Cultivation and Grazing Impacts on Extracellular Enzyme Activity in Alberta Grasslands

by

Dauren Kaliaskar

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Department of Renewable Resources
University of Alberta

Abstract

Grasslands cover a quarter of the planet's terrestrial surface and constitute 70% of the world's agricultural land area. Grasslands provide clean water, facilitate effective nutrient cycling, and provide necessary habitat and forage for livestock and wildlife. In addition, grasslands have the potential to mitigate greenhouse gas emissions by sequestering carbon (C) and nitrogen (N) in soil. Grazing is one of the most common uses of grasslands and may alter C and nutrient mineralisation. Therefore, understanding the impact of different grazing systems (i.e. continuous and rotational) on C and nutrient cycling, as well as past management practices (cultivation), climate and soil properties, is of significant interest. This study examined the role of grazing systems on soil biogeochemical cycling by measuring extracellular enzyme activity (EEA), which is an indicator of soil biological activity. The activities of six soil extracellular enzymes were analysed that are involved in C (xylosidase, β-glucosidase, cellobiosidase), nitrogen (N) (N-acetyl-β glucosaminidase, urease), and phosphorus (phosphatase) cycling. Soil samples were tested from 12 pairs of field sites (i.e., ranches) with varying grazing practices (i.e., AMP or non-AMP grazing, with divergent stocking rates) for at least five years prior. An information theoretic model selection approach was used to determine those independent variables (disturbance regime, climate, soil) that explained the variability of each EEA. Results showed that a long resting period (mainly present in AMP ranches) increased β-glucosidase activity, while a high stocking rate increased urease activity. In contrast, soils with known previous cultivation had lower xylosidase and phosphatase activities, suggesting a legacy effect of previous cropping. The main environmental factors regulating enzyme activity were available soil N and climatic aridity. Overall, grazing practices, as represented by grazing systems, appear capable of altering C and nutrient cycling, with AMP grazing increasing C mineralisation in

these Alberta grasslands. This finding highlights the importance of grazing practices that maintain soil biological activity.

Preface

This thesis is an original work by Dauren Kaliaskar. No part of this thesis has been previously published. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, Project Name "Grassland soil organic carbon, greenhouse gas emissions, water infiltration and biodiversity under grazing management practices in Canadian grasslands", No. Pro00078581, January 5, 2017.

"We might say that the earth has the spirit of growth: that its flesh is the soil ..."

- Leonardo da Vinci

To my beloved mother, Zhanna Kaliaskarova Yerbatirovna,

who sacrificed a lot for my best future,

with love, your son

Acknowledgments

Table of Contents

List of Tables

List of Figures

List of Symbols and Abbreviations

AMP – adaptive multi-paddock grazing system;

BAG – β-glucosidase;

C – carbon;

Cello – β-D-cellobiosidase;

CG – continuous grazing;

EEA – extracellular enzyme activity;

geomean – geometrical mean;

ha – hectare**;**

hr – hour**;**

MBC – microbial biomass carbon**;**

MBN – microbial biomass nitrogen;

N – nitrogen**;**

NAG – n-acetyl-β-glucosaminidase;

nmol – nanomole;

nAMP – grazing systems which are defined as non adaptive multi paddock**;**

P – phosphorus**;**

Phos – phosphatase;

RG – rotational grazing;

SOC – soil organic carbon;

SOM – soil organic matter;

Xylo – β-1,4-xylosidase;

μmol – micromole.

Chapter 1. Grazing System Effects on Soil Extracellular Enzyme Activity: Introduction and Literature Review

1.1 Introduction

The global area of grassland is larger than that of forests, and grasslands cover an estimated 52.5 M km^2 of the earth (Gibson, 2009; White et al., 2000), or a quarter of the planet's terrestrial surface and 70% of the world's agricultural land area (Henderson et al., 2015). Grasslands are often defined and distinguished based on plant species composition (grasses and shrubs) (Mueller-Dombois & Ellenberg, 1974; Schimper, 2011), climatic condition (Henzell, 1981), or a combination of these features (Gibson, 2009). In general terms, grasslands are characterized by relatively open land areas with a preponderance of largely herbaceous (grass, forb and grass-like) plant species, with a limited number and abundance of woody species (shrubs and trees), and are often subject to utilization by large herbivores, both wild and those representing closely managed livestock (White et al., 2000).

Grasslands exist in all continents, except Antarctica, and therefore occur under a wide range of conditions, including semi-arid to semi-humid regions of tropical and temperate climates. Temperate grasslands include the Eurasian steppes, North American prairies, South American pampas, South African and Australian temperate savanna and shrublands (Stokes et al., 1997). Soils of temperate grasslands are usually well-aggregated and have a thick A-horizon rich in organic matter (Hillel, 2007). Tropical grasslands include veld in Africa, tropical savannas in Africa and Australia, and tropical grasslands, savannas and shruborganci lands in the Americas (Briggs et al., 2008). Soils of tropical grasslands are typically porous and acidic with a thin A-horizon (Hillel, 2007). Most grasslands have distinct temporal changes in rates of plant growth throughout the year, often have dry and wet seasons, or cold and warm periods, creating

strong seasonal pulses in plant growth and forage availability. Rainfall in the wet season of tropical grasslands may reach 50-140 cm (Briggs et al., 2008).

For millennia, grasslands of the Great Plains in North America were grazed by bison, elk, antelope, and other ungulates. Climate, grazing, and wildfires were the main factors regulating grassland properties and function, with bison populations increasing with high forage abundance and decreasing under drought induced decreases in forage abundance (Bailey et al., 2010). Grasslands on all continents historically evolved with the presence of human activities. The first people came to the Great Plains at the end of the Ice Age around 12000-15000 years ago (Bailey et al., 2010). Indigenous people have hunted bison and used fire to maintain grasslands long before European settlement (Bailey et al., 2010). Following settlement and the introduction of modern agriculture, around 70-90% of grasslands in North and South America are now used as croplands or urban-industrial areas (Gibson, 2009). These changes markedly influenced grassland habitat for native plant and animal species, thereby altering their diversity, as well as ecosystem function. For example, conversion of arid grassland to cropland was a factor contributing to the Dust Bowl of the 1930s in western Canada. Around 5 to 10 M ha of prairies were negatively impacted during that period in Canada (Bailey et al., 2010).

Grasslands maintain the livelihood of people by supporting their animals, providing a clean water supply, facilitating nutrient cycles, as well as aiding soil C sequestration (White et al., 2000). Farber et al. (2006) grouped ecosystem services into four categories: provisioning services, supportive functions and structures, cultural services, and regulating services. Grassland provisioning services include providing forage for animals, and food, construction materials, as well as sources of fuel for people (Farber et al., 2006). Overall, the long-term supply of provisioning services is closely dependent on the maintenance of grassland forage quality.

Grassland supportive functions include nutrient cycling, pollination, hydrological cycling, and net primary production (Farber et al., 2006). Grassland soils store many nutrients such as nitrogen (N) and phosphorus (P), which are held mainly in organic forms as potential macronutrients for plants. Pollination by insects and animals is critical for supporting plant genetic diversity, but also increasing the supply of flowering plants with consumptive value. As part of the hydrological cycle, grasslands are critical for regulating water infiltration and storage in the soil profile, promoting ground water retention, and minimizing overland flood events, the latter of which also protects watersheds, stabilizes stream flows and maintains water quality (Farber et al., 2006; Gibson, 2009).

Grassland regulating services are vital for all living organisms by supporting, maintaining and even enhancing biogeochemical cycles and associated services such as climate regulation (Farber et al., 2006). Grassland soils are a major sink and source for nutrient elements involved in biogeochemical reactions between the atmosphere, vegetation, soil microbes/microfauna, and ungulates. Changes in these cycles can alter the availability of nutrients for plants and microorganisms, as well as nutrient storage in soil. Therefore, grassland plant growth is not only important as a source of forage, but also as a contributor to changes in soil chemical and biological properties. Soil covered with vegetation has been shown to have a lower surface temperature compared with bare soil (Jiang et al., 2010; Zeng et al., 2009), and this in turn, leads to less greenhouse gas (GHG) emissions. Modeling studies (Pitman et al., 2004) indicate that changes in land cover from native to seeded species contribute to increased soil temperatures and subsequent GHG emissions in Western Australia.

Since the middle of the 18th century, the surface temperature of the Earth has increased by 0.8°C (IPCC, 2007) and is projected to increase by 2 to 4°C by the end of the 21st century

(Bai et al., 2013). Global warming negatively affects natural systems and causes a wide range of ecological problems. Among the damaging effects are the extinction of animal and plant species, global rise in sea levels, decreased crop productivity in tropical and subtropical regions, and alteration of forage quantity and quality in grasslands due to changes in precipitation and temperature (Dumont et al., 2015; Mann, 2009).

Increases in GHG concentrations within the atmosphere are contributors to global warming by trapping energy that warms the Earth's surface (Morgan et al., 2010; Stocker et al., 2013). Since the Industrial Revolution, atmospheric concentrations of major GHG – namely carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4) – have substantially increased due to human activities (Wang et al., 2017). The global warming potential of CH_4 and N_2O is 25 and 310 equivalents of 1 CO_2 in a hundred-year period (Edenhofer & Seyboth, 2013). The agricultural and forestry sectors contribute about 24% of total global GHG emissions each year (Stocker et al., 2013).

Grasslands have the potential to mitigate GHG emissions by sequestering C in soil, which otherwise would contribute to atmospheric CO_2 levels. Compared to forests where C mostly present in above ground biomass (ratio of C storage in above ground: belowground 132-457: 481 Gt C), grasslands store the vast majority of carbon in the soil profile (ratio of C storage in above ground: belowground 14-48: 281 Gt C) (Gibson, 2009). Estimates of temperate and tropical grasslands indicate that these areas store 176 gigaton (Gt) and 247 Gt, respectively, of soil organic carbon (SOC) in the top 1 m of soil (Stockmann et al., 2013). On average, C sequestration in grassland soils can be as high as 0.35 Mg C ha^{-1} yr^{-1} in improved grazing management and 1.01 Mg C ha^{-1} yr^{-1} after conversion of cropland to pasture (Conant et al., 2001).

1.2 Carbon and Nutrient Cycles in Grassland

Global C cycling mainly consists of the continuous exchange of C among atmosphere, ocean, lithosphere, and land surface (Grace, 2013). The most common forms of C is carbon dioxide (CO_2) in the atmosphere, carbonate in soil ($CaCO_3$, $CaMg(CO_3)_2$, and $FeCO_3$) and ocean (H_2CO_3, HCO_3^-, and CO_3^{2-}), and as a product of anaerobic reactions – namely methane (CH_4) (Gibson, 2009; Holmén, 1992). Carbon cycling is divided into geological and biogeochemical cycles. The geological cycle can take millions of years to complete; C exchange proceeds slowly because the C within this cycle is mainly stored in the lithosphere (Grace, 2013). In biogeochemical cycles, C exchange occurs much faster and usually extends from hundreds to thousands of years (Soussana et al., 2004; Ussiri & Lal, 2017).

Carbon cycling is a process involving both biotic and abiotic reactions, attributed to both natural causes and human activities. One of the important C cycling reactions is photosynthesis in which autotrophic organisms consume CO_2 and produce O_2 (Gibson, 2009; Stockmann et al., 2013). Plants accumulate C in their bodies during photosynthesis, which becomes SOC after plant death, or is returned to the atmosphere via respiration or consumption (and digestion) by animals; those processes are repeated over time (Tan et al., 2007).

In the absence of human activity or other major disturbances, the biogeochemical C cycle in soil is typically in a steady state, with inputs balancing outputs, leading to stable ecosystem C (including within soil). Anthropogenic activity, including deforestation, prescribed burning, grassland conversion into croplands, mining and/or resource extraction, and any other activity that alters the plant community, including grazing, can alter C cycling by increasing C turnover in the soil, in turn increasing atmospheric CO_2 and CH_4 (Stockmann et al., 2013). These increases

can lead to global warming and climate change. As C is involved in two main GHGs, it is of significant interest to increase soil C sequestration potential, including in grasslands.

In addition to climate and soil properties, grassland management practices can influence soil C sequestration. According to previous studies, management activities that directly increase grassland productivity, and therefore C input, may increase soil C sequestration potential (Boehm et al, 2004; Conant et al, 2001; Gunina & Kuzyakov, 2014; Han et al., 2014; McNally et al., 2017; Schuman et al., 2002); for example, sowing of more productive grass species and legumes into grasslands, along with the addition of fertilizers, may increase soil C. Legumes may increase belowground biomass production and contribute to C sequestration (Crawford et al., 1996). On average, the improvements mentioned above increased soil C sequestration rate in the first four decades since new treatments were applied, mainly in the top 10 cm of soil (0.03 Mg C ha^{-1} yr^{-1} cm^{-1}) (Conant et al., 2001). At depths of 10-20 and 20-50 cm, 0.01 Mg C ha^{-1} yr^{-1} cm^{-1} was sequestered (Conant et al., 2001), while below this, at 50-100 cm depth, 0.008 Mg C ha^{-1} yr^{-1} cm^{-1} was sequestered (Conant et al., 2001). Improved grazing (e.g., moderate livestock stocking compared to low and high stocking) can lead to greater C sequestration rate (0.35 Mg C ha^{-1} yr^{-1}) than fertilization (0.30 Mg C ha^{-1} yr^{-1}) and irrigation (0.11 Mg C ha^{-1} yr^{-1}). Conversion of cultivated soils to perennial pasture is known to lead to a higher C sequestration rate (1.01 Mg C ha^{-1} yr^{-1}) than improved grazing practices (Conant et al., 2001). Grazing may increase soil organic C concentrations in regions with lower (400 mm) or higher (850 mm) precipitation (Pineiro et al., 2010).

Nitrogen is one of the main elements (along with C, H, and O) present in all organisms, primarily as amino acids in protein (Kuypers et al., 2018). The lithosphere stores the largest amount of N in ammonia form (1.8×10^{10} Tg N) (Kuypers et al., 2018). However, lithospheric N

does not comprise a main component of the biogeochemical N cycle. Instead, N is highly

abundant in the atmosphere (78%) but is not easily available to plants unless it is converted into

a form (NO_3^- or NH_4^+) that plants can take up.

Inorganic N forms include nitrogen gas (N_2), ammonium (NH_4^+), nitrite (NO_2^-), nitrate

(NO_3^-), nitrous oxide (N_2O), and nitric oxide (NO). Organic forms exist as part of proteinaceous

materials including purines and pyrimidines (Kieloaho et al., 2016). All these forms of N are

intricately involved in the biogeochemical cycle for N, which has six main processes:

assimilation, ammonification, nitrification, denitrification, anaerobic ammonium oxidation

(anammox), and N fixation (Kuypers et al., 2018). Among these processes, ammonification and

nitrification are the main processes that involve the largest fraction of N in the N biogeochemical

cycle (Kuypers et al., 2018).

Within grassland soils, plant available N forms are NH_4^+ and NO_3^-, and dissolved organic

N (DON) such as amino acids and nucleic acids (Zhong et al., 2015). These sources of N become

available through ammonification, nitrification processes, and DON leakage through the death

and lysis of plant and microbial cells (Conant et al., 2005). Nitrogen loss happens by

denitrification, leaching, and volatilization in grassland (Butterbach-Bahl et al., 2011). Grazing

animals consume N as protein and amino acids in forage, and following digestion and

subsequent metabolism of N, N loss occurs through the removal of animal products (wool, meat,

and milk), or as N loss from leaching/volatilization following urine or fecal deposition. However,

the majority of N from animals is recycled back to the soil as urine and retained within the

ecosystem. According to different studies, 60-65 % to 90-95 % of consumed N returns to soil by

urine (Chadwick et al., 2000, Haynes et al., 1993; Lantinga et al., 1987; Van Vuuren et al.,

1987).

Phosphorus is another major nutrient element and may be a limiting factor for plant growth in grasslands. High concentrations of P often occur in young soils but then decrease over time (Bünemann et al., 2010). In grassland soil total P can vary from 200 to 1100 mg kg^{-1} (Walker & Adams, 1958). Compared to C and N, the P cycle has two distinct characteristics. First, there is no gas phase, and second, the majority of soil P has insoluble and immobile forms (Gibson, 2009).

