LIMITED REPORT

Vulnerability of Prairie Grasslands to Climate Change

Prepared for
Prairies Regional Adaptation Collaborative (PRAC)

By Jeff Thorpe
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SRC Publication No. 12855-2E11

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SUMMARY

The purpose of this report is to assess the vulnerability to climate change of native grasslands and other natural ecosystems in the Prairie Ecozone of Alberta, Saskatchewan, and Manitoba.

Climate change is expected to cause major impacts in the Prairie Ecozone over the coming century. Temperatures are predicted to increase substantially, although the size of this change depends on which climate change scenario is used. Only small changes are predicted for annual precipitation and seasonal distribution of precipitation.

Vegetation zones are expected to shift northward, with forest replaced by aspen parkland and grassland, and with current Canadian grassland types replaced by those found in the U.S. Great Plains. Northward movement of species will probably lag behind the change in climate, so it is difficult to predict future vegetation exactly. However, the zonation results imply the following trends:

- decrease in tree cover in the southern boreal forest and aspen parkland, and reduced woody encroachment on grassland.
- decrease in species dependent on woody cover, and increase in species dependent on open grassland.
- change in grassland structure: decrease in midgrasses, increase in shortgrasses.
- decrease in cool-season (C_3) species and increase in warm-season (C_4) species.
- gradual introduction of plant and animal species currently found only in the U.S.
- new community types resulting from differences in migration rates among species.

Grassland production is expected to decrease, but the size of this loss ranges from slight in the cooler scenarios to moderate in the warmer scenarios. Decrease in average production implies decrease in sustainable stocking rates. The fertilizing effect of rising CO_2 concentrations could help to moderate production losses.

The change in average production could be less important than increased occurrence of low-production years (i.e. droughts). Besides the immediate reduction in growth, prolonged drought shifts grassland composition toward shorter or earlier-growing species.

For the livestock industry as a whole, the increased area of rangeland in formerly forested areas could help to compensate for reduced production in the drier areas.

Changes in grassland zonation and production will have broader implications for overall biodiversity. Species respond to climate change by moving (i.e. shifting ranges) or by adapting in place (by changing phenology or evolution). Species with long-distance dispersal and generalist habitat requirements will be more likely to keep pace with climate change, while slow-dispersing or habitat specialist species are more likely to lag behind.

Invasive species are likely to be winners under climate change, because of rapid dispersal, use of disturbed habitats, and capacity for rapid evolution. However, invasion also depends on resource availability, and increasing droughts may help to reduce invasion success.

Climate change is expected to reduce the number and area of wetlands, leading to losses in duck production and other wetland biodiversity. As with other climate change impacts, this effect will interact with changes in land use, which could be more immediately important.

Climate change will affect species at risk, but the impacts will vary depending on the biology and habitat requirements of the individual species. Some of those listed in Canada are northern fringe populations of species that are common in the U.S., so climate change could increase the climatic suitability for these species.

The overall impacts of climate change will vary among different types of grassland. Northern fescue prairie and other types of moister regions could be most severely impacted, because of low total area, high habitat fragmentation, and high potential for exotic invasion. The more widespread mixed prairie has relatively more capacity to adjust to climate change. One of the unknowns is the future development of former forest land; in many situations retreating forests are likely to be replaced by exotic grassland.

ACKNOWLEDGEMENTS

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1 INTRODUCTION

Climate change is expected to have major impacts on the Canadian Prairies (Sauchyn et al. 2010). This report focuses on the vulnerability of native grassland and associated natural ecosystems.

Native grassland in the Prairie Provinces is largely restricted to the Prairie Ecozone as mapped by ESWG (1996) (Figure 1). While most of the Prairie Ecozone has been cultivated, natural pasture is still estimated to make up 24% of the farm area (Table 1). Associated with grasslands are smaller areas of woodlands (mostly aspen[1] groves) and wetlands. These areas provide a grazing resource for livestock producers, and are also critically important for the biodiversity of the region, which is threatened by the extensive land conversion.
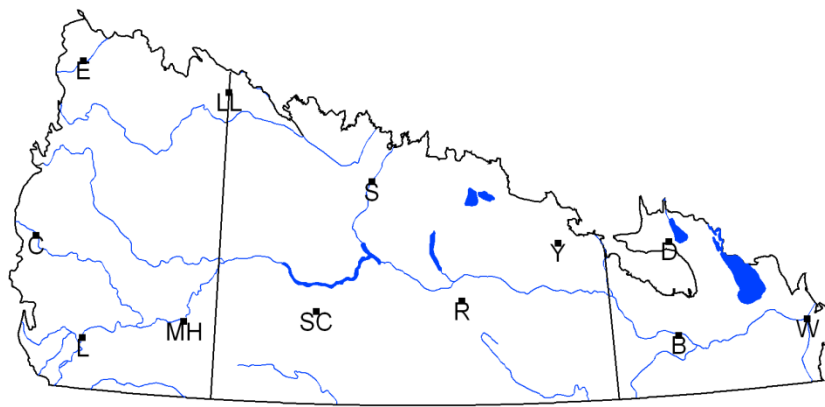
Figure 1 The Prairie Ecozone (ESWG 1996).

Prairie grasslands are subject to a variety of threats. In addition to the loss of most of the grassland area to cultivation, remaining areas are threatened by exotic invasion. In the moister parts of the ecozone, woodlands have encroached onto remaining grasslands since prairie fires were suppressed. On top of these threats, climate change will cause a new set of changes which could be important for both agriculture and biodiversity. Governments need to understand these changes, so that policies can be implemented to foster adaptation. While we cannot completely foresee the future, literature review and ecoclimatic modeling allow us to explore the range of probable outcomes for the coming century.

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[1] Scientific names of species referred to in the text are given in Appendix A.

Table 1. Area of natural pasture and tame pasture as a percentage of total farm area in the Prairie Ecozone, 2006.

	area (km2)	% of farm area
total farm area	403,325	
tame pasture	32,715	8%
natural pasture	96,831	24%

Source: Census of Canada for Agriculture data, interpolated to ecoregion boundaries by Agriculture Canada (http://www.agr.ca/nlwis-snite/index_e.cfm?s1=data_donnees&s2=details&page=ica-ira_plus, accessed July 31, 2008).

A detailed review of the scientific literature was conducted to address these questions, focusing on grasslands and their climatic relationships. In addition, ecoclimatic models were developed specifically for the Prairie Ecozone. Models for predicting the impact of climate on grassland production in the Canadian prairies were developed by Thorpe et al. (2004, 2008) and Thorpe (2007b). A model for predicting zonation of grassland types from climatic variables was developed by Vandall et al. (2006).   The current project made use of these existing models, but with substantial refinements. For consistency between the production and zonation analyses, both sets of models were recalibrated using a consistent set of climatic variables. Climatic mapping made use of the finer-resolution data surfaces that have become available in recent years, while the most recent outputs from Global Climate Models were used to project future changes.

2 PRESENT AND FUTURE CLIMATE

2.1 Baseline climatology

The convention in climate change modeling is to use the 1961-90 normals as a baseline. These 30-year normals are measured at an irregular network of Environment Canada climate stations. Their usefulness for mapping has been increased by interpolation among stations to form a continuous data surface for each climatic variable.   The latest and apparently best of these interpolations for western Canada uses the PRISM model, which was originally developed in the western U.S. by Daly et al. (1994). In addition to interpolating in the horizontal direction, this model adjusts variables for elevation using locally calculated lapse rates. Outputs are available for a 2.5 arc-minute grid (approximately 3 km east-west by 5 km north-south), providing a relatively fine-resolution representation of climate in relation to topography. This grid has been made available by Dr. Andreas Hamann at the University of Alberta (http://www.ales2.ualberta.ca/rr/people/hamann/data.htm). In order to encompass the Prairie Ecozone in each province, gridpoints up to 52° North were used in Manitoba, up to 54° North in Saskatchewan, and up to 54.5° North and 115° West in Alberta. For most subsequent mapping and analysis, these grids were trimmed to the boundaries of the Prairie Ecozone.

The baseline climatology represents monthly values for basic climatic variables:
- Tmax – monthly maximum temperature (i.e. mean of daily maximum values) (°C)
- Tmin – monthly minimum temperature (i.e. mean of daily minimum values (°C)
- Tmean – mean monthly temperature (calculated from Tmax and Tmin) (°C)
- PPT – monthly precipitation (mm)

In addition to these basic variables, a number of derived variables have been found useful for representing the impact of climate on vegetation:
- Growing degree days (GDD) is the sum of daily departures above a base temperature of 5°C. Development of plants is often closely related to GDD.
- Potential evapotranspiration (PET) is the amount of evaporation that would occur from a vegetated surface if soil water were freely available. PET depends mainly on temperature, although it is also influenced by other variables. A number of methods have been developed for estimating PET. For the current project, PET was estimated using Hogg's (1997) simplified Penman-Monteith method, which requires only temperature and elevation data. PET has the advantage of representing the thermal increase in the same units at PPT (i.e. millimetres of water), allowing direct comparison between the two variables.
- Hogg's (1994) Climatic Moisture Index (CMI) is calculated as PPT-PET. Hogg found that the forest/grassland transition in the Prairie Provinces is closely aligned with the isoline at CMI=0.
- The seasonal distribution of precipitation was represented by the proportion of annual precipitation falling in May through September (MAYSEP). A given amount of annual precipitation may have differing effects depending on how much of it falls during the growing season.

These derived variables were calculated for each of the PRISM model gridpoints. Monthly temperature data and gridpoint elevations were used to calculate potential evapotranspiration, while monthly precipitation data were used to calculate the proportion of precipitation in May through September. Maps were produced by drawing contours on each data surface using Geographic Information System (GIS) software.

2.2 Climate change scenarios

A large number of climate change scenarios are available, resulting from a variety of global climate models (GCMs) and emissions scenarios. The recommended approach for vulnerability analysis is to use several scenarios representing the range of variation, rather than any one scenario. Scenarios show changes from the baseline climate to the future, usually summarized in terms of future 30-year periods: 2011-2040 (for convenience referred to as the 2020s); 2041-2070 (the 2050s); and 2071-2100 (the 2080s).

Initial work on the grassland vulnerability assessment was based on Saskatchewan. Selection of climate change scenarios was based on an existing report. Barrow (2009) selected three of the most recent climate change scenarios to represent the range of climate changes anticipated for Saskatchewan over the coming century:

- GFCM20 B1
- CGCM3_T47_2 A1B
- MIMR B1

For the PRAC assessment, two additional scenarios were added to represent a greater range of climates (data downloaded from http://www.ales2.ualberta.ca/rr/people/hamann/data.html):
- HADCM3 A2
- ECHAM4 A2

When the assessment was extended to Manitoba, four scenarios were selected from http://www.ales2.ualberta.ca/rr/people/hamann/data.html) to represent the range of variation in Manitoba up to 52° North.
- ECHAM4 A2 – cool, medium precipitation
- HADCM3 B2 – medium temperature, high precipitation
- HADCM3 A2 – warm, medium precipitation
- CSIRO2 B2 – warm, low precipitation

When the assessment was extended to Alberta, the two scenarios common to the Manitoba and Saskatchewan assessments were used:
- HADCM3 A2
- ECHAM4 A2

This provided a common set of scenarios for mapping over the entire region. From the Manitoba and Saskatchewan assessments, it was found that these two scenarios represented much of the variation, with ECHAM4 A2 representing the cooler scenarios (i.e. those with more moderate temperature increases) and HADCM3 A2 representing the warmer scenarios.

For each province, monthly values of Tmean, Tmax, Tmin, and PPT for the 2020s, 2050s, and 2080s were downloaded from http://www.ales2.ualberta.ca/rr/people/hamann/data.html. These values are for gridpoints on the 2.5 arc-minute PRISM grid. For each gridpoint, the basic climatic data were used to calculate derived variables, as in the baseline climatology.

To show the differences between the cool and warm scenarios, averages over all gridpoints within the Prairie Ecozone are shown in Figures 2 to 5. Both scenarios show substantial warming from the baseline, as shown by higher values of growing degree-days (Figure 2) and potential evapotranspiration (Figure 3). However, the increase is much greater in the warm scenario, with growing degree-days (which average 1500-1700 in the baseline) rising to 2700-3000 by the 2080s, compared with 1900-2200 in the cool scenario. Potential evapotranspiration (which depends mainly on temperature) shows similarly large increases and differences between scenarios. By contrast, changes in annual precipitation vary from small increases in the warm scenario to small decreases in the cool scenario (Figure 4). Interestingly, the average precipitation is considerably higher in Manitoba than in Saskatchewan or Alberta. All of the scenarios show small decreases in the proportion of precipitation falling in summer, with the warm scenario in Manitoba showing the largest change (Figure 5).

Growing Degree-Days
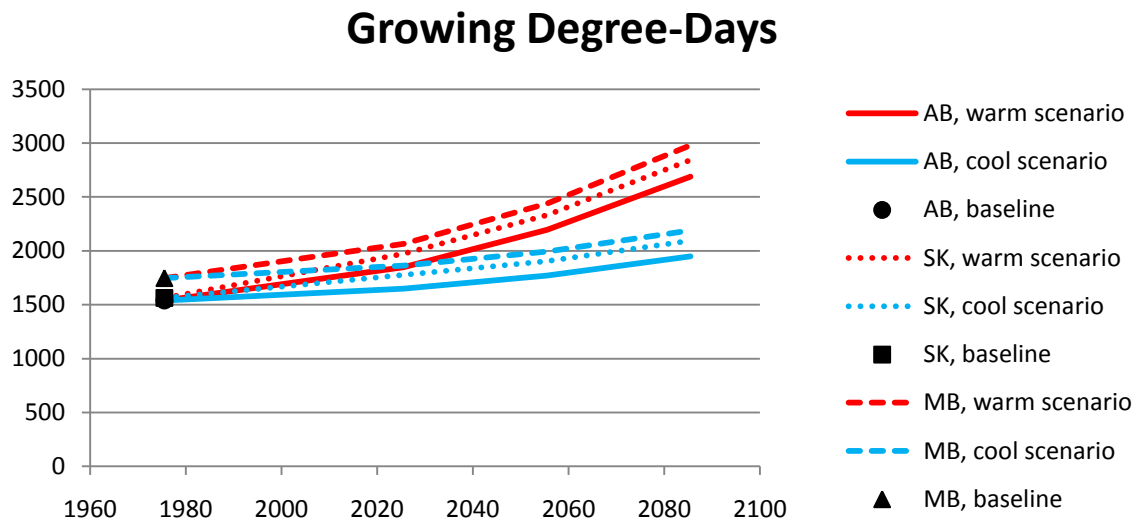
Figure 2. Average growing degree days for the Prairie Ecozone of Alberta, Saskatchewan, and Manitoba, in the 1961-90 baseline and in two scenarios for the 2020s, 2050s, and 2080s.

Potential Evapotranspiration (mm)
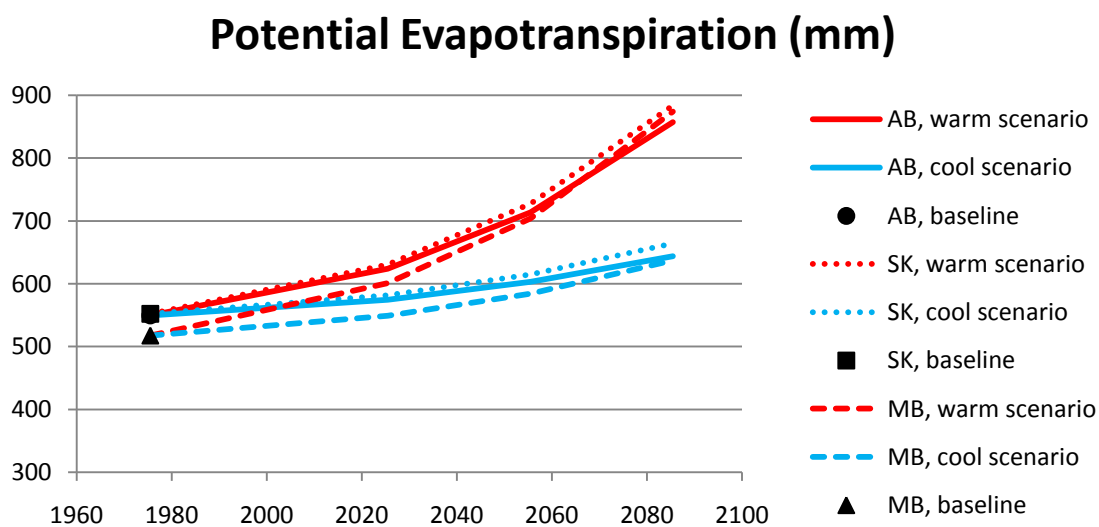
Figure 3. Average potential evapotranspiration for the Prairie Ecozone of Alberta, Saskatchewan, and Manitoba, in the 1961-90 baseline and in two scenarios for the 2020s, 2050s, and 2080s.

Annual Precipitation (mm)
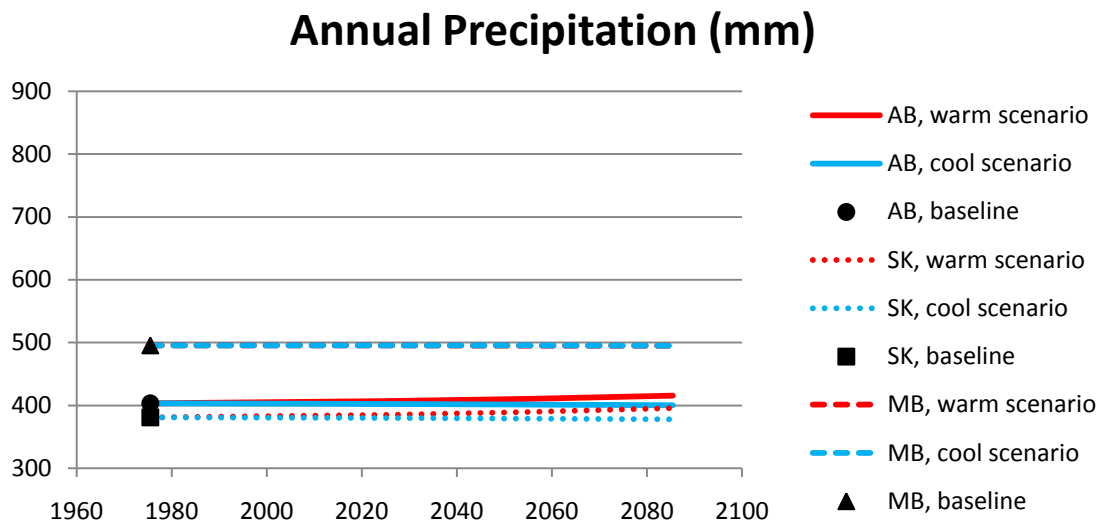
Figure 4. Average annual precipitation for the Prairie Ecozone of Alberta, Saskatchewan, and Manitoba, in the 1961-90 baseline and in two scenarios for the 2020s, 2050s, and 2080s.

Proportion of Precipitation in Summer
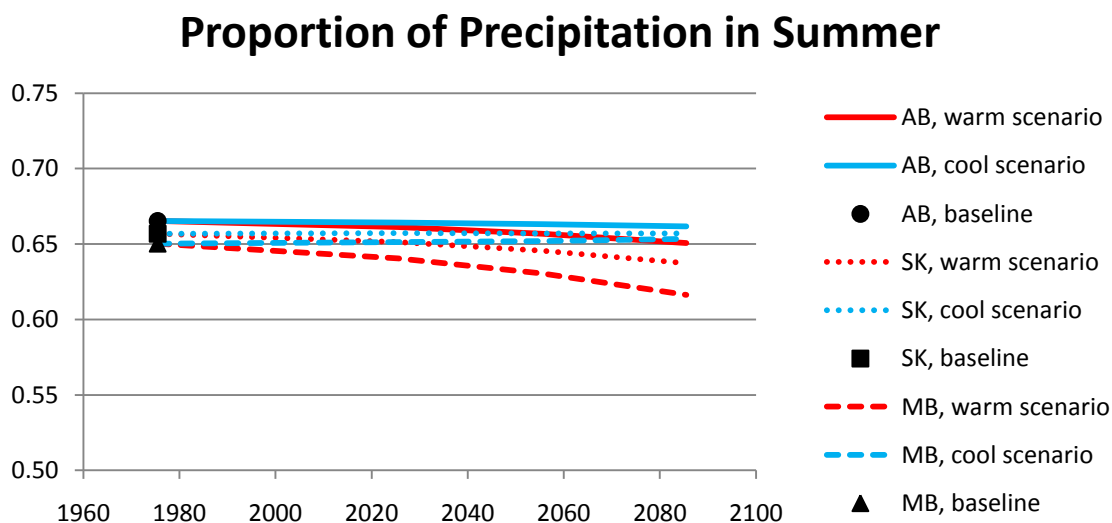
Figure 5. Average proportion of precipitation falling in May through September for the Prairie Ecozone of Alberta, Saskatchewan, and Manitoba, in the 1961-90 baseline and in two scenarios for the 2020s, 2050s, and 2080s.

3 IMPACTS OF CLIMATE CHANGE ON GRASSLAND ZONATION

3.1 Approach

Studies of shifts in vegetation zonation under climate change have typically been at the formation or biome level (e.g. Bachelet et al. 2003). Models in our region typically show grassland expanding north into the current boreal forest (Lenihan and Neilson 1995, Hogg and Hurdle 1995, Schneider et al. 2009). Lenihan and Neilson (1995) distinguished between "mixed

grass prairie" and "short grass prairie", and Hogg and Hurdle (1995) and Schneider et al. (2009) distinguished between "aspen parkland" and "grassland". However none of these studies have looked in detail at zonation of different types of grassland, including types currently found in the United States.

Vegetation zonation was modeled by relating the distribution of current vegetation zones to climatic variables. The vegetation and climate of the U.S. Great Plains were included in this analysis, to serve as analogues for the warmer future climates predicted for the Canadian Prairies. If models were calibrated with Canadian data only, future climates would be outside of the calibration range, leading to dangerous extrapolation. Zonation within Canada was represented by the national classification of ecoregions (ESWG 1996) (Figure 6). For the U.S., a variety of ecoregion classifications have been published, but most of them (Bailey 1978, 1981; Risser et al. 1981; Ricketts et al. 1999) are based at some level on Kuchler's (1964) classic map of the potential natural vegetation of the U.S. Analysis included the major Kuchler types occurring in or adjacent to the Central and Northern Great Plains, excluding types associated with azonal landscape features such as the Nebraska Sandhills (Figure 7). The area shown in Figure 7 includes Montana, Wyoming and Colorado down the west side and North Dakota, South Dakota, Nebraska and Kansas down the east side, encompassing the range of warming projected for the Canadian Prairies up to the 2080s.
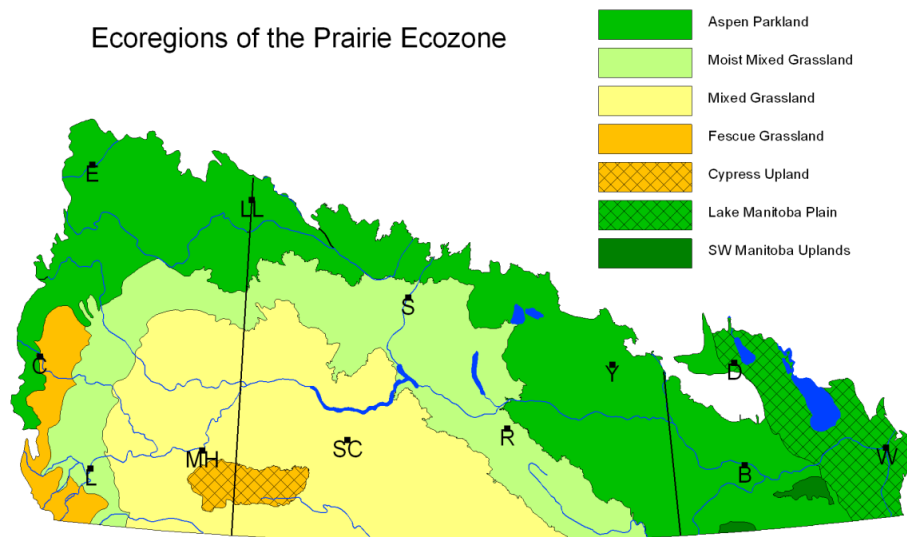
Figure 6. Ecoregions of the Prairie Ecozone in Alberta, Saskatchewan, and Manitoba (ESWG 1996).

