

**Structure, Function and Drought Resilience of Northern Prairie Communities,
50 Years After Grazing Disturbance**

By

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ABSTRACT

With climate change threatening the function of grassland ecosystems, conservation and restoration strategies are shifting from comparisons of species compositions with baseline conditions, to assessments of ecosystem functions and resilience. Here, I present research from Riding Mountain National Park, Manitoba, to illustrate the links between plant community composition, leaf traits of dominant plants, and grassland community function. I also discuss applications for the management of grassland ecosystems. I use plant community data, collected in 1973, 2010 and 2020, to understand the long-term effects of grazing on the function and resilience of northern fescue prairies. I test whether legacies of historic grazing continue to affect the structure, diversity, and composition of grassland communities, and whether historic grazing predicted community leaf trait composition in fescue grassland ecosystems. I also explore how nutrient and carbon cycling may be influenced by leaf traits of dominant plants, including their leaf carbon and nitrogen concentrations. Fifty years after grazing, heavily grazed prairies continued to have lower plant diversity. However, prairies with light grazing had lower spatial variation in plant composition. By 2020, community leaf trait composition could not be predicted by historic grazing, and instead, plant trait composition was driven by exotic species invasions. Similarity in traits between *Poa pratensis* and *Festuca hallii* resulted in a functional redundancy between lightly and heavily grazed grasslands. Invasions of *Poa pratensis* increased the values of leaf density, and leaf C:N over the years while *Bromus inermis* increased the value of specific leaf area (SLA), illustrating that changes in grassland composition correlate with changes in the traits of dominant plants that have the potential to affect the resilience of grasslands to drought as well as their function. This study describes how community trait composition can impact grassland drought tolerance and ecosystem functions, and the management implications of those consequences.

DEDICATION

This thesis is dedicated in loving memory of my dad. Although he is not here to see its completion, he will always be my inspiration to ask the questions and strive for excellence.

From a young age, my dad instilled a love and curiosity for the natural world into me, budding my passion for the ecological sciences and natural resource management.

This ones for you, Dad.

“Nature is ever at work building and pulling down, creating and destroying, keeping everything whirling and flowing, allowing no rest but in rhythmical motion, chasing everything in endless song out of one beautiful form into another.”

- **John Muir**

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GENERAL INTRODUCTION

Throughout recent history, grassland management strategies have evolved, and with them, strategies to evaluate the success of management of grassland ecosystems. Traditionally, comparisons of species composition with historic baselines were the most common approach to benchmark management success. However, with climate change causing rapid environmental changes in the northern Great Plains grasslands, recent approaches have turned to regarding ecosystem function as a more holistic approach to monitoring grassland health. The resilience of a grassland community to environmental change is an important consideration in the overall health and function of the ecosystem. In Riding Mountain National Park (RMNP), Manitoba, Parks Canada has identified the loss of biodiversity due to changes to the natural disturbance regime and forest encroachment in northern fescue grasslands as management concerns (Parks Canada 2007). This study examines how past management of northern fescue grasslands may impact their long-term resilience in the face of the changing climate, and how current management of grassland ecosystems may be adapted to better align with restoration goals.

In western Canada, Great Plains Rough Fescue grasslands overlay the black soil zone (Blood 1966; Looman 1969, Coupland and Brayshaw 1953), occupying an ecotone with aspen forest between more open grasslands to the south and coniferous forest to the north (Coupland and Brayshaw 1953). In the northern portion of the aspen zone, forest cover is broken by occasional patches of grassland, while in the southern portion, aspen stands are scattered throughout the grassland (Coupland and Brayshaw 1953). The altitude of fescue grasslands ranges from 730m in Manitoba to over 2000m in the Rocky Mountains and Southern British Columbia (Looman 1969). Plains rough fescue (*Festuca hallii*) dominates the vegetation community within northern fescue grasslands (Coupland and Brayshaw 1953; Blood 1966; Looman 1969) and is often codominant with wheatgrass (*Elymus trachycaulus*) (Looman 1969) or porcupine grass (*Hesperostipa spartea*) (Coupland and Brayshaw 1953). Frequency and abundance of forbs is generally higher in fescue prairies than that of mixed prairies to the south and includes Canada goldenrod (*Solidago canadensis*), prairie sage (*Artemisia ludoviciana*), and prairie smoke (*Geum triflorum*) (Thorpe et al. 2015). Shrub occurrence (*Dasiphora fruticosa*, *Sherperdia canadensis*) is common and depends on frequency of fire and other anthropogenic or natural disturbances (Coupland and Brayshaw 1953, Looman 1969; Thorpe et al. 2015). Shrubs tend to encroach rough fescue grasslands if not checked by fire or land management practices (Thorpe et al. 2015).

Historically, bison played a critical role in the maintenance of northern fescue grassland ecosystems, providing disturbance to maintain the grassland (Campbell et al. 1994). Bison provided disturbance by grazing, wallowing, and soil compaction (Campbell et al. 1994). However, due to the extirpation of bison prior to ecological studies during the 19th

century, their role in maintaining the resilience to drought is unknown. Fescue grasslands did not evolve under a heavy summer grazing regime, making them easily damaged by intense grazing (Trottier 1986), in contrast to mixed and short grass prairie associations, which evolved with heavier summer grazing (Heady 1975). The use of cattle to maintain disturbance was thought to be effective management of grassland ecosystems as a proxy for bison presence (Pykala 2005). However, recent studies have concluded that bison and cattle are not ecological synonyms (Kohl et al. 2013). Bison graze in grassland areas while cattle prefer to graze in riparian areas, meaning that cattle require active management to have a similar effect to bison on the landscape (Kohl et al. 2013). The long-term ecological role of cattle and other grazing livestock on community function in northern fescue prairie ecosystems is relatively unknown. Northern fescue grasslands in the aspen parkland region are at risk due to several threats including conversion to cropland (Moss and Campbell 1947; Grilz and Romo 1944; Gerling et al. 1995), invasion by exotic species (Grant et al. 2009), and loss of a natural disturbances (Strong 1977). The long-term interaction of these threats with reintroduced disturbance by cattle is an important factor when considering management for grassland diversity and ecosystem function.

Once grazing has been removed from a fescue grassland, the short-term species composition is dominated by subsets of ephemeral exotic or ruderal species, such as *Taraxacum officinale* (Sinkins and Otfinowski 2012). However, these suites of ephemeral species that flourish in response to grazing do not persist long-term (Sinkins and Otfinowski 2012). Ephemeral and ruderal species typically adopt a fast growth and reproductive strategy for a high investment of leaf nitrogen (Vukovic et al. 2014). A high proportion of these species in the community is likely to alter the community function and resilience by altering the representation of plant functional traits that define this strategy. However, in a fescue grassland ecosystem, by approximately 35 years after grazing, most ephemeral exotic species had virtually disappeared (Sinkins and Otfinowski 2012). Instead, grazed grasslands became dominated by persistent exotic graminoids *Bromus inermis* and *Poa pratensis* (Sinkins and Otfinowski 2012). Persistent exotic species typically adopt a strategy that prioritizes leaf longevity and greater carbon gains (Vukovic et al. 2014), which will alter community function and resilience. For example, a community dominated by persistent exotic species is likely to have less nitrogen cycling and greater carbon storage than a community dominated by ephemeral species (Vukovic et al. 2014).

The impacts of disturbance in plant communities are typically assessed by comparing the vegetation composition or diversity of the community to baseline historical conditions, or comparisons with an undisturbed state. However, restoration ecologists have become increasingly interested in quantifying the effect of disturbance on ecosystem function (Cardinale et al. 2006; Duffy et al. 2009). A common criticism of diversity-focused

research is that some species may exert a stronger control over ecological processes than others, and whether a diverse community performs any differently than the single species having the most influence (Cardinale et al. 2006). Even where a single species dominates a given ecosystem process, it is unlikely to dominate all the processes that are required of that vegetation community because different species maximize different ecosystem properties including water retention and distribution, nitrogen cycling and carbon storage. Therefore, plant communities that are more diverse are more likely to be persistent because multiple species contribute unequally to ecosystem processes (Duffy et al. 2009 Hautier et al. 2018). Representations of plant species that contribute to several ecosystem functions will increase the resilience of the ecosystem. For example, Cardinale et al. (2006) identified that accurately detailing how plant traits are related to the functional dominance in communities as a future challenge for research.

The structure and function of grassland ecosystems is also affected by environmental changes from climate and atmospheric composition. Each of the last three decades has been successively warmer than any other before, and the period from 1983 to 2012 was likely the warmest 30-year period of the last 1400 years (IPCC 2014). Global climate change is causing unprecedented warming on daily and seasonal timescales across almost all ecosystems worldwide (IPCC 2014). The business-as-usual climate model (Representative Concentration Pathway 8.5) predicts increased aridity across the North American grasslands (Hufkens et al. 2016). Increased aridity, triggering more severe and persistent drought than any of those in recorded history can cascade through an ecosystem to affect grassland composition and productivity (Clark et al. 2002). Drought is predicted to reduce surface vegetation cover and productivity, deplete groundwater aquifers, salinize soils, increase erosion, and alter biogeochemical cycling (Clark et al. 2002). As a result, the alteration of grassland communities by grazing disturbance may further impact the ability of the plant community to tolerate drought.

Fescue grasslands have functions that control the movement of energy, nutrients, and water (Kohler et al. 2017). Grasslands sequester carbon by storing carbon in their leaves and tissues during photosynthesis, and store carbon in the soil in root biomass and leaf litter (Lavorel and Grigulis 2012). Dead leaves, stems and roots contribute to the majority of soil carbon content. Root exudation contributes to more than 60% of total root C deposition to rhizosphere soils (Sun et al. 2021). Promoting carbon sequestration in native grasslands is becoming increasingly important when discussing climate change mitigation. Grassland plants influence key ecosystem functions such as growth and nutrient cycling through direct and indirect effects of moisture distribution (Pérez-Harguindeguy et al. 2013) and water flow regulation via aboveground biomass and underground root systems. Additionally, grassland plants also influence nutrient cycling through the accumulation and retention of soil from plant decomposition and erosion protection provided by plant residue (Lavorel and Grigulis 2012). Grasslands play a key

roll in regulating hydrological fluxes in terrestrial ecosystems, including the capture of precipitation, retention and spatial redistribution of water above and below ground and water loss through evaporation and transpiration (Pérez-Harguindeguy et al. 2013). The sustainability of ecosystem functions is determined by the resilience of the ecosystem to biotic and abiotic stress (Kohler et al. 2017). As a result, disturbances that alter the function of grassland ecosystems, including grazing, may jeopardize their ability to tolerate stress.

Grazing disturbance affects community trait composition by altering the community, such that the representation of grazing tolerant plants, with grazing tolerant leaf traits, is increased and becomes dominant. The representation of leaf traits has consequences in the ecosystem function and the potential response of the community to drought stress. In this study, I evaluate the relationship between community leaf trait composition and historic grazing disturbance and discuss the consequences of changing community traits of northern fescue grasslands on their resilience to drought and their function.

This study uses vegetation community composition data collected 4, 40, and 50 years after the removal of grazing from northern fescue grasslands in combination with plant trait data to evaluate the legacy of grazing disturbance on vegetation community composition, diversity, and leaf traits. I connect community leaf trait composition to community function and drought tolerance, including the cycling of nutrients and carbon, to better understand the legacy of grazing disturbance on northern fescue grasslands. To do this, I tested two hypotheses. First, I tested that legacies of grazing disturbance affects the structure, diversity, and species composition of northern fescue grasslands, even 50 years after the removal of grazing. I predicted that intensely grazed grasslands will have reduced diversity and a greater abundance of exotic species. Secondly, I tested that those legacies of grazing affect the community leaf trait composition, where grazing tolerant leaf traits will converge in intensely grazed grasslands. Finally, I discuss the ecological consequences of community leaf trait composition on community function and drought tolerance of grassland ecosystems, and its applications in ecosystem management.

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STRUCTURE, FUNCTION AND DROUGHT TOLERANCE OF NORTHERN PRAIRIE COMMUNITIES 50 YEARS AFTER GRAZING

Abstract

Grasslands provide critical ecosystem services such as carbon sequestration, water regulation, nutrient cycling, and biodiversity conservation. However, climate change is causing periods of increasingly frequent and prolonged drought in northern Great Plains ecosystems, changing the function of grassland communities. This research from Riding Mountain National Park, Manitoba, illustrates links between plant community composition, leaf traits of dominant plants, and the function of prairie grasslands. I used plant community data, collected in 1973, 2010 and 2020, to understand the long-term effects of grazing on the function and resilience of northern fescue prairies. I tested whether legacies of historic grazing continue to affect the structure, composition, and diversity of grassland communities, and whether species with drought tolerant leaf traits converge in historically grazed grasslands. I also explored how nutrient and carbon cycling may be influenced by leaf traits of dominant plants, including their leaf carbon and nitrogen concentrations. Fifty years after grazing, prairies that had been heavily grazed continued to have lower plant diversity and prairies that had been lightly grazed had lower spatial variation in plant composition. By 2020, community leaf trait composition could not be predicted by historic grazing, and instead, plant trait composition was driven by exotic species invasions. Similarity in traits between *Poa pratensis* and *Festuca hallii* resulted in a functional redundancy between lightly and heavily grazed grasslands. Invasions of *Poa pratensis* increased the values of leaf density, and leaf C:N over the years while *Bromus inermis* increased the value of specific leaf area (SLA), illustrating that changes in grassland composition correlate with changes in the traits of dominant plants. This study is the first to relate long-term legacies of grazing on mean community traits of northern fescue prairies and to help adapt the conservation and management of grasslands to changing climates.

Introduction

The distribution of plant species in grassland ecosystems is limited by environmental stress and disturbance. In grasslands, stress is typically associated with the availability of water and limited nutrient availability (Porporato et al. 2001). In contrast, disturbance in grasslands is associated with fire and grazing by herbivores (Grime 1977). Typically, plants that tolerate stress differ in strategy from those that tolerate disturbance (Grime 1977). Species with a competitive strategy use traits that maximize resource acquisition in productive, low stress environments (Grime 1977). Species with a stress-tolerant strategy maintain metabolic performance in unproductive, stressful environments (Grime 1977). Species with a ruderal strategy use rapid gene propagation and complete their lifecycle quickly in high disturbance environments where rapid regeneration is selected for (Grime 1977).

At the community level, the trade-offs in plant strategies are expressed by community diversity. The intermediate disturbance hypothesis predicts that species richness will be highest in communities with moderate levels of disturbance and at intermediate time spans following disturbance (Collins et al. 1995). Environmental stress and disturbance select for specialized plants and evolution of novel traits based on the plant strategy, driving the composition of grassland communities.

However, diversity in grassland communities can be expressed in terms of both the taxonomic diversity and diversity of plant strategies. As a result, trade-offs in plant strategies can also be expressed by the diversity of plant traits. The tolerance of plant species to stress or disturbance depends on the structure of the plant cells and organs. Plant traits are any morphological, physiological or phenological feature that is measurable for individual plants at the cell or whole organism level which may affect its ability to persist under certain conditions (Violle et al. 2007). Plant traits affect the demographic probabilities of immigration, growth, survival, and reproduction of a plant species (Shipley et al. 2016). If a species has the traits to match the requirements of its environment, it will have greater fitness in that environment, resulting in a greater abundance of that species (Shipley et al. 2016). Above-ground, the worldwide leaf economics spectrum summarizes relationships between plant strategy and plant traits (Wright et al. 2004). The leaf economics spectrum is a widely accepted key axis that describes the trade-off in plant morphology and anatomy that runs from quick to slow returns on investments of nutrients and dry mass in leaves (Wright et al. 2004).

The leaf economics spectrum places species along key dimensions of plant ecological strategy based on their traits relevant to growth, survival, and reproduction (Diaz et al. 2016). At one end of the spectrum, exploitative species with potential for quick return of investments of nutrients and dry mass in leaves use an acquisitive strategy (Wright et al. 2004; Diaz et al. 2016). These plants are characterized by low investment in structural

leaf tissues per unit area of light capturing surface, fast photosynthetic returns, and short lifespans (Wright et al. 2004) (Table 1). At the other end of the spectrum, species with a conservative strategy are expected to have a slower photosynthetic rate and slower potential rate of return on investments of nutrients and leaf dry mass than species with an acquisitive strategy (Wright et al. 2004, Diaz et al. 2016) (Table 1). As a result, conservative species have a longer leaf life span from greater investments in leaf tissue, which compensates for high construction costs per unit of leaf area (Wright et al. 2004) (Table 1).

Grazing is a disturbance which acts as a selective pressure in grassland communities, shaping the morphology, physiology, and life history of plants (Wright et al. 2005). Plant species can be grazing resistant by responding to grazing with either an avoidance or tolerance strategy. Plant species that avoid grazing are characterised by an acquisitive strategy on the leaf economics spectrum, which have a larger light-intercepting area per investment in leaf mass, allowing plants to grow faster as juveniles, compensating for lost surface area from grazing (Onoda et al. 2017). Therefore, grazing avoidant species can complete their life cycle before being affected by grazing. Alternatively, species that tolerate grazing are characterized by a conservative strategy. Their investment in structural tissues and high leaf density allows them to survive despite physical damage from grazing.

Plant leaf traits are the structures and morphology of plants that allow them to avoid or tolerate stress and disturbance. Specific leaf area (SLA) is an important trait when considering plant strategy and the trade off between carbon gains and leaf longevity (Pérez-Harguindeguy et al. 2013). SLA is expressed as the one-sided area of a leaf divided by the dry mass and describes the investment in leaf mass per unit of area (Cornelissen et al. 2003). Competitive and ruderal species (Grime 1977) use an acquisitive plant strategy and rapidly grow large, low dry mass leaves and may complete their life cycle quickly, in the case of ruderal species. Leaf traits that characterize these species include low leaf C:N, high SLA, and low leaf density. This leaf construction equates to a larger light intercepting surface for a given investment in leaf mass, allowing for faster photosynthetic gains and shorter leaf lifespan (Onoda et al. 2017). In contrast, stress-tolerant species that use a conservative strategy are those with slow growing, small leaves, thick leaf tissue that have a greater leaf longevity and resistance to physical hazards. Plant traits that characterize plants with a conservative strategy include high leaf C:N, low SLA, and high leaf density. Conservative leaf construction results in longer leaf lifespan and slower photosynthetic gains.

Table 1. Variables related to plant strategies on the worldwide leaf economics spectrum.

	Acquisitive	Conservative
Growth	rapid	slow
Lifespan	short	long
SLA	high	low
Leaf Density	low	high
C:N	low	high
Decomposition Rate	rapid	slow

Climate-induced environmental changes have the potential to affect the structure and function of grasslands ecosystems. The Representative Concentration Pathway 8.5 climate model predicts increased aridity across the North American grasslands (Hufkens et al. 2016). The Aspen Parkland region in Manitoba is predicted to see a significant increase in very hot days, with more than 30 days over 30 degrees Celsius predicted by the year 2050 (Prairie Climate Center 2019). Increased aridity and number of hot days, triggering more severe and persistent drought than in recorded history will affect grassland composition and productivity (Clark et al. 2002). Drought selects for species with a set of traits that can withstand extended periods without the availability of water. Species adapted to drought are characterized by structures that store water and reduce water loss during gas exchange (Wright et al. 2005), therefore, plant species that display a conservative strategy on the leaf economics spectrum, are likely to be drought tolerant (Coughenour 1985).