Inorganic P (PO_4^{3-}) is the main source of available P for plants and microorganisms. Inorganic forms of P are mostly water insoluble, and within acidic (< pH 4) or alkaline (> pH 8) soil, are precipitated or occluded in conjunction with Fe and Al, or Ca, respectively. Inorganic and organic forms of P are released to soil solution while P is taken from the soil solution by plants or microorganisms (Gibson, 2009). Organic P forms are a prevalent fraction of total soil P (Gibson, 2009). Mineralization of organic P depends on soil quality. In nutrient rich soil, P mineralization starts at an organic C to P ratio <100:1. Within low fertility soil, P mineralization starts at <200:1 organic C to P ratio. Also, P mineralisation depends on microorganisms, because their activity is known to immobilize available P forms (Brady & Weil, 2016).

Similar to the cycles of C and N, the grassland P cycle also depends on management actions (Costa et al., 2014; Craine & Jackson, 2010; Jones & Woodmansee, 1979; Roberts & Johnston, 2015; Schoumans et al., 2015; Zhou et al., 2017). Pasture and sugar cane plantations in southern Florida showed differences in P storage forms and availability (Castillo & Wright, 2008), with pastures having more Al-bound P forms, whereas sugar cane plantations had Ca-bound P forms due to limestone application (Castillo & Wright, 2008). In grazed grasslands, 10-40% of P removed by livestock is returned to soil in animal feces (Haynes & Williams, 1993). Phosphorus enrichment to soil as feces increases the organic P fraction, and has a positive

correlation with forage quality (Haynes & Williams, 1993). Increases in the organic P fraction may have a positive effect on plant available P. Studies in the Mediterranean and Pennsylvania have shown increases in organic P in pastureland and high decomposition rates with subsequent increases in available P within the soil (Dou et al., 2009; Nash et al., 2011; Nash et al., 2014).

Overall, nutrient cycling is important for forage production and C sequestration, two provisioning and regulating services, respectively. Availability of energy and nutrients for plant growth depends on SOM decomposition. Decomposition is carried out by enzymes, which are produced by microorganisms, plant roots, and invertebrates (Paul, 2006).

1.3 Soil Extracellular Enzymes

Enzymes are proteins responsible for increasing the rate of chemical reactions in biochemical pathways (Page et al., 1982). Soil enzymes can be categorised as extracellular or intracellular. Intracellular enzymes are present and function within living cells. Extracellular enzymes are produced and secreted (for example, into soil) from plant roots, live cells or during dead cell lysis. Fungi, bacteria, plants, termites, and ants all produce enzymes in the soil environment (Srinivasrao et al., 2017). Enzymes are typically active in soil solution where they can catalyze substrates. Enzymes attach to the substrate via their active site and subsequently alter the configuration of the substrate, including its bond structure. In dry soil, enzymes become immobile by adsorbing on to clay and humic colloids (Srinivasrao et al., 2017).

Soil extracellular enzyme activity (EEA) is important in regulating SOM decomposition and nutrient cycling, during which they alter soil quality, energy and nutrient transformation (Srinivasrao et al., 2017). Soil EEA are widely involved in the degradation of biopolymers, including cellulose, hemicellulose, chitin, and phosphoric acid monoester. The end product of

EEA is plant and microbe available forms of C and nutrients (N, P and S). The degradation of some biopolymers involves several enzymes because each enzyme is substrate specific (Table 1) (Richard et al., 2002). Therefore, in order to assess C cycling rates, it is necessary to test several enzymes because a single enzyme does not express total enzyme activity (Richard et al., 2002).

Compared to deoxyribonucleic acid (DNA), ribonucleic acid (RNA), and phospholipid - derived fatty acids (PLFA) analyses, soil EEA assay is relatively inexpensive and easy to conduct (Bandick et al., 1999; Trasar-Cepeda et al., 2008). While many soil (chemical and physical) properties do not respond quickly to environmental changes (e.g., alterations to land management and soil reclamation), enzymes respond relatively quickly to external changes (Srinivasrao et al., 2017). For example, increases of plant available P through the addition of fertilizer decrease phosphatase activity (Golub & Boesze-Battaglia, 2007). Enzyme synthesis is bioenergetically costly; as a result, microorganisms are unlikely to invest resources to produce enzymes if there are sufficient nutrients (e.g., P) in the soil. Conversely, changes in EEA are a useful metric to explore responses of microorganisms to environmental change (Trasar-Cepeda et al., 2008).

Local climate is the most important factor directly regulating EEA as it controls soil temperature and moisture content. In regions with >600 mm of mean annual precipitation (MAP), further increases in precipitation do not increase EEA. In contrast, in regions with <600 mm MAP, EEA increases with precipitation (Ren et al., 2017). In theory, decreases in soil moisture content within pre-existing wet soil will increase enzyme concentration, and thus levels of EEA (Sinsabaugh et al., 2008). However, in dry environments such as grasslands, increases in precipitation activate immobilized enzymes and thereby increase diffusion between enzymes and substrates, which in turn, can elevate EEA (Fierer et al., 2003; Ren et al., 2017). Moreover,

rewetting of dry soils increases biomass turnover through cell lysis, bringing additional enzymes into soil solution (Fierer et al., 2003).

Soil chemical and physical properties are important factors in the regulation of soil biochemical reactions. Soil pH accounts for the ionization of functional groups of enzymes or the ionization of substrate states, enzyme immobilization (adsorption degree), and control the solubility of co-factors (Frankenberger et al., 1982; Min et al., 2014). Typical soil pH values are in the range of 4 to 8. Laboratory experiments have shown that EEA can have a positive or negative correlation with soil pH; for example, increases in soil pH decrease C-degrading glucosidase and cellobiosidase activities (Sinsabaugh et al., 2008), while phosphatase has acid, neutral, and alkaline types with optimal activity at a soil pH of 4.8, 4.6-7.0, and 11.0, respectively (Herbien et al., 1990). As a result, phosphatase EEA must be interpreted in the context of the pH within the soil from which they originate.

Enzyme adsorption on soil particles also controls enzyme distribution and activity (Tietjen et al., 2003). Enzyme activity decreases when enzymes bind to clay with active sites. Many studies have found that phosphatase EEA decreases when this enzyme is highly adsorbed to clay materials (Bergaya et al., 2006; Chenu & Stotzky, 2002; Rakhsh & Golchin, 2018; Spaccini et al., 2001; Tietjen & Wetzel, 2003). Similarly, soils with greater clay content are known to have lower acid and alkaline phosphatase EEA. However, some EEA may increase due to adsorption because the substrate targeted by enzymes may also be adsorbed by clay particles, and thus the concentration of enzymes and substrate similarly increase in one location (Tietjen & Wetzel, 2003). Glucosidase EEA is also known to increase when more highly absorbed to clay, particularly when the concentration of glucosidase on clay particles is greater than that of the target substrate (Tietjen & Wetzel, 2003).

EEA responses to changes in clay content may also depend on the parent material and associated minerals within soil. Enzyme activity progressively decreases from kaolinite, to illite, and then to montmorillonite (Rakhsh & Golchin, 2018). This trend may be related to the mineral-specific surface area and associated cation exchange capacity (Rakhsh & Golchin, 2018). Kaolinite consists of one layer of Si-O and one layer of Al-OH bound together. In contrast, montmorillonite consists of many layers of aluminosilicates, that increases montmorillonite's adsorption potential compared to kaolinite and illite; thus, more enzymes become inactive by montmorillonite absorption which can occur very quickly (Tietjen et al., 2003).

1.4 Grassland Management Effects on Extracellular Enzyme Activity

Enzymes can have a relatively rapid response to changes in land management. The conversion of grasslands and forests to tilled cropland decreases EEA (Acosta-Martínez et al., 2008; Samuel et al., 2008). This confirms that in grassland and forest soils enzymes are mainly microbial in origin because tillage alters microbial structural diversity (e.g., ratio of fungi:bacteria) known to alter EEA (Acosta-Martínez et al., 2008; Kizilkaya & Dengiz, 2010; Six et al., 2006). For example, compared to non-tilled soil, the number of colonial fungi decrease while fungal hyphae increase with soil tillage (Deng & Tabatabai, 1994). Moreover, the addition of N and P fertilizers decreases EEAs involved in N and P mineralization. Microorganisms decrease enzyme synthesis when available nutrients are at a sufficient level in soil because enzyme synthesis is energy costly. Mulching of plant residues on the soil surface may also increase C mineralization because C degrading EEA is substrate limited, and substrate increases in the top soil (where microbes are more abundant) lead to greater EEA (Deng & Tabatabai, 1994).

Previous studies on EEA in grasslands give broad information about grazing effects on microbial activity (Banerjee et al., 2007; Chuan et al., 2020; Hewins et al., 2016, 2015). Compared to tilled agricultural lands, different grazing management actions can decrease, increase or have no influence on, levels of EEA. Studies in Patagonia and Inner Mongolia showed decreased EEA under continuous grazing with low, medium, and high intensities, but non-grazed periods of 5-10 years restored EEA levels to values similar to that of non-grazed sites (Prieto et al., 2011; Yong-Zhong et al., 2005). Overgrazing was thought to be the main factor decreasing EEA on these sites, and the arid climate necessitated a long recovery period to restore EEA within these grassland ecosystems. In contrast, well managed grazing may increase EEA. According to studies in South Africa and Brazil, compare to continuous grazing, rotational grazing can stimulate soil enzyme activity, thereby increasing nutrient mineralisation rates and positively influencing plant growth (Garcia et al., 2011; Kotzé et al., 2017).

Grazing experiments in the Canadian Prairies have reported similar results. Experimental results of soil biological quality in Manitoba concluded that increased cattle stocking rates decreased soil microbial activity, as well as C and N mineralization and phosphatase EEA (Banerjee et al., 2007). However, this study could not provide a clear understanding of the effect of different grazing systems on enzyme activity due to the short time span of the experiment (Banerjee et al., 2007). The study of EEA at grazed and ungrazed sites in Alberta grasslands concluded that grazing inhibited the activity of several C cycling enzymes, compared with greater enzyme activity found in non-grazed areas (Hewins et al., 2015). In a controlled defoliation experiment done in the Mixedgrass Prairie that simulated different grazing regimes, combined effects of grazing and environmental conditions were found on soil EEA. Intensive and frequent defoliation throughout the growing season (simulating continuous grazing) led to

decreased phosphatase and C-cycling EEA in a lowland (more mesic) ecosite, while cellobiosidase activity also declined in the same treatment on an upland (more xeric) ecosite (Hewins et al., 2016). Recent study in northern temperate grasslands (Chuan et al., 2020) evaluated long-term grazing effects on EEA within the plant litter derived from different common grass species. As EEA differed among grasses, long-term grazing induced changes to plant species composition in grasslands was considered a mechanism to increased C and P EEA, and the latter in turn, increased C and nutrient cycling (Chuan et al., 2020).

Based on previous studies, we can suggest that increases in livestock stocking rate and associated overgrazing appear to inhibit enzyme activity in grazed grasslands. However, there are many types of grazing systems, each of which has their own attributes. For example, continuous grazing (CG) is a system involving minimal livestock intervention wherein livestock (largely cattle in western Canada) graze at will within one expansive area for the entire grazing season; it requires low cost management with less labor and infrastructure (fencing, water, etc.) to undertake compared to other systems (Bailey et al., 2010). In contrast, rotational grazing (RG) involves the subdivision of large paddocks into smaller paddocks, which in turn, facilitates greater control over when, how often, and how intense a given area may be grazed by livestock (Bailey et al., 2010). Adaptive multi-paddock grazing (AMP) involves the use of a very large number of fields or paddocks for each herd (e.g. more than 20, often more than 50), thereby facilitating the use of high stocking densities for short and controlled periods, which in turn, facilitates a lengthy post-grazing recovery period to maximize vegetation regrowth (Hawkins et al., 2017; Holechek et al., 2016).

The effects of different grazing systems on soil C and nutrient cycling are of great interest to producers and land use planners alike. Allan Savory believes that holistic grazing

(from which AMP originates) may increase C sequestration in soil to the point of reversing half a century of rising CO_2 emission (Briske et al., 2014; Hawkins et al., 2017). Advocates of AMP grazing argue that this method is superior to CG and that previous studies examining the impact of this method on grassland properties and function (Briske et al., 2008) were flawed due to their improper methodology, including an inability to replicate 'ranch-level' grazing impacts due to the short duration (2-3 years), small paddock size (5-25 ha), and inflexible grazing regimes tested (Teague et al., 2009; Teague et al., 2013). Controversially, recent meta-analyzes have concluded that continuous grazing most often leads to similar impacts on plant production and rangeland condition compared to rotational grazing systems (Briske et al., 2008). Instead, these researchers argue that there is no superior grazing system, but that a proper, well managed grazing system regardless of its implementation throughout the grazing season, can be similarly economically and ecologically beneficial (Briske et al., 2014). Using this framework, the effectiveness of different grazing systems depend on a rangeland manager goals and his/her ability and willingness to regulate grazing impacts.

Overall, grasslands facilitate many vital ecological processes such as nutrient cycling and energy flow, the provision of clean water, food and forage, and are involved in soil C sequestration and the reduction of atmospheric GHGs. Climate, soil properties, and land management are primary factors regulating grassland condition and function. As the beef industry has a significant impact on the local economy in western Canada, and in Alberta alone, graze on nearly 10 M hectare of grassland, including 7 M ha of native grassland, understanding the effect of different grazing systems on soil biochemical processes is of great interest due to the importance of global grasslands in food production, GHG mitigation and C sequestration potential.

1.5 Research Objectives

Despite previous studies comparing different grazing systems for their effect on soil fertility and C sequestration, these results showed small differences between grazing systems (Briske et al., 2008). Some of the studies had small paddock sizes (5-25 ha) (Norton, 1998; Provenza, 2003; Teague et al., 2009), others a relatively short-lived implementation of a grazing system (2-3 yr) (Provenza, 2003; Teague et al., 2009), and all typically use a small number of ranches and/or study sites (3-4) (Briske et al., 2014; Teague et al., 2013). Collectively, these factors reduce the likelihood of finding a clear effect of grazing system in previous studies. Moreover, some conclusions have been made on the importance of these specialized grazing systems using anecdotal evidence without supportive data (Nordborg & Roos, 2016).

Given these limitations, field studies on working cattle ranches are needed to investigate the effects of grazing systems on key ecosystem properties, including nutrient cycling. Monitoring EEA represents an opportunity to evaluate potential nutrient mineralization rates in soil and detect management-induced changes to soil C, N and P biogeochemical cycling, particularly in comparison to changes in other soil properties.

This study investigates the effect of different grazing systems (and perhaps more importantly, land and grazing management practices) on soil EEAs involved in C and nutrient mineralization. Moreover, this study used ranches distributed across a wide agro-climatic gradient encompassing the Mixedgrass, Fescue Grassland, Central Parkland, and Lower Boreal Mixedwood subregions of Alberta.

The second chapter of this thesis includes results of a field experiment examining EEA in soil collected from these ranches. More specifically, the activity of six enzymes involved in C,

N, and P cycling were analysed on paired ranches from twelve sites in order to identify

differences between soils subject to different grazing practices. The latter were identified using

producer surveys and included cultivation history, as well as livestock stocking rates, and length

of grazing periods, together with length of recovery periods after grazing events. Samples

included assessments during early summer, mid summer and early autumn.

The synthesis summarizes the findings from the field experiment, highlights research

conclusions and provides implications for the management of these grasslands for multiple

environmental goods and services. It also outlines potential future research needs and

opportunities.

Table 1.1. Soil extracellular enzymes studied in this experiment and their function.

Enzyme	Cycles	Reaction	Product of reaction
β-α-cellobiosidase	carbon	hydrolysis of beta-D-glucosidic linkages in cellulose	disaccharides (cellobiose)
β-glucosidase	carbon	hydrolysis of non-reducing beta-D-glucosides residues	monosaccharides (glucose)
β-1,4-xylosidase	carbon	hydrolysis of beta-D-xylans	xylose
β-1,4-n-acetylglucosaminidase	nitrogen	hydrolysis of N-acetyl-beta-D-glucosaminide	N-acetylglucosamine
Urease	nitrogen	hydrolysis of urea	ammonia and CO_2
Phosphatase	phosphorus	hydrolysis of a phosphate monoester	Phosphate ion and an alcohol

Chapter 2. Effects of Land Use History, Climate, and Soil Properties on Extracellular Enzyme Activity Within Grazed Grasslands of Alberta

2.1 Introduction

Grasslands cover a quarter of the earth's terrestrial surface and are present in five continents (Henderson et al., 2015). Grasslands provide clean water and forage for animals, as well as habitat for many organisms, facilitate nutrient cycling, and are a source and sink of soil carbon (C) (White et al., 2000). Livestock grazing is known to alter C and nitrogen (N) cycles, and affect plant species distribution, soil microbial activity, and soil organic matter (SOM) mineralization (Hart et al., 1995; Teague et al., 2011). Levels of SOM mineralisation are driven by enzyme activities, which may be changed by long-term management practices associated with particular grazing systems (Hewins et al., 2016). While the impact of grazing on forage availability, nutrient cycling, SOM mineralisation and C sequestration potential in grasslands has frequently been studied in relation to the presence/absence of grazing in Canadian grasslands, less attention has been given to the specific impact of grazing systems and cultivation effects on grassland soil enzyme activity *in-situ*, including exposure to various cattle grazing practices.

