EFFECTS OF CHANGING PRECIPITATION PATTERNS AND CLIPPING ON THE SHRUB-STEPPE GRASSLAND PLANT COMMUNITIES OF THE SOUTHERN INTERIOR OF BRITISH COLUMBIA

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
Master of Science
in
Environmental Science
Thompson Rivers University

June 2013

ACKNOWLEDGEMENTS

I would like to thank my supervisor Dr. Lauch Fraser for support and guidance over the course of my project. Dr. Don Thompson with Agriculture and Agri-Food Canada helped with site selection and building grazing exclosures for this study. My supervisory committee; Don Thompson, Wendy Gardner and Jonathan Van Hamme for reviews, suggestions, and welcomed advice.

Tod Haughton with the BC Ministry of Environment approved permits to allow access and research in Lac du Bois Provincial Park. This study was conducted under permit # 102724 from BC Ministry of Environment, Park and Protected Areas Division.

My field assistants and lab mates for an interesting and educational working and learning environment; Cameron Carlyle, Amanda Schmidt, William Harrower, Percy Folkard, Ashleigh Gilbert, Marc Jones, Tessa Jongbloets, Anna Sapozhnikova, Laurenz Teuber.

This research was supported by a Future Forests Ecosystem Scientific Council (FFESC) grant to Lauch Fraser. I was supported through a National Science and Engineering Research Council (NSERC) Industrial Partner Scholarship with the Grasslands Conservation Council of BC.

ABSTRACT

Grasslands cover approximately 40% of the world's ice-free land area and occur on every continent. It is estimated that 25% of the world's land area is grazed by domesticated livestock. Managed grazing systems in rangelands are an essential economic resource for at least one third of the human population. It is unknown how global climate change and the interaction of grazing may influence grassland communities. This study looked at how shifting precipitation patterns combined with clipping (a surrogate for grazing) may affect the grassland plant community and nitrogen availability in soil. I found that grasslands around Kamloops, British Columbia, were resistant to changes in the seasonality and frequency of watering over two years. Lower and middle elevation, less productive, grassland plant communities were more susceptible to immediate degradation from clipping, compared to more productive higher elevation grasslands. Clipping decreased cover and biomass at lower and middle elevations but increased species richness at all elevations. Watering and clipping treatments had a significant and measurable effect on both the mean and variance of volumetric water content and temperature of soil. Nitrogen (NO_3^- and NH_4^+) from PRS™-probes was lowest in the weekly spring watering treatments, and increased as the growing season progressed. Nitrogen (NO_3^- and NH_4^+) extracted from soil samples increased with elevation and clipping. Understanding the combined effects of changing precipitation patterns and grazing on the grassland plant community will allow improved grassland conservation and management in the face of global climate change.

KEYWORDS

Climate change, diversity, gradient, grassland, grazing, nitrogen, precipitation

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LIST OF ABBREVIATIONS

BC = British Columbia
PRS™-probe = Plant Root Simulator™- probe
RS = Rainout shelter
LG = lower grassland (study site)
MG = middle grassland (study site)
UG = upper grassland (study site)
VWC = volumetric water content

NOMENCLATURE

Plant species were identified according to the Illustrated Flora of British Columbia, particularly Volume 7 (Douglas, Meidinger & Pojar 2001).

CHAPTER 1: GENERAL INTRODUCTION

Grasslands cover approximately 40% of the world's ice-free land area and occur on every continent (Loveland et al. 2000; White et al. 2000). Grassland communities represent 52.5 million km^2, including over 3 million km^2 in Canada (White et al. 2000). Grasslands can be defined based on different metrics, such as climate (White et al. 2000), vegetation (White et al. 2000; BECWeb 2012), soils, aridity, lack of woody plants, dominance of grass species (Gibson 2009), and grazing utility (Asner *et al.* 2004). They are commonly described as areas dominated by herbaceous, mainly graminoid, species, and where tree growth is limited by any one or combination of annual precipitation, fire, herbivory, and freezing (White et al. 2000; Bond & Parr 2010).

Grasslands provide many ecological goods and services. It is estimated that 25% of the world's land area is grazed by domesticated livestock (Asner *et al.* 2004). Managed grazing systems in rangelands are an essential economic resource for at least one third of the human population (von Wehrden et al. 2012), and several grasslands of the world are noted as biodiversity 'hotspots' with high species richness and endemism (Bond & Parr 2010). Grasslands also provide most of the world's grain species, as well as providing food, forage, fuel, medicines, shelter, habitat, climate regulation, cultural and religious sites, and recreation activities (White et al. 2000). And yet, grasslands are threatened by land clearing and alteration, desertification, over-grazing, afforestation, non-native invasive species, and global climate change (Asner *et al.* 2004; Havstad, Herrick & Tseelei 2008; Bond & Parr 2010).

According to the Intergovernmental Panel on Climate Change (IPCC), "Warming of the climate system is unequivocal…" (Solomon *et al.* 2007). Global air and ocean temperatures have risen by over 0.7ºC in the last 100 years, with temperatures in the arctic increasing at twice the global average (Solomon *et al.* 2007). Global climate change is caused by increasing levels of greenhouse gasses, primarily carbon dioxide (CO_2), in the atmosphere. Other greenhouse gasses include methane and nitrous oxide, which are predominantly released from agricultural practices. The majority of the increase in CO_2 has been caused by the burning of fossil fuels, and to a lesser extent land use changes and agriculture (Solomon *et al.* 2007). Over the past two decades, an increasing number of studies have addressed the effects and consequences of global climate change on plant communities and ecosystems. Most climate change field experiments either manipulate temperature by increasing it with open-top chambers (Henry & Molau 1997; Vodnik et al. 2008; Carlyle et al. 2011), or manipulate precipitation by reducing water availability with rain-out shelters (Yahdjian & Sala 2002; Dijkstra et al. 2012; Heisler-White et al. 2008; Heisler-White et al. 2009; Shinoda et al. 2010). While these experiments are important and a good first step in our understanding of the effects of climate change, they do not address the complexity of climate scenarios that will be affecting future ecosystems (White et al. 2011).

Precipitation and Nitrogen

Grasslands are generally considered primarily water limited (Gurevitch, Scheiner & Fox 2006). Precipitation amount and variability in dryland ecosystems are thought to be inversely proportional to each other, with grasslands at relatively lower annual precipitation and higher variability compared to forests (Bartha et al. 2008; Knapp et al. 2002; Knapp & Smith 2001; Loik et al. 2004; Wehrden et al. 2010). A similar relationship is found for pulsing in dryland ecosystems (Novoplansky & Goldberg 2001; Robertson et al. 2010; Schwinning & Sala 2004; Schwinning et al. 2004).

The majority of nitrogen (N) in natural environments comes from N fixation activity of bacteria, but other sources are human-mediated industrial fixation, and wet and dry atmospheric deposition (Gurevitch, Scheiner & Fox 2006). In grasslands, bacteria that fix N are present in biological soil crusts (BSC) and in associations with leguminous plants. BSC's are assemblages of mosses, lichens, cyanobacteria and algae (Evans & Belnap 1999). They function as sources of N, decrease water runoff and stabilize soils, and the metabolic function in BSC's across wide geographical areas are remarkably consistent (Strauss, Day & Garcia-Pichel 2011). Collins et al. (2008) proposed that water pulses available for plant growth and nitrogen fixation or mineralization may be temporally asynchronous. As the majority of rainfall events in arid and semi-arid areas are small (< 2 mm), it is unlikely they will stimulate plant growth. Microbial processes, however, can respond to small moisture pulses leading to a build-up of N in the soil, which may be more susceptible to leaching. A recent test of this hypothesis has shown that this may not be the case. Dijkstra et al. (2012) applied 10 and 20 mm water pulses to field plots and found that plants responded to the smaller pulses more than microbes, which showed a greater response to the larger pulses. Plants also maintained activity for longer after a pulse, possibly due to water present at lower soil depths and could, therefore, take up N fixed in the soil from these pulses. Though these were slightly larger pulses than those proposed by Collins et al. (2008), they indicate pulsing is an important component of the functioning of the soil community.

Over two decades ago Tilman & El Haddi (1992) stated climate change would lead to continued variability of precipitation in the future, with longer and more intense droughts. This statement has been proven correct and is an important area of research (Solomon et al. 2007; White et al. 2011). To prepare for current and future change in climates, researchers are pursuing studies that demonstrate how climate variables may affect plant communities and landscapes, and how these variables are linked to each other and other land uses (White et al. 2011).

Changes in precipitation patterns are linked to temperature changes caused by increased greenhouse gas emissions. British Columbia (BC) is expected to have greater warming and changes in precipitation than the global average (Spittlehouse 2008). The Southern Interior region around Kamloops, BC, is predicted to experience this change mostly with shifts in seasonal precipitation patterns, with more precipitation occurring in the winter and less in the summer (Spittlehouse 2008). This will likely have a substantial effect on Southern Interior grasslands, as these areas rely on winter snowfall and spring precipitation to make up the majority of plant-available water for the growing season (Environment Canada 2012). This is expected to cause grassland expansion and geographical shifts as grassland-appropriate climate envelopes change (Hamann & Wang 2006).

Grazing

Grazing is a globally important economic activity (White et al. 2000; Asner et al. 2004; Wehrden et al. 2012). It is also important industry in BC (Wilson 2009). As of January 1st, 2013 BC had just over 4.4% of Canada's cattle industry at 545 000 head of cattle (Statistics Canada 2013). In BC, one-third of the land area is included in grazing tenures, which includes 90 % of BC's grasslands (Wilson 2009).

Grazing has several impacts on plant communities including soil compaction and disturbance, inputs of concentrated fertilizer, removal and trampling of biomass.

Typically, grazers selectively remove portions of a plant's biomass, which causes changes in an individual plant's growth rate and fitness. This combined with the direct effects of grazers can cause shifts in plant community composition and structure (Gibson 2009). Plants with an evolutionary history of grazing can either be tolerant of grazing or unpalatable and therefore avoided (Gibson 2009). This can cause a shift in plant community by increasing the abundance of grazing-tolerant species with a decrease in those not evolutionarily adapted to or intolerant of grazing. Changes in community structure can follow the same pattern, with stoloniferous or annual plants replacing tall-statured, perennial or tussock plants (Díaz *et al.* 2007).

Study Site

Environmental gradients, such as precipitation, soil, latitude, and altitude, are important in structuring plant communities (Gentry 1988). Consideration of environmental gradients is therefore an important aspect of understanding biological responses to climate change (Dunne *et al.* 2004). As there is rarely an opportunity to study plant community changes over time scales exceeding a decade, gradients can be used to interpret how plant communities may change in the long-term (Dunne *et al.* 2004). Lac du Bois Grasslands Protected Area is a 15 000 hectare park in the Southern Interior of BC that encompasses a broad altitudinal scale from very hot, dry grasslands around 300 m to the grassland-forest ecotone at about 900 m, with dry Douglas-fir forests above. The grassland gradient of 300 – 900 m in Lac du Bois includes three distinct plant communities, the lower elevation dominated by *Pseudoroegneria spicata* (bluebunch wheatgrass), *Poa secunda* ssp. *secunda* (Sandberg's bluegrass), and the shrub *Artemisia tridentata* (big sagebrush). The middle grassland has a greater diversity of species and lower cover of sagebrush (van Ryswyk et al. 1966). The upper grasslands have a nearly continuous herbaceous cover, with sagebrush mainly excluded. Lac du Bois grasslands are also grazed by local cattle operators in agreement with BC Parks, so the plant communities reflect those developed under current land management. This location is ideally suited to study the effects of shifted precipitation patterns and clipping along an elevation and productivity gradient.

Outline of Thesis

In Chapter 2, I present a field experiment conducted in grasslands near Kamloops, BC. I studied how changes in the seasonality and frequency of precipitation may interact with disturbance caused by grazing (simulated by clipping) on three grassland plant communities of the Lac du Bois Grasslands. Since N is generally a limiting nutrient in grassland soils and N cycling in soil is tied to soil water conditions, I also tested the effect of precipitation and clipping on soil N availability. The purpose was to determine how probable changes in rainfall patterns may affect grassland plant communities while supporting a cattle grazing system that is nearly ubiquitous on rangelands in BC. In Chapter 3, I put the results from Chapter 2 in a broader ecological context, suggest future directions for research, and discuss how my results may inform grassland management and an economically robust cattle industry in the future with continued climate change.

CHAPTER 2: EFFECTS OF CHANGING PRECIPITATION PATTERNS AND CLIPPING ON THE SHRUB-STEPPE GRASSLAND PLANT COMMUNITIES OF THE SOUTHERN INTERIOR OF BRITISH COLUMBIA

Introduction

The Intergovernmental Panel on Climate Change (IPCC) is unequivocal in its contention that global climate change is occurring and that global warming is caused by human activity (Solomon *et al.* 2007). Climate change is predicted to effect ecosystems and the distribution and abundance of species populations. Some terrestrial plant populations have already shown a response to global climate change by extending their ranges toward the poles or to higher elevations (Parmesan & Yohe 2003). Furthermore, the phenologies of some plants have shifted with leaf expansion and flowering occurring earlier in the spring (Parmesan & Yohe 2003; Root et al. 2003). The main drivers of such changes are increased temperatures (Root *et al.* 2003) and alterations in precipitation patterns (Weltzin *et al.* 2003). Changes in phenology caused by extreme precipitation events have also been experimentally demonstrated (Jentsch *et al.* 2009).