Küchler Vegetation Types

Sagebrush steppe (*Artemisia-Agropyron*)
Wheatgrass-needlegrass shrubsteppe
(*Agropyron-Stipa-Artemisia*)

63 Foothills prairie
(*Agropyron-Festuca-Stipa*)

64 Grama-needlegrass-wheatgrass
(*Bouteloua-Stipa-Agropyron*)

65 Grama-buffalo grass
(*Bouteloua-Buchloë*)

66 Wheatgrass-needlegrass
(*Agropyron-Stipa*)

Wheatgrass-bluestem-needlegrass
(*Agrophyron-Andropogon-Stipa*)

Bluestem-grama prairie
(*Andropogon-Bouteloua*)

Bluestem prairie
(*Andropogon-Panicum-Sorghastrum*)

0   300 km

Source: Küchler, A. W. *Potential Natural Vegetation of the Conterminous United States*, American Geographical Society

Figure 7. Major zonal vegetation types in the central and northern Great Plains of the United States according to the classification of Kuchler (1964).

Combining the Canadian and U.S. classifications, the following vegetation zones were included in the analysis:

- Forest – Mainly southern boreal forest, a mosaic of broad-leaved forests (trembling aspen, balsam poplar, white birch) and conifer forests (white and black spruce, jack and lodgepole pine, balsam fir, tamarack). All Canadian gridpoints outside of the Prairie Ecozone were lumped in this category.
- Canada - Aspen Parkland Ecoregion: Mosaic of productive mid-height grasslands with aspen stands and shrubland. Dominant grasses are plains rough fescue, western porcupine grass, and northern wheatgrass. In the eastern part of the Parkland, tallgrass species (especially big bluestem) also become important. The Lake Manitoba Plain Ecoregion of central Manitoba was lumped with Aspen Parkland.
- Canada - Moist Mixed Grassland Ecoregion: Mixed prairie dominated by midgrasses (speargrasses, wheatgrasses, sometimes plains rough fescue).
- Canada - Mixed Grassland Ecoregion: Mixed prairie, usually dominated by midgrasses (western porcupine grass, needle-and-thread, northern and western wheatgrass), but with a shortgrass component (blue grama, sedges) which becomes more important in the drier parts of the region.

- Foothills Fescue – Productive grasslands of higher altitudes in the western part of the Prairies. Dominated by foothills rough fescue (or plains rough fescue in the Cypress Hills), Idaho fescue, Parry oatgrass, and bluebunch wheatgrass. Includes the Canadian Fescue Grassland and Cypress Upland Ecoregions as well as the similar Foothills Prairie mapped in the U.S.
- U.S. – Grama-Needlegrass-Wheatgrass: Mixed prairie dominated by midgrasses (needle-and-thread, western wheatgrass) but with an important shortgrass component (blue grama).
- U.S. – Wheatgrass-Needlegrass: Mixed prairie dominated by midgrasses (western and northern wheatgrass, porcupine grass, needle-and-thread, green needle grass).
- U.S. - Wheatgrass-Bluestem-Needlegrass: Mixed prairie dominated by midgrasses (western wheatgrass, porcupine grass, little bluestem), but with an important tallgrass component (big bluestem).
- U.S. – Bluestem Prairie: Tallgrass prairie, dominated by big bluestem, switchgrass, Indian grass, little bluestem.
- U.S. – Grama-Buffalo Grass: Shortgrass prairie dominated by blue grama and buffalo grass, but with an important component of midgrasses.
- U.S. – Sagebrush Steppe: Mixture of dense to open stands of short shrubs (big sagebrush, rabbitbrush, horsebrush) with mid- and shortgrasses (bluebunch wheatgrass, western wheatgrass, plains bluegrass, needle-and-thread).

These mapped zones impose discrete boundaries on continuous gradients in structure and composition. Tree cover declines sharply at the northern edge of the region, from forest (continuous tree cover) to Aspen Parkland (mosaic of woodland and grassland) to Moist Mixed Grassland (occasional tree cover). From the Mixed Grassland southward to U.S. – Grama-Buffalo Grass, the natural vegetation is predominantly open grassland with no tree cover, except in azonal sites such as streambanks or steep valley-slopes.

Within the grassland, the most obvious trend is in the height of the grass. Midgrasses (i.e. medium-height grasses) are highly dominant in Foothills Fescue, Aspen Parkland, Moist Mixed Grassland, and Grama-Needlegrass-Wheatgrass and Wheatgrass-Needlegrass. The proportion of shortgrasses increases southward and westward in the drier parts of the Mixed Grassland and in Grama-Needlegrass-Wheatgrass, and shortgrasses become dominant in Grama-Buffalo Grass. The proportion of tallgrasses increases eastward, in the eastern part of the Aspen Parkland and in Wheatgrass-Bluestem-Needlegrass, and tallgrasses become dominant in Bluestem Prairie. The tallgrass prairie actually comes a little way into Canada, in the Red River Valley of southern Manitoba.

Less obvious is the shift from cool-season to warm-season grasses. Cool-season plants (e.g. needlegrasses, wheatgrasses, fescues) have the C_3 photosynthetic pathway, and grow best at cooler temperatures. Warm-season plants (e.g. gramas, bluestems, dropseeds) have the C_4 pathway and grow best at warmer temperatures. Cool-season grasses are highly dominant in Foothills Fescue, Aspen Parkland, and Moist Mixed Grassland. Warm-season grasses become more important in the drier part of the Mixed Grassland and in Grama-Needlegrass-Wheatgrass as well as Wheatgrass-Needlegrass. Grama-Buffalo Grass and Bluestem Prairie are dominated by warm-season grasses.

Review of species lists (Vandall et al. 1996) shows that many species are wide-ranging, occurring at varying levels of dominance in many of the vegetation zones. Examples include: western wheatgrass, needle-and-thread, blue grama, June grass, sedges, sand reedgrass, pasture sage, prairie sage, scarlet mallow, moss-phlox, dotted blazing-star, broomweed, hairy golden-aster, plains prickly-pear, lance-leaved psoralea, skeletonweed, prairie coneflower, scarlet gaura, purple prairie-clover, western snowberry, and prairie rose. Other wide-ranging species, such as western porcupine grass, northern wheatgrass, and wolf-willow, have more northern distributions, while plains rough fescue is narrowly concentrated at the northern fringe of the region. A number of species, including foothills rough fescue, Idaho fescue, Columbia needlegrass, Richardson's needlegrass, Parry oatgrass, bluebunch wheatgrass, lupines, larkspurs, cranesbill, and shrubby cinquefoil are concentrated in the Foothills Fescue. Arrowleaf balsamroot occurs in both Foothills Fescue and Sagebrush Steppe. Some species are important in both Foothills Fescue and Aspen Parkland: awned wheatgrass, Hooker's oatgrass, timber oatgrass, mouse-ear chickweed, and northern bedstraw. Kentucky bluegrass (which is predominantly exotic in origin) is concentrated in the moister regions, both northern and southern: Foothills Fescue, Aspen Parkland, Wheatgrass-Needlegrass, Wheatgrass-Bluestem-Needlegrass, and Bluestem Prairie.

Other species are more characteristic of warmer climates. Little bluestem (a mid-sized warm-season grass) occurs widely in Canada, but increases in importance southward, especially in Wheatgrass-Bluestem-Needlegrass and Bluestem Prairie. Warm-season grasses such as big bluestem, Indian grass, prairie dropseed, side-oats grama, switchgrass, and prairie cordgrass are more restricted in Canada, occurring mainly in the southeastern part of the Aspen Parkland, and increase southward into Wheatgrass-Bluestem-Needlegrass and Bluestem Prairie.

Sagebrushes increase in drier regions, from the drier part of the Mixed Grassland Ecoregion (silver sagebrush only) to Grama-Needlegrass-Wheatgrass (both silver sagebrush and big sagebrush). Big sagebrush reaches its highest concentration in Sagebrush Steppe, where it is favoured by both the dry climate and the low proportion of precipitation in summer. Other species of warm, dry climates, including buffalograss, yucca, hairy grama, squirreltail, red three-awn, and bahia, become most important in Grama-Buffalo Grass. These species may also occur in neighbouring types, but are absent or rare in Canada.

3.2 Development of zonation model

Climatic data (1961-90 normals) for the zonation model were based on a grid of 0.5° latitude by 0.5° longitude. Data for the United States on this grid were developed for the VEMAP project (Kittel et al. 1995), and were available from www.cgd.ucar.edu/vemap/. This data source also showed the Kuchler type in which each gridpoint falls. Comparable half-degree data for Canada were developed by the author based on McKenney's grid of 1961-90 normals, which was available from www.cics.uvic.ca/scenarios/index.cgi. The half-degree gridpoints were overlaid on GIS coverage of the Canadian ecoregions to assign an ecoregion to each point. Datasets were edited to include Alberta, Saskatchewan and Manitoba up to 56° North Latitude, and to include the following states: Montana, North and South Dakota, Minnesota, Wyoming, Nebraska, Iowa, Colorado and Kansas. Previous work has shown that these states cover the range of future

climates predicted for the Canadian prairies (Vandall et al. 2006). U.S. gridpoints were further edited to eliminate points falling outside the target Kuchler types (Figure 7).

Modeling methods followed an earlier study (Vandall et al. 2006), with some refinements to increase compatibility with production modeling, and to incorporate the more recent climate change scenarios. The distribution of Canadian vegetation zones was modeled following the approach of Hogg (1994). The main zones are separated by thresholds of a climatic moisture index (CMI), defined as annual precipitation minus annual potential evapotranspiration (see Section 2). Thresholds were fine-tuned to optimize the separation of the calibration data (Table 2).

Table 2. Thresholds of the Climatic Moisture Index used to separate Canadian vegetation zones.

Ecoregion	Climatic Moisture Index
Forest	above -18 mm
Aspen Parkland	-18 to -143 mm
Moist Mixed Grassland	-143 to -220 mm
Mixed Grassland	below -220 mm

Foothills Fescue occupies approximately the same range of CMI values as Aspen Parkland, but differs by a lower concentration of precipitation in summer (Vandall et al. 2006). Therefore areas with CMI between -18 and -143 mm, but with less than 60% of the annual precipitation falling in May through September, were assigned to Foothills Fescue.

For the Kuchler vegetation types in the United States, a multinomial logistic regression (McCune et al. 2002) was calculated to predict type membership from precipitation (PPT), potential evapotranspiration (PET), and proportion of precipitation in summer (MAYSEP). This generates an equation for each vegetation type which calculates its log-likelihood ratio relative to a reference type (Table 3). Sagebrush Steppe was arbitrarily used as the reference type. The type with the highest log-likelihood ratio is that most likely to occur at given values of the independent variables.

Table 3. Coefficients of the logistic regression model used to separate U.S. vegetation zones.

type	intercept	PPT	MAYSEP	PET
Foothills Fescue	-41.923	0.031	42.221	0.006
Grama-Needlegrass-Wheatgrass	-36.271	0.007	46.822	0.011
Wheatgrass-Needlegrass	-83.350	0.043	92.405	0.014
Wheatgrass-Bluestem-Needlegrass	-216.767	0.114	245.962	0.007
Bluestem Prairie	-264.905	0.165	302.276	-0.020
Grama-Buffalo Grass	-100.699	0.025	96.991	0.037
Bluestem-Grama	-251.848	0.119	257.454	0.032
Sagebrush Steppe	0	0	0	0

In zonation predictions, the Canadian model was applied to climatic data within the range of Canadian climates in the 1961-90 baseline period. Climatic data warmer than this were assumed to be beyond the calibration range of the Canadian model, so the U.S. model was applied. Potential evapotranspiration of 631 mm was used as an approximate boundary for this purpose. The models were applied to all gridpoints in the 2.5 arc-minute PRISM grid to generate maps of predicted zonation for the 1961-90 baseline, the 2020s, the 2050s, and the2080s.

3.3 Zonation results

The zonation map predicted from the 1961-90 baseline climate (Figure 8) corresponds well with the actual pattern of vegetation types, indicating that the model is working. Note that the driest parts of the Mixed Grassland Ecoregion is shown as the U.S. type Grama-Needlegrass-Wheatgrass. This resulted from the relatively simple rule used to switch from Canadian to U.S. zonation models. However, the pattern is reasonable, because in fact this area has a drier, shorter type of grassland, more like the mixed prairie in Montana, compared to the Mixed Grassland Ecoregion as a whole.

The cool scenario for the 2080s shows the most moderate change, with Aspen Parkland (and Moist Mixed Grassland) still found in the northern part of the region, where it has pushed the current forest northward (Figure 9). However, in the southern part of the region, Canadian grassland types have been replaced by U.S. types: the drier Grama-Needlegrass-Wheatgrass in the west, and the intermediate Wheatgrass-Needlegrass in the east. Foothills Fescue persists in its current location in southwestern Alberta; note that Canadian and U.S. foothills fescue types were combined in the model, so this could represent northward shift of the Montana variant of the type.

The warm scenario for the 2080s, which results in lower moisture balance compared to the cool scenario, shows Grama-Needlegrass-Wheatgrass (the drier type of U.S. mixed prairie) extending over most of the current Prairie Ecozone, and Grama-Buffalo Grass (i.e. shortgrass prairie) appearing along the southern margin (Figure 10). The Aspen Parkland and the Boreal fringe have been largely replaced by Wheatgrass-Needlegrass (the intermediate type of U.S. mixed prairie). Foothills Fescue again persists in its current location.
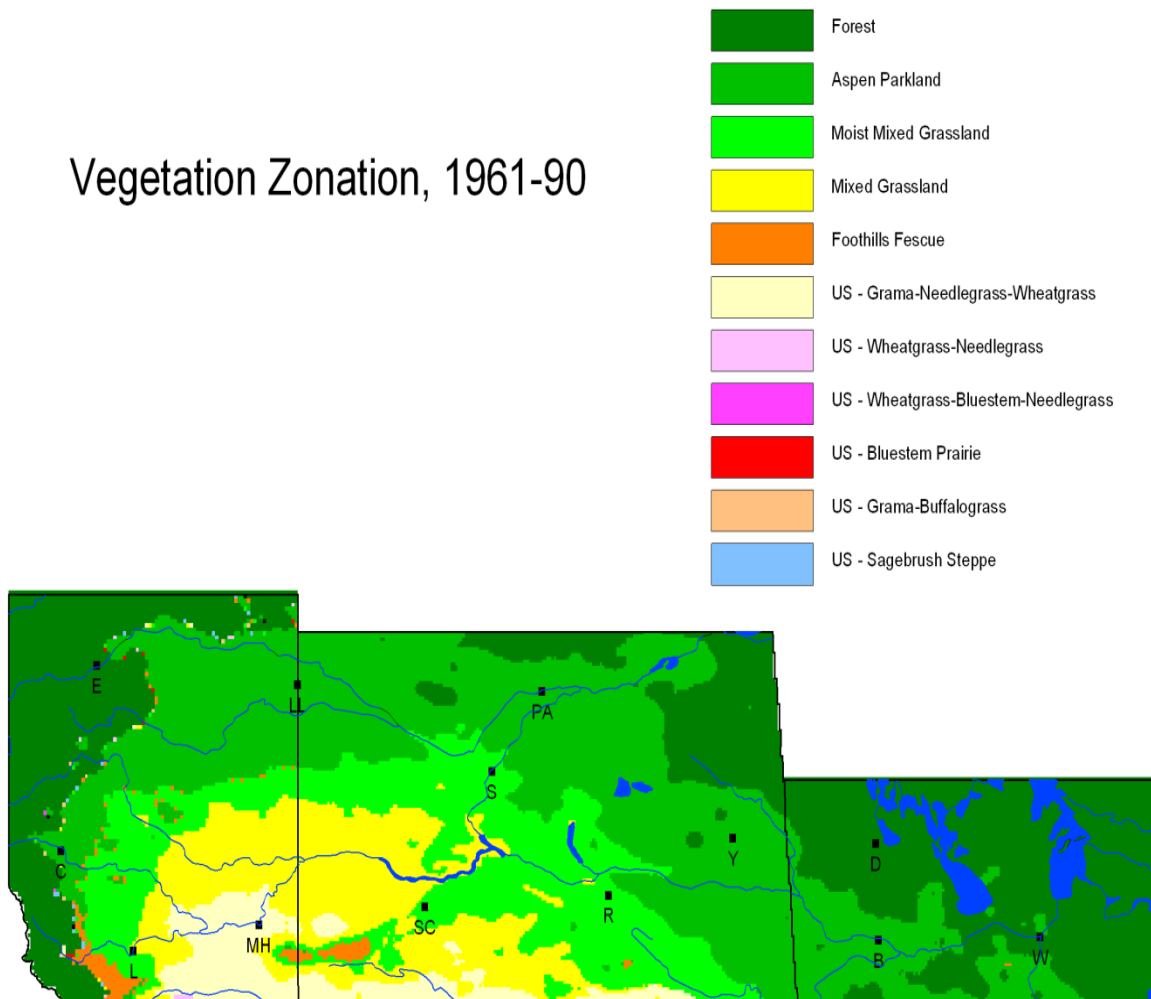
Figure 8. Predicted vegetation zonation based on climate data for the 1961-90 baseline.
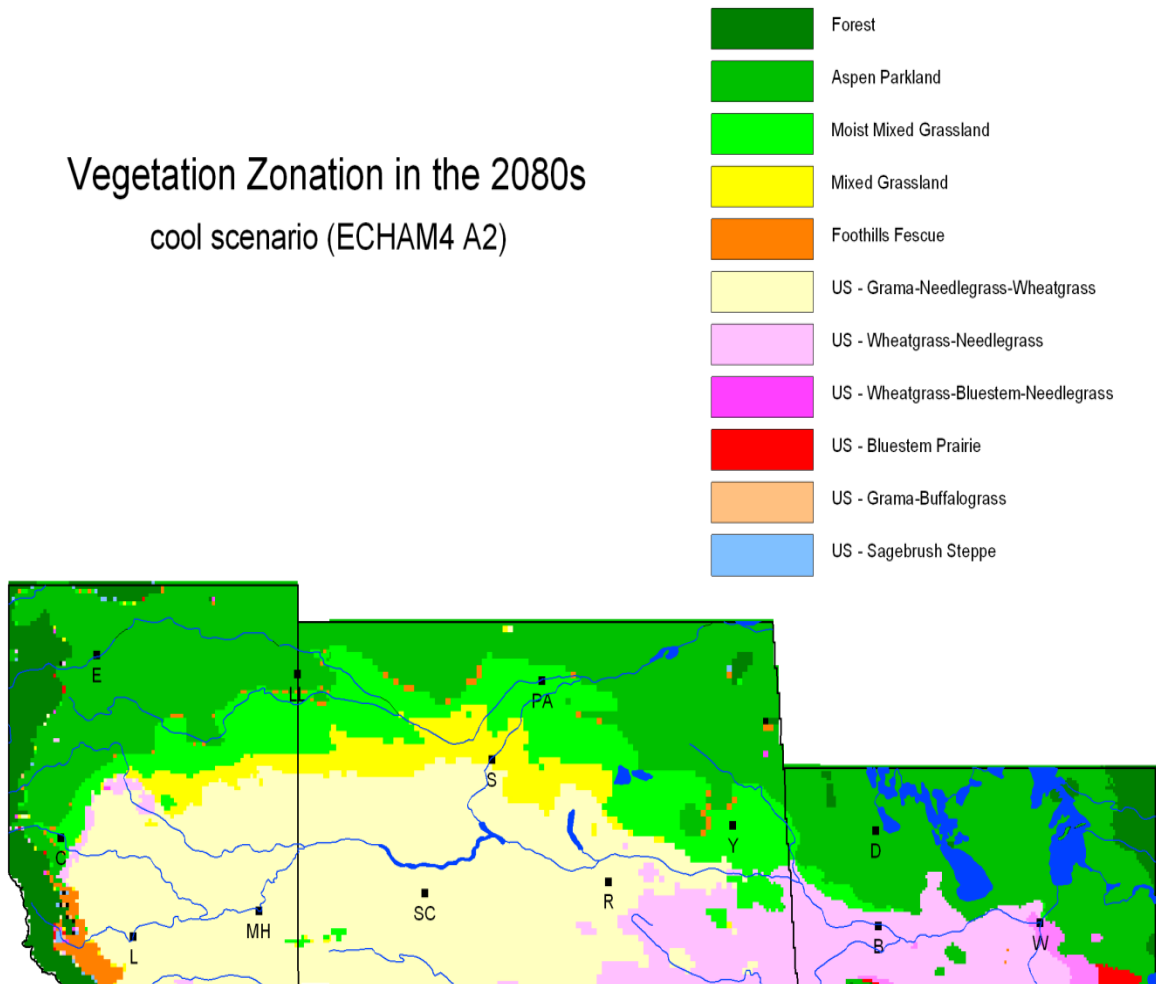
Figure 9. Predicted vegetation zonation based on the cool scenario for the 2080s.
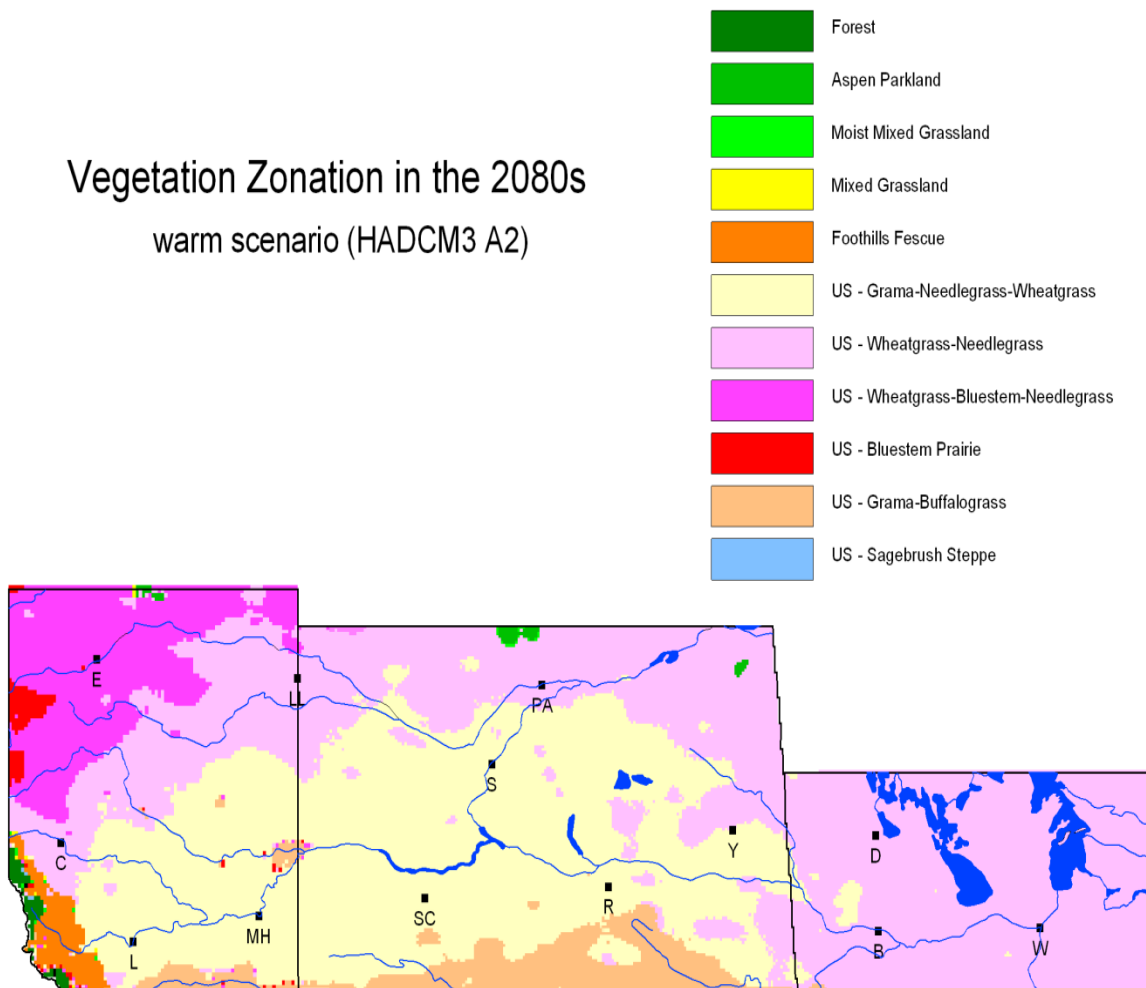
Figure 10. Predicted vegetation zonation based on the warm scenario for the 2080s.

