Rangeland Responses to Climate Change

Research Report #3 Prepared For: Alberta Sustainable Resource Development

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1. Introduction

Canada contains 22 M ha of land dedicated to range and forage production. This land supports 4 M cow/calf pairs, and overgrazing in some areas has resulted in many areas being in less than 'good' condition. Improving rangeland condition provides direct economic benefits and since native rangelands typically store more carbon than cropland and tame pasture, this also leads to increased carbon storage. A healthy rangeland stores equivalent carbon mass per ha as forested ecosystems, and because this carbon is primarily belowground, it is at a lower risk of release during fires. Unfortunately, we have a limited understanding of the belowground processes that drive rangeland dynamics, and a general lack of information on how increased temperature and/or altered precipitation patterns will impact the sustainability of these systems, particularly under sustained grazing. Moreover, sound fundamental information on the nature of climate-grazing interactions within rangelands has the potential to (1) improve carbon storage, (2) enhance native biodiversity and ecosystem functioning, and (3) provide positive economic returns.

To mitigate the potential impacts of climate change on the biodiversity and sustainable production of Canada's rangelands, it is essential to gain a mechanistic understanding of the links between temperature, precipitation, soil chemistry, microbial and invertebrate diversity and activity, primary production, and the dominant land use of livestock grazing. In this study, we are conducting replicated field experiments at several locations of Alberta, Saskatchewan, and Manitoba from 2006 to 2009. At each location, we will establish plots subjected to a variety of treatments, including combinations of defoliation and ambient warming (ambient or +2C using open-top greenhouses), and in the main study, precipitation (ambient, -70% using rainout shelters, +70% using watering) treatments as well for three growing seasons. We will measure primary productivity and range health, with a particular emphasis linking above and belowground dynamics. Using technology such as mini-rhizotrons (root periscope cameras) will allow for enhanced accuracy in estimating primary productivity and carbon flow. We will also measure changes in microbial and invertebrate communities, litter decomposition, and carbon and nitrogen cycling. We anticipate that changes in plant growth resulting from changed climatic conditions and management practices will have cascading effects on ecosystem resilience. From these data, we will identify a set of management recommendations for this

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sector of the agricultural community on how to alter grazing regimes to mitigate the varied impacts of future climate change.

This report has 2 objectives, including the following:

- Provide a summary of the second year responses (i.e. 2008) in the primary study examining Climate Change Impacts on Rangeland Function, being conducted from 2007 through 2009.
- Review the preliminary implications of the fore-mentioned results on rangeland management in the province of Alberta, which in turn, will enable Alberta Sustainable Resource Development to better meet their mandate for public land stewardship in the province.

2. Summary of Research Objectives, Experimental Design, and Scientific Methods in the Primary Rangeland Carbon Study

2.1. Summary

Canada contains 22 M ha of land dedicated to range and forage production. This land supports 4 M cow/calf pairs and overgrazing has resulted in less than 50% of this area listed in "good" condition. Improving rangeland condition provides direct economic benefits, and because native rangelands store more carbon (C) than annual cropland, this should also lead to increased C storage, with implications for feedback to climate systems both locally and globally. Globally, grasslands store more than twice as much soil C as forest, and since this C is primarily belowground, it is not released by fire. At present, we have a limited understanding of the belowground processes that drive rangeland dynamics, and a specific lack of information on how the increased temperature and altered precipitation patterns predicted to occur with climate change will impact the sustainability of these systems, particularly under grazing. Understanding climate-grazing interactions in rangelands has the potential to (1) increase C storage, (2) improve our understanding of ecosystem feedback on climate change, (3) enhance native biodiversity, ecosystem functioning and sustainability, and (4) provide positive economic returns. In this project we will identify key linkages between grazing, climate change, carbon storage, and primary production. Making this project particularly strong is our emphasis on detailed study of three main components of this system: (1) biomass production under climate change; (2) C and nitrogen (N) cycling and storage through altered microbial functioning and processes; and (3) soil invertebrate biodiversity and trophic structure. By emphasizing linkages between these components, we will identify the critical points at which climate change and land-use decisions interact, allowing the development of sound adaptation strategies.

We will conduct a replicated field experiment in the Parkland and /or Mixedgrass Prairie regions of Alberta, Saskatchewan, and Manitoba. At each location, we will establish plots subjected to combinations of defoliation, warming, and precipitation treatments for three growing seasons. We will measure primary productivity and range health, with a particular emphasis on belowground dynamics using mini-rhizotrons. We anticipate that changes in plant growth from these treatments will have cascading effects on ecosystem function.

From these data, we will identify a set of management recommendations for this sector of the agricultural community on how to alter grazing regimes to mitigate the impacts of climate change. This project is interdisciplinary by design, and as a group we have diverse research experiences. Several of the PIs have strong links with producer groups and industries, increasing our ability to communicate effectively with key stakeholders. The potential for outreach is further enhanced by having sites in all three prairie provinces, increasing both the generality of the project's outcomes as well as the potential number of interested industrial groups. The goals of this research parallel those of the Biosphere Adaptation to the Climate Change section of the Healthy Environment and Ecosystems project area. However, this project diverges in that its focus is on native rangeland, rather than forest or aquatic habitats.

Due to the amount of land area covered by native range, climate change in this habitat will have significant consequences both for Canada as a whole, as well as industry. An attractive aspect of addressing climate change impacts in rangelands is that grazing practices are dynamic, and thus the mitigation strategies developed through this research can be rapidly adopted, resulting in real benefits to Canada and producers. The long-term objectives of this research are to understand the ecological interactions present within rangeland ecosystems in the Prairie biome of western Canada, and how they are affected by changing environmental and management practices. By doing so, we will provide policy-relevant scientific data for sustainable management. We will seek further funding to extend the life of this experiment beyond this 3-year funding cycle, as long-term data are critical to achieve our long-term objectives.

2.2. Specific Objectives

- Determine how temperature, precipitation, and defoliation interact to impact the sustainability of native rangelands.
- Provide clear management suggestions to supporting organizations for increasing rangeland drought resistance and to maximize soil carbon storage and nitrogen cycling.
- Develop a synthetic model that incorporates the functional links between climate, grazing, root demography, soil invertebrate and microbial diversity, and carbon and nitrogen cycling.

2.3. Research Questions

- Do climate change and defoliation interact to affect root births, deaths, turnover, decomposition, and belowground carbon storage?
- What combinations of root size and depth distributions are associated with the highest level of forage production under different combinations of grazing and climate manipulation?
- How do the dominant forage species respond *in situ* to warming and precipitation treatments in terms of water use efficiency and rates of photosynthesis?
- How do rates of soil flux (e.g. soil respiration and N mineralization) change in response to varied grazing and climate treatments?
- Will climate change alter the diversity, biomass, or trophic function of grassland soil invertebrates?
- What functional links between climate, grazing, plant growth, microbial activity, and soil invertebrate diversity and distribution are most strongly associated with controlling forage production and net carbon storage under varied combinations of defoliation and climate?

2.4. Background and Current Developments

The western provinces are home to 83% of the beef herd. Of the land base used by cattle, 86% is rangeland, including 7.6 M ha in Alberta. The northern portion of this biome (the Aspen Parkland) is about 750,000 ha in size, and recognized as a 'tension zone' with a history of strong changes in climate and associated vegetation (*1*). Historical data indicate this region is susceptible to the influence of altered precipitation and warming associated with climate change. The temperature in the prairies is increasing. Over the short term, 2005/06 was the warmest winter since 1948, 4°C above normal (2). Temperatures in most seasons over the last 8 years have also been above normal (2). Over the long-term, temperatures are expected to increase by >4°C by 2080, increasing evaporation and reducing soil moisture availability. What remains unclear is whether precipitation will increase, decrease, or stay constant, though evaporation is expected to offset precipitation increases and could increase drought frequency and severity (2). Climate change will have direct and indirect effects on ecosystem sustainability. Our ability to mitigate potential negative outcomes (e.g. reduced forage production, release of vast stores of organic C in the Black and Dark Brown soils) is dependent upon a detailed understanding of the linkages between climate, grazing, plants, microbes, invertebrates, and soils.

Increased warming and drought frequency will reduce forage production over both the short and long-terms, providing a severe economic strain on rural western communities and industries. Precipitation is one of the most influential factors regulating plant growth in grasslands (*3*), including in the wetter northern prairies (*4*). However, drought alters not only current year production, but can change the distribution and size of roots in the soil profile (*5*) with functional consequences for the following year. Grazing can also influence root growth, though whether it reduces (*6*) or increases root growth (*7*) is unclear. Increased temperature is also associated with altered root growth, though the direction of effects is also variable among studies (*8-10*). Overall, there is consensus that grazing and climate change alter root growth, but there have not been enough studies to provide a clear indication of the direction and magnitude of effect, individually or in combination.

Understanding how warming, drought, and grazing interact to affect root growth is of critical importance in rangeland, where up to 92% of plant biomass exists belowground (11) and a healthy root structure is a prerequisite for sustained forage production. Additionally, most

plant competition in these systems occurs belowground (12), indicating that root traits will influence competition (13) and weed invasion. Seemingly minor differences among roots (e.g. diameter differences of 0.1mm) have dramatic effects on root survival (14) and nutrient uptake (15). Root turnover rates influence carbon and nitrogen cycling (16). In short, the impacts of climate change on rangeland sustainability will be determined by what happens belowground.

Changes in root growth can have direct impacts on production, as well as indirect effects through feedbacks into the soil system (*17*, *18*). The direction of feedbacks will in part be determined by whether climate change and grazing alters root growth through changes in root birth rates, or root death rates. For example, 1 kg of roots could be formed from 1 kg of production (low birth rates) and no root deaths, or from 10 kg of production (high birth rates) and 9 kg of root deaths. Though the standing pools of roots are the same in these scenarios, the difference in carbon inputs to the soil will have different consequences for carbon storage. To discriminate among these possibilities, this project uses an innovative technology known as a minirhizotron, or "root periscope", allowing non-destructive assessment of roots in the soil (*11*, *19*). This approach will enhance our understanding of root characteristics and function in relation to external abiotic factors and/or management influences.

Carbon inputs into the soil through dead roots, exudates, and leaf litter serve as the base of soil food webs (20). Changes in litter quantity or quality due to interactive effects of grazing and climate change can have cascading effects on microbial and soil invertebrate abundances, species composition and activity (21). This in turn will impact decomposition rates, soil respiration, and carbon and nitrogen cycling. A diversity of invertebrate animals inhabit soil, influencing its structure and composition through litter fragmentation, consumption of microbes, vectoring of fungal spores, and modification of pore-size distribution (20). These activities influence production and forage quality (22), and affect CO₂ generation from soil (23). Grazing is known to alter soil communities in Alberta grasslands (24), though it is unclear whether these effects were due to changes in root growth or soil microenvironment associated with litter removal. The few studies of the effects of changes in temperature and moisture on soil invertebrates show taxon-specific responses (25, 26). Overall, little is known about the biodiversity or community ecology of rangeland-dwelling invertebrates, particularly in Canada. Differentiation of these potential mechanisms of effect and taxonomic difference are critical to understanding the functional links between grazing, soil invertebrates, climate change, forage production, and carbon cycling.

In Mixed Prairie, studies on the impact of grazing on soil C have shown variable results (27, 28), and no studies have been conducted in the Aspen Parkland. More broadly, there are few studies of the warming effects on C and N cycling in rangeland systems (29), and even fewer focusing on interactions between warming, drought, and defoliation (30). The response of C and N fluxes to climate change and the resultant changes in ecosystem C and N stocks provide the feedback mechanism for further climate changes. Carbon and N cycling in the soil is mainly controlled by microbial processes (31), and how microbial function and diversity in Parkland regions will respond to climate change is unknown.

The development of mitigation measures for climate change in the Parkland is dependent upon a mechanistic understanding of the linkages between climate, grazing, plant growth, microbial activity, and soil fauna. Ecologists know these factors interact, yet studies testing the functional consequence of those interactions are rare, and non-existent within Canada's rangelands. This research will bridge a significant information gap, by linking the impact of ongoing routine management decisions by producers (i.e., defoliation intensity) with subsequent belowground root structure and development, and ultimately, with short and long-term forage production. Additionally, we will be able to measure changes in carbon and nutrient cycling, which combined with information on microbial activity and soil fauna, will allow us to determine how changes in management under climate change will impact carbon storage and turnover. This innovative research will establish a new framework for understanding and assessing the impact of common management practices, on the potential to improve forage production and carbon storage, and subsequently mitigate some negative consequences of climate change.

