13)	0.6 **a** (0.07)	0.4 **a** (0.06)	0.3 **a** (0.05)
Ecotone	0.7 **a** (0.07)	9.4 **a** (1.15)	2.1 **a** (0.39)	0.9 **a** (0.07)	0.6 **a** (0.07)	0.5 **a** (0.06)	0.3 **a** (0.05)
Grassland	0.7 **a** (0.49)	9.2 **a** (0.86)	2.6 **a** (0.31)	1.0 **a** (0.06)	0.7 **a** (0.08)	0.5 **a** (0.06)	0.4 **a** (0.06)
Coarse texture	0.7 **a** (0.04)	9.9 **a** (0.96)	2.5 **a** (0.26)	0.9 **a** (0.07)	0.5 **b** (0.04)	0.4 **b** (0.04)	0.3 **b** (0.04)
Fine texture	0.7 **a** (0.05)	10.0 **a** (0.89)	2.1**a** (0.19)	1.0 **a** (0.07)	0.8 **a** (0.06)	0.6 **a** (0.06)	0.4 **a** (0.05)

[1] Means within soil depth and plant community or within soil depth and soil texture class that are followed by the same letters are not statistically different (P>0.05).
[2] Fine root mass

Table 3.9. Average mass of medium roots in grassland, ecotone, and snowberry communities. Values for plant communities are means of nine study sites and those for soil texture classes are means of five coarse-textured soils or four fine-textured soils. The SE for means are in parentheses.

	Soil depth (cm)						
Plant community/ soil texture	0-50[1]	0-3	3-10	10-20	20-30	30-40	40-50
	MRM[2] ($kg\ m^{-2}$)	Medium root mass ($mg\ cm^{-3}$)					
Snowberry	0.9 **a** (0.08)	10.5 **b** (2.06)	3.3 **a** (0.30)	1.6 **a** (0.24)	0.9 **a** (0.18)	0.5 **a** (0.09)	0.5 **a** (0.07)
Ecotone	1.0 **a** (0.09)	16.5 **a** (2.05)	3.6 **a** (0.39)	1.3 **a** (0.10)	0.7 **a** (0.07)	0.3 **a** (0.04)	0.3 **a** (0.05)
Grassland	1.0 **a** (0.06)	14.6 **ab** (1.64)	3.3 **a** (0.27)	1.2 **a** (0.14)	0.8 **a** (0.07)	0.5 **a** (0.05)	0.4 **a** (0.06)
Coarse texture	0.9 **a** (0.05)	12.1 **a** (1.61)	3.2 **a** (0.22)	1.4 **a** (0.18)	0.8 **a** (0.14)	0.5 **a** (0.07)	0.4 **a** (0.05)
Fine texture	1.0 **a** (0.06)	16.5 **a** (1.66)	3.5 **a** (0.28)	1.3 **a** (0.11)	0.6 **a** (0.06)	0.3 **b** (0.03)	0.3 **a** (0.05)

[1] Means within soil depth and plant community or within soil depth and soil texture class that are followed by the same letters are not statistically different (P>0.05).
[2] Medium root mass.

Mass of large roots was not affected by the interaction of soil texture and plant communities (P>0.35). The mass of large roots was, however, greater ($P \leq 0.01$) in

the snowberry community than in the ecotone or grassland community in the 0-3, 3-10, and 10-20 and 0-50 cm depths (Table 3.10). Mass of large roots was 3.8, 3.1, and 2.5 mg cm^{-3} greater in the snowberry community than the ecotone for the 0-3, 3-10, and 10-20 cm depths, respectively. The mass of large roots was also 0.7 kg m^{-2} greater in the snowberry community than the grassland community for the 0-50 cm depth ($P \leq 0.01$). Similarly, the mass of large roots was 4.7, 6.1, and 3.2 mg cm^{-3} greater in snowberry than grassland communities for the 0-3, 3-10, and 10-20 cm depth increments, respectively and 1.1 kg m^{-2} greater in snowberry than grassland communities for the 0-50 cm depth (Table 3.10). However, the mass of large roots was not different ($P>0.05$) between the ecotone and grassland community at all soil depths except 3-10 and 0-50 cm (Table 3.10). Large root mass at the 3-10 and 0-50 cm depths was 3.0 mg cm^{-3} and 0.4 kg m^{-2} greater ($P \leq 0.05$) in the ecotone than the grassland community (Table 3.10). Mass of large roots was not different ($P>0.05$) between fine- and coarse-textured soils at all depths.

Table 3.10. Average mass of large roots in grassland, snowberry, and ecotone communities. Values for plant communities are means of nine study sites and those for soil texture classes are means of five coarse-textured soils or four fine-textured soils. The SE for means are in parentheses.

	Soil depth (cm)						
Plant community/ soil texture	0-50[1]	0-3	3-10	10-20	20-30	30-40	40-50
	LRM[2] (kg m^{-2})	Large root mass (mg cm^{-3})					
Snowberry	1.2 **a** (0.19)	5.6 **a** (1.31)	6.5 **a** (0.99)	3.5 **a** (0.71)	1.1 **a** (0.45)	0.4 **a** (0.16)	0.2 **a** (0.06)
Ecotone	0.5 **b** (0.08)	1.8 **b** (0.77)	3.4 **b** (0.54)	1.0 **b** (0.34)	0.6 **a** (0.30)	<0.1 **b** (0.01)	<0.1 **b** (0.01)
Grassland	0.1 **c** (0.04)	0.9 **b** (0.87)	0.4 **c** (0.13)	0.3 **b** (0.15)	0.1 **a** (0.07)	None present	None present
Coarse texture	0.5 **a** (0.21)	2.0 **a** (0.80)	3.3 **a** (0.98)	1.5 **a** (0.70)	0.7 **a** (0.40)	0.2 **a** (0.13)	0.1 **a** (0.04)
Fine texture	0.6 **a** (0.11)	3.5 **a** (1.04)	3.5 **a** (0.79)	1.7 **a** (0.39)	0.5 **a** (0.14)	0.1 **a** (0.04)	<0.1 **a** (0.03)

[1] Means within soil depth and plant community or soil depth and soil texture class that are followed by the same letters are not statistically different ($P>0.05$).

[2] Large root mass.

The % C, % N, and C:N ratios of fine and medium roots were compared in grassland and snowberry communities in the 0-3, 3-10, 10-20, and 20-30 cm depths. Percent C in fine and medium roots was the same (P>0.05) in grassland and snowberry communities at the 0-3, 10-20, and 20-30 cm depths (Table 3.11). Carbon content of medium roots in the 3-10 cm depth was 5.9% greater (P≤0.05) in the snowberry community than in grassland (Table 3.11). Nitrogen content and the C:N ratio of fine and medium roots from snowberry and grassland communities were the same (P>0.05) at all depths (Table 3.11). The C content of roots in fine-textured soil was 3.9% greater (P≤0.05) than those in coarse-textured soil. Similarly, The N content of roots in fine-textured soil was 0.4% greater (P≤0.05) than in coarse-textured soil. The C:N ratio was therefore greater (P≤0.05) in roots from coarse-textured soil (Table 3.11).

Table 3.11. Percent C and N, and the C:N ratio of fine, medium, and large roots at four soil depths in grassland and snowberry communities. Values for plant communities are means of nine study sites and those for soil texture classes are means of five coarse-textured soils or four fine-textured soils. The SE for means are in parentheses.

Soil depth (cm)	Plant community/ soil texture	Root size class	% organic C[1]	% N	C:N
0-3	Grassland	Fine	41.7 **a** (0.8)	2.2 **a** (0.1)	19.7 **a** (0.5)
	Snowberry		43.2 **a** (1.4)	2.3 **a** (0.1)	19.4 **a** (0.8)
	Grassland	Medium	46.0 **a** (0.8)	1.4 **a** (0.1)	35.1 **a** (2.3)
	Snowberry		50.4 **a** (0.9)	1.4 **a** (0.1)	36.3 **a** (1.7)
3-10	Grassland	Fine	39.4 **a** (1.7)	1.9 **a** (0.1)	21.9 **a** (1.2)
	Snowberry		43.2 **a** (2.0)	1.9 **a** (0.1)	22.8 **a** (1.1)
	Grassland	Medium	44.5 **b** (1.9)	1.2 **a** (0.1)	38.9 **a** (3.0)
	Snowberry		50.4 **a** (0.8)	1.1 **a** (0.1)	47.0 **a** (5.1)
10-20	Grassland	Fine	38.5 **a** (2.2)	1.6 **a** (0.2)	25.4 **a** (1.4)
	Snowberry		44.9 **a** (1.8)	1.8 **a** (0.1)	26.3 **a** (1.8)
	Grassland	Medium	47.1 **a** (1.6)	1.0 **a** (0.1)	47.6 **a** (1.9)
	Snowberry		51.2 **a** (0.4)	1.0 **a** (0.1)	54.9 **a** (7.3)
20-30	Grassland	Fine	39.2 **a** (1.7)	1.5 **a** (0.1)	27.4 **a** (1.6)
	Snowberry		44.7 **a** (1.8)	1.7 **a** (0.1)	27.1 **a** (1.4)
	Grassland	Medium	47.4 **a** (1.6)	1.1 **a** (0.2)	48.3 **a** (4.6)
	Snowberry		50.9 **a** (0.7)	0.9 **a** (0.1)	53.0 **a** (4.0)
All depths	Coarse texture		42.7 **b** (1.0)	0.9 **b** (0.1)	36.0 **a** (2.3)
	Fine texture		46.6 **a** (0.5)	1.3 **a** (0.1)	29.9 **b** (1.2)

[1] Means within soil depths, plant community and root size class, or within soil texture class that are followed by the same letters are not statistically different (P>0.05).

3.3.4 Properties of aboveground phytomass in grassland, ecotone, and snowberry communities

Herbaceous, litter, shrub, and total aboveground phytomass was different among grassland, ecotone and snowberry communities in most cases ($P<0.01$) (Tables 3.12). Herbaceous phytomass was greatest in the grassland community (142 g m^{-2}, SE= 16), intermediate in the ecotone (99 g m^{-2}, SE= 11), and least in the snowberry community (44 g m^{-2}, SE= 7). Herbaceous phytomass was 98 g m^{-2} greater in grassland community than the snowberry community, 55 g m^{-2} greater in the ecotone than snowberry community, and 43 g m^{-2} greater in grassland community than ecotone (Table 3.12). The mass of plant litter in the snowberry community (1084 g m^{-2}, SE= 304) was 815 and 861 g m^{-2} greater ($P\leq0.05$) than in the ecotone (269 g m^{-2}, SE= 47) and grassland (223 g m^{-2}, SE= 51), respectively. Similarly, the mass of snowberry (740 g m^{-2}, SE= 94) was 519 g m^{-2} and 737 g m^{-2} greater ($P\leq0.05$) in snowberry communities than in the ecotone (221 g m^{-2}, SE= 37) and grassland communities (7 g m^{-2}, SE= 5), respectively (Table 3.12). Total aboveground phytomass was the same ($P>0.05$) in the ecotone and grassland communities, but it was 1280 and 1497 g m^{-2} greater in snowberry (1868 g m-2, SE= 354) than in ecotone (588 g m-2, SE= 66) and grassland communities (371 g m-2, SE= 63), respectively (Table 3.12). Conversely, phytomass was the same between coarse and fine soils ($P>0.05$) (Table 3.12).

The % C, % N, and C:N ratios in herbaceous, snowberry, and litter phytomass was the same in grassland and snowberry communities ($P>0.05$) (Table 3.13). The C content of plant litter was 2.4% greater ($P<0.05$) in snowberry than grassland community. Average % C, % N, and C:N ratios in herbaceous, snowberry, and litter phytomass was the same for coarse- and fine-textured soils ($P<0.05$) (Table 3.13).

Table 3.12. Average aboveground herbaceous phytomass and mass of plant litter, snowberry, and total aboveground phytomass in grassland, ecotone, and snowberry communities. Values for plant communities are means of nine study sites and those for soil texture classes are means of five coarse-textured soils or four fine-textured soils. The SE for means are in parentheses.

Plant community/ soil texture	Herbaceous phytomass [1]	Litter phytomass	Snowberry phytomass	Total aboveground phytomass
	---------- Mass (g m^{-2})----------			
Snowberry	44 **c** (7)	1084 **a** (304)	740 **a** (94)	1868 **a** (354)
Ecotone	99 **b** (11)	269 **b** (47)	221 **b** (37)	588 **b** (66)
Grassland	142 **a** (16)	223 **b** (51)	7 **c** (5)	371 **b** (63)
Coarse texture	90 **a** (12)	392 **a** (90)	344 **a** (97)	827 **a** (175)
Fine texture	99 **a** (17)	658 **a** (258)	301 **a** (101)	1058 **a** (329)

[1] Means within plant communities and cover type and within soil type and cover type that are followed by the same letters are not statistically different (P>0.05).

Table 3.13. Average percent C and N and C:N ratios for grass, snowberry, and litter, in grassland and snowberry communities and for total aboveground phytomass in coarse and fine-textured soils. Values for plant communities are means of nine study sites and those for soil texture classes are means of five coarse-textured soils or four fine-textured soils. The SE for means are in parentheses. The SE of means are in parentheses.

Aboveground phytomass	Community/ soil texture class	% organic C [1]	% N	C:N
Herbaceous	Grassland	44.8 **a** (0.3)	1.2 **a** (0.1)	37.7 **a** (2.1)
	Snowberry	44.0 **a** (0.4)	1.2 **a** (0.2)	34.8 **a** (1.9)
Snowberry	Grassland	none present	none present	none present
	Snowberry	48.4 (1.0)	0.8 (0.1)	58.1 (3.0)
Litter	Grassland	41.0 **b** (0.9)	1.7 **a** (0.1)	24.2 **a** (1.4)
	Snowberry	43.4 **a** (1.0)	1.6 **a** (0.1)	27.1 **a** (1.2)
Average aboveground phytomass	Coarse texture	41.6 **a** (2.2)	1.2 **a** (0.1)	38.8 **a** (3.1)
	Fine texture	45.2 **a** (0.5)	1.4 **a** (0.1)	35.4 **a** (2.3)

[1] Means of % C, %N, or C:N within plant material type and community/soil texture class that are followed by the same letters are not statistically different (P>0.05).

3.4 Discussion

This research revealed that SOC did not vary among snowberry, ecotone, and grassland communities in Mixed and Moist Mixed Grasslands. The lack of correlation between SOC and cover or mass of shrubs differs from the response reported in other studies. For example, Jackson et al. (2002) concluded that relatively dry sites along a 200 to 1,100 mm precipitation gradient gained SOC following invasion of woody species, such as mesquite (*Prosopsis* spp.), creosote (*Larrea* spp.), and juniper (*Juniperus* spp.). Conversely, relatively wet sites along the precipitation gradient lost SOC following invasion by shrubs. SOC content increased in the upper 1 m of soil by up to 33% at dry sites and was reduced by up to 57% at wet sites (Jackson et al. 2002). This response of SOC to snowberry invasion reported by Jackson et al. (2002) may suggest SOC would be the same in grassland and snowberry communities at sites that are intermediate along the precipitation regime. At first glance, the neutral response of SOC to snowberry invasion in the Prairie Ecozone of Saskatchewan may seem to suggest that the study sites are intermediate along the precipitation gradient studied by Jackson et al. (2002). However, the study sites used for this research are comparable to the dry sites used by Jackson et al. (2002). The precipitation:evaporation ratio may be a better environmental gradient than annual precipitation for studying response of SOC to snowberry invasion because it would improve comparison of SOC responses across sites.

Different responses of SOC reported by Jackson et al. (2002) and those observed in the present study could be caused by the different shrub species. Another plausible explanation for the different responses reported in Jackson et al. (2002) and the present study may be related to the relatively large amount of SOC in the soils of Mixed Prairie. If the initial SOC content of soil is relatively large it would require a greater SOC response before differences between shrub and grassland communities could be detected. The use of coarse- and fine-textured soils in Saskatchewan accounted for this potential effect of initial carbon content in grassland because the

coarse textured soils have relatively low SOC content compared to fine-textured soils. However, the lack of response in SOC in the coarse-textured soils, which are SOC poor, refutes the latter argument.

Transport of sediment and C by wind into the shrub community is another possible explanation for the different amounts of SOC in shrub-invaded grassland in the present study and that of Jackson et al. (2002). Ground cover in the Mixed Prairie is greater than the desert communities described by Jackson et al. (2002). Wind-transported sediment may be greater in desert communities than in Mixed Prairie; furthermore sediments could be deposited in the shrub community and could be a source of C.

The hypothesis that snowberry invasion into grassland does not affect SOC content is supported by the present research. Aboveground plant phytomass was greater in the snowberry community than in the ecotone and grassland communities, but SOC was similar among snowberry, ecotone, and grassland communities. This conclusion is not supported by Hibbard et al. (2001) who concluded that soil C in the 0-10 cm depth was 0.84% in herbaceous communities and 1.4 to 2.3% in shrub or tree communities. However, this research was conducted in a subtropical savanna in Texas, where honey mesquite (*Prosopis juliflora* var. *glandulosa* Torr.) invaded herbaceous plant communities. Barth and Klemmedson (1978) also concluded that SOC declined by 55 to 60% in the upper soil depth and by 22 to 24% in the 30-60 cm depth as horizontal distance from palo verde (*Cercidium floridum* Benth.) or velvet mesquite (*Prosopis juliflora* (Swart) DC) increased. Hudak et al. (2003) also concluded that SOC at the 0-5 cm depth of the soil profile was greater in shrub than herbaceous plant communities. They speculated that this increase in SOC could be attributed to herbaceous plants, leading them to hypothesize that SOC declines as shrub cover increases and canopy cover of herbaceous plants declines. The assertion by Hudak et al. (2003) that herbaceous cover in the understory could affect SOC is not supported by the present research.

The measurement of SOC along the snowberry, ecotone, grassland plant community gradient in the present study was designed to determine if SOC increases or decreases when the plant community composition is comprised of: 1) high percent snowberry cover and low percent herbaceous cover (snowberry community); 2) mixed snowberry and herbaceous cover (ecotone); and 3) high percent herbaceous cover with no snowberry (grassland). Soil organic C was the same in the snowberry, ecotone, and grassland communities, but SOC was greater in fine-textured soils than coarse-textured soils. Soil texture plays a much greater role in governing SOC than does plant community composition. Studies that support the conclusion that SOC is mostly dependent on soil texture include Burke et al. (1989), Bosatta and Agren (1997), and Galantini et al. (2004). Explanations for the positive relationship between clay and silt and SOC include physical protection of organic matter and formation of organomineral complexes (Galantini et al. 2004) and lower decomposition rates in clayey soils relative to sandy soils (van Veen et al. 1985).

Similar root mass in the snowberry, ecotone, and grassland communities provides a possible explanation for the lack of increase or decrease of SOC following a change in species composition. However, this explanation is refuted by the lack of correspondence between SOC and greater mass of roots in some soil depths. For example, the mass of fine roots was greater in fine-textured soil than in coarse-textured soil at the 20-50 cm depths, but root mass did not correspond with SOC. The lack of correspondence between root mass and SOC is likely due to the relatively great amount of C in soil compared to the small amount of C that could be input to soil from roots at a point in time. In addition, it is likely that the mass of roots present changes more rapidly than SOC, thus it may not be possible to correlate the mass of roots at one point in time with SOC. Greater mass of fine roots in fine-textured soils is likely caused by slower decomposition relative to that in coarse-textured soils. This assertion is discussed in more detail in Section 5.0, where the decomposition of roots and leaves were studied. The mass of medium roots was not different among the three plant communities, except at the 0-3 cm depth where the mass of these roots was greater in

ecotone than in the snowberry community. As with fine roots however, the mass of medium roots did not correspond with SOC. Mass of large roots exhibited the greatest difference among the three plant communities. The mass of large roots in the 0-3, 3-10 and 10-20 cm depths was greater in the snowberry community than in the ecotone or grassland communities because the rhizomes of snowberry are larger than the roots of forbs and graminoids. Soil organic C did not correspond with the mass of large roots.

Carbon content of fine or medium roots did not correspond with SOC in the upper 10 cm of soil. This lack of correspondence does not explain why SOC was not greater in areas where the mass of roots was relatively great. A plausible explanation for the lack of correspondence between root mass and SOC may be that the SOC pool is so great that the mass of roots, as measured in a single growing season, is relatively insignificant. A second explanation is that the mass of roots is relatively constant over time as determined by production and decomposition. It is also possible that decomposers respond relatively rapidly to root production, and decomposition rate may correspond with root production in a growing season. However, evidence of this relationship is currently lacking.

3.5 Summary

Soil organic carbon was not different in snowberry, ecotone, or grassland communities. Therefore, the null hypothesis that SOC is similar between snowberry and grassland communities is accepted. However, the hypothesis that aboveground phytomass is equal in snowberry, ecotone and grassland communities is rejected because snowberry communities had the greatest phytomass while the grassland community had the least phytomass. The lack of correspondence between aboveground phytomass and SOC leads to the conclusion that phytomass production and species composition have less effect on SOC than was hypothesized.