Grazing systems regulate the timing, frequency, intensity and duration of defoliation, thereby altering interactions between herbivores, plants and the underlying soil (Howery et al., 2000). Both continuous grazing (CG) and rotational grazing (RG) are common grazing systems used in Canadian grasslands (Bailey et al., 2010). CG involves minimal livestock intervention wherein livestock (largely cattle in western Canada) graze at will within one expansive area for the entire grazing season; it requires little infrastructure (fencing and water development) and labor, and therefore is associated with a low cost as compared to other systems (Bailey et al., 2010). In contrast, RG involves the subdivision of larger paddocks into smaller paddocks, and facilitates greater control over when, how often, and how intense a given area may be grazed by

livestock (Bailey et al., 2010). Adaptive multi-paddock (AMP) grazing is a specialized form of RG employing a very large number of fields or paddocks for each herd (e.g., more than 20, often more than 50), thereby facilitating the use of high stocking densities for short and controlled periods, which in turn, facilitates a lengthy post-grazing recovery period (Hawkins et al., 2017; Holechek et al., 2016).

In theory, AMP grazing imitates historical grazing by wildlife, such as that which took place on grasslands grazed by large numbers of bison, elk, antelope, and horses with high intensity and short duration of grazing in one area (Teague et al., 2011b). Increased demand for vegetative parts of the most-palatable plants at high stocking density forces animals to consume less palatable plant species in the paddock. Such forms of grazing help regulate plant diversity and increase the uniformity of dung and urine deposition across the grassland (Teague & Barnes, 2017; Teague et al., 2011). The post-grazing recovery period in AMP grazing is generally long (45-100 days), which is intended to provide sufficient time for plants and microorganisms to regenerate, including the decomposition of dung and recycling of nutrients returned in urine (Dowling et al., 2005).

Decomposition of organic compounds in soil depends on the needs of microorganisms (Xiao et al., 2018). Soil microorganisms produce enzymes whose role is to degrade cellulose and other organic polymers to gain access to energy and nutrients (Bremmer et al., 1982). Extracellular enzymes are produced and excreted in soil where they are involved in the decay of detritus and the ongoing breakdown of SOM (Srinivasa et al., 2016). Levels of EEA depend on SOM content which is the main source of substrate for catalytic reactions (Srinivasa et al., 2016).

Past enzyme studies in grasslands provide insight on grazing effects on microbial activity and biogeochemical cycling of C and nutrients (Banerjee et al., 2007; Hewins et al., 2016, 2015).

The study of EEA at grazed and ungrazed sites in Alberta grasslands concluded that grazing inhibited the activity of several C cycling enzymes, resulting in greater EEA within non-grazed areas (Hewins et al., 2015). In another field experiment that imitated different grazing management practices through controlled defoliation regimes (intensity and frequency) under contrasting watering treatments, defoliation in temperate mixedgrass prairie had no effect on NAG (N cycling) and BAG (C cycling) activities. Levels of EEA were strongly affected by local soil-climatic (ecosite) conditions, whereas defoliation effects on biochemical processes were found to vary with ecosite texture and associated moisture regime (Hewins et al., 2016). However, this defoliation experiment did not include actual grazing, and excluded dung and urine deposition that would have altered EEA. This suggests that different grazing systems have the potential to alter biogeochemical cycling through changes in EEA, although further research is needed in grasslands that are subject to contrasting grazing practices over the long-term.

To investigate the effect of land use history and grazing practices on EEA, we analysed EEA in soil samples collected from 12 pairs of ranches in Alberta, Canada, practicing either AMP or 'conventional' (nAMP) grazing for at least ten years prior to the sampling. A ranch survey was conducted to characterize cultivation history, stocking rate, and rest to graze ratio. Extracellular enzymes, whose activity is essential for soil organic C, N, and P cycling, were studied. Detailed information about the enzymes examined is in Table 1.1. Our hypotheses were: 1) cultivation in the past will alter EEA, especially enzymes involved in C-cycling due to changes in SOC amount and forms caused by cultivation (Dormaar & Willms, 2000); 2) EEAs responsible for C cycling will be greater in soil from nAMP than AMP ranches due to higher substrate availability compared to intensively grazed AMP ranches; 3) high SR will increase urease EEA, and 4)

enzymes responsible for N and P cycling will be greater in AMP ranch soil compared to CG and RG ranches due to high plant demand of nutrients after intensive grazing events.

2.2 Methodology

2.2.1. Study sites

Study ranches (N = 24) were located in pairs at 12 sites within the Mixedgrass, Foothills Fescue, Aspen Parkland, and Boreal transition subregions of Alberta. All ranches were initially recruited by the voluntary participation of ranches considered to be practicing adaptive, multi-paddock (AMP) grazing. Interested participants completed an on-line survey regarding their willingness to participate and provided information on the pasture and grazing management activities across their property. Following a phone interview and subsequent site visit, 12 randomly selected AMP ranches were selected for sampling. All AMP ranches also had to have a neighboring property with similar cultivation history and a landowner/manager that was willing to participate (i.e., allow sampling), including providing detailed information on grazing practices taking place on the affected lands.

Study sites varied widely in annual precipitation and temperature (Table 2.1). Within each pair of ranches, one ranch employed AMP grazing techniques, which was ascertained using a combination of management survey responses and subsequent field reconnaissance. Neighboring nAMP systems employed a wide range of management practices, including season-long (continuous) grazing, to low (infrequent), moderate or even high intensity (relatively frequent) rotation of cattle through individual pastures. All ranchers managed their properties with a relatively stable system (AMP or conventional) for at least 5 yr, and commonly 10 yr or more, prior to the study. Most ranches within a ranch pair had the same cultivation history, with two

exceptions. In total, there were sixteen cultivated and eight non-cultivated ranches. Within a pair, ranches were located relatively close to each other (< 5 km) and had similar soil properties (texture, salinity), slope position, and elevation. A detailed survey of each ranch operator was conducted to obtain the information necessary to assess differences in soil EEA. Key metrics examined here are listed in Table 2.2 and include whether the area had been previously cultivated and the pattern of cattle use during the summer. The latter included the number of paddocks, average length of a grazing period, and the minimum length of the rest period during the early to mid-growing season (e.g., prior to August 1). These data were used to compute a rest:grazing ratio (RGR) that indicates the number of days of rest per day of active grazing during the growing season. Finally, information on the number of cattle, size of area grazed, and the entry and exit dates of cattle were used to compute an average stocking rate (SR) of cattle for the grazed area.

2.2.2. Soil sampling

Soil sampling was done three times in 2018: June 11 – 18 (it took a week to complete the sampling of all the ranches at each sampling time), July 23 – 30, and September 4 – 11, representing spring, mid-summer and fall, respectively. At each sampling, four soil cores (5 cm diameter x 15 cm deep) were collected from two lower and two upper slope positions within each ranch; slopes were randomly selected within the area. Thereafter, soil samples from the same slope position were combined and two composite soil samples (one upper and one lower slope) per ranch were placed on ice and transported to the lab for further processing. Once at the lab, samples were immediately sieved through a 2 mm sieve, refrigerated at -4 °C for 24 hours, and stored at -20 °C until used in further analyses.

2.2.3. Soil properties

Soil pH, NO_3^-, NH_4^+, microbial biomass C (MBC), and microbial biomass N (MBN) were analysed for the soil samples. To determine soil pH, a soil:water solution (10 g:50 mL) was tested using a pH meter (Orion, Thermo Fisher Scientific Inc., Beverly, MA, USA) (Robertson et al., 1999). Soil moisture content was analyzed by comparing weights before and after oven drying (105 °C). The analysed soil properties are presented in Table 2.1.

For determining soil available N (AN), 10 g of soil was mixed with 0.5M K_2SO_4 solution in a ratio of 1:5 (air-dried equivalent soil sample weight:K_2SO_4 solution). After mixing on a shaker at 180 rpm for an hour, samples were filtered using Q2 filter paper (Mulvaney, 1996). To determine nitrate (NO_3^-) and ammonium (NH_4^+) concentrations, soil extracts were mixed with vanadium chloride (Miranda et al., 2001) or phenol and hypochlorite at pH 11.2 (Keeney et al., 1982), respectively, and analyzed on a spectrophotometer (Genesys 10 UV-Vis, Thermo Spectronic). Three sub-samples of each extract were used to determine NO_3^- and NH_4^+.

The MBC and MBN were determined by ethanol-free chloroform fumigation, from one sub-sample (10 g of oven-dry equivalent) as described previously from a mixture of soil and 0.5 M K_2SO_4 solution (10 g:50 mL); while the other sub-sample was fumigated for 24 hours. Next, 50 mL of 0.5 M K_2SO_4 solution was added to fumigated soil subsamples, shaking for 1 hr at 180 rpm and filtered. Fumigated and unfumigated soil extracts were run on a Shimadzu TOC-V$_{CSN}$ analyser (Shimadzu, Kyoto, Japan). MBC and MBN were calculated by dividing the difference in C and N content between unfumigated and fumigated samples (Brookes et al., 1985).

Soil texture was analyzed with the hydrometer method (Kroetsch & Wang, 2008). Soil samples were mixed with a Calgon solution (50%) and distilled water (Calgon water ratio 1:40).

The soil-Calgon solution was shaken overnight, then transferred to a 1 L cylinder and its volume raised to 1 L with distilled water. Samples were pretreated to remove carbonate and organic carbon, respectively, by adding 1M HCL and 30% H_2O_2. A hydrometer was inserted to the cylinder and readings were taken after 40 seconds and 7 hr. Calculation of silt, sand, and clay was done by the following formulas.

$$Sand\% = 100 - (R_{40s} - R_L) * \frac{100}{oven\ dried\ soil\ (g)}$$

$$Clay\% = (R_{7hr} - R_L) * \frac{100}{oven\ dried\ soil\ (g)}$$

$$Silt\% = 100 - (sand\% + clay\%)$$

2.2.4. Extracellular Enzyme Assays

To assess EEA, a standard fluorometric method was used with 96-well microplates described by Sinsabaugh et al. (2003) with acetate buffer solution (pH 5.0). One gram of fresh soil and 125 mL of buffer were mixed to make a soil solution and 200 µL of the solution pipetted into each well of the microplate. Microplates with soil solutions and enzyme substrates were incubated depending on enzyme type for two (phosphotase), three (β-glucosidase, N-acetylglucosaminidase), four (xylosidase), or seven hours (Cello) at 25 °C. After incubation, microplates were read on a Biotek Synergy HT (Bio Tek Instruments, Inc, Vermont, USA) with 360 nm excitation and 460 nm emission. Resulting EEA rates were expressed in µmol per hour per gram oven-dry soil (µmol g soil^{-1} h^{-1}) using the following equation (Sinsabaugh et al., 2003).

$$Enzyme\ activity\ (\text{µmol g soil}^{-1}h^{-1}) = \frac{Signal \times 125\ ml}{1000 \times Time(h) \times 0.2\ ml \times W/(1+M)}$$

Where:

Enzyme activity rate is expressed in μmol per hour per g dry soil.

W is the fresh weight of soil in g.

M is the moisture content of soil per dry weight

$$Signal\ (nmol) = (Assay/E_c \times Q_c) - (Substrate/E_c) - (Soil/E_c \times Q_c) + (Buffer/E_c \times Q_c)$$

And where:

E_c is the emission coefficient

Q_c is the quench coefficient

For the urease activity assay, we followed the methodology used by Sinsabaugh et al. (2000). Dark 96-well microplates with a clear bottom (Fisher #CS003997) were chosen because a colorimetric method was used to determine urease activity. One 1 g of fresh soil was added to 100 mL 50 mM acetate buffer (soil pH 5.0). Microplates with soil solutions and an enzyme substrate were incubated for eighteen hours at 25 °C. After incubation, the microplates were read on the Biotek Synergy HT, which was calibrated for the colorimetric test. The EEA rate was expressed as nmol NH_4^+ released per hour per gram oven-dry soil (nmol NH_4^+ g^{-1} h^{-1}) using the following equation (Sinsabaugh et al. 2000).

$$Urease\ activtiy\ (nmol\ NH_4^+\ g^{-1}\ h^{-1}) = \frac{Net\ ABS \times 100\ ml}{(E \times Time(h) \times Soil(g) \times 0.2\ ml)}$$

Where:

Net ABS = Assay – Sample − Substrate

E is the extinction coefficient (25 $pmol^{-1}$)

Geometrical mean (geomean) of EEA involved in C-cycling was calculated to express average activity of C decomposing enzymes.

2.2.5. Statistical Analysis

Data were analysed using a linear mixed-effect model (glme), with response variables being the individual EEA values, as well as the total of all EEAs (geomean) responsible for C cycling (specifically Cello, Xylo and BAG). A model selection approach (Anderson et al., 2000) was used to compare models for their ability to explain each EEA response. Independent variables of interest in this study were grouped into three sub-groups, including 1) soil conditions (soil pH, texture, MBC and MBN, and AN), 2) macro- and microclimatic conditions (specifically AHM, and soil moisture content taken at the time of soil removal in the field), and 3) land management factors (comprised of animal stocking rates, whether the pasture had been previously cultivated, and the rest:grazing ratio) (Table 2.1). Prior to analysis, all independent variables were analyzed for their correlation with one another (cor.test, Pearson's method) to identify redundancy among variables, particularly among management factors. Only one variable from a correlated pair was chosen in each sub-group if the correlation coefficient was greater than 0.7 (Appendix A).

Model selection was done in two stages. First, models of independent variables were analysed within each sub-group (Table 2.2). Models tested at this stage were the same for all EEAs. In the second stage, the best model was chosen from each sub-group and they were run together, and if applicable, with interaction terms. Interactions were included where one of the management variables was a continuous variable (e.g., SR or RGR). After the best models were selected for each EEA, β coefficients, together with upper (UCI) and lower (LCI) confidence intervals (CI), were determined to assess the direction (positive vs negative), effect size (magnitude of the standardized β's), and strength (from CI's) of each independent variable on EEA activity. Significance was considered greater when the CI did not overlap with zero (Scrafford et al., 2017).

To compare and select the best model, AIC values corrected for small sample sizes (AICc) were compared, with the best model represented by the lowest AICc value. Models with a delta ≤ 2 AICc were considered to be similar in their explanatory ability.

$$AICc = -2log + 2K + \frac{2K(K+1)}{(n-K-1)}$$

Where:

K is the number of variables

n is sample size

Model evidence was calculated by Δ_i within each category.

$$\Delta i = AICci - minAICc$$

Model probability was determined by Akaike weight.

$$\omega i = \frac{\exp(-0.5\Delta i)}{\sum exp(-0.5\Delta r)}$$

Models with a delta ≤ 2 AICc were considered to be similar in their explanatory ability. In these cases, and particularly where multiple management factors in the initial analysis could explain a given EEA response, all management factors were tested in the derivation of the final models. The best models for various EEA predictor variables are presented in Tables 2.4 – 2.17. Final regression goodness of fit metrics (R^2), standardized β coefficients, and confidence intervals, are presented in Table 2.18.

Prior to running all models, predictor variables were centered and standardised using "scale" function. All models met assumptions of normality (Shapiro-Wilk normality test) and homogeneity of variance (Levene's test), except for the variable for Xylo which was log transformed. Values in tables with statistical results are based on transformed analyses, all other

values in tables and figures are non-transformed. All statistical analyses were conducted with R studio version 3.4.4 (R Foundation for Statistical Computing, Vienna, Austria).

