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Carbon Storage in Grazed Prairie Grasslands of Alberta

by

Darcy Christopher Henderson

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Master of Science

Department of Renewable Resources

Edmonton, Alberta

Fall 2000

0-612-59815-2

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ABSTRACT

Mitigation of global climate change currently involves research into land management for sequestering atmospheric CO_2 in soil organic matter (SOM). Soils from grazed and ungrazed treatments at nine native prairie grassland sites, across three soil zones, were sampled in southern Alberta. SOM was greatest in Black Chernozemic soils under subhumid fescue prairie and least in Brown under semiarid mixed prairie. Within a soil zone SOM was greater on ungrazed black and grazed brown and dark brown soil. Differences in grazing response were attributed to microclimatic alteration of both plant and soil microbial habitat. Using the natural abundance of ^{13}C technique on a site dominated by C_4 (blue grama) and C_3 (needle and thread) grasses, turnover rates of SOM were estimated to decline from 170 years at the surface to several thousand years at 20 cm depth. Turnover rates were slow and long-term grazing exclusion produced small changes in SOM mass.

DEDICATION

For my grandparents: James Christopher Henderson, Annie Faye Ross and Wilda Rachel Henderson. It took me a while, but I've come to understand why I chose this career path. Thank you for walks to the old house at the farm, mornings spent watching the bird feeder, afternoons hoeing potatoes in the garden, picking berries in the bush, barbecues at Little Red, fishing at Cecil ferry, pressing four-leafed clovers and releasing the bait frogs I caught for you.

ACKNOWLEDGEMENTS

I didn't know what to expect of a graduate supervisor when I arrived at the U of A. Maybe I was the benefactor of some dumb luck, but Dr. M. Anne Naeth was exactly what I needed from a supervisor. She quickly assessed whether I needed to have tabs kept on me or not. I was allowed a lot of freedom during my first year to take classes, set my own schedule and learn about graduate studies organically. However, this past year I needed a lot of help organizing this thesis and my life. Anne was always there when I needed her and knew exactly what to say and do. Thank you very much for helping me divert disaster.

I don't think Dr. Ben H. Ellert knew quite what to expect of an ecologist with my personality type assisting him with a mainly analytical, laboratory-based research project. Sometimes I know we were talking about the same thing, but more often than not thinking about it in a completely different way. It was a struggle for me, but I have learned an immense amount about soil science, analytical chemistry, biogeochemistry and the often unpleasant business of public institutional research/administration. Thank you for your patience, guidance, knowledge and sense of humour.

Thanks to committee members Dr. Edward W. Bork and Dr. Robert F. Grant for their useful editing suggestions to this final draft. Dr. Emanuel Mapfumo was invaluable for statistical advice and helping me understand the ins and outs of SAS.

Were it not for the helpful staff at AAFC Lethbridge Research Centre I would have never finished anything; not correctly anyway. Many thanks to Dr. Henry H. Janzen, Dr. Walter D. Willms, Dr. Johan F. Dormaar, Bruce Johnson, Clarence Gilbertson, Bruce Crowder, Yvonne Bruinsma, Linda Kremnek, Valerie Merrick, Mark Nadon, Elaine Nakonechney, Lorna Selinger, Edith Olson and Hugh McLean. Barry Adams and Darlene Moisey of AAFRD Public Lands were kind enough to provide data and other useful tidbits of information about my study sites. For beds, porcelain toilets, air conditioning and good food on the road I must thank Albert Middleton of AAFC Stavely Research Sub-station, Jim and Paula Gaub and Alan Ross of AAFC Onefour Research Sub-station and Dr. Barry Olson and the Olson clan of Lethbridge.

My fellow graduate students and friends from the U of A helped me learn more about myself and just what exactly I was doing here at university during our long, often

heated, discussions on statistics, philosophy, soil science, ecology, politics, teaching, love, sex, booze, drugs and life in general. Thanks to Wendy (girl who floats and sees colours) Gardner, Kelly (I was a man in a past life) Ostermann, Quinn (I'll never be a pilot) Bottorff, Kenton (don't get him upset) Rod, Colin (livin' the dream) Van Bostelin, Etienne (bohemian philosopher) Soulodre, Edith (I haven't got a problem, what's your problem?) Olson, Sara (got it together) Wilkinson, Warren (got nothing together) Fleming and Dr. Vanessa (overachiever) Bailey.

I managed to dupe many undergraduate students from Botany 204 to help out with some tedious lab work, sorting plant crowns from roots. Thanks to volunteers Teodora Alampi, Marie Beliveau, Britta Bentz, Anna Dabros, Mae Elsinger, Heather Fish, Paul Knaga, Meghan Mulligan, Julie Pierce, Angela Rogers, Fiona Sample and Charmaine Trottier.

The more time I spend apart from my family, the more I learn to appreciate what they have done and continue to do for me. Although I am not the ideal son, grandson, brother or relative (I rarely call, write, visit or say much when I do) I still think of you all everyday. The more I learn about myself, the more your influences seem to be part of everything I do. My mom, Lisa G. Henderson, influenced my critical side. Sometimes I stray into dark cynicism and distrust but I find these are healthy coping skills in my profession. My dad, George D. Henderson, influenced my analytical side. People end up coming to me with their questions and problems assuming I can help answer and deal with these. During the whole process I find my mannerisms and use of phrases much like yours. My grandparents influenced my emotional and spiritual side. The love and fascination I have for the natural world must have begun with you. You also taught me love is the most important thing whether it is someone in, or what you choose to do with, your life. I am so lucky to have grown-up with all of you in my life.

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1.1. CLIMATE CHANGE MITIGATION AND CARBON SEQUESTRATION

1.1.1. Kyoto Protocol: Impetus for This Research

Due to concern over the prospect of global climate change from industrial emissions of greenhouse gases, the international community formed the Kyoto Protocol to the Framework Convention on Climate Change in 1997. The Kyoto Protocol identifies carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) as greenhouse gases of particular concern. The overall goal was to achieve international consensus on the need to reduce greenhouse gas emissions and have groups of countries set common goals for such reductions. Canada set a goal of reducing greenhouse gas emissions by 6% below 1990 levels (Conference of the Parties 1997). Accommodation has been made for countries to use carbon credits, via carbon sequestration, in place of reduced emissions to meet their goals. Carbon sequestration involves removing atmospheric CO_2 through photosynthesis and storing it in terrestrial, aquatic and marine environments. Article 3.4 of the Kyoto Protocol outlines a need for standard methods to assess the potential and actual sequestration of carbon in agricultural soils (Bruce et al. 1999, Conference of the Parties 1997). This research addresses some methodology and assessment needs for native prairie rangelands in Alberta.

1.1.2. Agricultural Lands as Potential Carbon Sinks

In Canada approximately 612 000 km^2 of land are used for primarily agricultural purposes. Of that area, approximately 204 000 km^2 are native and non-native grasslands used for grazing livestock (Bruce et al. 1999). With consideration to the area involved, small changes in carbon inputs or outputs can have substantial impacts on greenhouse gas emissions and carbon sequestration (Allen-Diaz 1996). Cultivation of 408 000 km^2 of forested and prairie soils in Canada over the last two centuries is thought to have resulted in a loss of soil organic carbon (SOC) on the order of 1 Pg (Bruce et al. 1999). Most carbon loss occurred in the decade following land conversion, and rates of loss declined as equilibrium with the environment was approached. Thus, current rates of SOC loss are low relative to the period of settlement at the turn of the century (Houghton et al. 1983).

SOC under grazed native rangelands in Canada may be in equilibrium where little or no potential for further SOC gains or losses are possible. A significant shift from primarily high-density, low frequency migratory bison grazing to moderate-density and frequency sedentary cattle grazing has occurred (Johnston 1970). Whether the shift has caused an increase or decrease in SOC is not known. Overgrazing land can reduce plant productivity (carbon inputs) and increase erosional losses (carbon pool). Potential for increasing carbon storage is higher on lands that have lost carbon as a result of poor management. Across all rangelands, export of livestock for slaughter results in small nutrient and carbon losses from the system (Allen-Diaz 1996, Bruce et al. 1999). Fencing small parcels of land precludes importation of replacement nutrients as may have occurred under migratory bison grazing. The result is each land unit, be it a ranch or paddock, must be considered separately to determine carbon inputs, outputs, pool size and rate of increase or decrease.

Some research has focused on the effect of increased CO_2 concentration on plant production in the prairie ecozone (see reviews in Allen-Diaz 1996, Coughenour and Chen 1997, Polley 1997). Polley (1997) reviewed current research and found the most likely result of increased CO_2 concentrations would be latitudinal change in relative proportions of plant functional types (C_3 and C_4) which may alter patterns of range production and SOC sequestration. Allen-Diaz (1996) suggested redistribution of livestock to reduce stocking rates in sensitive areas, or during sensitive periods, would promote efficient nutrient cycling and conservation of SOC. Modeling by Coughenour and Chen (1997) suggests increases in CO_2 may increase plant productivity and offset SOC declines due to increased temperature and precipitation. Both Allen-Diaz (1996) and Polley (1997) recommend that rangeland research aimed at developing means to mitigate climate change must focus on soil, since this is where the bulk of grassland biomass and carbon is located.

This research stems from a larger research program into carbon sequestration initiated by the Greenhouse Emissions Management Consortium (GEMCo), and the research program of Dr. Ben H. Ellert, Biogeochemistry Research Scientist, Agriculture and Agri-Food Canada, Lethbridge. The original proposal for this thesis research outlined the following broad objectives from which this thesis research evolved.

1. Quantify soil carbon storage in representative rangeland ecosystems.
2. Evaluate the influence of livestock grazing on soil carbon storage.
3. Estimate the potential for increasing soil carbon storage by comparing soil carbon inputs and outputs.

1.2. GLOBAL CARBON CYCLES AND THE GREENHOUSE EFFECT

1.2.1. Global Carbon Pools and Cycles

Transfers of carbon between pools occur in both organic and inorganic forms. The following range of estimates were adapted from Schlesinger (1995) and Brady and Weil (1999). The exchange of carbon between the ocean and atmosphere is considerable (784 to 768 Pg C yr^{-1}). Biological CO_2 fixation and respiration accounts for 107 to 105 Pg yr^{-1} of this flux. Equilibrium is maintained across the CO_2 concentration gradient between the atmospheric pool (720 to 765 Pg C) and oceanic pool (38,000 to 39,000 Pg C) at any one point in time. However, diffusion of CO_2 into and out of, and formation of bicarbonate (H_2CO_3) within, oceans is slightly unbalanced and serve as a net sink for atmospheric CO_2. Carbonates and organic residues precipitate and accumulate in ocean sediments at the rate of 0.2 to 0.5 Pg C yr^{-1}. Biological addition of carbon to fossil fuel pools is included in that estimate. Release of CO_2 from geological pools occurs due to chemical weathering of uplifted carbonaceous rock (0.15 to 0.5 Pg C yr^{-1}) and volcanism (<0.05 Pg C yr^{-1}). Industrial fossil fuel combustion over the last century has greatly increased efflux of carbon (3 to 6 Pg C yr^{-1}) from geological to the atmospheric pool.

Approximately 90 to 130 Pg C yr^{-1} atmospheric CO_2 is fixed due to terrestrial photosynthesis. Half of the carbon fixed by plants is released relatively quickly by respiration, leaving approximately 40 to 70 Pg C yr^{-1} as net primary production (NPP). Organic carbon remaining as NPP is eventually returned to the atmosphere by consumer and decomposer respiration. Collectively, terrestrial organisms form a carbon pool of 560 to 800 Pg C. The global SOC pool is approximately twice that of terrestrial biota, at 1000 to 2000 Pg C (Schlesinger 1995, Brady and Weil 1999). Historical changes in land use have increased the efflux of CO_2 to the atmosphere and resulted in a net loss of SOC.

Cultivation, irrigation and deforestation combine to release an additional 1 to 3 Pg C yr^{-1} of carbon stored in biomass, peat and soil (Houghton et al. 1983). The net result of atmospheric inputs from human industrial activity has been an increase in atmospheric CO_2 from approximately 268 to 360 ppm over the last 150 years. Reforestation or establishing perennial forages on these lands would remove carbon from the atmosphere and possibly help mitigate greenhouse gas emissions (Allen-Diaz 1996, Bruce et al. 1999).

1.2.2. Terrestrial Biological Carbon Transformations

Plants fix atmospheric CO_2 through photosynthesis and, with H_2O and solar energy, create glucose (CH_2O) and oxygen (O_2). Glucose is an important energy source for metabolism and a building block for more complex organic molecules in plants and consumers at all other trophic levels. The biota of the earth are mainly a product of this process; since some chemoautotrophic organisms exist in environments restricted from the biosphere at large (Lehninger et al. 1993, Paul and Clark 1996). Respiration is a necessary function that involves the release of carbon into the atmosphere. CO_2 is respired under aerobic, and CH_4 under anaerobic, conditions. Although the concentration of CO_2 in the atmosphere is greater than CH_4, a single molecule of CH_4 has a greenhouse warming potential 30 to 40 times greater (Paul and Clark 1996). Approximately 50% of the CO_2 fixed during photosynthesis is lost via plant respiration, a significant proportion of which is respired from roots (Buyanovsky et al. 1987, Craine et al. 1999).

Soil respiration is the main source for CO_2 efflux in terrestrial environments. Fire and consumer respiration constitute the smaller remaining sources of CO_2 efflux from terrestrial biota. Aerobic soil microorganisms release CO_2 during decomposition of organic residues, a process of chemical oxidiation or functional mineralization (Paul and Clark 1996). Some organic residues added, or subsequently transformed, are more resistant to decomposition. Fractions of the SOC pool have been described on the basis of particulate size, radiocarbon age and chemical composition by several researchers (Paul 1984, Anderson and Coleman 1985, Roberts et al. 1989) from which the following four have been adapted:

1. Labile or Active Pool: composed mainly of coarse materials that are readily oxidized

and affected most by soil disturbance, residue inputs and climate.

2. Slowly Decomposed Pool: composed mainly of macroaggregates where mineralogy and soil aggregation are significant factors.
3. Very Slowly Decomposed Pool: composed mainly of water stable microaggregates.
4. Recalcitrant or Passive Pool: dependent on clay mineralogy of a soil and derived from microbial decomposition.

The ability of microorganisms to decompose these forms of SOC declines in the order listed. Vertical distribution of SOC in the soil is such that the upper 20 cm may contain >80% of total SOC (Paul 1984, Anderson and Coleman 1985, Roberts et al. 1989). Short-term management prescriptions for carbon sequestration are likely to have greater effects in soils with a large proportion of SOC in the labile pool (Bruce et al. 1999). Soil temperature, texture, moisture and nutrient availability are other factors affecting rates and potential for soil carbon transformations and CO_2 flux (Coughenour and Chen 1997, Parton et al. 1987).

1.2.3. Greenhouse Gases and Carbon Sinks

Photosynthesis and respiration are in dynamic equilibrium, but over millions of years there have been fluctuations in atmospheric O_2 and CO_2. Current atmospheric O_2 concentrations of 21% are a geologically recent phenomenon; produced, for the most part, by algae in the oceans. During the Mesozoic Era, CO_2 is thought to have occurred at much higher concentrations than it does currently (Sundquist 1993, Schlesinger 1995). Fluctuation in atmospheric CO_2 concentrations appears to be the best correlate with past climatic change since the Precambrian Era. High CO_2 correlates with the warm Mesozoic Era and low CO_2 correlates particularly well with Pleistocene glacial periods (Houghton et al. 1983, Sundquist 1993). Atmospheric fluctuations must be met by carbon uptake and/or release elsewhere in the environment.

A carbon sink may be considered any environment in which carbon influx from the atmosphere exceeds carbon efflux to the atmosphere per unit area and unit time (Lal et al. 1995). In the context of ecosystems, sinks occur where photosynthesis exceeds respiration, or NPP exceeds decomposition. Theory regarding ecological succession suggests NPP and decomposition are at equilibrium in either late successional ecosystems

(Odum 1969) or at intermediate stages of succession (Vitousek and Reiners 1975). Ecosystems such as arctic and alpine tundra, peatlands or wetlands are carbon sinks and may be considered in arrested development due to temperature and moisture limitations for decomposition. Ecosystems with high biomass to soil carbon ratios like tropical forests may have large carbon pools but are subject to high turnover and thus rapid losses or gains of carbon. Ecosystems with low biomass to soil carbon ratios like temperate grasslands may have small carbon pools but low turnover rates, low potential for substantial carbon loss and thus serve as effective carbon sinks (Eswaran et al. 1995).

1.3. ECOLOGICAL SETTING AND REGIONAL VARIATION IN PRAIRIE SOIL ORGANIC CARBON

1.3.1 Formation of Canadian Prairie Soils

Soils form as a product of time, climate, vegetation, topography and parent materials (Jenny 1941). Canadian temperate grasslands have developed over the last 10 000 years on glaciated landscapes. Parent materials were mainly derived from Cretaceous sedimentary deposits, and most soils have substantial amounts of soluble salts and inorganic carbon ($CaCO_3$) as a result. Often $CaCO_3$ carbon is more than twice the mass of SOC for a given soil to 1 m depth (Eswaran et al. 1995). Cold dry winters, cool wet springs and warm dry summers are characteristic of the subhumid to semiarid continental climate. Landscape variation in topography, parent material texture and chemistry affects the potential SOC mass at the polypedon scale. At the smaller scale, individual plants affect carbon inputs, microbial activity, organic matter density and depth within the solum (Schimel et al. 1985, ACECSS 1987, Eswaran et al. 1995).

Canadian prairie grasslands are dominated by soils of the Chernozem (Udoll and Ustoll) order (Table 1.1). Landscape variation in parent material and topography have produced localized polypedons of Solonetz (Natralboll), Vertisol (Cryert), Gleysol (Aquoll) and Regosol (Entisol) orders (ACECSS 1987, Brady and Weil 1999).

Schlesinger (1995) suggested recently glaciated environments are akin to seral ecosystems still in a process of carbon accumulation and serve as a net carbon sink. Grasslands may be efficient carbon sinks since a greater proportion of biomass occurs below ground where slow transformation into humus sequesters a considerable mass of carbon. However, based on reviews by Seastedt (1995) and Bruce et al. (1999) most SOC accumulation in the Canadian prairies took place during the first 1000 years of pedogenesis and carbon cycling is currently, for the most part, in dynamic equilibrium.

1.3.2. Regional Distribution of Prairie Ecoregions and Soil Zones

Regionally, there are three major ecoregions and soil zones recognized in the Canadian prairie ecozone: tallgrass prairie, mixed prairie and fescue prairie (Coupland 1961), and brown, dark brown and black soils (ACECSS 1989). Mixed prairie has been subdivided into two ecoregions (Strong and Leggat 1991). Needle and thread (*Stipa comata* Trin.&Rupr.), blue grama (*Bouteloua gracilis* [HBK] Lag.), sedges (*Carex* spp.) and wheatgrasses (*Agropyron* spp.) dominate dry mixed prairie on brown soils in southwestern Saskatchewan and southeastern Alberta. Moist mixed prairie corresponds with dark brown soils surrounding brown soils on the west, north and east. Within this ecoregion blue grama decreases in abundance and moist microsites support fescues (*Festuca* spp.) in the north and west. Sagebrush (*Artemisia cana* Pursh) and rose (*Rosa woodsii* Lindl.) are common shrubs in mixed prairie (Coupland 1950). Black soils in eastern Saskatchewan and southwestern Manitoba supported moist mixed prairie, interspersed with tallgrass prairie species and trembling aspen (*Populus tremuloides* Michx.) in a region known as the aspen parklands (Bird 1961).

British Columbia has bluebunch wheatgrass (*Agropyron spicatum* [Pursh] Scribn.&Smith) and big sagerush (*Artemisia tridentata* Nutt.) dominated palouse prairie and ponderosa pine (*Pinus ponderosa* Laws.) on brown and dark brown soils. These areas are restricted to interior warm, semiarid valleys from 250 to 1000 m above sea level (asl) (van Ryswyk et al. 1966).

Fescue prairie has also been subdivided into two ecoregions (Strong and Leggat 1991). Rough fescue (*Festuca campestris* Rydb.) is dominant in foothills fescue prairie on black soils between 49° and 51° N, and 1000 m to 2000 m asl in southwestern Alberta (Moss and Campbell 1947). This ecoregion occurs at similar latitudes and elevations in parts of the interior Douglas fir (*Pseudotsuga menziezii* [Mirb.] Franco) biogeoclimatic zone in British Columbia (van Ryswyk et al. 1966). Plains rough fescue (*Festuca hallii*

[Vasey] Piper) is dominant in parkland fescue prairie of southwestern Manitoba, central Saskatchewan and Alberta on black soils north of the dark brown soil zone (Coupland 1961). Big bluestem (*Andropogon gerardii*) once dominated tallgrass prairie on black soils in southern Manitoba. Parkland associations between tallgrass prairie, aspen and bur oak (*Quercus macrocarpa* Michx.) also occurred. Western snowberry (*Symphoricarpos occidentalis* Hook.), silverberry (*Elaeagnus commutata* Bernh. ex. Rydb.) and saskatoon (*Amelanchier alnifolia* Nutt.) are common shrubs throughout the black soil zone (Bird 1961).

1.3.3. Regional Variation in Carbon Pools, Inputs and Outputs

A variety of environmental variables correlate with these ecoregions along a gradient. Annual precipitation increases from approximately 300 mm in semiarid brown soils at the Alberta-Saskatchewan-Montana border, to approximately 500 mm in subhumid black soils to the west, north and east. Mean summer temperature decreases along the same gradient from approximately 20 to 15 °C (Strong and Leggat 1991). The interaction of precipitation and temperature decreases potential evapotranspiration and increases soil moisture along the gradient. Temperature and precipitation are the two best correlates with plant production in prairie grasslands (Sims et al. 1978, Cannon and Nielsen 1984, Smoliak 1986, Tieszen et al. 1997). Increases in annual NPP (ANPP) from 539 to 2576 kg ha^{-1} and litter standing crop from 192 to 4879 kg ha^{-1} occur along the gradient in southern Alberta (Moisey and Adams 1999).

Temperature, moisture and plant production have combined to influence the development of different soil zones. Cold to cool, subhumid black soils have thicker, darker Ah horizons with more SOC and N whereas cool to warm, semiarid brown soils have lighter coloured, thinner Ah horizons with correspondingly less SOC and N (ACECSS 1987, Anderson 1995). There remains, however, considerable variation in estimates of SOC mass in each soil zone (Table 1.2).

Physical, chemical and biological characteristics of soil organic matter differ along the soil zone gradient. Ah horizon C:N ratios generally increase from a low of 9 in brown to a high of 13 in black soils (Smoliak et al. 1972, Roberts et al. 1989, Dormaar and Willms 1998). The increase in C:N ratios has been attributed to both differences in the biochemical composition of humus in different soils and decreased nitrogen availability in black soils. Moisture limitations for decomposition in brown soils result in retention of proportionately more labile particulate organic matter to soil humus. The proportion of recalcitrant humus is greater in black soils (Anderson and Coleman 1985, Dormaar 1975). Research has demonstrated soil lignin and water soluble carbon contents are lower and polysaccharides more stable in black soils (Dormaar et al. 1984, Dormaar and Willms 1993, Amelung et al. 1997). Available nitrogen (NO_3), as a proportion of total nitrogen, is slightly greater in semiarid brown soils due to higher demands for nitrogen for litter decomposition in subhumid black soils (Burke et al. 1997, 1998). Insam (1990) found microbial biomass carbon was greater in warmer southern mixed prairie than northern, and predicted the ratio of microbial biomass carbon to SOC was greater in semiarid than subhumid climates.

Vertical and temporal variations in soil characteristics exist among and within soil zones. SOC mass/concentration and the proportion of labile to total organic matter declines exponentially, and C:N ratios linearly, with increasing depth in prairie soils (van Veen and Paul 1981, Anderson 1995). The latter two characteristics are related as humification by repeated microbial transformations reduces C:N ratios and increases stability of organic matter compounds (Paul and Clark 1996). Accumulation of NO_3 at depth due to leaching has also been identified as a factor in C:N ratio changes with depth (Amelung et al. 1997). CO_2 flux research by Ham and Knapp (1998) demonstrate grasslands act as carbon sinks in summer and sources the remainder of the year due to changes in the photosynthesis to decomposition ratio. Seasonal variation in carbon inputs and outputs results in peak SOC concentrations in late fall to early winter and lowest concentrations in late spring to early summer (Dormaar et al. 1977, 1984). In mixed prairie, litter is incorporated into SOC over winter and surface litter mass is lowest in spring (Lauenroth and Whitman 1977, Buyanovsky et al. 1987). In fescue prairie, most decomposition of litter from the previous year occurs in summer and fall and production from a given year persists through winter and the following spring (Buyanovsky et al. 1987, Willms et al. 1998).

Landscape variation may occur due to differences in topography, texture and ecological disturbance such as grazing or cultivation. SOC mass increases with clay or decreases with sand content in brown and dark brown soils (Cannon and Nielsen 1984, Bauer et al. 1987, Anderson 1995). This relationship appears to be more pronounced in the warmer southern Great Plains (Nichols 1984, McDaniel and Munn 1985, Amelung et al. 1997). Although some research indicates root and plant production are greater in sandy soils (Weaver and Darland 1949, Cannon and Nielsen 1984, Sala et al. 1988), clay mineral-organic matter complexes stabilize and retain more SOC (Tiessen et al. 1984, Anderson and Coleman 1985). Black soils are not moisture limited and soil textural differences in plant production are less pronounced.

1.4. ECOLOGICAL DISTURBANCE AND CARBON CYCLING IN PRAIRIES

1.4.1 Land Use on Canadian Prairies

Most original native prairie grasslands in Alberta have been cultivated for non-native annual and perennial crop production (Table 1.1). The most productive soils are almost entirely under cultivation (Johnston 1970). In 1996, approximately 210 400 km^2 in Alberta was privately owned and leased land used primarily for agricultural production (known as the white zone) (AAFRD 1996). A smaller area of crown forest land (within the green zone) is used extensively for livestock grazing. Most of the land used for agriculture was originally prairie grassland. South of the boreal forest, the three prairie soil zones comprise 158 140 km^2 of Alberta; this does not include grassland soils in the green zone and Peace River region (AGRASID 1999). As of 1996 approximately 65 000 km^2 of white and green zone land was uncultivated prairie grassland (Prairie Conservation Forum 1997). Nearly 70% of Alberta prairie grasslands have been cultivated or otherwise developed. Much of the uncultivated land occurs on poorly drained saline and solonetzic soils, rapidly drained regosolic dune sand and areas where stones, steep slopes or frost risk prevented plowing. Proportionately more prairie grassland has been lost in Saskatchewan and Manitoba where solonetzic soils and rolling topography are not as extensive. Most remaining grassland is grazed extensively by livestock May to October (Dormaar and Willms 1990a, Willms and Jefferson 1993).

1.4.2. Grazing Optimization and Suppression of Plant Productivity

McNaughton (1983) proposed the compensatory growth hypothesis (a.k.a. grazing optimization) whereby herbivory can stimulate plant productivity. Controversy over this hypothesis has resulted from evidence to the contrary in most ecosystems and difficulty supporting mutualistic over antagonistic coevolutionary adaptations of plants to herbivory (Southwood 1985, Belsky 1986, Milchunas et al. 1988). Whether stimulation of plant production by herbivores translates to improved soil nutrient retention has yet to be determined (Holland et al. 1992, de Mazancourt et al. 1998).

1.4.2.1. Productivity and Biomass Allocation Patterns in Plants

Fischer and Turner (1978) determined maximization of productivity was an unlikely adaptation to be selected for in plants from arid and semiarid environments. Conservation of energy reserves and moisture appears to be the rule and these species have adapted by decreasing transpirational water losses, increasing water use efficiency per unit of CO_2 fixed and shifting dominance of biomass to belowground organs.

The type of photosynthetic pathway affects patterns of variation in productivity over the season. Peak production for most C_3 species occurs in late June to early July, whereas C_4 species peak in late July to early August. Peak photosynthetic efficiency also differs along a temperature gradient from 20 °C for C_3 to 35 °C for C_4. Canadian prairies are the northernmost limit for most C_4 species and maximum potential growth may never be attained at these latitudes (Lauenroth and Whitman 1977, Smedley et al. 1991, Willms and Jefferson 1993, Frank et al. 1995, Coughenour and Chen 1997). Willms and Jefferson (1993) provide ratios for aboveground ANPP of three key species in Canadian mixed prairie that demonstrate variance between C_3 and C_4 production. For blue grama (C_4), needle and thread (C_3) and western wheatgrass (C_3) the ratio of ANPP among them is 1:2:4 respectively.

In mixed prairie the ratio of above ground to below ground plant biomass may be as much as 1:6. Blue grama has a larger root:shoot ratio relative to most prairie grass and forb species. The relative contribution to belowground biomass in prairies varies among plant functional types (caespitose versus rhizomatous) and individual species (Weaver 1950, Coupland and Johnson 1965, Sims and Coupland 1979). Clipping abovegound

ANPP provides one means of measuring carbon inputs, but belowground ANPP is less well understood (Willms and Jefferson 1993).

1.4.2.2 Response of Plant Communities to Herbivory

Removal of grass leaves and stems by clipping stimulates tillering and regrowth, at the expense of carbohydrate reserves in, and production of, new roots (Fischer and Turner 1978). In situ responses of plants to herbivory are a product of more than defoliation. A review by Milchunas and Lauenroth (1993) revealed ANPP in most arid to humid, tropical to temperate grassland environments declined with grazing. Litter removal and defoliation cause ANPP to decrease in semiarid mixed prairie (Willms et al 1986, 1993). This decrease is attributable to decreased soil moisture and a shift towards less productive and palatable species (Milchunas and Lauenroth 1993, Willms and Jefferson 1993).

