## Adaptive Multi-paddock Grazing Increases Organic Carbon in Grassland Soils

by

Laio Silva Sobrinho

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Soil Science

Department of Renewable Resources University of Alberta

© Laio Silva Sobrinho, 2023

#### Abstract

Grasslands cover 30% of the planet's terrestrial surface and provide habitat and forage for livestock and wildlife. In addition, grasslands have the potential to mitigate climate change by sequestering substantial amounts of carbon (C) in the soil. However, the ability of grassland soils to sequester C varies greatly depending on the grazing management system adopted. This study examined the difference in soil organic C (SOC) mass between two different grazing systems, including adaptive multi-paddock (AMP) grazing, which involves rotating livestock through many small paddocks based on forage availability and allowing extended rest periods between grazing events, and conventional grazing (i.e., neighboring to AMP, hereafter n-AMP, varying from continuous to slow or fast rotational grazing, representative of the typical variation in grazing practices observed on-farm). I evaluated the effects of diverse grazing practices on SOC in soil depths up to 1 meter, using equivalent soil mass (ESM) to offset differences in soil bulk density among different paddocks, thus ensuring the proper comparison of grazing system effects on SOC mass. Soil samples were collected from 26 ranch pairs, where one ranch practiced AMP while the other n-AMP grazing across the Canadian prairies. In addition to assessing differences in equivalent SOC mass between grazing systems at the treatment level (AMP vs. n-AMP), I used an information theoretic model selection approach to assess the influence of nuanced grazing management practices, including stocking rate, animal stock density, and rest intervals, on SOC. My results show AMP grazed grasslands with higher stocking rates and extended rest periods sequestered significantly more SOC in the 10-30 cm ESM soil layer than n-AMP grazed grasslands. Conversely, n-AMP can sequester more SOC than AMP grazing at stocking rates lower than 3.5 AUM ha<sup>-1</sup>. These results highlight the importance of using sampling protocols that encompass deeper soil layers to adequately quantify

ii

the effect of grazing management on SOC. This study emphasizes the potential for enhancing soil C sequestration in grazed grasslands through the use of rotational grazing systems at adequate stocking rates.

#### Preface

This thesis is an original work by Laio Silva Sobrinho. 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.

Data analysis, interpretation and conclusions in Chapter 2 and are my original work, as well as the literature review in Chapter 1 and conclusions in Chapter 3. The laboratory work, data collection, data analysis and the manuscript composition were my responsibility. Dr. Scott Chang, Dr. Edward Bork, Dr. Cameron Carlyle, Dr. Mark Boyce, and Dr. Timm Döbert played supervisory roles in this work. "We do not inherit the earth from our ancestors, we borrow it from our children."

- Native American Proverb

#### Acknowledgements

I extend my profound gratitude to my supervisor, Dr. Scott Chang, whose guidance has been instrumental in shaping this research. I am also immensely thankful to my supervisory committee members, Drs. Edward Bork and Cameron Carlyle, for their valuable supervision, participation, and input.

Special acknowledgments go to Dr. Mark Boyce and Dr. Timm Doebert for their insightful input, and to Dr. Bharat Shrestha for his expert direction during the sample processing and analysis phases.

I am thankful for the support from and collaboration with my lab mates, including Cole Gross, Gleb Kravchinsky, Kiah Leicht, Dauren Kaliaskar, and Tien Weber. Additionally, I would like to express my heartfelt gratitude to the research assistants and volunteers, including Lakshay Bansal, Sandford Hu, Mayumi Pinongcos, Xueyao Chen, Jillian Calvert, Hang Chen, Tony Shao, Andrew Johnstone, Anabel Dombro, Mary Villeneuve, Ashutosh Gupta, Justin Kailan, Megan Johns, Muhammad Younas, Arvin Lim, Leah Stachniak, and Sarah Breitkreuz. Their tireless contributions throughout the laborious processing of soil samples have been invaluable.

On a personal note, I am especially thankful to my partner, Camila Honorato, for her unwavering love and support. My gratitude also extends to my grandparents Antonio and Zilda Sobrinho and for my aunt Celida Costa, for their unconditional love and care, and to my parents Joacy and Francisca Sobrinho, along with my siblings, Laila and Breno Sobrinho, whose encouragement and love have been my strength.

Finally, I thank Agriculture and Agri-Food Canada agency (AAFC) for their support through a grant from the Agricultural Greenhouse Gases Program (AGGP). Special

vi

acknowledgment is due to Dr. Mark Boyce, the Principal Investigator, whose leadership has greatly contributed to the success of this project.

### **Table of Contents**

Abstract	ii
Preface	iv
Acknowledgements	vi
List of Tables	X
List of Figures	xii
List of Symbols and Abbreviations	xv
Chapter 1. Grazing System Effects on Soil Organic Carbon: Introduction and Literature Revie	ew 1
1.1 Introduction	1
1.2 Overview of Grassland Distribution and Ecology	2
1.3 Role of Grasslands in C Storage and Sequestration	3
1.4 Effects of Grazing on Grassland Plant Communities and Soil Properties	4
1.5 Different Grazing Management Practices (Continuous vs. AMP grazing)	7
1.6 AMP Grazing Impacts on Soil Organic C	8
1.7 Research Objectives	. 10
	. 10
Chapter 2. Effects of Grazing Management on Soil Organic C in Grassland Soils of Western	
Canada	12
2.1 Introduction	12
2.7 Materials and Methods	15
2.2 Materials and Methods 2.2.1 Study Area	15
2.2.1 Study Alea 2.2.2 Experimental Design	16
2.2.2 Experimental Design	17
2.2.5 Soil Core Processing	18
2.2.4 Soil Analysis	10
2.2.5 Son Analysis 2.2.6 Grazing Metrics	20
2.2.0 Grazing Metrics	20
2.2.7 Data Analysis	21
2.5 Results	24
2.3.1 Differences in Orazing Tractices Detween Awn and in-Awn and SOC Mass	24
2.3.2 Effect of Overall Grazing Treatment on All Horizon Depth and SOC Mass.	23
Equivalent SOC Mass	25
2.3.4 Interaction Between Binary Grazing Treatment and Stocking Pate on Ah	23
Horizon Denth and SOC Mass	28
2.4 Discussion	20
2.4. Discussion	29
2.4.1 AMF and n-AMF Affect An Horizon Depth and Equivalent SOC Mass	29
Equivalent SOC Mass	20
2 4 2 Polo of Stocking Poto on Ah Horizon Donth	
2.4.5 Kole of Stocking Kale on All Homzon Deput	30
2.4.4 The Distribution of SOC Across the Soll Profile	38 11
2.5 Conclusions	41
Chapter 2 Synthesis and Future Descareb	12
2 1 Synthesis of Findings	43 12
2.2 Deficiencies and Limitations	43 11
5.2 Denciencies and Limitations	44

3.3 Future Research Directions	
3.4 Conclusions	
References	59
Appendices	
Appendix A. Location of study sites	80
Appendix B. Management information of study ranches	82
Appendix C. Results of Pearson correlation analysis of management variables	85
Appendix D. Average soil organic carbon mass per study ranch	
Appendix E. Mixed model analysis results	

#### **List of Tables**

- **Table 1**: Summary of the nuanced grazing metrics within the adaptive multi-paddock (AMP) andconventionally (n-AMP) grazed beef cattle operations assessed during 2018 and 2019 inthe prairie provinces of western Canada. Values are means ( $\pm$ SE). Bold means differfrom each other at a significance level of P < 0.05 (n = 26). AUM ha<sup>-1</sup> = animal-unit-months per hectare. AU ha<sup>-1</sup> = Animal units per hectare.48

- Table 4: Summary table for Ah horizon depth and soil organic carbon (SOC) mass distinguished between adaptive (AMP) vs conventionally (n-AMP) grazed grasslands as a fixed effect, and combined with other grazing practices. Random intercepts were specified for 'ranch pair' to account for the paired study design. The random effect accounts for geographic variation in soils and climate. The variance explained by just the fixed effects (R<sup>2</sup><sub>m</sub>) and

the variance explained by both fixed and random effects $(R^2_c)$ were calculated after	
Nakagawa & Schielzeth (2013). Standardised coefficients are provided to determine	
effect size ( $\omega$ p2) and 95% confidence intervals (CI) as a measure of significance; bold	
variables have CIs that do not overlap zero	52

#### **List of Figures**

- Figure 3: (a) Relationship between soil organic carbon (SOC) mass within the Ah horizon and stocking rate (in animal-units-month per hectare) distinguished between adaptive (AMP) and conventionally (n-AMP) grazed grasslands. Solid circles indicate raw means, with the associated linear regression lines and 95% confidence intervals (shaded areas) being provided (n = 26). (b) Models demonstrating the relationship between SOC mass within

Figure 5: (a) Relationship between soil organic carbon (SOC) mass within the 0-80 cm equivalent soil mass (ESM) depth and stocking rate (in animal-units-month per hectare) distinguished between adaptive (AMP) and conventional (n-AMP) grazing systems.
Solid circles indicate raw means, with the associated linear regression lines and 95%

#### List of Symbols and Abbreviations

- °C degrees Celsius
- AHM: annual heat moisture index
- AICc Akaike Information Criterion adjusted for small sample size
- AMP adaptive multi-paddock (grazing system)
- AU animal unit
- AUD animal unit density
- AUM animal unit month
- C-carbon
- $\operatorname{cm}-\operatorname{centimeter}$
- DOC dissolved organic carbon
- ESM equivalent soil mass
- F:B fungi:bacteria ratio
- GHG greenhouse gas
- ha-hectare
- MAP mean annual precipitation
- n-AMP neighboring to adaptive multi-paddock (grazing system operators)
- MAT mean annual temperature
- Mg Megagram
- mm millimeter
- RGR rest:grazing ratio
- SGS start of the grazing season
- SOC soil organic carbon;

SOM – soil organic matter

TOC – total organic carbon

yr – year

Chapter 1. Grazing System Effects on Soil Organic Carbon: Introduction and Literature Review

#### **1.1 Introduction**

Grasslands are one of the most extensive biomes on Earth, covering over 52 M km<sup>2</sup> globally and comprising approximately 4% of Canada's total land area (White et al., 2000; Statistics Canada, 2021). As a major terrestrial carbon (C) sink, storing about 10-30% of the global soil organic C (SOC), grasslands play a vital role in regulating the climate (Batjes, 2018; Lal, 2004). Over-grazing of grasslands has degraded grassland ecosystems, decreasing grassland productivity and its ability to store C. One such strategy is the use of adaptive multi-paddock (AMP) grazing, which involves rotating livestock through many small paddocks based on forage availability and allowing extended rest periods between grazing events. The AMP grazing system has been claimed to offer benefits like increased productivity, soil carbon sequestration, and resilience to degradation (Teague et al., 2011).

The potential of AMP grazing to sequester SOC, however, remains disputed, with studies showing mixed results (Briske et al., 2008). Moreover, current findings predominantly come from agricultural grasslands situated within the United States, and which differ considerably from the northern temperate grasslands typically found in Canada that are often moister and heavily dominated by cool-season plant species. This knowledge gap on the effectiveness of AMP grazing in the Canadian context limits adoption among producers in Canada. Therefore, this study aims to evaluate the impact of AMP grazing on SOC sequestration specifically within Canadian grasslands. The findings will elucidate the potential climate change mitigation benefits of adopting AMP grazing in Canada and inform sustainable rangeland management strategies.

#### **1.2 Overview of Grassland Distribution and Ecology**

Grasslands are defined as lands dominated by grasses and herbaceous plants, with woody vegetation accounting for less than 10% of the ground cover (DiGaudio et al., 2017). They constitute one of the most extensive biomes globally, representing approximately 30% of the Earth's land area excluding Greenland and Antarctica, and are able to thrive under varied conditions from semi-arid to semi-humid climates in both tropical and temperate regions (Gibson, 2012).

Major grassland regions include the steppes of Eurasia, the prairies of North America, the pampas of South America, the savannas of Africa, and the rangelands of Australia (Watkinson, and Ormerod, 2001). Eurasian steppes extend from Ukraine to northeastern China, while the North American prairies cover the Great Plains of the United States and the Prairie Provinces of Canada. The South American pampas extends from Argentina to the Andean foothills, while Savannas are found extensively in sub-Saharan Africa as well as in South America and Australia. Each grassland region harbors unique biological communities shaped by regional climate patterns, evolutionary history, and human land use over millennia. As such, grasslands play a vital role in human livelihoods by ensuring a pure water supply, assisting in nutrient cycling, and supporting livestock (White et al., 2000).

In Canada, grasslands extend over the Prairie Provinces, namely Alberta, Saskatchewan, and Manitoba (Statistics Canada, 2021). For thousands of years, the vast grasslands of the Prairies served as the grazing grounds for bison, elk, antelope, and other ungulates. The characteristics and performance of these grasslands were primarily governed by climatic conditions, grazing practices, and wildfires. Bison populations thrived in conditions where forage

was plentiful and dwindled during periods of drought, which decreases forage availability (Bailey et al., 2010). Grasslands continue to face threats from agricultural expansion, urbanization, invasion of invasive species, and climate change worldwide (Bardgett et al., 2021). Therefore, sustainable management is essential to preserve the ecological integrity, biodiversity, and functionality of grasslands.

#### 1.3 Role of Grasslands in C Storage and Sequestration

Grasslands play a vital role in the global C cycle and climate regulation through their ability to sequester and store substantial amounts of C. In fact, with an estimated SOC pool of approximately 343 Pg C (Conant, 2010), grasslands contain over 30% of the total global SOC stock (Follet and Kimble, 2000; Lal, 2002; Schuman et al., 2002; Derner and Schuman, 2007), highlighting their significance as a terrestrial C sink.

The high SOC stocks in grasslands are due to the perennial nature of grasses, which enable constant C input from aboveground vegetation, along with large contributions of C to subsoils through root exudates and the decomposition of deep roots (Zimmermann et al., 2011). In addition, the extensive root systems of grasses, especially compared to contemporary annual crops, facilitate additional SOC accumulation in deeper soil layers (Lorens and Lal, 2018; Omonode and Vyn et al., 2006). Consequently, the main repository for C storage in grasslands is not above ground, but rather belowground, embedded within the soil matrix (Liu et al., 2022). In fact, some global grasslands contain up to 60% of their soil C below the first 30 cm of the soil (Ward et al., 2016). Nonetheless, a preponderance of soil C research has been skewed towards the uppermost soil layers, with the median depth of such studies in grasslands standing at only 20 cm as of 2017 (Conant et al., 2017). Consequently, C storage in deeper soils remains relatively unexplored and would be much higher than currently estimated (Upton et al., 2020).

Estimated C sequestration rates in grasslands range between 0.03 to 1 Mg C ha<sup>-1</sup> year<sup>-1</sup> (Smith et al., 2008). Therefore, grasslands represent an important natural solution to achieve climate change mitigation. However, conversion of grasslands to croplands or degradation through improper grazing management leads to substantial SOC loss (Guo and Gifford, 2002; Dlamini et al., 2016). The adoption of proper management practices of grasslands is therefore critical for harnessing their C sequestration potential and for climate change mitigation.

#### 1.4 Effects of Grazing on Grassland Plant Communities and Soil Properties

Grazing by large herbivores, especially cattle, which represents the most prevalent disturbance experienced in grasslands (Dixon et al., 2014), can substantially impact grassland plant communities and soils through processes such as trampling, defoliation, and excretion (Lezama and Paruelo, 2016; Zhang et al., 2022). These grazing-induced disturbances influence vegetation structure (Cingolani et al., 2003), biodiversity (Tallowin et al., 2005), and nutrient cycling (de Faccio Carvalho et al., 2010).

Defoliation from grazing removes photosynthetic tissue, which can curtail plant growth (Ferraro and Oesterheld, 2002). However, at moderate intensities, it can also stimulate regrowth and tiller proliferation in grasses due to compensatory growth (McNaughton, 1983; Díaz et al., 2007). The degree of compensatory response also depends on factors such as the time available for recovery and availability of associated resources (water, nutrients) (Oesterheld and McNaughton, 1991). Notably, while compensatory growth has been observed under experimental defoliation in grassland environments, such responses were ephemeral, lasting only

a single growing season (Bork et al., 2017). As such, there's a pressing need for more extensive research to discern the impacts of varying grazing systems on grassland production.

By altering plant productivity and litter inputs, grazing can also modify soil organic matter (SOM) accumulation and soil C storage. Some studies suggest that grazing increases SOC by mixing plant litter into mineral soil layers and stimulating root growth (Schuman et al., 1999; Reeder and Schuman, 2002). For example, Smoliak et al. (1972) found a 25% increase in SOC after a decade of heavy grazing, which the authors attributed to increased root biomass in the uppermost soil layer, primarily due to an increase in the shallow-rooted, grazing tolerant grass *Bouteloua gracilis* (blue grama grass). Additionally, recent meta-analyses have indicated that grazing might boost SOC levels (Sollenberger et al., 2019; Mutema et al., 2022), but only when stocking rates are at low to moderate levels (e.g., Zhou et al., 2017; Bork et al., 2023).

In contrast, other research points to a potential decrease in soil C under grazing, particularly after overgrazing associated with excess stocking (Tanentzap and Coomes, 2012; Dlamini et al., 2016). For instance, Dormaar and Willms (1998) reported higher SOC inside grazing exclosures, with 29-46% less SOC under moderate-heavy grazing. The authors attributed this to reduced soil moisture and nitrogen availability outside exclosures. Other studies report similar variable results across different regions, grazing intensities, and methods (Naeth et al., 1991; Steffens et al., 2008). Generally, any land management approach that diminishes plant inputs, via specific grazing practices that exceed the tolerance of vegetation based on the frequency, timing, and intensity of defoliation, could likely lead to a reduction in SOC (Conant et al., 2001). However, shifts in land use and better grazing management could bolster SOM and its associated soil C storage.

Furthering our understanding of the effect of grazing intensity on SOC stocks is multifaceted and varies based on factors such as regional climate and plant community types. According to Lai and Kumar (2020), global grazing intensities have differential impacts on SOC: heavy grazing generally diminishes SOC and increases soil compaction, whereas light grazing can elevate SOC levels. Cattle grazing has a more pronounced influence on soil compaction and SOC than sheep grazing, and climate further modulates these effects.

Grazing effects on SOC storage are influenced by climate conditions. As reported by Abdalla et al. (2018), across all climatic zones, grazing usually results in diminished SOC storage. Yet, exceptions were found; for instance, under moist warm climates all grazing intensities led to augmented SOC stocks (+7.6%), while moist cool climates saw reduced SOC stocks (-19%). Considering the uniqueness of specific climates, such as dry warm and dry cool, only low and low-to-medium grazing intensities, respectively, were associated with increased SOC stocks, and further supports other recent findings (e.g., Bork et al., 2023). High grazing intensities may also benefit SOC more in C4-dominated grasslands than in C3-dominated or mixed grasslands.

The impact of grazing on SOC is complex and varies depending on multiple factors. McSherry and Ritchie (2013) highlighted this context-specificity of grazing impacts on SOC. Their analysis underscored the interactive effects of soil texture, precipitation, grassland type, and grazing intensity, on SOC. Both C4-dominated and C4-C3 mixed grasslands revealed an upsurge in SOC with increased grazing intensity, contrasting starkly with grasslands solely dominated by C3 vegetation, which exhibited a decline. These findings emphasized that to optimize SOC and potentially mitigate greenhouse gas (GHG) emissions, grazing management

strategies must be directed to specific regional and ecological contexts (Lai and Kumar, 2020; Abdalla et al., 2018; McSherry and Ritchie, 2013).

#### **1.5 Different Grazing Management Practices (Continuous vs. AMP grazing)**

Grazing management practices are multifaceted, with optimal application requiring careful consideration of several interconnected factors, such as stocking rate, stocking density, the timing of grazing relative to plant growth stage (and tolerance to defoliation), and the frequency of grazing, as well as the length of recovery (rest period) between grazing events.

