



# Grazing, regional climate and soil biophysical impacts on microbial enzyme activity in grassland soil of western Canada



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## ABSTRACT

Grasslands cover more than 25% of the terrestrial surface of the Earth and hold 30% of the world's terrestrial carbon (C) pool. While nearly all native grassland ecosystems are used for livestock production, sustainably managed grasslands also provide many ecosystem goods and services such as C storage. Despite the importance of grasslands to the global C cycle, little is known about how long-term management practices, including the presence or absence of grazing, directly and indirectly affect the soil microbial processes that regulate C and nutrient cycling. We measured the effect of long-term cattle grazing on microbial extra cellular enzyme activity (EEA) at 12 locations stratified among three distinct grassland types (foothills fescue, aspen parkland, and mixed grass prairie) across Alberta, Canada. Each location included paired grazed and non-grazed plant communities managed this way for at least 30 years. Specifically, we quantified EEA of enzymes responsible for C ( $\beta$ -1,4-glucosidase,  $\beta$ -D-cellobiosidase,  $\beta$ -xylosidase), C and nitrogen (*N*-actyl-glucosaminidase), and phosphorous (phosphatase) cycling in soil from 0 to 15 and 15–30 cm depths. Although grazing effects on EEA remained weak ( $0.05 \leq p \leq 0.10$ ) they were relatively consistent among enzymes ( $n = 3/5$ ), with  $\beta$ -D-cellobiosidase, *N*-actyl-glucosaminidase, and phosphatase EEAs all greater in non-grazed plant communities than in grazed communities. All EEAs were greater in the foothills fescue and mixed grass regions than in the parkland with the exception of  $\beta$ -1,4-glucosidase, which was relatively high at all locations. Multivariate analyses suggested the soil properties that best describe EEA are soil pH, organic matter and moisture content, together with total nitrogen (N). Additionally, EEAs were correlated with the cover of several dominant plant species. Four of five EEAs were positively correlated with the grass *Festuca campestris*, while N and C degrading enzymes were negatively correlated with the grasses *Bouteloua gracilis* and *Koeleria macrantha*, respectively. Net C cycling appears to be strongly controlled by  $\beta$ -1,4-glucosidase. In conclusion, grazing and associated changes in plant communities appear to decrease the EEAs of some enzymes, suggesting that microbes in non-grazed communities are actively decomposing a relatively greater amount of organic matter. However, when working across broad spatial ranges, our marginally significant results and post-hoc power analysis suggest the need for larger sample sizes (>23 replicates) to further elucidate relationships between EEAs and low intensity disturbances such as cattle grazing.

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## 1. Introduction

Grassland ecosystems are ubiquitous across the globe covering an estimated 25% of the terrestrial surface of the Earth and store up to 30% of soil carbon (C) (Schuman et al., 2002; Derner and

Schuman, 2007; Svejcar et al., 2008). These ecosystems provide many beneficial ecological goods and services (EG&S) including forage production, water purification, biodiversity and wildlife habitat (Havstad et al., 2007). Grasslands are also increasingly being recognized as both a reservoir of soil C and potential C sink, particularly as management practices improve and large areas of heavily disturbed grasslands recover (Lal, 2002,2004; Derner and Schuman, 2007; Havstad et al., 2007). The influence of grazing on

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plant species composition and production has been studied widely in native grasslands (Willms and Jefferson, 1993), while few studies directly assess the effect of long-term grazing by large ungulates on belowground processes (Daryanto et al., 2013). Especially limited are studies that investigate the role of soil C and nutrient cycling by microbes, which has left a knowledge gap in the role of grazing on these cycles.

Soil C is the largest terrestrial C pool, holding an estimated 2300 Pg C, more than twice that in the atmosphere (Jobbágy and Jackson, 2000; Percival et al., 2000; Chapin III et al., 2009). Rates of soil carbon and nutrient cycling are controlled by decomposer organisms that produce extracellular enzymes that target litter substrates (Allison et al., 2007; Schlesinger and Bernhardt, 2013). Once litter and organic matter is degraded energy and nutrients can be taken up by plants and microbes from the soil solution. The rate at which organic compounds are broken down and incorporated into the soil matrix is important for regulating soil C storage, as well as N and P availability.

Improvements in management and condition of grasslands are estimated to sequester 0.5 Pg C yr<sup>-1</sup> (Lal, 2002; Derner and Schuman, 2007). Due to their large size, potential as C sinks and widespread use for livestock production, understanding the effect of grazing on the controls of C and associated biogeochemical cycling in grasslands is of great importance. An improved understanding of grassland biogeochemistry under grazing could lead to the development of management practices that increase sequestration of atmospheric C, and improve overall soil fertility and health by enhancing nutrient cycling.

