PLANT COMMUNITIES OF THE GRASSLANDS AND THE FOREST-GRASSLAND MOSAIC IN THE CARIBOO-CHILCOTIN REGION OF BRITISH COLUMBIA

by

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ABSTRACT

Plant communities and soils of grasslands on an elevation gradient and the forest-grassland mosaic in the Cariboo-Chilcotin of British Columbia were examined. Vegetation change along an elevation-climate gradient was analysed, including plant cover, litter cover, species composition, and species richness. Grassland plant communities were compared with associated climate variables and biogeoclimatic classifications. Based on results, an updated classification of grassland ecosystems is proposed with suggestions for management and research. Plant community and soil moisture characteristics of adjacent forests and grasslands were compared. Ten-year-old slash and burn treatments of young forests, and areas of forest encroachment on grasslands were studied to detect potential change between forest and grassland states. Results did not suggest change in ecosystem state between grasslands and forests, with persistent ecosystem legacies a potential source of long-term resilience. Land-use legacies manifested as encroachment of forests on areas of historical grasslands and high cover values of exotic species.

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BACKGROUND

Inland Douglas-fir forests and intermountain grasslands reach their most northern geographic extent in the Cariboo-Chilcotin region of British Columbia. The Douglas-fir biogeoclimatic zone is primarily on the plateau surrounding the Fraser River, while grasslands are centred on low elevations of the Fraser and Chilcotin River Valleys and extend to higher elevations on adjacent parts of the Fraser Plateau (Steen and Coupe, 1997). Grassland ecosystems of North America are highly fragmented, with most productive types being converted to cultivation agriculture (Samson et al., 2004; Looney and Eigenbrode, 2012; Augustine et al., 2019). In the Cariboo-Chilcotin region, extensive native grasslands remain because of low human population density and absence of widespread cultivation. Within the region, there is a wide climate gradient due to influence of the Coast Mountains rainshadow and large changes in elevation (Steen and Coupe, 1997). This is a unique landscape with an intact gradient of grassland ecosystems of semi-arid to sub-humid climates, and the transition to a forested landscape.

Grassland ecosystems of North America were described in comprehensive ecological studies predominantly published in the early- to mid-20th century (e.g. Daubenmire, 1942; Tisdale, 1947; Weaver and Bruner, 1954; Coupland, 1961; van Ryswyk et al. 1966). The comprehensive studies formed the foundation for subsequent experimental research and for ecosystem conservation and management. The Cariboo-Chilcotin grasslands may be the largest grassland ecosystem that has not been described in a comparable comprehensive study. While it may not be possible to identify causal factors for plant community and soil changes along a climate gradient (Dunne et al., 2004), baseline descriptive studies are vital in informing experimental research. Furthermore, the long-term livestock exclosures of the Range Reference

Area program provide an experimental basis to compare grazed and non-grazed grassland plant communities, and climate modelling (Wang et al., 2016) permits the establishment of ecosystem-climate relationships at the sub-regional level.

A landscape mosaic of forests and grasslands occurs on the plateau surrounding the Fraser and Chilcotin Rivers. Like other grasslands of North America, trees have encroached on these grasslands in the 20th century (Bai et al., 2004; Steele et al., 2007). Tree encroachment on grasslands of the region has been documented with historical photo-imagery (Bai et al., 2004; Steele et al., 2007) and reconstructed through dendrochronological studies of grassland-adjacent trees (Strang and Parminter, 1980; Harvey and Smith, 2017). Encroachment has been associated with the introduction of livestock grazing, fire suppression, and end of First Nations traditional burning practices (Tisdale, 1950; Strang and Parminter, 1980; Arno and Gruell, 1986; Blackstock and McAllister, 2004; Heyerdahl et al., 2006). Recently, grassland restoration practices (cutting and prescribed burning of young forests) have been applied to areas of tree encroachment on grasslands. However, the effects of forest encroachment on plant communities have not been studied. Also, the effectiveness of treatments in “restoring” grassland plant communities is not known.

Water availability is a leading determinant of plant composition in drylands (Brown et al., 1997; Weltzin et al., 2003). Vegetation and soil moisture can often act as a positive feedback in woody vegetation dynamics (D'Odorico et al., 2007). Therefore, soil moisture should be the subject of studies on the effects of forest encroachment in a water-limited environment. In ecosystems near the boundary between grassland- and forest-associated climates, tree cover establishes slowly or is limited to pulses of establishment during infrequent high-precipitation years (Arno and Gruell, 1986; League and Veblen, 2006; Weidenmaier et al., 2010).

Modification of soil moisture conditions by the plant community is a factor in maintaining an ecosystem state. For example, the high concentration of fine roots in grassland soils can prevent tree seedling establishment by reducing soil moisture (James et al., 2003). As trees encroach on the grasslands, the likelihood of subsequent tree establishment increases due to shading, increased soil moisture content and associated tree seedling survival (Kennedy and Sousa, 2006). Further, woody plant growth on grasslands interrupts the relatively homogenous spatial distribution of soil moisture, resulting in resource-poor patches and deterioration of the grassland plant community (Schlesinger et al., 1990).

Frequent surface fires are often a factor in excluding trees from grasslands (Heyerdahl et al., 2006). There is potentially a relationship between the spatial distribution of soil moisture and the fire disturbance regime in grasslands. The relatively homogenous spatial distribution of soil moisture in grasslands is reflected above ground as continuous cover of vegetation and litter (Schlesinger et al. 1990). This is expected to influence the grassland fire regime, as spatial connectivity of fine fuels is a condition required to support surface fires (Krawchuck and Moritz 2011). Higher elevation grasslands are associated with a cooler-wetter climate and greater net primary productivity (NPP) (van Ryswyk et al., 1966; Carlyle et al., 2014). Greater NPP supports a frequent fire return interval fire regime, with fine fuel accumulations supporting higher intensity and greater spatial connectivity of fires (Krawchuck and Moritz, 2011; Moritz et al., 2012). Therefore, on the cooler and wetter part of the climate gradient, the relationship between NPP and the fire disturbance regime likely plays a substantial role in preventing forest encroachment on grasslands.

Forests have greater spatial heterogeneity of soil moisture than grasslands (Kleb and Wilson, 1997). Mature Douglas-fir forests facilitate patches of tree seedling survival, as the heterogenous canopy provides a balance of precipitation throughfall, light transmission, and shading (Simard, 2009). At the northern extent of the Interior Douglas-fir biogeoclimatic zone, the forest canopy thermal cover is an important factor in reducing tree seedling mortality caused by growing season frost (Reich and Kamp, 1993). Variable soil moisture conditions in dry Douglas-fir forests result in clump and patch patterns of tree regeneration, and understorey vegetation that is sparse in comparison to adjacent grasslands (Steen and Armleder, 2008; Lemay et al., 2009). This could contribute to Interior Douglas-fir forests having a mixed-severity stand maintaining disturbance regime. The mixed-severity disturbance regime of Interior Douglas-fir forests is spatially and temporally heterogeneous and results in structurally diverse stand conditions across the landscape (Klenner et al., 2008; Heyerdahl et al., 2012; Harvey et al., 2017). Therefore, there may be a relationship between spatially heterogeneous soil moisture, vegetation patterns, and the fire disturbance regime.

RESEARCH OBJECTIVES

The purpose of this research is to develop an understanding of grassland ecosystems of the Cariboo-Chilcotin region, and to determine potential factors contributing to the long-term persistence of forest and grassland states within a grassland-forest mosaic. Chapter 1 is based on the sampling of previously established grazed and non-grazed grassland permanent paired plots. Based on this sampling, I describe grassland plant communities and soils on a climate-elevation gradient. I also examine the effects of grazing of grassland plant communities. In chapter 2, I use grassland restoration treatments and areas of forest encroachment on historical grasslands to examine effects of recent forest establishment on plant communities and soil moisture conditions. These plant community and soil moisture observations are compared to baseline conditions found in adjacent mature forests, and adjacent grasslands that have not been affected by forest encroachment.

While field sampling was in progress, the Hanceville wildfire burned the forest-grassland mosaic part of the study area in late July 2017. This event created an opportunity to sample plant communities and soil moisture one year after a burn, where “pre-burn” sampling had been completed in the same month that the fire occurred. Therefore, there is an additional objective of studying the effects of burning on plant communities and soil moisture (Chapter 2).

Objective 1:

a) Characterize grassland plant communities and associated soils of the Cariboo-Chilcotin on an elevation gradient.
b) Examine the effects of grazing on grassland plant communities.

Objective 2:

a) Describe the effects of forest encroachment and ecological restoration treatments on grassland plant communities.
b) Compare the soil moisture of forests and grasslands and determine if forest encroachment causes a change in soil moisture.
c) Examine the effects of burning on plant communities and soil moisture in the forest-grassland mosaic.

CHAPTER 1: GRASSLAND PLANT COMMUNITIES AND ASSOCIATED SOIL CHARACERTISTICS ALONG AN ELEVATION GRADIENT FROM BRITISH COLUMBIA'S CARIBOO-CHILCOTIN REGION

Introduction

The Cariboo-Chilcotin grasslands are a geographically isolated most northern extension of the intermountain grasslands that are found in interior British Columbia and western United States. Grassland climatic factors of the region include a strong rainshadow effect of the Coast Mountains and very cold winter temperatures from the influence of northern Arctic air masses (Steen and Coupe, 1997). The low to middle elevation grasslands have similar species composition to low- to mid-elevation grasslands described in the Thompson-Nicola region of southern interior British Columbia (Tisdale, 1947; van Ryswyk et al., 1966) and the inland northwest of the United States (Daubenmire, 1942). Like the intermountain grasslands to the south of the region, leading species at low elevations are bluebunch wheatgrass (*Pseudoroegnaria spicata*), needle-and-thread grass (*Hesperostipa comata*), Sandberg's bluegrass (*Poa secunda* var. *sandbergii*), and big sagebrush (*Artemisia tridentata*). Notably, rough fescue (*Festuca campestris*) and Idaho fescue (*Festuca idahoensis*) are absent. The dominance of needlegrasses (*Achnatherum rihardsonii* and *Hesperostipa curtiseta*) in the upper grasslands at all seral stages is distinct from grasslands of other regions. In the upper grasslands, there are botanical similarities to northern grasslands including the fescue grasslands of the northern Great Plains (Coupland, 1961) the Rocky Mountain foothills (Moss et al., 1947), and small grassland patches in the sub-boreal forests of central British Columbia (Pojar, 1982).

Livestock severely overgrazed the Cariboo-Chilcotin grasslands from the 1860s to the 1920s, resulting in deterioration of grasslands and presence of early seral plant communities (Tisdale et al., 1954; Bawtree and Zabek, 2011). Early records of grassland composition include descriptions of extensive bare soil and the presence of ruderal species, and there are no descriptions of species composition that pre-date grazing. Extensive bare ground and lack of plant cover can be seen in early photographs of the region such as at Toosey range reference area in 1923 (Figure 1.1). The first Grazing Act of 1918 brought about the regulation of grazing on crown land (Thistle, 2009), resulting in gradual reduction of livestock use across the study area from the 1920s to the 1990s. Conservation grazing measures have resulted in increases of native and non-native grasses and forbs, and an increase in productivity. However, there is abundance of exotic species and apparent lack of successional change in the upper grasslands, with the exotic grass *Poa pratensis* often being the leading species. From the late 1980s to the mid 1990s, an effort was undertaken in building range reference areas (RRAs) throughout the grassland elevation gradient (Province of British Columbia, 2020 a). The effort in constructing RRAs was intended to determine ecosystem potential and plant community successional stages of various grassland types. In this study, I collect plant and soil data from those RRAs in order to complete the following objectives:

1. Characterize the species composition and soils of Cariboo-Chilcotin grasslands on a climate-elevation gradient.
2. Determine the effects of grazing on Cariboo-Chilcotin grassland plant communities.

Figure 1.1. Toosey Range Reference Area near Riske Creek in 1923. The livestock exclosure was recently installed and growth of *Koeleria macrantha* can be seen inside the exclosure.

Methods

Study Area

The study was conducted in the Cariboo-Chilcotin grasslands along the Fraser River Valley and adjacent plateaus from Big Bar North to Riske Creek, an area that is approximately 120 by 40 km in size (Figure 1.2). The grasslands of this region occur along the Fraser and Chilcotin River Valleys and their adjacent plateau areas. The grasslands occur within the Bunchgrass and Interior Douglas-Fir biogeoclimatic zones (Steen and Coupe, 1997), and have been classified into the elevation categories of the lower, middle and upper grasslands (Tisdale, 1947; van Ryswyk et al., 1966; Delesalle et al., 2009). The grasslands are found on an elevation gradient from approximately 400 to 1200 metres. Higher elevations are associated with cooler and wetter conditions. From the lowest to highest elevation, mean annual temperature (MAT) is estimated to range from 7.7 to 3.0 C^o, and mean annual precipitation (MAP) from 309 to 499 mm

(Wang et al., 2016). The soils have been grouped into Brown Chernozems at the lowest elevations, and Dark Brown and Dark Gray Chernozems at mid to high elevations (Valentine et al., 1987). The parent material of the study area is a veneer of eolian fine sand and silt overlaying skeletal glaciofluvial deposits (Valentine et al., 1987).

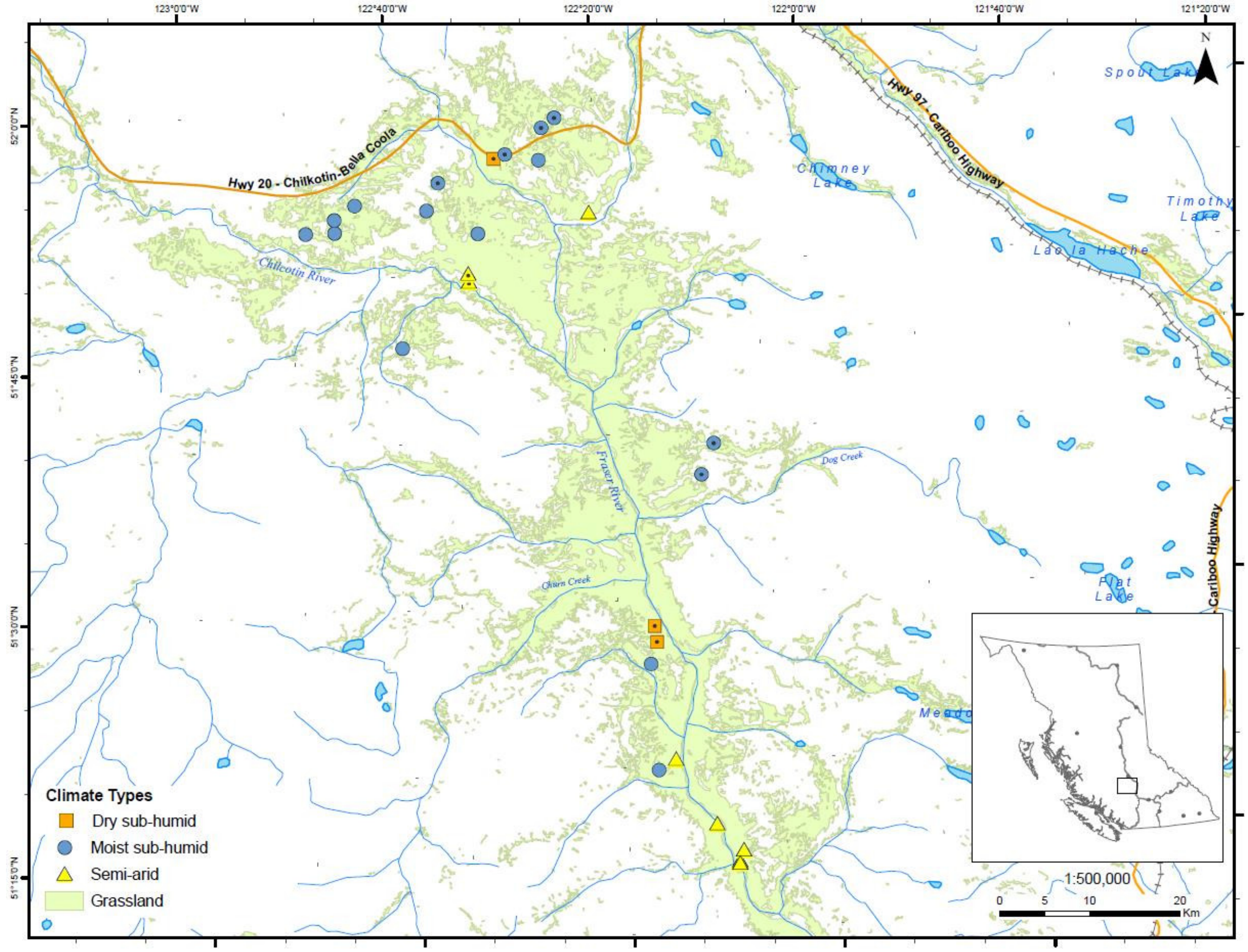


Figure 1.2. The study area with RRAs categorized into climate categories: semi-arid (triangles), dry sub-humid (squares), and moist sub-humid (circles).

Experimental design

Twenty-eight grassland range reference areas (RRAs) were selected for vegetation sampling (Appendix 1). The selection excluded reference areas with steep slopes, saline soils, and riparian vegetation. Each range reference area consists of a permanent plot inside a 0.5 to 1-hectare livestock exclosure and an adjacent paired plot outside the exclosure. Therefore, “inside” refers to plots inside an exclosure that have not been grazed since exclosure installation, and “outside” plots are grazed annually. These RRAs were established 20 to 35 years before the sampling for this study, apart from a 60-year-old and 95-year-old reference area. At the time of establishment, permanent plot locations were selected to represent a uniform plant community within and between inside and outside plots. Sampling took place on five parallel transects that are 30 metres length and spaced 5 metres apart.

Vegetation was sampled between 2013 and 2017 at the expected peak productivity of the site: early June for low elevations and July or August for higher elevations. Vegetation and substrates were sampled with 50 Daubenmire frames (20 cm by 50 cm) using the cover class method (Daubenmire, 1959). Ten frames were placed at random locations on each of the five transects. The cover class category of individual vascular plant and moss species was visually estimated in each frame, with categories representing 0-5, 5-25, 25-50, 50-75, 85-95, and 95-100% cover. The mid-point of each cover class category was used to for statistical determinations of the mean cover for each species. Sampling characterized the cover of all vascular species as well as litter and bare soil.

Soil was sampled in September 2019 in a sub-set of 11 RRA inside plots selected to represent intervals of the elevation gradient. The sampling was designed to ensure representation of soil characteristics for the plot area. Samples were taken using a 7 cm diameter corer to 15 cm depth. Two composite samples were taken from each plot. The first composite sample was taken from the second transect and the second composite sample from the third transect. Each composite sample consisted of six sub-samples taken from randomized locations along the transect and mixed in one container.

Climate Analyses

Climate data for each RRA was obtained from the ClimateBC model (Wang et al.,2016, downloaded from http://climatemodels.forestry.ubc.ca/climatebc/downloads) based on monthly averages from 1980 to 2010. The climate category for each RRA was determined using the definition of semi-arid climates (Bailey, 1979). Like the Thornthwaite (1948) index, Bailey's index is a moisture index based on annual precipitation and temperature. However, Bailey's index takes greater account for the effectiveness of precipitation by taking account of season (mean monthly temperature) and variability of precipitation throughout the year. The climate categories were determined using the Bailey's equation $\sum_{1}^{12} 0.18p/1.045\text{\textasciicircum}t$ where p is monthly precipitation (mm) and t is mean monthly temperature in degrees Celsius. Based on this calculation, RRAs were placed in climate categories: semi-arid ($2.5 < SA < 4.7$), dry sub-humid ($4.7 < DSH < 6.37$), and moist sub-humid ($6.37 < MSH < 8.7$).

Records

Four pedons were classified according to standard methods (Soil Classification Working Group, 1998) and accessed from the provincial RRA database (Appendix 2). These pedons were selected to represent mid and high elevation grasslands; a low elevation grassland pedon classification was not completed. Historical information was accessed from the Province of BC

RRA files, kept at Ministry of Forests, Lands and Natural Resource Operations and Rural Development, Prince George, British Columbia, 2000 South Ospika Blvd.

Plant Community Analyses

Nonmetric multidimensional scaling (NMS; PC-ORD v. 7, McCune and Mefford, 2016) was used on vegetation data collected inside plots to describe patterns in species composition along the environmental gradient. A random starting multivariate distance measure was applied to the NMS and the Bray-Curtis distance measure was applied (Bray and Curtis, 1957). Species associated with environmental gradients were determined using multiple Pearson correlations with ordination axes.

Linear regressions were used to determine the relationships between elevation and litter cover and vegetation cover. The coefficient of variation (CV) was used to characterize the heterogeneity of litter cover at each plot. Species richness was determined using a simple count of vascular species recorded per RRA inside plot. Spearman's rank correlation was used to characterize the relationship between elevation and species richness.

Based on NMS analysis, plant communities were divided into lower, middle and upper grasslands (Tisdale, 1947; Deleselle et al., 2009) in order to reduce variability between plots for statistical analysis. Grazed and non-grazed grassland plant communities were compared using paired t-tests of plant community characteristics (vegetation cover, litter cover, proportion of native grass cover, proportion of exotic species cover, and bluebunch wheatgrass cover). Analyses were completed on grouped plant communities (upper, middle, and lower grasslands) rather than grasslands of climate categories in order to reduce variability within groups. Statistics were completed in SPSS version 24.0 (IBM Corp. 2016).

Soil Analyses

The Bouyoucos (1962) hydrometer method was used for soil particle size analysis. The calcium chloride method was used to measure pH. For subsequent analysis, soil samples were dried at 35 C° to constant mass, flail ground, and sieved to <2mm. Total carbon and nitrogen were measured using a Flash 2000 elemental analyser based on Thermo Application Note (ThermoFisher Scientific, Waltham, MA., USA). Within the Flash system, samples are combusted at 950 C° in the presence of a catalyst in the reactor tube. During combustion, N and C are oxidized and gasses are analyzed in a thermal conductivity detector. Cation exchange capacity (CEC) and cation concentrations were measured using the $BaCl_2$ method (Hendershot and Duquette 1986; USEPA Method 200.7, 1994). The extracts of the $BaCl_2$ method were analyzed using ICP-OES (inductively coupled plasma, optical emission spectroscopy). Inorganic carbon was measured using a Skalar Primacs analyzer using the Skalar Application note (Skalar Inc, Brampton ON., Canada). Within the SKALAR Primacs system, samples are acidified with phosphoric acid, converting inorganic carbon to carbon dioxide. Carbon dioxide is then analyzed using an infrared detector. The average was taken from the results of the two composite samples from each RRA.