Subhumid fescue prairie is more productive and litter standing crop can be 15 to 25 times that of mixed prairie (Willms et al. 1986, Moisey and Adams 1999). Burke et al. (1998) distinguish between these two ecosystems as one dominantly water limited (mixed prairie), and the other nitrogen and light limited (fescue prairie). Temperature limitation is a third factor in fescue prairie productivity. Litter has a cooling effect on soil. Once litter is removed, growing season soil temperature increases and leads to an increase in ANPP (Johnston 1961, 1971, Knapp and Seastedt 1986, Willms et al. 1986, 1993). There is an upper limit to this response however, as very heavy grazing appears to consistently reduce ANPP in fescue prairie (Dormaar and Willms 1990a). Other anomalies to the ANPP response to grazing have been reported by Johnston (1961) for fescue prairie and Shariff et al. (1984) and Manley et al. (1995) for mixed prairies.

1.4.2.3. Plant, Soil and Herbivore Interactions

Grazing causes a shift in rangeland species composition towards less productive communities adapted to drier conditions (Sims and Coupland 1979, Milchunas and Lauenroth 1993, Willms and Jefferson 1993). Grazing dry mixed grass prairie generally increases the abundance of blue grama. Blue grama has a high root:shoot ratio and mass of fine roots relative to other grasses (Coupland and Johnson 1965). Inputs from blue grama below ground may increase SOC relative to adjacent ungrazed prairie dominated by C_3 species (Smoliak et al. 1972, Dormaar et al. 1977, 1984, Sims and Coupland 1979, Dormaar and Willms 1990a, Frank et al. 1995, Derner et al. 1997, Kelly and Burke 1997). Grazing the mainly C_3 foothills fescue prairie results in a decrease of the dominant species, rough fescue (Dormaar and Willms 1990a). Rough fescue has a large root mass and is replaced by species with smaller root masses characteristic of mixed prairie communities and less organic residue is contributed to the SOC pool in grazed treatments (Johnston 1971, Dormaar and Willms 1990a, 1998).

Previous research suggests root biomass may be directly related to SOC mass/concentration. Researchers have demonstrated a correlation between root biomass and plant community composition or soil texture (Bauer et al. 1987, Sala et al. 1988). Differences in root productivity, turnover, respiration and addition of exudates are difficult to quantify in situ, although these may be equally or more important than biomass as determinants of, and correlates with, SOC (Sims and Coupland 1979).

Grazing optimization of plant production may occur on a sustained basis only under set conditions. For example, de Mazancourt et al. (1998) described a scenario whereby plant production may be suppressed in environments with reduced nutrient availability due volatilization, erosion or demands for litter decomposition. If grazing animals were introduced to such an environment nutrient cycles could increase in efficiency and more nutrients (nitrogen and phosphorus primarily) would remain in the soil. Under these conditions, grazing could theoretically enhance productivity if nutrient losses from livestock export are less than the losses caused by other sources (Holland et al. 1992, de Mazancourt et al. 1998).

1.4.3. Grazing Impacts on Soil Organic Carbon Transformations

1.4.3.1. Grazing and Patterns of Soil Organic Carbon Mass/Concentration

In a review of grazing impacts on grasslands around the globe, Milchunas and Lauenroth (1993) found no consistent relationship between grazing impacts and SOC storage. In several cases the results of studies in the same ecosystem were contradictory. Research from the northern Great Plains indicates SOC is greater under grazed treatments in brown soils and greater under exclosures in black soils with few exceptions (Table 1.3). Two of five studies in brown soils sampled the same heavily grazed treatment at different periods in time using the same technique (Smoliak et al. 1972, Dormaar and Willms 1990b). Differences in SOC among treatments were more pronounced at shallow depths.

Three of five studies in black soils were conducted at the same research site at different periods in time using different fractionation methods and chemical analyses (Johnston et al. 1971, Naeth et al. 1991, Dormaar and Willms 1998). Differences between treatments were rarely statistically significant. Regardless, all three studies consistently demonstrated a trend toward greater SOC mass/concentration under exclosures and progressively less SOC under increasing grazing intensity. Naeth et al. (1991) found Ah SOC was greater beneath the exclosure in foothills fescue, but greater beneath grazing treatments in plains rough fescue on black soils.

Responses to grazing treatment in dark brown soils were variable. SOC mass/concentration was greater under moderate to heavy grazing treatments (Dormaar et al. 1984, Frank et al. 1995) while in other cases SOC was greater beneath exclosures (Bauer et al. 1987, Frank et al. 1995, Derner et al. 1997). Only Bauer et al. (1987) used replicates of treatments at different locations. That research demonstrated the difference between grazed treatments and 75 year old exclosures was more pronounced in sandy soils and less in clay textured soils.

All comparisons of SOC mass/concentration between treatments may reflect responses to grazing or grazing exclusion, or both. Experimental and statistical methodology would imply the variable we manipulate (grazing intensity, duration, timing, frequency) is the treatment variable (Steele et al. 1997). However, ecologically prairie grasslands can not be considered as realistic controls in the absence of grazing and fire (Sims et al. 1978). Response variables selected and hypotheses formulated for grazing treatment effects have focused on herbivore-plant interactions within grazed treatments, whereas soil-plant-atmosphere interactions within ungrazed treatments have for the most part been ignored.

1.4.3.2. Grazing and Changes in Soil Physical Properties

Trampling by livestock compacts soil, increases bulk density and reduces average soil aggregate diameter and mass of the macroaggregate fraction of soil (Johnston 1971, Naeth et al. 1990). Infiltration rates are reduced in compacted soils and runoff increases, leading to soil and/or plant residue losses with erosion. Compacted soils also have less moisture holding capacity as the pore space is reduced (Lodge 1954, Johnston 1971, Naeth et al. 1991, Unger and Kaspar 1994, Manley et al. 1995). Reduced habitable pore space for mesofauna and microflora may affect detrital food webs. Litter reductions due to herbivory and trampling allow more solar radiation to reach the soil surface. Mean soil temperature and the amplitude of daily and seasonal temperature fluctuations increase with grazing and litter removal. Increases in temperature can increase evaporation rates (Rice and Parenti 1978, Knapp and Seastedt 1986, Willms et al. 1986, 1993, Facelli and Pickett 1991).

The interaction of defoliation, trampling and litter removal impacts soil microclimate. In water limited semiarid brown soils grazing creates drier and warmer microsites that are less productive but favour C_4 species which use water more efficiently. In temperature limited subhumid black soils, where litter mass may be 15 times that of mixed prairie, grazing creates warmer microsites that are more productive and stimulate tillering (Johnston 1961, 1971, Willms et al. 1986, Dormaar and Willms 1990a).

1.4.3.3. Grazing and Changes in Soil Chemical Properties

Most nitrogen, phosphorus, potassium and sulfur consumed by livestock is returned quickly via urine and faeces. A small portion of these nutrients is lost by through assimilation and export of livestock. In terms of carbon, most of that consumed is released as CO_2 through respiration. Trampling of plant residues by herbivores and addition of dung returns organic matter to the soil with increased surface area and mineralized nutrients (N, P) readily available for microbial immobilization (Shariff et al. 1984, Dormaar and Willms 1990, Holland et al. 1992).

Grazing results in consistently lower C:N ratios of organic matter at the soil surface (Smoliak et al. 1972, Dormaar and Willms 1990, 1998, Frank et al. 1995). This is an indicator of lower carbon or greater nitrogen concentrations with grazing. Lignin content of plant litter influences the rate of decomposition. Species with high C:N ratios in leaves, stems and/or roots will decompose more slowly (Parton et al. 1987). Dormaar and Willms (1993) found partially decomposed blue grama residues had less lignin and more nitrogen relative to rough fescue buried in litter bags, although lignin concentration increased in both species buried in black soils. Shariff et al. (1984) found litter decomposed more quickly and nitrogen mineralization rates were higher under moderately grazed mixed prairie, relative to both ungrazed and heavily grazed treatments. Soil nitrate (NO_3) concentrations relative to total N appear to increase under grazed treatments in mixed prairie. Drier conditions inhibit both decomposition and NPP, reducing competition for NO_3 (Sharrif et al. 1984, Dormaar and Willms 1993, Frank et al. 1995, Derner et al. 1997). As well, increases in nitrogen use efficient species like blue grama may reduce available nitrogen demand and lead to accumulations of NO_3 relative to ungrazed sites (Burke et al. 1997, 1998).

1.4.3.4. Grazing and Changes in Soil Biological Activity

The interacting effects of defoliation, trampling and litter removal via livestock grazing impact soil microbial habitat, which in turn affects microbial activity and CO_2 efflux. Decomposition accounts for 60 to 70% of CO_2 efflux in tallgrass prairie (Buyanovsky et al. 1987, Craine et al. 1999). Soil respiration (both decomposition and root respiration) in tallgrass prairie varies from 0.4 to 0.04 mg CO_2 m^{-2} s^{-1} (Wildung et al. 1975, Ham and Knapp 1998). Soil temperature and moisture are the two main factors affecting microbial activity, and thus mineralization of SOC. Wildung et al. (1975) found soil microbial respiration was maximized at gravimetric soil water contents of 6 to 10%, and temperatures above 15 °C in black soils.

Litter removal due to grazing increases soil temperature and, in a temperature limited but moist environment, could increase microbial respiration (Buyanovsky et al. 1987). It is possible SOC mineralization declines in cooler, moister ungrazed fescue prairie on black soils. In dry environments microbial activity may decrease as temperature increases following grazing due to evaporative water loss (Johnston 1971, Willms et al. 1986, Willms 1988). It is possible SOC mineralization increases in ungrazed mixed prairie on brown soils. Holt (1997) found heavily grazed semiarid grasslands in Australia had less microbial biomass, peptidase and amidase (enzymes involved in N mineralization) activities, despite no change in SOC over six to ten years. Changes in these soil characteristics were attributed to warmer, drier conditions on grazed treatments resulting in decreased microbial activity.

1.4.3.5. Relationship of Plant Species to Soil Organic Carbon

Dormaar and Willms (1993) speculated an increase in blue grama on grazed mixed prairie was the cause for greater SOC on grazed treatments. Research in Alberta appears to consistently demonstrate blue grama cover and Ah SOC increased directly with grazing intensity (Smoliak et al. 1972, Dormaar and Willms 1990b, Dormaar et al. 1994). Frank et al. (1995) found SOC differed little between heavily grazed and ungrazed mixed prairie treatments, but moderately grazed had less SOC than the two extremes. Less SOC on grazed mixed prairie in North Dakota was attributed to reduced root biomass (Bauer et al. 1987); even though blue grama increased on grazed treatments. Manley et al. (1995) found SOC was greater on moderately grazed mixed prairie, although blue grama was absent in both grazed and ungrazed treatments in Wyoming. Shariff et al. (1994) found grazing, particularly moderate intensity, increased ANPP and root biomass in North Dakota mixed prairie. One is left to ponder whether blue grama has anything to do with observed SOC responses to grazing treatments.

Johnston (1961) noted that light grazing in the fescue prairie increased root biomass; contrary to the results of clipping experiments of rough fescue in the greenhouse. Dormaar et al. (1984) found heavily grazed fescue prairie had more SOC than an adjacent ungrazed exclosure. This one exception to previous research at the same site was attributed to differences in topographic position and microclimate between treatments that may have affected pedogenesis, subsequent erosion and the apparent response to grazing.

It is difficult to determine whether any grazing treatment has had an effect on the SOC pool in either mixed prairie or fescue prairie. A lack of statistically significant differences between treatments indicates considerable underlying spatial variability, or that changes are small relative to variability. Small treatment differences in the labile pool of SOC may also be difficult to detect against a substantial background mass of recalcitrant SOC (Bruce et al. 1999).

1.4.4. Cultivation Impacts on Soil Organic Carbon Transformations

Turnover of prairie grassland SOC between fractions and over time has been studied in cultivated soils or paired comparisons of cultivated and uncultivated soils. The dynamics of SOC under native prairie has been inferred from cultivated land studies. Disturbance due to cultivation or grazing exclusion provides a necessary manipulation whereby plant and soil characteristics can be studied over time (Martel and Paul 1974, Tiessen et al. 1982, Schimel et al. 1985, Aguilar et al. 1988). Turnover represents the time required for the cumulative input or output of carbon to equal the SOC pool size; assuming steady state conditions. Crude estimates of turnover can be made from the input perspective using SOC mass, aboveground ANPP from clippings, and an assumed root:shoot ratio to account for total ANPP. Soil respiration, minus root respiration, can be used in place of ANPP to calculate turnover from the output perspective. Use of a tracer such as ^{13}C can provide a more accurate measure of turnover (Paul and Clark 1996).

1.4.4.1. Effect of Cultivation in Prairie Grasslands

Cultivation of prairie soils is known to cause several changes in soil characteristics. Tillage equipment and erosion/deposition redistributes soil in cultivated lands from hilltops and shoulder slopes to toe slopes and basins (Aguilar et al. 1988, Pennock et al. 1994). Tillage also disrupts soil structure and leads to decreases in macroaggregate fractions (Dormaar and Smoliak 1985, Six et al. 1998).

SOC declines with cultivation. Litter removal and initial decreases in bulk density expose macroaggregates and buried plant residues. Mineralization of these labile SOC fractions results in a rapid decline in SOC (Holland and Coleman 1987). Martel and Paul (1974) determined SOC loss was proportional in all chemical fractions initially then mainly from labile fractions over time. Combined with reduced residue inputs from annual crops, the mean residence time of SOC increases, since remaining SOC is in older recalcitrant forms (Table 1.4). Total soil nitrogen, phosphorus and microbial biomass carbon also decline with cultivation. Both the ratio of mineralizable C: total C, and mineralizable N: total N increase with cultivation, and are related to decomposition of previously stabilized, now labile, organic matter. Statistically significant changes in SOC on level fields have only been detected in the upper-most increments or A horizon. Losses also appear to be more rapid in sandy soils relative to silt or clay (Tiessen et al. 1982, Schimel et al. 1985, Aguilar et al. 1988). The loss of carbon from soil follows first order kinetics, whereby a rapid decline in the first decade or two begins to level out over the next few decades until a new equilibrium of inputs and outputs is reached (Paul and Clark 1996).

1.4.4.2. Soil Organic Matter Recovery and Succession in Prairie Grasslands.

Abandoned cultivated land will revegetate naturally under moderate grazing pressure and soil organic matter increases with time. Rates of organic matter recovery are slow (Dormaar et al. 1990). After as few as 10 years cultivation recovery for black soils has been estimated to take 150 years (Dormaar et al. 1990, Kindscher and Tieszen 1998) and greater than 50 (possibly 75) years for brown soils (Dormaar et al. 1990, Burke et al. 1995). Recovery of the labile fraction occurs initially, followed by reformation of macroaggregates (Buyanovsky 1987). Increases in resistant polysaccharide and phenolic compounds do occur but much more slowly (Tiessen et al. 1984, Dormaar and Smoliak 1985). A persistent soil characteristic of most abandoned cultivated land is the higher ratio of potentially mineralizable N: total N (Dormaar and Smoliak 1985, Dormaar et al. 1990, Ajwa et al. 1998). Contrary to these findings, Burke et al. (1995) found no difference in potentially mineralizable N, C or microbial biomass C after 50 years of recovery on shortgrass prairie. Tiessen et al. (1984) pointed out soils with high $CaCO_3$ promote stabilization of undecomposed residues in brown soils and may be a factor in the rate and fractional proportions of SOC recovery.

Stage of plant community succession does not infer stages in soil organic matter recovery. Abandoned cultivated land superficially resembling adjacent uncultivated land did not differ in composition or cover of shortgrass prairie, although SOC was lower on the abandoned side after 50 years (Burke et al. 1995). Both Dormaar and Smoliak (1985) and Kindscher and Tieszen (1998) found species richness, vegetation cover, root biomass and SOC lower on 25 to 55 year old abandoned land. ANPP was greater on abandoned land in the brown soil zone of Alberta (Dormaar and Smoliak 1985). The increase in production was attributed to increased N availability, despite the fact abandoned land had a greater proportion of blue grama, a less productive species. SOC recovery rates were shown to be linear by Dormaar et al. (1990) for brown soils. Plant community succession may be a factor in this because shallow-rooted annuals tend to dominate prairie for as much as a decade before deep-rooted perennials begin to dominate (Weaver and Albertson 1936, Judd and Jackson 1940, Booth 1941, Costello 1944, Tomanek et al. 1955). There may be a linear increase in root biomass and residue inputs to SOC with succession on these lands.

1.5. RESEARCH GAPS AND DIRECTIONS FOR THIS RESEARCH

1.5.1. Gaps in Research

Whether it is within grazed or ungrazed treatments that the SOC pool changes is unknown because no preliminary sampling to quantify baseline conditions and spatial variability was conducted. Hypotheses regarding, and measurement of grazing treatment effects tend to focus on herbivore-plant interactions within grazed treatments, whereas soil-plant-atmosphere interactions within ungrazed treatments have for the most part been ignored. Variation in treatment responses may reflect lack of site replication and consistency in sampling and analyses in previous research (Bowman 1991, Veldkamp and Weitz 1994, Dutilleul 1993). Consistent, quantitative methods for sampling and analyzing more than one site provide useful contrasts among soil zones or ecoregions (Naeth et al. 1991) and soil texture classes (Bauer et al. 1987). Replicates within dominant soil texture classes nested within each soil zone or ecoregion would be ideal for comparing grazed and ungrazed treatments. Accomplishing this is difficult due to the expense necessary to analyze a sufficient number of samples in one study. Exclosures were established at different times and grazing history has not been recorded with sufficient detail in nearly all studies. Qualitative range condition categories are often all that is available for describing grazed treatments. The above are important factors limiting statistical and ecological inference.

In most studies the Ah horizon, which contains up to 80% of prairie plant root biomass, was sampled and analyzed. However, early work by Weaver (1950) and Coupland and Johnson (1965) demonstrated prairie grasses and forbs commonly have root systems that extend beyond 1 to 2 m deep. Blue grama was one of the more shallow rooted species. SOC mass in the Ah may be equivalent to underlying B and C horizons to 100 cm based on regional and site specific research (Table 1.2). Treatment differences at the surface may be less dramatic when considered against background SOC mass at depth (Herrick and Whitford 1995, Bruce et al. 1999).

Long term range production monitoring conducted by federal, provincial and state agencies in the northern Great Plains facilitate estimation of carbon input rates. Estimates of carbon outputs are complicated by the difficulty distinguishing plant root respiration from soil organic matter decomposition (Ham and Knapp 1998). In semiarid systems timing appears to be important for soil carbon efflux because it is closely tied to spring snow melt and infrequent rainfall events (Ellert 2000). In situ estimates of carbon turnover (balance of input and output) rates using an isotopic tracer have been conducted for prairie soils supporting annual crops and perennial tame forages. However, estimates from intensively managed crop systems cannot necessarily be applied to extensively grazed systems on native range.

Carbon content determinations have been made using several techniques (for example, dry combustion or incubation and gas chromatography, or solution extraction and titration) not all of which yield comparable results. Carbon content has also been reported as % total C, % organic C, % organic matter, g kg^{-1} or kg m^{-2}. Often sampling was qualitative (for example carbon concentration in Ah horizon of variable depth), as opposed to quantitative (carbon mass per soil volume, or per equivalent soil mass). Concentration data can be used to identify treatment differences but not extrapolated to estimate SOC pool size or turnover rates for a given area. Reporting mass per area data with associated bulk density or on an equivalent mass basis for each increment is necessary for evaluating predictive carbon cycle models (Ellert and Janzen 1996).

1.5.2. Research Objectives

The first objective of this thesis research is to quantify differences in the organic carbon pool among grazed and ungrazed treatments along an environmental gradient from black soils under subhumid fescue prairie to brown soils under semiarid mixed prairie in southern Alberta. The carbon pool will be separated into belowground (fine soil and macro-organic matter) and aboveground (litter, vegetation and crowns) fractions. Regional gradient analyses will be applied to describe how SOC mass changes with precipitation, temperature, elevation, soil and vegetation characteristics. Previous research placed considerable emphasis on the role blue grama plays in patterns of SOC mass between grazing treatments. Separate analyses of mixed prairie data will be used to assess the influence of increasing blue grama cover in grazed treatments on SOC.

The second objective is to estimate turnover rate of SOC among depth increments in grazed, native prairie grassland using the natural abundance of ^{13}C as a tracer. Differences in ^{13}C discrimination during photosynthesis in C_3 and C_4 plants will be exploited to trace the movement between, and turnover time within, organic matter fractions. Turnover rates are important for determining expected rates of change following treatment applications or management prescriptions intended to affect the SOC pool. This will be the first time two adjacent native, perennial mixed C_3 and C_4 grassland communities have been used to estimate SOC turnover.

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Table 1.1. Soil zones, landscapes and land use in the prairie ecozone of southern Alberta.

Landform	Soil Zones			Percentage of Land Base
	Black	Dark Brown	Brown	
Plains				
Area (km^2)	40 118	26 088	32 856	62.6
Parent materials	till, fluvial, lacustrine	till, fluvial, lacustrine	till, fluvial, lacustrine	
Major orders	CH, SZ	CH, SZ	CH, SZ	
Uplands				
Area (km^2)	15 306	11 491	5 043	20.1
Parent materials	till	till	till	
Major orders	CH	CH	CH	
Valleys/Coulees				
Area (km^2)	6 607	1 826	3 477	7.5
Parent materials	eroded, fluvial	eroded, fluvial	fluvial, eroded	
Major orders	RG, CH	RG, CH	CH, RG	
Hills/Escarpments				
Area (km^2)	4 491	1 266	326	3.9
Parent materials	till	till	till	
Major orders	CH	CH	CH	
Benches/Plateaus				
Area (km^2)	1 681	2 520	634	3.1
Parent materials	till, fluvial	till, fluvial	till, fluvial	
Major orders	CH	CH	CH, SZ	
Lowlands/Basins				
Area (km^2)	946	358	2 252	2.2
Parent materials	lacustrine	lacustrine	lacustrine	
Major orders	CH, SZ, GL	CH, SZ, GL	CH, SZ, GL	
Dunefields				
Area (km^2)			857	0.5
Parent materials			aeolian	
Major orders			CH, RG	
Total Area (km^2)	69 149	43 549	45 445	100.0
1996 Crop/Fallow Area (km^2)	37 100	19 566	11 746	43.3
Other Developed Area (km^2)	?	?	?	25.6
Remaining Native Area (km^2)	?	?	?	31.1

CH= chernozem, GL= gleysol, RG= regosol, SZ= solonetz.
Soil orders and landforms adapted from Agricultural Region of Alberta Soil Information Database (1999).
Annually cultivated area estimated from municipality statistics (Alberta Agriculture Food and Rural Development 1996).
Remaining native adapted from Prairie Conservation Forum (1996).
Other developed calculated from difference of all other land uses and includes farmsteads, urban, roadways and possibly seeded range and non-native pasture.

Table 1.2. Soil organic carbon mass estimates for northern Great Plains native rangeland.

Brown Soil (Mg ha^{-1})	Dark Brown Soil (Mg ha^{-1})	Black Soil (Mg ha^{-1})
80 (100 cm) Anderson and Coleman 1985		150 (100 cm)
69 to 111 (45 cm range of sand to clay) Bauer et al. 1987		
50 (20 cm under shortgrass) Burke et al. 1989 [z]		80 (20 cm under tallgrass prairie)
64 to 74 (30 cm range of sand to clay) 117 to 140 (107 cm range of sand to clay) Frank et al. 1995		
20 (100 cm Regosol badlands) 0 to 20 (20 cm range of sand to clay) Franzmeier et al. 1985 [z]		210 (100 cm Vertisol under tallgrass) 80 to 100 (20 cm range of sand to clay under tallgrass prairie)
45 and 109 (30 and 90 cm) Manley et al. 1995		
38 and 70 (Ah and 100 cm) McGill et al. 1988	60 and 105 (Ah and 100 cm)	100 and 160 (Ah and 100 cm)
35 to 45 (20 cm range of sand to clay) Parton et al. 1987 [z]		45 to 60 (20 cm range of sand to clay under tallgrass prairie)
Tiessen et al. 1982	109 (100 cm clay)	87 (100 cm sand)
63 and 83 (40 and 80 cm clay) van Veen and Paul 1981		
45 to 88 (100 cm under palouse prairie) van Ryswyk et al. 1965	68 to 130 (100 cm under palouse prairie)	163 to 250 (100 cm)

[z] Regional average of spatially interpolated data from a large (N>100) sample of pedons.

Unless otherwise indicated, estimates for soil zones correspond to loam textured Chernozemic soils within mixed and fescue prairie ecosystems.

Table 1.3. Grazing and soil organic carbon in brown, dark brown and black soil zone native rangelands.

Soil Zone State/Prov.	Plant Community	Depth (cm) Increment	SOC Grazed (site note)	SOC Ungrazed (duration)	Reference
			Mg ha^{-1}		
Brown	blue grama	0 to 5	8 (M)	4 (55 yrs.)	Derner et al.
Colorado		5 to 15	11	7	1997
		15 to 30	13	12	
Brown (SZ)	blue grama	0 to 7.6	20 (L)	14.5 (11 yrs.)	Manely et al.
Wyoming	wheatgrass		20 (H)		1995
			20 (RH)		
			21 (HRM)		
		7.6 to 30	37.5 (L)	31.5	
			37 (H)		
			31 (RH)		
			38 (HRM)		
			% C		
Brown	blue grama	0 to 2	2.70 (HM)	1.40 (35 yrs.)	Dormaar and
Alberta	spear grass ^{z}	2 to 10	1.34	0.98	Willms 1990
		10 to 30	0.82	0.69	
Brown (SZ)	blue grama	Ah horizon	1.15 (L)	1.10 (19 yrs.)	Smoliak et al.
Alberta	spear grass ^{z}		1.16 (M)		1972
			1.38 (H)		
			Mg ha^{-1}		
Brown (SZ)	blue grama	Ah horizon	25 (EAM)	26 (50 yrs.)	Naeth et al.
Alberta	spear grass		31 (LAM)		1991
Dark Brown	little bluestem	0 to 5	19 (M)	26 (85 yrs.)	Derner et al.
Kansas		5 to 15	28	29	1997
		15 to 30	29	25	
Dark Brown	spear grass	0 to 30.4	64 (M)	72 (78 yrs.)	Frank et al.
North Dakota	blue grama		74 (H)		1995
		30.4 to 106.7	53 (M)	69	
			66 (H)		
Dark Brown	spear grass	0 to 7.6	29 (clay)	31 (75 yrs.)	Bauer et al.
North Dakota	blue grama		27.5 (loam)	29	1987
			22 (sand)	20	
		7.6 to 46	71 (clay)	80	
			64.5 (loam)	60	
			44 (sand)	66	
			% C		
Dark Brown	spear grass	Ah horizon	3.26 (MH)	2.79 (13 yrs.)	Dormaar et al.
Alberta	blue grama				1994
Black	foothill rough	Ah horizon	11.71 (L)	(20 yrs.)	Johnston et al.
Alberta	fescue ^{y}		11.23 (M)		1971
			10.74 (H)		

Soil Zone State/Prov.	Plant Community	Depth (cm) Increment	SOC Grazed (site note)	SOC Ungrazed (duration)	Reference
			%	C	
Black Alberta	foothill rough fescue ^{y}	Ah horizon	11.0 (L) 8.5 (H) 7.5 (VH)	11.4 (42 yrs.)	Dormaar and Willms 1998
Black Alberta	foothill rough fescue	Ah horizon	4.27 (HRM)	4.90 (4 yrs.)	Dormaar et al. 1989
			Mg	ha^{-1}	
Black Alberta	foothill rough fescue ^{y}	Ah horizon	63 (L) 63 (M) 70 (H) 64 (VH)	74 (39 yrs.)	Naeth et al. 1991
	plains rough fescue	Ah horizon	42 (EAL) 43 (EAH) 40 (LAL) 57 (LAH)	38 (46 yrs.)	

SZ = solonetzic soil, otherwise all soils were chernozemic.

Grazing intensity: L = light, M = moderate, H = heavy, VH = very heavy, RH = rotation heavy, HRM = high rotation management, EA = early season, LA = late season.

z Same heavy intensity treatment sampled separately in two studies (AAFC Onefour Research Sub-station).

y Same site and treatments sampled separately in three studies (AAFC Stavely Research Sub-station).

Table 1.4. Mean residence time (MRT) estimates for soil organic carbon in northern Great Plains native rangeland soils.

Horizon or Depth (cm)	Brown Soil	Dark Brown Soil	Black Soil
		MRT (years)	
Ah			385 z
B			2420 z 1910 y
0 to 10	193 x 545 w	560 x	216 to 575 x 250 w
10 to 20	1528 x		
20 to 30	2398 x	1825 x	700 to 930 x
30 to 40	4068 x		

z Anderson 1995.
y Anderson and Paul 1984.
x Paul et al. 1997.
w Martel and Paul 1974.

II. GRAZING MEDIATED CHANGES IN THE SOIL ORGANIC CARBON POOL OF ALBERTA PRAIRIE GRASSLANDS

2.1. INTRODUCTION

Current research into carbon sequestration has been driven by concerns over the rise in atmospheric carbon dioxide (CO_2) concentrations over the last two centuries and the implications for global climate change. Mitigation of CO_2 emissions has involved research into agricultural land management which may promote CO_2 influx via photosynthesis and/or suppress CO_2 efflux via decomposition to effectively create carbon sinks or increase the efficiency of existing sinks (Lal et al. 1995, Seastedt 1995, Allen-Diaz 1996). Original grasslands in Alberta were representative of northern mixed prairie in semiarid regions and fescue prairie in subhumid regions (Coupland 1961). The organic carbon pool in these grasslands is mainly in the form of soil organic carbon (SOC) (Sims and Coupland 1979, Van Veen and Paul 1981, Roberts et al. 1989, Anderson 1995, Eswaran et al. 1995, Seastedt 1995). Thus, when considering carbon sequestration in prairie grasslands, management influences on the SOC pool are most important (Bruce et al. 1999).

SOC varies both temporally and spatially along a hierarchy of scales. During centuries and millennia, regional climate and vegetation are the major factors affecting the SOC pool mass (Anderson and Coleman 1985, McDaniel and Munn 1985, Parton et al. 1987, Amelung et al. 1997). Across landscapes, variation in parent material texture and recent land use affect the SOC pool (Weaver and Darland 1949, Nichols 1984, McDaniel and Munn 1985, Sala et al. 1988, Anderson 1995). Smaller scale SOC variation due to topoedaphic influences on soil moisture, temperature, erosion and deposition have been investigated (Franzmeier et al. 1985, Schimel et al. 1985, Yonker et al. 1988, Roberts et al. 1989, Herrick and Whitford 1995). At still smaller scales there are individual perennial plant effects on the vertical and horizontal distribution of SOC in the solum (Bowman 1991, Hook et al. 1991, Derner et al. 1997, Kelley and Burke 1997, Burke et al. 1998).