Traditional approaches to grassland monitoring involve surveys for species composition using cover estimates. These data are then analysed for alpha or beta diversity that can be compared with baseline values or undisturbed conditions (Kvalseth 1991; Legendre and Legendre 2012). Composition-based approaches to plant community monitoring document the changes in community structure but may not explicitly measure function or account for functional redundancy between species (Koehl 1996). Focusing on key traits of organisms that predispose species to influence ecosystem functions can make biodiversity research more realistic and applicable (Kohler et al. 2017). A trait-based approach captures important mechanisms for resistance, resilience, and transformation of ecosystem functions by examining the morphology and physiology of individual plant species (Kohler et al. 2017). Studying community function in addition to structure can provide insights into how an ecosystem functions, regardless of whether the composition of the community is identical to baseline conditions (Craine et al 2011; Hoover et al. 2014; Li et al. 2018).

Grassland ecosystem functions are dependent on the traits of plants in the grassland community. Plant traits scale to drive ecosystem functions based on the representation of species within a vegetation community. Plant traits contribute to community functions

differently, and the representation of plant traits will alter the community function. The community assemblage that will affect ecosystem properties is the result of sorting processes among species with the appropriate response traits that allow them to respond to environmental change (Suding et al. 2008). Sorting is the result of the non-random demographic process of dispersal, growth, survival, and reproduction of individuals belonging to different species as determined by the traits that they possess (Shipley et al. 2006). The ecological sorting process will result in species that have the appropriate response traits to persist through environmental change to become more abundant in the community (Shipley et al. 2006). Abundant species are the most functionally important due to their greater representation in the community (Grime 1998; Suding et al. 2008). Response traits determine community response overlap with effect functional traits that determine effects on ecosystem functioning (Lamarque et al. 2014). For example, fertilization favours plants with nitrogen-rich leaves because nitrogen-rich soil selects for species with high leaf nitrogen content. A community dominated by nitrogen rich leaves promotes high above ground primary productivity (Lamarque et al. 2014). Consequently, the altered community will impact ecosystem processes via changes in the representation of effect traits (Suding et al. 2008). For example, the nitrogen cycling and decomposition rate in the community will increase due to an increase representation of nitrogen-rich leaves.

Response traits are plant traits that impact the ability of the plant to respond to the external environment (Suding et al. 2008). Plant traits provide adaptations that help species to resist disturbance and stress from environmental changes. Acquisitive leaf traits, including high specific leaf area and low leaf density are not adapted to retain water in the leaf, causing the plant to be intolerant to drought (Wright et al. 2005, Vitra et al. 2019). Alternatively, species that use a conservative strategy, have plant traits that retain water and allow leaf persistence under very dry conditions, including low specific leaf area and high leaf density providing structural support to prevent xylem cavitation during drought stress (Wright et al. 2005, Vitra et al. 2019). Therefore, leaf traits that allow plants to resist grazing provide similar benefits to plants when subjected to drought (Coughenour 1985). Grazing in a grassland is likely to change the long-term trait composition to a more conservative, or grazing tolerant, assembly of plant traits (Pazos et al. 2007; Streit et al. 2022). Because conservative plant traits may make a plant more tolerant to drought, a convergence of conservative traits in a grassland ecosystem is likely to make the plant community more drought tolerant.

In contrast, effect traits define the ability of a plant to affect functions or processes in its external environment (Suding et al. 2008). Leaf traits may contribute to the function of the ecosystem while they are on the plant or as leaf litter during decomposition (Cornwell et al. 2008; McSherry and Ritchie 2013). Leaf C:N is a leaf traits that contributes to the cycling of nutrients and carbon in the ecosystem. Species with an acquisitive plant

strategy require an increased leaf nitrogen content to support the high photosynthetic rate and rapid growth of plants (Onoda et al. 2017), therefore, when these species decompose the increased nitrogen content in their leaves will result in increased nitrogen availability in the ecosystem (Lamarque et al. 2014). Furthermore, leaf nitrogen content has important implications in community function because high nitrogen content of leaves is associated with high nutritional content to herbivores (Pérez-Harguindeguy et al. 2013). Alternatively, species that have adopted a conservative strategy have an increased C:N. High carbon leaves decompose slowly (von Lutzow et al. 2006), resulting in increased litter accumulation (Cornwell et al. 2008), and decreased available nitrogen (Lamarque et al. 2014; Wright et al. 2005). Eventually, the slow decomposition of these plants contributes to greater carbon storage in the ecosystem (von Lutzow et al. 2006). Understanding how plant traits drive ecosystem functions is a growing area of research and is important to fully understand the impact of environmental change and disturbance on grassland ecosystems.

This project focuses on a long-term experiment in Riding Mountain National Park (RMNP), Manitoba to evaluate the legacies of historic grazing of northern fescue grasslands on grassland structure, diversity, and function, including susceptibility to drought. This research will expand existing long-term data and incorporate plant traits into an analysis of historically grazed grassland communities. I tested two hypotheses: First, that legacies of historic grazing continue to affect the structure, diversity, and composition of grassland communities, 50 years after the removal of grazing. Secondly, that those legacies of grazing affect the community plant trait composition so that conservative leaf traits converge in grazed grasslands. In addition, I explored how the cycling of nutrients and carbon in historically grazed grasslands may be influenced by plant leaf traits. Finally, I discussed the consequences of community trait composition on grassland community drought tolerance and ecosystem function.

Methods

Study Region

This research was conducted in Riding Mountain National Park (RMNP), approximately 300km northwest of Winnipeg, Manitoba, Canada (Latitude: 50.6580; Longitude: -99.9721). The park contains 2,978km² of Mixedwood Boreal Forest and protects much of the last remaining plains rough fescue grassland communities in Western Canada (Trottier 1986). RMNP is characterized by a mean annual precipitation of 450-500mm and a growing season of 168-173 days (Leeson et al. 2005). Mean temperatures range between -12°C in February and 18°C in July (Government of Canada n.d.).

Approximately 75km² of RMNP is grassland ecosystem, and approximately 25km² of that are classified as fescue grassland (Trottier 1986). Fescue prairies in RMNP are distributed along its southern and western portions. Remnant fescue grasslands in the park are isolated and small (mean = 0.08km²; max = 2.12km²) and are often associated with broad river valleys and rich soils formed over base parent material (Blood 1966). Native ungulate species are present in the park, including elk (*Cervus elaphus canadensis*), moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*). Of these, elk are found most frequently in the fescue grasslands, and their populations are small and well distributed (Parks Canada [unpublished data]). Historically, the fescue grasslands in RMNP were important habitat for plains bison (*Bison bison*), however, only reintroduced bison confined to a fenced enclosure remain in the park today. Records of fire history in the park date back to its establishment in 1933. Park grasslands are burned frequently, with the date of the last burn in major grasslands ranging from 2005 to 2016 (Parks Canada [unpublished data]).

Historic Grazing and Monitoring of Grassland Recovery

Hay harvesting, and grazing by cattle, horses, and sheep were permitted in the region of the present RMNP, starting in 1895 and persisted through its change in status from a Forest Reserve to a National Park in 1933 (Trottier 1986). Grazing by domestic animals was terminated in 1970 due to deterioration of grassland condition and complete defoliation in some heavily used regions (Trottier 1986). Grazing was concentrated within seven grazing compartments (Figure 1) in the grassland areas of RMNP (Trottier 1986). Up to 1,400 cattle were grazed in the park on an annual basis between 2 to 5 months per year between 1895 and 1970 (Trottier 1986).

Starting in 1969, Riding Mountain National Park established a program to monitor the recovery of historically grazed prairies. Plant communities in historically grazed grasslands were surveyed along 33 permanent transects, distributed across the park (Trottier 1986) (Figure 1). Shortly after grazing was removed, these were classified into three grazing classes based on the degree of defoliation by livestock (Sinkins and Otfinowski 2012): lightly grazed (n=11), moderately grazed (n=13), and heavily grazed

(n=9). Since surveyed grasslands are confined to areas previously measured for livestock grazing, it is not possible to include control sites (Sinkins and Otfinowski 2012). Vegetation inventories of historically grazed transects were completed in 1973 (Trottier 1986), 1995 (Slogan 1997), 2010 (Sinkins and Otfinowski 2012), 2015 (Pinchbeck and Otfinowski 2015), and 2020. In this study, I evaluate the affects of historic grazing on the structure, function, and composition of northern fescue grasslands, and determine whether historic grazing affects community trait composition. I then discuss the consequences of community trait composition on community drought tolerance and ecosystem functions.

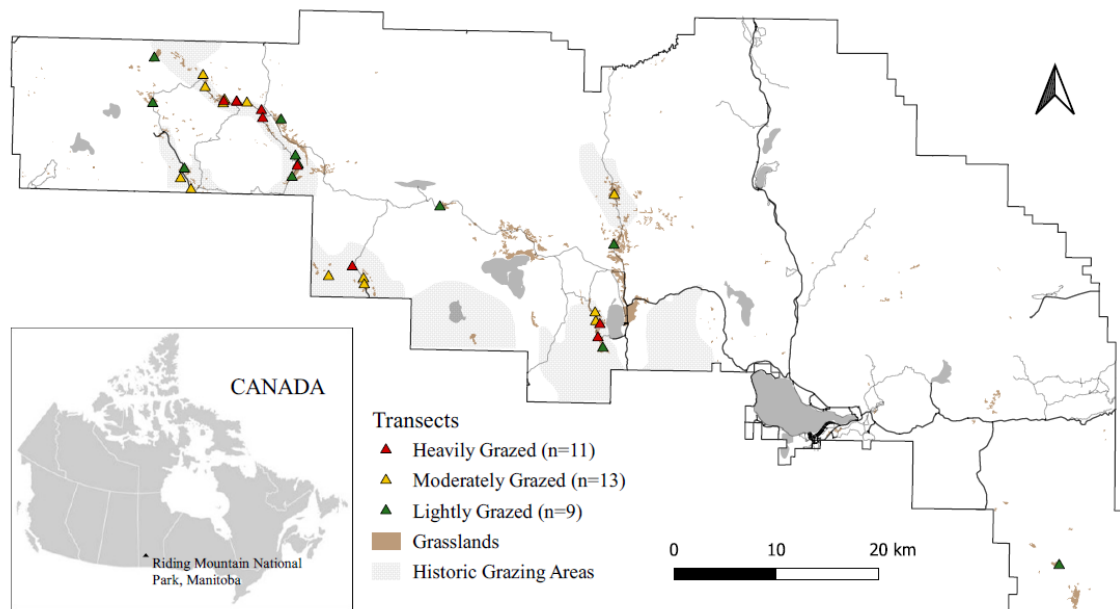


Figure 1. Distribution of 33 long term-monitoring transects in historically grazed northern fescue grasslands in Riding Mountain National Park, Manitoba, Canada. Map was produced using Transverse Mercator projection and NAD83 UTM Zone 14U coordinate reference system.

Vegetation Species Inventory

The first objective of this research was to determine whether legacies of historic grazing continue to affect the structure, diversity, and composition of grassland communities. Surveys of plant communities followed methods used in 1973 (Trottier 1986) and 2010 (Sinkins and Otfinowski 2012). Inventories of plants were conducted during peak growing season. Vegetation community data were collected by stretching a measuring tape between two permanent transect markers at either end of the 30.5 m linear transect. A metal pin (3 mm diameter) was lowered at 30.5 cm intervals along the transect and each plant species that touched the pin at each of the 100 intervals was recorded (Sinkins

and Otfinowski 2012). Each species of vascular plant was only recorded a maximum of one time at each interval; therefore, each species has a maximum count of 100 hits per transect (Sinkins and Otfinowski 2012).

Species of *Carex* were not separated during the long-term grassland monitoring inventories in 1973 or 2020. To identify commonly occurring *Carex* species, I referred to recent databases of vascular plants in the grasslands of RMNP. Based on this review, I determined *C. torreyi* and *C. inops* represent the functional diversity of upland sedges in the fescue grassland ecosystem.

Plant nomenclature throughout this study follows VASCAN (<https://data.canadensys.net/vascan/>). Voucher specimens of species identified on the transects were collected and verified using herbarium collections at The University of Winnipeg (UWPG) and the University of Manitoba (WIN). Vouchers will be housed in the University of Winnipeg herbarium.

Plant Trait Inventory

The second objective of my research was to determine how the traits of dominant plant species affect the function and drought tolerance of historically grazed grasslands. I predicted that conservative leaf traits converge in grasslands with legacies of heavy grazing disturbance. Using historical surveys from the grazed transects (1973, 2010, 2020), thirty plant species were selected for trait measurements. Selected focal species were dominant in historic plant communities, defined as those that contribute to 70% of the total standing biomass (Cornelissen et al. 2003).

Measurements of leaf structure were completed within 2-3 hours after sunrise and 3-4 hours before sunset (Cornelissen et al. 2003). Plants for trait analysis were chosen from a representative grassland area, and ten representative individuals of each pre-determined dominant species were selected for analysis. Representative individuals were well grown, robust plants in well lit areas (Cornelissen et al. 2003). In a case where a species has only one full grown leaf to be harvested, 20 representative individuals were selected for analysis. These included *Poa pratensis* and *Thalictrum venulosum*.

Characteristics of the selected plants, including plant height and plant developmental stage were recorded to standardize relative plant maturity. Plant height was recorded in meters by measuring the aboveground biomass from the soil surface to the top of the inflorescence while vertically stretching the plant (Cornelissen et al. 2003). In forbs, developmental stages included vegetative, flower bud, flowering or in fruit. In graminoids, developmental stage categories included stem elongation, booting, inflorescence emergence, anthesis, milk, dough, and ripening (Larsen et al. n.d.).

Leaf traits were measured on two representative leaves collected from each of the ten selected plants for each species (Cornelissen et al. 2003). Representative leaves were those in full sun conditions, relatively young but fully expanded, mature leaves from adult plants, and without obvious symptoms of pathogen or herbivore attack (Cornelissen et al. 2003). When measuring leaf traits, any petiole, rachis, and veins were included as part of the leaf. Leaf thickness was measured using an electronic micrometer (0.001 mm accuracy) on a section of the leaf off the midrib that was representative of the leaf thickness. Following thickness measurements, leaves were harvested and transported to a field laboratory in moist bags to measure leaf area. Harvested leaves were placed in a plastic report cover and passed through a portable leaf area meter (LI-3000C, LI-COR Inc. Lincoln, NE USA). Measured leaves were dried (60°C, 72h) and weighed for leaf dry mass (Cornelissen et al. 2003).

Leaf traits specific leaf area (SLA) and leaf density were calculated for community leaf trait analyses. SLA was calculated as the one-sided area of the leaf divided by the leaf dry mass (mm^2/mg) (Cornelissen et al. 2003). Leaf density was calculated by dividing the dry mass of the leaf by the leaf volume, calculated by multiplying leaf thickness and leaf area (mg/mm^3). Each focal species had 10 replicates of SLA and leaf density except species that had one leaf collected per individual, which had 20 replicates.

Dried leaves were ground and analyzed for total carbon and nitrogen content using an elemental analyzer which uses the modified Duman method (ThermoFisher *FlashSmart* <https://www.thermofisher.com/order/catalog/product/11206100> #/11206100). Leaf carbon and nitrogen were expressed in trait profiles as C:N ratio. Each focal species had 5 replicates of C:N, except *Carex torreyi* and *C. inops*, which had 3 replicates each. All plant material for leaf C:N was collected within 1 year of analysis.

Data Management and Statistical Analyses

Species composition data, plant trait data, and transect data was stored in a relational database, postgresSQL 9.4 (<https://www.postgresql.org/>). I determined how the legacies of historic grazing continued to affect the structure, composition, and diversity of grassland communities by comparing the species composition between historic grazing classes in 1973, 2010, and 2020. In addition, I compared the community weighted mean plant leaf traits, SLA, leaf density, and leaf C:N, between historic grazing classes.

Plant community diversity and composition

My first hypothesis examines if historic grazing legacies continued to impact the structure, diversity, and composition of grassland communities, 50 years after the removal of grazing. Effects of historic grazing intensity on the species diversity of prairies were based on measures of alpha diversity (richness, effective richness, Shannon-Wiener index) and beta diversity (Bray-Curtis dissimilarity) (Kvalseth 1991; Legendre

and Legendre 2012). Species richness (S) is the number of species identifies on a transect. The Shannon-Wiener diversity index is defined as:

$$Eq. 1 \quad H' = - \sum_{i=1}^R p_i \ln p_i$$

Where p_i is the proportion of individuals belonging to the i th species. The Shannon-Wiener Index quantifies the uncertainty in predicting the species identity of an individual that is taken at random from the dataset, therefore, transects with a higher Shannon-Wiener index (H') have a higher alpha diversity (Legendre and Legendre 2012). Effective richness describes plant communities based on the proportional abundance of species. Effective richness was calculated as:

$$Eq. 2 \quad N_1 = e^{H'}$$

Where H' is equal to the Shannon-Wiener diversity index and e is equal to the mathematical constant Euler's number. Effective richness can be interpreted as the species richness if the evenness is the same across all species.

Beta diversity is the variability in community composition among grassland transects, expressed as the ratio between regional and local species diversity (Jost 2007). The Bray-Curtis index estimates beta diversity by quantifying the compositional dissimilarity between two different transects, j and k . Bray-Curtis index is defined as:

$$Eq. 3 \quad BC_{jk} = \frac{\sum_{i=1}^p |X_{ij} - X_{ik}|}{\sum_{i=1}^p (X_{ij} + X_{ik})}$$

The Bray-Curtis index is bound between 0 and 1, where two sites that have the same composition cannot be distinguished and have a Bray-Curtis index of zero (Legendre and Legendre 2012). Univariate analysis of variance (ANOVA) on diversity indices for each survey transect was used to compare the means of diversity indices between historic grazing intensities.

Redundancy analysis (RDA) of survey sites, species composition data and historic grazing intensity for 1973, 2010 and 2020 datasets were used to compare vegetation community composition between transects with histories of varying grazing intensities. RDA is a constrained ordination model was used to quantify the proportion of variance in the community vegetation or trait composition that can be explained by historic grazing intensity. Following RDA, a Monte-Carlo permutation test was used to determine the significance of RDA axes (Legendre and Legendre 2012).

Plant trait composition

The second objective of my research was to determine the affect of historic grazing intensity on the leaf traits of dominant plant species. Using the abundance proportion from the composition survey (p_{ik}) of each species (i) in a transect (k), community weighted means (*CWM*) were calculated for each plant trait (j). Where t_{ij} is the value of trait j for species i . *CWM* quantifies the average trait values per unit of biomass expressed by the vegetation community (Sonnier et al. 2010).

$$Eq. 4 \quad CWM_{jk} = \sum_{i=1}^s p_{ik} t_{ij}$$

I calculated *CWM* for all leaf traits for each species on each of the transects to construct a trait profile of each transect. Community weighted means of leaf traits for 1973, 2010, and 2020 were calculated using plant trait data collected in 2019-2021 and species abundance survey data from 1973, 2010, and 2020, respectively.

To determine whether a convergence of conservative leaf traits was observed in grasslands with a legacy of heavy grazing, I used RDA to quantify the proportion of variance in the mean plant leaf trait composition between survey sites which could be explained by historic grazing intensity. Furthermore, I used ANOVA to compare log-transformed means of SLA, leaf density, and leaf C:N between historic grazing classes.

Results

Structure, Diversity and Composition of Grazed Northern Fescue Grasslands

Historic grazing affected the structure, diversity, and composition of grassland communities in all years since the removal of grazing. In 1973, grasslands of all grazing classes were dominated by graminoids and had low cover of shrubs (Table 2). By 2010, lightly grazed grasslands were still dominated by graminoids, however, shrub cover was greatest in heavily grazed grasslands ($F_{2,30} = 5.61$, $p = 0.008$) and graminoid cover was greatest in lightly grazed grasslands ($F_{2,30} = 4.13$, $p = 0.026$). By 2020, shrub cover stabilized between grazing classes ($F_{2,30} = 0.11$, $p = 0.896$), while graminoid cover remained high in lightly grazed grasslands ($F_{2,30} = 3.39$, $p = 0.047$).