In a continuous grazing system, a single herd grazes on one pasture throughout the season. This system often involves stable (set) stocking rates and densities with no defined rest periods or variation in the specific timing and frequency of defoliation (Allen et al., 2011). Although this is a less labor-demanding management system, it may lead to patchy grazing patterns and overgrazing of preferred plant species (Teague et al., 2003). Overgrazing can have far-reaching impacts, such as reduced plant productivity, leading to insufficient forage availability (Mysterud, 2006). It can also negatively impact biodiversity by favoring certain species over others (Olff and Ritchie, 1998). Soil health can be significantly degraded, with erosion and compaction resulting from trampling, which in turn, affects the soil's water-holding capacity and nutrient cycling (Bai et al., 2012; Wang and Batkhishig, 2014). Overgrazing has also been linked to a decline in C sequestration, as the diminished plant cover leads to a loss of SOC, counteracting efforts to mitigate climate change (Ganjegunte et al., 2005).

Rotational grazing systems, on the other hand, aim to prevent overgrazing by allowing regular rest periods for pastures between grazing events, while also promoting more homogeneous grazing of vegetation across the landscape (Briske et al., 2008). A specific form of rotational grazing is the AMP (adaptive, multi-paddock) grazing system. AMP grazing, first

conceptualized as "rational grazing" (Voisin, 1959) and incorporated into other systems such as "holistic grazing" and "management-intensive grazing" (Savory and Butterfield, 2016; Gerrish, 2004), adaptively manages grazing pressure to accommodate plant growth, foraging conditions, and animal needs. It employs high stock densities for short grazing periods and allows sufficient plant recovery periods between grazing events (Teague and Barnes, 2017). In an AMP grazing system, a pasture is subdivided into several small paddocks, often centered around a water source, and involves high-density, frequent movement of livestock among these paddocks (Teague and Kreuter, 2020). The AMP grazing allows for extended rest periods for each paddock, which has been claimed to offer several benefits, such as improved soil water infiltration, homogeneous grazing, increased productivity and animal gain, and higher stocking rates (Savory, 1983; Teague et al., 2011).

AMP grazing is thus a distinct approach that integrates stocking rates, stocking density, timing and frequency of defoliation, together with rest periods, into a comprehensive management practice that seeks to align several ecological principles with the fundamental requirements of both land (vegetation and soils) and livestock. Proponents assert that AMP grazing provides ecological benefits, including improved soil health, increased productivity, more uniform grazing (i.e., utilization) of vegetation biomass, and higher C sequestration, as compared to continuous grazing (Savory and Butterfield, 2016; Teague et al., 2011). However, evidence on the efficacy of AMP grazing is debated (Briske et al., 2013).

#### **1.6 AMP Grazing Impacts on Soil Organic C**

AMP grazing has been highlighted due to its effectiveness in counteracting the detriments of conventional (largely continuous) grazing (Teague et al., 2011). Ecosystem-based benefits of

AMP grazing over conventional methods, as documented in several studies, include increased soil water infiltration (Döbert et al., 2021), improved water holding capacity, reduced soil erosion, and enhanced biomass productivity (Grenke PhD thesis), among other benefits (Apfelbaum et al., 2022; Park et al., 2017; Wang et al., 2021).

Specifically, Apfelbaum et al. (2022) found that SOC stocks to a depth of 1 meter were over 13% greater in AMP grazed areas compared to conventionally grazed ranches. Johnson et al. (2022) noted a 20.6% increase in SOC in the top 10 cm of the soil profile and a 19.52% reduction in soil C (CO<sub>2</sub>) respiration rates with AMP grazing. Mosier et al. (2021) reported that AMP grazing sites had on average 13% more soil C compared to conventional grazing sites over a 1-meter depth. Furthermore, in another study, Mosier et al. (2022) illustrated that farms using AMP grazing management had greater C stocks within the soil A-horizon across multiple SOM fractions.

Findings from past work emphasize AMP grazing's potential to offset GHG gas emissions via soil C sequestration, with studies documenting a 4-year C sequestration rate of 3.59 Mg C ha<sup>-1</sup> yr<sup>-1</sup> (Stanley et al., 2018). Owing to these ecological advantages, AMP grazing has seen increased adoption among North American producers.

However, the effectiveness of AMP grazing remains disputed. This is partially due to the lack of extensive research and the limitations posed by small sample sizes, which fail to encompass the wide range of environmental factors and adaptive (i.e., flexible) management practices inherent in cattle grazing (Teague et al., 2013). Moreover, current studies on the impact of AMP grazing on SOC sequestration have not sufficiently accounted for potential confounding factors, such as soil compaction associated with high stocking densities commonly found under AMP grazing (Apfelbaum et al., 2022; Mosier et al., 2021, 2022; Johnson et al., 2022).

Studies asserting higher SOC sequestration under AMP grazing have been restricted to specific climatic zones in the United States, predominantly in moist and warm regions with a relatively high abundance of warm-season C4 plant species (Apfelbaum et al., 2022; Johnson et al., 2022; Mosier et al., 2021, 2022). Such environments differ significantly from the moist and cool climate typically found in Canadian grasslands, limiting the applicability of these findings. Thus, a comprehensive understanding of the effects of AMP grazing on C sequestration within the context of Canadian grasslands remains elusive. Further research in these settings is necessary to validate or refute the proposed benefits of AMP grazing.

#### **1.7 Research Objectives**

Previous comparative grazing studies have had limitations including small scales, a limited number of replications, a lack of adaptive grazing practices, and a reliance on anecdotal evidence rather than on-farm data (Briske et al., 2008; Nordborg, 2016; Norton, 1998; Teague et al., 2013). To better evaluate grazing impacts, long-term studies across diverse working landscapes are needed.

The objective of this study was to compare SOC dynamics between commercial cattle ranches using AMP grazing versus neighboring (hereafter conventional; n-AMP) operations across the northern temperate grasslands of western Canada. The specific goals of this study were to:

• Evaluate differences in SOC stock between AMP and n-AMP at the ranch/pasture level.

- Examine how nuanced grazing practices affect SOC stocks.
- Assess grazing impacts on SOC distribution across various soil depths.

This research encompassed 26 neighboring AMP and n-AMP ranch pairs distributed across major ecoregions in Alberta, Saskatchewan and Manitoba. Detailed grazing management histories were obtained through producer surveys, and were documented by Bork et al. (2021). Soil cores to 1 m depth were collected during summer over two years for SOC analysis.

Chapter 2 describes the study areas, soil sampling and analytical methods, grazing metrics, and statistical approaches used. The grazing management attributes of AMP and n-AMP ranches are characterized and compared. Statistical analyses examine differences in SOC stocks between AMP and n-AMP systems and relationships to specific grazing practices.

Chapter 3 summarizes key findings from the thesis research, highlights overall research conclusions, and discusses implications for grazing management strategies to support SOC sequestration. It outlines future research opportunities to uncover mechanisms driving subsurface SOC accrual under specialized grazing regimes such as AMP.

Ultimately, this thesis provides new insights into grazing practices to inform climatesmart livestock management across northern grasslands.

# Chapter 2. Effects of Grazing Management on Soil Organic C in Grassland Soils of Western Canada

#### **2.1 Introduction**

Grasslands comprise approximately 40% of the Earth's terrestrial surface (White et al., 2000) and are a significant source of ecological goods and services (EG&S), including wildlife habitat, forage production, and soil carbon (C) storage (Bengtsson et al., 2019). Notably, grasslands store over 10% of terrestrial biomass C and as much as 30% of the soil organic C (SOC) stock (Scurlock and Hall, 1998). Despite their importance, many grassland areas have suffered losses of SOC over recent decades due to conversion to alternative agricultural use (i.e., cropping) and improper grazing management (Bardgett et al., 2021). Under conventional grazing management, grasslands are continuously grazed throughout the grazing season, which enables cattle to selectively defoliate preferred forage plants, resulting in spatially patchy distribution of livestock grazing, bare ground patches, high rates of soil erosion, reduced productivity and biodiversity (Teague et al., 2011; Zhou et al., 2019). Furthermore, inappropriate grazing, including that occurring under high stocking rates, particularly under continuous grazing with little no rest, has been found to decrease SOC in grasslands worldwide (Byrnes et al., 2018). Although this loss of SOC to the atmosphere denotes a substantial disturbance to the global C cycle, it also represents an opportunity for managing current greenhouse gas (GHG) emissions by sequestering SOC back into the soil through improved grassland management (Conant et al., 2016).

Improved grassland management has been recognized as a climate change mitigation strategy of high impact due to its large potential area of adoption and potential to sequester up to

1.6 Pg CO<sub>2</sub> (eq) yr<sup>-1</sup> (Paustian et al., 2016). Importantly, rotational grazing has been deemed capable of reversing the damage caused by conventional grazing (Byrnes et al., 2018). Numerous forms of rotational grazing have been shown to restore or improve ecosystem function and have beneficial impacts on the soil (Teague and Kreuter, 2020), all of which broadly consist of dividing large grazing areas into smaller ones, and rotating livestock through them (Savory and Butterfield, 1998). Rotational grazing systems can be prescriptive, with predefined rotations (fixed spatiotemporal arrangement) or flexible, with rotations based on available pasture, forage conditions, and animal needs (Undersander et al., 2002). One such rotational grazing system is adaptive multi-paddock (AMP) grazing, which involves adaptively regulating grazing pressure to accommodate plant growth and foraging conditions while supporting animal needs. AMP practitioners use relatively high stock densities for short grazing periods (hours to days, depending on available forage and livestock numbers) while allowing sufficient plant recovery (regrowth) periods between each grazing event (Teague and Barnes, 2017). The practices utilized in AMP grazing were first conceptualized as "rational grazing" (Voisin, 1959) and are incorporated within other progressive grazing systems, including "holistic grazing" (Savory and Butterfield, 1998) and "management-intensive grazing" (Gerrish, 2004).

Several studies have reported on the ecological benefits of AMP management compared to conventional grazing, including enhanced soil water infiltration and improved water holding capacity (Döbert et al., 2021; Apfelbaum et al., 2022), reduced soil erosion (Park et al., 2017), and increased biomass productivity (Johnson et al., 2022), among others (Wang et al., 2021). Additionally, AMP grazed pastures have documented the potential to offset GHG emissions through soil C sequestration, with a 4-year C sequestration rate of 3.59 Mg C ha<sup>-1</sup> yr<sup>-1</sup> (Stanley et al., 2018). For its purported positive impact on pasture condition, productivity, and utilization,

AMP grazing has been increasingly used by producers in North America. However, in despite of its purported benefits for SOC sequestration and other ecological benefits, the effectiveness of AMP grazing is still a matter of dispute, partly due to the lack of extensive research and the small sample sizes typically used that fail to capture the wide range of management practices and environmental factors involved in cattle grazing (Briske et al., 2013; Teague et al., 2013; Bork et al., 2021). Furthermore, the studies conducted on the effect of AMP grazing on SOC sequestration so far have failed to avoid the potential confounding effect of soil compaction associated with the high stocking densities commonly adopted in AMP (e.g., Apfelbaum et al., 2022; Mosier et al., 2021, 2022; Johnson et al., 2022).

In an effort to better understand the role of grazing management on SOC sequestration across northern temperate grasslands, I conducted a study to compare the SOC mass of pastures under AMP grazing to those of neighboring pastures subjected to conventional grazing management systems, henceforth called n-AMP grazing (Bork et al., 2021). In this context, n-AMP grazed areas represent a random sample of beef cattle production operators found across grasslands of western Canada. Furthermore, I evaluated the influence of various grazing practices on SOC mass, in addition to the effect of grazing as a dichotomous treatment (i.e., AMP vs. n-AMP). Additionally, this investigation included assessing the impact of various grazing practices on SOC at greater soil depths (up to 1-m) while avoiding the potential confounding effect of soil compaction by using equivalent soil mass (ESM) in SOC mass calculations. I hypothesized that extended rest periods following early-season grazing for short periods at high stocking densities under AMP grazing would increase SOC sequestration. The significance of these findings is discussed in the context of sustainable grazing management and

the development of resilient agricultural production systems in the face of changing climatic conditions.

#### 2.2 Materials and Methods

#### 2.2.1 Study Area

This study was conducted on grasslands associated with 52 ranches located across Alberta (n = 20), Saskatchewan (n = 24), and Manitoba (n = 8), in the prairie region of western Canada (Appendix A). Sites included in this study correspond to those reported in Döbert et al. (2021) in the assessment of water infiltration, and consist of a smaller subset of ranches reported in Bork et al. (2021). All ranches were privately owned except two, which are owned by the University of Alberta.

The 52 ranches represented an agro-climatic gradient that captured broad variation in climate, soil type, vegetation type and land management across the temperate Canadian grasslands. The ranches were, in order of increasing aridity, situated within the Boreal transition (n = 10), Fescue Grasslands of the foothills and parkland regions (n = 36), and Mixedgrass Prairie (n = 6). Ranches in the Boreal transition were dominated by introduced grasslands (i.e., planted forage on previously cultivated lands) intermingled with boreal forest. Those in the Fescue Grasslands were dominated by native rough fescue (*Festuca campestris* and *F. hallii*) on non-cultivated soil, or more commonly, seeded grasses such as Kentucky bluegrass (*Poa pratensis*), smooth brome (*Bromus inermis*), and timothy (*Phleum pratense*) in addition to introduced legumes such as clover species (*Trifolium spp.*) and alfalfa (*Medicago sativa*). The Mixedgrass Prairie grasslands were comprised of grasses of varying height, including western and northern wheatgrass (*Pascopyrum smithii* and *Elymus lanceolatus*, respectively), blue grama

grass (*Bouteloua gracilis*), spear grasses (*Hesperostipa comata* or *H. curtiseta*), and junegrass (*Koeleria macrantha*). Across grasslands of the study region, the climate normal over 30 years (1989 - 2018) ranged from 326.2 to 629.2 mm for mean annual precipitation (MAP), and 1.2 °C to 4.8 °C for mean annual temperature (MAT). The annual heat moisture index (AHM, [AHM = (MAT + 10)/(MAP/1000)]), an index of aridity that accounts for both changes in temperature and moisture, ranged from 21.6 in moist areas to 45.3 in arid areas. Predominant soils varied from Black, Eluviated Black and Dark Gray Chernozems (Fescue Grasslands) to Brown Chernozems (Mixedgrass Prairie) and Gray Luvisols (Boreal Transition).

#### **2.2.2 Experimental Design**

This study followed a split-plot experimental design using 26 neighboring pairs of beef cattle ranches, with each ranch pair consisting of an AMP ranch and an n-AMP (neighboring) ranch. The latter can be regarded as representative of the wide range of typical grazing operations found within the regional cattle industry (Bork et al. 2021). AMP ranches were selected from an online self-identification questionnaire advertised at grazing workshops and conferences. Prospective candidates responded to numerous questions regarding their grazing practices. Those questions were structured to identify producers who adopted highly flexible (i.e., adaptive), multi-paddock grazing to facilitate short grazing periods and long rest intervals during the growing season, as described previously (Bork et al., 2021).

Eligible AMP ranches were restricted to those that used this system for a minimum of 10 years and had a neighboring (typically within 5 km) n-AMP ranch with a similar cultivation history and ecosite conditions (e.g., landform, slope, soil texture, and soil type) supporting cattle grazing. Most ranches had a history of cultivation (42/52) and seeding, with an average of

approximately 19 years since the last cultivation occurred (Appendix B). Additionally, AMP ranches had to have an area available for soil sampling greater than 10 ha, which had not been subject to bale feeding to avoid confounding effects of additional C inputs from supplemental feed. These conditions were confirmed through phone interviews and field visits. The ranch pairs were distributed across a large geographic area approximately 1,300 km from east to west, and nearly 550 km from north to south, with a minimum distance of 25 km between pairs. Within this framework, each ranch pair served as the whole plot factor, while the grazing system functioned at the sub-plot level, allowing for a detailed comparative analysis of different grazing systems and their effects on SOC.

#### 2.2.3 Soil Sampling

Fifteen sampling points were randomly selected within a representative grassland area of 10 ha on each of the 52 studied ranches. Wetlands, watering points, fences, or areas subject to anomalous disturbances (i.e., prairie dog burrows, pocket gophers, and ant hills) were avoided. A large diameter (5-cm) core was used to sample the mineral soil at each sampling point to a maximum depth of 100 cm using a Giddings hydraulic soil sampler (Giddings Machine Company, Windsor, CO, USA) mounted on a Polaris Ranger 6 x 6. A total of 780 soil cores were collected, with 24 and 28 ranches sampled in July and August of 2017 and 2018, respectively. Although not all cores reached 100 cm depth, total coring depth averaged 96.1 cm for AMP ranches and 95.9 cm for n-AMP ranches. The 5-cm diameter soil cores were extracted in plastic sleeves, capped at both ends to create a sealed 100-cm length soil sample, stored in a large heavy-duty crate, and transported to the Forest Soils Lab at the University of Alberta for processing and soil C analysis.

#### 2.2.4 Soil Core Processing

In the laboratory, soil cores were divided into sections using a hybrid approach. The topsoil, classified as the Ah horizon in accordance with the Canadian System of Soil Classification (Canadian Agricultural Services Coordinating Committee, 1998), is characterized by high organic C content and was separated into genetic strata. The B horizon (i.e., subsoil) was stratified into fixed depth increments. After the LFH layer (i.e., litter, fragmented litter, and humus) was removed from the top of each soil core, the thickness of the Ah horizon was measured and separated into strata of varying depths according to apparent differences in soil color and texture. For instance, the Ah horizon from a given soil core might be stratified into two strata: 0 to 9 cm (Ah1<sub>0-9cm</sub>) and 9 to 27 cm (Ah2<sub>9-27cm</sub>). The subsoil (soil horizon below Ah) was stratified in fixed depth increments from the bottom of the Ah horizon to 60 cm (e.g., B1<sub>27-60cm</sub>), and from 60 to 100 cm (e.g., B1<sub>60-100cm</sub>). The separation and stratification approach adopted for the Ah and B horizons, respectively, was guided by distinct considerations for the SOC content. The Ah horizon was sampled separately to avoid mixing or cross-contamination (from the dust generated during the processing and grinding of the Ah horizon samples) with the less humified mineral soils below, as this could substantially increase the SOC analysis in the soil below the Ah, leading to inaccurate representations. On the other hand, the B horizon was stratified in fixed depth increments, as SOC was not expected to be very different among soil layers or horizons below the Ah. This approach ensured that the unique characteristics of the Ah horizon were preserved, while providing a consistent method for examining the subsoil, aligning with the objectives of understanding SOC distribution.

Soil from each core section was air-dried at room temperature and sieved using a 2 mm screen to remove coarse fragments (larger than 2 mm in diameter), litter and roots. Coarse

fragments were weighed, and their volume quantified through the water displacement method (Carter and Gregorich, 2007). A portion (20 g) of each sample was oven-dried at 105° C until a constant weight was reached to determine soil moisture content. The soil volume in each core section was calculated as a function of the core diameter (5 cm) and section length. Bulk density of the fine earth was calculated using Eq. 1:

BDi  $(g \text{ cm}^{-3}) = (dry \text{ soil}_{[g]} - \text{ coarse fragment}_{[g]})/(sample \text{ vol}_{[cm^3]} - \text{ coarse fragment vol}_{[cm^3]})$  Eq.1

#### 2.2.5 Soil Analysis

One sub-sample of an air-dried soil sample was ground to a fine powder (<0.1 mm) using a ball mill (Retsch MM200 Mixer Mill, Thomas Scientific, Swedesboro, NJ, USA) and analyzed for total C by dry combustion using an automated elemental analyzer (Vario El Cube CHNS, Elementar Analysensysteme GmbH, Langenselbold, Germany). A sulfanilamide standard was run after every 10<sup>th</sup> sample to correct for drift in the instrument. Soil pH was measured using a pH meter (Thermo Fisher Scientific, Waltham, MA, USA) with a 1:5 (*w:v*) mix of soil:water (Hendershot et al., 2006).