The null hypothesis that the mass of fine and medium roots is equal in snowberry and grassland communities is accepted. However, the null hypothesis that

the mass of large roots is equal among snowberry, ecotone, and grassland communities is rejected. It is possible the origin of SOC is primarily from fine and medium roots, which are relatively consistent along the snowberry-ecotone-grassland gradient.

Coarse-textured soils had less SOC than fine-textured soils. Conversely, aboveground phytomass was not statistically different on coarse- and fine-textured soils and soil texture had negligible effects on root mass. The role of soil texture in the SOC balance of snowberry and grassland communities therefore is not to regulate SOC by influencing the species and phytomass produced. It is, however, likely that soil texture plays a role in the C budget by regulating C efflux from soil. The efflux is regulated by the chemical and physical protection of organic matter in a soil; the capacity of soil to protect soil organic matter increases with clay content.

An assumption made at the outset of this research was that changes to the amount and type of plants on a site affect soil carbon content. However, aboveground phytomass and root mass was not different in coarse- and fine-textured soils but mass of SOC was different in these soils. The lack of change of SOC suggests that species composition, aboveground phytomass and root mass are not primary factors that determine the SOC content in the Prairie Ecozone, at least not in the plant communities studied. The hypothesis that SOC is greater on sites with greater phytomass is therefore not accepted because SOC is greater in fine-textured soils, despite similar amounts of phytomass at sites with fine- and coarse-textured soils. Snowberry invasion into grasslands did not reduce SOC.

4.0 EFFECTS OF CATTLE GRAZING ON THE MASS OF ROOTS, ABOVEGROUND PHYTOMASS, AND SOIL ORGANIC CARBON IN THE PRAIRIE ECOZONE OF SASKATCHEWAN

4.1 Introduction

Livestock grazing has potential to indirectly alter the soil carbon balance by impacting the physical, chemical, and biological processes that regulate it. Herbivores influence grassland soil functions by accelerating nutrient cycling in patches where wastes are deposited (Day and Delting 1990, Jaramillo and Delting 1992). Herbivores also increase decomposition rates by reducing C:N ratios of plant shoots (Holland et al. 1992) and roots (Risser and Parton 1982, Seastedt 1985) and by affecting mineralization (Holland and Delting 1990, Frank and Groffman 1998). Herbivory may affect the soil food-web, and therefore SOC, by influencing root exudates which in turn affect soil organisms (Bardgett et al. 1998). Longer-term effects of grazing on soil organisms may be triggered by herbivory if root and belowground net primary production are altered, if plant litter quality changes, or if plant species composition changes (Bardgett et al. 1998). Grazing management may therefore affect factors that control the quality and quantity of SOC in grasslands.

Grazing management strategies that maintain grassland species composition and structure are predicted to increase SOC on grasslands in the United States relative to overgrazed grassland where species composition is modified (Schuman et al. 2002). Conversely, overgrazing may reduce SOC by altering C input from litter, increasing soil temperature, altering microbial activity, and increasing the frequency of wet-dry cycles (Abril and Bucher 2001). However, previous studies indicate that the response of SOC to grazing management is variable. Conant et al. (2001) noted that the majority of studies concluded grazing increased soil C most in warm, dry regions. They also concluded that the average annual rate of SOC increase was 7.7 %

for studies in areas with a long history of grazing while sites with a relatively short grazing history lost an average of 1.8%. Other studies that indicate total soil C is influenced by grazing management include Bauer et al. (1987) and Conant et al. (2003). Conversely, studies that indicate grazing does not alter SOC include Milchunas and Lauenroth (1993), Mathews et al. (1994) and Manley et al. (1995).

The varied conclusions about the effect of grazing on SOC suggests that SOC may be dependent on the grazing regime, site conditions, or grassland community composition. For example, heavy grazing did not affect SOC relative to an exclosure, but soil in the moderately grazed grassland contained less organic carbon than the exclosure (Frank et al. 1995). Frank et al. (1995) speculated that carbon removal by grazing animals in the moderately grazed grassland may reduce SOC while an increase in the dense shallow roots of blue grama (*Bouteloua gracilis* (HBK) Lag.) in heavily grazed grassland accounted for maintenance of SOC relative to the control. Total carbon, alcohol/benzene extractable carbon, and alkaline-soluble carbon increased following 19 years of heavy grazing relative to light or no grazing because the amount and kind of roots changed with species composition in heavily grazed areas (Smoliak et al. 1972). Total carbon and concentration of carbon increased following grazing, and the increases were caused by replacement of species such as needle-and-thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth) with blue grama (Dormaar et al. 1984, Dormaar and Willms 1990). Alternatively, 12 years of heavy grazing on previously ungrazed Mixed Prairie in Wyoming did not alter SOC in the 0-60 cm depth relative to light grazing (Schuman et al. 1999). In Alberta, grazing had no affect on SOC despite greater mass of vegetation and litter in ungrazed than in grazed grassland (Henderson et al. 2004).

SOC decreased as stocking rate increased on one soil type while SOC was similar in grazed and ungrazed treatments for another soil (Potter et al. 2001). Soils where SOC decreased with increasing stocking rate had greater sand content and less initial SOC in the control relative to the soil in which grazing effects were not detected. It therefore appears that the effect of grazing on SOC may be dependent on

site factors such as soil texture and the initial SOC content. Spatial and temporal variability of climate, soil characteristics, disturbance history, and other site and environmental conditions may determine whether grazing increases or decreases SOC. This conclusion would explain why reports are contradictory as a whole, despite conclusive site-specific findings.

The research reported herein provides additional information on the effect of grazing on sequestration of SOC in the Brown and Dark Brown Soil Zones in Saskatchewan. The primary objective of the research described in this chapter was to determine if SOC corresponded with plant community characteristics in ungrazed or heavily grazed grasslands. The second objective was to determine if SOC corresponded with the mass of roots, aboveground phytomass or soil texture. The hypothesis relevant to the first objective of this research is that SOC does not correspond with species composition in grassland. The hypotheses related to the secondary objectives are that: (1) SOC corresponds with root mass in grassland; (2) SOC decreases where above ground phytomass production is reduced by heavy grazing, and; (3) the effect of grazing on SOC was different between coarse-textured and fine-textured soils.

4.2 Materials and methods

4.2.1 Site selection and description

Nine heavily grazed grasslands in fair or poor range condition and nine ungrazed grasslands in good or excellent condition were selected for this study (Abouguendia 1990) (Table 4.1). Sites in good or excellent range condition were located first and a suitable heavily grazed site within 2 km was located for comparison. The grazed sites were heavily grazed for more than 10 years before the present study was conducted.

4.2.2 Experimental design

Three transects were established at each study site and four, 2 x 2 m study plots were located along each transect (Figure 4.1). Each study site consisted of a grazed and an ungrazed treatment. Two plots per transect were located in the ungrazed area and two were located in the grazed area (6 plots in grazed and six plots in ungrazed at each replicated study site). Plots within the grazed and ungrazed grassland were located about 10 to 50 m apart. Although assignment of grazing treatments were paired in this manner, soil texture varied in grazed and ungrazed treatments at some sites, particularly those where the grazing treatments were greater than 1 km apart. This textural difference led to classification of sites by soil texture and grazing treatment for the analyses.

Figure 4.1 Diagram of the transect and plot layout at one site for studying the effect of livestock grazing on plant species composition, standing crop, and soil organic carbon.

Table 4.1 Descriptions of nine study sites in central and southern Saskatchewan for studying the effect of grazing on soil organic carbon, root mass, and aboveground phytomass.

Site and study year	Soil association Landscape class, and Ecoregion	Dominant graminoids	Township	Grazing history
Matador North 2003	Sceptre Lacustrine plain Mixed Grassland	*Elymus lanceolatus* ((Scribn. & J.G. Sm.) Gould)) *Koeleria macrantha* (Ledeb.) J.A. Schultes *Nassella viridula* (Trin.) Barkworth	S13 T20 R14 W3	Ungrazed plots protected from livestock for over 15 years. Grazed plots heavily grazed for over 15 years
Matador South 2003	Sceptre Lacustrine plain Mixed Grassland	*Nassella viridula* *Elymus lanceolatus* *Bouteloua gracilis*	T20 R14 W3 (1 km south of Matador North)	Ungrazed plots protected from livestock for over 15 years. Grazed plot heavily grazed for over 15 years
Biddulph 2003	Dune Sand Fluvial plain Moist Mixed Grassland	*Hesperostipa comata* *Koeleria macrantha*	S12 T34 R5 W3	Ungrazed plots protected from livestock for over 15 years. Grazed plots heavily grazed for over 15 years
Kernen 2004	Elstow (ungrazed) Weyburn (grazed Lacustrine plain Moist Mixed Grassland	*Festuca hallii* (Vasey) Piper *Elymus lanceolatus*	S9 T37 R4 W3	Ungrazed plots protected from livestock for over 15 years. Grazed plots heavily grazed for over 10 years
Outlook 2004	Dune Sand Lacustrine plain Moist Mixed Grassland	*Hesperostipa comata* *Koeleria macrantha*	T29 R8 W3	Ungrazed plots protected from livestock for about 15 years. Grazed plots heavily grazed for over 10 years
Monet 2004	Haverhill Hummocky Shallow Lacustrine Mixed Grassland	*Elymus lanceolatus* *Hesperostipa comata*	T24 R15 W3	Ungrazed plots protected from livestock for about 10 years. Grazed plots moderately grazed for over 15 years
Kindersley 2004	Haverhill Shallow lacustrine plain Moist Mixed Grassland	*Hesperostipa comata* *Elymus lanceolatus*	T29 R24 W3	Ungrazed plots protected from livestock for over 8 years. Grazed plots moderately grazed for over 15 years
Aberdeen 2004	Weyburn Hummocky Morainal Moist Mixed Grassland	*Hesperostipa comata* *Elymus lanceolatus* *Festuca hallii*	T37 R2 W3	Lightly grazed plots are located in a remote section of the range management unit. Grazed plots heavily grazed for more than 10 years.
Macrorie 2004	Haver Hummocky morainal Moist Mixed Grassland	*Elymus lanceolatus*	T26 R9 W3	Ungrazed plots protected from livestock for over 15 years. Grazed plots heavily grazed for over 10 years

4.2.3 Biophysical data collection

Dependent variables measured or estimated included aboveground phytomass, species composition, percent canopy and basal cover of vascular species, soil organic carbon, root mass, soil texture, and bulk density. Aboveground phytomass, species composition, and percent canopy cover were determined in August 2003 or 2004 in a 1 x 1 m subplot. Litter was collected from the soil surface by raking it and collecting it in paper bags. Live and recently senesced forb and graminoid plant material was clipped at ground level and stored in separate paper bags. Litter and forbs and graminoids were dried at 85^{o} C to a constant mass.

Species composition and percent canopy cover were determined by identifying and recording all species within 8, 0.5 x 0.5 m subplots per plot in August 2003 or 2004 (24 subplots in grazed and 24 in ungrazed treatments per site) (Bonham 1989). Ground cover of litter, bare ground, feces, and rock was also estimated. The eight subplots were positioned in the same location as aboveground phytomass was sampled and adjacent to the area where soil sample cores were extracted. Canopy cover was visually estimated to the nearest 5% for all species in each subplot. Mean percent cover per plot was calculated by summing the estimated percent cover of each species and dividing by the number of subplots (n=8).

Basal cover in grazed and ungrazed treatments was also measured in 2003 or 2004 using the point frame method (Hanson 1934, Bonham 1989). The point frame consisted of 20 pins (points) with 2.5 cm spacing. A starting point in each treatment was randomly determined and frames were placed along a linear transect originating from that point. Data were collected at 600 points (30 frames) in each grazing treatment at the nine study sites. Basal cover was determined by lowering a pin at about an 85^{o} angle to the soil surface and recording the species or ground cover category present where the sharpened point of the pin met the soil surface.

Soil samples for measuring root mass were collected in June 2003 or 2004. A hydraulic-powered punch with a 6.5 cm diameter core was used to collect three soil cores (subsamples) from 0 to 50 cm deep at each plot. Plant litter was removed from the soil surface before collecting soil samples. Soil cores were divided into 0-3, 3-10, 10-20, 20-30, 30-40, and 40-50 cm depth increments and the three subsamples for each soil depth increment were pooled. Pooled samples for each increment were stored in paper bags, labeled, and stored at room temperature for more than 2 months before determining the mass of roots.

Root mass was determined by placing the pooled soil sample from one plot on a 3 x 3 mm mesh screen that was placed over a 20 L pail. A second screen with 1 x 1 mm mesh was draped inside the pail and underneath the 3 x 3 mm screen. Warm water was sprayed onto the soil and root sample and large and medium roots were collected from the 3 x 3 mm screen after the soil was removed. Roots remaining on top of the 3 x 3 mm screen were sorted by hand into large (greater than 3 mm diameter) and medium (less than 3 mm diameter) size classes. Roots that remained on the 1 x 1 mm screen were also collected and combined with the medium roots from the 3 x 3 mm screen. Plant materials floating in the water after the 1 x 1 mm screen was removed were collected with a hand-held sieve with mesh size less than 0.5 x 0.5 mm. Roots collected from the water were categorized as fine.

Roots in the large and medium categories were easily identifiable as roots. However, the small plant fragments that comprise the fine samples were unidentifiable, and consisted of small roots, fractions of roots, sloughed root epidermis, and fragmented and partly decomposed leaves and stems. All root samples for each depth increment were stored in tin cans, oven dried at 85^{o} C to a constant mass and weighed using a closed microbalance. Root material was stored at room temperature in labeled paper envelopes.

Bulk density of soil was determined using the core method (Blake and Hartge 1986). Bulk density was determined for the 0-3, 3-10, 10-20, 20-30, 30-40, and 40-50 cm depths. The soil samples were collected by digging a hole in each plot with a spade

and inserting a bulk density tube into the soil at the midpoint of each depth increment. Soil tubes were pushed into the coarse-textured soil by hand or pounded into fine-textured soils. Bulk density tubes were extracted from the soil by digging out a section of soil in front of the tubes. Soil was then shaved off the openings of the tubes using a knife. Soil samples from the cores at each depth increment for all plots were placed in tin cans and transported to the laboratory. Soil samples were dried at 85^{o} C to a constant mass and weighed.

Soil samples were air dried and ground after removing recognizable plant materials by sieving or hand-picking; however, some plant materials could not be removed from soil clods. Approximately 50 g of dried soil was placed in a ball grinder for 2 to 3 minutes, or until the sample was either a fine powdery texture (fine-textured soil) or the sample was comprised exclusively of individual soil particles (coarse-textured soil). The ground soil samples were stored in plastic drum vials at room temperature after grinding. A Leco CR-12 Carbon Analyzer was used to measure SOC (Wang and Anderson 1998). Approximately 0.15 g of the finely ground soil was placed into the carbon analyzer which was set at 840^{o} C (Wang and Anderson 1998). Organic carbon in each sample was completely oxidized within 2 minutes. The carbon analyzer measured percent organic carbon in the soil sample.

Sample adequacy for measuring SOC was determined by Bowman (1991) for loamy and sandy loam soil. According to Bowman (1991), 9 and 16 samples, respectively, are adequate for measuring SOC having a 95% confidence limit and an error of 10%. For this study, the sample adequacy was calculated using Equation 4.1 from Bowman (1991), where t is the Student's t-value at p=0.05, CV is the coefficient of variation, and E is the allowable error. Consequently, 18 subsamples per treatment were collected and pooled for measuring SOC at all study sites.

$$n = (t)^2 (CV\%)^2 / (E\%)^2 \qquad \text{(Equation 4.)}$$

The percent sand, silt, and clay in the A horizon of samples collected from each plot was determined using a hydrometer method similar to that described by Gee and Bauder (1979) and based on Bouyoucos (1962). The analysis was completed as described in section 3.2.3.

4.2.4 Century model simulation

The Century model is a process model that simulates soil organic matter cycles in a variety of ecosystems (Parton et al. 1987). The model consists of several submodels including soil organic matter and plant production submodels. The soil organic matter submodel, which was the focus of this simulation, compartmentalizes SOC into active, slow, and passive pools. These pools are described in more detail in section 2.0. The model is useful for describing these different pools because it calculates the flow of carbon between them as determined by microbial decomposition which is regulated in the model by the environmental parameters specified.

Century version five was used to model total soil carbon and the active, slow, and passive SOC fractions. Default site parameters were used for a temperate grassland with the exception of maximum and minimum air temperature, total precipitation, and soil texture. The model uses a monthly time step to calculate output values, thus the driving variables are monthly average maximum air temperature, monthly precipitation, soil texture, dead plant material nutrient and lignin content, and atmospheric and soil inputs of N (Parton and Rasmussen 1994). Monthly mean precipitation and temperature data were obtained from the Environment Canada weather station nearest to the site being modeled (Environment Canada 2004). Data from the Environment Canada weather station were also used to calculate monthly standard deviations and skewness for each environmental variable. Soil texture data were obtained from Biddulph, and Matador North, which are the two sites that were modeled for the simulation. These sites were chosen because soils are coarse-textured at Biddulph and fine-textured at Matador.

The management regime for the simulation was set up to run using climate normals for all simulations. Year 1 through 1924 was run without grazing to reach an approximate equilibrium in the carbon balance. Grazing was introduced in 1925 and it continued through 2504. Data were reported at 1924, 2004 and every 100 years thereafter through 2504. The management regime was programmed with grass initiating growth in May and senescing in August. The simulation was repeated three times for each study site; once for no grazing from year 1 through 2504, once with no grazing from year 1 through 1924 and light grazing from 1925 through 2504, and once with no grazing from year 1 through 1924 and heavy grazing from 1925 through 2504. The heavy grazing regime was programmed to have a quadratic effect on production while light grazing did not affect production. The grazing in the light and heavy grazing strategies was programmed to start in early June and end on October 31. The output variables from the simulation used in the analysis were total soil carbon and the active, slow, and passive SOC pools.

The Century model was originally validated by simulating steady-state soil C and N levels and above ground production for 24 sites in the Great Plains (Parton et al. 1987). The model was validated for this study by comparing simulation scenarios to measured total soil organic carbon values in the 3 to 10 cm soil depth from the two study sites. The model was deemed to be parameterized appropriately for the simulation of the test sites because the simulation of total soil C was within 10 %, of the actual measured values at the study sites.

4.2.5 Data analysis

The General Linear Model analysis of variance for a randomized complete block design was used to analyze effects of grazing treatments and soil texture class and their interactions (Zar 1999). A Tukey multiple comparison test was used for pairwise comparisons of means (Zar 1999). All analyses were conducted using Minitab® Release 14.1 (Minitab Inc. 2003) and a critical value of $P \leq 0.05$ was used for evaluating statistical significance.

The averages of grazed and ungrazed treatments at each of the nine study sites were analyzed for each dependent variable. Sites were also classified as coarse-textured (< 45% sand) or fine-textured (>45 % sand) for the analyses. Effects were determined for grazing treatments, soil texture, and the interaction of grazing and soil texture. The potential correlation among species composition, environmental variables, and study sites was explored using ordination techniques available in CANACO (version 4.5) (ter Braak and Šmilauer 2002). The initial ordination analysis performed was a detrended canonical correspondence analysis (DCCA). The DCCA was conducted to determine the standard deviation of the plant species gradients for each ordination axis. The standard deviation of the first axis was less than three and indicated that the model is linear (ter Braak and Šmilauer 2002). Redundancy analysis (RDA) is therefore an appropriate technique for exploring the relationship among species and the biophysical variables comprising this dataset. The RDA was run using Hill's technique to scale species response and species scores were divided by standard deviations to reduce the dominant effect that species with large variance have on the ordination diagram (ter Braak and Šmilauer 2002). Environmental data were also centered and standardized because units of measure vary among the variables and scaling was focused on inter-sample distances instead of inter-species distances (ter Braak and Šmilauer 2002). Species that occurred in fewer than 5% of the study plots were omitted from the RDA to reduce the influence of rare species (McCune and Grace 2002). Correlated environmental variables were also removed from the RDA using manual forward selection (ter Braak and Šmilauer 2002). Forward selection is a step-wise process that uses a Monte Carlo test with 9999 unrestricted permutations to calculate the significance of each environmental variable (ter Braak and Šmilauer 2002). Variables with $P > 0.05$ were omitted from the RDA model. The Pearson product moment correlation coefficient was used to measure the degree of linear relationship between pairs of variables that were included in the RDA model.

4.3 Results

4.3.1 Effects of grazing on plant cover and phytomass

Grazing reduced herbaceous, litter, and total aboveground phytomass in the grasslands. Herbaceous phytomass was 241 g m^{-2} (SE= 29) and 111 g m^{-2} (SE=15) in ungrazed and grazed grasslands ($P<0.01$), respectively, while mass of litter was 46 g m^{-2} (SE= 22) and 252 g m^{-2} (SE=35) in grazed and ungrazed grasslands, respectively. Total aboveground phytomass was 493 g m^{-2} (SE= 46) and 157 g m^{-2} (SE= 27) in ungrazed and grazed grassland, respectively (P=(Table 4.2). However, the herbaceous phytomass (182 g m^{-2}, SE= 31 and 172 g m^{-2}, SE= 33), litter (151 g m^{-2}, SE= 43 and 147 g m^{-2}, SE= 48), and total aboveground phytomass (333 g m^{-2}, SE= 61 and 314 g m^{-2}, SE= 73) were not different ($P>0.77$) between coarse and fine soils, respectively (Table 4.2).