Precipitation can be a major factor driving plant community composition and productivity, especially in arid and semi-arid environments (Knapp & Smith 2001; Hamann & Wang 2006). Heavy precipitation events, the amount of rainfall from heavy events, and the total area affected by drought has increased since the 1960’s as a result of climate change (Solomon *et al.* 2007). Climate change is expected to continue to alter precipitation patterns across the globe, with an increased likelihood of extreme climate events (Solomon *et al.* 2007). The increase in extreme events will likely be caused by warming air temperature, which increases the water holding capacity of the atmosphere. The greater concentration of water vapour in the atmosphere can lead to fewer, more intense precipitation events (Solomon *et al.* 2007). The effects of extreme events are largely unknown (Jentsch & Beierkuhnlein 2008), but may have species, community, or context-dependent effects (Jentsch *et al.* 2009). Studying the effects of frequency and seasonality of precipitation as proposed by Beier et al. (2012) will draw a more complete picture of how climate changes will affect plant communities.

Changing precipitation event frequency and intensity can have important impacts on soil water conditions. Increasing rainfall event size while decreasing frequency in grassland ecosystems may lead to small increases in plant-available soil water during rainfall pulses, while increasing the length and intensity of drought in the interpulse period (Knapp *et al.* 2002). Knapp et al. (2002) found that less frequent rainfall events had a significant positive effect on plant species diversity and aboveground net primary productivity in the tall-grass prairie ecosystem when there was no change in total rainfall amount. One possible mechanism for this effect is the two-phase resource dynamics hypothesis (Goldberg & Novoplansky 1997). Frequency of water pulses have been shown to cause shifting dominance from fast growing to slow growing grass species as the interpulse period increases (Novoplansky & Goldberg 2001). Therefore, the length of the interpulse period may have a significant effect on plant dominance and species diversity (Goldberg & Novoplansky 1997). Besides species-specific drought tolerance traits, nitrogen dynamics in soil will be affected by water pulses.

Nitrogen (N) mineralization is tied to water availability within soil. Bacterial growth increases in a few hours after rewetting dry soil, to growth rates and respiration levels much higher than soils kept constantly moist. It has been shown that approximately 4 days after wetting growth rates return to the same as constantly moist soils (Iovieno & Bååth 2008). This increased activity during a water pulse can cause a 25-30% increase in overall bacterial growth, compared to constantly moist soils (Iovieno & Bååth 2008). Soils that go through drying/rewetting phases are also likely to have an overall decrease in bacterial biomass, with a simultaneous increase in fungal biomass (Bapiri, Bååth & Rousk 2010). Compared to mean annual changes in precipitation, less research has focused on changes in the seasonality and frequency of precipitation events that may arise from climate change. As these changes can affect the plant and microbial communities directly and indirectly, understanding how grasslands will respond to changes in precipitation patterns is essential for sustainable grassland management.

The effect of grazing on plant communities depends on three factors: the seasonal timing of grazing, location on the plant of biomass removal, and intensity of removal. Herbivory by ungulates does not usually kill mature plants but can be extremely detrimental to seedling survival (Crawley 1997). Domestic cattle are kept at higher densities within pastures than wild herbivores. This causes greater grazing intensity on plants making it likely that an individual plant will be grazed more than once. This also means there is less selectivity across the landscape for preferred forage species (Crawley 1997). Clipping treatments, used as a surrogate for grazing, hold the timing and selectivity of biomass removal constant while the severity of removal is determined by the experimental design. Therefore, clipping may be more representative of domestic, rather than wild grazing. A plant's ability to compensate for herbivory depends mainly on timing, with grazing earlier in the growing season allowing more time for the plant to replace biomass and recover lost resources before the dormant season. The amount of stored nutrients, available soil nutrients, and intensity of grazing also influence plant recovery (Crawley 1997). Grazing can change the species composition of a community, with tall, perennial and tussock plants being replaced by annual, short-statured, or stoloniferous plants (Díaz *et al.* 2007).

Stress has been defined as the external constraints that restrict the production of plant biomass (Grime 1977). However, the definition of stress, and the scales at which it may be used, is not without debate (Korner 2003, 2004; Lortie *et al.* 2004; Marrs 2004; Weiher 2004). Disturbance is defined as the partial or total destruction of biomass (Grime 1977). Disturbance also occurs along a continuum of severity from minimal (herbivory or trampling) to complete destruction. Stress and disturbance play a large role in controlling the structure and composition of plant communities (Grime 2001), and the relative importance of these processes may change along productivity gradients due to differences in resource availability. Grazing by both wild and domestic animals is extremely extensive (Asner *et al.* 2004), and therefore is it important to study multiple factors of interest in a community (Knapp *et al.* 2012).

Climate manipulations can affect the plant community on a short-term scale. Changing climate patterns combined with continued grazing have the potential to change productivity, nutrient cycling, relative species abundance and composition of the grassland plant community. Therefore, integrating climate change experiments with natural productivity gradients is a useful way of assessing both short and long-term plant community dynamics (Dunne *et al.* 2004; Fraser *et al.* 2009). Designing a study along a primary productivity gradient allows more informed conclusions to be reached about the effects climate change variables have on plant communities (Weltzin *et al.* 2003).

Understanding the combined stress and disturbance effects of changing precipitation patterns and grazing on the grassland plant community will allow improved grassland conservation and management in the face of global climate change. I tested the interacting effects of precipitation and clipping (a surrogate of grazing) along a natural primary productivity gradient. I asked the following three questions (1) how do variation in seasonality and frequency of precipitation events affect grassland community diversity and productivity? (2) How do precipitation patterns and grazing interact and affect grassland community diversity and productivity along a productivity gradient? (3) How does N availability change with seasonality and frequency of precipitation along a natural productivity gradient?

Methods

Study Site

My study was carried out in Lac du Bois Grassland Protected Area, British Columbia, Canada and an adjacent crown property (Figure 2.1). Lac du Bois is a recreation area 15 000 ha in size containing bunchgrass, ponderosa pine and interior Douglas-fir biogeoclimatic ecological classification (BEC) zones (BC Parks 2007; BECWeb 2012). Sites are located along an elevational gradient positively corresponding to primary productivity.

The lower elevation site is on crown land managed by the Ministry of Environment located at 580 m asl (meters above sea level) (NAD 83, 10U 680869E 5622735N). Soil at this site is classified as Brown Chernozem (van Ryswyk et al. 1966). Vegetation at this site is dominated by the grass *Pseudoroegneria spicata* (Pursh) A. Love, *Poa secunda* J. Presl, and the woody shrub *Artemisia tridentata* Nutt. The middle elevation site is 755 m asl (NAD 83, 10U 0680873E, 5625967N) and the soil at this site is classified as Dark Brown Chernozem (van Ryswyk et al. 1966). Species richness at the middle elevation site is higher than the lower elevation site, and is dominated by *Pseudoroegneria spicata* and *Poa secunda* ssp. *secunda* J. Presl. The upper elevation site is 900 m asl (NAD 83, 10U 0679866E, 5629464N) with Black Chernozem soil (van

Ryswyk et al. 1966). The climax vegetation community is typically dominated by *Festuca campestris* Rydb (also see Chapter 1). Both the middle and upper elevation sites are located within the Lac du Bois Grassland Protected Area (Figure 2.1).

Growing season precipitation measured from May to October at the lower and middle elevations, respectively, were 95.8 mm and 112.4 mm averaged over 2007 and 2008, while the upper elevation had 145 mm in 2007 (Carlyle 2012). Though these recent measurements are lower in total amounts, the same increase in precipitation with elevation was recorded in an earlier paper by van Ryswyk et al. (1966). The increase in precipitation corresponds to changes in soil type, plant community, and increasing productivity with elevation of the sites (Tisdale 1947; van Ryswyk et al. 1966).

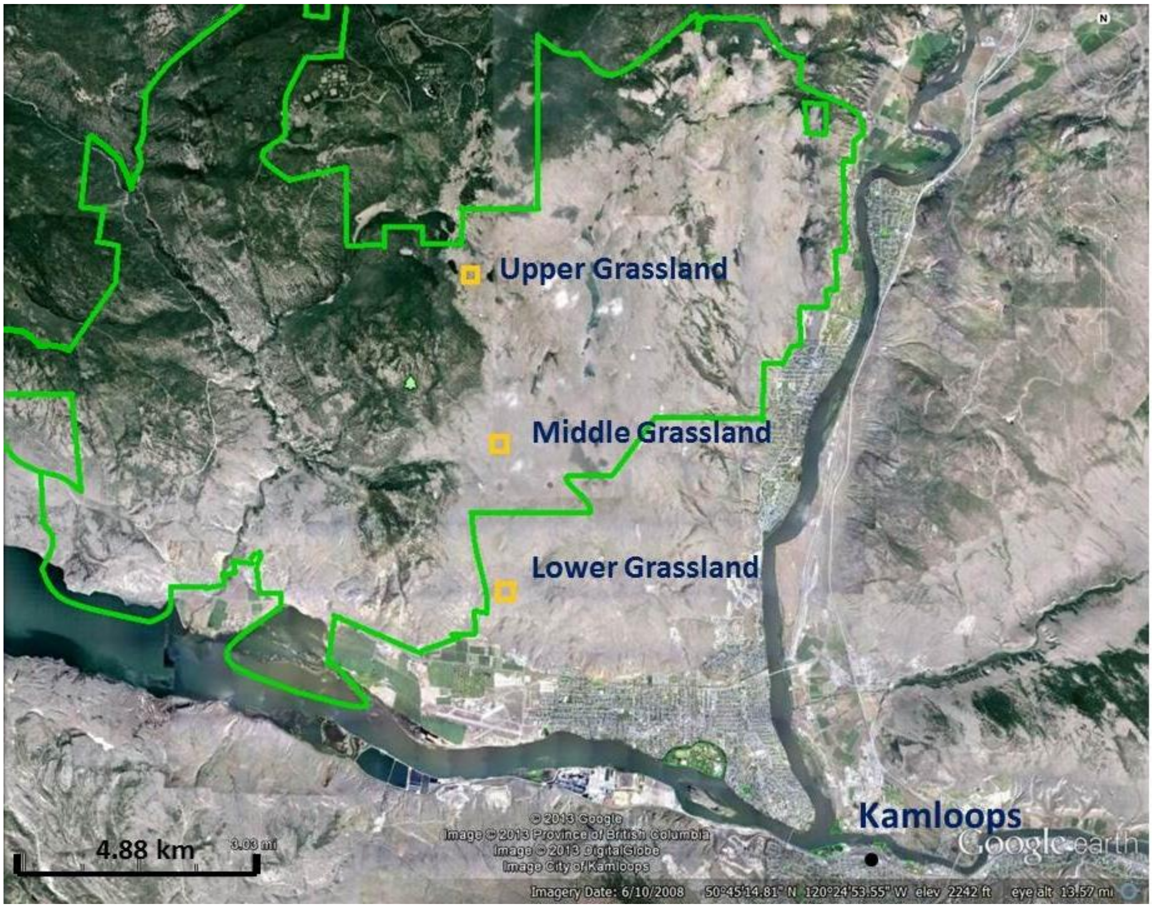

Figure 2.1: Map of Lac du Bois Grassland Provincial Park outlined in light green. Locations of study sites from UTM coordinates are marked with boxes (Lower-, Middle- and Upper Grasslands) (Google Earth 2011).

Experimental design

In April 2010, one cattle exclosure (approximately 30 m x 30 m) was erected at each of three sites by the Agriculture and Agri-Food Canada Kamloops office (Figure 2.2). Experimental plots within the exclosures were set up and treatments started the first week of May 2010. Plots were 1 x 1 m square with an average of 1 m between plots (minimum of 0.5 m). Sagebrush (*Artemisia tridentata*) plants were deliberately avoided and any shading from sagebrush onto plots was minimized. This was done purposefully as the research questions focused on the herbaceous plant community. All sites were in areas grazed by cattle in previous years.

Two treatment types, hand watering and clipping, were applied to study the effects of precipitation change and grazing on the grassland plant community in 2010 and 2011. All watering treatment plots were covered with temporary rainout shelters (RS) in both spring (May-June) and fall (September-October), to block the majority of natural precipitation on the watering treatment plots. Unmanipulated ambient precipitation (control) plots were not covered by RS's. The RS's were removed from plots during July and August, and were similar in design to Kochy & Wilson (2004) and Carlyle et al. (2011) (Figure 2.3). The shelter consisted of a thin sheet of plastic (Tufflite IV™ 6mil Polyethylene film, Tyco Plastics and Agricultural Films Monroe, LA, USA) attached to four wooden stakes at the corners of the plot. The plastic was anchored at 1 m height on the north-west side of the plot, and at 30 cm on the other three corners. Aside from the unmanipulated control plots, four combinations of watering treatments were applied by hand watering: 1) spring watering applied every week, 2) spring watering applied every four weeks (monthly), 3) fall watering applied every week, 4) fall watering applied every four weeks (monthly). The water addition amount was a 50% increase in the historical 30-year average for the respective month of watering (Table 2.1). Water addition was applied slowly to minimize surface runoff.

Disturbance was achieved by clipping biomass to 5 cm above the soil or litter surface to simulate heavy grazing by cattle (Brown & Archer 1999; Carlyle 2012). All treatments were applied in a fully factorial design, creating 10 treatment and control plots in a block. Blocks were replicated six times at each of three sites to control for spatial heterogeneity within a site. Treatments were randomly assigned to plots within each block.