Soil samples with a pH > 6.4 were assessed for soil inorganic C through a method adapted from Snyder and Trofymow (1984). Briefly, 10 mL of 0.5 N NaOH in a 20 mL vial and 2 g of soil in a 50 mL beaker were placed in a 1.0 L reaction vessel and sealed. Five mL of 1 N HCl solution was then added to the 2 g soil through a rubber septum located on the lid of the reaction vessel. A 24 h incubation period was allowed, during which the CO<sub>2</sub> released from soil carbonates was absorbed by the NaOH solution. Subsequently, 2 mL of 2N BaCl<sub>2</sub> was added into the NaOH solution to precipitate the absorbed CO<sub>2</sub> as BaCO<sub>3</sub>. After adding four drops of phenolphthalein indicator, the non-consumed NaOH was back-titrated with a 0.5 N HCl solution using a microburet accurate to 0.001 mL. To account for ambient CO<sub>2</sub> within the jar, four blanket (control) NaOH samples were analyzed for every 70 soil samples. Each blanket NaOH sample corresponded to a reaction vessel where no soil was subject to reaction with HCl. Recovery tests were conducted using known graded CaCO<sub>3</sub> samples that contained 0.5 mg, 1 mg, 5 mg, 10 mg, 25 mg, 40 mg, and 55 mg of C. On average, a 99.01% recovery rate of SIC was obtained. Total organic C was determined using Eq. 2.

$$TOC = TCi\% - ICi\%$$
 Eq.2

Where:

 $TOC_i$ % = Percentage of total organic C in the soil horizon i.

 $TC_i\%$  = Percentage of total C in the soil horizon i, as measured by the elemental analyzer. IC<sub>i</sub>% = Percentage of inorganic C (%) in soil horizon i, obtained through titration and calculated as follows (Eq. 3).

ICi%= ((Blank HCli [ml] – Titration HCli [ml]))/((Soil samplei [g])) x 100 Eq.3

Finally, soil C mass was computed by multiplying TOC concentrations by soil bulk density and the depth of each layer, thereby deriving soil C mass. Depth of the Ah horizon from each soil core and SOC mass from each soil layer were regarded as subsamples and averaged to the ranch level (Appendix D).

#### 2.2.6 Grazing Metrics

Through surveys, I characterized the grazing management metrics that reflected the unique grazing practices adopted at each ranch regardless of treatment classes: AMP vs n-AMP Bork et al. (2021). The following grazing metrics were obtained for each ranch: stocking rate (aggregate year-long intensity of forage use), stock density while grazing (herd effect),
rest:grazing ratio (recovery period allowed following early season grazing), and the start of the grazing season (alleged range readiness) (Appendix B). Stocking rate [animal-unit-months (AUM) ha<sup>-1</sup>] for each ranch was calculated from the total area grazed, number of cattle, stock class (yearlings vs mature cows/bulls), and grazing entry and exit dates. Animal unit equivalencies for yearlings, mature cows and bulls were set at 0.8, 1.25, and 1.5, respectively (Bao et al., 2019). Average stocking densities while grazing (animal-units (AU) ha<sup>-1</sup>) were calculated as a function of average paddock size and herd size while grazing. The rest:grazing ratio was the number of days of rest provided following early season grazing (prior to August 1) standardized to the number of days of grazing during the early grazing typically was reported to occur. The earliest possible start date of the grazing season was set to March 15. I used a binary cultivation history metric (cultivated/non-cultivated) to indicate whether a grassland had previously been cultivated and seeded (Appendix B).

#### 2.2.7 Data Analysis

All statistical analyses were performed in Rstudio (version 3.5.2., R Development Core Team, Vienna, Austria) using linear mixed model analysis in the 'lme4' R package (Bates et al., 2014) with ranch pairs included as a random factor. As a first step, I used a mixed model analysis of variance to test if the nuanced grazing management practices of stocking rate, animal stock density, rest:grazing ratio, and start of grazing season differed among operations considered to practice AMP grazing and neighboring properties (n-AMP). By assessing a slightly larger group of ranches from which this study is part, Bork et al. (2021) found these metrics to be suitable indicators of the distinct management practices that characterized AMP and n-AMP ranches. I

intended to assess if the results found by Bork et al. (2021) are replicated in this subset of ranches, and subsequently evaluated the effect of grazing attributes on Ah horizon depth and SOC mass in all soil layers.

To avoid having soil compaction as a confounding effect when calculating SOC mass (Mg ha<sup>-1</sup>), I computed equivalent soil masses (ESM) per layer (Ah horizon, 0-10, 10-30, 30-60, and 60-80 cm) and for the total (0-80 cm) ESM using MB32AMP as the reference site. MB32AMP was selected as it had a relatively low soil bulk density without being an outlier compared to other sites. This was done using the Rstudio script created by von Haden et al. (2020). The SOC masses and Ah horizon depth were tested for normality and equality of variances using Shapiro-Wilk and Levene's tests, respectively, after which data were log-transformed to meet model assumptions. Prior to producing graphs, all data were back-transformed using the *antilog.pred* function in R.

The effect of grazing management (AMP vs n-AMP) on SOC mass within the Ah horizon and on total Ah horizon depth (cm) at the pasture level was evaluated by calculating F-tests using the *Anova* function in the 'car' package (Fox and Weisberg, 2018), with significance set at P <0.05. Using the same analytical procedure, I evaluated the effect of grazing management on incremental and cumulative SOC mass at increasing depths. Subsequently, I used a model selection approach to compare the ability of nuanced grazing practices to explain variation in SOC mass and Ah horizon depth. The tested models, which were the same for SOC mass and Ah horizon depth, contained either one or two grazing metrics as predictor variables, with interaction terms when applicable (see Appendix E for an overview of the predictors, and associated models).

To avoid model redundancy, prior to the analysis I assessed multicollinearity between the set of continuous independent variables based on a collinearity threshold of  $|\mathbf{r}| < 0.7$  using Pearson's correlation (Dormann et al., 2013). To verify if the binomial variable of grazing system was correlated with any of the continuous grazing metrics, I included grazing system in the analysis of multicollinearity by dummy-coding n-AMP as 0 and AMP as 1. No predictor variables were correlated with each other above the threshold (Appendix C). All independent variables were centered and standardized using the *scale* function in R.

I used Akaike Information Criterion adjusted for small sample size (AICc) to identify the most parsimonious candidate models. Models with a  $\Delta \leq 2$  AICc were considered to be similar in their ability to explain SOC mass and Ah horizon depth (Symonds and Moussalli, 2011). Null models with a random-effects structure (ranch pair) only were among the candidate models, thereby accounting for regional edapho-climatic variations. Since I was selecting models that contained different fixed effects and the same random factors, I deactivated the restricted maximum likelihood function (*REML* = *FALSE*) in the 'lmer' package (Fox et al., 2015). Finally, I used the *standardize\_parameters* function from the 'effectsize' package in R (Ben-Shachar et al., 2020) to assess the direction (positive vs negative) and effect size (magnitude of the standardized  $\beta$ 's) of model coefficients as well as their confidence intervals to assess variable significance (Cumming, 2009).

The linear mixed model containing the interaction between stocking rate and rest:grazing ratio was among the most robust models explaining variation in Ah horizon depth and SOC mass in the Ah horizon, as well as SOC mass in the 10-30 and 0-80 cm ESM layers. Regression models were developed with  $\beta$  estimates derived from a linear mixed model to demonstrate how Ah horizon depth and SOC mass in the 10-30 and 0-80 cm ESM layers were influenced by the

length of the rest period along a stocking rate gradient. In order to visually 'depict' differences in the sensitivity of SOC data relative to various rest periods, six levels of rest:grazing ratios were used, as follows: 0 rest (representing n-AMP ranches, which provided pastures little to no rest from grazing; Table S1), and 20, 40, 60, 80, and 100 days of rest to each day of early season grazing prior to August 1 (representing the spectrum of rest-rotation practices adopted by the AMP ranchers in this study; Appendix B). Because 50 of the 52 ranches in this study adopted a stocking rate between 0.32 and 5.78 AUM ha<sup>-1</sup> (Appendix B), I used a maximum stocking rate of 5.78 ha<sup>-1</sup> for model visualization.

Based on the finding that rest:grazing ratio (a grazing metric that clearly distinguishes AMP from n-AMP ranches) interacted with stocking rate to influence Ah horizon depth, I then tested the interactive effect of grazing system and stocking rate on SOC mass and Ah horizon depth. This allowed us to assess whether the underlying interaction between rest:grazing and stocking rate ratio would result in different trends between AMP and n-AMP grazed grasslands at the pasture/ranch level along a continuous range of stocking rates.

## 2.3 Results

#### 2.3.1 Differences in Grazing Practices Between AMP and n-AMP

There was no significant difference in stocking rates (AUM ha<sup>-1</sup>) between AMP and n-AMP ranches (P = 0.257; Table 1). However, AMP ranches had a mean animal stock density (AU ha<sup>-1</sup>) nearly 22 times larger than n-AMP ranches (Table 1). Known early adopters of AMP also began the grazing season earlier in the year, with the grazing season starting on average around April 29 while n-AMP operations started grazing close to May 20 (Table 1). In addition, AMP ranchers provided a longer recovery time after each grazing event compared to n-AMP ranchers, averaging nearly 6 weeks of rest for each day of early-season grazing in AMP operations; on the other hand, n-AMP ranchers used longer individual grazing periods and shorter subsequent rest intervals, averaging <1 day of rest to each day of grazing (Table 1). Similar results were reported by Bork et al. (2021) regarding a larger subset of ranches from which the present study was derived.

# 2.3.2 Effect of Overall Grazing Treatment on Ah Horizon Depth and SOC Mass

Evaluated at the binary treatment level (i.e., as two categorical classes), no differences in Ah horizon depth and SOC mass within the Ah horizon were found between AMP and n-AMP ranches (Table 2). Similarly, incremental and cumulative equivalent SOC mass were not different between grasslands subject to different grazing systems down to an 80 cm ESM depth (Fig. 1). As expected, SOC mass decreased with increasing depth, with ESM depths of 0-10, 10-30 cm, 30-60 cm, and 60-80 cm, representing 34.8%, 30.4%, 26.5%, and 7.5%, respectively, of the total SOC mass in the soil profile of the study grasslands.

# 2.3.3 Association of Specific Grazing Practices with Ah Horizon Depth and Equivalent SOC Mass

Through the selection of the most parsimonious linear mixed models among several candidate models, I identified if any of the underlying nuanced grazing practices characterizing all ranches across the AMP and n-AMP treatments were robust in explaining the depth of the Ah horizon and equivalent SOC mass across the soil layers. The most parsimonious models to predict Ah horizon depth consistently included stocking rate alone, and the interaction of stocking rate with rest:grazing ratio (Appendix E). For further validation, I calculated model estimates and weights for each fixed effect to account for model selection uncertainty (Table 3).

Results from the model validation suggest that stocking rate alone was a more robust fixed effect related to Ah horizon depth, as demonstrated by its 95% CI (Table 3; Fig. 2a), followed by the model with the interaction between stocking rate × rest:grazing ratio (Table 3). Although the latter model was non-significant in predicting Ah horizon depth based on its 95% CI (Table 3), it was the most robust (based on model weights) in predicting SOC mass within the Ah horizon and the 10-30 cm ESM layer, as well as across the entire 0-80 cm ESM soil profile, where it was significant based on its 95% CI (Appendix E; Table 3). Notably, equivalent SOC mass within the 10-30 cm ESM and the 0-80 cm ESM layers had nearly identical leading models as the most robust, which was likely due to the fact that the equivalent SOC mass within the 0-80 cm ESM profile is cumulative of all embedded soil layers, including that from the 10-30 cm layer. No model had greater performance than the null model (>2 AICc units) in predicting equivalent SOC mass within the shallow topsoil (0-10 cm ESM), or the 30-60 cm and the 60-80 cm ESM layers (Appendix E).

Results obtained from the linear regression models show that higher stocking rates were associated with thicker Ah horizons (Fig. 2a). Moreover, this occurred even in the absence of rest periods (rest:grazing ratio = 0), with topsoil depths ranging from ~17.2 cm at 0.32 AUM ha<sup>-1</sup> to ~19.1 cm at 5.78 AUM ha<sup>-1</sup> (Fig. 2b). An even stronger positive association existed at the highest rest period (rest:grazing ratio = 100), as Ah horizon depth increased from ~15.8 cm at 0.32 AUM ha<sup>-1</sup> to ~23.2 cm at 5.78 AUM ha<sup>-1</sup> (Fig. 2b). A different pattern occurred for modeled SOC mass data from the Ah horizon (Fig. 3b), where increasing stocking rates negatively impacted SOC mass within the Ah horizon at a rest:grazing ratio of 0 (which were grasslands comprised only of n-AMP ranches); SOC mass decreased from ~47 Mg ha<sup>-1</sup> at 0.32 AUM ha<sup>-1</sup> to ~43 Mg ha<sup>-1</sup> at 5.78 AUM ha<sup>-1</sup> in grasslands lacking rest. In comparison, within grasslands

having a rest:grazing ratio of 100, SOC mass in the Ah horizon increased from  $\sim 28$  Mg ha<sup>-1</sup> at 0.32 AUM ha<sup>-1</sup> to  $\sim 68$  Mg ha<sup>-1</sup> at 5.78 AUM ha<sup>-1</sup> (Fig. 3b).

Within the 10-30 ESM cm depth, at a stocking rate of 5.78 AUM ha<sup>-1</sup>, equivalent SOC increased by  $\sim 10$  Mg ha<sup>-1</sup> between the lowest and the highest rest:grazing ratio (Fig. 4b). Conversely, within the same soil layer, at a stocking rate of 0.32 AUM ha<sup>-1</sup> the highest rest:grazing ratio was associated with a reduction of  $\sim 12$  Mg ha<sup>-1</sup> of SOC compared to the lowest rest:grazing ratio. Similarly, across the 0-80 cm ESM layer (i.e., whole soil profile) the highest rest:grazing ratio had ~20 Mg ha<sup>-1</sup> more SOC than the lowest rest:grazing ratio at a stocking rate of 5.78 AUM ha<sup>-1</sup> and ~40 Mg ha<sup>-1</sup> less SOC than the lowest rest:grazing ratio at a stocking rate of 0.32 AUM ha<sup>-1</sup> (Fig. 5b). Overall, these results indicate that 1) higher stocking rates alone were associated with thicker Ah horizons regardless of the grazing system adopted, and that 2) longer rest periods only resulted in increased SOC sequestration if higher stocking rates (higher than approximately 3.5 AUM ha<sup>-1</sup>) were used. Furthermore, since the Ah horizon (mean Ah depth =  $21.42 \pm 0.82$  cm) extended well beyond the 0-10 cm ESM layer and into the upper half of the 10-30 cm ESM layer (i.e., 10-20 cm), and considering that the interaction between stocking rate × rest: grazing ratio had a positive association with SOC stocks in the Ah horizon and in the 10-30 cm ESM layer, but not in the 0-10 cm ESM layer, the interactive effect of stocking rate × rest: grazing ratio on SOC stocks within the Ah horizon likely occurred below the 10 cm depth and was a function of increasing Ah depth below 10 cm.

At lower stocking rates (lower than approximately 3.5 AUM ha<sup>-1</sup>), none of the rest periods attributed to AMP grazing (i.e., 20, 40, 60, 80, and 100 rest:grazing ratios) had a positive effect on SOC sequestration depth compared to the n-AMP grazers that had no rest period while summer grazing (i.e., rest:grazing ratio  $\sim$  0). Considering that ranches in this study averaged

94.35 Mg SOC ha<sup>-1</sup> in total to 80 cm (ESM depth) (Appendix D) and that the interactive effect between stocking rate × rest:grazing ratio explained 5% of the total variation in SOC within the 0-80 cm ESM soil profile ( $R^2_c = 0.05$ , Table 3), the total effect of the interaction between these two management practices amounted to an average increase of 4.71 Mg SOC ha<sup>-1</sup> from AMP grazing across all ranches.

# 2.3.4 Interaction Between Binary Grazing Treatment and Stocking Rate on Ah Horizon Depth and SOC Mass

Stocking rate alone was associated with Ah horizon depth (Table 4). For SOC mass within the Ah horizon, the interaction between grazing system and stocking rate was significant (Table 4), with SOC mass increasing within AMP ranches under increasing stocking rates, but decreasing in n-AMP with escalating stocking (Fig. 3a). While grazing system and stocking rate did not affect SOC mass at the 0-10 cm ESM layer, their interactive (multiplicative) effect on SOC was evident within the 10-30 and 0-80 cm ESM layers, in which increasing stocking rates had a positive effect on incremental equivalent SOC mass in grasslands subject to AMP grazing; in contrast, for n-AMP grasslands this relationship was negative (Fig. 4a and Fig. 5a), and thus consistent overall with the more detailed assessment of grazing management practices. The interaction between grazing system × stocking rate had a significant effect on SOC mass within the exact same soil layers in which the model containing the interaction between the rest:grazing ratio and stocking rate were identified as more robust in predicting SOC mass. This could be attributed to the significant correlation between grazing system and rest:grazing ratio (r = 0.69; Appendix C).

### 2.4. Discussion

#### 2.4.1 AMP and n-AMP Affect Ah Horizon Depth and Equivalent SOC Mass

The lack of differences in Ah horizon depth and equivalent SOC mass detected between grazing systems across all soil layers in a binary comparison (AMP vs. n-AMP) is in contrast to previous studies that found AMP significantly increases SOC mass in grasslands compared to n-AMP grazing, especially within surface soil layers (Johnson et al., 2022; Mosier et al., 2021). This reported impact on SOC in surface soil is attributed elsewhere to the intensified trampling of soil and vegetation caused by high animal stocking densities, resulting in the fragmentation of plant material and its incorporation into the surface soil, which in turn facilitates microbial assimilation of shoot litter C into the SOC pool (Wei et al., 2021). Since saprotrophic fungi are the key regulators of plant litter decomposition and C incorporation into the soil (Crowther et al., 2012), increased SOC sequestration due to grazing practices that intensify trampling (i.e., those like AMP with a high stocking density) have been associated with increased fungal abundance and higher fungi:bacteria (F:B) ratios (Liu et al., 2015; Teague et al., 2011). However, when assessing microbial communities within the 0-15 cm soil layer in 15 of the same 26 ranch pairs included in this study, Khatri-Chhetri et al. (2022) found that AMP grazed soils did not increase fungal abundance or fungi:bacteria ratio compared to those subject to n-AMP grazing. This indicates that the management practices adopted in the AMP grasslands of this study may not have led to changes in the soil microbial community that purportedly have led to increases in SOC sequestration elsewhere, partially explaining why equivalent SOC mass within the 0-10 cm ESM layer remained similar between AMP and n-AMP grasslands. Therefore, more research is needed to clarify this.

Furthermore, discrepancies between these findings and other studies might be due to differences in sampling methodology, vegetation type, or climate. For instance, the studies conducted by Apfelbaum et al. (2022), Johnson et al. (2022), and Mosier et al. (2021, 2022) that found AMP grazing sequestered more SOC than n-AMP grazing in binary comparisons, were each performed in a small number of ranches and restricted to relatively smaller regions within moist and warm climatic zones in the south or south-central United States under environments intrinsically different from the generally moist and cool northern temperate climates of western Canada. Of the paired sites in this study only 3 of the 26 ranch pairs were located in an ecoregion of high aridity, and all were cool temperate, with most to all of the biomass derived from cool season C3 plant species regardless of location. Therefore, the difference in findings between my results and others' might be because plant communities in my study sites respond to changes in grazing management practices differently compared to other regions. Furthermore, the broad variation in management practices among ranch operations, including within each of the AMP and n-AMP grazing treatments in my study (Bork et al., 2021), even regardless of their dichotomous treatment classes, might also explain why the binary comparison of their effect on equivalent SOC mass revealed no significant difference. These results provide evidence of the challenges related to identifying management practices that are beneficial to SOC sequestration in the northern Great Plains given its wide variability in edapho-climatic conditions.