Results

Species composition

Species composition of the non-grazed grasslands of the semi-arid, dry sub-humid, and moist sub-humid climates is summarized in Tables 1.1 to 1.3. Species composition of the semi-arid grasslands is summarized in Table 1.1. Leading species include the native bunchgrasses

Hesperostipa comata and *Pseudoroegnaria spicata*, and the low shrub *Artemisia frigida,* and the large shrub *Artemisia tridentata*.

Table 1.1. Mean cover and standard deviation of vascular plant species in the semi-arid grasslands (n=9).

Semi-arid		
Species	Cover (%)	SD
Hesperostipa comata	14.37	12.91
Pseudoroegnaria spicata	6.69	7.39
Artemisia frigida	5.79	8.51
Artemisia tridentata	2.95	5.17
Sporobolus cryptandrus	1.34	2.48
Phacelia linearis	0.66	0.86
Opuntia fragilis	0.57	0.38
Orthocarpus luteus	0.46	1.21
Bromus tectorum	0.27	0.64
Achnatherum hymenoides	0.17	0.39

Artemisia tridentata cover was variable depending on fire history, with a 2010 wildfire significantly reducing cover of the species at the Cavanagh Creek RRA near Big Bar (Image 2). Grasslands were dominated by *Hesperostipa comata* or *Pseudoroegnaria spicata* depending on grazing history, with *Hesperostipa comata* present at all sites. The cactus species *Opuntia fragilis* is a reliable indicator of semi-arid grasslands, as it is present on all RRAs in this climate (sometimes at trace levels), and was not found in other climate categories. The warm-season (C4 photosynthesizing) native bunchgrass *Sporobolus cryptandrus* was present on sites with past heavy grazing and is an early seral plant community indicator, although it was sometimes present at trace levels at late seral stages. The native bunchgrass *Achnatherum hymenoides* was an indictor of patches of coarse soil substrates. Plant and litter cover were discontinuous and heterogenous, with spaces between plants (Figure 1.3 and Figure 1.4). Spaces between plants had high cover of biological soil crust (BSC). Diversity of vascular species is low, typically with 10-

11 species per RRA. Farwell Big Sage RRA (Figure 1.5) located at Farwell Canyon is an example of a semi-arid grassland with high cover values of *Artemisia tridentata*.

Figure 1.3. Overview of Cavanagh RRA near Big Bar, in the semi-arid climate at 468 m elevation. The site is dominated by *Pseudoroegnaria spicata* with traces of *Hesperostipa comata* and *Poa secunda* var. *sandbergii*. The 2017 photograph was taken after *Artemisia tridentata* plants were substantially reduced by a wildfire in 2010.

Figure 1.4. Ground shot at Cavanagh RRA showing the spaces between plants and BSC cover. Litter cover is low. A young *Artemisia tridentata* plant that has seeded in post-wildfire is in the lower left part of the image.

Figure 1.5. Overview of semi-arid grasslands at Farwell Canyon, 515 m elevation. *Artemisia tridentata* is present. *Hesperostipa comata* is the leading species by cover, followed by *Pseudoroegnaria spicata*.

Species composition of dry sub-humid grasslands is summarized in Table 1.2. *Pseudoroegnaria spicata* is the dominant species in grasslands of the dry sub-humid climate. The grasslands also have a greater diversity of forbs than the semi-arid grasslands. The exotic sod-forming grass species *Poa pratensis* is present but at low cover levels. *Artemisia frigida* is the second most abundant species, and the forbs *Astragalus miser* and *Achillea millefolium* are present. The low stature native bunchgrass *Koeleria macrantha* has higher cover in early seral condition and has lower cover but is still present in late seral stages. Species richness is intermediate, with 20 vascular species per RRA being typical.

Table 1.2. Mean cover and standard deviation of vascular plant species in the dry sub-humid grasslands (n=3).

Dry sub-humid		
Species	Cover (%)	SD
Pseudoroegnaria spicata	18.22	14.42
Artemisia frigida	4.87	7.60
Achillea millefolium	4.28	7.03
Astragalus miser	3.17	5.48
Koeleria macrantha	3.12	0.54
Poa pratensis	2.98	5.13
Tragopogon pratensis	2.95	5.11
Hesperostipa comata	2.87	4.95
Taraxacum offifinale	0.80	1.39
Eriogonum heracleoides	0.62	1.07

Plant and litter cover were greater than in the semi-arid grasslands but more variable (heterogenous) than in the moist sub-humid grasslands. *Hesperostipa comata* was absent from late seral stages. The exotic species *Tragopogon pratensis* is one of the leading forbs. There was encroachment of Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and lodgepole pine (*Pinus contorta* var. *latifolia*) trees on the higher elevation part of the dry-sub humid grasslands. Toosey RRA (Figure 1.6) is near the highest elevation of the dry-sub humid grasslands (904 m).

Figure 1.6. Dry sub-humid climate grasslands at Toosey RRA, 904 m elevation. *Pseudoroegnaria spicata* is the leading species. Levels of heterogeneity of plant cover is intermediate between lower grassland and upper grasslands. There is sparse encroachment of Douglas-fir and lodgepole pine, but all the pine trees have died

Species of the moist sub-humid grasslands are summarized in Table 1.3. *Poa pratensis* is present throughout the grasslands and is often the leading species. *Achnatherum richardsonii* and *Hesperostipa curtiseta* are also often present and sometimes co-dominant with *Poa pratensis*. *Pseudoroegnaria spicata* is sometimes the leading species or co-dominant at the lower elevations of this zone but is generally absent on level terrain and gentle slopes over 1000 m elevation.

Shrub cover is low (<4 % cover), with *Rosa acicularis* often being present at low cover values and *Symphoricarpos occidentalis* generally restricted to swales. *Tragopogon pratensis* is always present and is sometimes the most abundant forb species. There is greater species richness than found in semi-arid or dry sub-humid grasslands, with 25-40 vascular species per RRA. However, most of these species are low in cover (<4%), after the 1-3 leading grass species. Plant and litter cover are continuous with low spatial heterogeneity.

Table 1.3. Mean cover and standard deviation of vascular plant species in the moist sub-humid grasslands (n=16).

	Moist sub-humid	
Species	Cover (%)	SD
Poa pratensis	23.49	20.57
Achnatherum richardsonii	11.40	13.02
Pseudoroegnaria spicata	6.93	9.30
Tragopogon pratensis	6.29	5.33
Hesperostipa curtiseta	4.06	9.24
Antennaria umbrinella	3.51	7.02
Astragalus miser	3.17	4.88
Koeleria macrantha	2.06	3.72
Achillea millefolium	1.94	2.58
Artemisia frigida	1.31	2.42

An overview of moist sub-humid grasslands at Becher's prairie near Loran RRA (970 m elevation) is presented as Figure 1.7. Encroachment of trees on the moist sub-humid grasslands is common and sometimes dense. Figure 1.8. shows an area of grasslands near Riske Creek with lodgepole pine encroachment that was burned in the 2017 Hanceville wildfire (970 m elevation).

Figure 1.7. Moist sub-humid grasslands at 970 m elevation with *Poa pratensis*, *Achnatherum richardsonii*, and *Hesperostipa curtiseta*. Note the continuous plant and litter cover.

Figure 1.8. Moist sub-humid grasslands at 970 m elevation with lodgepole pine trees burned in the 2017 Hanceville wildfire.

NMS Analysis

Multivariate species-space distances among sample units are show in Figure 1.9. Axis 1 includes 71.2% of the variation, and axis 2 accounts for 15.3% of the variation, for a total of 86.5% of variation in species composition explained by the distance matrix, measured by the Bray-Curtis distance measure (Bray and Curtis, 1957). The distribution of the points (RRAs) is driven by species composition, with similar plant communities being placed close together in the distance matrix. There are two gradients in the matrix represented by Axis 1 and Axis 2. The distance matrix axes were correlated with climate variables of mean annual temperature (MAT) and mean annual precipitation (MAP), and with plant community characteristics (litter cover, vegetation cover, and species richness). Elevation is also correlated with the distance matrix as a combined climate (MAP and MAT) factor.

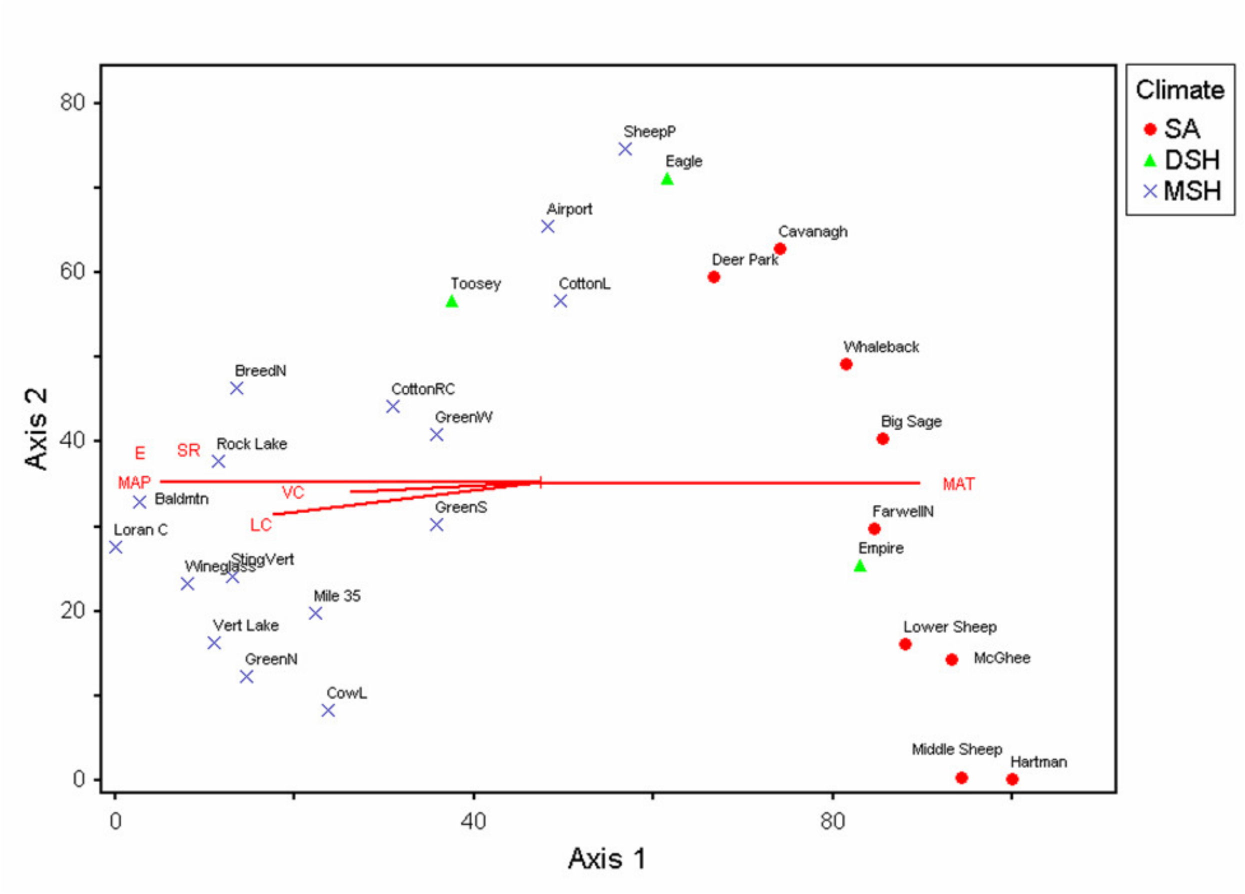


Figure 1.9. NMS ordination of 28 inside plots and 78 species of the Range Reference Areas. The climate categories assigned to plots are: SA=Semi-arid, DSH=Dry sub-humid, MSH=Moist sub-humid. The climate and environmental variables correlated with the ordination axes: E= elevation, SR = Species Richness, MAP= Mean Annual Precipitation, MAT= Mean Annual Temperature, VC= Vegetation Cover, LC = Litter Cover, MAT= Mean Annual Temperature. Both axes are significant (Monte Carlo Test p=0.004), total stress = 10.05.

Species associated with Axis 1 are summarized on Table 1.4. *Hesperostipa comata* abundance has the strongest positive correlation with the axis. Other species positively correlated with Axis 1 include CAM photosynthesizing *Opuntia fragilis* prickly-pear cactus and C4 photosynthesizing native bunchgrass *Sporobolus cryptandrus*. The native bunchgrass *Achnatherum richardsonii* and the exotic sod-forming grass *Poa pratensis,* and the exotic forb *Tragopogon pratensis* are negatively associated with Axis 1. Axis 2 (summarized on Table 1.5) is positively associated with *Pseudoroegnaria* and negatively associated with *Hesperostipa comata* and *Poa pratensis* abundance.

Table 1.4. Pearson correlations of plant species abundance with NMS Axis 1.

Axis 1 Associated Species			
Negative (-)		Positive (+)	
Achnatherum richardsonii	0.676	*Hesperostipa comata*	0.711
Poa pratensis	0.643	*Opuntia fragilis*	0.704
Cerastium arvense	0.609	*Phacelia linearis*	0.47
Tragopogon pratensis	0.555	*Artemisia tridentata*	0.437
Geum triflorum	0.543	*Artemisia frigida*	0.427
Agoseris glauca	0.455	*Sporobolus cryptandrus*	0.405
Galium boreale	0.444	*Achnatherum hymenoides*	0.349
Fragaria virginiana	0.422	*Kali tragus*	0.327
Danthonia intermedia	0.401	*Bromus tectorum*	0.302
Elymus trachycaulus	0.391	*Lepidium densiflorum*	0.295

Table 1.5. Pearson correlations of plant species abundance with NMS Axis 2.

Axis 2 Associated Species			
Negative (-)		Positive (+)	
Hesperostipa comata	0.537	*Pseudoroegnaria spicata*	0.861
Poa pratensis	0.442	*Arabis hoelbolii*	0.564

Climate variables correlated with the ordination matrix axes are summarized in Table 1.6. Axis 1 of the ordination matrix has a negative relationship with MAP and elevation, and a positive relationship with MAT. Axis 2 is not correlated with any of the climate variables. This demonstrates that Axis 1 represents a climate gradient, with higher elevations and cool-wet conditions correlated with the negative end of Axis 1, while lower elevations and warm-dry conditions correlated with the positive end of Axis 1. There is a concentration of moist sub-humid RRAs on the negative end of Axis 1 and semi-arid RRAs on the positive end of Axis 1.

Table 1.6. Pearson correlations of climate variables and Axis 1 and Axis 2 of the ordination space. Elevation and mean annual precipitation are negatively correlated with Axis 1, and MAT is positively correlated with Axis 1. There is not a relationship between the climate variables and Axis 2.

Variable	Axis 1 (R^2= 71.2)	Axis 2 (R^2=15.3)
Elevation	-0.914	0.032
MAP	-0.92	0.063
MAT	0.919	-0.071

Axis 2 is positively correlated with greater percent cover values of *Pseudoroegnaria spicata*. There were low cover values of *Pseudoroegnaria spicata* at the positive and negative ends of the climate gradient. *Pseudorognaria spicata* gradually increases and then decreases on Axis 2 moving from negative to positive along the climate gradient (Axis 1).

Grassland Plant Community Categorizations

Based on ordination analysis, grassland plant communities were organized into lower, middle, and upper grasslands (Tisdale, 1947; Deleselle et al., 2009). The relationships between plant communities, elevation, climate categories, and biogeoclimatic zones is summarized in Table 1.7. There is a gradual change in plant community composition along the elevation gradient. Lower grassland plant communities can be identified by the presence of *Hesperostipa comata* and *Opuntia fragilis*, the middle grasslands by *Pseudoroegnaria spicata* and greater vascular species richness than the lower grasslands; the upper grasslands are characterized by *Poa pratensis*, *Achnatherum richardsonii*, and *Hesperostipa curtiseta* as leading species.

Table 1.7. Distribution of grassland plant community categorizations with biogeoclimatic ecosystem classification (BEC) and climate classification systems. The symbol ** means the grassland category is widely distributed with the BEC subzone, while * means the category may be found within the BEC subzone but is not widely distributed. Climate categories are SA = semi-arid, DSH = dry sub-humid, and MSH = moist sub-humid. Bolded letters denote the climate that the grassland category is primarily associated.

BEC and climate	Lower Grasslands	Middle Grasslands	Upper Grasslands
BG xh	**		
BG xw	**	*	
IDF xm		**	**
IDF dk			*
climate	**SA**, DSH	**DSH**, MSH	**MSH**
elevation (m)	380-700	700-950	950-1200

The grassland plant communities were related with biogeoclimatic and climate categories but did not perfectly overlap. There were also plant communities that were intermediate between the grassland categorizations that occurred near the elevational boundaries.

The effects of grazing on species composition

The mean cover and frequency of species of grazed and un-grazed plant communities are included in Table 1.8 (upper grasslands), Table 1.9 (middle grasslands), and Table 1.10 (lower grasslands).

Table 1.8 Mean cover and frequency of species of inside and outside plots in the upper grasslands.

Upper Grasslands					
Inside, n = 13			Outside, n = 12		
Species	mean	freq	Species	mean	freq
Poa pratensis	28.84	1	*Poa pratensis*	25.97	1
Achnatherum richardsonii	13.39	0.92	*Achnatherum richardsonii*	7.54	0.67
Tragopogon pratensis	7.12	1	*Hesperostipa curtiseta*	5.74	0.75
Hesperostipa curtiseta	4.99	0.77	*Antennaria umbrinella*	4.87	0.67
Antennaria umbrinella	3.53	0.77	*Potentilla hippiana*	3.22	0.83
Pseudoroegnaria spicata	3.38	0.69	*Tragopogon pratensis*	2.85	1
Astragalus miser	2.60	0.77	*Koeleria macrantha*	2.69	0.75
Achillea millefolium	1.82	1	*Geranium viscosissimum*	2.55	0.25
Galium boreal	1.51	0.54	*Hesperostipa comata*	1.66	0.42
Koeleria macrantha	1.22	0.85	*Pseudoroegnaria spicata*	1.55	0.42

Table 1.9 Mean cover and frequency of species on inside and outside plots of the middle grasslands.

Middle Grasslands					
Inside, n = 5			Outside, n = 5		
Species	Mean	freq	Species	Mean	freq
Pseudoroegnaria spicata	23.99	1	*Pseudoroegnaria spicata*	8.09	1
Astragalus miser	5.28	0.6	*Koeleria macrantha*	7.03	1
Koeleria macrantha	4.60	1	*Poa pratensis*	4.57	0.8
Achillea millefolium	4.06	1	*Artemisia frigida*	4.29	1
Antennaria microphylla	3.66	0.2	*Antennaria umbrinella*	2.63	0.4
Tragopogon pratensis	3.40	0.6	*Artemisia tridentata*	2.50	0.2
Antennaria umbrinella	2.17	0.4	*Linum lewisii*	2.39	0.4
Poa pratensis	1.95	0.6	*Achillea millefolium*	1.62	0.8
Artemisia frigida	1.94	1	*Hesperostipa comata*	1.60	0.6
Achnatherum richardsonii	1.65	0.2	*Artemisia campestris*	1.57	0.6

Table 1.10 Mean cover and frequency of species of inside and outside plots of the lower grasslands.

Lower Grasslands					
Inside, n = 10			Outside, n = 9		
Species	Mean	freq	Species	Mean	freq
Hesperostipa comata	13.79	1	*Hesperostipa comata*	9.94	0.89
Artemisia frigida	6.57	0.8	*Sporobolus cryptandrus*	5.39	0.89
Pseudoroegnaria spicata	6.19	0.8	*Pseudoroegnaria spicata*	4.63	0.56
Sporobolus cryptandrus	1.21	0.4	*Artemisia frigida*	1.83	0.89
Artemisia tridentata	1.16	0.6	*Artemisia tridentata*	0.98	0.56
Phacelia linearis	0.59	0.5	*Opuntia fragilis*	0.89	1
Opuntia fragilis	0.54	1	*Phacelia linearis*	0.83	0.33
Koeleria macrantha	0.43	0.4	*Salsola kali*	0.81	0.22
Orthocarpus luteus	0.41	0.2	*Koeleria macrantha*	0.78	0.33
Bromus tectorum	0.24	0.5	*Bromus tectorum*	0.56	0.33

The results of paired t-tests for grazed and un-grazed plots for each plant community are summarized in Table 1.11. The only significant effects of grazing were reduced vegetation cover ($p = 0.02$) and reduced *Pseudoroegnaria* cover ($p=0.001$) in the middle grasslands. Potential or marginal effects of grazing that did not meet the alpha level ($p \leq 0.05$) of significance were reduced plant cover in lower grasslands ($p= 0.08$), reduced native forbs in lower grasslands ($p = 0.08$), and reduced litter in upper grasslands ($p = 0.08$). In the lower grasslands, grazed plots were associated with a decrease in *Pseudoroegnaria* and an increase in *Sporobolus*, but statistical analysis could not be completed due to low frequency of occurrence (4 occurrences on inside plots for *Sporobolus* and 5 occurrences on outside plots for *Pseudoroegnaria*).

Table 1.11. Mean cover and coefficient of variation for ecosystem traits for inside and outside plots of each grassland category. The p-value is the result of paired t-tests and significance of the difference between inside and outside plots. Significant values are bolded.