The shifts in vegetation zonation presented in Figures 8 to10 are a type of community change. In current range science, such change is represented by "state-and-transition" diagrams (Westoby et al. 1989, Rodriguez Iglesias and Kothmann 1997, Bestelmeyer et al. 2003, Stringham et al. 2003, Briske et al. 2005). These are used to show the various directions in which communities may change as a result of different transitional processes. These may include irreversible changes between stable states, as well as the reversible changes that occur among communities within a stable state (Briske et al. 2005). Typically these diagrams have been used to represent processes such as grazing, fire, erosion, or exotic invasion. However, they can be extended to represent the

impacts of climate change. State-and-transition diagrams developed by Thorpe (2007a) for Saskatchewan rangelands have been modified for this purpose. These diagrams are for the "Loam Ecosite", which includes native rangelands on well-drained uplands with loamy soil texture.

The diagram for the Dry Mixed Grassland of southwestern Saskatchewan (Figure 11) shows Northern Wheatgrass - Needle-and-thread as the potential community under lightly grazed conditions. Heavy grazing can alter it to the other communities shown below it in the diagram (Needle-and-thread – Wheatgrass – June Grass – Blue Grama, and Blue Grama – Needle-and-thread – June Grass – Western Wheatgrass). All of these communities are enclosed by a solid box, representing a stable state which could be thought of as "native grassland under the current climate". Changes among these three communities are shown with arrows in both directions, indicating that the changes are reversible depending on grazing management. The single arrow to the left indicates a transition caused by exotic invasion, which is relatively irreversible, at least without extreme management inputs. The single arrows to the right represent impacts of climate change, which are also relatively irreversible. Both the cool and warm scenarios are predicted to shift this community toward the Blue Grama – Needle-and-thread – Western Wheatgrass community found in Montana and Wyoming. The warm scenario predicts a shift with further climate change to the Blue Grama – Buffalograss community found in Colorado.

The diagram for the Mixed Grassland in central Saskatchewan (Figure 12) is similar, except that the reference community in this somewhat moister climate is Western Porcupine Grass – Northern Wheatgrass. Climate change is predicted to shift it, first toward the Northern Wheatgrass – Needle-and-thread community found in southwestern Saskatchewan (Figure 11), and then to the Blue Grama – Needle-and-thread – Western Wheatgrass" community found in Montana and Wyoming.

In the moister climate of Aspen Parkland, the potential community is Plains Rough Fescue – Western Porcupine Grass – Northern Wheatgrass (Figure 13). Here, another pathway related to woody encroachment in the absence of fire is shown, while the most common types of exotic communities are dominated by smooth brome and Kentucky bluegrass. Climate change under the cool scenario shifts this community to Western Porcupine Grass – Northern Wheatgrass (i.e. the Mixed Grassland of Figure 12), while the warm scenario causes a shift to Northern Wheatgrass – Needle-and-thread (i.e. the Dry Mixed Grassland of Figure 11), and then to the even drier Blue Grama – Needle-and-thread – Western Wheatgrass.

```
┌─────────────┐          ┌──────────────────────┐              ┌──────────────┐
│  Crested    │          │ ┌──────────────────┐ │  climate     │  Blue Grama  │
│ Wheatgrass  │ ←exotic  │ │    Northern      │ │  change      │  – Needle-   │
│ – native    │ invasion │ │  Wheatgrass –    │ │  (cool       │  and-thread –│
│  grasses    │          │ │  Needle-and-     │ │  scenario)   │   Western    │
└─────────────┘          │ │   thread         │ │   →          │  Wheatgrass  │
                         │ │  (reference      │ │              └──────────────┘
                         │ │   community)     │ │
                         │ └──────────────────┘ │  climate     ┌──────────────┐   climate     ┌──────────────┐
                         │                      │  change      │  Blue Grama  │   change      │              │
                         │   ↓heavy grazing     │  (warm       │  – Needle-   │   (warm       │ Blue Grama - │
                         │     recovery↑        │  scenario)   │  and-thread –│   scenario)   │ Buffalograss │
                         │ ┌──────────────────┐ │   →          │   Western    │    →          │              │
                         │ │  Needle-and-     │ │              │  Wheatgrass  │               └──────────────┘
                         │ │   thread –       │ │              └──────────────┘
                         │ │  Wheatgrass –    │ │
                         │ │  June Grass –    │ │
                         │ │  Blue Grama      │ │
                         │ └──────────────────┘ │
                         │                      │
                         │   ↓heavy grazing     │
                         │     recovery↑        │
                         │ ┌──────────────────┐ │
                         │ │  Blue Grama –    │ │
                         │ │  Needle-and-     │ │
                         │ │  thread – June   │ │
                         │ │  Grass – Western │ │
                         │ │  Wheatgrass      │ │
                         │ └──────────────────┘ │
                         └──────────────────────┘
```

Figure 11. State-and-transition diagram for the Loam Ecosite in the Dry Mixed Grassland of southwestern Saskatchewan.

Crested Wheatgrass – native grasses	←exotic invasion	Western Porcupine Grass – Northern Wheatgrass (reference community)	climate change (cool scenario) →	Northern Wheatgrass – Needle-and-thread	climate change (cool scenario) →	Blue Grama – Needle-and-thread – Western Wheatgrass
			climate change (warm scenario) →	Northern Wheatgrass – Needle-and-thread	climate change (warm scenario) →	Blue Grama – Needle-and-thread – Western Wheatgrass
		↓heavy grazing recovery↑				
		Western Porcupine Grass – Northern Wheatgrass – Sedge – Pasture Sage				
		↓heavy grazing recovery↑				
		Blue Grama – Pasture Sage – June Grass				

Figure 12. State-and-transition diagram for the Loam Ecosite in the Mixed Grassland of central Saskatchewan.

```
                              ┌─────────────────┐
                              │   Snowberry –   │
                              │  native grasses │
                              └─────────────────┘

                                  ↓fire   no fire↑

┌──────────┐              ╔═══════════════════╗        climate      ┌──────────────┐
│  Smooth  │              ║ ┌───────────────┐ ║        change        │   Western    │
│  Brome – │  ←exotic     ║ │ Plains Rough  │ ║        (cool         │  Porcupine   │
│  native  │  invasion    ║ │   Fescue –    │ ║        scenario)     │   Grass –    │
│  grasses │              ║ │   Northern    │ ║          →           │   Northern   │
└──────────┘              ║ │  Wheatgrass – │ ║                      │  Wheatgrass  │
                          ║ │   Western     │ ║                      └──────────────┘
┌──────────┐              ║ │ Porcupine     │ ║
│ Kentucky │              ║ │ Grass         │ ║        climate    ┌──────────────┐ climate   ┌──────────────┐
│Bluegrass–│  ←exotic     ║ │ (reference    │ ║        change     │   Northern   │ change    │ Blue Grama   │
│  native  │  invasion    ║ │  community)   │ ║        (warm      │  Wheatgrass  │ (warm     │ – Needle-    │
│  grasses │              ║ └───────────────┘ ║        scenario)  │  – Needle-   │ scenario) │ and-thread – │
└──────────┘              ║                   ║          →        │  and-thread  │   →       │   Western    │
                          ║                   ║                   └──────────────┘           │  Wheatgrass  │
                          ║  ↓heavy grazing   ║                                              └──────────────┘
                          ║    recovery↑      ║
                          ║ ┌───────────────┐ ║
                          ║ │    Western    │ ║
                          ║ │ Porcupine Grass│ ║
                          ║ │  – Northern   │ ║
                          ║ │  Wheatgrass – │ ║
                          ║ │ Sedge – Pasture│ ║
                          ║ │     Sage      │ ║
                          ║ └───────────────┘ ║
                          ║                   ║
                          ║  ↓heavy grazing   ║
                          ║    recovery↑      ║
                          ║ ┌───────────────┐ ║
                          ║ │ Sedge – Pasture│ ║
                          ║ │ Sage – Western │ ║
                          ║ │ Porcupine Grass│ ║
                          ║ │  – Northern   │ ║
                          ║ │   Wheatgrass  │ ║
                          ║ └───────────────┘ ║
                          ╚═══════════════════╝
```

Figure 13. State-and-transition diagram for the Loam Ecosite in the Aspen Parkland of north-central Saskatchewan.

3.4 Discussion of vegetation zonation

There is little other literature on predicting zonation of different types of grassland, with most modeling focused on the transition from grassland to forest. Epstein et al. (1998) modeled the ecoclimatic distributions of individual plant species in U.S. Great Plains grasslands. Sykes (2008) used a simulation model to predict changes in botanical composition of grasslands at Saskatoon and Melfort. Under the current climate (1961-90), plains rough fescue was predicted to be the dominant species, while climate change scenarios for the 2020s, 2050s, and 2080s

caused a gradual shift to dominance by northern wheatgrass. This is consistent with the shift from aspen parkland to mixed prairie shown in the current models.

While the results have been discussed as shifts in vegetation zones, it would be more accurate to describe them as "shifts to a climate that is capable of supporting a different vegetation zone". Even if these climatic shifts occur by the 2050s or 2080s, there may be a lag in the change in vegetation composition. The perennial plants already established may persist even as the climate becomes less suitable for them, while new southern plant species may be unable to migrate northward as fast as the climate changes. The rate and success of migration will vary among species because of differences in environmental tolerance, genetic variation, and dispersal rates. This variation implies that new combinations of species (i.e. new plant communities) could emerge (Singh and Wheaton 1991, Peters 1992), as occurred in the northward migration of tree species following deglaciation (Davis 1981). Many wind-dispersed species can easily migrate fast enough to keep up with climatic warming, but others may be limited by slow dispersal or restriction to particular habitats (Malcolm and Pitelka 2000).

Some adjustment will occur through changes in the abundances of species that are already present. For example, increase in shortgrasses could initially occur by increase in the proportion of blue grama, which is already a widely distributed shortgrass in Canadian grassland. Migration of buffalo grass, the other major component of U.S. shortgrass prairie, into the region can be expected to be a much slower process. Buffalo grass actually occurs in Saskatchewan and Manitoba, but as a "species at risk" with a tiny population along the Souris River. Assuming a larger role in future grasslands would require substantial migration.

Because of these factors that complicate the adjustment of vegetation to climate change, the results should not be interpreted as showing the actual composition of the vegetation in the 2050s, but rather as showing the direction of change.

One of the major expected trends relates to the proportions of warm-season and cool-season plant species. Warm-season species have the C_4 photosynthetic pathway, and are adapted to growth at higher temperatures. Cool-season species have the C_3 pathway, and grow best when it is cooler. Where warm-season and cool-season species occur together, the cool-season species tend to grow earlier in the season. These temperature adaptations are also reflected in the geographic distributions of species. Across the Canadian and U.S. Great Plains, Thorpe et al. (2004) found that dominance by warm-season species increases with annual growing degree-days, and is higher on sand than on loam. Canadian and northern U.S. grasslands with cooler regional climates are dominated by cool-season grasses such as speargrasses, wheatgrasses and bluegrasses, while warm-season grasses such as bluestems, gramas, and switchgrass become more abundant in the warmer climates further south. The relationship with soil texture can be seen in Canadian grasslands, where warm-season grasses such as sand reedgrass and sand dropseed are more common on sands than on finer-textured soils. Other studies based on U.S. data have obtained similar results (Paruelo and Lauenroth 1996, Epstein et al. 1997a, 1998). Collatz et al. (1998) and Winslow et al. (2003) developed physiological models to explain the differences in distribution. Models of the impacts of climate change have predicted decreasing proportions of cool-season species and shifts toward warm-season dominance in the northern Great Plains (Coffin and Lauenroth 1996, Epstein et al. 2002). These trends could be modified

by changes in seasonal distribution of precipitation. Winslow et al. (2003) and Epstein et al. (1997a) modeled the proportions of C_3 and C_4 species as influenced by the seasonal availability of moisture, and concluded that a higher proportion in spring should favour C_3s while a higher proportion in summer should favour C_4s.

The direct fertilization effect of rising CO_2 concentrations theoretically provides a greater relative benefit to cool-season than warm-season species (Long and Hutchin 1991, Parton et al. 1994, Polley 1997). However, experimental results have shown that this advantage may be eliminated under dry grassland conditions (Nie et al. 1992; Campbell and Stafford Smith 2000). In Colorado shortgrass prairie, Morgan et al. (2004) found that increased CO_2 favoured one of the dominant C_3 grasses (needle-and-thread) but not the other (western wheat-grass), over the dominant C_4 (blue grama). They suggested that CO_2 enrichment could favour increases in needle-and-thread, which if true would be opposed to the climatic effect favouring increases in blue grama. In some systems, elevated CO_2 is predicted to increase woody cover at the expense of grasses (Campbell and Stafford Smith 2000). Polley (1997) suggested that in systems where there is a tension between shrub and grass cover, CO_2 fertilization may slow the depletion of upper soil moisture by grasses, increasing percolation to deeper layers that support shrubs. In an experiment with CO_2 enrichment in shortgrass prairie, the sub-shrub pasture sage showed a clear increase in cover (Morgan et al. 2007). However, in pot experiments with sagebrush steppe species, Lucash et al. (2005) found that grass growth is more responsive than sagebrush growth to increasing CO_2. In managed grasslands, CO_2 enrichment has been observed to favour legumes over grasses (Campbell and Stafford Smith 2000).

The shifts in zonation shown by the models imply that the climate will become less suitable for trees and shrubs and more suitable for open grassland. While we do not know how fast forest will be replaced by parkland, and parkland by grassland, the implied trend is toward declining woody cover. This could occur by failure of tree regeneration following disturbances (e.g. fire, timber harvesting), or it could occur by dieback of mature trees during drought years (see Section 5.4). Under the current climate, grasslands in the moister ecoregions such as Aspen Parkland are continually being invaded by shrubs and trees, depending on disturbance regimes. The models imply that this woody encroachment should decrease over time as the climate becomes less suitable for woody plants. Both declining tree cover and reduced woody encroachment could significantly increase the area of grassland in the Prairies, which would be beneficial for livestock grazing.

Neilson (2003), in developing models for predicting vegetation zonation, used the two-layer hypothesis which says that grasses draw water mainly from the upper soil, while woody plants draw from both upper and lower layers. Neilson argued that concentration of precipitation in summer favours grasses over woody plants, depending on the total annual precipitation. Summer precipitation tends to be immediately transpired, limiting recharge of deep soil moisture which is needed to sustain woody plants. It also tends to be variable because it comes mainly from convective events, leading to extended dry periods which trees may not survive. Models based on these relationships successfully predict the "Prairie Peninsula" of the Upper Midwest, which has relatively high precipitation (equal to forested regions further east), but with higher concentration in summer. Conversely, the northwestern U.S. has a summer-dry, winter-wet regime which favours deep-rooted woody plants, even in the interior where total precipitation is

low. In sagebrush-bunchgrass steppe, Svejcar et al. (2003) hypothesized that a shift to more summer precipitation would favour grasses over shrubs, and the reverse for a shift to more winter precipitation, although experimental results from artificial water treatments did not support these hypotheses. In the current analysis, the climate change scenarios show declining summer concentration of precipitation (Figure 5). However, the predicted change is small, with the most extreme scenario for the 2080s still showing more than 60% of annual precipitation falling in the five-month period of May through September. This summer concentration will continue to favour grasses over trees in transitional areas.

4 IMPACTS OF CLIMATE CHANGE ON GRASSLAND PRODUCTION

4.1 Methods

Analysis of the impacts of climate change on grassland production was based on existing models (Thorpe et al. 2004, 2008, Thorpe 2007b). The general approach was to relate measured grassland production to average climate (1961-90 normals) at the measurement locations, using multiple linear regression. Data were assembled for grasslands spanning the Prairie Provinces and the Great Plains states to the south, in order to develop statistical relationships that apply to the entire range of present and future climates. Thorpe (2007b) limited the dataset to loamy range sites (i.e. well-drained sites with loam to clay loam soils), to remove the effect of soil variation, resulting in 47 data points. For the current project, this dataset was reanalyzed using the same three climatic variables as in the zonation analysis: annual precipitation (PPT), annual potential evapotranspiration (PET), and proportion of precipitation falling in May through September (MAYSEP). The best regression model was Equation 1 (notes that units are kg/ha for production and mm for PPT and PET, while MAYSEP is a proportion).

Equation 1: Production = -3004 + (4.72*PPT) + (-0.98*PET) + (5316*MAYSEP)
R^2 = 58.6%; all coefficients statistically significant (p<0.05)

In the previous studies, it was found that a somewhat closer-fitting regression could be developed for Canada-only data. Reanalysis based on the standard three variables used in the current study gave Equation 2.

Equation 2: ln(production) = 2.973 + (0.00453*PPT) + (-0.00259*PET) + (6.187*MAYSEP)
R^2 = 68.7%; all coefficients statistically significant (p<0.05)

As in the previous studies, future production was predicted by applying Equation 1 to baseline and future climate data, calculating the percent change in predicted production, and applying this percent change to the baseline production predicted by Equation 2. These calculations were applied to each gridpoint in the baseline climate grid (approximately 3 km east-west by 5 km north-south) to give a data surface for grassland production. GIS software was then used to develop contour maps for production. It should be noted that these maps apply to native grasslands on loamy range sites. For other range sites, production can be estimated using average ratios (e.g. ratio of production on wet meadow sites to production on loamy sites) (Thorpe 2007b).

4.2 Production results

Production results are presented in two ways: as maps with production contours for the baseline and the 2080s (Figures 14 to 16), and as a graph showing the changes through time for individual locations (Figure 17).