2.3 Results

Most ranches within a given sampling pair had the same cultivation history (all but two; see Table 2.3), with a total of sixteen ranches having a history of cultivation, and another eight were lacking previous cultivation. The same number of ranches were subject to cultivation (8 of 12) within each grazing treatment. Adaptively grazed ranches had RGR varying from 6.4-90 (Table 2.3), while nAMP ranches generally had much lower RGR values, ranging from 0 (season-long grazing with no rest) to 3.5. One pair of AMP and nAMP ranches sampled had the same RGR (20). Stocking rates varied across ranches but did not demonstrate any difference (P = 0.12) between sample ranches exposed to different grazing systems (Table 2.3).

All soil parameters including MBC, MBN, AN, and soil moisture content, were variable among sampling locations (i.e., pairs), but remained overall similar (P = 0.33, 0.34, 0.94, and 0.98, respectively) between the core grazing treatments (Table 2.3). Among all C-cycling EEAs, mean BAG activity was the highest (184 nmol g soil^{-1} h^{-1}, Table 2.4). In contrast, EEA of Xylo and NAG were typically the lowest among all EEA examined (29 and 69 nmol g soil^{-1} h^{-1}, respectively).

2.3.1. Comparative management effects on extracellular enzyme activity

Within the management subgroup, widely varying fixed effects were evident, depending on the EEA examined. For example, cultivation was of primary importance in affecting Xylo (Table 2.5) but played a lesser role as an alternative explanatory model for each of NAG (Table 2.11) and Phos (Table 2.15), together with the geomean of C-cycling EEAs (Table 2.17).

In contrast, SR was the leading management factor accounting for variation in EEA for each of Cello (Table 2.9), NAG (Table 2.11), Phos (Table 2.15), urease (Table 2.13), as well as the sum of all C-cycling EEAs (Table 2.17), but also provided an equally plausible variable in accounting for observed variation in Xylo (Table 2.5) and BAG (Table 2.7). Overall, SR appeared to be of importance in all EEAs tested. Unlike SR, RGR was of primary importance in explaining variance in BAG (Table 2.7), and potentially Cello (Table 2.9), NAG (Table 2.11), Phos (Table 2.15) as well as the sum of C cycling EEAs (Table 2.17).

2.3.2. Comparative climate effects on extracellular enzyme activity

Values of aridity, as represented by measures of AHM, were most often the leading climatic variable (rather than soil moisture content) accounting for variance in EEA. This was true for all enzymes except for urease (Table 2.13), for which soil moisture was most important, and Xylo, for which the combination of AHM + soil moisture content at field sampling were included. As a result, AHM was included in the final model selection analysis for all EEAs, except for urease.

2.3.3. Comparative effects of soil properties on extracellular enzyme activity

Among the soil physical and chemical properties measured, total AN was the most important variable regulating activity of EEAs responsible for C and N cycling, with only Phos and urease lacking AN in the top models. Soil AN was the sole leading fixed factor accounting for variance in Xylo (Table 2.5), Cello (Table 2.9), NAG (Table 2.11), and total C cycling EEA (Table 2.17), and was an equally plausible factor accounting for variance in BAG EEA (Table 2.7), along with soil pH and the sand:clay ratio. The latter two variables were also the leading factors responsible for variance in Phos EEA (Table 2.15). Urease activity was unrelated to AN, soil pH and soil texture, and was instead related to MBC (Table 2.13).

2.3.4. Overall fixed model effects on individual extracellular enzyme activities

When leading fixed factors from the management, climatic and soil subgroups were tested, select management factors were significant for individual EEAs, depending on the identity of the EEA (Table 2.19). In general, management factors were only significant for Xylo, BAG, and the sum of all C-cycling EEAs, along with Phos and urease. Final fixed effects accounted for 33-54% of the variance in individual C-cycling EEAs, and 37% and 55% of the variance in Phos and NAG activity, respectively (Table 2.19).

The activity of Phos was effected by the combination of cultivation history, sand:clay ratio in soil, and soil pH (Table 2.16), although an alternative model that contained SR instead of cultivation provided a similarly plausible outcome, as did a simpler model containing only texture and pH (Table 2.16). Final beta coefficients showed that activity of Phos increased with greater SR ($\beta = 0.22$; Fig.1), but declined with increases in soil pH ($\beta = -0.47$), a shift to a greater proportion of sand in the soil ($\beta = -0.67$), and the known presence of previous cultivation ($\beta = -0.29$; Table 2.19). Cultivation reduced Phos EEA from 161.62 ± 13.38 to 153.87 ± 8.42 nmol g soil^{-1} h^{-1}. Among these fixed effects, both soil texture and pH appeared to be the most important factors regulating Phos EEA, as evidenced by the lack of overlap of confidence intervals with 0 (Table 2.19). Also of note is that neither soil pH nor soil texture appeared in any other final models for the other EEAs assessed (Table 2.19).

The only other EEA in which cultivation history was a significant factor was Xylo (Table 2.6), in which it appeared in combination with soil AN, either as a simple additive model or a multiplicative model. The simple model was 1.57 times more likely to be the final solution. Final assessment of Xylo responses indicated strong divergence in the impact of these factors on Xylo EEA, with past cultivation reducing Xylo activity from 34.43 ± 4.61 to 25.56 ± 1.44 nmol g

soil^{-1} h^{-1} (β = -0.28) , and greater AN increasing Xylo activity (β = 0.47; Table 2.19; Fig. 2).
Between these two fixed effects, AN appeared to be a more robust factor regulating Xylo activity
based on the confidence intervals (Table 2.19).

Levels of Cello EEA (Table 2.10), together with NAG (Table 2.12), were closely tied to
both AN and AHM. For both these enzymes, their activity declined with greater aridity (β = -
0.14 and -0.42) but increased as soil AN increased (β = 0.38 to 0.70; Table 2.19; Figs. 3A, 3B).
Between these factors, soil AN appeared to be the more robust fixed effect regulating the activity
of these enzymes, as demonstrated by their confidence intervals (Table 2.19). Notably, urease
activity was associated with a very different set of fixed factors compared to NAG in the final
analysis among group variables (Table 2.14). Urease was the only enzyme impacted by cattle
SR, with greater urease activity observed in relation to increased stocking (β = 0.29; Fig.4), a
response that appeared to be robust based on associated confidence intervals (Table 2.19).
Urease activity was also the only EEA to be directly associated with soil moisture (β = 0.31) and
MBC (β = 0.30) in the final analysis (Table 2.14). Urease activity generally increased in wetter
soils, and was positively associated with MBC (Table 2.19).

The final C-cycling enzyme, BAG, was the only enzyme for which RGR appeared in the
final model (Table 2.8). Activity of BAG increased in relation to a greater RGR (β = 0.10; Table
2.19; Fig. 5). This same enzyme also increased sharply with greater soil AN (β = 0.43) but
declined markedly in relation to increasing aridity (β = -0.37), as represented by regional AHM
values of individual ranch locations (Table 2.19). Of note is that the overall mean activity of all
three C-cycling enzymes (Table 2.18) responded very similar to that of BAG (Table 2.8), albeit
with dampened beta coefficients; total C-cycling EEA increased with a longer RGR (β = 0.14)
and greater soil AN (β = 0.34), but declined with aridity (β = -0.17; Table 2.19; data not shown).

2.4 Discussion

2.4.1. Management factors

This field study highlights the importance of analysing the activities of a variety of enzymes to assess changes in soil biogeochemical activity in response to grassland management and environmental factors. Enzymes responsible for macronutrient (N and P) cycling, as well as C cycling, were found to respond to management activities, though the identity of the significant activities varied depending on the mineral involved and the specific chemical pathway represented by the EEA.

Grasslands with a reported history of cultivation had lower soil EEA for both Xylo and Phos, even though five or more years had passed since the last cultivation event. The finding that cultivation decreased Xylo and Phos EEA is consistent with the hypothesis that cultivation altered soil EEA. Depressed Xylo and Phos EEAs in cultivated grassland soil suggests that legacy effects of previous soil disturbance exist that changed SOM composition, in turn leading to reductions in substrate and enzyme synthesis. For example, cultivation is known to enhance soil microbial decomposition of organic matter, which can markedly decrease soil C levels (Whalen et al, 2003), and this alone may account for the reduction in Xylo activity. Moreover, subsequent seeding of forage species into cultivated land may not be able to replace lost SOM at the same rate as ongoing decomposition (Dormaar & Willms, 2000). Alternatively, a change in the composition of SOM due to cultivation (Katsalirou et al., 2010) may alter opportunities for C cycling, including the amount of microbial biomass C (Katsalirou et al., 2010; Wallenius et al., 2011), and thus impact Xylo activity. While Xylo was impacted by cultivation, it is notable that neither BAG nor Cello responded to this disturbance, and suggests the primary C transformation pathway altered by cultivation within these grasslands at this point in time is through the degradation of oligosaccharides of xylose (i.e., hemicellulose) rather than cellulose. However,

cultivation may not have been the sole factor that decreased Xylo EEA. Previous studies of tilled and no-tilled grasslands (Masciandaro & Ceccanti, 1999; Štursová & Baldrian, 2011; Wal et al., 2006) showed similar results where Xylo EEA decreased in cultivated fields. Xylosidase is generally of saprotrophic basidiomycetes origin (Štursová & Baldrian, 2011) and soil cultivation destroys basidiomycetes mycelia and results in a relative decrease of Xylo synthesis in cultivated soils (Šnajdr et al., 2008; Štursová & Baldrian, 2011).

In the case of reduced P cycling, cultivation may have increased the ratio of C:NaOH-extractable organic P, which would increase plant available P in soil due to decreased Phos EEA (Dormaar & Willms, 2000). This in turn, would reduce the need for phosphatase activity to promote P supply, and therefore account for the observed reduced in Phos activity. In all likelihood, cultivation impacts on biogeochemical cycling can be expected to decline several years after the practice is stopped (Dormaar & Willms, 2000), particularly with the ongoing addition of OM inputs from perennial plant growth and cattle dung deposition. However, our results suggest that these legacy effects persist for some time.

Among the subgroup of management factors tested, SR was a key factor regulating the EEA of all enzymes examined, although in the final comparative analysis with environmental factors, SR was of greatest importance in regulating only the activity of urease and Phos. This supports the third hypothesis posed in this study. Both urease and Phos activity increased in relation to greater SR, and may reflect the fact that cattle excreta (urine and dung) returns the vast majority of N (urine, including urea) and P (dung) consumed by grazing animals to the soil, leading to its rapid mineralisation and ample supply of these nutrients for microbes (Lantinga et al., 1987). Greater SR would return larger amounts of excreta, in turn providing more urea for microbial breakdown. This finding agrees with previous studies that concluded high urea

deposition under high SR were responsible for increasing urease EEA (Cui & Holden, 2015; Kizilkaya & Dengiz, 2010), with a similar finding for Phos (Adetunji et al., 2017; Criquet et al., 2007; Nannipieri et al., 2011). The close direct (i.e., positive) association between MBC and urease EEA further reinforces that soil microorganisms were likely the main urease degrading organisms present within these grassland soils (Sarathchandra et al., 1984).

High activity of Phos in all grasslands regardless of the grazing system used may indicate a low concentration of P and high competition for plant available P in the study soils. A previous study examining defoliation effects on EEA in the Mixedgrass subregion in Alberta (Hewins et al., 2016) had similar results showing high Phos activity in plots with varying defoliation frequency and intensity, likely due to high competition for available P between plants and microorganisms. The latter was explained by the requirement of ample available P for plants to recover within intensively defoliated sites, and thereby continue their growth under less frequent and less intensive defoliation regimes (Hewins et al., 2016); in both cases low available P was the trigger for the high Phos EEA.

An important objective in this study was the comparative assessment of AMP and non-AMP grazing. While grasslands subject to these different grazing practices did not differ in SR, they did differ in the temporal pattern of grassland use by livestock, as exemplified by the length of the rest period relative to grazing events during the growing season (Table 2.3, Appendix C), and therefore provided a key distinguishing characteristic of AMP grazing. This metric (rest to grazing ratio, or RGR), was found to be an important factor for five different enzymes when assessed within the management subgroup, and in the final analysis (including environmental factors), also explained variance in both BAG activity, as well as the total activity of C-cycling

enzymes. The lack of strong effects for Xylo and Cello suggests that BAG was a particularly responsive enzyme to RGR, to the point of contributing to the overall response in C-cycling.

Of note is that BAG EEA was greater within grassland soil from soil subject to higher RGR, and this leads us to reject our hypothesis related to grazing system effects on C-cycling enzymes. While the specific mechanism for this effect is unknown, there are several possible explanations. AMP ranches with long rest periods relative to individual grazing periods may have had greater BAG activity because cattle tended to graze individual paddocks more evenly, and this could allow for more uniform dung deposition across the grassland (Teague et al., 2009). A large number of cattle in a short period of time may increase substrate availability for enzymes in pulse events by increasing dung and urea deposition on the soil surface, while long post-grazing periods may give sufficient time for microorganisms to recover and grow in an undisturbed environment.

Alternatively, brief grazing periods may promote either plant growth (Bork et al., 2017; Broadbent et al., 2019), or the retention of select plant species capable of withstanding that disturbance regime (Broadbent et al., 2016), and thereby alter the quality (i.e., composition) of plant (shoot and root) mass inputs. For example, if a high RGR leads to greater retention of certain plant species, including grazing tolerant grasses, that may lead to leaf and root litter deposition that is higher in more degradable forms of C, in turn supporting BAG activity. Previous studies in Alberta grasslands have found that EEA in grass litter is dependent on the identity of the plant species, with the EEA in litter of *Poa pratensis* L., a species known to increase under grazing due to its tolerance to defoliation (Willms & Quinton, 1995), having particularly high decomposition rates and coincident with elevated EEA (Chuan et al., 2020). Differences in EEA were apparent among different forage grasses, including those native and

introduced to Alberta (Chuan et al., 2020), and could also account for the differences in EEA detected in relation to cultivation reviewed earlier. Moreover, as AMP grazing can lead to more uniform defoliation impacts on vegetation (Teague et al., 2009), plant regrowth could be more uniform under less patchy grazing, with a greater likelihood for plant inputs to be younger, further altering substrate quality and observed EEA.

In contrast to ranches with a high RGR, grasslands experiencing longer periods of cattle use and limited recovery during the growing season may lead to increased selective grazing (including patch grazing, and possibly localized overgrazing), with uneven dung distribution (Teague et al., 2009). These alterations may decrease EEA in places with low substrate availability, as well as lead to nutrient leaching and C loss in places with high dung deposition (Schipper et al., 2017).

The resulting EEA documented here also showed the importance of analysing not one but several enzymes of each nutrient element. Based on both previous work (Hewins *et al.*, 2015, 2016) and the current study it is important to include BAG, Cello, NAG, and Phos EEA in any assessment of grassland soil responses. Furthermore, it is important to include in future studies other enzymes that are important in nutrient cycling, for example, the group of nitrogenase metalloenzymes that fix dinitrogen from air to ammonia form (Kuypers et al., 2018) and ammonia monooxygenase that can oxidize ammonia to nitrite (Kuypers et al., 2018). This information would provide a better understanding of nutrient cycling processes in grazed grasslands.

2.4.2. Soil and climatic regulators of EEA

Despite the importance of management factors in regulating EEAs, soil properties and climatic factors (macro and micro-climatic) were often the primary factors regulating the activity of enzymes related to C, N and P-cycling. Urease was the only enzyme best explained by soil moisture itself, presumably because soil water is a necessary precursor to allow microbes to actively break down urea into ammonia and carbon dioxide (Sahrawat, 1984). For most other C and N-cycling enzymes (BAG, Cello, NAG), macroclimate conditions, as represented by increasing aridity (AHM) demonstrated a strong negative relationship with EEA. Increased aridity may have decreased EEA due to diffusion losses of substrate (Steinweg et al., 2012). As AHM will be closely correlated with several other environmental metrics, such as soil organic matter, due to its impact on plant growth and associated C input to the ecosystem, it is also possible that the negative impact of AHM reflects a generalized decrease in soil organic substrates. Notably, MBC was only found to be a major factor regulating Phos activity. Not surprisingly, Phos EEA increased with MBC levels, and for this same enzyme, no climatic metric appeared in the top explanatory model, possibly because MBC was inversely correlated with AHM (Appendix A).