	Lower			Middle			Upper		
Trait	In	Out	p	In	Out	p	In	Out	p
Vegetation	32.5 (35.5)	27.7 (2.6)	0.08	59.6 (13.73)	**46.74 (10.33)**	**0.02**	82.7 (7)	75.5 (6.64)	0.37
Litter	24.1 (3.9)	21.7 (2.43)	0.71	41.6 (12.05)	39.56 (12.68)	0.47	71.9 (4.91)	61 (6.3)	0.08
Native Grass	0.71 (0.07)	0.75 (0.05)	0.64	0.62 (0.12)	0.47 (0.06)	0.26	0.32 (0.06)	0.3 (0.06)	na
Native Forb	0.25 (0.07)	0.14 (0.04)	0.08	0.31 (0.09)	0.3 (0.09)	0.89	0.26 (0.04)	0.31 (0.04)	0.238
Exotic	0.01 (0.002)	0.05 (0.02)	na	0.07 (0.05)	0.09 (0.05)	na	0.43 (0.05)	0.38 (0.08)	0.47

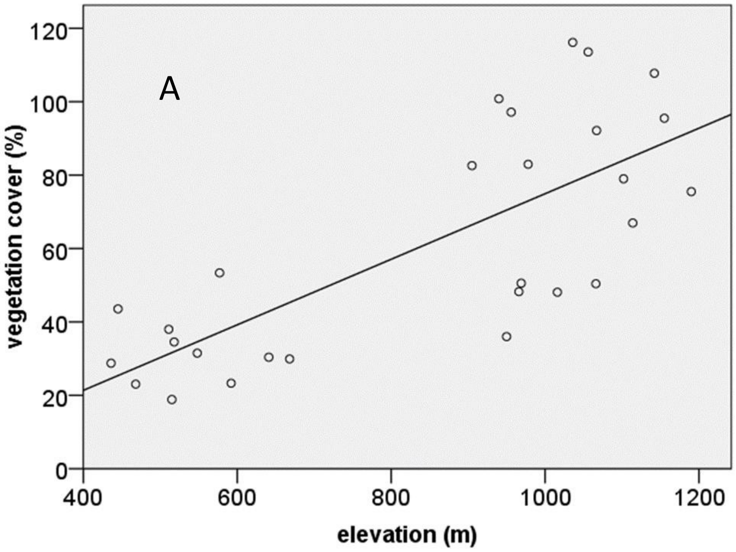
Species composition of grazed and non-grazed upper grasslands were similar. *Poa pratensis* was leading on grazed and non-grazed plots there, while *Achnatherum richardsonii* and *Hesperostipa curtiseta* are frequent secondary species. Average combined cover of native bunchgrass species was slightly lower than average cover of *Poa pratensis.*

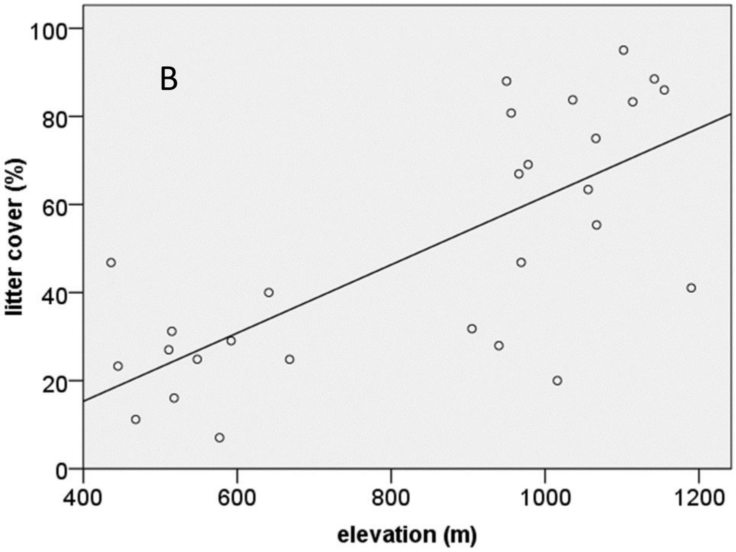
Plant community characteristics on an elevation-climate gradient

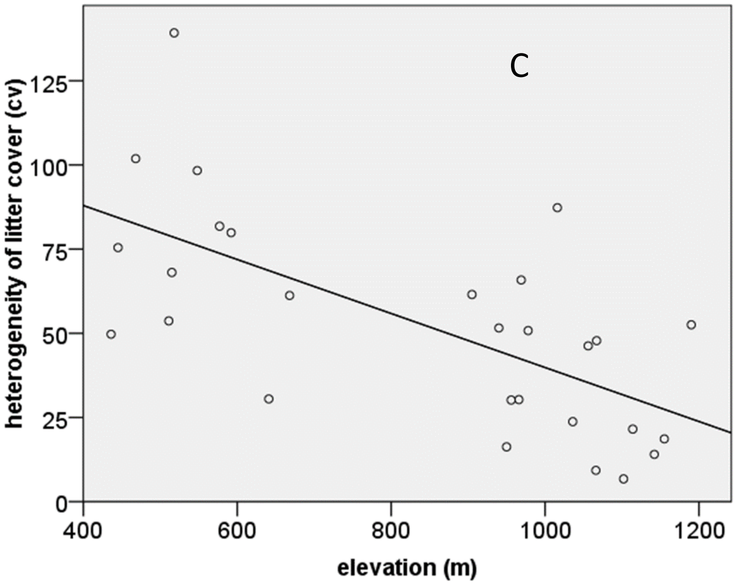
The relationship between elevation and plant community characteristics are summarized in Table 1.12. and shown in Figure 1.10. The cooler-wetter end of the climate gradient was associated with increased vegetation cover ($R^2=0.548$; $p <0.001$), increased litter cover ($R^2=0.532$; $p<0.001$), and reduced heterogeneity of litter cover ($R^2=0.432$; $p <0.001$). There was also a significant positive relationship between elevation and species richness (Spearman correlation=0.813; $p <0.001$). Average vegetation cover and litter cover increased from averages of 32.5 and 24.1%, respectively, in the lower grasslands to 82.7 and 71.9%, respectively, in the upper grasslands. Plots had an average species count of 10.5 in lower grasslands, 20.6 in middle grasslands, and 28.1 in upper grasslands. The native forb component of upper grasslands was a source of diversity despite high cover values of exotic species.

Table 1.12. Results of linear regressions showing relationships between plant community characteristics and elevation.

Variable	n	F	R^2	p	intercept	slope coefficient
Vegetation cover	28	33.77	0.548	0.000005	-14.4	0.09
Litter cover	28	29.53	0.532	0.000011	-15.7	0.08
Hetergoeneity of litter cover	28	19.75	0.432	0.000146	120	-0.08







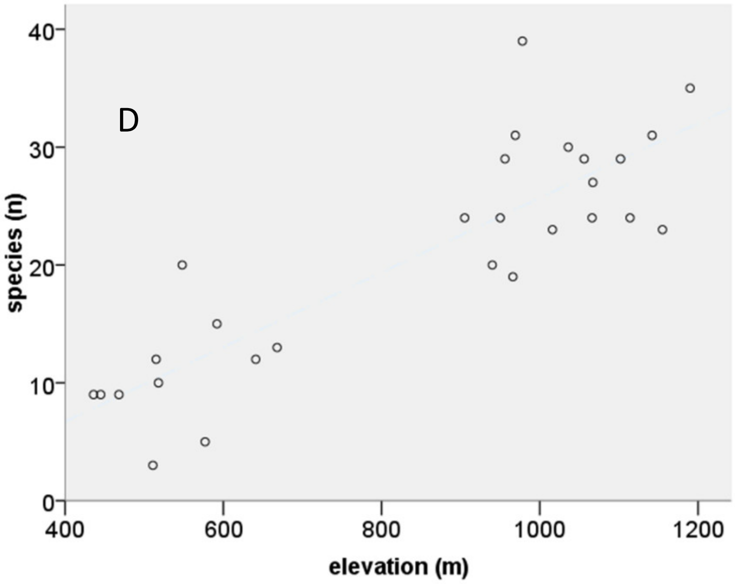


Figure 1.10. Relationships between elevation and plant community characteristics including **A.** total vegetation cover (%), **B.** litter cover (%), **C.** litter cover heterogeneity (coefficient of variation; CV), and **D.** number of vascular species per plot (n).

Soil characteristics on an elevation-climate gradient

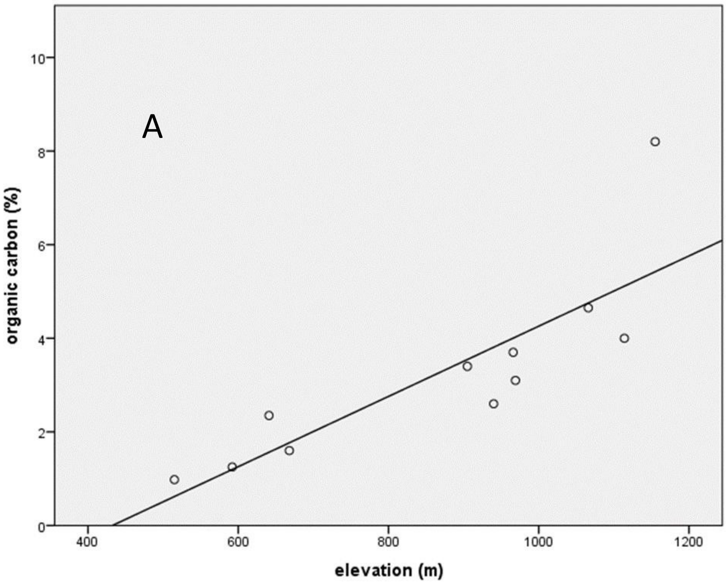
A summary of soil characteristics of range reference areas collected along the elevation gradient are summarized on Table 1.13. Relationships between elevation, carbon and nitrogen are summarized on Table 1.14. and shown on Figure 1.11.

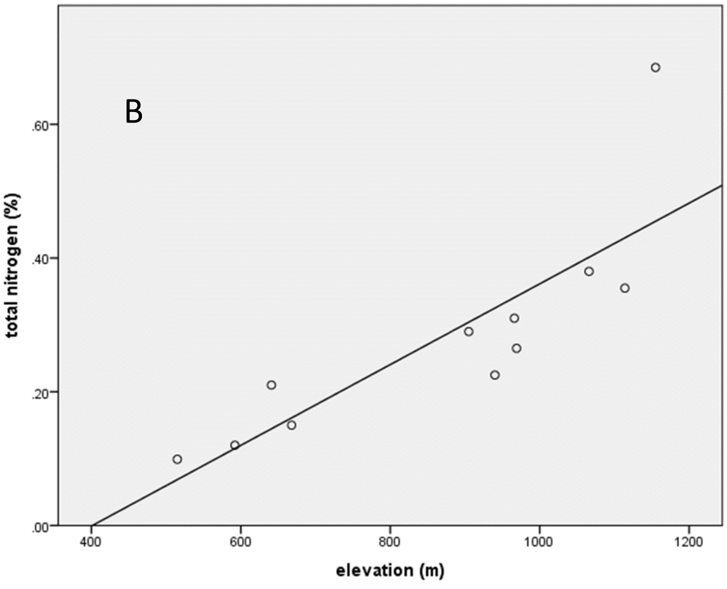
Table 1.13. Summary of soil characteristics of RRAs selected from the elevation gradient.

Reference Area	elevation (m)	MAP	MAT	organic C (%)	total N (%)	C/N ratio	pH	Clay (%)	Silt (%)	Sand (%)	texture
Farwell Big Sage	515	313	6.3	0.98	0.099	9.90	7.12	12.8	38.4	48.8	Loam
Farwell Needlegrass	592	334	5.9	1.25	0.12	10.42	6.77	9.0	47.4	43.7	Loam
Eagle Tree	641	318	5.8	2.35	0.21	11.19	6.51	17.9	46.0	36.1	Loam
Empire Valley	668	364	5.9	1.6	0.15	10.67	6.56	14.1	53.7	32.2	Silt Loam
Toosey	905	411	4.4	3.4	0.29	11.72	6.39	17.9	49.9	32.2	Loam
Cotton Lake	940	420	4.2	2.6	0.225	11.56	6.39	16.6	47.2	36.2	Loam
Loran	966	436	4.1	3.7	0.31	11.94	5.96	21.7	43.5	34.8	Loam
Rock Lake	969	438	4.0	3.1	0.265	11.70	6.17	17.9	42.2	39.9	Loam
Sting and Vert	1066	471	4.0	4.65	0.38	12.24	6.34	14.0	35.7	50.3	Loam
Vert Lake	1114	480	3.8	4	0.355	11.27	6.78	21.7	39.6	38.7	Loam
Bald Mountain	1155	478	3.2	8.2	0.685	11.97	5.86	11.5	47.3	41.3	Loam

Table 1.14. Results of linear regressions showing relationship between soil characteristics and elevation.

Variable	n	F	R^2	p	intercept	slope coefficient
organic carbon (%)	11	20.84	0.698	0.001	-3.25	0.0075
total nitrogen (%)	11	20.13	0.691	0.002	-0.24	0.0006
C/N ratio	11	19.75	0.738	0.001	8.91	0.0028





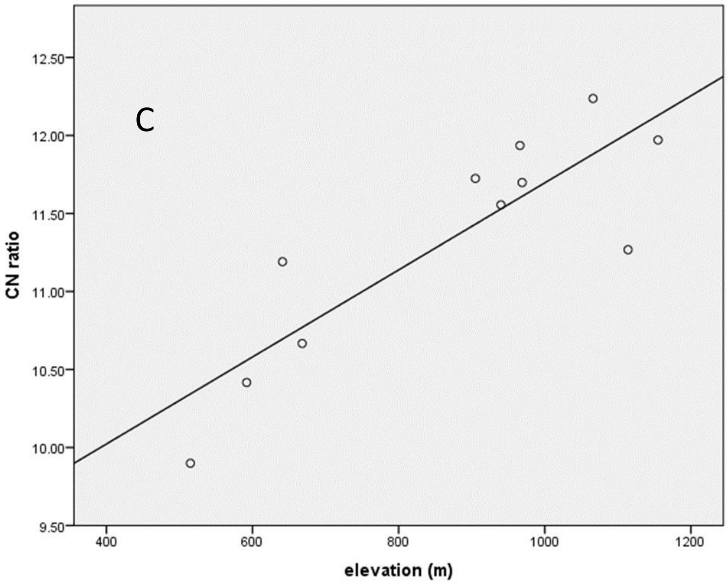


Figure 1.11. Relationships between elevation and **A.** organic carbon (%), **B.** total nitrogen (%), and **C.** C/N ratio.

There was a significant increase in soil organic C (%), total N (%), and C/N ratio with cooler and wetter climate conditions. However, the magnitude of change in C/N was small (ranging from 9.9 to 12.24), compared to the increase in total N across the climate gradient (from 0.099 to 0.685 %). The inorganic carbon concentrations generally were below the detection limit (except for one sub-sample that was slightly above the detection limit), indicating the absence of calcium carbonates in the Ah horizon. Of four sub-humid zone soils, three were classified as orthic dark brown chernozems, and one as a calcareous dark brown chernozem (Appendix 1). There was low variability in soil texture among soil samples despite being collected at various elevations over a large geographic area. All samples were classified as a loam or silt loam, with similar concentrations of combined silt and clay.

Discussion

The presence of spatially contiguous grasslands along a large (~800 m) elevation gradient provided an opportunity for the comparison of grassland ecosystems of different climates in a relatively small geographic area. Elevation was a strong predictor of plant community characteristics, soil qualities, and species composition. The cooler-wetter climates were associated with increases of soil carbon content, vegetation cover, litter cover, and species richness. Warm-dry conditions were associated with greater heterogeneity of litter cover. Grazing caused moderate changes in the plant community in middle and lower grasslands, notably the reduction in *Pseudoroegnaria* cover. In the lower grasslands, *Hesperostipa comata* had the greatest cover on grazed and non-grazed plots, and *Pseudoroegnaria* had higher frequency and cover on non-grazed plots than grazed plots. *Sporobolus cryptandrus* had higher cover on grazed lower grasslands. I did not find any significant differences between grazed and non-grazed grasslands in the sub-humid climate upper grasslands.

Tisdale (1947) created the categorization of lower, middle, and upper grasslands for southern interior British Columbia. This convention was supported by subsequent research in the Thompson-Nicola grasslands (e.g., van Ryswyk et al., 1966; Carlyle et al., 2014; Lee et al., 2014; Cumming et al., 2016) and is applied in conservation and grazing management (Deleselle et al., 2009; Province of British Columbia, 2020 b). In the Thompson-Nicola region, the Bunchgrass very dry hot (BG xh), Bunchgrass very dry warm (BG xw) (Nicholson et al., 1991) and Interior Douglas-fir very dry hot (IDF xh) biogeoclimatic subzones (Hope et al., 1991) correspond with the lower, middle, and upper grasslands (Tisdale, 1947; Lee et al., 2014). Additionally, the changes in leading species composition that represent the categories are spatially abrupt (Lee et al., 2014). In the Cariboo-Chilcotin, the progression of biogeoclimatic zones and grassland plant communities along the elevation gradient do not completely coincide. Creating grassland categorizations is more challenging because species composition, plant cover, litter cover, and soil characteristics changed gradually and continuously along the elevation gradient. Furthermore, because of the gradual changes along the elevation gradient, there are plant communities that are intermediates between categorizations.

Based on NMS ordination analysis, a re-configuration of this classification for the Cariboo-Chilcotin grasslands is proposed. Steen and Coupe (1997) distinguish the BG xh from the BG xw by the presence of *Artemisia tridentata*, with the BG xh having greater cover values of the species. Deleselle (2009) also separates the lower and middle grasslands on the difference in *Artemisia tridentata* cover. In the RRAs, the frequent absence of *Artemisia tridentata* means it is not a reliable indicator for grassland plant communities. Therefore, the lower grasslands category is defined by more consistent observations. Observations include the presence of *Hesperostipa comata* at all seral stages (although *Pseudoroegnaria spicata* is leading at late seral stages), relatively low litter and plant cover, and the presence of *Opuntia fragilis*. The BG zone spatially approximates the proposed definition of the lower grasslands, although the transition to middle grasslands may occur in the higher elevation part of the BG xw. The definition of the middle grasslands includes greater cover values of *Pseudoroegnaria spicata*, the absence of *Hesperostipa comata* at late seral stages, and absence of *Opuntia fragilis*. The middle grassland categorization can be obscured by grazing which reduces *Pseudoroegnaria spicata* and because *Hesperostipa comata* may be present at early seral stages. In this case, greater species richness (>15 vascular species per plot), the presence of *Poa pratensis*, and *Achnatherum nelsonii* are indicators of the middle grasslands. The upper grasslands have one or a combination of *Poa pratensis, Achnatherum richardsonii*, and *Hesperostipa curtiseta* as leading species. The upper grasslands also have greater plant cover and litter cover, and greater species richness than other grassland categories. The IDF xm contains areas of middle and upper grasslands, while the upper grasslands also extend into the IDF dk. There is a broad transition between the middle and upper grasslands that occurs between approximately 900 to 950 m elevation. In this transition, there is sometimes substantial cover of *Pseudoroegnaria spicata* as well as grass species associated with the upper grasslands.

This study uses a framework of climate categories in analysis and discussion. The framework is useful because there is a great quantity of scientific literature that describes ecosystems characteristics for each climate category. Characteristics include productivity, carbon and nitrogen dynamics, biological and abiotic decomposition processes, and disturbance regimes. The bunchgrass biogeoclimatic zone and the lower grasslands roughly correspond with the semi-arid climate. The middle grasslands occur in the dry sub-humid and drier parts of the moist sub-humid climates. The transition from middle to upper grasslands and the entirety of the upper grasslands occur in the moist sub-humid climate. Climate categories will be used when comparing the Cariboo-Chilcotin grasslands to those of other regions because climate categories are equivalent, while species composition-based categories are not directly comparable. Discussion on the effects of grazing and of within-region characteristics will use the lower, middle, and upper grassland categories.

Patterns of plant cover changed from discontinuous to continuous on a gradient from semi-arid to sub-humid climate grasslands. The same pattern has been described in the Burke et al. (1998) review of global temperate grasslands. Total plant cover in grasslands is strongly correlated with productivity (Carlyle et al., 2014). Aboveground productivity in grasslands is strongly correlated with below-ground productivity and accumulation of organic carbon

(Anderson, 1987). Root litter is the primary source of soil organic carbon in grassland (Steinaker and Wilson, 2005). Soil organic carbon increases with wetter conditions because of increased productivity of organic matter and with cooler conditions because of lower decomposition rates (Anderson, 1987; Pennock et al., 2011). Burke et al. (1989) and Hewins et al. (2018) found that climate and soil texture explain most of the variation in grassland soil organic carbon content at the regional level. Smaller particle sizes (silt + clay) are a greater source of organic carbon retention capacity than larger particle sizes (sand) because of greater surface area, and because particles provide physical and biochemical C stabilization factors (Plante et al., 2006). In this study, the relative uniformity of soil texture (silt + clay content) in the aeolian veneer effectively created a controlled variable, permitting a representation of the climate-soil organic matter relationship with a small sample size.

The semi-arid grasslands have low concentrations of soil organic carbon and total nitrogen. Sub-humid grassland patterns of decomposition are closely linked to the growth of the microbial community, while in semi-arid grasslands, above- and below-ground processes are uncoupled from these patterns (Parton et al., 2007). Like below-ground processes, above-ground decomposition is limited by low microbial activity. Low litter covers found in the semi-arid grasslands result from low productivity (Zhou et al., 2009), and abiotic decomposition processes such as photodegradation (Austin and Vivanco, 2006). The Collins et al. (2008) review concluded that due to the lack of a rich carbon and nitrogen "pool", nutrient cycling in semi-arid ecosystems is more likely to operate in a direct "loop". The loop works by transferring nutrients from the biological soil crusts directly to plants through a fungal network. Therefore, the diverse biological soil crust communities of the Cariboo Chilcotin grasslands as described by Marsh et al. (2006) are likely critical for supporting productivity. Initial observations suggest that BSC is reduced or absent from heavily grazed grasslands. Caputa et al. (2013) has demonstrated biological soil crusts deliver substantial amounts of nitrogen to the grassland ecosystem, with high levels of temporal heterogeneity depending on water availability and soil surface temperature.

The results indicate that availability of N is most limited by retention capacity in semi-arid grasslands and by nitrogen inputs in sub-humid grasslands. There was a relatively constant C/N ratio in comparison to the large increase in total nitrogen along the elevation gradient. However, there were small but statistically significant increases in C/N ratio. Grassland root litter has lower nitrogen content than forest root litter, which contributes to higher C/N ratios in grassland than forest soils (Steinaker and Wilson, 2005). Despite low nitrogen content of root litter in grasslands, greater concentrations of SOC (soil organic carbon) are associated with increased soil nitrogen, as SOC provides a substrate to capture nitrogen inputs (Barrett and Burke, 2000). Barrett and Burke (2002) demonstrate that greater SOC content increased soil nitrogen retention in a fertilization experiment. Luo et al. (2017) found with increasing aridity, the proportion of ecosystem nitrogen (combined plant and soil) shifted to above-ground plant matter in comparison to the concentration of soil N. The concentration of nitrogen in foliage rather than soil is an indicator of the link between microbial communities and plants that bypass the soil. Luo et al. (2017) also found that increasing levels of SOC dilute the concentration of nitrogen in the ecosystem. It is likely that increases in soil N content along the elevation gradient were related to greater retention capacity provided by SOC, while the C/N ratio increased because of the dilution effect of increased SOC. Lack of nitrogen inputs to meet the retention capacity of soils in the sub-humid climate may also be a factor in the increasing C/N ratio.