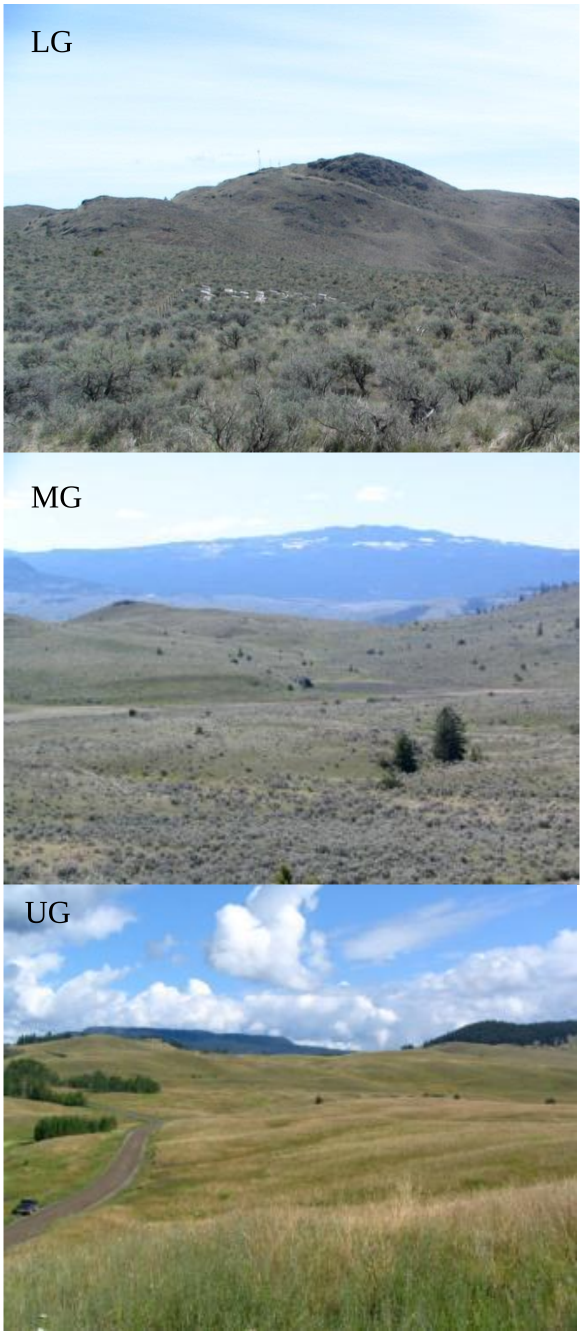

Figure 2.2: Lower (LG), middle (MG) and upper (UG) grasslands at or near study sites. Cover, biomass, species richness and diversity, and precipitation increase with elevation.

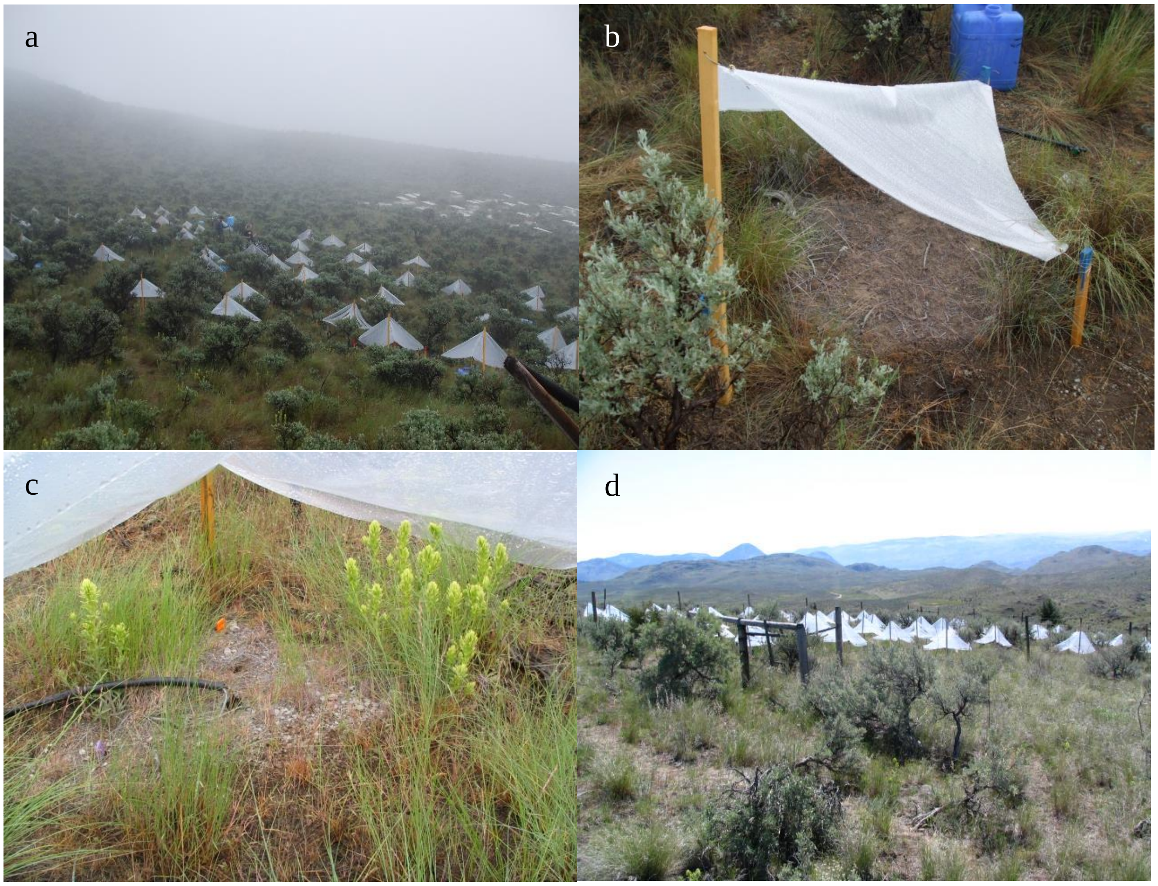

Figure 2.3: Design and performance of rainout shelters (RS) at lower grassland site (a and b) and middle grassland (c and d). Soil moisture and temperature probes, and PRS™-probe (orange) visible in (c).

Table 2.1 Water amounts added to plots for the 1 week and 4 week treatments in the respective month of addition. Average precipitation was based on historical (1971-2000) data (Environment Canada 2012).

	May	**June**	**September**	**October**
Average Precipitation (mm)	24.4	35.2	28	16.2
50% increase (mm):	36.6	52.8	42	24.3
Amount per 1 week (L):	9.15	13.2	10.5	6.075
Amount per 4 weeks (L):	36.6	52.8	42	24.3

Measurements

Percent cover estimates of each species present were used to determine plant community composition of each treatment and control plot. Estimates were performed after peak biomass accumulation, starting early July 2010. The sampling area was the centre 50 x 50 cm (0.25 cm^2) of each plot. This left a 25 cm border between the plot edge and sampling area to account for edge effects. In a similar study, Yahdjian & Sala (2002) found edge effects extending up to 20 cm under the rainout shelters; therefore, the 25 cm border was considered an adequate buffer.

Clipping occurred after spring watering treatments were completed, at the height of the growing season in July and August 2010, and July 2011. Clipped biomass was discarded from plots. Biomass and litter were collected at the end of the second field season in November 2011. This was approximately 4 months after clipping treatment was applied. Biomass from the centre 0.25 m^2 sampling area was clipped to soil surface, sorted to species, dried at 65°C for two days, and weighed.

Soil moisture as volumetric water content (VWC) and temperature (°C) measurements were logged every half hour from May through October. Moisture and temperature probes were placed in one block at each of the three sites. Soil moisture probes (Soil Moisture Smart Sensor, S-SMB-M005 using an $ECH_2O^{®}$ Dielectric Aquameter probe, Decagon Devices, Inc.) were 10 cm long and placed vertically into the soil. Measurements were averaged over the length of the probe. The probes were connected to a HOBO® Micro Station data logger or Weather Station data logger, Onset Computer Corporation. Soil moisture data was calibrated for soil type as in Carlyle (2012). Soil temperature probes (TMC50-HD, connected to a HOBO® U12 Data Logger, Onset Computer Corporation) were placed approximately 5 cm below the soil surface.

Plant-available nitrogen (N) was measured using Plant Root Simulator (PRS)™-probes (Western Ag Innovations Inc 2010) placed in two replicate blocks per site. These probes consisted of an ion-replacing membrane held in a plastic frame (15 cm x 2.5 cm x 0.5 cm) that captured free ions in the soil. N forms of interest were nitrate (NO_3^-) and ammonium (NH_4^+). Two probes were needed for each analysis – one that captured and replaced anions (NO_3^-), and one for cations (NH_4^+). Probes were replaced every sixty days, according to the three measurement seasons of spring, summer and fall. The three sets of probes allowed a continuous measurement of soil N dynamics over the entire six-month study season.

A second method of analyzing N in the plot soils was done to test the correlation between extractable NO_3^- and NH_4^+ to the relative amounts measured by PRS™-probes. Samples of the 0-15 cm soil surface were collected from the same plots as the probes in early November 2011, shortly after the final watering treatments were completed. Samples were air dried then sieved using a 2 mm mesh. Separate sub-samples were oven-dried to allow for the results to be corrected to and reported on an oven-dry basis. The samples were extracted for 1 hour at a ratio of 2.5 g soil: 25 ml 2N KCl and the centrifuged extracts analyzed for available NH_4^+- N and NO_3^--N using an OI-Analytical "Alpkem FSIV" segmented flow analyzer. Analysis was performed at the Technical Services Laboratory for the BC Ministry of Environment (Ministry of Environment 2012).

Statistical analysis

Study design allowed three-way analysis of variance (ANOVA) using site, watering treatment and clipping as factors to be tested on the data from 2010 and 2011; cover, species richness, and Simpson's and Shannon-Weiner diversity indices, biomass, litter, biomass and litter combined. Species richness, Simpson's and Shannon-Weiner diversity indices were determined from cover estimate data. Biomass and 2011 cover were also analysed separately by each site. Data were either natural log +1 transformed or square root transformed to meet the ANOVA assumption of equality of variances. This usually resulted in normalized distributions for the data; in the instances where it did not ANOVA is robust to deviations of normality. Tukey's HSD tests were performed on the data after ANOVAs if there were significant treatment effects. Soil moisture and temperature were analysed using a repeated-measures ANOVA.

Two types of soil N measurements were analysed, PRS™– probe N and soil extractable N. The PRS™ data had four factors of interest; site, water treatment, clipping and season of measurement, and three replicate measurement seasons; spring, summer, and fall. Therefore the Akaike Information Criterion (AIC) stepwise test was used to determine the best model for a repeated measures ANOVA. The soil extractable N data was analysed using a three-way ANOVA followed by a Tukey's HSD test. A correlation was performed on the PRS™ – probe N and extractable N data.

All analyses were performed using R (version 2.15.2) (R Development Core Team 2012) packages 'car'(Fox & Weisberg 2011) and 'vegan' (Oksanen *et al.* 2011).

Results

Soil Moisture

Data were analysed using a repeated measures ANOVA on measurements taken in 2011 (Figure 2.4). Daily mean and variance were analysed for each site separately with watering and clipping treatments as factors. No interactions were analysed.

The lower grassland showed an effect of watering treatment for daily mean ($F = 11.290$, $df = 5$, $P = 0.009$), with the weekly fall water treatment having a higher VWC than all other plots at 19.2 %, followed by the ambient control plot at 17.2%. Daily variance was also significant ($F = 17.689$, $df = 5$, $P = 0.003$), with weekly fall watering lower than ambient. There was no effect of clipping.

Spring, summer and fall seasons were also analysed separately. Daily mean VWC was affected by watering in all three seasons. In the spring, fall watered plots were lower at 14.6 and 15.1 % VWC than either spring watered or ambient ($F = 15.942$, $df = 5$, $P = 0.004$). During the summer, spring plots watered weekly and fall plots watered monthly were lower than the others, at 16.1 and 16.3 % VWC, respectively ($F = 7.614$, $df = 5$, $P = 0.022$). During the fall, spring watered plots were lower than the others at 6.3 and 7.7 % VWC, respectively ($F = 85.097$, $df = 5$, $P \leq 0.001$). During the summer, the clipping treatment increased soil moisture from 16.8 % in the ambient control plot to 18.1 % VWC ($F = 6.041$, $df = 1$, $P = 0.057$). Daily variances by season were also affected by water treatment, indicating fall RS's decreased variability in the spring ($F = 8.848$, $df = 5$, $P = 0.016$), weekly spring and monthly fall watering decreased variability during the summer ($F = 8.177$, $df = 5$, $P = 0.019$), while fall watering increased moisture variability in the fall ($F = 323.042$, $df = 5$, $P \leq 0.001$).

Daily mean VWC in the middle grassland was not significantly affected by either watering or clipping treatments. However, watering had a significant effect on daily variance (F = 4.684, df = 5, P = 0.089), where it appears that fall watering increased variability from the ambient 0.66 to 0.85 and 0.91 for weekly and monthly watering, respectively. Spring, summer and fall seasons were also analysed separately. There were no significant effects of either watering or clipping in the spring or summer, but watering caused significant increase in VWC in the fall season (F = 11.111, df = 5, P = 0.018). Water treatment had a significant effect on the variance of VWC data in both spring and fall (spring: F = 10.982, df = 5, P = 0.010; fall: F = 11.642, df = 5, P = 0.017).

The upper grassland showed less response to water manipulations. Daily mean VWC was not affected by either watering or clipping treatments, but clipping caused a significant decrease on daily variance, from 1.4 in the unclipped to 1.2 in the clipped plot (F = 6.585, df = 1, P = 0.050). There was no effect of either treatment on daily mean VWC in spring or summer, but there was an increase in VWC from weekly and monthly fall watering in the fall season compared to control and spring watered plots (F = 5.961, df = 5, P = 0.086). Daily variance, however, was affected by the watering treatment in both spring and fall (spring: F = 4.806, df = 5, P = 0.055; fall: F = 37.226, df = 5, P = 0.007).