Table 4.2. Average herbaceous phytomass, litter mass, and total aboveground phytomass in grazed or ungrazed grasslands with coarse- or fine-textured soil. Values for grazing treatment are means of nine study sites and means of texture classes are of five coarse-textured or four fine-textured soils. The SE for means are in parentheses.

Grazing treatment/ soil class	Herbaceous phytomass [1]	Litter	Total aboveground phytomass
	----------Mass (g m^{-2})----------		
Grazed	111 **b** (15)	46 **b** (22)	157 **b** (27)
Ungrazed	241 **a** (29)	252 **a** (35)	493 **a** (46)
Coarse texture	182 **a** (31)	151 **a** (43)	333 **a** (61)
Fine texture	172 **a** (33)	147 **a** (48)	314 **a** (73)

[1] Means within phytomass type and grazing or soil texture classes that are followed by the same letters are not statistically different ($P>0.05$).

Grazing reduced the basal cover of decreaser graminoids (P=0.05), which are species that decrease in relative importance under continued heavy grazing (Abouguendia 1990), and litter ($P<0.01$). Basal cover of increaser forbs was also different (P=0.05) averaging 36 (SE= 11.3) and 11 % (SE= 6.6) in grazed and the

ungrazed grasslands, respectively (Table 4.3). The basal cover of decreaser graminoids was twice as great in ungrazed than in the grazed grassland (Table 4.3). Litter cover was also 40 % greater in ungrazed than grazed grassland while bare ground was about 20 % more on grazed than ungrazed areas (Table 4.3).

An ordination joint plot of the RDA indicated that species composition was different between grazed and ungrazed grassland (Figure 4.2). Rough fescue (*Festuca hallii* (Vasey) Piper), northern wheatgrass (*Elymus lanceolatus* (Scribn. & J.G. Sm.) Gould), porcupine grass (*Hesperostipa curtiseta* (A.S. Hitchc.) Barkworth), and green needlegrass (*Nassella viridula* (Trin.) Barkworth) corresponded positively with ungrazed swards. Conversely, fringed sage (*Artemisia frigida* Willd.), clubmoss (*Selaginella densa* Rydb.), blue grama, and needle-and-thread corresponded positively with heavy grazing.

Table 4.3. Average basal cover of forbs and graminoids and ground cover on grazed and ungrazed sites with coarse or fine soils (n=600). The SE for means are in parentheses.

Grazing treatment/ soil class	Decreaser forb[1]	Increaser forb	Decreaser graminoid	Increaser graminoid	Litter	Bare ground	lichen	Moss
Grazed	0.1 **a** (0.1)	36.3 **a** (11.3)	3.4 **b** (1.2)	4.3 **a** (1.4)	28.3 **b** (6.9)	21.6 **a** (9.2)	5.2 **a** (2.1)	None
Ungrazed	0.2 **a** (0.1)	11.3 **b** (6.6)	7.7 **a** (1.5)	2.4 **a** (0.4)	68.6 **a** (7.3)	0.7 **b** (0.3)	3.7**a** (1.3)	5.2 (4.5)
Fine texture	0.31 **a** (0.18)	30.7 **a** (12.0)	6.5 **a** (1.4)	4.2 **a** (1.3)	45.4 **a** (1.7)	8.1 **a** (5.4)	4.0 **a** (1.5)	0.4 **a** (0.2)
Coarse texture	0.03 **a** (0.03)	18.3 **a** (8.4)	4.8 **a** (1.6)	2.7 **a** (0.7)	50.9 **a** (9.3)	13.6 **a** (8.4)	4.7 **a** (1.9)	4.4 **a** (4.1)

[1] Means within a cover type and grazing or within cover type and soil texture class that are followed by the same letters are not statistically different (P>0.05).

Species that did not correspond with grazing treatment included rose (*Rosa* sp.), hairy golden aster (*Heterotheca villosa* (Pursh) Shinners), Missouri goldenrod (*Solidago missouriensis* Nutt.), and sand grass (*Calamovilfa longifolia* (Hook.) Scrib). Percent sand, % N in the 3-10 cm depth, mass of medium roots in the 3-10 cm and 30-40 cm depths, mass of fine roots in the 10-20 cm depth, percent clay, and herbaceous phytomass were statistically significant environmental variables and were included in the RDA model (Table 4.4). The first four axes of the RDA

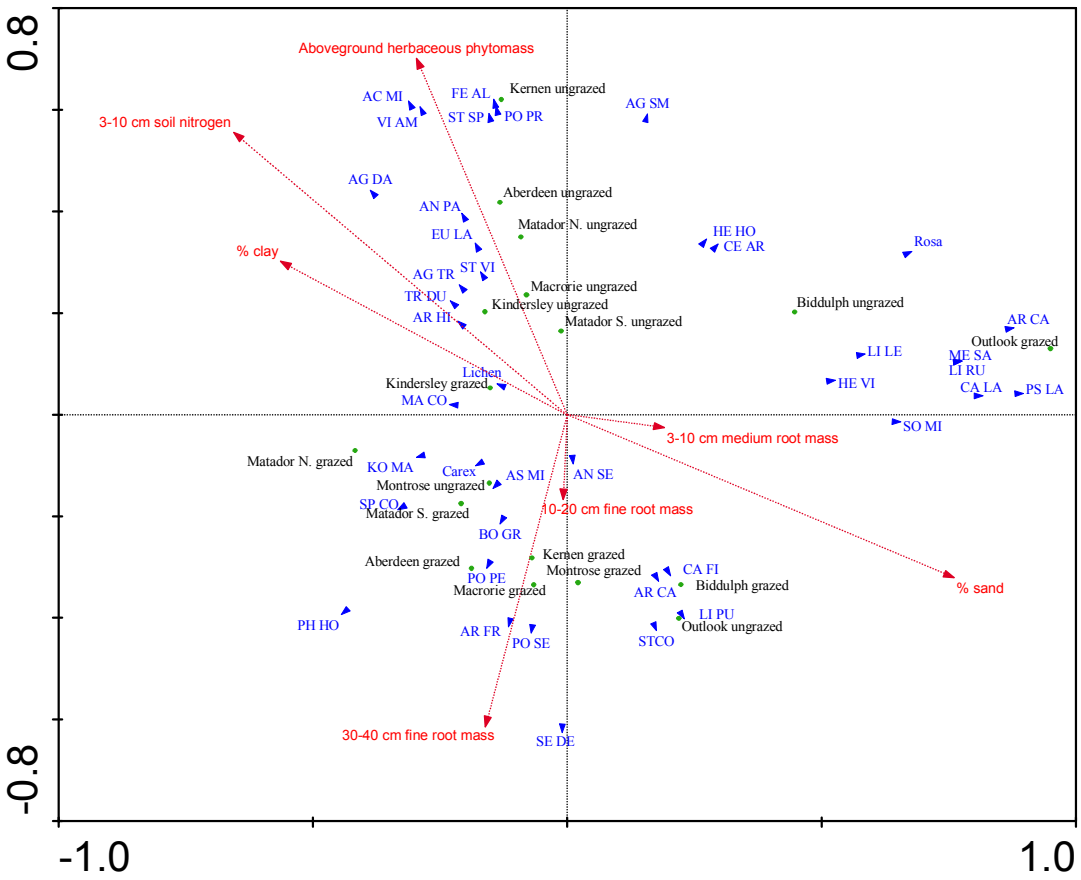

Figure 4.2. Redundancy analysis joint plot of linear combinations of species and biophysical variables from nine study sites with grazed and ungrazed treatments. (Graze = grazed, Ungra = ungrazed, Ma = Macrorie, Ou = Outlook, Mo = Montrose, Ab = Aberdeen, MS = Matador South, MN = Matador North, Bi = Biddulph, Ke = Kernen, Ki = Kindersley). Species codes are derived from the first two letters of the genus name followed by the first two letters of the species name. Complete genus and species names can be determined from Appendix 4.1.

Table 4.4 Additional variance explained (λ_A) and P-value of each biophysical variable studied at grazed and ungrazed sites derived from a redundancy analysis with manual forward selection and a Monte Carlo test with 9999 unrestricted permutations.

Biophysical variable	λ_A	P-value
% sand	0.13	**0.00**
3-10 cm soil nitrogen	0.10	**0.00**
3-10 cm medium root mass	0.08	**0.02**
30-40 cm fine root mass	0.09	**0.02**
10-20 cm fine root nitrogen	0.08	**0.03**
% clay	0.07	**0.04**
Aboveground herbaceous phytomass	0.07	**0.03**
Percent litter cover	0.06	0.08
20-30 cm medium root mass	0.05	0.14
40-50 cm SOC	0.05	0.22
3-10 cm medium root mass	0.05	0.14
0-50 cm medium root mass	0.05	0.13
10-20 cm fine root mass	0.05	0.15
0-3 cm medium root mass	0.05	0.23
30-40 cm SOC	0.04	0.29
0-3 cm fine root mass	0.04	0.35
30-40 cm medium root mass	0.05	0.26
0-50 cm fine root mass	0.04	0.37
10-20 cm medium root mass	0.04	0.46
10-20 cm medium root nitrogen	0.04	0.53
20-30 cm SOC	0.04	0.44
0-50 total root mass	0.04	0.43
40-50 cm medium root mass	0.05	0.25
3-10 cm fine root mass	0.04	0.34
0-3 cm SOC	0.03	0.54
Annual daily average temperature	0.05	0.20
Plant carbon content	0.04	0.54
Litter mass	0.06	0.11
Total phytomass	0.06	0.11
10-20 cm soil nitrogen	0.03	0.67
40-50 cm fine root mass	0.03	0.62
20-30 cm fine root mass	0.03	0.73
10-20 cm SOC	0.04	0.48
3-10 cm fine root nitrogen	0.04	0.42
3-10 cm SOC	0.03	0.77
Annual rainfall	0.03	0.74
Annual snowfall	0.05	0.22
Plant nitrogen content	0.02	0.86

explained 47 % of the variation in species composition and 76 % of the species-environment relationship (Table 4.5). Percent sand corresponded most strongly with Axis 1 (r= 0.70) while aboveground herbaceous phytomass corresponded most strongly with Axis 2 (r= 0.71) and percent clay (r= 0.70) and mass of medium roots in the 3-10 cm depth (r= 0.86) corresponded with axes three and 4, respectively (Figure 4.2). Grazed and ungrazed treatments were generally separated by Axis 2.

Canopy cover of sand grass, Missouri goldenrod, and hairy golden aster corresponded positively with Axis 1 whereas Junegrass and sun-loving sedge corresponded negatively with Axis 1 (Figure 4.2). Conversely, aboveground phytomass and canopy cover of rough fescue, Kentucky bluegrass (*Poa pratensis* L.), and porcupine grass corresponded positively with Axis 2.

Table 4.5 Redundancy analysis summary statistics from species and biophysical data, including importance value of each axis and variance of species composition explained by each axis, cumulative variance explained, and the sum of all canonical eigenvalues.

	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalues[1]	0.16	0.12	0.11	0.08	1.00
Species-environment correlations	0.95	0.99	0.97	0.95	
Cumulative percentage variance:					
of species data	15.9	28.1	38.8	47.2	
of species-environment relationship	25.7	45.3	62.4	75.9	
Sum of all eigenvalues					1.00
Sum of all canonical eigenvalues					0.62

[1] Eigenvalue: 0= unimportant, 1= very important

4.3.2 Effects of grazing on soil organic carbon, bulk density, % N, and the C:N ratio

Redundancy analyses indicated SOC was not useful for explaining the variability observed in species composition among study sites; SOC did not correspond with species composition or with grazing treatments (Table 4.4). Alternatively, % sand, soil N and mass of medium roots in the 3-10 cm depth, mass of

fine roots in the 30-40 cm depth, % clay and aboveground phytomass accounted for much of the variability observed in species composition (Table 4.4). Redundancy analyses also indicated soil N in the 3-10 cm depth corresponded negatively with coarse-textured soils (Table 4.6).

The interacting effects of grazing treatments and soil texture on SOC was not significant at the 0-50 cm depth (P=0.97), nor was the main effect of grazing (P=0.19). Conversely, SOC in the 0-50 cm depth was greater in fine-textured soil than in coarse-textured soil (P=0.02). An exception occurred, however, at the 40 to 50 cm depth where SOC was 0.4% (SE= 0.08) in grazed grassland and 0.5% (SE= 0.08) in ungrazed grassland (Table 4.7). A possible explanation for greater SOC in ungrazed grassland at the 40-50 cm depth could be that roots in ungrazed grassland grow deeper and thereby enable SOC sequestration deeper in the soil. However, the mass of roots in the 40- 50 cm depth was not different in grazed and ungrazed grassland. The mass of roots at each soil depth are described in more detail in section 4.4.3 (Tables 4.10 and 4.11).

Table 4.6. Redundancy analysis correlations for pairs of environmental variables.

	Aboveground herbaceous phytomass	% sand	% clay	30-40 cm FRM[1]	3-10 cm MRM[1]	3-10 cm soil N	10-20 cm fine root N
Aboveground Herbaceous phytomass	1.00						
% sand	-0.13	1.00					
% clay	0.02	-0.87*	1.00				
30-40 cm FRM	-0.06	-0.24	0.05	1.00			
3-10 cm MRM	-0.34	0.19	-0.11	-0.46	1.00		
3-10 cm soil N	0.21	-0.64*	0.31	0.17	-0.11	1.00	
10-20 cm fine root N	-0.37	0.05	0.04	-0.16	0.17	-0.05	1.00

[1] Fine root mass (FRM) and medium root mass (MRM).

***** The correlation is significant ($P \leq 0.05$)

Table 4.7. Average soil organic carbon in grazed or ungrazed sites with coarse or fine texture soil. Values for grazing treatment are means of nine study sites and means of texture classes are of five coarse-textured or four fine-textured soils. The SE for means are in parentheses.

	Soil depth (cm)						
Grazing treatment/ soil class	0-50[1]	0-3	3-10	10-20	20-30	30-40	40-50
	Soil organic carbon ($kg\ m^{-2}$)	Soil organic carbon (%)					
Grazed	5.5 **a** (0.7)	3.3 **a** (0.57)	1.5 **a** (0.25)	0.9 **a** (0.17)	0.7 **a** (0.13)	0.5 **a** (0.09)	0.4 **b** (0.08)
Ungrazed	6.8 **a** (0.9)	4.1 **a** (0.61)	2.1 **a** (0.38)	1.2 **a** (0.22)	0.8 **a** (0.13)	0.7 **a** (0.09)	0.5 **a** (0.08)
Fine texture	7.6 **a** (0.8)	4.4 **a** (0.62)	2.3 **a** (0.33)	1.5 **a** (0.19)	1.1 **a** (0.10)	0.8 **a** (0.06)	0.7 **a** (0.05)
Coarse texture	5.1 **b** (0.7)	3.1 **a** (0.54)	1.4 **a** (0.30)	0.7 **b** (0.11)	0.5 **b** (0.05)	0.4 **b** (0.04)	0.3 **b** (0.03)

[1] Means within grazing treatment and soil depth or soil texture and soil depth that are followed by the same letters are not statistically different ($P>0.05$).

Soil organic carbon was not affected by soil texture at the 0-3 and 3-10 cm depths ($P>0.05$) (Table 4.7). Conversely, SOC was 0.8%, 0.6,% 0.4%, and 0.4% greater in fine-textured soil than in coarse-textured soil in the 10-20, 20-30, 30-40, and 40-50 cm depths, respectively ($P\leq0.05$) (Table 4.7). In addition, SOC was 2.5 kg m^{-2} greater ($P>0.05$) in fine-textured soil than in coarse-textured soil at the 0-50 cm depth (Table 4.7).

Bulk density in the upper 3 cm of the soil profile was not different between grazed and ungrazed treatments ($P\geq0.05$). The bulk density was 0.14 g m^{-3} in grazed than ungrazed grasslands at the 3-10 cm depth. It is also worth noting, that a trend of greater bulk density at soil depths beyond 10 cm was observed in grazed grassland than in the ungrazed grasslands. Bulk density of soil from grazed grassland ranged from 1.05 g cm^{-3} (SE= 0.12) in the 0-3 depth to 1.45 g cm^{-3} (SE= 0.06) in the 40-50 cm depth; bulk density of soil from ungrazed grassland ranged from 0.89 g cm^{-3} (SE= 0.01) to 1.43 g cm^{-3} (SE= 0.03) in the 0-3 and 40-50 cm depths, respectively (Table 4.8). In addition, the bulk density of coarse-textured soil was greater than that of fine-textured soil at all depths (Table 4.8).

Table 4.8. Average bulk density from six soil depths in grazed or ungrazed grassland with coarse or fine soil texture. Values for grazing treatment are means of nine study sites and means of texture classes are of five coarse-textured or four fine-textured soils. The SE for means are in parentheses.

Grazing treatment/ soil class	Soil depth (cm) 0-3[1]	3-10	10-20	20-30	30-40	40-50
	Bulk density (g cm^{-3})					
Grazed	1.05 **a** (0.12)	1.29 **a** (0.07)	1.35 **a** (0.07)	1.39 **a** (0.06)	1.40 **a** (0.06)	1.45 **a** (0.06)
Ungrazed	0.89 **a** (0.01)	1.15 **b** (0.06)	1.26 **a** (0.06)	1.33 **a** (0.05)	1.36 **a** (0.05)	1.43 **a** (0.03)
Fine texture	0.81 **a** (0.11)	1.06 **a** (0.06)	1.14 **a** (0.05)	1.23 **a** (0.03)	1.25 **a** (0.03)	1.31 **a** (0.03)
Coarse texture	1.13 **b** (0.09)	1.38 **b** (0.04)	1.46 **b** (0.03)	1.49 **b** (0.04)	1.50 **b** (0.04)	1.57 **b** (0.04)

[1] Means within soil depth and grazing treatment or soil depth and texture that are followed by the same letters are not statistically different (P>0.05).

Grazing had no affect on the C:N ratio (P>0.46) of soil in the 3-10 and 10-20 cm depths (P>0.05) (Table 4.9). Similarly, the C:N of soil in the 3-10 and 10-20 cm depths was not different between coarse-textured soil and fine-textured soil, averaging 16.7:1 (SE= 3.1) and 11.8:1 (SE= 1.2), respectively. The % N in soil was the same in fine- (0.26, SE= 0.02) and coarse-textured (0.17, SE= 0.03) soils at the 3-10 cm depth but it was greater in the fine-textured (0.19, SE= 0.01) soil than in coarse-textured (0.10, SE= 0.01) soil at the 10-20 cm depth ($P \leq 0.05$).

Table 4.9. Average % N and C:N ratios of soil in grazed or ungrazed grassland with coarse or fine soil texture. Values for grazing treatment are means of nine study sites and means of texture classes are of five coarse-textured or four fine-textured soils. The SE for means are in parentheses.

Grazing treatment/ soil class	Soil depth (cm) 3-10	10-20	3-10	10-20
	Soil %N		Soil C:N	
Grazed[1]	0.19 **a** (0.02)	0.13 **a** (0.02)	12.6 **a** (1.9)	14.5 **a** (3.0)
Ungrazed	0.25 **a** (0.04)	0.16 **a** (0.02)	11.9 **a** (1.5)	14.5 **a** (2.3)
Fine texture[1]	0.26 **a** (0.02)	0.19 **a** (0.01)	10.5 **a** (0.3)	11.8 **a** (1.2)
Coarse texture	0.17 **a** (0.03)	0.10 **b** (0.01)	13.6 **a** (2.1)	16.7 **a** (3.1)

[1] Means within soil depth and grazing treatment or soil depth and texture that are followed by the same letters are not statistically different (P>0.05).

4.3.3 Effects of grazing on the mass, % C, % N, and the C:N ratio of roots

The interactions between grazing treatment and soil texture and the main effect of grazing were not significant for fine root mass in the 0-50 cm depth at P>0.78 and P>0.32, respectively. The mass of fine roots was not statistically different in grazed and ungrazed grassland averaging 0.9 kg m^{-2} (SE= 0.09) and 0.8 kg m^{-2} (SE= 0.06) in the 0-50 cm depth in grazed and ungrazed grassland, respectively (Table 4.10). The effect of soil texture on the mass of fine roots was not significant (P>0.07) at the 0-50 cm depth where the mass of fine roots was 0.9 kg m^{-2} (SE= 0.08) in fine-textured soil and 0.7 kg m^{-2} (SE= 0.06) in coarse-textured soil. The mass of fine roots was not affected by soil texture at other soil depths either. The exception occurred in the 3-10 cm depth where the mass of fine roots was 2.1 (SE= 0.18) mg cm^{-3} in coarse soil and 2.9 (SE= 0.27) mg cm^{-3} in fine soils (Table 4.10). However, the greater mass of fine roots in fine soil at the 3-10 cm increment did not correspond with greater SOC content therein. The mass of fine roots in the 0-50 cm depth was not different between fine and coarse soils (Table 4.10).

Table 4.10. Average mass of fine roots from six soil depths in grazed or ungrazed grassland with coarse or fine soil texture. Values for grazing treatments are means of nine study sites and means of texture classes are of five coarse-textured or four fine-textured soils. The SE for means are in parentheses.