The species composition of the upper grasslands consists of early- to mid-seral species or indicators of past disturbance. Species composition of grazed and non-grazed plant communities are similar, and no statistically significant differences between communities inside and outside of exclosures were detected. *Poa pratensis* is the leading species, with most areas having a substantial component of *Achnatherum richadsonii* and *Hesperostipa curtiseta*. *Achnatherum nelsonii* as a frequent trace species. *Poa pratensis* is an exotic cool-season grass that invades after heavy grazing and is persistent in grasslands across humid and sub-humid (mesic) grasslands of North America (White et al.,2013; DeKeyser and Dennhardt, 2015; Printz and Hendrickson, 2015). *Hesperostipa curtiseta* is rare in the grasslands of interior British Columbia outside of the of the Cariboo-Chilcotin region but is common in the northern Great Plains. In the Great Plains, *Hesperostipa curtiseta* is an indicator of past grazing disturbance in the plains-rough fescue (*Festuca hallii*) grasslands (Coupland, 1961; Coupland and Brayshaw, 1953). In the Thompson-Nicola grasslands of southern interior British Columbia, *Achnatherum richardsonii* and *Achnatherum nelsonii* are a substantial part of early- to mid-seral plant communities in the higher elevation upper grasslands that are dominated by mountain-rough fescue (*Festuca campestris*) in the late seral stage (Province of British Columbia, 2020 c). The presence of early seral associated grasses and absence of a dominant late seral species normally associated with sub-humid climates may have contributed to lack of successional direction in the upper grasslands. Furthermore, grazed and non-grazed grasslands may have recovered at similar rates after being severely over-grazed in earlier decades, when bare ground and lower stature grasses such as *Festuca saximontana* and *Koeleria macrantha* were more common.

Species richness increases continually along the elevation gradient coincidentally with greater plant cover and litter cover. In a worldwide meta-analysis of grassland species richness, Fraser et al. (2015) found a humped-back relationship between productivity and species richness. While there is debate on whether the humped-back relationship of productivity and species richness is consistent worldwide (Laanisto and Hutchings, 2015), it appears the humped-back relationship at least predominates across temperate and high-latitude grasslands (Partel et al., 2007) In a subsequent review, Koerner et al. (2018) attributed lower species richness associated with productive grasslands to the monopolization of resources by dominant species. The continuous increase in number of species along the elevation gradient in the Cariboo-Chilcotin grasslands is an outlier of the normal humped-back productivity-species richness relationship. In the climate-elevation gradient of this study, a relatively cool-wet climate and increased availability of soil resources was correlated with greater species richness. This suggests that due to the absence of dominant species, resource availability is the driving factor in species richness.

Poa pratensis was the leading species in the upper grasslands, while *Tragopogon pratensis* was a high frequency low cover species. Similarly, White et al. (2013) found that *Poa pratensis* invasion reduced native species cover but not native species presence or richness at a site in the sub-humid foothills-fescue region of Alberta. *Bromus tectorum* (cheatgrass) is frequent but with low cover in the lower grasslands and may be a recent invader. Cheatgrass has invaded millions of hectares of North American rangelands (Mack, 1981), with semi-arid sagebrush (*Artemisia tridentata*) grasslands being particularly susceptible to invasion (Chambers et al., 2007). Cheatgrass invasions have serious consequences for ecosystem services due to the associated deterioration of native plant cover and soil properties, and their ability to support recurrent wildfires (Chambers et al., 2014). Therefore, cheatgrass may pose a significant threat to the semi-arid grasslands.

The soils of the sub-humid grasslands have considerably lower soil organic matter content than those described for grasslands in the sub-humid climates of Alberta (Hewins et al., 2018), and the upper grasslands of the Thompson-Nicola region of British Columbia (van Ryswyk et al., 1966; Carlyle et al.,2014). This is despite the upper grasslands climate of the study area being considerable wetter and cooler than the upper grasslands location used in van Ryswyk et al. (1966) and Carlyle et al. (2014) studies (as per ClimateBC estimates; Wang et al.,2016). Further, black chernozems are the dominant soils of sub-humid grasslands of Canada (Soil Classification Working Group, 1998). The dominant grassland soils of the study area are dark brown chernozems, which have lower soil organic carbon content than the black chernozems and are more typical of semi-arid rather than sub-humid climate grasslands (Soil Classification Working Group, 1998). Dark Gray Chernozems are also found in the region (Valentine et al., 1987), indicating that forests and grasslands have both occupied some sites over time (Soil Classification Working Group, 1998). It is suggested that the dominance of early-seral grasses and the lack of a high productivity late-seral grass species may have prevented the accumulation of greater concentrations of soil organic carbon. The presence of a large stature species with a high biomass root system may be a necessary factor in the accumulation of organic carbon found in black chernozems. Rough fescue has a large root system in comparison to other grassland species (Johnston, 1961). Johnston et al. (1971) found that the long-term removal of rough fescue by heavy grazing may have resulted in the loss of organic carbon and a change from a black to dark brown soil colour. Coupland and Brayshaw (1953) determined that late seral rough fescue grasslands on the northern Great Plains produced a total weight of root material 50% greater than under an early seral grassland dominated by *Hesperostipa curtiseta* and *Koeleria macrantha*. The geographic isolation of these central British Columbia grasslands may have prevented the migration of the typical late seral species *Festuca campestris*, therefore limiting the buildup of soil organic carbon.

Reduced frequency of fires has resulted on the encroachment of lodgepole pine (*Pinus contorta* var. *latifolia*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) trees on the Cariboo-Chilcotin grasslands in the past ~100 years (Strang and Parminter 1980; Bai et al., 2004). The greatest amount of forest encroachment occurred at higher elevations (Bai et al., 2004; Steele et al., 2007). Forest encroachment on grasslands in sub-humid climates is often associated with degradation from intensive livestock grazing and loss of fine fuels that contribute to periodic fires that suppressed encroachment in the past (Archer et al., 2017). Fire activity increases across a resource gradient as primary productivity provides a greater amount and spatial connectivity of fine fuels (and declines again due to high fuel moisture content) (Krawchuck and Moritz, 2011). In the upper grasslands, the high cover values of plant cover and litter, and the reduced heterogeneity of litter cover, are expected to support the spread of spatially contiguous fires. Therefore, it is likely that historically there was a higher frequency and larger size of fires in the upper grasslands than in the lower grasslands.

The long-term predominance of grassland plant communities in parts of the sub-humid climate is evidenced by grassland-associated soil characteristics. These include the accumulation of organic carbon in the Ah horizon, and the dissolution of carbonates from the A horizon and precipitation to the C horizon as is characteristic of chernozemic soils (Appendix 1). There is evidence that the process of precipitation of carbonates to the C horizon takes longer periods of time than the accumulation of organic carbon in the Ah horizon (Anderson, 1977). Water limitation is the leading factor controlling the vegetation of the semi-arid bunchgrass biogeoclimatic zone, as trees do not typically grow on zonal sites and grasslands predominate due to drought (Nicholson et al.,1991). Trees can grow on the sub-humid grasslands, as demonstrated in the 20th century as trees encroached on historical grasslands. Correspondingly, Burke et al. (1998) describes a resource gradient from semi-arid to sub-humid grasslands: water limitation controls plant-soil interactions in the semi-arid climates, and fire and grazing disturbances become more important as vegetation cover increases along a precipitation gradient. Despite the trend of afforestation, it is predicted that northern sub-humid forests will be susceptible to degradation due to climate change and drought, increased land use and resource extraction, and the presence of invasive species (Timoney, 2003). In the past, the cycle of vegetation and litter buildup and curing, followed by spatially continuous fires, has maintained areas in the grassland state over long periods of time. First Nations burning practices were likely an important part of this plant and soil relationship as well (Blackstock and McAllister, 2004).

Conclusions

The plant community composition of Cariboo-Chilcotin grasslands is unique and distinct in comparison to the grasslands of other regions. Above-ground patterns of plant and litter cover are consistent with those expected with a transition from semi-arid to sub-humid grasslands. Below-ground carbon and nitrogen dynamics are also consistent with other grassland climate gradients, except for the unexpectedly lower organic carbon concentrations found in the sub-humid upper grasslands.

Management of exotic species will be a challenge, with different strategies required depending on the grassland type (upper, middle, or lower). In the upper grasslands, *Poa pratensis*is the leading species under the existing grazing regime and under the passive restoration found inside grazing exclosures. Therefore, research and management efforts should focus on strategies to reduce *Poa pratensis* and increase native bunchgrass cover. This may include prescribed burning and altered grazing practices. In the middle grasslands, management should be aimed at maintaining and enhancing *Pseudoroegnaria* cover. In the lower grasslands, research should focus on strategies to prevent the spread of *Bromus tectorum* and to maintain biological soil crust cover.

CHAPTER 2: ECOLOGICAL LEGACIES PERSIST AFTER FOREST ENCROACHMENT, ECOLOGICAL RESTORATION TREATMENTS, AND WILDFIRE IN A GRASSLAND-FOREST MOSAIC

Introduction

In the Cariboo-Chilcotin region of British Columbia, spatially abrupt grassland-forest boundaries are historically stable despite variations in climate and frequent fires. In this region, warm aspects and lower elevation increase the probability of a site being grassland, cool aspects and higher elevation increase the probability of a site being forested (Bai et al., 2004). However, the largest area of both grassland and forest occur on level terrain, with extensive grassland areas at higher elevations (Bai et al., 2004). This suggests that in addition to landscape position factors, ecosystem legacies may be important for maintaining the forest and grassland states after disturbances. Stand-level disturbance histories of dry forests of interior British Columbia reveal frequent low-severity fires, punctuated by spatially and temporally heterogeneous high-severity fires (Heyerdahl et al., 2012; Harvey et al., 2017). These disturbance patterns create a mixed severity disturbance regime that contributes to diverse stand conditions over the landscape (Klenner et al., 2008). Meanwhile, grasslands of the dry forest zone have experienced frequent fires (average 10-year return interval), until the early 20th century when grassland fires become infrequent (Strang and Parminter, 1980). Historical grassland fires have been linked to inter-annual climate variability (Harvey and Smith, 2017), and spatial connectivity of fine fuels (Krawchuck and Moritz 2011; Harvey et al., 2017; Harvey et al., 2018;).

Ecosystem legacies are defined as “a physical or biological condition of a previous ecosystem that persists after a disturbance, often guiding ecosystem re-organization” (Jogiste et al. 2017). In dryland ecosystems, spatial and temporal distribution of soil resources is a driving factor in post-disturbance regime shift or re-organization to the same state. Changes in vegetation patterns caused by land uses can re-distribute the spatial and temporal distribution of soil moisture (Breshears and Barnes, 1999). Livestock grazing and anthropogenically altered disturbance regimes have caused an increased spatial heterogeneity of soil resources, resulting in the expansion of woody vegetation into grasslands (Schlesinger et al., 1990; Okin et al., 2009; Bestelmeyer et al., 2018). Increased spatial heterogeneity in soil moisture is considered a feedback that favours regeneration of trees, as trees reinforce increased spatial soil moisture heterogeneity (Kleb and Wilson, 1997; Partel and Wilson, 2002). Grasslands experience greater temporal heterogeneity of soil resources. In grasslands, average soil moisture is greater than in adjacent forests during periods of high precipitation, but drought conditions are more severe due to greater evaporation and water uptake through the high concentration of fine roots near the soil surface (Wilson and Kleb, 1996; James et al. 2003; McLaren et al. 2004).

Heterogenous light and soil moisture conditions are important in creating microsites for tree seedling establishment in Douglas-fir forests (Gray, 1995). In the dry Douglas-fir forests of interior British Columbia, a heterogeneous canopy structure is thought to provide “zones of regeneration” for tree seedlings through a balance of shading and reduced precipitation interception in openings (Simard, 2009). The concept of resource heterogeneity is related to the size of plants and scale of resource distribution. Trees create heterogeneity on a larger scale than grasses, as tree canopies cause uneven distribution of precipitation and tree root systems have variable water uptake over a larger area (Wilson, 2000). This spatial heterogeneity influences the patchy pattern of dry forests, as tree seedling establishment is typically limited to patches of higher resource availability. Characteristic grassland ecosystems require a relatively uniform spatial distribution of resources because individual grass plants cannot reach outside resource-poor patches. Meanwhile, native bunchgrasses are better adapted to surviving temporal heterogeneity of soil moisture typical of grasslands by storing energy below ground in root systems during wet conditions and entering dormancy during drought.

Forest cover has encroached on grassland ecosystems of this region in the 20th century (Bai et al., 2004). Forest encroachment on grasslands has resulted from interruption of the relationship between litter, vegetation, and the fire disturbance regime on grasslands. Livestock grazing reduces litter cover and interrupts fine fuel spatial connectivity in grasslands, preventing the spread of fires and associated mortality of tree seedlings. Encroachment has been linked to fire suppression (Tisdale, 1950), reduced litter cover due to livestock grazing (Strang and Parminter, 1980; Arno and Gruell, 1986), and the reduction in traditional First Nations burning practices (Blackstock and McAllister, 2004). In the Cariboo-Chilcotin region, forest cover has encroached on 200 km^2 of grasslands from the early 1960's to the 1990's (Cariboo-Chilcotin Grasslands Strategy Working Group, 2001).

While "ecosystem memory" is the totality of all ecosystem legacies (Jogiste et al., 2017), legacies identified as being important to dryland systems are examined because memory is likely beyond the scope of any single study. Spatial and temporal distributions of soil moisture and plant communities that persist after disturbance are viewed as ecosystem legacies. These variables are used because soil water is the most limiting resource in grasslands (Burke et al. 1998) and dry Douglas-fir forests (Littell et al., 2008). It is predicted that patterns of resource distribution and plant communities interact with patterns of disturbance, including 1) heterogeneous distribution combined with a spatially mixed fire severity regime in forests, and 2) spatially homogenous patterns of resources and vegetation and relatively uniform spread of fire in grasslands. The high level of temporal heterogeneity of soil moisture in grasslands could contribute to the fire regime through periods of high soil moisture and high productivity, followed by drought and curing of litter and vegetation. These disturbance patterns combined with a frequent fire return interval may contribute to the reorganization of the forested and grassland states.

It is hypothesized that forest and grassland associated plant communities and soil moisture patterns will persist after disturbances, contributing to the resilience and recovery of each ecosystem state. Soil moisture, plant species composition, and substrates in adjacent forest and grassland plant communities were measured. In order to detect persistent plant and soil moisture legacies, areas of tree encroachment on grasslands, as well as restored grasslands (slash and burn treatments of forest encroachment on grasslands) were compared to stable-state grasslands and forests. After initial sampling, the study area was unintentionally burned in a wildfire. Vegetation and soil moisture were re-sampled to determine the effect of fire on grassland-associated and forest-associated patterns of soil moisture, as well as recovery of plant communities immediately after wildfire.

Methods

Study Area

The study was conducted near Riske Creek, British Columbia, in an area known as Becher's Prairie. Becher's Prairie is a level to gently rolling grassland and forest parkland area on the Chilcotin Plateau ranging from 900 to 1100 m elevation within the very dry mild subzone of the Interior Douglas-fir biogeoclimatic zone (IDF xm; Steen and Coupe, 1997). The climate is continental sub-humid, with a mean annual temperature of 4.3 ° C and mean annual precipitation 416 mm for the 1981 to 2010 period (Wang et al., 2016).

The area is provincial crown land with grazing tenures allocated according to the *Range Act* and grazing management plans created under the *Forest and Range Practices Act*. The area has been grazed since the 1860's, with early grazing practices creating early seral grassland plant communities (Bawtree, 2005). Reductions in stocking rates and the introduction of rotational grazing in the past 50 years have resulted in the partial recovery of native grassland ecosystems. Forest encroachment on grasslands has occurred on Becher's prairie. A mapped boundary known as the "grassland benchmark" demarcates the extent of grasslands in the region based on the earliest available aerial photographs (Cariboo-Chilcotin Grasslands Strategy Working Group, 2001; Steele et al., 2007). In the case of Becher's prairie, aerial photographs are from 1962. Grassland ecosystem restoration has been applied in parts of the grassland benchmark where trees establishing on grasslands has been cleared and excess material burned in a raised container (sloop) above the soil surface in order to reduce soil heating (see sloop burning: https://www.ccerc.net/photo-gallery-2/sloop10-018/). These treatments were followed by an early spring prescribed burn. In late July 2017, the study area was unintentionally burned in the Hanceville Fire wildfire.

Climate and weather

The Riske Creek weather station is maintained within the study area. The weather station has recorded April to October daily maximum and hourly temperature and daily precipitation data beginning in 1980, with some gaps in the data due to periodic maintenance. Table 2.1 includes the average precipitation per month taken from the Riske Creek weather station, as well as the precipitation recorded for the 2017 and 2018 growing seasons when data were collected for this study. April 2017 had slightly greater precipitation than average, followed by below-average precipitation from May to September. A record low (2 mm) for the month of June precipitation occurred in 2017. Lower than average precipitation continued through the 2018 growing season.

Table 2.1 Precipitation (precip., mm) and temperature (temp., ºC) values from the Riske Creek weather station site. The 2017 and 2018 values are the total monthly precipitation and average daily temperature per month, measured directly from the weather station. The average values for total month precipitation (Precip. ave) and average month temperature (Temp. ave) are the spatially interpolated averages (Wang et al., 2016) for the same location as the weather station.

Climate variable	April	May	June	July	Aug	Sep.
Precip. ave.	27.0	33.0	48.0	49.0	36.0	31.0
Temp. ave.	4.7	9.5	13.0	15.7	15.1	10.8
2017 precip.	32.2	23.2	2	22	7.8	26
2017 temp.	3.96	11.50	15.51	17.51	17.56	12.09
2018 precip.	NR	10.6	40.4	26.8	12	57
2018 temp.	NR	14.65	13.93	17.89	16.76	8.39

NR = not recorded.

Historical weather data for combined May to August precipitation are shown on Figure 2.1. The mean May-August precipipitation for the period 1980-2018 (based on 36 complete 3 month periods) is 153.1 mm, with a high level of interannual variability. The lowest growing season precipitation of all recorded years occurred in 2017 (55 mm), with below-average precipitation continuing in 2018 at 89.8 mm. The 2017 wildfire was preceded by an above-average precipitation season in 2016 (183.6 mm). There has been a significant decline in May-August precipitation over the 1980 to 2018 time period.

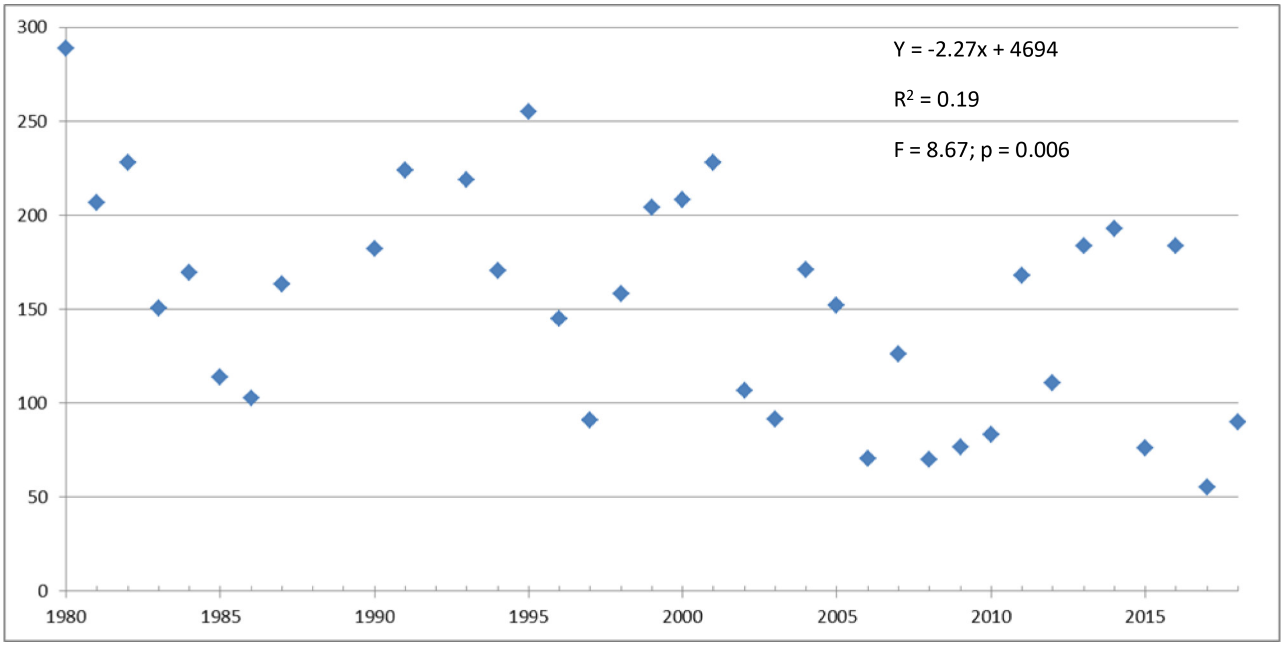


Figure 2.1. Combined May to August precipitation (mm) recorded at the Riske Creek weather station from 1980 to 2018. There is a significant trend ($p = 0.006$) in lower precipitation over time expressed by the slope coefficient (-2.27), constant (4694), and regression values ($F = 8.67$; $R^2 = 0.19$).

Site Selection

A post-hoc experimental design was created based on the division of the forest-grassland ecotone into four categories: 1. *Young Forests* are areas within the grassland benchmark that have become densely forested; 2. *Restored Grasslands* are within the grassland benchmark, had been covered with dense forest, but forest cover has been removed using grassland restoration treatments; 3. *Mature Forests* are forest stands outside the grassland benchmark but adjacent to grassland benchmark areas; and 4. *Stable State Grasslands* are grasslands within the grassland benchmark area that have not been affected by forest encroachment, and are adjacent to mature forest stands. Grassland restoration treatments occurred between 2007 and 2009. These treatments included winter cutting of stems, burning of excessive slash loads in an elevated steel container, and a low-severity prescribed burn in early spring.