2.5. Research Team

The research team consists of accomplished, well-respected researchers from a diversity of disciplines, and includes:

- 1. Dr. J.F. Cahill (Biological Sciences) University of Alberta
- 2. Dr. E.W. Bork (Agricultural, Food, and Nutritional Science) University of Alberta
- 3. Dr. S.X. Chang (Renewable Resources) University of Alberta
- 4. Dr. H.C. Proctor (Biological Sciences) University of Alberta
- 5. Dr. S.D. Wilson (Biology) University of Regina

Cahill, Bork, and Wilson have proven track records in the grasslands of Western Canada, and are uniquely positioned to conduct the plant component of this project. Cahill and **Wilson** have published extensively on root ecology and plant-soil feedbacks, and both use minirhizotrons in their research. Bork, Chang, and Wilson have strong records in applied ecology and conservation biology. **Bork** is a rangeland ecologist and grazing management specialist, with extensive ties to industry partners and other stakeholder groups. Wilson and Chang have both addressed issues of soil carbon storage and climate change. Proctor and Chang are well suited to lead the carbon/nitrogen cycling and soil invertebrate diversity components of this project. Chang has an extensive body of research in understanding climate-soil interactions, with strong ties to the network of climate change researchers in Canada. He has published extensively on soil biogeochemistry, soil respiration and microbial functional diversity and is experienced with basic physiological measurements and stable isotope techniques. Proctor is one of the world's experts on soil mites and associated mesofauna. She has a broad understanding of soil invertebrates, and her ecological knowledge allows for integration of these data with other aspects of the study. All team members have experience with field experiments and are familiar with the logistical difficulties involved. All have records of finishing studies on time and within budget, while emphasizing the training of HQP. The team is committed to this work and see genuine potential for achieving an integrative understanding of how climate change will alter rangeland sustainability and the potential feedback mechanisms for regional and global climate change.

2.6. General Experimental Design

Locations: Logistical considerations require us to restrict our research to a few locations across the Prairie biome, including the Mixedgrass Prairie and Aspen Parkland. The Parkland is a transition zone between the mixed prairie and boreal forest. Parkland structure is a product of complex interactions between the plant communities, grazing management, climatic conditions, and nutrient inputs, and is likely particularly sensitive to climate change. Similarly, the Mixedgrass is known to be moisture limiting for plant growth, with productivity intricately tied to the timing and amount of rainfall. Three field sites will be established: (1) Kinsella, AB, in the Parkland, (2) White Butte, SK, in the Mixed Prairie, and (3) Spruce Woods, MB, in the Parkland-Boreal transition. All sites are mosaics of grasslands with aspen stands restricted to moister areas. Grassland areas are more heavily grazed than the aspen stands in all regions, and are therefore the focus of this work.

Layout: We will use a factorial design to determine the interactive effects of temperature (2 levels), precipitation (3 levels), and defoliation (3 levels) on a suite of response variables (see below). Field sites will be chosen in areas with no obvious environmental gradients, allowing the use of a fully randomized design, with five replicates of each treatment combination. It is not feasible to increase the number of replicates without reducing the number of locations or treatment combinations. Each plot (the unit of replication) will be approximately 2 x 2 m in size, with a 1 m buffer zone separating plots. Plot size is limited by the physical constraints imposed by our warming treatment (see below). Plots and blocks will be marked immediately after snowmelt in spring 2007, followed shortly by climate manipulations. Livestock will be excluded during the experiment.

<u>*Warming:*</u> Warming will be achieved by the use of open-top chambers (OTC). This method is used around the world (*32*), and consists of a 40 cm high x 2 m diameter cone, with the side made of a fibreglass material positioned at a 60° angle. The fibreglass allows transmission of visible, but not infra-red light, creating a greenhouse effect within the chambers of around 2-4° C above ambient (*32*). The exact warming achieved (along with any confounding effects) will be measured using HOBO data loggers to record air and soil temperature, humidity, and soil moisture in 78 of the 210 plots spread across the three locations (3-5 replicates per treatment combination). The costs associated with data logging all 210 plots are prohibitive

(\$100,000 more). Additional micro-environmental measures (PAR, and more plots for temperature and soil moisture) will be collected periodically using handheld devices.

<u>Precipitation:</u> Plots will be individually modified to receive approximately ambient, -70%, or + 70% growing season rainfall using a modified design of Zhou et al. (*30*). In brief, water addition is achieved by gravity feeding rainfall collected outside a plot, and water reduction occurs by using a transparent rainout shelter to intercept approximately 70% of rainfall. All plots of all treatments will have similar shelters built around them to control for potential confounding effects of the structures on air temperature and shading, differing in whether the rain is directed inwards (+70%), outwards (-70%), or allowed to pass through (control). Micro-climatic effects of the shelters will be determined using data loggers as described above. This approach will not affect the frequency of rainfall events in the plots, just their magnitude. The risk of this approach is that the actual precipitation manipulations will depend upon actual rainfall, a value that is highly variable in rangelands. Due to logistical constraints the MB and SK sites will not include a water addition treatment.

Defoliation: The presence of OTC devices precludes the use of cattle, and instead we will defoliate vegetation manually within plots (none, low, high). The low and high intensity treatments consist of clipping at a stubble height of approximately 7.5 and 2.5 cm, which roughly corresponds to the removal of 30% and 80% of standing current annual biomass in low and high intensity plots (exact removal amounts will be determined). These levels coincide with conservative and excessive use for native rangelands. Defoliation will occur in mid summer (June 15-30), similar to what is done by local producers.

<u>Plot Disturbance</u>: We are aware that our research activity could negatively impact the ecological functioning of plots (*33*). To minimize this risk, there will only be two destructive harvests in each plot each year. All destructive sampling (clipping, soil coring, etc) will occur in the same area within a plot at each sampling period, reducing the overall extent of damage to the plots. Holes left behind will be refilled and their locations marked. Although this reduces our ability to describe within-year patterns, it is sufficient to make reliable between-treatment comparisons. Environmental measures will be made with installed probes and handheld devices and will therefore not cause further disturbance.

2.7. Subproject 1: Enhancing the sustainability of biomass production during climate change (Bork, Wilson, Cahill, and Chang)

The overall goal of this subproject is to determine how climate change and defoliation will interact to alter biomass production, plant phenology and forage quality. More specifically, this goal is subdivided into (1) biomass production and C and N pools and (2) root growth and turnover. A Ph.D. student will lead the project testing the impacts of altered grazing and climate on forage production and standing C and N pools. In all three locations, a permanent 50 x 50 cm quadrat will be marked on the surface of all 210 plots in spring 2007, allowing for repeated nondestructive measurement of plant phenology, and species composition and cover each growing season. The cover estimates will be converted to rough estimates of biomass using doublesampled plots located outside the immediate study area. Direct measures of shoot biomass will be assessed within each plot (but outside the permanent quadrats described above) by clipping a 20 x 50 cm subplot in each plot in May (spring) and late July (peak biomass). Clipped materials will be sorted to species, dried, and weighed. To provide estimates of forage quality, biomass samples will be pooled by growth form (grasses, forbs, shrubs) and ground for analysis of %C and N, and forage quality parameters (neutral and acid detergent fiber). Leaf litter will also be removed from the clipped plots, dried, weighed, ground, and %C and N determined. Within each clipped quadrat, root C and N content and biomass will be assessed through the sampling of replicate bulked 5 cm diameter soil cores at two depths (0-15cm and 15-30cm). Roots will be sieved/washed from the soil, analyzed for root length (WinRhizo), dried, weighed, and with %C and N determined. Additional soil cores will be taken for assessment of soil total and available carbon and nitrogen, pH, moisture content, bulk density, and other chemical and physical properties.

An M.Sc. student will test the treatment effects on root growth and demography. To achieve this, we will combine the previously described biomass data with demographic data obtained with a mini-rhizotron camera system (Bartz Technology). In spring 2007, we will install a mini-rhizotron tube (5 cm diameter, 1 m long, clear extruded acrylic) at a 45° angle in all plots. To allow for plant recovery following the disturbance associated with tube installation, we will not collect root image data until the following growing season (2008). Starting in spring 2008, we will conduct monthly imaging through the rooting zone throughout the growing season

for two consecutive years. Images will be collected in a belted transect along the tube, with 13 mm image widths. To limit the number of images requiring processing, we will process only every fourth image. This choice still provides substantial data (approximately 15-20 images per tube per month), while reducing the workload associated with image processing. To process an image, a lab technician needs to trace each root by hand (using a digitizing program), from which demographic information can be recorded (root birth dates, death dates, length, diameter, etc.). Prior experience indicates that this takes approximately 1 hour per tube per session. With 210 tubes over two years, this results in substantial computer work. Our experience shows that no software currently available reliably automates this takes.

Statistical analysis will be conducted to achieve two main goals: (1) determination of how precipitation, temperature and defoliation, alone and in combination, influence a variety of response variables (e.g., root birth, abundance, growth and death, root and shoot biomass, carbon storage, range health, species composition, etc.), and (2) determination as to which combination of root characteristics produces the most desired community function (e.g., biomass production during drought, carbon storage, etc.). In the former analyses, generalized linear mixed models (GLMM) will be conducted that include temperature, defoliation, and moisture treatment as fixed effects. In analyses that include all three locations, location will be included as a random effect. Repeated measures analyses will be conducted when appropriate. Root demographic analyses will involve traditional population analyses, such as the use of proportional hazards models. Tests of treatment effects on community structure will involve a variety of multivariate approaches such as multi-response permutation procedures and indicator species analyses. To determine how different rooting characteristics (e.g. depth x length distributions of the community) are associated with desired ecosystem function (e.g. low abundance of invasive species, biomass production during reduced precipitation), we will again use generalized linear models, however, we will also include a variety of measures (e.g. root turnover rate) as continuous variables in the analysis. We specifically want to know if there are certain rooting characteristics which are associated with particular community functions (e.g. drought resistance). If so, then the initial sets of analyses would provide us the management suggestions necessary to cause those rooting traits to develop.

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2.8. Subproject 2: Climate-induced shifts in C and N fluxes and microbial activity (Chang and Cahill)

Two graduate students will be associated with this subproject designed to determine the impacts of climate change and defoliation on C and N fluxes and microbial activity and functional diversity. The project will be split into one study (Ph.D) addressing treatment impacts on decomposition, water use efficiency, respiration, and photosynthesis, and a second study (M.Sc.) addressing treatment effects on microbial populations, activity, and community structure.

Carbon and nitrogen stocks in biomass will be quantified as described in Subproject 1. Additional measures (twice per year) include: microbial C and N, soluble C and N, and net and gross N mineralization rates. All soil sampling will occur in the clipped quadrats described above, and will be to a depth of 30 cm, which consists of the main rooting zone in these systems (Cahill and Wilson, pers. obs.). Soluble C and N concentrations will be extracted with water and determined on a Shimadzu TOC-TN analyser. Net N mineralization rates will be determined with the buried bag method and gross N mineralization rates with the 15N pool dilution method, in-situ (35). Microbial biomass C and N concentrations will be measured using the chloroformfumigation extraction (36) as well as by the analysis of the phospholipid fatty acid (PLFA) profiles (37). The latter method will provide information on the relative composition of bacteria and fungi in the soil and provide an indication of microbial community composition. Microbial functional diversity will be assessed with the BiologTM technique based on substrate utilization patterns (38), and combined with the C and N flux measurements, will allow us to link soil chemical and microbiological properties with ecosystem functions.

Decomposition rates will be measured using small litter bags filled with known amounts of roots (buried at 10 cm below soil surface) and shoots (incubated at soil surface) collected in year 1. Material will be collected and placed in the field each fall in all plots, with replicate bags retrieved in the spring, summer, and fall. Materials in the bag will be dried, weighed, and determined for %C and N and ash content. Ash-free dry weight will be determined to correct for soil contamination. CO_2 and N_2O fluxes from the soils to the atmosphere will be measured biweekly throughout each growing season. Due to logistical constraints, these soil-atmosphere fluxes will only be measured at the Alberta site. Intensive measurements (daily and diurnal measurements) will be conducted following rainfall and extended droughts to characterize the response of the systems to such events, to allow us to quantify the effects of extreme weather conditions on C and N fluxes and to scale up the measurements to an annual basis. The Daycent ecosystem model (34) will be calibrated to model the dynamics of C and N fluxes in the system and determine how they are affected by the imposed treatments. This will further improve our ability to scale up the C and N fluxes to an annual basis.