The objective of this research is to describe differences in SOC in response to livestock grazing and long-term grazing exclusion. Milchunas and Lauenroth (1993) reviewed studies from both tropical and temperate rangelands and found no consistent relationship between grazing and SOC. Inconsistent patterns or explanations for the physiological mechanisms involved in SOC differences among treatments in the northern Great Plains have been reported. For instance, increases in SOC or root biomass with grazing have been attributed to changes in plant species composition and increases in productivity (Johnston 1961, Smoliak et al. 1972, Dormaar 1990, Shariff et al. 1994, Manley et al. 1995), while decreases in SOC or root biomass with grazing have been attributed to decreases in plant productivity (Weaver 1950, Johnston 1971, Bauer et al. 1987, Dormaar and Willms 1998). Frank et al. (1995) found SOC mass was lower on moderately grazed mixed prairie in North Dakota, but slightly higher in the control and heavily grazed treatments. Dormaar et al. (1984), studying foothill fescue prairie in Alberta, found SOC concentration was greater under high intensity than moderate intensity grazing but still less than under the ungrazed control. In other cases variation was too large for significant differences to be detected among treatments (Lodge 1954, Naeth et al. 1991).

As grazing intensity increases in grasslands, litter biomass and climax plant species decline, while subdominants increase and invaders colonize (Dyksterhuis 1949, Milchunas and Lauenroth 1988, Wroe et al. 1988). The effect of grazing on plant productivity is less clear, particularly in relation to root production (Lauenroth and Whitman 1977, Sims and Coupland 1979, Milchunas and Lauenroth 1993, Willms and Jefferson 1993, Shariff et al. 1994). An intermediate grazing duration or intensity has been postulated to increase total annual forage production (Vitousek and Reiners 1975, Fischer and Turner 1978, McNaughton 1983, Milchunas and Lauenroth 1988). This grazing optimization hypothesis may not be universally true for plant root production or long-term soil nutrient retention (de Mazancourt et al. 1998). There may be subtle changes in the SOC pool, whereby some plant species promote SOC accumulation through addition of residues low in nitrogen and high in complex carbohydrates resistant to decomposition, or release of exudates that inhibit decomposition (Dormaar and Willms 1993, de Mazancourt et al. 1998).

When considering the SOC pool the most important effect of grazing may not be directly related to production inputs, but rather decomposition outputs due to changes in soil microbial habitat. Changes in soil chemical and physical characteristics, as a result of grazing, may influence microbial activity and transformations of organic matter. Microorganisms are ultimately responsible for decomposition of organic residues and formation of soil humus. Plant residues are part of a rapidly turning over, or active, pool of SOC. Microbially transformed products of plant residues become more and more stable, less susceptible to mineralization and collectively form a slowly turning over, or passive, pool of SOC (Vossbrinck et al. 1979, Grant and Rochette 1994, Anderson 1995, Schlesinger 1995, Seastedt 1995, Bruce et al. 1999). To understand the dynamics of the SOC pool both input and output patterns and mechanisms must be determined. Organic carbon pool patterns identified in this research are intended to guide further research into the mechanisms for change.

2.2. MATERIALS AND METHODS

2.2.1. Study Sites

Long-term grazed and ungrazed treatments on native prairie grassland were sampled at nine sites in southern Alberta, Canada between July 1998 and August 1999 (Table 2.1, Figure A.1). Sites were selected on the basis of grazing exclusion duration (>20 years), lack of stones to facilitate sampling to a 110 cm depth and representation of major plant community types within fescue and mixed prairie ecoregions. Sampling avoided edge effects of exclosure fence lines at each site. The small size (100 to 1800 m^2) of seven out of nine exclosures restricted the number of subsample points established in each experimental unit. The experimental unit was considered an adjacent grazed or ungrazed area of equivalent area and topography at each site. Small exclosures simplified selection of the adjacent ungrazed unit. Sampling locations at two larger (>40 ha) exclosures were restricted to the same area (approximately 1 ha) sampled by Alberta Agriculture, Food and Rural Development (AAFRD), Public Lands for long-term forage production monitoring. Different numbers of subsamples were taken from each experimental unit (3 to 6 per unit) to account for local spatial variation.

These nine sites represent an environmental and ecological gradient within southern Alberta. Two sites (Stavely B and C) were located in a subhumid, high elevation region where vegetation was typical of foothill rough fescue (*Festuca campestris* Rydb.) prairie (Moss and Campbell 1947). One site (Twin River) was transitional, with both Black and Dark Brown Chernozemic soils and vegetation a complex of communities representative of the fescue prairie association, *Stipa-Agropyron* faciation of mixed prairie (Coupland 1961) and *Festuca-Agropyron* Palouse prairie (van Ryswyk et al. 1965). The six remaining sites were located in semiarid, low elevation regions where vegetation was typical of northern mixed prairie (Strong and Leggat 1991) and representative of the *Stipa-Bouteloua* faciation of mixed prairie (Coupland 1961).

Accurate stocking data at all sites but Stavely have not been regularly recorded. Range condition classification from 1997 sampling was based on methods outlined in Wroe et al. (1988) and reported by Moisey and Adams (1999). Exclosure herbaceous annual net primary production (ANPP) represents the mean of 1989 to 1999 aboveground clippings collected by Alberta Public Lands (Moisey and Adams 1999). ANPP data from grazing cages was not available for all sites for the same time period. Precipitation and temperature data were adapted, and in some cases interpolated by simple distance weighted averaging, from Environment Canada climate normals 1961 to 1990 (Environment Canada 1996). Landscape and soil characteristics were derived from the Agricultural Region of Alberta Soil Inventory Database (AGRASID 1998) and field classification (Agriculture Canada Expert Committee on Soil Survey [ACECSS] 1987).

2.2.2. Vegetation Sampling

Percent cover of vascular vegetation, bare ground, cattle dung and non-vascular plants (lichens and algae) were visually estimated from three to six 0.25 m^2 quadrats placed within each experimental unit (Table A.1). Percent biovolume of all vascular plant species was estimated. Moss (1994) was used as the authority for identification and nomenclature. Biovolume is a visual estimate of the percentage biomass contribution of one species to all live vegetation rooted within a quadrat, similar to relative foliar cover (Wroe et al. 1988). Three aboveground biomass fractions were removed from each quadrat: litter, vegetation and dung. All standing and surface litter was raked with hands, rooted vascular plants were clipped at ground level and non-vascular plants and cattle dung were hand picked. Samples were oven dried at 70 °C for 48 hours prior to determination of dry weight biomass. All three fractions were fine ground first in a Wiley Mill, then Cyclotec grinder, to pass a 0.1 mm sieve prior to chemical analyses (Ellert and Johnson 1997). Dung mass values were later combined with litter due to similarity in carbon concentration and difficulties separating the two fractions in the field.

2.2.3. Soil Sampling and Processing

Within each clipped and raked quadrat, three soil cores (6.7 diameter x 110 depth cm) were extracted with a heavy-duty hydraulic corer mounted on a one-ton truck and combined. Locations of the three cores within a quadrat were selected to proportionately represent the basal cover of plant crowns, little clubmoss (*Selaginella densa* Rydb.) and bare ground. Common depth increments for cores were based on natural horizons identified in the field (Figure A.2). Due to gravel at all sites but Picture Butte and/or bedrock at Onefour-B and Stavely-B it was not always possible to obtain cores to a 110 cm depth, but 65 cm was the minimum. Up to 10 depth increments were selected at each site for a total of 741 field soil samples collected from 90 subsample points. Field soil samples were stored in a cold room (-0.5 °C) up to two days before being processed in the lab (Bates 1993).

Subsamples, 50 to 75 g wet weight, of each field soil sample were oven dried at 110 °C for 48 hours prior to weighing for bulk density determination (Culley 1993). The remainder of each field soil sample was air-dried prior to organic residue and stone fractionation (Bates 1993). Up to four fractions were separated from each sample: plant crowns, macro-organic matter (MOM) >0.5 mm, stones >2 mm and fine soil. Plant crowns represent those aboveground portions (stem and leaf material) of vascular plants, and whole little clubmoss plants that could not be removed by clipping. MOM represents a combination of live and partially decomposed roots and plant debris, seeds, insect exuviae and other organic debris larger than 0.5 mm (Gregorich and Ellert 1993). Stones and MOM larger than 2 mm were first separated by hand crushing each air-dried field soil sample and sieving through a 2 mm mesh (Sheldrick and Wang 1993). Additional MOM was separated from fine soil by two to three repetitions of hand crushing, sieving (0.5 mm mesh) and winnowing. For winnowing a tabletop grain cleaner was used to separate heavy particles (soil) and light particles (MOM) between 0.5 and 2 mm in size.

Soil that passed a 0.5 mm sieve was combined with heavy particles (0.5 to 2 mm) from the winnowing process to comprise the fine soil fraction. Plant crowns in the 0 to 10 cm increment from each of the 90 subsample point were separated from MOM by hand picking. Stones and MOM were oven dried at 110 °C and 70 °C, respectively, for 48 hours and dry weight determined for correction of bulk density and MOM C calculations. Plant crown and MOM fractions were fine ground first in a Wiley Mill, then Cyclotec grinder, and fine soil fractions in a roller mill, to pass a 0.1 mm sieve prior to chemical analyses (Ellert and Johnson 1997).

2.2.4. Chemical Analyses

Total C, organic C and total N of all fractions (except stones) were determined by automated dry combustion and gas chromatography using a Carlo-Erba NC2100 elemental analyzer (Pella 1990, Nelson and Sommers 1996). Fine ground subsamples (10 to 40 mg) of fine soil in Ag cups were acidified with 6M HCl to evolve inorganic CO_3^{-2} before SOC determination (Nelson and Sommers 1996). All fine ground subsamples for total fine soil, plant crown and MOM fraction C were not acidified and combusted in Sn cups (Ellert and Johnson 1997). Analytical precision was calculated as the average standard deviation of soil and vegetation standards replicated in each run. Analytical variation for % C was ±0.057 % for soil, and ±0.363 % for organic residue standards.

2.2.5. Data Analyses

When using SOC on a mass basis there is a risk any observed treatment effect will largely be an artifact of differences in soil mass. Ellert and Janzen (1996) promote reporting SOC on an equivalent mass basis, which provides a measure of carbon concentration independent of bulk density differences. SOC mass and bulk density data were reported separately to facilitate comparison with other research, but allow for equivalent mass calculation. SOC mass per volume (Mg ha^{-1} for a given increment) was calculated by multiplying organic C percent concentration by dry soil mass, corrected by subtracting crown, MOM and stones mass and volume. Fine soil and MOM C and N data were weighted by soil layer thickness to achieve common depth increments among sites for statistical comparison. Analyses were restricted to increments above 65 cm, due to unbalanced numbers of subsamples within units below this depth.

Grazed and ungrazed treatments at each site were initially compared by t-tests, assuming equal variance. Data were then organized into two 2 x 3 and one 2 x 2 factorial experimental designs prior to ANOVA (Table 2.2). Three designs were used to attempt to partition and test regional and landscape scales of variation. The error term for Type III sums of squares in SAS PROC MIXED was used to calculate estimated mean squares as this allows the best test for the main effects in an unbalanced design (SAS Institute 2000, Shaw and Mitchell-Olds 1993). Factors were considered fixed and replicates random in all factorial designs. Comparisons between grazing treatments within each regional or landscape factor, and among these factors were made with P values from Fisher's least significant difference test (Table B.1) (Steel et al. 1997).

Several researchers suggest there is a dependent relationship between an increase in SOC with grazing and an increase in the cover of blue grama (*Bouteloua gracilis* HBK) on mixed prairie. The dense mass of fine roots produced by this species reportedly leads to increased residue inputs and thus SOC (Smoliak et al. 1972, Dormaar et al. 1977, 1984, Sims and Coupland 1979, Dormaar 1990, Frank et al. 1995, Derner et al. 1997, Kelly and Burke 1997). Linear regression was applied to both SOC and MOM C mass at four increments as dependent variables against both estimated blue grama carbon mass (% biovolume X vegetation carbon mass) and total vegetation carbon mass at 40 sample points where the species was present (Graybill and Iyer 1994).

Correlation coefficients (r) of the linear relationship between selected variables along the environmental gradient of ungrazed sites were calculated. All subsets multiple linear regression was used to find the best models for predicting SOC mass along the gradient. Both the coefficient of determination (r^2) and Mallow's C_p criterion were used to select best subsets (Graybill and Iyer 1994).

2.3. RESULTS AND DISCUSSION

2.3.1. Grazing Effects at the Site Scale

There was a trend towards greater vegetation and litter carbon mass in ungrazed treatments across all sites (Table 2.3). Vegetation was similar between grazing treatments at Onefour sites as sampling occurred during a drought year (1998) and production is moisture limited in this ecoregion (Smoliak 1986). At eight of nine sites litter carbon mass was significantly greater ($P \leq 0.05$) within exclosures. Crown carbon mass treatment effects were not statistically significant, likely due to difficulty achieving a consistent clipping height (rough fescue tussocks in particular) and inclusion of little clubmoss in the crowns fraction at mixed prairie sites. Sims et al. (1978) also found crown biomass response to grazing treatments and ecoregions was not predictable. Crowns of rough fescue tussocks could not be clipped as closely to the ground surface as other vegetation, thus increasing that fraction at ungrazed Stavely sites. Little clubmoss was more abundant in Turin to Onefour-C sites (Table A.1) therefore contributing substantially to the crowns fraction.

Greater root penetration in sandy soil sites (Picture Butte and Turin) led to a trend toward greater MOM carbon mass at depth relative to other sites (Table 2.3). There was no statistically significant grazing treatment effect in MOM carbon mass across sites. At Stavely and Onefour-B sites there was a trend towards greater MOM carbon mass in grazed treatments, but a decrease at all other sites. Within exclosures at Stavely, new tiller growth was suppressed and broad interspaces between rough fescue tussocks were unvegetated beneath accumulated litter. Field observation of grazed treatments suggests there may be a greater density of tillers relative to exclosures, which may partly explain the trend toward greater MOM C mass in the upper 10 cm of grazed units. The trend towards increased MOM C mass on grazed treatments at Stavely was possibly a function of vegetation spatial structure (tiller density and distribution) as affected by release from light and temperature limitations for new tiller development and plant establishment. Such a response would be consistent with mechanisms proposed by the grazing optimization hypothesis (McNaughton 1983) and litter raking trials in fescue prairie (Weaver and Roland 1952, Willms et al. 1986, 1993).

SOC mass was greater in grazed treatments in the 0 to 10 cm increment at all sites, though statistically significant only at Stavely and Picture Butte (Table 2.3). Observed SOC treatment effects at Stavely may have been a function of soil microbial respiration rate as affected by soil moisture and temperature. Although ANPP increases with grazing (Sims et al. 1978) decomposition may have increased proportionately more. More of the carbon contributed by plant residues in cooler, moister exclosure soils may have been sequestered. Soils within exclosures at Stavely have high organic matter contents similar to organic soils. ACECSS (1987) identifies organic soils as those with SOC contents >17% and the upper 10 cm of soils at Stavely had contents as high as 13.9%. The response of SOC mass to grazing was not as clear among dark brown and brown soil sites where soil texture may have been an influence. Less compacted soils in exclosures could have greater porosity and the opportunity for mineralization of SOC could have increased (Unger and Kaspar 1994) explaining apparent increases in SOC with grazing. Significant differences in SOC mass in the 35 to 65 cm increment likely reflect spatial variation rather than a treatment effect.

SOC mass is a function of soil mass and carbon concentration. The trend for fine soil carbon concentration was not consistent, and was greater in the 0 to 10 cm increment at five ungrazed sites (Table 2.4). Across sites there was a trend towards greater bulk density in the 0 to 10 cm increment of grazed treatments at seven of nine sites, though statistically significant in only five of those. It is important to note that each site where bulk density was significantly greater in the 0 to 10 cm increment of grazed treatments had lower carbon concentrations. Comparison of SOC mass with bulk density and carbon concentration between 0 and 35 cm for Stavely-B most clearly demonstrates the role treatment differences in bulk density have on SOC mass estimates. Concentration data, or SOC mass per equivalent soil mass may be the more useful response variable for measuring grazing treatment effects. Significant differences in both carbon concentration and bulk density in the 35 to 65 cm increment likely reflect spatial variation rather than a treatment effect.

Changes in soil C:N ratios were not consistent among sites or depths. MOM C:N ratios demonstrate a trend towards increasing with grazing in mixed prairie sites, and decreasing in fescue prairie (Stavely) sites in the 0 to 10 cm increment. MOM C:N ratios also demonstrate a trend towards increasing with depth. These C:N ratios possibly reflect slower rates of humification and carbon mineralization in exclosures (Paul and Clark 1996) or additions of cattle dung in grazed treatments. The MOM fraction is subject to more variability among sites and depths due to the fractionation method. In black soils, deep penetrating shrub roots were included in the MOM fraction resulting in large C:N ratios and significant spatial variation, such as that observed in the 35 to 50 cm increment. At all sites, inclusion of soil in the MOM fraction could decrease the ratio.

2.3.2. Interaction of Grazing and Regional or Landscape Factors

Variability in soil organic matter on multiple spatial scales masked the small grazing treatment effects in this study. Regional and landscape scale differences in SOC pool by ecoregion, soil zone and texture class were expected and observed (Tables B.2 to B.18). For carbon mass, concentration and soil bulk density variables tested, the main effect of all regional and landscape factors was significant ($P \leq 0.05$); with the exception of MOM carbon mass from 35 to 65 cm.

The main effects of grazing within soil zones and texture classes were significant for carbon concentration in the 10 to 35 cm increment ($P=0.005$ and 0.006, respectively). There were also significant interactions, but these were due to the overriding influence of differences at Stavely but no other sites. The same was true for grazing effects on SOC within texture classes ($P = 0.091$) in the 0 to 10 cm increment, and within soil zones ($P = 0.020$) in the 10 to 35 cm increment. Grazing effects were significant ($P \leq 0.05$) for both vegetation and litter carbon mass regardless of the regional or landscape factor.

Comparisons among soil zones and texture classes indicate black soils with high organic matter contents (Stavely) were consistently different from all other sites for all response variables. Brown soils were not statistically different from dark brown for all variables except vegetation carbon mass. The differences between coarse and fine textured soils were statistically significant for several variables in the 0 to 10 cm increment. Bulk density was significantly lower, and SOC, MOM C and carbon concentration greater in fine soils relative to coarse. The magnitude of the grazing effect appeared to be greater in black soils relative to dark brown and brown, or greater in organic relative to fine textured soils. Mean changes in SOC mass were a decrease of 12.78 Mg ha^{-1} in grazed black, relatively high organic matter soils under fescue prairie, and an increase of 5.79 Mg ha^{-1} in grazed dark brown and brown soils under mixed prairie. Use of decrease and increase does not, however, imply the direction of change since it is unknown which treatment experiences the change.

2.3.3. Relationship of Plant Roots to Soil Organic Carbon

MOM C mass was positively correlated with both blue grama and total vegetation C mass in the 10 to 35 ($P \leq 0.05$), 35 to 65 ($P \leq 0.1$) and composite 0 to 65 ($P \leq 0.05$) cm increments (Table 2.5). Total vegetation was a better overall correlate. SOC mass was positively correlated with vegetation C mass in the 0 to 35 ($P \leq 0.1$) increment. Blue grama C mass was negatively correlated with SOC mass in the 35 to 65 cm increment. During sampling, position of the three cores in each quadrat included cover of plant crowns proportional to vegetation basal cover, but sampling error is still a possible source of significant variation.

Similar grazing treatment effects on SOC were observed for Onefour and Stavely sites in previous studies (Johnston 1971, Dormaar et al. 1977, Dormaar 1990, Dormaar and Willms 1998). Dormaar and Willms (1998) suggested the shift in species composition with grazing leads to two things. In fescue prairie, grazing decreases the cover of rough fescue and results in a loss of root biomass. In mixed prairie, grazing increases blue grama and increases soil root biomass (Dormaar et al. 1977). An increase or decrease in root biomass or plant residue inputs was suggested as the mechanism for observed SOC patterns. It is possible crowns were not distinguished from roots in previous studies. Inclusion of blue grama crowns may result in overestimation of root biomass for this species. More obvious explanations for grazing treatment differences in SOC may be associated with changes in plant residue decomposability (Parton et al. 1987), carbon mineralization rates and humus formation as a function of change in the soil physical environment due to grazing.

Changes in plant communities may contribute little to variation in SOC between treatments. Much of the SOC may be ancient and a product of previous plant communities and environments during the more than 10 000 years since deglaciation, or millions of years old lignite coal in the parent material (Anderson 1995, Seastedt 1995). If the influence of past environments dominates, it may be unwise to equate current range condition, or responses of individual plant species to grazing, with changes in SOC.

MOM C mass should be influenced by grazing more than SOC, as the MOM fraction is more labile and representative of short-term changes in plant community composition and production. However, sampling the MOM standing crop may not be the most effective way to detect changes because of inert charcoal contamination, differences in root decomposition rates at different depths and seasonal or grazing effects on root productivity and turnover (Gregorich and Janzen 1996).

2.3.4. Regional Environmental Gradient Pattern

SOC mass increased from brown to black soil zones. There were significant correlations between SOC mass (0 to 65 cm) and several environmental and site variables (Table 2.6). July mean temperature and annual precipitation were the two best individual predictors. Litter C mass, MOM C mass and January mean temperature were also significant, in decreasing order. Both July mean temperature and little clubmoss plus lichen basal cover were inversely related to SOC, MOM C and litter C mass. July mean temperature was significantly related to vegetation basal cover, SOC, MOM C and litter C mass. Best subset models for predicting SOC mass were: MOM C x July mean T ($r^2 = 96.8$, $C_p = 0.4$); MOM C x July mean T x January mean T ($r^2 = 97.0$, $C_p = 2.2$); and MOM C x July mean T x litter C ($r^2 = 96.9$, $C_p = 2.2$). Linear relationships between SOC mass with the five best environmental and organic residue predictors are in Figures 2.1 and 2.2.

Various linear correlates with SOC (Franzmeier et al. 1985, McDaniel and Munn 1985, Sims and Neilsen 1986, Parton et al. 1987, Burke et al. 1989, Amelung et al. 1997) and ANPP (Sims et al. 1978, Cannon and Nielsen 1984, Sala et al. 1988, Burke et al. 1997) along similar environmental gradients have been identified in the northern Great Plains. Data from 29 rangeland benchmark sites in southern Alberta indicate direct linear relationships between annual precipitation, elevation, January mean temperature and litter biomass in ungrazed prairie (Tables C.1, C.2, Figures C.1, C.2). Aboveground ANPP in ungrazed exclosures was not linear and reached an asymptote at approximately 400 mm annual precipitation and 1000 m elevation. Sims and Neilsen (1986) found elevation and precipitation were the best predictors of SOC based on 78 sites from Montana. Sims et al. (1978) identified a similar pattern for ungrazed prairie grasslands from across North America. Sala et al. (1988) identified 370 mm annual precipitation as the point at which this same phase transition occurs in the northern Great Plains. The asymptote observed at the transition between subhumid and semiarid prairie grasslands is true for ungrazed prairie, whereas the increase in ANPP continues linearly with annual precipitation in grazed prairie (Sims et al. 1978, Burke et al. 1989). Sims et al. (1978) summed up the differential response as litter accumulation in ungrazed prairie imposes a biotic control on microclimate, N availability and ANPP, whereas litter removal in grazed prairie imposes an abiotic (regional temperature and precipitation) control.

Although plant productivity appeared to be promoted by herbivory in subhumid prairie, there may also be an enhanced rate of decomposition and little net change in the SOC pool. A predictive spatial model used by Parton et al. (1987) identified a few key relationships between biotic and abiotic effects on grassland SOC pools. Temperature and precipitation were the dominant controls on ANPP and decomposition. Meanwhile, variability in plant species residue decomposability and soil texture affected SOC turnover rates.

The key variables identified in our analysis may be useful for verification of spatial and hierarchical carbon pool models. Two large scale factors, temperature and precipitation, can be interpolated from meterological station data. At smaller scales ground truthing to assess SOC within a landscape could utilize litter mass of ungrazed (>20 years) exclosures. Although soil texture has not been a successful predictor of SOC mass across ecoregions, within moisture limited mixed prairie it may be a key variable to identify SOC mass variation between landscapes within an ecoregion (McDaniel and Munn 1985, Burke et al. 1989, Amelung et al. 1997).

2.3.5. Influence of Bulk Density

While overall grazing treatment differences were not statistically significant, there was a trend toward bulk density increases under grazing in the 0 to 10 cm increment. Bulk density was significantly different at five of nine sites ($P \leq 0.05$) (Table 2.4). In dark brown soils bulk density was nearly equal among grazing treatments. Texture classes were significantly different ($P \leq 0.05$) in the 0 to 10 cm increment. Within texture classes the magnitude of the grazing treatment difference was greatest in organic and least in fine textured soils. Statistically significant differences in soil mass at depth were due to natural variation in soil parent material (Picture Butte and possibly other sites) and differing amounts of stones (all sites except Picture Butte which had no stones).

Bulk density differences in the upper 10 cm of soil can be explained. Soils with high clay content (Hays and Onefour-C) or high organic matter content (Stavely) increased in bulk density with grazing, whereas sandy soils (Picture Butte and Turin) did not change as much. Sandy soils are less sensitive to compaction from grazing relative to soils rich in clay or organic matter (Brady and Weil 1999). The duration of grazing exclusion was greater at Stavely and Onefour sites (>50 years) than other sites (<30 years). Thus, more time elapsed for plant root growth to ameliorate compaction in exclosures and produce statistically significant grazing treatment differences. Grazing during the spring or fall period when soils are moist increases susceptibility to soil compaction (Unger and Kaspar 1994). At Onefour-C, winter grazing traditionally occurred under frozen or dry conditions and may have reduced the effect of grazing on soil compaction.

2.3.6. Proposed Mechanisms for Grazing Effect Trends

Grazing effects that may promote range productivity appear to promote decomposition and SOC loss. A conceptual problem arises in the search for answers to these observed treatment effects on the mass of SOC. In rangelands, grazing season, duration, frequency and intensity are manipulated and thus considered treatment variables (Holochek et al. 1998). However, in grassland ecosystems on the northern Great Plains continuous grazing by large ungulates has been the norm for 10 000 years (Wells 1970, Axelrod 1985). SOC has accumulated over this period and current estimates of turnover rates suggest significant change in the SOC pool require centuries to millennia (Anderson 1995, Eswaran et al. 1995). From an ecological perspective, grazing exclusion has been imposed for a short period of time (20 to 70 year). Sims et al. (1978) suggested consideration of grasslands without the interaction of herbivores is unnatural. Modification of the grazing regime may have less of an effect than exclusion on a carbon pool subjected to grazing for millennia. Exclosures should be viewed as the extreme manipulation. Grazing animal impacts on ANPP due to trampling, herbivory and addition of N through urine and faeces are equally important response variables to quantify as exclosure impacts on soil respiration due to decreased soil temperature and increased moisture.

The strongest response, and most consistent difference between grazed and ungrazed treatments, was the accumulation of litter within exclosures. In the absence of livestock trampling, plant root growth loosens soil, forms more macro-pores and increases infiltration (Naeth 1990, Facelli and Pickett 1991). Litter moderates the soil microclimate such that shade lowers temperatures during summer and insulation lengthens the frost-free period during spring and fall. Litter also reduces evaporation and retains soil moisture (Knapp and Seastedt 1986, Willms et al. 1986, 1993, Facelli and Pickett 1991). Thus, the primary treatment effect may be a response to grazing exclusion whereby litter accumulates and the soil physical environment changes. The change in SOC mass would be inversely related to change in the activity of aerobic heterotrophic microorganisms, assuming little or no change in plant productivity.

In subhumid fescue prairie moisture is not limiting for production or decomposition. In exclosures, substantial litter cover increases soil moisture and decreases soil temperature that may decrease microbial activity (Holland and Coleman 1987). Anaerobic conditions can briefly result following rainfall events and during spring runoff (Brady and Weil 1999). Within exclosures, these anaerobic conditions may persist longer than on grazed areas. The overall effect of grazing exclusion and litter accumulation is to decrease mineralization and retain more SOC.

In semiarid mixed prairie there is relatively less humified soil organic matter and more fine particulate matter due to physical breakdown via freeze-thaw, photochemical degradation and trampling (Sims and Coupland 1979, Vossbrinck et al. 1979, Dormaar and Willms 1993). Under natural conditions, this water-limited environment limits humification through microbial decomposition relative to black soils under fescue prairie (Van Veen and Paul 1981, Anderson and Coleman 1985, Seastedt 1995). Within exclosures, there is increased soil moisture, moderated soil temperature and increased porosity. The overall effect of grazing exclusion and litter accumulation may increase mineralization and decrease SOC relative to grazed areas. There would be intense competition for both moisture and nitrogen between plants and microorganisms that may reduce the magnitude of the SOC reduction (Holland and Coleman 1987, Facelli and Pickett 1991, Burke et al. 1998). A change in composition with grazing toward more water use and nitrogen efficient species like blue grama (Burke et al. 1997) may change the production:decomposition ratio in favour of carbon sequestration.

2.3.7. Management and Future Research Recommendations

Despite the lack of statistically significant results, the trend in this and other research is worthy of comment. In mixed prairie, improved spatial and temporal range utilization to more evenly compress soil and prevent excessive litter accumulation could promote SOC sequestration. However, current range management practices promote 50% ANPP carryover as litter due to the positive effect litter accumulation has on moisture retention and range forage production (Wroe et al. 1988, Willms and Jefferson 1993). Careful attention should be paid to balancing sustainable grazing practices (the primary land use) with carbon sequestration practices.