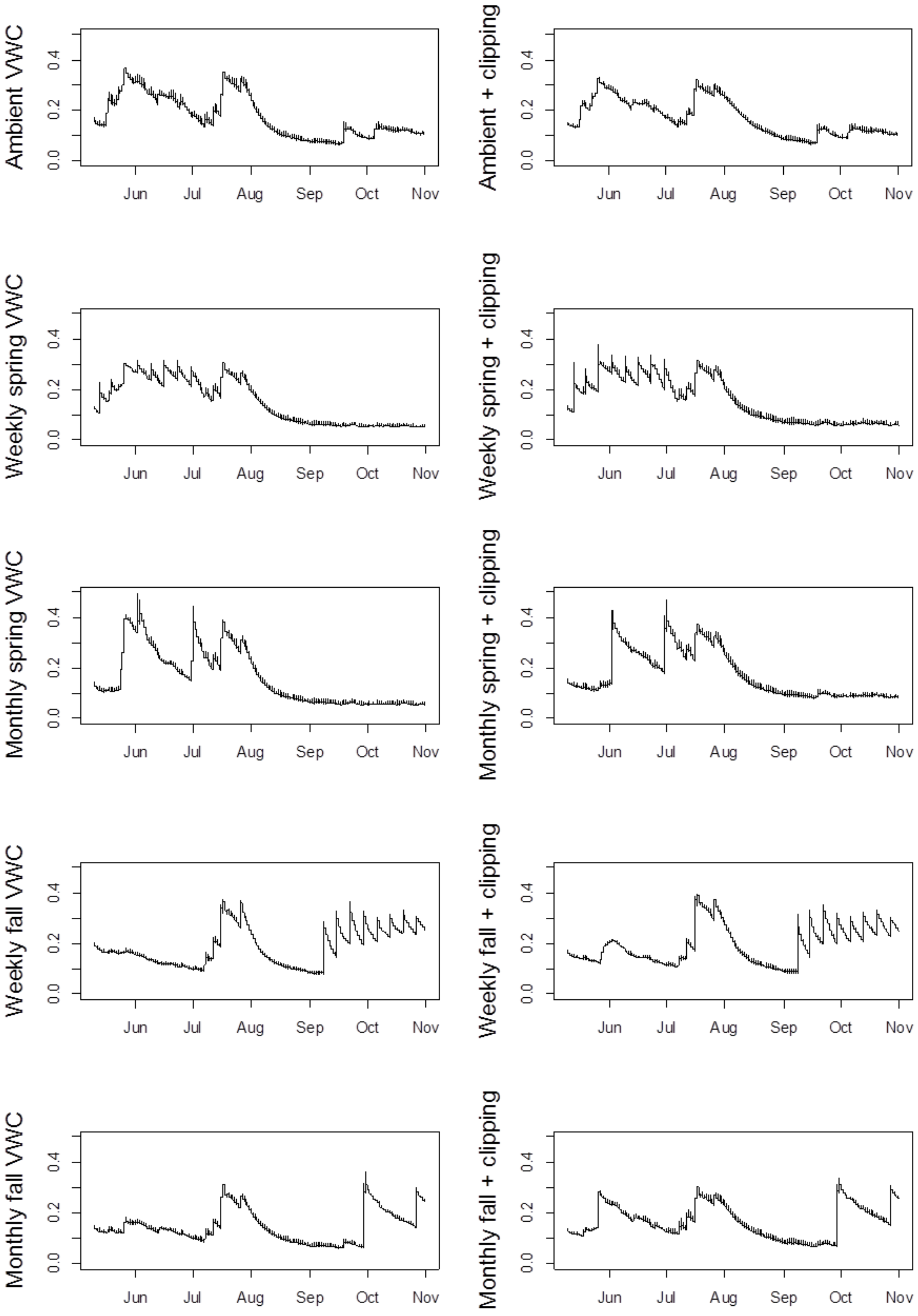
Ambient VWC
Ambient + clipping
Weekly spring VWC
Weekly spring + clipping
Monthly spring VWC
Monthly spring + clipping
Weekly fall VWC
Weekly fall + clipping
Monthly fall VWC
Monthly fall + clipping
0.0
0.2
0.4
Jun
Jul
Aug
Sep
Oct
Nov

Figure 2.4: (Previous Page) Lower grassland volumetric water content (VWC) in ambient (control) and watering treatment plots (spring/ fall, weekly/ monthly). Figures on the left are measurements from unclipped plots, while those on the right are measurements from clipped plots.

Soil Temperature

Data were analysed using a repeated measures ANOVA on measurements taken in 2011. Daily mean and variance were analysed for each site separately with watering and clipping treatments as factors. No interactions were analysed. Seasons (spring, summer and fall) were also analysed separately. In the lower grassland, there were no significant effects of either water or clipping treatment on daily mean or variance. Nor were there effects of water or clipping on daily mean or variance in the spring and summer seasons, and daily mean in the fall. However, fall variance was significantly affected by both watering treatment (F = 5.210, df = 4, P = 0.069) and clipping (F = 6.253, df = 1, P = 0.067). The variance of the control (ambient precipitation) plot was 47.338, which was similar to both spring watering treatments (weekly: 51.727, monthly: 44.546), and the monthly fall treatment at 41.728. However, the weekly fall watering treatment had a much higher variance of 88.833. The unclipped treatment plots had variances of 45.620, while clipped plots were 64.208.

There was an error in two probes in the middle grassland resulting in no logged values for the monthly spring watering treatment. The repeated measures ANOVA did not show significant effects of daily mean or variance across the whole season. However, summer daily mean was affected by both water (F = 6.485, df = 3, P = 0.0795) and clipping (F = 12.980, df = 1, P = 0.0367) treatments. It appears that watering decreased soil temperature from the ambient 22.2°C, to 21.2°C and 21.4°C in the weekly spring and fall watered plots, respectively. Clipping increased temperature to an average 21.9°C compared to the unclipped plots of 21.3°C. Fall daily mean was also affected by water (F = 18.230, df = 3, P = 0.020) and clipping (F = 6.465, df = 1, P = 0.085) treatments. Clipping, as was seen in the summer, increased temperature from the ambient 13.1°C to 13.3°C. The significant watering factor indicates that the spring watering treatments, which are under RS's in the fall, have higher mean temperatures at 13.9°C than the ambient (13.0°C) or fall watering treatments (weekly: 12.8°C, monthly: 13.2°C). There were no significant effects on mean or variance in any time period in the upper grassland. This includes the whole six-month season, and each season analysed separately.

Cover

Site, watering treatment, and block were used in a three-way ANOVA on 2010 cover estimates. Site was the only significant factor ($F = 63.239$, $df = 2$, $P \leq 0.001$). Neither watering treatment nor block had any significant effects. Blocking, to account for site heterogeneity, was not included in any further analyses as no differences were seen between blocks within sites. Clipping treatment was not included in the analysis, as the clipping treatment was applied after the cover estimates were recorded in 2010. According to the Tukey's HSD test, the upper grassland site had more cover than both lower and middle sites ($P \leq 0.001$), which were not different from each other ($P = 0.709$) (Figure 2.5 (a)).

For 2011 data, cover of all sites increased with elevation in the three-way ANOVA ($F = 168.722$, $df = 2$, $P \leq 0.001$) and Tukey's ($P \leq 0.001$ for all) (Figure 2.5 (b)). Clipping also significantly decreased cover ($F = 10.760$, $df = 1$, $P = 0.001$), but no interactions were significant.

Grassland sites were also analysed separately for the 2011 data. Clipping caused a significant decrease in the lower ($F = 9.501$, $df = 1$, $P = 0.003$) and middle sites ($F = 3.577$, $df = 1$, $P = 0.064$), but not in the upper grassland. Neither watering treatments nor interactions were significant in any grassland community.

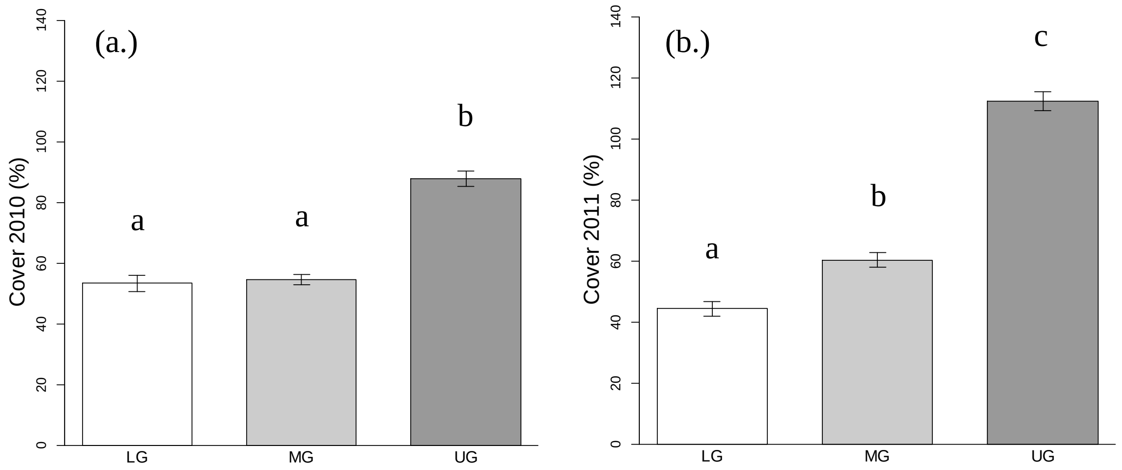

Figure 2.5: Combined cover of all species present from (a.) 2010 and (b.) 2011 estimates. Letters indicate site differences in the Tukey's HSD test.

Biomass

The three-way ANOVA showed there was a significant effect of site (F = 76.241, df = 2, $P \leq 0.001$) and clipping (F = 178.771, df = 1, $P \leq 0.001$) at the end of two years of field treatments. No other factors or interactions were significant. Tukey's test showed there was no significant difference in biomass between the lower and middle grasslands (P = 0.679), while the upper grassland had higher biomass than the others ($P \leq 0.001$ for both; Figure 2.6 (a)). Clipping decreased biomass in all sites.

Grassland sites were also analysed separately. As with the grouped analyses, only clipping decreased biomass at each site (LG: F = 51.352, df = 1, $P \leq 0.001$; MG: F = 81.314, df = 1, $P \leq 0.001$; UG: F = 60.141, df = 1, $P \leq 0.001$).

Litter

Litter data were natural log transformed to meet assumptions of equal variances, although the transformation did not normalize the data. Factors of site, clipping and water were used in the three-way ANOVA. Site (F = 234.718, df = 2, $P \leq 0.001$), clipping (F = 5.255, df = 1, P = 0.023), and a site: clipping interaction (F = 3.637, df = 2, P = 0.029) were all significant. The Tukey's test showed litter was significantly different at each site ($P \leq 0.001$; Figure 2.7 (a)), and clipping caused a significant decrease in litter. For the site x clipping interaction, clipping caused a significant decrease only in the lower grassland ($P = 0.037$). There was no difference in clipping treatment for either the middle ($P = 0.520$) or upper ($P = 0.975$) grassland sites. The lower and middle grassland unclipped treatments were significantly different from each other ($P = 0.063$).

Biomass & Litter:

Data was natural log transformed but this transformation did not normalize the data or equalize the variances to an $\alpha = 0.05$ significance level, however the variances had less than a 3x difference from each other which are acceptable variance values for ANOVA. Site was a significant factor ($F = 199.779$, $df = 2$, $P \leq 0.001$), as was clipping ($F = 60.177$, $df = 1$, $P \leq 0.001$). There was also a site x clipping interaction ($F = 8.493$, $df = 2$, $P \leq 0.001$). According to the Tukey's all sites were significantly different from each other ($P \leq 0.006$ for all). Clipping caused a decrease in combined biomass and litter ($P \leq 0.001$). For the site x clipping interaction, clipping significantly reduced biomass and litter only in the lower ($P \leq 0.001$) and middle ($P \leq 0.001$) grasslands (Figure 2.7 (b)). The upper grassland site had much higher cover, biomass, and litter than either the lower or middle grasslands. The combined biomass and litter collected from the upper grassland was approximately 687 g/m^2, compared to 127 g/m^2 and 152 g/m^2 for the lower and middle grasslands.

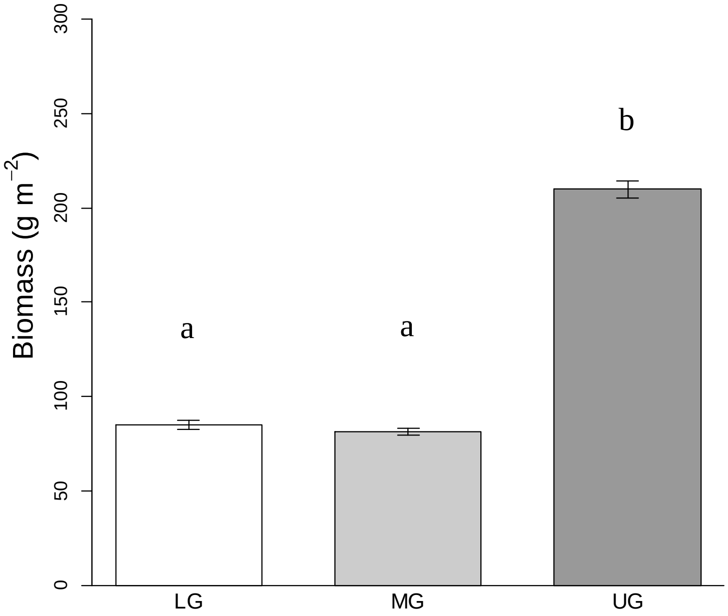

Figure 2.6: Biomass for lower (LG), middle (MG), and upper (UG) grasslands, water and clipping treatments grouped. Letters indicate significant differences between sites from the Tukey's. Bars are means (g m^{-2}) ± SE.