Soil texture and pH were of relatively minor importance in regulating the EEA of C and N cycling enzymes, but were of primary importance for P. Soil pH varied from acid to neutral, and soils with high (close to neutral) soil pH levels led to decreased Phos EEA. Our finding of a soil pH effect on Phos suggests that low pH levels triggered Phos synthesis, which may reflect a low concentration of available P in acid soils (Devau et al., 2009). Also, soils with high clay content decreased Phos activity, and is similar to results of other studies (Rakhsh & Golchin,

2018; Tietjen & Wetzel, 2003). Decreases of Phos activity may be explained by immobilization by adsorbing enzymes on clay particles (Steinweg et al., 2012; Tietjen & Wetzel, 2003).

Among soil properties, soil AN was the main fixed factor associated with greater soil EEA, appearing for all C-cycling enzymes as well as NAG. My finding is consistent with the literature about biochemical C cycling in Alberta ranches (Chuan et al., 2020; Hewins et al., 2016, 2015). Increased AN concentration in soil may have enhanced C-cycling EEAs by decreasing the ratio of C:N in plant tissues, and greater relative N concentrations may create more optimal conditions for increasing microbial activity, as exemplified by C mineralising EEAs (Chuan et al., 2020).

Chitin degrading NAG activity was one of the lowest in the soils studied, which may be related to the low concentrations of fungi found in these soils since chitin is a major part of fungi cells. Previous studies have found a correlation between NAG EEA and fungal biomass in soil (Miller et al., 1998; Sinsabaugh et al., 2008). Moreover, trampling by cattle might destroy fungal mycelia and decrease fungal growth in rangeland (Clegg, 2006), although in this case a greater impact could be expected from either higher SRs or a longer RGR, neither of which occurred. Importantly, the results here for the N cycling enzymes (NAG and urease) do not implicate differences among grazing systems (i.e., RGR).

2.5 Conclusion

I conclude that grassland management, climate, and soil properties all effected EEAs related to C and nutrient (N and P) cycling. This study showed that both cultivation history and ongoing grazing practices (SR and RGR) had both positive and negative effects on EEAs. While high SR and longer RGR were associated with increased EEAs (urease, Phos, BAG, and geomean of C-

cycling enzymes), cultivation decreased activity of those enzymes responsible for C (Xylo) and P (Phos) cycling. Notably, enzyme activities related to C mineralization (BAG) were greater in soils with longer RGR, as emphasized on ranches employing AMP grazing. Among environmental factors, soil N availability was the main factor altering EEAs, followed by climatic conditions. Nitrogen (NAG) and P EEAs were related to available sources of these nutrients and environmental conditions. Future research on microbial composition, and more detailed C dynamics in soil, as well as nitrification and denitrification pathways, could be essential in understanding the mechanisms regulating C and nutrient cycling, with implications for C sequestration and greenhouse gas dynamics in grazed grasslands of Alberta.

Chapter 3. Synthesis and Future Research

Grasslands occupy a quarter of the planet's terrestrial surface and constitute 70% of the world's agricultural land area (Henderson et al., 2015). Grasslands maintain the livelihood of people by providing forage for cattle, supporting clean water supply, and facilitating nutrient cycling (White et al., 2000). Grasslands have the potential to mitigate GHG emissions by sequestering C in soil, which otherwise would contribute to increasing atmospheric CO_2 levels. Climate, soil properties, and land management are primary factors regulating grassland condition and function.

In this study, I examined the effects of previous management (cultivation) and ongoing grazing activities on soil EEA involved in C and nutrient (N and P) mineralization within 24 Alberta ranches. The second chapter of this thesis includes results of a field experiment examining extracellular enzyme activity (EEA) in grassland soils from these ranches. More specifically, the activity of six enzymes involved in C, N, and P cycling were analysed on paired ranches in order to identify the effect of management and environmental factors. In the synthesis I summarised key findings of this study and review the implications of these findings for future C storage and nutrient cycling within Alberta grasslands.

Results showed that both historical and current ranch management altered EEAs responsible for C and nutrient cycling. Ranches with a history of cultivation had lower Xylo and Phos EEA, which has implications for long-term C and P storage in grasslands. On the one hand, soil disturbance by tillage may have changed soil structure and microenvironment that was likely to increase available P and therefore decrease Phos activity. On the other hand, cultivation could also have shifted soil microbial composition and decreased Xylo activity, in turn leading to

decreased C mineralisation and storage in soil. The latter is a significant concern as it may lead to an overall decrease in SOM (Cenini et al., 2016).

Lengthy rest periods after grazing during the growing season increased BAG EEA in soil. The increase in BAG activity, which is involved in the latter stages of cellulose decomposition, could again reflect fundamental changes in microbial activity, organic matter decomposition and therefore associated C turnover, thereby altering C accumulation in grazed soils. In contrast, high SR may be responsible for increasing GHG emissions due to enhanced urease activity that produces ammonium and CO_2. Findings of this study provide evidence that enzyme activity is regulated by both grazing management practices, including more nuanced aspects of the grazing system, and the history of soil management even decades after last cultivation.

Regional climate and soil properties were also primary factors regulating soil EEAs in the grasslands studied. Available N was positively correlated with all C-cycling enzymes, indicating that changes in soil C:N ratio may alter C and N mineralisation. Meanwhile, increased aridity of the grassland, as represented by AHM, decreased those EEAs responsible for C-cycling and C turnover. Further work is needed to understand the optimal ranch management practices necessary to optimize soil C storage and GHG mitigation, including more mechanistic linkages between EEAs, N availability and moisture conservation measures, that in turn, may alter SOM mineralisation (either positively or negatively).

Overall, this research provides a better understanding of grazing systems and environmental effects on grassland C dynamics and nutrient cycling. To further develop our understanding, it will be important to study the intensity and directionality of SOM decomposition in grassland soils during grazing and post grazing periods, including linkages to EEA during these periods. It is important to identify the optimal length of rest period, and how

this may depend on AHM, as the latter was the main limiting factor that determined EEA activity responsible for C and N mineralisation in Alberta grasslands. Furthermore, it will be valuable to study the effect of seeding of plants with different chemical composition and biomass inputs, including in comparison to native grasslands, on C-cycling EEA within soils and corresponding and decomposition of SOM. Additional research may identify the optimal available soil N levels that will alter C-cycling EEAs and C mineralisation such that C storage can be maximized. Finally, I did not analyse plant available P in these soils and its relationship with Phos EEA. It may be of interest to study soil P because of its importance in increasing forage quality and plant resistance to drought. Last, while this thesis describes the importance of disturbance and grazing management in regulating EEA, further work is needed to understand how these changes in biogeochemical cycling translate into the provision of various grassland services, which include soil C storage and GHG uptake, but also other socio-economic benefits such as forage quantity and quality, as well as ecosystem biodiversity.

Table 2.1. Description of predictor variables by subgroup used in the analysis of extracellular enzyme activity in ranches.

Subgroup	Predictor variable	Description
Management	Cultivated	Presence/absence of known cultivation history in a ranch
	Stocking rate	Measure of grazing intensity, computed from survey information on the number of animals and the specific length of grazing, reported in animal-unit-months (AUM) per ha. An AUM is a 454 kg cow, with or without a calf, grazing for one month.
	Rest to graze ratio	The number of days of rest per day of active grazing during the growing season (May 1 to July 1)
Climate	AHM[†]	Index of aridity, derived from the combination of MAT[‡] and MAP[§], AHM = (MAT+10)/(MAP/1000)
	Soil moisture	Actual soil moisture (%) at the time of soil sampling (removal) in the field
Soil properties	Sand:Clay	Ratio of %sand to %clay
	Soil pH	Soil acidity/alkalinity
	AN	Plant available nitrogen concentration in soil
	MBC	Microbial biomass C

† AHM – annual heat moisture index

‡ MAT – mean annual temperature, MAT = sum of mean temperature (January-December)/12

§ MAP – mean annual precipitation, average of rainfall of last 30 years

Table 2.2. Baseline regression models examined in the initial analysis, split into the sub-groups of management factors, macro- and microclimate, and local soil properties, for the EEA associated with soil (0-15 cm layer) removed from individual ranches. Null model (interaction only) present in italic.

Groups	Regression models
Null	*1 + (Pair/Ranch)[†]*
Management	Cultivated + (Pair/Ranch)
	SR[‡] + (Pair/Ranch)
	RGR[§] + (Pair/Ranch)
	Cultivated + SR + (Pair/Ranch)
	Cultivated + RGR + (Pair/Ranch)
	Cultivated + SR + RGR+ (SR * RGR) + (Pair/Ranch)
Climate	AHM[#] + (Pair/Ranch)
	Soil moisture + (Pair/Ranch)
	AHM + Soil moisture + (Pair/Ranch)
Soil properties	Sand:Clay + (Pair/Ranch)
	Soil pH + (Pair/Ranch)
	AN[††] + (Pair/Ranch)
	MBC[‡‡] + (Pair/Ranch)
	Sand:Clay + Soil pH + (Pair/Ranch)
	Sand:Clay + Soil pH + AN + (Pair/Ranch)
	Sand:Clay + Soil pH + AN + MBC + (Pair/Ranch)

† fixed effect, one AMP and one nAMP ranches within a pair

‡ stocking rate

§ rest to graze ratio

annual heat moisture index

†† plant available nitrogen

‡‡ microbial biomass carbon

Table 2.3. Summary of the average (Mean), minimum (Min), maximum (Max), and standard deviation (StDev) of various management, climatic, and soil parameters encountered across study ranches in the adaptive multi-paddock (AMP) and non-adaptive multi-paddock (nAMP) groups during the growing season of 2018, in Alberta, Canada. Means of different grazing treatments with an * differ, at P < 0.05.

Response	df	F-stat	P	Mean	Min-Max	StDev	Mean	Min-Max	StDev
					AMP			nAMP	
SR[†], AUM ha^{-1}	23	0.51	0.42	3.47	1.37-6.97	1.96	2.90	0.33-8.39	2.74
RGR[‡]	23	21.78	0.01	26.22*	6.43-90	25.66	2.55*	0-20	5.50
MAT[§], °C	23	1.04	0.96	3.10	2.-4.1	0.58	3.10	2-4.1	0.57
MAP[#], mm	23	0.94	0.99	454.29	332.30-539.80	59.07	454.29	332.30-539.80	60.79
AHM[††]	23	0.97	0.98	30.08	24.30-44.10	5.01	30.10	24.30-44.20	5.08
Soil moisture, %	23	1.08	0.98	20.23	2.48-51.91	9.49	20.28	2.47-42.39	9.09
Soil pH	23	1.03	0.41	5.98	4.67-7.40	0.62	6.13	5.37-7.5	0.61
AN[‡‡], mg kg^{-1}	23	0.94	0.64	18.87	3.56-47.26	10.68	17.41	5.00-49.69	10.97
MBC[§§], mg kg^{-1}	23	0.62	0.33	122.66	22.39-362.74	72.16	145.62	24.82-356.22	91.50
MBN[##], mg kg^{-1}	23	0.53	0.34	43.77	6.86-98.46	22.90	51.45	6.84-111.63	31.31
Clay, %	23	1.54	0.97	24.34	2.30-41.20	10.86	24.41	4.1-34	8.75
Sand, %	23	1.33	0.41	37.96	17.9-90.5	18.19	41.98	30.5-90.1	15.76
Silt, %	23	1.72	0.18	37.71	7.20-51.40	11.97	33.61	5.8-41.3	9.12
Sand:Clay	23	3.42	0.56	4.72	0.58-39.35	10.72	3.29	0.91-21.97	5.79

† stocking rate
‡ rest to graze ratio
§ mean annual temperature
# mean annual precipitation
†† annual heat moisture index
‡‡ available nitrogen
§§ microbial biomass carbon
microbial biomass nitrogen

Table 2.4. Mean activity and standard error of extracellular enzyme activities responsible for carbon, nitrogen and phosphorus cycling in grassland soils, subject to either adaptive multi-paddock (AMP) grazing, or conventional (nAMP) grazing, across 12 pairs of ranches sampled in June, July, and September 2018 in Alberta, Canada. Units are nmol g^{-1} h^{-1} for xylosidase (Xylo), β-glucosidase (BAG), cellobiosidase (Cello), N-acetylglucosidase (NAG), and phosphatase (Phos) activities and nmol NH_4^+ g^{-1} h^{-1} for urease activity.

Grazing system	Xylo	BAG	Cello	NAG	Urease	Phos
AMP	29.1 ± 2.7	184.0 ± 11.1	163.3 ±13.9	66.6 ± 3.5	69.1 ± 0.04	161.8 ±10.8
nAMP	27.9 ± 2.7	165.2 ±10.3	161.8 ±13.6	67.9 ±5.1	70.3± 0.05	151.1 ± 9.2

Table 2.5. Summary results comparing regression models within each sub-group for factors impacting xylosidase activity. The best model within each subgroup is in bold. Alternative model within the management subgroup considered to be equally plausible (based on ΔAICc ≤ 2) are underlined.

Candidate models	K[†]	AICc[‡]	ΔAICc[§]	ω_i[#]
Management Subgroup				
Cultivated	**5**	**42.51**	**0.00**	**0.428**
SR[††]	5	44.30	1.79	0.175
RGR [‡‡]	5	44.85	2.34	0.128
Cultivated + SR	6	44.87	2.36	0.133
Cultivated + RGR	6	45.01	2.50	0.122
Cultivated + SR + RGR + (SR * RGR)	8	49.94	7.43	0.010
Climate Subgroup				
AHM[§§]	5	39.87	1.36	0.215
Soil moisture	5	38.82	0.31	0.362
AHM + Soil moisture	**6**	**38.51**	**0.00**	**0.423**
Soil Subgroup				
Sand:Clay	5	39.69	10.79	0.003
Soil pH	5	44.67	15.87	0.001
AN[##]	**5**	**28.80**	**0.00**	**0.714**
MBC[†††]	5	43.02	14.22	0.001
Sand:Clay + Soil pH	6	41.28	12.48	0.001
Sand:Clay + Soil pH + AN	7	31.28	2.48	0.207
Sand:Clay + Soil pH + AN + MBC	8	33.36	4.56	0.073

† number of model parameters
† number of model parameters
‡ Akaike information criterion corrected
§ difference between AICc and the smallest AICc
# model weight (probability)
†† stocking rate
‡‡ rest to graze ratio
§§ annual heat moisture index
plant available nitrogen
††† microbial biomass carbon

Table 2.6. Summary results comparing regression models on xylosidase activity responses as a function of leading variables from the management, climate, and soil parameter subgroups. The best model is in bold, the null and global (all variables) models are italicized, while alternative models considered to be equally plausible (based on $\Delta AIC_c \leq 2$) to the leading model are underlined.

Ranked model categories	K[†]	AIC$_c$[‡]	ΔAIC$_c$[§]	ω_i[#]
Cultivation + AN[††]	**6**	**27.80**	**0.00**	**0.349**
<u>Cultivation + AN + (Cultivation*AN)</u>	7	28.70	0.90	0.223
<u>AN</u>	5	28.89	0.99	0.213
SR + AN + (SR * AN)	7	30.62	2.82	0.085
SR + AN	6	31.37	3.57	0.059
AHM[‡‡] + Soil moisture + AN	7	31.94	4.14	0.044
Cultivation + SR + AHM +Soil moisture + AN	*8*	*30.93*	*3.13*	*0.018*
Cultivation + AHM+ Soil Moisture	7	37.55	9.75	0.003
Cultivation + Soil moisture	6	38.39	10.49	0.002
AHM +Soil moisture	6	38.58	10.68	0.002
Cultivation +AHM	6	39.24	11.44	0.001
SR + Soil moisture	6	40.60	12.80	0.001
SR + AHM + Soil moisture	7	40.96	13.16	0.000
SR + AHM	6	42.33	14.53	0.000
Null	*4*	*42.43*	*14.63*	*0.000*
Cultivation	5	42.50	14.70	0.000
SR	5	44.29	16.49	0.000

† plant available nitrogen
‡ Akaike information criterion corrected
§ difference between AIC$_c$ and the smallest AIC$_c$
# model weight (probability)
†† plant available nitrogen
‡‡ annual heat moisture index

Table 2.7. Summary results comparing regression models within each sub-group for factors impacting β-glucosidase activity. The best model within each subgroup is in bold. Alternative models within the management and soil subgroups considered to be equally plausible (based on ΔAICc ≤ 2) are underlined.