# 2.4.2 Specific Role of Stocking Rate, Rest:Grazing Ratio, and Stock Density on Equivalent SOC Mass

Past research on the effect of nuanced grazing practices on C sequestration have largely focused on the isolated effects of either rest periods, grazing intensity or stock density, relative to

SOC sequestration. For instance, extended rest periods prior to regrazing are thought to increase C sequestration by enabling ample shoot regrowth between grazing episodes, consequently promoting root growth (since plant belowground biomass is even more abundant than aboveground biomass) and improving root distribution and microbial activity (Teague and Kreuter, 2020). Conversely, while rest periods have a clearer association with SOC mass, the effect of grazing intensity on SOC is less obvious, varying by region, climate, and plant type (Abdalla et al., 2018), with some previous studies reporting a positive effect (Li et al., 2011; Silveira et al., 2014), some a negative effect (Ma et al., 2020), and yet others a lack of association between grazing intensity and SOC (Willms et al., 2002). Divergent results may be related to the fact that studies examining long-term stocking are frequently restricted to a few locations (e.g., Silveira et al., 2014), lack adequate replication (e.g., Han et al., 2008), are limited to pastures under continuous grazing management only (Willms et al., 2002), or included rotationally grazed pastures but did not report on the effect of potentially confounding factors such as the length of the rest period between grazing events (e.g., Bork et al., 2020). As a result, several meta-analyses conclude that high grazing intensity reduces soil C (Lai and Kumar, 2020; Lu et al., 2017; Zhou et al., 2017), especially in pastures dominated by C3 plants (Abdalla et al., 2018; McSherry and Ritchie, 2013), which are also dominant across all of my study locations. However, since none of these meta-analyses differentiated between the effect of grazing intensity between pastures under continuous or rotational grazing, it is possible that their findings are biased towards the effect of stocking rate for pastures under continuous grazing and do not reflect its effect on rotationally grazed pastures. For instance, pastures under continuous grazing represented the majority of the 28 studies from North America included in the meta-analysis conducted by Lai and Kumar (2020), with only five (or 17%) of those studies reporting on

rotational grazing. While high grazing intensities under a continuous grazing system lead to reduced SOC mass by altering the plant root system and its associated microbial community (Klumpp et al., 2009), these results suggest grazing intensity has the opposite effect on SOC mass if pastures are provided ample rest before being regrazed, potentially through the enhanced grassland biomass production and plant composition change (Grenke PhD thesis).

Beyond the dichotomic comparison between AMP and n-AMP, a more thorough examination of the role of distinct cattle management practices provides novel understanding of how specific grazing metrics might alter SOC sequestration. First, while the metrics of stocking rate and rest: grazing ratio influenced SOC in subsurface layers, none of the nuanced grazing management practices included in this study influenced SOC mass within the immediate surface soil layer, highlighting the importance of assessing SOC within the collective soil profile including the deeper soil layers. Secondly, I found that at stocking rates lower than 3.5 AUM ha <sup>1</sup>, n-AMP grazed grasslands sequestered more SOC in subsurface soil (below 10 cm depth) relative to AMP grazed grasslands at comparable stocking rates; importantly, however, as stocking rates gradually increased across n-AMP grazed grasslands, subsurface equivalent SOC mass decreased. In contrast, in AMP ranches, subsurface equivalent SOC mass increased with increasing combinations of both stocking rate and rest: grazing ratios (i.e., symptomized by longer periods of rest between early-season grazing events), with the point of intersection between AMP and n-AMP (the point at which AMP sites had more equivalent SOC mass than n-AMP sites) being a stocking rate of around 3.5 AUM ha<sup>-1</sup>, regardless of the rest:grazing ratio adopted in AMP ranches.

Several mechanisms might be responsible for the differences in subsurface equivalent SOC mass along different levels of stocking rates and rest periods in n-AMP and AMP ranches.

Different levels of grazing intensity, for instance, have been shown to affect root biomass (Zhou et al., 2017), root C contents (Ma et al., 2021), and root exudation (Sun et al., 2017), all of which influence the allocation of C to belowground, and consequently, the sequestration of SOC within greater soil depths (Bai and Cotrufo, 2022; Wilson et al., 2018; Zhou et al., 2017). In a metaanalysis of the impact of continuous grazing at various grazing intensities on subsurface soil layers, Jiang et al. (2020) found both light and moderate grazing intensities had greater belowground biomass and total C in deeper soil layers (20-40 cm and >40 cm) compared to a heavy grazing intensity, which is in agreement with my results that within n-AMP grazed grasslands, equivalent SOC mass in the 10-30 cm ESM layer (and consequently, across the entire 0-80 cm ESM layer) gradually decreased with increasing stocking rate. This can be explained by the fact that in continuous grazing systems (such as in part of the n-AMP ranches included in this study), low and intermediate stocking rates (and thus, presumably light and moderate grazing intensities) stimulate the allocation of belowground C by promoting the modification of root architecture and dynamics, enabling the creation of more fine roots (Derner et al., 2006). Although I did not measure root length, Ma et al. (2020) found root length was more responsive than biomass to climate and grazing treatments in Canadian grasslands. Their results imply subtle root morphological changes could be contributing to the subsurface SOC accumulation I observed under certain grazing regimes. Enhanced root growth and turnover may increase rhizodeposition and SOC stabilization in deeper layers. Further research on root traits would provide greater insight into grazing effects on soil C sequestration.

The study by Smoliak et al. (1972) also provides useful insights on grazing impacts on prairie soils and vegetation. They examined a *Stipa-Bouteloua* grassland in Alberta grazed by sheep at light, moderate and heavy intensities over 19 years. Under heavy grazing, they observed

compositional shifts towards more shallow-rooted grasses and increases in root biomass near the surface. This accumulation of root biomass aligns with my findings of thicker A horizons and enhanced subsurface SOC stocks at higher stocking rates. Although I did not assess species shifts, Smoliak et al.'s results imply heavy continuous grazing favors shallow-rooted plants, which could contribute to subsurface SOC accrual. Their findings lend additional support that specialized grazing regimes alter root traits in ways that increase subsurface SOC sequestration. While species such as *Poa pratensis* may play a role, the broader dataset of sites analyzed by Bork et al. (2021) indicates this was not a dominant species across most ranches. Without available data on floristic shifts specific to my sites, I am unable to conclusively identify which species are involved in the observed subsurface SOC accumulation patterns.

Allocating more biomass to roots can give plants greater access to moisture and nutrients (Zhou et al., 2014) while representing a conservative strategy to avoid damage and maintain the ability to recolonize in frequently disturbed habitats (Ning et al., 2014). On the other hand, continuous grazing at high stocking rates (or high grazing intensity) generally leads to overgrazing, which causes plants to reduce leaf photosynthetic functions (Ren et al., 2017). As a consequence, root biomass and the allocation of C belowground are decreased at the same time that shoot respiration is increased to resist disturbance and maintain plant survival (Liu et al., 2021), all of which might ultimately lead to the loss of subsoil SOC over time.

Unlike in n-AMP ranches, equivalent SOC mass within the 10-30 and 0-80 cm ESM layers in AMP ranches increased with increasing stocking rates, corroborating the results reported on by Bork et al. (2020), who found stocking rates were positively associated with equivalent SOC mass within the 0-60 cm soil layer in 32 rotationally grazed Mixedgrass Prairie pastures located across a large geographic area in Saskatchewan, Canada. With rotational grazing

systems such as AMP grazing, plants can recover leaf photosynthetic functions by regrowing aboveground biomass during extended periods of rest (Teague et al., 2011). In fact, in a study conducted in a subset of the same 26 ranch pairs used in this study, Grenke et al. (n.d) found AMP increased aboveground shoot biomass relative to n-AMP grazed pastures. As a consequence of greater biomass production, plants in AMP grazed pastures can continue allocating C to roots even after being heavily grazed (Ma et al., 2021), presumably because highly disturbed but sufficiently rested (recovered) plants are more prone to enhancing root growth and translocating C belowground. Additionally, Grenke et al. (n.d) also found that AMP grazing increased pasture utilization rates compared to n-AMP, which is thought to improve root turnover rates (Frank et al., 2002), ultimately leading to the accumulation of root-derived C deeper in the soil profile. In line with this, my findings indicate that soils from the AMP ranches that had adopted higher cattle stocking in combination with longer rest periods were more effective in sequestering SOC in subsoil layers (defined as below 10 cm depth) compared to AMP ranches that practiced shorter rest periods and implemented lower stocking rates. On the other hand, the AMP grasslands in which stocking rates were lower than ~3.5 AUM ha<sup>-1</sup> had lower SOC compared to n-AMP grasslands at comparable stocking rates, regardless of the rest:grazing ratio adopted. This finding suggests that the use of excessively long rest periods may reduce C fixation by vegetation and subsequent inputs to soil, particularly when insufficient stocking rates (i.e., reduced herbivore offtake) are applied. While the mechanisms for this are not altogether clear, this could arise if extended rest under low stocking impair plant growth, as might occur when growing conditions are ideal for plant growth thereby allowing vegetation to rapidly develop and senesce before the end of the growing season, or when an excessive accumulation of aboveground litter arises, both of which could reduce overall plant growth and

thus SOC sequestration within AMP ranches. Excessive litter accumulation on the soil surface hinders new biomass production by reducing canopy light penetration, decreasing soil surface temperature, and delaying spring green-up (Deutsch et al., 2010a; Deutsch et al., 2010b). The problems related to the accumulation of litter, particularly under elevated levels of plant production (Grenke, PhD thesis), are thought to reduce SOC mass in grasslands (Reeder and Schuman, 2002) and might explain the low SOC observed within the AMP ranches here that adopted stocking rates lower than ~3.5 AUM ha<sup>-1</sup>. From the 52 ranches included in this study, only 15 had a stocking rate higher than ~3.5 AUM ha<sup>-1</sup>, nine of which were AMP and five were n-AMP. This indicates that new or existing AMP operators who intend to promote SOC sequestration within northern temperate grasslands should strive to adopt relatively higher stocking rates, although admittedly this is only possible as pasture conditions warrant (e.g., through increased forage production attained via extended rest). Additionally, it should be pointed out that while some advocates of multi-paddock grazing have suggested that the use of such systems can support much higher levels of grazing (e.g., double stocking, see Savory, 1989), our results here do not support this generalization, with instead more conservative increases in use likely to enhance SOC.

Another important finding in this study was the lack of the herd effect (i.e., stocking density) on SOC mass in surface and subsurface soil layers. The high stocking densities applied in AMP grazing systems are thought to decrease selectivity in foraging, thereby increasing biomass removal uniformity and decreasing bare soil areas, thus improving soil hydrological functioning (Teague et al., 2013). Furthermore, high stocking densities are believed to increase the return of dung and urine, leading to improved nutrient cycling and subsequently enhanced plant growth (Drewry et al., 2008; Schrama et al., 2013). Additionally, high stocking densities

result in more intense hoof action, the trampling and fragmentation of vegetation, and the incorporation of litter into the soil (Mancilla-Leytón et al., 2013), ultimately promoting soil microbial activity (Lee et al., 2014). These effects associated with high stocking densities are collectively understood to boost C storage in surface soil layers (Wei et al., 2021). However, stocking density here did not affect equivalent SOC mass in this study, which further indicates that the observed increase in SOC mass associated with grazing management practices was likely regulated by belowground (root-associated) rather than aboveground (shoot-associated) C allocation processes. Similar null results for stocking density were reported by Grenke et al. (2022), who hypothesized that because AMP and n-AMP ranches did not differ in stocking rate, they might not actually differ in grazing selectivity despite differences in stocking density. Additionally, it might be possible that because I used ESM in my calculations of SOC mass, I accounted for any potential soil compaction issues associated with high stocking densities (von Haden et al., 2020), which could otherwise result in artificially inflated estimates of SOC mass in AMP ranches and potentially falsely indicate stocking density as an influential grazing management metric to soil C.

Alternatively, alterations in botanical composition could also account for the increase in SOC within AMP ranches that adopted high stocking rates and longer rest periods, in contrast to n-AMP ranches (Apfelbaum et al., 2022). This is further underscored by a recent assessment reporting that alterations to grassland forb biomass and grass quality (C:N ratio) under grazing were important in regulating SOC within a large network of Alberta grasslands (Bork et al., 2023). However, a study conducted by Grenke et al. (2022) on 18 of the 26 ranch pairs investigated in this study did not reveal marked changes in plant composition and diversity as a result of AMP grazing compared to n-AMP grazing. Furthermore, any increase in SOC mass

related to changes in vegetation composition would likely be manifested to the greatest extent within surface soil layers, because the majority of roots in grasslands are located within the 0-15 cm soil layer, and elevated stocking rates direct pasture composition towards species with shallow root systems (Smoliak et al., 1972). Nevertheless, as discussed earlier, the increase in equivalent SOC mass in AMP ranches occurred largely in subsurface soil layers (e.g., below 10 cm but above 30 cm), which would suggest that if changes in plant composition do play a role in altering SOC, it may be at least partially due to the location and distribution of roots of various plant species within the profile, and would require further testing for direct linkages to responses to changes in stocking and the timing and/or frequency of grazing, including rest periods.

### 2.4.3 Role of Stocking Rate on Ah Horizon Depth

One of the important findings of this study was the positive association between stocking rate and Ah horizon depth, as evidenced by its 95% CI (Table 4). However, this finding may not necessarily be a causal relationship. Thicker A horizons may be associated with higher biomass productivity (Kazemi et al., 1990), which in turn, can support higher stocking rates via enhanced forage availability (Bork et al., 2020). Therefore, the observed positive association between stocking rate and Ah horizon depth may simply reflect the underlying relationship between Ah horizon depth and grassland productivity, rather than a direct effect of stocking rate on Ah horizon depth.

#### 2.4.4 The Distribution of SOC Across the Soil Profile

Increased rhizodeposition might be associated with the increases in equivalent SOC mass in the subsurface soil layers of the AMP sites under high stocking rates and extended rest periods. Broadly, plant rhizodeposits consist of root exudates, active secretions such as secondary organic metabolites, proteins, fine roots sloughed during root elongation and senesced root tissue (Uren, 2000). Despite the priming effect, which is the increase in the decomposition rate of soil organic matter (SOM) by soil microbes after fresh organic C input to soil (Fontaine et al., 2003), rhizodeposition can lead to higher net C storage in soil (Liang et al., 2018). For instance, Villarino et al. (2021) found that rhizodeposition inputs are more efficient in forming mineral-associated organic C (46%), which constitutes the more stable and longer-term C pool in the soil, compared to above ground inputs (7%) or roots (9%). In a temperate grassland study, Ma et al. (2021) used 13C pulse labeling to show that high intensity defoliation the prior growing season increased allocation of newly fixed photosynthates to live roots. This supports the concept that defoliation can stimulate belowground C allocation, which may occur through increased rhizodeposition. In a study conducted in a temperate grassland using similar grazing intensities (e.g., stocking rates) but different rest periods between grazing systems, rotational grazing was found to increase the mean C residence time of belowground rhizodeposits and C used for root respiration by approximately 52% compared to continuous grazing (Liu et al., 2021), indicating that the contribution of rhizodeposits to C sequestration might be exacerbated under rotational grazing systems such as AMP grazing. Analogously, in a study assessing the effect of cattle stocking on rhizodeposits while maintaining the same rest period between treatments (i.e., 21 days), Sun et al. (2017) found moderate and heavy grazing intensities increased root exudation by approximately 25 and 40%, respectively. The authors attributed the differences in root exudation between treatments to changes in defoliation-induced root processes (Sun et al., 2017). Collectively, these studies seem to indicate that the beneficial effects of rotational grazing on mechanisms that benefit soil C sequestration, including rhizodeposition, might be dependent on

both the length of the rest period and on the grazing intensity adopted within each rotationally grazed ranch, supporting my findings.

Previous research has indicated that the movement of dissolved organic C (DOC) into deeper soil layers is responsible for the redistribution of C added by root litter, creating a profile of SOC even deeper than the distribution of living roots (Kalks et al., 2020; Rumpel and Kögel-Knabner, 2010). Additionally, due to decomposition rates that vary from a few years to millennia (Ota et al., 2013), DOC has been found to sorb, stabilize, and accumulate in subsurface layers of clay-rich Chernozemic soils (Mayes et al., 2012) such as found in many of my grassland sites, ultimately representing up to 14% of the total SOC below the surface 20 cm of grassland soils (Sanderman and Amundson, 2008). Therefore, DOC might represent a substantial proportion of the soil C sequestered in the subsurface layers (below 10 cm) of the AMP ranches that use longer rest periods and high cattle stocking rates. In fact, Khatri-Chhetri et al. (2022) found that AMP grazing increased the DOC concentration in the 0-15 cm soil layer compared to n-AMP grazing in a subset of my study sites. At the same time, Döbert et al. (2021) found AMP grazing improved water infiltration within the 0-15 cm soil layer of my study sites, which can facilitate the percolation of soluble C such as DOC deeper into the soil profile (Evans et al., 2020). Enhanced water infiltration combined with higher concentrations of DOC in the topsoil in the AMP ranches studied (Döbert et al., 2021; Khatri-Chhetri et al., 2022) could be one mechanism causing the leaching and redistribution of C to deeper soil layers (Kalbitz and Kaiser, 2008), thereby leading to SOC accumulation in the 10-30 cm ESM layer and enhancing soil C storage in that layer. Similar results have been reported by Dong et al. (2021), who found rotationally grazed pastures under high cattle stocking had higher concentrations of DOC compared to pastures under medium and low cattle stocking levels. While DOC might have played an

important role in the sequestration of soil C in subsurface layers, I did not analyze its concentration in my study.

#### 2.5 Conclusions

This study has important implications for the management of grazing practices to enhance SOC sequestration within northern temperate grasslands. First, n-AMP grazed grassland can sequester more SOC than AMP grazed grassland at stocking rates lower than 3.5 AUM ha<sup>-1</sup>, while AMP grazed grasslands with high stocking rates appear capable of sequestering significantly more SOC than n-AMP grasslands at the same stocking levels. This indicates that new or existing AMP operators within the northern temperate grasslands should strive to modify their grazing system over time in order to attain relatively high stocking rates and thereby promote SOC sequestration. Ultimately, the exact stocking rates to be adopted in each operation will be context specific (considering the ecoregion, climate, and vegetation composition of each ranch) rather than generalized from the present study, and any changes in management, including the use of high stock densities, extended rest, and elevated stocking will ultimately need to be phased in as conditions (forage responses and grassland condition) permits. Second, my results demonstrate the value to AMP operators of using longer rest periods, showing that stocking rate is not the only factor changing the effect of grazing management on the sequestration of SOC. Furthermore, since the observed changes in equivalent SOC mass due to improved management practices were found in subsurface soil layers (below 10 cm depth) and not in surface layers, my results highlight the importance of using sampling protocols that encompass deeper soil layers to properly quantify the effect of grazing management on SOC (FAO, 2019), in addition to using the ESM method to account for potential differences in bulk soil associated with soil

compaction. Importantly, because the adoption of AMP grazing at higher stocking rates is associated with the sequestration of C in the deeper soil, where turnover rates of C may be slower, grasslands subject to this grazing practice may be able to store more C over time. Finally, my results indicate further research is required to understand the tradeoff of varying stocking rates and rest periods on SOC sequestration in northern temperate grasslands, including the potential role of root growth, rhizodeposition, and DOC transportation on the accumulation of C in subsurface soil layers.

## **Chapter 3. Synthesis and Future Research**

This thesis research aimed to elucidate the impacts of adaptive multi-paddock (AMP) grazing practices on soil organic carbon (SOC) stocks compared to conventional grazing systems in the northern temperate grasslands of western Canada. The key findings can be summarized as follows:

### **3.1 Synthesis of Findings**

- When compared categorically, no significant differences in SOC stocks were found between AMP and conventional grazing systems across soil depths to 80 cm (ESM depth). This contrasts with previous studies conducted in other regions, such as the south-central United States, that reported 20.6% higher SOC stocks under AMP grazing in shallow surface layers (0-10 cm) compared to conventional grazing (Johnson et al., 2022). The lack of categorical differences observed in my study may be attributed to high variability in grazing practices and environmental conditions across the broad geographic extent of the Canadian grasslands studied.
- An in-depth examination of specific grazing practices revealed that higher cattle stocking rates alone were associated with increased thickness of the Ah horizon, regardless of the grazing system or rest periods provided. This corroborates the findings of Smoliak et al. (1972), who reported greater accumulation of root biomass near the soil surface under long-term heavy grazing.
- Longer rest periods between grazing events only resulted in greater SOC accumulation in subsurface layers (10-30 cm ESM depth) when combined with higher stocking rates above

approximately 3.5 AUM ha<sup>-1</sup> in AMP systems. This interactive effect of stocking rate and rest periods aligns with the proposed mechanisms of increased belowground C allocation and root growth during extended recovery periods (Teague & Kreuter, 2020).