The map for the baseline climate (Figure 14) conforms with our understanding of regional production differences, indicating that the model is working. The change from the baseline to the 2080s is slight for the cool scenario (Figure 15), whereas the warm scenario shows moderate shifts towards lower production (Figure 16).
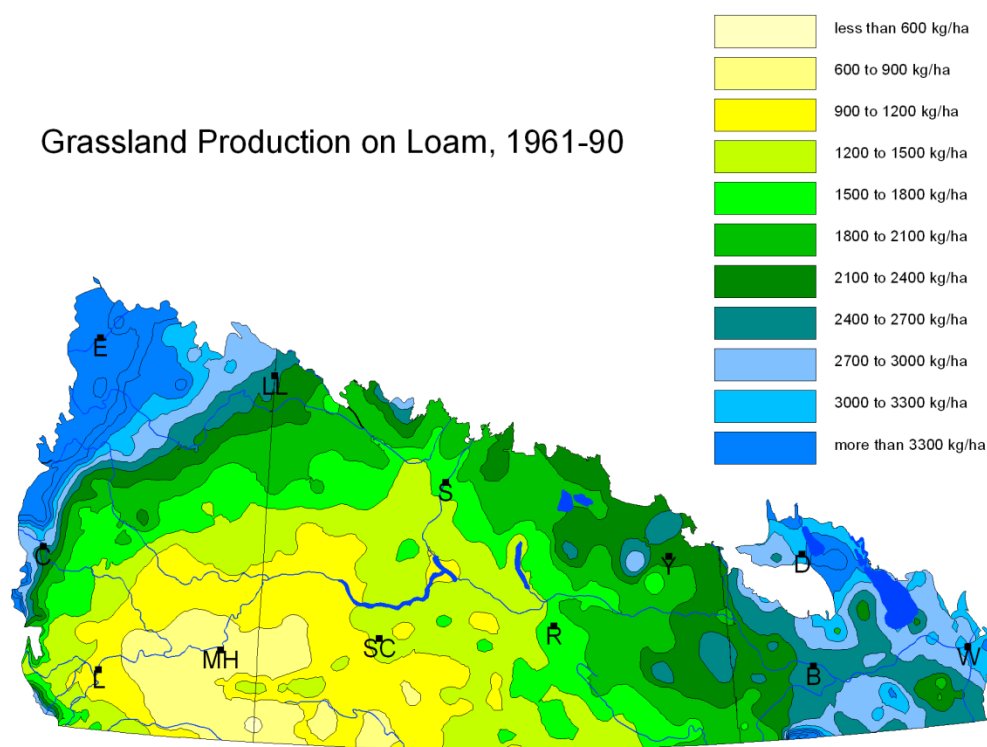

Figure 14. Predicted grassland production on Loam Ecosite based on climate data for the 1961-90 baseline.
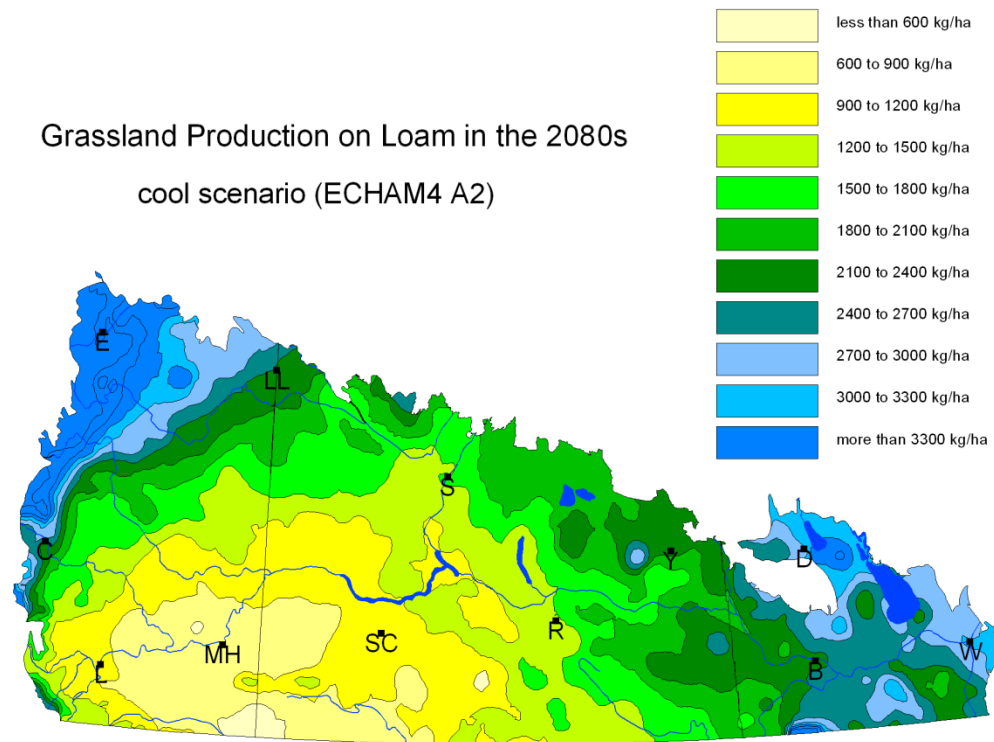
Figure 15. Predicted grassland production on Loam Ecosite based on the cool scenario for the 2080s.
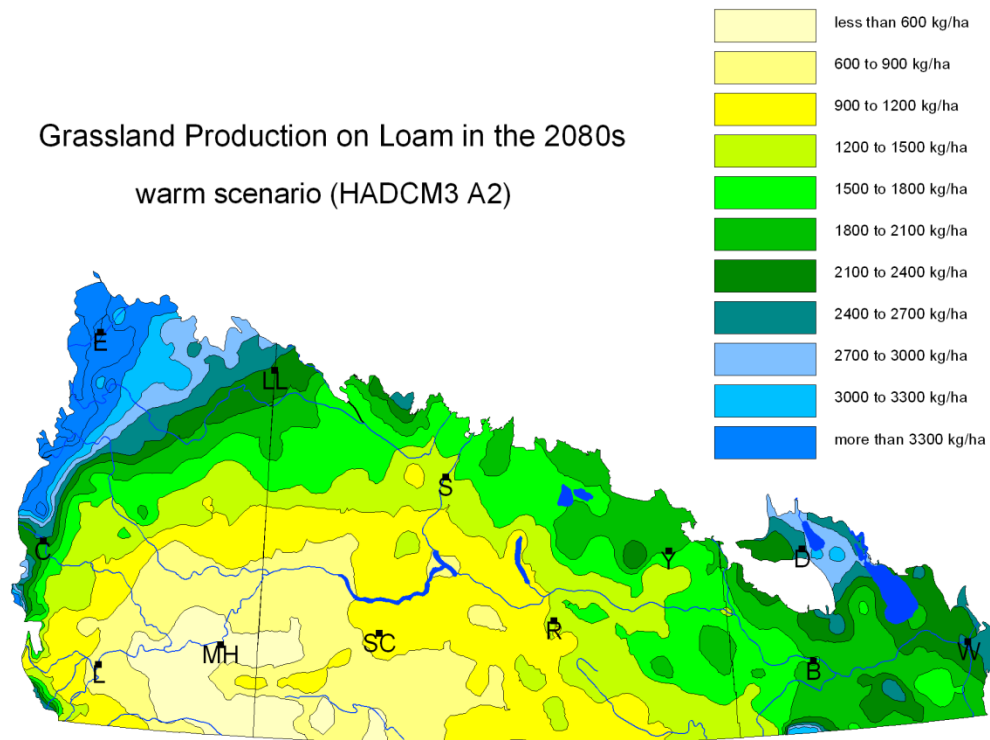
Figure 16. Predicted grassland production on Loam Ecosite based on the warm scenario for the 2080s.

Figure 17 provides a different view of production changes, by tracking them for individual locations distributed across the region. The location labelled "49°N/110°W" is the corner of Alberta, Saskatchewan, and Montana, the driest part of the region. The location labelled "SE Manitoba" is the southeast corner of the Prairie Ecozone, at the U.S. border south of Winnipeg. This figure shows that production decreases for both scenarios and all locations, with greater decreases for the warm scenario. For the cool scenario, decreases from the baseline to the 2080s are modest, ranging from 83 to 165 kg/ha among locations. For the warm scenario, decreases range from 161 to 632 kg/ha among locations. The greater decreases in the warm scenario are most evident for locations in the eastern part of the region: Estevan, Dauphin, and SE Manitoba. The warm scenario in these locations leads to substantial decreases in production.

Grassland Production on Loam (kg/ha)
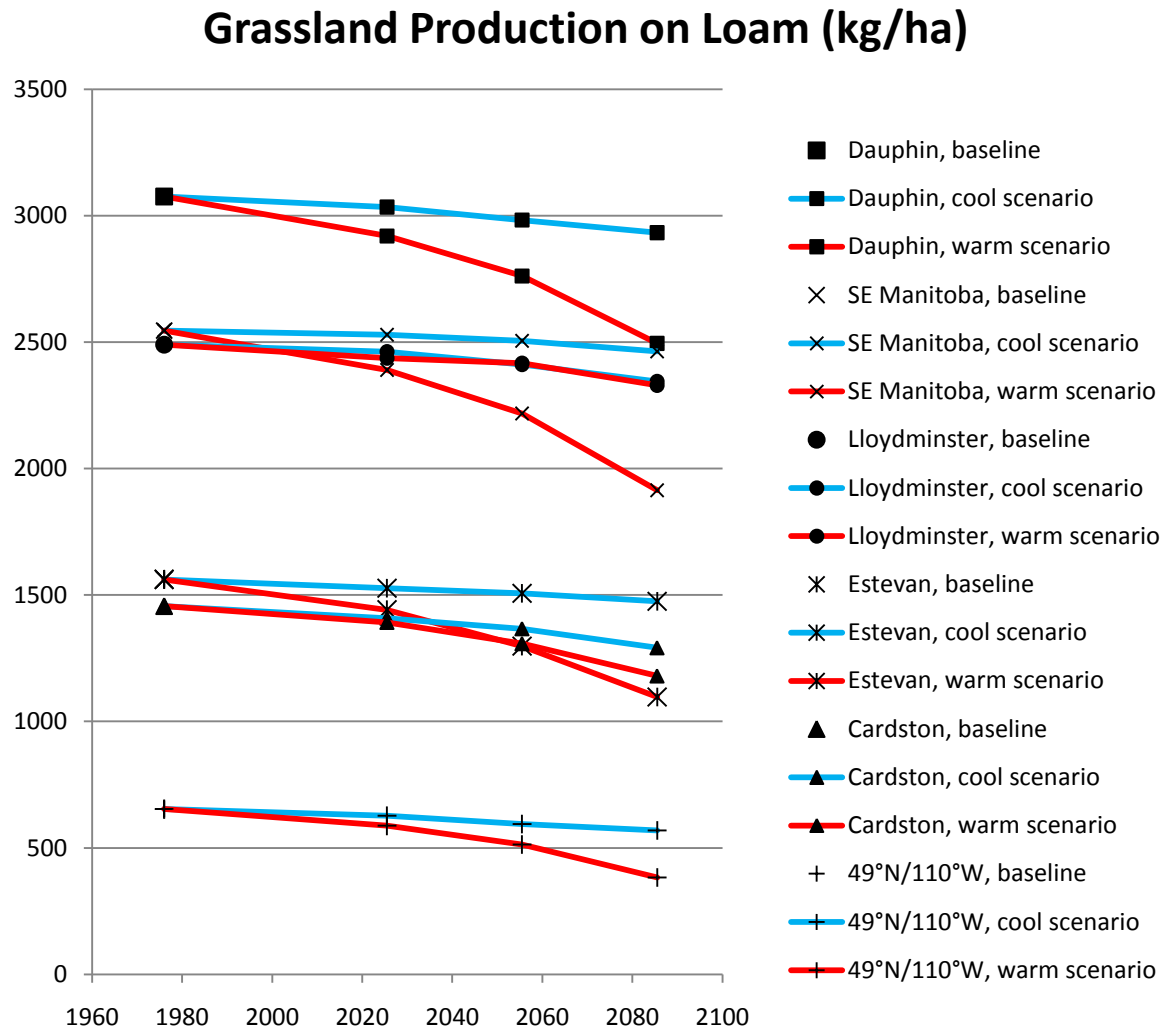
Figure 17. Trends from the 1961-90 baseline to the 2080s in predicted production from high-condition grassland on loamy upland soils at six locations.

4.3 Discussion of production results

Modeling based on the warmer climate change scenario shows significant decreases in grassland production (up to 40% losses in some areas). On the other hand, the cool scenario shows negligible changes in production. Both scenarios show significant warming, with much higher potential evapotranspiration than in the baseline climate. It might be thought that this would lead to more drastic losses of production, as implied by talk of "desertification" in some quarters. However, the regression model is more strongly influenced by precipitation than by potential evapotranspiration, and only small changes in precipitation are predicted in the climate change scenarios.

Other studies have shown the strong relationship between annual precipitation and grassland production, across climates varying widely in temperature (Sims et al. 1978, Sala et al. 1988,

Epstein et al. 1996, 1998). In the U.S. both precipitation and grassland production show a simple westward decline across the Great Plains (Schimel et al. 1990). Campbell et al. (1997) generalized that 90% of the variance in production in grassland systems can be accounted for by annual precipitation. According to Lauenroth and Sala (1992), precipitation has a large explanatory effect for production in arid and semiarid regions because it is both low and variable. It would appear that the primary limiting factor for grassland production is the amount of water input from annual precipitation. Rises in temperature have a secondary negative effect (e.g. Sims et al. 1978, Epstein et al. 1996, 1997b), possibly related to increases in direct evaporation from the soil surface. Decreases in the proportion of annual precipitation falling in summer (as expressed by the MAYSEP variable used in the current analysis) also have a secondary negative effect, probably because the proportion of annual precipitation lost in spring runoff is higher if MAYSEP is lower. However, a significant part of fall and winter precipitation goes to recharging soil moisture, which in turn is used by plants in the growing season, so winter precipitation should not be considered inconsequential for production.

The relatively modest changes in production predicted by this analysis receive support from several ecosystem simulation studies in U.S. grasslands using older GCM scenarios. Schimel et al. (1990) applied the CENTURY model to a site in central U.S., using the GISS scenario for CO_2 doubling. Both temperature and precipitation increased in this scenario. The model predicted an increase in net primary production, related to both the increase in precipitation and the increase in nitrogen availability with faster decomposition at warmer temperatures. Schimel et al. (1991) extended CENTURY simulations to the entire Great Plains using spatial data for climate and soil texture. This again showed an increase in net primary production for the northern plains, attributed to the increase in precipitation in the GISS scenario. Parton et al. (1996) and Ojima et al. (1996) applied CENTURY to grassland sites around the world, using the GFDL and CCC climate change scenarios, and obtained similar results to the Schimel studies for sites in Montana and Colorado. Similar results were obtained by Baker et al. (1993), who applied the SPUR model to U.S. rangelands, using the GISS, GFDL, and UKMO climate change scenarios. All of the simulations resulted in an increase in grassland production in the northern part of the Great Plains, except that the GFDL scenario showed a decrease in the eastern part of the northern plains (North and South Dakota). The three climate change scenarios showed a decrease in soil organic matter in the northern plains, related to faster decomposition at higher temperatures, and a decrease in the carbon: nitrogen ratio in soil.

While the changes are more moderate than might be expected from the large predicted warming, those predicted by the warmer scenario would have significant impacts. A 25% decrease in average production implies a 25% decrease in sustainable stocking rates, which would negatively impact on financial returns to livestock producers, other factors being equal. It also implies a shift to a lower, less dense grassland community, which could change habitat properties for grassland birds or other wildlife. On the other hand, if the future climate were to follow the cooler scenario, these impacts could be minor.

In addition to effects on forage quantity, climate change could affect forage quality. Craine et al. (2009) analyzed the quality of forage used by cattle in different regions of the United States. Both crude protein and digestible organic matter tend to decrease with mean annual temperature, and increase with annual precipitation. From these trends, they concluded that a rise in

temperature or a decrease in precipitation will tend to reduce forage quality. Declines in forage quality would tend to exacerbate declines in production, because grazers would have to consume a greater amount of forage for a given weight gain.

This analysis has considered only climatic effects on grassland production. Another factor that could affect production is the fertilizing effect of rising CO_2 concentrations. The rate of photosynthesis increases with atmospheric CO_2 concentration, with C_4 species reaching saturation (i.e. not responding to further increases) before C_3 species (Polley 1997). Increasing CO_2 also reduces stomatal conductance and leaf transpiration rates, meaning that water use efficiency (i.e. amount of production per unit of transpiration) increases and soil moisture is not used up as fast (Polley 1997). Parton et al. (1996) and Ojima et al. (1996) used an ecosystem model (CENTURY) to simulate the effect of doubling CO_2 concentrations on grassland sites around the world, and found increases in production. Similar results were obtained by Baker et al. (1993), who used the SPUR model to simulate CO_2 doubling without climate change in U.S. rangelands. Field experiments with CO_2 enrichment chambers in grasslands around the world have shown increases in production averaging 17%, and ranging from 0 to 30%, with doubling of ambient CO_2 concentrations (Campbell and Stafford Smith 2000). Experiments of this type in Colorado shortgrass prairie averaged 41% production increases with CO_2 doubling (Morgan et al. 2004). This study also showed higher soil moisture and leaf water potential, demonstrating the benefit of increased water use efficiency.

Comparing grassland experiments around the globe, Campbell and Stafford Smith (2000) found no relationship between the response to CO_2 and the overall level of production. A greater response to CO_2 is often observed when water is limited as in dry years, probably because of increases in water use efficiency (Polley 1997, Campbell and Stafford-Smith 2000). In fact, increases in grassland growth are attributed primarily to increases in water use efficiency, and only secondarily to increases in photosynthetic rate (Morgan et al. 2004). However these effects are relative to a given climatic state. The shift to a drier climate will tend to reduce production, and the extent to which the CO_2 fertilization effect will compensate for the climatic drying effect is uncertain.

Other factors, such as heavy grazing, nutrient deficiency, or low temperature, could reduce or eliminate the ability of plants to take advantage of the CO_2 fertilization effect (Polley 1997). Besides the effect on forage quantity, some research has shown a reduction in forage quality (lower N, higher carbohydrates) with CO_2 fertilization (Campbell and Stafford Smith 2000). Morgan et al. (2004) found a significant decrease in forage digestibility with CO_2 enrichment in shortgrass prairie, implying that while forage production may increase, cattle would have to consume more forage to achieve comparable weight gains.

CO_2 fertilization provides a greater benefit in terms of photosynthetic rate to C_3 than C_4 species (Long and Hutchin 1991, Parton et al. 1994, Polley 1997). However, experimental results have shown that this advantage is reduced under field conditions in dry grasslands (Nie et al. 1992, Polley 1997, Campbell and Stafford Smith 2000). The increase in water use efficiency occurs in both C_3 and C_4 species, probably explaining why growth responses do not differ more than they do (Morgan et al. 2004). In Colorado shortgrass prairie, one of the dominant C_3 species (needle-

and-thread) responded strongly to CO_2 enrichment whereas the other dominant C_3 (western wheatgrass) and the dominant C_4 (blue grama) showed no significant response.

Changes in grassland production, whether caused by climate change or CO_2 fertilization, are important to the livestock industry because they imply changes in sustainable stocking rates. However, these changes occur in the context of other economic factors affecting livestock producers. Campbell and Stafford Smith (2000) cautioned that changes in production may not be so significant economically once other factors (biophysical, market, or institutional) are taken into account   Changes in species composition may be as important as changes in production (Campbell and Stafford Smith 2000).

5 CLIMATE CHANGE AND DROUGHT

5.1 Drought in the Prairies

The analysis in the preceding section dealt with average levels of production. These are important, because they determine the long-term grazing capacities that are used in planning of grazing operations (Wroe et al. 1988, Abouguendia 1990). However, our grasslands show wide year-to-year variation in production related to weather.   Study of trends in long-term research sites has shown that grassland production is more variable than that of either forests (moister climates) or deserts (drier climates), indicating that grasslands could be the most responsive to climate change (Knapp and Smith 2001). For grazing operations, any increase in the frequency or duration of drought could be as important as changes in average production levels.

The Prairie Ecozone is one of the more drought-susceptible areas of Canada, and multiyear droughts have occurred in Canada during the 1890s, 1910s, 1930s, 1960s and 1980s, and most recently at the beginning of the 2000s (Bonsal 2008). In the future the prairies may be even more susceptible to drought than the rest of Canada.   For the period 1900 to 1998 there was a significant increase in annual precipitation across southern Canada with the exception of southern Alberta and Saskatchewan (Bonsal 2008).   Southwestern Saskatchewan and southeastern Alberta have the both the lowest precipitation and the highest coefficient of variation in precipitation (Sauchyn et al. 2009).

Bonsal and Regier (2006, 2007) and Bonsal (2008) reviewed historical droughts in the Canadian Prairies. The drought of 2001-2002 was the most severe on record at several stations (Bonsal and Regier 2007). However, the drought of 1915 to the 1930s had much greater spatial extent. Prior to the historical period, the occurrence of even more prolonged droughts has been inferred from tree rings, lake sediments, and dune activation. The 20th Century may have been the most benign of the past 750 years with respect to drought occurrence (Sauchyn et al. 2009).

Several studies have predicted increasing drought in the coming century. Sheffield and Wood (2007) defined a "drought month" as having simulated soil moisture below the once-per-10 years threshold for that month based on the 20th Century distribution. They defined droughts in terms of consecutive sequences of dry months. Their analysis of GCM outputs indicated increasing frequency and extent of droughts for Western North America to 2090. Wang (2005) presented similar analysis.

Based on transient runs of a global climate model, Kharin and Zwiers (2000, 2005) found that the relative increase in extreme daily precipitation totals will be greater than the increase in average precipitation. However, they found that changes in the lengths of wet and dry periods will be modest outside of the tropics, so their results do not specifically indicate increased drought in temperate latitudes.

For the Canadian Prairies, Bonsal and Regier (2006) projected the Standardized Precipitation Index (SPI) and Palmer Drought Severity Index (PDSI) into the future based on analysis of GCM outputs. SPI is based on standardized departures in precipitation from a probability distribution based on historic records. PDSI is based on a water balance approach, so is affected by temperature (through evaporative losses) as well as by precipitation. The climatic record from 1915 to 2002 was used to characterize the baseline distribution for each index. The analysis showed relatively benign results based on SPI, because precipitation is generally predicted to increase, but not based on PDSI which is affected by increasing temperatures. In an 88 year future series, the worst drought on record (1924 for spatial extent and 1931 for severity) is exceeded over 20 times in a warm-dry scenario, 6-8 times in a warm-wet scenario, and 2-4 times in a cool-wet scenario.

5.2 Short term drought effects on grassland

The effects of drought on grasslands are well understood. The immediate effect is a decrease in production.

The longest record of grassland production in the Prairies is at Agriculture Canada's research station near Manyberries in southeastern Alberta (Smoliak 1986, W. Willms, Agriculture Canada, personal communication) (Figure 18). While the average production over this period was 426 kg/ha, yearly production varied from lows of 100 kg/ha to highs of 900 kg/ha. The low production through the 1930s, and the effects of more recent drought years such as 1961 and 1988, can be seen in these results.

Several studies have related this variation to yearly weather. Clarke et al. (1943) found that drought, as indicated by below normal April-to-July precipitation and decreased annual precipitation-to-evaporation ratios, caused substantial reduction in plant cover on both ungrazed areas and grazed areas. They demonstrated a close relationship between production and the precipitation-to-evaporation ratio over a nine year period. Smoliak (1956) later analyzed data for the 1930 to 1953 period at Manyberries and found that the variation in May-June precipitation explained 74% of the variation in forage yield. Smoliak (1986) analyzed the longer series of data from 1930 to 1983, and found that the best regression used September (of the previous year) plus April to July precipitation, which accounted for 59% of the variation in forage production. Thorpe et al. (2004) recalculated these regressions including the additional years of data collected at this site since Smoliak's analysis, and found that actual evapotranspiration (calculated from a water-balance model) had somewhat higher predictive value.
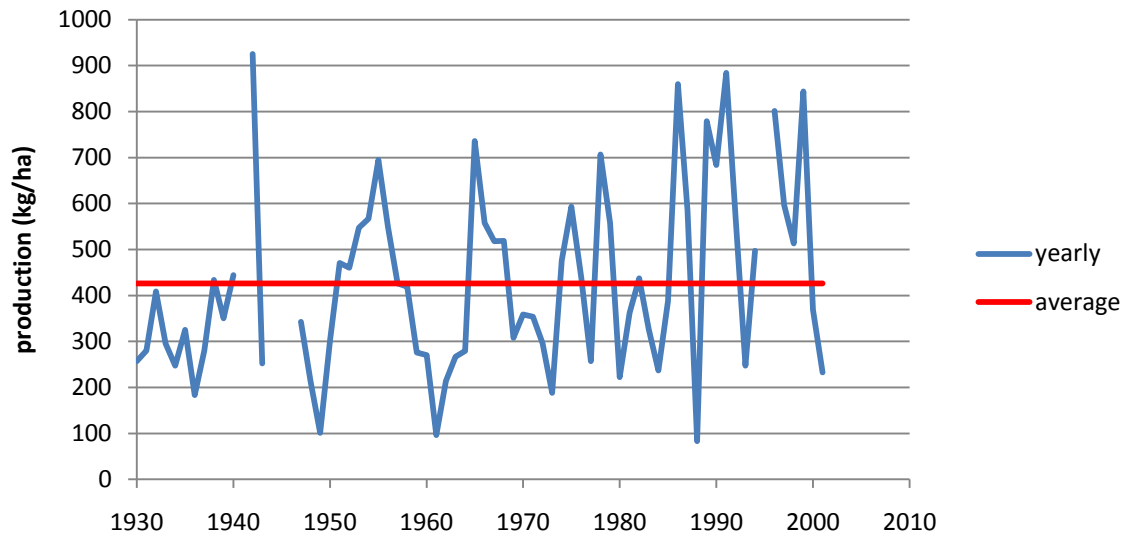
Figure 18. Year-to-year variation in production from mixed prairie at Manyberries, Alberta.