In fescue prairie, grazing exclusion would lead to aspen (*Populus tremuloides* Michx.) invasion and the formation of luvisolic soils. This would transfer dominance of the carbon pool from SOC to woody biomass. Acids in leaf litter would promote leaching of SOC and a decline in accumulated humus (Fuller and Anderson 1993). To avoid aspen invasion but retain surface litter a region-wide change towards winter grazing, instead of the current May to October season, is recommended. Cattle would browse aspen in winter to suppress further invasion (Fitzgerald and Bailey 1984). Soil would be less compacted while it was frozen and litter breakdown would be reduced through trampling and incorporation into the soil surface. The end result would maintain soil macro-porosity, greater surface litter coverage and thus SOC storage. Future research to confirm these hypotheses with empirical data is necessary.

Coincidentally, the pattern of intense summer utilization of mixed prairie and more dispersed winter utilization of fescue prairie was that of migratory herds of bison in this region prior to 1850 (Epp 1988). Migratory bison grazing was perhaps the most effective mechanism for maintaining optimum SOC pools in Canadian prairie grasslands.

Further research into CO_2 flux (soil respiration) dynamics and the soil physical environment of adjacent grazed and ungrazed treatments are necessary to complement currently collected ANPP data. Fractionation of soil humus would help determine if differences in the ratio of humic materials exist between treatments and replicates. These data, in combination with particle size, available nitrogen and ^{14}C dating, would be useful for partitioning spatial and temporal variation in observed SOC patterns between sites and treatments. Differences in plant community composition, soil texture, period of grazing exclusion and grazing intensity hampered statistical inference for treatment effects in this study. Long-term manipulative experiments are necessary to identify the mechanisms for treatment differences in the SOC pool. Experimental units or blocks should be grouped along a hierarchy of soil zones or ecoregions, parent material texture, soil order and grazing regime (Figure 2.3). Sampling a particular management (experimental) unit then requires consideration of topographic and microsite variation.

2.4. CONCLUSIONS

Changes in SOC mass due to grazing were small in proportion to the total SOC pool, and rarely statistically significant. Responses to grazing appear to differ between ecoregions that differ in regional climate. The threshold for this changeover in response is along the boundary of cool semiarid and subhumid prairie grasslands. Within a soil zone SOC mass was on average 12.78 Mg ha^{-1} greater in ungrazed black and 5.79 Mg ha^{-1} greater in grazed brown and dark brown soil. While changes were small (less than 5% of the SOC pool) and not statistically significant, the actual amount of carbon involved relative to the area of rangeland in Alberta prairie grasslands (approximately 65 Mha) is substantial. SOC mass was overall greatest in black soils and least in brown soils. Climatic variables provided the best correlates with SOC mass. Two additional variables, litter and macro-organic matter mass, were also good predictors of SOC mass. Mass of litter raked from grazing exclosures may provide a quick and efficient means of estimating SOC mass in southern Alberta range production benchmark sites not already sampled in this research.

The potential for changing range management practices to sequester carbon is still not clear based on this research. Grazing treatment differences were restricted to the upper 35 cm of soil, and the actual change in SOC differs depending on whether mass per unit volume or concentration is considered. Management recommendations for carbon sequestration are consistent with past recommendations for optimizing range productivity. The assumption that comparisons in space are equivalent to those in time may be unwise given the underlying spatial variability and the incorrect assertion that exclosures represent baseline conditions. Exclosures still represent the most extreme contrast with grazing, and detectable differences between these two treatments are more likely than between different grazing regimes. It remains unclear whether carbon pool changes occur in the ungrazed, grazed or both treatments. Regardless, the stability of the SOC pool and slow turnover rate in prairie environments may require waiting centuries for treatment differences to become detectable.

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Table 2.1. Selected characteristics of study sites.

Characteristic	Stavely B, C	Twin River	Picture Butte	Turin	Hays	Onefour A, B, C
Ecoregion	foothills fescue	foothills fescue	mixedgrass	mixedgrass	dry mixedgrass	dry mixedgrass
Soil Zone	black	dark brown	dark brown	dark brown	brown	brown
Soil Order	orthic chernozem	orthic chernozem	rego chernozem	orthic chernozem	orthic chernozem	solodized solonetz orthic chernozem
Parent Material	glacial till	glacio-lacustrine overlying till	glacio-lacustrine	glacio-fluvial	glacio-lacustrine overlying till	glacio-fluvial overlying bedrock
Soil Texture Class	loam	loam	sandy-loam	sand	clay-loam	sandy to silty-loam
Elevation (m)	1 366	1 242	878	846	796	937
Mean Annual Precipitation (mm)	476	390	374	360	328	351
Mean July T. (°C)	14.7	18.0	18.2	18.3	19.2	19.3
Mean January T. (°C)	-6.8	-7.5	-8.7	-8.9	-9.9	-11.4
Year Exclosure Established	1949	1970	1978	1976	1979	1948 (A) 1927 (B, C)
Exclosure ANPP (kg ha^{-1})	2632^{z}	2167	1626	891	687	799 (A)
Grazing Duration and Season	5 months May to Oct.	5 months May to Oct.	5 months May to Oct.	5 months May to Oct.	5 months May to Oct.	6 months May to Oct. (A, B) Nov. to Apr. (C)
1997 Grazed Range Condition	good (B)	fair	poor	poor	fair	good (A)

z ANPP monitored in an exclosure adjacent to B field approximately 250 m from the exclosure sampled in this investigation.

Table 2.2. ANOVA table for three experimental designs and multiple comparisons.

2 x 2 Factorial by Ecoregions	2 x 3 Factorial by Soil Zone	2 x 3 Factorial by Texture Class
	Main Effects and Interaction	
Ecoregion	Soil Zone	Texture Class
Grazing	Grazing	Grazing
Ecoregion X Grazing Interaction	Soil X Grazing Interaction	Texture X Grazing Interaction
	L.S.D. Comparisons	
	Black ≠ Dark Brown	Organic ≠ Coarse
	Black ≠ Brown	Coarse ≠ Fine
	Dark Brown ≠ Brown	Fine ≠ Organic
Fescue Grazed ≠ Ungrazed	Black Grazed ≠ Ungrazed	Organic Grazed ≠ Ungrazed
Mixed Grazed ≠ Ungrazed	Dark Brown Grazed ≠ Ungrazed	Coarse Grazed ≠ Ungrazed
	Brown Grazed ≠ Ungrazed	Fine Grazed ≠ Ungrazed

Table 2.3. Mean organic carbon pool for grazed (GR) and ungrazed (EX) treatments in nine native rangeland sites in southern Alberta.

Depth (cm)	Stavely B		Stavely C		Twin River		Picture Butte		Turin		Hays		Onefour A		Onefour B		Onefour C	
	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX
	Vegetation Carbon Mass (Mg ha^{-1})																	
	1.40	1.98	1.43*	2.29*	0.72*	1.06*	0.79	1.19	0.57	0.97	0.39	0.57	0.37	0.33	0.35	0.34	0.38	0.32
	Litter Carbon Mass (Mg ha^{-1})																	
	1.39*	3.32*	1.82*	5.76*	0.83*	2.15*	0.44*	1.74*	0.23*	0.61*	0.13*	0.39*	0.18*	0.47*	0.31	0.33	0.22*	1.32*
	Crowns Carbon Mass (Mg ha^{-1})																	
	0.59	2.17	1.81	3.86	0.70	0.48	1.16	0.81	1.27	1.48	1.80	1.27	1.14	1.60	1.27	2.03	2.63	1.63
	Macro-organic Matter Carbon Mass (Mg ha^{-1})																	
0 to 10	7.08	7.08	9.29*	7.07*	4.17	3.74	3.52	3.68	4.35	3.60	5.99	6.39	2.99	3.11	2.79*	5.16*	5.27*	4.01*
10 to 35	3.26	2.97	3.07	3.00	1.06	1.09	1.59	1.87	0.94	1.26	0.89	0.93	0.98	1.07	2.44	2.09	2.29	1.95
35 to 65	0.97	0.43	1.06*	0.60*	0.52	0.56	1.03	1.42	0.42	0.59	0.61	0.67	0.41	0.46	1.49*	0.84*	0.86	1.02
65 to 110	0.26	0.17	0.38	0.30	0.23	0.35	0.57	0.91	0.17	0.49	0.23	0.37	0.13	0.18	0.86	0.08	0.20	0.37
	Fine Soil Organic Carbon Mass (Mg ha^{-1})																	
0 to 10	60.02*	50.05*	66.46	59.60	31.36	27.29	30.78*	25.84*	18.74	18.10	28.73	27.42	15.92	15.33	17.97	17.21	26.82	21.57
10 to 35	83.55*	101.59*	85.16	99.90	45.27	44.67	40.51	39.80	30.07	26.26	30.90	34.23	28.31	29.28	29.96	31.08	25.45	24.02
35 to 65	43.36	53.17	53.09	49.10	31.00	27.74	34.24*	22.38*	20.92	23.73	29.08*	32.05*	20.28*	15.88*	19.06*	14.62*	19.56	16.80
65 to 110	36.29	38.59	40.85	42.34	29.10	27.60	33.72	38.83	16.26	17.16	30.03	32.42	19.88	15.41	15.09	6.27	25.79	24.12
Grand Total	238.17	261.52	264.42	273.82	144.96	136.73	148.35	138.47	93.94	94.25	128.78	136.71	90.59	83.12	91.59	80.05	109.47	97.13

Pairs of values followed by an asterix within each site are significantly different ($P \leq 0.05$, Student's t-test assuming equal variance).
The 65 to 110 cm increment was not tested because soils at Turin were only sampled to 95 cm and at Onefour B-EX to 80 cm.

Table 2.4. Selected mean soil characteristics for grazed (GR) and ungrazed (EX) treatments in nine native rangeland sites in southern Alberta.

Depth (cm)	Stavely B		Stavely C		Twin River		Picture Butte		Turin		Hays		Onefour A		Onefour B		Onefour C	
	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX
	Fine Soil Organic Carbon Concentration (%)																	
0 to 10	9.10*	10.87*	10.78	11.25	3.16	2.73	2.50	2.18	1.36	1.29	2.66	2.83	1.35	1.52	1.39	1.58	2.51	2.12
10 to 35	3.62*	5.12*	3.44	4.58	1.56	1.49	1.18	1.14	0.80	0.68	0.96	1.06	0.95	1.01	0.92	1.01	0.78	0.74
35 to 65	1.20*	1.53*	1.55*	1.30*	0.73	0.69	0.81*	0.49*	0.48	0.51	0.72*	0.84*	0.53*	0.39*	0.50*	0.37*	0.47	0.39
65 to 110	0.58	0.64	0.68	0.68	0.40	0.43	0.52	0.59	0.35	0.36	0.45	0.53	0.30	0.22	0.24	0.08	0.40	0.37
	Bulk Density of Fine Soil Fraction (Mg m^{-3})																	
0 to 10	0.66*	0.47*	0.62*	0.54*	0.99	1.01	1.24	1.18	1.38	1.41	1.08*	0.97*	1.19*	1.02*	1.29*	1.09*	1.06	1.02
10 to 35	0.93*	0.80*	0.99*	0.88*	1.16	1.20	1.37	1.40	1.51	1.54	1.29	1.30	1.19	1.17	1.31*	1.23*	1.31	1.30
35 to 65	1.21	1.16	1.15*	1.26*	1.42	1.34	1.41*	1.52*	1.44*	1.55*	1.35	1.27	1.28	1.40	1.28	1.31	1.38	1.43
65 to 110	1.39	1.35	1.33	1.39	1.61	1.41	1.44	1.47	1.55	1.58	1.48	1.35	1.46	1.56	1.38	1.70	1.44	1.45
	Fine Soil Organic C: Total N Ratio																	
0 to 10	11.36*	11.87*	11.12	11.16	11.11	10.35	10.14	10.25	11.15	11.26	11.98	11.76	9.06*	9.67*	9.13	10.07	11.00*	10.05*
10 to 35	10.76*	11.23*	10.98	10.86	9.32*	8.81*	9.12	8.96	11.13	11.29	12.39	11.71	8.23	8.59	8.36	8.66	8.20	8.00
35 to 65	9.31	9.27	9.69	9.55	8.42	8.82	8.69	8.38	9.96	9.44	9.09	10.85	7.34	7.49	7.34*	5.86*	7.34	6.87
65 to 110	7.59	7.57	7.33	7.86	8.24	9.17	8.32	8.90	9.57	9.37	8.99	8.93	7.86	7.51	6.28	3.31	7.38	7.34
	Macro-organic Matter C:N Ratio																	
0 to 10	19.71	20.58	19.23	19.33	31.20	27.16	20.88	19.05	25.59	21.26	28.66	26.07	28.95	26.05	27.65	28.45	29.97	24.26
10 to 35	24.41*	31.42*	25.24	28.34	44.05	37.94	22.66	23.65	30.32	25.96	44.89	39.91	35.15	31.75	32.67	35.75	30.69	29.41
35 to 65	29.34*	45.55*	24.74*	31.51*	45.67	39.62	18.80*	20.57*	27.89	25.24	29.71	32.26	31.82	30.97	26.22	28.89	28.65	30.36
65 to 110	38.56	43.56	27.18	32.85	37.52	41.45	19.95	22.76	31.43	28.43	27.34	30.41	32.16	33.84	30.17	36.02	23.83	22.33

Pairs of values followed by an asterix within each site are significantly different ($P \leq 0.05$, Student's t-test assuming equal variances).
The 65 to 110 cm increment was not tested because soils at Turin were only sampled to 95 cm and at Onefour B-EX to 80 cm.

Table 2.5. Linear regression analyses of estimated blue grama aboveground carbon mass (% biovolume X aboveground carbon mass Mg ha^{-1}) and total aboveground carbon mass versus macro-organic matter and fine soil organic carbon mass (Mg ha^{-1}).

Depth (cm)	Macro-organic Matter Carbon				Fine Soil Organic Carbon			
	Blue Grama		Total		Blue Grama		Total	
	r	P	r	P	r	P	r	P
0 to 10	0.085	0.604	0.257	0.110	0.142	0.383	0.301	0.059
10 to 35	0.415	0.008	0.369	0.019	0.099	0.545	0.264	0.099
35 to 65	0.310	0.052	0.264	0.100	-0.114	0.483	0.044	0.787
0 to 65	0.322	0.042	0.434	0.005	0.040	0.808	0.227	0.159

Analyses for 40 quadrats (subsamples) where blue grama was present at mixed prairie sites.

Table 2.6. Correlation matrix for ten variables across nine ungrazed prairie grassland sites in southern Alberta.

	Soil Organic Carbon Mass	Macro-organic Matter Carbon Mass	Soil C:N	Mean Annual Precipitation	July Mean Temperature	January Mean Temperature	Litter Carbon Mass
Macro-organic Matter Carbon Mass	0.827*	1.00	- -	- -	- -	- -	- -
Soil C:N	0.554	0.524	1.00	- -	- -	- -	- -
Mean Annual Precipitation	0.948*	0.715*	0.345	1.00	- -	- -	- -
July Mean Temperature	-0.973*	-0.748*	-0.494	- -	1.00	- -	- -
January Mean Temperature	0.823*	0.487	0.570	- -	- -	1.00	- -
Litter Carbon Mass	0.898*	0.693*	0.302	0.920*	-0.901*	0.780*	1.00
Litter Basal Cover	0.210	0.164	0.235	0.272	-0.210	0.239	0.487
Grass and Forb Basal Cover	0.627	0.359	0.335	0.701*	-0.708*	0.686*	0.410
Selaginella and Lichen Basal Cover	-0.558	-0.335	0.0	-0.665	0.614	-0.651	-0.724*

Significant correlation indicated by asterix * ($P \leq 0.05$).

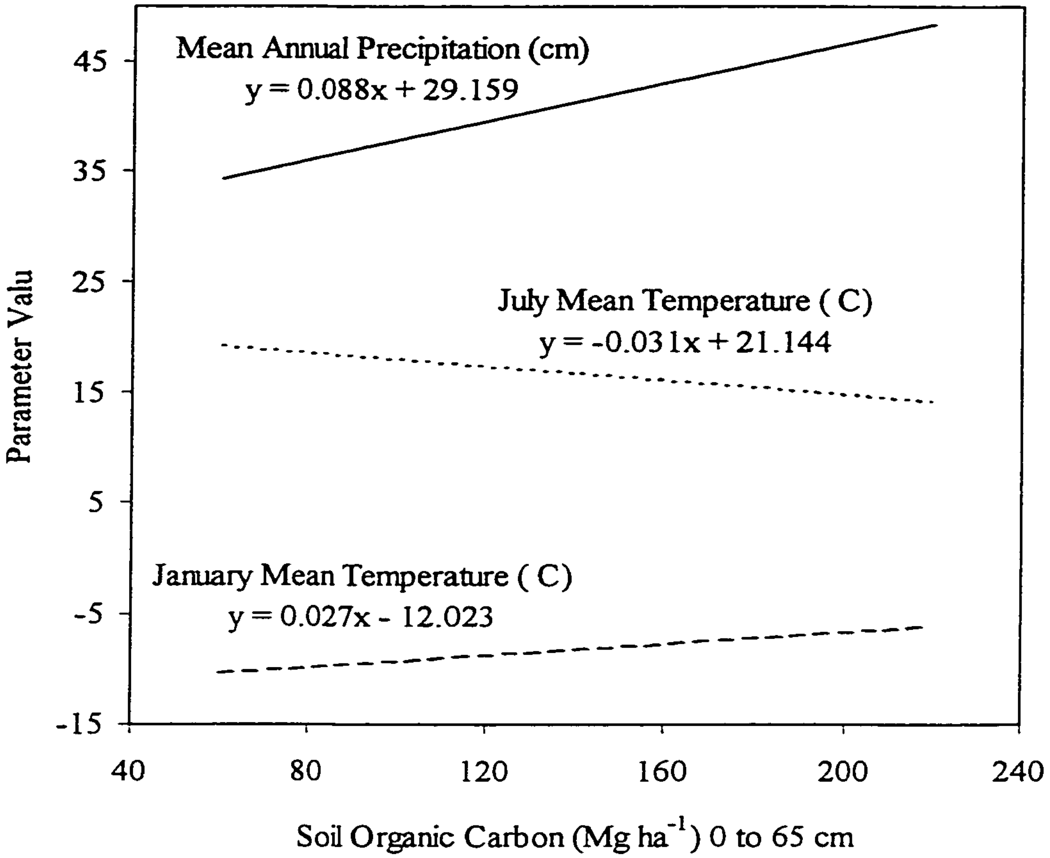

Figure 2.1. Linear relationships between soil organic carbon mass and environmental variables in ungrazed prairie grasslands of southern Alberta between 49° and 51° N.

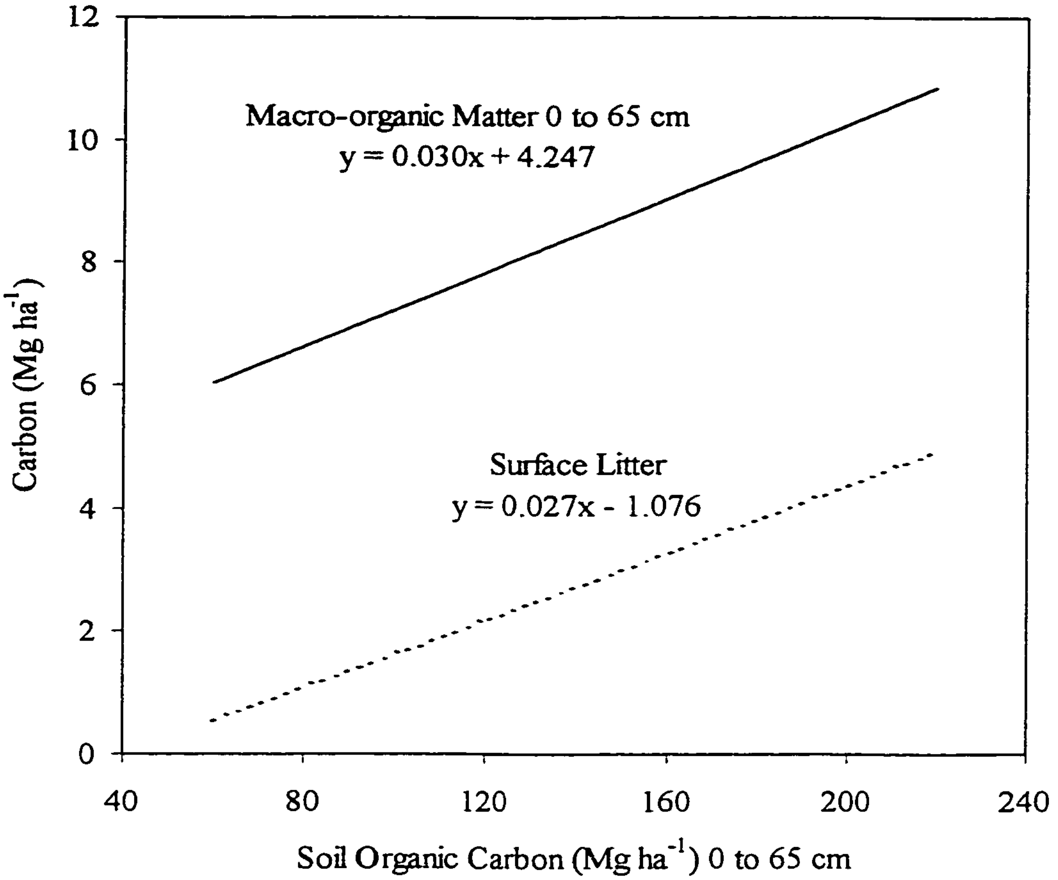

Figure 2.2. Linear relationships between soil organic carbon mass and organic residues in ungrazed prairie grasslands of southern Alberta between 49° and 51° N.

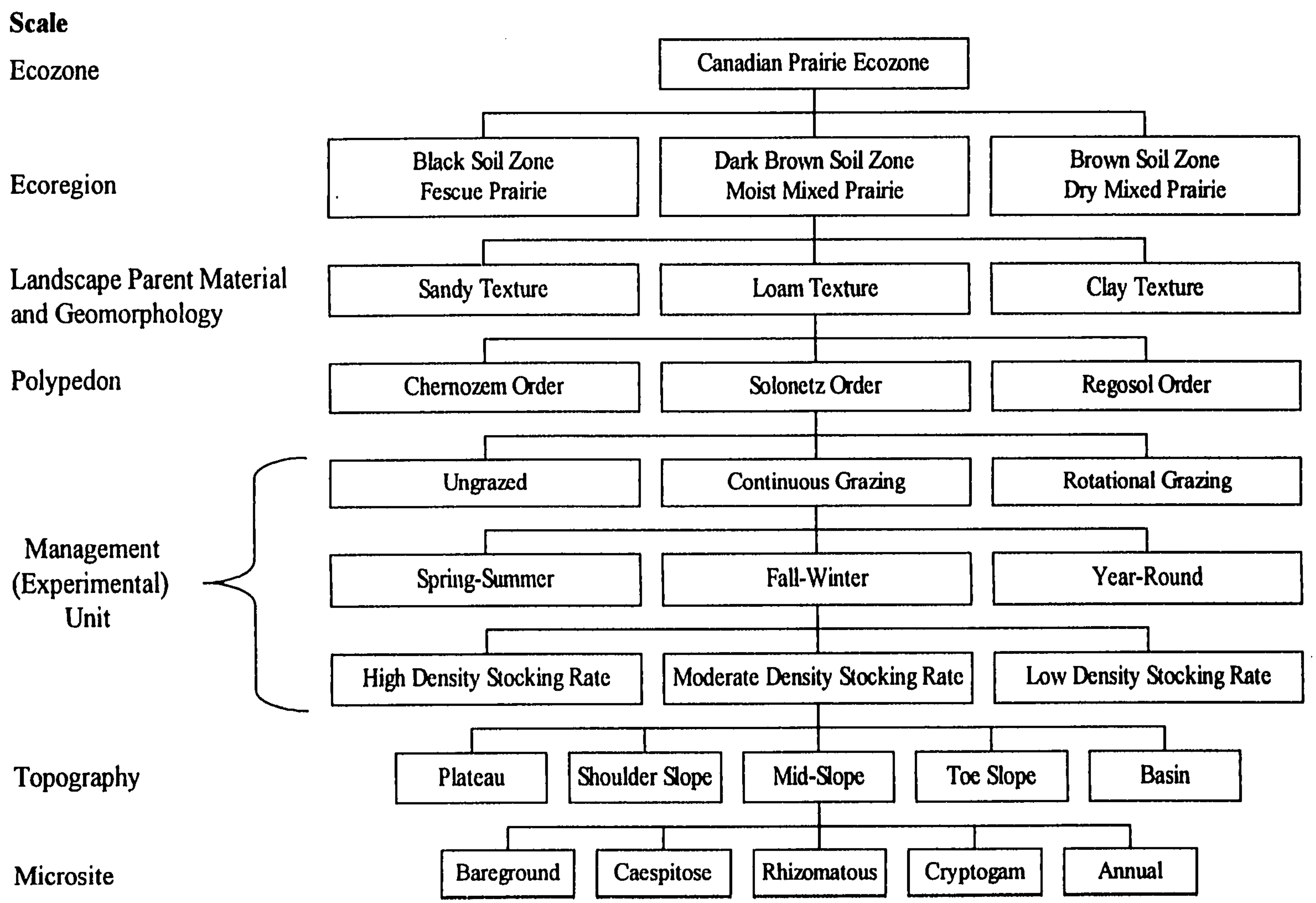

Figure 2.3. Hierarchical structure of accounting for spatial variation in experimental designs and sampling for rangeland soils. Each level in the hierarchy represents a factor (controlled by randomized sampling, blocking or incorporated as a main effect).

III. UTILITY OF ^{13}C TECHNIQUE FOR CARBON TURNOVER ESTIMATION IN GRAZED NORTHERN MIXED PRAIRIE

3.1. INTRODUCTION

Current research into carbon sequestration has been driven by concerns over the rise in atmospheric carbon dioxide concentrations over the last two centuries and the implications for global climate change. Mitigation of CO_2 emissions has involved research into agricultural land management that may promote CO_2 influx via photosynthesis and/or suppress CO_2 efflux via decomposition to effectively create carbon sinks or increase the efficiency of existing sinks. Any soil may be an effective carbon sink if inputs can be maximized and outputs minimized (Lal et al. 1995). Clipping herbaceous aboveground annual net primary production (ANPP) facilitates estimates of photosynthetic carbon inputs in grasslands. However, in-situ estimates of soil respiration outputs due to decomposition are difficult to partition from root respiration. Change in the natural abundance of ^{13}C in soil organic matter is one of few in-situ techniques available for estimating rates of soil organic carbon (SOC) turnover (Wolf et al. 1994, Paul and Clark 1996). Turnover represents the time required for the cumulative input or output of carbon to equal the SOC pool size; assuming steady state conditions (Paul and Clark 1996). The primary objective of this investigation was to identify soil organic matter turnover rates for two fractions to a depth of 1 m in a cool, semiarid mixed prairie grassland.

Approximately 1% of carbon in the environment is ^{13}C. Discrimination against $^{13}CO_2$ in the carboxylation reactions of photosynthesis varies among functional groups of plants and results in unique $^{13}C/^{12}C$ ratios within tissues (Boutton 1991a). A clear distinction between C_3 (cool season) and C_4 (warm season) photosynthetic pathway types can be made based on the ratio of $^{13}C/^{12}C$ (Smith and Epstein 1971, Boutton 1991b). Ehleringer and Monson (1993) reviewed hypotheses for the evolutionary development of different photosynthetic pathways. C_3 plants discriminate against ^{13}C with the enzyme ribulose biophosphate carboxylase to a greater degree than in C_4 plants where discrimination occurs during carbon fixation by phosphenol pyruvate carboxylase (Boutton 1991b).

Measurement of isotopic ratios has been facilitated by the development of automated, continuous flow mass spectrometric techniques. The standard unit of measurement in geochemistry is $\delta^{13}C$ ‰. The ratio of $^{13}C/^{12}C$ in an oxidized sample is compared to a standard, or reference, CO_2. Originally a standard derived from Pee Dee Beleminite (PDB), a limestone from the SE United States, was used; now several standards are in use though all calibrated against the original PDB reference. PDB is enriched with ^{13}C relative to the atmosphere and all terrestrial organic matter (Boutton 1991a, Wolf et al. 1994). As such, the $\delta^{13}C$ ‰ values for C_3 and C_4 plants are negative. On average, C_3 plants are -27‰, C_4 are -13‰ and the modern atmosphere varies from -7.4‰ to -8.4‰ (Smith and Epstein 1971, Terri and Stowe 1976, Boutton 1991b).

The natural abundance of ^{13}C in soil organic matter reflects the $\delta^{13}C$ ‰ of plant residue inputs over time. Where a transition from C_3 to C_4, or C_4 to C_3, dominated communities have occurred comparison of the initial soil organic carbon (SOC) $\delta^{13}C$ ‰ with SOC some time after facilitates measurement of older SOC loss and new SOC inputs (Wolf et al. 1994, Paul and Clark 1996). SOC turnover has been estimated in C_4 pastures established on formerly C_3 tropical forests (Volkoff and Cerri 1987, Skjemstad et al. 1990, Veldkamp and Weitz 1994), annual C_4 corn (*Zea mays*) crops on formerly C_3 temperate deciduous forests (Balesdent et al. 1987, Gregorich et al. 1995) and annual C_3 wheat (*Triticum aestivum*) crops and perennial pastures on formerly C_4 prairie (Balesdent et al. 1988, Jastrow et al. 1996, Follet et al. 1997). Generally, turnover rates are most rapid, and proportionately more of the SOC pool is labile, at the surface and both decline exponentially with depth. Fine scale SOC turnover has been investigated from similar treatments, but along a hierarchy of soil aggregate size or amongst humic fractions (Tiessen and Stewart 1983, Balesdent et al. 1988, Jastrow et al. 1996). Generally, turnover rates are most rapid, and proportionately more of the SOC pool is labile, in macroaggregates vs. microaggregates. Mean residence time of carbon is shorter in fulvic acids and longer in humic acids.

This research involved use of a mixed prairie site formerly dominated by a C_4 (blue grama, *Bouteloua gracilis* HBK) community, disturbed by cultivation in 1928, abandoned in 1931 and revegetated naturally to a C_3 (needle and thread, *Stipa comata* Trin.&Rupr.) dominated community (Dormaar et al. 1994). The unique challenge was to identify SOC turnover to depths of 110 cm using the $\delta^{13}C$ technique in a grazed, mixed

C_3 and C_4 community with no management inputs via tillage, fertilization or irrigation for 67 years. Turnover rates are expected to be slower in such a perennial system, compared to estimates for annually cultivated lands on the Great Plains (Jastrow et al. 1996, Follet et al. 1997).