- At stocking rates below ~3.5 AUM ha<sup>-1</sup>, conventional grazing accrued more subsurface SOC than AMP grazing systems regardless of rest period length. This contrasts with the finding of Bork et al. (2020) that stocking rates were positively associated with subsurface SOC in rotational grazing systems. It suggests that excessive rest without sufficient defoliation may impair plant growth and SOC sequestration.
- The positive effects of specialized AMP grazing practices on SOC stocks occurred between 10-30 cm ESM depth, rather than in shallow surface layers (0-10 cm ESM depth). This distribution pattern points to the importance of subsurface processes in SOC accrual, rather than surface litter fragmentation and incorporation.
- Overall, nuanced grazing practices explained a relatively small amount (2-5%) of variability in subsurface SOC stocks. This highlights the complexity of interacting factors regulating soil C sequestration and the context-specific nature of grazing impacts.

#### **3.2 Deficiencies and Limitations**

• The exclusion of roots and the litter, fragmented litter, and humus (LFH) layer from the soil samples analyzed in my study provides a likely explanation for the lack of detectable differences in surface SOC stocks between AMP and n-AMP grazing systems. By omitting these key C pools from SOC measurements, I may have overlooked substantial amounts of C especially within the surface layers. A recent study by Bork et al. (2023) quantified up to 15 Mg ha<sup>-1</sup> of C in the LFH layer alone. If this C-rich surface mulch layer had been

included in my sampling, it could have represented a sizable missing pool of SOC, particularly in AMP grazed soils where litter fragmentation and incorporation are enhanced. The absence of roots, which are predominantly concentrated near the soil surface, may also have led to the exclusion of appreciable C in the topsoil. At lower stocking rates where SOC differences between grazing systems are smaller, the omission of surface litter and roots likely precluded detection of any changes in shallow SOC stocks. Overall, the removal of these influential C pools prior to analysis provides a probable explanation for the unchanging surface layer SOC observed between AMP and n-AMP grazed grasslands.

- There was no quantification of the uncertainty in the measurement of SOC stocks through collection of bulk density core replications and propagation of errors. Assessing uncertainty would indicate the sensitivity and statistical significance of grazing impacts on subsurface SOC storage (Rossi et al., 2009).
- The experimental design lacked stratification by landscape positions (e.g. summit, backslope, footslope, etc.) within each ranch for soil sampling. Stratified random sampling accounting for topo-edaphic variability would improve characterization of SOC distribution (Conant & Paustian, 2002).

# **3.3 Future Research Directions**

While my thesis revealed the potential for AMP grazing practices to enhance grassland SOC sequestration under certain management regimes, it also exposed major knowledge gaps regarding the belowground mechanisms governing subsurface SOC accumulation. Further research integrating advanced assessment of soil processes, plant attributes, and microbial communities could provide vital insights into these linkages. Specific future research directions could include:

- Examining root dynamics below 10 cm depth using techniques such as pulse-labeling with 14C or 13C tracers (Denef et al., 2007). These techniques allow for the tracking and quantification of C allocation within root systems, essential for understanding how different grazing practices affect belowground carbon dynamics and subsurface SOC accrual (Reeder & Schuman, 2002).
- Investigating organomineral associations and SOC stabilization in subsurface soils through density and particle size fractionation (Cyle et al., 2016). This approach can uncover the relationships between soil minerals and organic matter, essential to understanding the mechanisms that physically protect and stabilize SOC, especially in the dense rooting zone.
- Quantifying dissolved organic C (DOC) production, leaching and sorption within the soil profile using methods such as sorption experiments and suction lysimeters (Fröberg et al., 2003). Given higher water infiltration under AMP grazing (Döbert et al., 2021), DOC dynamics may drive subsurface SOC accrual.
- Assessing uncertainty in SOC stock changes by collecting bulk density core replications across treatments (Maillard et al., 2017). Propagating measurement errors through SOC calculations with this method will enhance the statistical robustness of the findings, providing more accurate representations of grazing impacts on subsurface SOC storage.

Additionally, connecting my findings on subsurface SOC accumulation to related ecosystem attributes studied concurrently on the ranch network could reveal important linkages. For instance, overlaying SOC distribution patterns with data on plant community composition,

diversity and aboveground productivity from Grenke et al. (2022) could elucidate connections between vegetation responses and soil C sequestration under different grazing regimes.

# **3.4 Conclusions**

This thesis demonstrates the potential for specialized grazing practices like AMP grazing to increase SOC sequestration within northern temperate grasslands, thereby promoting climate change mitigation. However, it also highlights the context-dependency of grazing impacts based on regional environment, management nuances, and their complex interactions. The accrual of SOC in deeper soil layers points to knowledge gaps regarding belowground processes governing subsurface C storage. Further research integrating state-of-the-art assessment of soils, microbial communities, plant attributes and their interconnectivity could provide valuable insights into mechanisms and help refine grazing strategies to optimize soil C sequestration. Overall, advancing knowledge in this area can inform climate-smart, regenerative grazing practices within resilient cattle production systems.

**Table 1**: Summary of the nuanced grazing metrics within the adaptive multi-paddock (AMP) and conventionally (n-AMP) grazed beef cattle operations assessed during 2018 and 2019 in the prairie provinces of western Canada. Values are means ( $\pm$ SE). Bold means differ from each other at a significance level of P < 0.05 (n = 26). AUM ha<sup>-1</sup> = animal-unit-months per hectare. AU ha<sup>-1</sup> = Animal units per hectare.

Grazing practice	AMP	n-AMP	F-stat	<i>P</i> -value
Stocking rate (AUM ha <sup>-1</sup> )	3.18 (0.29)	2.57 (0.23)	1.31 (1, 50)	0.257
Stocking density (AU ha <sup>-1</sup> )	44.30 (10.0)	2.04 (0.22)	8.87 (1, 50)	0.004
Start of grazing season (Julian day)	119.00 (3.84)	140.0 (3.69)	10.50 (1, 50)	0.003
Rest:grazing ratio	40.10 (4.11)	0.96 (0.15)	45.16 (1, 50)	< 0.001

**Table 2**: Depth of the Ah horizon and its associated equivalent soil organic carbon (SOC) mass as distinguished between adaptivemulti-paddock (AMP) and conventionally (n-AMP) grazed grasslands. Values are means ( $\pm$ SE) (n = 26).

Soil parameter	AMP	n-AMP	F-stat	<i>P</i> -value
Ah horizon depth (cm)	21.41 (0.58)	21.43 (1.21)	0.001	0.971
Equivalent SOC mass	56 80 (1 60)	56.00 (4.12)	0.004	0.050
(Mg ha <sup>-1</sup> )	50.67 (1.07)	50.77 (4.15)	0.004	0.950

**Table 3**: Summary table of the most parsimonious linear mixed models ( $\leq \Delta 2$ AIC units) for Ah horizon depth and soil organic carbon (SOC) mass derived from Appendix E in which all grazing factors were included as continuous variables (i.e., grazing treatment was not included as a categorical effect). Random intercepts were specified for 'ranch pair' to account for the paired study design. The variance explained by just the fixed effects ( $R^2_m$ ) and the variance explained by both fixed and random effects ( $R^2_c$ ) were calculated for the top models after Nakagawa & Schielzeth (2013). Standardised coefficients are provided to determine effect size ( $\omega p2$ ) and 95% confidence intervals as a measure of significance; bold variables have CIs that do not overlap zero.

Soil	Response				Estimat			
		$\mathbf{R}^{2}\mathbf{m}$	R <sup>2</sup> c	Explanatory variable		SE	ω <sub>p</sub> <sup>2</sup>	95% CI
layer	variables				e			
	Depth	0.01	0.29	Intercept	1.2230	0.0335	0.00	[0.00, 0.00]
				Stocking rate	0.0157	0.0071	0.12	[0.01, 0.23]
		0.02	0.29	Intercept	1.2419	0.0374	0.00	[0.00, 0.00]
Ah				Stocking rate	0.0067	0.0095	0.09	[-0.02, 0.21]
horizon				Rest:grazing ratio	-0.0005	0.0008	0.02	[-0.07, 0.11]
				Stocking	0.0002	0.0002	0.06	
				rate*Rest:grazing ratio	0.0002	0.0002	0.00	[-0.03, 0.13]
	SOC mass	0.03	0.41	Intercept	1.6767	0.0473	0.00	[0.00, 0.00]

				Stocking rate	-0.0046	0.0114	0.07	[-0.05, 0.18]
				Rest:grazing ratio	-0.0023	0.0009	-0.03	[-0.12, 0.06]
				Stocking	0.0007	0.0002	0.14	[0.05.0.22]
				rate*Rest:grazing ratio	0.0007	0.0002	0.14	[0.03, 0.23]
10.20	SOC mass	0.03	0.46	Intercept	1.4238	0.0434	0.00	[0.00, 0.00]
10-30				Stocking rate	-0.0052	0.0099	0.07	[-0.04, 0.19]
cm				Rest:grazing ratio	-0.0029	0.0008	-0.09	[-0.17, -0.01]
(ESM								
				Stocking				
depth)				Stocking rate*Rest:grazing ratio	0.0007	0.0002	0.16	[ 0.07, 0.24]
depth)	SOC mass	0.05	0.49	Stocking rate*Rest:grazing ratio	<b>0.0007</b> 1.9710	<b>0.0002</b> 0.0034	<b>0.16</b>	[ <b>0.07</b> , <b>0.24</b> ]
depth) 0-80	SOC mass	0.05	0.49	Stocking   rate*Rest:grazing ratio   Intercept   Stocking rate	<b>0.0007</b> 1.9710 -0.0085	<b>0.0002</b> 0.0034 0.0079	<b>0.16</b> 0.00 0.07	[ 0.07, 0.24] [0.00, 0.00] [-0.06, 0.21]
depth) 0-80 cm	SOC mass	0.05	0.49	Stocking rate*Rest:grazing ratio Intercept Stocking rate Rest:grazing ratio	0.0007 1.9710 -0.0085 -0.0027	0.0002 0.0034 0.0079 0.0006	0.16 0.00 0.07 -0.13	[0.07, 0.24] [0.00, 0.00] [-0.06, 0.21] [-0.23, -0.02]
depth) 0-80 cm (ESM	SOC mass	0.05	0.49	Stocking rate*Rest:grazing ratio Intercept Stocking rate Rest:grazing ratio Stocking	0.0007 1.9710 -0.0085 -0.0027	0.0002 0.0034 0.0079 0.0006	0.16 0.00 0.07 -0.13	[0.07, 0.24] [0.00, 0.00] [-0.06, 0.21] [-0.23, -0.02]

\* = additive and multiplicative interactions between model predictors. ESM-Equivalent soil mass.

**Table 4**: Summary table for Ah horizon depth and soil organic carbon (SOC) mass distinguished between adaptive (AMP) vs conventionally (n-AMP) grazed grasslands as a fixed effect, and combined with other grazing practices. Random intercepts were specified for 'ranch pair' to account for the paired study design. The random effect accounts for geographic variation in soils and climate. The variance explained by just the fixed effects ( $R^2_m$ ) and the variance explained by both fixed and random effects ( $R^2_c$ ) were calculated after Nakagawa & Schielzeth (2013). Standardised coefficients are provided to determine effect size ( $\omega$ p2) and 95% confidence intervals (CI) as a measure of significance; bold variables have CIs that do not overlap zero.

Soil	Soil	<b>D</b> 2	<b>D</b> <sup>2</sup>		F 4. 4	<u>e</u> re	2	
layer	parameter	K <sup>2</sup> m	K <sup>2</sup> c	Explanatory variable	Estimate	SE	<b>⊕</b> ը²	95% CI
	Depth	0.02	0.30	Intercept	1.255	0.037	0.00	[0.00, 0.00]
				Grazing system	-0.065	0.035	-0.02	[-0.09, 0.05]
				Stocking rate	0.005	0.009	0.12	[0.01, 0.23]
Ah				Grazing system * Stocking rate	0.018	0.010	0.07	[-0.01, 0.16]
horizon	SOC mass	0.03	0.42	Intercept	1.692	0.046	0.00	[0.00, 0.00]
				Grazing system	-0.144	0.038	-0.03	[-0.10, 0.04]
				Stocking rate	-0.007	0.011	0.10	[-0.01, 0.21]
				Grazing system * Stocking rate	0.044	0.012	0.15	[0.07, 0.23]

	SOC mass	0.03	0.48	Intercept	1.419	0.044	0.00	[0.00, 0.00]
10-30 cm								
(ECM				Grazing system	-0.130	0.035	-0.06	[-0.12, 0.01]
(ESM				Stocking rate	-0 001	0.010	0 11	
depth)				Stocking fate	-0.001	0.010	0.11	[ 0.01, 0.22]
1 /				Grazing system * Stocking rate	0.034	0.010	0.13	[ 0.05, 0.21]
0.00	SOC mass	0.01	0.29	Intercept	1.960	0.037	0.00	[0.00, 0.00]
0-80  cm								
0 00 0111				Grazing system	-0 098	0.033	-0.04	[_0 14 0 28]
(ESM				Grazing system	-0.098	0.033	-0.04	[-0.14, 0.28]
(ESM				Grazing system Stocking rate	-0.098 -0.005	0.033 0.009	-0.04 0.08	[-0.14, 0.28] [-0.06, 0.23]
(ESM depth)				Grazing system Stocking rate	-0.098 -0.005	0.033 0.009	-0.04 0.08	[-0.14, 0.28] [-0.06, 0.23]

\* = additive and multiplicative interaction between model predictors. ESM-Equivalent soil mass.



**Figure 1**: Soil organic carbon (SOC) mass within each incremental equivalent soil mass (ESM) depth (a) and cumulative soil mass (b) associated with adaptive (AMP) and conventionally (n-AMP) grazed grasslands. Points are means and error bars represent  $\pm$ SE (n = 26). There was no statistically significant difference (P > 0.05) in incremental and cumulative SOC mass between categories of AMP and n-AMP grazing.



**Figure 2**: (a) Relationship between Ah soil horizon depth and stocking rate (in animal-unitsmonth per hectare) across all grasslands sampled irrespective of categorical grazing system (n = 26). Solid circles indicate raw means, with the associated linear regression lines and 95% confidence intervals (shaded areas) being provided. (b) Regression models demonstrating the relationship between Ah horizon depth and stocking rate as influenced by six rest:grazing ratios (RGR): 0, 20, 40, 60, 80, and 100. The rest:grazing ratio of 0 represents exclusively conventionally grazed (n-AMP) ranches while all other rest:grazing ratios (20, 40, 60, 80, and 100) represent the different levels of rest:grazing ratio used, with a rest:grazing ratio of 100 limited exclusively to adaptive grazed (AMP) ranches. The regression in (b) was developed with beta estimates coefficients derived from the most parsimonious model (Table 4). The points shown in (a) and (b) were obtained from log back-transformed calculations.



**Figure 3**: (a) Relationship between soil organic carbon (SOC) mass within the Ah horizon and stocking rate (in animal-units-month per hectare) distinguished between adaptive (AMP) and conventionally (n-AMP) grazed grasslands. Solid circles indicate raw means, with the associated linear regression lines and 95% confidence intervals (shaded areas) being provided (n = 26). (b) Models demonstrating the relationship between SOC mass within the Ah horizon and stocking rate as influenced by six rest:grazing ratios (RGR): 0, 20, 40, 60, 80, and 100 days of rest to each day of grazing. The rest:grazing ratio of 0 represents exclusively n-AMP ranches while all other rest:grazing ratios (20, 40, 60, 80, and 100) represent varying levels of rest:grazing ratio adopted in AMP ranches. The regression in (b) was developed with beta estimates derived from the most parsimonious model (Table 4). The points shown in (a) and (b) were obtained from log back-transformed calculations.


equivalent soil mass (ESM) depth and stocking rate (in animal-units-month per hectare) distinguished between adaptive (AMP) and conventionally (n-AMP) grazed grasslands. Solid circles indicate raw means, with the associated linear regression lines and 95% confidence intervals (shaded areas) being provided (n = 26). (b) Model demonstrating the relationship between SOC mass within the 10-30 cm ESM depth and stocking rate as influenced by six rest:grazing ratios (RGR): 0, 20, 40, 60, 80, and 100. The rest:grazing ratio of 0 represents exclusively n-AMP ranches while all other rest:grazing ratios (20, 40, 60, 80, and 100) represent the varying levels of rest:grazing ratio adopted in AMP ranches. The regression in (b) was developed with beta estimates derived from the most parsimonious model (Table 4). The points shown in (a) and (b) were obtained from log back-transformed calculations.



**Figure 5**: (a) Relationship between soil organic carbon (SOC) mass within the 0-80 cm equivalent soil mass (ESM) depth and stocking rate (in animal-units-month per hectare) distinguished between adaptive (AMP) and conventional (n-AMP) grazing systems. Solid circles indicate raw means, with the associated linear regression lines and 95% confidence intervals (shaded areas) being provided (n = 26). (b) Models demonstrating the relationship between SOC mass within the 0-80 cm ESM depth and stocking rate as influenced by six rest:grazing ratios (RGR): 0, 20, 40, 60, 80, and 100. The rest:grazing ratio of 0 represents exclusively n-AMP ranches while all other rest:grazing ratios (20, 40, 60, 80, and 100) represent the varying levels of rest:grazing ratio adopted in AMP ranches. The regression in (b) was developed with beta estimates derived from the most parsimonious model (Table 4). The points shown in (a) and (b) were obtained from log back-transformed calculations.

#### References

- Abdalla, M., Hastings, A., Chadwick, D. R., Jones, D. L., Evans, C. D., Jones, M. B., Rees, R. M., & Smith, P. (2018). Critical review of the impacts of grazing intensity on soil organic carbon storage and other soil quality indicators in extensively managed grasslands. *Agriculture, Ecosystems and Environment*, 253, 62–81. https://doi.org/10.1016/J.AGEE.2017.10.023
- Allen, V. G., Batello, C., Berretta, E. J., Hodgson, J., Kothmann, M., Li, X., ... & Sanderson, M. (2011). An international terminology for grazing lands and grazing animals. *Grass and forage science*, 66(1), 2. https://doi:10.1111/j.1365-2494.2010.00780.x
- Apfelbaum, S. I., Thompson, R., Wang, F., Mosier, S., Teague, R., & Byck, P. (2022).
  Vegetation, water infiltration, and soil carbon response to Adaptive Multi-Paddock and Conventional grazing in Southeastern USA ranches. *Journal of Environmental Management*, 308. https://doi.org/10.1016/j.jenvman.2022.114576
- Bai, Y., & Cotrufo, M. F. (2022). Grassland soil carbon sequestration: Current understanding, challenges, and solutions. *Science*, 377(6606).
   https://doi.org/10.1126/SCIENCE.ABO2380
- Bai, Y., Wu, J., Clark, C. D., Pan, Q., Zhang, L., Chen, S., ... & Han, X. (2012). Grazing Alters Ecosystem Functioning and C:n:p Stoichiometry Of Grasslands Along A Regional Precipitation Gradient. *Journal of Applied Ecology*, 6(49), 1204-1215. https://doi.org/10.1111/j.1365-2664.2012.02205.x
- Bailey, A. W., Schellenberg, M. P., & McCartney, D. (2010). Management of Canadian prairie rangeland (No. 10144). Ottawa, Canada: Agriculture and Agri-Food Canada.