In the current project, we reanalyzed the Manyberries data using "forage-year precipitation" (i.e. the total from September of the previous year to August of the current year) as the predictive variable. The regression for the years from 1961-1990 explained 71.5% of the variation, slightly better than the regression based on AET. Predictions from this model closely track the measured yearly yields (Figure 19).

A comparable analysis for a long time series of production data in the Colorado shortgrass prairie showed a linear relationship between yearly forage production and yearly precipitation (Lauenroth and Sala 1992). The Colorado analysis differed in showing lags in recovery of production after some drought years, by contrast with the apparently immediate response in the Alberta data (Figure 19). In Wyoming mixed prairie, Derner and Hart (2007) found that peak standing crop is statistically related to April+May+June precipitation.

Kochy and Wilson (2004) confirmed this immediate response by experimentally watering mixed prairie plots in Saskachewan at levels corresponding to the driest, intermediate, and wettest years on record. At the end of one growing season there were significant differences in standing crop. Heitschmidt et al. (2005) artificially imposed a drought treatment on Montana mixed prairie, and found 20-40% reduction in production in the drought year, followed by substantial recovery during the first post-drought year, and nearly full recovery within two years. By contrast with these results indicating a direct tracking of yearly weather, Haddad et al. (2002) found that after a severe drought in tall-grass prairie, there was a two-year oscillation in grassland production for the next 15 years that was independent of the weather in those years.
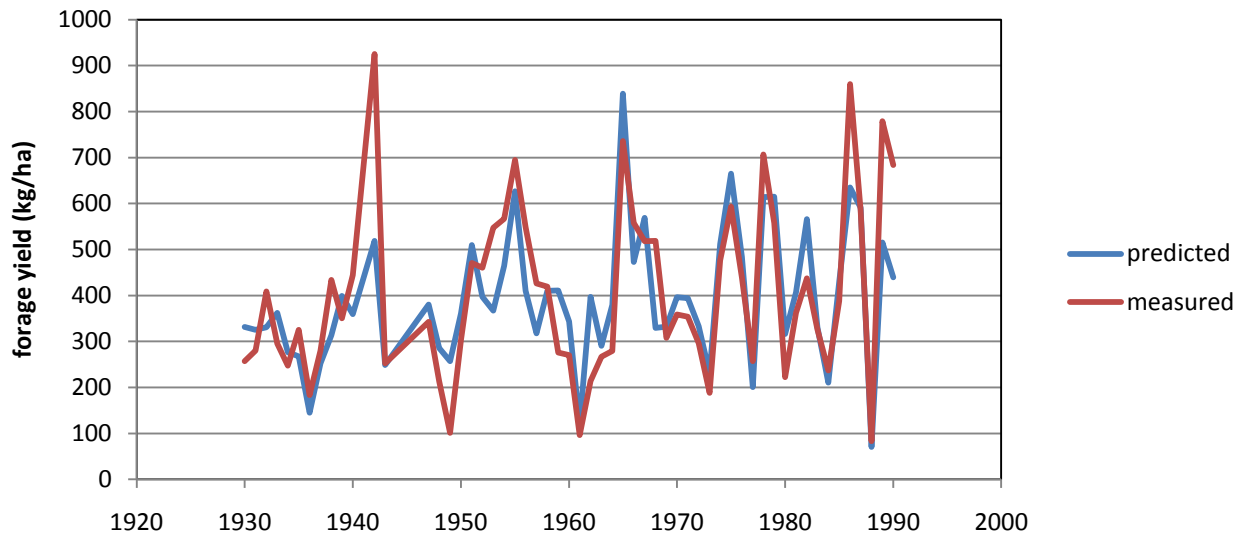
Figure 19. Predicted production of mixed prairie at Manyberries, Alberta, based on forage-year precipitation, compared with measured yield, for the period from 1930 to 1990.

Seasonal timing of precipitation is important. Heitschmidt et al. (1999) found that an artificially imposed late spring to early fall drought had relatively little effect on yield of a mixed prairie in Montana. They attributed this to the dominance of cool-season grasses, which complete most of their growth in spring. Conversely, an artificially imposed April-May-June drought reduced production considerably, mainly by reducing growth of cool-season perennials such as western wheatgrass (Heitschmidt et al. 2005). Based on these results, it might be thought that summer precipitation is unimportant in Northern Mixed Prairie. However, Heitschmidt and Vermeire (2006) showed that even after spring drought, mixed prairie in Montana responded to added moisture in summer by some increase in production, mainly of the warm-season grass blue grama. However, this response was limited to about 50% of the production that would have been produced in a year with normal spring moisture.

These results show that yearly moisture availability has a direct effect on yearly production in prairie grasslands. According to Coupland (1958), the immediate effect is a reduction in leaf height, while only with prolonged drought is there a reduction in plant cover. Conversely, with increased moisture availability, the first response is increase in leaf height.

One of the predictions from some climate models is a shift towards more extreme precipitation events. Fay et al. (2003) simulated this change in Kansas tallgrass prairie, and found that concentration of a given total amount of rainfall into fewer, larger events resulted in more runoff, leading to lower soil moisture and correspondingly lower production. Dominance by the C4 grass big bluestem was reduced, because it was stressed by the longer dry periods. Analysis of a long time series of production data in the Colorado shortgrass prairie showed that precipitation events of 15-30 mm had the largest effect on grassland production (Lauenroth and Sala 1992).

In the mixed prairie, drought interacts with other causes of reduced production, such as wildfire (Erichsen-Arychuk et al. 2002). Grazing can function similarly to drought in removing

protective plant cover and reducing litter. This increases insolation levels and wind speeds at ground level, both of which result in higher evaporative losses from the soil. According to Coupland (1958), moderate grazing is less important than drought in reducing plant cover, but heavy grazing is at least as influential. Heitschmidt et al. (2005) found that periodic grazing during drought in Montana mixed prairie had little effect on production. Willms et al. (1986) found that removing litter reduced yield both in foothills fescue at Stavely, AB, and in dry mixed prairie at Manyberries, AB. The reduction was about 25% (compared to control yields) in fescue, regardless of the number of years litter removal was repeated, whereas the reduction in dry mixed prairie ranged from 28% with one year of removal up to 57% with three years of removal. Willms et al. (1993) found that removing litter from mixed prairie near Lethbridge reduced herbage production by up to 60% in three out of four years studied. However, they found that the effect of litter was least in an extremely dry year (when there was no water to conserve) and in a relatively wet year (when there was sufficient water across all treatments). Litter amount was negatively correlated with heat accumulation (degree days above 5°C) in the soil, indicating the cooling effect of litter cover. Plants of all species (including increasers such as blue grama and sedges) responded to litter removal by reduced plant heights and yields.

5.3 Modeling of climate change, drought, and production

In order to model the effects of drought on production, we made use of the recently developed SRC Forage Calculator. The basis for this tool was an analysis of time series of production measurements in native rangeland reference areas. The objective of this analysis was to develop a method for predicting yearly production from yearly weather data. The best predictive variable was found to be "forage-year precipitation", defined as the sum of precipitation from the previous September to the current August. However, the prediction varied among locations with different average levels of precipitation and production. To make the prediction more general, the percent deviation in production was related to the percent deviation in precipitation. In each case, the current-year value was compared to the long-term average value, and percent deviation was calculated as: (current − average) / average. Over all available data, the following relationship was found:

% deviation in production = 1.078 * % deviation in forage-year precipitation.

The Forage Calculator applies this relationship to actual precipitation data for a location of interest, estimates the percent deviation in production, then applies this to the average production for the location to estimate current-year production.

Several locations across the Prairie Ecozone were chosen for modeling drought effects under climate change using this tool. The average production for the location was estimated from climatic normals (see Section 2). The historic time series of monthly precipitation values for the location was downloaded from http://cfs.nrcan.gc.ca/subsite/glfc-climate/namonthly. Forage-year precipitation (PPTfy) was calculated for each year in the 1961-90 period. The t-distribution based on the mean and standard deviation of this time-series was used to determine the PPTfy value below which 20% of the distribution lies. This value was considered the "dry threshold", because the driest 20% of years would fall below this threshold. This threshold was expressed as a percent deviation from the average PPTfy. The Forage Calculator was then used to estimate the percent deviation in production, which was applied to the average production value to

estimate the dry-threshold production level corresponding to the dry-threshold precipitation value.

The analysis as described above assumes that the historic variability in precipitation will persist into the future. This is the usual approach in studies of this kind (e.g. Bonsal and Regier 2006). However, there have also been indications from the literature that variability in precipitation may increase (see Section 5.1). While we have not yet seen an estimate of this increase, an indication of its effect can be obtained by arbitrarily increasing the variability in the above analysis. The standard deviation of annual precipitation values was assumed to increase 10% by the 2020s, 20% by the 2050s, and 30% by the 2080s. Dry-threshold values of precipitation and production were then recalculated.

For each location, the trends in average production and dry-threshold production were plotted from the 1961-90 baseline to the 2080s (Figures 20 to 25). Results are shown for the warm scenario only. Dry-threshold values trend downward, more or less in parallel with average production values. For example, for the southwest corner of Saskatchewan (49° N, 110° W), average production decreases from 653 kg/ha to 383 kg/ha, while the dry threshold decreases from 490 kg/ha to 291 kg/ha (assuming constant variability). This implies that by the 2080s under the warm scenario, the driest 20% of the years will have production less than 291 kg/ha. If we assume that variability in precipitation will increase, the dry threshold will be even lower (264 kg/ha by the 2080s). Increasing variability implies a broader distribution of yearly precipitation values, meaning that the lower tail of the distribution defined by the dry threshold will be further from the mean.

It should be remembered that the decreases in average production were more moderate under the cool scenario than the warm scenario (see Section 4), so the dry thresholds would also be more moderate. However, if we take the warm scenario as the "worst-case scenario", this analysis shows that not only will production be lower on average, but the dry years under that scenario will be extremely low in production.
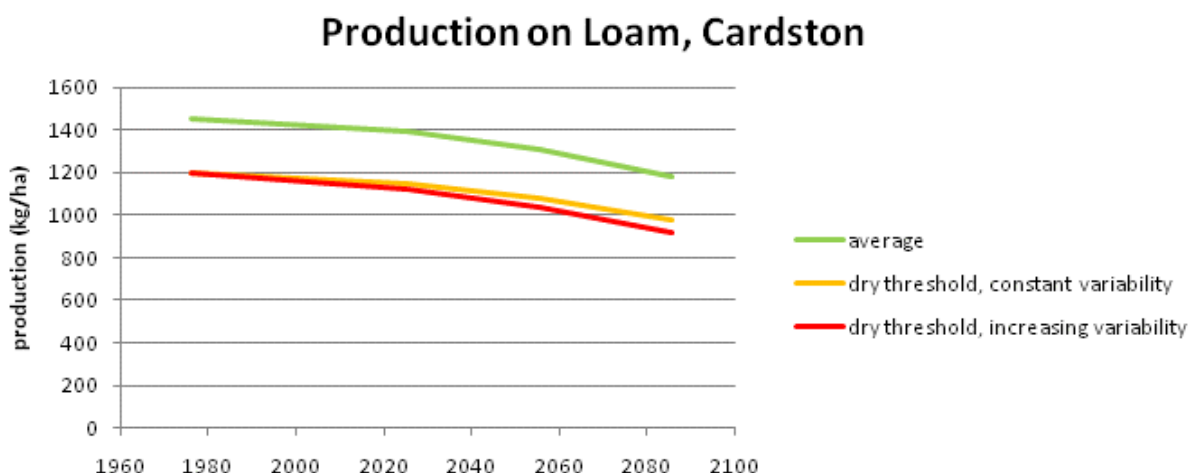
Figure 20. Predicted changes in average production and "dry threshold" production for Cardston, AB, under the warm scenario.

Production on Loam, Lloydminster
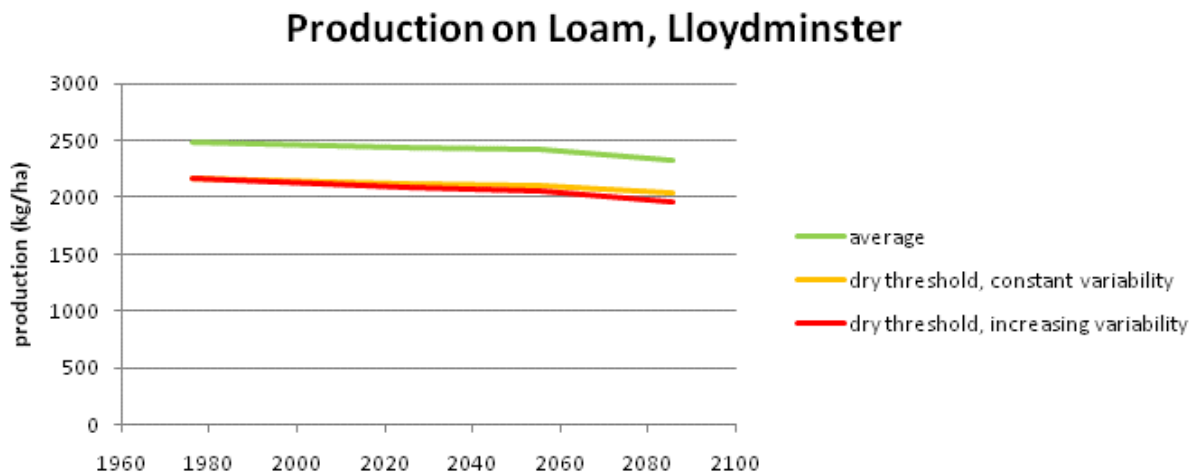
Figure 21. Predicted changes in average production and "dry threshold" production for Lloydminster, AB/SK, under the warm scenario.

Production on Loam, 49°N 110°W

Figure 22. Predicted changes in average production and "dry threshold" production for the corner of Saskatchewan, Alberta, and Montana under the warm scenario.

Production on Loam, Estevan

Figure 23. Predicted changes in average production and "dry threshold" production for Estevan, SK, under the warm scenario.

Production on Loam, Dauphin

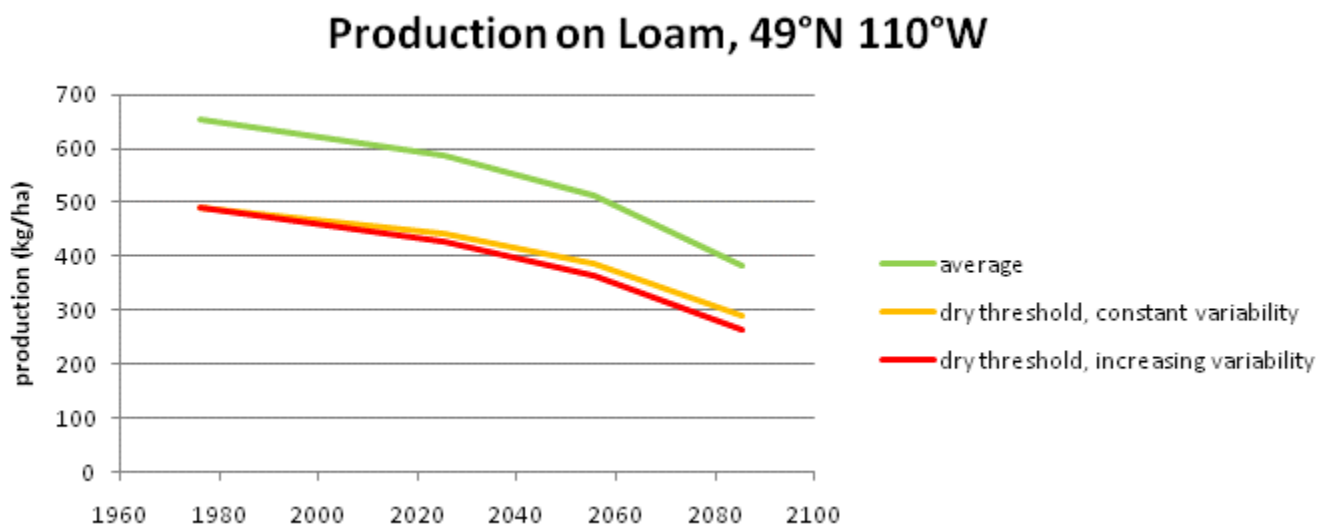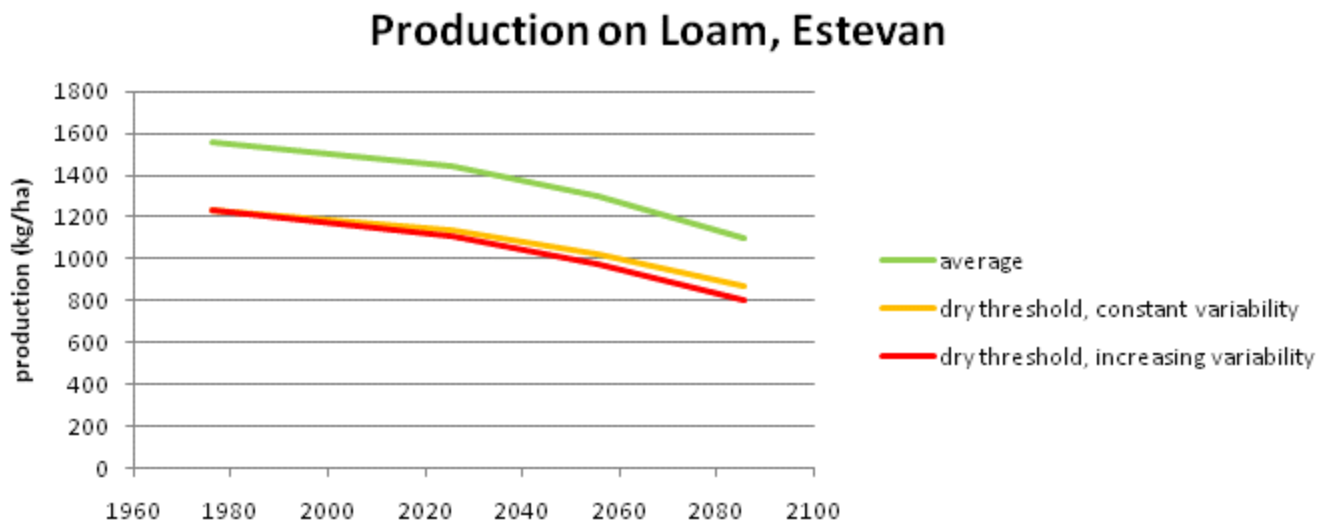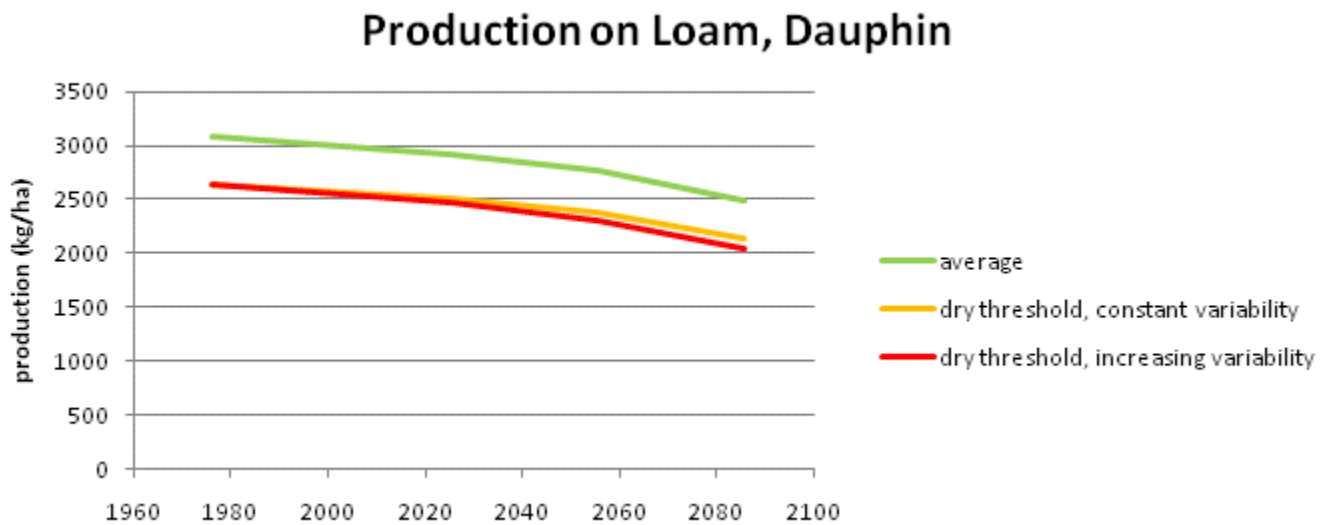**Figure 24. Predicted changes in average production and "dry-threshold" production for Dauphin, MB, under the warm scenario.**
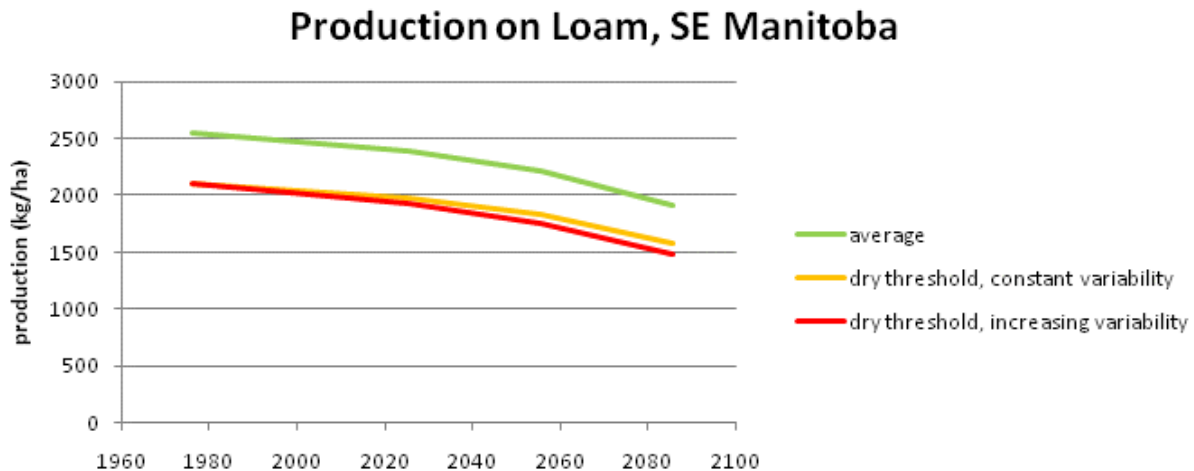
Production on Loam, SE Manitoba

Figure 25. Predicted changes in average production and "dry-threshold" production for the southeast corner of the Prairie Ecozone under the warm scenario.

It should be noted that increasing precipitation variability could also lead to increased occurrence of extreme wet years. Most of the attention by range managers has focused on the dry end of the cycle, which can be severely limiting to livestock producers. Because high precipitation leads to more grass growth, it is often assumed that wet years are benign. However, the record wet summer of 2010 created major challenges for producers, especially in Manitoba, through flooding of low-lying pastures. This impact of precipitation variability is much harder to model compared to production changes, because it is specific to particular topographic situations.