Short-term treatment effects on photosynthesis and stomatal conductance will be measured using a Li-Cor 6400 at the Alberta site. Longer term effects of the treatments on stomatal conductance, water stress and use efficiency, and N cycling can be revealed by 13C and 15N concentrations in plant tissues (39). These will be measured in all plots twice each year, using the material collected in Subproject 1.

Analyses will include the Daycent modeling approach with, as well as series of GLMM as described in Subproject 1. A full assessment of the impact of climate change and management practices on ecosystems C and N fluxes and their feedback to the climate system will be performed.

2.9. Subproject 3: Effects of climate change and grazing pressure on biodiversity and trophic structure of soil mesofauna (Proctor, Cahill, Wilson)

A Ph.D. student will lead the subproject testing the impact of climate change and defoliation on soil invertebrate communities. We will target mesofauna (mites and springtails), the dominant invertebrates documented in arid Alberta grasslands (24). Broad-scale, but coarse, comparisons of soil invertebrates among locations will be conducted using the mini-rhizotron images collected within Subproject 1. During image processing, numbers of mesofauna at different depths will be recorded. This will allow us to see vertical shifts in distribution, but image quality is too poor to allow identification of taxa beyond "mite" or "collembolan". A more detailed understanding of treatment effects on invertebrates requires soil extraction. Because extraction and identification require substantial time in the laboratory, we will conduct this aspect of the subproject only at the Alberta site. Two cores (3 cm diameter, 10 cm deep) will be taken from each plot in each of the sampling periods (spring and peak biomass) each

year. Because we predict the influence of treatment to be strongest in the upper layer of soil, each core will be divided into a 5 cm upper and 5 cm lower section, and invertebrates extracted separately. Tullgren-style extractors will be used with invertebrates extracted into 70% EtOH. Because some groups of mesofauna are more resistant to this desiccation-based extraction method than others, we will also extract a subset of the residual cores via kerosene.

We plan on a rapid approach to biomass estimation. Mesofauna from a set of trial extractions will be split into groups based on body structure (e.g. collembolans, hard-bodied mites, soft-bodied mites). For each morphogroup, we will estimate the total area of a gridded Petri dish that they cover when densely packed. Animals will then be dried and weighed to give a per-surface-area estimate of biomass. Thus, when a treatment sample is sorted, we will first arrange the animals into morphogroups, note the area covered, and then continue to sort finely for taxonomic identification. For identification, animals will be sorted, counted, and representatives cleared and mounted. We hope to identify to genus, but recognize that in many cases (e.g. juveniles), family or superfamily may be the finest level possible. Voucher specimens will be deposited at the Canadian National Collection of Insects and Arachnids in Ottawa. We will also classify taxa into 'trophic groups' to help in construction of the network of plant-soil-animal interactions. Although omnivory is common, one can often make generalizations about the most usual diet at the family level. For taxa that ingest solid particles (e.g. most Oribatida), we will examine gut contents of slide mounted individuals to determine some aspects of their diet.

The statistical approach will be similar to that described in Subproject 1, a combination of univariate and multivariate analyses to determine how altered climate and defoliation interact to affect mesofauna abundance, distribution, biomass and composition. Relationships between mesofauna abundance and biomass, as well as microbial biomass and diversity, will be explored to understand the food web and the interrelationships between different components in the ecosystem.

2.10. Synthesis (Cahill, Bork, Wilson, Chang, Proctor)

An innovative aspect of this project is the emphasis on the linkages between soil chemistry, microbial activity, soil invertebrates, plant growth, grazing, and climate change, rather than viewing these as discrete projects. A critical analytical objective will be the integration of the datasets generated in each subproject, allowing us to test broader questions about the interactions between climate change and ecosystem sustainability. This more synthetic approach is enhanced by having field sites distributed over a broad geographic area. Synthesis will be facilitated through integrated database management overseen by the project manager. We will use a variety of analytical approaches, including Structured Equation Modelling, Information Theoretic Approaches, and Simulation Building to explore the relative strengths of the different potential functional links amongst our response variables. For example, we will develop a model to explore the relative contributions of alternative plausible causal factors (e.g. root turnover, microbial activity, etc.) which could alter carbon storage with decreased soil moisture and increased temperatures. This approach will allow us to identify which of the countless numbers of potential linkages are functionally most critical in this system for any particular management goal or concern.

2.11. Project Work Plan and Communication

Cahill will serve as the primary group leader and as the direct supervisor of the Project Manager who we will hire to oversee the logistics of the research and to conduct active research, such as the synthesis of the datasets. Communication among the team members will happen on a regular basis (daily or weekly as needed). Team members based in Regina will travel to Edmonton for meetings twice each year, and will participate via teleconferencing for other meetings. Communication with supporting organizations and other interested stakeholders will occur informally throughout the project, as well as more formal annual two-day meetings. During these meetings, students and PIs will report on progress to date, identify key milestones yet to be achieved, and welcome input on direction and dissemination. This project will run from approximately October 2006 – September 2009, allowing for three field seasons (2007, 2008, and 2009). The initial priorities will be to hire/recruit students and technical staff, build research equipment, and install plots in time prior to the first growing season. All analytical samples from one growing season will be processed prior to the initiation of the next growing season, such that all students and technical staff will be very active 12 months/year. To facilitate communication among team members, the general public, potential students, media groups, and other researchers, the project coordinator will construct a high-quality web page describing this project and related research. Technology transfer notes will be developed for dissemination of research results to the collaborating organizations, user groups, and policy makers.

2.12. Access to Equipment, Field Sites, and Infrastructure

We have access to the infrastructure needed for this project, including field sites, computer labs (UA, UR), plant and soil sample processing facility (UA), biogeochemical analytical facilities (UA), three mini-rhizotron cameras (UA, UR), a Li-Cor 6400 for measures of respiration and photosynthesis (UA), and a fabrication shop for building equipment (UA). The Alberta field site is equipped with trailers, and provides a base of operations for the largest component of this project. The satellite sites are provincial natural areas that are supportive of field research and easily accessible. Resource use in this project involves four major areas: (1) Construction of rainout shelters and OTC units, along with associated data loggers and probes to measure their effectiveness. Without the ability to manipulate temperature and precipitation, along with the ability to accurately record the level of manipulation, this project can not be conducted. (2) People. A strength of this project is that we are using a variety of subdisciplines to address a single unified question. However, this also means that we need a large group of diverse HQP to conduct the research. (3) Travel. The field locations in this study span three provinces, and there will be substantial travel between sites and home universities. Additionally, numerous students will be living in the field for extended periods. (4) Analytical analyses. We will be taking a large number of samples for C and N determination and measures of stable isotopes. We are able to conduct all of these analyses at UA, at a cost greatly below commercial rates. The comprehensive approach we are taking is a cornerstone of this innovative research project.

2.13. Training of HQP

Over the course of three years, this project will train 2 M.Sc., 3 Ph.D. students, a project manager, an image analyst (roots), 11 summer field assistants, and 15 undergraduate lab assistants during the academic year (Total HQP = 33). This is a large number of HQP and reflects the integrative nature of this research and our commitment to training HQP. Most graduate students will be co-supervised. Two graduate students are already in place with one having started in 2005 and the second starting in 2006. We will employ a full time Grade 8 technician (University of Alberta personnel scale) to help with coordination of research across the field sites, supervision of students in the field, and with sample processing during the academic year. Prior experiences with multi-investigator projects have taught us that this position is critical to the integration of communication of information amongst team members and to help keep all members working towards the same goal.

The supporting organizations will play an important role in the training of the HQP in this project. Behan-Pelletier of the National Collection will assist with oribatid identifications and training of the PhD student associated with Subproject 3. Ducks Unlimited and Alberta Sustainable Resource Development will provide support for the graduate students with hands-on training on range management issues and techniques. The graduate students in turn will provide input to upgrade the producers' knowledge about current developments and particularly results from this project. Additional interactions with industry and other research will be facilitated through support from the Agricultural Research and Extension Council of Alberta and the Alberta Cooperative Conservation Research Unit. Each of the three subproject components will train people to fill current and future gaps in expertise in our supporting (and other related) organizations. All HQP will develop skills in plant identification, experimental design, statistical analysis, and working in a large team. Subproject 1 will create rangeland ecologists able to assess range health and address long-term rangeland sustainability. Subproject 2 will produce people skilled in field and laboratory assessment of soil biogeochemistry. The Ph.D. student from Subproject 3 (invertebrates) will graduate at a time when many of the mite taxonomists in Canada are retiring or have already retired. Undergraduate technicians involved in all subprojects would also gain skills that could be applied to research at AAFC stations anywhere in the country.

Overall this project represents an outstanding opportunity for the training of HQP. The PIs have diverse backgrounds, and established relationships with a variety of supporting organizations. As a result, students will be trained in numerous technical skills, and more importantly, they will be trained in an environment which encourages discussion and communication across disciplines. We are taking a holistic approach with this research project that will provide an excellent environment for the training of HQP.

2.14. Supporting Organizations

We have received support from various organizations in western Canada concerned with the sustainable management of rangelands, including Ducks Unlimited Canada (DUC), the Agricultural Research and Extension Council of Alberta (ARECA), and Alberta Sustainable Resource Development (ASRD). Ducks Unlimited is Canada's self-proclaimed "Conservation Company", with interest in maintaining habitat through land stewardship, particularly native rangelands. ASRD and ARECA recognize the importance of rangelands to the economic wellbeing of rural communities in western Canada. Additional support from Agriculture and Agri-Food Canada indicates the realization that an understanding of the organisms which live in rangelands soil is critical to any realistic long-term plan for sustainable production.

The potential impact of our work to increase understanding of the impacts of climate change, along with the development of mitigation strategies is in part evidenced by the large commitment BIOCAP Canada is willing to make to this project. Additional support from the Faculty of Agriculture, Forestry and Home Economics at the University of Alberta further highlights the interest in improving sustainable management of rangelands in the face of climate change. PIs and graduate students will have substantial opportunities to interact with other BIOCAP research groups, integrating our research focus with their prior and current work. For example, this project can contribute to the Landscape Scale Research Group whose mandate is to develop an understanding of how a variety of land use practices interact with climate change and mitigation efforts. We will also encourage data sharing among groups, increasing the value of these data through broader access.

Our plan for knowledge transfer will take advantage of the centralized research activities associated with the Kinsella Research Station and its various outreach activities. The Kinsella station is frequently used for demonstrations, field tours, and special seminars or workshops by various commodity and interest groups in rural Alberta, as well as other visiting researchers to the University of Alberta. We will also hold annual field days with invitations extended to all interest groups, including stakeholder organizations such as ASRD, to review the field sites, examine and discuss results, and provide feedback on the project. Throughout the research, frequent communication will be made with provincial Alberta Agriculture, Food, and Rural Development forage and beef extension specialists, as well as associated interest groups to ensure they are kept informed of the results of the research. Similar outreach will occur in SK and MB with producers and provincial and federal agricultural agencies in the communities surrounding the two satellite field sites. We also anticipate our web page describing the project will facilitate information dissemination to the general public, media, supporting organizations, other researchers, and other interested groups.

Interim and final results of this research will be presented at various forums, including international and national scientific meetings as well as regional meetings such as the annual ARECA meeting, the Western Range Science Seminar, the Western Canadian Grazing Conference, the Alberta Soil Science Workshop, and workshops organized by Climate Change Central and BIOCAP Canada. Final results of this research will be published in peer-reviewed articles for prompt transfer to other scientists (i.e., Ecology, Ecological Applications, Journal of Applied Ecology, Soil Biology and Biochemistry, and Rangeland Ecology and Management), and will be summarized in articles prepared for various popular press media, including Cattlemen's Magazine, Alberta Crops and Beef, Country Guide, and Rangelands. Final results of this research will also be adapted into producer-friendly extension publications (e.g., AgDex Factsheets on "Strategies to Manipulate Root Growth for Maximum Drought Resistance"), for dissemination by the AAFRD extension office.