	Soil depth (cm)						
Grazing treatment/ soil class	0-50[1]	0-3	3-10	10-20	20-30	30-40	40-50
	FRM[2] (kg m^{-2})	Fine root mass (mg cm^{-3})					
Grazed	0.9 **a** (0.09)	9.0 **a** (0.91)	2.8 **a** (0.25)	1.4 **a** (0.17)	1.0 **a** (0.15)	1.0 **a** (0.11)	0.7 **a** (0.11)
Ungrazed	0.8 **a** (0.06)	8.7 **a** (0.82)	2.2 **a** (0.25)	1.2 **a** (0.14)	1.0 **a** (0.14)	0.8 **a** (0.11)	0.7 **a** (0.11)
Coarse texture	0.7 **a** (0.06)	8.3 **a** (0.81)	2.1 **a** (0.18)	1.1 **a** (0.13)	0.8 **a** (0.09)	0.7 **a** (0.08)	0.6 **a** (0.08)
Fine texture	0.9 **a** (0.08)	9.3 **a** (0.86)	2.9 **b** (0.27)	1.4 **a** (0.16)	1.2 **a** (0.16)	1.0 **a** (0.11)	0.8 **a** (0.11)

[1] Means within soil depth and a grazing or soil texture class that are followed by the same letter are not statistically different (P>0.05).
[2] Fine root mass (FRM)

The main effects of grazing, soil texture and their interaction were not significant for the mass of medium roots in the 0-50 cm depth at P>0.90, P>0.99, and P>0.92, respectively. The mass of medium roots averaged 0.6 kg m^{-2} in the 0-50 cm increment in grazed and ungrazed grassland. Similarly, the mass of SOC was 0.6 kg m^{-2} in the 0-50 cm increment in coarse and fine soils (Table 4.11).

Table 4.11. Average mass of medium roots from six depths in grazed or ungrazed grassland with coarse or fine texture. Values for grazing treatments are means of nine study sites and means of texture classes are of five coarse-textured or four fine-textured soils. The SE for means are in parentheses.

	soil depth (cm)						
Grazing treatment/ soil class	0-50[1]	0-3	3-10	10-20	20-30	30-40	40-50
	MRM (kg m^{-2})	Medium root mass (mg cm^{-3})					
Grazed	0.6 **a** (0.06)	8.9 **a** (1.42)	1.9 **a** (0.26)	0.8 **a** (0.10)	0.4 **a** (0.05)	0.3 **a** (0.05)	0.2 **a** (0.05)
Ungrazed	0.6 **a** (0.07)	8.1 **a** (1.12)	1.8 **a** (0.27)	0.8 **a** (0.08)	0.5 **a** (0.06)	0.3 **a** (0.05)	0.3 **a** (0.05)
Fine texture	0.6 **a** (0.09)	7.6 **a** (1.52)	1.9 **a** (0.35)	0.8 **a** (0.07)	0.4 **a** (0.07)	0.4 **a** (0.07)	0.3 **a** (0.07)
Coarse texture	0.6 **a** (0.04)	9.2 **a** (1.04)	1.7 **a** (0.19)	0.8 **a** (0.05)	0.4 **a** (0.03)	0.3 **a** (0.03)	0.2 **a** (0.03)

[1] Means within soil depth and grazing treatment or soil depth and texture that are followed by the same letters are not statistically different (P>0.05).
[2] Medium root mass (MRM)

Grazing had no effect on % C (P>0.41) or % N (P>0.07) of fine or medium roots in any of the soil depths tested, nor did grazing affect the C:N ratio of fine roots in the 3-10 cm depth (P>0.45). However, the C:N ratio of medium roots in the 10-20 cm depth decreased with grazing (P=0.04), averaging 43:1 (SE= 1.9) and 50:1 (SE= 2.5) in grazed and ungrazed grassland, respectively (Table 4.12).

Soil texture had no effect on % C of fine or medium roots in all soil depths (P>0.05) except for medium roots in the 3-10 cm depth where % C was 2 % greater in roots from coarse soil (Table 4.12). In addition, the % N of fine roots from the 3-10 and 10-20 cm depths was similar in fine- and coarse-textured soil (P>0.05), but % N of medium roots in the 10-20 cm depth was 0.2% greater in coarse-textured soils than

fine-textured soils (P≤0.05) (Table 4.12). The % N of medium roots in the 3-10 cm depth was similar (P>0.05) in fine- and coarse-textured soils.

Table 4.12. Average % C, % N, and C:N ratios of fine and medium roots from two soil depths in grazed or ungrazed grassland with coarse or fine texture. Values for grazing treatments are means of nine study sites and means of texture classes are of five coarse-textured or four fine-textured soils. The SE for means are in parentheses.

	----------3-10 cm fine root----------			----------3-10 cm medium root----------		
Grazing treatment/ soil class	% C[1]	% N	C:N	% C	% N	C:N
Grazed	33.1 **a** (1.0)	1.7 **a** (0.1)	19.9 **a** (0.7)	46.4 **a** (0.7)	1.1 **a** (0.1)	40.1 **a** (2.2)
Ungrazed	31.9 **a** (0.9)	1.7 **a** (0.1)	19.6 **a** (0.8)	45.5 **a** (0.6)	1.0 **a** (0.1)	42.8 **a** (2.5)
Fine texture	33.1 **a** (0.7)	1.6 **a** (0.1)	21.0 **a** (0.8)	44.8 **b** (0.4)	1.0 **a** (0.1)	44.5 **a** (1.4)
Coarse texture	32.0 **a** (1.0)	1.7 **a** (0.1)	18.8 **b** (0.5)	46.8 **a** (0.6)	1.2 **a** (0.1)	39.0 **a** (2.6)
	----------10-20 cm fine roots----------			----------10-20 cm medium roots--------		
Grazed	32.3 **a** (0.1)	1.6 **a** (0.1)	21.5 **a** (0.9)	45.4 **a** (1.2)	1.0 **a** (0.1)	42.8 **b** (1.9)
Ungrazed	31.1 **a** (0.8)	1.4 **a** (0.1)	22.5 **a** (0.9)	45.2 **a** (0.8)	0.9 **a** (0.1)	49.6 **a** (2.5)
Fine texture	32.2 **a** (0.6)	1.4 **a** (0.1)	23.7 **a** (0.9)	44.3 **a** (0.8)	0.9 **b** (0.0)	49.7 **a** (1.5)
Coarse texture	31.3 **a** (1.0)	1.5 **a** (0.1)	20.6 **b** (0.5)	46.0 **a** (1.0)	1.1 **a** (0.1)	43.4 **b** (2.6)

[1] Paired means for %C, %N, or C:N within a soil depth and root size class and a grazing or soil texture class that are followed by the same letters are not statistically different (P>0.05).

The C:N ratio of fine roots was greater in fine- than in coarse-texture soils (P≤0.05) (Table 4.12). The C:N ratios for fine roots from the 3-10 cm depth averaged 21:1 (SE= 0.8) and 19:1(SE= 0.5) for fine- and coarse-texture soil, respectively, while the ratios were about 24:1 (SE= 0.9) and 21:1 (SE= 0.5) for fine roots from the 10-20 cm depth in fine- and coarse-textured soil, respectively (Table 4.12). The C:N ratio of medium roots in the 10-20 cm depth was about 50:1 (SE= 1.5) and 43:1 (SE=2.6) (P≤0.05) in fine- and coarse-texture soils, respectively. Conversely, the C:N ratio of medium roots in the 3-10 cm depth was not different (P>0.05) in fine- and coarse-texture soil, averaging 44:1 (SE= 1.4) and 39:1 (SE= 2.6), respectively (Table 4.12).

The % C, % N and C:N ratio of grass and litter was similar (P>0.05) in grazed and ungrazed grassland (Table 4.13). Conversely, % N of grass was greater (P<0.05) in coarse-textured soils than fine-textured soils averaging 1.5 % (SE= 0.07) and 1.2 %

(SE= 0.09), respectively (Table 4.13). The % N content of litter was also greater (P=0.01) in coarse- than fine-textured soil averaging 1.3 % (SE= 0.07) and 1.6 % (SE= 0.08), respectively (Table 4.13). Conversely, % C and the C:N ratio of graminoids were similar (P>0.05) in coarse- and fine-texture soils (Table 4.13).

Table 4.13. Average % C, % N, and C:N ratios of graminoids and litter in grazed or ungrazed grassland with coarse or fine textured soil. Values for grazing treatments are means of nine study sites and means of texture classes are of five coarse-textured or four fine-textured soils. The SE for means are in parentheses.

	----------Graminoids----------			----------Litter----------		
Grazing treatment/ soil class	% C[1]	% N	C:N	% C	% N	C:N
Grazed	44.3 **a** (0.61)	1.4 **a** (0.09)	31.8 **a** (2.22)	39.6 **a** (2.76)	1.4 **a** (0.10)	29.9 **a** (2.91)
Ungrazed	44.8 **a** (0.41)	1.3 **a** (0.09)	35.5 **a** (2.51)	41.1 **a** (1.15)	1.5 **a** (0.07)	27.5 **a** (1.29)
Fine texture	43.8 **a** (0.56)	1.2 **b** (0.09)	36.9 **a** (2.99)	38.4 **a** (2.36)	1.3 **b** (0.07)	30.2 **a** (2.31)
Coarse texture	45.1 **a** (0.41)	1.5 **a** (0.07)	31.1 **a** (1.55)	42.3 **a** (0.94)	1.6 **a** (0.08)	27.3 **a** (1.80)

[1] Paired means within a grazing or soil texture classes that are followed by the same letters are not statistically different (P>0.05).

4.3.4 Century model analysis of the effects of grazing on total soil organic carbon and the active, slow, and passive fractions of soil organic carbon

The Century model was used to simulate soil organic carbon at two of the sites used in this research program. Soil at the Biddulph site was coarse-textured while soil was fine-textured at Matador. Biddulph is about 180 km northeast of Matador. The simulation was programmed to run for 1924 years before grazing is introduced.

After 1924 years total SOC in the upper 20 cm of the soil profile was 3.0 and 6.2 kg m^{-2} at Biddulph and Matador, respectively (Table 4.14). The simulation was also programmed to run until the year 2504 under no grazing, light grazing, or heavy grazing. The estimated loss of total SOC between 1924 and 2004 was about 0.1 kg m^{-2} in lightly grazed grassland and 0.3 kg m^{-2} in heavily grazed grassland at Biddulph. The same simulation indicated total SOC decrease about 0.1 and 0.4 kg m^{-2} for light and heavy grazing at Matador (Table 4.14). The reduced total SOC under light or heavy

grazing was therefore approximately equal when compared to ungrazed grassland over this 80-year period (Table 4.14). Conversely, the model indicated that heavy or light grazing for 500 years (1924 to 2504) reduced total SOC relative to ungrazed grassland. The difference in total SOC between ungrazed grassland in 1924 and lightly and heavily grazed grassland in 2504 was predicted to be 0.4 and 0.8 kg m^{-2}, respectively, at Biddulph and 0.3 and 1.0 kg m^{-2}, respectively at Matador (Table 4.14). The Century model therefore indicated SOC will decline more on heavily grazed than on lightly grazed grassland over the same period and that the proportional loss of total SOC from 1924 to 2504 would be 27.2% in the coarse-texture soils at Biddulph and 16.2% in fine-texture soils at Matador (Table 4.14). The proportional differences in total SOC lost in coarse-textured and fine-textured soils is a function of the amounts of carbon in the active, slow, and passive fractions and the simulated effect of grazing on each fraction. Total SOC generated from the simulation indicates that more carbon is present in fine-textured soil than in coarse-textured soil. In addition, the majority of the carbon in both soils is in the slow and passive fractions with the active fraction comprising about 3 % of the total SOC. Heavy grazing from 1924 to 2504 reduced the passive SOC by 0.2 kg m^{-2} at Biddulph and by 0.3 kg m^{-2} at Matador (Table 4.14). Proportionally, these reductions were greater at Biddulph than at Matador because the initial amount of SOC is greater in fine-texture soils than soils with coarse texture.

The reduction of passive SOC was similar in lightly and heavily grazed grassland over the 2004 to 2504 period. About 0.2 kg m^{-2} of passive SOC were lost over this 500-year period (Table 4.14). However, the proportional loss of passive SOC was about 15% at Biddulph and 6% at Matador.

Table 4.14. Summary of the effect of simulated grazing on the active, slow, and passive soil carbon fractions at Biddulph and Matador using the Century carbon model.

Simulation year	Grazing treatment	Biddulph SOC				Matador SOC			
		Total[1]	Active	Slow	Passive	Total[1]	Active	Slow	Passive
		kg m^{-2} (% of total)							
1924	None	3.0	0.1	1.6	1.3	6.2	0.1	2.6	3.5
2004		2.9	0.1	1.6	1.3	6.1	0.1	2.6	3.4
2504		2.6	0.1	1.5	1.1	6.0	0.1	2.6	3.3
1924	Light	3.0	0.1	1.6	1.3	6.2	0.1	2.6	3.5
2004		2.9	0.1	1.5	1.3	6.1	0.2	2.6	3.4
2504		2.6	0.1	1.4	1.1	5.9	0.1	2.5	3.3
1924	Heavy	3.0	0.1	1.6	1.3	6.2	0.1	2.6	3.5
2004		2.7	0.1	1.4	1.3	5.8	0.1	2.3	3.4
2504		2.2	<0.1	1.1	1.1	5.2	0.1	1.9	3.2

[1] Total carbon in the upper 30 cm of the soil.

The effect of light or heavy grazing was similar on the slow and passive SOC. For example, light grazing from 1924 to 2004 reduced slow SOC by 0.1 kg m^{-2} or less at Biddulph and Matador (Table 4.14). Light grazing through 2504 reduced slow soil carbon by another 0.1 kg m^{-2} at Biddulph and at Matador. Conversely, about 0.2 kg m^{-2} (12.5 %) of the slow SOC was lost between 1924 and 2004 and 0.3 kg m^{-2} (21.5 %) was lost from 2004 to 2504 in heavily grazed grassland at Biddulph (Table 4.14). Similarly, heavy grazing at Matador reduced slow SOC by 0.3 kg m^{-2} (11.5 %) from 1924 to 2004 and by 0.4 kg m^{-2} (17.3 %) from 2004 to 2504 (Table 4.14). Slow soil carbon may thus be reduced with one century of heavy grazing with reductions gradually increasing over the next 5 centuries. Conversely, light grazing had a relatively minor effect on the slow SOC fraction over 500 years.

The reduction in active SOC with light and heavy grazing was similar at Biddulph and Matador. Grazing had no affect on active SOC at Biddulph or Matador from 1924 to 2004 (Table 4.14). The small amount of C in this fraction may be one reason why a change in active SOC was not detected with simulated grazing.

In summary, about 2% to 4% of the total soil carbon was classified as active at Biddulph and Matador (Table 4.14). The remainder of the soil carbon was classified as slow or passive, but proportionately more carbon was allocated to the slow fraction at Biddulph than at Matador. On the other hand, proportionally more SOC was allocated to the passive fraction at Matador than at Biddulph. This allocation of SOC was expected because physical protection of SOC in fine-textured soils is greater than in coarse-textured soils. Grazing had no effect on the amount of active SOC in the soils over the 500-year simulation, but slow and passive pools were reduced. Reduction of slow and passive SOC depended on grazing intensity with heavy grazing reducing SOC more than light grazing.

4.4 Discussion

Soil organic carbon was not affected by grazing in the present study. Previous reports indicate that improved grazing management could increase SOC on grasslands in the United States by 0.1 to 0.3 Mg C ha^{-1} $year^{-1}$ (Schuman et al. 2002). This prediction is supported by other studies on the effect of grazing on soil carbon (Conant et al. 2001). Soil C in overgrazed grasslands also decreased by an average of 0.19 Mg ha^{-1} $year^{-1}$ relative to moderately grazed sites (Conant et al. 2001). In Alberta, SOC was greater in ungrazed (4.23%) than grazed (3.51%) grassland (Dormaar et al. 1989) and Johnston et al. (1971) concluded that the concentration of SOM was 11.7 % in lightly grazed grassland and 9.7 % in very heavily grazed fescue grassland. In contrast, SOC in grazed and ungrazed grassland in the present study was not different at 5.5 and 6.8 kg m^{-2} , respectively, in the upper 50 cm of soil. However, organic carbon in the upper 45 cm of soil was 1.27 kg m^{-2} greater in relict grassland relative to grazed grassland when C values were averaged over soil textures (Bauer et al. 1987). Bauer et al. (1987) speculated that the difference in organic carbon in grazed and ungrazed grasslands could be caused by the cumulative removal of C by animals.

Abril and Bucher (2001) estimated 58 Mg C ha^{-1} or 78% of the pre-grazing amount of C was removed by cattle grazing in semi-arid savannas and woodlands in Argentina. They attributed the reduction of SOC in their study to reduced C input from litterfall, increased soil temperature, and greater frequency of wet dry cycles. The reduction of SOC in grazed grassland is contrary to the lack of increase or decrease caused by grazing in the present research. However the heavily grazed site studied by Abril and Bucher (2001) was denuded, whereas the heavily grazed site in the present study was covered by vegetation and the mass of roots in grazed and ungrazed sites was similar. Different site conditions and/or grazing intensity are potential reasons why conclusions about the effect of grazing and SOC were different between Abril and Bucher (2001) and the present research.

There was no evidence that SOC, root mass, and grazing were correlated in the present study. Similarly, grazing did not consistently increase or decrease SOC or root mass in Alberta (Henderson et al. 2004). The present study and that of Henderson et al. (2004) were conducted in Mixed Prairie where cover of species such as blue grama and Junegrass persist in heavily grazed swards. Persistence of vegetative cover is likely important for maintaining the root mass and SOC because these species have extensive root systems (Coupland and Johnson 1965). Contribution of C from roots of plants that persist in grazed swards in Mixed Prairie may be why SOC was similar in grazed and ungrazed Mixed Prairie, despite reductions in aboveground phytomass in grazed sites.

Despite differences in plant community composition and greater aboveground phytomass in ungrazed grassland as compared to grazed grassland, SOC was not different in the two grazing treatments. Twelve years of heavy grazing in Wyoming modified plant community composition, but the total amount of C in the upper 60 cm of soil was not different in grazed and ungrazed sites (Schuman et al. 1999). Similarly, Grazing in Mixed Prairie did not change soil C relative to ungrazed controls (Manley et al. 1995), while excluding grazing for 50 years did not cause measurable differences in the concentration of C in the upper 5 cm of the soil in sandhill grassland (Berg et al.

1997). The consequence of livestock grazing on SOC is therefore contentious. A review of 236 studies lead Milchunas and Lauenroth (1993) to conclude SOC response to grazing was almost equally divided between positive and negative responses.

Disparate responses of SOC to grazing is confounded by variability among grazing treatments and the response of plants to grazing. Grazing regimes that cause short-term reductions in the amount of aboveground phytomass are not likely to cause a great change in SOC content because aboveground phytomass represents a relatively small portion of the total ecosystem C, and most plant-based SOC is derived from roots (Follett 2001). This lack of short-term effects of grazing on SOC is supported by the Century simulation. Less than 3 % of the total SOC is in the active fraction which could be influenced by short-term management. In addition, aboveground phytomass can recover relatively quickly after grazing. The time required to have a measurable effect on SOC is greater than the recovery of aboveground phytomass because some SOC is recalcitrant (Follett 2001). The lack of correspondence between SOC and aboveground phytomass production in a given year suggests that extended periods of heavy grazing may be required to change SOC. The Century simulation supports this assertion because about one-half of the total SOC is in the passive fraction and slightly less than one-half is in the slow fraction. Carbon in the passive pool resists decomposition for physical reasons such as occlusion with soil structures and attachment to clay and for chemical reasons such as formation of refractory organic compounds (Amundson 2001). Reductions of SOC in the passive pool will therefore be gradual and measurable differences are not likely to be detected for centuries. This characteristic of the SOC pool indicates that about 100 years of heavy grazing is insufficient to change the amount SOC.

The response of SOC to grazing is delayed in the short-term by recalcitrant C fractions in the soil and in the long-term by a shift in species composition. The resistance of slow and passive SOC to decomposition may therefore cause a temporal lag from the time that the aboveground phytomass production is depleted by grazing to the time when SOC changes. Defoliation reduces aboveground phytomass more

than roots (Ferraro and Oesterheld 2002). Roots, are, however, reduced by grazing, but unlike aboveground plant parts, roots are not removed to the same extent as above ground phytomass is (Weaver 1950). The gradual reduction in root mass is therefore one reason why SOC is the same in grazed and ungrazed grassland despite the reduction in aboveground phytomass in grazed grassland. In addition, the temporal lag may be lengthened when decreaser plant species are replaced by increaser species that persist in heavily grazed grassland. For example, blue grama and clubmoss are found on heavily grazed grassland (Coupland 1961, Smoliak 1965) and they have dense root systems (Coupland and Johnson 1965, Lutwick and Dormaar 1976, Dormaar et al. 1981) that may function to maintain SOC, even if above ground phytomass production is reduced by grazing. Thus, since the majority of SOC is root-derived, and increaser species can persist in heavily grazed grassland, they can continue to contribute to the SOC pool despite reduced aboveground production; SOC levels are then likely to be maintained.