5.4 Long-term drought effects on grassland

While grasslands respond immediately to moisture stress through reduced growth, prolonged drought can result in plant mortality, particularly of the more robust, higher-producing grass species. The areas opened up by the loss of these species may be recolonized by the less productive, more drought-tolerant species. Plant mortality may also facilitate invasion by exotic species.

Some of the first studies of the effects of drought on grassland communities were conducted during the drought of the 1930s. Results of these studies were summarized by Coupland (1958a, 1959). One of the effects was decreasing plant cover in grasslands. For example, in Mixed Prairie in southeastern Alberta, basal cover declined from 26% to 14%. In North Dakota, a decrease from 30% to 13% was measured. The loss of basal cover was sometimes less in moderately grazed pastures, attributed to the effect of previous grazing in favoring drought-resistant species such as buffalo grass. Under heavy grazing, however, the loss in cover was greatest.

Changes in species composition were variable among regions (Coupland 1958a, 1959). In communities with both mid and short grasses, drought eliminated the midgrasses. In western Kansas, blue grama and buffalo grass were almost the only grasses surviving, indicating a shift to shortgrass prairie. Blue grama actually suffered less than buffalo grass, but buffalo grass

bounced back faster after the return of rain. In little bluestem communities in west-central Kansas, little bluestem was eliminated while blue grama and side-oats grama persisted. In tallgrass prairie, there was a shift from little bluestem to western wheatgrass, blue grama, porcupine grass, prairie and sand dropseed, and buffalo grass. The reduction of midgrasses was less severe in the northern part of the Great Plains. In western North Dakota and southeastern Montana, there was a decrease of blue grama, buffalo grass, needle-and-thread, western wheatgrass, June grass, little bluestem, and sand reedgrass, while a number of early-growing species (thread-leaved sedge, low sedge, Sandberg's bluegrass) persisted. A similar trend was seen in southeastern Alberta, where needle-and-thread, western wheatgrass, and blue grama decreased (but were not eliminated), while June grass and especially Sandberg's bluegrass increased. These species apparently evade drought by using the moisture available early in the season, then going dormant during the summer. It is not surprising that this strategy appeared in the northern areas, where snowmelt creates a temporary pulse of soil moisture in early spring. Native forbs also suffered great reductions. From Oklahoma to South Dakota, many of the less drought-tolerant forbs had practically disappeared, leaving only six to eight of the most xerophytic native species regularly represented. Scarlet mallow was the only generally distributed native, non-grassy species, aside from cactus, that increased in Mixed Prairie. Prickly-pear cactus increased so greatly in abundance that it constituted a serious weed problem. Coupland summarized the changes as follows: midgrass communities were replaced by mixedgrass communities, mixedgrass communities by shortgrass communities, and there were changes in composition within shortgrass communities.

Coupland (1958a, 1959) also summarized the succession following the return to normal moisture conditions. Badly denuded range went first to an annual weed stage (Russian-thistle, horseweed), followed by weedy grasses and some perennial forbs, then an early native grass stage with western wheatgrass and sand dropseed, then a late grass stage with other native species approaching their previous abundance. Sand dropseed was often important in recovery on sandy loam soils. Many forbs increased in number and size, while scarlet mallow and prickly-pear cactus declined to their former levels. Basal cover recovered even under moderate grazing.

Recovery from the 1930s drought in the Canadian mixed prairie was shown by monitoring of 48 sites in southeastern Alberta and southwestern Saskatchewan (Coupland 1959). These sites were sampled in the early to mid-1940s, shortly after the drought, and in 1955-57 following more than a decade of higher precipitation. The average changes in species composition are shown in Table 4. On average over all sites, the community was dominated by needle-and-thread and blue grama in the 1940s, but by the late 1950s had shifted to dominance by western porcupine grass and wheatgrasses.   These changes resulted in Coupland (1961) revising his classification of grassland communities of the Canadian prairies, because he realized that earlier descriptions of "shortgrass prairie" dominated by blue grama were made during or shortly after the drought. Excessive stocking rates in the early 20th Century also contributed to the shortgrass appearance of the drier regions (Adams et al. 2004). The return to normal precipitation, coupled with better grazing management, showed that these areas were capable of supporting mid-grass dominated communities (Coupland 1961, Adams et al. 2004).

Table 4. Changes in percentage of biomass of major graminoid species in Canadian mixed prairie from 1944 (following drought) to 1955-56 (following moister weather) (after Coupland 1959).

	1944	1955-56
Western porcupine grass (*Stipa curtiseta*)	13.6	26.7
Wheatgrasses (*Agropyron* spp.)	15.2	23.3
Plains reedgrass (*Calamagrostis montanensis*)	0.8	5.0
Thread-leaved sedge (*Carex filifolia*)	2.0	2.3
Low sedge (*Carex stenophylla*)	3.4	3.2
June grass (*Koeleria cristata*)	9.2	8.9
Blue grama (*Bouteloua gracilis*)	24.2	14.9
Needle-and-thread (*Stipa comata*)	29.3	12.8

While compositional changes are most likely to occur as a result of multi-year drought, they can occur even in a single year. Tilman and El Haddi (1992) found that species richness of old-field grasslands in Minnesota declined after the severe drought of 1988. Many of the species that were lost were annuals, while among the perennials, low-abundance species were most likely to disappear.

Drought impacts have also been measured in the woodlands of the Aspen Parkland. Hogg et al. (2005) showed that most of the variation in aspen growth between 1951 and 2000 was explained by interannual variation in a climatic moisture index, combined with insect attacks. Hogg et al. (2008) monitored aspen stands in Parkland and Boreal Forest during the severe drought of 2001-2002, and found that net biomass increment changed from 2.2 t ha^{-1} yr^{-1} to near zero. Both reduced growth and increased mortality contributed to this decline. Aspen stands in the Parkland, where the drought was most severe, showed the highest levels of dieback.

Many other examples of recent tree mortality attributed to drought and heat stress have been documented around the world (Allen et al. 2010). For example, in the southwestern U.S., dieback of ponderosa pine at the dry margin of its range has led to shifts in the boundary between pine forest and pinon-juniper woodland (Allen and Breshears 1998).   The authors pointed out that tree mortality leads to more rapid vegetation shifts than changing rates of natality or growth. In Oklahoma, DeSantis et al. (2011) found that drought-caused mortality of oaks during the 20th Century accelerated their replacement by junipers. Rehfeldt et al. (2009) modeled the bioclimatic envelope of aspen in the western United States, and predicted decreases in its range with climate change.

These results have interesting implications for the changes in vegetation zonation discussed in Section 3. It is often assumed that mature trees will persist once they are established, and that a tree-killing disturbance such as fire or logging is required to catalyze the change from woodland to grassland. According to Jackson et al. (2009), trees have a narrower range of conditions in which sexual reproduction can occur, compared to the broader range of conditions for adult survival. However, forest dieback studies have shown that vegetation change could occur by

mortality of mature trees. If severe droughts become more common, aspen dieback could result in relatively rapid loss of tree cover in the Parkland, accelerating the shift to open grassland.

6 IMPACTS OF CLIMATE CHANGE ON BIODIVERSITY

6.1 Responses of species to climate change

The analysis of impacts on vegetation zonation in Section 3, and of the effects of drought in Section 5, focused on changes in the major plant species that characterize plant communities. However, these changes will affect the whole range of species, including the less common plants as well as animals and microbes. Because of the importance of all components of biodiversity, the impacts of climate change should be considered more broadly.

According to Running and Mills (2009), wild species can adapt to climate change either by moving (i.e. shifting range limits) or by adapting in place (either through phenotypic plasticity or evolution). Unsuccessful adaptation results in population decline and eventual extinction.

Parmesan and Yohe (2003) reported a meta-analysis of studies of 20th Century ecological changes around the world. They found average shifts of range boundaries of 6.1 km per decade northward or 6.1 metres per decade upward in elevation. Of species showing range shifts, 80% were in the direction predicted by climate change.

Among the many examples of range shifts given by Parmesan (2006), the most visible are northward shift in the Arctic treeline and upward shift in the alpine treeline. Upward elevational shifts of plant species and vegetation types in mountainous areas have been documented by Walther (2003) and Kelly and Goulden (2008). In the case of Arctic treelines, some studies have shown shifts (i.e. establishment of tree seedlings beyond the current treeline) while other studies have shown stable treelines over the past half century, possibly because of poor availability or dispersal of seeds, or a requirement for disturbance for tree recruitment (Walther 2003). Shifts in treelines are thought to be episodic rather than gradual (Walther 2003). Jackson et al. (2009) described a "ratchet mechanism" in range expansion of woody plants, in which colonization of new areas occurs during favourable periods, followed by persistence of established plants during unfavourable periods. This is related to the narrower range of conditions in which sexual reproduction can occur, compared to the broader range of conditions for adult survival. An example is the 13th and 14th Century expansion of piñon pine in the southwestern U.S., by a series of establishment events coinciding with wet periods (Gray et al. 2006). These patterns show that the current range of a species may be contingent on a series of preceding events, rather than simply being in equilibrium with the current climate.

Mechanisms of range shifts have been worked out in detail for some groups. Edith's checkerspot, a California butterfly, suffered increased extinction at its southern and lower boundaries (caused by unusual weather events), but had stable populations at its northern and upper boundaries (Parmesan et al. 2000). Tree species vary in tolerance for extreme winter cold, with boreal species able to survive temperatures below -40°C which are lethal to temperate species (Woodward 1987). Similarly, pest species that are limited by low winter temperatures have been able to expand northward in response to milder winters, with the mountain pine beetle

in British Columbia being a conspicuous example (Carroll et al. 2003, Thomson 2009). Root (1988) found that the northern range limits of wintering bird species in North America are related to mean minimum January temperature, length of the frost-free season, and potential vegetation. However, Parmesan et al. (2005) showed that, while physiological tolerances to climatic thresholds are important in determining range boundaries, other processes such as competition, predation, or specialized soil requirements may also be important.

In some cases, range shifts may lead to smaller range sizes, depending on how much area with the appropriate future climate is available. Thomas et al. (2004) used climatic envelope modeling (i.e. defining the climatic boundaries of current species ranges, and assuming that these boundaries will shift north with climate change) to predict global risks of extinction resulting from decreases in range size. Over all regions and taxonomic groups, 15-37% of species were predicted to be "committed to extinction" by 2050. Risks increased from minimal-change to high-change climate scenarios. Peterson (2003) modeled niches of Great Plains and Rocky Mountain bird species, and predicted shifts in range with climate change. While expansions tended to take place along northern borders, and retractions along southern borders, there were many variations. Effects on range size were generally negative for Great Plains species, but varied over a wide range.

Pearson and Dawson (2003) summarized the criticisms of the bioclimatic envelope approach. The success of a species may be determined by biotic interactions (e.g. competition, predation), and not merely by tolerances to environmental variables. However, proponents respond that the envelope approach is suitable at broad geographic scales where climate is the dominant control on species distributions. Another criticism is that species differ widely in dispersal capacity, and slow-moving species may not keep pace with climate change. However, it is usually assumed that envelope models show the potential range of a species under a new climate, not the actual range, which may be affected by barriers to dispersal (Pearson and Dawson 2003).

The rate and success of migration will vary among species because of differences in environmental tolerance, genetic variation, and dispersal rates. This variation implies that new combinations of species (i.e. new communities) could emerge (Singh and Wheaton 1991, Peters 1992). This has been demonstrated in the case of the northward migration of North American tree species following deglaciation (Davis 1981, Davis and Shaw 2001). For plants, many wind-dispersed species can easily migrate fast enough to keep up with climatic warming, but others may be limited by slow dispersal or restriction to particular habitats (Malcolm and Pitelka 2000). Models of the synergistic effects of climate change and habitat fragmentation suggest that habitat specialists, especially those with poor dispersal ability, are least able to keep pace with climate change (Travis 2003). Dobrowski et al. (2011) analyzed the measured range shifts of California plants associated with 20th Century warming. They found that species with long-distance dispersal strategies (wind dispersal, animal dispersal) appeared to track the shifting climate more closely than species with shorter-range dispersal. Endemic species (i.e. those found only in California) tracked climate less closely than wider-ranging species, but this again appeared to be linked to reproductive strategy (short-range dispersal, dependence on fire for regeneration). Neilson et al. (2005) speculated that rapid climate change will lead to sorting of species along a migrational front, led by the most invasive and trailed by the least invasive. Even among native

species, rapid dispersers may invade more sedentary late-successional communities, increasing the risk of local extinction of some species.

The adjustment to climatic change may also occur at the level of genetic variation within species. For example, Rehfeldt et al. (1999) showed that a wide-ranging species such as lodgepole pine includes populations that differ widely in climatic adaptation. Climate change may lead to northward migration of southern genotypes within such a species. Successful migration may also require evolutionary change within species (Davis and Shaw 2001). For example, southern species may be adapted to the warmer temperatures that will be found in Canada in the future, but not to the longer summer days at northern latitudes. Northward migration may be accompanied by selection for new genetic combinations of photoperiod and temperature response.

By contrast with the above examples of shifts in range boundaries, Running and Mills (2009) considered phenological change to be an example of "adaptation in place". The meta-analysis of studies of 20th Century ecological changes by Parmesan and Yohe (2003) included many studies of phenological change in plants, birds, butterflies and amphibians. These studies showed a mean shift towards earlier spring timing of 2.3 days per decade. While 27% of species showed no trends and 9% showed delayed spring timing, the remaining 62% showed earlier spring timing. Root et al. (2003) and Walther (2003) also documented significant shifts to earlier timing over large numbers of species.

Many examples of phenological change are given by Parmesan (2006). In the Prairie Ecozone, the Plantwatch program has been compiling phenological observations for several plant species (Beaubien 2001). At Edmonton, the first-flowering date of trembling aspen advanced by about 26 days from 1901 to 1997 (Beaubien and Freeland 2000). At Delta Marsh in southern Manitoba, a 63-year record of first spring sightings of bird species was analyzed to show trends in migration phenology (Murphy-Klassen et al. 2005). Of 27 species showing significant trends, 25 species showed a trend toward earlier arrival dates through this period, while only two species showed later arrival dates. About half of the species showed significant relationships between arrival date and mean temperature of their month of arrival.

While phenological changes appear benign, in that they imply the capacity of species to adapt rapidly to climate change, they can lead to other problems (McCarty 2001). Differing rates of phenological change may lead to mismatches in timing between predators and their prey, herbivorous insects and their host plants, parasitoids and their host insects, and insect pollinators with flowering plants (McCarty 2001, Parmesan 2006, Visser and Both 2005). One striking example is snowshoe hare, in which the timing of colour change is matched to the timing of snow-melt. Hares that are still white after the snow cover disappears are more vulnerable to predation. Colour change is driven largely by day length, and it is not yet known whether the hare can evolve changes in timing fast enough to match the shortening period of snow cover (Running and Mills 2009).

This raises the other mechanism of adaptation in place, by evolution (i.e. shifts in gene frequencies) (Running and Mills 2009). Contemporary evolution in thermal tolerance in response to climate change has been observed in frogs, insects, and plants (Skelly et al. 2007). Skelly et

al. (2007) argued that the "climatic envelope" approach distorts the probability of extinction because it implicitly assumes that species cannot evolve in response to climate change. However studies of some plant and animal species have in fact shown "niche conservatism", consistent with the climatic envelope approach; for example, range shifts in mammal species recovering from the Pleistocene glaciation followed predictable climatic regimes (Peterson 2003, Pearson and Dawson 2003, Martinez-Meyer et al. 2004). Parmesan (2006) argued that in the history of post-glacial change, evolution in place was less important than shifts in range limits.

According to Running and Mills (2009), "evolutionary rescue" of a species is favoured by:
- large population size and/or rapid population growth; because of this, other stressors such as habitat fragmentation of overharvest can compromise adaptive capacity.
- short generation time
- strong directional selection
- medium level of gene flow, because high gene flow into a population will deter local adaptation.
- generalist species, because specialists will be less likely to possess the variation needed for evolutionary adaptation.

Parmesan and Yohe (2003) recognized that most short-term population changes are caused not by climate change but rather by land-use change and natural fluctuation. In estimating the overall impacts of global change on biodiversity, Sala et al. (2000) considered the largest driver to be land-use change, because of its devastating effects on habitat availability. However, they considered climate change to be the second-most important driver. Parmesan and Yohe (2003) argued that finding significant climate signals (e.g. phenological change, range shifts) amid the noise of biological data indicates important climate change effects over the long term. McCarty (2001) argued that research on recent ecological changes shows that climate change must be considered a current, not just a future, threat to species.

Nevertheless, the effects of climate change can only be understood in synergy with other stressors such as habitat loss and fragmentation (Opdam and Wascher 2004, Running and Mills 2009). Parmesan et al. (2000) contrasted the situation following the Pleistocene glaciation, in which most species were capable of shifting their ranges northward, with the current situation in which range shifts may be impeded by fragmentation. Travis (2003) incorporated this synergy into models of species persistence. For both climate change and habitat loss, these models show species persisting up to a critical threshold, then declining rapidly. Synergistically, under climate change the habitat threshold occurs sooner, while in fragmented habitats the climate change impact is more severe. Opdam and Wascher (2004) reported empirical evidence for animal species that showed this kind of synergy. Fragmentation could affect both the leading edge of a range shift (reducing establishment rates) and the trailing edge (increasing extinction rates) (Opdam and Wascher 2004). In fragmented landscapes, the source area for dispersal is smaller than in natural landscapes, while the success of dispersal may be limited by the distance between habitat patches (Parmesan et al. 2000). Favourable climate episodes may effectively increase the size of habitat patches, thus improving dispersal (Jackson et al. 2009). However, empirical data on these relationships are lacking because most studies of range shifts have not considered landscape pattern (Opdam and Wascher 2004).

Widespread declines in amphibian populations have been linked to pollution and disease, but climate change may also be a major factor. Reading (2007) found that common toads in the UK showed declines in female body condition and body size, egg production, and survival rate that were correlated with rising temperatures, and suggested that declines were related to partial hibernation during mild winters. McMenamin et al. (2008) related the decline of amphibians in Yellowstone National Park to increase in drought and decrease in number of wetlands. They presented a general model linking amphibian decline to climate warming, decrease in effective moisture, loss of pond habitat, changes in phenology, and increased risk of disease.

6.2 Drought and biodiversity

As discussed earlier in relation to forage production (see Section 5), climate change may affect not just the average conditions, but also the occurrence of extremes. Shifts toward drier average conditions also imply that the dry years will become even drier, especially if variability of precipitation increases. Therefore it is important to consider the effect of droughts on biodiversity.

Wiens (1974) found that Great Plains grasslands have generally low diversity of bird species (averaging only 3-4 species per 10 ha plot), and argued that this is related to production "bottlenecks" during drought years to which only a few species are adapted, coupled with the lack of "refugia" that could shelter less adapted species during droughts. Rotenberry (1980) reached similar conclusions from analysis of diets of shrubsteppe birds. Rotenberry and Wiens (1991) found that Sage Sparrow and Brewer's Sparrow on Oregon shrubsteppe had significantly greater reproductive success during wet years than dry years. Igl and Johnson (1997) found that most North Dakota grassland birds were more abundant in wet years (1967 or 1993) than in a dry year (1992). However, there are differences among species in response to drought. George et al. (1992) monitored grassland birds before, during, and after the 1988 drought in western North Dakota. They found a decline in bird species richness during the dry year, but recovery by the following year. The decline was related to decreases in Grasshopper Sparrow, Sprague's Pipit, Clay-coloured Sparrow, and Baird's Sparrow, while Horned Lark and Western Meadowlark were unaffected so became more dominant in the bird community. The authors noted that the shift was similar to that associated with heavy grazing. Wiens (1974) reported similar changes during a 1970-1971 drought in Texas, with increases in Horned Lark, intermediate responses of Western Meadowlark, and decreases of Lark Bunting and Grasshopper Sparrow during the drought, followed by the reverse when rain returned. In a North Dakota study over a long time sequence (1980-2004), Niemuth et al. (2008) found relationships (either positive or negative) between abundance and annual moisture conditions for 17 out of 19 grassland bird species.

Insect populations are well known to be climate-dependent. Tepedino and Stanton (1981) found that patterns of bee diversity on shortgrass prairie do not indicate continuous competition for resources, and suggested that this is because of the wide variation in resource availability from year to year. Hawkins and Holyoak (1998) showed that a wide range of insect taxa from across North America declined during the severe drought of the late 1980s. Experimental irrigation of shortgrass prairie significantly increased the biomass of grassland insects (Kirchner 1977). However, destructive outbreaks of plant-eating insects are often preceded by warm, dry weather,

because of a variety of processes including faster development of the insect and weakened defenses by the plant (Mattson and Haack 1987).

Grasshoppers are the most destructive insect pests of grasslands and cereal crops in many parts of the Prairies (Johnson 1993). They are not introduced, but rather are natural grassland herbivores. In the Matador Study in southern Saskatchewan, Bailey and Riegert (1973) found that 10% of grassland production was harvested by grasshoppers, although most of this was dropped on the ground and only 2% was actually ingested. Grasshopper populations undergo outbreaks followed by return to more moderate levels. Several consecutive years of warm, dry weather precede major grasshopper outbreaks (Johnson 1993). Powell et al. (2007) found that grasshopper density in Alberta is negatively related to summer soil moisture level. Whitman et al. (cited by Coupland 1958), estimated that grasshoppers removed 30 to 40% of grass growth during a drought year in western North Dakota.

Forest tent caterpillar and other insects cause significant defoliation of trembling aspen in the Aspen Parkland in some years (Brandt 1997). Defoliation is highly variable, with some years characterized by severe defoliation and others with very little. Ives (1981) found that outbreaks of forest tent caterpillar are favoured by mild winters and warm, dry summers. The synergistic effects of drought in favouring insect outbreaks and reducing growth of trees can contribute to forest dieback. Hogg et al. (2005) showed that most of the variation in aspen growth between 1951 and 2000 was explained by interannual variation in a climatic moisture index, in combination with outbreaks of forest tent caterpillar.

6.3 Impacts of climate change on wetlands

In addition to grasslands and woodlands, wetlands are important natural ecosystems in the Prairie Ecozone. While much smaller in area than grasslands, wetlands make a large contribution to the biodiversity of the region, supporting a whole suite of plants and animals that require wet environments. Of these, most attention has focused on waterfowl.

Waterfowl biologists base much of their analysis on an area called the Prairie Pothole Region (PPR), which includes the agricultural portion of the Canadian prairies plus glaciated portions of Montana, North and South Dakota, Minnesota, and Iowa. This area comprises 10% of North American waterfowl breeding habitat, but produces 50-80% of the continent's ducks (Batt et al. 1989).

Duck production in the PPR varies widely among years, because the wetlands on which it is based fluctuate in number and area. Bethke and Nudds (1995) showed that duck abundance in the Canadian prairies is statistically related to wetland conditions, which in turn depend on precipitation in the two previous years. Larson (1995) developed regressions for the PPR predicting the percentage of wetland basins holding water, depending on yearly weather. She predicted that a 3° C rise in temperature with no change in precipitation would result in a 15% decrease in basins holding water in the grassland, and a 56% decrease in the aspen parkland where basin density is much higher.