- Bao, T., Carlyle, C. N., Bork, E. W., Becker, M., Alexander, M. J., DeMaere, C., de Souza, D.
  M., Farr, D., McAllister, T. A., & Selin, C. (2019). Survey of cattle and pasture management practices on focal pastures in Alberta. *Canadian Journal of Animal Science*, 99(4), 955–961.
- Bardgett, R. D., Bullock, J. M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., ... & Shi, H. (2021). Combatting global grassland degradation. *Nature Reviews Earth & Environment*, 2(10), 720-735. https://doi.org/10.1038/s43017-021-00207-2
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *ArXiv Preprint ArXiv*:1406.5823.
- Batjes, N. H. (2018). Technologically Achievable Soil Organic Carbon Sequestration In World Croplands and Grasslands. *Land Degradation Development*, 1(30), 25-32. https://doi.org/10.1002/ldr.3209
- Bengtsson, J., Bullock, J. M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P. J., Smith, H. G., & Lindborg, R. (2019). Grasslands—more important for ecosystem services than you might think. *Ecosphere*, 10(2), e02582. https://doi.org/10.1002/ECS2.2582
- Ben-Shachar, M. S., Lüdecke, D., & Makowski, D. (2020). Effectsize: Estimation of effect size indices and standardized parameters. *Journal of Open Source Software*, 5(56), 2815.
- Bork, E. W., Broadbent, T. S., & Willms, W. D. (2017). Intermittent growing season defoliation variably impacts accumulated herbage productivity in mixed grass prairie. *Rangeland Ecology & Management*, 70(3), 307-315. https://doi.org/10.1016/j.rama.2016.10.007
- Bork, E. W., Döbert, T. F., Grenke, J. S. J., Carlyle, C. N., Cahill, J. F., & Boyce, M. S. (2021). Comparative Pasture Management on Canadian Cattle Ranches With and Without

Adaptive Multipaddock Grazing. *Rangeland Ecology and Management*, 78, 5–14. https://doi.org/10.1016/j.rama.2021.04.010

- Bork, E. W., Hewins, D. B., Lamb, E. G., Carlyle, C. N., Lyseng, M. P., Chang, S. X., ... & Iravani, M. (2023). Light to moderate long-term grazing enhances ecosystem carbon across a broad climatic gradient in northern temperate grasslands. Science of The Total Environment, 164978. https://doi.org/10.1016/j.scitotenv.2023.164978
- Bork, E. W., Raatz, L. L., Carlyle, C. N., Hewins, D. B., & Thompson, K. A. (2020). Soil carbon increases with long-term cattle stocking in northern temperate grasslands. *Soil Use and Management*, 36(3), 387–399. https://doi.org/10.1111/sum.12580
- Briske, D. D., Bestelmeyer, B. T., Brown, J. R., Fuhlendorf, S. D., & Polley, H. W. (2013). The savory method cannot green deserts or reverse climate change. *Rangelands*, 35(5), 72-74. https://doi.org/10.2111/RANGELANDS-D-13-00044.1
- Briske, D. D., Derner, J. D., Brown, J. R., Fuhlendorf, S. D., Teague, W. R., Havstad, K. M., ...
  & Willms, W. D. (2008). Rotational grazing on rangelands: reconciliation of perception and experimental evidence. *Rangeland Ecology & Management*, 61(1), 3-17. https://doi.org/10.2111/06-159R.1
- Byrnes, R. C., Eastburn, D. J., Tate, K. W., & Roche, L. M. (2018a). A Global Meta-Analysis of Grazing Impacts on Soil Health Indicators. *Journal of Environmental Quality*, 47(4), 758– 765. https://doi.org/10.2134/jeq2017.08.0313
- Canadian Agricultural Services Coordinating Committee. Soil Classification Working Group, National Research Council Canada, Canada. Agriculture, & Agri-Food Canada. Research Branch. (1998). *The Canadian system of soil classification* (No. 1646). NRC Research Press.

- Cingolani, A. M., Cabido, M. R., Renison, D., & Solís Neffa, V. (2003). Combined effects of environment and grazing on vegetation structure in Argentine granite grasslands. *Journal* of Vegetation Science, 14(2), 223-232. https://doi.org/10.1111/j.1654-1103.2003.tb02147.x
- Conant, R. T. (2010). Challenges and opportunities for carbon sequestration in grassland systems (Vol. 9). Rome, Italy: FAO.
- Conant, R. T., Cerri, E. P., Osborne, B. B., & Paustian, K. (2016). Grassland management impacts on soil carbon stocks: a new synthesis.
- Conant, R. T., Paustian, K., & Elliott, E. T. (2001). Grassland management and conversion into grassland: effects on soil carbon. *Ecological applications*, 11(2), 343-355.
- Conant, R., Cerri, C., Osborne, B., Paustian, K. (2017). Grassland management impacts on soil carbon stocks: a new synthesis. *Ecological applications*, 2(27), 662-668. https://doi.org/10.1002/eap.1473
- Crowther, T. W., Boddy, L., & T Jones, H. (2012). Functional and ecological consequences of saprotrophic fungus–grazer interactions. *The ISME journal*, 6(11), 1992-2001.
- Cumming, G. (2009). Inference by eye: Reading the overlap of independent confidence intervals. *Statistics in Medicine*, 28(2), 205–220.
- Cyle, K. T., Hill, N., Young, K., Jenkins, T., Hancock, D., Schroeder, P. A., & Thompson, A. (2016). Substrate quality influences organic matter accumulation in the soil silt and clay fraction. Soil Biology and Biochemistry, 103, 138-148. https://doi.org/10.1016/j.soilbio.2016.08.014
- de Faccio Carvalho, P. C., Anghinoni, I., de Moraes, A., de Souza, E. D., Sulc, R. M., Lang, C. R., ... & Bayer, C. (2010). Managing grazing animals to achieve nutrient cycling and soil

improvement in no-till integrated systems. *Nutrient Cycling in Agroecosystems*, 88, 259-273. https://doi.org/10.1007/s10705-010-9360-x

- Denef, K., Bubenheim, H., Lenhart, K., Vermeulen, J., Van Cleemput, O., Boeckx, P., & Müller, C. (2007). Community shifts and carbon translocation within metabolically-active rhizosphere microorganisms in grasslands under elevated CO 2. Biogeosciences, 4(5), 769-779. https://doi.org/10.5194/bg-4-769-2007
- Derner, J. D., & Schuman, G. E. (2007). Carbon sequestration and rangelands: a synthesis of land management and precipitation effects. *Journal of soil and water conservation*, 62(2), 77-85.
- Derner, J. D., Boutton, T. W., & Briske, D. D. (2006). Grazing and Ecosystem Carbon Storage in the North American Great Plains. *Plant and Soil*, 2006 280:1, 280(1), 77–90. https://doi.org/10.1007/S11104-005-2554-3
- Deutsch, E. S., Bork, E. W., & Willms, W. D. (2010a). Separation of grassland litter and ecosite influences on seasonal soil moisture and plant growth dynamics. Plant Ecology, 209, 135-145. https://doi.org/10.1007/s11258-010-9729-6
- Deutsch, E. S., Bork, E. W., & Willms, W. D. (2010b). Soil moisture and plant growth responses to litter and defoliation impacts in Parkland grasslands. Agriculture, ecosystems & environment, 135(1-2), 1-9. https://doi.org/10.1016/j.agee.2009.08.002
- Díaz de Otálora, X., Epelde, L., Arranz, J., Garbisu, C., Ruiz, R., & Mandaluniz, N. (2021).
  Regenerative rotational grazing management of dairy sheep increases springtime grass production and topsoil carbon storage. *Ecological Indicators*, 125.
  https://doi.org/10.1016/J.ECOLIND.2021.107484

- Diaz, S., Lavorel, S., McIntyre, S. U. E., Falczuk, V., Casanoves, F., Milchunas, D. G., ... & Campbell, B. D. (2007). Plant trait responses to grazing–a global synthesis. *Global change biology*, 13(2), 313-341. https://doi.org/10.1111/j.1365-2486.2006.01288.x
- DiGaudio, R., Dybala, K., Seavy, N., Gardali, T. (2017). Population and Habitat Objectives For Avian Conservation In California's Central Valley grassland–oak Savannah Ecosystems. San Francisco Estuary and Watershed Science, 1(15). https://doi.org/10.15447/sfews.2017v15iss1art6
- Dixon, A. P., Faber-Langendoen, D., Josse, C., Morrison, J., & Loucks, C. J. (2014). Distribution mapping of world grassland types. *Journal of biogeography*, 41(11), 2003-2019. https://doi.org/10.1111/jbi.12381
- Dlamini, P., Chivenge, P., Chaplot, V. (2016). Overgrazing Decreases Soil Organic Carbon
   Stocks the Most Under Dry Climates And Low Soil Ph: A Meta-analysis Shows.
   Agriculture, Ecosystems & Environment, (221), 258-269.
   https://doi.org/10.1016/j.agee.2016.01.026
- Döbert, T. F., Bork, E. W., Apfelbaum, S., Carlyle, C. N., Chang, S. X., Khatri-Chhetri, U., Silva Sobrinho, L., Thompson, R., & Boyce, M. S. (2021). Adaptive multi-paddock grazing improves water infiltration in Canadian grassland soils. *Geoderma*, 401. https://doi.org/10.1016/j.geoderma.2021.115314
- Dong, L., Martinsen, V., Wu, Y., Zheng, Y., Liang, C., Liu, Z., & Mulder, J. (2021). Effect of grazing exclusion and rotational grazing on labile soil organic carbon in north China. *European Journal of Soil Science*, 72(1), 372–384. https://doi.org/10.1111/ejss.12952
- Dormaar, J. and Willms, W. (1998). Effect of forty-four years of grazing on fescue grassland soils. *Journal of range management*, 1(51), 122. https://doi.org/10.2307/4003574

- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., & Leitão, P. J. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46.
- Drewry, J. J., Cameron, K. C., Buchan, G. D., Drewry, J. J., Cameron, K. C., & Buchan, G. D. (2008). Pasture yield and soil physical property responses to soil compaction from treading and grazing — a review. *Soil Research*, 46(3), 237–256. https://doi.org/10.1071/SR07125
- Evans, L. R., Pierson, D., & Lajtha, K. (2020). Dissolved organic carbon production and flux under long-term litter manipulations in a Pacific Northwest old-growth forest. *Biogeochemistry*, 149(1), 75–86. https://doi.org/10.1007/s10533-020-00667-6
- FAO. (2019). Measuring and modelling soil carbon stocks and stock changes in livestock production systems: Guidelines for assessment (Version 1). FAO-Livestock Environmental Assessment and Performance (LEAP) Partnership.

http://www.fao.org/partnerships/leap/publications/en/

- Ferraro, D. O., & Oesterheld, M. (2002). Effect of defoliation on grass growth. A quantitative review. *Oikos*, 98(1), 125-133. https://doi.org/10.1034/j.1600-0706.2002.980113.x
- Follett, R. F., & Kimble, J. M. (Eds.). (2000). The potential of US grazing lands to sequester carbon and mitigate the greenhouse effect. CRC press.
- Fontaine, S., Mariotti, A., & Abbadie, L. (2003). The priming effect of organic matter: a question of microbial competition? *Soil Biology and Biochemistry*, 35(6), 837–843. https://doi.org/10.1016/S0038-0717(03)00123-8
- Fox, G. A., Negrete-Yankelevich, S., & Sosa, V. J. (2015). Ecological statistics: contemporary theory and application. Oxford University Press, USA.
- Fox, J., & Weisberg, S. (2018). An R companion to applied regression. Sage publications.

- Frank, D. A., Kuns, M. M., & Guido, D. R. (2002). Consumer control of grassland plant production. *Ecology*, 83(3), 602-606. https://doi.org/10.1890/0012-9658(2002)083[0602:CCOGPP]2.0.CO;2
- Fröberg, M., Berggren, D., Bergkvist, B., Bryant, C., & Knicker, H. (2003). Contributions of Oi, Oe and Oa horizons to dissolved organic matter in forest floor leachates. Geoderma, 113(3-4), 311-322. https://doi.org/10.1016/S0016-7061(02)00367-1
- Ganjegunte, G., Vance, G. F., Preston, C. M., Schuman, G. E., Ingram, L. J., Stahl, P. D., ... & Welker, J. M. (2005). Soil Organic Carbon Composition In a Northern Mixed-grass Prairie. *Soil Science Society of America Journal*, 6(69), 1746-1756. https://doi.org/10.2136/sssaj2005.0020
- Gerrish, J. (2004). Management-intensive grazing: the grassroots of grass farming. Green Park Press, Ridgeland, Missouri.
- Gibson, D. I. (2012). Grassland Biome. *Ecology*. https://doi.org/10.1093/obo/9780199830060-0032
- Grenke, J. S. J., Bork, E. W., Carlyle, C. N., Boyce, M. S., & Cahill, J. F. (2022). Limited impacts of adaptive multi-paddock grazing systems on plant diversity in the Northern Great Plains. *Journal of Applied Ecology*. https://doi.org/10.1111/1365-2664.14181
- Guo, L. B. and Gifford, R. M. (2002). Soil Carbon Stocks and Land Use Change: A Meta Analysis. *Global Change Biology*, 4(8), 345-360. https://doi.org/10.1046/j.1354-1013.2002.00486.x
- Han, G., Hao, X., Zhao, M., Wang, M., Ellert, B. H., Willms, W., & Wang, M. (2008). Effect of grazing intensity on carbon and nitrogen in soil and vegetation in a meadow steppe in Inner

Mongolia. Agriculture, Ecosystems & Environment, 125(1–4), 21–32. https://doi.org/10.1016/J.AGEE.2007.11.009

Hendershot, W., Lalande, H., & Duquette, M. (2006). Soil Reaction and Exchangeable Acidity. In Soil Sampling and Methods of Analysis. Carter, M., Gregorich, E., Eds. CRC Press.

Jiang, Z. Y., Hu, Z. M., Lai, D. Y. F., Han, D. R., Wang, M., Liu, M., Zhang, M., & Guo, M. Y. (2020). Light grazing facilitates carbon accumulation in subsoil in Chinese grasslands: A meta-analysis. *Global Change Biology*, 26(12), 7186–7197. https://doi.org/10.1111/gcb.15326

- Johnson, D. C., Teague, R., Apfelbaum, S., Thompson, R., & Byck, P. (2022). Adaptive multipaddock grazing management's influence on soil food web community structure for: increasing pasture forage production, soil organic carbon, and reducing soil respiration rates in southeastern USA ranches. *PeerJ*, 10, e13750. https://doi.org/10.7717/peerj.13750
- Kalbitz, K., & Kaiser, K. (2008). Contribution of dissolved organic matter to carbon storage in forest mineral soils. *Journal of Plant Nutrition and Soil Science*, 171(1), 52–60. https://doi.org/10.1002/JPLN.200700043
- Kalks, F., Liebmann, P., Wordell-Dietrich, P., Guggenberger, G., Kalbitz, K., Mikutta, R.,
  Helfrich, M., & Don, A. (2020). Fate and stability of dissolved organic carbon in topsoils and subsoils under beech forests. *Biogeochemistry*, 148(2), 111–128.
  https://doi.org/10.1007/S10533-020-00649-8/TABLES/3
- Kazemi, M. L., Dumenil, L. C., & Fenton, T. E. (1990). Effects of accelerated erosion on corn yields of loess-derived and till-derived soils in Iowa. Unpublished technical report, Dept of Agronomy, Iowa State University.

- Khatri-chhetri, U., Thompson, K. A., Quideau, S. A., Boyce, M. S., Chang, S. X., Kaliaskar, D.,
  Bork, E. W., & Carlyle, C. N. (2022). Adaptive multi-paddock grazing increases soil
  nutrient availability and bacteria to fungi ratio in grassland soils. *Applied Soil Ecology*,
  179(June), 104590. https://doi.org/10.1016/j.apsoil.2022.104590
- Klumpp, K., Fontaine, S., Attard, E., le Roux, X., Gleixner, G., & Soussana, J. F. (2009). Grazing triggers soil carbon loss by altering plant roots and their control on soil microbial community. *Journal of Ecology*, 97(5), 876–885. https://doi.org/10.1111/J.1365-2745.2009.01549.X
- Lai, L., & Kumar, S. (2020). A global meta-analysis of livestock grazing impacts on soil properties. *PloS One*, 15(8), e0236638. https://doi.org/10.1371/journal.pone.0236638
- Lal, R. (2002). Soil carbon dynamics in cropland and rangeland. *Environmental pollution*, 116(3), 353-362. https://doi.org/10.1016/S0269-7491(01)00211-1
- Lal, R. (2004). Soil carbon sequestration impacts on global climate change and food security. *Science*, 304(5677), 1623-1627. https://doi.org/10.1126/science.1097396
- Lee, H., Fitzgerald, J., Hewins, D. B., McCulley, R. L., Archer, S. R., Rahn, T., & Throop, H. L. (2014). Soil moisture and soil-litter mixing effects on surface litter decomposition: A controlled environment assessment. *Soil Biology and Biochemistry*, 72, 123–132. https://doi.org/10.1016/J.SOILBIO.2014.01.027
- Lezama, F., & Paruelo, J. M. (2016). Disentangling grazing effects: trampling, defoliation and urine deposition. *Applied vegetation science*, 19(4), 557-566. https://doi.org/10.1111/avsc.12250
- Li, W., Huang, H. Z., Zhang, Z. N., & Wu, G. L. (2011). Effects of grazing on the soil properties and C and N storage in relation to biomass allocation in an alpine meadow. *Journal of Soil*

*Science and Plant Nutrition*, 11(4), 27–39. https://doi.org/10.4067/S0718-95162011000400003

- Liang, J., Zhou, Z., Huo, C., Shi, Z., Cole, J. R., Huang, L., Konstantinidis, K. T., Li, X., Liu, B.,
  Luo, Z., Penton, C. R., Schuur, E. A. G., Tiedje, J. M., Wang, Y. P., Wu, L., Xia, J., Zhou,
  J., & Luo, Y. (2018). More replenishment than priming loss of soil organic carbon with
  additional carbon input. *Nature Communications*, 2018 9:1, 9(1), 1–9.
  https://doi.org/10.1038/s41467-018-05667-7
- Liu, L., Sayer, E. J., Deng, M., Li, P., Liu, W., Wang, X., ... & Piao, S. (2022). The grassland carbon cycle: Mechanisms, responses to global changes, and potential contribution to carbon neutrality. *Fundamental Research*. https://doi.org/10.1016/j.fmre.2022.09.028
- Liu, M., Ouyang, S., Tian, Y., Wen, S., Zhao, Y., Li, X., Baoyin, T. tao, Kuzyakov, Y., & Xu, X.
  (2021). Effects of rotational and continuous overgrazing on newly assimilated C allocation. *Biology and Fertility of Soils*, 57(2), 193–202. https://doi.org/10.1007/s00374-020-01516-2
- Liu, N., Kan, H. M., Yang, G. W., & Zhang, Y. J. (2015). Changes in plant, soil, and microbes in a typical steppe from simulated grazing: explaining potential change in soil C. *Ecological Monographs*, 85(2), 269–286. https://doi.org/10.1890/14-1368.1
- Lorenz, K. and Rattan, L. (2018). Carbon sequestration in agricultural ecosystems. https://doi.org/10.1007/978-3-319-92318-5
- Lu, X., Kelsey, K. C., Yan, Y., Sun, J., Wang, X., Cheng, G., Neff, J. C., Lu, X., Kelsey, K. C., Yan, Y., Sun, J., Wang, X., Cheng, G., & Neff, J. C. (2017). Effects of grazing on ecosystem structure and function of alpine grasslands in Qinghai–Tibetan Plateau: a synthesis. *Ecosphere*, 8(1), e01656. https://doi.org/10.1002/ECS2.1656

- Ma, Z., Chang, S. X., Bork, E. W., Steinaker, D. F., Wilson, S. D., White, S. R., & Cahill Jr, J. F. (2020). Climate change and defoliation interact to affect root length across northern temperate grasslands. Functional Ecology, 34(12), 2611-2621.
  https://doi.org/10.1111/1365-2435.13669
- Ma, Z., Bork, E. W., Li, J., Chen, G., & Chang, S. X. (2021). Photosynthetic carbon allocation to live roots increases the year following high intensity defoliation across two ecosites in a temperate mixed grassland. *Agriculture, Ecosystems & Environment*, 316, 107450. https://doi.org/10.1016/J.AGEE.2021.107450
- Maillard, É., McConkey, B. G., & Angers, D. A. (2017). Increased uncertainty in soil carbon stock measurement with spatial scale and sampling profile depth in world grasslands: A systematic analysis. Agriculture, Ecosystems & Environment, 236, 268-276. https://doi.org/10.1016/j.agee.2016.11.024
- Mancilla-Leytón, J. M., Sánchez-Lineros, V., & Martín Vicente, A. (2013). Influence of grazing on the decomposition of Pinus pinea L. needles in a silvopastoral system in Doñana, Spain. *Plant and Soil*, 373(1–2), 173–181. https://doi.org/10.1007/S11104-013-1788-8/METRICS
- Mayes, M. A., Heal, K. R., Brandt, C. C., Phillips, J. R., & Jardine, P. M. (2012). Relation between Soil Order and Sorption of Dissolved Organic Carbon in Temperate Subsoils. *Soil Science Society of America Journal*, 76(3), 1027–1037. https://doi.org/10.2136/SSSAJ2011.0340
- McNaughton, S. J. (1983). Compensatory plant growth as a response to herbivory. *Oikos*, 329-336. https://doi.org/10.2307/3544305
- Mcsherry, M. E., & Ritchie, M. E. (2013). Effects of grazing on grassland soil carbon: A global review. *Global Change Biology*, 19(5), 1347–1357. https://doi.org/10.1111/gcb.12144

Mosier, S., Apfelbaum, S., Byck, P., Calderon, F., Teague, R., Thompson, R., & Cotrufo, M. F. (2021). Adaptive multi-paddock grazing enhances soil carbon and nitrogen stocks and stabilization through mineral association in southeastern US grazing lands. *Journal of Environmental Management*, 288, 112409.

https://doi.org/10.1016/j.jenvman.2021.1124093

- Mosier, S., Apfelbaum, S., Byck, P., Ippolito, J., & Cotrufo, M. F. (2022). Improvements in soil properties under adaptive multipaddock grazing relative to conventional grazing. *Agronomy Journal*, 114(4), 2584-2597. https://doi.org/10.1002/agj2.21135
- Mutema, M., Buthelezi, N., Muchaonyerwa, P., Cerri, C., Chaplot, V., Chaplot, V. (2022). On the impact of grassland management on soil carbon stocks: a worldwide meta-analysis. *Geoderma* regional, (28), e00479. https://doi.org/10.1016/j.geodrs.2021.e00479
- Mysterud, A. (2006). The concept of overgrazing and its role in management of large herbivores. *Wildlife Biology*, 12(2), 129-141.
- Naeth, M., Bailey, A., Pluth, D., Chanasyk, D., Hardin, R. (1991). Grazing impacts on litter and soil organic matter in mixed prairie and fescue grassland ecosystems of alberta. *Journal of Range Management*, 1(44), 7. https://doi.org/10.2307/4002629
- Ning, Y., Zhang, Z. X., Cui, L. J., & Zou, C. L. (2014). Adaptive Significance of and Factors Affecting Plasticity of Biomass Allocation and Rhizome Morphology: a Case Study of the Clonal Plant Scirpus planiculmis (Cyperaceae). *Polish Journal of Ecology*, 62(1), 77–88. https://doi.org/10.3161/104.062.0108

Nordborg, M. (2016). Holistic management-a critical review of Allan Savory's grazing method.