3.2. MATERIALS AND METHODS

3.2.1. Study Area and Experimental Design

Field sampling on a mixed prairie rangeland site was conducted at Picture Butte, approximately 20 km NE of Lethbridge, Alberta, Canada between July and August 1998. The 40 ha study area is representative of the *Stipa-Bouteloua* faciation of northern mixed prairie (Coupland 1950). A detailed vegetation inventory and site history is given in Dormaar et al. (1994). Soil is classified as a sandy-loam textured Orthic Dark Brown Chernozem developed on glacio-fluvial parent material. Climate is cool, semi-arid continental with approximately 400 mm of annual precipitation. In 1928 an 8 ha portion was cultivated and seeded to annual cereal crops until abandonment in 1931. The abandoned cultivated land revegetated naturally to a native plant community compositionally distinct from the adjacent uncultivated portion. Uncultivated grassland is dominated by blue grama and cultivated grassland by needle and thread. In 1977 an exclosure (30 x 60 m) straddling the old plow-line was established as part of Alberta Agriculture, Food and Rural Development, Public Lands range production benchmark sites (Moisey and Adams 1999). These disturbances created four distinct treatments: grazed native, grazed abandoned, ungrazed native and ungrazed abandoned.

Sampling avoided edge effects of the plow-line and exclosure fence-line. As the primary focus of this study was to observe isotopic changes in the plant community resulting from cultivation and abandonment, transects were established parallel to the plow line on either side. Small dimensions of the exclosure, and a desire to disturb as little area as possible during sampling, restricted the number of sample points to four in each of the two ungrazed treatments. Each grazed treatment had eight sample points. The unique character of this site, that makes possible this study, precluded any opportunity for replication at another location. Individual quadrats were therefore considered replicates within a completely randomized design in statistical analyses.

Consequently, results are treated as a case study to test the utility of the ^{13}C technique.

3.2.2. Vegetation Sampling

Percent cover of vascular vegetation, bare ground, cattle dung and non-vascular plants (lichens and algae) were visually estimated from four to eight 0.25 m^2 quadrats placed systematically along transects within each treatment (Table 3.3). Percent biovolume of all vascular plant species was estimated. Moss (1994) was used as the authority for identification and nomenclature. Biovolume is a visual estimate of the percentage biomass contribution of one species to all live vegetation rooted within a quadrat, similar to relative foliar cover (Wroe et al. 1988). Three aboveground biomass fractions were removed from each quadrat: litter, vegetation and dung. All standing and surface litter was raked with hands, rooted vascular plants were clipped at ground level and non-vascular plants and cattle dung were hand picked. Samples were oven dried at 70 °C for 48 hours prior to determination of dry weight biomass. All three fractions were fine ground first in a Wiley Mill, then a Cyclotec grinder, to pass a 0.1 mm sieve prior to chemical analyses (Ellert and Johnson 1997). Dung mass values were later combined with litter due to similarity in carbon concentration and difficulties separating the two fractions in the field.

3.2.3. Soil Sampling and Processing

Within each clipped and raked quadrat, three soil cores (6.7 diameter x 110 depth cm) were extracted with a heavy-duty hydraulic corer mounted on a one-ton truck and combined. In the two grazed treatments sampling depth alternated from 50 to 110 cm among sample points. Locations of the three cores within a quadrat were selected to proportionately represent the basal cover of plant crowns and bare ground. Common depth increments for cores were based on natural horizons identified in the field (Figure A.2). Up to 9 depth increments were selected at each site for a total of 204 field soil samples collected from within 24 sample points. Field soil samples were stored in a cold room (-0.5 °C) up to two days before being processed in the lab (Bates 1993).

Subsamples, 50 to 75 g wet weight, of each field soil sample were oven dried at 110 °C for 48 hours prior to weighing for bulk density determination (Culley 1993). The remainder of each field soil sample was air-dried prior to organic residue fractionation (Bates 1993). Up to three fractions were separated from each sample: plant crowns, macro-organic matter (MOM) >0.5 mm and fine soil. Plant crowns represent those aboveground portions (stem and leaf material) of vascular plants that could not be removed by clipping. MOM represents a combination of live and partially decomposed roots and plant debris, seeds, insect exuviae and other organic debris larger than 0.5 mm (Gregorich and Ellert 1993). MOM larger than 2 mm was first separated by hand crushing each air-dried field soil sample and sieving through a 2 mm mesh (Sheldrick and Wang 1993). Additional MOM was separated from fine soil by two to three repetitions of hand crushing, sieving (0.5 mm mesh) and winnowing. For winnowing a tabletop grain cleaner was used to separate heavy particles (soil) and light particles (MOM) between 0.5 and 2 mm in size. Soil that passed a 0.5 mm sieve was combined with heavy particles (0.5 to 2 mm) from the winnowing process to comprise the fine soil fraction. Plant crowns in the 0 to 10 cm increment from each of the 24 quadrats were separated from MOM by hand picking. MOM was oven dried at 70 °C for 48 hours and dry weight determined for correction of bulk density and MOM C calculations. Plant crown and MOM fractions were fine ground first in a Wiley Mill, then a Cyclotec grinder, and fine soil fractions in a roller mill, to pass a 0.1 mm sieve prior to chemical analyses (Ellert and Johnson 1997).

3.2.4. Chemical Analyses

Percent concentration of total carbon, organic carbon and total nitrogen of all fractions was determined by dry combustion, gas chromatography and thermal conductivity detection in a Carlo-Erba NA-1500 elemental analyzer (Pella 1990, Nelson and Sommers 1996). Fine ground subsamples (10 to 40 mg) of fine soil in Ag cups were acidified with 6M HCl to evolve inorganic CO_3^{-2} before SOC determination (Nelson and Sommers 1996). All fine ground subsamples for total fine soil, plant crown and MOM C were not acidified and combusted in Sn cups (Ellert and Johnson 1997). Analyses of $^{13}C/^{12}C$ for all fractions (except coarse fragments) were conducted with an automated Micromass Optima continuous flow mass spectrometer coupled to the Carlo-Erba, using a PDB calibrated standard as the reference gas (Boutton 1991a). Analytical precision of the Carlo-Erba NA-1500 differed from an average standard deviation for each set of ±0.64 % C for organic residue standards and ±0.05 % C for soil standards. Analytical precision of the mass spectrometer was ±0.23 ‰ standard deviations for organic residue and ±0.30 ‰ for soil standards. Mass spectrometer deviations were greater than the 0.05 to 0.1 ‰ range expected (Balesdent et al. 1988, Boutton 1991a, Skjemstad et al. 1990, Veldkamp and Weitz 1994, Follet et al. 1997). Ehleringer (1991) suggests variation on the order of ±0.4 ‰ can be expected for intrapopulation samples as a result of genetic differences in physiology and phenology.

3.2.5. Data Analyses

The organic carbon mass per area was calculated by multiplying the percent concentration of organic carbon by dry weights of each fraction. SOC mass per volume (Mg ha^{-1} for a given increment) was calculated by multiplying organic C percent concentration by dry soil mass, corrected by subtracting crown and MOM dry mass and volume (assuming a density of 1 Mg m^{-3}). Fine soil and MOM C and N data were weighted by soil layer thickness to achieve common depth increments among sites for statistical comparison.

Carbon mass for all fractions was analyzed within a completely randomized design by ANOVA, using SAS PROC GLM with Fisher's L.S.D. test used to identify significant ($P \leq 0.05$) differences among the four treatments (Table B.1) (SAS Institute 2000, Steele et al. 1996). The unbalanced number of subsamples in this investigation may have limited statistical inference (Hurlbert 1984). Application of the ^{13}C technique for estimating carbon turnover among spatially separate treatments (compared to the ideal temporal separation) makes use of a single mean SOC mass for each depth increment from the manipulated (abandoned) treatment (Veldkamp and Weitz 1994, Wolf et al. 1994). Statistical comparison between treatments allows a measure of bias due to spatial variability.

The following differential formula (Equation 1) from Wolf et al. (1994) was used to calculate the mass of SOC and MOM added to the soil following isotopic change of the input plant community.

$$\text{Proportion New SOC} = \left(\frac{(\delta^{13}\text{C‰ A Soil} - \delta^{13}\text{C‰ N Soil})}{(\delta^{13}\text{C‰ A Residue} - \delta^{13}\text{C‰ N Soil})} \right) \quad \text{(Eq. 1)}$$

$$\text{New SOC (Mg ha}^{-1}\text{)} = \text{Total SOC (Mg ha}^{-1}\text{)} * \text{Proportion New SOC}$$

δ^{13}C‰ A Soil refers to SOC of the grazed, cultivated and abandoned treatment for each depth increment. δ^{13}C‰ N Soil refers to SOC of the grazed, uncultivated treatment for each depth increment. δ^{13}C‰ A Residue refers to the mean of vegetation, litter and crowns (–25.67 ‰) of the grazed, cultivated and abandoned treatment. To determine SOC mass derived from the new plant community, SOC mass at each depth increment was multiplied by the calculated proportion of new inputs for each respective depth. The same equation was applied to MOM C mass and δ^{13}C at each depth, using the same δ^{13}C‰ A Residue value. Proportions provide a measure of net input since the disturbance.

Organic carbon loss following cultivation and the rate of new carbon incorporation into the SOC fraction is not linear but follows first order kinetics (Paul and Clark 1996). A portion of residue inputs since disturbance have subsequently been mineralized and lost as CO_2. Turnover rate as calculated by first order kinetics represents the time required for the cumulative annual input or output of carbon to equal SOC pool size; assuming steady state conditions. Mean SOC turnover time was determined by taking the reciprocal of the first order rate constant (k), calculated for each depth increment (Equation 2).

$$k = \frac{\left(-\ln (\%C_4\ A / \%C_4\ N) \right)}{\text{Years Elapsed Since Disturbance}} \quad \text{(Eq. 2)}$$

$$\text{Turnover (Years)} = 1 / k$$

Values for $\%C_4$ were calculated for both abandoned (A) and native (N) treatments from a simple mixing equation where pure C_3 derived SOC is –27 ‰, and pure C_4 derived SOC is –13 ‰ (Equation 3) (Boutton 1991b).

$$\%C_4 = \left(\frac{(-27\ ‰ - \text{Sample } \delta^{13}\text{C } ‰)}{(-27\ ‰ - -13\ ‰)} \right) * 100 \qquad \text{(Eq. 3)}$$

Sample δ^{13}C ‰ is the SOC or MOM C sample for which an estimate of %C_4 is desired.

Estimates of minimum sample size requirement for SOC %, SOC δ^{13}C and MOM δ^{13}C were made using the iterative method, pooled sample variance and values from Student's t distribution for $\alpha = 0.05$ (Steele et al. 1996).

3.3. RESULTS

3.3.1. Carbon Pool and Soil Characteristics

Vegetation standing crop and litter carbon mass differed more as a function of grazing than between native and abandoned treatments (Table 3.1). Litter accumulations in the exclosure were six times that of the grazed area. Crown and MOM carbon mass reflected a difference between native and abandoned treatments more than grazed and ungrazed effects. MOM carbon mass was consistently greater in native than abandoned treatments in the upper 35 cm of soil. For each of abandoned and native treatments, MOM carbon mass was greater in ungrazed than grazed treatments at most depth increments. Ungrazed native treatment had the greatest MOM carbon mass to 110 cm. SOC mass was not significantly different between grazed abandoned and native treatments for all but the 0 to 5 cm increment where native grazed SOC was greater than abandoned grazed. SOC mass in the ungrazed area was consistently less than the grazed area, to 80 cm depth. The grazed native treatment had the greatest SOC mass to 110 cm.

Soil bulk density was greater in grazed than ungrazed treatments at the 0 to 5 cm increment (Table 3.2). MOM C:N ratios averaged 20.1 and were highly variable within and among treatments, but was consistently lowest in the uppermost increments. Grazed native MOM C:N was consistently greater than grazed abandoned between 0 to 50 cm depth. SOC C:N ratios declined with depth in all but the grazed abandoned treatment;

where C:N ratio was greater between 5 and 20 cm than 0 to 5 cm. Surface SOC C:N ratios tended to be highest in native treatments between 0 to 5 cm and highest in abandoned treatments between 5 to 20 cm.

3.3.2. Vegetation and Litter

Bare ground was greatest on the abandoned cultivated land (Table 3.3). Litter cover was fairly even in ungrazed treatments and covered 40 to 60% more of the surface than within the grazed area. With grazing, greater vegetation basal cover is attributable to an abundance of low, mat-forming blue grama. Needle and thread was the single dominant on grazed abandoned land but ranked seventh among species on grazed native land. Blue grama accounted for less than half of vegetation biovolume, but was still the most abundant species on grazed native land. Differences in species composition and biovolume between native and abandoned treatments were less pronounced in the exclosure.

3.3.3. Carbon Isotopes

Isotopic variation of vegetation between grazed abandoned and native treatments were related to the proportion of blue grama biovolumes (Figure 3.1). Clipped vegetation was lower in ^{13}C than the crown fraction. Crowns were considerably more variable than any other fraction. Biovolumes appear to have overestimated aboveground blue grama biomass on native treatments and underestimated on the abandoned treatments. MOM δ^{13}C‰ in the 0 to 5 cm increment was isotopically more similar to crowns on the native treatment and to litter on the abandoned treatment. MOM δ^{13}C‰ was consistently lower on the abandoned treatment throughout the solum. ^{13}C enrichment between 20 to 70 cm in both treatments may reflect dominance of blue grama roots or carbonate contamination at this depth. Except for the 0 to 5 cm increment, abandoned SOC δ^{13}C‰ was not consistently depleted relative to the native treatment (Figure 3.2). The dominantly C_3 plant community had SOC δ^{13}C‰ enriched to a greater degree than under C_4 vegetation. There was considerable variation within treatments, although native SOC δ^{13}C‰ declined steadily with depth from 20 to 110 cm. Mean ^{13}C enrichment of SOC relative to MOM from the same increments was 1.05‰ on the native grazed side (Figure 3.3).

3.3.4. Turnover Calculations

Differences in δ^{13}C‰ for 0 to 5 and 5 to 10 cm allowed for SOC turnover calculations (Table 3.4). Although the δ^{13}C‰ difference between treatments for the 10 to 20 cm increment was not statistically significant ($P \geq 0.05$), turnover calculations were derived. Calculations between abandoned and native treatments were restricted to the 16 sample points on grazed treatments (8 replicates abandoned, 8 replicates native). The proportion of new SOC contributed over the 70 year period declined rapidly with depth to 20 cm. Below 20 cm differences between abandoned and native treatments were highly variable and mean differences inconsistent. The mass of new SOC contributed in the 0 to 5 cm increment was nearly three times that in the 5 to 10 cm increment. Turnover time for the SOC pool ranged from 165 years near the surface to more than 6000 years near the interface of the Ah and Ck horizons. The proportion of new MOM C contributed over the same period also declined with depth to 110 cm. Relative to SOC, MOM C turnover was more rapid and the proportion added to this fraction over the last 70 years was greater at all depth increments. MOM C turnover rates were less than a third of SOC in the 0 to 5 and 5 to 10 cm increments (Table 3.4).

3.3.5. Sample Size Requirements

The largest minimum sample size requirement for assessing differences in SOC % between treatments was 30 (Table 3.5). Sample sizes for detecting differences in δ^{13}C ‰ were less, at 19 for SOC and 10 for MOM. Variability due to depth was most evident in the SOC fraction. Sample requirements were greater in the 0 to 5 cm depth for SOC %, whereas minimum requirements increased markedly below 65 cm for SOC δ^{13}C. Actual sample variance was higher for SOC δ^{13}C samples below 50 cm where only 4 points were available to estimate variance.

3.4. DISCUSSION

3.4.1. Validity of Turnover Calculations

Turnover calculations assumed first order kinetics for both SOC and MOM fractions. The negative exponential loss of original carbon should reflect rapid loss of labile fractions and slow release of increasingly recalcitrant soil organic matter (Balesdent et al. 1988). Similarly, the addition of new carbon would be primarily in the form of labile plant residues and macroaggregate associated carbohydrates derived from root exudates (Dormaar and Willms 1990). Changes in the $\delta^{13}C$ of SOC over 67 years of natural recovery possibly reflects changes mainly in the light fraction (MOM <0.5 mm) and more readily mineralized, macroaggregate associated SOC (Cambardella and Elliott 1994, Jastrow et al. 1996). Turnover rates between 0 and 10 cm were within the estimated 50 to 1200 year range based on ^{14}C and ^{13}C dates (Jastrow et al. 1996, Paul et al. 1997). However, soils under long-term cultivation had longer mean residence times than beneath native range apparently due to a proportional decline in the active SOC fraction, since this pool is not adequately replaced by residues from shallow-rooted annual crops. SOC turnover rate between 10 to 20 cm exceeded, and MOM fell short of, the estimated 635 to 2155 year range of ^{14}C mean residence times for similar soils (Paul et al. 1997). Although sample size was sufficient, the 10 to 20 cm $\delta^{13}C$ SOC treatment difference was not statistically significant and the mean difference of 0.1 ‰ for SOC at this increment was within the range of analytical variation. Thus the accuracy of the 6615 year turnover rate should be viewed as poor.

MOM C turnover rates between 50 and 80 cm were less than between 35 and 50, and 80 and 110 cm. Variability (small sample size, rooting depth, carbonate contamination and other factors discussed in subsequent sections) resulted in a greater shift in $\delta^{13}C$ ‰ among native and abandoned treatments than expected between 50 and 80 cm. Because the MOM fraction includes live roots and relatively more undecomposed residues than the SOC fraction, turnover rates were expected to be more rapid than for SOC. Sims and Singh (1978) calculated proportional root turnover of 0.10 to 0.72 per year, indicating relatively short (2 to 10 years) turnover rates for live roots. Turnover rates in excess of this would indicate increasingly greater proportions of undecomposed residues in the MOM fraction. The 95 to 110 cm MOM treatment difference was not statistically significant and the mean difference of 0.13 ‰ for MOM at this increment was within the range of analytical variation. Thus the accuracy of our 2850 year turnover rate should be viewed as poor.

3.4.2. Variation due to Physiological ^{13}C Fractionation

Differences in water use efficiency of plant species may confound $\delta^{13}C$ differences due to photosynthetic pathway. Water use efficient plants restrict diffusivity of CO_2 by reducing air-flow through stomata. Isotopic enrichment of water use efficient plants, like needle and thread, may be as much as 4.4‰ (O'Leary 1988, Farquhar et al. 1989, Ehleringer 1991). Large inputs from needle and thread belowground relative to all C_3 vegetation aboveground may result in overestimation of C_4 inputs.

Differential discrimination occurs within a plant during biosynthesis of structural compounds and within a community due to phenology. Cellulose is 1 to 2‰ enriched and lignin 2 to 6‰ depleted in ^{13}C relative to the plant as a whole (Boutton 1991b). The relative contribution of these compounds to belowground plant parts and SOC fractions could affect the final turnover estimate. For example, belowground, non-photosynthetic tissues may be 2 to 4‰ enriched relative to aboveground green vegetation (O'Leary 1988). Patterns of C_3 and C_4 plant production within a season vary, with C_3 peaking in June and C_4 in July (Lauenroth and Whitman 1977, Ehleringer 1978, Ode et al. 1980, Monson and Williams 1982, Monson et al. 1986, Tieszen et al. 1997). Thus, sampling aboveground vegetation should be restricted to the intermediate peak production period or in late fall once all vegetation has become dormant.

Enrichment of 0.5 to 1.5‰ is also possible through microbial transformation of organic residues (Balesdent et al. 1988). Multiple transformations of plant residues through soil faunal and microbial communities can enrich SOC by 1.5 to 6.5‰ from the original plant residue. An additional factor is variation in atmospheric ^{13}C concentration. A depletion of 1.4‰ has occurred over the last century in response to atmospheric pollution from fossil fuel combustion (Boutton 1991b). Older SOC should be enriched by an equal amount; although it may have undergone further microbial transformations and thus not differ isotopically from younger SOC.

These factors combined could explain the observed enrichment of approximately 1 to 4‰ in crown and MOM relative to litter and vegetation fractions (Figure 3.1). Litter mixed with MOM is incorporated into the upper increments (0 to 10 cm). SOC at these increments was approximately 2 to 3‰ depleted relative to that between 10 and 60 cm (Figure 3.2).

3.4.3. Variation in SOC Mass due to Three Seasons of Tillage

Cultivation for three seasons, and subsequent abandonment, was sufficient to deplete SOC mass in the 0 to 5 cm increment (Table 3.1). Below 5 cm, differences among treatments were not statistically significant, though mean SOC mass was often greater on the abandoned treatment. A study of long-term cultivation effects on grassland soils, at multiple time intervals, indicated little or no change in SOC mass in the first 4 years of cultivation (Tiessen et al. 1982). Kelly and Burke (1997) investigated changes in SOC within surface soils immediately beneath dead blue grama individuals. There was an initial 9 month period in which SOC rapidly increased as plant crowns and roots decomposed and entered the SOC pool. A total of 36 months was necessary for SOC to decline to previous levels. This effect reflected transient changes in the labile fraction of SOC.

Tillage exposes soil aggregates to increased oxidation and accelerates SOC loss from this slowly oxidized fraction (Mann 1986, Buyanovsky et al. 1987). Aggregates of similar size from cultivated soils often have SOC several centuries older than adjacent rangeland soils as a result of accelerated oxidation and carbon loss (Martel and Paul 1974, Balesdent et al. 1988, Cambardella and Elliott 1994, Follet et al. 1997, Paul et al. 1997). With continued cultivation, resistant humus and microaggregate SOC comprises relatively more of the remaining SOC pool (Paul et al. 1997). Recovery of the light fraction, or labile pool, of SOC is expected to be rapid (Buyanovsky et al. 1987, Balesdent et al. 1988). On the abandoned treatment there may have been a SOC loss from more slowly oxidized pools that have not yet recovered. This difference in SOC pools between treatments may be a contributing factor to the observed SOC C:N and $\delta^{13}C$ difference in the 0 to 5 cm increment (Schimel et al. 1985, Aguilar et al. 1988, Burke et al. 1989, Burke et al. 1995). Dormaar and Smoliak (1985) suggested 75 to 150 years were required for complete recovery of SOC on abandoned cultivated land. The initial loss of carbon from the cultivated and abandoned treatment was not accounted for and both SOC and MOM turnover rate estimates are biased if inferences about northern mixed prairie communities other than a needle and thread dominated ones were to be made.

3.4.4. Variation in ^{13}C due to Differences in Rooting Depth

In previous studies belowground $\delta^{13}C$ ‰ enrichment occurred with depth (Follet et al. 1997). Repeated microbial transformation of older SOC at depth has been suggested as the mechanism for progressive enrichment. In this study, enrichment with depth was observed to approximately 45 cm for MOM and 20 cm for SOC. ^{13}C depletion occurred below these depths. Previous investigations often did not involve samples below 50 cm. In this study, C:N ratios of SOC declined with depth and suggest increased humification occurred as expected (Paul and Clark 1996).

Differences in rooting depth and subsequent dominance of the rooting zone by different plant species may explain the above pattern. In both abandoned and native treatments, the upper 20 cm of organic matter was primarily derived from residues of C_3 vegetation. The presence of shallow-rooted annual C_3 weeds such as bluebur (*Lappula echinata* Gilib.) and the perennial graminoids Sandberg's bluegrass (*Poa sandbergii* Vasey) and sedges (*Carex* spp.), combined with relatively greater litter production by needle and thread may explain SOC ^{13}C depletion in the upper horizon. At depth, deep-rooted needle and thread plants may have been more abundant relative to more shallow-rooted blue grama. Only in the 20 to 70 cm zone did blue grama comprise more MOM relative to aboveground cover. Based on what is known of these species' rooting patterns (Weaver and Darland 1949, Weaver 1950, Coupland and Johnson 1965), rooting depth appears to be a more straightforward explanation for this pattern than multiple microbially mediated transformations. The rooting depth explanation does assume little vertical redistribution of SOC over time.

Correlation of turnover estimates by $\delta^{13}C$ ‰ with ^{14}C estimates of mean residence time would assist to determine whether rooting depth variation was important. Use of $\delta^{13}C$ to identify rooting depth of C_4 species in C_3 dominated communities may also facilitate future investigations into interspecific competition, niche theory and physiological ecology.

3.4.5. Spatial Scales and Sources of Variation

Both Veldkamp and Weitz (1994) and Wolf et al. (1994) suggest use of adjacent sites (treatments in space) versus repeated sampling (treatments in time) results in a more variable data set and potential for errors in turnover estimates. On our site there were two scales of spatial heterogeneity. Juxtaposition of abandoned and native treatments to other landscape elements differed at the large scale. An irrigated field was located approximately 100 m north of the abandoned treatment and the Oldman River valley escarpment was within 100 m south of the native treatment. Although the area sampled was relatively level (< 1% slope), there may have been an underlying moisture gradient affecting the distribution of plant species, ANPP and rates of SOM transformations. Dormaar et al. (1994) reported ungrazed abandoned treatment aboveground ANPP was nearly twice that of the ungrazed native treatment. The presence of crested wheatgrass (*Agropyron cristatum* Gaertn.) in the exclosure may account for this difference. Previous studies on the natural distribution of C_4 plants in mixed prairie indicate an increase in C_4 cover is inversely correlated with soil moisture (Ayyad and Dix 1964, Baines 1973, Ode et al. 1980, Barnes et al. 1983, Archer 1984). The native treatment would be expected to have more blue grama simply due to this moisture gradient. Mean SOC $\delta^{13}C$ ‰ at depth indicated the opposite was true and the abandoned treatment historically had more C_4 vegetation.

A clear depletion in SOC ^{13}C from native to abandoned treatments was necessary to meet assumptions of the turnover calculations (Wolf et al. 1994). The degree of SOC ^{13}C enrichment relative to plant residues may vary from 0.5 to 4‰, dependent on the quality of SOC fractionation and proportion of recalcitrant humus in the SOC fraction (Boutton 1991a, 1991b). Gradual enrichment of SOC $\delta^{13}C$ with depth was expected (Follet et al. 1997). SOC $\delta^{13}C$ instead became more depleted from 10 to 110 cm on the native treatment. SOC $\delta^{13}C$ on the abandoned treatment similarly became more depleted beneath the 20 to 35 cm increment. Kindscher and Tieszen (1998) and Collins et al. (1999) found a similar pattern beneath uncultivated and restored tallgrass prairie when samples 80 to 100 cm deep were analyzed.

Soil bulk density variation among treatments could have affected accuracy of SOC mass comparisons and resulting turnover calculations (Veldkamp and Weitz 1994). Bulk density was not significantly different between abandoned and native treatments; although Dormaar et al. (1994) found it was lower in the upper 6 cm of the abandoned side. Differences in bulk density due to cultivation and abandonment were not observed at other mixed prairie sites after as much as 50 years (Dormaar and Smoliak 1985) or as little as 4 years (Tiessen et al. 1982).

Although bulking cores within an experimental unit reduced within-unit variation, there was still enough between unit variation to obscure statistically significant $\delta^{13}C$ ‰ differences between treatments for both MOM and SOC. Both Skjemstad et al. (1990) and Veldkamp and Weitz (1994) found such spatial heterogeneity was the largest source of variation. At the treatment scale individual plant basal area and density differed. Bunches of needle and thread had smaller basal areas than patches of blue grama. Field observations and a previous study by Dormaar et al. (1994) indicated individual blue grama patches covered more surface area than individual bunches of needle and thread and accounted for greater basal area and biomass of crowns on the native side. Burke (1995) found SOC beneath blue grama patches were significantly greater than beneath patch interspaces. The effect did not extend very deep and only the 0 to 5 cm increment demonstrated a significant difference between treatments (Burke 1995).

3.4.6. Temporal Scales and Sources of Variation

Temporal sources of variation stemmed from both natural succession and pedogenesis. Throughout the process of natural succession on this site it is unknown how composition differed at earlier seral stages. Pioneer and weedy C_4 annuals may have dominated the site for a period (see Table C.3 for list of C_4 species in Alberta). This was a typical pattern in studies of recovering abandoned farmland following the 1930s drought in Colorado (Costello 1944), Nebraska (Judd and Jackson 1940) and Kansas (Weaver and Albertson 1936, Albertson and Tomanek 1965). Residue inputs from shallow-rooted annual species would have been limited to the litter stratum and upper few cm of soil. Although little residue may have been contributed by early successional species, a delay in C_3 production would have caused an initial lag in SOC recovery and an overestimate of SOC turnover.

During the interglacial hypsithermal 5 to 7 thousand years before present (k ybp) C_4 species may have been more abundant on this site (Follet et al. 1997). Pedogenesis in this region was limited to the last 10 000 years. The hypsithermal period was warmer and more arid than conditions of the past century (Axelrod 1985). There was both more

C_4 derived MOM and SOC belowground than can be accounted for by the present abundance of blue grama. Differences in rooting depth and possible biochemical mechanisms for this variation have already been discussed. Accepting the hypsithermal hypothesis requires evidence of substantial MOM contamination with both ancient charcoal and undecomposed residue throughout the solum. Visual examination of samples in this study, and in a study elsewhere by Skjemstad et al. (1990), confirm charcoal and rarified residues were present at depth.

Contamination of the MOM C fraction with CO_3^{-2} ($\delta^{13}C$ approximately = 0 ‰) could account for the belowground MOM $\delta^{13}C$ pattern. The ^{13}C enrichment shift between 20 and 70 cm is within the zone of CO_3^{-2} accumulation (leached from surface, deposited in subsurface) based on the mass of inorganic carbon in the soil (data not reported). Previous analyses of acidified and non-acidified MOM indicates CO_3^{-2} contamination is statistically significant and accounts for 0.5 ‰ enrichment of non-acidified MOM (Table C.4). Although carbonate concentration between 20 and 70 cm is greater than above 20 cm, there is not an obvious zone of accumulation in the fine soil fraction (Figure C.3). Accumulation in the MOM fraction is possible when compared to the SOC fraction (Figure 3.3).