In the U.S. portion of the PPR, Sorenson et al. (1998) showed that both pond counts and duck numbers are closely related to May values of the Palmer Drought Severity Index (PDSI). Application of either a $2xCO_2$ scenario or a transient scenario for the 2050s resulted in substantial lowering of the average May PDSI (relative to the 1955-1996 base period), and roughly halved the predicted numbers of both ponds and ducks. However, the authors pointed out that these results relate to duck numbers settling within the PPR. During drought years, many ducks overfly the region and nest in boreal and tundra habitats. Habitats in these regions are more stable (i.e. less prone to drying out in drought years), but duck production is thought to be lower. Moreover, with climate change, these northern regions will themselves change in hydrology. Thus there are uncertainties about the overall effect on North American duck populations.

Johnson et al. (2005) developed a simulation model for pothole hydrology, based on a semipermanent wetland in North Dakota, then applied the model to historic climates of other parts of the PPR to show temporal and spatial variability in wetlands. Wetlands in the PPR change dramatically through time, from drying out during droughts to overflowing during wet periods. Drier parts of the region have longer periods in which wetlands are dry, and the ratio of open water to emergent cover increases from dry to moist climates. A simulated temperature increase of 3° C reduced the ratio of open water to emergent cover at all locations. However, a 20% precipitation increase compensated for the temperature rise, resulting in about the same cover/open water pattern as under historic climates.

Johnston et al. (2010) expanded this model to include temporary, seasonal and semipermanent wetlands. They then applied warmer temperatures to simulate climate change. Even temporary wetlands continued to recharge with water in spring, but higher spring evapotranspiration led to a shorter wet period. Semipermanent wetlands showed greater proportional losses, because their wet period extends into summer, when the higher evapotranspiration rates had greater effect. The authors pointed out that these results could be altered if winter warming leads to increased sublimation and reduced snowpack. Results would also be altered for wetlands in highly permeable substrates, in which inflow from groundwater would play a bigger role in maintaining water depth.

Johnston et al. (2010) discussed the concept of a "vegetation cover cycle" in wetlands, oscillating from dry stages with dense cover and little open water, to completely flooded lake stages. Faster cover cycles (i.e. more frequent oscillation) more often produce the "hemi-marsh" stage (i.e. roughly equal proportions of cover and water) which is most productive for waterfowl. Because the cover cycle is driven by climatic variability, the fluctuating climate of the prairie region contributes to its high production for waterfowl. The fastest cover cycles and most productive wetlands have historically been in the "core" of the PPR, in southeastern Saskatchewan, southwestern Manitoba, and the Dakotas; the drier area further west tends to persist in the vegetation cover stage, whereas the moister area in Minnesota and Iowa tends to persist in the open water stage. Simulating climate change by applying warmer temperatures to their model of wetland hydrology results in declining production in the core area, suggesting that it will become a more episodic, less reliable source of waterfowl production, similar to the drier areas further west. Favourable water and cover conditions will be found further north and east, except that many of the eastern U.S. wetlands have already been drained.

As with biodiversity in general, climate change impacts on wetlands can only be understood in the context of other human-caused stressors. Many prairie wetlands have been eliminated or degraded by artificial drainage. Monitoring transects across the Canadian Prairies showed that both the wetland area and the number of wetland basins decreased by 5% from 1985 to 2001 (Watmough and Schmoll 2007). Drainage of wetlands in eastern Saskatchewan is increasing streamflow (Sauchyn et al. 2009). Bethke and Nudds (1995) invoked land use change to explain duck numbers that were lower than would be expected from wetland conditions. Running and Mills (2009) argued that, because ducks formerly dealt with drought by moving to other wetlands, the anthropogenic loss of wetlands increases vulnerability to climate change. Even where wetlands have not been drained, changes in cropping practices (continuous cropping, minimum tillage) have increased efficiency of water use, but have reduced runoff to wetlands and recharge of groundwater (Sauchyn et al. 2009). Conversion from cropland to grassland, a practice beneficial to soil conservation and upland habitat, also has the negative effect of reducing runoff to wetlands (Van der Kamp et al. 1999). This illustrates the complexity of deciding on beneficial management practices.

6.4 Impacts of climate change on invasive species

Climate change creates novel environments, and invasive species are by definition suited to succeed in these environments (Bradley et al. 2010). According to Dukes and Mooney (1999), rapid climatic change would disadvantage native species that cannot quickly expand their ranges, or could leave ill-adapted plant communities that are susceptible to invasion, while invasive species tend to be rapid dispersers, so should be quick to shift their ranges. Successful invaders tend to have large native ranges, so therefore may have broad climatic tolerances (Dukes and Mooney 1999, Hellmann et al. 2008). Many invasive species have characteristics that favour rapid range shifts, such as low seed mass and short time to maturity (Hellmann et al. 2008). Among animal species, specialists that rely on a particular plant community are more likely to be disadvantaged by climate change compared to generalist species that can use a variety of plant communities (Dukes and Mooney 1999).

However successful invasion has also been found to be affected by resource availability. The "fluctuating resource hypothesis" says that a temporary excess of resources such as water or nutrients favours invasion (Dukes and Mooney 1999). Carbon fertilization as a result of rising CO_2 concentrations has been shown to favour invasive plants over a range of species and growth habits (Bradley et al. 2010). In arid and semiarid regions, increase in moisture favours invasion (Dukes and Mooney 1999). Experimental moisture manipulation in German grassland and heath communities supported this hypothesis, with drought reducing invasibility and heavy rainfall increasing invasibility (Kreyling et al. 2008). Similarly, artificial enrichment (water plus nitrogen) of Colorado shortgrass prairie led to invasion by both exotic and native weeds (Milchunas and Lauenroth 1995). Blumenthal et al. (2008) found that experimentally increasing snow accumulation on mixedgrass prairie plots increased growth of seeded invasive species, with more significant effects than summer irrigation. If climate change leads to increased drought frequency, this could place a limit on invasive species by reducing availability of a critical resource. Conversely, if the frequency of extreme wet years increases, invasive species could benefit.

Invasive species, like any other species, are constrained by climatic suitability. Bradley (2009) analyzed the climatic envelope of cheatgrass, an important invasive plant in the intermountain region of the western United States. This study found that the range of suitable climates for cheatgrass could either expand or contract, depending on the climate change scenario. Scenarios with decreasing summer precipitation favoured range expansion. The median scenario showed cheatgrass expanding into parts of Montana and Wyoming that are not now suitable. Cheatgrass occurs in the Canadian prairies but is not yet a major invasive, so any tendency towards increased climatic suitability would be of concern for our region.

An alternative strategy besides range shifts is adaptation in place by evolution. Invasive species have traits that improve their chances of rapid evolution in response to climate change, including large population size, rapid population growth, short generation times, high habitat connectivity (because of use of disturbed habitats), and generalist phenotypes (Running and Mills 2009).

While climate change could affect invasion for the reasons discussed above, it is important to remember that the most important factor is physical disturbance related to land use (Bradley et al. 2010). As with biodiversity in general, the impact of climate change interacts with land use change. Conservation measures such as protection of natural ecosystems, reduction of fragmentation, and careful grazing management to maintain range health, could help to mitigate any tendency towards increased invasion.

6.5 Impacts of climate change on species at risk

Much of the focus in biodiversity discussions has been on species at risk, which receive special attention under the federal Species at Risk Act (SARA) as well as legislation in the various provinces. To shed light on climate change impacts on species at risk, a case study area in Manitoba was analyzed. The "West Souris River Basin" is a 4300 km^2 area in the southwest corner of Manitoba, bounded by the U.S. border on the south, the Saskatchewan border on the west, the Souris River on the east, and a watershed boundary in the north. Soils consist of Black Chernozems on loamy glacial till in the west, and on sandy glacio-fluvial material in the east. A large area of the sand plain in the northeast is poorly drained (Gleysolic soils), and a portion has been modified into dunes (the Lauder Sandhills). The land cover includes 53% annual cropland, 5% forage crops, 29% grassland (concentrated in in sandy areas), 6% woodland (concentrated in dunes), plus smaller areas of wetlands and other types. Growing degree days are predicted to increase from 1900 in the present climate to 2400-3200 (depending on the scenario) by the 2080s. Annual precipitation is about 470 mm in the present climate, and by the 2080s could decrease to 430 mm, increase to 495 mm, or not change, depending on the scenario

Species at risk that have been recorded in the case study area are listed in Table 5. This includes Schedule 1 species under SARA.

Most of these species are not rare globally (ranks G4 or G5), because of large populations in the U.S. Great Plains. Their at-risk status in Canada results from being at the northern fringe of the range. For such species, the shift of vegetation zones northward could increase the area of suitable habitat within Canada, other things being equal. Exceptions to this are the Dakota Skipper and possibly the Piping Plover, which have rarer global ranks (G2 and G3 respectively). The Northern Leopard Frog is the only one of these species with a significant range north of the grassland (i.e. in the Boreal Forest).

Table 5. SARA-listed species at risk in the West Souris River Basin case study area.

SCIENTIFIC NAME	COMMON NAME	G RANK	S RANK	SARA Schedule 1
Birds:				
Anthus spragueii	Sprague's Pipit	G4	S2B	Threatened
Athene cunicularia	Burrowing Owl	G4	S1B	Endangered
Charadrius melodus	Piping Plover	G3	S1B	Endangered
Lanius ludovicianus excubitorides	Loggerhead Shrike	G4T4	S2B	Threatened
Herptiles:				
Eumeces septentrionalis	Northern Prairie Skink	G5	S1	Endangered
Lithobates pipiens	Northern Leopard Frog	G5	S4	Special Concern
Insects:				
Hesperia dacotae	Dakota Skipper	G2	S2S3	Threatened
Vascular plants:				
Buchloe dactyloides	Buffalograss	G4G5	S1	Threatened
Dalea villosa var. villosa	Hairy Prairie-clover	G5T5	S2S3	Threatened
Tradescantia occidentalis	Western Spiderwort	G5	S1	Threatened

Information on the biology of these species has been reviewed to assess the likely impacts of climate change. This review shows that the impacts are likely to vary widely, depending on the characteristics and requirements of the individual species.

Sprague's Pipit is endemic to the Northern Great Plains, with 60% of its breeding habitat in Canada (COSEWIC 2010). It prefers to nest in open native grasslands of intermediate height and density with moderate litter accumulation and low shrub cover. Tame grassland is less suitable, but supports some breeding. Breeding is more successful on larger patches of grassland. It is estimated that the population of this species has declined by 83% over the last 40 years.

Habitat loss and fragmentation associated with cultivation, road development, and energy development are the main threats to Sprague's Pipit. Heavy livestock grazing, resulting in lower grassland structure as well as disturbance and trampling of nests, is also a threat (COSEWIC 2010). Measures aimed at conserving remaining native grassland, restoring cropland to permanent cover, and improving grazing management, are beneficial for this species.

A 2010 workshop with species-at-risk experts in southwestern Saskatchewan indicated that climate change scenarios favouring a shift to shorter, less productive grassland would negatively impact on Sprague's Pipit because of loss of habitat structure. Increased precipitation variability leading to more frequent droughts would have further negative impacts on structure. On the other hand, more frequent wet years leading to flooding could have a short-term negative impact

on nest success. Decline in Sprague's Pipit was measured during the 1988 drought in North Dakota (George et al. 1992).

Burrowing Owl is found in all three provinces of the Prairie Ecozone, where it represents the northern fringe of the species' breeding range. Preferred breeding habitat is open, sparsely vegetated grassland with animal burrows for nesting. However, adjacent taller grasslands are used for foraging (COSEWIC 2006).

The Canadian population of Burrowing Owl declined by 90% from 1990 to 2000, with the trend slowing to 50% for the period 1994 to 2004 (COSEWIC 2006). The population is thought to be stable in the core range in the U.S., but it has disappeared from the eastern and northern fringe of its range, in a band averaging about 200 km wide, extending from the Gulf of Mexico into Manitoba and across Saskatchewan and Alberta (COSEWIC 2006). The main threat is thought to be habitat loss resulting from cultivation, as well as fragmentation and degradation of the remaining grasslands (COSWEIC 2006).

A 2010 workshop with species-at-risk experts in southwestern Saskatchewan indicate that climate change scenarios predicting shifts from parkland to open grassland would be beneficial for Burrowing Owl because habitat area would increase. Shifts to drier, less productive grassland types should provide the kind of vegetation structure favoured by this species. Increased frequency of dry years could have opposing impacts on prey availability: ground squirrels would decrease, but grasshoppers may increase. On the other hand, flood events could cause loss of nests or chicks. Warming could also affect migration: if winter habitat becomes available further north, migration distances could decrease.

Loggerhead Shrike has a wide breeding range in North America, of which the population in the Canadian Prairies represents the northern fringe (COSEWIC 2004a). Habitat includes a variety of open vegetation types, including grassland, sagebrush, and cropland. However Loggerhead Shrike requires scattered trees or shrubs, especially thorny species, for perching and nesting (COSEWIC 2004a).   The Canadian population has declined by 80% since 1968. The primary threat is thought to be conversion of native grassland to cropland, with pesticides, predation, and vehicle collisions also considered threats (COSEWIC 2004a).

A 2010 workshop with species-at-risk experts in southwestern Saskatchewan indicated that climate change scenarios predicting a loss of woody cover could eliminate habitat for Loggerhead Shrike, because completely open grassland would provide no perching sites. Increases in climatic extremes could also have a negative impact, because nests are frequently destroyed by severe thunderstorms (COSEWIC 2004a).

Piping Plover occurs in the prairie portions of Alberta, Saskatchewan, and Manitoba (and occasionally further north) where it represents the northern edge of the breeding range. It is a shorebird which uses sandy/gravelly beaches, islands, and peninsulas on saline and freshwater lakes and rivers. Because of hydrologic fluctuations, these habitats can be unpredictable. The most consistently available habitat is wide gravelly shores on permanent saline water bodies (Environment Canada 2006).

The Prairie Canada population declined by 32% from 1991 to 2001, and by 42% from 1996 to 2001. The primary threat in the Prairies is thought to be predation on eggs and chicks. Disturbance by livestock and humans is an additional threat (Environment Canada 2006).

Impacts of climate change on Piping Plover are not clear. However, the loss of wetlands predicted by some models could reduce habitat availability.

Northern Prairie Skink is a small lizard. In Canada, it is found only in a small area in southwestern Manitoba, the extreme northern outlier of the main range in the U.S. Great Plains. Most of the Manitoba population is in the Carberry Sandhills, but there is a small population in the Lauder Sandhills. It is found on grassland or shrubland on sandy soil, but nesting sites are usually under objects such as boards, shingles, or sheets of tin. The main threats are conversion of sandy prairie to potato farming, aspen encroachment on grassland, and invasion by leafy spurge (COSEWIC 2004b).

In winters with poor snow cover, skinks may be killed in their hibernacula when freezing temperatures penetrate more deeply (COSEWIC 2004b). Climate change scenarios predicting shifts to milder winters, possibly with higher winter precipitation, should be beneficial to this species.

Northern Leopard Frog has a wide range across Canada and the United States. Breeding habitat consists of shallow, open wetlands. Frogs also forage in adjacent meadow and grassland habitats. For wintering, frogs require cold, well-oxygenated water bodies that do not freeze to the bottom (COSEWIC 2009).

Northern Leopard Frog is threatened by loss of wetlands through artificial drainage (COSEWIC 2009). Watmough and Schmoll (2007) measured a 5% loss in wetland number and wetland area across the Prairies from 1985 to 2001. Other threats include road mortality, habitat damage by livestock, disease, introduction of non-native fish and plants, and pesticides (COSEWIC 2009).

A 2010 workshop with species-at-risk experts in southwestern Saskatchewan indicated that scenarios leading to drier average conditions would have negetative impacts on Northern Leopard Frog, because of reduced river flows (loss of overwintering habitat) and decreases in ephemeral water sources (loss of breeding habitat). McMenamin et al. (2008) related the decline of amphibians in Yellowstone National Park to increase in drought and decrease in number of wetlands. They presented a general model linking amphibian decline to climate warming, decrease in effective moisture, loss of pond habitat, changes in phenology, and increased risk of disease. On the other hand, trends towards increased variability of precipitation could lead to more frequent flooding events, which would be beneficial for Northern Leopard Frog.

Dakota Skipper is a small butterfly which is rare both locally and globally. In Canada, it occurs in southern Manitoba and extreme southeastern Saskatchewan, where it is restricted to patches of tall-grass and mixed-grass prairie. This represents the northern fringe of its range, but its distribution in the United States is also small, being restricted to North Dakota and small areas of South Dakota and Minnesota (COSEWIC 2003).

The main threats to Dakota Skipper are conversion of grassland to cropland, fragmentation of the remaining grassland, heavy grazing impacts, prescribed burning, and exotic invasion which displaces the native plants needed by this species (COSEWIC 2003).

Impacts of climate change are not clear. However, Dakota Skipper appears to be associated with the moister grasslands of the eastern prairies. The drier climate change scenarios, which favour a shift to the shorter mixed prairie found in eastern Montana and Wyoming, could make the grassland less suitable for Dakota Skipper.

Buffalograss is a short perennial grass that is extremely rare in Canada, with two small populations along the Souris River in southeastern Saskatchewan and southwestern Manitoba. However, it is a common and even dominant species in the U.S. Great Plains. While it occurs across a range of sites in its core range, it is most abundant on clay soils (Environment Canada 2007).

Threats in Canada include loss of grassland to coal mining and other disturbances, and invasion by taller exotic species. Livestock grazing is not considered a threat, because Buffalograss tends to increase with grazing intensity. Lack of grazing in protected areas could actually reduce the viability of Buffalograss populations (Environment Canada 2007).

Climate change scenarios and modeling of vegetation zonation have direct implications for the future of Buffalograss in the Canadian Prairies. The drier kind of mixed prairie (Grama-Needlegrass-Wheatgrass), found in eastern Montana and Wyoming, is predicted to expand into Canada in most scenarios. While this grassland type is similar in dominant species to Canadian mixed prairie, one of the important differences is greater abundance of southern species such as Buffalograss. The extension of this trend is the shortgrass prairie (Grama-Buffalograss) of eastern Colorado, where Buffalograss is one of the dominant species. The warmest and driest climate change scenarios show this type expanding into the southern edge of the Canadian prairies by the 2050s or 2080s. These shifts imply that the climate should become increasingly suitable for Buffalograss in the coming century, which could lead to expansion of the existing populations and removal from "species-at-risk" status.

Hairy Prairie-clover is a perennial legume which is extremely rare in Canada, being found at only a few locations in Saskatchewan and Manitoba. However, this is the northern fringe of a much larger range in the U.S. Great Plains, where it is not considered rare. It grows on active or partially stabilized sand dunes, including the Carberry Sandhills and the Lauder Sandhills (COSEWIC 2000).

Threats to Hairy Prairie-clover include the ongoing trend towards stabilization of dunes, and invasion by exotics, particularly leafy spurge. The impacts of livestock grazing are uncertain. It is possible that heavy livestock use helps to keep dunes active, maintaining the early-successional habitats used by Hairy Prairie-clover. For this reason, exclusion of grazing in protected areas may not be the best management for this species (COSEWIC 2000).

The impacts of climate change are uncertain. However climate change scenarios and vegetation zonation models predict a shift towards U.S. grassland types where Hairy Prairie-clover is more

common. This implies that the climate should become more suitable for this species, potentially increasing its viability and population size. Climate change is also expected to favour activation of dunes (Wolfe and Thorpe 2005), which would help to maintain habitat for this species.

Western Spiderwort is a perennial forb. Most of what has been said about Hairy Prairie-clover applies also to Western Spiderwort. It is rare in Canada, found in only a few locations in Alberta, Saskatchewan, and Manitoba, but has a much wider U.S. range where it is not considered rare. It grows on active or partially stabilized sand dunes, including the Routledge Sandhills and the Lauder Sandhills (COSEWIC 2002).

Threats include dune stabilization and invasion by leafy spurge. Effects of livestock grazing may be either positive or negative. Western Spiderwort is grazed by both cattle and deer. On the other hand, livestock impacts may help to activate dunes, maintaining some early-successional habitats (COSEWIC 2002).

As with Hairy Prairie-clover, we have no specific information on climate change impacts. However, climate change scenarios and zonation models imply that the climate should become more suitable for Western Spiderwort, and should favour the active dune habitats it requires.

7 RANGELAND VERSUS CROPLAND UNDER CLIMATE CHANGE

While this report has focused on climate change impacts on native prairie, adaptation measures may involve tradeoffs among different land uses. Therefore, it is useful to compare impacts on prairie with those on arable land.

Brklacich et al. (1999) summarized the literature (up to 1997) on impacts of climate change on Canadian agriculture. Warmer frost-free seasons will accelerate the development of grain crops and reduce the time between seeding and harvest. In northern regions where crop maturation is limited by early fall frosts, climate change will extend the geographic range over which annual crops can be grown. Predicted impacts on grain yields in the Prairies vary from increases to decreases, depending on whether the scenarios predict increases or decreases in precipitation. Under one scenario, yields will decrease in the western part of the Prairies, but increase in the eastern part. The economic models reviewed by Brklacich et al. (1999) predict relatively minor effects. For example, the estimated effects of climate change on cash receipts from farming in Alberta are in the -7% to +5% range. A variety of adaptation options have been discussed, including expanding agriculture northward into former forest land, switching to longer-season spring-seeded cereal cultivars, increasing use of winter wheat in the southern part of the region, and use of water management techniques such as snow-trapping to address moisture deficits.

A detailed climate change analysis by Nyirfa and Harron (2001) applied the Land Suitability Rating System (LSRS) for spring-seeded small grains to the Canadian prairies. Application of a climate change scenario for the 2050s resulted in significant shifts in suitability zones. In particular the driest part of the region (roughly the Brown Soil Zone or Mixed Grassland Ecoregion) shifted from predominantly Class 3A, which is at the low end of suitable climates for spring-seeded small grains, to predominantly Class 4A, which is unsuitable. The moister areas (Dark Brown and Black Soil Zones) shifted from predominantly 2A to predominantly 3A. However, it should be noted that the LSRS model is driven by a climatic moisture index

(precipitation [PPT] – potential evapotranspiration [PET]), and the authors acknowledge that the LSRS ratings have never been validated for the more extreme aridity ratings (i.e. low values of PPT – PET) predicted by the 2050s scenario. The climate change scenarios for our region show large increases in PET but only small changes in PPT (see Section 2), so the PET change probably dominates the shift in suitability zones found by these authors. In the current grassland analysis, it was found that changes in PPT have a larger influence on production than changes in PET. This implies that an index that gives equal weight to both types of change could lead to distortion if extended outside its calibration range.

McGinn et al. (2001) used four climate change scenarios to drive a soil water balance model for the prairie region. Temperature increases were predicted to allow earlier seeding and increased crop maturation rates. Predicted effects on growing-season soil moisture ranged from no change to significant increases, depending on the scenario. They concluded that climate-related constraints on crop production will range from unchanged to somewhat reduced compared to the present climate.   They also pointed out that carbon fertilization will tend to increase crop production.