Norton, B. E. (1998). The application of grazing management to increase sustainable livestock production. *Animal production in Australia*, 22(1), 15-26.

- Oesterheld, M., & McNaughton, S. J. (1991). Effect of stress and time for recovery on the amount of compensatory growth after grazing. *Oecologia*, 85, 305-313. https://doi.org/10.1007/BF00320604
- Olff, H., & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Trends in* ecology & evolution, 13(7), 261-265. https://doi.org/10.1016/S0169-5347(98)01364-0
- Omonode, R. A. and Vyn, T. J. (2006). Vertical Distribution Of Soil Organic Carbon and Nitrogen Under Warm-season Native Grasses Relative To Croplands In West-central Indiana, Usa. *Agriculture, Ecosystems & Environment*, 2-3(117), 159-170. https://doi.org/10.1016/j.agee.2006.03.031
- Ota, M., Nagai, H., Koarashi, J. (2013). root and dissolved organic carbon controls on subsurface soil carbon dynamics: a model approach. *Journal of Geophysical Research Biogeosciences*, 4(118), 1646-1659. https://doi.org/10.1002/2013jg002379
- Park, J. Y., Ale, S., & Teague, W. R. (2017). Simulated water quality effects of alternate grazing management practices at the ranch and watershed scales. *Ecological Modelling*, 360, 1-13. https://doi.org/10.1016/j.ecolmodel.2017.06.019
- Paustian, K., Lehmann, J., Ogle, S., Reay, D., Robertson, G. P., & Smith, P. (2016). Climatesmart soils. *Nature*, 532(7597), 49–57. https://doi.org/10.1038/NATURE17174
- Porensky, L. M., Augustine, D. J., Derner, J. D., Wilmer, H., Lipke, M. N., Fernández-Giménez, M. E., & Briske, D. D. (2021). Collaborative Adaptive Rangeland Management,
  Multipaddock Rotational Grazing, and the Story of the Regrazed Grass Plant. *Rangeland Ecology and Management*, 78, 127–141. https://doi.org/10.1016/j.rama.2021.06.008

- Reeder, J. D., & Schuman, G. E. (2002). Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. *Environmental pollution*, 116(3), 457-463. https://doi.org/10.1016/S0269-7491(01)00223-8
- Ren, W., Hu, N., Hou, X., Zhang, J., Guo, H., Liu, Z., Kong, L., Wu, Z., Wang, H., & Li, X. (2017). Long-term overgrazing-induced memory decreases photosynthesis of clonal offspring in a perennial grassland plant. *Frontiers in Plant Science*, 8, 419. https://doi.org/10.3389/FPLS.2017.00419/BIBTEX
- Roy, P. S., Ramachandran, R. M., Paul, O., Thakur, P. K., Ravan, S., Behera, M. D., ... & Kanawade, V. P. (2022). Anthropogenic land use and land cover changes—A review on its environmental consequences and climate change. *Journal of the Indian Society of Remote Sensing*, 50(8), 1615-1640. https://doi.org/10.1007/s12524-022-01569-w
- Rumpel, C., & Kögel-Knabner, I. (2010). Deep soil organic matter—a key but poorly understood component of terrestrial C cycle. *Plant and Soil*, 2010 338:1, 338(1), 143–158. https://doi.org/10.1007/S11104-010-0391-5
- Sanderman, J., & Amundson, R. (2008). A comparative study of dissolved organic carbon transport and stabilization in California forest and grassland soils. *Biogeochemistry*, 89(3), 309–327. https://doi.org/10.1007/S10533-008-9221-8/FIGURES/9
- Savory, A. (1983). The Savory grazing method or holistic resource management. Rangelands Archives, 5(4), 155-159.
- Savory, A., & Butterfield, Jody. (1998). Holistic management : a new framework for decision making. 616.
- Savory, A., Butterfield, J. (2016). Holistic management: a commonsense revolution to restore our environment, 3rd. Island Press, Washington, DC.

- Schrama, M., Heijning, P., Bakker, J. P., van Wijnen, H. J., Berg, M. P., & Olff, H. (2013). Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. *Oecologia*, 172(1), 231–243. https://doi.org/10.1007/S00442-012-2484-8/METRICS
- Schuman, G. E., Janzen, H. H., & Herrick, J. E. (2002). Soil carbon dynamics and potential carbon sequestration by rangelands. *Environmental pollution*, 116(3), 391-396. https://doi.org/10.1016/S0269-7491(01)00215-9
- Schuman, G. E., Reeder, J. D., Manley, J. T., Hart, R. H., & Manley, W. A. (1999). Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. *Ecological applications*, 9(1), 65-71. https://doi.org/10.1890/1051-0761(1999)009[0065:IOGMOT]2.0.CO;2
- Scurlock, J. M. O., & Hall, D. O. (1998). The global carbon sink: a grassland perspective. *Global Change Biology*, 4(2), 229–233. https://doi.org/10.1046/J.1365-2486.1998.00151.X
- Silveira, M. L., Xu, S., Adewopo, J., Franzluebbers, A. J., & Buonadio, G. (2014). Grazing land intensification effects on soil C dynamics in aggregate size fractions of a Spodosol. *Geoderma*, 230–231, 185–193. https://doi.org/10.1016/J.GEODERMA.2014.04.012
- Smith, P., Martino, D., Cai, Z., Gwary, D., Janzen, H., Kumar, P., ... & Smith, J. (2008).
  Greenhouse gas mitigation in agriculture. Philosophical transactions of the royal Society B: *Biological Sciences*, 363(1492), 789-813. https://doi.org/10.1098/rstb.2007.2184
- Smoliak, S., Dormaar, J., Johnson, A. (1972). Long-term grazing effects on stipa-bouteloua Prairie soils. *Journal of range management*, 4(25), 246. https://doi.org/10.2307/3896903
- Snyder, J. D., & Trofymow, J. A. (1984). A rapid accurate wet oxidation diffusion procedure for determining organic and inorganic carbon in plant and soil samples. *Communications in*

Soil Science & Plant Analysis, 15(5), 587–597.

https://doi.org/10.1080/00103628409367499

- Sollenberger, L., Kohmann, M., Dubeux, J., Silveira, M. (2019). Grassland Management affects delivery of regulating and supporting ecosystem services. *Crop Science*, 2(59), 441-459. https://doi.org/10.2135/cropsci2018.09.0594
- Stanley, P. L., Rowntree, J. E., Beede, D. K., DeLonge, M. S., & Hamm, M. W. (2018). Impacts of soil carbon sequestration on life cycle greenhouse gas emissions in Midwestern USA beef finishing systems. *Agricultural Systems*, 162, 249–258. https://doi.org/10.1016/J.AGSY.2018.02.003
- Statistics Canada. (2016). Accounting for ecosystem change in Canada: 2.0 Ecosystem extent and drivers of change. Retrieved from https://www150.statcan.gc.ca/n1/pub/16-201x/2021001/sec-2-eng.htm#shr-pg0
- Steffens, M., Kölbl, A., Totsche, K. U., & Kögel-Knabner, I. (2008). Grazing effects on soil chemical and physical properties in a semiarid steppe of Inner Mongolia (PR China). *Geoderma*, 143(1-2), 63-72. https://doi.org/10.1016/j.geoderma.2007.09.004
- Sun, G., Zhu-Barker, X., Chen, D., Liu, L., Zhang, N., Shi, C., He, L., & Lei, Y. (2017).
  Responses of root exudation and nutrient cycling to grazing intensities and recovery practices in an alpine meadow: An implication for pasture management. *Plant and Soil*, 416(1–2), 515–525. https://doi.org/10.1007/s11104-017-3236-7
- Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65(1), 13–21.

- Tallowin, J. R. B., Rook, A. J., & Rutter, S. M. (2005). Impact of grazing management on biodiversity of grasslands. *Animal Science*, 81(2), 193-198. https://doi.org/10.1079/ASC50780193
- Tanentzap, A. J., & Coomes, D. A. (2012). Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter?. *Biological Reviews*, 87(1), 72-94. https://doi.org/10.1111/j.1469-185X.2011.00185.x
- Teague, R. and Kreuter, U. (2020). Managing grazing To Restore Soil Health, Ecosystem Function, and Ecosystem Services. *Frontiers in Sustainable Food Systems*, (4). https://doi.org/10.3389/fsufs.2020.534187
- Teague, R., & Barnes, M. (2017). Grazing management that regenerates ecosystem function and grazingland livelihoods. *African Journal of Range and Forage Science*, 34(2), 77–86. https://doi.org/10.2989/10220119.2017.1334706
- Teague, R., & Kreuter, U. (2020). Managing Grazing to Restore Soil Health, Ecosystem Function, and Ecosystem Services. In Frontiers in Sustainable Food Systems (Vol. 4). *Frontiers Media S.A.* https://doi.org/10.3389/fsufs.2020.534187
- Teague, R., Provenza, F., Kreuter, U., Steffens, T., & Barnes, M. (2013). Multi-paddock grazing on rangelands: Why the perceptual dichotomy between research results and rancher experience? In *Journal of Environmental Management* (Vol. 128, pp. 699–717). https://doi.org/10.1016/j.jenvman.2013.05.064
- Teague, W. R., Dowhower, S. L., Baker, S. A., Haile, N., DeLaune, P. B., & Conover, D. M. (2011). Grazing management impacts on vegetation, soil biota and soil chemical, physical and hydrological properties in tall grass prairie. *Agriculture, Ecosystems and Environment*, 141(3–4), 310–322. https://doi.org/10.1016/J.AGEE.2011.03.009

- Upton, R. N., Checinska Sielaff, A., Hofmockel, K. S., Xu, X., Polley, H. W., & Wilsey, B. J. (2020). Soil depth and grassland origin cooperatively shape microbial community cooccurrence and function. *Ecosphere*, 11(1), e02973. https://doi.org/10.1002/ecs2.2973
- Uren, N. (2000). Types, Amounts, and Possible Functions of Compounds Released into the Rhizosphere by Soil-Grown Plants. *The Rhizosphere*, 35–56. https://doi.org/10.1201/9780849384974-8
- Villarino, S. H., Pinto, P., Jackson, R. B., & Piñeiro, G. (2021). Plant rhizodeposition: A key factor for soil organic matter formation in stable fractions. Science Advances, 7(16), 3176–3190. https://doi.org/10.1126/SCIADV.ABD3176/SUPPL\_FILE/ABD3176\_SM.PDF

Voisin, A. (1959). Grass Productivity. Philosophical Library, Inc., New York.

- von Haden, A. C., Yang, W. H., & DeLucia, E. H. (2020). Soils' dirty little secret: Depth-based comparisons can be inadequate for quantifying changes in soil organic carbon and other mineral soil properties. *Global Change Biology*, 26(7), 3759–3770. https://doi.org/10.1111/gcb.15124
- Wang, F., Apfelbaum, S. I., Thompson, R. L., Teague, R., & Byck, P. (2021). Effects of adaptive multiple paddock and continuous grazing on fine-scale spatial patterns of vegetation species and biomass in commercial ranches. *Landscape Ecology*, 36(9), 2725–2741. https://doi.org/10.1007/s10980-021-01273-z
- Wang, Q. and Batkhishig, O. (2014). Impact Of Overgrazing On Semiarid Ecosystem Soil
  Properties: a Case Study Of The Eastern Hovsgol Lake Area, Mongolia. *Journal of Ecosystem & Ecography*, 01(04). https://doi.org/10.4172/2157-7625.1000140

- Ward, S. E., Smart, S. M., Quirk, H., Tallowin, J. R., Mortimer, S. R., Shiel, R. S., ... & Bardgett,
  R. D. (2016). Legacy effects of grassland management on soil carbon to depth. *Global change biology*, 22(8), 2929-2938. https://doi.org/10.1111/gcb.13246
- Waters, C. M., Orgill, S. E., Melville, G. J., Toole, I. D., & Smith, W. J. (2017). Management of Grazing Intensity in the Semi-Arid Rangelands of Southern Australia: Effects on Soil and Biodiversity. *Land Degradation and Development*, 28(4), 1363–1375. https://doi.org/10.1002/LDR.2602
- Watkinson, A. and Ormerod, S. (2001). Grasslands, Grazing and Biodiversity: Editors' Introduction. *Journal of Applied Ecology*, 2(38), 233-237. https://doi.org/10.1046/j.1365-2664.2001.00621.x
- Wei, Y., Zhang, Y., Wilson, G. W. T., Guo, Y., Bi, Y., Xiong, X., & Liu, N. (2021). Transformation of litter carbon to stable soil organic matter is facilitated by ungulate trampling. *Geoderma*, 385. https://doi.org/10.1016/j.geoderma.2020.114828
- White, R. P., Murray, S., Rohweder, M., Prince, S. D., & Thompson, K. M. (2000). Grassland ecosystems (p. 81). Washington, DC, USA: World Resources Institute.
- White, R. P., Murray, Siobhan., Rohweder, Mark., & World Resources Institute. (2000). Pilot analysis of global ecosystems. *Grassland ecosystems*. World Resources Institute.
- Willms, W. D., Dormaar, J. F., Adams, B. W., DOUWES Walter D Willms, H. E., Douwes, H.E., & J, C. T. (2002). Response of the mixed prairie to protection from grazing (Vol. 55).
- Wilson, C. H., Strickland, M. S., Hutchings, J. A., Bianchi, T. S., & Flory, S. L. (2018). Grazing enhances belowground carbon allocation, microbial biomass, and soil carbon in a subtropical grassland. *Global Change Biology*, 24(7), 2997–3009. https://doi.org/10.1111/GCB.14070

- Zhang, T., Li, F. Y., Li, Y., Shi, C., Wang, H., Wu, L., ... & Wang, Z. (2022). Disentangling the effects of animal defoliation, trampling, and excretion deposition on plant nutrient resorption in a semi-arid steppe: The predominant role of defoliation. *Agriculture, Ecosystems & Environment*, 337, 108068. https://doi.org/10.1016/j.agee.2022.108068
- Zhou, G., Zhou, X., He, Y., Shao, J., Hu, Z., Liu, R., Zhou, H., & Hosseinibai, S. (2017). Grazing intensity significantly affects belowground carbon and nitrogen cycling in grassland ecosystems: a meta-analysis. *Global Change Biology*, 23(3), 1167–1179. https://doi.org/10.1111/GCB.13431
- Zhou, X., Zhang, Y., & Niklas, K. J. (2014). Sensitivity of growth and biomass allocation patterns to increasing nitrogen: A comparison between ephemerals and annuals in the Gurbantunggut Desert, north-western China. *Annals of Botany*, 113(3), 501–511. https://doi.org/10.1093/aob/mct275
- Zhou, Y., Gowda, P. H., Wagle, P., Ma, S., Neel, J. P. S., Kakani, V. G., & Steiner, J. L. (2019).
   Climate Effects on Tallgrass Prairie Responses to Continuous and Rotational Grazing.
   *Agronomy* 2019, Vol. 9, Page 219, 9(5), 219.
  - https://doi.org/10.3390/AGRONOMY9050219
- Zimmermann, J., Dauber, J., Jones, M. P. (2011). Soil Carbon Sequestration During the Establishment Phase Of Miscanthus × Giganteus: A Regional-scale Study On Commercial Farms Using 13c Natural Abundance. *GCB Bioenergy*, 4(4), 453-461. https://doi.org/10.1111/j.1757-1707.2011.01117.x

## Appendices

#### Appendix A. Location of study sites



**Figure A1.** Map of the Canadian prairie grasslands comprising the provinces of Alberta, Saskatchewan and Manitoba (from left to right). Natural ecoregions include the Boreal Transition (dark green), Fescue Grasslands of the foothills and parkland regions (light green) and Mixedgrass Prairie (bright green). Also shown are the 26 ranch pairs comprising 26 adaptive multi-paddock (AMP) grazing ranches and an equal number of ranches employing regionally representative conventional grazing for comparison (Döbert et

al., 2021). AGGP = Agricultural Greenhouse Gases Program. Ecoregion data were obtained from Natural Resources Canada, available at https://www.nrcan.gc.ca/maps-tools-publications/tools/geodetic-reference-systems/forest-maps/16874.

## Appendix B. Management information of study ranches

**Table B1**. Ranch-averaged summary of grazing metrics used in the statistical analysis, with predictor variables grouped by grassland management. RanchID = the identification number of a study ranch; Grazing system (GS) = adaptive multi-paddock (AMP) and conventional (n-AMP) ranches; SR = Stocking rate in animal-units-month per hectare (AUM ha<sup>-1</sup>); AUD = Animal unit density per hectare (AU ha<sup>-1</sup>), RGR = Rest:grazing ratio, CH = Cultivation history (cultivated – Y, non-cultivated – N).