Evidence of buried horizons in the solum indicates past periods of surface destabilization and recovery. Another C_4 species on site, but not within the area sampled, was sand reed grass (*Calamovilfa longifolia* Hook.); a species known to colonize and stabilize drifting sand and soil (Moss 1994). It is possible this C_4 was the sole species on the study site for extended periods following soil drift events. Undecomposed residues in the 20 to 70 cm depth may represent inputs from sand reed grass 5 to 7 k ybp, and residues below 70 cm represent older C_3 dominated communities. ^{14}C analyses of both SOC and MOM are required to assist in answering that question. Palynological investigation of wetland sediments in the region to identify relative proportions of C_4 grass pollen through time might also be useful. Paleoecological investigations may use $\delta^{13}C$ analysis of soil profiles to complement pollen analysis of wetland sediments.

3.5. CONCLUSION

Substantial natural variation in native, mixed C_3 and C_4 plant communities and arid conditions limiting turnover rate limited the utility of the ^{13}C technique for SOC turnover estimation. The largest δ^{13}C differences occurred in the 0 to 5 cm increment at 5.6 ‰ for MOM and 2.9 ‰ for SOC fractions. Soil organic matter pool turnover rates declined rapidly with depth from 51 years for MOM at the 0 to 5 cm increment, to 6615 years for SOC at the 10 to 20 cm increment. Inclusion of live roots in the MOM fraction resulted in more rapid turnover estimates than the SOC fraction. Multiple sources of variation were possible. Detailed site management and successional history, ^{14}C radiocarbon dating and analytical quality control are necessary to account for the relative contribution of each source of variation. Locating and sampling sites with similar management histories and plant community shifts would further support the results of this study. Some potentially useful ecological applications for this technique were suggested for plant competition and paleoecological investigations.

3.6. REFERENCES

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Table 3.1. Mean organic carbon pool mass for abandoned and native, grazed and ungrazed treatments at Picture Butte.

Depth (cm)	Grazed		Ungrazed	
	Abandoned	Native	Abandoned	Native
	Vegetation Carbon Mass (Mg ha^{-1})			
	0.91 a ±0.12	0.84 a ±0.12	1.45 b ±0.44	1.32 b ±0.36
	Litter Carbon Mass (Mg ha^{-1})			
	0.25 a ±0.05	0.30 a ±0.22	2.13 b ±0.54	1.98 b ±0.72
	Crowns Carbon Mass (Mg ha^{-1})			
	0.74 a ±0.18	1.26 b ±0.40	0.71 a ±0.32	1.01 b ±0.22
	Macro-organic Matter Carbon Mass (Mg ha^{-1})			
0 to 5	2.15 a ±0.67	2.59 ab ±0.55	2.45 ab ±0.30	3.10 b ±0.47
5 to 10	0.46 a ±0.18	0.70 b ±0.08	0.53 ab ±0.26	0.57 a ±0.10
10 to 20	0.46 a ±0.14	0.81 b ±0.08	0.80 ab ±0.51	0.77 b ±0.09
20 to 35	0.70 a ±0.21	0.90 ab ±0.19	0.86 ab ±0.37	1.10 b ±0.16
35 to 50	0.70 a ±0.23	0.62 a ±0.17	0.58 a ±0.16	0.84 a ±0.29
50 to 65	0.42 a ±0.20	0.39 a ±0.02	0.37 a ±0.16	0.58 a ±0.34
65 to 80	0.38 a ±0.06	0.27 b ±0.03	0.28 ab ±0.14	0.43 ab ±0.17
80 to 95	0.21 a ±0.04	0.18 ab ±0.05	0.14 b ±0.01	0.29 ab ±0.14
95 to 110	0.12 a ±0.03	0.12 a ±0.03	0.14 a ±0.07	0.18 a ±0.05
Subtotal	5.60	6.58	6.15	7.86
	Fine Soil Organic Carbon Mass (Mg ha^{-1})			
0 to 5	15.25 a ±2.41	18.04 b ±1.58	12.22 c ±0.84	14.11 ac ±1.75
5 to 10	13.02 a ±1.02	12.84 ab ±0.92	11.23 c ±0.66	11.73 bc ±0.55
10 to 20	21.19 a ±1.12	19.96 ab ±1.21	18.15 c ±0.91	18.57 bc ±1.24
20 to 35	20.54 ab ±2.74	21.97 a ±1.64	19.03 b ±1.00	21.23 a ±1.28
35 to 50	14.02 ab ±4.86	18.15 a ±4.56	10.52 b ±0.73	12.65 b ±1.94
50 to 65	16.47 a ±5.49	16.04 a ±3.81	8.06 b ±0.48	9.73 c ±1.10
65 to 80	16.93 a ±4.03	12.80 ab ±4.40	7.66 c ±0.86	10.93 b ±1.48
80 to 95	15.58 a ±2.96	11.31 ab ±4.09	9.63 b ±1.19	13.08 a ±4.04
95 to 110	13.45 a ±4.08	9.61 a ±4.83	11.44 a ±2.85	14.83 a ±2.41
Subtotal	146.45	140.72	107.94	126.86
Grand Total	153.95	149.70	118.38	139.03

For each row, numbers followed by the same letter are not significantly different (L.S.D. $P \leq 0.05$). Standard deviations follow means.

Table 3.2. Selected mean soil characteristics for abandoned and native, grazed and ungrazed treatments at Picture Butte.

Depth (cm)	Grazed		Ungrazed	
	Abandoned	Native	Abandoned	Native
	Bulk Density (Mg m^{-3})			
0 to 5	1.18 a ±0.06	1.18 a ±0.08	1.06 b ±0.04	1.04 b ±0.01
5 to 10	1.36 a ±0.05	1.35 a ±0.09	1.30 a ±0.04	1.33 a ±0.05
10 to 20	1.32 a ±0.03	1.38 b ±0.08	1.34 ab ±0.03	1.38 b ±0.02
20 to 35	1.42 a ±0.05	1.40 a ±0.01	1.43 a ±0.03	1.41 a ±0.03
35 to 50	1.51 a ±0.05	1.43 b ±0.05	1.51 a ±0.02	1.50 a ±0.04
50 to 65	1.49 ab ±0.09	1.41 b ±0.03	1.57 a ±0.06	1.54 a ±0.03
65 to 80	1.45 ab ±0.07	1.44 b ±0.04	1.55 a ±0.02	1.52 a ±0.05
80 to 95	1.44 a ±0.02	1.44 a ±0.03	1.54 a ±0.03	1.46 a ±0.07
95 to 110	1.46 a ±0.01	1.48 a ±0.03	1.47 a ±0.11	1.45 a ±0.01
	Macro-organic Matter C:N Ratio			
0 to 5	15.11 a ±0.90	19.89 b ±1.68	15.17 a ±2.76	16.16 a ±0.28
5 to 10	18.82 a ±3.10	23.20 b ±1.48	25.46 b ±7.98	21.94 ab ±2.23
10 to 20	21.75 a ±3.04	24.95 b ±2.14	23.80 ab ±2.03	23.68 ab ±1.25
20 to 35	18.93 a ±1.14	22.49 b ±1.38	22.06 b ±2.11	23.63 b ±1.36
35 to 50	17.77 a ±0.99	20.51 b ±1.17	20.91 b ±2.68	21.57 b ±0.73
50 to 65	17.51 a ±1.02	18.11 a ±1.09	21.03 a ±4.31	19.91 a ±0.34
65 to 80	19.23 ab ±1.81	18.38 a ±0.74	20.94 ab ±2.04	21.51 b ±2.06
80 to 95	19.88 a ±0.29	20.80 a ±1.40	20.71 a ±0.98	23.25 b ±2.89
95 to 110	20.58 a ±1.56	20.67 a ±1.09	21.14 a ±1.19	23.51 b ±1.11
	Fine Soil Organic C: total N Ratio			
0 to 5	9.54 a ±0.36	10.71 b ±0.46	10.23 b ±0.75	10.82 b ±0.38
5 to 10	9.74 ab ±0.19	9.52 b ±0.21	9.96 a ±0.38	9.68 ab ±0.12
10 to 20	9.60 a ±0.11	9.32 b ±0.16	9.42 b ±0.06	9.32 b ±0.06
20 to 35	8.69 a ±0.27	8.79 a ±0.28	8.80 a ±0.07	8.72 a ±0.19
35 to 50	8.45 a ±0.56	8.63 a ±0.37	8.64 a ±0.52	8.50 a ±0.52
50 to 65	8.98 a ±0.57	8.73 ab ±0.15	7.94 b ±0.13	8.26 ab ±0.72
65 to 80	8.99 a ±0.36	8.17 a ±0.74	8.16 a ±0.43	8.78 a ±0.20
80 to 95	9.20 a ±0.27	8.63 a ±0.51	9.11 a ±0.43	9.19 a ±0.32
95 to 110	8.84 a ±0.23	8.15 a ±1.64	8.49 a ±0.56	8.75 a ±0.29

For each row, numbers followed by the same letter are not significantly different (L.S.D. $P \leq 0.05$). Standard deviations follow means.

Table 3.3. Mean vegetation basal cover and species biovolume visual estimates for abandoned and native, grazed and ungrazed treatments at Picture Butte July 1998.

Stratum	Grazed		Ungrazed		$\delta^{13}C$ ‰
Species	Abandoned	Native	Abandoned	Native	
			Basal Area (%)		
Litter	8.6	12.1	67.9	52.0	
Bare Ground	46.8	19.3	2.0	0	
Vegetation	44.6	68.6	30.1	48.0	
			Biovolume (%)		
Stipa comata Trin.&Rupr.	78.4	2.9	42.5	34.4	-25.6
Bouteloua gracilis HBK	2.2	39.1	4.1	18.8	-13.4
Eurotia lanata Pursh		14.0	15.0	25.3	-29.1
Poa sandbergii Vasey	11.8	9.5	14.1	4.2	-28.2
Carex spp. L.	1.0	9.8	0.4	6.5	-27.3
Lappula echinata Gilib.	1.5	16.0	1.2	0.3	
Koeleria macrantha Ledeb.			6.6	4.2	
Sphaeralcea coccinea Pursh	3.6	1.9	1.7	2.1	
Agropyron cristatum Gaertn.			8.3		
Tragopogon dubius Scop.			2.9	1.6	
Lygodesmia juncea Pursh		4.2			
Agropyron smithii Rydb.		2.2		1.0	
Erigeron caespitosus Nutt.				1.6	
Mamillaria vivipara Nutt.	0.3	0.1	0.8		
Taraxacum officinale Weber	0.3		0.8		
Allium textile Nels.&Macbr.		0.2	0.8		
Artemisia frigida Willd.	0.1	0.1	0.8		
Solidago missouriensis Nutt.	0.8				

$\delta^{13}C$ values for the five most common species are the mean of five bulk samples of each species collected at random from across the study area.

Table 3.4. Soil organic matter turnover for grazed northern mixed prairie grassland.

Depth (cm)	Macro-organic Matter Carbon			Fine Soil Organic Carbon		
	Proportion[1] New Carbon in 70 years	New Carbon[1] (kg ha^{-1}) in 70 years	Carbon Turnover[2] (years)	Proportion[1] New Carbon in 70 years	New Carbon[1] (Mg ha^{-1}) in 70 years	Carbon Turnover[2] (years)
0 to 5	0.90	2142	51	0.40	6.66	165
5 to 10	0.62	360	98	0.18	2.27	403
10 to 20	0.47	297	146	0.02	0.45	6615
20 to 35	0.24	193	316			
35 to 50	0.17	114	446			
50 to 65	0.24	99	308			
65 to 80	0.33	109	220			
80 to 95	0.11	21	807			
95 to 110	0.03	4	2850			

1. Based on equation 1 in methods.
2. Based on equation 2 in methods, using 70 years as time since disturbance.

Table 3.5. Minimum sample size estimates for soil organic carbon and δ^{13}C‰ to 95% confidence.

Depth (cm)	Fine Soil %C			Fine Soil Organic δ^{13}C ‰			Macro-organic Matter δ^{13}C ‰		
	Pooled Variance	Estimated Minimum Difference	Estimated Minimum n	Pooled Variance	Estimated Minimum Difference	Estimated Minimum n	Pooled Variance	Estimated Minimum Difference	Estimated Minimum n
0 to 5	0.17	0.16 %	30	0.27	0.90 ‰	5	2.02	1.19 ‰	9
5 to 10	0.04		10	0.48		6	1.97		9
10 to 20	0.01		5	0.30		5	1.25		7
20 to 35	0.01		6	0.53		6	1.07		7
35 to 50	0.06		12	0.40		6	2.19		10
50 to 65	0.06		13	0.93		8	1.29		7
65 to 80	0.05		11	1.85		13	1.77		9
80 to 95	0.03		8	2.87		17	0.68		6
95 to 110	0.04		10	3.33		19	1.08		7

Estimated n derived from the iterative method using pooled sample variance and the t distribution (Steel et al. 1996).

Pooled Variance was derived from variance for abandoned and native, grazed treatments.

Estimated Mean Difference derived from (3 * analytical standard deviation) to account for 99.7% of analytical variation. For macro-organic matter δ^{13}C additional variation of 0.5 ‰ was added to account for carbonate contamination variation.

Actual n from which pooled sample variances were estimated, were n = 8 from 0 to 50 cm, and n = 4 from 50 to 110 cm.

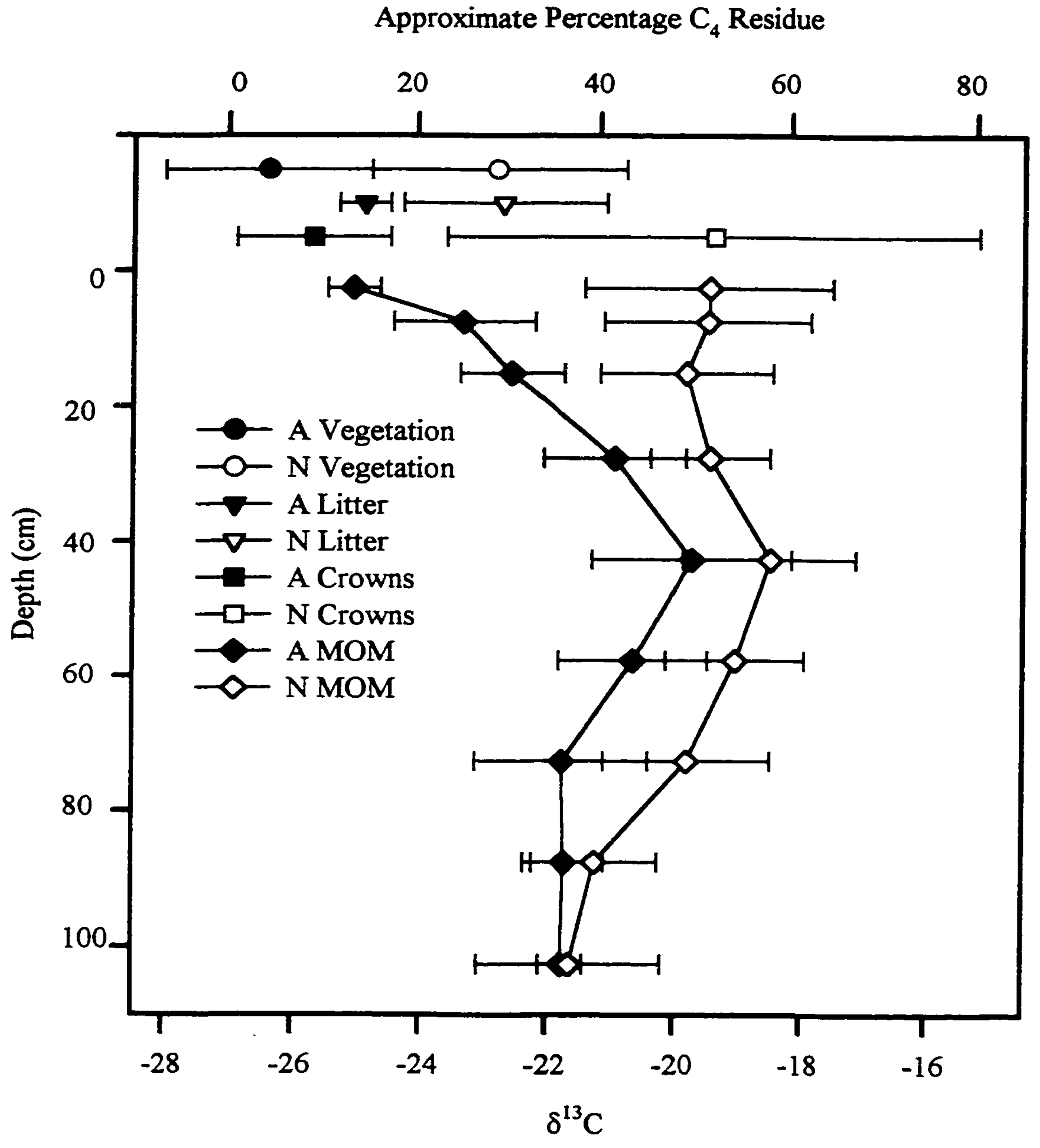


Figure 3.1. Organic residue $\delta^{13}C$ for vegetation, litter, crown and macro-organic matter (MOM) fractions across abandoned (A) and native (N) grazed treatments.
Error bars are standard deviations.

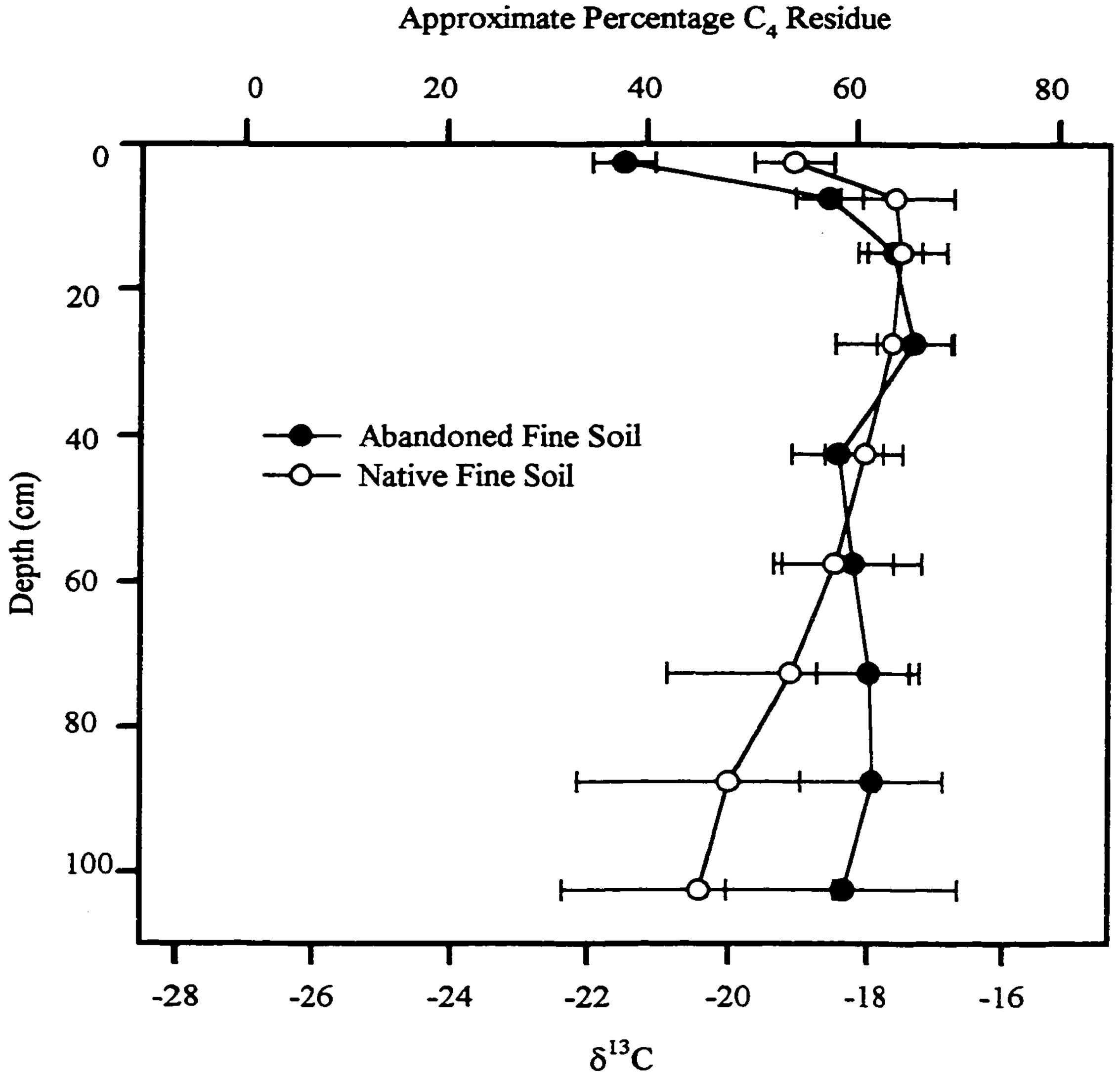


Figure 3.2. Fine soil organic carbon $\delta^{13}C$ across abandoned (A) and native (N) grazed treatments.
Error bars are standard deviations.

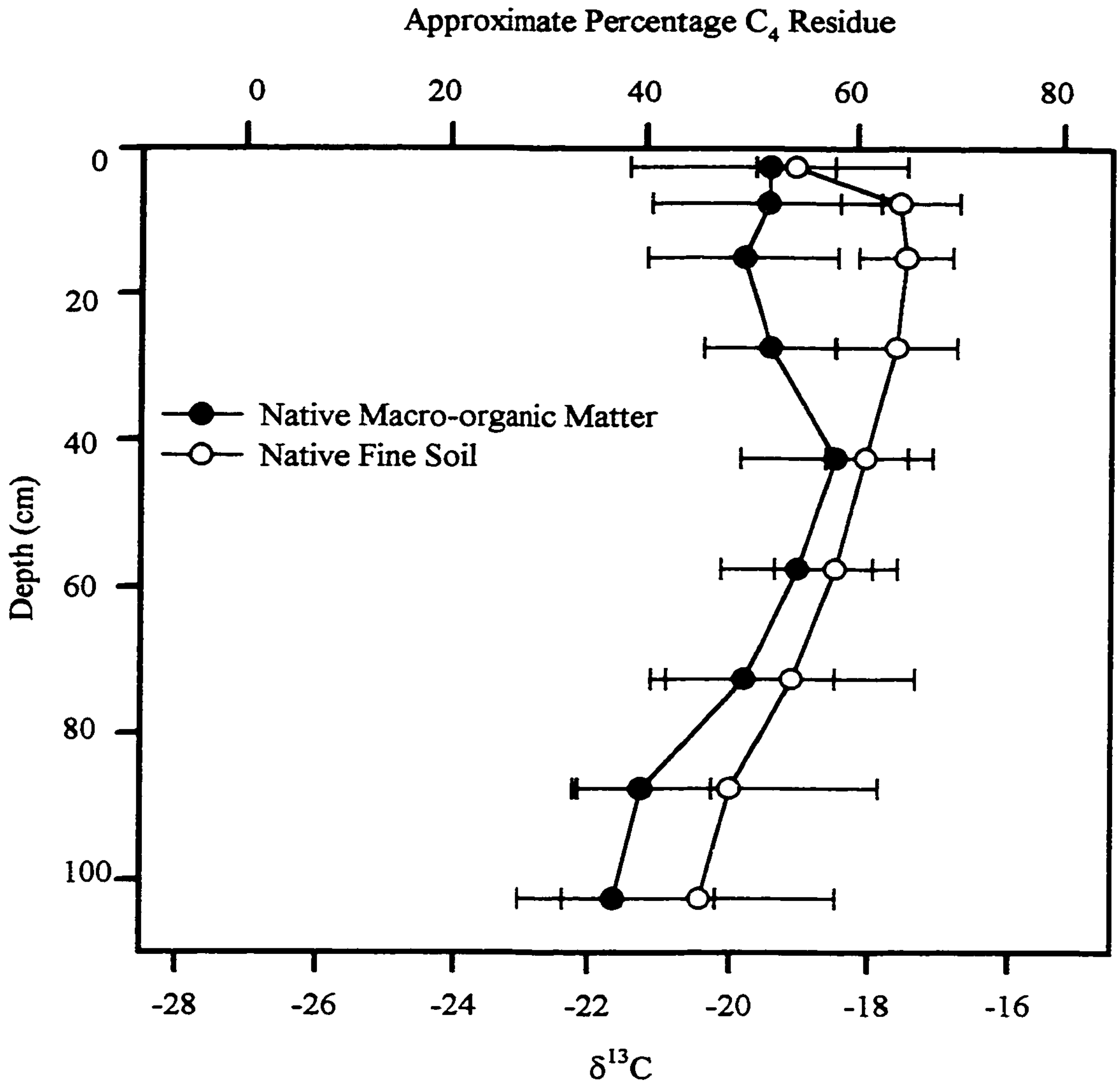


Figure 3.3. Comparison of fine soil organic carbon and macro-organic matter carbon $\delta^{13}C$ within the native grazed treatment. Mean difference between fractions is 1.05 %. treatments.

Error bars are standard deviations.

APPENDIX A. STUDY SITE DESCRIPTIONS

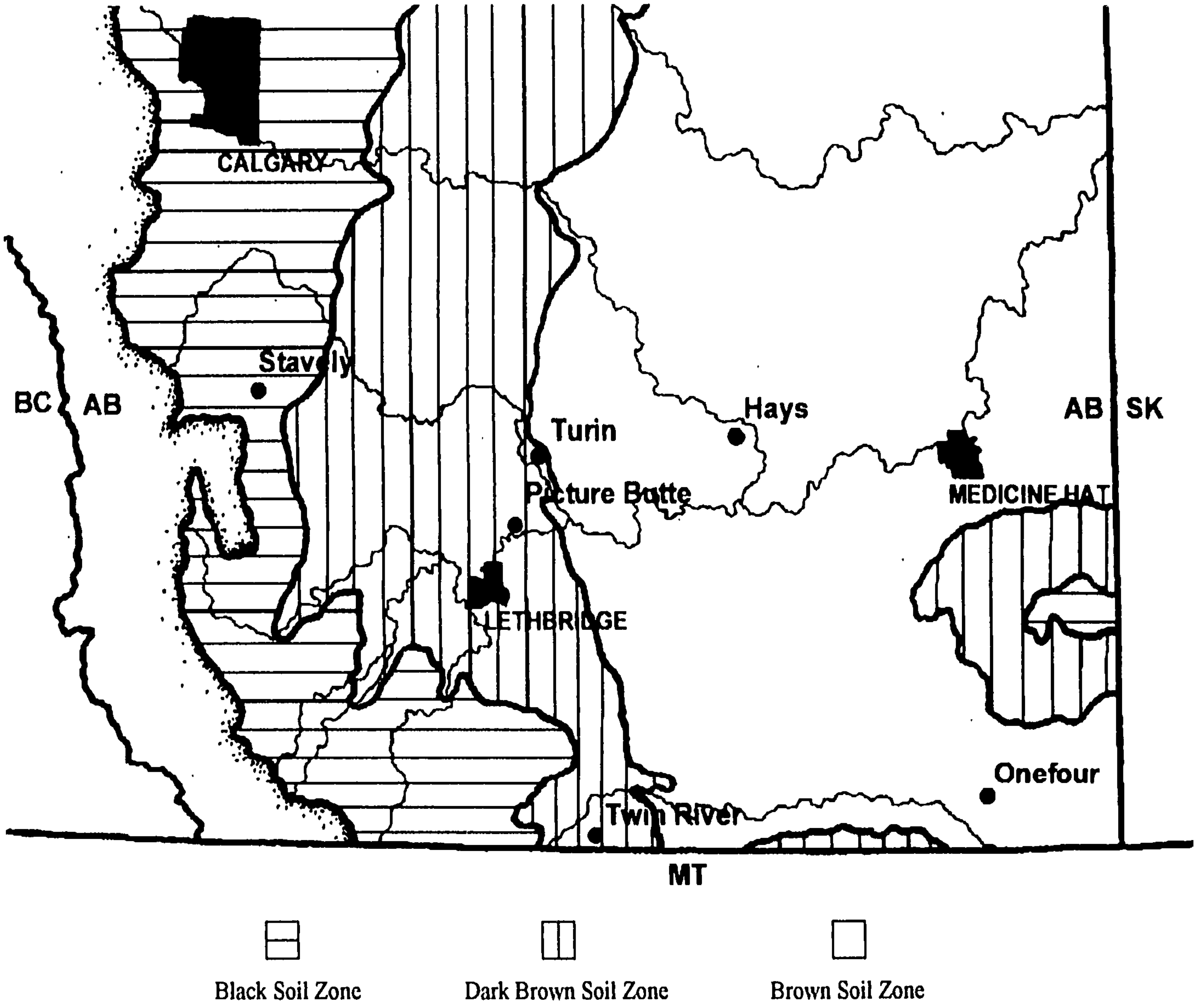


Figure A.1. Southern Alberta study area with approximate site locations.

Table A.1. Vegetation composition and cover summary for grazed (GR) and exclosures (EX) at all sites.