2.15. Benefits to Canada

Significant economic benefits are likely to arise from this research, mainly through the ability to predict and anticipate changes in the quantity and quality of rangeland resources. These resources are far larger that the 4.7% of Canada's area occupied by the grassland biome, because this biome is also the home of 14% of the country's population, and 15% of its gross domestic product. At current prices, cattle in the Prairie Provinces are worth nearly \$10 billion (Statistics Canada 2006), a figure that does not include the associated infrastructure such as farms, feedlots, transportation and packing houses. Thus, increasing the value of this industry by only a small amount would yield enormous economic benefits (e.g. a 1% increase in the value of cattle is \$100 million). We will contribute value by allowing managers to predict and anticipate changes in range carrying capacity in response to the now widely-accepted warming trend. For example, it is possible that drought-adapted prairie grasses will be little affected by small increases in temperature. If so, then current grazing regimes can be maintained. Alternatively, a reduced carrying capacity would signal a need for either reduced cattle numbers or alternative feeding strategies.

A secondary long-term economic benefit will result from the knowledgeable stewardship of rangeland soils. Environmental benefits will accrue for increasing our ability to store soil carbon. We will learn how storage can be controlled via grazing, a wide-spread and relatively easy to manage activity which, in contrast to forest growth, can be altered over relatively short time frames. Grasslands store significantly more carbon belowground than do other vegetation types, such as boreal forest. This fact combined with the total area of temperate grasslands, means that temperate grasslands store 245% more C than boreal forests on a global scale [grasslands: 119.7 x 1015 g; boreal forest: 48.7 x 1015 g (40)]. This information will allow Canada to make an important contribution to global management of C storage. Canada is in a unique position to provide information about the northern Great Plains, where lower temperatures cause C storage to be likely greater than in the well-studied more southern grasslands of the US. The data and understanding generated in this project will help fill critical holes in our current understanding of carbon cycling, and will increase our ability to adequately inventory Canada's carbon stores.

An additional environmental benefit will be the conservation of biodiversity in native grasslands used for cattle production. The only productive alternative to grazing in this region is cultivation-based agriculture with consequent losses of habitat and soil organic matter. Social benefits include an enhanced ability to keep ranchers employed growing livestock and conserving native grassland, with consequent positive effects on rural prairie communities.

This investigation will also train unique Highly Qualified Personnel at all levels, including > 10 undergraduate assistants, 5 graduate students and two research technicians. Training of HQP is of strategic importance to Canada and will benefit the country in technology development and economic growth in the long run. Good public policy has science as one of its foundations. As noted above, our understanding of C storage in grassland soils is very weak compared with that of forests. Much of the scientific literature about grasslands originates from warmer and wetter climates, and the applicability of these results to Canadian issues is uncertain. This project will address an important knowledge gap to society and the agriculture community in particular.

2.16. References

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3. Summary of Second Year Results in the Study Examining Climate Change Impacts on Rangeland Function

3.1. Environmental Responses

3.1.1. Precipitation

Mean precipitation reduction in the plots with rainout shelters, and hence mean precipitation addition to the "augmented rainfall" plots, was calculated at +/-48% rather than 70%, with values ranging from 36% to 59%. Rainfall interception by the rainout shelters was calculated using the equation:

% reduction = Vol._{H2O Collected} / Vol._{H2O Theoretical} * 100%,

where: $Vol_{H2O Collected}$ = volume of water collected and diverted from each -70% precipitation plot, and $Vol_{H2O Theoretical}$ = theoretical volume of ambient precipitation in each plot

The volume of water collected was calculated based on average water height in tanks containing runoff from the -70% plots, while the theoretical precipitation volume was calculated as rainfall (mm) recorded on site multiplied by the effective plot area. As there was a discrepancy in total rainfall recorded by the two rain gauges at the study site, the larger recorded rainfall was used to calculate the theoretical precipitation volume, ensuring that the estimated magnitude of treatment effects was conservative.

Although our moisture modification treatments were slightly below anticipated values, a 48% reduction (or increase) in moisture still represents a major perturbation to the plant communities examined. Moreover, a 50% increase or decrease in rainfall provides moisture values across our experimental plots that are consistent with deviations considered typical of variation within and between growing seasons in grasslands of western Canada (Fig. 1).

3.1.2. Air Temperature

Open-top chambers (OTCs) were effective in raising air temperatures 10 cm above the soil surface. There were significant warming x sampling time interactions on air temperature for all months, with the presence of OTCs significantly raising air temperatures during the day but

not at night (Table 1, Figs. 2-5). The magnitude of the warming effect varied by month, from a moderate mean daytime increase in air temperature of 1.9°C in June, to a more substantial increase of 3.2°C in July (Figs. 2-5). There were also significant precipitation x sampling time and precipitation effects on air temperature in June and July, respectively (Table 1), although the magnitude of these effects was minimal (Figs. 3, 4).

Observed temperature changes are important because they increase the potential for evaporation of water during and after rainfall events. In addition, these temperature changes may impose greater stress on vegetation during peak temperatures at mid afternoon, particularly within a plant community dominated by cool season C3 species. Conversely, increased mid-day temperatures may favor warm season C4 species such as *Bouteloua gracilis* over time.

3.1.3. Relative Humidity

Relative humidity was affected by a variety of main effects and interactions among the warming, defoliation, and precipitation treatments, as well as sampling time, depending on the month of assessment (Table 2). Main effects of warming and precipitation were present for all months, as was a time of day effect. Warming raised relative humidity near the ground surface by 1.6 - 4.0%, depending on the month (Figs. 6-9). Although the magnitude of differences among precipitation treatments varied among months, the general trend remained consistent whereby relative humidity increased from the -70%, through the ambient and +70% precipitation treatments. Maximum differences in humidity between treatments within a month varied from a low of 2.0% in May to a high of 7.7% in July (Figs. 6-9). Relative humidity was 35 - 38% greater at night than during the day (Figs. 6-9). In addition to these effects, there was a significant precipitation treatment x sampling time effect in June, July, and August. For these months, the effects of precipitation treatment on relative humidity were more pronounced during the day than at night. A number of other significant and near-significant effects were observed for one or two months, and are summarized in Table 2.

Relative humidity is an important factor regulating water use and conservation in grasslands, with high humidity leading to reduced moisture loss, both through evaporation and transpiration mechanisms. Conversely, the lower observed humidity associated with reductions

in precipitation is more likely to reduce plant growth by forcing water conservation in plants during photosynthesis, and may account for reductions in yield during drought periods.

3.1.4. Soil Temperature

There were significant warming and sampling time effects on soil temperature in both the 0-5 cm and 5-20 cm soil layers during all months (Tables 3, 4). Warming increased soil temperature $0.6 - 1.9^{\circ}$ C in the 0-5 cm profile depending on month, with a significantly greater warming effect observed during the day than at night in May and July (Table 3, Figs. 10-13). Significant warming x time effects at the 5-20 cm depth soil temperature were observed for all months (Table 4), with OTCs increasing temperatures $1.1 - 1.6^{\circ}$ C during the day and $0.2 - 0.6^{\circ}$ C at night (Figs. 14-17).

There were significant defoliation main effects on soil temperatures in both soil depth layers for all months, with the exception of the 0-5 cm profile in August (Tables 3, 4). Additionally, there were significant defoliation x time interactions in the 0-5 cm profile in May, June, and July (Table 3). Increasing defoliation intensity resulted in high soil temperatures in all months for the 5-20 cm layer, with the maximum variation between treatments ranging from 0.5°C in August to 1.2°C in July (Figs. 14-17). This pattern generally held in the 0-5 cm layer, but with a significantly greater range in temperatures observed during the day than at night. Maximum variation between treatments during the day varied from 1.0°C in August to 2.4°C in July, and from 0.2°C in August to 0.4°C in July at night (Figs. 10-13). Summaries of all significant and near significant interactions are in Tables 3 and 4.

Increased soil temperatures, particularly in the day during mid-summer, and in the presence of defoliation, are important as they reinforce the effectiveness of the OTCs in increasing the temperature that vegetation and soils are exposed to within our warmed plots. Even small increases of 1-2°C are important in that they greatly increase the potential for evaporation, as well as influence key biological/ecological processes such as rates of nutrient cycling (i.e. decomposition). The influence of defoliation in increasing temperatures is not surprising given that the removal of biomass (both living plant material and litter) is likely to increasing the amount of solar radiation reaching the soil surface following loss of the protective insulating layer.
3.1.5. Soil Moisture

Not surprisingly, the precipitation treatments significantly affected soil moisture during all eight sampling times listed here, with significant warming main effects and/or interactions with precipitation for all eight times as well (Table 5). There was no consistent pattern in soil moisture for those times where only a precipitation main effect was observed (May 15 and August 15, 30). However, the May sampling time occurred only 7 days after the precipitation shelters were installed for the season, so it is likely that these treatments were not in place long enough to lead to any measurable effect. Patterns for the August sampling times were generally as expected, with greater than ambient soil moisture in the +70% plots for both times and lower than ambient soil moisture in the -70% plots during August 30 (August 15: 28.5% VWC Ambient, 30.1% -70% Precipitation, 34.3% +70% Precipitation) (Fig. 18). As there was approximately 80 mm of rainfall at the site on August 11, it could be that there was insufficient time for the drought treatment to re-establish an effect (i.e. produce measurable moisture deficits) by the time of sampling.

There was a consistent relationship between the +70% and -70% treatments when significant warming x precipitation interactions were present, with soil moisture in the -70% plots approximately 40% of that recorded in the +70% plots (Fig. 18). Soil moisture in the ambient plots, however, was more similar to that recorded in the -70% plots when OTCs were present, and similar to that recorded in the +70% plots when OTCs were absent. These findings suggest that there may have been increased evapo-transpiration within warmed plots. Alternatively, this observation may be an artifact of the OTCs preventing precipitation from entering the sides of these plots, and will require further examination. Temporal variation in precipitation effects for both the 0-5 cm and 5-20 cm soil layers can be seen in Fig. 18.

Warming x depth interactions were observed for all but two of the sampling times. The general pattern of the interaction was for slightly lower soil moisture in warmed plots than control plots in the 5-20 cm layer, but greater soil moisture in control plots than warmed plots in the 0-5 cm layer. Differences between control and warmed plots in the 5-20 cm layer ranged from 0.3% to 2.6% VWC, while differences between control and warmed in the 0-5 cm layer ranged from 5.8% to 10.3% VWC. A summary of all significant and near-significant treatment effects and interactions is presented in Table 5.

Overall, our soil moisture data reinforce the effectiveness of our treatments, including rainout shelters and OTCs, in altering soil moisture availability and/or subsequent use by vegetation. Changes in soil moisture are likely the result of many factors, including altered precipitation, evaporation, infiltration, and transpiration, as evidenced by the changes in air and soil temperature, as well as relative humidity, documented previously. Regardless of the causal mechanism(s), changes in soil moisture are likely to be the single most important factor regulating plant growth and ultimately, forage production and quality, within the grasslands examined in this study.

3.2. Plant Species Diversity and Composition

There was no effect of precipitation or year on species richness. The interaction between defoliation and temperature, however, had a significant effect (p=0.02) on richness in both 2007 and 2008 (Fig. 19). In the absence of defoliation during the growing season, warming from the OTCs led to greater species richness compared to unwarmed plots. In contrast, within those plots receiving high defoliation, the additional presence of warmed conditions led to a reduction in species richness (Fig. 19). Moreover, the magnitude of this reduction appeared to increase from 2007 to 2008 (Fig. 19).

Year also had an effect on species evenness, and the two years were subsequently analysed separately. During 2007, defoliation had an effect on evenness (p=0.002, Fig. 20), with undefoliated plots having greater species evenness than either of those defoliated in mid summer. There was also a marginally significant (p=0.08) warming by precipitation interaction on evenness in 2007. During that year, evenness declined with warming under ambient precipitation, but increased with the addition of warming to drought (Fig. 21).

One year later in 2008, precipitation, but not defoliation, had a significant effect on species evenness, with significantly greater evenness in droughted plots compared to those receiving either ambient or added rainfall (p=0.02; Fig 22).

Ordination of species data using NMS resulted in a three-dimensional solution with a stress value of 17.75 and instability of 0.008. Axis 1 explained 26.3% of the variance, Axis 25.1%, and Axis 3 27.6%, for a total variance explained (r²) of 78.9%. Examining the ordination

output graphs, Axis 3 separated the three defoliation treatments (Fig. 23), and Axes 2 (Fig. 24) and 3 (Fig. 25) separated the three precipitation treatments. Temperature did not contribute to variation in community composition.