The CO_2 exchange in grazed pastures and ungrazed exclosures in Shortgrass Steppe was similar over the growing season (LeCain et al. 2002). Since livestock grazing may not alter the CO_2 exchange rate in grassland, it is possible grazing may reduce SOC indirectly. Indirect effects of grazing on SOC may eventually occur when aboveground cover becomes depleted and soils erode. Alternatively, long-term, heavy grazing would change the carbon balance if grazing eventually depletes the source of carbon and the site is devoid of vegetation. If grassland is grazed this intensively and annual input of carbon by plants is eliminated, the CO_2 exchange process will be reliant on recalcitrant SOC in the soil, which will eventually be depleted. The Century simulation indicated heavy grazing slowly decreased the amount of SOC in the slow and passive fractions over a 580 year period. Many years of no carbon input from plants may therefore be required before recalcitrant SOC pools begin to decline, after which, a grazing effect may be observed. It is therefore probable that the several decades of heavy grazing was insufficient to change SOC in the present study. It is also possible that any amount of grazing that maintains a

permanent cover of plants and a perpetual source of carbon via roots can maintain SOC.

The present study also indicates the amount of SOC in grazed grassland is determined by soil texture. SOC and silt-plus-clay content of soil corresponded positively, but SOC corresponded negatively with the content of sand (McGrath and Zhang 2003, Henderson 2004) because decomposition is hindered in fine-textured soil (Jenkinson 1977, Sorensen 1981). Clay particles retain more carbon than sand (Jenkinson 1977, Christiansen 2001) and they are the basic building blocks of soil aggregates and organomineral complexes that stabilize organic matter in soil (Paul and Clark 1996). The conclusion that soil texture has greater control over SOC than grazing was supported by the Century simulations in this research and by research that indicates factors such as topographic position, soil texture and/or parent material explain much of the landscape-scale variation observed among C pools (Aguilar and Heil 1988, Hook and Burke 2000).

In the present study soil texture was the primary factor influencing the amount of SOC in grasslands. The magnitude of the existing SOC pool, especially in fine-textured soil, makes it difficult to identify the effects of short-term grazing on SOC despite visually obvious grazing effects on other components of the carbon balance, such as the amount of aboveground phytomass.

4.5 Summary

SOC quantity may be more stable than originally hypothesized at the outset of this research. The null hypothesis that SOC in grazed and ungrazed grassland is equal is therefore accepted. Similarly, the null hypothesis that the mass of roots is equal in grazed and ungrazed grasslands is accepted. The lack of correspondence between grazing and root mass and between grazing and SOC occurred despite a reduction in aboveground phytomass in grazed grassland. The cumulative effects of livestock grazing on SOC over the past century are not likely great enough to cause a

measurable change in SOC despite altered plant community composition and reduced aboveground phytomass. It remains possible that continued removal of C in exported animals, loss of carbon during ruminant metabolism, and reduced carbon flow through the plant community may eventually cause a change in SOC. The lack of consistent correlation between SOC and grazing in the literature may be the product of different grazing histories among study sites and the difference in evolutionary history of grasslands.

In conclusion there appear to be two main opposing hypotheses about the effect of grazing on SOC. First, it may be may predicted that SOC will remain relatively constant in a given soil because any defined area of land will have a maximum production capacity and therefore a maximum C input. The amount of C fixed for a defined land area is therefore determined by the production constraints of that area, and not by plant species composition. Consequently, there will be a relatively constant supply of C in the system, regardless of the species composition. In addition, processes such as decomposition and plant community succession may function to maintain the carbon balance by reducing or increasing the rate of C loss in response to changing conditions. Second, it may be hypothesized, as was done at the outset of this research, that any change in species composition will change the physical and chemical properties of C on a site, disrupting the C balance. The research presented herein supports the former of these two hypotheses.

5.0 RATES OF DECOMPOSITION OF ROOT AND LEAF LITTER FROM GRASS AND SNOWBERRY

5.1 Introduction

Energy flow and nutrient cycling are major processes that are part of ecosystem functioning. The primary factors that control the rate of nutrient cycling and decomposition, are the decomposer organisms, the physio-chemical environment, and the quality of the organic material (Swift et al. 1979). The effect of the decomposers on organic matter is related to their functional ecology and distribution pattern while the physio-chemical environment is related to nutrient and water availability, aeration, oxygen availability, pH, and temperature (Swift et al. 1979). The quality of the organic matter, on the other hand, is related to its value as a food source for other organisms.

The content of nitrogen, lignin, and phosphorus in plant materials are properties that influence the rate of decomposition of that material (Mun and Whitford 1998, Hendrickson et al. 2001, Moretto and Distel 2003). Plants with a greater C:N ratio, and those that have a relatively great concentration of lignin, decompose more slowly and species with these characteristics are often referred to as poor-quality. Similarly, Taylor et al (1989b) found that N content and the C:N ratio were better indicators of decomposition rates for leaf litter than the lignin:N ratio. However, the decomposition of roots corresponded negatively with initial lignin concentration (Mun and Whitford 1998). The effect of phytomass chemistry on decomposition is an indication that different species and different plant organs (roots, leaves, culms) are likely to decompose at different rates. This assertion is supported by research that indicated the rate of decomposition of leaves is greater than that from stems (Koukoura et al. 2003).

Understanding decomposition becomes more complicated when the effects of environmental conditions are considered. The primary environmental factors affecting decomposition are soil texture, temperature and water availability (Oades 1988, Taylor and Parkinson 1988b, Hassink et al. 1997, Kochy and Wilson. 1997). Interaction of

these factors complicates studies of the decomposition process and non environmental factors such as lignin content may affect decomposition differently across climatic regions (Meentemeyer 1978). Couteaux et al. (1995) also suggested that decomposition will be more constrained by litter quality in areas where temperature and water are less limiting, such as in tropical environments.

This study was undertaken with anticipation that site-specific information about decomposition rates would be useful for explaining SOC differences observed in the snowberry and grazing studies conducted as part of this research program. Information on the decomposition of Mixed Prairie plants is lacking in the literature and it was deemed important because plants that decompose fast or slow may contribute more or less to the SOC pool.

The objectives of the study were to determine if decomposition of dominant plants in Mixed Prairie varied among plant parts and plant growth forms and whether their decomposition was affected by soil texture. The hypotheses tested were that decomposition is equal between leaves and roots and between snowberry (*Symphoricarpos occidentalis* Hook.) and graminoids and that the decomposition of graminoids or snowberry from different plant communities is equal.

5.2 Materials and methods

The study was conducted at Kernen and Biddulph in 2004 and repeated at both sites in 2005. Plant material was collected at both sites and material from each site was placed at both sites in a reciprocal arrangement. Plant material was placed in the field in October of the year prior to data collection. The envelopes containing air-dried material were randomly assigned positions within each study site. Envelopes containing leaves of grasses or snowberry were placed on the soil surface and secured to the ground using bamboo skewers. Envelopes containing root material of snowberry or graminoids were buried 15 cm deep and flagged using bamboo skewers. All samples were placed in the grassland community.

5.2.1 Site selection and plant material descriptions

Biddulph is a sandy site that is dominated by Mixed Prairie while Kernen is a fine-textured site and is dominated Fescue Prairie. The Soil associations for these sites are Dune Sand at Biddulph and Elstow at Kernen (Table 4.1). Leaves and roots of grasses and snowberry used for this study were collected at both sites. The grassland community at Biddulph, from which plant material was collected, was dominated by needle-and-thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth) , Junegrass (*Koeleria macrantha* (Ledeb.) J.A. Schultes), and thread-leaved sedge (*Carex filifolia* Nutt.) while the graminoid community at Kernen is dominated by rough fescue (*Festuca hillii* (Vasey) Piper), porcupine grass (*Hesperostipa curtiseta* ((A.S. Hitchc.) Barkworth)), and northern wheatgrass (*Elymus lanceolatus* (Scribn. & J.G. Sm.) Gould). Snowberry patches were dominated by snowberry at both sites.

All plant materials were collected in mid-September. Snowberry leaves and roots were collected near the centre of a snowberry patch while grass leaves and roots were collected in the adjacent grassland. Snowberry leaves were collected by hand-picking them off of the shrubs and grass leaves and stems were collected by clipping plants near ground level and retaining only the current-year growth. Roots were collected from the 3 to 20 cm depth of soil in grassland and snowberry communities. The plant material classes for this study are: Kernen-grassland leaves, Kernen-snowberry leaves, Kernen-grassland roots, Kernen snowberry roots, Biddulph-grassland leaves, Biddulph-snowberry leaves, Biddulph- grassland roots and Biddulph-snowberry roots.

Roots were prepared for the study by placing a soil sample from a community (snowberry or grassland) on a 3 x 3 mm mesh screen that was placed over a 20 L pail. Warm water was sprayed onto the soil and root sample using a garden spray nozzle. All roots were collected from the 3 x 3 mm screen after the soil was washed off the sample and stored in paper bags and dried to a constant mass at room temperature.

Leaves were prepared by air-drying the material at room temperature to a constant mass. Five grams of the air-dried leaves or roots were weighed using an electronic balance and placed in fiberglass screen envelopes with 1x1 mm mesh. These envelopes were 10 x 15 cm and were sewn together using polyester and monofilament thread.

Soil temperature, air temperature above the plant canopy, temperature at the ground surface and ambient precipitation were measured and recorded using a data logger. The data logger was programmed to record average hourly air temperature above the plant canopy, ground surface temperature and soil temperature. It was also programmed to record total daily precipitation. Two temperature probes were used to measure air temperature above the canopy (approximately 30 cm above the soil surface), two probes were used to measure air temperature at the ground surface, and two probes were used to measure soil temperature. All air temperature probes were wrapped with aluminum foil. The probes for measuring air temperature above the canopy were suspended above the ground using wooden stakes. The probes measuring temperature at the ground surface were secured to the ground using wire anchors. Probes for measuring soil temperature were 10 cm below the soil surface. One gauge was installed to measure precipitation. The gauge was located about 15 cm above the soil surface on a wooden platform.

5.2.2 Experimental design

Plant material types were applied in a factorial randomized complete block design with five blocks at each site. The eight plant material types were replicated five times within each block at both study sites for the 2004 and 2005 studies. Each of these eight replications within blocks represents a different potential collection date. For example, material was collected from the field once per month from May through September, thus 5 of the 8 replications were randomly collected from each block. It was necessary to place eight replications per block in the field, however, because loss or damage of some litterbags was anticipated.

5.2.3 Data analysis

Data were analyzed using an ANOVA and terms in the significant interactions ($P \leq 0.05$) were reanalyzed using ANOVA and Tukey multiple comparisons (Zar 1999). All analyses were completed using Minitab® release 14. The correlation between decomposition and macroclimatic variables was also analyzed using the Pearson product moment correlation coefficient, which tested the linear relationship between pairs of variables.

5.2.4 Data collection

The procedure for measuring decomposition of plant material was destructive because percent organic matter loss was calculated as ash free mass of the plant material (Cepeda-Pizarro and Whitford 1990). New sample bags were therefore collected once per month from May through September. Samples for each collection date were oven dried at 85^{o} C to a constant mass. Each dried sample was removed from the fiberglass envelope and weighed. Soil that infiltrated the bag while it was in the field was not removed from a sample before it was weighed. The amount of soil contamination was determined by placing the dried and weighed sample from an envelope into a muffle furnace and incinerating the organic material at 700^{o} C for 4 hours (Dormaar and Willms 1993). The mass of soil remaining after incineration was determined by weighing on a micro balance and was subtracted from the original oven-dried mass of the plant material and soil mixture (Equations 5 and 6). Percent organic matter loss was therefore calculated as ash free mass of the plant material (Cepeda-Pizarro and Whitford 1990). The mass of organic matter in the soil that infiltrated the litterbags was estimated by collecting six soil samples from the 3-10 cm depth and measuring the organic matter content with a Leco CR-12 Carbon Analyzer. Approximately 0.15 g of the finely-ground soil was placed into the Leco CR-12 which was set at 840^{o} C.

$$d = \frac{I+A-Y}{Si} - F \qquad \text{(Equation 5)}$$

$$\%d = \frac{d \times 100}{I-Y} \qquad \text{(Equation 6)}$$

Where:
d = Estimated organic matter loss
Y= Mass of initial inorganic content of sample (before being placed in the litter bags)
I = Initial dry mass of the sample
A = Mass of ash after retrieval from the field
Si = Estimated organic matter content of soil around the litterbags using a Leco CR-12 Carbon Analyzer
F = Final dry mass of the sample

Annual decay rate constants were calculated for plant material that was placed in the field in October 2003 and retrieved in September 2004 and for material placed in the field in October 2004 and retrieved in September 2005. Annual rate constant was calculated as a single negative exponential (Equation 7) (Olsen 1963). The single exponential model is the most commonly used model in decomposition research (Wieder and Lang 1982).

$$k = -\text{Ln}\,(X/X_o) \qquad \text{(Equation 7)}$$

Where:
k= the annual rate constant
X= the mass of material remaining after 1 year
X_o= the mass of the material at the start of the experiment

Gravimetric soil water content was measured on each collection date. Soil water content in the 0-10 cm depth was measured by collecting soil from the 0-10 cm depth with a 2 cm-diameter probe at three locations in each block. Soil was collected in tin cans and wet soil weight was recorded. All soil samples were oven-dried to a constant mass at 85^{o}C. Soil water content was calculated using Equation 8.

% soil water = (wet soil weight – dry soil weight)/ dry soil weight (Equation 8)

5.3 Results

5.3.1 Average monthly decomposition and C:N ratios of grass and snowberry leaves and roots collected at Biddulph

The average monthly mass lost from different plant materials indicated that plant material type (leaves or roots) was the key factor affecting decomposition, not growth forms (graminoids or snowberry). Leaves of grasses and snowberry lost more mass than roots and this trend was relatively consistent in 2004 and 2005 at both study sites. The best example of this trend was illustrated by material collected from Biddulph in 2004 and studied at Kernen. The grass and snowberry leaves from Biddulph lost 3.2 % (SE= 0.12) and 2.8 % (SE= 0.08) of their mass per month, while grass and snowberry roots from Biddulph lost 2.4 % (SE= 0.18)) and 2.2 % (SE= 0.08) of their mass per month, respectively (Table 5.1). This difference between grass and snowberry leaves and roots was not expected, however because the initial C:N ratios of these materials did not correspond with the measured decomposition. For example, decomposition was not different between grass and snowberry leaves from Biddulph in 2004 but the C:N ratios for these materials were different at 33:1 (SE= 0.01) and 47:1 (SE= 0.33), respectively (Table 5.2). The greater loss of mass from leaves than roots that was observed for plant material collected at Biddulph and studied at Kernen in 2004 was similar to that of snowberry root material collected at Biddulph and studied at Kernen in 2005. Average monthly decomposition of Biddulph snowberry leaves was greater than snowberry roots at 3.0 % (SE= 0.13) compared to 2.4 % (SE=0.13). However, decomposition was not different ($P>0.05$) when Biddulph grass leaves were compared to Biddulph grass roots in 2005 (Table 5.1).

Table 5.1. Average monthly decomposition of leaves and roots of snowberry and grasses. Values within sites are means of four sample collection dates. The SE for means are in parentheses.

			Study site and year			
Material origin	Plant material		Kernen 2004[1]	Kernen 2005	Biddulph 2004	Biddulph 2005
			Average mass per month (%)			
Biddulph[2]	Leaves	Grass	3.2 **a** (0.12)	3.4 **a** (0.15)	3.1 **a** (0.11)	3.4 **a** (0.14)
		Snowberry	2.8 **a** (0.08)	3.0 **a** (0.13)	2.9 **ab** (0.09)	2.8 **b** (0.07)
	Roots	grass	2.4 **b** (0.18)	3.8 **a** (0.29)	2.5 **b** (0.29)	2.7 **b** (0.24)
		Snowberry	2.2 **b** (0.08)	2.4 **b** (0.13)	2.9 **ab** (0.17)	2.4 **b** (0.13)
Kernen	Leaves	Grass	4.0 **a** (0.15)	5.0 **a** (0.19)	4.1 **a** (0.14)	4.5 **a** (0.11)
		Snowberry	3.5 **b** (0.10)	3.7 **b** (0.09)	3.8 **ab** (0.08)	3.4 **b** (0.06)
	Roots	Grass	2.7 **c** (0.12)	3.3 **c** (0.20)	3.9 **ab** (0.19)	2.9 **c** (0.15)
		Snowberry	2.9 **c** (0.08)	3.1 **c** (0.09)	3.5 **b** (0.09)	3.1 **bc** (0.12)

[1] Means of plant material types within an origin site and a study year that are followed by the same letters are not statistically different ($P>0.05$).
[2] Material from each site was collected in the same year of the study (i.e. 2004, and 2005).

The pattern of decomposition rates of plant materials from Biddulph at Kernen in 2004 and 2005 was not repeated at Biddulph in 2004 or 2005, but there were similarities between the study sites. For example, average monthly decomposition of Biddulph grass leaves was 3.1 % (SE=0.11) and 3.4 % (SE=0.14) at Biddulph in 2004 and 2005, respectively, which is greater than the 2.5 % (SE=0.29) lost from Biddulph grass roots in 2004 and 2.7 % (SE=0.24) in 2005 (Table 5.1). Average monthly decomposition of leaves and roots of snowberry from Biddulph at Biddulph was not different in 2004 or 2005 (Table 5.1). This lack of difference between leaves and roots was not expected because the C:N ratio of snowberry leaves was different ($P\leq0.05$) in 2004 and 2005 at 47:1 (SE=0.33) in 2004 and 26:1 (SE=0.01), respectively while that of roots was also different at 36:1 (SE=0.01) in 2004 and 41:1 (SE=0.57) in 2005, respectively (Table 5.2).

Table 5.2. Average % C, % N, and C:N ratios of leaves and roots of grasses and snowberry collected at Kernen and Biddulph in 2004 and 2005. Values within sites are means of four sample collection dates. Numbers in parentheses are S.E. of the means.

			--------Material collected in 2004--------			------Material collected in 2005-------		
Material origin	Plant material		% C[1]	% N	C:N	% C	% N	C:N
Biddulph	Leaves	Grass	40.6 **b** (3.97)	1.2 **a** (0.10)	33 **d** (<0.01)	46.1 **b** (1.50)	0.9 **d** (0.03)	49 **a** (0.33)
		Snowberry	50.3 **a** (0.43)	1.1 **a** (<0.01)	47 **a** (0.33)	52.5 **a** (0.07)	2.0 **a** (<0.01)	26 **c** (<0.01)
	Roots	Grass	47.5 **a** (0.12)	1.2 **a** (0.03)	38 **b** (0.58)	34.3 **c** (0.48)	1.6 **b** (<0.01)	22 **d** (0.33)
		Snowberry	46.5 **a** (0.22)	1.3 **a** (<0.01)	36 **c** (<0.01)	49.2 **ab** (0.12)	1.2 **c** (<0.01)	41 **b** (0.57)
Kernen	Leaves	Grass	44.2 **ab** (0.24)	1.2 **ab** (<0.01)	38 **b** (<0.01)	43.2 **c** (0.03)	1.1 **c** (<0.01)	40 **a** (0.33)
		Snowberry	49.2 **a** (0.21)	1.0 **b** (0.06)	50 **a** (2.33)	50.8 **a** (0.03)	1.5 **a** (<0.01)	33 **c** (<0.01)
	Roots	Grass	44.8 **a** (1.13)	1.0 **b** (0.06)	45 **ab** (2.08)	41.3 **d** (0.07)	1.3 **b** (<0.01)	32 **c** (0.33)
		Snowberry	43.5 **b** (1.78)	1.5 **a** (0.07)	30 **c** (<0.01)	47.5 **b** (0.07)	1.3 **b** (<0.01)	37 **b** (<0.01)

[1] Means of plant material types within an origin site and a collection year that are followed by the same letters are not statistically different (P>0.05).

5.3.2 Average monthly decomposition and C:N ratios of grass and snowberry leaves and roots collected at Kernen

The trends of decomposition rates from plant material collected at Kernen were less consistent than the trends observed for plant materials collected at Biddulph. The decomposition of Kernen grass leaves (4.1%, SE= 0.14) was not different (P>0.05) from that of Kernen grass roots (3.9%, SE=0.19) at Biddulph in 2004 (Table 5.1). However, decomposition of grass leaves was greater than that for grass roots from Kernen when studied at Kernen in 2004 and 2005 and at Biddulph in 2005 ($P \leq 0.05$) (Table 5.1). The greater loss of mass from grass leaves than grass roots was not expected because the C:N ratio was not different between grass leaves and grass roots collected at Kernen in 2004 (P>0.05), but the C:N ratio of grass leaves (40:1, SE= 0.33) was greater than that of grass roots (32:1, SE= 0.33) from Kernen in 2005. The C:N ratios of plants collected from Kernen 2005 were therefore consistent with the expectation that material with greater initial C:N ratios will decompose less

rapidly. Conversely, decomposition of grass leaves was greater than that of snowberry leaves at Kernen in 2004 despite similar C:N ratios of (Tables 5.1 and 5.2).