Candidate models	K[†]	AICc[‡]	ΔAICc[§]	ω_i[#]
Management Subgroup				
Cultivated	5	-148.29	3.39	0.091
SR[††]	5	-149.84	1.84	0.198
RGR[‡‡]	**5**	**-151.60**	**0.00**	**0.496**
Cultivated + SR	6	-147.34	4.34	0.057
Cultivated + RGR	6	-149.01	2.61	0.135
Cultivated + SR + RGR + (SR * RGR)	8	-145.50	6.10.	0.024
Climate Subgroup				
AHM[§§]	**5**	**-159.30**	**0.00**	**0.771**
Soil moisture	5	-150.19	9.19	0.000
AHM + Soil moisture	6	-156.89	2.49	0.222
Soil Subgroup				
Sand:Clay	5	-158.43	5.43	0.036
Soil pH	5	-150.02	13.82	0.001
AN[##]	5	-162.52	1.32	0.277
MBC[†††]	5	-148.45	15.45	0.000
Sand:Clay +Soil pH	6	-157.54	6.34	0.023
Sand:Clay +Soil pH + AN	**7**	**-163.80**	**0.00**	**0.537**
Sand:Clay +Soil pH + AN + MBC	8	-161.09	2.89	0.127

† number of model parameters
† number of model parameters
‡ Akaike information criterion corrected
§ difference between AICc and the smallest AICc
# model weight (probability)
†† stocking rate
‡‡ rest to graze ratio
§§ annual heat moisture index
plant available nitrogen
††† microbial biomass carbon

Table 2.8. Summary results comparing regression models on β-glucosidase responses as a function of leading variables from the management, climate, and soil parameter subgroups. The best model is in bold, the null and global (all variables) models are italicized, while alternative models considered to be equally plausible (based on ΔAICc ≤ 2) to the leading model are underlined.

Ranked model categories	K[†]	AICc[‡]	ΔAICc[§]	ωi[#]
RGR + AHM + AN	**7**	**-166.24**	**0.00**	**0.321**
RGR + AN		-164.94	1.29	0.168
RGR[††] +AHM[‡‡] +Sand:Clay+soil pH+AN[§§]	9	-164.21	2.03	0.116
Sand:Clay+Soil pH+ AN	7	-163.85	2.38	0.097
RGR+AN+(RGR*AN)	7	-163.47	2.77	0.080
AHM+Sand:Clay+soil pH +AN	8	-162.67	3.56	0.054
SR + AHM + AN		-162.62	3.62	0.052
RGR + SR +AHM +Sand:Clay+soil pH+AN		*-161.71*	*4.52*	*0.033*
SR + AN		-160.25	5.99	0.016
SR +AHM +Sand:Clay+soil pH+AN		-160.18	6.05	0.016
SR + AN + (SR * AN)		-159.90	6.33	0.014
AHM	5	-159.33	6.90	0.010
RGR+AHM	6	-159.15	7.09	0.009
SR + AHM		-157.16	9.07	0.003
RGR+AHM+RGR*AHM	7	-156.56	9.68	0.003
SR + AHM + (SR * AHM)		154.06	12.81	0.001
RGR	5	-151.62	14.62	0.000
Null	*4*	*-150.72*	*15.52*	*0.000*
SR		-149.78	16.46	0.000

† number of model parameters
‡ Akaike information criterion corrected
§ difference between AICc and the smallest AICc
# model weight (probability)
†† rest to graze ratio
‡‡ annual heat moisture index
§§ plant available nitrogen

Table 2.9. Summary results comparing regression models within each sub-group for factors impacting cellobiosidase activity. The best model within each subgroup is in bold. Alternative model within the management subgroup considered to be equally plausible (based on ΔAICc ≤ 2) are underlined.

Candidate models	K†	AICc‡	ΔAICc§	ωi#
Management Subgroup				
Cultivated	5	-137.27	2.02	0.165
SR††	**5**	**-139.29**	**0.00**	**0.452**
<u>RGR‡‡</u>	5	-137.50	1.79	0.184
Cultivated + SR	6	-136.94	2.35	0.139
Cultivated + RGR	6	-134.89	4.40	0.050
Cultivated + SR + RGR + (SR * RGR)	8	-131.73	7.56	0.010
Climate Subgroup				
AHM§§	**5**	**-145.16**	**0.00**	**0.676**
Soil moisture	6	-139.80	5.36	0.046
AHM + Soil moisture	6	-143.38	1.78	0.277
Soil Subgroup				
Sand:Clay	5	-142.57	7.18	0.018
Soil pH	5	-137.62	12.13	0.002
AN##	**5**	**-149.75**	**0.00**	**0.655**
MBC†††	5	-138.70	11.05	0.003
Sand:Clay +Soil pH	6	-140.90	8.85	0.008
Sand:Clay +Soil pH + AN	7	-147.69	2.06	0.234
Sand:Clay +Soil pH + AN + MBC	8	-145.64	4.11	0.084

† number of model parameters
† number of model parameters
‡ Akaike information criterion corrected
§ difference between AICc and the smallest AICc
# model weight (probability)
†† stocking rate
‡‡ rest to graze ratio
§§ annual heat moisture index
plant available nitrogen
††† microbial biomass carbon

Table 2.10. Summary results comparing regression models on cellobiosidase activity responses as a function of leading variables from the management, climate, and soil parameter subgroups. The best model is in bold, the null and global (all variables) models are italicized, while alternative models considered to be equally plausible (based on $\Delta AIC_c \leq 2$) to the leading model are underlined.

Ranked model categories	K[†]	AIC_c[‡]	ΔAIC_c[§]	ω_i[#]
AHM[††] +AN[‡‡]	**6**	**-151.77**	**0.00**	**0.387**
<u>AN</u>	5	-149.77	2.00	0.142
SR[§§] +AHM+AN	7	-149.40	2.37	0.118
RGR +AHM+AN	7	-149.29	2.48	0.112
SR+AN	6	-147.88	3.89	0.055
RGR + AN + (RGR * AN)	7	-147.77	3.99	0.052
RGR + AN	6	-147.67	4.09	0.050
RGR + SR + AHM + AN	*8*	*-146.84*	*4.92*	*0.033*
SR+AN+(SR*AN)	7	-145.32	6.45	0.015
AHM	5	-145.20	6.57	0.015
SR+AHM+(SR*AHM)	7	-143.62	8.14	0.006
SR+AHM	6	-143.43	8.34	0.004
RGR + AHM	6	-142.66	9.11	0.001
RGR + AHM + (RGR * AHM)	7	-140.12	11.65	0.001
Null	*4*	*-139.75*	*12.02*	*0.001*
SR	5	-139.28	12.49	0.001
RGR	5	-137.48	14.28	0.000

† number of model parameters
‡ Akaike information criterion corrected
§ difference between AIC_c and the smallest AIC_c
# model weight (probability)
†† annual heat moisture index
‡‡ plant available nitrogen
§§ stocking rate

Table 2.11. Summary results comparing regression models within each sub-group for factors impacting N-acetyl-β glucosidase. The best model within each subgroup is in bold. Alternative models within the management subgroup considered to be equally plausible (based on ∆AICc ≤ 2) are underlined.

Candidate models	K[†]	AICc[‡]	∆AICc[§]	ωi[#]
Management Subgroup				
<u>Cultivated</u>	5	-233.73	0.70	0.249
SR[††]	**5**	**-234.43**	**0.00**	**0.352**
<u>RGR[‡‡]</u>	5	-233.50	0.93	0.221
Cultivated + SR	6	-231.94	2.49	0.101
Cultivated + RGR	6	-231.11	3.32	0.067
Cultivated + SR + RGR + (SR * RGR)	8	-227.14	7.29	0.009
Climate Subgroup				
AHM[§§]	**5**	**-239.03**	**0.0**	**0.525**
Soil moisture	5	-237.20	1.83	0.210
AHM + Soil moisture	6	-237.66	1.37	0.265
Soil Subgroup				
Sand:Clay	5	-239.03	22.13	0.000
Soil pH	5	-233.51	27.65	0.000
AN[##]	**5**	**-261.16**	**0.00**	**0.673**
MBC[†††]	5	-237.55	23.61	0.000
Sand:Clay +Soil pH	6	-236.86	24.30	0.000
Sand:Clay +Soil pH + AN	7	-258.88	2.28	0.215
Sand:Clay +Soil pH + AN + MBC	8	-257.57	3.59	0.112

† number of model parameters
† number of model parameters
‡ Akaike information criterion corrected
§ difference between AICc and the smallest AICc
# model weight (probability)
†† stocking rate
‡‡ rest to graze ratio
§§ annual heat moisture index
plant available nitrogen
††† microbial biomass carbon

Table 2.12. Summary results comparing regression models on N-acetyl-β glucosidase activity responses as a function of leading variables from the management, climate, and soil parameter subgroups. The best model is in bold, the null and global (all variables) models are italicized, while alternative models considered to be equally plausible (based on $\Delta AIC_c \leq 2$) to the leading model are underlined.

Ranked model categories	K[†]	AIC$_c$[‡]	ΔAIC$_c$[§]	ω$_i$[#]
AN[††]	**5**	**-261.11**	**0.00**	**0.360**
<u>AHM[‡‡] +AN</u>	6	-259.78	1.36	0.180
Cultivated + AN	6	-258.75	2.36	0.110
SR[§§] +AN	6	-258.51	2.60	0.098
RGR[##] +AN	6	-258.50	2.61	0.097
Cultivated+AN+(Cultivated*AN)	7	-258.17	2.94	0.083
RGR+AN+RGR*AN	7	-256.89	4.22	0.044
SR+AN+SR*AN	7	-255.81	5.30	0.025
Cultivated+SR+RGR+AHM+AN	*9*	*-251.18*	*9.93*	*0.003*
AHM	5	-238.97	22.14	0.000
Cultivated + AHM	6	-237.10	24.01	0.000
SR + AHM	6	-236.65	24.46	0.000
RGR + AHM	6	-236.39	24.72	0.000
Cultivated + AHM+(Cultivated *AHM)	7	-236.12	24.99	0.000
Null	*4*	*-235.96*	*25.15*	*0.000*
SR	5	-234.39	26.72	0.000
SR+ AHM + (SR * AHM)	7	-234.36	26.75	0.000
RGR + AHM + (RGR * AHM)	7	-233.90	27.21	0.000
Cultivated	5	-233.70	27.41	0.000
RGR	5	-233.46	27.65	0.000

† number of model parameters
† number of model parameters
‡ Akaike information criterion corrected
§ difference between AIC$_c$ and the smallest AIC$_c$
# model weight (probability)
†† plant available nitrogen
‡‡ annual heat moisture index
§§ stocking rate
rest to graze ratio

Table 2.13. Summary results comparing regression models within each sub-group for factors impacting urease activity. The best model within each subgroup is in bold. Alternative models considered to be equally plausible (based on ΔAICc ≤ 2) are underlined.

Candidate models	K[†]	AICc[‡]	ΔAICc[§]	ωi[#]
Management Subgroup				
Cultivated	5	12.20	3.65	0.098
SR[††]	**5**	**8.55**	**0.00**	**0.601**
RGR[‡‡]	5	12.21	3.64	0.093
Cultivated + SR	6	11.23	2.62	0.163
Cultivated + RGR	6	14.65	6.10	0.028
Cultivated + SR + RGR + SR * RGR	8	16.16	7.61	0.013
Climate Subgroup				
AHM[§§]	5	7.49	11.14	0.003
Soil moisture	**5**	**-3.65**	**0.00**	**0.784**
AHM + Soil moisture	6	-1.05	2.60	0.213
Soil Subgroup				
Sand:Clay	5	5.81	5.25	0.022
<u>Soil pH</u>	5	2.51	1.95	0.119
AN[##]	5	7.95	7.39	0.008
MBC[†††]	**5**	**0.56**	**0.00**	**0.316**
<u>Sand:Clay +Soil pH</u>	6	2.09	1.53	0.147
<u>Sand:Clay +Soil pH + AN</u>	7	1.37	0.81	0.210
<u>Sand:Clay +Soil pH + AN + MBC</u>	8	1.70	1.14	0.179

† number of model parameters
† number of model parameters
‡ Akaike information criterion corrected
§ difference between AICc and the smallest AICc
# model weight (probability)
†† stocking rate
‡‡ rest to graze ratio
§§ annual heat moisture index
plant available nitrogen
††† microbial biomass carbon

Table 2.14. Summary results comparing regression models on urease activity responses as a function of leading variables from the management, climate, and soil parameter subgroups. The best model is in bold, the null and global (all variables) models are italicized, while alternative models considered to be equally plausible (based on $\Delta AIC_c \leq 2$) to the leading model are underlined.

Ranked model categories	K[†]	AIC$_c$[‡]	ΔAIC_c[§]	ω_i[#]
SR[††] +Soil moisture+MBC[‡‡]	*7*	*-6.10*	*0.00*	*0.334*
SR+Soil moisture	6	-5.06	1.04	0.199
SR+MBC	6	-4.50	1.60	0.150
Soil moisture	5	-3.72	2.38	0.102
Soil moisture+MBC	6	-3.31	2.79	0.083
SR+MBC+SR*MBC	7	-2.95	3.15	0.069
SR+Soil moisture+SR*Soil moisture	7	-2.38	3.72	0.052
MBC	5	0.52	6.62	0.012
SR	5	8.56	14.66	0.000
Null	*4*	*9.82*	*15.92*	*0.000*

† number of model parameters
‡ Akaike information criterion corrected
§ difference between AIC$_c$ and the smallest AIC$_c$
# model weight (probability)
†† stocking rate
‡‡ microbial biomass carbon

Table 2.15. Summary results comparing regression models within each sub-group for factors impacting phosphatase activity. The best model within each subgroup is in bold. Alternative models considered to be equally plausible (based on ΔAICc ≤ 2) are underlined.

Candidate models	K[†]	AICc[‡]	ΔAICc[§]	ωi[#]
Management Subgroup				
Cultivated	5	-163.23	1.07	0.201
SR[††]	**5**	**-164.30**	**0.00**	**0.344**
RGR[‡‡]	5	-162.96	1.34	0.176
Cultivated + SR	6	-162.66	1.64	0.151
Cultivated + RGR	6	-161.83	2.47	0.100
Cultivated + SR + RGR + SR * RGR	8	-159.25	5.05	0.028
Climate Subgroup				
AHM[§§]	**5**	**-163.90**	**0.00**	**0.581**
Soil moisture	5	-162.04	1.86	0.229
AHM + Soil moisture	6	-161.66	2.24	0.190
Soil Subgroup				
Sand:Clay	5	-165.16	10.26	0.003
Soil pH	5	-170.60	4.82	0.042
AN[##]	5	-167.40	8.02	0.008
MBC[†††]	5	-162.24	13.18	0.001
Sand:Clay +Soil pH	**6**	**-175.42**	**0.00**	**0.465**
Sand:Clay +Soil pH + AN	7	-175.04	0.38	0.386
Sand:Clay +Soil pH + AN + MBC	8	-172.26	3.16	0.096

† number of model parameters
† number of model parameters
‡ Akaike information criterion corrected
§ difference between AICc and the smallest AICc
# model weight (probability)
†† stocking rate
‡‡ rest to graze ratio
§§ annual heat moisture index
plant available nitrogen
††† microbial biomass carbon

Table 2.16. Summary results comparing regression models on phosphatase activity responses as a function of leading variables from the management, climate, and soil parameter subgroups. The best model is in bold, the null and global (all variable) models are italicized, while alternative models considered to be equally plausible (based on $\Delta AIC_c \leq 2$) to the leading model are underlined.