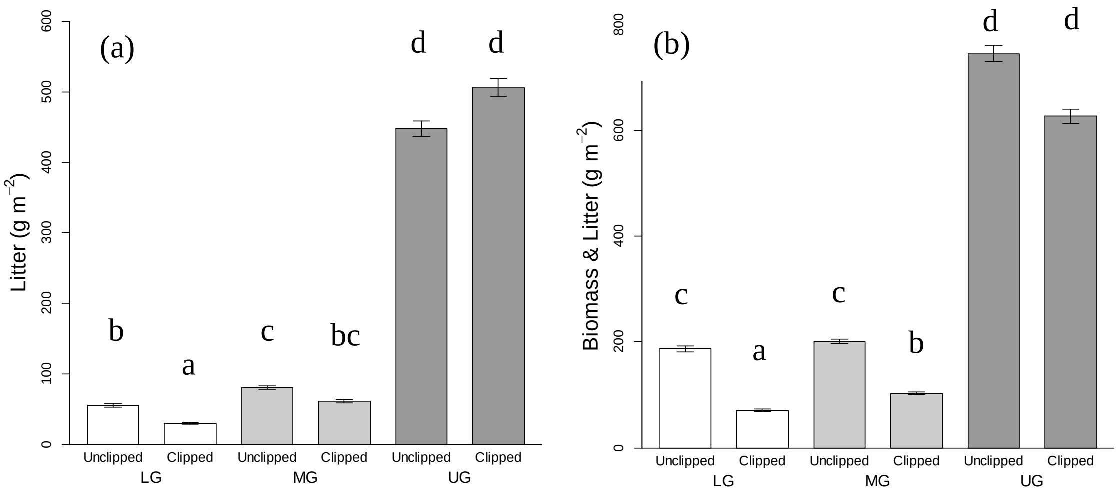

Figure 2.7: Interacting effects of site x clipping on (a) litter, and (b) biomass + litter (mean g m^{-2} ± SE). Letters indicate significant differences between sites and clipping treatments, note differences in y-axis scales.

Functional Groups

To determine effects of treatments on different functional groups in the plant community, data from cover estimates and biomass collection in 2011 were divided into four groups; graminoids, forbs, legumes and shrubs. Cover estimates were made immediately before the clipping treatment was applied, and therefore reflect the clipping treatment from the 2010 growing season. Biomass was harvested in November 2011, approximately 4 months after the clipping treatment was applied and reflects two years of clipping treatments. MANOVA results showed a significant effect of site (Pillai = 0.965, F = 34.465, $P \leq 0.001$) and clipping (Pillai = 0.192, F = 8.744, $P \leq 0.001$) on cover. There was a similar pattern for biomass (site: Pillai = 0.579, F = 15.067, $P \leq 0.001$; clipping: Pillai = 0.428, F = 27.511, $P \leq 0.001$), with a significant site: clipping interaction (Pillai = 0.208, F = 4.292, $P \leq 0.001$). The univariate test for each variable was then performed. Significant results are listed in Table 2.2. Site factors showed a consistent increase of cover and biomass in all functional groups with elevation and a general decrease with clipping. Graminoids showed the clearest response to treatments (Figure 2.8 (a) and Figure 2.9 (a)), with forbs following the same trend (Figure 2.8 (b) and Figure 2.9 (b)). While legume cover showed a significant interaction between water and clipping in the ANOVA (F = 2.072, df = 4, P = 0.087), the Tukey test did not show any significant differences, and there was no effect for biomass.

Table 2.2: ANOVA results: F and P values on cover and biomass (2011) for functional groups. Only significant values (P ≤ 0.1) are shown.

		Cover			Biomass		
Functional group	Factors	df	F value	P value	df	F value	P value
Graminoids	Site	2	52.209	≤ 0.001	2	52.593	≤ 0.001
	Clipping	1	32.845	≤ 0.001	1	94.266	≤ 0.001
	Site x Clipping	2	NS	NS	2	4.853	0.009
Forbs	Site	2	89.459	≤ 0.001	2	13.009	≤ 0.001
	Clipping	1	NS	NS	1	21.388	≤ 0.001
	Site x Clipping	2	NS	NS	2	8.135	≤ 0.001
Legumes	Site	2	48.550	≤ 0.001	2	6.325	0.002
	Clipping	1	2.758	0.099	1	15.114	≤ 0.001
	Water x Clipping	4	2.072	0.087	4	NS	NS
	Site x Clipping	2	NS	NS	2	6.016	0.003
Shrubs	Site	2	18.037	≤ 0.001	2	5.869	0.004

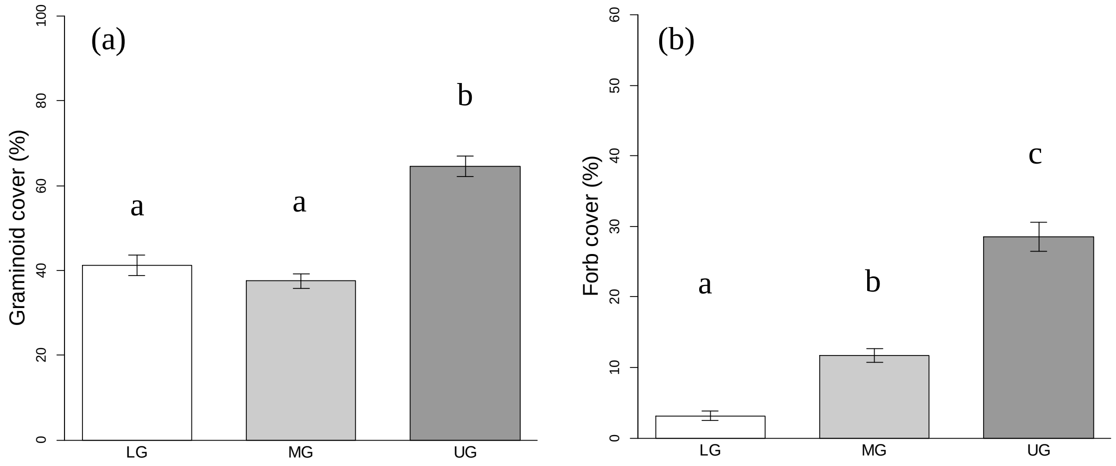

Figure 2.8: Graminoid cover (a) and forb cover (b) for 2011 by site, water and clipping treatments grouped. Note differences in y-axis scales. Letters indicate significant differences in the Tukey's; bars are means ± SE.

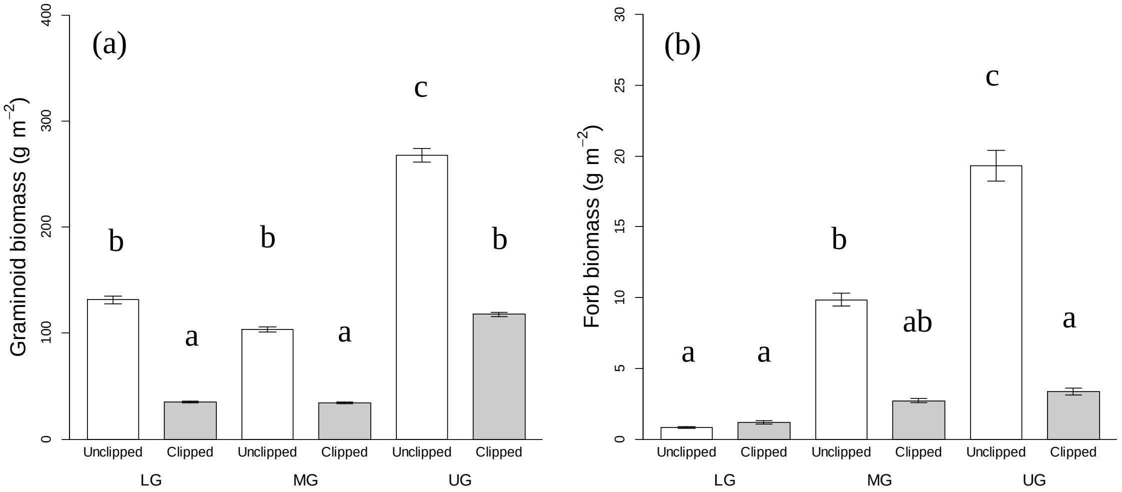

Figure 2.9: Interacting effects of site x clipping on (a) graminoid biomass and (b.) forb biomass for 2011, water and clipping treatments grouped. Bars are means ± SE, note differences in y-axis scales. Letters indicate significant differences between treatments.

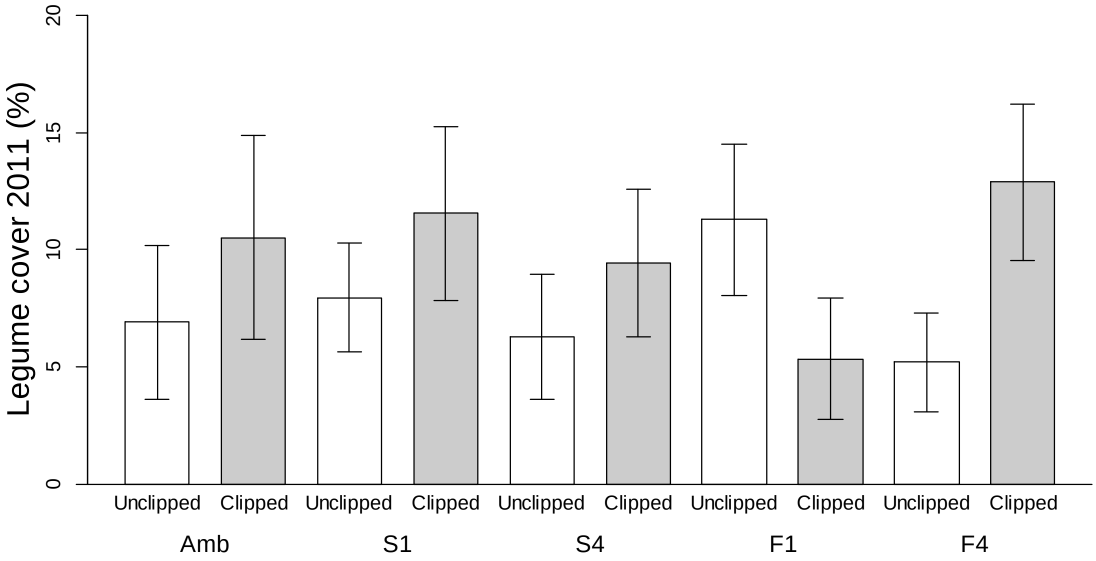

Figure 2.10: Interacting effects of watering treatment x clipping on legume cover for 2011. Amb = ambient rainfall; S1 = weekly spring watering; S4 = monthly spring watering; F1 = weekly fall watering; F4 = monthly fall watering. Bars are means ± SE.

Species Richness

Data were not normally distributed, but had equal variances (P = 0.196), so were not transformed. Clipping had not been applied as a treatment in the 2010 prior to the

2010 estimates, and therefore was not included in the ANOVA with the site and watering factors. Site was the only significant factor at $P \leq 0.001$ (df = 2, F = 88.057). From the Tukey's, species richness was significantly less in the lower grassland compared to either the middle or upper grassland ($P \leq 0.001$ for both), and was not significantly different between the middle and upper sites (P = 0.588).

For the 2011 measurements, site, clipping, and water were factors in the three-way ANOVA. Site and clipping were both significant at $P \leq 0.001$ (df = 2, F = 106.500) and $P \leq 0.008$ (df = 1, F = 7.116). According to the Tukey's, species richness was significantly lower in the lower grassland compared to either middle or upper grasslands ($P \leq 0.001$ for both). The difference between middle and upper grasslands was significant with P = 0.089. Clipped plots had higher species richness than unclipped (P = 0.009) (Figure 2.11), there were no significant interactions. To determine if any changes occurred in species richness between years, the difference between 2011 and 2010 was also analysed. There were no significant effects.

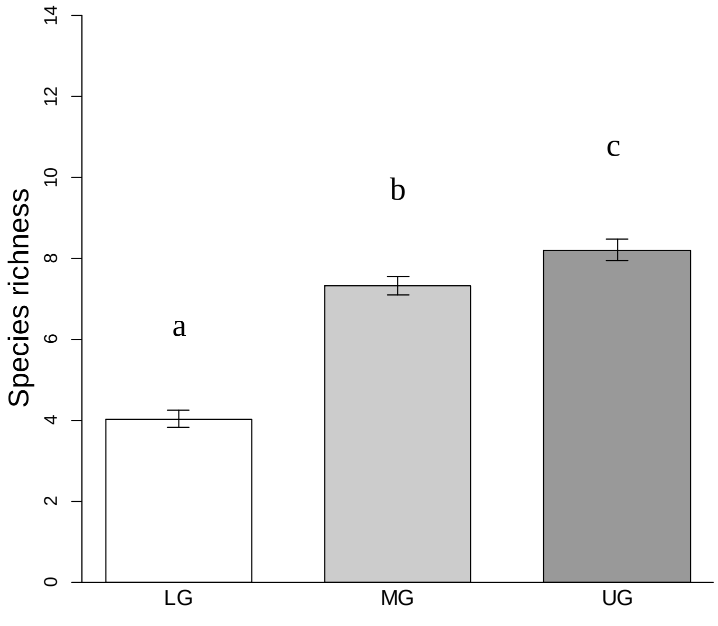

Figure 2.11: Species richness (mean ± SE) by site for 2011, water and clipping treatments grouped. Bars are means ± SE, letters indicate significant differences between sites.