Decomposition of Kernen snowberry leaves (3.5 %, SE= 0.10 in 2004 and 3.7 %, SE=0.09 in 2005) was greater than that of Kernen snowberry roots (2.9 %, SE= 0.08 in 2004 and 3.1 %, SE= 0.09 in 2005) when studied at Kernen. Conversely, decomposition was not different between snowberry leaves and roots when studied at Biddulph in 2004 or 2005 (Table 5.1). Decomposition of Kernen grass leaves was also greater than snowberry leaves at Biddulph in 2005, while a difference was not detected between these plant materials in 2004 at Biddulph (Table 5.1). The C:N ratios for these materials were not consistent with decomposition results because the C:N ratio of Kernen snowberry leaves was 50:1 (SE= 2.33) compared to 38:1 (SE= 0.01) for Kernen grass leaves in 2004 ($P \leq 0.05$). Conversely, the C:N ratio of Kernen snowberry leaves was 33:1 (SE= 0.01) compared to 40:1 (SE= 0.33) for Kernen grass leaves in 2005 ($P \leq 0.05$) (Table 5.2). Decomposition of Kernen snowberry roots and grass roots was the same at both study sites ($P > 0.05$) (Table 5.1). The lack of difference in decomposition rates between grass and snowberry roots at Kernen or Biddulph occurred despite differing C:N ratios between snowberry and grass roots in both years ($P \leq 0.05$) (Table 5.2).

5.3.3 Correlation of decomposition and environmental data

Total monthly precipitation and mean monthly air, soil surface, and ground temperature were measured to determine if environmental variables corresponded with decomposition of plant material. However, the data set is incomplete due to equipment malfunctions. In addition, some precipitation data were compromised by material that blew into the rain gauge or by animals and people that periodically disrupted the gauge. The entire data set was therefore inspected, and data that were deemed unreliable were deleted. Data were not considered if the recorded values were not

plausible, such as temperatures below freezing in summer and occurrence of large precipitation events during times when no precipitation was received. The remaining data were supplemented with data from an Environment Canada weather station at Kernen; however, an Environment Canada weather station was not located near Biddulph and weather data for this study site were incomplete.

June had the greatest precipitation while July had the greatest air, ground surface, and soil temperatures (Figures 5.1, 5.2, 5.3, 5.4). Soil water content in 2004 was greater in May and June than in subsequent months, while soil water content in 2005 was greatest in September with May and June having the next greatest soil water content (Figure 5.3).

Most correlations between cumulative decomposition and environmental conditions were not statistically significant (P>0.05). Exceptions were positive correlations between air temperature and decomposition of grass leaves, soil temperature and decomposition of grass leaves, and total monthly precipitation and decomposition of grass roots (Table 5.4).

Table 5.3. Average gravimetric soil water content in the 3 to 10 cm depth at Biddulph and Kernen in 2004 and 2005. Values within sites are means of four sample collection dates. Numbers in parentheses are S.E. of the means.

		---------- Study site ----------	
Year	Month	Kernen [1]	Biddulph
		----------% soil water----------	
2004	May	22 **b** (0.8)	10 **ab** (0.2)
	June	29 **a** (0.6)	10 **a** (0.3)
	July	19 **c** (0.7)	5 **c** (0.3)
	August	17 **c** (0.5)	4 **c** (0.9)
	September	27 **ab** (0.8)	8 **b** (0.4)
2005	May	24 **b** (1.0)	8 **b** (0.4)
	June	20 **c** (1.3)	12 **a** (1.5)
	July	18 **c** (0.7)	5 **c** (0.3)
	August	16 **d** (1.0)	5 **c** (0. 2)
	September	28 **a** (0.8)	11 **a** (0.3)

[1] Means within a study year and a study site that are followed by the same letters are not statistically different (P>0.05).

Table 5.4. Correlation coefficients for cumulative decomposition of leaves and roots of grasses and snowberry with air, soil surface, and soil temperature and total monthly precipitation.

	Grass leaves	Snowberry leaves	Grass roots	Snowberry roots
	----------Correlation coefficient----------			
Air temperature	0.47*	0.19	0.17	-0.09
Soil surface temperature	0.31	0.08	-0.01	-0.11
Soil temperature	0.46*	0.13	0.03	-0.22
Total monthly precipitation	0.28	0.21	0.61*	0.02

* The correlation is statistically significant ($P \leq 0.05$).

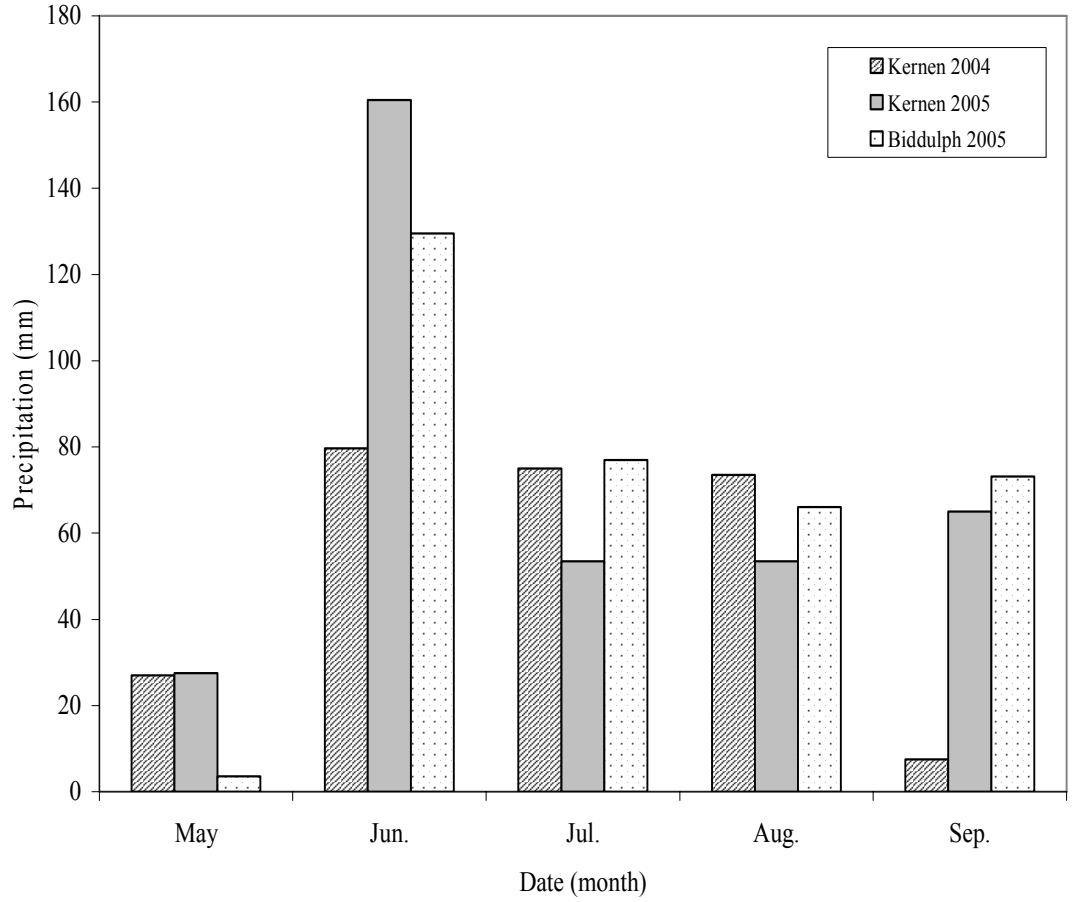

Figure 5.1. Total monthly precipitation at Kernen in 2004 and 2005 and at Biddulph in 2005.

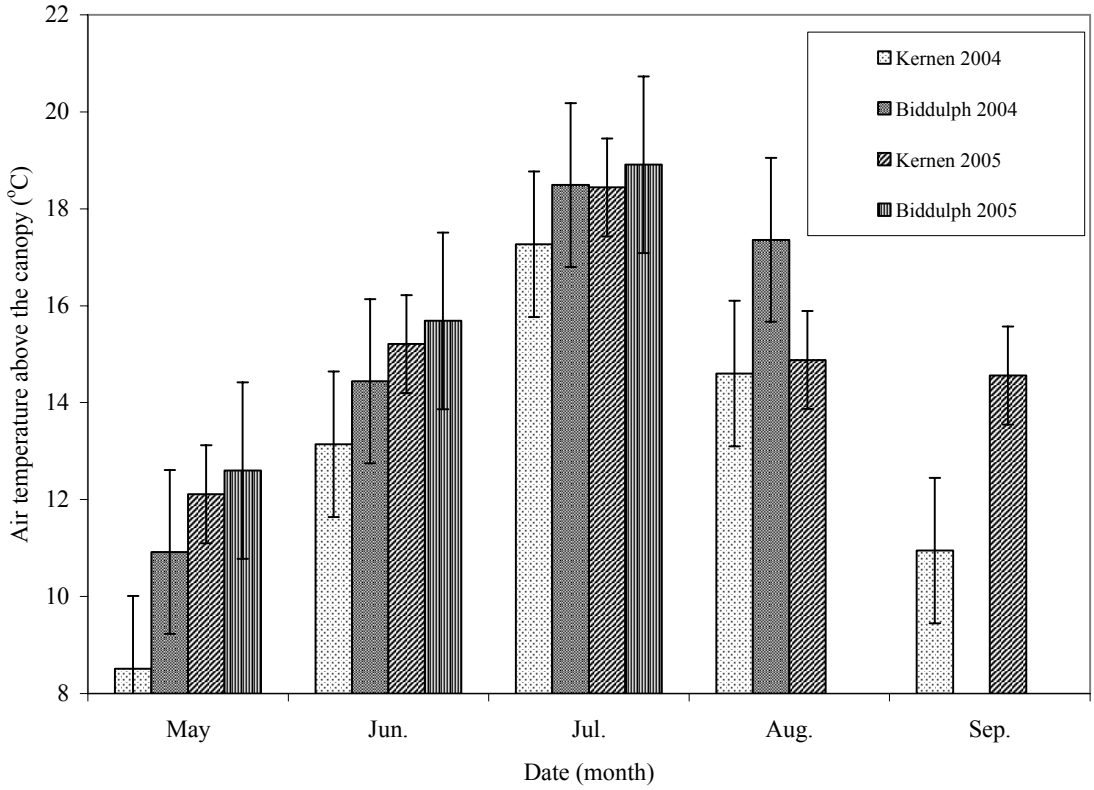

Figure 5.2. Mean monthly air temperature at Kernen and Biddulph in 2004 and 2005. Vertical bars are SE of the monthly mean and were calculated from daily averages for that month.

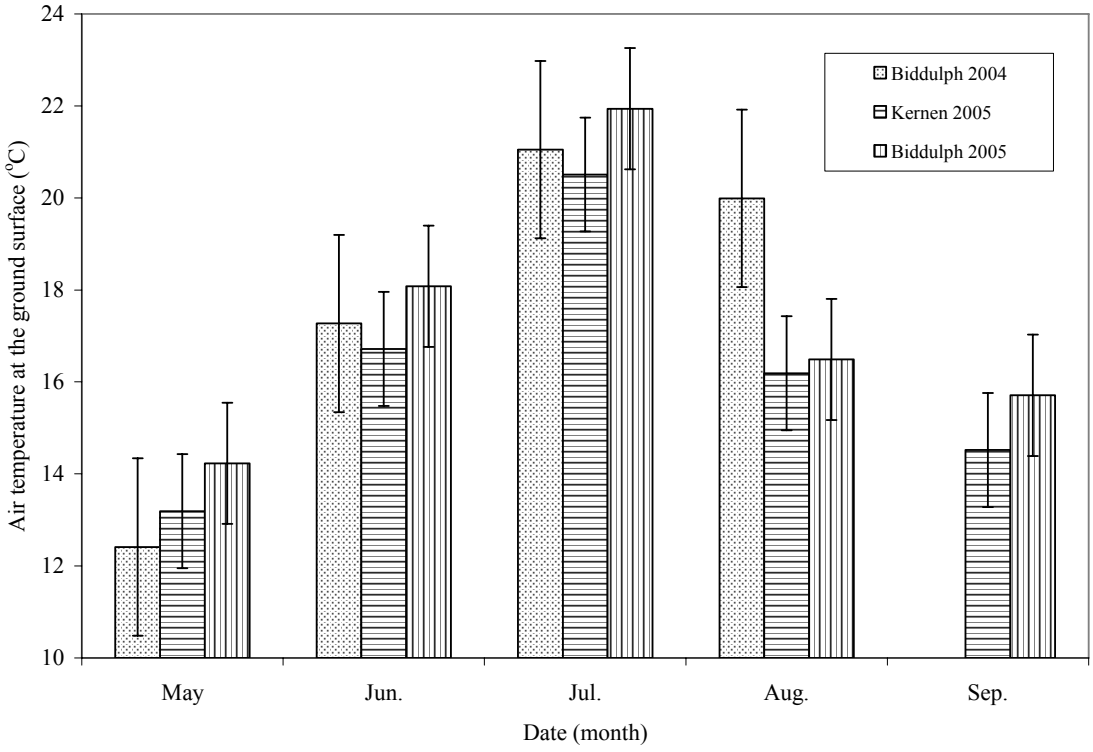

Figure 5.3. Mean monthly air temperature at the ground surface at Kernen and Biddulph in 2004 and 2005. Vertical bars are SE of the monthly mean and were calculated from daily averages for that month.

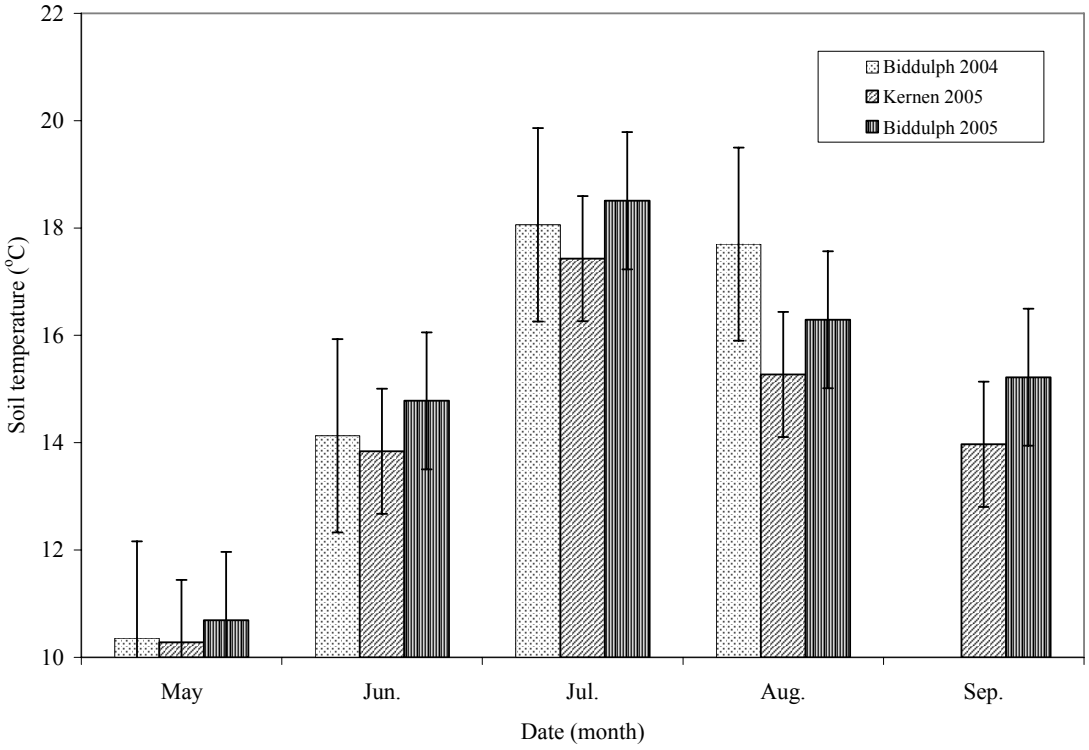

Figure 5.4. Mean monthly soil temperature 10 cm below the surface at Biddulph in 2004 and 2005 and Kernen 2005. Vertical bars are SE of the monthly mean and were calculated from daily averages for that month.

5.3.4 Cumulative decomposition of leaves and roots of snowberry and grasses

Decomposition of leaves was consistent at both study sites in 2004 and 2005. Grass leaves from Kernen lost more mass than the other materials at both study sites in 2004 and 2005 (Figures 5.5 to 5.8). The rate of decomposition was intermediate for grass leaves from Biddulph and snowberry leaves from Kernen while decomposition of snowberry leaves from Biddulph was least at both study sites in 2004 and 2005. The most mass lost from leaves occurred at Kernen in 2005 when grass leaves from this site lost 61 % of their mass over 12 months. Comparatively, mass lost from Kernen grass leaves was 50, 50, and 51 % over this same period at Biddulph in 2004 and 2005 and Kernen in 2004, respectively (Figures 5.5 to 5.8). Decomposition of grass leaves from Biddulph and snowberry leaves from Kernen was also consistent in all site and year combinations. Decomposition of Biddulph grass leaves was 40, 43, 42, and 45 % while decomposition of Kernen snowberry leaves was 41, 41, 38, and 43 % for Biddulph in 2004 and 2005 and Kernen in the same years, respectively (Figures 5.5 to 5.8). Conversely, the decomposition of snowberry leaves from Biddulph was slower than that for all other plant materials in all replications. Decomposition of Biddulph snowberry leaves was 34, 35, 32, and 37 % at Biddulph in 2004 and 2005 and Kernen in 2004 and 2005, respectively (Figures 5.5 to 5.8).

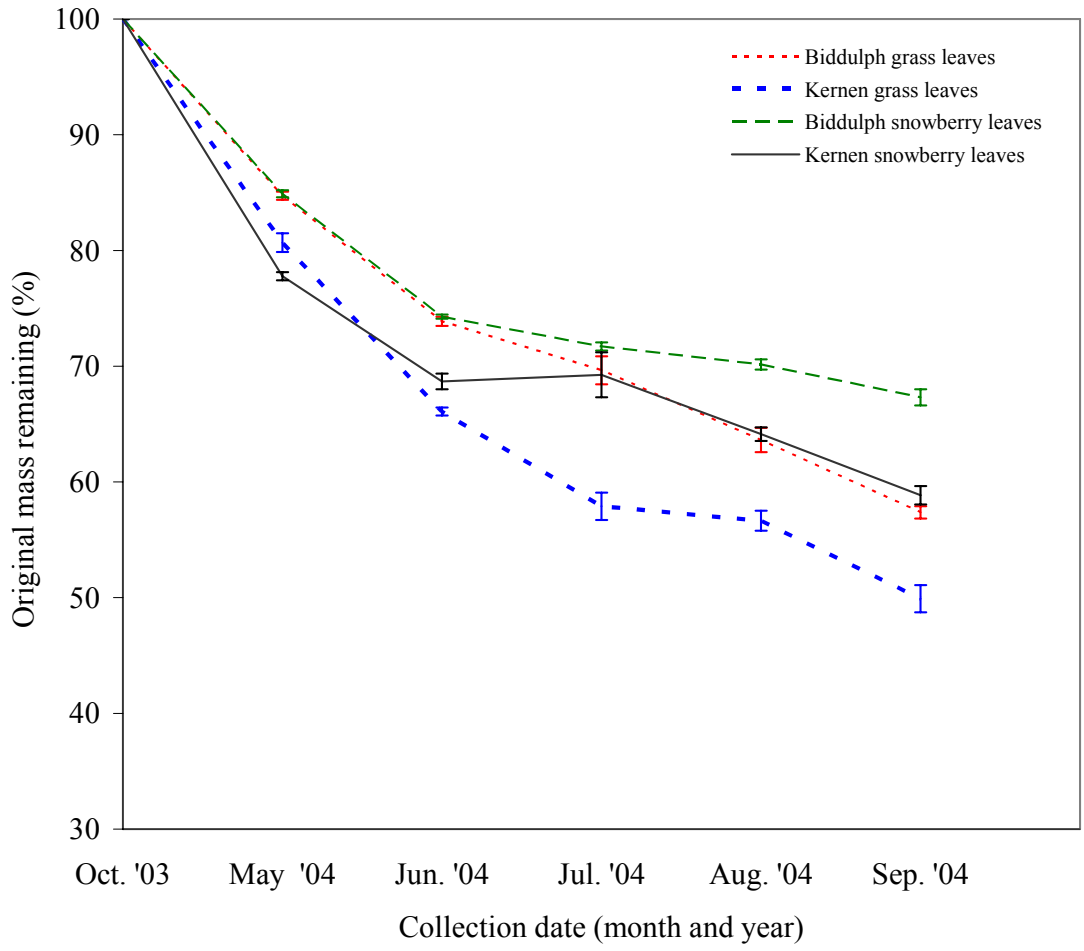

Figure 5.5. Cumulative percent decomposition of grass and snowberry leaves at Kernen in 2004. Decomposition was based on ash free mass. Vertical bars are SE of the means.