In all years, grazing intensity significantly affected grassland diversity (Table 3). Species richness ($F_{2,90} = 53.22$, $p < 0.001$) and Shannon's diversity ($F_{2,90} = 29.61$, $p < 0.001$) remained lowest in heavily grazed treatments (Table 3B), even 50 years after the removal of grazing (Table 3A). However, beta diversity declined significantly in transects with historically low grazing intensities ($F_{2,166} = 5.29$, $p = 0.006$) (Table 3A). As a result, grazing intensity, but not time since the removal of grazing, continued to significantly affect all measures of grassland diversity over the course of the experiment (Table 3B).

Historic grazing intensity was a good predictor of plant community composition for all sampling years. Four years after the removal of grazing, grazing history accounted for 39.4% of the variance in the plant community ($F_{1,30} = 20.04$, $p = 0.001$; Figure 2A) and separated lightly grazed communities, dominated by *Festuca hallii* from heavily grazed communities dominated by *Poa pratensis* (Figure 2A). Forty years after grazing, the proportion of variance in plant communities explained by historic grazing intensity remained high (27.4%; $F_{1,30} = 6.12$, $p = 0.047$) (Figure 2B). Lightly grazed transects continued to be characterized by native graminoids (eg. Plains rough fescue - *Festuca hallii*, Richardson's needlegrass - *Achnatherum richardsonii*) and heavily grazed grasslands remained dominated by exotic graminoids (eg. Kentucky bluegrass - *Poa pratensis* and smooth brome - *Bromus inermis*) and shrubs (eg. Western Snowberry - *Symphoricarpos occidentalis*) (Figure 2B). By 2020, historic grazing intensity continued to explain a significant proportion of the variance in the plant community (22.3%; $F_{1,30} = 8.90$, $p = 0.001$) (Figure 2C). Lightly grazed grasslands were still dominated by native graminoids (eg. Plains rough fescue - *Festuca hallii*) and historically heavily grazed grasslands were characterized by exotic graminoids (eg. Kentucky bluegrass - *Poa pratensis* and smooth brome - *Bromus inermis*) (Figure 2C).

Table 2. Mean vegetation community composition and structure across historic grazing intensities in Riding Mountain National Park, Manitoba, Canada northern fescue prairies in 1973, 2010 and 2020. Within each year, species representing 70% of the overall standing biomass are listed. Species highlighted in bold are exotic to North America (Brouillet et al. 2010). Unidentified *Carex* species may include *C. torreyi*, *C. inops*, *C. hookeriana*, *C. deweyana* and *C. capillaris*.

Group A - Light			Group B - Moderate			Group C - Heavy		
Species	Mean Hits	Std. Dev.	Species	Mean Hits	Std. Dev.	Species	Mean Hits	Std. Dev.
1973								
<i>Festuca hallii</i>	52.0	15.4	<i>Poa pratensis</i>	51.8	26.8	<i>Poa pratensis</i>	77.7	29.5
<i>Carex sp</i>	22.1	15.5	<i>Carex sp</i>	21.2	10.8	<i>Elymus trachycaulus</i>	23.1	25.1
<i>Koeleria macrantha</i>	14.3	7.7	<i>Elymus trachycaulus</i>	15.2	13.3	<i>Carex sp</i>	12.1	17.3
<i>Hesperostipa spartea</i>	14.2	12.7	<i>Festuca hallii</i>	15.0	11.5	<i>Vicia americana</i>	9.2	12.7
<i>Poa pratensis</i>	12.0	14.3	<i>Koeleria macrantha</i>	10.5	9.7	<i>Achillea millefolium</i>	7.8	10.5
<i>Elymus trachycaulus</i>	7.4	3.9	<i>Vicia americana</i>	9.8	8.3	<i>Fragaria virginiana</i>	7.8	9.5
<i>Galium boreale</i>	7.4	7.7	<i>Hesperostipa spartea</i>	9.7	10.7			
<i>Solidago rigida</i>	5.8	2.9	<i>Taraxacum officinale</i>	7.4	7.1			
<i>Symphyotrichum laeve</i>	5.5	6.5	<i>Galium boreale</i>	6.6	4.2			
<i>Geum triflorum</i>	5.4	3.7	<i>Achillea millefolium</i>	6.5	4.4			
<i>Fragaria virginiana</i>	5.4	8.2	<i>Fragaria virginiana</i>	6.3	8.2			
Graminoid	141.2	25.3	Graminoid	139.5	33.5	Graminoid	121.8	47.3
Forb	70.1	23.5	Forb	78.4	16.5	Forb	73.4	53.7
Shrub	3.8	7.6	Shrub	5.0	5.8	Shrub	2.6	6.6
2010								
<i>Festuca hallii</i>	56.7	21.6	<i>Poa pratensis</i>	78.8	18.5	<i>Poa pratensis</i>	82.3	12.8
<i>Poa pratensis</i>	42.3	30.6	<i>Festuca hallii</i>	25.6	24.2	<i>Symphoricarpos occidentalis</i>	29.6	26.2
<i>Achnatherum richardsonii</i>	19.6	14.1	<i>Elymus trachycaulus</i>	17.0	12.2	<i>Carex sp</i>	16.2	20.2
<i>Carex sp</i>	19.5	14.1	<i>Carex sp</i>	12.2	7.9	<i>Bromus inermis</i>	14.2	15.3
<i>Galium boreale</i>	15.3	8.1	<i>Symphyotrichum laeve</i>	11.6	11.9	<i>Galium boreale</i>	11.1	6.1
<i>Bryophyte sp</i>	10.5	14.2	<i>Galium boreale</i>	11.5	7.3	<i>Calamagrostis canadensis</i>	7.6	21.2
<i>Elymus trachycaulus</i>	9.3	5.8	<i>Bryophyte sp</i>	10.1	17.3	<i>Solidago canadensis</i>	7.4	16.0
<i>Hesperostipa spartea</i>	9.3	9.5	<i>Artemisia ludoviciana</i>	6.4	3.7			
<i>Bromus ciliatus</i>	7.8	9.3	<i>Bromus inermis</i>	5.6	20.2			
<i>Symphyotrichum laeve</i>	7.6	6.6	<i>Thalictrum venulosum</i>	5.1	4.0			
<i>Geum triflorum</i>	7.2	8.0						
Graminoid *	172.3	27.7	Graminoid	149.8	31.8	Graminoid	132.8	31.4
Forb	91.0	33.3	Forb	87.1	37.5	Forb	72.8	53.3
Shrub	12.5	12.5	Shrub	10.8	6.7	Shrub *	31.0	27.4
2020								
<i>Poa pratensis</i>	71.5	34.4	<i>Poa pratensis</i>	89.6	14.5	<i>Poa pratensis</i>	89.0	9.8
<i>Festuca hallii</i>	61.4	22.8	<i>Festuca hallii</i>	27.1	27.3	<i>Bromus inermis</i>	25.1	26.8
<i>Carex sp</i>	25.4	14.6	<i>Carex sp</i>	24.4	16.6	<i>Symphoricarpos occidentalis</i>	20.1	16.6
<i>Galium boreale</i>	12.4	7.3	<i>Galium boreale</i>	13.5	9.2	<i>Carex sp</i>	17.6	16.8
<i>Fragaria virginiana</i>	11.9	8.7	<i>Thalictrum venulosum</i>	12.8	9.7	<i>Solidago canadensis</i>	17.6	21.3
<i>Achnatherum richardsonii</i>	11.8	7.4	<i>Fragaria virginiana</i>	12.5	11.9	<i>Anemone canadensis</i>	12.1	16.0
<i>Symphyotrichum laeve</i>	8.9	6.2	<i>Symphyotrichum laeve</i>	9.4	8.1	<i>Galium boreale</i>	10.9	8.0
<i>Schizachne purpurascens</i>	8.3	7.5	<i>Lathyrus ochroleucus</i>	8.3	8.2	<i>Elymus repens</i>	8.0	18.0
<i>Rosa acicularis</i>	7.2	7.2	<i>Elymus trachycaulus</i>	6.8	5.4	<i>Calamagrostis canadensis</i>	7.8	17.6
<i>Elymus trachycaulus</i>	7.0	4.1	<i>Symphoricarpos occidentalis</i>	6.5	6.8			
<i>Hesperostipa spartea</i>	6.5	6.7	<i>Achnatherum richardsonii</i>	5.8	8.4			
			<i>Bromus inermis</i>	5.5	20.0			
Graminoid *	213.5	39.2	Graminoid	178.3	44.2	Graminoid	170.1	37.2
Forb	99.5	35.5	Forb	114.5	60.3	Forb	100.2	75.3
Shrub	20.0	15.700	Shrub	22.9	17.8	Shrub	23.1	18.7

* mean significantly different between grazing groups

Table 3. Mean species richness, Shannon-Wiener diversity, effective species richness and Bray-Curtis dissimilarity across the historic grazing intensities in northern fescue grasslands of Riding Mountain National Park, Canada in each of 1973, 2010, and 2020 (A). One-way (A) and two-way (B) Analysis of variance (ANOVA) results are shown.

A	Group A - Light		Group B - Moderate		Group C - Heavy		ANOVA grazing intensity		
	mean	std. dev.	mean	std. dev.	mean	std. dev.	F value	D.F.	p-value
1973									
Species Richness (S)	31.2	3.8	27.5	3.6	14.2	8.4	26.94	2,30	<0.001
Shannon-Weiner Diversity (H')	2.7	0.2	2.6	0.3	1.6	0.9	14.83	2,30	<0.001
Effective Species Richness (N1)	14.9	2.5	14.3	3.5	6.5	4.2	18.30	2,30	<0.001
Bray-Curtis Dissimilarity	0.4	0.1	0.5	0.1	0.5	0.2	2.46	2,166	0.089
2010									
Species Richness (S)	31.4	4.1	28.9	6.2	17.8	8.1	15.45	2,30	<0.001
Shannon-Weiner Diversity (H')	2.7	0.2	2.5	0.3	2.0	0.5	11.47	2,30	<0.001
Effective Species Richness (N1)	14.7	3.0	13.0	4.0	8.1	3.9	11.19	2,30	<0.001
Bray-Curtis Dissimilarity	0.5	0.1	0.5	0.1	0.5	0.1	0.485	2,166	0.617
2020									
Species Richness (S)	33.2	5.3	28.9	6.2	19.6	6.4	13.16	2,30	<0.001
Shannon-Weiner Diversity (H')	2.7	0.3	2.5	0.3	2.2	0.5	4.99	2,30	0.013
Effective Species Richness (N1)	14.9	4.0	13.0	4.0	9.6	4.6	1.74	2,30	0.193
Bray-Curtis Dissimilarity	0.4	0.1	0.5	0.1	0.5	0.1	5.29	2,166	0.006

B	ANOVA grazing intensity			ANOVA year			ANOVA grazing intensity*year		
	F value	D.F.	p-value	F value	D.F.	p-value	F value	D.F.	p-value
Species Richness (S)	53.22	2,90	<0.001	1.83	2,90	0.167	0.426	4,90	0.790
Shannon-Weiner Diversity (H')	29.61	2,90	<0.001	0.646	2,90	0.527	2.48	4,90	0.050
Effective Species Richness (N1)	20.94	2,90	<0.001	0.240	2,90	0.787	1.60	4,90	0.181
Bray-Curtis Dissimilarity	3.32	2,498	0.037	2.05	2,498	0.130	2.31	4,498	0.057

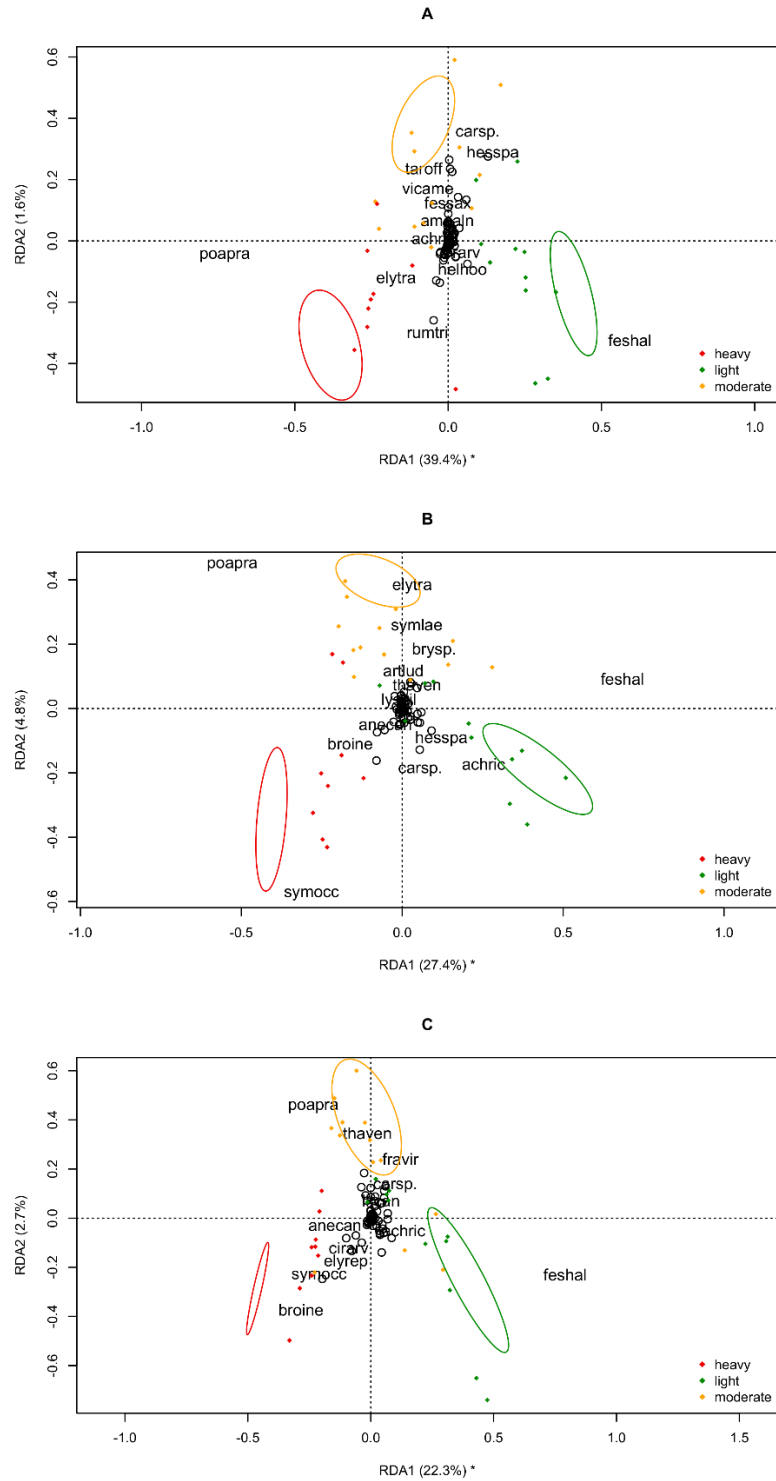


Figure 2. Redundancy analysis of sampling sites, vegetation community composition and historic grazing treatments for 1973 (A), 2010 (B), and 2020 (C) in northern fescue grasslands in Riding Mountain National Park, Manitoba, Canada. Abbreviations represent the first three letters of species binomials. See Appendix A for species names. Ellipses represent 95% confidence standard error for each grazing group.

Plant Trait Composition of Grazed Northern Fescue Grasslands

The effect of historic grazing intensity on the trait composition of grasslands depended on time since the removal of grazing. Four years after the removal of grazing, the mean community composition of leaf traits could not be predicted by historic grazing intensity. The means of SLA ($F_{2,30} = 0.68$, $p = 0.513$), leaf density ($F_{2,30} = 1.12$, $p = 0.339$), and leaf C:N ($F_{2,30} = 1.97$, $p = 0.158$) were unchanged between the three grazing classes (Table 4A) (Figure 3), and grazing intensity explained only 3.5% of the variance in leaf trait composition ($F_{1,30} = 1.09$, $p = 0.596$) (Figure 4A).

However, by 2010, forty years after the removal of grazing, grazing intensity explained 16.9% of the variance in leaf trait composition of grasslands ($F_{1,30} = 6.12$, $p = 0.037$) (Figure 4B). Historically intensely grazed grasslands became dominated by plants with acquisitive leaf traits and lightly grazed grasslands were dominated by conservative leaf traits. The community weighted means of leaf density ($F_{2,30} = 4.23$, $p = 0.024$) and leaf C:N ($F_{2,30} = 5.91$, $p = 0.007$) were lowest in grasslands with a history of intense grazing and highest in grasslands with a history of light grazing (Table 3A) (Figure 3). However, there was no effect of historic grazing intensity on the community weighted mean of specific leaf area (SLA) of grasslands ($F_{2,30} = 0.09$, $p = 0.917$) (Table 4A) (Figure 3).

The effect of historic grazing on the leaf trait composition of grasslands did not persist. Fifty years after the removal of grazing, the means of SLA ($F_{2,30} = 0.02$, $p = 0.985$), leaf density ($F_{2,30} = 0.39$, $p = 0.683$), and leaf C:N ($F_{2,30} = 1.10$, $p = 0.345$) no longer differed between the three grazing classes (Table 4A) (Figure 3) and historic grazing intensity explained an insignificant portion of variance in the community trait composition ($F_{1,30} = 0.88$, $p = 0.680$) (Figure 4C).

Regardless of historic grazing intensity, the community weighted mean values of all leaf traits increased between 1973 and 2020 (Figure 3). Mean SLA ($F_{2,90} = 30$, $p < 0.001$), mean leaf density ($F_{2,90} = 19.73$, $p < 0.001$), and mean leaf C:N ($F_{2,90} = 17.45$, $p < 0.001$) all increased significantly between 1973 and 2020 (Table 4B).

Independent of historic grazing intensity, the composition of grasslands changed over time. As a result, survey year, indicating the time since grazing, predicted 9.6% of the variance in the vegetation community composition ($F_{1,96} = 10.246$, $p = 0.001$) (Figure 5). Between 1973 and 2020 grasslands shifted in composition from native graminoids, including *Elymus trachycaulus*, *Koeleria macrantha*, and *Hesperostipa spartea*, (Figure 5) to exotic graminoids, including *Poa pratensis* and *Bromus inermis* (Figure 5). In addition, grasslands in 2020 were characterized by native graminoid plains rough fescue (*Festuca hallii*), as well as forbs (eg. Canada anemone – *Anemone canadensis*, veiny meadow-rue – *Thalictrum venulosum*, northern bedstraw – *Galium boreale*), and shrub (eg. western snowberry - *Symphoricarpos occidentalis*) (Figure 5).

Table 4. Mean specific leaf area (SLA), leaf density, and leaf C:N across the historic grazing intensities in northern fescue grasslands of Riding Mountain National Park, Manitoba, Canada in each of 1973, 2010, and 2020 (A). Two-way Analysis of variance (ANOVA) results are shown for within each sample year (A) and across all years (B).