Results from the PerMANOVA support the visual assessment of the ordination: defoliation treatment had a significant effect on the ordination (p=0.0002), as did the precipitation treatment (p=0.002), while temperature had no effect on the ordination (p=0.73) (Table 6). All levels of precipitation led to a significant effect on community composition, as did all defoliation treatments (Table 7), although the high and low defoliation treatments were marginally different (p=0.06).

Warmed and undefoliated plots had greater richness than unwarmed, undefoliated plots. These results suggest the latter treatments were relatively stable in composition, while the former plots were susceptible to species compositional change, potentially invasion or opportunistic increases in existing species adapted to the warmer, dryer conditions within the plant community. However, it is also important to note that warmed plots experiencing high defoliation exhibited low richness, indicating defoliation may have offset any compositional changes generated by the warming treatment alone. The combined effects of defoliation and warming may also have led to environmental conditions that allowed only a few species to dominate.

Notably, our results differ from those of other defoliation studies, where increased defoliation generally increased plant diversity. For example, in the study by Harmens et al. (2004), forb species richness increased with defoliation, while species evenness did not exhibit a clear response. Perhaps because our study has been historically grazed, and species richness is likely to be high due to previous grazing influences, a much longer time frame would be required for plots to respond to defoliation, including the lack thereof. Notably, richness at our prairie grassland site was not sensitive to temperature, unlike the study by Klein et al. (2004) within alpine grasslands where richness declined with warming. Differences in responses between these studies are understandable, and are attributed to the sharply contrasting experimental locations, with differences in plant communities, environmental conditions, and the associated adaptation of the community to environment, likely to dictate observed responses.

Precipitation and defoliation affected overall community composition, while temperature did not affect the community. These results suggest that community composition is more

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sensitive to defoliation and precipitation changes than temperature. This is perhaps not surprising given the high impact of defoliation (up to 70 or 80% biomass removal) and precipitation (a 40% increase or decrease in moisture) treatments relative to the more subtle warming effects. While effects of a 2°C change in temperate are likely to manifest in community changes over the long-term (i.e. over many year or decades), the plant community examined here is likely resistant to a short-term increase in temperature of this magnitude. While Harmens et al. (2004) found that temperature had an effect on community composition, the effect was weaker than that of defoliation.

To assess species responses to treatments, an Indicator Species Analysis was performed on the cover data collected in July 2008. A total of 7 species responded to various combinations of warming, precipitation and defoliation (p < 0.10) (Table 8). These species included blue grama grass, milkvetch, upland sedges, fairy candelabra, western porcupine grass, pasture sage, and moss.lichens. Among species, all preferred unwarmed conditions with the exception of pasture sage. The response of sage indicates that this unpalatable plant may become more problematic under a general shift towards a warmer climate. The lack of a response by blue grama grass to warming was somewhat surprising given that this species was expected to respond positively to warm conditions due to its adaptation to these conditions as a C4 species.

Among the 7 species responding to treatments (Table 8), not surprisingly most preferred conditions of high rainfall, particularly sedges and forbs (i.e. milkvetch, fairy candelabra, and pasture sage). The only exceptions were western porcupine grass and blue grama grass, which were linked to ambient rainfall, and the cover of moss and lichen, which was tied to a reduction in rainfall.

Finally, the 7 species in Table 8 were differentially linked to the defoliation treatments. Western porcupine grass and pasture sage preferred no defoliation, sedges low defoliation, and all other species high defoliation. Most species responding positively to defoliation were known to be disturbance tolerant, including fairy candelabra, blue grama grass, and the cover of moss.lichen.

In summary, defoliation and precipitation effected community composition, although the latter was relatively robust to short term changes in temperature. As warming is likely to increase in significance over time, and some individual species will continue to respond to temperature changes (e.g. pasture sage), it is evident that Alberta's grasslands are susceptible to

ongoing climate change impacts, particularly rainfall in the short-term. As a result, the modification of grazing may be important in limiting any undesirable impacts of combined defoliation, precipitation change, and warming, during this transition.

3.3. Range Health

Range health assessments were conducted on all plots in July of 2007 and 2008 using ASRD range health criteria. Results of the initial assessment in 2007 indicated that all plots exposed to the control and warming treatment alone were healthy, regardless of the presence of drought (Fig. 26), reinforcing the notion that this grassland was in excellent condition at the start of the study. With light defoliation, a small to moderate number of plots were designated as 'healthy with problems' (Fig. 26), likely due to the loss of litter and associated changes in species richness that were previously described. Moreover, the addition of drought to light defoliation and warming resulted in a further increase in the frequency of plots rated as 'healthy with problems'. Under heavy defoliation, an even larger proportion of plots were rated as 'healthy with problems' (Fig. 26). Only 1 plot out of the 90 examined was rated as unhealthy.

Based on the summary of 2008 range health assessments, those plots receiving additional precipitation appeared better able to resist changes in range health due to low defoliation (Fig. 28). Our data also indicated an important interaction existed between warming and precipitation on range health. Warmed plots had greater range health than unwarmed plots, but only under high precipitation. Conversely, warmed plots led to lower health scores under ambient precipitation. These results are important in that they highlight the uncertainty associated with future range health trend under climate change, given varying scenarios of changes in temperature and rainfall amounts and/or patterns. That is, while warmer conditions may allow for enhanced plant growth provided increased moisture is available to offset increases in evapotranspiration, the opposite is true should rainfall remain the same or even decline. Finally, defoliation had the strongest effect on observed range health during 2008 (Fig. 28). This is not surprising given the marked negative impact of moderate to heavy defoliation on plant vigor, associated litter levels, and other important community characteristics.

As a potential undesirable weed responding to warming, we conducted a further assessment on the cover of pasture sage across the treatments (Fig. 28). Pasture sage cover generally increased with greater rainfall, and declined sharply with dry conditions. Under drought conditions, little effect of warming was apparent. However, under either ambient or above normal rainfall, warming had a sharply contrasting impact that depended on defoliation intensity. In the absence of defoliation, warming increased the cover of pasture sage (Fig. 28). However, under high defoliation warming actually resulted in a reduction in pasture sage cover. Given that defoliation was not selective (i.e. sage was also defoliated), the latter result represents a reduction in resilience (i.e. recovery) of sage under warmed conditions following heavy defoliation.

Overall, these results suggest that the range health assessment appears capable of capturing variation in treatment responses, including that of warming, precipitation change and defoliation. Future changes in range health rating scores are likely as the cumulative effects of all three treatments continue to develop over the next several years. Data from 2009 in particular, will provide clearer evidence of the utility of the range health scores for assessing rangeland resistance to degradation under each disturbance, and may provide insight into the disturbance thresholds likely to cause accelerated loss of range condition.

3.4. Vegetation Biomass

Year had an effect on productivity of all three growth forms, and thus years were analyzed separately. In both years, total productivity was affected by precipitation and defoliation (2007: def p<0.0001, precip p=0.001; 2008: def p=0.002, precip p=0.0002) (Fig. 29), but not temperature. During 2007 total productivity increased with greater severity of defoliation, although the extent of the increase was much larger under ambient moisture than droughted plots (Fig. 29). Among growth forms, grass production in 2007 was affected by all the treatments, (def p<0.0001, precip p=0.001, temp p=0.06; Fig. 30). Grass productivity was reduced by drought, but increased with defoliation of any severity (Fig. 30).

One year later in 2008, total production once again increased in plots receiving either moderate or high severity defoliation (Fig. 29). Similarly, production closely followed the total

amount of moisture as determined by the rainfall treatments. However, grass productivity was affected by precipitation only (p<0.0001), decreasing with a reduction in precipitation. Unlike the year before, forb productivity responded to treatments in 2008: forb productivity declined with defoliation (p=0.02), and there was an additional temperature by precipitation interaction (p=0.03) (Fig. 31). Under ambient and increased precipitation, forbs within the warmed treatment had lower biomass than the unwarmed treatments, while under decreased precipitation levels, forbs in the warmed treatment produced more biomass across all defoliation treatments (Fig. 31).

Our results documenting temperate grassland responses to climatic factors in central Alberta contrast those from arctic and alpine environments, which generally respond strongly to climate and defoliation manipulations (Walker et al., 2006, Klein et al., 2004, Rustad et al., 2001). For example, in the meta-analysis by Rustad et al. (2001) of warming experiments, primary productivity in grasslands responded both positively and negatively to warming, with an average response near zero.

One theory that explains the disparity between temperate grassland responses to stresses like defoliation, precipitation, and temperature changes, is that these responses depend closely on successional status (Grime et al. 2000). After five years of precipitation and temperature manipulation in two grassland sites, the later successional site had no response to the treatments, but productivity and community composition in the early successional grassland responded to all treatments (Grime et al., 2000). Our site was historically moderately grazed prior to the initiation of the experiment, and thus our site may be mid-successional, explaining why we saw some treatment responses, but not as many as Grime observed at the early successional site.

In another study by Harmens et al. (2004), forb biomass increased in response to high (frequent) defoliation coupled with warming, but declined with low defoliation and warming. This outcome is similar to our results, although temperature interacted with precipitation instead of defoliation to increase forb biomass. Plots exposed to the combined stress of decreased precipitation (i.e. drought) and warming had greater forb biomass than unwarmed plots. Additionally, within plots receiving ambient or high precipitation, forbs had lower biomass when exposed to warming compared to the unwarmed treatments. Thus, it appears that forbs likely have a competitive advantage under stressful growing conditions.

3.5. Soil Carbon and Nitrogen Dynamics

Summary results of the analysis of soil carbon and nitrogen data are provided in Table 9, while data on gas fluxes are provided in Table 10.

3.5.1. Soil Microbial Biomass Carbon and Nitrogen

Soil microbial biomass carbon (MBC) showed strong inter-annual variability at both shallow (0-5 cm) and deeper (5-15 cm) soil depths, with MBC greater during the second year of the study. From the first to the second year of the study, MBC increased from 2.9 to 4.3, and 0.9 to 1.16 g/kg in the 0-5 and 5-15 cm soil layers, respectively (Fig. 32).

Within the 0-5 cm soil layer, high intensity defoliation decreased MBC from 3.5 to 2.5 g/kg in 2007. Similarly, levels of MBC declined from 4.29 (non-defoliation) and 5.19 (low defoliation) to 3.4 g/kg (high defoliation) in 2008 (Fig. 32). In contrast, low defoliation had no influence on soil MBC. In contrast to defoliation, warming increased MBC from 2.4 to 3.5 g/kg in 2007 (Fig. 32). Precipitation also influenced MBC. Values of MBC increased at the 0-5 cm soil depth from 4.6 g/kg in control plots to 5.3 g/kg under high precipitation, but decreased to 2.9 g/kg under reduced precipitation in 2008 (Table 9 and Fig. 32).

At the deeper soil depth (5-15 cm), defoliation also influenced MBC in 2007 (Table 9), similar to that observed in the 0-5 cm soil layer. Soil MBC under reduced precipitation (1.04 g/kg) was lower than that documented under high precipitation (1.31 g/kg) during 2008.

Soil microbial biomass nitrogen (MBN) exhibited considerable inter-annual variability at both soil depths (Table 9). During 2008, MBN was significantly greater at 0-5 cm (values ranged from 2.9 to 4.3 g/kg) than at 5-15 cm (0.93 to 1.16 g/kg) soil depth (Figure 33). Levels of MBN increased from 0.34 to 0.49 g/kg in response to warming in the 0-5 cm soil layer in 2007. Precipitation was a key factor determining soil MBN in both 2007 and 2008 (Table 9). Reduced precipitation decreased soil MBN in both years. In 2008, soil MBN was significantly greater within precipitation addition plots (1.7 g/kg) compared to plots with ambient rainfall (1.1 g/kg).

The strong effect of defoliation on soil microbial biomass in our study illustrates the influence of important belowground (i.e. soil) and aboveground (i.e. plant) processes interacting

with one another (Grime, 2001; Wardle *et al.*, 2004; Bardgett *et al.*, 2005). Soil microbial populations directly influence carbon substrate quantity and quality (Bardgett *et al.*, 1997). Defoliation tended to decrease MBC and MBN because of the removal of plant biomass and organic matter from these plots, decreasing soil organic carbon input and availability to microbial populations, resulting in the reduction in soil MBC (Garcia, 1992; Zhang *et al.*, 2005).