Diversity Indices

Simpson's diversity index data could not be transformed to satisfy assumptions of equal variances or normality. As the ANOVA is robust to these deviations it was used anyway. A non-parametric alternative (Friedman's test) is sensitive to non-equal variances, so was inappropriate to use.

Data for 2010 and 2011 were analysed separately. In 2010 Simpson's diversity increased with elevation (ANOVA: $F = 112.774$, $df = 2$, $P \leq 0.001$; Tukey's: $P \leq 0.001$ for all). In 2011 Simpson's diversity again increased with elevation ($F = 214.831$, $df = 2$, $P \leq 0.001$), and there was a site x clipping interaction ($F = 2.385$, $df = 2$, $P = 0.096$). Clipping was not significant in either the ANOVA or Tukey's tests. The site x clipping interaction in the ANOVA indicates that Simpson's diversity decreased with clipping in the LG, but increased with clipping in the UG (Figure 2.12). However, the Tukey's HSD test did not show a significant interaction.

To determine if any changes occurred in Simpson's diversity between years, the difference between 2011 and 2010 was also analysed. The upper grassland had a higher increase in the Simpson's diversity index than either lower or middle grasslands (ANOVA: $F = 47.868$, $df = 2$, $P \leq 0.001$; Tukey's: $P \leq 0.001$ for both) (Figure 2.13).

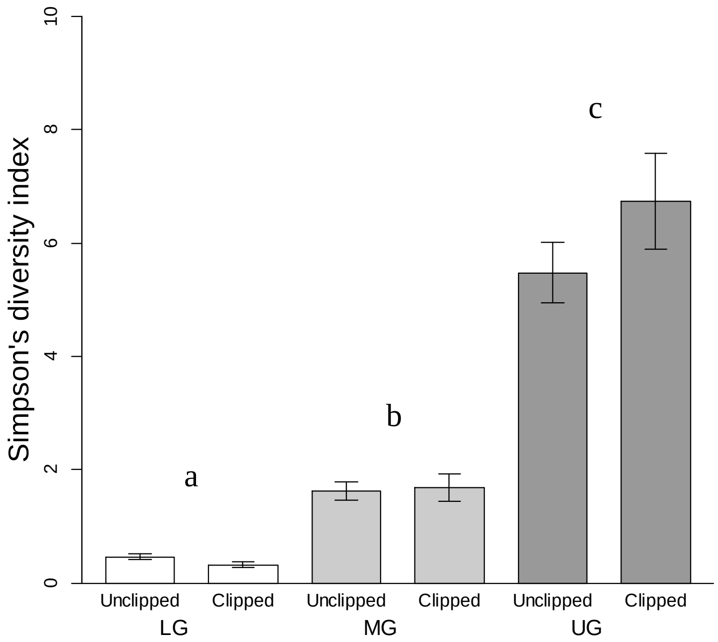

Figure 2.12: Simpson's diversity index (means ± SE) on cover estimates, 2011. Letters indicate significant differences between sites.

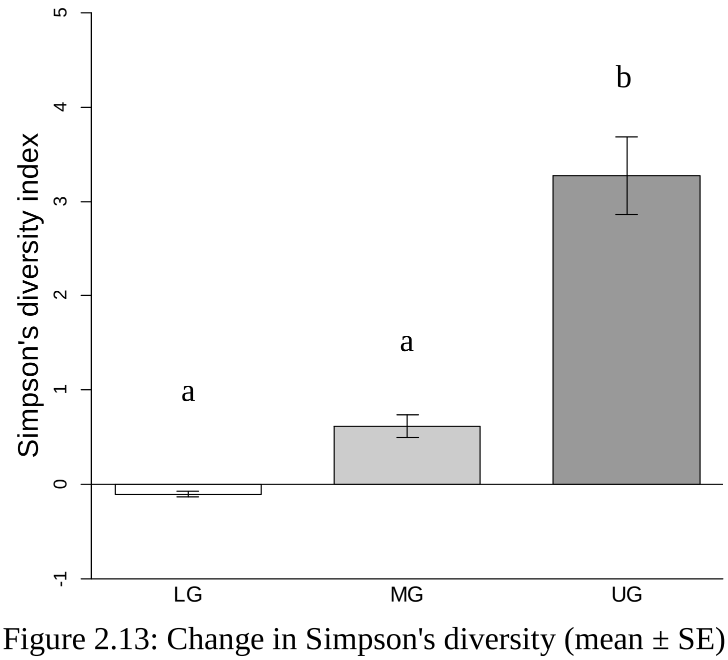

Figure 2.13: Change in Simpson's diversity (mean ± SE) from 2010 to 2011, water and clipping treatments grouped. Positive values are an increase in diversity, negative are a decrease. Letters indicate significant differences between sites.

The Shannon-Weiner diversity index data did not need to be transformed. Data from 2010 and 2011 were analysed separately. As clipping had not yet been applied at the time of the 2010 estimates, this factor was not included in the ANOVA. Diversity was lower in the lower grassland than either middle or upper grasslands (ANOVA: F = 109.684, df = 2, P ≤ 0.001; Tukey's: P ≤ 0.001 for both), which were not different from each other (P = 0.354). In 2011 the lower grassland had lower diversity than either the middle or upper (ANOVA: F = 171.558, df = 2, P ≤ 0.001; Tukey's: P ≤ 0.001 for both), which were not significantly different from each other (Figure 2.14). Clipping increased Shannon-Weiner diversity overall (F = 14.568, df = 1, P ≤ 0.001).

To determine if any changes occurred in species richness between years the difference in diversity between 2011 and 2010 was analysed. An ANOVA was performed on this data, and showed both site (F = 2.701, df = 2, P = 0.070) and clipping (F = 4.140, df = 1, P = 0.044) as significant factors. According to the Tukey's, the upper grassland had higher species richness than the lower (P = 0.085; Figure 2.15), and clipping increased diversity (P = 0.044).

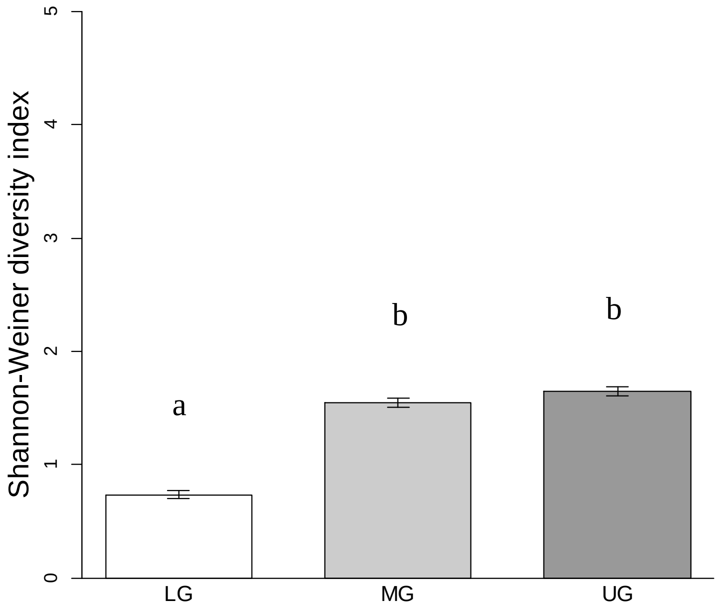

Figure 2.14: Shannon-Weiner diversity index (mean ± SE) for site in 2011, water and clipping treatments grouped. Letters indicate significant differences between sites.

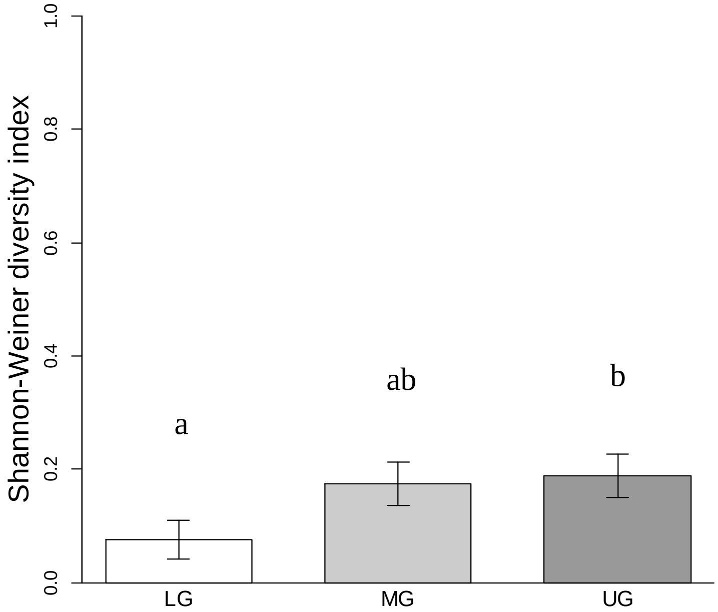

Figure 2.15: Change in Shannon-Weiner diversity index between 2010 and 2011. Positive values show an increase in diversity. Letters indicate significant differences between sites.

Nitrogen

Data from the 2011 PRS™- probes were natural log +1 transformed to satisfy the assumption of normality of variances, although this did not normalise the data. PRS™-probes were placed in spring 2011 and replaced at the start of the summer and fall in the same spots allowing a continuous measurement of N over three seasons. The lowest scoring AIC model used all four factors (site, watering treatment, clipping, season of measurement) and interactions of; site x season, water x season, site x clipping, season x clipping, and the three-way interaction of site x season x clipping. The same plots were sampled three times – once per season of measurement – so a repeated measure ANOVA was performed on the data followed by a Tukey's HSD, with the above factors and interactions. Watering treatment and season of measurement were significant factors in the ANOVA (F = 4.910, df = 4, P = 0.002; F = 72.947, df = 2, $P \leq 0.001$, respectively). From the Tukey's, the weekly spring watering treatment had lower N than the other water treatments, but not ambient control. N increased with each successive season ($P \leq 0.009$

for all). There were also interactions between site and season (F = 4.309, df = 4, P = 0.003; Figure 2.16), watering and season (F = 2.058, df = 8, P = 0.048; Figure 2.17), and a three-way interaction between site, season and clipping (F = 3.106, df = 4, P = 0.019). The three-way interaction indicates that in the spring, upper grassland clipped plots were significantly lower than all other treatment combinations, and the spring measurements were generally lower than all others. The highest measurements were from the fall, regardless of clipping treatment or site (Figure 2.18).

Soil samples were also analysed at the Technical Services Laboratory with the Ministry of Environment (2012) for NO_3^- and NH_4^+. These combined measurements (for total N) were log +1 transformed. Site, watering treatment and clipping were used in the ANOVA, followed by a Tukey's HSD test. The amount of N (mg Kg^{-1}) increased by site with elevation (F = 12.091, df = 2, $P \leq 0.001$) and increased with clipping treatment (F = 2.993, df = 1, P = 0.096; Figure 2.19). No interactions were significant.

To compare the results of the PRS™- probe measurements with the total N extracted from the soil, a correlation was run between the datasets. The correlation coefficient of the log-transformed data was 0.180 (Figure 2.20).

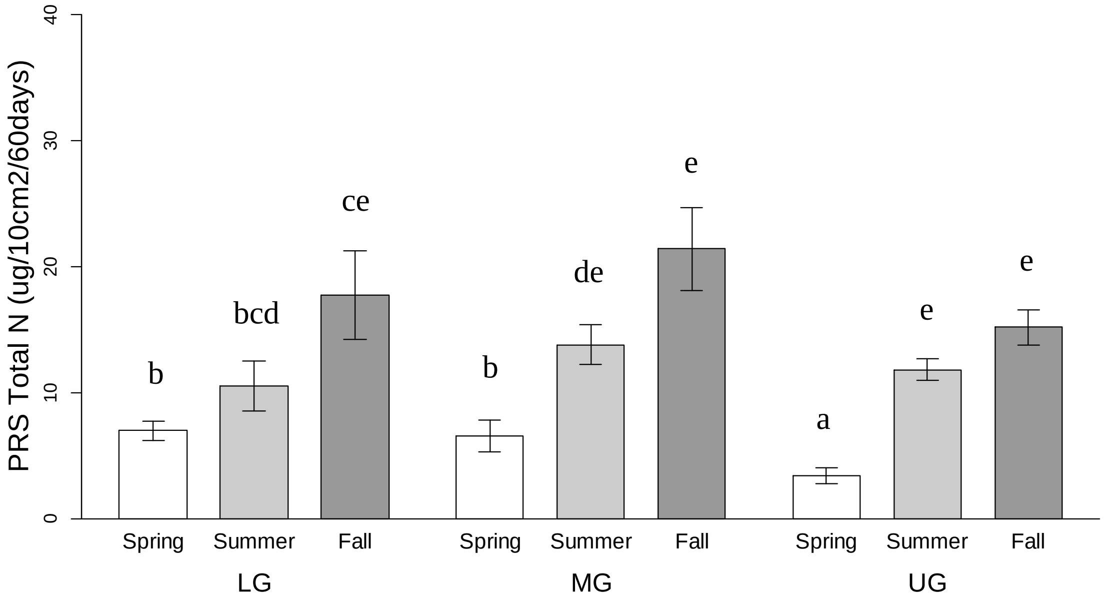

Figure 2.16: PRS™ – probe data from 2011 showing site x season of measurement interactions. Bars are means ± SE, different letters indicate significant differences between treatments.