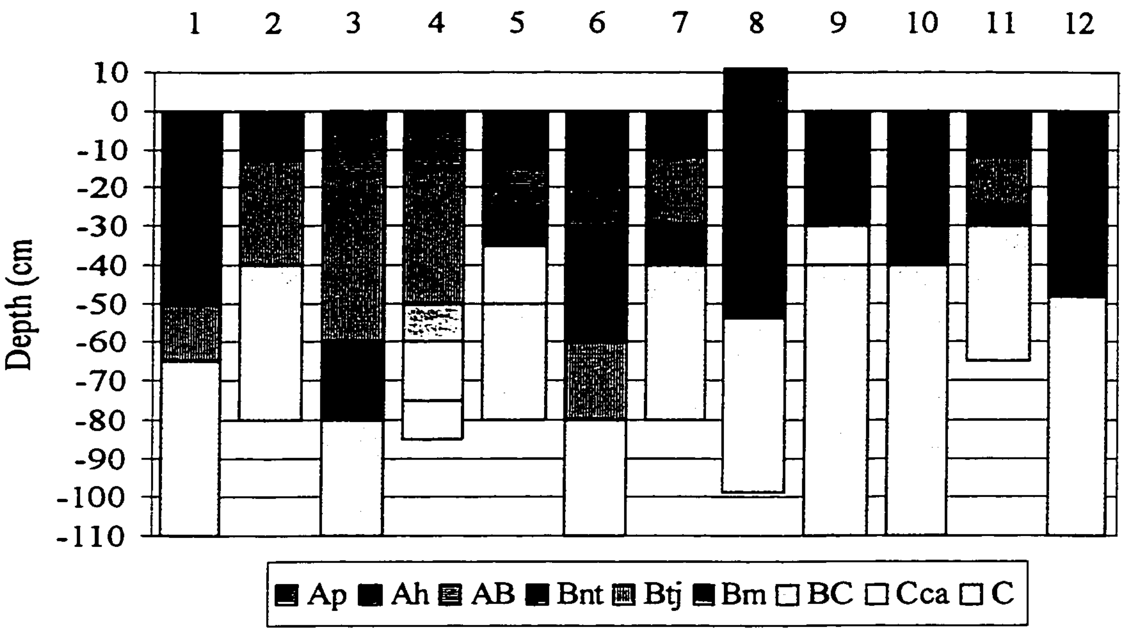
Stratum Species	ST-B		ST-C		TW		PB		TN		HY		OF-A		OF-B		OF-C	
	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX
<u>Grasses</u>																		
Agropyron dasystachyum	1.0	0.2	1.7	0.7	0.3	41.0							3.9	8.5	1.3	1.3	5.7	20.3
Agropyron smithii	0.7	0.2	4.7			1.3			0.8	4.7				2.0				
Agropyron subsecundum	0.3		0.5		0.3													
Bouteloua gracilis					0.3	0.2	20.0	9.0	13.0	2.7	17.7	5.0	9.5	3.8	22.7	14.7	8.7	0.3
Bromus inermis/pumpellianus	0.5	7.5	3.5	2.8														
Carex spp	0.9	5.8	2.5	1.7	16.0	0.5	8.8	3.1	2.7	1.8	4.7	7.3	0.8	2.4	5.3	3.7	12.3	1.3
Danthonia parryi	1.3		14.2	2.8														
Festuca campestris	0.7	10.7		20.0		0.2												
Festuca idahoensis	0.3		0.5	0.5	19.3	6.0												
Koeleria macrantha		0.1	0.2					2.0	3.3	0.2	1.0	0.5	0.5	0.7		0.7		
Phleum pratense	0.5																	
Poa pratensis	35.5	18.0	8.3	1.1														
Poa sandbergii							6.5	2.0						2.7				
Stipa comata	0.9			0.5			3.0	16.5	21.0	35.7	6.7	20.0	15.3	22.0	20.0	19.7	10.7	5.0
Stipa curtiseta					3.7													
<u>Forbs</u>																		
Achillea millefolium		2.5	3.4	1.8	1.3	0.2												1.0
Agoseris glauca	1.3		0.2			0.2												
Allium cernuum			0.2															
Allium textile							0.3											
Anemone cylindrica			0.3															
Anemone patens			0.3															
Antennaria spp.					0.2				0.2									
Artemisia frigida					2.3	4.3							3.8	1.3	0.2	1.0	0.3	
Artemisia ludoviciana		1.3		0.5														
Aster laevis	0.2	0.7		4.8														
Aster ericoides	1.0		1.7	0.3														
Aster spp.													0.8					

Stratum Species	ST-B		ST-C		TW		PB		TN		HY		OF-A		OF-B		OF-C	
	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX
Astragalus pectinatus					0.7										0.2			
Astragalus spp.		0.3																
Campanula rotundifolia	0.2		0.7	0.3														
Chrysopsis villosa									1.0	0.2				1.0				
Cirsium arvense		2.7																
Comandra pallida									2.0	0.7								
Erigeron caespitosus								0.8										
Gaillardia aristata	0.2			0.3														
Galium boreale	5.0	3.4	4.7	2.6														
Geranium viscosissimum	0.1	0.3	0.1															
Hedysarum alpinum	0.5	0.8	0.3															
Huechera richardsonii			0.2															
Lactuca pulchella		0.5																
Lappula echinata							16.8	0.1										
Lathyrus ochroleucus				0.1														
Liatris punctata									1.3	3.3								
Lithospermum spp.			0.2															
Lupinus argenteus	0.8		0.7	0.5														
Lygodesmia juncea							0.5								0.2	0.3		
Mamillaria vivipara							0.1											
Phlox hoodii					2.5						0.2	0.5	1.8	3.1		4.7		
Plantago patagonica															0.2		1.5	
Potentilla argentea	1.5		1.8															
Potentilla pensyllvanica					2.7					1.7								
Scenecio spp.			0.1	0.2														
Solidago missouriensis	1.0	1.5	2.0	1.2			0.1							0.2				
Sphaeralcea coccinea					0.7		2.0	1.0	0.2	0.3	1.8	1.3	0.7	1.2		0.3	2.3	1.0
Taraxacum officinale	0.3		0.2											0.2				
Thalictrum venulosum		1.3																
Thermopsis rhombifolia	2.2	0.2	2.7						1.0	5.7								
Tragopogon dubius	0.2		0.2		0.2	0.3		0.8						0.3				
Vicia americana	1.5	0.3	0.3	0.3														
Viola spp.			0.2	0.3														

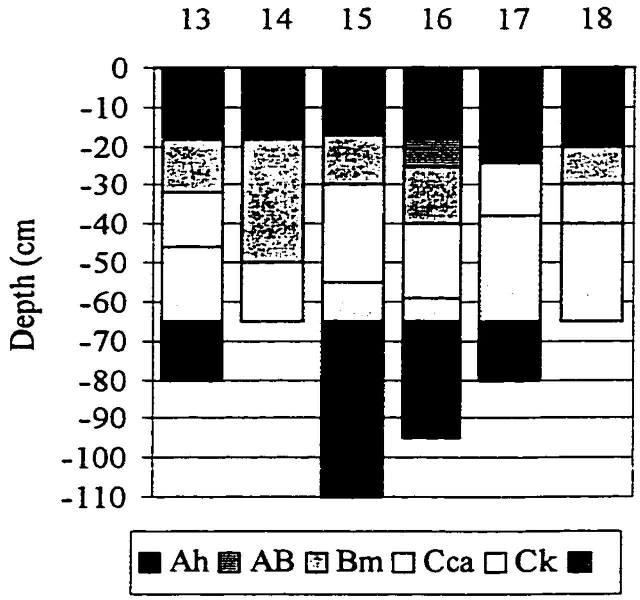
Stratum Species	ST-B		ST-C		TW		PB		TN		HY		OF-A		OF-B		OF-C	
	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX	GR	EX
<u>Shrubs</u>																		
Artemisia cana														0.2				
Eurotia lanata							7.3	12.3					0.3		1.0			1.3
Potentilla fruiticosa	0.2	3.8		3.0														
Symphoricarpos occidentalis		3.3																
Rubus idaeus		0.3																
Rosa woodsii	2.3	2.7	2.7	4.5														
<u>Low Vegetation</u>																		
Algae							0.5											
Lichen					0.7	0.2	0.4		8.3	1.3	0.7	0.5	8.5	1.2	5.3	4.0	6.3	1.2
Bryophyte		0.1		0.8														
Selaginella densa					3.7	0.5			26.7	23.3	49.7	32.0	36.2	28.1	18.3	29.3	21.7	1.2
Litter	34.0	32.0	44.0	49.0	33.0	48.0	9.8	51.0	13.0	16.0	10.0	23.3	2.3	19.0	9.7	16.0	6.3	66.3
Cattle Dung	6.4		1.8		0.7		0.3						2.1		0.5		1.2	
Bare Ground	0.5	0.2	0.2	0.2	7.3	0.3	25.0	1.3	6.7	7.7	7.7	5.3	14.7	4.7	16.0	2.3	23.3	1.5

ST = Stavely, TW = Twin River, PB = Picture Butte, TN = Turin, HY = Hays, OF = Onefour.
Names follow Moss (1994).

Figure A.2. Soil profile descriptions and series classification for all sites.

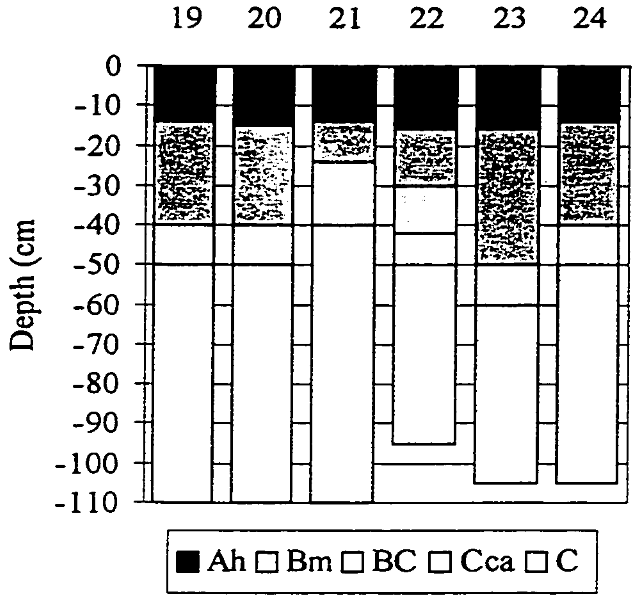


Onefour-A: CHINZ Solonetzic Brown Chernozem, loam, glaciolacustrine*
(grazed 1-6, exclosure 7-12)

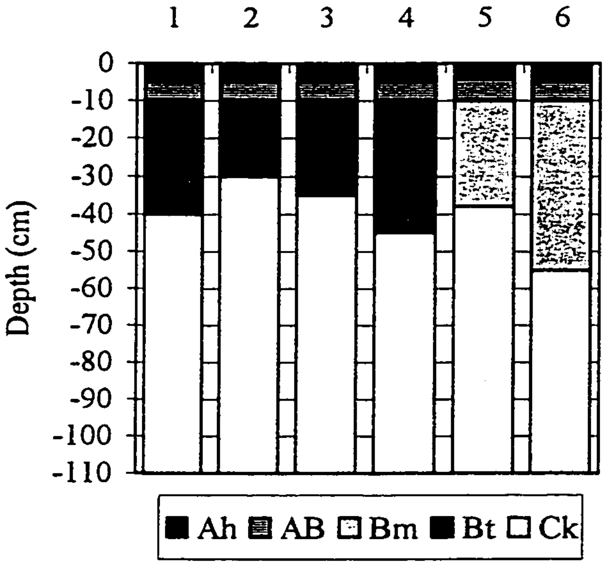


Onefour-B: COMREY Orthic Brown Chernozem, sandy-loam, glaciofluvial
(grazed 13-15, exclosure 16-18)

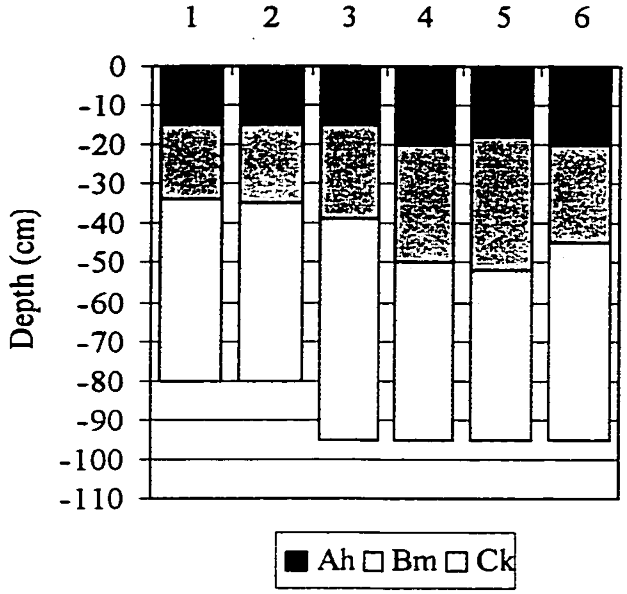
Onefour-C: MASINASIN Orthic Brown Chernozem, silty-loam, till
(grazed 19-21, exclosure 22-24)



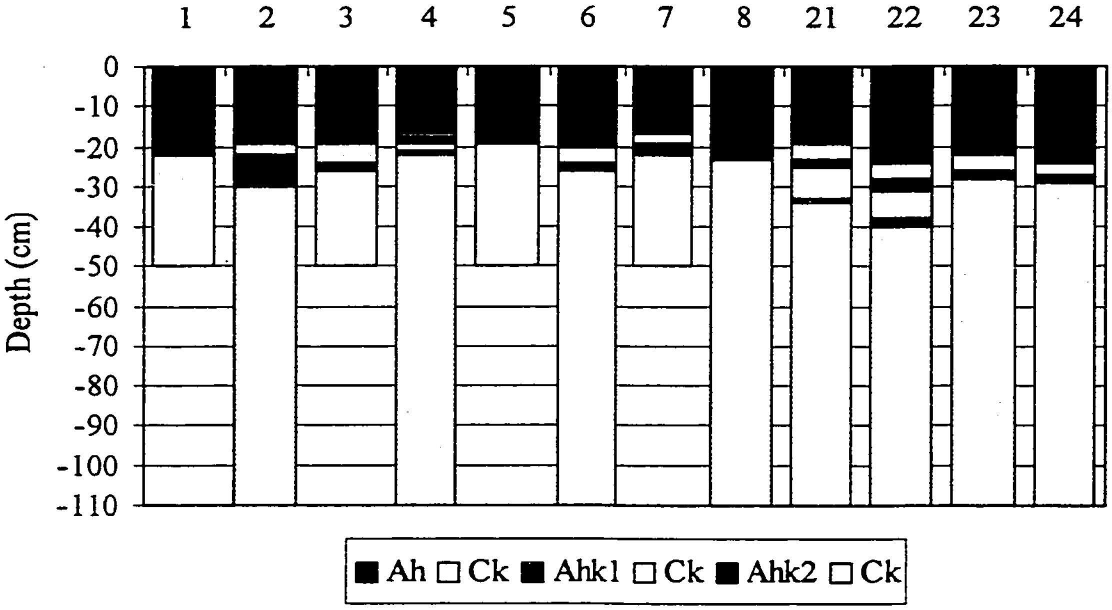
Hays - CRANFORD Orthic Brown Chernozem, clay-loam, glaciolacustrine over till
(grazed 1, 3, 5, exclosure 2, 4, 6)



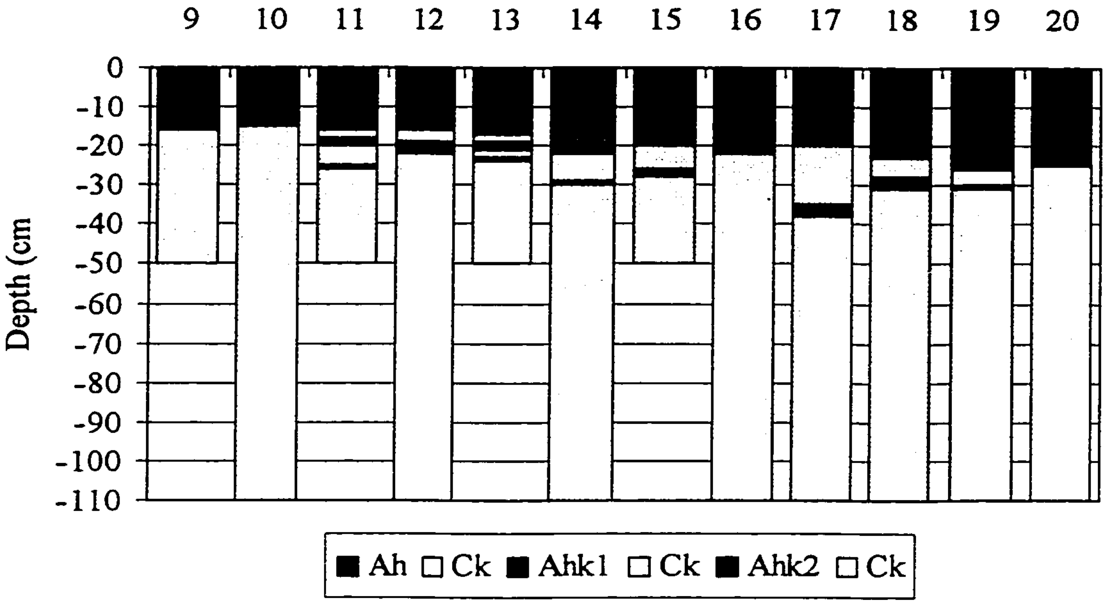
Turin - KESSLER Orthic Dark Brown Chernozem, sand, glaciofluvial
(grazed 1, 3, 5, exclosure 2, 4, 6)



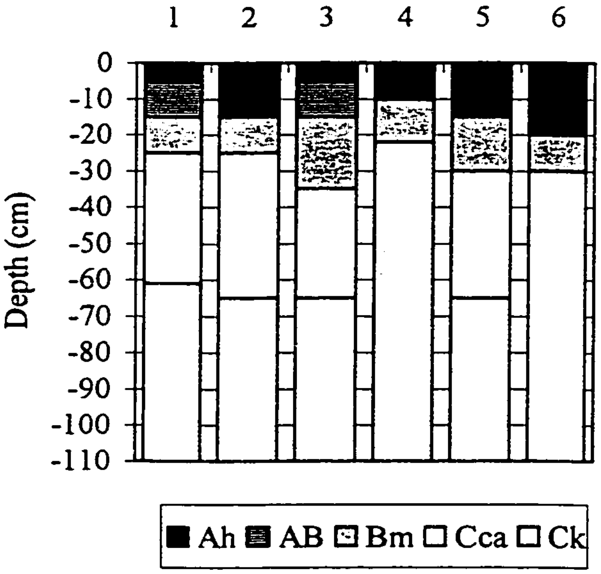
Picture Butte (A): LETH Orthic Dark Brown Chernozem, loam, glaciolacustrine**
(grazed 1-8, exclosure 21-24)



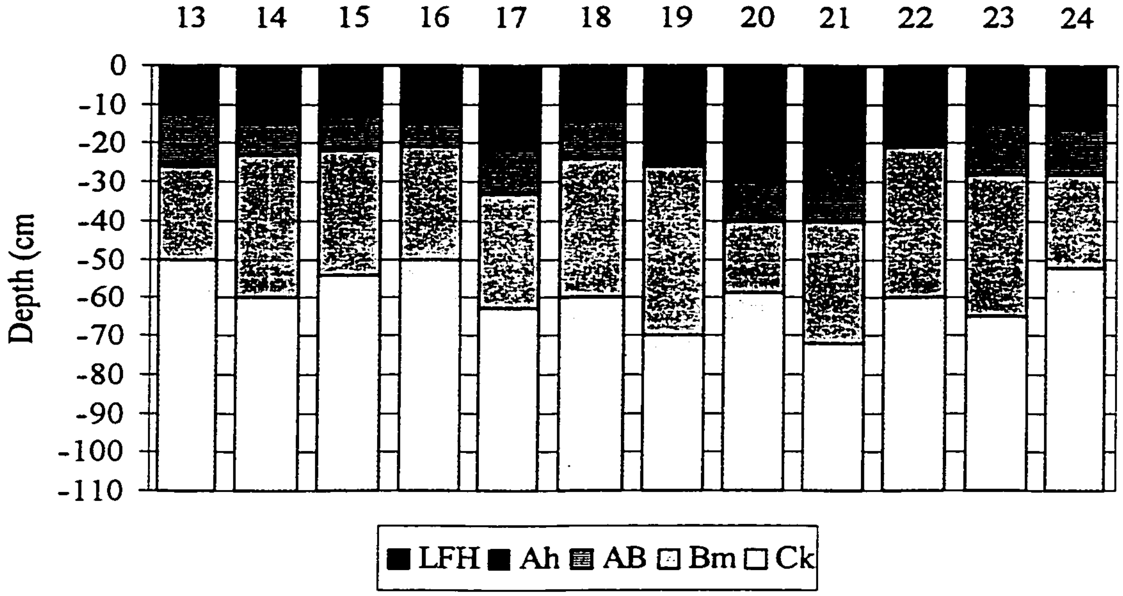
Picture Butte (N): LETH Orthic Dark Brown Chernozem, loam, glaciolacustrine**
(grazed 9-16, exclosure 17-20)



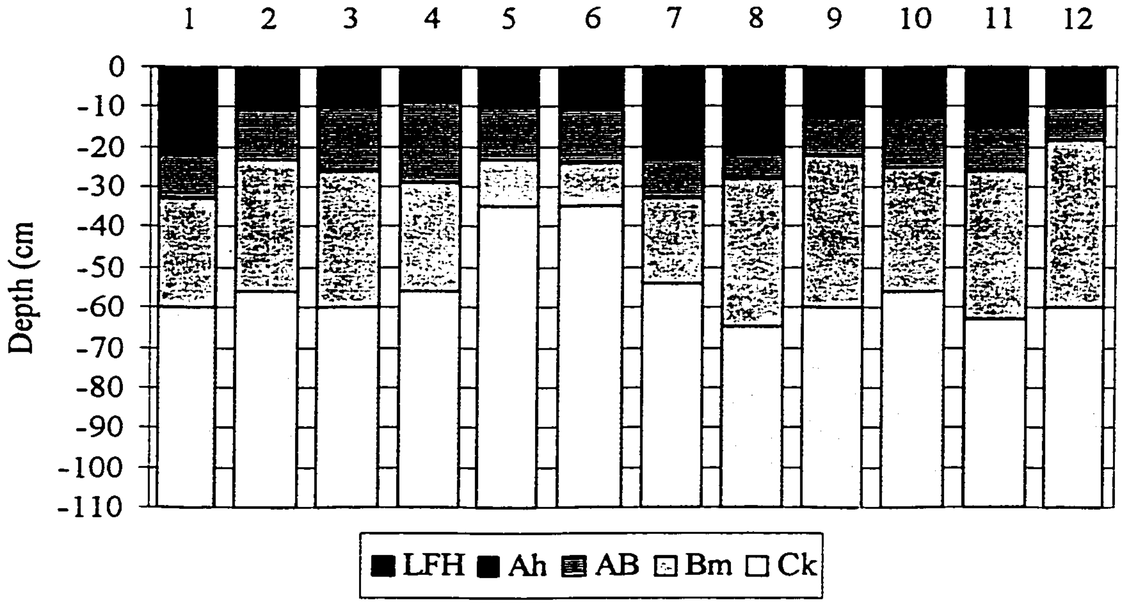
Twin River: LUPEN Orthic Dark Brown Chernozem, silty-loam, glaciolacustrine over till
(grazed 1, 3, 5, exclosure 2, 4, 6)



Stavely-B: DUNVARGAN Orthic Black Chernozem, silty-loam, till
(grazed 13-18, exclosure 19-24)



Stavely-C: DUNVARGAN Orthic Black Chernozem, silty-loam, till
(grazed 1-6, exclosure 7-12)



* SHOULD BE RECLASSIFIED - Site (originally classified by Moisey and Adams 1999) was not lacustrine, though CHINZ is intermediate between the other two possible soils in all other characteristics. Site is a complex of BUNTON Orthic Brown Chernozem, loam on glaciofluvial fan and STEVEVILLE Brown Solodized Solonetz, loam on till overlying bedrock based on AGRASID (1998) and field characteristics described using ACECSS (1987) criteria.

** SHOULD BE RECLASSIFIED - Site (originally classified by Moisey and Adams 1999) sandy with no distinct B horizon, and presence of buried horizons. Soil most likely a KESSLER-ZR Rego Dark Brown Chernozem, sandy-loam on glaciofluvial deposit based on series present in AGRASID (1998) and field characteristics described using ACECSS (1987) criteria.

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AGRASID. 1998. Agricultural region of Alberta soil inventory database, version 1.0. Alberta Agriculture, Food and Rural Development. Edmonton, AB.

Moisey, D. and B.W. Adams. 1999. Annual summary - rangeland benchmark network monitoring program within the grassland natural region. Unpublished report. Alberta Agriculture, Food and Rural Development - Public Lands Division. Lethbridge, AB.

Moss, E.H. 1994. Flora of Alberta. University of Toronto Press. Toronto, ON. 687 pp.

APPENDIX B. DATA ANALYSIS SUMMARIES

Table B.1. Statistical models and SAS procedures.

Chapter 2 - 2 X 3 and 2 X 2 Factorial designs

Levels of Regional (R) Factor = 3 (soil zone or texture), 2 (ecoregion)
Levels of Grazing (G) Factor = 2 (grazed, ungrazed)
Experimental Units = 18
Replicates = 2 - 5

$$\gamma_{ijkl} = \mu + R_i + G_j + RG_{ij} + \varepsilon_{ijk} + s_{(ij)l}$$

SAS code:

```
PROC MIXED;
     CLASS REGION GRAZING REPLICATE SUBSAMPLE;
     MODEL CARBON=REGION GRAZING REGION*GRAZING/DDFM=SATTERTH;
     RANDOM REPLICATE(REGION*GRAZING);
     LSMEANS REGION/PDIFF;
     LSMEANS REGION*GRAZING/PDIFF;
RUN;
```

Note: Error term the sum of pooled subsample variance (s_{ijk}) and replicate variance (ε_{ijk}) within each soil zone factor. The MIXED procedure was used to accommodate an unbalanced design and fixed factors. The LSMEANS REGION statement was not used for "ECOREGION" because there were only two.

Chapter 3 - Completely randomized design

Treatments = 4
Experimental Units = 24
Replicates = 4 - 8

$$\gamma_{ij} = \mu + \tau_i + \varepsilon_{ij}$$

SAS code:

```
PROC GLM;
     CLASS TREATMENT REPLICATE;
     MODEL CARBON=TREATMENT REPLICATE;
     RANDOM REPLICATE(TREATMENT)/TEST;
     MEANS TREATMENT/LSD;
RUN;
```

Note: Pooled subsample variance for the error term (quadrat was the experimental unit). GLM was used in place of ANOVA to accommodate the unbalanced number of units in each treatment.

SAS Institute. 2000. SAS/STAT User's Guide, Version 8. SAS Institute Inc. Cary, NC. 3884 pp.

Note 1: The following abbreviations apply to all subsequent tables (B.2. to B.18.):

GR = grazed treatment, EX = ungrazed treatment.

BL = black soil zone treatment, DB = dark brown soil treatment, BR = brown soil zone treatment.

ORG = organic texture class treatment, CRS = coarse texture class treatment, FIN = fine texture class treatment.

Note 2: P values for the grazing treatment, and the BL and ORG (same replicates from Stavely) treatments are not comparable among designs because the MIXED procedure in SAS calculates unique values for each model.