In general, warming increased soil microbial biomass in our study, for which there are several potential explanations, including that 1) warming accelerated organic matter breakdown leading to greater organic carbon availability for microbial population growth during decomposition, or 2) warming enhanced plant growth, particularly belowground. Positive responses of plant biomass to warming are known to increase soil C substrate available for microbes (Wan *et al.*, 2005; Belay-Tedla *et al.*, 2009). Soil microbial responses to experimental warming in other studies have been inconsistent. For example, 12 years of experimental warming decreased the size of some microbial populations due to a reduction in labile C availability (Frey *et al.*, 2008).

The reduction in MBC and MBN with reduced precipitation may partially be explained by a decline in soil C substrate as a consequence of suppressed plant growth (Peters *et al.*, 2007), or by the fact that soil wetting after a drought situation can induce bacteria lysis (Fierer *et al.*, 2003), thereby substantially decreasing total soil microbial biomass (Kassem *et al.*, 2008). Increased precipitation increased microbial N. The addition of precipitation resulted in an obvious and predictable stimulation in grass productivity, which in turn, increased inputs of plant biomass C and associated soil C substrates. Ultimately, this would enhance belowground C allocations (Zak *et al.*, 1994) and consequently support larger soil microbial populations.

3.5.2. Soil Dissolved Organic Carbon and Nitrogen

Soil dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) showed few responses to treatments over the first two years of data collection (Table 9; Figs. 34, 35). However, annual variability of DOC between growing seasons was significant at both soil depths. Concentrations of DOC were greater in the 0-5 cm soil layer than in 5-15 cm soil. The limited differences found here suggest that either warming, defoliation and precipitation were not key factors regulating soil DOC, or alternatively that the complex interactions among these factors canceled out their effects on DOC at either soil depth during 2007 and 2008. Instead, significant annual variability in dissolved organic C and N concentrations were evident. Annual variation in the inputs of plant litter, nutrient throughfall (Schwendenmann & Veldkamp, 2005), rhizo-deposition and root-mycorhizal turnover (Nguyen, 2003), could all be significant factors affecting the annual-variation of DOC. Our findings suggest that the dynamics of DOC are complex, and are affected by climatic factors, grazing intensities, and their interactions, rather than their individual effects.

3.5.3. Soil Greenhouse Gas Efflux

Inter-annual variability was large for soil carbon dioxide emissions (Table 10, Figure 36). Neither warming nor defoliation influenced soil carbon dioxide emissions during the two years of the study to date. The main effect of precipitation on CO_2 emissions was significant during both years (Table 10). Carbon dioxide efflux increased in the precipitation addition plots (from 2.9 to 4.09 µmol m⁻²s⁻¹), and decreased due to precipitation reduction (from 2.7 to 1.2 µmol m⁻²s⁻¹ and from 2.9 to 1.2 µmol m⁻²s⁻¹ in 2007 and 2008, respectively), as compared with the control.

Precipitation was a strong driver of soil CO₂ efflux in our study. Given that grassland soils are typically moisture-limited (Knapp, 1985), small changes in soil moisture content could potentially have large impacts on soil microbial (Maier & Kress, 2000) and plant root respiration (Innes *et al.*, 2000). These changes, in turn, may explain why reduced precipitation decreased soil CO₂ emission while the addition of moisture increased soil CO₂ emission. Soil CO₂ efflux was highly correlated with soil temperature and volumetric water content in each year of the study. Soil temperatures in both the 0-5 and 5-15 cm soil depths, combined with soil volumetric water content in the top 5 cm, explained as much as 45% of soil CO₂ emissions in 2007.

Similarly, almost 26% of the variation in CO_2 efflux during 2008 was explained by soil temperature in the shallow (0-5 cm) soil layer together with soil volumetric water content at both

soil depths. Soil volumetric water content at 0-5 cm was the main contributor to variation in CO_2 emissions during both years (25 and 22% in 2007 and 2008, respectively).

Soil nitrous oxide (N₂O) emissions did not show significant inter-annual variability (Table 10) (Figure 37). Emission of N₂O did not respond significantly to either warming or defoliation in either year. During the first year, only precipitation influenced soil N₂O emission. Uptake of N₂O was evident within the low rainfall precipitation treatment. Efflux of N₂O decreased from 7.9 x 10^{-5} under ambient precipitation to $-7.2 \times 10^{-5} \mu mol m^{-2} s^{-1}$ in the reduced precipitation treatment. Overall, effects of our treatments on soil N₂O efflux were complex and usually consisted of numerous interactions among treatments.

The decreasing effect of lower precipitation on N_2O emission was expected. It is established that under drought conditions the emission of NO is more important than that of N_2O (Firestone & Davidson, 1989). Additionally, decreased soil moisture inhibits denitrification and N_2O production.

In the present study, grassland soils are a sink for atmospheric methane. Aerobic methanotrophs are a primary biological sink for methane because they oxidize atmospheric CH_4 as energy sources (Hanson & Hanson, 1996). Consistent with our study, grassland ecosystems have been shown to be a net CH_4 sink (Hutchinson & Mosier, 1981; Mosier et al., 1991). However, environmental conditions and grazing practices may influence CH_4 consumption in grasslands (vandenPolvanDasselaar *et al.*, 1997).

Abiotic factors (e.g., soil temperature and moisture) have been found to affect CH₄ variability in terrestrial ecosystems (Boon & Mitchell, 1995; Ball *et al.*, 1997; Miyajima *et al.*, 1997; Livesley *et al.*, 2008). During 2007, slight significant responses to warming were evident (Table 10). Soil CH₄ uptake decreased from -6 x 10^{-4} to -5 x 10^{-4} µmol m⁻²s⁻¹ due to increased temperatures.

The effects of defoliation and precipitation on soil CH₄ emission were strong in the second year of study (Table 10). Uptake of CH₄ decreased due to defoliation (from -8 x 10^{-4} µmol m⁻²s⁻¹ to -7 x 10^{-4} and -6 x 10^{-4} µmol m⁻²s⁻¹, in the low and high intensity defoliation treatments, respectively) (Figure 38). Low intensity defoliation increased soil CH₄ uptake in this study. To date, very little is known on the effect of defoliation intensity on CH₄ emission in grassland ecosystems.

Our results show that the responses in CH₄ uptake varied by defoliation intensity, similar to that observed within wetland ecosystems (Freeman *et al.*, 2002). We propose that the effects of defoliation on CH₄ uptake depend on plant-microbe relationships rather than soil moisture content and temperature within the grassland ecosystem studied here. Regression analysis did not show a strong relationship between CH₄ efflux and soil moisture content and temperature. Moreover, precipitation suppressed CH₄ uptake in both high and low moisture treatments. CH₄ uptake was greatest within ambient (-9 x $10^{-4} \mu \text{mol m}^{-2}\text{s}^{-1}$) plots, and declined significantly due to both reduced precipitation (-7 x $10^{-4} \mu \text{mol m}^{-2}\text{s}^{-1}$) and increased precipitation (i.e. legume vs non-legume), and nitrifier and methanotoph competition for NH₄⁺-N (Niklaus *et al.*, 2006; Livesley *et al.*, 2008). The response of CH₄ consumption was consistent with our hypothesis and previous findings that propose temperature and moisture impacts on soil CH₄ flux (Jury *et al.*, 1991; Torn & Chapin, 1993; Smith *et al.*, 2000).

3.6. Litter Decomposition

Litter decomposition comprises a significant component of the global carbon budget (Aerts 2006). Decomposition is sensitive to temperatures (e.g. Murphy et al. 1998), and it has been hypothesized that climatic warming will lead to increased litter decomposition, especially in cold biomes, where decomposition is strongly temperature limited (Hobbie et al. 2002, Robinson 2002). In addition, studies suggest that global warming will lead to increased litter decomposition rates only if there is sufficient moisture (e.g.Robinson et al. 1995, Rustad and Fernandez 1998, Verburg et al. 1999, Shaw and Harte 2001, Sjögersten and Wookey 2004).

On the other hand, human-induced land-use practices, including livestock grazing, have been shown to alter plant species composition (Milchunas and Lauenroth 1993), which has strong effects on ecosystem processes (Chapin et al. 2000, Diaz and Cabido 2001) such as litter decomposition and nutrient cycling (Anderson 1991, Vitousek 1997). Grazing is therefore expected to influence decomposition rates through effects on local environmental parameters and litter quality (e.g. Semmartin et al. 2004). Litter quality is often the best predictor of decomposition rates within a particular climatic region (Silver and Miya 2001, Parton et al. 2007).

Litter decomposition at the Alberta and Manitoba study sites after 6 months did not differ significantly between treatments (Fig. 39 and 41); however, the interaction between precipitation and defoliation had a significant effect on litter mass loss at Saskatchewan ($F_{2, 23} = 3.63$, P = 0.042; Fig. 40). Grazing increases light penetration and albedo (Ritchie et al. 1998), which can subsequently increase soil temperature, but can also lead to a drastic reduction in soil water content (Naeth et al. 1991). In this case, positive effects conferred by precipitation could have smoothed out the potential negative effects of defoliation (high evapo-transpiration and/or drought) which suppress litter decomposition. In some cases, it has even been shown that soil moisture overrides the importance of increased temperature on litter decomposition (Murphy et al. 1998).

After 1 year of incubation, precipitation had pronounced effects on litter mass loss at the Alberta and Manitoba study sites ($F_{2,36} = 5.27$, P = 0.01; Fig. 42 and $F_{1,17} = 19.73$, P = 0.001; Fig. 44, respectively), but not at Saskatchewan ($F_{1.18} = 1.18$, P = 0.29; Fig. 43). Within the former sites, mass loss was significantly greater in either ambient or water addition treatments than in drought treaments. Separately, temperature also had a significant effect on litter decomposition at Manitoba and Saskatchewan ($F_{1,17} = 5.64$, P = 0.03; Fig. 44, and $F_{1,18} = 7.67$, P = 0.013; Fig. 43, respectively). Although earlier studies emphasize that litter decomposition will only increase in a warmer world if the soil moisture is sufficiently high (e.g. Shaw and Harte 2001; Rustard and Fernandez 1998; Verburg et al., 1999; Robinson et al., 1995; Sjörgersten and Wookey, 2004), the results found here suggest that temperature and precipitation can independently affect rates of litter mass loss. The interplay between defoliation and climatic effects was only exhibited at Saskatchewan after 1 year incubation ($F_{2,18} = 2.84$, P = 0.085; Fig. 43). This finding appears to be the only result to date that corroborates the suggestion that litter decomposition rates should be influenced to a greater extent by the interaction between warming and moisture. However, contrary to expectations, there was greater litter mass loss in control than warming plots in this scenario (Fig. 43).

Further investigations on litter decomposition dynamics in these grassland ecosystems are necessary, and these will include:

- a) Determination of how grazing alters local environmental parameters which signifacntly affect decomposition rates and related carbon and nitrogen fluxes (*environment-effect*).
- b) Assessing how grazing changes plant species composition, which inherently alters chemical quality of plant/litter material and therefore decomposition rates and related Cand N fluxes (*quality-effect*).
- c) Finally, comparison of above- and belowground decomposition rates and associated C and N fluxes. Since above- and belowground litter are affected by different environmental parameters, it is expected that root and shoot litter decomposition rates will differ with considerable consequences for nutrient cycling (Giese et al., 2009 but see Seastedt et al., 1992; Moretto et al., 2001; Biondini et al., 1998).

3.7. Soil Microfauna

We are studying the taxonomic composition of soil arthropod assemblages and comparing these communities between treatments. Sample species are shown in Fig. 45. In addition, we will estimate arthropod biomass and document new species. Data presented here refer to soil cores collected in July 2007. Progress on sorting and identifying samples has been slower than expected. Nonetheless, over 4500 individuals have been counted and a total of 69 taxa have been identified, most of them mites (Arachnida: Acari). Non-mite groups include 8 orders of macro-invertebrates and 3 families of Collembola (springtails). Mites include 2 families of Astigmata, 2 families of Endeostigmata, 15 families of Prostigmata (including 4 families of Heterostigmata) and 16 families of Oribatida (consisting of 25 genus or species-level taxa). The remaining oribatids from 2007 samples will be sorted to genus or species when possible. All other mites will continue to be sorted to the level of family.

We have identified 2 species new to science, and expect to find more. A member of the genus *Trachyuropoda* (Mesostigmata: Trachyuropodidae) is in the process of being described by Dr. Proctor in collaboration with Jeno Kontschan from Hungary, an expert on the genus. Its proposed name is *Trachyuropoda kinsella*. The other species is a member of the spider mite subfamily Bryobiinae (Prostigmata: Tetranychidae), which will be described if additional

specimens are found. This species might be of particular interest because some of its relatives are plant pest species.