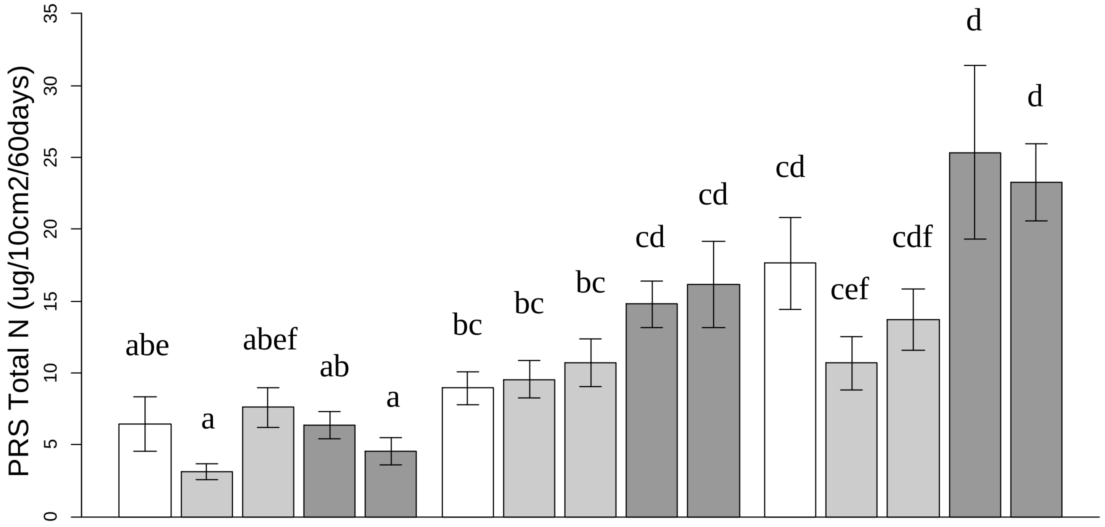

Figure 2.17: PRS™ – probe total N amounts by season of measurement (spring, summer, fall), and watering treatment (Amb = ambient rainfall; S1 = weekly spring watering; S4 = monthly spring watering; F1 = weekly fall watering; F4 = monthly fall watering). Bars are means ± SE, different letters indicate significant differences between treatments.

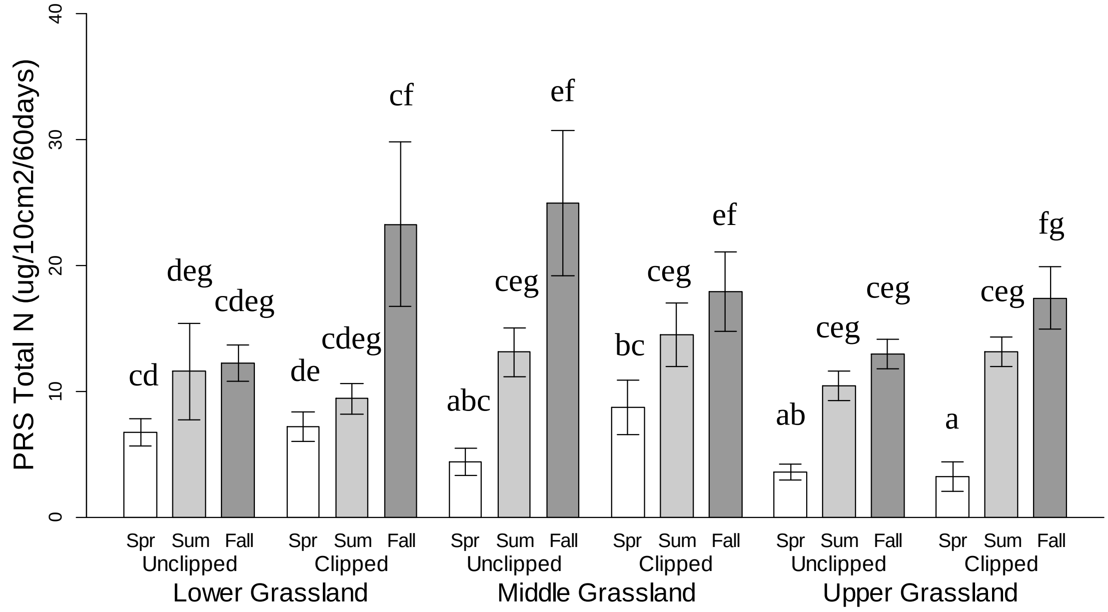

Figure 2.18: Three-way interaction between site, clipping and season of measurement. Bars are means ± SE, different letters indicate significant differences between treatments.

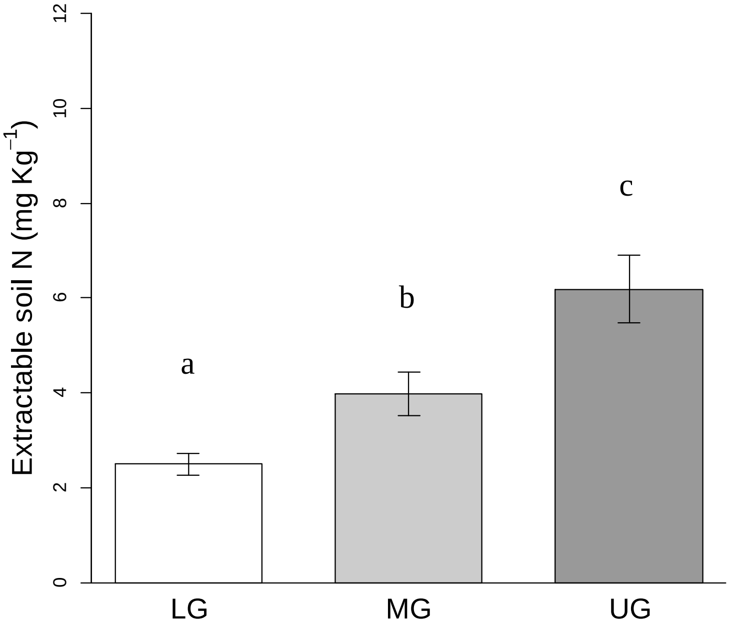

Figure 2.19: Total extractable soil N. Bars are means ± SE of unclipped and clipped plots from lower (LG), middle (MG), and upper (UG) grassland sites. Letters indicate significant differences between sites.

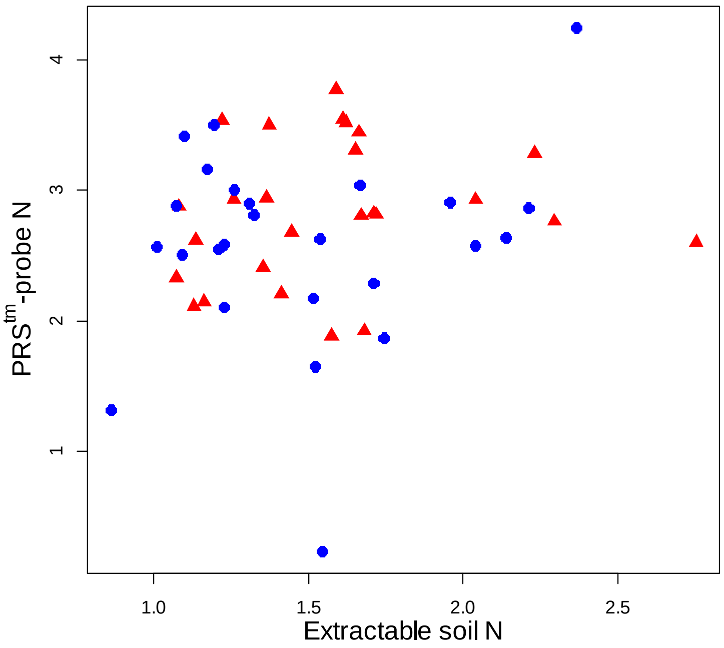

Figure 2.20: Relationship between PRS™ – total N (red triangles) and soil extractable total N (blue circles). Both axes are log +1 transformed. Correlation coefficient is 0.180.

Discussion

Shifting the season and frequency of water had a significant effect on mean and variance of volumetric water content (VWC), and to a lesser degree on variance of soil temperature. Legume cover seems to show a variable effect of fall watering that depends on watering frequency. Measures of cover, biomass, litter, species richness and diversity indices were not affected by watering treatments, but did see an effect of clipping on the plant community. Clipping had variable effects on cover and biomass depending on site productivity. Clipping generally increased species richness and, potentially, plant-available N as well.

Soil Moisture

All three elevational sites showed significant effects, with weekly and monthly treatment peaks in VWC (Figure 2.4). The lower grassland VWC was more responsive to watering treatments than either middle or upper grasslands. Mean daily VWC was significantly affected over the whole field study as well as in plots that were watered in each season of analysis. There were differences in responses to mean VWC and the variance of VWC. While the lower grassland exhibited responses to water treatment in both daily mean and daily variance of VWC, the middle and upper grasslands mainly exhibited responses in daily variance. This indicates that the mean VWC in these grasslands was less influenced by watering treatments than natural soil moisture and precipitation, but watering treatments did influence the range of moisture levels measured in plots.

Welker et al. (1991) saw that water from small precipitation events (less than 3 mm) caused by natural rainshowers or by irrigation had approximately the same residence time in soil. For larger events (above 6 mm) the irrigated water addition stayed significantly longer than water from natural rainfalls. Water from precipitation events < 10 mm remained in the soil for about two days, while water from those > 10 mm stayed consistently longer. As the smallest water addition I applied was 6.075 mm, I can assume VWC was increased in the plots and persisted for a minimum of several days after each watering, as was seen in a similar study in the same area (Carlyle, Fraser & Turkington 2011). This is the pattern seen in the lower grassland, where moisture levels were significantly elevated by treatments. In contrast, the middle and upper grassland soil moisture levels may have returned to ambient faster after water treatment resulting only in significant variance of VWC.

A minor drawback of my study is that I considered all sites to have the same amount of rainfall. However, a minor increase in rainfall amount has been measured along the elevational gradient in Lac du Bois (Tisdale 1947; Carlyle 2012). I also used historical precipitation records from the Kamloops Airport, which is at a slightly lower elevation than my lower grassland site.

I did not alter the precipitation amount on plots evenly across the year. I chose to use the historical monthly means for the watering treatments in each month, despite months receiving different amounts of water, i.e. fall months (September and October) overall received less water than spring (May and June). I did this because the RS’s can only be expected to reduce soil moisture by about half (Carlyle, Fraser & Turkington 2011). Thus, watering was applied at historical averages plus 50% for each respective month of watering to account for the decreased precipitation in the opposite season (either spring or fall). It would have been arbitrary to decide on a single amount applied in all months, seeing as they do vary, and the sampling design followed logical increases in water addition.

Soil Temperature

Contrary to soil moisture, soil temperature exhibited less of a response to water or clipping treatments; however, there are still some interesting findings. In the lower grassland, a significant effect of both water and clipping treatments was observed in the fall, such that the variability of temperature was increased in weekly fall watered and clipped plots. This indicates that while the daily mean was not affected, both treatments caused the soil temperature to fluctuate to a greater degree than in plots that were unwatered or unclipped.

The middle grassland showed an unusual pattern in soil temperature. During the summer season when all RS's were removed, both weekly spring and fall watering treatments had lower mean daily temperature than the ambient control plot. The spring watered plot may have had carry-over effects into the summer from being watered every week during the spring, increasing soil moisture and the energetic requirement for increasing soil temperature. The weekly fall watered plot, however, was covered with a RS during the spring making it more likely to have a lower soil moisture than ambient, and therefore more likely to increase in temperature faster during the summer (as was seen in Carlyle et al. 2011). However, there were no significant effects of any treatment on soil moisture during the summer, making it unlikely there was any carry-over of water treatments that would affect plot temperature in the summer. There was no response in any way in the upper grassland to these treatments, suggesting the amount they may have affected soil temperature was to a lesser degree than the natural climate.

Community responses to precipitation treatments

Few of the factors I measured showed a response to water manipulations over the course of two years. This is a similar result to a previous study in the same area where water addition had variable effects on plant growth over four years (Carlyle 2012). A three year study in the Colorado shortgrass prairie also showed C3 plants did not respond to watering treatments which maintained field capacity, whereas C4 plants increased (Kirchner 1977). Similarly, a four year study involving watering treatments had no effect on bunchgrasses in a sagebrush-steppe ecosystem in Idaho (Morris 2001).

My conclusion is two-part: 1) two years of an altered precipitation pattern is not a long enough time period to measure a significant biomass or diversity response in the grassland communities I studied. 2) The precipitation increase I chose was within the boundaries of natural variation for this ecosystem, and not likely to cause a dramatic change in this short time span.

Though there are a number of climate change papers that do show an immediate response to climate manipulations in grasslands (Grime *et al.* 2000; Heisler-White, Knapp & Kelly 2008; Heisler-White *et al.* 2009), this likely depends on the plant community involved (Grime *et al.* 2000, 2008). Long-term studies on climate variables are difficult to undertake and maintain despite their importance in ecological understanding (Magnuson 1990; Schindler 1998; Silvertown *et al.* 2006; Hobbs, Yates & Mooney 2007; Knapp *et al.* 2012). Some experiments that have been conducted in grassland ecosystems show a delayed response from the plant community, or that the first few years do not predict outcomes of later years (Bates *et al.* 2006; Adler & Levine 2007; Chimner *et al.* 2010; Carlyle 2012). Short-term studies cannot adequately measure shifting species dominance, richness, and reproduction or recruitment. They are also constrained by logistical (accurate precipitation simulation, external environmental effects, etc.) and conceptual (timing, magnitude, natural variation, scaling, choosing appropriate variables for measurement) difficulties (Weltzin *et al.* 2003). Only the changing presence and absence of annual species and the biomass of perennial species can be measured in the short-term. This also does not take into account species that have periods of dormancy with no above-ground biomass produced in some years.