A	Group A - Light		Group B - Moderate		Group C - Heavy		AVOVA grazing intensity		
	mean	std.dev.	mean	std.dev	mean	std.dev	F value	D.F.	p-value
	1973								
SLA (mm ² /mg)	24.72	4.90	29.32	7.78	29.57	13.55	0.68	2,30	0.513
Leaf Density (mg/mm ³)	0.39	0.07	0.39	0.10	0.35	0.20	1.12	2,30	0.339
Leaf C:N	36.56	6.37	35.30	9.18	30.47	17.04	1.97	2,30	0.158
	2010								
SLA (mm ² /mg)	34.06	4.91	33.44	5.20	33.34	6.65	0.09	2,30	0.917
Leaf Density (mg/mm ³)	0.54	0.06	0.44	0.08	0.43	0.15	4.23	2,30	0.024
Leaf C:N	47.53	5.12	39.14	7.16	36.09	10.39	5.91	2,30	0.007
	2020								
SLA (mm ² /mg)	42.79	7.15	43.62	10.46	42.70	9.79	0.02	2,30	0.985
Density (mg/mm ³)	0.60	0.12	0.56	0.14	0.57	0.17	0.39	2,30	0.683
Leaf C:N	54.18	11.00	49.23	11.81	46.54	12.29	1.10	2,30	0.345

B	AVOVA grazing intensity			ANOVA year			AVOVA grazing intensity*year		
	F value	D.F.	p-value	F value	D.F.	p-value	F value	D.F.	p-value
SLA (mm ² /mg)	0.328	2,90	0.721	30.00	2,90	<0.001	0.464	4,90	0.762
Leaf Density (mg/mm ³)	3.25	2,90	0.043	19.73	2,90	<0.001	0.706	4,90	0.590
Leaf C:N	6.32	2,90	0.003	17.46	2,90	<0.001	0.519	4,90	0.722

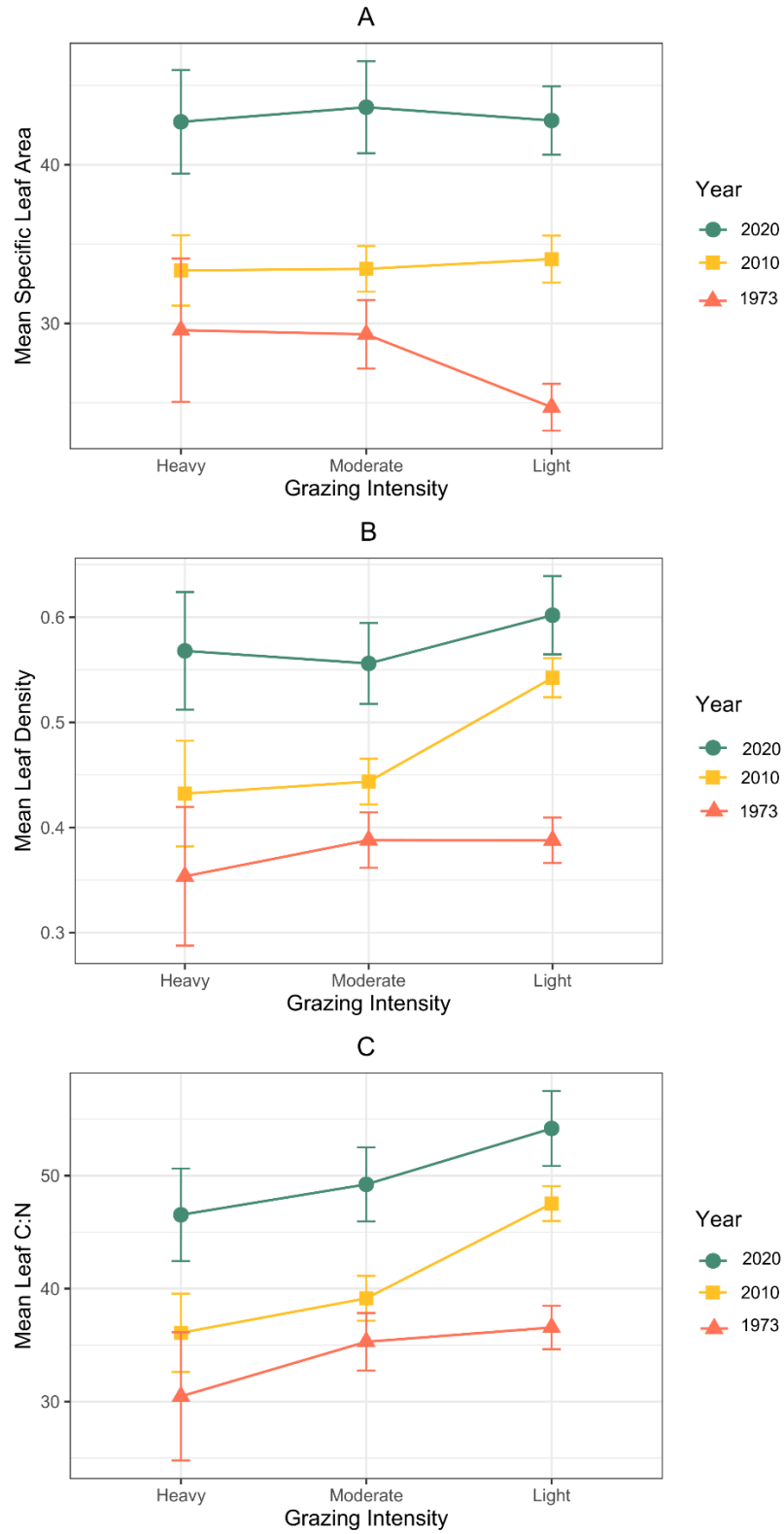


Figure 3. Interaction plots of the community weighted mean specific leaf area (A), leaf density (B), and leaf C:N (C) in each historic grazing class in Riding Mountain National Park, Manitoba, Canada northern fescue grasslands for 1973, 2010, and 2020.

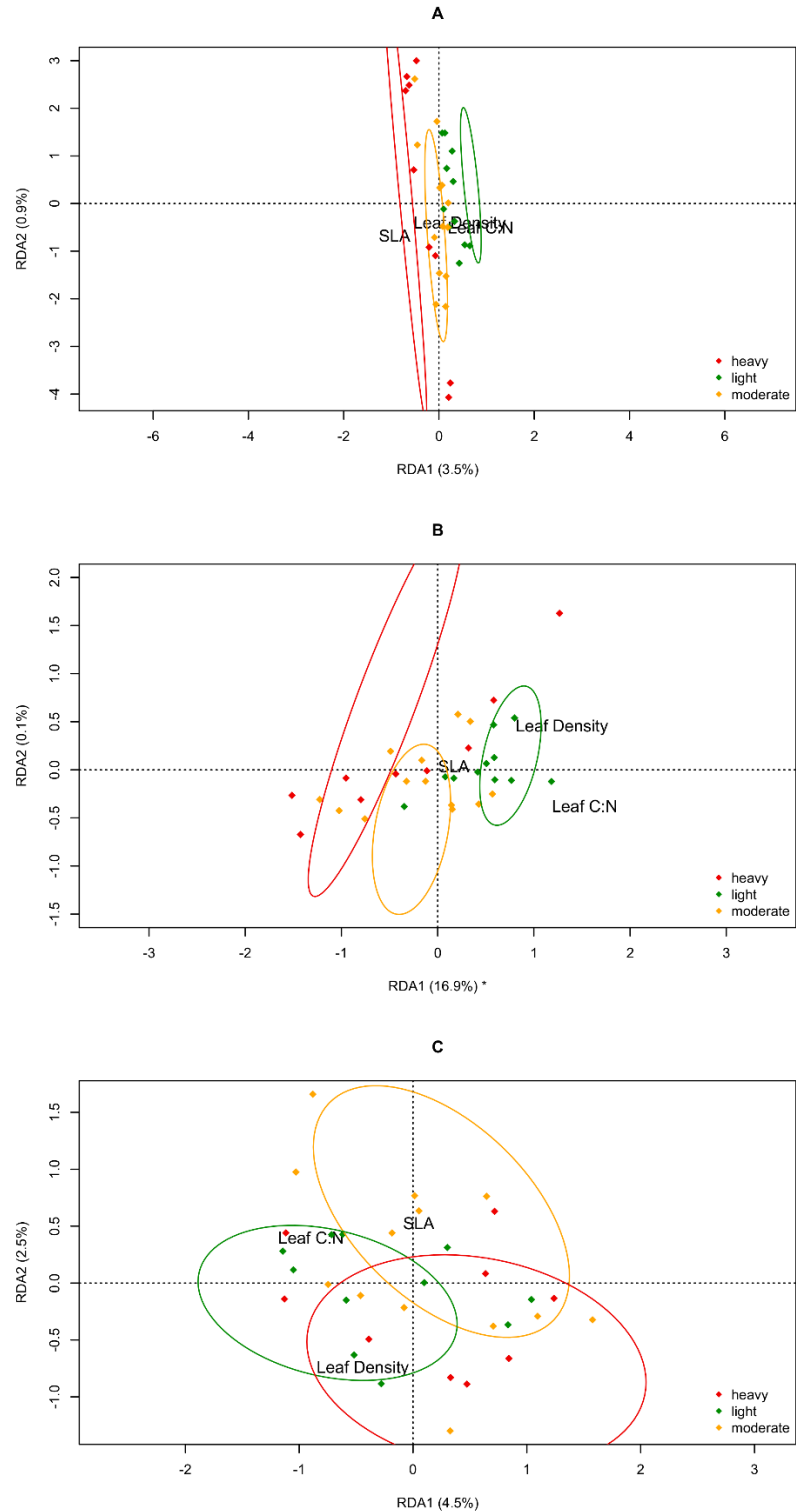


Figure 4. Redundancy analysis of sampling sites, community weighted mean leaf traits, and historic grazing treatments for 1973 (A), 2010 (B), and 2020 (C) in northern fescue grasslands in Riding Mountain National Park, Manitoba, Canada. See Table 3 for full details of traits. Ellipses represent 95% confidence standard error for each grazing group.

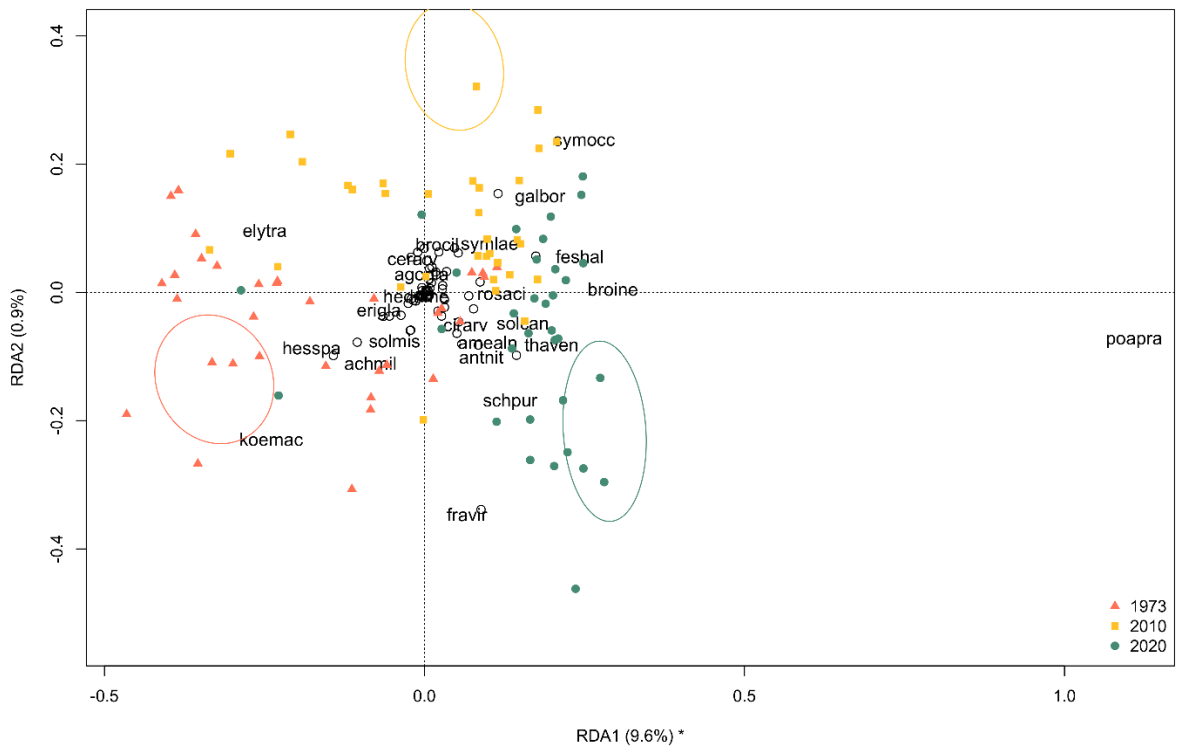


Figure 5. Redundancy analysis of sample sites, vegetation community composition and survey year for northern fescue grasslands in Riding Mountain National Park, Manitoba, Canada sampled in 1973, 2010 and 2020. Abbreviations represent the first three letters of species binomials. See table 1 for dominant species names. Ellipses represent 95% confidence standard error for each grazing group.

Discussion

Impacts of Grazing on Fescue Prairie Plant Communities

My results suggest that legacies of livestock grazing continue to alter the structure, diversity, and composition of northern fescue prairie communities, even 50 years after the removal of grazing. The proportion of shrubs increased in historically heavily grazed grasslands over the sample years. This effect could be explained by cattle preferentially grazing grasses and forbs but avoiding shrubs (Anderson et al. 2010), resulting in an increase in shrub abundance with grazing. After the removal of grazing, it is possible that shrub abundance continued to increase due to the lack of disturbance to limit the proliferation of shrubs. The significant decline in alpha diversity in historically heavily grazed grasslands has persisted for 50 years since the removal of grazing. Grasslands with a history of heavy grazing were dominated by exotic invaders in all years of the experiment. However, the composition of exotic species has transitioned from an association of ephemeral exotic species including *Taraxacum officinale* in 1973 to perennial, clonal invaders like *Poa pratensis* and *Bromus inermis* in 2010 (Sinkins and Otfinowski 2012). By 2020, all but one grassland in RMNP were invaded by *Poa pratensis*. This exotic species significantly invaded heavily and moderately grazed grasslands first (Trottier 1983), allowing these sites to act as foci for the proliferation of the species into other grasslands by 2020. The pattern of exotic species establishing in disturbed areas and dispersing into unaffected areas has been observed in other natural ecosystems (Duncan et al. 1997; Moody et al. 1988; DeKeyser et al. 2015). As a result, the invasion of *Poa pratensis* into lightly grazed grasslands was likely independent of historic livestock management. Gifford and Otfinowski (2013) noted the ability of exotic species *Poa pratensis* and *Bromus inermis* to spread by anthropogenic vectors, such as roads and trails, after initial introduction.

After 50 years of recovery, grasslands that were historically lightly grazed had significantly less spatial heterogeneity than moderately and heavily grazed grasslands. As a result, vegetation community composition became increasingly similar between historically lightly grazed grasslands. In 2020, lightly grazed grasslands were dominated by native graminoids *Festuca hallii* and *Achnatherum richardsonii*, and occasionally *Poa pratensis*. Grassland ecosystems require disturbance to maintain spatial heterogeneity (Fuhlendorf et al. 2008). Without significant natural disturbance cycles and little impact of livestock grazing, grasslands with a history of light grazing lacked the disturbance necessary to maintain beta diversity. In moderately and heavily grazed grasslands, beta diversity remained consistent from 1973 to 2020, and did not differ between the two grazing classes. Many rangeland studies have generally concluded that spatial heterogeneity decreases with grazing intensity, however, these studies were often conducted in paddocks, where grazing is more uniform and concentrated than in natural grasslands (Barnes et al. 2008; Onatibia and Aguilar 2018). However, Adler et al. (2001)

and Marion and Bouzille (2010) found that managing grazing to be patchy increased the spatial heterogeneity in vegetation communities, which better reflects the historic grazing conditions in this study.

Impacts of Grazing on Fescue Prairie Trait Composition

I predicted that conservative plant traits would converge in grazed grasslands. However, plant trait composition was only predicted by historic grazing 40 years after grazing was removed. I also expected that long-term grazing would result in communities dominated by grazing tolerant plants, characterized by conservative traits, such as high leaf density, high leaf C:N and low SLA that help plants to resist grazing (Coughenour 1985). However, I observed a convergence of conservative traits in lightly grazed grasslands and a convergence of acquisitive leaf traits in intensely grazed grasslands only in 2010.

The competitive sorting model predicts that changes to disturbance in a grassland can cause the distribution of plants with different life strategies to undergo a transition phase where the ecological sorting process is not stabilized (Gitay and Wilson, 1995). This transition period may result in a mix of acquisitive and conservative plant strategies. Four years after grazing was removed from RMNP, the community trait composition was not associated with the legacies of historic grazing. Although plant community composition was distinct between grazing classes, the strategies of those communities, and therefore plant traits, were not distinct. The removal of grazing pressure provided an opportunity for ruderal species and competitors that would have previously been checked by grazing to flourish in sparsely vegetated areas. This effect caused a mix of plant species with conflicting strategies, and therefore leaf traits, to occupy vegetation communities, regardless of the grazing history. This pattern of variable plant trait assemblages is common in grassland early succession after disturbance (Spasojevic et al. 2010).

In 2010, 40 years after the removal of grazing, conservative plant traits converged in grasslands with legacies of light grazing and acquisitive plant traits converged in grasslands with legacies of intense grazing. According to the competitive sorting hypothesis, the ecological sorting process eventually stabilizes, and plant strategy reflects the legacy of disturbance (Gitay and Wilson, 1995). In this system, the ecological sorting process stabilized after 40 years, and community trait composition reflected the historic disturbance. The convergence of conservative leaf traits in lightly grazed grasslands can be attributed to their dominance by native grass species, particularly *Festuca hallii*. In contrast, grasslands with a history of intense grazing saw a convergence of acquisitive leaf traits, characteristic of species of *Carex* spp., *Bromus inermis*, *Galium boreale*, and *Calamagrostis canadensis*. Grazed grasslands are likely to have greater soil nitrogen due to manure impacts from livestock (Guo et al. 2017), selecting for acquisitive traits

(Onoda et al. 2017), which may offer a possible explanation for the observed convergence of acquisitive traits.

Fifty years after the removal of grazing from RMNP, there was no legacy of grazing remaining on plant trait composition. Over time, ecological or environmental factors likely caused the distribution of plant species to shift and no longer be associated with a legacy of the historic disturbance, (Gitay and Wilson 1995). For example, with time, the encroachment of exotic graminoids and shrubs had a greater impact on grassland trait composition than historic grazing disturbance. By 2020, grasslands in RMNP were dominated by either *Poa pratensis* where historic grazing was heavy or moderate, or *Festuca hallii* and *Poa pratensis* associations where historic grazing was light.

The similarity in leaf traits between *Poa pratensis*, abundant in historically heavy and moderately grazed grasslands, and *Festuca hallii*, characteristic of grasslands with histories of less intense grazing, raised questions about the provenance of the *Poa pratensis* found in these native fescue grasslands. Both *Poa pratensis* and *Festuca hallii* shared high leaf density and leaf C:N, and low SLA. Palit et al. (2021) also noted the similarities in plant morphological traits between *Poa pratensis* and native grass species. According to Murovec et al. (2009), genetic variability in natural populations of *Poa pratensis*, may be reflected in morphological characters and adaptations. Some of these variants are closer in structure and strategy to native graminoid species (Murovec et al. 2009), making them better adapted to the stress and disturbance in Canadian grasslands than more exotic varieties. This functional similarity between *Poa pratensis* and *Festuca hallii* could explain the ability of *Poa pratensis* to invade and take over fescue grasslands in the northern great plains. *Poa pratensis* has invaded most fescue and mixed grass prairies across the northern Great Plains (Perkins et al. 2019; Palit and DeKeyser 2021; DeKeyser et al. 2015; Toledo et al. 2014), making it one of the primary management concerns across the ecosystem (Perkins et al. 2019). More importantly, my results suggest that, based on leaf traits, grasslands dominated by *Festuca hallii* and *Poa pratensis* may have functional similarities. This finding raises important questions about the effect of exotic species on natural ecosystems and points to other traits, including those describing roots, that need to be quantified in order to fully contrast traits describing native and exotic plants. Furthermore, the observed functional similarity between the leaf traits of *Poa pratensis*, an exotic plant, and *Festuca hallii*, a native graminoid, highlights the importance of trait-based measurements in the study of grassland restoration. The species abundance-based trait modelling used in this study to determine differences in community leaf traits could not detect a difference between historic grazing classes because they were all dominated by graminoids with conservative plant traits. Considering a broader suite of plant traits may help to distinguish the ecological differences between these species.