Ranked model categories	$K^\dagger$	$AIC_c^\ddagger$	$\Delta AIC_c^\S$	$\omega_i^\#$
Cultivated + Sand:Clay + Soil pH	**7**	**-175.66**	**0.00**	**0.286**
<u>SR†† + Sand:Clay + Soil pH</u>	7	-175.50	0.16	0.265
<u>Sand:Clay + Soil pH</u>	6	-175.44	0.22	0.256
RGR‡‡ + Sand:Clay + Soil pH	7	-173.53	2.13	0.099
AHM§§ + Sand:Clay + Soil pH	7	-172.75	2.91	0.067
Cultivated + SR + RGR + AHM + Sand:Clay+Soil pH	*10*	*-170.43*	*5.23*	*0.021*
Null	*4*	*-164.49*	*11.17*	*0.001*
SR	5	-164.35	11.31	0.001
AHM	5	-163.88	11.78	0.001
Cultivated	5	-163.27	12.39	0.001
RGR	5	-163.01	12.65	0.001
SR+AHM	6	-162.86	12.80	0.000
Cultivated + AHM	6	-162.78	12.88	0.000
RGR+AHM	6	-161.99	13.67	0.000
RGR+AHM+RGR*AHM	7	-160.71	14.95	0.000
SR+AHM+SR*AHM	7	-160.54	15.12	0.000
Cultivated + AHM + Cultivated*AHM	9	-158.01	17.65	0.000

† number of model parameters
‡ Akaike information criterion corrected
§ difference between AIC_c and the smallest AIC_c
\# model weight (probability)
†† stocking rate
‡‡ rest to graze ratio
§§ annual heat moisture index

Table 2.17. Summary results comparing regression models within each sub-group for factors impacting the geometrical mean of all carbon cycling extracellular enzyme activities, including xylosidase, β-glucosidase, and cellobiosidase activities. The best model within each subgroup is in bold. Alternative models considered to be equally plausible (based on ΔAICc ≤ 2) are underlined.

Candidate models	K[†]	AICc[‡]	ΔAICc[§]	ωi[#]
<u>Cultivated</u>	5	-206.65	0.60	0.238
SR[††]	**5**	**-207.25**	**0.00**	**0.321**
<u>RGR[‡‡]</u>	5	-206.60	0.65	0.232
Cultivated + SR	6	-205.04	2.21	0.106
Cultivated + RGR	6	-204.73	2.52	0.091
Cultivated + SR + RGR+ SR * RGR	8	-200.55	6.70	0.011
AHM[§§]	**5**	**-212.68**	**0.00**	**0.618**
Soil moisture	5	-208.73	3.95	0.086
AHM + Soil moisture	6	-211.20	1.48	0.296
Sand:Clay	5	-211.54	14.64	0.000
Soil pH	5	-207.30	18.88	0.000
AN[##]	**5**	**-226.18**	**0.00**	**0.601**
MBC[†††]	5	-207.30	18.88	0.000
Sand:Clay +Soil pH	6	-211.32	14.86	0.000
Sand:Clay +Soil pH + AN	7	-224.74	1.44	0.293
Sand:Clay +Soil pH + AN + MBC	8	-222.69	3.49	0.105

† number of model parameters
† number of model parameters
‡ Akaike information criterion corrected
§ difference between AICc and the smallest AICc
# model weight (probability)
†† stocking rate
‡‡ rest to graze ratio
§§ annual heat moisture index
plant available nitrogen
††† microbial biomass carbon

Table 2.18. Summary results comparing regression models on the geometrical mean of all carbon cycling extracellular enzyme activates, including xylosidase, β-glucosidase, and cellobiosidase activities, as a function of the leading variables from the management, climate, and soil parameter subgroups. The best model is in bold, the null and global (i.e., all variable) models are italicized, while alternative models considered to be equally plausible (based on $\Delta AIC_c \leq 2$) to the leading model are underlined.

Ranked model categories	K[†]	AIC$_c$[‡]	ΔAIC$_c$[§]	ω$_i$[#]
AHM[††] +AN[‡‡]	**6**	**-226.61**	**0.00**	**0.373**
RGR[§§]+AN	6	-225.50	1.11	0.214
Cultivated+AN	6	-224.13	2.48	0.108
SR[##] +AN	6	-223.82	2.79	0.092
SR+AN+(SR*AN)	7	-223.67	2.94	0.086
RGR+AN+RGR*AN	7	-223.10	3.51	0.065
Cultivated+AN+(Cultivated*AN)	7	-222.37	4.24	0.045
Cultivated+SR+RGR+AHM+AN	*9*	*-220.43*	*6.18*	*0.017*
Cultivated+AHM	6	-211.58	15.03	0.000
SR+AHM	6	-210.51	16.10	0.000
RGR+AHM	6	-210.38	16.23	0.000
Cultivated+AHM+(Cultivated*AHM)	7	-209.10	17.51	0.000
Null	*4*	*-208.36*	*18.25*	*0.000*
SR+AHM+SR*AHM	7	-208.04	18.57	0.000
RGR+AHM+RGR*AHM	7	-207.83	18.78	0.000
SR	5	-207.19	19.42	0.000
Cultivated	5	-206.60	20.01	0.000
RGR	5	-206.54	20.07	0.000

† number of model parameters
‡ Akaike information criterion corrected
§ difference between AIC$_c$ and the smallest AIC$_c$
# model weight (probability)
†† annual heat moisture index
‡‡ available nitrogen
§§ rest to graze ratio
stoking rate

Table 2.19. The best and alternative model fixed effects for xylosidase, β-glucosidase, cellobiosidase, N-acetyl-β glucosidase, urease, phosphotase, and the geometrical mean of carbon cycling enzymes activities. Given are the standardised regression coefficients (β), their standard errors (R^2), and upper and lower confidence intervals (CI) for various predictor variables of each enzyme activity significance. Effects with CI bounds that do not overlap with 0 demonstrate a greater likelihood of significance. Alternative fixed effects from the management and climate subgroups are italicized.

Fixed effect	β	SE	Lower CI	Upper CI
Xylosidase				
Cultivated	-0.28	0.13	-0.557	0.010
AN[†]	0.47	0.10	0.127	0.316
Best Model	R^2mar = 0.33[§§]	R^2cond = 0.85[##]		
β-glucosidase				
RGR[‡]	0.20	0.10	-0.0001	0.021
AHM[§]	-0.37	0.16	-0.037	-0.0005
AN	0.43	0.12	0.008	0.035
Best model	R^2mar = 0.54	R^2cond = 0.72		
Cellobiosidase				
AHM	-0.42	0.18	-0.05	-0.003
AN	0.38	0.11	0.009	0.04
Best model	R^2mar = 0.45	R^2cond = 0.75		
N-acetyl-β glucosaminidase				
AN	0.70	0.10	0.010	0.019
AHM	*-0.14*	*0.13*	*-0.147*	*0.131*
Best model	R^2mar = 0.55	R^2cond = 0.63		
Urease				
SR[††]	0.29	0.11	0.013	0.130
Soil moisture	0.31	0.14	0.004	0.160
MBC[‡‡]	0.30	0.14	-0.0006	0.149
Best model	R^2mar = 0.42	R^2cond = 0.42		
Phosphotase				
Cultivated	-0.29	0.16	-0.06	0.008
SR	*0.22*	*0.13*	*-0.004*	*0.025*
Sand/Clay	-0.67	0.19	-0.049	-0.009
Soil pH	-0.47	0.12	-0.035	-0.012
Best model	R^2mar = 0.37	R^2cond = 0.80		
Geometrical mean of carbon cyling enzymes				
RGR	*0.14*	*0.11*	*-0.005*	*0.017*
AHM	-0.17	0.23	-0.032	0.015
AN	0.34	0.13	0.003	0.029
Best model	R^2mar = 0.16	R^2cond =0.68		

† available nitrogen
‡ rest to graze ratio
§ annual heat moisture
# model weight (probability)

†† stocking rate
‡‡ microbial biomass carbon
§§ marginal R^2
conditional R^2
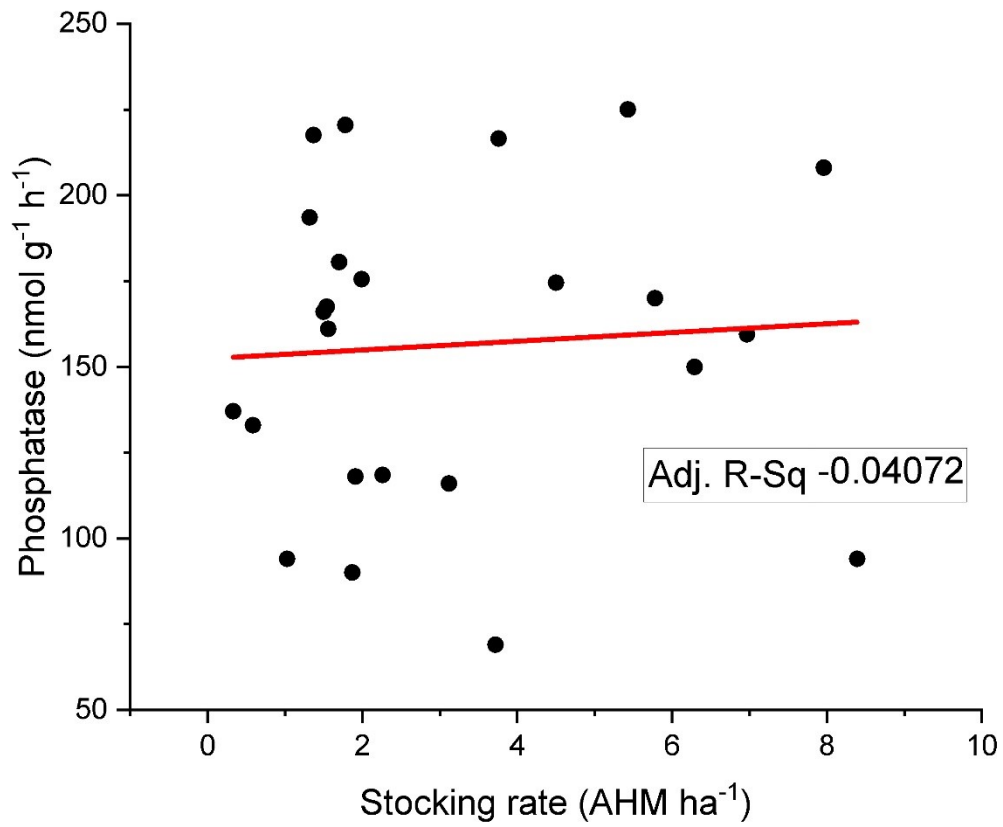
Figure 1. The relationship between phosphatase activity (nmol g^{-1} h^{-1}) and stocking rate (animal unit month ha^{-1}).
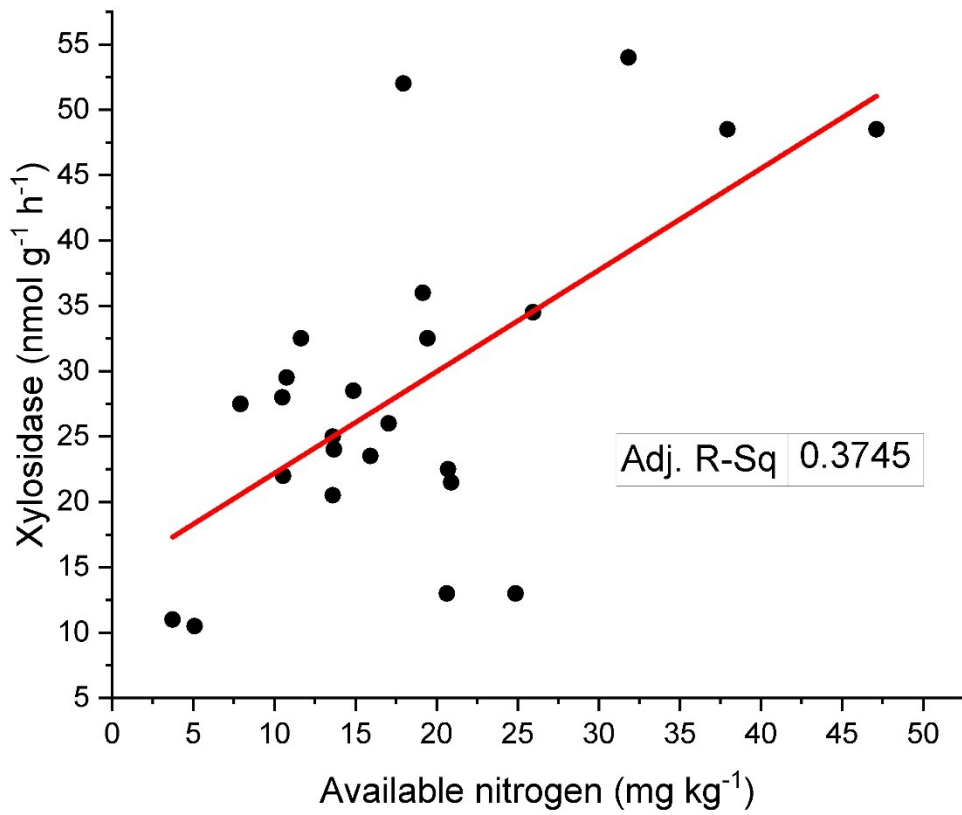
Figure 2. The relationship between xylosidase activity (nmol g^{-1} h^{-1}) and available nitrogen (mg kg^{-1}).
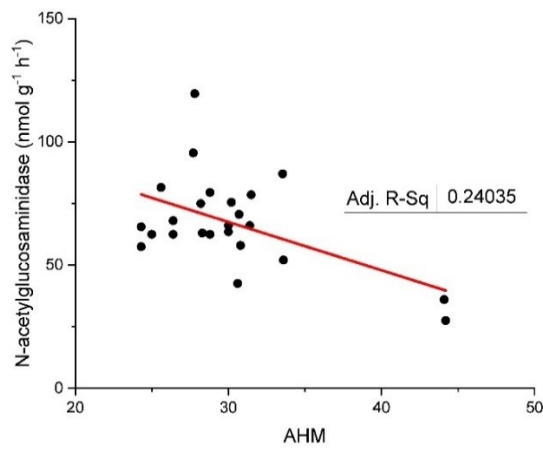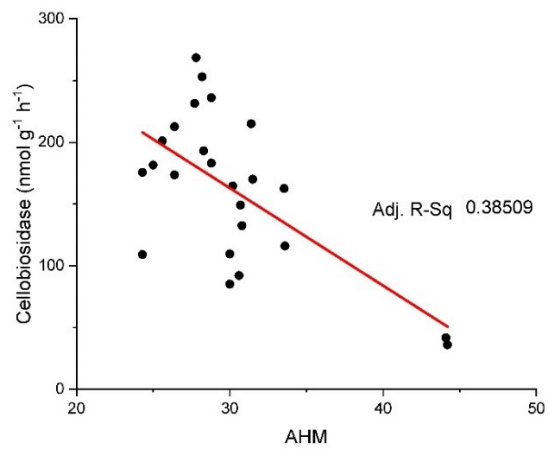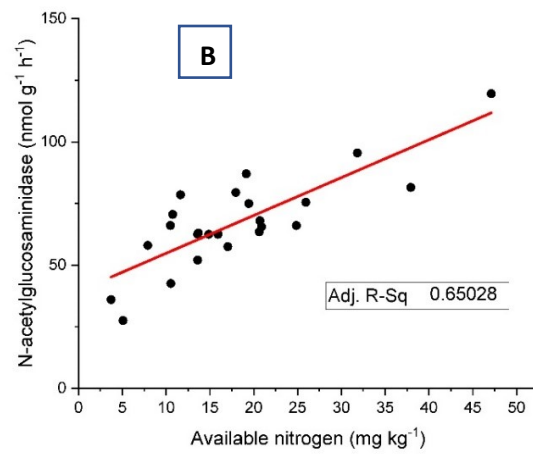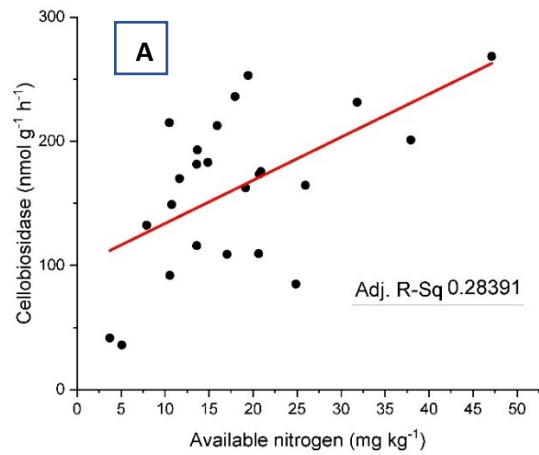
Figure 3. The relationship of cellobiosidase (A), N-acetylglucosaminidase (B) activities (nmol g^{-1} h^{-1}) with annual heat moisture (AHM) index and available nitrogen (mg kg^{-1}).
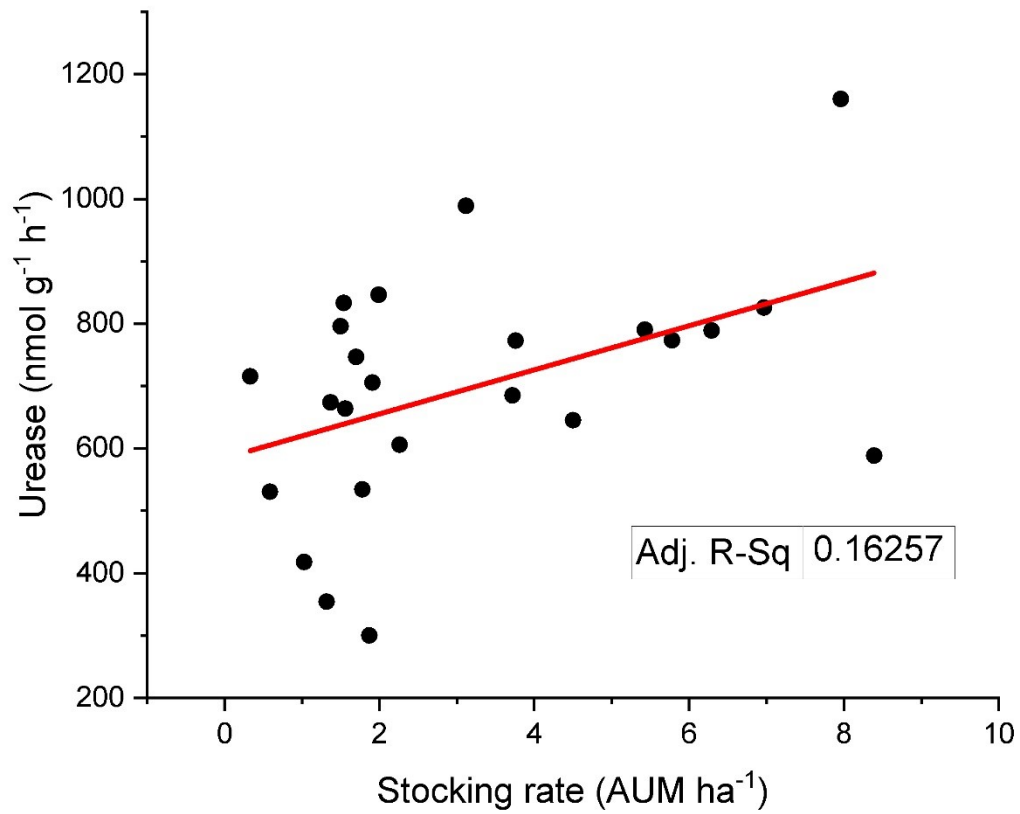
Figure 4. The relationship between urease activity (nmol g^{-1} h^{-1}) and stocking rate (animal unit month ha $^{-1}$).
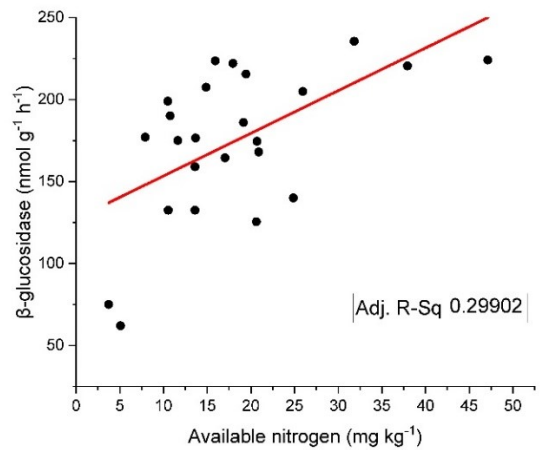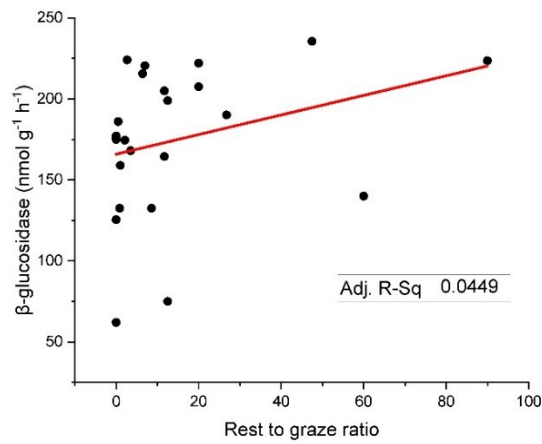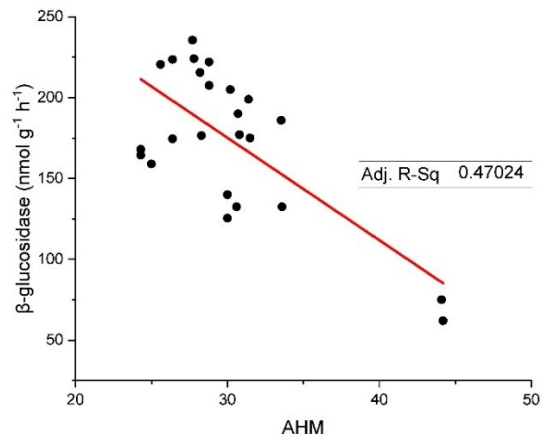
Figure 5. The relationship between β-glucosidase activity (nmol g^{-1} h^{-1}) and rest days to grazed days ratio, annual heat moisture (AHM) index and available nitrogen (mg kg^{-1}).