More extreme alterations to precipitation patterns may have caused an immediately measureable response in the plant communities' production or diversity. The precipitation shifts I simulated were designed to be predictable and consistent with climate projections for the Southern Interior of BC in the future (Spittlehouse 2008), but were still within the bounds of natural precipitation variability for this area. The difference my study treatments would have compared to long-term data is that precipitation shifts are more likely to happen on a regular basis with continued climate change rather than as extreme events occurring rarely over three decades.

Community responses to clipping treatments

One of the more important outcomes of the analysis is that the lower and middle grasslands saw decreased cover and biomass with clipping. While there was generally a trend present of decreasing cover and biomass in the upper grassland, it did not show a significant response even after two years. The trend would likely require a slightly longer time scale to become significantly lower from unclipped control plots. This indicates that the lower and middle grassland communities are more susceptible to immediate degradation than the more diverse and productive upper grassland.

All sites were grazed in the years prior to study initiation. An increase in biomass may have resulted from the lack of cattle grazing for the duration of the study regardless of clipping treatments, leading to non-significant results from clipping in the upper grassland. Another explanation may be that grasses in the more productive areas with access to more available resources, may have compensated or even overcompensated for biomass lost to clipping. Hawkes & Sullivan (2001) performed a meta-analysis on plant responses to herbivory and found that only graminoids (as opposed to dicot forbs or woody plants) in high resource environments responded to herbivory by compensating or overcompensating in growth. This supports the compensatory continuum hypothesis proposed by Maschinski & Whitham (1989). However, the Maschinski & Whitham study used fruit production as a measure of compensation, rather than biomass. Another supporting explanation to my results, particularly in the lower grassland, is that grazing and watering can cause nutrients to become limiting factors. According to the extractable N data, the lower grassland has the lowest amount of N in the soil. Bagchi & Ritchie (2011) found that clipping without added nutrients caused a decreased in above and below ground biomass, even with irrigation.

Litter alone and in combination with biomass also showed significant interactions between site and clipping. Litter alone decreased with clipping only in the lower grassland, while litter and biomass combined decreased in the lower and middle grasslands. This suggests that the lower elevation grasslands that are characterized by more widely spaced individual plants, warmer temperature and lower precipitation than higher elevation areas (van Ryswyk et al. 1966; Carlyle 2012), are more susceptible to immediate decreases in plant cover, and therefore litter, caused by clipping.

Functional Groups

The dominant and sub-dominant grasses in my study sites are long-lived bunchgrasses, aside from the rhizomatous *Poa pratensis* in the upper grassland. It is reasonable to expect these bunchgrasses to be relatively less responsive to precipitation manipulation than other functional groups, because they generally have deeper root systems (Gayton 2003; Morecroft *et al.* 2004). Zavaleta et al. (2003) found increased precipitation increased above-ground production of forb species but had no effect on grasses after three years. Consistent spring watering treatment may favour production of species that have the majority of their growth during the spring. This growth, in both annual and perennial species, would normally be dependent on spring precipitation (as well as winter snow melt) and then become dormant as the summer progresses and soil moisture decreases. Legumes may play important functions within plant communities by increasing biodiversity and increasing N levels in soil. Legume cover showed a significant water x clipping interaction in the ANOVA (Table 2.2). Though this interaction was not significant in the more conservative Tukey's HSD test, there may be an interacting effect of clipping and the frequency of fall watering on legumes (Figure 2.10) that warrants further investigation.

Species Richness & Diversity Indices

Species richness increased with elevation. In 2010 there was no difference between the middle and upper grasslands, however, in 2011 the upper grassland had higher species richness than the middle. Clipping increased species richness compared to unclipped plots using pooled sites. Previous work in Lac du Bois was performed on 30-year old exclosures (Carlyle 2012). These upper grassland sites were heavily rough-fescue dominated, with lower species diversity than middle grassland areas. As the sites I studied had all been grazed in previous years, this disturbance and the clipping treatment I applied was likely to decrease competition by the dominant bunchgrasses as predicted in Grime (1979), allowing a higher diversity than would be seen in undisturbed sites. This decrease in dominant plant cover may allow the subdominants to germinate or put more energy into above-ground growth due to an increase in available resources. However, it is unlikely that light is a limiting resource in these grasslands unless litter plays a large role in suppression (Facelli & Pickett 1991). According to Austin et al. (2004), ecosystems with less than about 600 mm precipitation per year will be water limited. Kamloops receives approximately 280 mm per year and is considered chiefly water limited. In comparison, the short-grass steppe ecosystem of the American prairies has approximately 333 mm precipitation per year with a high amount of light available at the soil surface (Lane *et al.* 2000). This indicates light is not a limiting resource in the prairie ecosystem or in the Lac du Bois study sites. Light availability decreases as competition increases with precipitation in mixed-grass and especially in tall-grass prairies.

Simpson's diversity index groups the lower and middle grasslands together in diversity with the upper grassland much higher, while the Shannon-Weiner index has a low value for the lower grassland and groups the middle and upper grasslands together at a higher diversity. This shows an important difference between the sensitivities of the two indices to rare versus common species. My results clearly show how the Shannon-Weiner index gives a greater weight to rare species, which occur mostly in the middle grassland, than the Simpson's index. A combination of these two indices is useful for comparison and to better inform conclusions on how manipulation or management regimes affect rare versus common species.

Nitrogen

Combined NO_3^- and NH_4^+ - N measurements from PRS™- probes increased with each successive season of measurement (spring through fall), and did not change with elevation. This is somewhat contrary to previous research on N availability in a Californian grassland to shrubland gradient, where N availability decreased as the growing season progressed (Goedhart, Pataki & Billings 2010), and in previous PRS™ measurements in Lac du Bois where N increased with elevation (Carlyle 2012). PRS™-probes measure free ions in the soil, which is dependent on lateral movement of water through soil to bring the ions into contact with the probe membrane. Considering the semi-arid conditions of the grassland sites in this study and that water is one of, if not the limiting resource in this ecosystem, lateral water movement is likely limited to spring snowmelt or extreme summer rainshowers. This is a specific measurement of the amount of N in soil, and does not necessarily represent the entire pool. N measurements were likely different from the previous work by Carlyle (2012), because of different sites selected between the two studies. As previously discussed, my study sites were grazed in years prior to study with different species abundances leading to different N dynamics in the soil.

The increase in available N in the fall may be due to a combination of increased ambient precipitation, watering treatments, and reduced plant growth during the fall growing season. These conditions may lead to a temporal decoupling of N availability and uptake as previously proposed (Austin *et al.* 2004; Collins *et al.* 2008). Moist soil conditions provide the opportunity for microbes to mineralize labile N, but lower plant growth or fewer plants that are active in the fall make it likely that N uptake is lower leading to accumulation of N in the soil.

Extracted N from soil samples show almost the opposite from the PRS™- probes. N levels increased with elevation and clipping, whereas there was no change between sites or with clipping for the PRS™ measurements. This second form of N measurement is a different way of estimating available N by extracting NO_3^- and NH_4^+ from a larger soil sample than the PRS™- probes, and is not dependent on water movement through soil.

The two methods of N analysis I used did not correlate well, with a coefficient of only 0.18. I conclude that the means by which N amount (and/or form) is measured in soil is dependent on the questions being asked. PRS™-probes are one way of easily gauging the amount of readily available, dissolved N in soil. A more complete picture may be found by a combination of PRS™-probes and N extraction methods.

Conclusion

After two years of field treatments there was no measureable effect of changing precipitation patterns on the grassland plant community. Watering treatments were effective in altering mean and variability of soil moisture, and variability of soil temperature. Clipping decreased plant cover, biomass and litter, and had the most pronounced and immediate effect on the lower grassland plant community. Similar patterns were seen for functional groups, species richness, and the two diversity indices.

N availability in the soil can be altered by both watering treatments and clipping. Climate factors play a large role in regulating rates of N mineralization and uptake, and the effects of these can change dramatically during a single growing season.

The climate model this study was designed after was from Spittlehouse (2008), which shows potential for the Southern Interior to see little change in annual mean precipitation but a shift in precipitation from summer to winter with an increase in temperature. My study design mimicked an extension of the growing season into either the spring or fall. As it is unclear how accurate global circulation models are in predicting future scenarios of precipitation pattern changes on small biologically meaningful units, a range of scenarios should be considered. Therefore my study looked at increased and decreased precipitation in both spring and fall, while avoiding the experimentally difficult approach of trying to manipulate snow loads.

CHAPTER 3: GENERAL CONCLUSION

Southern interior grasslands appear to be resistant to changes in cover, biomass and diversity from short-term alterations in precipitation pattern. Clipping causes an immediate and pronounced decrease in plant cover that extends into at least the next year's growing season, with a similar effect on biomass and diversity. This trend is less pronounced in upper grasslands with higher productivity. Though I have two years of field manipulation data, larger climate systems such as the El Niño Southern Oscillation (ENSO; Holmgren et al. 2006) can have a large impact on the outcome of experiments, and this is difficult to quantify unless multiple years of the same study are performed (Vaughn & Young 2010).

Long term studies are an essential component of successful ecological research (Magnuson 1990). The Park Grass Experiment in the UK was initiated in 1856, is the oldest functioning ecological experiment in the world, and has provided a unique glimpse of changing plant dynamics over its extensive history. The original purpose was to answer agricultural questions about the effects of different fertilization treatments on soils and plant communities. However, the extensive list of studies that it has supported since are still the beginning of potential questions and answers it can provide (Silvertown *et al.* 2006). The Long-Term Ecological Research (LTER) Network is a field ecology based network of studies in the USA. The value of long term research networks such as this allows both the measurement of responses to treatments that may not appear until years after initiation, as well assessment of the mechanisms behind the responses (Knapp *et al.* 2012). Having a broad geographical reference also allows results to be expanded to the global scale on which current issues such as climate change occur (Fraser *et al.* 2013).

As my study is a small investigation into how we can expect grasslands to respond to changing climate patterns, I have suggestions for future work in this developing area:

- Assess the different types of precipitation on plant communities, eg. differences in snow versus rain, and snow pack duration as suggested by Loik et al. (2004) and initiated by Chimner et al. (2010).

- Drought and extreme event studies (Jentsch, Kreyling & Beierkuhnlein 2007; Jentsch & Beierkuhnlein 2008), preferably in coordination with a multisite network as proposed by Fraser et al. (2012).
- Formation of dedicated long-term studies, structured similar to the Park Grass Experiment (Silvertown *et al.* 2006), or the Long-Term Ecological Research (LTER) Network (Knapp *et al.* 2012).

Climate change induced changes in mean or seasonal temperature and precipitation will continue to affect grasslands. Grazing has well-known effects on grassland plant communities in the Southern Interior of BC. As grasslands are affected by changing precipitation and temperature patterns, grazing systems will have to evolve to suit the plant communities that support this grazing. Managers should be extremely cautious to not heavily graze lower elevation grasslands, as these are very susceptible to degradation. Promoting and adopting grazing strategies that best maintain grassland ecosystem function (Maestre *et al.* 2012) is the best way to insure these ecosystems against degradation in the 21st century.

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APPENDIX A

Table A.1: Species list of identified plants in all sites divided into graminoid, forb, legume and shrub functional groups. Five species were unidentifiable and not included in this list.

Scientific Name	Common Name
Graminoids:	
Achnatherum nelsonii	Nelson's needlegrass
Achnatherum richardsonii	Richardson's needlegrass
Bromus tectorum	cheatgrass
Carex sp.	sedge sp.
Elymus glacus	blue wildrye
Festuca campestris	rough fescue
Hesperostipa comata	needle and thread grass
Juncus balticus	Baltic rush
Koeleria macrantha	junegrass
Phleum pratense	common timothy
Poa pratensis	Kentucky bluegrass
Poa secunda ssp. *secunda*	Sandberg's bluegrass
Pseudoroegneria spicata	bluebunch wheatgrass
Vulpia octoflora	six-week fescue
Forbs:	
Achillea millifolium	yarrow
Arabis holboellii	Holboell's rockcress
Aster campestris var. *campestris*	meadow aster
Aster ericoides ssp. *pansus*	tufted white prairie aster
Balsamorhiza sagittata	arrow-leaved balsamroot
Calochortus macrocarpus	sagebrush mariposa lily
Campanula rotundifolia	common harebell
Castilleja thompsonii	Thompson's paintbrush
Cerastium arvense	field chickweed
Chenopodium album	lamb's-quarters

Scientific Name	Common Name
Cirsium hookerianum	Hooker’s thistle
Comandra umbellate	pale comandra
Crepis atrabarba	slender hawksbeard
Erigeron corymbosus	long-leaved daisy
Erigeron filifolius	thread-leaved daisy
Erigeron flagellaris	trailing daisy
Eriogonum heracleoides	parsnip-flowered buckwheat
Fritilaria pudica	yellow bell
Gallium boreal	northern bedstraw
Lithospermum ruderale	lemonweed
Lomatium macrocarpum	large-fruited desert-parsley
Microsteris gracilis	pink twink
Opuntia fragilis	brittle prickly-pear cactus
Polygonum douglasii	Douglas’s knotweed
Potentilla hippiana	woolly cinquefoil
Rhinanthus minor	yellow rattle
Taraxacum officinale	common dandelion
Tragopogon dubius	yellow salsify
Verbascum thapsus	mullein
Zygadenus venenosus	meadow death-camas
Legumes:	
Astragalus agrestis	field milk-vetch
Astragalus collinus	hillside milk-vetch
Astragalus miser	timber milk-vetch
Medicago lupulina	black medic
Vicia americana	American vetch
Shrubs:	
Antennaria neglecta	field pussytoes
Antennaria rosea	rosy pussytoes
Antennaria umbrinella	umber pussytoes

Scientific Name	Common Name
Artemisia frigida	pasture sage
Artemisia tridentata	big sagebrush
Ericameria nauseosus	common rabbit-brush