Between 1973 and 2020, the community weighted mean values of SLA, leaf density and leaf C:N increased in the northern fescue grasslands of RMNP, regardless of historic grazing disturbance. This results suggests that a suite of plants with conservative leaf traits (high leaf density, high leaf C:N low SLA) increased in abundance in some prairies while simultaneously, a suite of plants with acquisitive leaf traits (high SLA, low leaf density, low leaf C:N) increased in other grasslands. The increase in SLA from 1973 to 2020 suggests that a suite of species with acquisitive leaf traits increased in abundance in a subset of the surveyed grasslands. Based on our results quantifying the distribution of species abundance across survey years, the increase in SLA can likely be attributed to the increased abundance of *Galium boreale* and *Bromus inermis* over the course of the experiment. Exotic species, *Bromus inermis*, is invading grasslands across the northern Great Plains (Fink and Wilson 2011), however, changes in community mean SLA over time have been variable (Bauer and Albrecht 2020; Ridding et al. 2020; Luo et al. 2019; Griffin-Nolan et al. 2019), as it is easily affected by local conditions, particularly drought (Luo et al. 2019). The increase in leaf density and leaf C:N between 1973 and 2020 can be attributed to the invasion of *Poa pratensis*. *Poa pratensis* has significantly invaded grasslands across the northern Great Plains (Perkins et al. 2019; Palit and DeKeyser 2021; DeKeyser et al. 2015), and an increase in conservative leaf traits associated with Kentucky bluegrass has been observed (DeKeyser et al. 2015). In this study, *Poa pratensis* invasion was reflected in an increase in conservative leaf traits in grasslands where the abundance of *Poa pratensis* increased.

Drought Tolerance and Ecosystem Function

Drought Tolerance

Grasslands dominated by grazing tolerant, conservative, leaf traits were predicted to be more drought tolerant than grasslands dominated by acquisitive leaf traits (Wright et al. 2005; Vitra et al. 2019; Quiroga et al. 2010). Resource conservative leaf traits, including low SLA and high leaf density limit water lost through leaves, resulting in greater drought tolerance (Wright et al. 2005; Vitra et al. 2019) (Figure 6). Forty years after grazing, conservative leaf traits converged in lightly grazed grasslands, while acquisitive leaf traits converged in intensely grazed grasslands. As a result, 40 years after grazing historically intensely grazed grasslands were less drought tolerant than lightly grazed grasslands. These results contrast with Quiroga et al. (2010), who concluded that grasslands with a history of high grazing pressure select for drought-resistance. However, Souther et al. (2020) found that grassland communities dominated by native grass species with high species richness and low abundances of exotic species were the most resilient to the ecological impacts of drought. Managing grasslands to be lightly disturbed by grazing may promote the proliferation of native grass species with drought resilient leaf traits, resulting in higher drought tolerance.

Community mean SLA was increasing in a subset of grasslands that were dominated by *Bromus inermis* and *Galium boreale* (Figure 6). Plants with a high specific leaf area have a decreased ability to tolerate drought stress. Acquisitive leaves depend on large light-intercepting surfaces, which are less efficient at retaining moisture in times of drought (Onoda et al. 2017). Based on the leaf traits in this study, grasslands dominated by exotic *Bromus inermis* may be particularly vulnerable to drought. This result may suggest that the susceptibility of *Bromus inermis* to drought may aid passive restoration of some invaded grasslands against the invader. However, the deeply penetrating root system and rhizomatous nature of *Bromus inermis* may also affect its drought tolerance (Wang et al. 2020).

In contrast, I also found that leaf density and leaf C:N had increased from 1973 to 2020 as a result of *Poa pratensis* invasion (Figure 6). *Poa pratensis* is characterized by conservative leaf traits that can conserve moisture in the leaf during drought (Wright et al. 2005; Vitra et al. 2019) Based on these leaf traits, grasslands where *Poa pratensis* is dominant are likely to be more drought tolerant. As drought becomes more frequent and intense (IPCC 2014; Hufkens et al. 2016), it will cause acquisitive, drought intolerant species to become less common in a vegetation community and be replaced by drought tolerant species, like *Poa pratensis*. There is evidence indicating that *Poa pratensis* can persist under drought conditions (Chai et al. 2010), however, the long-term response of *Poa pratensis* abundance to drought stress in northern Great Plains grasslands is unknown. Kirwan et al. (2021) observed that *Poa pratensis* produced similar biomass in drought conditions than non-drought conditions.

Ecosystem Function

The breakdown of plant leaves by microorganisms influences the cycling of carbon and nitrogen in grassland ecosystems, as well as organic carbon accumulation in plant litter and in soil (von Lützo et al. 2006; Cotrufo et al. 2013). The nitrogen and carbon content of leaves, dictated by plant traits, defines their contribution towards the rates of carbon and nitrogen cycling. Forty years after the removal of grazing disturbance, leaf C:N was significantly higher in lightly grazed grasslands than intensely grazed grasslands, reflecting the accumulation of conservative leaf traits in these grasslands. Leaves with greater density and higher C:N decompose slowly, tying up nitrogen in their leaf litter and in soil (Cornwell et al. 2008), resulting in reduced nitrogen availability to plants (Figure 6). Ultimately, prairies with a high representation of conservative leaf traits, including leaf C:N, produce the carbon-rich organic soils representative of grassland ecosystems (Lamarque et al. 2014). In an empirical study, McSherry et al. (2013) concluded that soil carbon content increased with grazing disturbance in C4 dominated and C4/C3 mixed grasslands, but decreased in C3 dominated grasslands, indicating that the effect of leaf traits on soil organic carbon stores is dependent on the species composition and differences in leaf structure among functional plant groups.

In contrast to the lightly grazed grasslands, historically intensely grazed grasslands were characterized by acquisitive leaf traits 40 years after the removal of grazing, including low community weighted leaf C:N values. Acquisitive leaves are characterized by high leaf nitrogen contents, as the acquisitive strategy depends on high investments of nitrogen for large leaves with a high photosynthetic rate (Onoda et al. 2017). The increased nitrogen content in these leaves is also attractive to herbivores and species with an acquisitive strategy may be susceptible to grazing (Fuhlendorf et al. 2008). However, in contrast to conservative traits, an increase in acquisitive leaf traits in grasslands may result in greater organic nitrogen in soil (Onoda et al. 2017). As a result, rapid leaf decomposition in grasslands with a convergence of low C:N leaves likely resulted in soils rich in organic nitrogen but reduced carbon storage (Onoda et al. 2017; von Lutzow et al. 2006) (Figure 6). These results contrast with the empirical results of Wang et al. (2014), where grazed grasslands increased the carbon storage in the top 15cm of soil, however it was noted that this effect can be highly dependent on livestock management.

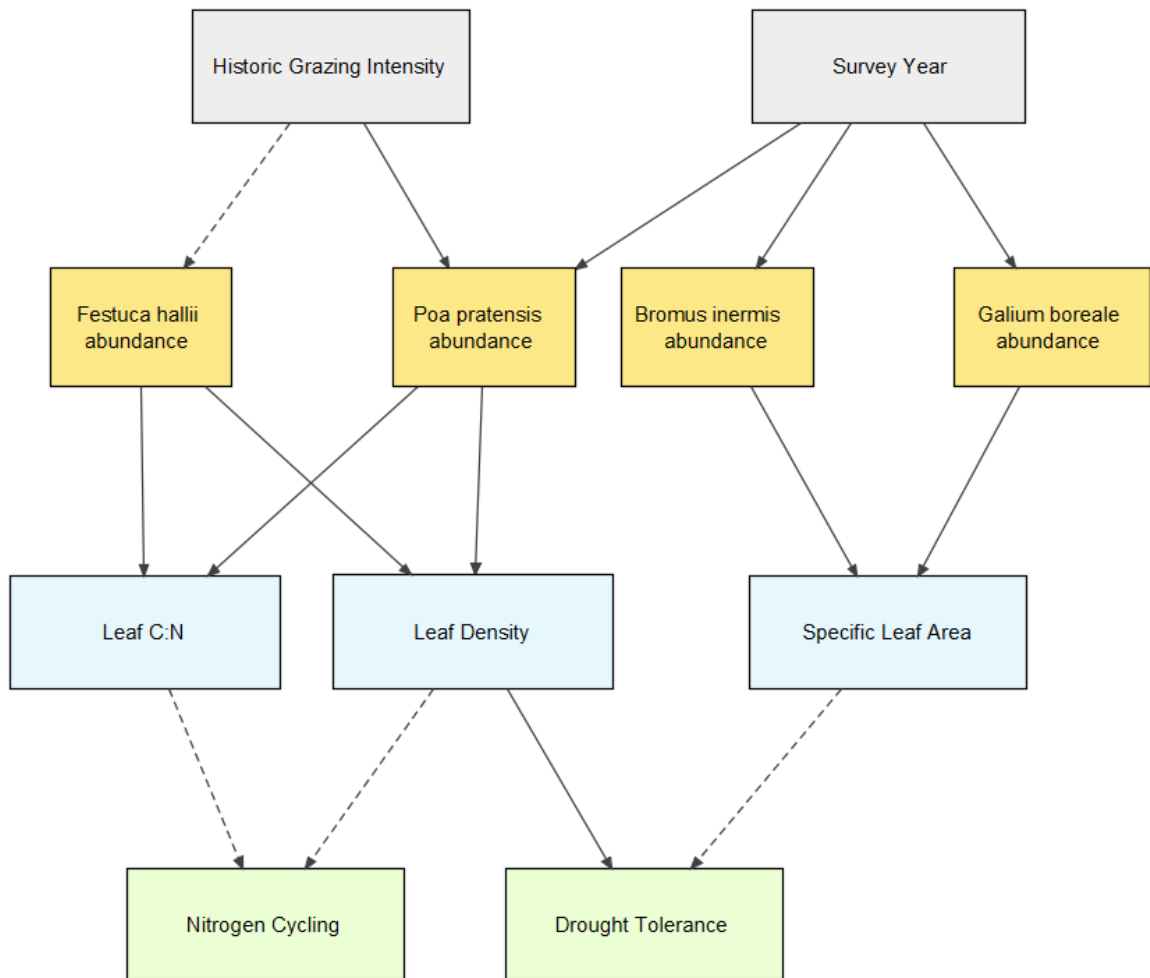


Figure 6. Theoretical model outlining the interactions between grazing disturbance, species composition, plant traits and community function from historically grazed northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. Solid arrows represent positive interaction and dotted arrows represent negative interactions.

Significance and Applications

Fifty years after the removal of livestock grazing from RMNP, its influence continued to be reflected in the structure, diversity, and composition of northern fescue prairie communities. Historic grazing decreased the alpha diversity of heavily grazed grasslands. However, in the absence of grazing, grasslands with legacies of light grazing declined in beta diversity. Heavily grazed grasslands continued to be dominated by exotic grasses, particularly *Poa pratensis*, which became dominant in nearly all grasslands in RMNP. Lightly grazed grasslands remained dominated by *Festuca hallii*, but there were no signs of *Festuca hallii* recovery in heavily grazed grasslands.

Although the legacies of grazing were strongly reflected in species composition, that effect was not consistent with community plant trait composition. Plant trait composition was only predicted by historic grazing in 2010, when conservative traits converged in lightly grazed grasslands and acquisitive traits converged in heavily grazed grasslands. By 50 years after the removal of grazing, the dominance of conservative graminoids, *Poa pratensis* in heavily and moderately grazed grasslands and *Festuca hallii* in lightly grazed grasslands, prevented our model from distinguishing leaf traits between historic grazing classes. Dominance by *Poa pratensis* and *Festuca hallii* caused grasslands with variable grazing intensities to become functionally similar based on SLA, leaf density and leaf C:N. Further research encompassing a broader range of traits for these species may help distinguish functional differences.

Overall, community weighted mean values for all plant traits increased in the northern fescue grasslands on RMNP from 1973 to 2020. Suites of species with opposite traits simultaneously increased in different grassland remnants, with conservative traits attributed to *Poa pratensis* invasion and acquisitive traits attributed to the increase in abundance of *Bromus inermis* and *Galium boreale*.

Grasslands dominated by conservative leaf traits have a greater drought tolerance than grasslands dominated by acquisitive leaf traits, suggesting that northern fescue prairies are the most drought resistant at intermediate time periods after light disturbance. Furthermore, grasslands dominated by species with drought susceptible leaf traits, such as *Bromus inermis*, may be the least resilient to the changing climate and may require specific management attention. Souther et al. (2020) found that heavy grazing in grasslands decreased their tolerance to drought and increased their invadability by exotic species. Heavy grazing selected for disturbance-adapted species, hastening the spread of exotic and weedy species (Souther et al. 2020). Therefore, resource managers should use caution when considering introducing grazing into grasslands dominated by *Poa pratensis* because concentrated grazing is likely to cause a competitive release allowing the species the further proliferate and herbivores are likely to carry seeds into unaffected

areas (Dornbusch et al. 2020). Generally, restoring grasslands to associations of native grass species with drought tolerant traits will improve their climate resilience.

Conservative leaf trait dominance in grasslands is likely to result in reduced nitrogen availability to plants, as nitrogen is tied up in high carbon content leaf litter, however, the fate of carbon rich leaves in the form of soil organic carbon is highly dependent on livestock management. Grasslands dominated by acquisitive leaf traits will be rich in nitrogen, as photosynthetically active, nitrogen-rich leaves rapidly decompose. High representation of acquisitive leaves in a grassland can be attractive to herbivores, causing these areas to be at risk of overgrazing if grazing intensity is not closely managed.

The use of plant leaf traits allowed me to consider the functional consequences of historic grazing legacies. The results of this study suggest that the management of historically grazed grasslands should not only focus on the diversity and species composition of grassland remnants, but also be tailored to the specific functional challenges of each grassland. Generally, grasslands dominated by native grass species have the highest resilience to the changing climate. These results extend the current knowledge of the long-term legacy of historic grazing disturbance on vegetation community trait composition, and illustrate the recovery of northern fescue grasslands, 50 years after the removal of grazing.

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GENERAL DISCUSSION AND CONCLUSIONS

Management Applications

Much of the historic extent of northern fescue grasslands were found in the black soil zone of the northern great plains and Aspen Parkland (Moss and Campbell 1947; Coupland 1961). In Western Canada, grassland areas, including fescue prairies, were the first to be converted to cropland following settlement. As a result, the most significant remnants of northern fescue grassland ecosystems exist where they were protected from widespread conversion to cropland and severe grazing pressure (Trottier 1986). However, in the Riding Mountain Forest Reserve, and later Riding Mountain National Park (RMNP), seasonal grazing and haying permits were granted to local ranchers until 1969 (Trottier 1986).

Northern fescue grasslands in RMNP have been primarily managed with passive restoration, however, prescribed fire and bison grazing are used to maintain grassland ecosystems. Parks Canada has completed 17 prescribed burns in the grasslands included in this study since the establishment of the park in 1933 (Parks Canada [unpublished data]). On average, these prairies have been burned two times each, with the most recent burn occurring in the western grasslands in 2016, including 14 survey sites (Parks Canada [unpublished data]). Other notable recent burns include the Lake Audy area in 2005, including five survey sites and the Kinnis meadows burn in 2010 including two study sites (Parks Canada [unpublished data]). Parks Canada also maintains a bison display herd of approximately 40 animals in a 493-hectare enclosure in a rough fescue grassland area near Lake Audy (Parks Canada [unpublished data]). No survey sites in this study were located inside the bison enclosure.

Parks Canada (2007) has identified the loss of biodiversity due to changes to the natural disturbance regime and forest encroachment in northern fescue grasslands as management concerns in RMNP. The results of this study apply directly to the management of fescue grasslands in RMNP but can also be applied to grazed grassland ecosystems across the northern great plains. Current assessment of grassland health and the efficacy of management is typically based on measures of species diversity and grassland structure and composition (Wilsey et al. 2005). In this study, I proposed approaching grassland management and monitoring through ecosystem function and resilience using leaf traits, in addition to community composition and diversity indices. Plant leaf traits were measured for the 30 top species identified in the northern fescue grasslands from 1973 to 2020 (Appendix C). Leaf trait data will be submitted to a global database (Kattge et al. 2011) so resource managers can use the plant trait values measured in this study in combination with community composition data to draw conclusions about community function and drought tolerance.

Fifty years after grazing, legacies of intense grazing continued to reduce alpha diversity and drive the species composition of grasslands. However, legacies of grazing had no effect on leaf trait composition. Instead, invasive grass species dictated leaf trait composition. By 2020, moderately and heavily grazed grasslands were dominated by *Poa pratensis* and *Bromus inermis*, and *Festuca hallii* dominated lightly grazed grasslands. *Poa pratensis* and *Festuca hallii* have similar, conservative, leaf traits. Because of this similarity in leaf traits, grasslands dominated by *Poa pratensis* and *Festuca hallii* are functionally similar and create a functional redundancy, despite having distinct species compositions. Palit et al. (2021) also noted the similarities in plant morphological traits between *Poa pratensis* and native grass species.

Generally, grasslands dominated by conservative leaf traits are more drought tolerant than grasslands dominated by acquisitive leaf traits (Wright et al. 2004; Vitra et al. 2019; Quiroga et al. 2010). I predicted that I would see a convergence of conservative, drought tolerant, leaf traits in heavily grazed grasslands, as grazing disturbance increased the representation of conservative, grazing tolerant leaf traits. However, plant community traits were driven by exotic species instead of historic grazing intensity, making drought tolerance a function of exotic species over grazing history. Souther et al. (2020) found that grassland communities dominated by native grass species with high species richness and low abundances of exotic species were the most resilient to the ecological impacts of drought. Alternatively, they found that dominance by exotic and weedy species reduced drought resilience (Souther et al. 2020).

Poa pratensis has invaded most fescue and mixed grass prairies across the northern great plains (Perkins et al. 2019; Palit et al. 2021; DeKeyser et al. 2015; Toledo et al. 2014), making it one of the primary management concerns across the ecosystem (Perkins et al. 2019). Based on my results, *Poa pratensis* has conservative leaf traits, allowing it to persist through drought while species with acquisitive leaf traits will likely become less common (Chai et al. 2010). *Poa pratensis* may become more abundant in grasslands as it takes the space of other less drought tolerant species. However, with the observed functional redundancy between *Poa pratensis* and *Festuca hallii* dominated grasslands, *Poa pratensis* grasslands are likely to provide some ecosystem functions that *Festuca hallii* and other native grass species would provide. This concept is consistent with the shift in conservation ethic that has been observed recently, where ecological research and measures of grassland health are transitioning away from comparisons of species composition with historic baselines, towards measures of ecosystem functions and services (Craine et al. 2011; Hoover et al. 2014; Li et al. 2018). With climate change, species compositions are going to shift (Yang et al. 2011; Stanik et al. 2021; Batbaatar et al. 2022). In response, conservation and restoration of grassland ecosystems is also shifting to a community function focus, regardless of the species composition, acknowledging that even grasslands invaded by exotic species may be providing

important ecosystem functions. For example, in an empirical study assessing the function of urban grasslands, van der Walt et al. (2015), found that despite reduced plant species diversity, the function of urban grasslands made them worthy of conservation. As a result, conservation resources may be better used to maintain the ecological value of uninvaded grasslands by preventing new introductions of exotic species than restoring grasslands from *Poa pratensis* dominance.