Two-hectare plots were located in four representative examples of each of the four vegetation categories, for a total of sixteen plots. Potential sites were selected based on forest cover criteria using current and historical aerial imagery overlaid with the grassland benchmark layer. In the field, plots locations were selected from the potential sites by controlling for terrain (excluding steep slopes) and excluding riparian ecosystems. In order to ensure that stable state grasslands, restored grasslands, and young forest plots were historically grasslands, soils were inspected to confirm the presence of an Ah horizon meeting the soil colour and structure requirements of a Chernozemic soil. Mature forest plots met the conditions for a Luvisolic or Brunisolic forest soil (Soil Classification Working Group, 1998). Evidence of a grassland soil consisted of an Ah horizon at least 10 cm in depth and having a Munsell colour value darker than 3.5 when moist. The forest soils had an Ah horizon less than 10 cm in depth, with a Bm or Bt horizon. A map of the study area is included in Figure 2.2; a historical aerial photographs of part of the study area are included in Appendix 3.

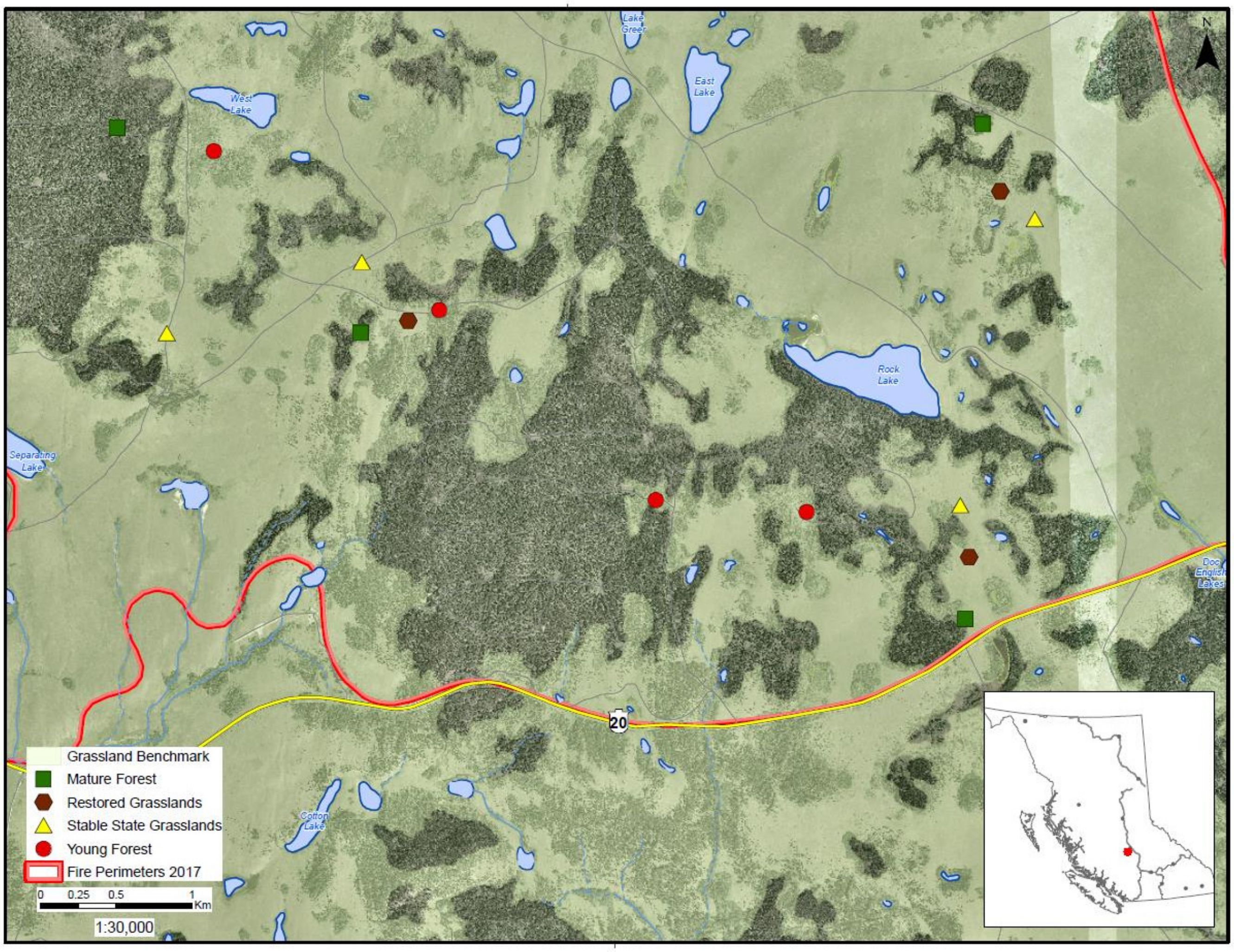


Figure 2.2. Study area with plots. The transparent green layer represents the extent of grasslands (the grassland benchmark) from 1962 aerial photography. The red/pink line denotes the area burned in the 2017 Hanceville wildfire. Red circles are young forest, yellow triangles are stable state grasslands, the brown hexagons are restored grasslands.

Field methods: Plant Communities

Within each replicate plot, vegetation and substrates were sampled using the Daubenmire (1959) method with sixty 50 cm x 20 cm frames randomly placed on five 50-metre transects (12 frames per transect). The cover class category of individual vascular plant and moss species was visually estimated in each frame, with categories representing 0-5, 5-25, 25-50, 50-75, 85-95, and 95-100% cover. *Peltigera* spp. was included with vegetation cover, with other lichens counted as part of the biological soil crust substrate. Other substrates measured for cover included litter, soil, rock, and wood. In forested plots, the tree layer was sampled using the point-centred quarter method (Cottam and Curtis 1956) for trees greater than or equal to 2 metres height. According to the point-centred quarter method, four quadrants were created by using a line perpendicular to the transect at each randomized sampling (centre) point. The distance to the closest tree in each quadrant from the centre point, tree species, and the stem diameter at breast height (DBH, at 1.3 m) were recorded. An image of the point-centred quarter method used is available in Mueller-Dombois et al. (2003). Vegetation was first sampled in the second week of July 2017 and re-sampled at the same transect locations in the second week of July 2018.

Field methods: Soil Moisture

Soil moisture heterogeneity was measured during spring (May 8-11) 2017, before the wildfire that burned the study area in late July 2017. A late-summer re-sampling was planned for 2017 was prevented by access restrictions due to extensive fire activity in and around the study area. Sampling was repeated after the wildfire in spring (May 8-11) 2018, and for a third time in late summer (August 20-23) 2018. Sampling was completed over three periods in order to measure temporal variability, and to detect the effects of wildfire on soil moisture heterogeneity.

Soil volumetric water content (soil moisture) was sampled *in situ* using a Decagon GS3 sensor (Decagon Devices, http://www.ictinternational.com/pdf/?product_id=253). The sensor uses an electromagnetic field to measure dielectric permittivity of the medium, measuring soil moisture in a 300 cm^3 area of influence around a sensor. Within each plot, soil moisture was measured at 30 points. Points were located at six randomized points on five 50 m long transects.

Measurements were taken horizontally at a depth of 10 cm from the mineral soil surface. At each point, a hole was dug by removing a clump of soil, and then a sensor was inserted into the sidewall of the hole at 10 cm depth. After measurement, the clump was pressed back into the hole for repeat measurements.

The spatial scales of measurement were carefully considered; 50 metre length transects were intended to capture the influence of clumps and gaps within the forest type. The small area of influence of the soil sensor (300 cm^3 or a radius of less than 4.2 cm) was selected to detect the fine level of variability that is important for growth of tree germinants and fine-rooted forbs and grasses.

Analyses: Vegetation

Each plot was used as a separate experimental unit. Species and substrate cover at each plot were calculated by averaging the mid-point of the 60 recorded Daubenmire cover class categories. Summaries of each ecosystem category were prepared by calculating the average cover of species and substrate from each plot. Species diversity was characterized by calculating unevenness of the community using Shannon's Diversity Index (H) (Shannon and Weaver, 1949), formulated by spreadsheet. Repeated measures analysis of variance was used to detect differences in the post-wildfire ecosystem conditions from pre-wildfire conditions for plant community and substrates. The variables tested include mean cover for leading species, plant functional groups, litter, and bare soil. Species and substrate values were log-transformed to normalize data for analysis.

Non-Metric Multidimensional Scaling (NMS) in PC-ORD v. 7, (McCune and Mefford, 2016) was used to: 1. Characterize the species composition of new grasslands and new forests along the forest to grassland ecological gradient; 2. Detect changes in the plant communities resulting from wildfire; and 3. Relate vegetation trends to environmental gradients and wildfire effects. The Bray-Curtis distance measure (Bray and Curtis, 1957) was used with 500 iterations in a 2-dimensional solution. A Monte Carlo test based on 250 randomized runs was used to determine the significance of the resulting matrix. Pearson correlations were used to find relationships between the ordination axes, species abundance, and environmental variables. Spearman correlation r values greater than 0.45 were reported. Successional vectors were used to show the change in plant communities one year after wildfire. Parametric statistics were completed in SPSS version 24.0 (IBM Corp. 2016).

Analyses: Soil moisture

A total of 1410 soil moisture observations were recorded: 16 plots x 30 measurements per plot x 3 sampling periods, minus one un-sampled missed plot in August 2018. As this missed plot was a mature forest, an average of the three mature forests plots for August 2018 were used for the missing data. Plots were analyzed as separate experimental units, each consisting of 30 soil moisture measurements per sampling period. The average soil moisture for each plot was calculated by using the mean of the 30 measurements. The coefficient of variation (CV), defined as the ratio of the standard deviation to the mean) of the 30 measurements was used to measure spatial variability in soil moisture for each plot. The CV was used as the measure of variability because it controls for the difference in mean soil moisture between plots and sampling periods. Repeated measures ANOVAs were used to determine the changes in mean soil moisture and heterogeneity of soil moisture (CV) over the sampling periods and between ecosystem categories.

Burn Severity

In August 2017, the level of burn severity on the ground was measured along vegetation transects using the line intercept method. Burn severity was separated into 5 categories: (0) fire did not burn all the way through vegetation and litter; (1) all vegetation and litter is burned to the mineral soil, plant and litter still present but blackened; (2) all vegetation and litter are completely consumed, leaving fine white ash; (3) Red coloured mineral soil indicating higher burn temperatures; and (4) Underground roots burned, leaving depressions. The transect distance of each plot (250 m total) was measured in cm with the sum of each category used as a plot total. Rock substrates were measured and subtracted from the total distance for calculating burn severity. Average burn severity for each plot was determined based on: sum of (burn severity category x distance/total distance of the plot). Heterogeneity of burn severity for each plot was calculated using the Shannon diversity index (H) (Shannon and Weaver, 1949), based on the plot total of each burn severity category

Results

Forest and Grassland Plant Communities

Summaries of vegetation cover for all plots are included in Table 2.2. A total of 83 species were observed and used in analysis of vegetation for each treatment. Axis 1 of the NMS ordination Axis 1 (Figure 2.3) is associated with the forest-grassland ecological gradient. Pearson correlation analysis of the abundance of individual species with this gradient (Table 2.3) shows that the forests are associated with *Calamagrostis rubescens*, *Vicia americana, Epilobium angustifolium*, *Pleurozium schreberi*, *Arctostaphylos uva-ursi*, *Lathyrus nevadensis*, *Lathyrus ochroleucus*, and *Eurybia conspicua*. Grasslands are associated with *Poa pratensis*, *Cerastium* *arvense*, *Hesperostipa curtiseta*, *Achnatherum richardsonii*, and *Potentilla hippiana*. The mature forests and stable state grasslands represent distinct plant communities rather than an ecological gradient considering there is little overlap in species composition between these types. Among the forest-associated species, only *Vicia americana* also occurred in the stable state grasslands. In the mature forests, native bunchgrass species represent 0.42% total cover and 1.2% as a proportion of total plant cover. *Poa pratensis* is the most abundant species in grasslands and also occurs in mature forests.

Restored grasslands and forest encroachment

The young forest plots had traces of forest and grassland associated species but were dominated by exotics. Remnants of native bunchgrass community were surviving under a forest canopy and combined with the presence of the forest-associated moss *Pleurozium schreberi*. The plots have trace levels of native bunchgrass species; an average of 3.6% cover compared to 23.7% cover found in stable state grasslands. There is 5.1% cover of the forest moss species, *Pleurozium schreberi*. The most abundant species in the understorey of young forest plots were the exotics grass *Poa pratensis* and the exotic forb *Tragopogon pratensis*. Native bunchgrass cover consisted primarily of *Achnatherum richardsonii* and *Achnatherum nelsonii*. There is an almost complete absence of grassland-associated *Hesperostipa curtiseta* in young forests, suggesting this species has low tolerance for forest conditions.

The restored grasslands appear in the same cluster as the stable state grasslands in the NMS analysis. Like stable state grassland, *Poa pratensis* is the most abundant species. There is an average 14.6% native bunchgrass cover, representing 29% as a proportion of vegetation, compare to 46.9% proportion in stable state grasslands. There is also similarity in composition of the native forb community. The forest-associated species *Pleurozium, Calamagrostis*, *Lathyrus* and *Eurybia* are not present. There are traces of *Arctostaphylos* present on some plots.

Table 2.2. Average species cover of plots recorded in 2017 and 2018. Due to wildfire evacuation, one young forest plot and one stable state grassland plot were not sampled in 2017. The plots were burned in a wildfire except one restored grassland and one stable state grassland plot.

Forested Plots			
2017			
Stable State N=4		Young Forest N=3	
Pleurozium schreberi	18.4	*Poa pratensis*	12.3
Calamagrostis rubescens	6	*Tragopogon pratensis*	7
Arctostaphylos uva-urs	2.5	*Pleurozium schreberi*	5
Peltigera spp.	1.4	*Achnatherum. richardsonii*	2.7
Poa pratensis	1	*Peltigera spp.*	1.5
Fragaria virginiana	0.7	*Achnatherum nelsonii*	0.8
Tragopogon pratensis	0.6	*Fragaria virginiana*	0.7
Polytrichum spp.	0.4	*Astragalus miser*	0.7
Rosa acicularis	0.4	*Juniperus communis*	0.5
Antennaria microphylla	0.4	*Galium boreale*	0.4
2018			
Stable State N=4		Young Forest N=4	
Calamagrostis rubescens	4.5	*Tragopogon pratensis*	15.4
Epilobium angustifolium	4.1	*Poa pratensis*	11.8
Tragopogon pratensis	1.3	*Epilobium angustifolium*	1.1
Pleurozium schreberi	0.8	*Achnatherum. richardsonii*	0.6
Poa pratensis	0.8	*Galium boreale*	0.6
Fragaria virginiana	0.5	*Achillea millefolium*	0.5
Lathyrus nevadensis	0.4	*Taraxacum officinale*	0.3
Taraxacum officinale	0.4	*Achnatherum nelsonii*	0.2
Galium boreale	0.3	*Geranium viscossisium*	0.2
Achnatherum. richardsonii	0.2	*Astragalus miser*	0.2

Table 2.2. Continued

Grassland Plots

2017			
Stable State N=3		Restored N=4	
Poa pratensis	18.5	*Poa pratensis*	19.6
A. richardsonii	14.4	*Achnatherum richardsonii*	10.2
Hesperostipa curtiseta	7.9	*Tragopogon pratensis*	4.7
Juncus balticus	1.8	*Hesperostipa curtiseta*	2.2
Antennaria microphylla	1.2	*Geum triflorum*	1.7
Cerastium arvense	0.9	*Achillea millefolium*	0.9
Potentilla hippiana	0.7	*Achnatherum nelsonii*	0.7
Tragopogon pratensis	0.7	*Geranium viscossisium*	0.7
Achillea millefolium	0.5	*Cerastium arvense*	0.7
Achnatherum nelsonii	0.4	*Solidago spathulata*	0.6
2018			
Stable State N=4		Restored N=4	
Poa pratensis	21.5	*Poa pratensis*	16.5
Achnatherum richardsonii	8.7	*Achnatherum. richardsonii*	5
Tragopogon pratensis	4.3	*Hesperostipa curtiseta*	4.1
Hesperostipa curtiseta	4.2	*Tragopogon pratensis*	3.4
Geum triflorum	1.3	*Achillea millefolium*	1.8
Achillea millefolium	0.8	*Astragalus miser*	1.1
Geranium viscossisium	0.7	*Achnatherum nelsonii*	1.1
Cerastium arvense	0.7	*Cerastium arvense*	0.6
Solidago spathulata	0.5	*Taraxacum officinale*	0.5
Potentilla hippiana	0.4	*Fragaria virginiana*	0.4

NMS Analysis

The NMS analysis including all plots (Figure 2.3) is statistically significant for Axis 1 (p=0.004) and Axis 2 (p=0.004). The final stress for the solution is 9.85. Axis 1 explains 74.5% of the variation, and the second matrix represents 16.3% of the variation. The two axes explain 90.8% of the variation in species composition.

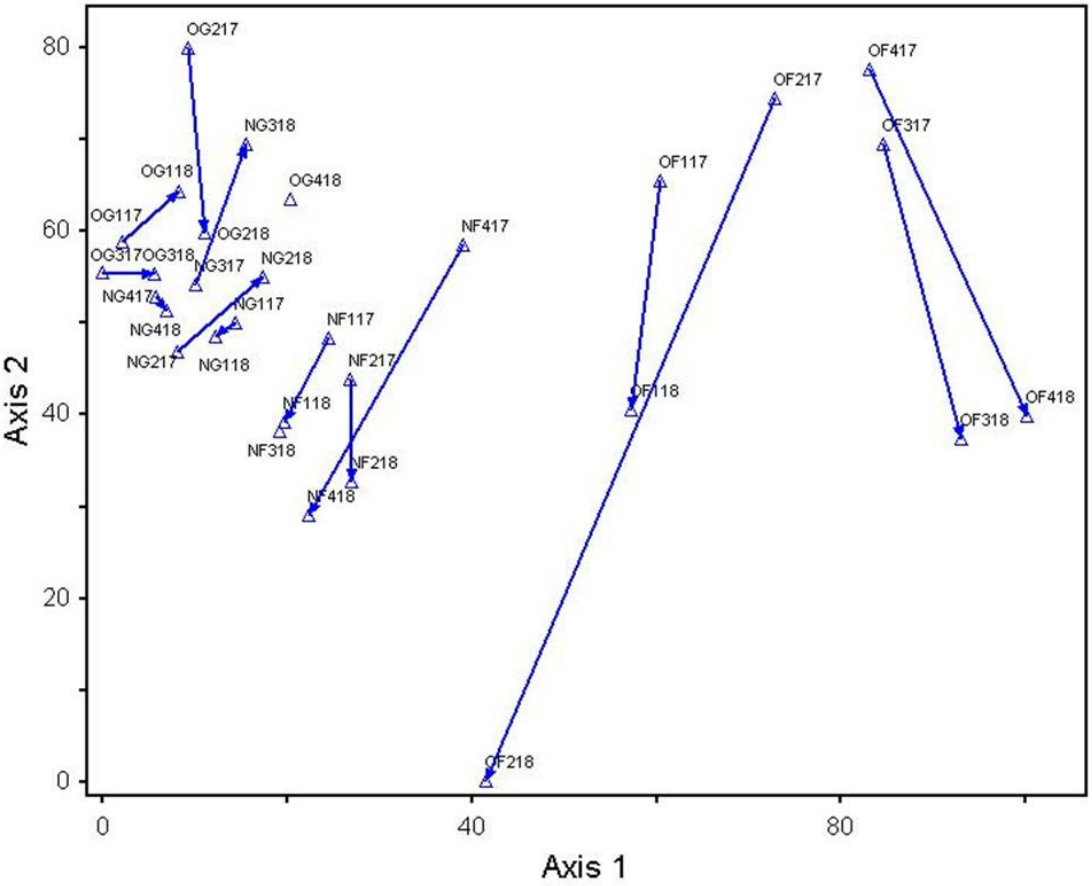


Figure 2.3. Nonmetric multidimensional scaling ordination showing of all plots. (a) the position of sites according to species composition; (b) labelled with plot category (OF = mature forest, OG = stable state grassland, NF = young forest, NG = restored grassland); and (c) vectors showing the change from pre-wildfire to post-wildfire along ordination axes. n=14 plots measured twice, and 2 plots measured once for a total of 30 plots; 83 species.

Table. 2.3. Pearson correlation of species associated with NMS ordination axes. Axis 1 species are associated with forests (+) or grasslands (-), while Axis 2 is associated with pre-wildfire (+) and post-wildfire species composition (-).

Species	Axis 1 (R^2 = 0.745)	Axis 2 (R^2 = 0.163)
Calamagostis rubescens	0.87	0.18
Poa pratensis	0.80	0.00
Vicia americana	0.61	0.00
Dracocephalum parviflorum	0.07	-0.60
Epilobium angustifolium	0.59	-0.32
Pleurozium schreberi	0.58	-0.45
Arctostaphylos uva-ursi	0.58	0.43
Cerastium arvense	-0.57	0.31
Lathyrus nevadensis	0.56	-0.21
Hesperostipa curtiseta	-0.56	0.28
Eurybia conspicua	0.55	0.20
Lathyrus ochroleucus	0.53	0.37
Tragopogon pratensis	0.25	-0.52
Achnatherum richardsonii	-0.47	0.36

Effects of Fire on plant communities

The change in species composition of forested plots is associated with consistent movement to the negative end of Axis 2 of the NMS ordination (Figure 2.3). Photographs of plant communities immediately after wildfire and one year after wildfire are included in Appendices 4 and 5. For the forested plots, wildfire caused a significant reduction in *Pleurozium* cover (p=0.000179). The negative end of the Axis 2 represents the post-wildfire forest condition, is associated with lower levels of *Pleurozium* (-0.45; Table 2.3). The Axis 2 post-wildfire forest condition was also associated with *Dracocephalum parviflorum* (-0.6), a native forb of the mint family that is dependent on fire for breaking seed dormancy (Van Veldhuizen and Knight, 2006). The results of repeated measures ANOVAs are included in Table 2.4.