Previous research shows that livestock grazing has complex effects on the environment, with vegetation being impacted both morpho-physiologically at the individual plant level (Belsky, 1986), through the population and community levels by altering plant species structure, abundance, and eventually composition, including diversity (Coughenour, 1991). These changes in turn, alter the composition and chemistry (e.g. lignin content) of plant material entering the litter pool (Naeth et al., 1991; Barger et al., 2004; Steffens et al., 2008). Furthermore, land uses such as grazing have the potential to alter ground cover of vegetation and litter, which has cascading effects on the microclimate of the soil environment (e.g. moisture and temperature) and associated plant growth (Deutsch et al., 2010; Deutsch et al., 2011). Despite substantive evidence highlighting the effect of grazing on the macro-scale ecology of native grasslands, little is known about how grazing affects mechanisms controlling ecosystem processes such as C cycling, including the impact on soil biochemical transformations (Esch et al., 2013). For example, research describing C pools in grasslands shows that grazing can have neutral, positive or negative effects on terrestrial C storage (Derner and Schuman, 2007), and potentially the microbial extracellular enzymes that control organic matter transformations in litter and soil (Patra et al., 2005).

Given the ambiguity around grazing impacts on soil C, a better mechanistic understanding of how this land use affects the global C cycle is needed (Derner and Schuman, 2007). Presently, there is no conclusive evidence to explain the role of grazing and associated plant community changes on microbial C and nutrient cycling in Rangeland soils, and the response of extracellular enzyme activity (EEA) to grazing is inconsistent across studies. Some investigations show a reduction in EEA with grazing; for example, in Australia, soils degraded by heavy grazing had decreased peptidase and amidase activity (Holt, 1997), and in a two-year short duration grazing trial of fescue grasslands at one site within the same study region examined here, phosphatase and dehydrogenase activity was reduced under grazing compared to non-grazed enclosures (Dormaar et al., 1989). Other investigations report no effects of grazing on EEAs including a study on the high plains of West Texas (Bell et al., 2006), and a study in the Chihuahuan Desert of New

Mexico (Liu et al., 2000). Lastly, in a comparison of light versus intense grazing in permanent grasslands of France, intense grazing enhanced enzyme activity across two topographic ecosites (Patra et al., 2005). Microplate methods now make it possible to measure the activities of a broad range of extracellular enzymes in environmental samples and quantify the potential mineralization of litter and soil organic matter (SOM) in the environment (Saiya-Cork et al., 2002; Allison et al., 2007; Bell et al., 2013).

To better understand the effect of long-term grazing and subsequent changes in plant communities, we measured microbial EEA in soil samples collected from paired grazed and non-grazed grassland sites in three distinct grassland climates (i.e. aspen parkland, foothills fescue and mixed grass prairie) in Alberta, Canada. Extracellular enzymes produced by microbes and select plants are the biochemical basis for C and nutrient cycling in the natural world (Allison et al., 2007; Chapin III et al., 2011). In theory, microbes regulate the production of extracellular enzymes in ecosystems when and where substrates are available for decomposition as a means of accessing energy and nutrients, or conversely extracellular enzymes may be produced in high concentrations when nutrient (i.e. P) substrate availability is low (Allison et al., 2007; Sinsabaugh et al., 2008). As a result, greater EEA and subsequently greater potential rates of biogeochemical cycling are expected in samples with more organic substrate availability (Allison et al., 2007). Here, we use EEA as a proxy for biogeochemical cycling by soil microbial communities.

We hypothesized that EEAs in mineral soil horizons would not differ between areas exposed and protected from long-term livestock grazing. However, we predicted that enzyme activity would vary among natural sub-regions because of the associated effect of climate on soil and vegetation characteristics (e.g. productivity, composition and species richness). Furthermore, we hypothesized that enzyme activity will be proportional to soil moisture content and the concentration of soil organic matter (SOM), soil C, and soil total nitrogen (N), and will be greatest in environments where pH is optimized.

## 2. Methods

### 2.1. Field sites and sampling

Our study sites are located within 3 distinct grassland natural sub-regions: the aspen parkland, foothills fescue and mixed grass prairie in Alberta, Canada (Downing and Pettapiece, 2006). These sub-regions cover broad spatial distributions and 3 distinct climates (e.g. MAT: 2.3°C, 3.9°C, 4.4°C; and MAP: 441 mm, 470 mm and 394 mm, in the aspen parkland, foothills fescue and mixed grass prairie, respectively) (Downing and Pettapiece, 2006). Among regions, changes in precipitation and temperature combine to result in a strong gradient in moisture availability, which is reflected in the precipitation: evapo-transpiration ratio varying from 0.3 in the mixedgrass, to 0.8 in the parkland and more than 1.0 in the foothills (Strong and Leggat, 1992). These differences among regions have led to distinctly divergent plant community assemblages, as well as soil characteristics (e.g. organic matter content). In order to capture the variation present across each individual sub-region, we sampled four sites (within ca. 161 km of one another) within each of the 3 regions (Fig. 1; N = 12 sites). Each site is part of the long-term Rangeland reference area (RRA) stewardship program managed by Alberta Environment and Parks. These long-term grazing enclosures (30–50 y old, and at least 25 × 25 m in area) are maintained to prevent domestic livestock grazing, while areas outside the enclosures are grazed at light to moderate intensity each year. Although enclosures do not exclude wild ungulates, the latter are generally at low densities, and previous studies have found that wildlife tend to avoid using enclosures of this size (Gross and Knight, 2000). Using

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