Table B.2. Factorial ANOVA table for vegetation carbon mass within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
		Main Effects			
Ecoregion	<0.001	Soil Zone	<0.001	Texture Class	<0.001
Grazing	0.069	Grazing	<0.001	Grazing	0.037
		Interaction			
Ecoregion X Grazing Interaction	0.241	Soil X Grazing Interaction	<0.001	Texture X Grazing Interaction	0.293
		L.S.D. Comparisons			
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	<0.001	CRS ≠ FIN	0.825
		DB ≠ BR	<0.001	FIN ≠ ORG	<0.001
Fescue GR ≠ EX	0.070	BL GR ≠ EX	<0.001	ORG GR ≠ EX	0.033
Mixed GR ≠ EX	0.531	DB GR ≠ EX	0.003	CRS GR ≠ EX	0.417
		BR GR ≠ EX	0.987	FIN GR ≠ EX	0.574

Table B.3. Factorial ANOVA table for litter carbon mass within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
Main Effects					
Ecoregion	<0.001	Soil Zone	<0.001	Texture Class	<0.001
Grazing	0.002	Grazing	<0.001	Grazing	0.002
Interaction					
Ecoregion X Grazing Interaction	0.037	Soil X Grazing Interaction	0.027	Texture X Grazing Interaction	0.046
L.S.D. Comparisons					
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	<0.001	CRS ≠ FIN	0.468
		DB ≠ BR	0.138	FIN ≠ ORG	0.001
Fescue GR ≠ EX	0.003	BL GR ≠ EX	0.001	ORG GR ≠ EX	0.002
Mixed GR ≠ EX	0.257	DB GR ≠ EX	0.096	CRS GR ≠ EX	0.354
		BR GR ≠ EX	0.410	FIN GR ≠ EX	0.169

Table B.4. Factorial ANOVA table for crowns carbon mass within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
Main Effects					
Ecoregion	0.595	Soil Zone	0.059	Texture Class	0.178
Grazing	0.152	Grazing	0.114	Grazing	0.172
Interaction					
Ecoregion X Grazing Interaction	0.124	Soil X Grazing Interaction	0.061	Texture X Grazing Interaction	0.055
L.S.D. Comparisons					
		BL ≠ DB	0.021	ORG ≠ CRS	0.085
		BL ≠ BR	0.253	CRS ≠ FIN	0.857
		DB ≠ BR	0.116	FIN ≠ ORG	0.152
Fescue GR ≠ EX	0.071	BL GR ≠ EX	0.014	ORG GR ≠ EX	0.019
Mixed GR ≠ EX	0.918	DB GR ≠ EX	0.821	CRS GR ≠ EX	0.616
		BR GR ≠ EX	0.988	FIN GR ≠ EX	0.376

Table B.5. Factorial ANOVA table for macro-organic matter carbon mass at the 0 to 10 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
		Main Effects			
Ecoregion	0.014	Soil Zone	0.001	Texture Class	<0.001
Grazing	0.657	Grazing	0.557	Grazing	0.464
		Interaction			
Ecoregion X Grazing Interaction	0.512	Soil X Grazing Interaction	0.574	Texture X Grazing Interaction	0.417
		L.S.D. Comparisons			
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	0.001	CRS ≠ FIN	0.033
		DB ≠ BR	0.391	FIN ≠ ORG	0.001
Fescue GR ≠ EX	0.500	BL GR ≠ EX	0.349	ORG GR ≠ EX	0.262
Mixed GR ≠ EX	0.854	DB GR ≠ EX	0.745	CRS GR ≠ EX	0.532
		BR GR ≠ EX	0.646	FIN GR ≠ EX	0.618

Table B.6. Factorial ANOVA table for macro-organic matter carbon mass at the 10 to 35 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
		Main Effects			
Ecoregion	0.025	Soil Zone	0.001	Texture Class	<0.001
Grazing	0.890	Grazing	0.917	Grazing	0.815
		Interaction			
Ecoregion X Grazing Interaction	0.863	Soil X Grazing Interaction	0.801	Texture X Grazing Interaction	0.883
		L.S.D. Comparisons			
		BL ≠ DB	0.001	ORG ≠ CRS	0.001
		BL ≠ BR	0.001	CRS ≠ FIN	0.724
		DB ≠ BR	0.567	FIN ≠ ORG	<0.001
Fescue GR ≠ EX	0.847	BL GR ≠ EX	0.699	ORG GR ≠ EX	0.699
Mixed GR ≠ EX	0.977	DB GR ≠ EX	0.641	CRS GR ≠ EX	0.798
		BR GR ≠ EX	0.776	FIN GR ≠ EX	0.845

Table B.7. Factorial ANOVA table for macro-organic matter carbon mass at the 35 to 65 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
Main Effects					
Ecoregion	0.529	Soil Zone	0.998	Texture Class	0.840
Grazing	0.393	Grazing	0.482	Grazing	0.453
Interaction					
Ecoregion X Grazing Interaction	0.291	Soil X Grazing Interaction	0.331	Texture X Grazing Interaction	0.418
L.S.D. Comparisons					
		BL ≠ DB	0.999	ORG ≠ CRS	0.802
		BL ≠ BR	0.962	CRS ≠ FIN	0.563
		DB ≠ BR	0.960	FIN ≠ ORG	0.789
Fescue GR ≠ EX	0.242	BL GR ≠ EX	0.175	ORG GR ≠ EX	0.178
Mixed GR ≠ EX	0.857	DB GR ≠ EX	0.496	CRS GR ≠ EX	0.993
		BR GR ≠ EX	0.736	FIN GR ≠ EX	0.776

Table B.8. Factorial ANOVA table for macro-organic matter carbon mass at the 0 to 65 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
Main Effects					
Ecoregion	0.016	Soil Zone	<0.001	Texture Class	<0.001
Grazing	0.619	Grazing	0.459	Grazing	0.382
Interaction					
Ecoregion X Grazing Interaction	0.493	Soil X Grazing Interaction	0.458	Texture X Grazing Interaction	0.331
L.S.D. Comparisons					
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	<0.001	CRS ≠ FIN	0.158
		DB ≠ BR	0.297	FIN ≠ ORG	<0.001
Fescue GR ≠ EX	0.468	BL GR ≠ EX	0.197	ORG GR ≠ EX	0.167
Mixed GR ≠ EX	0.869	DB GR ≠ EX	0.934	CRS GR ≠ EX	0.556
		BR GR ≠ EX	0.861	FIN GR ≠ EX	0.694

Table B.9. Factorial ANOVA table for fine soil organic carbon at the 0 to 10 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
Main Effects					
Ecoregion	<0.001	Soil Zone	<0.001	Texture Class	<0.001
Grazing	0.397	Grazing	0.144	Grazing	0.091
Interaction					
Ecoregion X Grazing Interaction	0.660	Soil X Grazing Interaction	0.667	Texture X Grazing Interaction	0.565
L.S.D. Comparisons					
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	<0.001	CRS ≠ FIN	0.022
		DB ≠ BR	0.224	FIN ≠ ORG	<0.001
Fescue GR ≠ EX	0.431	BL GR ≠ EX	0.175	ORG GR ≠ EX	0.117
Mixed GR ≠ EX	0.719	DB GR ≠ EX	0.520	CRS GR ≠ EX	0.638
		BR GR ≠ EX	0.653	FIN GR ≠ EX	0.420

Table B.10. Factorial ANOVA table for fine soil organic carbon at the 10 to 35 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
Main Effects					
Ecoregion	<0.001	Soil Zone	<0.001	Texture Class	<0.001
Grazing	0.495	Grazing	0.020	Grazing	0.122
Interaction					
Ecoregion X Grazing Interaction	0.489	Soil X Grazing Interaction	0.003	Texture X Grazing Interaction	0.117
L.S.D. Comparisons					
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	<0.001	CRS ≠ FIN	0.577
		DB ≠ BR	0.002	FIN ≠ ORG	<0.001
Fescue GR ≠ EX	0.400	BL GR ≠ EX	<0.001	ORG GR ≠ EX	0.031
Mixed GR ≠ EX	0.993	DB GR ≠ EX	0.704	CRS GR ≠ EX	0.694
		BR GR ≠ EX	0.772	FIN GR ≠ EX	0.941

Table B.11. Factorial ANOVA table for fine soil organic carbon at the 35 to 65 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
		Main Effects			
Ecoregion	<0.001	Soil Zone	<0.001	Texture Class	<0.001
Grazing	0.812	Grazing	0.674	Grazing	0.786
		Interaction			
Ecoregion X Grazing Interaction	0.646	Soil X Grazing Interaction	0.662	Texture X Grazing Interaction	0.599
		L.S.D. Comparisons			
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	<0.001	CRS ≠ FIN	0.196
		DB ≠ BR	0.091	FIN ≠ ORG	<0.001
Fescue GR ≠ EX	0.891	BL GR ≠ EX	0.613	ORG GR ≠ EX	0.632
Mixed GR ≠ EX	0.551	DB GR ≠ EX	0.394	CRS GR ≠ EX	0.314
		BR GR ≠ EX	0.600	FIN GR ≠ EX	0.848

Table B.12. Factorial ANOVA table for fine soil organic carbon at the 0 to 65 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
		Main Effects			
Ecoregion	<0.001	Soil Zone	<0.001	Texture Class	<0.001
Grazing	0.987	Grazing	0.939	Grazing	0.996
		Interaction			
Ecoregion X Grazing Interaction	0.764	Soil X Grazing Interaction	0.542	Texture X Grazing Interaction	0.646
		L.S.D. Comparisons			
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	<0.001	CRS ≠ FIN	0.139
		DB ≠ BR	0.032	FIN ≠ ORG	<0.001
Fescue GR ≠ EX	0.861	BL GR ≠ EX	0.440	ORG GR ≠ EX	0.496
Mixed GR ≠ EX	0.785	DB GR ≠ EX	0.452	CRS GR ≠ EX	0.558
		BR GR ≠ EX	0.762	FIN GR ≠ EX	0.767

Table B.13. Factorial ANOVA table for bulk density at the 0 to 10 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
Main Effects					
Ecoregion	<0.001	Soil Zone	<0.001	Texture Class	<0.001
Grazing	0.349	Grazing	0.173	Grazing	0.076
Interaction					
Ecoregion X Grazing Interaction	0.965	Soil X Grazing Interaction	0.602	Texture X Grazing Interaction	0.743
L.S.D. Comparisons					
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	<0.001	CRS ≠ FIN	0.003
		DB ≠ BR	0.128	FIN ≠ ORG	<0.001
Fescue GR ≠ EX	0.580	BL GR ≠ EX	0.297	ORG GR ≠ EX	0.183
Mixed GR ≠ EX	0.396	DB GR ≠ EX	0.982	CRS GR ≠ EX	0.170
		BR GR ≠ EX	0.170	FIN GR ≠ EX	0.613

Table B.14. Factorial ANOVA table for bulk density at the 10 to 35 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
Main Effects					
Ecoregion	<0.001	Soil Zone	<0.001	Texture Class	<0.001
Grazing	0.574	Grazing	0.478	Grazing	0.485
Interaction					
Ecoregion X Grazing Interaction	0.661	Soil X Grazing Interaction	0.556	Texture X Grazing Interaction	0.645
L.S.D. Comparisons					
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	<0.001	CRS ≠ FIN	0.240
		DB ≠ BR	0.115	FIN ≠ ORG	0.001
Fescue GR ≠ EX	0.540	BL GR ≠ EX	0.277	ORG GR ≠ EX	0.304
Mixed GR ≠ EX	0.913	DB GR ≠ EX	0.723	CRS GR ≠ EX	0.893
		BR GR ≠ EX	0.736	FIN GR ≠ EX	0.902

Table B.15. Factorial ANOVA table for bulk density at the 35 to 65 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
		Main Effects			
Ecoregion	0.017	Soil Zone	<0.001	Texture Class	0.004
Grazing	0.611	Grazing	0.295	Grazing	0.492
		Interaction			
Ecoregion X Grazing Interaction	0.533	Soil X Grazing Interaction	0.962	Texture X Grazing Interaction	0.366
		L.S.D. Comparisons			
		BL ≠ DB	<0.001	ORG ≠ CRS	0.002
		BL ≠ BR	0.005	CRS ≠ FIN	0.486
		DB ≠ BR	0.015	FIN ≠ ORG	0.006
Fescue GR ≠ EX	0.943	BL GR ≠ EX	0.674	ORG GR ≠ EX	0.723
Mixed GR ≠ EX	0.337	DB GR ≠ EX	0.402	CRS GR ≠ EX	0.130
		BR GR ≠ EX	0.529	FIN GR ≠ EX	0.586

Table B.16. Factorial ANOVA table for fine soil carbon concentration at the 0 to 10 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
		Main Effects			
Ecoregion	<0.001	Soil Zone	<0.001	Texture Class	<0.001
Grazing	0.816	Grazing	0.426	Grazing	0.314
		Interaction			
Ecoregion X Grazing Interaction	0.789	Soil X Grazing Interaction	0.331	Texture X Grazing Interaction	0.183
		L.S.D. Comparisons			
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	<0.001	CRS ≠ FIN	0.008
		DB ≠ BR	0.548	FIN ≠ ORG	<0.001
Fescue GR ≠ EX	0.759	BL GR ≠ EX	0.138	ORG GR ≠ EX	0.061
Mixed GR ≠ EX	0.976	DB GR ≠ EX	0.671	CRS GR ≠ EX	0.995
		BR GR ≠ EX	0.937	FIN GR ≠ EX	0.689

Table B.17. Factorial ANOVA table for fine soil carbon concentration at the 10 to 35 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
		Main Effects			
Ecoregion	<0.001	Soil Zone	<0.001	Texture Class	<0.001
Grazing	0.326	Grazing	0.005	Grazing	0.006
		Interaction			
Ecoregion X Grazing Interaction	0.337	Soil X Grazing Interaction	0.002	Texture X Grazing Interaction	0.003
		L.S.D. Comparisons			
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	<0.001	CRS ≠ FIN	0.442
		DB ≠ BR	0.179	FIN ≠ ORG	<0.001
Fescue GR ≠ EX	0.237	BL GR ≠ EX	0.001	ORG GR ≠ EX	0.001
Mixed GR ≠ EX	0.984	DB GR ≠ EX	0.749	CRS GR ≠ EX	0.976
		BR GR ≠ EX	0.772	FIN GR ≠ EX	0.989

Table B.18. Factorial ANOVA table for fine soil carbon concentration at the 35 to 65 cm increment within three experimental designs.

2 x 2 Factorial by Ecoregions	P Value	2 x 3 Factorial by Soil Zone	P Value	2 x 3 Factorial by Texture Class	P Value
		Main Effects			
Ecoregion	<0.001	Soil Zone	<0.001	Texture Class	<0.001
Grazing	0.800	Grazing	0.625	Grazing	0.702
		Interaction			
Ecoregion X Grazing Interaction	0.696	Soil X Grazing Interaction	0.784	Texture X Grazing Interaction	0.590
		L.S.D. Comparisons			
		BL ≠ DB	<0.001	ORG ≠ CRS	<0.001
		BL ≠ BR	<0.001	CRS ≠ FIN	0.170
		DB ≠ BR	0.320	FIN ≠ ORG	<0.001
Fescue GR ≠ EX	0.933	BL GR ≠ EX	0.804	ORG GR ≠ EX	0.792
Mixed GR ≠ EX	0.581	DB GR ≠ EX	0.453	CRS GR ≠ EX	0.251
		BR GR ≠ EX	0.653	FIN GR ≠ EX	0.975

APPENDIX C. ADDITIONAL STUDY AREA CHARACTERISTICS

CORRELATES BETWEEN ALBERTA RANGE BENCHMARK SITES

Data for these analyses taken from Moisey and Adams (1999).

Elevation is the best overall predictor of herbaceous annual net primary production (ANPP) and litter standing crop within the 49° to 51° N latitude zone of prairie grasslands (Table C.1). July mean temperature is superior to annual precipitation as a predictor of both ANPP and litter standing crop. The influence of elevation represents changes in the ratio of precipitation/evaporation as an interaction between annual precipitation and July mean temperature. The influence of growing season length is indicated by the relationship between ANPP and January mean temperature.

Table C.1. Correlation matrix of monitored variables at all AAFRD benchmark sites in southern Alberta (n=29). (* $P \leq 0.05$)

	Elevation	Precipitation	Litter	ANPP
Precipitation	0.826*	1.000	- -	- -
Litter	0.762*	0.607	1.000	- -
ANPP	0.791*	0.696*	0.882*	1.000
Jul. mean T	-0.784*	- -	-0.615	-0.694*
Jan. mean T	0.576	- -	0.490	0.650

Table C.2. Correlation matrix of monitored variables at all mixed prairie AAFRD benchmark sites in southern Alberta (n=21). (* $P \leq 0.05$)

	Elevation	Precipitation	Litter	ANPP
Precipitation	0.339	1.000	- -	- -
Litter	0.300	0.534	1.000	- -
ANPP	0.295	0.668*	0.950*	1.000
Jul. mean T	-0.095	- -	-0.214	-0.281
Jan. mean T	0.437	- -	0.505	0.520

Precipitation is the best predictor of ANPP and litter mass within mixed prairie between 49° and 51° N latitude (Table C.2). January mean temperature was likely related to growing season length, with more production occurring in warmer zones. The relationship between ANPP and litter standing crop is more strongly correlated in mixed prairie, as litter has a positive effect on production. The cooling effect of litter becomes an inhibitor of production in fescue prairie at higher elevations, and results in the smaller correlation coefficient for all sites combined.

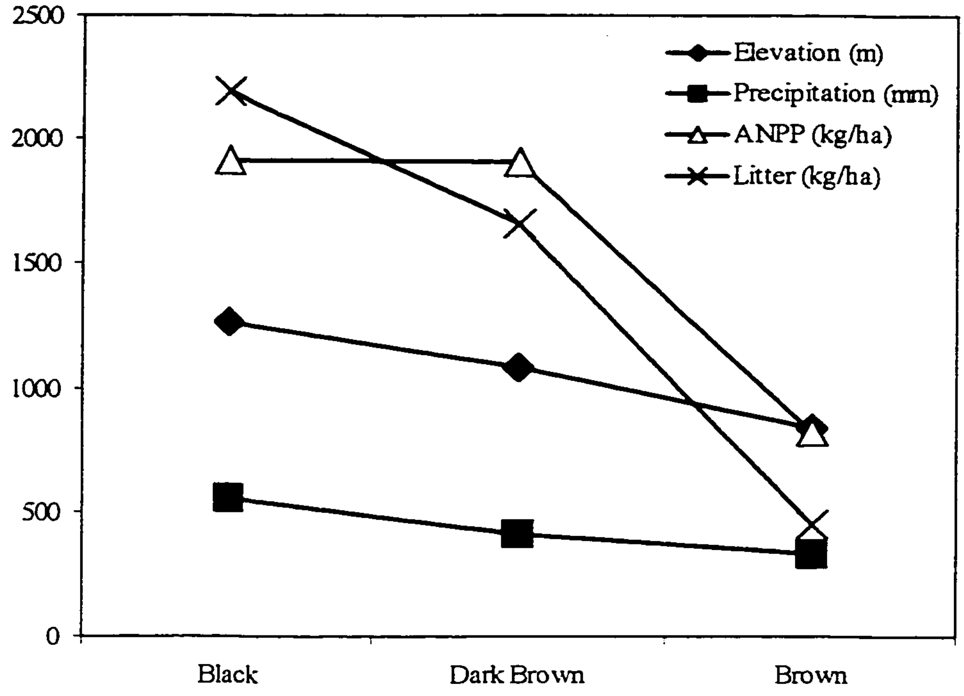

Figure C.1. Relationship between mean values for four variables along the environmental gradient from west (black soils) to east (brown soils).

Transition between fescue and mixed prairie occurs in the dark brown soil zone. Between 450 to 500 mm precipitation, and 1050 to 1150 m elevation, litter accumulations begin to have a negative effect on ANPP due to decreased soil temperature during growing season and competition for nitrogen with fungal decomposers of litter. In the mixed prairie precipitation is the limiting factor and litter standing crop is tightly linked to ANPP.

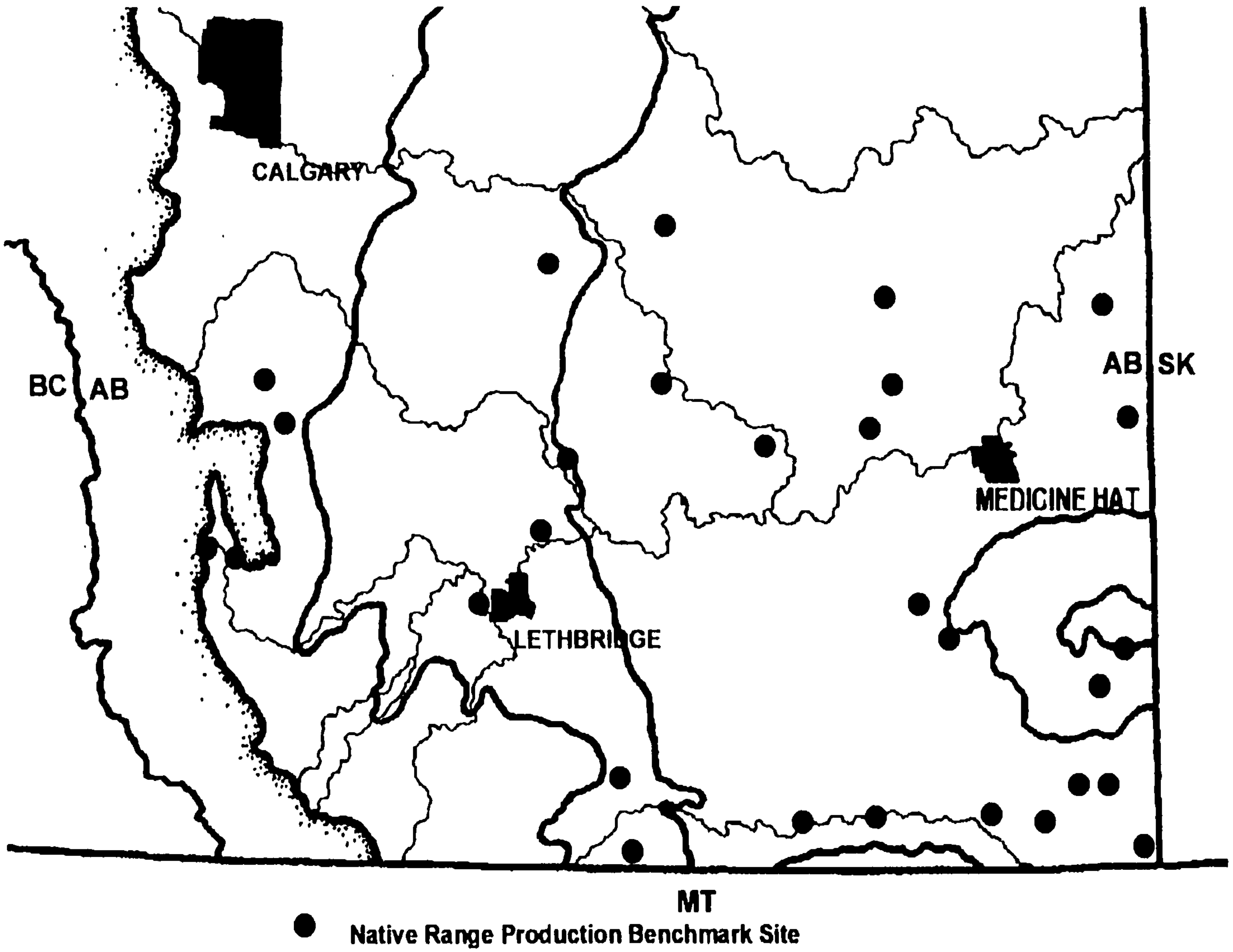

Figure C.2. Approximate location of AAFRD native range production benchmark sites in southern Alberta.

Table C.3. Known and suspected C_4 plants in Alberta.

Species	Life History	Habitat	Notes
Grasses:			
Aristida longiseta Steud.	perennial	warm dry prairie	native, rare
Bouteloua gracilis (H.B.K.) Lag.	perennial	warm dry prairie	native, common
Calamovilfa longifolia Hack.	perennial	sand dunes	native, common
Distichlis stricta (Torr.) Rydb.	perennial	saline prairie	native, common
Muhlenbergia asperifolia Nees & Mey.	perennial	saline meadow	native, uncommon
Muhlenbergia cuspidata (Torr.) Rydb.	perennial	warm dry prairie	native, uncommon
Muhlenbergia glomerata (Willd.) Trin.	perennial	acid bog and fen	native, uncommon
Muhlenbergia recemosa (Michx.) BSP	perennial	sand dunes	native, rare
Muhlenbergia richardsonis (Trin.) Rydb.	perennial	prairie & meadow	native, uncommon
Schedonnardus paniculatus (Nutt.) Trel.	perennial	disturbed soil	native, uncommon
Spartina pectinata Link.	perennial	saline wetlands	native, uncommon
Sporobolus cryptandrus (Torr.) Gray	perennial	sand dunes	native, uncommon
Schizachyrium scoparium Michx.	perennial	warm dry prairie	native, rare
Eragrostis cilianensis (All.) Lutati.	annual	disturbed soil	exotic, uncommon
Digitaria ischaemum Schreb.	annual	urban turf	exotic, rare
Digitaria sanguinalis (L.) Scop.	annual	disturbed soil	exotic, rare
Echinochloa crusgalli (L.) Beauv.	annual	disturbed soil	exotic, common
Panicum capillare L.	annual	disturbed soil	exotic, uncommon
Panicum miliaceum L.	annual	disturbed soil	exotic, uncommon
Setaria glauca (L.) Beauv.	annual	disturbed soil	exotic, common
Setaria viridis (L.) Beauv.	annual	disturbed soil	exotic, common
Forbs:			
Atriplex rosea L.	annual	disturbed soil	exotic, uncommon
Atriplex spp. ?	annual/perennial	saline/disturbed	native
Axyris amaranthoides L.	annual	disturbed soil	exotic, common
Chenopodium spp. ?	annual	saline/disturbed	native/exotic
Kochia scoparia (L.) Schrad.	annual	disturbed soil	exotic, common
Salicornia rubra A. Nels. ?	annual	saline meadow	native, common
Salsola kali L.	annual	dry disturbed soil	exotic, common
Sarcobactus vermiculatus L. ?	perennial	saline prairie	native, uncommon
Suaeda calceoliformis (Hook.) Moq.	annual	saline meadow	native, common
Suaeda moquinii (Torr.) Greene	perennial	saline meadow	native, rare
Suckleya suckleyanna (Torr.) Rydb. ?	annual	saline meadow	native uncommon
Amaranthus retroflexus L.	annual	disturbed soil	exotic, common
Amaranthus spp. ?	annual	disturbed soil	native
Portuclaca oleracea L.	annual	disturbed soil	exotic, common
Euphorbia spp. ?	annual/perennial	disturbed soil	native/exotic
Senecio spp. ?	perennial	prairie	native

Native forb species suspected C_4 for which no published $\delta^{13}C$ values were found are indicated by ? following the name or genus.
Adapted from Bender (1971), Waller and Lewis (1979) and Moss (1994).

Table C.4. Comparisons of acidified (6 M HCl) and non-acidified macro-organic matter (MOM) carbon and nitrogen percent concentration and $\delta^{13}C$ from Picture Butte.

Sample Number	Carbon		Nitrogen		$\delta^{13}C$	
	Acidified	Non-Acidified	Acidified	Non-Acidified	Acidified	Non-Acidified
G0022	17.37	18.16	1.28	1.28	-24.54	-24.92
G0023	11.83	13.12	0.71	0.77	-22.94	-22.58
G0024	17.64	18.11	1.01	0.95	-22.15	-21.71
G0025	16.54	16.67	0.88	0.83	-23.45	-22.29
G0026	19.12	19.88	0.99	0.97	-22.92	-21.78
G0027	18.66	19.81	1.12	1.07	-21.75	-21.48
G0028	23.89	24.16	1.45	1.43	-21.07	-20.09
G0029	22.50	22.96	1.38	1.36	-20.65	-20.41
G0030	27.47	26.55	1.46	1.32	-22.70	-22.28
G0031	19.74	20.17	1.08	1.00	-22.90	-21.99
G0101	38.27	39.28	2.11	2.14	-19.07	-19.37
G0102	23.62	22.79	1.14	1.12	-20.36	-20.53
G0103	28.23	29.02	1.32	1.29	-22.60	-22.43
G0104	20.59	20.78	1.13	1.06	-21.28	-20.64
G0105	22.41	23.50	1.22	1.18	-20.89	-20.48
G0106	20.84	22.88	1.16	1.19	-20.93	-20.43
G0107	20.48	21.71	1.17	1.17	-21.41	-20.33
G0108	20.30	21.24	1.12	1.11	-22.38	-21.74
G0109	19.35	19.84	0.90	0.89	-23.65	-22.68
G0110	22.46	22.38	1.20	1.09	-24.28	-23.28
G0149	28.04	28.63	1.09	1.08	-24.53	-23.55
G0150	30.99	32.35	1.30	1.30	-23.91	-23.03
G0151	24.89	26.73	1.27	1.26	-21.53	-20.96
G0152	24.84	25.01	1.30	1.25	-20.85	-20.70
G0153	29.95	31.12	1.59	1.58	-22.75	-22.24
G0154	34.09	35.43	1.53	1.58	-25.85	-26.11
G0155	32.91	33.40	1.50	1.44	-25.31	-25.10
Mean	23.59	24.28	1.24	1.21	-22.47	-21.97
Variance	36.44	37.31	0.07	0.08	2.67	2.66
Paired	t stat =.	-10.06	t stat =	3.03	t stat =	-5.73
t-test	t crit 2 tailed =	2.06	t crit 2 tailed =	2.06	t crit 2 tailed =	2.06
Results	P value =	1.86×10^{-10}	P value =	0.01	P value =	4.91×10^{-6}

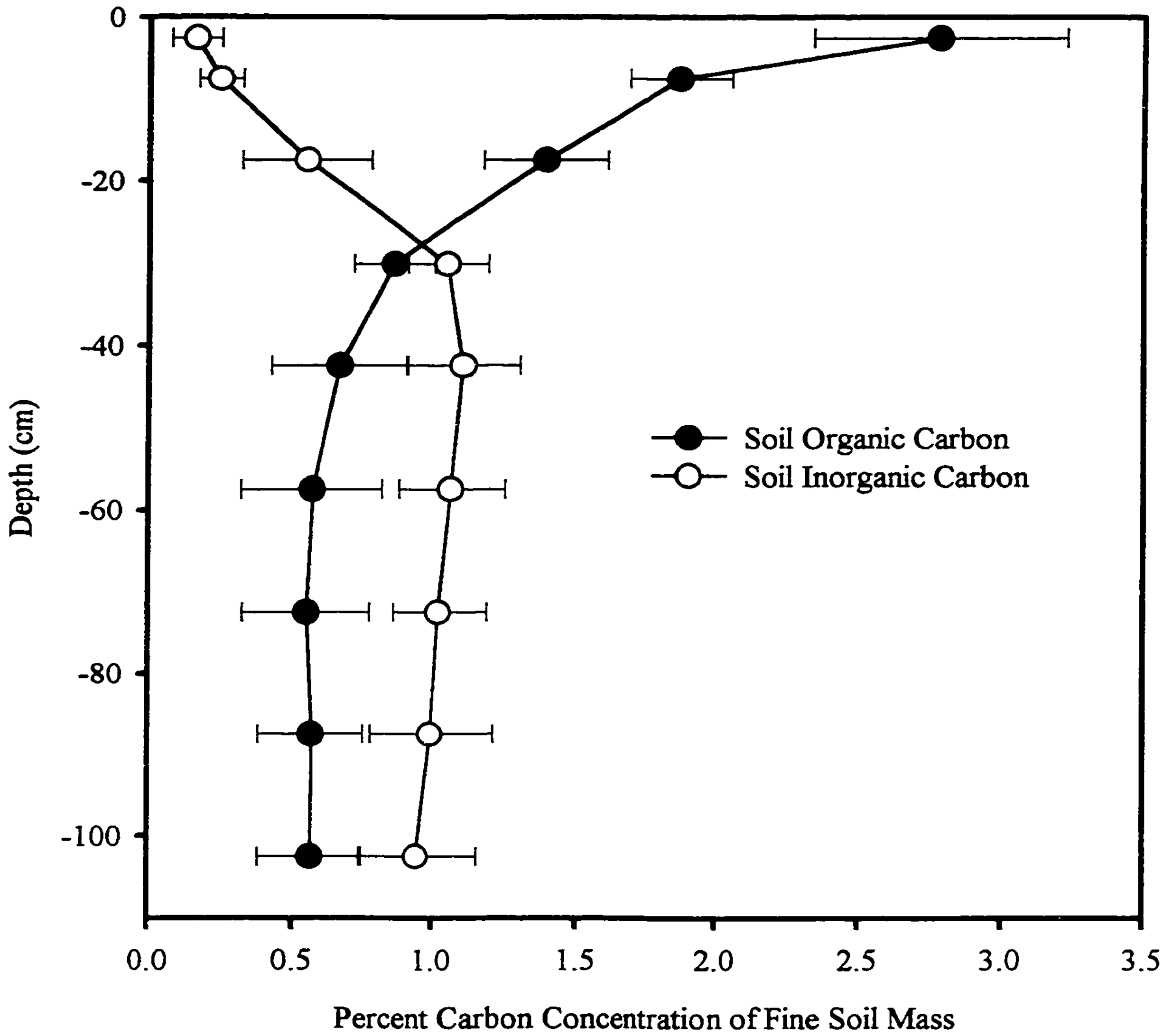

Figure C.3. Comparison of soil organic and inorganic carbon vertical distribution at Picture Butte.
Error bars are standard deviations.

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