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Appendix A. Results of Pearson Correlation Analysis

Appendix A. Results of the Pearson correlation analysis between various management factors, climate, and soil property variables

Variables	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. SR†															
2. RGR‡	0.18														
3. MAP§	0.16	0.14													
4. MAT#	-0.10	-0.04	-0.02												
5. AHM††	-0.23	-0.16	-0.91***	0.41**											
6. Soil moisture	0.15	0.23	0.58***	-0.17	-0.63***										
7. Soil pH	0.29*	0.07	0.38**	-0.08	-0.43**	0.37*									
8. Clay	-0.23	-0.12	0.63***	-0.01	-0.67***	0.42**	0.23								
9. Silt	0.29*	0.17	0.59***	-0.43**	-0.76***	0.58***	0.36*	0.37*							
10. Sand	-0.05	0.03	-0.74***	0.36*	0.87***	-0.61***	-0.36*	-0.81***	-0.84***						
11. NO3	-0.16	-0.31*	-0.04	-0.09	0.07	0.25	0.37*	0.36*	0.20	-0.34*					
12. NH4	0.21	0.13	0.57***	0.14	-0.47***	0.66***	0.09	0.43**	0.36*	-0.48***	0.03				
13. AN‡‡	0.20	0.10	0.56***	0.13	-0.48***	0.68***	-0.03	0.45**	0.38**	-0.50***	0.03	1.00***			
14. MBC§§	-0.02	0.45**	0.41**	0.06	-0.40**	0.64***	0.48***	0.47**	0.36*	-0.50***	0.51***	0.38**	0.42**		
15. MBN##	0.02	0.03	0.48**	0.08	-0.46**	0.73***	0.50***	0.48***	0.42**	-0.54***	0.52***	0.48***	0.52***	0.97***	
16. Sand:Clay	-0.15	0.04	-0.62***	0.49***	0.83***	-0.55***	0.45**	-0.71***	-0.77***	0.89***	-0.32*	0.36*	-0.39**	0.41**	-0.44**

*$p < 0.5$
**$p < 0.01$
***$p < 0.001$
† stocking rate
‡ rest to graze ratio
§ mean annual precipitation
# mean annual temperature
†† annual heat moisture index
‡‡ available nitrogen
§§microbial biomass carbon
microbial biomass nitrogen

Appendix B. Climate Conditions

Appendix B. Climatic data for each ranch studied, including mean annual precipitation (MAP), mean annual temperature (MAT), and annual heat:moisture index (AHM) of each study ranch

PairID	RanchID	Grazing	MAP (mm)	MAT (°C)	AHM
Pair-1	AMP01	AMP	533.3	2.8	24.3
Pair-1	nAMP02	nAMP	533.3	2.8	24.3
Pair-2	AMP03	AMP	489.8	2.8	26.4
Pair-2	nAMP04	nAMP	490.5	2.8	26.4
Pair-3	AMP05	AMP	477.2	3.3	28.2
Pair-3	nAMP06	nAMP	476.9	3.3	28.3
Pair-4	AMP07	AMP	539.8	3.4	25.6
Pair-4	nAMP08	nAMP	549.2	3.4	25
Pair-5	AMP09	AMP	455.6	3.3	30
Pair-5	nAMP10	nAMP	454.7	3.3	30
Pair-6	AMP11	AMP	510.6	3.8	27.7
Pair-6	nAMP12	nAMP	509.7	3.8	27.8
Pair-7	AMP13	AMP	455.7	2.9	28.8
Pair-7	nAMP14	nAMP	455.4	2.9	28.8
Pair-8	AMP15	AMP	430.1	3.3	31.4
Pair-8	nAMP16	nAMP	429.6	3.3	31.5
Pair-9	AMP17	AMP	332.3	4.1	44.1
Pair-9	nAMP18	nAMP	331.3	4.1	44.2
Pair-10	AMP19	AMP	409.5	2.2	30.7
Pair-10	nAMP20	nAMP	408.4	2.3	30.8
Pair-11	AMP21	AMP	408.6	3.3	33.6
Pair-11	nAMP22	nAMP	409.6	3.3	33.5
Pair-12	AMP23	AMP	409	2	30.2
Pair-12	nAMP24	nAMP	404.1	2	30.6

Appendix C. Management Information of Study Ranches

Appendix C. Mean stocking rate (SR), rest to graze ratio (RGR), and cultivation history (cultivated – Y, non-cultivated – N) in each study ranch during the growing season of 2018 in Alberta, Canada. Also shown are the size of the entire ranch, number of paddocks, typical length of a grazing period (Gr length) within a paddock, and the herd size (Cattle)

PairID	RanchID	Grazing	SR	RGR	Cultivated	Grazed area, ha	Paddocks	Gr length	Cattle
Pair-1	AMP01	AMP	6.2	11.6	N	61.9	16	1-5/14§§	83.4
Pair-1	nAMP02	nAMP	2.2	3.5	Y	129.5	2	6/14†	84
Pair-2	AMP03	AMP	4.5	90	Y	603.0	77	1	320
Pair-2	nAMP04	nAMP	3.1	2.1	Y	323.7	12	18	210
Pair-3	AMP05	AMP	1.7	6.4	Y	647.5	35	7	156
Pair-3	nAMP06	nAMP	0.3	0	Y	607.0	30	75	60
Pair-4	AMP07	AMP	1.9	7	N	10117.5	120	10	1680
Pair-4	nAMP08	nAMP	0.6	1	N	2023.5	20	30	342
Pair-5	AMP09	AMP	3.7	60	Y	687.9	70	1/3-4§§	460
Pair-5	nAMP10	nAMP	8.4	0	Y	40.4	1	215	48
Pair-6	AMP11	AMP	1.3	47.5	N	5261.1	120	3-5/5-15§§	600
Pair-6	nAMP12	nAMP	5.4	2.6	N	259.0	5	45	192
Pair-7	AMP13	AMP	6.9	20	Y	161.8	15	2	120
Pair-7	nAMP14	nAMP	7.9	20	N	101.2	6	3/7§§	180
Pair-8	AMP15	AMP	5.8	12.5	Y	78.9	44	2	136
Pair-8	nAMP16	nAMP	1.5	0	Y	141.6	5	142	45.6
Pair-9	AMP17	AMP	1.8	12.5	N	4977.8	50	4/14§§	1020
Pair-9	nAMP18	nAMP	1.0	0	N	1537.8	1	163s/fall§§	300
Pair-10	AMP19	AMP	1.8	26.8	Y	1618.8	100	2-3/14	348
Pair-10	nAMP20	nAMP	1.3	0	Y	64.7	1	61	42.6
Pair-11	AMP21	AMP	1.9	8.5	Y	1052.2	30	7	300
Pair-11	nAMP22	nAMP	1.5	0.5	Y	303.5	8	60	84
Pair-12	AMP23	AMP	3.7	11.6	Y	809.4	100	3	880
Pair-12	nAMP24	nAMP	1.5	0.8	Y	323.7	10	25	88

Appendix D. Soil Properties of Study Ranches

Appendix D. Mean soil pH, soil moisture, microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), and plant available N (AN) of each study ranch sampled in June, July, and September during the growing season of 2018 in Alberta, Canada

PairID	RanchID	Grazing	pH	Soil moisture	MBC	MBN	AN
Pair-1	AMP01	AMP	5.4 ± 0.2	18.9 ± 1.9	81.1 ± 11.7	29.2 ± 4.1	17.0 ± 3.0
Pair-1	nAMP02	nAMP	6.1 ± 0.4	26.3 ± 1.8	131.0 ± 13.4	49.0 ± 4.8	20.9 ± 6.2
Pair-2	AMP03	AMP	6.2 ± 0.1	23.4 ± 2.9	119.3 ± 10.0	38.4 ± 3.7	15.9 ±2.5
Pair-2	nAMP04	nAMP	6.7 ±0.2	29.1 ± 13.2	233.9 ± 64.2	76.5 ± 17.6	20.7 ±6.2
Pair-3	AMP05	AMP	6.3 ± 0.2	20.2 ± 0.3	97.5 ± 12.5	35.6 ± 5.1	10.8 ± 3.3
Pair-3	nAMP06	nAMP	6.8 ± 0.4	24.4 ± 2.4	183.1 ± 29.5	68.7 ± 11.7	12.7 ± 2.6
Pair-4	AMP07	AMP	6.0 ± 0.1	25.3 ± 2.5	161.5 ±37.1	65.4 ± 16.8	46.5 ± 6.5
Pair-4	nAMP08	nAMP	6.5 ± 0.1	21.4 ± 3.4	250.8 ± 64.1	87.4 ± 24.9	14.5 ± 2.4
Pair-5	AMP09	AMP	6.1 ± 0.0	32.4 ± 19.4	118.9 ± 33.3	53.5 ± 13.3	24.8 ± 4.6
Pair-5	nAMP10	nAMP	6.2 ± 0.1	16.1 ± 4.6	59.5 ± 9.8	30.7 ± 5.9	20.6 ± 6.3
Pair-6	AMP11	AMP	5.7 ± 0.0	25.5 ± 0.3	198.4 ± 35.1	69.3 ± 14.6	31.8 ± 5.2
Pair-6	nAMP12	nAMP	5.7 ± 0.1	31.6 ± 3.4	261.3 ±22.5	95.2 ±11.1	47.1 ± 9.4
Pair-7	AMP13	AMP	6.4 ±0.3	22.2 ± 1.5	124.8 ±20.1	48.0 ± 8.5	14.8 ± 3.3
Pair-7	nAMP14	nAMP	6.2 ±0.2	24.5 ± 0.8	205.1 ± 19.0	69.7 ± 7.6	17.9 ± 6.4
Pair-8	AMP15	AMP	6.8 ± 0.5	12.7 ± 2.3	95.9 ± 11.7	32.6 ± 5.3	10.4 ± 2.1
Pair-8	nAMP16	nAMP	5.6 ± 0.1	12.1 ± 0.7	95.7 ± 12.7	29.2 ± 3.5	11.6 ± 2.1
Pair-9	AMP17	AMP	4.8 ± 0.1	2.5 ± 0.01	24.4 ± 3.1	7.4 ± 1.0	3.7 ± 0.4
Pair-9	nAMP18	nAMP	5.5 ± 0.0	2.5 ± 0.06	28.3 ± 2.6	8.0 ± 1.0	5.0 ± 0.3
Pair-10	AMP19	AMP	6.0 ± 0.5	16.1 ± 0.2	88.7 ± 14.7	30.2 ± 7.3	10.7 ±1.8
Pair-10	nAMP20	nAMP	5.5 ± 0.1	16.4 ± 0.7	97.7 ± 12.0	31.8 ± 4.4	7.9 ± 1.0
Pair-11	AMP21	AMP	6.2 ± 0.0	19.2 ± 1.8	273.2 ±2.6	77.3 ±10.1	13.6 ±3.4
Pair-11	nAMP22	nAMP	5.6 ± 0.2	22.4 ± 1.8	139.3 ± 15.8	51.8 ±5.3	19.1 ± 3.6
Pair-12	AMP23	AMP	5.4 ± 0.0	24.0 ± 2.5	133.1 ± 21.4	50.7 ±3.6	25.9 ± 5.2
Pair-12	nAMP24	nAMP	5.6 ± 0.2	16.2 ± 0.07	61.27 ± 6.0	18.7 ± 2.8	10.5 ± 3.9