Table. 2.4. Results of repeated measures ANOVA on cover values for environmental variables and leading species, before and after fire. Not all plots were available for before and after comparison because they did not burn or were not sampled in 2017. For native bunchgrasses and native forbs, the absolute value, and the proportion of the total vegetation cover (pr.) are compared. Forested plots consist of all plots with forest cover that were measured in pre-fire and post-fire condition. Grassland plots consist of restored grassland stable state grassland plots that were measured in pre-fire and post-fire condition. Thirteen of sixteen plots were analysed, as some plots were not sampled in 2017 due to wildfire.

	Combined Forests, n=7				Combined Grasslands, n=6			
	2017	2018	F	p	2017	2018	F	p
Native Bunchgrass	1.78	0.52	8.79	**0.025**	18.98	11.21	4.77	0.081
Native Bunchgrass pr.	0.052	0.026	1.74	0.235	0.38	0.32	0.493	0.514
Forbs	4.42	5.37	0.951	0.367	7.02	6.57	0.066	0.807
Forbs pr.	0.131	0.265	3.56	0.108	0.14	0.18	2.3	0.191
Diversity (H)	2.62	2.23	5.26	0.062	2.68	2.66	0.117	0.746
Litter	53.96	40.38	2.32	0.179	62.65	29.3	12.65	**0.016**
Bare soil	1.74	25.5	13	**0.011**	1.4	22.17	23.08	**0.005**
Tragopogon pratensis	3.25	7.22	2.6	0.158	2.67	1.75	2.74	0.159
Poa pratensis	5.83	5.48	0	0.998	19.08	14.18	2	0.216
Pleurozium schreberi	12.66	0.49	66.88	<0.001	0	0	NA	NA

Wildfire caused a significant increase in bare soil in grasslands (p=0.011) and in forests (p=0.005). Litter was reduced in grasslands (p=0.016), but an effect on litter was not detected in forests. This is likely due to post-wildfire needle shedding. In forests, there was a reduction in cover of native bunchgrasses (p=0.025), although this change was not significant when calculated as a proportion of total vegetation cover (p=0.235). There was not a significant change in native forb cover for forests or grasslands. There was not a significant change in cover of native bunchgrasses or native forbs in the grasslands.

There was a significant reduction in *Pleurozium schreberi* cover in young forests and mature forests. However young forest plant communities did not increase in similarity to either grasslands or mature forests. This result is reflected in the repeated measures ANOVA showing that total cover of native bunchgrasses were reduced in forests. The mature forest-associated species *Calamagrostis rubescens* was a trace species or not present on forest encroachment plots and did not increase with wildfire. The most abundant species on post-wildfire young forest plots were *Tragopogon pratensis* and *Poa pratensis* (Table 2.2).

Soil Moisture

Soil moisture conditions were recorded from each plot in May 2017, May 2018 and August 2018. The summer 2017 measurement was not recorded due to wildfire suppression activities. The mean soil moisture for each ecosystem category over three sampling periods is presented in Table 2.5 and shown in Figure 2.4. The grassland plots had higher soil moisture content than forested plots for the May 2017 sampling period following above-average precipitation conditions. Stable state grasslands had the highest soil moisture content followed by restored grasslands, forest encroachment, and mature forests. As drought conditions prevailed during the 2018 sampling, grassland soil moisture declined rapidly. Mature forests started with the lowest soil moisture in May 2017 but had the least change in soil moisture over the three sampling periods. At the sampling period in August 2018, mature forests had the greatest average soil moisture content.

Table 2.5. Mean soil moisture values (with standard deviation) for ecosystem categories over three sampling periods.

Category	May 2017	May 2018	August 2018
Stable state grasslands	33.17 (4.17)	23.24 (0.86)	12.04 (1.93)
Restored grasslands	31.85 (3.95)	26.18 (1.36)	12.40(2.1)
Young forests	29.61 (3.29)	30.74 (3.5)	12.79 (0.36)
Mature forests	24.17 (2.58)	27.33 (2.08)	15.21 (0.74)

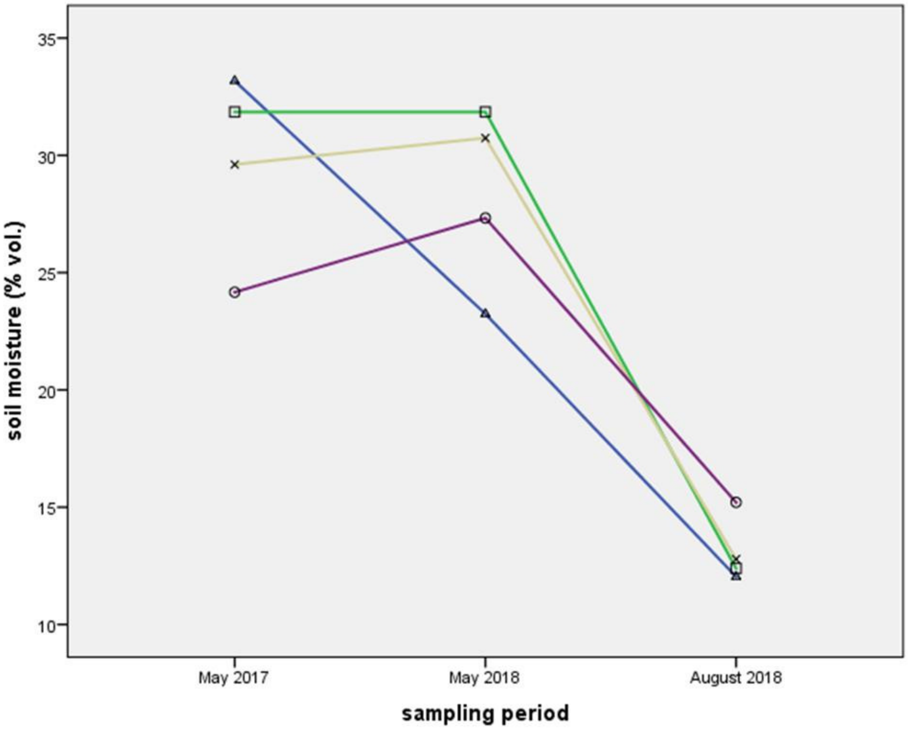


Figure 2.4. Mean soil moisture content over three sampling periods for: stable state grasslands (triangles), mature forests (circles), young forests (x's), and restored grasslands (squares). N=4 plots per type, with each plot value the mean of 30 measurements.

A repeated measures analysis of variance for average soil moisture content demonstrated a significant change in soil moisture over time (F = 238.58; $p < 0.001$), and a significant interaction effect between category and time (F = 9.43; $p < 0.001$). However, a post-hoc analysis did not detect significant differences among the four ecosystem categories, with p values ranging from 0.639 to 1.0. Therefore, to determine if soil moisture was greater in forests than grasslands, mean soil moisture content of all plots with forest cover (n = 8) was compared to combined restored grasslands and stable state grasslands (n=8).

The repeated-measures ANOVA results for mean soil moisture content comparing all of grassland plots to all forested plots are presented in Table 2.6. This analysis shows that there is a significant difference in soil moisture content over the three sampling periods ($p<0.001$), but that there is not a significant difference between the mean forest and mean grassland soil moisture content, p = 0.914. However, there is a significant interaction effect between the ecosystem categories and sampling period ($p<0.001$). An insignificant difference in mean soil moisture between categories, combined with a significant interactive effect over time, can occur when there is a crossover relationship between categories. This crossover relationship is shown on Figure 2.4, with stable state grasslands having high soil moisture content in May 2017, and lower soil moisture content than other categories for the May 2018 and August 2018 sampling periods.

Table 2.6. Results of repeated measures ANOVA of mean soil moisture over three sampling periods. Forested categories include combined encroachment forest and mature forest plots, grassland category includes restored grasslands and stable grasslands.

Mean soil moisture	F	Partial Eta squared	p
Sampling period	175.54	0.926	<0.001
Category x sampling period	14.57	0.51	<0.001
Between categories	0.012	0.001	0.914

The results of spatial variability in soil moisture content as expressed by coefficient of variation (CV) is presented in Table 2.7. The forested plots have greater spatial heterogeneity of soil moisture than grassland plots across the three sampling periods, with mature forests having substantially greater levels of heterogeneity than other categories. This relationship continues as mean soil moisture changes over time, and after wildfire.

Table 2.7. Mean coefficient of variation (CV; heterogeneity) of soil moisture for ecosystem categories over three sampling periods.

Category	May 2017	May 2018	August 2018
Stable state grasslands	0.089	0.0915	0.0948
Restored grasslands	0.09	0.111	0.0865
Young forests	0.163	0.12	0.17
Mature forests	0.208	0.167	0.232

Due to the large difference in spatial heterogeneity between ecosystem types, a repeated measures anova ananlysis for all four ecosystem categories was completed (Table 2.8), with post-hoc results presented in Table 2.9. The level of heterogeneity in soil moisture changes over time (p=0.039), and there is a significant interactive effect between category and sampling period (p = 0.017). However, the more significant results are found in the post-hoc analysis between categories, as shown in Table 2.9 and Figure 2.5. According to the post-hoc analysis, all categories are significantly different (p less than or equal to 0.001), except for stable state grasslands and restored grasslands, which have similar CV values, p=1. Over time there are susbstantial changes in soil moisture heterogeneity. However, the ranked relationship between young forests and mature forests is constant over the three sampling periods despite the differences in season and post-wildfire condition. Forested plots mainain greater heterogeneity than grasslands across the three sampling periods.

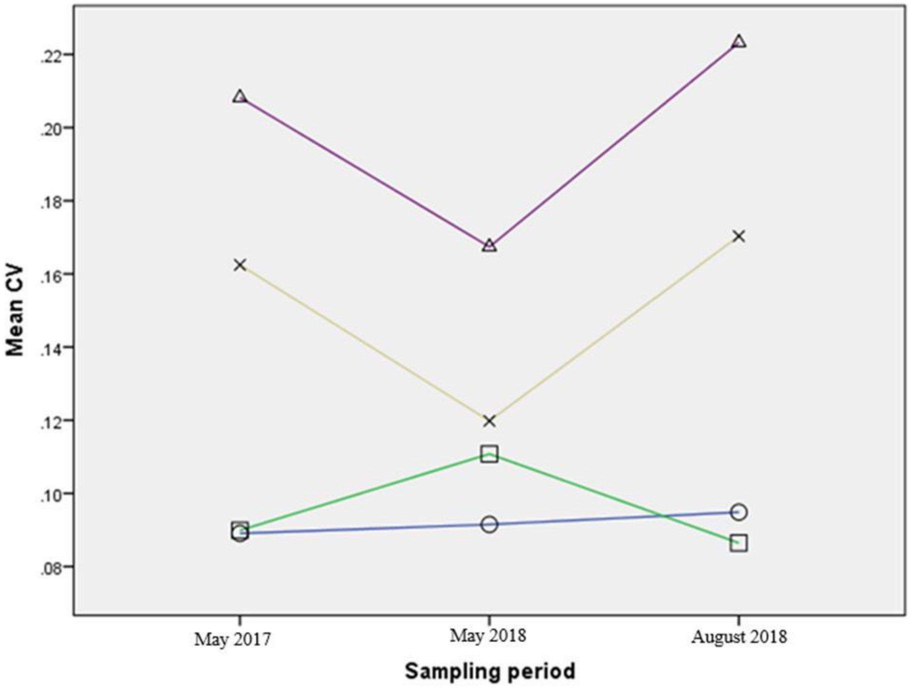


Figure 2.5. Mean coefficient of variation (CV; heterogeneity) of each ecosystem category over three sampling periods. Each category represents the average of four plots, with the CV of volumetric soil water content of 30 measurements in each plot. Triangle = mature forest, x = young forest, square = restored grasslands, circle = stable state grasslands.

Table 2.8. Results of repeated measures ANOVA for coefficient of variation (CV; heterogeneity) of soil moisture for four categories over three sampling periods.

Mean CV of soil moisture	F	Partial Eta squared	p
Sampling period	3.73	0.237	0.039
Category x sampling period	3.3	0.452	0.017

The more important results of homogeneity of soil moisture conditions are found in the post-hoc analysis in Table 2.9. The level of variability is significantly different for all plots, except for stable state grasslands and restored grasslands.

Table 2.9. Results of Bonferroni post-hoc analysis (p-values) for statistical significance of between category comparisons after repeated measures ANOVA for coefficient of variation (CV; heterogeneity).

Category	Stable State Grasslands	Restored Grasslands	Young Forest	Mature Forest
Stable State Grasslands	-	1	<0.001	<0.001
Restored Grasslands	1	-	<0.001	<0.001
Young Forest	<0.001	<0.001	-	0.001
Mature Forests	<0.001	<0.001	0.001	-

There is a difference in homogeneity of soil moisture resources over time and between vegetation types. The wildfire disturbance that occurred after the first sampling period did not change the overall relationship between the vegetation types. Figure 4 shows that mature forests had greater heterogeneity of soil resources over all sampling periods, despite large changes in mean soil moisture content.

Forest Cover, Substrates, and Wildfire Severity

Tree species density for forest categories are summarised in Table 2.10. *Pseudotsuga menziesii* is the leading tree species in all the mature forest plots, while the forest encroachment plots have a higher proportion of *Pinus contorta*. The mature forest plots have greater basal area and greater average DBH than encroachment plots. There is also greater variability in DBH for the mature forest plots due to the presence of overstorey and understory canopy layers. Differences in percent of canopy burned between plots is highly variable, with no relationship detected between category or any measure variable.

Table 2.10. Mean forest stand characteristics with standard deviation for mature forests and young forests. Percent burned is the average area burned per tree by height. Proportion of each tree species is by percent of total trees (> 2m height) recorded.

Category	DBH (cm)	Density, stem/ha	Douglas-fir	lodgepole pine	Aspen	Basal area, m^2/ha	% burned
Young Forests	7.95 (0.74)	1247.75 (505)	22.5 (26.7)	74 (23.8)	3.5 (6)	10.3 (5.2)	51.25 (38.7)
Mature Forests	16.1 (4.2)	712.25 (270.1)	85.875 (17.9)	7.5 (10.5)	7.6 (9.5)	20.5(2.7)	52.75 (36.2)

Ground-level burn severity is summarised in Table 2.11. There was higher burn severity and greater spatial diversity in severity in the mature forests than other categories. An example of high variability of burn severity in a mature forest is shown in Figure 2.6. Spatial variability and severity were similar between the forest encroachment and restored grassland categories. The stable state grasslands burn severity was highly contiguous and spatially uniform (Figure 2.7). This occurred despite the plots being distributed among forested plots that burned at various levels of severity. Field observations noted that the remnants of a forest humus layer increased the spatial variability of litter and burn patterns on the restored grasslands.

Table 2.11 Results for ground substrate burn severity using the line intercept method. The mean severity is based on the sum of each burn category divided by the total distance. The diversity is the Shannon's diversity index (H) is based on the proportions of each burn severity category. Plots that are not applicable (NA) fell outside the wildfire boundary due to a fireguard.

	Mature Forests		Young Forests		Restored Grasslands		Stable State Grasslands	
Plot	Severity	Diversity	Severity	Diversity	Severity	Diversity	Severity	Diversity
1	0.95	1.11	0.52	0.82	0.78	0.56	1	0
2	1.64	0.84	1.2	0.55	0.72	0.95	1	0
3	2.12	1.1	0.82	0.61	0.86	0.56	1	0
4	2.16	0.92	1.12	0.39	N/A	N/A	N/A	N/A
Mean	1.72	0.99	0.92	0.59	0.79	0.69	1	0

Figure 2.6. Mature forests burn severity was highly variable, sometimes following clump and gap patterns. This plot has areas categorized as non-burned (0), black ash (1), and white ash (3).

Figure 2.7. Stable state grasslands had low variability of burn severity and all fell within the black ash (1) category.

Despite the large differences in burn severity of the forest canopy (Table 2.10) and ground-level burn severity (Table 2.11), there were not large differences in soil moisture content or heterogeneity of soil moisture between lightly burned and severely burned forest plots.

Table 2.12 summarizes the litter cover of plots before and after wildfire. The highest litter cover before wildfire was in stable state grasslands (78.5%). Litter was significantly reduced in grasslands plots, but a significant effect was not detected in forests because of needle fall from burned trees. The post-fire litter cover in grasslands was reduced to a greater extent than cover estimates indicate, because ashy burned litter material was still counted as litter cover.

Table 2.12. Mean litter cover (with standard deviation) for plots before (2017) and after (2018) wildfire with standard deviation for plots that were measured before and after wildfire.

Year	Stable state grasslands	Restored grasslands	Young forests	Mature forests
2017	78.54 (6.72)	46.76 (10.11)	64.4 (5.61)	46.14 (4.14)
2018	26.76 (11.74)	31.83 (5.67)	40.83 (19.79)	40.04 (24.67)

Discussion

Forest and grassland associated plant communities are essentially mutually exclusive, having very little overlap in species composition. Therefore, the grasslands and forests of this region should be understood as a mosaic of adjacent but mutually exclusive patches rather than a continuous cline or gradient. Similarly, forests and grasslands are different in terms of spatial and temporal distribution of soil moisture, which is expected to be a driving factor in plant community assemblage in this water limited environment. In mature forests, burning caused a change in abundance of species that were present in before wildfire, but did not cause a directional change toward the grassland state. Burning did not change grassland plant communities in the year after fire, and small differences could be attributed to inter-annual variability in the plant community or slight differences in data collection. These results suggest that forest and grassland recovery are strongly influenced by belowground physical and biological legacies, in addition to effects of the aboveground physical structure in forests.

The Forest Legacy

Forest cover promotes the survival of seedlings through the canopy effect of moderating soil moisture conditions during drought. The study period of 2017-2018 occurred in severe drought conditions, with the lowest growing season rainfall recorded in over 30 years. After the first soil moisture sampling period in May 2017, forested plots were burned at various levels of severity in a wildfire that occurred under drought conditions and high summer temperatures. During drought conditions, mature forests had greater soil moisture content than other plot categories. However, a post-hoc analysis did not find the differences to be statistically significant, likely because of low sample size ($n = 4$). Analysis of combined forested and grassland plots demonstrated that drought was moderated on forested plots including after wildfire. While all forested plots had greater spatial variability in soil moisture content than grassland plots, mature forests had substantially greater levels of variability than encroachment forests. This suggests that structural attributes of mature forests such as larger diameter and taller trees, multiple canopy layers, and large-diameter dead wood and snags create greater spatial heterogeneity in soil moisture resources. Furthermore, the 2018 post-wildfire sampling periods indicate that heterogeneous soil moisture conditions persisted after various levels of fire severity, one year after the fire disturbance. It is possible that in the more severely burned forests ecosystem legacy effects could be reduced over time. However, it is expected that post-fire soil moisture conditions will contribute to survival of tree seedlings and re-establishment of the forest canopy.

In mature forests, *Calamagrostis rubescens* (pinegrass) was slightly reduced in the first year after wildfire but became the leading understorey species due to the greater reduction in cover of other species. In interior Douglas-fir forests, *Calamagrostis* recovers by 2-5 years after fire disturbance (Stark et al., 2006; Bassett, 2019). The species is well adapted to surviving wildfire in forests due to its strongly rhizomatous growth form and prolific post-fire disturbance seed production. It was noted in post-wildfire observations that even within high severity areas of the wildfire, *Calamagrostis* rhizomes survived in small patches of lightly or moderately burned forest floor. It is expected that *Calamagrostis* rhizomes will spread from these patches to re-colonize the area. Although *Calamagrostis* does not typically produce inflorescences and seeds while growing under a forest canopy, fire disturbance and open conditions causes an increase in flowering and seed production (Dobb and Burton, 2013). Seed production combined the increased bare soil substrate also likely contribute to the spread of pinegrass.

The largest effects of fire on forested plots were a significant reduction in *Pleurozium schreberi* cover. The plant community expected for level to gently sloping sites for the IDFxm subzone is expected to be a Pinegrass (mean cover 7-15%) – and Feathermoss (mean cover >15%) plant community, with cooler aspects having a greater abundance of feathermoss (Steen and Coupe, 1997). Feathermoss is susceptible to fire-related mortality because it is highly flammable during dry spells and it lacks connection to the soil substrate (Tesky, 1992). *Pleurozium* re-established to pre-fire conditions after 90 years in a study in the eastern boreal forest (Foster, 1985), and is associated with late successional stages in the boreal forest of Alaska (Mack et al., 2008), and the hemi-boreal forests of Europe (Marozas et al., 2007). In this study, the significant loss of *Pleurozium* cover at all levels of burn severity indicates that fire spreads through this moss layer while missing adjacent patches of grasses and forbs. Considering that the historic fire return interval for dry Douglas-fir forests of this region averages approximately 20 years (Wong and Iverson, 2004) to 25 years (Harvey et al., 2017), it is likely that the high levels of pre-fire *Pleurozium* cover were outside the historical range of variability. Therefore, the wildfire-induced reduction in *Pleurozium* followed by dominance of *Calamagrostis* may represent a return to historical dry forest understorey conditions.

The Grassland Legacy

Average soil moisture of restored and stable-state grasslands was greater than soil moisture of forested plots at the first sampling period in May 2017. This sampling period followed an above-average level of precipitation for April 2017 and for the preceding year of 2016. Subsequently, drought conditions set in and grassland soil moisture content remained below forest soil moisture content for the May 2018 and August 2018 periods. There was low spatial heterogeneity of soil moisture in grasslands, with a relatively even distribution of soil moisture resource within plots. The higher soil moisture content of grasslands during cool and wet conditions is likely due to the absence of precipitation interception and other effects provided by a forest canopy. The relatively even distribution of soil resources is related to the relatively even distribution of vegetation, fine roots of grasses, and litter. The more severe drought conditions that occur in grasslands could result from lack of shading from the canopy, as well as higher transpiration rates associated with the high concentration of grass roots near the soil surface (James et al. 2003).

There is evidence that cycles of wet conditions and high biomass production followed by dry conditions and intense drying contribute to the high-frequency fire regime in the grasslands. Grassland fires of the Cariboo region have been linked to inter-annual climate variability

(Harvey and Smith, 2017). The compilation of weather data from Riske Creek confirms that there is a high level of inter-annual variability in growing season precipitation. Grassland aboveground net primary production increases with greater precipitation of the current year, as well as the preceding year (Yang et al., 2008). Furthermore, the low spatial variability of soil moisture resources in grassland soils contributes to relatively uniform levels of productivity and a continuous layer of cured vegetation and litter during drought conditions. The cool-season native bunchgrass species of interior British Columbia survive intense drought conditions by entering a dormant stage (Gayton, 2013). These conditions contribute to a spatially continuous layer of cured (dormant) vegetation and litter thatch across the grasslands during dry conditions. Spread of fire in grasslands is limited by connectivity and accumulation of fine fuels (Krawchuk and Moritz, 2011), and fire history reconstruction of the region demonstrates a relationship between buildup of fine fuels and grassland fires (Harvey et al., 2017; Harvey et al., 2018). Stable-state grasslands had greater pre-fire litter cover than all other vegetation types, as well as the most severe drought conditions. These conditions contributed to the spatially continuous distribution and spread of fire across the mature grasslands.