Almost all data used for the following analyses are from the plots in block 1 (with the exception of plot 2-1, which was substituted for plot 1-3) producing a sample size of 12. Note that the plots containing water addition treatments have not been included because these treatments had not yet been applied. We performed an ordination analysis on our taxa using PATN version 3 software (http://www.patn.com.au/patn_v3.htm). As extrinsic factors we used all available environmental and vegetation data (including vegetation-cover evenness and diversity indices), with the exception of the continuous temperature and soil humidity data. These data will be used in later analyses. Multivariate analysis using all taxa identified to the finest levels was difficult to interpret and did not offer much useful information due to the high number of identified taxa relative to sample size. However, when taxa were combined into larger groups (i.e. orders) a distinct pattern was evident (Fig. 46).

Precipitation manipulation was the only treatment showing a significant (p<0.05) separation of the two groups using ANOSIM (analysis of similarity). Ordination of the precipitation treatment revealed separation between ambient precipitation plots compared to the droughted (i.e. rainfall reduced) plots. All mite taxa appeared to be more abundant under drier conditions. When analyzing the same data using ANOVA (using SPSS version 17, http://www.spss.com/statistics/) this interpretation was further supported (Fig. 47).

Exploring the complete dataset using Bivariate Pearson correlation analysis (using SPSS version 17) indicated that abundance of Tydeidae, a family within the Prostigmata, was significantly negatively correlated with soil moisture (p<0.01) (Fig. 48). Similarly, the majority of Oribatida consisted of unidentified juveniles, which were also negatively correlated with soil moisture (p<0.05). Using ANOVA we established that taxon richness of arthropods (at the family level) significantly increased within the droughted plots (p<0.05). This was not the case for either the grazing or the temperature treatments.

We had expected to see lower abundances and lower taxon richness in the drought treatments. Instead, we saw the abundance and taxonomic richness of mites actually increasing. A large part of this response was due to the Tydeidae. Previous studies have shown that members of this family dominate dry soils, and they appear able to quickly capitalize on harsh conditions. We expect that as more soil cores are processed, other taxa will also take up such 'indicator' roles with regard to changes in environmental variables.

Additional sets of samples will be taken from the plots at the end of the 2009 field season. One set will be processed using the kerosene flotation protocol used for the initial (i.e. 2007) samples, and the other set will be rapidly extracted using Tullgren funnels. The former extraction is exhaustive but labor intensive, and will allow us to recognize within-plot changes in micro-arthropod community assemblages between 2007 and 2009, which in turn can be linked to the treatments imposed (warming, precipitation and defoliation). As the Tullgren samples can be rapidly processed they will be used to estimate biomass for the integrated modeling portion of the overall project.

3.8. Root Dynamics

Assessment of rooting dynamics, specifically measures of root length, using the images obtained from the root periscope is in the early stages. However, some preliminary results have been obtained and are providing a unique assessment of changes in root abundance in relation to the main experimental treatments being tested in this investigation.

While warming produced no significant change in mean root length (Fig. 49, top), altered precipitation had a profound influence on observed root length. In particular, the presence of drought conditions resulted in more than a 50% reduction in mean root length (Fig. 49, bottom), suggesting vegetation within these plots was unable to support ongoing root production, and more likely, the maintenance of existing roots.

Not surprisingly, defoliation also had a strong influence on measured root length (Fig. 50). Heavy defoliation resulted in a large reduction in root presence, falling to approximately half that observed within undefoliated check plots. While light defoliation appeared to produce a modest increase in mean root length, this value remained statistically similar to that observed under no defoliation (Fig. 50). The strong reduction in root length is consistent with several other studies conducted in the mixedgrass and fescue grasslands of Alberta, all of which indicate that changes in root abundance, including the depth of roots, are likely to occur, particularly under heavy and repeated defoliation.

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Appendix 1:

Summary Data Results for the Second Year Effects of Warming, Precipitation, and Defoliation on Rangeland Function

Environmental Responses

Table 1. Monthly significant and near-significant main effects and interactions at α =0.05 of warming, defoliation, and precipitation treatments and time of measurement (3 PM or 3 AM) on air temperature recorded within study plots containing dataloggers. Analyses were conducted using the Proc GLM module of SAS 9.1.3. Individual plot values were averaged over each month.

Month	Significant/Near Sig. Term	df	F-value	P-value
May	Warming	1	138.30	<0.0001
-	Time	1	28137.00	<0.0001
	Warming*Time	1	243.72	<0.0001
June	Warming	1	133.08	<0.0001
	Precipitation	2	7.41	0.0023
	Time	1	32636.90	<0.0001
	Warming*Time	1	185.84	<0.0001
	Precipitation*Time	2	3.35	0.0478
July	Warming	1	130.20	<0.0001
-	Precipitation	2	3.67	0.0368
	Time	1	12606.50	<0.0001
	Warming*Time	1	147.49	<0.0001
August	Warming	1	82.06	<0.0001
Ũ	Time	1	10594.50	<0.0001
	Warming*Time	1	93.86	<0.0001

Table 2. Monthly significant and near-significant main effects and interactions at α =0.05 of warming, defoliation, and precipitation treatments and time of measurement (3 PM or 3 AM) on relative humidity recorded within study plots containing dataloggers. Analyses were conducted using the Proc GLM module of SAS 9.1.3. Individual plot values were averaged over each month.

Month	Significant/Near Sig. Term	df	F-value	P-value
May	Warming	1	16.34	0.0003
	Precipitation	2	8.76	0.0009
	Time	1	8471.63	<0.0001
June	Warming	1	17.54	0.0002
	Defoliation	2	5.71	0.0076
	Precipitation	2	58.33	<0.0001
	Defoliation*Precipitation	4	2.62	0.0530
	Time	1	3275.39	<0.0001
	Precipitation*Time	2	15.56	<0.0001
July	Warming	1	23.40	<0.0001
	Defoliation	2	2.96	0.0664
	Precipitation	2	30.47	<0.0001
	Time	1	2192.08	<0.0001
	Warming*Time	1	4.36	0.0448
	Precipitation*Time	2	8.38	0.0012
August	Warming	1	16.50	0.0003
-	Precipitation	2	29.18	<0.0001
	Time	1	2025.71	<0.0001
	Precipitation*Time	2	5.90	0.0061
	Defoliation*Precipitation*Time	4	2.53	0.0572

Table 3. Monthly significant and near-significant main effects and interactions at α =0.05 of warming, defoliation, and precipitation treatments and time of measurement (3 PM or 3 AM) on soil temperature (0-5cm) recorded within study plots containing dataloggers. Analyses were conducted using the Proc GLM module of SAS 9.1.3. Individual plot values were averaged over each month.

Month	Significant/Near Sig. Term	df	E-value	D-valuo
Morr			1-Value	
May	vvarming	1	15.74	0.0004
	Defoliation	2	6.36	0.0047
	Warming*Defoliation	2	3.98	0.0287
	Time	1	672.11	<0.0001
	Warming*Time	1	5.10	0.0308
	Defoliation*Time	2	3.25	0.0519
June	Warming	1	6.08	0.0192
	Defoliation	2	5.26	0.0106
	Warming*Defoliation	2	4.25	0.0231
	Warming*Defoliation*Precipitation	4	2.74	0.0457
	Time	1	737.30	<0.0001
	Defoliation*Time	2	3.56	0.0403
	Precipitation*Time	2	4.23	0.0234
July	Warming	1	9.59	0.0041
	Defoliation	2	6.19	0.0054
	Time	1	394.59	<0.0001
	Warming*Time	1	4.52	0.0413
	Defoliation*Time	2	3.06	0.0610
	Precipitation*Time	2	4.29	0.0224
August	Warming	1	8.07	0.0074
	Time	1	298.35	< 0.0001

Table 4. Monthly significant and near-significant main effects and interactions at α =0.05 of warming, defoliation, and precipitation treatments and time of measurement (3 PM or 3 AM) on soil temperature (5-20cm) recorded within study plots containing dataloggers. Analyses were conducted using the Proc GLM module of SAS 9.1.3. Individual plot values were averaged over each month.

Month	Significant/Near Sig. Term	dt	F-value	P-value
May	Warming	1	26.14	<0.0001
	Defoliation	2	8.19	0.0015
	Precipitation	2	3.56	0.0409
	Time	1	155.29	<0.0001
	Warming*Time	1	3.67	0.0651
June	Warming	1	15.36	0.0005
	Defoliation	2	10.26	0.0004
	Precipitation	2	4.80	0.0158
	Warming*Defoliation*Precipitation	4	3.82	0.0130
	Time	1	206.76	<0.0001
	Warming*Time	1	5.86	0.0220
July	Warming	1	20.01	0.0001
	Defoliation	2	9.42	0.0008
	Warming*Precipitation	2	5.23	0.0123
	Warming*Defoliation*Precipitation	4	2.56	0.0623
	Time	1	134.21	<0.0001
	Warming*Time	1	7.15	0.0128
August	Warming	1	14.75	0.0005
	Defoliation	2	2.87	0.0706
	Warming*Precipitation	2	9.19	0.0006
	Time	1	122.19	<0.0001
	Warming*Time	1	6.56	0.0151

Table 5. Temporal variation in significant and near-significant main effects and interactions at α =0.05 of warming, defoliation, and precipitation treatments and soil depth (0-5 cm or 5-20 cm) on soil moisture recorded within study plots containing dataloggers. Analyses were conducted using the Proc GLM module of SAS 9.1.3. Readings were recorded at 3 PM on each sampling date.

Sampling				
Date	Significant/Near Sig. Term	df	F-value	P-value
15-May-08	Warming	1	6.72	0.0140
	Precipitation	2	18.39	<0.0001
	Warming*Depth	1	3.90	0.0565
30-May-08	Warming	1	3.71	0.0638
	Precipitation	2	14.40	<0.0001
	Warming*Precipitation	2	4.04	0.0280
	Warming*Depth	1	4.62	0.0398
15-Jun-08	Precipitation	2	18.03	<0.0001
	Warming*Precipitation	2	4.59	0.0186
30-Jun-08	Precipitation	2	14.17	<0.0001
	Warming*Precipitation	2	3.20	0.0572
15-Jul-08	Warming	1	8 15	0 0085
	Warming*Defoliation	2	5.30	0.0000
	Precipitation	2	12 41	0.0002
	Warming*Precipitation	2	3.56	0.0436
	Warming*Depth	1	4.54	0.0432
30lul-08	Precipitation	2	4 00	0 0296
	Warming*Precipitation	2	2 94	0.0200
	Denth	1	6 79	0.0145
	Warming*Depth	1	14.74	0.0006
15-Aug-08	Warming	1	4 62	0 0388
10-Aug-00	Warming*Defoliation	2	4.02	0.0000
	Precipitation	2	4.40	0.0132
	Denth	2 1	4.03	0.2300
	Warming*Depth	1	3.87	0.0492
00.4	- ·	,	0.70	0.04.40
30-Aug-08	vvarming	1	6.72	0.0140
	Precipitation	2	18.39	<0.0001
	vvarming [*] Depth	1	3.90	0.0565



Figure 1. Long-term variation in annual precipitation in the Edmonton region from 1883 through 2003.



Figure 2. Warming, defoliation, and precipitation treatment effects on mean air temperature recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during May 2008. All error bars are ± 1 S.E.



Figure 3. Warming, defoliation, and precipitation treatment effects on mean air temperature recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during June 2008. All error bars are ± 1 S.E.

b)



Figure 4. Warming, defoliation, and precipitation treatment effects on mean air temperature recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during July 2008. All error bars are ± 1 S.E.



Figure 5. Warming, defoliation, and precipitation treatment effects on mean air temperature recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during August 2008. All error bars are ± 1 S.E.



Figure 6. Warming, defoliation, and precipitation treatment effects on mean relative humidity recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during May 2008. All error bars are ± 1 S.E.



Figure 7. Warming, defoliation, and precipitation treatment effects on mean relative humidity recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during June 2008. All error bars are ± 1 S.E.



Figure 8. Warming, defoliation, and precipitation treatment effects on mean relative humidity recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during July 2008. All error bars are ± 1 S.E.



Figure 9. Warming, defoliation, and precipitation treatment effects on mean relative humidity recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during August 2008. All error bars are ± 1 S.E.



Figure 10. Warming, defoliation, and precipitation treatment effects on mean soil temperature (0-5 cm) recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during May 2008. All error bars are ± 1 S.E.