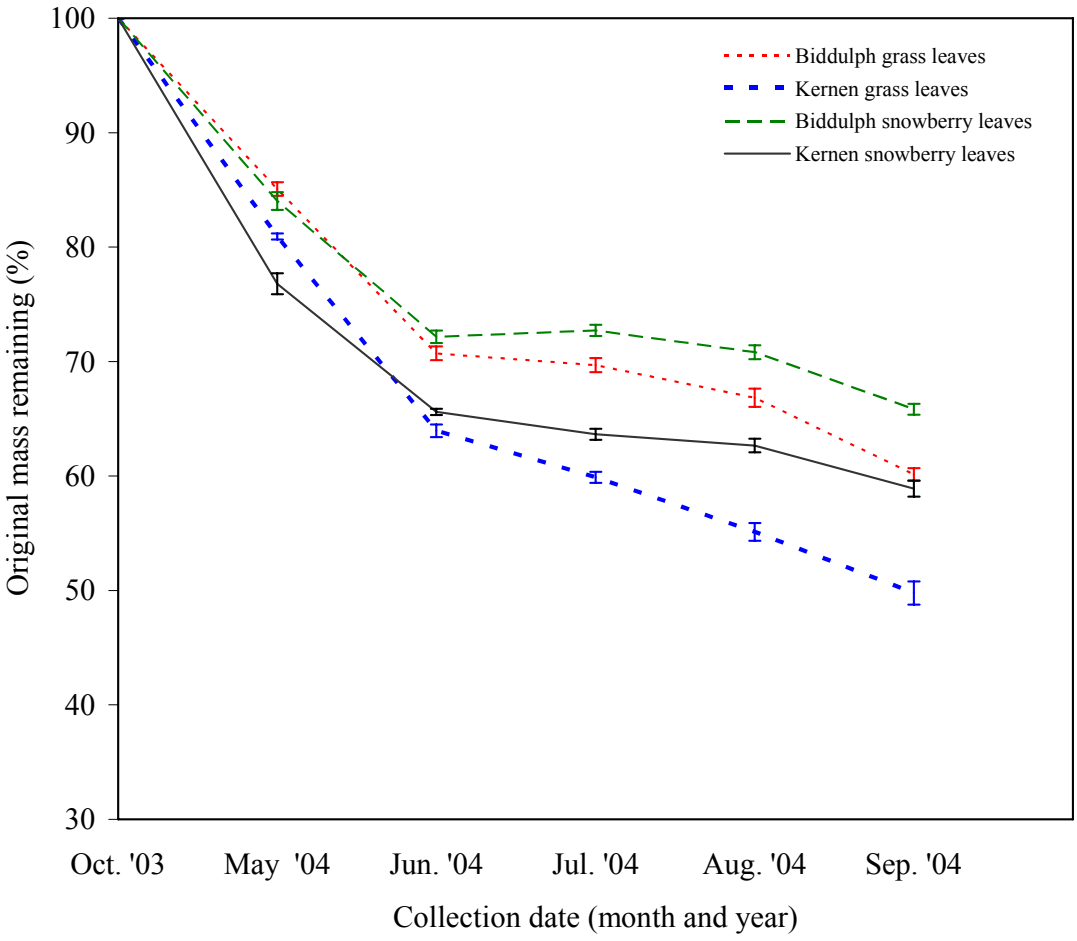

Figure 5.6. Cumulative percent decomposition of grass and snowberry leaves at Biddulph in 2004. Decomposition was based on ash free mass. Vertical bars are SE of the means.

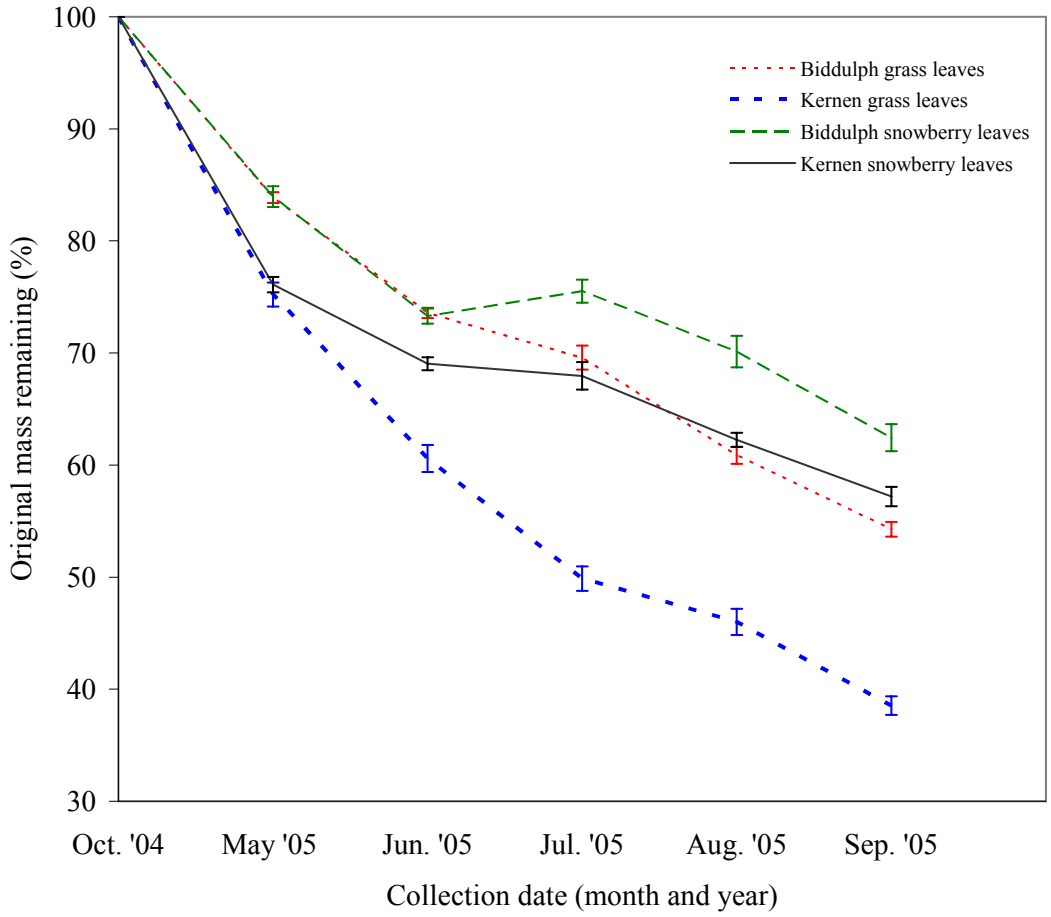

Figure 5.7. Cumulative percent decomposition of grass and snowberry leaves at Kernen in 2005. Decomposition was based on ash free mass. Vertical bars are SE of the means.

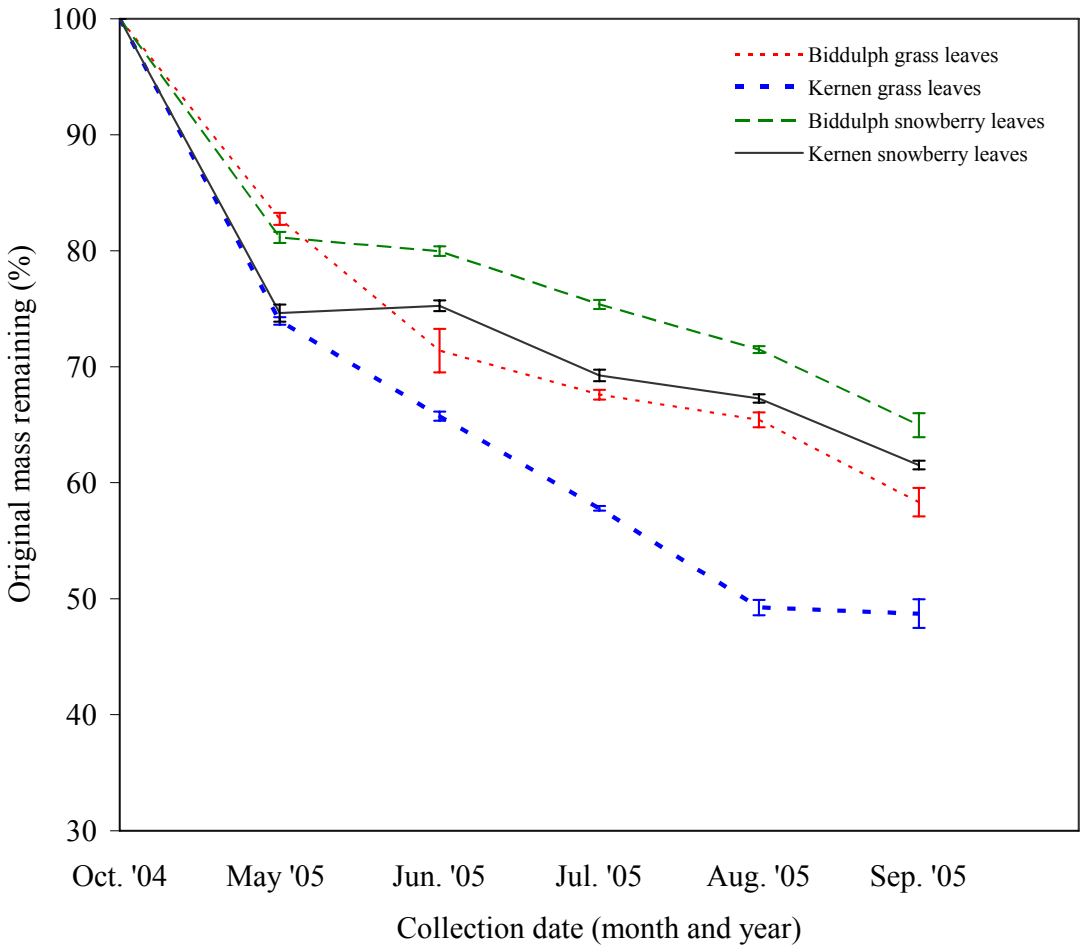

Figure 5.8. Cumulative percent decomposition of grass and snowberry leaves at Biddulph in 2005. Decomposition was based on ash free mass. Vertical bars are SE of the means.

Decomposition of roots was inconsistent over the study period (Figures 5.9 to 5.12). The inconsistency in decomposition of roots was likely caused by growth of roots from surrounding plants into the sample bags. This error was observed during collection of samples and was verified by the gain in mass of root samples during the growing season and an increase in the rate of decomposition thereafter. For example, Biddulph grass roots gained mass from May through July and lost mass from July through August, however, most of the gains are within the SE of the mean (Figure 5.9). All other root samples gained mass over one or more months from May through September (Figures 5.9 to 5.12). The inconsistency of decomposition from roots was further revealed when the correlation analysis indicated some correlations between decomposition and C:N were positive, and some were negative. Experimental error caused by roots growing into the sample bags was therefore a problem for measuring decomposition of roots in this study. Inconsistent decomposition rates for roots is not attributed to soil contamination because all root samples were incinerated in a muffle furnace and the amount of mineral soil in each sample was measured and accounted for when decomposition was calculated. There were periods when mass of leaves also increased during the growing season, but these increases were smaller than those observed in root samples.

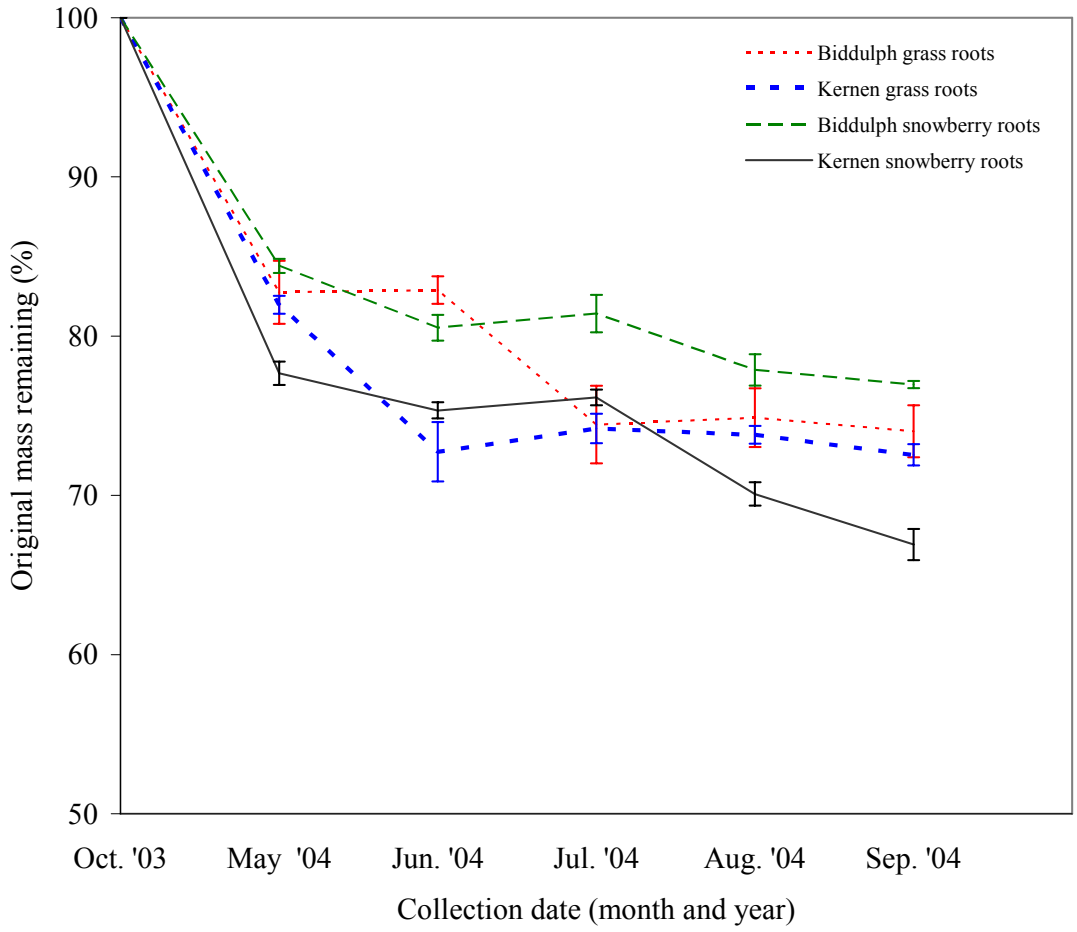

Figure 5.9. Cumulative percent decomposition of grass and snowberry roots at Kernen in 2004. Decomposition was based on ash free mass. Vertical bars are SE of the means.

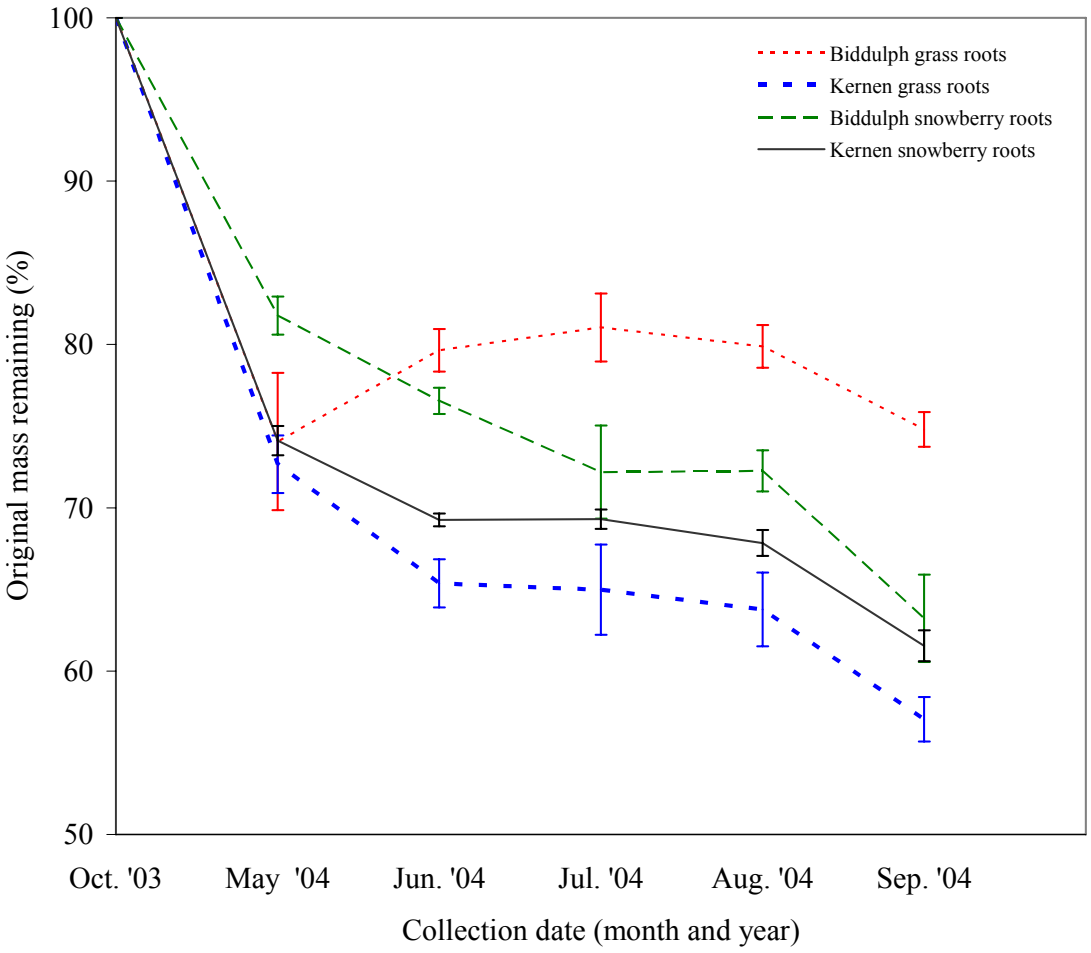

Figure 5.10. Cumulative percent decomposition of grass and snowberry roots at Biddulph in 2004. Decomposition was based on ash free mass. Vertical bars are SE of the means.

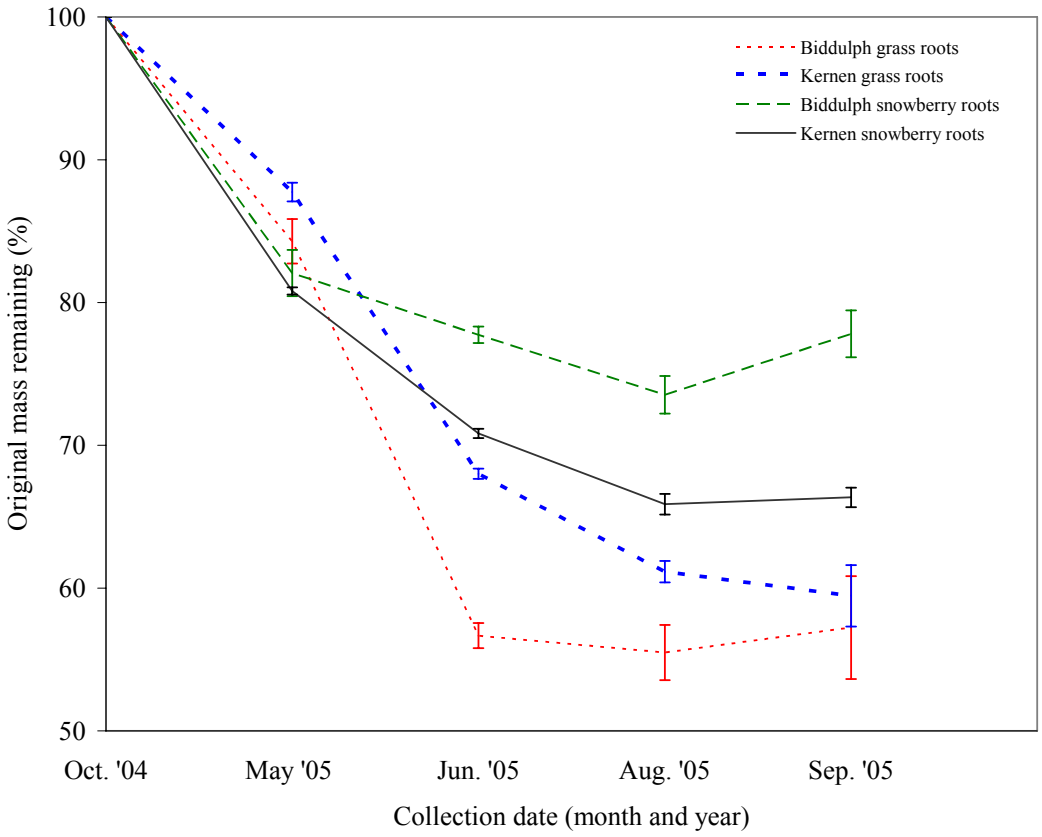

Figure 5.11. Cumulative percent decomposition of grass and snowberry roots at Kernen in 2005. Decomposition was based on ash free mass. Vertical bars are SE of the means.