The Hanceville wildfire of 2017 is likely the first landscape-scale grassland fire in the region since Strang and Parminter (1980) reported the cessation of grassland fires at nearby Dester Ridge (11 km west of this study area) in the 1920s. Similarly, Harvey et al. (2017) reported on the cessation of frequent grassland fires in the late 19th century at Churn Creek (approximately 60 km south of the study area). In 2017, wildfire reached the grasslands at Dester Ridge and Churn Creek, as well as the grasslands of the study area at Riske Creek. This is an indication that despite an approximately 100-year absence of frequent fire from the grassland landscape, the soil legacy of resource patterns and plant propagules can support spatially continuous grassland fires. A high frequency, spatially continuous disturbance regime historically prevented the encroachment of forests on grasslands within the Interior Douglas-Fir biogeoclimatic zone.

Native bunchgrass species are a major component of the restored grasslands plots, as well as a remnant under forest cover on grasslands. Native bunchgrasses were not significantly reduced in burned grasslands. However, wildfire caused a significant reduction in native bunchgrasses under young forests. These results are likely due to substrates; bunchgrasses within moss and humus layers in the forest are susceptible to fire due to the root systems being above the mineral soil, while the rhizomatous growth form of *Calamagrostis* could be an adaptation to surviving fire disturbances in forest substrates. The grassland restoration treatments mechanically removed the forest canopy and reduced the moss and humus components with a low-severity prescribed burn. The low-severity disturbances of the treatments likely reduced mortality of the remnant bunchgrass plants, over time resulting in recovery of the bunchgrass component close to the levels observed in stable state grasslands. These results suggest that grassland restoration treatments can be used to restore grassland legacies existing in the understorey of young forests.

Land-Use Legacies

Species composition of grassland ecosystems has been altered by livestock grazing and altered fire regimes, while the age distribution, structure, and stem density of Douglas-fir forests have been altered by logging and fire suppression (Dawson,1996; Lemay et al., 2009; Harvey et al., 2017). In the grasslands, the presence of the exotic grass *Poa pratensis* indicates a past history of heavy grazing; the species is known to be persistent decades after more sustainable grazing practices or grazing exclusion are introduced (Sinkins and Otfinowski 2012; White et al., 2013; Dekeyser et al., 2015;). However, distinct patterns of spatial and temporal distribution of soil moisture, as well as native plant species associated with forests and grasslands are present before and after a wildfire that occurred under severe drought conditions. Therefore, it appears that these ecosystems have maintained the capacity to recover after wildfire disturbances, despite existing land use legacies. In the case of restored grasslands, native bunchgrass communities recovered to a large extent, 10 years after restoration treatments. Remnants of forest humus and litter were also present in restored grasslands. The burn severity of the remnant forest humus patches was more variable than burn severity in grassland litter, resulting in greater overall variability of burn severity than in stable-state grasslands. The removal of these last forest remnants in the 2017 fire event may restore grassland-associated patterns of fire disturbance in the future.

The overwhelming presence of exotic species in young forests indicates they are essentially an anthropogenic land use legacy resulting from fire suppression, livestock grazing, and species introductions of the past ~100 years. In young forests, the wildfire reduced the leading forest moss species *Pleurozium schreberi*, as well as grassland-associated native bunchgrasses, leaving a post-wildfire ecosystem dominated with the exotic species *Tragopogon pratensis* and *Poa pratensis* (mean 84% exotic species as a proportion of vegetation cover). *Tragopogon* is well adapted to the young forest habitat because it is a prolific seed producer (Qi et al., 1996), and its seeds germinate and survive on a wide variety of substrates including litter and plant substrates (Gross and Werner 1982, Gross 1984). *Poa pratensis* is a relatively shade tolerant (Lin et al., 1998) mesic ecosystem specialist (DeKeyser et al., 2015; Printz and Hendrickson, 2015), and is more abundant than drought-adapted native bunchgrasses in the cooler and shaded microclimate of the young forests. The absence of pinegrass in young forest could be a result of absence of fire-induced seed production, or lack of substrate conditions suitable for germination. The presence or absence of soil legacies not measured in this study, such as seed banks, propagules, and grassland-associated or forest-associated mycorrhizal communities may have also limited establishment of forest-associated plant communities in young forests.

Young forests moderated drought conditions and reduced soil moisture in the cool-wet period. Although young forest spatial heterogeneity of soil moisture is significantly greater than found in grasslands types, it is significantly lower than in mature forests. There is a large difference between young forest and mature forest spatial heterogeneity, suggesting that structures supporting the mature forest-imposed levels of spatial heterogeneity take long periods of time to develop. The species composition of tree species in the young forests is also different than in mature forests, with a greater proportion of *Pinus contorta*. This is likely a result of seedling survival in the grasslands due to greater tolerance to frost. Growing season frost causes mortality of *Pseudotsuga* seedlings in large openings, with thermal cover provided by forest canopy improving seedling survival (Steen et al., 1990). Therefore, in parts of the Cariboo region, cold-tolerant *Pinus contorta* seedlings have greater survival rates than *Pseudotsuga* seedlings in open cutblocks (Reich et al., 1993). Considering that *Pseoudotsuga* has greater drought tolerance than *Pinus contorta*, young forests may be more susceptible to drought-associated mortality than mature forests.

Conclusions

Post-wildfire ecosystem legacies include spatial and temporal patterns of soil moisture, and the propagules of forest-adapted and grassland-adapted species. It is expected that these and other legacies will promote the re-organization and recovery of forest and grassland plant communities after wildfire and other disturbances. Differences in soil conditions suggest that ecological memory, defined as "the totality of information and material legacies" (Jogieste et al., 2017), developed over long periods of time in both grasslands and forests, and provides a source of resilience for each of these ecosystem states.

In a case of afforestation of grasslands in Europe, Kimberley et al. (2019) demonstrated that species' rates of extinction and colonization vary between species and habitats. In the Kimberley et al. (2019) analysis, afforestation caused the loss of grassland species, but forest species did not colonize at the same rate as the species lost. Similarly, the reproductive and dispersal characteristics of understorey forest species may have prevented their colonization of young forests in this study. On the *Festuca hallii* prairie (rough fescue) of Manitoba, the removal of tree plantations from historical grassland areas did not result in the return of rough fescue 20 years after tree removal treatments (Coffey and Otfinowski, 2018). The Coffee and Otfinowski (2018) result contrasts from the results of this study where leading native grassland species did re-colonize areas where young forests were removed. Therefore, the ability of a plant community to become established or to re-establish may depend on the characteristics of the individual species and local conditions.

It is unlikely the historical landscape experienced frequent regime shifts between forest and grasslands states. As the climate associated with the bunchgrass biogeoclimatic zone is projected to shift into dry forest zones (Hamann and Wang, 2006), ecosystem legacies will provide some resilience for forests to resist a permanent regime shift to a grassland state. However, there is uncertainty regarding the maximum levels of climate change and disturbance severity that will still allow forest ecosystems to re-organize. Analysis of the Riske Creek weather station data shows that there is already a downward trend in growing season precipitation, which may already have affected productivity and disturbance regimes. Further, the establishment of young forests on benchmark grasslands did not result in levels of soil moisture heterogeneity, forest cover heterogeneity, or plant communities associated with mature forest. Similarly, the long-term loss of mature forest cover may not result in the rapid establishment of grassland associated plant communities. Young forests on the grassland benchmark (historical grassland areas) can be restored to grassland conditions with ecosystem restoration treatments. Management of the forest-grassland mosaic should focus on restoring historical patterns of resource distribution and disturbance regimes.

CONCLUSIONS AND RECOMMENDATIONS

Grassland plant communities

The baseline characterization of grasslands on an elevation gradient provides direction for management and research. The upper grasslands have high productivity in comparison to low and middle elevation grasslands, manifested in greater vegetation and litter cover levels. In recent years there have been efforts to reintroduce prescribed burning to the grasslands, and it is likely that the practice will become more common. The reintroduction of fire can be used to prevent the establishment of trees on grasslands. Livestock grazing occurs to various levels and frequencies on virtually all grasslands of the Cariboo-Chilcotin. Therefore, maintaining litter and plant cover levels that will carry prescribed fires and support livestock grazing will be focus of management. Consequently, research should focus on prescribed burning and grazing practices that will maintain healthy native plant communities.

Attaining knowledge on the autecology of leading species will be a key step in managing for greater abundance of native bunchgrasses in the upper grasslands. An important species trait of interest is the response to presence of litter. Litter accumulation drives grassland plant community composition via leaf traits (Letts et al., 2015). Litter can form a dense thatch in the upper grasslands, and litter cover levels can be manipulated through grazing and burning. Hilger and Lamb (2017) found that grassland productivity peaks at an intermediate amount of litter. A second important autecological trait is the response of species to defoliation at various levels of severity, timing, and frequency. Defoliation studies have contributed to management of native grasslands of other regions (e.g., MacLean and Wikeem, 1985). There is an absence of literature on the effects of defoliation for leading native grasses of the upper grasslands in the Cariboo-Chilcotin (particularly *Achnatherum richardsonii* and *Hesperostipa curtiseta*). Finding the effects of litter cover and defoliation on key species will provide information on optimal frequency and severity of grazing and prescribed burning. Too frequent or severe defoliation and litter removal can result in reduced species richness (Bai et al., 2001), increased bare ground cover and soil erosion (Facelli and Pickett, 1991), more severe drought conditions (Deutsch et al., 2010), and reduced grassland productivity (Willms et al., 1986; Zhang and Romo, 1994). The exotic cool-season *Poa pratensis* is the leading species in the upper grasslands, and ~30 years of grazing exclusion has not reduced its abundance. *Poa pratensis* is known to have a competitive advantage in situations where there is frequent defoliation (Tannas, 2011), and where there is excessive litter cover (Bosy and Reader, 1995). Intermediate levels of disturbance may create competitive advantages for native grass species and contribute to reduced cover of *Poa pratensis*.

The low soil organic carbon content of sub-humid grassland soils in comparison to other sub-humid grassland regions is a topic of interest. Isolating the covarying effects of plant community and climate on soil organic carbon has been a challenge for regional scale studies. The Cariboo-Chilcotin sub-humid grasslands present a unique situation in having lower soil organic carbon than sub-humid climate grasslands of other regions. The lower than expected organic carbon levels may be attributed to species composition that includes leading grass species that are normally considered early- to mid-seral, and perhaps less productive than late seral grasses of other regions. Historical overgrazing may also be a factor in the lower than expected soil organic carbon content. Comparative studies on productivity of fine roots between species of the Cariboo-Chilcotin and leading species of other sub-humid grasslands may provide new insights in soil organic carbon accumulation. Researchers may also experiment with introduction of higher productivity grass species and measure inputs of litter and organic carbon to the mineral soil.

In lower grasslands, biological soil crusts (BSC) cover the large inter-plant spaces that result from low productivity and the bunchgrass growth form of leading species. BSC cover data was excluded from analysis of this study because the Daubenmire (Daubenmire, 1959) cover class method was found to be inaccurate in measurement of BSC as total substrate and species levels abundance. Future research on measuring abundance of BSC species may obtain more accurate results using a point-based method (e.g., as described by Booth et al., 2006), as it would be more appropriate for the size and spatial distribution of the crust species. The diversity of BSC species and their potential contribution to soil nitrogen content in the Cariboo Chilcotin region has been described (Marsh et al., 2006; Caputa et al., 2013). However, there are gaps in knowledge on the links between BSC and grassland productivity, the effects of various grazing practices on BSC, effects of burning on BSC, and the potential links between mycorrhizal fungi to BSC species and vascular grassland species. BSC cover has also been demonstrated to reduce the germination rates of exotic annual grass *Bromus tectorum* in semi-arid ecosystems (Deines et al., 2007). An investigation into the role of BSC in controlling the spread of *Bromus tectorum* in the Cariboo-Chilcotin region may provide valuable information. Finally, the use of fungal pathogens for biological control to prevent the spread of *Bromus tectorum* (Meyer et al., 2008) is also a topic of interest.

The Forest and Grassland Mosaic

The "grasslands benchmark area" is a demarcated area of grassland ecosystem and is the central policy to protect grasslands from forest encroachment (Cariboo-Chilcotin Grasslands Strategy Working Group, 2001). The grassland benchmark represents the extent of grasslands based on the earliest available aerial imagery, which dates from the 1960s to 1970s (Steele et al., 2007). Ecosystem restoration treatments can be used to remove forest encroachment within the benchmark, and provincial re-forestation obligations are not attached to logging activities (British Columbia CORE, 1995). The concept of the grasslands benchmark as a delineated area with an abrupt grasslands boundary is supported by measurement of conditions on the ground. There is very little overlap in species composition between adjacent forests and grasslands. Encroachment of forest cover on the grassland benchmark has not resulted in the establishment of mature-forest-associated plant communities. Therefore, the grassland-forest boundary should be considered representative of boundaries in a complex mosaic rather than a continuous ecotone.

Leading species in young forests were exotic *Poa pratensis* and *Tragopogon pratensis.* Removal of young forests on the benchmark area resulted in the re-establishment of native grassland communities, although with high cover values of *Poa pratensis* (like the baseline condition in adjacent grasslands). In mature forests, pinegrass was present before wildfire, and was the leading species re-established after wildfire. In terms of silviculture, pinegrass is often considered a nuisance species as it may compete for moisture with conifer plantations. After logging and wildfire, efforts are made in reducing pinegrass abundance using herbicide and mechanical treatments (Simard et al., 1998; Swift and Turner, 2004). The policy of removing pinegrass should be reconsidered; after wildfire, pinegrass was the most important species for reducing bare ground cover in mature forests. Pinegrass may play a role in reducing soil erosion, capturing nutrients, and contributing organic matter to burned soils. The importance of pinegrass as forage for livestock is well known (MacLean et al., 1969; MacLean, 1972), but its ecological role as dominant species in dry forests of interior British Columbia has not been recognized by researchers and resource managers.

Mature forests had greater heterogeneity of soil moisture than grasslands or young forests. Grasslands had spatially homogenous soil moisture and experienced the highest average and lowest average soil moisture conditions over the study period. Soil moisture conditions of young forests were intermediate between grasslands and mature forests, with heterogeneity being more like grasslands. The high spatial heterogeneity of soil moisture was measured in mature forests before and after wildfire. Several studies have linked structural diversity to successful regeneration in Douglas-fir forests. There was greater variability in stem density and stem size in mature forests than young forests. Therefore, soil moisture heterogeneity in mature forests may result from greater structural heterogeneity in than found in encroachment forests.

As the climate is projected to become warmer and drier (Hamann and Wang, 2006), creating heterogeneity in forest stand structure may be a strategy for maintaining recruitment of trees. Interior Douglas-fir (*Pseodotsuga menziesii var. glauca*) is shade tolerant, (Klinka et al., 2000) (unlike Coastal Douglas-fir, *Pseudotsuga menziesii var. menziesii* which is shade intolerant) (Drever and Lertzman, 2001). The forest canopy reduces understorey drought conditions through buffering of air and soil temperatures (Simard, 2009). However, interception reduces the amount of precipitation that reaches the soil directly beneath forest the forest canopy (Pypker et al., 2005). Simard (2009) has hypothesized that edges of canopy gaps and edges of the dripline of mature trees are zones of regeneration due to a balance of shading and precipitation throughfall. Lemay et al. (2009) found that in dry interior Douglas-fir forests, tree regeneration was densely clustered near large diameter trees, and the clustered pattern of regeneration was likely due to higher moisture microsites. In the same study, there was high mortality of small trees (<7 cm dbh) due to competition in these dense patches of regeneration. Therefore, a strategy in recruiting healthy trees into the canopy may include protecting large diameter trees while using low-severity prescribed burns or mechanical treatments to reduce stem density in regenerating patches and to create or maintain canopy gaps. Lemay et al. (2009) and Simard (2009) associated patches of Douglas-fir regeneration with large trees and canopy gaps, while this study associated greater soil moisture heterogeneity with mature forests. The ecological processes that caused the patches of more favourable soil moisture conditions were not measured directly. A high level of soil moisture heterogeneity persisted after a severity burn, indicating that standing dead trees (and possibly other forest legacies) continue to contribute to higher moisture microsites one year after the fire disturbance. However, the period that these greater heterogeneity conditions will persist is not known; in summer 2018, many dead trees still had needles and the shading effects may be reduced with needle fall. Where there is greater distance to live trees, seed dispersal may be a limiting factor. Due to the large areas burned in 2017 and 2018, there are opportunities to study the effects of standing dead trees and other forest legacies on forest regeneration. Also, studies should aim to identify how particular forest attributes create the soil moisture conditions that permit the growth of tree seedlings during drought. Variables of interest include canopy gap size, tree height, light conditions, density, stem flow, presence of veteran trees, and precipitation interception and throughfall.

In the in the 2017 wildfire, surface cover in mature forests burned at the highest severity and had the greatest variation (diversity) of burn severity. Dendrochronological studies have found that interior Douglas-fir forests historically burned at various levels of severity, but that the high severity burn patches were limited in area by heterogeneity of stand structure and topography (Heyerdahl et al., 2007; Heyerdahl et al. 2012; Harvey et al. 2017). In mature forests, some large high-severity burn patches were likely outside of the historical range of variation. Dry Douglas-fir forests should be managed for lower stem densities and heterogenous patterns of clumps and gaps in order to prevent the spread of high-intensity wildfires (Harvey et al., 2017).

There are several lines of evidence that ecological legacies will prevent the rapid shifting between grassland and forest ecosystem states. Evidence includes: the failure of mature forest-associated plant communities to establish in young forests, the re-establishment of grassland plant communities in restored grassland, and the re-establishment of forest-associated communities in mature forests after wildfire. Legacies that prevent change between states may include soil characteristics associated with forests and grasslands, remnant forest floor and stand structure in burned forests, the presence of plant propagules, and soil mycorrhizal communities, among others. Although climate change altered disturbance regimes are expected to expand the extent of grasslands (Hamann and Wang, 2006; Seidl et al., 2017) managing for changes in ecosystem state should be considered carefully. First steps may include experimental treatments on small areas and recording long term ecological trends.

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APPENDIX 1

Range Reference Areas (RRAs) and associated information included year of exclosure construction and plot layout (created), elevation (m), climate category, grassland plant community type, and location in decimal degrees. Soil samples were collected from bolded RRA's. SA = semi-arid, DSH = dry sub-humid, MSH = moist sub-humid.

Range Reference Area	created	elevation (m)	climate	type	location
Lower Sheep	1997	436	SA	lower	51.230, -122.160
Middle Sheep	1997	445	SA	lower	51.234, -122.160
Cavanagh	1997	468	SA	lower	50.982, -121.900
Hartman Flats	1997	511	SA	lower	51.271, -122.193
Big Sage Farewell	**1986**	**515**	**SA**	**lower**	**51.824, -122.546**
McGhee Flats	1997	518	SA	lower	51.337, -122.253
Deer Park	1990	548	SA	lower	51.887, -122.348
Whaleback	1997	577	SA	lower	51.243, -122.153
Farwell Needlegrass	**1986**	**592**	**SA**	**lower**	**51.832, -122.547**
Fraser North Eagle Tree	**1997**	**641**	**DSH**	**middle**	**51.457, -122.273**
Empire Valley	**1994**	**668**	**DSH**	**middle**	**51.473, -122.277**
Toosey	**1921**	**905**	**DSH**	**middle**	**51.950, -122.495**
Cotton Lake	**1995**	**940**	**MSH**	**middle**	**51.951, -122.478**
Airport flats	1997	950	MSH	middle	51.435, -122.285
Cotton Ranch Corrals	1995	956	MSH	upper	51.944, -122.424
Loran C	**1995**	**966**	**MSH**	**upper**	**51.986, -122.396**
Rock Lake	**1963**	**969**	**MSH**	**upper**	**51.981, -122.426**
Mile 35	1995	978	MSH	upper	51.873, -122.529
Sheep Point	1997	1016	MSH	upper	51.329, -122.281
Cow Lake	1990	1036	MSH	upper	51.762, -122.658
Greenfield W	1986	1056	MSH	upper	51.880, -122.806
Sting and Vert	**1988**	**1066**	**MSH**	**upper**	**51.652, -122.163**
Greenfield S	1986	1067	MSH	upper	51.880, -122.760
Wineglass Big B	1987	1102	MSH	upper	51.898, -122.609
Vert Lake	**1996**	**1114**	**MSH**	**upper**	**51.622, -122.190**
Greenfield N	1986	1142	MSH	upper	51.893, -122.760
Bald mtn. Holding Ground	**1995**	**1155**	**MSH**	**upper**	**51.926, -122.589**
Breeding pasture N	1986	1190	MSH	upper	51.908, -122.726