However, my research suggests that leaf traits of invasive species will affect the function of grassland communities, including their response to drought. For example, grasslands dominated by the exotic grass, *Bromus inermis*, will likely respond the most dramatically to increased drought. *Bromus inermis* invasions are a primary management concern in RMNP and across grassland ecosystems in the northern Great Plains (Otfinowski et al. 2007; Fink and Wilson 2011). High abundances of *Bromus inermis* in a grassland increases the representation of drought susceptible leaf traits. Species with acquisitive traits, like *Bromus inermis*, are poorly adapted to tolerate drought, and therefore, are likely to become less abundant in grasslands with the introduction of drought stress. Increasing frequency and intensity of drought stress in the northern great plains and aspen parkland regions may aid in the long-term passive restoration of grasslands invaded by smooth brome. However, without looking at plant root traits, this study does not give an entire picture of drought tolerance in grassland ecosystems. *Bromus inermis* has deeply penetrating roots and forms and readily proliferates through underground rhizomes (Wang et al. 2020; Otfinowski and Kenkel 2008), which may make the species more drought tolerant than it appears based on my data (Wang et al. 2020).

The breakdown of plant leaves by microorganisms influences the cycling of carbon and nitrogen in grassland ecosystems, as well as carbon accumulation in soils (von Lutzow et al. 2006; Cotrufo et al. 2013). In general, species with an acquisitive strategy contain more leaf nitrogen, resulting in a lower leaf C:N value than species with a conservative strategy (Lamarque et al. 2014; Onoda et al. 2017). Acquisitive leaves have a high investment of nitrogen for quick photosynthetic returns without investing in highly structural leaves (Onoda et al. 2017). Conservative leaves have a lower investment of nitrogen for slower photosynthetic gains but have a higher investment in long-lived leaves (von Lutzow et al. 2006).

Grasslands with a high representation of conservative leaf traits, including *Poa pratensis* dominance, will have leaf litter that decomposes slowly, as the high carbon content leaves are resistant to degradation (von Lutzow et al. 2006). The slow decomposition in these grasslands can increase the accumulation of leaf litter (Cornwell et al. 2008), which may cause fires in the area to spread rapidly and burn intensely (Fidelis et al. 2010), damaging shallow-rooting plants (Snyman 2005). Additionally, leaves that are slow to decompose tie up nitrogen in their leaf litter (Cornwell et al. 2008), decreasing the availability of nitrogen in soils (Lamarque et al. 2014). Letts et al. (2015) found that an

accumulation of leaf litter will select against plants with acquisitive strategies that have a high nitrogen requirement from establishing. Eventually, these high-carbon leaves decompose and contribute to high carbon storage in these grasslands.

In contrast, grassland communities dominated acquisitive species, including *Bromus inermis*, have a high representation of acquisitive leaf traits. A dominance of nitrogen-rich leaves in a grassland is attractive to herbivores and may be susceptible to overgrazing if not closely managed (Fuhlendorf et al. 2008). Kobiela et al. 2017 found that the abundance of *Bromus inermis* increased in grazed sites. *Bromus inermis* is an aggressive invader and will tend to increase in abundance by rhizomatous growth when a competitive release is provided by grazing, despite a reduction in aboveground biomass (Kobiela et al. 2017). Nitrogen-rich leaf litter decomposes rapidly and increases nitrogen availability in soils (Onoda et al. 2017; von Lutzow et al. 2006). Piper et al. (2015) found that *Bromus inermis* invasion did not change inorganic nitrogen content of grassland soils, but nitrogen mineralization rates and total soil nitrogen were higher in invaded soils.

Based on my results, intensive grazing is detrimental to the health of northern fescue grasslands. Low to moderate intensity grazing is more in line with the pre-settlement natural processes of these grasslands (Trottier 1986). Low to moderate livestock grazing during the early spring months has been successful to enhance native species diversity (Towne and Kemp 2008). My results suggest that a reintroduction of low-intensity grazing may enhance the beta diversity of northern fescue grasslands, while maintaining alpha species diversity. Grazing may help to reduce litter accumulation in grasslands (Chuan et al. 2018), allowing a more diverse understory to emerge (Letts et al. 2015; Zou et al. 2016). Resource managers should exercise caution and monitor grazing intensity when reintroducing grazing into areas invaded by exotic species, including *Poa pratensis*, as the presence of large herbivores may cause further proliferation of the species into uninvaded areas (Dornbusch et al. 2020). Hendrickson et al. (2020) and Dornbusch et al. (2020) noted the ability of *Poa pratensis* to replace native species and become a near monoculture in overgrazed grasslands.

Cattle have successfully been used as a proxy for bison in grassland ecosystems to maintain disturbance (McIntyre et al. 2003; Pykala 2004; Hayes and Holl 2003), however, in Canadian national parks, a reintroduction of bison may enhance the ecological and cultural value of grasslands. Bison and cattle are not ecological synonyms (Kohl et al. 2013). Cattle tend to spend time in wet areas, while bison tend to spend time in open grasslands (Kohl et al. 2013). If large herbivores are being used as grassland management and restoration tools, cattle likely need to be corralled in varying grassland sections to ensure they graze grassland areas relatively evenly (Veblen and Porensky 2019), while the behaviour of bison keeps them on the grassland (Kohl et al. 2013), requiring little management.

Ultimately, a restoration of the pre-settlement disturbance regime will provide grasslands with the best resilience to the changing climate. Pre-settlement disturbance involved a combination of grazing by large herbivores and fire. A grazing and fire model in a North American tallgrass prairie created variable patterns of heterogeneity which caused plant species with multiple strategies to coexist (Fuhlendorf et al. 2009). Communities that are variably disturbed by grazing and fire will have a more even representation of different plant strategies than uniformly disturbed communities, reflecting the evolutionary disturbance pattern of grassland ecosystems. Variable plant strategies coexisting in one prairie will equate to a more even representation of plant traits along the leaf economics spectrum, while uniformly disturbed communities will have a representation of a particular set of plant traits that represents that disturbance (Suding et al. 2008). Recent research has considered the theory that grasslands with a high diversity of plant traits have a high functional diversity (Hughes 2014; Craven et al. 2016). A significant argument exists for variable representation of response traits resulting in grasslands that are more resilient to variable biological and environmental stressors in the face of a changing climate (Craven et al. 2016; Chillo et al. 2011; Mori et al. 2013).

According to Fuhlendorf et al (2009), restoring the natural disturbance regime using a combination of light to moderate grazing and prescribed fire may more effectively restore grasslands to native species communities and control shrub encroachment than grazing alone. A combination of early spring burning and spring and fall grazing has been successful to reduce the cover of exotic species (Bahm et al. 2011), increase spatial heterogeneity of grasslands (Fuhlendorf et al. 2009), and enhance the proliferation of native species (Towne and Kemp 2008). Repeated burning has been successful to significantly reduce *Poa pratensis* cover and provide a competitive release for native grasses to proliferate (Bahm et al. 2011; Towne and Kemp 2008). Promoting drought tolerance in the fescue grasslands by increasing the cover of native species will result in more resilient grasslands to the effects of the changing climate.

Future Research

Most of the function of grassland ecosystems depends on processes below the soil surface (Gould et al. 2016). The roots of grassland species have a large part in dictating a species' response to drought (Lozano et al. 2020). The representation of root traits and belowground plant anatomy are important factors when considering the function of grassland ecosystems and their restoration (Otfinowski and Coffey 2020). To get a more complete picture of grassland function following disturbance, analysis of root traits and soil community should be included for the historically grazed northern fescue grasslands. Furthermore, this study, exploring only leaf traits, suggested that prairie communities dominated by exotic *Poa pratensis* and native *Festuca hallii* have similar functions and drought tolerance. However, Murphy and Grant (2005) found that the abundance of *Poa pratensis* declined with drought conditions, suggesting that there may be other attributes

of *Poa pratensis*, not encompassed in this study, that are contributing to drought tolerance. Analysis of root traits may provide insight on the difference in function between these communities. For example, Looman 1969 has reported that the rooting depth of *Festuca hallii* exceeds one meter, but the roots of *Poa pratensis* reach only the top six to ten inches of soil (Beard 1973). A high representation of the longer root length in *Festuca hallii* is likely to result in a more drought resilient grassland, while a greater representation of shorter, *Poa pratensis*, roots is likely to result in a grassland that is susceptible to drought.

The similarity in leaf traits between *Poa pratensis* and *Festuca hallii* raised questions about the provenance of the *Poa pratensis* variation found in the fescue grasslands of RMNP. Both *Poa pratensis* and *Festuca hallii* had conservative traits with low SLA, high leaf density and high leaf C:N. According to Murovec et al. (2009), genetic variability exists in natural populations of *Poa pratensis*, which is reflected in morphological characters and adaptations. Some of these variants are closer in structure and strategy to native graminoid species (Murovec et al. 2009), making them better adapted to the stress and disturbance in Canadian grasslands. Genetic analysis could be carried out to determine the variety of *Poa pratensis* found in the rough fescue grasslands of RMNP and its genetic similarities to native grass species, particularly *Festuca hallii*. This analysis would inform best management practices to combat *Poa pratensis* invasion in RMNP. Additionally, genetic analysis of *Poa pratensis* in fescue grassland ecosystems would further knowledge on the hybridization of *Poa pratensis* and other exotic species with native species, and the impact of such varieties on vegetation community dynamics.

Trait-based ecological studies often assume that plant traits are stable across time and space. This assumption allows plant trait data to be stored in global databases (Kattge et al. 2011) and applied to ecological studies around the world (Smimova et al. 2018; Butler et al. 2017; Loranger et al. 2012). In this study, I assumed that plant traits collected in a donor grassland in RMNP were broadly applicable to all surveyed grasslands. Additionally, I applied plant traits collected in 2019-2021 to community composition data collected in 1973 and 2010. New research in the field of trait-based ecology is suggesting that the traits of plants may change when exposed to stress and disturbance (Luong and Loik 2021). A future challenge of this research will be to assess the differences in species-specific plant trait values measured at survey sites which were historically grazed at varying intensities.

Summary and Final Conclusions

The effects of the changing climate, and anticipated environmental changes, have caused grassland management strategies to evolve. With that change, strategies used to evaluate the efficacy of management actions has evolved. Recent advancements in the ecological science have turned to community function and resilience as an indicator of grassland

health. This study used historically grazed northern fescue grasslands in Riding Mountain National Park, Manitoba, as a model to demonstrate the use of community species composition and plant leaf traits to assess the long-term impact of livestock grazing on grassland structure, diversity, function, and drought tolerance.

I found that legacies of heavy grazing decreased the species diversity of grasslands in all survey years, however, by 2020, beta diversity declined in grasslands that lacked disturbance. Species composition was predicted by historic grazing intensity in every survey year, but that relationship was only reflected in community plant trait composition in 2010. My results suggested that at intermediate time periods after grazing disturbance, acquisitive, drought susceptible, leaf traits converge in intensely grazed grasslands, while conservative, drought tolerant, leaf traits converge in lightly grazed grasslands. By 2020, the effects of exotic species invasions were more prominent than the effects of historic grazing. Dominance of grasslands by either *Poa pratensis* or *Festuca hallii* resulted in functionally similar communities, based on three leaf traits. I found that community mean values of SLA, leaf density and leaf C:N increased from 1973 to 2020. The increase in trait values can be attributed to the simultaneous invasion of *Poa pratensis* and *Bromus inermis* into different prairie remnants.

Community plant traits composition has consequences on community drought tolerance and ecosystem function. Communities that see a convergence of acquisitive leaf traits, like those dominated by *Bromus inermis*, are the most susceptible to drought. However, a convergence of conservative traits, such as *Poa pratensis* dominance, results in drought tolerant communities. To further advance the knowledge of the impacts of grazing on ecosystem function and drought tolerance, studies that include plant root traits and soil community should be considered. Important root traits include acquisitive traits, specific root length and nitrogen content, and conservative traits, root density and carbon content (Sun et al. 2021). Nitrogen availability is greater in grasslands dominated by acquisitive traits than grasslands dominated by conservative traits. Finally, grasslands with a convergence of conservative traits will have a slower litter decomposition rate and greater carbon storage. Future research considering invasions by exotic grass species in the context of climate change, based on their traits, will be important to adapt management techniques to changing environmental conditions.

In the Riding Mountain National Park Management Plan (Parks Canada 2007), Parks Canada identified the loss of biodiversity due to changes to the natural disturbance regime and forest encroachment in northern fescue grasslands as management concerns. A pyric herbivory model that reflects the pre-settlement disturbance regime will increase the spatial heterogeneity of grasslands and increase resilience to future biological and environmental threats.

In the face of our changing climate, ecological research and grassland ecosystem management is adapting to value the resilience of grassland ecosystem functions to drought over purely species composition and diversity-based approaches. The results of this study are directly applicable to the management of historically grazed northern fescue grasslands in RMNP, and can be widely applied to understand the structure, function, and drought tolerance of historically grazed grasslands in the northern great plains.

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APPENDICES

Appendix A. All species identified on the long-term monitoring transects in 1973, 2010, and 2020 with species code, family association and vernacular name.

Species	Code	Family	Vernacular Name
<i>Achillea millefolium</i> Linnaeus	achmil	Asteraceae	common yarrow
<i>Achnatherum richardsonii</i> (Link) Barkworth	achric	Poaceae	Richardson's needlegrass
<i>Agastache foeniculum</i> (Pursh) Kuntze	agafoe	Lamiaceae	blue giant hyssop
<i>Agoseris glauca</i> (Pursh) Rafinesque	agogla	Asteraceae	pale agoseris
<i>Agrostis scabra</i> Willdenow	agrsca	Poaceae	rough bentgrass
<i>Allium stellatum</i> Fraser ex Ker Gawler	allste	Amaryllidaceae	autumn onion
<i>Amelanchier alnifolia</i> (Nuttall) Nuttall ex M. Roemer	amealn	Rosaceae	saskatoon
<i>Androsace septentrionalis</i> Linnaeus	andsep	Primulaceae	northern fairy-candelabra
<i>Anemonastrum canadense</i> (Linnaeus) Mosyakin	anecan	Ranunculaceae	canada anemone
<i>Anemone cylindrica</i> A. Gray	anecyl	Ranunculaceae	long-headed anemone
<i>Anemone multifida</i> Poiret	anemul	Ranunculaceae	cut-leaved anemone
<i>Antennaria neglecta</i> Greene	antneg	Asteraceae	field pussytoes
<i>Anthoxanthum nitens</i> (Weber) Y. Schouten & Veldkamp	antnit	Poaceae	vanilla sweetgrass
<i>Antennaria parvifolia</i> Nuttall	antpar	Asteraceae	small-leaved pussytoes
<i>Arabis hirsuta</i> (Linnaeus) Scopoli	arahir	Brassicaceae	hairy rockcross
<i>Arctostaphylos uva-ursi</i> (Linnaeus) Sprengel	arcuva	Ericaceae	common bearberry
<i>Artemisia biennis</i> Willdenow	artbie	Asteraceae	biennial wormwood
<i>Artemisia dracunculus</i> Linnaeus	artdra	Asteraceae	dragon wormwood
<i>Artemisia ludoviciana</i> Nuttall	artlud	Asteraceae	silver wormwood
<i>Astragalus canadensis</i> Linnaeus	astcan	Fabaceae	Canada milk-vetch
<i>Astragalus laxmannii</i> Jacquin	astlax	Fabaceae	Laxmann's milk-vetch
<i>Boechnera stricta</i> (Graham) Al-Shehbaz	boestr	Brassicaceae	Drummond's rockcross
<i>Botrychium lunaria</i> (Linnaeus) Swartz	botlun	Ophioglossaceae	common moonwort
<i>Bromus ciliatus</i> Linnaeus	brocil	Poaceae	fringed brome
<i>Bromus inermis</i> Leysser	broine	Poaceae	smooth brome
<i>Calamagrostis canadensis</i> (Michaux) Palisot de Beauvois	calcan	Poaceae	bluejoint reedgrass
<i>Campanula rotundifolia</i> Linnaeus	camrot	Campanulaceae	harebell
<i>Carex atherodes</i> Sprengel	carath	Cyperaceae	wheat sedge
<i>Carex sp</i>	carsp.	Cyperaceae	sedges
<i>Cerastium arvense</i> Linnaeus	cerarv	Caryophyllaceae	field chickweed
<i>Chamaenerion angustifolium</i> (Linnaeus) Scopoli	chaang	Onagraceae	fireweed
<i>Cirsium arvense</i> (Linnaeus) Scopoli	cirarv	Asteraceae	canada thistle
<i>Cirsium drummondii</i> Torrey & A. Gray	cirdru	Asteraceae	Drummond's thistle
<i>Comandra umbellata</i> (Linnaeus) Nuttall	comumb	Santalaceae	bastard toadflax
<i>Crataegus chrysoarpa</i> Ashe	crachr	Rosaceae	Fireberry hawthorn narrow-leaved
<i>Crepis tectorum</i> Linnaeus	cretec	Asteraceae	hawkbeard
<i>Danthonia intermedia</i> Vasey	danint	Poaceae	timber oatgrass
<i>Danthonia spicata</i> (Linnaeus) P. Beauvois ex Roemer & Schultes	danspi	Poaceae	poverty oatgrass
<i>Dasiphora fruticosa</i> (Linnaeus) Rydberg	dasfru	Rosaceae	shrubby cinquefoil
<i>Descurainia sophia</i> (Linnaeus) Webb ex Prantl	dessop	Brassicaceae	flixweed
<i>Drymocallis arguta</i> (Pursh) Rydberg	dryarg	Rosaceae	tall wood beauty
<i>Elymus repens</i> (Linnaeus) Gould	elyrep	Poaceae	quackgrass
<i>Elymus trachycaulus</i> (Link) Gould ex Shinners	elytra	Poaceae	Slender Wildrye
<i>Equisetum arvense</i> Linnaeus	equarv	Equisetaceae	field horsetail
<i>Erigeron glabellus</i> Nuttall	erigla	Asteraceae	streamside fleabane
<i>Festuca hallii</i> (Vasey) Piper	feshal	Poaceae	plains rough fescue
<i>Festuca saximontana</i> Rydberg	fessax	Poaceae	Rocky Mountain fescue
<i>Fragaria virginiana</i> Miller	fravir	Rosaceae	wild strawberry
<i>Gaillardia aristata</i> Pursh	gaiari	Asteraceae	great blanketflower
<i>Galium boreale</i> Linnaeus	galbor	Rubiaceae	northern bedstraw
<i>Galium labradoricum</i> (Wiegand) Wiegand	gallab	Rubiaceae	Labrador bedstraw
<i>Gentianella amarella</i> (Linnaeus) Börner	genama	Gentianaceae	autumn dwarf gentian
<i>Geum aleppicum</i> Jacquin	geuale	Rosaceae	yellow avens