Figure 11. Warming, defoliation, and precipitation treatment effects on mean soil temperature (0-5 cm) recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during June 2008. All error bars are ± 1 S.E.



Figure 12. Warming, defoliation, and precipitation treatment effects on mean soil temperature (0-5 cm) recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during July 2008. All error bars are ± 1 S.E.



Figure 13. Warming, defoliation, and precipitation treatment effects on mean soil temperature (0-5 cm) recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during August 2008. All error bars are ± 1 S.E.



Figure 14. Warming, defoliation, and precipitation treatment effects on mean soil temperature (5-20 cm) recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during May 2008. All error bars are ± 1 S.E.



b)

Figure 15. Warming, defoliation, and precipitation treatment effects on mean soil temperature (5-20 cm) recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during June 2008. All error bars are ± 1 S.E.



Figure 16. Warming, defoliation, and precipitation treatment effects on mean soil temperature (5-20 cm) recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during July 2008. All error bars are ± 1 S.E.



Figure 17. Warming, defoliation, and precipitation treatment effects on mean soil temperature (5-20 cm) recorded at a) 3 PM and b) 3 AM within study plots containing dataloggers during August 2008. All error bars are ± 1 S.E.



Figure 18. Temporal variation in precipitation treatment effects on soil moisture at two depths recorded in study plots containing dataloggers during summer 2008, with bars clustered by a) sampling date, and b) precipitation treatment. All error bars are ± 1 S.E.

b)

Plant Diversity and Composition

Table 6. Results of one-way PerMANOVAs testing for significance of temperature, defoliation and precipitation treatments.

Treatment	F-stat	p-value
Temperature	0.64	0.73
Defoliation	5.39	0.0002
Precipitation	7.41	0.0002

Table 7. Results of one-way PerMANOVAs pairwise comparisons comparing treatment levelswithin defoliation and precipitation.

Treatment	Comparison	t-value	p-value
Defoliation	High vs Undef	3.01	0.0002
	High vs Low	1.44	0.06
	Low vs Undef.	2.22	0.0004
Precipitation	+Precip vs Ambient	1.53	0.03
	+Precip vs - Precip	3.66	0.0002
	Ambient vs -Precip	2.44	0.0002

	Max	Max Group	IV from randomized				
	Group	IV	Observed	grou	р-		
Species	IV Code	Treatment	IV	Mean	SD	value	
Bouteloua gracilis	СНА	Unwarmed, High Def, Ambient	16	10.1	2.67	0.034	
Astragalus sp	CN+	Unwarmed, Undef, +Precip Unwarmed,	19.6	11.5	3.81	0.039	
Carex spp	CL+	LowDef, +Precip Unwarmed.	9.5	8.1	0.74	0.045	
Androsace septentrionalis	CH+	HighDef, +Precip	21.8	10.1	4.92	0.048	
Moss and lichen	CH-	HighDef, - Precip Unwarmed,	15.6	10.9	2.96	0.072	
Stipa curtiseta	CNA	Undef, AmbientPrecip	9	8	0.63	0.072	
Artemisia frigida	WN+	Warmed, Undef, +Precip Warmed.	14.2	11.4	1.89	0.078	
Spphaeralcea coccinea	WH+	HighDef, +Precip Warmed.	17.6	10.9	6.07	0.100	
Elymus glaucus	WNA	NoDef, Ambient	26.7	9.7	6.89	0.114	

Table 8. Results of Indicator Species Analysis in response to warming, precipitation, and defoliation treatments in July 2008.



Figure 19. Effect of defoliation and warming on species richness in 2007 (top) and 2008 (bottom).



Figure 20. Effect of defoliation on species evenness during 2007.



Figure 21. Effect of precipitation and warming on species evenness during 2007.



Figure 22. Effect of precipitation on species evenness during 2008



Figure 23. NMS ordination diagram showing axes 1 and 3 separating community composition among plots receiving the three defoliation treatments. Red symbols represent plots undergoing high defoliation, green triangles low defoliation, and blue triangles the undefoliated treatment.



Figure 24. NMS ordination diagram showing axis 1 and 2 separating community composition among plots due to the three precipitation treatments. Red symbols represent plots undergoing high precipitation, green triangles ambient precipitation, and blue triangles the low precipitation treatment.



Figure 25. NMS ordination diagram showing axes 1 and 3 separating community composition among plots receiving the three precipitation treatments. Red symbols represent plots undergoing high precipitation, green triangles ambient precipitation, and blue triangles the low precipitation treatment.

Range Health





Figure 26. Frequency of plots with unhealthy, healthy with problems, and healthy range assessments within droughted (top) and ambient rainfall (bottom) plots during 2007.



Figure 27. Summary of mean range health scores associated with the main effects of warming, precipitation and defoliation during 2008. Scores of 1, 2 and 3 coincide with unhealthy, healthy with problems, and healthy range, respectively. No plots had a range health score of 1.



Figure 28. Cover of *Artemisia frigida* (pasture sage) in relation to precipitation, warming and defoliation during August 2008.

Vegetation Biomass



Figure 29. Effect of defoliation and precipitation on total productivity in 2007 (top) and 2008 (bottom).



Figure 30. Effect of defoliation, temperature and precipitation on grass productivity in 2007.



Figure 31. Effect of defoliation, temperature and grazing on forb productivity in 2008.

Soil Carbon and Nitrogen Dynamics

Sources	Year	$\mathbf{W}^{\mathbf{a}}$	Db	Pr ^c	W× D	W×Pr	D×Pr	W×D×Pr	Yr ^d
0-5 cm									
MBC ^e	2007	0.001	0.09	0.88	0.34	0.79	0.1	0.68	
	2008	0.97	0.01	<.0001	0.9	0.08	0.33	0.2	
MBN ^r	2007	0.06	0.14	0.06	0.2	0.3	0.6	0.23	
	2008	0.99	0.01	<.0001	0.99	0.05	0.08	0.39	
DOC ^g	2007	0.32	0.73	0.52	0.32	0.55	0.26	0.35	
	2008	0.48	0.45	0.54	0.2	0.24	0.01	0.42	
DON ⁿ	2007	0.22	0.62	0.63	0.04	0.24	0.59	0.55	
	2008	0.61	0.38	0.57	0.22	0.21	0.02	0.45	
5-15									
cm									
MBC	2007	0.4	0.01	0.005	0.01	0.72	0.14	0.25	
	2008	0.9	0.49	0.05	0.48	0.71	0.46	0.38	
MBN	2007	0.7	0.45	0.51	0.92	0.81	0.05	0.9	
	2008	0.8	0.42	<.0001	0.65	0.65	0.71	0.35	
DOC	2007	0.73	0.36	0.22	0.93	0.51	0.8	0.61	
	2008	0.33	0.42	0.64	0.42	0.42	0.42	0.69	
DON	2007	0.43	0.85	0.41	0.8	0.53	0.86	0.86	
	2008	0.74	0.9	0.32	0.42	0.64	0.54	0.68	

Table 9. Summary P-value results from the ANOVA of soil response variables in 2007-2008 using repeated measures.

Note: W, D, and Pr represent warming, defoliation and precipitation, respectively.

Sources	CO ₂ ^a		N_2O^a		CH ₄ ^a	
	2007	2008	2007	2008	2007	2008
W	0.48	0.44	0.29	0.53	0.07	0.34
D	0.77	0.69	0.53	0.74	0.74	0.04
Pr	<.0001	<.0001	0.03	0.27	0.44	<.0001
$W \times D$	0.06	0.81	0.54	0.98	0.14	0.19
$W \times Pr$	0.08	0.58	0.004	0.62	0.77	0.27
$\mathbf{D} \times \mathbf{Pr}$	0.97	0.79	0.15	0.61	0.67	0.24
$\mathbf{W} \times \mathbf{D} \times \mathbf{Pr}$	0.18	0.76	0.84	0.41	0.31	0.03
Date	<.0001	<.0001	0.99	0.86	<.0001	<.0001
W × Date	0.65	0.41	0.39	0.24	0.33	0.02
D × D ate	0.01	0.71	0.96	0.37	0.06	0.56
Pr × Date	0.0009	0.0002	0.1	0.26	0.6	<.0001
$W \times D \times Date$	0.24	0.88	0.88	0.96	0.11	0.89
$W \times Pr \times Date$	0.44	0.67	0.0003	0.85	0.83	0.78
$\mathbf{D} \times \mathbf{Pr} \times \mathbf{Date}$	0.63	0.27	0.03	0.91	0.89	0.99
$W \times D \times Pr \times Date$	0.91	0.9	0.81	0.03	0.59	0.82

Table 10. Summary P-values results from the ANOVA of soil CO_2 , N_2O and CH_4 efflux in 2007 and 2008 using repeated measures.

Note: W, D, and Pr represent warming, defoliation and precipitation, respectively.



Figure 32. Defoliation, precipitation and warming effects on average soil microbial biomass carbon (MBC) during the 2007 and 2008 growing seasons at 0-5 cm depth (left) and 5-15 cm depth (right). Error bars represent 1 SE.



Figure 33. Defoliation, precipitation and warming effects on average soil microbial biomass nitrogen (MBN) during the 2007 and 2008 growing seasons at 0-5 cm depth (left) and 5-15 cm depth (right). Error bars represent 1 SE.



Warmed



Figure 34. Defoliation, precipitation and warming effects on average dissolved soil organic carbon (DOC) during the 2007 and 2008 growing seasons at 0-5 cm depth (left) and 5-15 cm depth (right). Error bars represent 1 SE.



Control

Warmed

Figure 35. Defoliation, precipitation and warming effects on average dissolved soil organic nitrogen (DON) during the 2007 and 2008 growing seasons at 0-5 cm depth (left) and 5-15 cm depth (right). Error bars represent 1 SE.





Figure 36. Defoliation, precipitation and warming effects on soil carbon dioxide (CO_2) efflux during the 2007 and 2008 growing seasons. Error bars represents 1 SE.



Figure 37. Defoliation, precipitation and warming effects on soil nitrous oxide (N_2O) efflux during the 2007 and 2008 growing seasons. Error bars represents 1 SE.



Figure 38. Defoliation, precipitation and warming effects on soil methane (CH₄) efflux during the 2007 and 2008 growing seasons. Error bars represents 1 SE.

Litter Decomposition



Figure 39. Aboveground litter mass loss after 6 months within plains rough fescue grassland at the Alberta study site in response to precipitation, warming and defoliation. Error bars represent ± 1 SE.



Figure 40. Above ground litter mass loss after 6 months within mixed prairie grassland at the Saskatchewan study site in response to precipitation, warming and defoliation. Error bars represent ± 1 SE.



Figure 41. Above ground litter mass loss after 6 months within grassland at the Manitoba study site in response to precipitation, warming and defoliation. Error bars represent ± 1 SE.

a) Alberta



Figure 42. Aboveground litter mass loss after 12 months within plains rough fescue grassland at the Alberta study site in response to precipitation, warming and defoliation. Error bars represent ± 1 SE.



Figure 43. Aboveground litter mass loss after 12 months within mixed prairie grassland at the Saskatchewan study site in response to precipitation, warming and defoliation. Error bars represent ± 1 SE.



Figure 44. Aboveground litter mass loss after 12 months within grassland at the Manitoba study site in response to precipitation, warming and defoliation. Error bars represent ± 1 SE.
Soil Microfauna



Mesostigmata



Oribatida



Prostigmata



Collembola

Figure 45. Sample images of various micro-organisms, extracted from soil samples in the main climate change study area in July 2007.



Figure 46. 3-D PATN ordination of soil arthropods showing axes 1 and 3. Gray circles represent droughted plots, while black circles represent ambient precipitation treatments. Stress is a measure for how reliable the ordination is, with 0.0873 being in the range of good to very good.



Figure 47. Average abundance of taxa within the ambient and droughted precipitation treatments at the Alberta study site in 2007. Significance is indicated as follows: * p<0.05, ** p<0.01. Error bars are +/- 1 SD.



Figure 48. Scatter plot of Tydeidae (gray squares) and oribatid juveniles (black triangles) abundance (y-axis) in relation to volumetric soil moisture (x-axis).

Root Dynamics



Figure 49. Mean root length measures in response to the main effects of warming (top) and precipitation (bottom), as calculated using images obtained with a root periscope.



Figure 50. Mean root length responses under the 3 defoliation treatments as assessed from images collected with the root periscope.