Site	Management								
RanchIDs	GS	SR	AUD	SGS	RGR	СН			
AB02AMP	AMP	4.50	40.87	91.00	90.00	Y			
AB02nAMP	n-AMP	3.12	7.78	167.00	2.11	Y			
AB03AMP	AMP	1.70	8.43	131.00	6.43	Y			
AB03nAMP	n-AMP	0.33	2.96	106.00	0.00	Y			
AB04AMP	AMP	1.99	19.93	75.00	7.00	Ν			
AB04nAMP	n-AMP	0.59	3.38	151.00	1.00	Ν			
AB05AMP	AMP	3.72	46.80	136.00	60.00	Y			
AB05nAMP	n-AMP	8.39	1.19	75.00	0.00	Y			
AB06AMP	AMP	1.37	13.69	75.00	47.50	Ν			
AB06nAMP	n-AMP	5.43	3.71	152.00	2.67	Ν			
AB08AMP	AMP	5.78	75.98	147.00	12.50	Y			
AB08nAMP	n-AMP	1.50	1.61	152.00	0.00	Y			
AB10AMP	AMP	1.87	10.25	116.00	12.50	Ν			

AB10nAMP	n-AMP	1.03	0.20	136.00	0.00	Ν
AB11AMP	AMP	1.78	21.49	129.00	26.80	Y
AB11nAMP	n-AMP	1.32	0.66	162.00	0.00	Y
AB12AMP	AMP	1.91	8.55	101.00	8.57	Y
AB12nAMP	n-AMP	1.54	2.21	136.00	0.50	Y
AB13AMP	AMP	3.76	108.78	139.00	11.67	Y
AB13nAMP	n-AMP	1.56	2.72	142.00	0.84	Y
MB32AMP	AMP	3.32	8.28	91.00	40.00	Y
MB32nAMP	n-AMP	2.34	0.52	151.00	0.00	Y
MB34AMP	AMP	5.33	15.09	136.00	80.00	Y
MB34nAMP	n-AMP	4.07	0.74	152.00	0.00	Y
MB35AMP	AMP	2.87	15.66	121.00	21.67	Y
MB35nAMP	n-AMP	2.15	1.98	152.00	1.67	Y
MB37AMP	AMP	2.58	30.83	141.00	30.00	N
MB37nAMP	n-AMP	2.61	2.08	151.00	3.00	Ν
SK14AMP	AMP	2.85	13.04	75.00	18.75	Y
SK14nAMP	n-AMP	3.43	4.11	75.00	0.80	Y
SK15AMP	AMP	10.91	108.64	131.00	60.00	Y
SK15nAMP	n-AMP	4.65	3.32	121.00	0.82	Y
SK16AMP	AMP	2.97	370.63	75.00	90.00	Y
SK16nAMP	n-AMP	3.88	1.11	91.00	0.00	Y
SK17AMP	AMP	1.79	11.67	145.00	90.00	Y
SK17nAMP	n-AMP	1.86	1.11	181.00	0.00	Y
	l					

SK18AMP	AMP	1.29	3.24	136.00	11.00	Ν
SK18nAMP	n-AMP	1.20	0.45	140.00	1.00	Ν
SK19AMP	AMP	4.43	53.41	141.00	40.00	Y
SK19nAMP	n-AMP	2.53	0.61	162.00	0.00	Y
SK21AMP	AMP	2.64	25.72	91.00	30.00	Y
SK21nAMP	n-AMP	1.26	1.57	146.00	2.63	Y
SK22AMP	AMP	2.20	36.50	152.00	40.00	Y
SK22nAMP	n-AMP	3.26	1.94	152.00	2.00	Y
SK23AMP	AMP	3.96	29.65	106.00	95.00	Y
SK23nAMP	n-AMP	2.05	0.38	121.00	0.00	Y
SK24AMP	AMP	0.78	25.66	136.00	45.00	Y
SK24nAMP	n-AMP	1.89	2.67	145.00	2.50	Y
SK25AMP	AMP	0.93	4.94	172.00	7.50	Y
SK25nAMP	n-AMP	1.93	1.75	158.00	0.00	Y
SK28AMP	AMP	5.32	45.35	101.00	60.00	Y
SK28nAMP	n-AMP	2.80	2.22	151.00	3.43	Y





**Figure C1**. A correlation matrix assessing collinearity among five grassland management variables: SR = stocking rate in animal- units-month per hectare (AUM ha<sup>-1</sup>); RGR = rest:grazing ratio; AUD = stock density in animal units per hectare (AU ha<sup>-1</sup>); SGS = Start of the grazing season across 52 ranches. GS = Grazing system, with n-AMP dummy being coded as 0 and AMP being coded as 1. Red lines illustrate average trends. Correlation coefficients (Pearson) provided.

\*\*\* = Significant correlation at P<0.001.

- \*\* = Significant correlation at P < 0.01.
- \* = Significant correlation at P<0.05.

# Appendix D. Average soil organic carbon mass per study ranch

 Table D1. Ranch-averaged summary of dependent soil parameters used in the statistical

 analyses. Variables are grouped by soil layers between the Ah horizon and equivalent soil mass

 (ESM) depths. Horizon depth = averaged total depth of the Ah horizon (cm); SOC mass = soil

 organic carbon mass (Mg ha<sup>-1</sup>).

Site	Ah ho	rizon	SOC mass per ESM depth					
RanchID	Horizon depth	SOC mass	0-10 cm	10-30 cm	30-60 cm	60-80 cm	0-80 cm	
AB02AMP	18.30	70.87	47.01	32.48	23.95	8.24	109.77	
AB02nAMP	13.17	68.09	64.96	23.99	13.93	8.04	109.20	
AB03AMP	25.53	78.92	37.27	39.50	43.93	6.62	149.98	
AB03nAMP	26.60	106.85	52.26	64.75	36.29	5.24	148.90	
AB04AMP	34.93	115.42	65.17	56.11	53.53	16.47	176.53	
AB04nAMP	23.73	80.63	63.74	47.28	51.18	10.57	167.41	
AB05AMP	10.80	60.14	60.70	14.34	18.66	4.91	85.04	
AB05nAMP	13.20	43.16	35.76	14.66	14.51	10.69	72.94	
AB06AMP	19.30	60.46	60.69	26.00	39.63	5.42	128.07	
AB06nAMP	22.20	80.25	70.20	33.57	44.38	21.19	170.17	
AB08AMP	21.07	71.98	35.21	38.59	34.20	10.73	118.72	
AB08nAMP	17.73	67.28	49.48	38.54	29.59	7.86	125.82	
AB10AMP	14.53	15.78	10.04	9.20	9.58	12.95	48.90	
AB10nAMP	20.8	22.54	9.93	11.72	12.88	4.99	47.40	

AB11AMP	11.47	36.97	31.23	26.66	26.59	7.45	92.14
AB11nAMP	11.47	34.11	25.22	23.80	25.82	8.73	86.03
AB12AMP	18.07	57.26	32.16	32.91	22.97	9.41	98.45
AB12nAMP	30.93	82.96	36.38	37.86	28.61	7.11	114.96
AB13AMP	20.07	68.73	40.57	36.11	25.89	8.47	113.76
AB13nAMP	15.47	48.83	30.16	30.72	26.41	9.48	96.77
MB32AMP	22.27	43.76	25.41	27.04	27.62	5.36	76.73
MB32nAMP	18.8	36.09	20.56	24.11	21.53	6.00	76.54
MB34AMP	42.07	90.92	19.02	34.67	44.48	11.45	113.75
MB34nAMP	32.07	71.54	22.63	34.62	32.66	5.20	95.10
MB35AMP	22.27	60.12	32.37	30.02	20.88	5.69	122.63
MB35nAMP	29.70	73.55	29.30	37.21	30.49	5.33	100.09
MB37AMP	14.00	41.64	32.78	18.20	12.18	9.81	71.43
MB37nAMP	11.60	41.63	39.41	10.78	10.08	4.05	65.18
SK14AMP	14.00	24.63	16.98	16.37	19.48	11.30	71.60
SK14nAMP	14.63	27.82	19.76	20.62	23.54	6.41	72.62
SK15AMP	21.60	75.60	41.24	36.64	11.08	5.83	96.05
SK15nAMP	14.60	40.43	26.17	20.38	7.59	7.06	62.51
SK16AMP	23.13	23.03	8.87	13.36	20.66	6.93	45.45
SK16nAMP	23.19	20.19	7.18	13.48	28.83	15.19	63.78
SK17AMP	24.70	22.36	7.58	12.32	19.99	7.04	46.68
SK17nAMP	20.67	21.50	10.48	14.92	20.78	6.23	52.65
SK18AMP	15.40	42.20	33.88	27.62	15.51		77.01
	l		l				

16.53	50.69	39.03	30.96			70.00
22.13	60.70	31.39	31.23	15.35	5.28	84.61
25.60	72.65	41.33	26.42	18.75	6.94	98.65
20.20	55.22	37.22	25.97	29.71	4.91	86.63
21.40	60.48	36.07	34.29	31.06	2.59	113.84
21.40	63.80	35.94	27.87	19.67	2.45	81.71
28.93	70.41	31.58	33.26	21.01	2.12	88.04
23.67	67.28	31.55	35.00	25.83	6.53	101.20
19.07	50.89	19.06	35.85	29.43	1.42	90.67
19.13	35.70	14.63	20.14	13.92	4.07	52.76
22.07	66.47	25.74	34.36	28.17	1.73	101.91
26.47	72.77	37.51	34.65	21.74	3.31	95.73
37.73	88.24	23.37	35.91	37.29	5.95	103.12
30.33	62.78	27.76	28.96	17.48	3.16	80.82
26.07	57.51	27.19	27.33	20.09	3.72	85.77
	16.53         22.13         25.60         20.20         21.40         21.40         28.93         23.67         19.07         19.13         22.07         26.47         37.73         30.33         26.07	16.5350.6922.1360.7025.6072.6520.2055.2221.4060.4821.4063.8028.9370.4123.6767.2819.0750.8919.1335.7022.0766.4726.4772.7737.7388.2430.3362.7826.0757.51	16.5350.6939.0322.1360.7031.3925.6072.6541.3320.2055.2237.2221.4060.4836.0721.4063.8035.9428.9370.4131.5823.6767.2831.5519.0750.8919.0619.1335.7014.6322.0766.4725.7426.4772.7737.5137.7388.2423.3730.3362.7827.7626.0757.5127.19	16.5350.6939.0330.9622.1360.7031.3931.2325.6072.6541.3326.4220.2055.2237.2225.9721.4060.4836.0734.2921.4063.8035.9427.8728.9370.4131.5833.2623.6767.2831.5535.0019.0750.8919.0635.8519.1335.7014.6320.1422.0766.4725.7434.3626.4772.7737.5134.6537.7388.2423.3735.9130.3362.7827.7628.9626.0757.5127.1927.33	16.5350.6939.0330.9622.1360.7031.3931.2315.3525.6072.6541.3326.4218.7520.2055.2237.2225.9729.7121.4060.4836.0734.2931.0621.4063.8035.9427.8719.6728.9370.4131.5833.2621.0123.6767.2831.5535.0025.8319.0750.8919.0635.8529.4319.1335.7014.6320.1413.9222.0766.4725.7434.3628.1726.4772.7737.5134.6521.7437.7388.2423.3735.9137.2930.3362.7827.7628.9617.4826.0757.5127.1927.3320.09	16.5350.6939.0330.9622.1360.7031.3931.2315.355.2825.6072.6541.3326.4218.756.9420.2055.2237.2225.9729.714.9121.4060.4836.0734.2931.062.5921.4063.8035.9427.8719.672.4528.9370.4131.5833.2621.012.1223.6767.2831.5535.0025.836.5319.0750.8919.0635.8529.431.4219.1335.7014.6320.1413.924.0722.0766.4725.7434.3628.171.7326.4772.7737.5134.6521.743.3137.7388.2423.3735.9137.295.9530.3362.7827.7628.9617.483.1626.0757.5127.1927.3320.093.72

-- Inexistent mineral soil layer due to shallow parent material

### Appendix E. Mixed model analysis results

**Table E1**. Linear mixed models used to assess the independent effects of nuanced grazing practices on Ah horizon depth (cm) and soil organic carbon (SOC) mass across grasslands of 52 ranches. A null model is specified with random structure only. Random intercepts were specified for 'ranch pair' to account for the paired study design. The random effect accounts for geographic variation in soils and climate. AIC<sub>c</sub> = Akaike Information Criterion adjusted for small sample size. Bold indicates most parsimonious models within a  $\Delta \leq 2$  AICc.

			log-		Delta	AICc
Soil layer	Model	K	Likelihood	AICc	AICc	weight
Ah	Ah horizon depth ~ Stocking rate	4	95.13	-180.18	0.00	0.38
horizon	Ah horizon depth ~ Stocking rate * Rest:grazing ratio	6	96.22	-178.29	1.88	0.15
	Ah horizon depth ~ 1 (Null)	3	92.82	-177.59	2.59	0.10
	Ah horizon depth ~ Rest:grazing ratio	4	93.69	-177.30	2.88	0.09
	Ah horizon depth ~ Stocking rate * Start of grazing season	6	95.56	-176.98	3.20	0.08
	Ah horizon depth ~ Start of grazing season	4	93.33	-176.59	3.59	0.06
	Ah horizon depth ~ Stocking rate * Animal stock density	6	95.31	-176.47	3.70	0.06
	Ah horizon depth ~ Animal stock density	4	93.01	-175.94	4.24	0.05

0-10 cm	SOC stocks ~ 1 ( <i>Null</i> )	3	364.96	-721.86	0.00	0.23
	SOC stocks ~ Start of grazing season * Rest:grazing ratio	6	34.25	-54.35	10.47	0.00
	SOC stocks ~ Animal stock density * Rest:grazing ratio	6	34.56	-54.98	9.84	0.00
	SOC stocks ~ Animal stock density * Start of grazing season	6	35.06	-55.98	8.84	0.01
	SOC stocks ~ Start of grazing season	4	33.71	-57.34	7.48	0.02
	SOC stocks ~ Animal stock density	4	33.92	-57.76	7.06	0.02
	SOC stocks ~ Rest:grazing ratio	4	33.99	-57.90	6.92	0.02
	SOC stocks ~ 1 (Null)	3	33.67	-59.29	5.53	0.04
	SOC stocks ~ Stocking rate * Animal stock density	6	37.09	-60.03	4.79	0.06
	SOC stocks ~ Stocking rate	4	35.46	-60.84	3.98	0.09
	SOC stocks ~ Stocking rate * Start of grazing season	6	37.69	-61.23	3.59	0.11
	SOC stocks ~ Stocking rate * Rest:grazing ratio	6	39.48	-64.82	0.00	0.64
	season	6	93.55	-172.95	7.23	0.01
	Ah horizon depth ~ Animal stock density * Start of grazing					
	Ah horizon depth ~ Animal stock density * Rest:grazing ratio	6	93.72	-173.30	6.87	0.01
	Ah horizon depth ~ Start of grazing season * Rest: grazing ratio	6	93.82	-173.49	6.69	0.01

	SOC stocks ~ Stocking rate * Rest:grazing ratio	6	367.71	-721.28	0.58	0.17	
	SOC stocks ~ Start of grazing season	4	365.41	-720.74	1.12	0.13	
	SOC stocks ~ Animal stock density	4	365.10	-720.13	1.73	0.10	
	SOC stocks ~ Stocking rate	4	365.03	-719.98	1.88	0.09	
	SOC stocks ~ Rest:grazing ratio	4	364.96	-719.85	2.01	0.08	
	SOC stocks ~ Stocking rate * Animal stock density	6	366.66	-719.17	2.69	0.06	
	SOC stocks ~ Stocking rate * Start of grazing season	6	366.31	-718.48	3.38	0.04	
	SOC stocks ~ Animal stock density * Start of grazing season	6	366.24	-718.33	3.53	0.04	
	SOC stocks ~ Start of grazing season * Rest:grazing ratio	6	366.13	-718.11	3.75	0.04	
	SOC stocks ~ Animal stock density * Rest:grazing ratio	6	365.47	-716.80	5.06	0.02	
10-30 cm	SOC stocks ~ Stocking rate * Rest:grazing ratio	6	140.51	-266.87	0.00	0.92	
	SOC stocks ~ Stocking rate	4	134.78	-259.49	7.38	0.02	
	SOC stocks ~ Stocking rate * Animal stock density	6	136.69	-259.24	7.64	0.02	
	SOC stocks ~ 1 (Null)	3	133.32	-258.59	8.28	0.01	
	SOC stocks ~ Rest:grazing ratio	4	133.40	-256.71	10.16	0.01	
	SOC stocks ~ Animal stock density	4	133.35	-256.61	10.26	0.01	
	SOC stocks ~ Start of grazing season	4	133.34	-256.61	10.27	0.01	
----------	---	---	--------	---------	-------	------	--
	SOC stocks ~ Stocking rate * Start of grazing season	6	135.11	-256.08	10.79	0.00	
	SOC stocks ~ Animal stock density * Start of grazing season	6	134.01	-253.86	13.01	0.00	
	SOC stocks ~ Animal stock density * Rest:grazing ratio	6	133.90	-253.66	13.21	0.00	
	SOC stocks ~ Start of grazing season * Rest:grazing ratio	6	133.45	-252.75	14.13	0.00	
30-60 cm	SOC stocks ~ 1 (Null)	3	-62.86	133.78	0.00	0.29	
	SOC stocks ~ Animal stock density	4	-62.47	135.04	1.26	0.16	
	SOC stocks ~ Start of grazing season	4	-62.84	135.77	1.99	0.11	
	SOC stocks ~ Rest:grazing ratio	4	-62.85	135.80	2.02	0.11	
	SOC stocks ~ Stocking rate	4	-62.86	135.81	2.03	0.11	
	SOC stocks ~ Stocking rate * Rest:grazing ratio	6	-60.89	135.95	2.17	0.10	
	SOC stocks ~ Stocking rate * Animal stock density	6	-61.87	137.92	4.14	0.04	
	SOC stocks ~ Stocking rate * Start of grazing season	6	-62.10	138.37	4.59	0.03	
	SOC stocks ~ Animal stock density * Rest:grazing ratio	6	-62.35	138.87	5.09	0.02	
	SOC stocks ~ Animal stock density * Start of grazing season	6	-62.39	138.95	5.17	0.02	
	SOC stocks ~ Start of grazing season * Rest:grazing ratio	6	-62.80	139.77	5.99	0.01	

60-80 cm	SOC ~ Stocking rate * Animal stock density	6	-149.60	313.43	0.00	0.28	
	SOC ~ Start of grazing season	4	-152.32	314.76	1.34	0.15	
	SOC ~ Stocking rate	4	-152.36	314.83	1.40	0.14	
	SOC ~ 1 ( <i>Null</i> )	3	-153.51	315.10	1.67	0.12	
	SOC ~ Stocking rate * Rest:grazing ratio	6	-150.61	315.45	2.02	0.10	
	SOC ~ Animal stock density	4	-153.44	317.00	3.57	0.05	
	SOC ~ Rest:grazing ratio	4	-153.51	317.13	3.70	0.04	
	SOC ~ Start of grazing season * Rest:grazing ratio	6	-151.59	317.40	3.97	0.04	
	SOC ~ Stocking rate * Start of grazing season	6	-151.63	317.48	4.05	0.04	
	SOC ~ Animal stock density * Start of grazing season	6	-151.96	318.14	4.71	0.03	
	SOC ~ Animal stock density * Rest:grazing ratio	6	-153.13	320.48	7.05	0.01	
0-80 cm	SOC ~ Stocking rate * Rest:grazing ratio	6	266.21	-518.19	0.00	0.87	
	SOC ~ Stocking rate * Animal stock density	6	263.18	-512.15	6.04	0.04	
	$SOC \sim 1$ (Null)	6	262.81	-511.39	6.80	0.03	
	SOC ~ Stocking rate	3	258.74	-509.39	8.80	0.01	
	SOC ~ Stocking rate * Start of grazing season	4	259.54	-508.96	9.23	0.01	

SOC ~	Animal stock density	6	261.46	-508.71	9.48	0.01
SOC ~	- Start of grazing season	4	259.36	-508.59	9.60	0.01
SOC ~	Animal stock density * Start of grazing season	4	259.33	-508.54	9.65	0.01
SOC ~ Rest:grazing ratio		6	261.11	-508.00	10.19	0.01
SOC ~	Animal stock density * Rest: grazing ratio	4	259.02	-507.91	10.28	0.01
SOC ~	Start of grazing season * Rest: grazing ratio	6	260.41	-506.60	11.59	0.00

\* = indicates additive and multiplicative effect between model predictors