<i>Geum macrophyllum</i> Willdenow	geumac	Rosaceae	large-leaved avens
<i>Geum triflorum</i> Pursh	geutri	Rosaceae	three-flowered avens
<i>Glechoma hederacea</i> Linnaeus	glehed	Lamiaceae	ground-ivy
<i>Hedysarum americanum</i> (Michaux ex Pursh) Britton	hedame	Fabaceae	alpine hedysarum
<i>Helictochloa hookeri</i> (Scribner) Romero Zarco	helhoo	Poaceae	Hooker's oatgrass
<i>Hesperostipa spartea</i> (Trinius) Barkworth	hesspa	Poaceae	plains porcupine grass
<i>Heuchera richardsonii</i> R. Brown	heuric	Saxifragaceae	Richardsons alumroot
<i>Hieracium umbellatum</i> Linnaeus	hieumb	Asteraceae	umbellate hawkweed
<i>Juncus balticus</i> Willdenow	junbal	Juncaceae	baltic rush
<i>Koeleria macrantha</i> (Ledebour) Schultes	koemac	Poaceae	Prairie junegrass
<i>Lathyrus ochroleucus</i> Hooker	latoch	Fabaceae	cream-coloured vetchling
<i>Lathyrus venosus</i> Muhlenberg ex Willdenow	latven	Fabaceae	veiny vetchling
<i>Liatris ligulistylis</i> (A. Nelson) K. Schumann	lialig	Asteraceae	meadow blazing-star
<i>Linum lewisii</i> Pursh	linlew	Linaceae	wild blue flax
<i>Lithospermum canescens</i> (Michaux) Lehmann	litcan	Boraginaceae	hoary puccoon
<i>Lysimachia ciliata</i> Linnaeus	lyscil	Primulaceae	fringed yellow loosestrife
<i>Maianthemum stellatum</i> (Linnaeus) Link	maiste	Asparagaceae	solomon's seal
<i>Mertensia paniculata</i> (Aiton) G. Don	merpan	Boraginaceae	tall bluebells
<i>Monarda fistulosa</i> Linnaeus	monfis	Lamiaceae	wild bergamot
<i>Muhlenbergia cuspidata</i> (Torrey ex Hooker) Rydberg	muhcus	Poaceae	plains muhly
<i>Muhlenbergia racemosa</i> (Michaux) Britton, Sterns & Poggenburgh	muhrac	Poaceae	marsh muhly
<i>Muhlenbergia richardsonis</i> (Trinius) Rydberg	muhric	Poaceae	mat muhly
<i>Mulgedium pulchellum</i> (Pursh) G. Don	mulpul	Asteraceae	blue lettuce
<i>Nabalus racemosus</i> (Michaux) Hooker	nabrac	Asteraceae	glaucous rattlesnakeroot
<i>Nassella viridula</i> (Trinius) Barkworth	nasvir	Poaceae	green needlegrass
<i>Oxytropis lambertii</i> Pursh	oxylam	Fabaceae	Lambert's locoweed
<i>Phleum pratense</i> Linnaeus	phlpra	Poaceae	common timothy
<i>Poa compressa</i> Linnaeus	poacom	Poaceae	Canada bluegrass
<i>Poa palustris</i> Linnaeus	poapal	Poaceae	fowl bluegrass
<i>Poa pratensis</i> Linnaeus	poapra	Poaceae	kentucky bluegrass
<i>Polygala senega</i> Linnaeus	polsen	Polygalaceae	Seneca snakeroot
<i>Populus tremuloides</i> Michaux	poptre	Salicaceae	trembling aspen
<i>Potentilla gracilis</i> Douglas ex Hooker	potgra	Rosaceae	slender cinquefoil
<i>Prunus virginiana</i> Linnaeus	pruvir	Rosaceae	chokecherry
<i>Ranunculus rhomboideus</i> Goldie	ranrho	Ranunculaceae	prairie buttercup
<i>Ribes hirtellum</i> Michaux	ribhir	Grossulariaceae	swamp gooseberry
<i>Ribes oxycanthoides</i> Linnaeus	riboxy	Grossulariaceae	Canada gooseberry
<i>Rosa acicularis</i> Lindley	rosaci	Rosaceae	prickly rose
<i>Rubus idaeus</i> (Michaux) Focke	rubida	Rosaceae	North American red raspberry
<i>Rudbeckia hirta</i> Farwell	rudhir	Asteraceae	black-eyed Susan
<i>Rumex triangulivalvis</i> (Danser) Rechinger f.	rumtri	Polygonaceae	triangular-valve dock
<i>Salix</i> sp	salsp.	Salicaceae	willows
<i>Schizachne purpurascens</i> (Torrey) Swallen	schpur	Poaceae	purple false melic
<i>Scirpus</i> sp	scisp.	Cyperaceae	sedges
<i>Sisyrinchium montanum</i> Greene	sismon	Iridaceae	strict blue-eyed grass
<i>Solidago canadensis</i> Linnaeus	solcan	Asteraceae	canada goldenrod
<i>Solidago glutinosa</i> Nuttall	solglu	Asteraceae	sticky goldenrod
<i>Solidago missouriensis</i> Nuttall	solmis	Asteraceae	Missouri goldenrod
<i>Solidago rigida</i> Linnaeus	solrig	Asteraceae	stiff goldenrod
<i>Sonchus arvensis</i> Linnaeus	sonarv	Asteraceae	field sow-thistle
<i>Spiraea alba</i> Du Roi	spialb	Rosaceae	white meadowsweet
<i>Sporobolus heterolepis</i> (A. Gray) A. Gray	spohet	Poaceae	prairie dropseed
<i>Stachys palustris</i> Linnaeus	stapal	Lamiaceae	marsh hedge-nettle
<i>Stellaria longipes</i> Goldie	stelon	Caryophyllaceae	long-stalked starwort
<i>Symphotrichum ciliolatum</i> (Lindley) Á. Löve & D. Löve	symcil	Asteraceae	Lindleys aster
<i>Symphotrichum ericoides</i> (Linnaeus) G.L. Nesom	symeri	Asteraceae	white heath aster
<i>Symphotrichum laeve</i> (Linnaeus) Á. Löve & D. Löve	symlae	Asteraceae	smooth aster
<i>Symphotrichum lanceolatum</i> (Willdenow) G.L. Nesom	symlan	Asteraceae	white paniced aster
<i>Symphoricarpos occidentalis</i> Hooker	symocc	Caprifoliaceae	western snowberry

<i>Taraxacum officinale</i> F.H. Wiggers	taroff	Asteraceae	common dandelion
<i>Thalictrum dasycarpum</i> Fischer & Avé-Lallemant	thadas	Ranunculaceae	purple meadow-rue
<i>Thalictrum venulosum</i> Trelease	thaven	Ranunculaceae	veiny meadow-rue
<i>Thlaspi arvense</i> Linnaeus	thlarv	Brassicaceae	field pennycress
<i>Trifolium repens</i> Linnaeus	trirep	Fabaceae	white clover
<i>Urtica dioica</i> Linnaeus	urtdio	Urticaceae	stinging nettle
<i>Vicia americana</i> Muhlenberg ex Willdenow	vicame	Fabaceae	American vetch
<i>Viola adunca</i> Smith	vioadu	Violaceae	hooked violet
<i>Viola canadensis</i> Linnaeus	viocan	Violaceae	Canada violet
<i>Zizia aptera</i> (A. Gray) Fernald	zizapt	Apiaceae	heart-leaved alexanders

Appendix B. Proportional species abundances of the top 30 species contributing 70% of the vegetation communities on the long-term monitoring transects in Riding Mountain National Park, Manitoba in 1973 (A), 2010 (B). 2020 (C). Species codes represent the first three letters of species binomials. See Appendix A for a full list of species names.

Transect	Graze	achmil	achric	anecan	artlud	brocil	broine	calcan	carsp.	cirarv	elyrep	elytra	feshal	fravir	galbor	geutri	hesspa	koemac	latoch	monfis	poapra	rosaci	schpur	solcan	solrig	symlae	symocc	taroff	thaven	vicame	
A	AP1	Heavy	0.09	0.15	0	0	0.14	0	0	0.54	0	0	0.41	0	0.24	0.07	0	0	0.01	0.04	0	0.5	0	0	0.37	0	0.07	0	0.02	0.24	0.11
	AP2	Light	0.02	0.05	0	0	0.01	0	0	0.06	0	0	0.09	0.73	0.01	0.28	0.04	0.42	0.18	0	0.03	0.01	0.01	0	0.09	0.08	0.01	0	0	0	
	AP3	Moderate	0.02	0	0	0.04	0.1	0	0	0.18	0	0	0.2	0.21	0.23	0.05	0	0.09	0.12	0	0	0.65	0.01	0.04	0	0.06	0.09	0	0.17	0	0.01
	AP4	Heavy	0.08	0.03	0	0.07	0.12	0	0	0.14	0.01	0	0.44	0	0.12	0.02	0	0	0	0	0	0.88	0	0	0.13	0	0	0	0.06	0.03	0.02
	AP5	Moderate	0.04	0.01	0	0	0.05	0	0	0.35	0	0	0.18	0.2	0.05	0.04	0.01	0.22	0.38	0.01	0	0.05	0.03	0	0	0.01	0.08	0	0	0	0.03
	BH1	Light	0.03	0.08	0	0	0.01	0	0	0.25	0	0	0.06	0.48	0	0.03	0.1	0.23	0.09	0.02	0	0.04	0	0	0	0.01	0.02	0	0	0	0
	BL1	Moderate	0.09	0.02	0	0.05	0.01	0	0	0.04	0	0	0.03	0	0	0.03	0	0.01	0.02	0.01	0	0.87	0	0	0	0	0	0	0.11	0	0.1
	BL2	Heavy	0.04	0	0	0.06	0	0	0	0.03	0	0	0.06	0	0.01	0.15	0	0	0	0	0	0.96	0.01	0	0	0	0.02	0	0.05	0	0.19
	BL3	Moderate	0.03	0.04	0	0	0	0	0	0.25	0	0	0.21	0.31	0	0.09	0	0	0.18	0	0	0.31	0.01	0.01	0	0.11	0.03	0.01	0.03	0	0.05
	BL4	Moderate	0.02	0.03	0.12	0	0.03	0	0	0.22	0	0	0.11	0.13	0.03	0.06	0	0	0.16	0	0.02	0.11	0	0	0	0.09	0.02	0.04	0	0	0.01
	BTS1	Light	0.1	0.01	0.04	0.06	0.02	0	0	0.09	0	0	0.06	0.44	0	0.12	0.04	0.14	0.23	0.04	0.05	0.3	0	0	0	0.06	0.01	0.03	0	0	0.1
	BTS2	Heavy	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.92	0	0	0.03	0	0	0.01	0.1	0	0
	BTS3	Light	0.02	0	0	0.07	0.01	0	0	0.13	0	0	0.07	0.4	0	0.04	0.11	0.25	0.15	0	0	0.37	0	0	0	0.1	0	0.06	0	0	0.09
	BTS4	Light	0.07	0.02	0	0.11	0.12	0	0	0.32	0	0	0.07	0.27	0.02	0.01	0.07	0.2	0.14	0	0.02	0.33	0	0	0	0.07	0.05	0	0	0	0.02
	BTV1	Moderate	0.13	0.05	0	0.02	0	0	0	0.25	0	0	0.08	0.15	0.02	0.07	0.02	0.02	0.07	0	0	0.68	0	0.01	0	0.01	0.03	0	0.2	0	0.15
	BTV10	Heavy	0	0	0	0	0	0	0	0	0.02	0	0	0	0	0	0	0	0	0	0	0.98	0	0	0	0	0	0	0	0	0
	BTV2	Moderate	0.05	0.09	0	0.03	0	0	0	0.14	0	0	0.06	0.3	0.05	0.02	0.09	0.31	0.06	0	0	0.47	0.01	0	0	0.05	0.04	0.05	0.07	0	0.09
	BTV3	Moderate	0.12	0.03	0	0.03	0.03	0	0	0.15	0	0	0.3	0.23	0	0.1	0	0.21	0.02	0	0	0.71	0.02	0	0	0.01	0.01	0	0.05	0	0.26
	BTV4	Heavy	0	0	0	0	0	0	0	0.18	0	0	0.08	0	0.1	0.08	0	0	0	0	0	0.11	0	0	0	0	0	0.2	0.06	0	0
	BTV5	Moderate	0.14	0	0	0	0.01	0	0	0.2	0	0	0.5	0	0.19	0.07	0	0	0.08	0	0	0.79	0	0	0	0	0.03	0	0.18	0	0.23
	BTV6	Heavy	0.1	0	0	0	0	0	0	0.04	0.03	0	0.45	0	0.21	0.14	0	0	0	0	0	0.97	0	0	0	0	0	0	0.03	0	0.14
	BTV7	Moderate	0.05	0.08	0	0.01	0.02	0	0	0.34	0	0	0.14	0.21	0.01	0.11	0	0.14	0.04	0.05	0.02	0.8	0.01	0	0	0.17	0.03	0	0.08	0	0.18
	BTV8	Heavy	0.04	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0.95	0	0	0	0	0	0	0.04	0	0
	BTV9	Heavy	0.34	0	0.01	0	0.01	0	0	0.16	0	0	0.64	0	0.02	0.07	0	0	0.13	0.01	0	0.72	0	0.02	0	0	0.09	0	0.2	0.09	0.37
	DL1	Moderate	0.02	0	0	0.06	0.03	0	0	0.03	0	0	0.01	0	0.05	0.06	0	0	0.13	0	0	0.42	0	0	0	0.03	0	0	0.05	0	0.04
	DL2	Light	0	0.04	0	0	0.02	0	0	0.18	0	0	0.03	0.62	0	0.08	0.03	0.15	0.17	0	0.01	0.13	0	0	0	0.04	0.01	0	0	0	0.06
	DL3	Moderate	0.09	0.05	0	0.07	0.03	0	0	0.38	0	0	0.06	0	0	0.16	0	0.2	0.08	0	0	0.28	0.03	0	0	0.01	0.03	0.03	0.02	0	0.09
	KM1	Light	0.05	0.01	0.03	0.02	0.05	0	0	0.49	0	0	0.08	0.45	0.19	0.05	0	0.02	0.28	0.01	0	0.08	0	0	0.03	0.01	0.22	0	0	0	0.1
	KM2	Moderate	0.04	0.01	0.01	0.01	0.06	0	0	0.22	0	0	0.1	0.21	0.19	0	0	0.06	0.03	0.02	0.02	0.6	0.02	0	0	0	0	0	0.07	0.03	0.02
	MP1	Light	0.05	0.01	0	0.06	0.03	0	0	0.31	0	0	0.07	0.36	0	0.02	0.09	0.07	0.06	0.01	0.06	0	0.02	0	0	0.06	0.02	0	0	0	0
	MV1	Light	0.01	0.08	0	0	0	0	0	0.14	0	0	0.02	0.74	0.18	0.11	0.07	0.01	0.12	0	0	0	0	0	0.02	0.08	0.07	0	0	0	0.02
	PP1	Light	0.08	0.11	0.01	0	0.08	0	0	0.44	0	0	0.17	0.58	0.17	0.03	0.01	0.06	0	0.01	0	0.05	0	0.09	0.02	0.05	0.11	0	0	0	0
	SL1	Light	0.01	0.03	0	0.04	0.01	0	0	0.02	0	0	0.09	0.65	0.02	0.04	0.03	0.01	0.15	0.02	0.03	0.01	0.02	0.02	0	0.07	0.01	0.01	0	0	0.04

Transect	Graze	achmil	achric	anecan	artlud	brocil	broine	calcan	carsp.	cirarv	elyrep	elytra	feshal	fravir	galbor	geutri	hesspa	koemac	latoch	monfis	poapra	rosaci	schpur	solcan	solrig	symlae	symocc	taroff	thaven	vicame
AP1	Heavy	0.01	0	0.08	0.02	0.18	0.11	0.04	0.57	0	0	0.15	0	0.08	0.11	0	0	0	0	0	0.62	0	0.05	0.46	0	0.03	0.01	0	0	0.05
AP2	Light	0.03	0.29	0	0.01	0.01	0	0	0.16	0	0	0.19	0.72	0.01	0.21	0.02	0.22	0.02	0.02	0.06	0.28	0.16	0	0	0	0	0	0	0	0.07
AP3	Moderate	0.04	0.02	0.04	0.03	0.01	0	0	0.14	0	0	0.45	0.26	0.04	0.15	0	0.09	0.08	0.02	0.01	0.77	0.07	0.02	0	0.03	0.09	0.03	0	0.11	0.13
AP4	Heavy	0.07	0	0.39	0	0.19	0	0.64	0.04	0.1	0	0.07	0	0	0.09	0	0	0	0.03	0	0.77	0	0.02	0.21	0	0.01	0.03	0.01	0.04	0.05
AP5	Moderate	0.02	0	0.21	0.11	0.04	0	0	0.1	0	0	0.08	0.02	0.01	0.09	0	0.01	0.01	0.04	0.1	0.86	0.06	0.01	0	0	0.04	0	0	0.11	0.02
BH1	Light	0.03	0.37	0	0	0.02	0	0	0.52	0	0	0.11	0.55	0	0.09	0.25	0.05	0.02	0	0	0.01	0	0.03	0	0.03	0.14	0	0	0.02	0.02
BL1	Moderate	0.01	0	0	0.06	0.01	0	0	0	0	0	0.22	0	0.02	0.1	0	0	0.02	0	0.07	0.95	0.01	0	0	0.04	0.13	0.01	0	0.05	0.02
BL2	Heavy	0.02	0	0.04	0.03	0.01	0.18	0	0.06	0	0	0.07	0.01	0	0.13	0.02	0	0	0	0	0.88	0	0.01	0	0	0.06	0.02	0	0.05	0.09
BL3	Moderate	0.03	0.02	0	0.05	0	0	0	0.04	0	0	0.2	0.05	0	0.01	0	0	0	0	0.03	0.98	0.06	0.01	0	0	0.03	0	0.01	0.03	0
BL4	Moderate	0.05	0.05	0	0.09	0.01	0	0	0.01	0	0	0.04	0.39	0.03	0.09	0	0	0.01	0	0.13	0.43	0.04	0.04	0.02	0.03	0.17	0.02	0	0.03	0.05
BTS1	Light	0.04	0.05	0.01	0.03	0.02	0	0	0.11	0	0	0.03	0.65	0.01	0.24	0.02	0.08	0	0.01	0.02	0.49	0.03	0	0	0	0	0	0	0.05	0.07
BTS2	Heavy	0.01	0.02	0	0.1	0	0.2	0	0.07	0	0	0	0.04	0	0.09	0	0	0	0	0	0.93	0.08	0	0	0	0	0.49	0	0.02	0.01
BTS3	Light	0.03	0	0	0.19	0.01	0	0	0.02	0	0	0.01	0.3	0.01	0.31	0.02	0	0.01	0	0	0.89	0.15	0	0	0.02	0.02	0.2	0	0.15	0.06
BTS4	Light	0.02	0.11	0.11	0.05	0.09	0	0	0.1	0	0	0.08	0.53	0	0.14	0.03	0.11	0	0.01	0.04	0.74	0.07	0	0	0.01	0.1	0.04	0	0.04	0.07
BTV1	Moderate	0.01	0.06	0	0.08	0.02	0	0	0.15	0	0	0.18	0.62	0.02	0.14	0.02	0.02	0.01	0	0	0.63	0	0	0	0.02	0.27	0	0	0.04	0.03
BTV10	Heavy	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.76	0	0	0	0	0.01	0.62	0	0	0
BTV2	Moderate	0	0	0.04	0.11	0.04	0	0	0.08	0	0	0.06	0.27	0.02	0.16	0.05	0.01	0	0.06	0	0.88	0.01	0	0	0.03	0.43	0.11	0	0.02	0.07
BTV3	Moderate	0.01	0.09	0	0.06	0.01	0	0	0.16	0	0	0.31	0.77	0.09	0.09	0.07	0.01	0	0	0.05	0.42	0.01	0	0.03	0.02	0.14	0	0	0.03	0.06
BTV4	Heavy	0	0	0	0	0	0.21	0	0.04	0.02	0	0	0	0.15	0	0	0	0	0	0	0.88	0	0	0	0	0	0.56	0	0.01	0
BTV5	Moderate	0.07	0	0.05	0	0	0	0	0.21	0.04	0	0.22	0.15	0.01	0.13	0	0	0	0.07	0	0.9	0	0	0.01	0	0.07	0.06	0	0.1	0
BTV6	Heavy	0.01	0	0.11	0	0	0	0	0.42	0.07	0	0.01	0	0	0.23	0	0	0.01	0.02	0	0.91	0	0.01	0	0	0.04	0.39	0	0	0.02
BTV7	Moderate	0	0.01	0.12	0.01	0	0	0	0.18	0	0	0.11	0.3	0	0.19	0	0	0	0.11	0.02	0.87	0.01	0	0.02	0	0.02	0.03	0	0.1	0.13
BTV8	Heavy	0.01	0	0	0.09	0	0	0	0.04	0.03	0	0	0	0	0.11	0	0	0	0	0	1	0	0	0	0	0.03	0.05	0.03	0	0.01
BTV9	Heavy	0.01	0	0.04	0	0	0.48	0	0.22	0	0	0.09	0	0	0.09	0	0	0	0.19	0	0.66	0	0	0	0	0.03	0.49	0	0	0.13
DL1	Moderate	0.01	0	0	0.05	0	0.73	0	0.21	0	0	0	0.1	0.01	0.06	0	0	0	0	0	0.81	0.02	0	0	0.25	0.06	0.01	0	0	0
DL2	Light	0.02	0.27	0	0.03	0.01	0	0	0.11	0	0	0.02	0.57	0.04	0.13	0.06	0.04	0	0.02	0.1	0.46	0.11	0.02	0	0.01	0.04	0.02	0	0.07	0.05
DL3	Moderate	0.03	0.16	0	0.06	0.05	0	0	0.24	0	0	0.12	0.4	0	0.01	0	0	0.02	0	0	0.8	0.03	0	0	0.01	0	0.07	0	0.04	0.02
KM1	Light	0.06	0.04	0.16	0.03	0.2	0	0	0.26	0	0	0.17	0.16	0.1	0.22	0	0.05	0.01	0	0	0.56	0	0	0.21	0.05	0.07	0	0	0.17	0.01
KM2	Moderate	0.07	0	0.06	0.12	0.08	0	0	0.06	0	0	0.22	0	0	0.28	0	0	0	0.1	0.02	0.94	0	0	0.39	0	0.06	0.01	0	0	0.08
MP1	Light	0.01	0.25	0	0.04	0.04	0	0	0.36	0	0	0.12	0.66	0.09	0.11	0.19	0.21	0.02	0.01	0.04	0.2	0.01	0.03	0.02	0.11	0.19	0	0	0.02	0.04
MV1	Light	0.09	0.17	0	0.01	0.19	0	0	0.17	0	0	0.12	0.99	0.11	0.1	0.08	0	0.04	0	0	0	0	0	0	0.04	0.17	0	0	0.01	0.02
PP1	Light	0.03	0.17	0.02	0	0.26	0.04	0	0.22	0	0	0.1	0.48	0.13	0.06	0.02	0	0	0.04	0	0.79	0	0.02	0.05	0.04	0.07	0	0	0.05	0.04
SL1	Light	0	0.44	0	0.02	0.01	0	0	0.12	0	0	0.07	0.63	0.01	0.07	0.1	0.26	0.01	0	0.02	0.23	0.09	0	0	0	0.04	0.06	0	0.03	0