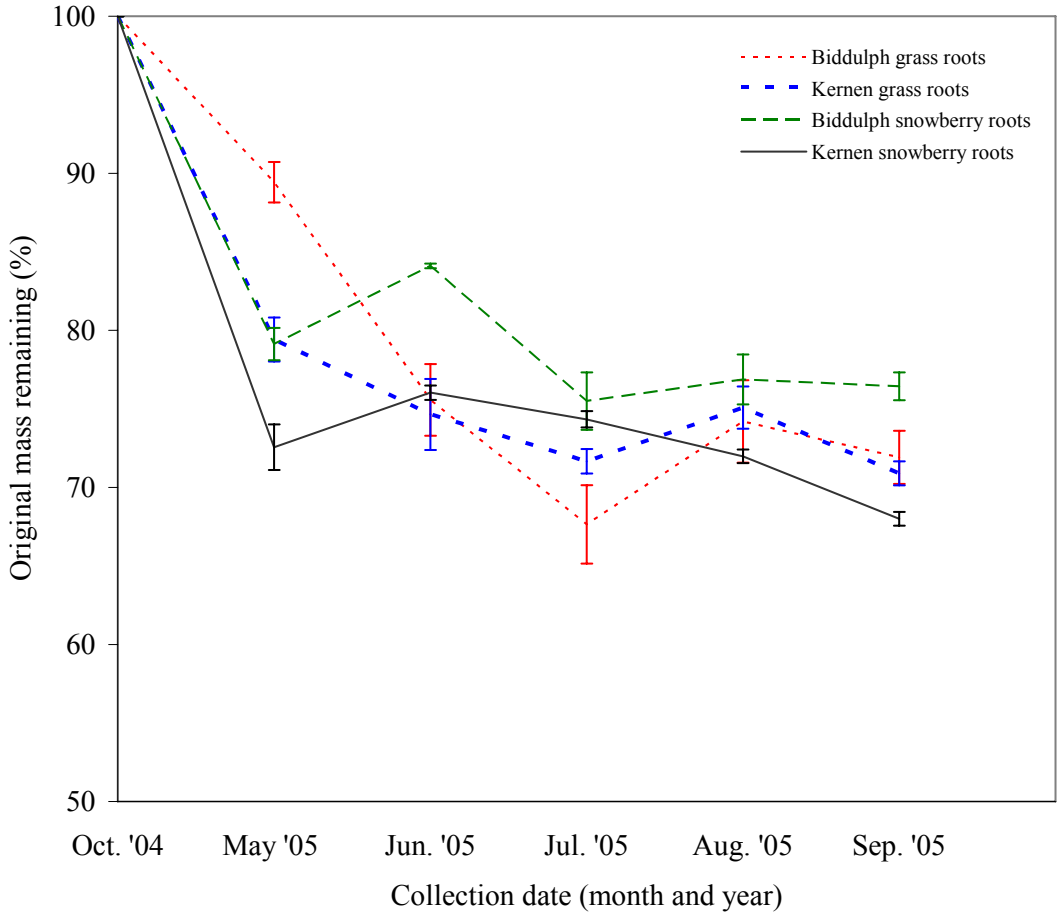

Figure 5.12. Cumulative percent decomposition of grass and snowberry roots at Biddulph in 2005. Decomposition was based on ash free mass. Vertical bars are SE of the means.

Cumulative mass loss of plant materials was quantified by calculating and analyzing the decomposition rate constants. The 2-way interactions between plant material type, origin of the plant material, study site, and study year were significant ($P \leq 0.05$). The significant interactions were reanalyzed within factors to identify if differences among mean rate constants occurred within study sites, study years or material origin. Histograms of errors were also generated and they revealed that the distribution of errors for rate constants is approximately normal.

Mean rate constants of the plant materials were different in all cases ($P<0.03$) (Table 5.5). Grass leaves had the greatest rate constants for material originating at Biddulph (0.57 yr^{-1}, SE= 0.01) and Kernen (0.71 yr^{-1}, SE= 0.02). In addition, the decay rate for grass leaves (0.57 yr^{-1}, SE= 0.01 and 0.52 yr^{-1}, SE= 0.03) was greater than that of snowberry leaves (0.46 yr^{-1}, SE= 0.01 and 0.48 yr^{-1}, SE= 0.01) and snowberry roots (0.34 yr^{-1}, SE= 0.03 and 0.38 yr^{-1}, SE= 0.02) for material originating at Biddulph and Kernen, respectively (Table 5.5). Grass leaves also decayed faster than grass roots (0.42 yr^{-1}, SE= 0.03) for material originating at Kernen ($P>0.05$), but there was no difference between the rates of decay for leaves and roots of grass from Biddulph (Table 5.5). Snowberry roots decayed slower than all other plant materials from Biddulph and Kernen. The decay rate of grass and snowberry leaves was not different within the Biddulph and Kernen study sites ($P>0.05$) (Table 5.5). However, decay was slowest for grass roots (0.36 yr^{-1}, SE= 0.03) at Kernen while decay of grass and snowberry roots were slowest at Biddulph at 0.44 yr^{-1} (SE= 0.01). Decay rates of snowberry roots and leaves of snowberry or grasses were similar ($P>0.05$) at Biddulph (Table 5.5). The decay rates of grass leaves, snowberry leaves, and snowberry roots were not different in the study conducted in 2004 ($P>0.05$), but grass roots (0.44 yr^{-1}, SE= 0.03) decomposed more slowly than snowberry leaves (0.55 yr^{-1}, SE= 0.05) (Table 5.5). Conversely, grass leaves (0.58 yr^{-1}, SE= 0.03) and snowberry leaves (0.58 yr^{-1}, SE= 0.03) decomposed faster than grass roots (0.36 yr^{-1}, SE= 0.03) and snowberry roots (0.39 yr^{-1}, SE= 0.02) during the 2005 study ($P \leq 0.05$) (Table 5.5).

Table 5.5. Mean annual decay rates for leaves and roots of grasses and snowberry within plant material origin, study site, and study year. Decay rates were calculated from a negative exponential model. The SE for means are in parenthesis.

	-----Plant material origin----		----------Study site----------		----------Study year----------	
Plant material	Biddulph[1]	Kernen	Biddulph	Kernen	2004	2005
	---------- k (yr^{-1}) ----------					
Grass leaves	0.57 **a**	0.71 **a**	0.52 **a**	0.52 **a**	0.45 **ab**	0.58 **a**
Grass roots	0.47 **ab**	0.42 **bc**	0.44 **b**	0.36 **b**	0.44 **b**	0.36 **b**
Snowberry leaves	0.46 **b**	0.48 **b**	0.58 **a**	0.55 **a**	0.55 **a**	0.58 **a**
Snowberry roots	0.34 **c**	0.38 **c**	0.44 **b**	0.41 **ab**	0.46 **ab**	0.39 **b**

[1] Means of plant materials within columns that are followed by the same letters are not statistically different (P>0.05).

5.4 Discussion

Annual decomposition of leaves ranged from 33% to 62% while that of roots ranged from 23% to 43%. Decomposition of these materials was comparable to or greater than that of grass leaves from other studies (Lauenroth and Whitman 1977, Dormaar and Willms 1993, Moretto and Distel 1997, Koukoura 1998, Hendrickson et al. 2001). For example, decomposition of leaves reported a range from 20 to 50% (Lauenroth and Whitman 1977, Abouguendia and Whitman 1979) while decomposition of roots ranged from 18 to 57% (Lauenroth and Whitman 1977, Sims and Coupland 1979).

The rate constants for decomposition of leaves in the first year of the present study were variable among previous studies. The single exponential rate constants of leaves in the present study ranged from 0.45 yr^{-1} to 0.71 yr^{-1} while that of roots ranged from 0.36 yr^{-1} to 0.47 yr^{-1}. The use of different plants species and different methods for calculating rate constants for decomposition make direct comparisons with the present study impractical, but rates of decomposition in the present study are plausible when compared to the range of decay rates reported by others (Blaire et al. 1990, Kochy and Wilson 1997). Rates of decomposition of leaves and roots for snowberry and grasses from the present study varied within origin, study site, and year. Variability in rates of

decomposition among years have been attributed to variability of cellulose, lignin, and ash contents (Taylor and Parkinson 1988a).

Roots typically decompose more slowly than leaves or, less commonly, at the same rate (Waid 1974). Kemp et al. (2003) indicated shrub leaf litter decomposed faster than shrub root litter in the Chihuahuan Desert. In the present study, average monthly decomposition of grass leaves was always greater than grass and snowberry roots and this greater decomposition was consistent among material origin site, study site, and year. Average decomposition of snowberry leaves was less consistent than that of grass leaves and varied among material origins, study sites, and years. Textural differences between shoots and roots of fescue (*Festuca arundinacea* Schred.) explain why roots decomposed more slowly than shoots (Malone and Reichle 1973). Malone and Reichle (1973) also concluded that roots require fragmentation by soil fauna before microorganisms can decompose the material. Conversely, shoot litter on the soil surface loses mass via leaching relatively quickly in the early stages of decomposition (Swift et al. 1979). However, roots undergo a period of rapid decomposition and a long period when decomposition is slow (Mun and Whitford 1998). Leaching of soluble materials from leaves did not explain why leaves lost more mass than roots in the first year of decomposition because precipitation did not correspond with decomposition of leaves.

The inconsistent rates of decay for leaves and roots in the present study may be explained by the different responses of individual plant species or materials to site and environmental factors. For example, decomposition of leaf litter may be predominantly controlled by chemical composition of the material and characteristics of the site while decomposition of roots may be predominantly controlled by their chemical composition (Moretto and Distel 2003). Leaves and roots could have similar decay rates, despite differences in their chemical composition if the microenvironment of buried roots is better suited to decomposition than that of leaves on the soil surface (Moretto and Distel 2003). It is likely that differences in the microsites aboveground and belowground complicated their comparison.

Cornelissen and Thompson (1997) concluded that monocot leaves decomposed more slowly than dicot leaves because the former are physically tougher and have more silicon. Previous studies on decomposition of leaf litter in Saskatchewan also indicated that decomposition rates of aspen (*Populus tremuloides* Michx.) leaves were less than that of grass litter Kochy and Wilson (1997). Different decomposition rates for aspen and grass were attributed to greater N in grass leaves. The N content of snowberry and grass leaves in the present study was not different in 2004, but snowberry leaves had more N than grass leaves in 2005 and decomposition did not correspond with N in the present study

As with N content of leaves, environmental conditions did not correspond with decomposition of leaves and roots. The lack of correlation between decomposition of some plant materials and air temperature and precipitation was unexpected given that it is generally accepted that temperature and precipitation affect decomposition (Swift et al. 1979). However, lack of correlation between decomposition and temperature and precipitation suggests that while macro-climatic variables may be important regulators of the overall decomposition process (Swift et al. 1979), factors such as litter quality dominate at a local scale (Meentemeyer 1984). The relatively small scale of this study and the coarse scale of temperature and precipitation measurement may explain why environmental variables corresponded poorly with average monthly decomposition. It is also possible that more temporal replication of the study is necessary to show correlation between environmental variables and decomposition.

The rapid initial decomposition rate observed during some studies, such as Koukoura (1998), may also confound the correlation analysis between decomposition and environmental variables. The initial rapid decomposition is caused by leaching of water-soluble constituents from litter in the first year of the study. This speculation is supported by decomposition curves that consistently indicate initial decomposition is greater than subsequent decay rates because soluble plant constituents are leached early in the decomposition process (Swift et al. 1979). This initial leaching of material

in the present study occurred during late fall and winter when the plant material was covered by snow. Decomposition of grass and forbs that were in direct contact with snow ranged from 30% to 51%, depending on the species studied (Bleak 1970).

Collectively, the literature concerning the role of precipitation on decomposition of plant material weakly support the decomposition of grass and snowberry in the present study. Precipitation may have leached soluble material from leaves more rapidly than from roots and this leaching from leaves was approximately equal among sites and materials. In addition, subsequent decomposition after the initial rapid leaching occurred at a relatively slow rate and these latter rates were consistent among the plant material, sites, and years comprising the study. Greater decomposition of leaves than roots in this study is therefore likely caused by the rapid leaching of material from leaves. Decomposition occurring after the initial rapid loss phase was therefore less dependent on precipitation because the range of moisture-holding capacity that permits decomposition is relatively great. It is likely that the amount of precipitation was either sufficient to maintain decomposition throughout the study, and/or that water availability in litter dropped below or above the functioning thresholds consistently among sites and years during the present study. The exceptions to this hypothesis occurred when decomposition of grass roots corresponded positively with total monthly precipitation. It remains possible that soil water content plays a role in the relative decomposition rates of leaves at the soil surface and roots buried in the soil. Future studies of decomposition in Mixed Prairie could be designed to test the different thresholds for maximizing leaching above- and below-ground.

The poor correlation between decomposition and temperature in the present study is also supported by previous research. Temperature may not correspond with SOM decomposition because temperature may not limit microbial activity in soil (Giardina and Ryan 2000). Conversely, decomposition of litter was best described as linear function of temperature and moisture with moisture increasing in importance as temperature increased (Taylor and Parkinson 1988c). Temperature also had a greater influence on decomposition of aspen and pine leaves (*Pinus contorta* Loud. x *Pinus*

banksiana Lamb.) than watering rate (Taylor and Parkinson 1988b, 1988c). On the other hand, raising soil temperature by 3 to 5^{o} C did not affect decomposition of birch leaves (*Betula pubescens* Ehrh) after 1 year (Verburg et al. 1999).

The initial N and C:N ratios did not correspond with decomposition in this study. Inconsistent effects of C:N ratio as a predictor of decomposition may be caused by the amount of lignin (Aber et al. 1990) and the amount of N in the surrounding substrate (Melillo et al. 1982). Thus, in the present study, if N was a greater limiting factor at either Kernen or Biddulph then the correlation between decomposition and C:N may be complicated by pooling data from the two sites. However, data analysis in the present study included separating the interacting effects of site and material which should account for this potential effect of different nutrient availability between the two study sites. Grass leaves decayed faster than grass roots at both study sites. Snowberry leaves also decayed faster than snowberry roots at Biddulph, but there was no difference in the rate of decay at Kernen.

The initial N content and C:N ratio corresponded with decomposition of plant litter in other studies conducted at a single site (Koukoura et al. 2003). It is possible that the N content of the samples increased during the present study because N from an outside source was deposited in the litterbags (Melillo et al. 1982). For example, N content of blue grama roots in litterbags increased in a study in the Mixed Prairie and Fescue Prairie, while the N content of rough fescue decreased (Dormaar and Willms 1993). Potential, unconfirmed, sources of N include fixation, absorption of atmospheric ammonia, dust, green litter, fungal translocation and/or immobilization (Melillo et al. 1982).

The potential effect of litterbags on decomposition is another factor that could complicate the correlation between decomposition and plant litter quality. The size of the openings in the mesh used for the litter bags controls the type of organisms that can access the plant material (Koukoura et al. 2003, Smith and Bradford 2005). The effect of litter quality on decomposition was dependent on the composition of soil fauna and the length of exposure. For example, after 30 days litter quality and decomposition

were positively correlated for the most complex decomposer community (Smith and Bradford 2005). This correlation declined with declining mesh size and exclusion of some soil organisms. Conversely, after 60 days, decomposition was most strongly affected by litter quality in the litter bags with the smallest mesh size while litter quality and decomposition were not correlated when bags with larger mesh were used. It is therefore possible that the mesh size used in the present study was large enough to permit all or most functional groups of decomposers to access the plant material. This factor could therefore encourage relatively uniform decomposition of plant material, even if some plant material is relatively poor quality because greater diversity of the decomposer community should increase the likelihood that some species are present which are capable of decomposing poor quality organic matter.

A second complicating factor caused by litterbags is related to the location of leaf litter relative to the soil surface. Decomposition of leaves can be slower when materials are suspended above the soil surface relative to material that contacted soil (Seastedt et al. 1992). The litterbags in this study may have acted as a barrier between the sample material and the physical environment which could reduce the decomposition of leaves.

5.5 Summary

Decomposition varied between species, plant parts, sites, and years in the present study but leaves generally decomposed faster than roots. Unfortunately, attempts to show that decomposition corresponded with the initial C, N and C:N ratio of plant material were not successful in the present study. Future attempts to find evidence of correlation between the initial N and C:N content of plants and decomposition should also consider the C:N and N in the soil or plant materials around the plant samples over the duration of the experiment. The effects of temperature, water availability, and chemical composition of plant materials on decomposition are relatively well understood at large spatial scales. However, correlation of these

variables with decomposition was poor in the present study. It may therefore be necessary to increase the temporal replication to gain a better understanding of the relationship between decomposition and environmental factors. In addition, application of knowledge about macroclimatic factors at small scales, such as that studied by the litterbag method, may be inappropriate because they may not reflect conditions at that small scale.

Decomposition rate constants were calculated as an alternative to the average monthly decomposition. In general, conclusions based on the rate constants were similar to those drawn from the average monthly decomposition. The hypothesis that decomposition of plant material is affected by material origin, location, and year is therefore accepted. An alternate hypothesis that decomposition of grass leaves is equal to that of snowberry leaves is not accepted, nor is the hypothesis that decomposition of grass roots is equal to that of snowberry roots. More detailed studies are required to gain a better understanding of the actual differences between these plant materials at different sites. Subsequent research on decomposition should involve intensive environmental monitoring and intensive analysis of plant chemistry. Microhabitat also has potential to play a large role in regulating decomposition. This dependence of decomposition on microhabitat further suggests that decomposition experiments should be designed with greater spatial replication to account for the variability among environmental conditions at large scale.

6.0 GENERAL DISCUSSION AND SYNTHESIS

Agricultural soils are targeted for C sequestration because they are extensive, soil organic carbon content of may be below historic amounts and the potential for sequestration of C in the soil may be great. Grassland used for livestock grazing may have potential to sequester C in soils (Follett et al. 2001). Grasslands have the potential for carbon sequestration because they are the most extensive major natural vegetation formation at a global scale (Gould 1968). Grasslands are also present on most continents and have relatively consistent climate, flora, fauna, growth form, and physiognomy (Carpenter 1940). Collectively, grasslands occupied 3.2 billion ha, or 24 percent of the global land area. Throughout the North American grasslands, overgrazing and shrub encroachment can be addressed by changing land management practices and these practices may affect SOC. These land management practices may include modified timing, intensity, and/or duration of grazing and it may include prescriptive burning in some areas where fire has been intentionally excluded from ecosystems that evolved with fire.

Aboveground phytomass was greater in ungrazed grassland than in grazed grassland at 488 and 157 g m^{-2}, respectively. Conversely, grazing did not effect the mass of fine and medium roots. The mass of fine roots was 0.9 and 0.8 kg m^{-2} in grazed and ungrazed grassland while that of medium roots was 0.6 kg m^{-2} in both grazing treatments. Replacement of decreaser plants by increaser plants in grazed grassland may be a compensatory mechanism that maintains root mass at the plant community scale. This compensatory growth at the community scale could be the reason why total SOC in the upper 50 cm of soil was not affected by livestock grazing.

The effect of livestock grazing on distribution of SOC through the profile was also studied and differences between grazed and ungrazed grassland were not found

for the 0-3, 3-10, 10-20, 20-30, 30-40 cm depths. It therefore appears that current land management regimes are consistent with goals related to maintenance of SOC in Mixed Prairie. Furthermore, maintaining cover of plants, and therefore roots, in grasslands may be the key to maintaining SOC while managing for a specific plant community may be less important for maintaining SOC. It remains likely, however, that swards with relatively large amounts of aboveground production of native plants may be beneficial for other management goals, but species composition and aboveground phytomass in grazed or ungrazed grassland were not identified as key factors for maintaining SOC.

Encroachment of snowberry into native prairie was also studied to determine if invasion in grassland by this species is consistent with goals related to soil carbon sequestration. Total aboveground phytomass in the snowberry community was more than triple that of the snowberry-grassland ecotone and was 6-times greater than that of grassland. Total organic carbon sequestered in shrub communities is about 5-times greater than that in grassland vegetation. However, the amount of C sequestered in vegetation is less than 9 % of the amount of C stored in soil.

The mass of large roots was greater in the snowberry community than in ecotones or grassland. Conversely, the mass of fine and medium roots was not different in these three communities. The differences in aboveground phytomass among plant communities did not correspond with greater SOC in the snowberry community. The SOC in the upper 50 cm of soil was 8.3, 7.9, and 7.9 kg m^{-2} in snowberry, ecotone, and grassland communities, respectively. As with the grazing study, plant species composition did not correspond with SOC content. Invasion of snowberry into grassland therefore appears to be consistent with goals related to maintaining SOC in Mixed Prairie.

Soil texture had a greater effect on SOC content than management of the aboveground plant community in the present studies. The SOC content of fine-textured soil was 10.5 kg m^{-2} in the snowberry invasion study, while that of coarse-textured soil was 6.2 kg m^{-2}. SOC in fine- and coarse-textured soil was 7.6 and 5.1 kg m^{-2},

respectively, in the grazing study. The lack of correspondence between SOC, plant community, and aboveground phytomass was interpreted to be an indication that the massive amount of C in soil acts as a buffer to management activities. This interpretation is plausible because the small annual effects of altered input from plants is insignificant relative to the total SOC pool, even when these effects are cumulative over several decades. In addition, the structure and composition of a plant community may change in the short term, but below ground production may not change or there may be a lag period before changes occur. For example, heavy grazing changes plant community composition, but the rhizosphere changes much more slowly, thereby ensuring input of carbon from roots occurs. Most ecosystem carbon occurs below ground in the Mixed Prairie studied; changes in aboveground phytomass are relatively insignificant, even when snowberry replaces graminoids.

Although some differences between decomposition of roots and leaves were detected in the decomposition study, there were few differences in decomposition within leaf and root classes. Species composition may therefore be less important for maintaining SOC than originally thought. However, this conclusion is provided with the caution that other ecological reasons likely warrant prudent management of grassland resources so that the natural composition of plants is maintained.

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