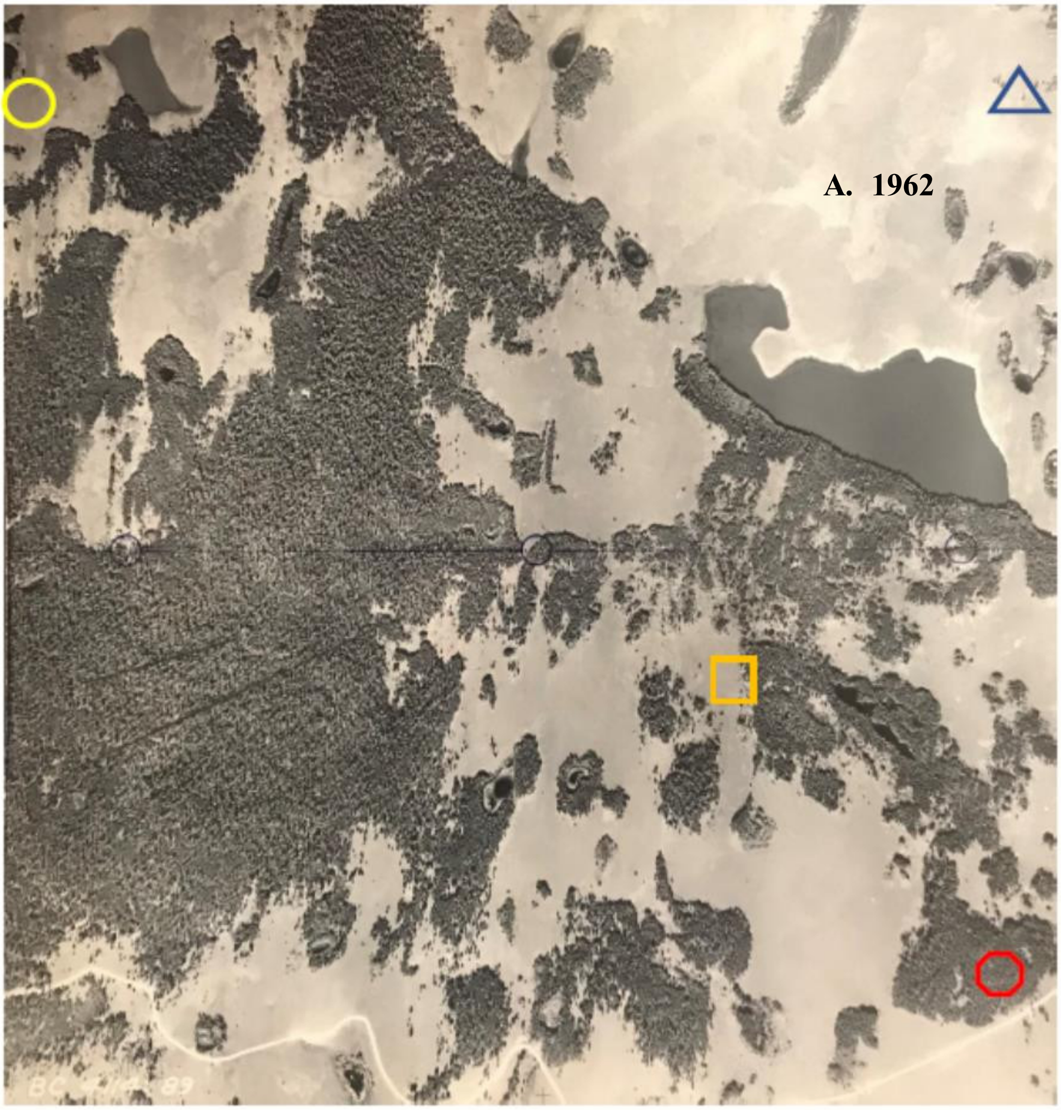
APPENDIX 2

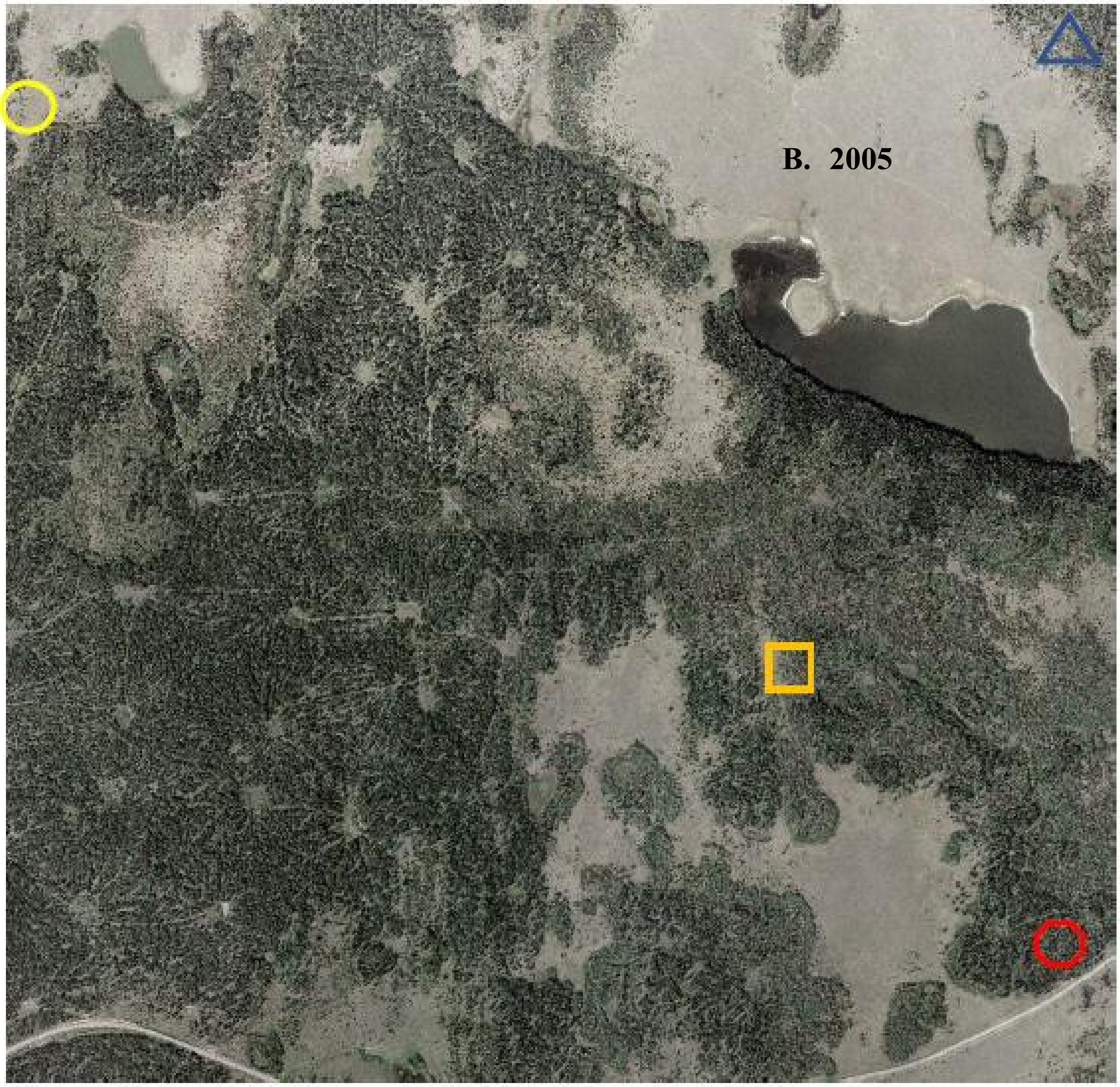
Morphological descriptions of pedons from the Cariboo-Chilcotin grasslands. Colour values are recorded as moist. Pedon data was accessed from the RRA database, BC Ministry of Forests, Lands and Natural Resource Operations.

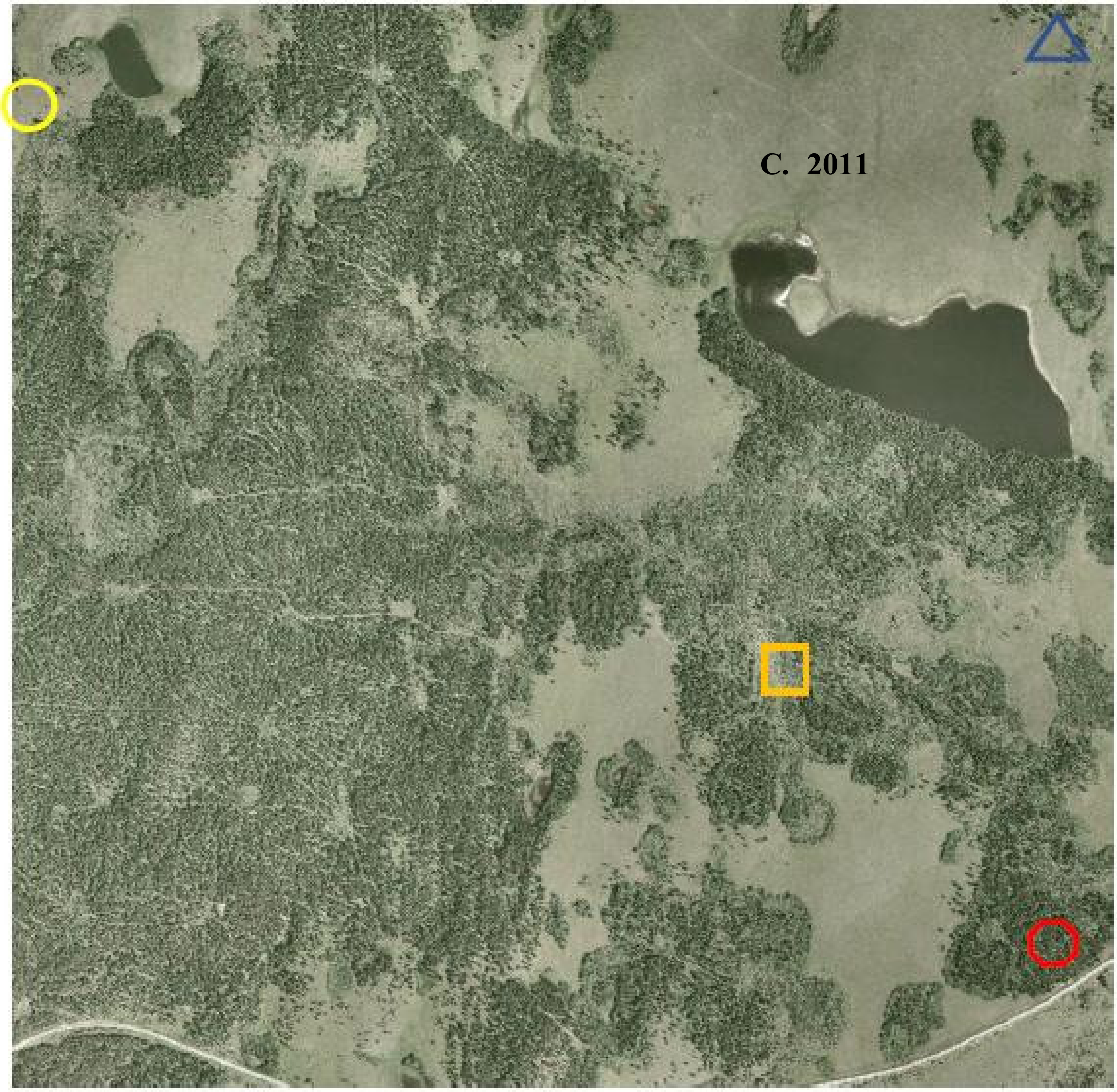
	Depth (cm)	Description
		Toosey: Orthic Dark Brown Chernozem
Ah1	0-11	very dark gray (10 YR 3/1); silt loam; weak to moderate, fine granular; abundant, fine, oblique roots within soil matrix
Ah2	11-26	dark yellowish brown (10 YR 3/4); silt loam; moderate, medium subangular blocky; abundant, fine, oblique roots within peds
Bt	26- 40	brown (10 YR 4/3); clay loam; moderate to strong, medium angular blocky; plentiful, fine, oblique roots within peds
Ck	40+	light olive brown (2.5 Y 5/3); sandy loam; moderate to strong; medium angular blocky; very few, very fine, oblique roots
		Rock Lake: Orthic Dark Brown Chernozem
Ah	0-15	very dark brown (10 YR 2/2); silt loam; moderate, medium subangular blocky; abundant, fine, oblique roots within peds
Bm	15-26	dark grayish brown (10 YR 4/2); loam; moderate, medium subangular blocky; plentiful, fine, oblique roots within peds
Bt	26-36	Brown (10 YR 4/3); clay loam; moderate to strong, medium angular blocky; plentiful, fine, oblique roots within peds
BCca	36- 45	dark grayish brown (10 YR 4/2); loam; moderate, medium angular blocky; few, fine, oblique roots along ped surfaces
Ck	45+	dark olive brown (2.5 Y 3/3); loam; moderate, medium angular blocky
		Sting and Vert: Calcareous Dark Brown Chernozem
Ah 1	0-9	very dark brown (10YR 2/1.5); silt loam; moderate, medium granular; abundant, fine, oblique roots within soil matrix
Ah 2	9-26	very dark grayish brown (10YR 3/2); silt loam; medium, subangular blocky; abundant, fine, oblique roots within soil matrix
Bmk	26-36	very dark grayish brown (10YR 3/2.5); sandy loam; weak, fine subangular blocky; plentiful, very fine, oblique roots within soil matrix
Cca	36-55	dark grayish brown (2.5Y 4/2); sandy loam; weak, medium subangular blocky; few, very fine, oblique roots within soil matrix
Ck	55+	very dark grayish brown (2.5Y 3/2); sandy loam; weak, medium subangular blocky
		Vert Lake: Orthic Dark Brown Chernozem
Ah1	0 -12	very dark brown to black (10YR 2/1.5); silt loam; moderate, medium granular; abundant, fine, oblique roots within soil matrix
Ah2	12 -23	very dark brown (10YR 2.5/2); silt loam; moderate, medium subangular blocky; abundant, fine, oblique roots within peds
Bmk	23- 35	dark brown (10YR 3/2.5); loam; moderate, medium subangular blocky; plentiful, very fine, oblique roots within peds
Cca	35- 55	dark grayish brown (2.5Y 4/2.5); loam, moderate to strong, medium angular blocky; very few, very fine, oblique roots within peds
Ck	55+	very dark grayish brown (2.5Y 3/2.5); loam; strong, medium angular blocky

APPENDIX 3

Riske Creek (Becher's Prairie) aerial photographs showing **A**. 1962 benchmark for extent of forests and grasslands, **B.** 2005 showing extent of forest encroachment on grasslands, and **C.** 2011 after grassland restoration treatments removed young forest encroachment from portions of the grassland benchmark. Shapes indicate an example of each ecosystem category, with an approximate location: stable state grassland (yellow circle), restored grassland (blue triangle), young forest (orange square), and mature forest (red octagon). Aerial Photographs provided by Province of British Columbia, Ministry of Forests, Lands and Natural Resource Operations.



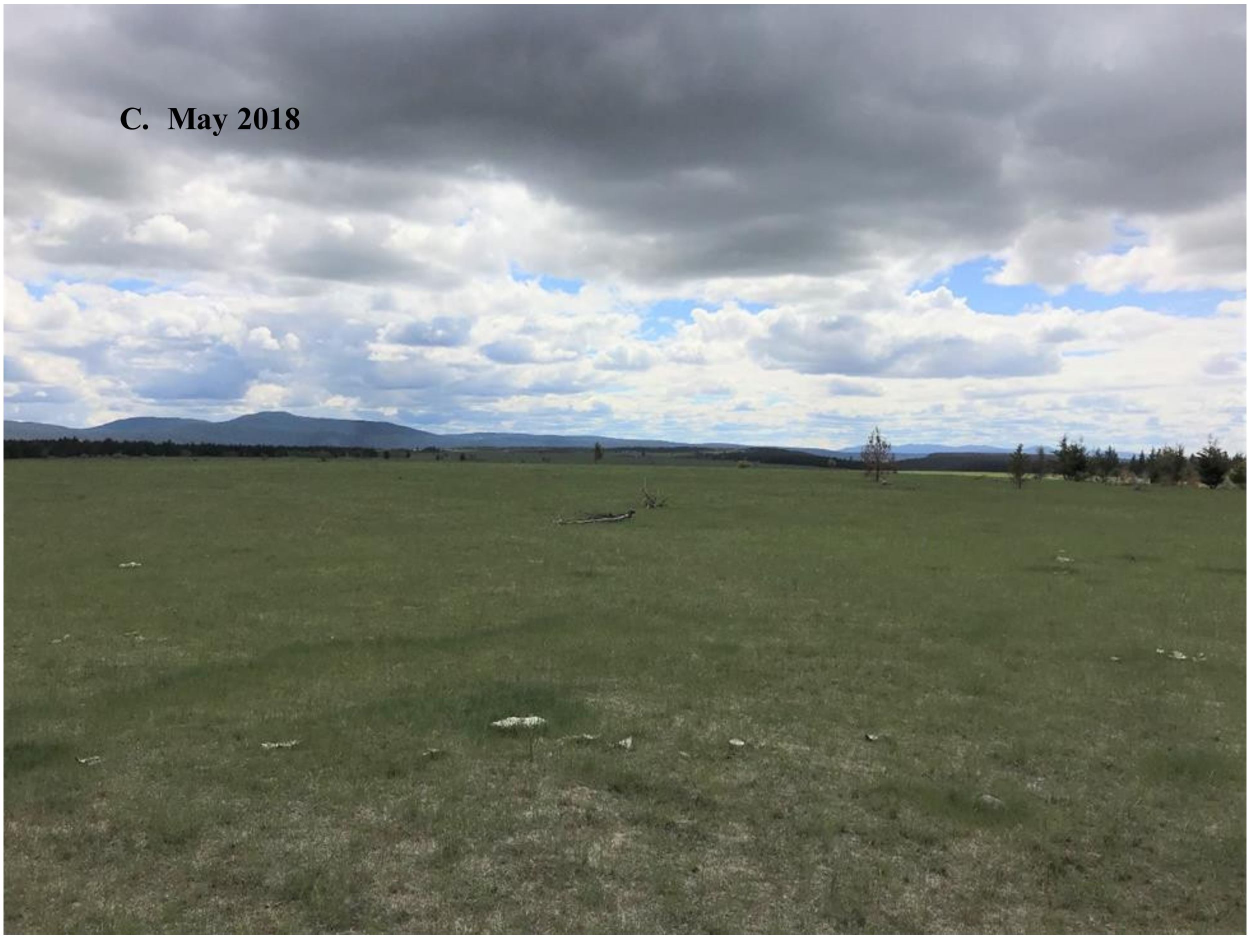

B. 2005


C. 2011

APPENDIX 4

Photographs of stable state grasslands **A.** before wildfire in July 2017, **B.** after wildfire in August 2017, **C.** May 2018, and **D.** September 2019. Continuous plant and litter cover resulted in low diversity (H) of burn severity. After wildfire, the plant community recovered to a similar species composition by July 2018, although litter cover was reduced and there was increased bare ground cover. It appears that there may be higher cover of native needlegrasses and reduced *Poa pratensis* in September 2019; however, this needs to be verified with future research.

B. August 2017



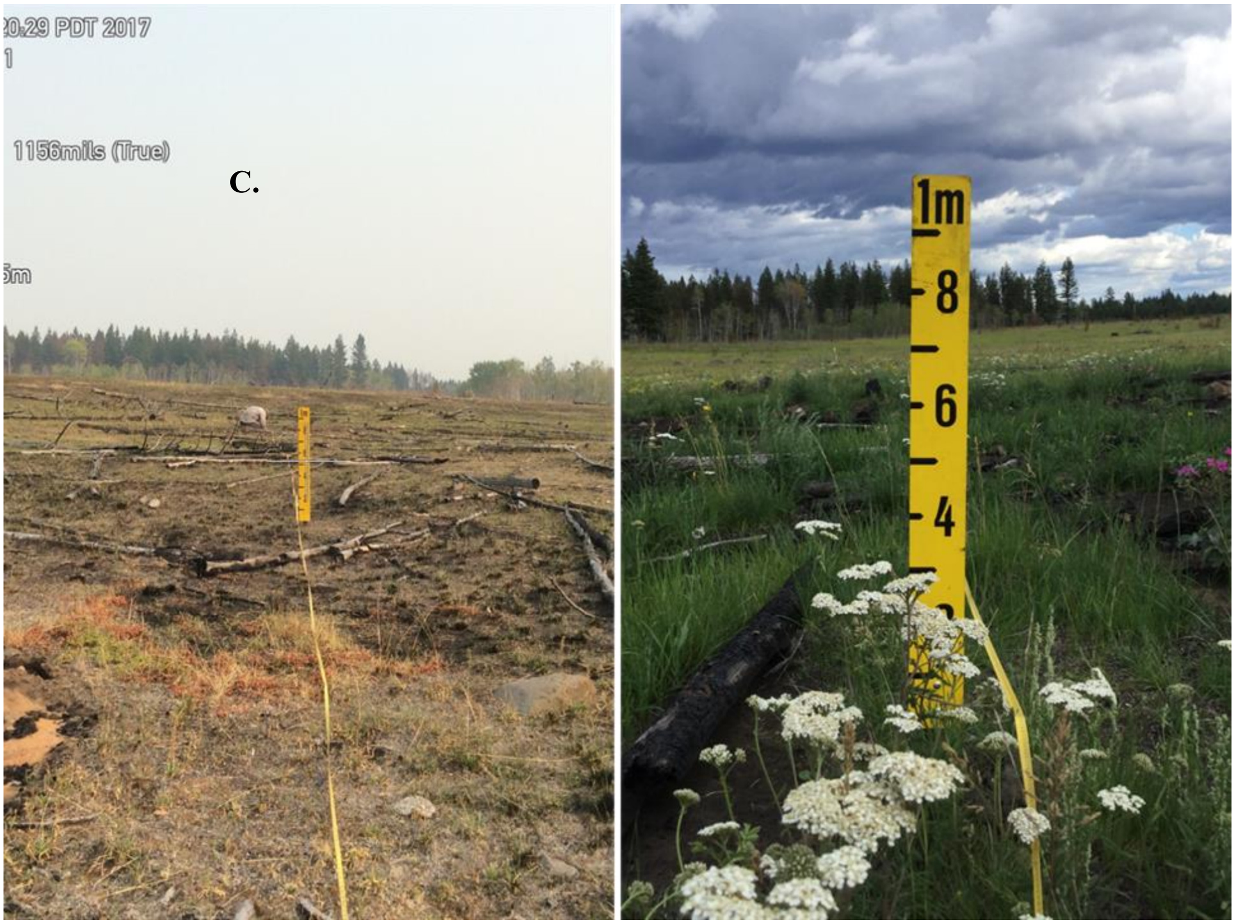
C. May 2018

D. September 2019

APPENDIX 5

Before and after photographs of plant communities several weeks after wildfire (August 2017) and one year after wildfire (July 2018) including: **A.** mature forests, **B.** young forest, and **C.** restored grassland. The wildfire resulted in increased dominance of *Calamagrostis rubescens* in mature forests, an increase in exotic species *Tragopogon pratensis* in young forests, and no detected change in species composition of restored grasslands. Diversity of burn severity in restored grasslands and young forests was intermediate between mature forests which had high diversity and stable state grasslands low diversity (H).


Tue Sep 5 17:05:04 PDT 2017
N 537248 5758681
m
-84
ring: 102° S78E 1813mils (True)
gle: +03.6°
e: -00.4°
trans 3@ 20m
B.


20.29 PDT 2017
1
1156mils (True)
C.
5m
1m
8
6
4