Transect	Graze	achmil	achric	anecan	artlud	brocil	broine	calcan	carsp.	cirarv	elyrep	elytra	feshal	fravir	galbor	geutri	hesspa	koemac	latoch	monfis	poapra	rosaci	schpur	solcan	solrig	symlae	symocc	taroff	thaven	vicame
AP1	Heavy	0	0.14	0.21	0.01	0.08	0.2	0.18	0.53	0.01	0	0.15	0	0.03	0.12	0	0	0.01	0.12	0	0.76	0	0.22	0.59	0	0.02	0	0	0.13	0.09
AP2	Light	0.03	0.08	0	0.09	0	0	0	0.3	0	0	0.13	0.82	0.14	0.18	0.04	0.11	0.02	0.05	0.08	0.81	0.19	0.03	0	0.01	0.05	0	0	0.05	0.01
AP3	Moderate	0.05	0	0.18	0.05	0.01	0	0	0.36	0	0	0.1	0.15	0.41	0.29	0	0	0	0.09	0.07	0.97	0.11	0	0	0.05	0.1	0.21	0	0.32	0.05
AP4	Heavy	0.02	0	0.42	0	0.09	0.03	0.52	0.2	0.05	0	0.17	0	0.04	0.23	0	0	0	0.17	0	0.75	0	0.22	0.34	0	0.08	0.05	0.01	0.09	0.04
AP5	Moderate	0	0.01	0.15	0	0.02	0	0	0.43	0	0	0.15	0.23	0.15	0.06	0	0.01	0.05	0.05	0.01	0.96	0.05	0.08	0	0	0.04	0.07	0	0.25	0.03
BH1	Light	0.11	0.17	0	0.02	0.03	0	0	0.46	0	0	0.04	0.86	0.06	0.04	0.09	0.1	0.11	0.01	0	0.15	0.01	0.22	0	0.17	0.09	0	0	0.03	0.02
BL1	Moderate	0.09	0.01	0	0.02	0.01	0	0	0.13	0	0	0.04	0	0.07	0.06	0	0	0.02	0.01	0.04	0.95	0.07	0	0	0.06	0.24	0.01	0	0.07	0.03
BL2	Heavy	0	0	0.06	0.03	0.02	0.61	0	0.11	0	0	0.03	0.05	0	0.16	0	0	0	0.02	0	0.87	0.03	0.01	0.05	0	0.21	0	0	0.11	0.03
BL3	Moderate	0	0.02	0	0.07	0	0	0	0.05	0	0	0	0.02	0	0.1	0	0	0	0.04	0	0.98	0.15	0.03	0	0	0.04	0.01	0	0.06	0.04
BL4	Moderate	0.04	0.09	0	0.01	0	0	0	0.08	0	0	0.04	0.45	0.05	0.28	0	0	0.03	0.05	0.04	0.56	0.03	0.05	0	0.03	0.18	0.05	0	0.05	0.01
BTS1	Light	0	0.04	0	0.13	0	0	0	0.13	0	0	0.06	0.43	0	0	0.01	0	0.03	0.02	0.02	1	0.08	0.04	0.01	0.01	0.06	0	0	0.05	0
BTS2	Heavy	0.01	0	0	0.13	0	0.38	0	0.04	0	0	0	0.01	0	0.12	0	0	0	0.01	0.01	0.99	0.09	0	0	0	0	0.29	0	0.02	0.01
BTS3	Light	0.01	0	0	0.11	0	0	0	0.03	0	0	0.05	0.32	0	0.07	0	0	0.01	0	0.02	1	0.14	0	0	0.06	0.01	0.13	0	0.03	0.02
BTS4	Light	0	0.1	0.07	0.09	0.05	0	0	0.41	0	0	0.02	0.39	0.11	0.17	0.07	0.1	0.03	0	0.22	0.91	0.02	0	0.04	0	0.2	0.13	0	0.06	0.02
BTV1	Moderate	0.01	0.29	0	0.07	0	0	0	0.15	0	0	0.02	0.79	0.14	0.05	0.04	0	0	0.01	0.08	0.93	0.04	0.02	0	0.02	0.14	0.03	0	0.14	0.03
BTV10	Heavy	0.01	0	0	0	0	0.72	0	0	0.12	0.07	0	0	0	0	0	0	0	0	0	0.93	0	0	0	0	0.01	0.39	0	0	0.06
BTV2	Moderate	0.02	0	0.06	0.1	0	0	0	0.08	0	0	0.09	0.3	0.17	0.21	0.03	0.02	0	0.22	0.01	0.95	0.02	0	0	0.02	0.22	0.14	0	0.12	0.06
BTV3	Moderate	0.1	0.1	0	0.01	0	0	0.19	0.15	0	0	0.18	0.78	0.25	0.11	0.03	0.07	0	0.02	0.07	0.59	0.03	0.08	0.07	0.04	0.13	0	0	0.07	0.08
BTV4	Heavy	0	0	0	0.05	0	0	0	0.18	0.12	0.55	0	0	0	0.01	0	0	0	0	0	0.98	0.04	0	0	0	0	0.32	0	0.02	0.01
BTV5	Moderate	0.01	0	0.08	0	0	0	0	0.2	0.11	0	0.03	0.03	0.15	0.18	0	0	0	0.16	0	1	0	0	0.03	0	0.05	0.05	0	0.28	0.06
BTV6	Heavy	0.01	0	0.07	0	0	0.07	0	0.28	0.15	0	0	0	0.14	0.09	0	0	0	0.11	0	0.94	0	0	0.02	0	0.04	0.37	0	0.02	0.04
BTV7	Moderate	0.01	0.05	0.11	0.03	0	0	0	0.47	0	0	0.04	0.43	0	0.17	0	0	0	0.22	0.04	0.99	0.01	0	0.01	0	0	0.16	0	0.11	0.08
BTV8	Heavy	0.04	0	0	0.04	0	0	0	0	0.21	0.1	0	0	0	0.2	0	0	0	0.01	0	0.99	0	0	0.24	0	0	0.07	0	0	0.03
BTV9	Heavy	0	0	0.33	0	0.41	0.25	0	0.24	0	0	0	0	0	0.05	0	0	0	0.04	0	0.8	0.01	0	0.34	0	0.01	0.32	0	0.12	0.08
DL1	Moderate	0.02	0.03	0	0	0.01	0.72	0	0.18	0	0	0.02	0.04	0.01	0	0	0	0.02	0.01	0	0.93	0.01	0	0	0.26	0.03	0.01	0	0	0.02
DL2	Light	0.05	0.15	0	0.02	0.01	0	0	0.03	0	0	0.02	0.67	0.12	0.21	0.01	0	0.03	0.02	0.14	0.76	0.18	0.01	0	0	0.03	0.06	0	0.07	0
DL3	Moderate	0.04	0.15	0	0.04	0.11	0	0	0.55	0	0	0.07	0.24	0.02	0.06	0	0.11	0	0.02	0	0.91	0.05	0.04	0	0.04	0.02	0.1	0	0.12	0.02
KM1	Light	0.02	0.03	0	0.06	0.03	0	0	0.3	0.03	0	0.04	0.34	0.12	0.07	0	0	0.02	0.11	0	0.99	0	0.18	0.12	0.03	0.03	0	0	0.05	0.04
KM2	Moderate	0.15	0	0.14	0.01	0.19	0	0.07	0.34	0.03	0	0.1	0.07	0.2	0.19	0	0	0.03	0.18	0.07	0.93	0.02	0.18	0.44	0	0.03	0	0	0.07	0.21
MP1	Light	0.06	0.14	0.02	0.05	0.04	0	0	0.4	0	0	0.14	0.77	0.25	0.16	0.14	0.05	0.05	0.03	0.05	0.71	0.05	0.1	0.03	0.05	0.14	0	0	0.04	0.03
MV1	Light	0.11	0.16	0	0.03	0.04	0	0	0.23	0	0	0.1	0.91	0.21	0.19	0.07	0.02	0.08	0.01	0	0	0	0.14	0	0.09	0.16	0	0	0.04	0.01
PP1	Light	0.05	0.2	0	0	0	0.31	0	0.29	0	0	0.09	0.45	0.24	0.08	0	0.14	0.04	0.06	0	0.94	0.02	0.11	0.03	0.03	0.14	0	0	0.08	0.14
SL1	Light	0.06	0.23	0	0.01	0.01	0	0	0.21	0	0	0.08	0.79	0.06	0.19	0.01	0.19	0.01	0.07	0.07	0.59	0.1	0.08	0	0.02	0.07	0.08	0	0.05	0.02

Appendix C. Leaf traits measured for the top 30 species contributing to 70% of the vegetation communities on the long-term monitoring transects in Riding Mountain National Park (RMNP), Manitoba. Leaf traits were measured from plants collected in at a reference prairie within RMNP. *Carex* sp. is the mean of *C. inops* and *C. torreyi*.

Species	SLA (mm²/mg)	Leaf Density (mg/mm³)	Leaf C:N
<i>Festuca hallii</i>	7.5	0.460	25.4
<i>Poa pratensis</i>	7.8	0.429	25.4
<i>Symphoricarpos occidentalis</i>	9.2	0.371	21.9
<i>Cirsium arvense</i>	9.5	0.150	21.2
<i>Hesperostipe spartea</i>	10.0	0.333	22.1
<i>Solidago rigida</i>	11.0	0.211	22.0
<i>Achillia millefolium</i>	11.4	0.342	20.3
<i>Achnatherum richardsonii</i>	11.5	0.331	23.4
<i>Geum triflorum</i>	11.5	0.189	22.3
<i>Fragaria virginiana</i>	12.4	0.347	17.1
<i>Solidago canadensis</i>	13.8	0.215	20.6
<i>Anenome canadensis</i>	14.2	0.158	21.0
<i>Elymus trachycaulus</i>	14.8	0.238	19.4
<i>Rosa acicularis</i>	15.3	0.256	21.6
<i>Symphoritrichan lavae</i>	15.4	0.201	17.9
<i>Thalictrum venulosum</i>	16.6	0.205	18.2
<i>Artemisia ludoviciana</i>	17.2	0.185	16.5
<i>Monarda fistulosa</i>	17.4	0.146	17.9
<i>Vicia americana</i>	17.6	0.173	14.4
<i>Elymus repens</i>	18.5	0.204	18.1
<i>Bromus inermis</i>	19.6	0.174	19.5
<i>Koeleria macrantha</i>	20.5	0.186	21.5
<i>Bromus ciliatus</i>	20.5	0.173	21.9
<i>Lathyrus ochroleucus</i>	20.8	0.160	14.1
<i>Schizachne purpurascence</i>	22.1	0.217	21.1
<i>Carex torreyi</i>	22.1	0.157	16.4
<i>Carex sp.</i>	22.4	0.168	19.0
<i>Carex inops</i>	22.6	0.179	21.6
<i>Calamagrosis canadensis</i>	23.3	0.171	16.5
<i>Galium boreal</i>	25.6	0.140	20.8
<i>Taraxacum officinale</i>	28.2	0.105	17.6

Appendix D. Community weighted mean leaf trait profile for each survey site in Riding Mountain National Park, Manitoba in 1973(A), 2010 (B), 2020 (C).

A	Grazing			
	Transect	Intensity	Mean SLA (mm²/mg)	Mean Leaf Density (mg/mm³)
AP1	Heavy	50.4	0.655	56.2
AP2	Light	28.7	0.441	45.3
AP3	Moderate	36.7	0.457	42.7
AP4	Heavy	34.8	0.464	37.9
AP5	Moderate	26.3	0.377	36.9
BH1	Light	18.9	0.331	31.1
BL1	Moderate	24.2	0.284	23.4
BL2	Heavy	28.1	0.302	25.9
BL3	Moderate	25.8	0.350	33.4
BL4	Moderate	17.7	0.280	24.7
BTS1	Light	29.0	0.423	38.8
BTS2	Heavy	19.6	0.184	16.2
BTS3	Light	27.9	0.379	36.7
BTS4	Light	27.1	0.440	38.2
BTV1	Moderate	32.9	0.419	37.0
BTV10	Heavy	17.5	0.174	14.5
BTV2	Moderate	29.3	0.415	39.0
BTV3	Moderate	35.7	0.484	43.4
BTV4	Heavy	14.0	0.157	15.2
BTV5	Moderate	41.2	0.500	45.0
BTV6	Heavy	35.1	0.427	36.9
BTV7	Moderate	39.7	0.513	47.1
BTV8	Heavy	18.2	0.191	15.7
BTV9	Heavy	48.4	0.628	55.7
DL1	Moderate	16.4	0.188	16.3
DL2	Light	22.2	0.332	32.8
DL3	Moderate	24.8	0.375	32.1
KM1	Light	31.8	0.477	45.0
KM2	Moderate	30.2	0.403	38.1
MP1	Light	17.8	0.304	27.5
MV1	Light	22.6	0.363	35.2
PP1	Light	27.5	0.494	43.6
SL1	Light	18.5	0.283	28.0

B	Grazing		Mean SLA	Mean Leaf Density	Mean Leaf C:N
	Transect	Intensity	(mm²/mg)	(mg/mm³)	
AP1	Heavy	42.0	0.573	46.2	
AP2	Light	34.3	0.575	51.8	
AP3	Moderate	42.4	0.524	49.3	
AP4	Heavy	40.4	0.717	52.5	
AP5	Moderate	32.1	0.417	33.9	
BH1	Light	29.0	0.572	48.8	
BL1	Moderate	28.7	0.319	28.9	
BL2	Heavy	27.6	0.347	28.8	
BL3	Moderate	25.8	0.301	25.9	
BL4	Moderate	26.0	0.358	32.9	
BTS1	Light	29.2	0.415	37.9	
BTS2	Heavy	34.0	0.409	35.4	
BTS3	Light	41.1	0.466	42.1	
BTS4	Light	36.3	0.543	47.6	
BTV1	Moderate	32.8	0.477	44.5	
BTV10	Heavy	25.3	0.257	24.5	
BTV2	Moderate	36.7	0.470	44.1	
BTV3	Moderate	34.2	0.516	48.0	
BTV4	Heavy	31.3	0.351	31.5	
BTV5	Moderate	33.8	0.422	37.1	
BTV6	Heavy	37.4	0.450	39.5	
BTV7	Moderate	37.1	0.443	39.7	
BTV8	Heavy	24.0	0.266	22.0	
BTV9	Heavy	38.1	0.521	44.5	
DL1	Moderate	32.5	0.548	44.0	
DL2	Light	32.5	0.495	43.7	
DL3	Moderate	30.7	0.461	38.7	
KM1	Light	40.1	0.565	47.1	
KM2	Moderate	41.9	0.514	41.7	
MP1	Light	37.3	0.627	57.3	
MV1	Light	28.1	0.564	49.7	
PP1	Light	38.3	0.603	49.9	
SL1	Light	28.3	0.542	47.0	

C Transect	Grazing	Mean SLA	Mean Leaf Density	Mean Leaf C:N
	Intensity	(mm ² /mg)	(mg/mm ³)	
AP1	Heavy	60.1	0.815	65.5
AP2	Light	48.8	0.672	62.0
AP3	Moderate	61.2	0.710	64.9
AP4	Heavy	56.0	0.823	65.2
AP5	Moderate	47.8	0.559	50.8
BH1	Light	39.0	0.640	58.3
BL1	Moderate	31.4	0.373	34.0
BL2	Heavy	36.2	0.538	44.0
BL3	Moderate	28.7	0.299	26.4
BL4	Moderate	32.4	0.430	40.1
BTS1	Light	33.5	0.425	37.6
BTS2	Heavy	33.9	0.450	36.5
BTS3	Light	33.0	0.382	34.9
BTS4	Light	49.6	0.669	60.1
BTV1	Moderate	44.5	0.645	57.3
BTV10	Heavy	35.2	0.518	41.7
BTV2	Moderate	45.8	0.546	50.4
BTV3	Moderate	46.3	0.685	61.9
BTV4	Heavy	41.9	0.440	40.1
BTV5	Moderate	43.6	0.454	41.2
BTV6	Heavy	39.0	0.463	40.7
BTV7	Moderate	47.6	0.602	53.3
BTV8	Heavy	34.3	0.372	31.1
BTV9	Heavy	47.7	0.694	53.9
DL1	Moderate	33.1	0.545	43.6
DL2	Light	40.3	0.539	49.3
DL3	Moderate	42.6	0.594	51.0
KM1	Light	43.5	0.523	45.8
KM2	Moderate	62.3	0.786	65.0
MP1	Light	52.0	0.758	67.9
MV1	Light	35.3	0.600	54.6
PP1	Light	51.9	0.758	65.9
SL1	Light	43.6	0.654	59.6