On the negative side, the advantage given by climate change to invasive species (see Section 6.4) will apply equally to those that are cropland pests. Ziska et al. (2011) reviewed the ways in which climate change could increase damage from crop pathogens, invasive insects, and weeds. Crop losses due to weeds are currently greater in the southern U.S. compared to the north because of the presence of weed species that are limited by low winter temperatures.

Because of the variability and uncertainties is the above analyses, it is difficult to judge whether cropland is more or less vulnerable to climate change compared to rangeland. Agricultural production from both types of land use will be affected by climate change, with the size and even the direction of the impact depending on which scenario is used. However one impact showing clear differences between cropland and rangeland is soil degradation. Sauchyn and Kennedy (2005) modeled sensitivity to land degradation in southern Saskatchewan as a function of climate, soil, and land cover. They found that sensitivity increases under two out of three 2050s climate change scenarios, with cultivated land much more sensitive than permanent cover. It is well known that native prairie plays a valuable role in soil protection on sites which are sensitive because of slope steepness or coarse texture. Any increase in climatic tendency to soil degradation would increase the importance of this function of grasslands.

8 SYNTHESIS OF IMPACTS

8.1 General trends

This analysis indicates the following general trends for Canadian grasslands in the coming century:
- Declining tree and shrub cover.
- Less invasion of grassland patches by shrubs and poplar sprouts.
- Increase in open vegetation suitable for livestock grazing.
- Decreases in animal species dependent on woody cover.
- Increases in animal species dependent on open grassland.
- Shifts in structure of grasslands: decrease of midgrasses, increase of shortgrasses.

- Decrease in cool-season grasses, increase in warm-season grasses.
- Gradual introduction of plant and animal species currently found only in the U.S.
- New community types caused by differences in rate of northward migration.
- Increases in invasion by exotic plants.
- Loss of wetland area and shifts from more permanent to more temporary types of wetlands.
- Small to medium decreases in average rates of grass production and grazing capacity per unit area, depending on the scenario. However the increase in open vegetation types associated with declining woody cover could increase the total area of rangeland.
- More frequent drought years with low production, but possibly also more frequent extreme wet years with flooding of low-lying pastures.

These trends will not apply equally to all areas. To examine regional differences, the following discussion focuses on particular types of grassland.

8.2 Mixed prairie

The core of the Prairie Ecozone, the Mixed Grassland Ecoregion, accounts for the largest area of remaining native prairie in Canada (Table 6). Because of the drier climate, there has been less cultivation than in the other large ecoregions. While fragmentation of grassland patches by cultivated fields and roads has seriously affected all parts of the Prairies, the Mixed Grassland is somewhat less fragmented than other areas. The large area of grassland south of the Cypress Hills in Saskatchewan and Alberta is contiguous with grassland in northeastern Montana.

Table 6 Areas of grassland/shrubland in Ecoregions of the Prairie Ecozone. Based on 1990s remote sensing data (Riley et al. 2007); Lake Manitoba Plain not shown because of incomplete data.

Ecoregion	Area (ha)	Percent of ecoregion
Mixed Grassland	5,532,996	41%
Moist Mixed Grassland	1,855,550	19%
Aspen Parkland	2,196,020	13%
Fescue Grassland	524,039	35%
Cypress Upland	623,633	73%
SW Manitoba Uplands	15,079	7%

Native vegetation in this ecoregion is largely "mixed prairie", so called because it is a mixture of midgrasses and shortgrasses. More productive mixed prairie also occurs in the Moist Mixed Grassland Ecoregion. As detailed in Section 3, the proportion of shortgrasses increases southward, and there are other shifts in species composition along the north-south gradient. The climate change models show the Canadian mixed prairie shifting toward the kind of mixed prairie found in central Montana and central Wyoming, with an increasing proportion of shortgrasses and with some new species. The warmest climate change scenario shows the southern edge of our mixed prairie shifting toward the shortgrass prairie found in eastern Colorado, a grassland type dominated by warm-season shortgrasses.

The mixed prairie probably has better odds of adjusting to climate change than other grassland types. Because of the mixture of growth-forms and photosynthetic types in existing grasslands, shifts in species composition can occur initially by increasing proportions of species already present (e.g. blue grama, little bluestem). Northward migration of southern species is more likely to be successful, because of the larger grassland area and relatively lower level of fragmentation. The dry climate and the incidence of drought years, which may increase with climate change, will tend to reduce exotic invasion problems which are expected to become more acute in moister regions. However, prolonged, severe droughts are most likely to occur in the mixed prairie, so the chances of ecological disruption by soil erosion are greatest here. From the agricultural perspective, severe drought years are most likely to reduce forage yield to very low levels in the mixed prairie. On the other hand, livestock producers in this area already tend to practice conservative stocking and to have drought planning measures in place, so should be best equipped to deal with future droughts.

8.3 Northern fescue prairie

Northern fescue prairie occurs in the Aspen Parkland and parts of the Moist Mixed Grassland Ecoregion (referred to as Northern Fescue Subregion in Alberta). This grassland type is dominated by plains rough fescue, while a variety of mixed prairie species are also present and tend to increase with overgrazing. The area of remaining grassland is much lower in these moister regions where the climate favours cultivation (Table 6). The remaining grassland patches are heavily fragmented by cropland, roads, and other disturbances.

Much of the northern fescue occurs in a patchwork with shrublands and aspen groves. Indeed, in many areas the greatest current threat to fescue prairie is woody encroachment, favoured by the elimination of prairie fires. The climate change models indicate that the climate will become less suitable for woody growth, eventually leading to shrinking of aspen groves. The evidence of aspen dieback in the Parkland during recent droughts shows that this could happen relatively rapidly. Presumably the problem of woody encroachment should ease, which should make it easier to maintain grassland areas. These trends could be beneficial for livestock grazing, for which grassland is preferred over woodland.

However, within the grassland patches, the climate change models imply that the northern fescue prairie will shift toward mixed prairie, with the extent of the shift varying among the scenarios. This implies that the unique character of this dense, fescue-dominated community will be lost, as grasslands shift toward a more common type. Initially at least, this shift can occur by expansion of the mixed-prairie components (needlegrasses, wheatgrasses, etc.) that are already present in fescue prairie.

Probably the greatest concern for the future of northern fescue prairie is exotic invasion. Much of this grassland type is already invaded, with exotics such as smooth brome and Kentucky bluegrass favoured by the relatively moist climate. If climate change is likely to increase invasion problems, as indicated by the literature review, then this is more likely to occur in northern fescue than in mixed prairie because of the moister climate. The disruption to existing communities resulting from climatic stress, exacerbated by the high fragmentation which will

create barriers to movement of new native species, could provide new opportunities for exotics to expand.

Shifting of the northern fescue prairie to new habitats to the north will be impeded by the high fragmentation of native habitats in this region. Moreover, the available native habitats are generally forested at present, raising questions about how forested lands will develop as the climate becomes less suitable for tree growth (see below).

8.4 Foothills fescue prairie

The other type of fescue grassland occurs in the foothills of the Rocky Mountains (the Fescue Grassland Ecoregion or Foothills Fescue Subregion). This grassland is dominated by foothills rough fescue, while subordinate species include both mixed prairie and western cordilleran species.

The climate zonation models indicate that foothills fescue will persist in more or less its current location. The current Canadian type of foothills fescue will probably shift toward the similar type found in Montana. However, concerns about increasing exotic invasion apply equally to this relatively moist area.

8.5 Eastern grasslands

The grasslands of the eastern end of the Prairie Ecozone show some unique features. There are a number of east-west trends across the aspen parkland from central Saskatchewan into Manitoba: decreasing occurrence of fescue prairie (perhaps because of a longer history of grazing impact); increasing abundance of exotics (especially Kentucky bluegrass); and increasing occurrence of tallgrass prairie species. Another feature of much of southern Manitoba is low relief and poor drainage, with many areas showing a pattern of upland grasslands on gentle rises and wet meadows on gentle depressions.

Much of the "native" grassland in Manitoba and southeastern Saskatchewan is really a blend of native species with Kentucky bluegrass, while smooth brome and other exotics are also widespread. The tendency of climate change to favour invasion is very likely to be expressed here, where exotics are already widespread, and where the moist climate and prevalence of moist soils tend to favour invasion. It may be increasingly difficult to maintain native species composition in these eastern grasslands. On the other hand, the climate change models indicate a shift toward a drier mixed prairie environment, which may not be quite as favourable to exotics. As with aspen parkland in general, this shift should eventually reduce the amount of woody encroachment, helping to maintain or increase the area of grassland. This aspect of the impact should be beneficial for livestock grazing.

The occurrence of tallgrass prairie species is another unique feature in eastern grasslands. The northern extension of tallgrass prairie into Canada is usually mapped in only a small area of the Red River basin south of Winnipeg. However, tallgrass species, especially big bluestem, appear along with mixed prairie species and Kentucky bluegrass across much of southern Manitoba and southeastern Saskatchewan. The adjoining area of north-central North Dakota is mapped as Wheatgrass-Bluestem-Needlegrass, indicating the same admixture. The tallgrass species are generally warm-season (C_4) species. Climate change is expected to increase the suitability for

warm-season grasses, which include big bluestem, little bluestem, Indian grass, switchgrass, and prairie dropseed. However, tallgrasses require relatively high moisture. Climate change models for southern Manitoba indicate a shift toward somewhat drier conditions, favouring the Wheatgrass-Needlegrass type found in western North and South Dakota, where tallgrasses are less important. While the warmer climate should favour warm-season species, the increasing aridity will reduce the suitability for the taller warm-season grasses. In an experimental study in Kansas tallgrass prairie, Nie et al. (1992) found that the taller C_4s (big bluestem and Indian grass) did better under a high-water treatment, whereas the shorter C_4 little bluestem did better under a low-water treatment. Also in Kansas tallgrass prairie, modeling by Craine et al. (2011) showed that a reduction in annual precipitation would preferentially reduce the more moisture-requiring lowland species; similarly, in a measured 16 year record, lowland species tended to decrease in years with low precipitation.

If variability increases with future warming, one consequence could be increased frequency of extreme wet years. While analysis of climatic extremes has focused on drought years, extreme wet years such as 2010 have shown that excessive moisture can cause problems for livestock producers such as flooded pastures. These problems are more evident in Manitoba than in the other provinces, because of the generally wetter climate and the extent of poorly drained land.

8.6 New grasslands on former forest land

One aspect of future grassland composition that has received little attention is the new grassland on formerly forested land. Climate change models show the southern boreal forest being pushed back, replaced by aspen parkland in the cooler scenarios, or even by mixed prairie in the warmer scenarios. This change could substantially increase the area of grassland in the region, which would increase the forage resource for livestock grazing. However, the question is: what kind of grassland?

The transition from forest to grassland could occur either by gradual tree mortality (as in the aspen dieback observed in recent droughts), or by regeneration failure following fire or timber-harvesting. In either case, the lower plants immediately available for filling the growing space will be shade-adapted forest understory species. The initial transition, as in the aspen dieback scenario, could be from closed forest to open forest, with more lush growth of the understory species as the canopy opens. Some of the shrubs such as chokecherry, saskatoon, snowberry and rose can grow either in shade or sun, so could persist as shrubland even after all the trees are gone. However, especially among the native herbaceous species, there is surprisingly little overlap between forest and grassland communities. For example, the major forest grasses (e.g. rough-leaved rice-grass, purple oat-grass, hairy wild-rye) are rarely found in grassland, whereas the major grassland grasses (e.g. rough fescue, needlegrasses, wheatgrasses, bluestems) are rarely found in forest (awned wheatgrass is one exception). Therefore, in many situations the shade-adapted forest species will have to be replaced by sun-adapted grassland species.

In the best-case scenario, the declining forest stand would be surrounded by native grassland, as in intact areas of aspen parkland. In this situation, we could expect propagules of native grassland species to gradually spread into the opening forest, with increasing competitive success as light levels increase. In this situation there could be a smooth transition from native forest to native grassland. From central Alberta to central Saskatchewan, this would usually be northern fescue prairie.

However, in many situations the propagules that will be most available will be exotics, including smooth brome, Kentucky bluegrass, timothy, Canada thistle, and others. Anywhere in the region where there are roads with ditches, there will be a source of smooth brome. Stands of seeded forages also provide a source of exotic propagules. Brome and Kentucky bluegrass may already have invaded the grassland, and will probably spread more aggressively than the native grassland species. In the worst-case scenario, the forest will already have these exotics growing in the understory, usually where it has been disturbed by heavy livestock grazing; several of these species are capable of growing in both sun and shade. In all of these situations, we can expect a transition from forest to exotic grassland.

In the boreal forest (i.e. north of the aspen parkland), there is little native grassland to provide a source of propagules. In this situation it is even more likely that the source of sun-adapted plants will be exotics spreading from roadsides or seeded pastures. However, even in the forest this may not always be the case. Aspen forests along the southern edge of the boreal zone have often resulted from invasion of grassland in the recent past. In some cases in this region there are pockets of the original prairie, for example on south-facing slopes, which could provide a source of native propagules. Some open stands, especially on sandy soils, will even have a few grassland species (e.g. golden-bean, pasture sage, crocus) in the understory. However, the more common source for propagules is likely to be the brome-infested roadside.

9 LITERATURE CITED

Abouguendia, Z.M. 1990. Range plan development: a practical guide to planning for management and improvement of Saskatchewan rangeland. New Pasture and Grazing Technologies Project, Regina.

Adams, B., J. Carlson, D. Milner, T. Hood, B. Cairns, and P. Herzog. 2004. Beneficial Grazing Management Practices for Sage-Grouse (*Centrocercus urophasianus*) and Ecology of Silver sagebrush (*Artemisia cana* Pursh subsp. *cana*) in Southeastern Alberta. Alberta Sustainable Resource Development.

Allen, C.D., A.K. Macalady, H. Chencouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D.D. Breshears, E.H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J-H Lim, G. Allard, S.W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660-684.

Allen, C.D., and D.D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proceedings of the National Academy of Sciences USA, 95:14839-14842.

Bachelet, D., R.P. Neilson, T. Hickler, R.J. Drapek, J.M. Lenihan, M.T. Sykes, B. Smith, S. Sitch, and K. Thonicke. 2003. Simulating past and future dynamics of natural ecosystems in the United States. Global Geochemical Cycles 17(2), 1045, doi:10.1029/2001GB001508.

Bailey, C.G., and P.W. Riegert. 1973. Energy dynamics of *Encoptolophus sordidud costalis* (Scuder) (Orthoptera: Acrididae) in a grassland ecosystem. Canadian Journal of Zoology 51:91-100.

Bailey, R.G. 1978. Description of the ecoregions of the United States. USDA Forest Service.

Bailey, R.G. 1981. Ecoregions of North America after the classification of J.M. Crowley. Map at 1:12,000,000.

Baker, B.B., Hanson, J.D., Bourdon, R.M., Eckert, J.B. 1993. The potential effects of climate change on ecosystem processes and cattle production on U.S. rangelands. Climate Change, 25: 97-117.

Barrow, E. 2009. Climate scenarios for Saskatchewan. Prairie Adaptation Research Collaborative, University of Regina. 131 pp.

Batt, B.D.J., M.G. Anderson, C.D. Anderson, and F.D. Caswell. 1989. The use of prairie potholes by North American ducks. pp. 204-227 in A.G. van der Valk (ed.). Northern Prairie Wetlands. Iowa State University Press.

Beaubien, E.G. 2001. Canada Plantwatch: trends to earlier spring development. In Proceedings of the Sixth Prairie Conservation and Endangered Species Workshop, February 2001. Edited by D. Blouin. Manitoba Habitat Heritage Corporation.

Beaubien, E.G. & Freeland H.J. 2000. Spring phenology trends in Alberta, Canada : links to ocean temperature. International Journal of Biometeorology 44 :53-59.

Bestelmeyer, B.T, J.R. Brown, K.M. Havstad, R.Alexander, G. Chavez, and J.E. Herrick. 2003. Development and use of state-and-transition models for rangelands. Journal of Range Management 56:114-126.

Bethke, R.W. and Nudds, T.D. 1995. Effects of climate change and land use on duck abundance in Canadian prairie-parklands. Ecological Applications 5:588–600.

Blumenthal, D., R.A. Chimner, J.M. Welker, and J.A. Morgan. 2008. Increased snow facilitates plant invasion in mixedgrass prairie. New Phytologist 179:440-448.

Bonsal, B. 2008. Droughts in Canada: An overview. CMOS Bulletin SCMO. 36:79-86.

Bonsal, B., and M. Regier. 2006. The 2001 and 2002 Canadian drought: historical context and potential future occurrence. CCIAP A932 " Canadian agricultural adaptations to 21st century droughts: preparing for climate change". Environment Canada.

Bonsal, B., and M. Regier. 2007. Historical comparison of the 2001/2002 drought in the Canadian Prairies. Climate Research 33:229-242.

Bradley, B.A. 2009. Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. Global Change Biology 15:196-208.

Bradley, B.A., D.M. Blumenthal, D.S. Wilcove, and L.H. Ziska. 2010. Predicting plant invasions in an era of global change. Trends in Ecology and Evolution 25:310-318.

Brandt, J.P. 1997. Forest health monitoring in west-central Canada in 1996. Canadian Forest Service, Northern Forestry Centre, Information Report NOR-X-351.

Briske, D.D., S.D. Fuhlendorf, and F.E. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. Rangeland Ecology and Management 58:1-10.

Brklacich, M., C. Bryant, B. Veenhof, and A. Beauchesne. 1999. Implications of global climatic change for Canadian agriculture: a review and appraisal of rsearch from 1984 to 1997. Chapter 4 in G. Koshida and W. Avis (editors). The Canada country study: climate impacts and adaptation. Environment Canada.

Campbell, B.D., and D.M. Stafford Smith. 2000. A synthesis of recent global change research on pasture and rangeland production: reduced uncertainties and their management implications. Agriculture, Ecosystems and Environment 82:39-55.

Campbell, B.D., D.M. Stafford Smith, and G.M McKeon. 1997. Elevated CO_2 and water supply interactions in grasslands: a pastures and rangelands management perspective. Global Change Biology 3:177-187.

Carroll, A.L., S.W. Taylor, J. Regniere, and L. Safranyik. 2003. Effects of climate change on range expansion by the mountain pine beetle of British Columbia. Canadian Forest Service, Pacific Forestry Centre.

Clarke, S.E., E.W. Tisdale, and N.A. Skoglund. The effects of climate and grazing practices on short-grass prairie vegetation. 1943. Canada Department of Agriculture.

Coffin, D.P., and W.K. Lauenroth. 1996. Transient Responses of North-American Grasslands to Changes in Climate. Climatic Change, 34:269-278.

Collatz, G.J., J.A. Berry, and J.S. Clark. 1998. Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C_4 grasses: present, past, and future. Oecologica 114:441-454.

COSEWIC. 2000. COSEWIC asessment and update status report on the Hairy Prairie-clover *Dalea villosa* var. *villosa* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 22 pp. (www.sararegistry.gc.ca/status/staus_e.cfm)

COSEWIC. 2002. COSEWIC asessment and update status report on the Western Spiderwort *Tradescantia occidentalis* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 25 pp. (www.sararegistry.gc.ca/status/staus_e.cfm)

COSEWIC. 2003. COSEWIC asessment and update status report on the Dakota Skipper *Hesperoa dacotae* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 35 pp. (www.sararegistry.gc.ca/status/staus_e.cfm)

COSEWIC. 2004a. COSEWIC asessment and update status report on the Loggerhead Shrike *excubitorides* subspecies *Lanus ludovicianus excubitorides* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 24 pp. (www.sararegistry.gc.ca/status/staus_e.cfm)

COSEWIC. 2004b. COSEWIC asessment and update status report on the Prairie Skink *Eumeces septentrionalis* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 22 pp. (www.sararegistry.gc.ca/status/staus_e.cfm)

COSEWIC. 2006. COSEWIC asessment and update status report on the Burrowing Owl *Athene cunicularia* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 31 pp. (www.sararegistry.gc.ca/status/staus_e.cfm)

COSEWIC. 2009. COSEWIC asessment and update status report on the Northern Leopard Frog Lithobates pipiens, Rocky Mountain population, Western Boreal/Prairie populations and Eastern populations, in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 69 pp. (www.sararegistry.gc.ca/status/staus_e.cfm)

COSEWIC. 2010. COSEWIC assessment and status report of the Sprague's Pipit *Anthus spragueii* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 28 pp. (www.sararegistry.gc.ca/status/staus_e.cfm)

Coupland, R.T. 1958. The effects of fluctuations in weather upon the grasslands of the Great Plains. Botanical Review 24:273-317.

Coupland, R.T. 1959. Effects of changes in weather conditions upon grasslands in the Northern Great Plains. In: Grasslands. Pub. 53, American Society for the Advancement of Science, Washington, DC, pp. 291-306.

Coupland, R.T. 1961. A reconsideration of grassland classification in the Northern Great Plains of North America. Journal of Ecology 49:135-169.

Craine, J.M., A.J. Elmore, K.C. Olson, and D. Tolleson. 2009. Climate change and cattle nutritional stress. Global Change Biology doi: 10.1111/j.1365-2486.2009.02060.x

Craine, J.M., J.B. Nippert, E.G. Towne, S. Tucker, S.W. Kembel, A. Skibbe, and K.K. McLauchlan. 2011. Functional consequences of climate change-induced plant species loss in a tallgrass prairie. Oecologica 165:1109-1117.

Daly, C., Neilson, R.P., and Phillips, D.L. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33: 19.

Davis, M.B. 1981. Quaternary history and the stability of forest communities. Pp. 132-153 in D.C. West, H.H. Shugart, and D.B. Botkin (eds.). Forest succession: concepts and application. Springer-Verlag, New York.

Davis, M.B., and R.G. Shaw. 2001. Range shifts and adaptive responses to quaternary climate change. Science 292:673-679.

Derner, J.D., and R.H. Hart. 2007. Grazing-induced modifications to peak standing crop in Northern Mixed-grass Prairie. Rangeland Ecology and Management 60:270-276.

DeSantis, R.D., S.W. Hallgren, and D.W. Stahle. 2011. Drought and fire suppression lead to rapid forest composition change in a forest-prairie ecotone. Forest Ecology and Management 261:1833-1840.

Dobrowski, S.Z., J.H. thorne, J.A. Greenberg, H.D. Safford, A.R. Mynsberge, S.M. Crimmins, and A.K. Swanson. 2011. Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. Ecological Monographs 81:241-257.

Dukes, J.S., and H.A. Mooney. 1999. Does global change increase the success of biological invaders. Trends in Ecology and Evolution 14:135-139.

Epstein, H.E., Lauenroth, W.K., Burke, I.C., and Coffin, D.P. 1996. Ecological responses of dominant grasses along two climatic gradients in the Great Plains of the United States. Journal of Vegetation Science 7: 777-788.

Epstein, H.E., Lauenroth, W.K., Burke, I.C., and Coffin, D.P. 1997a. Production patterns of C_3 and C_4 functional types in the U.S. Great Plains. Ecology 78:722-731.

Epstein, H.E., W.K. Lauenroth, and I.C. Burke. 1997b. Effects of temperature and soil texture on ANPP in the U.S. Great Plains. Ecology 78:2628-2631.

Epstein, H.E., Lauenroth, W.K., Burke, I.C., and Coffin, D.P. 1998. Regional productivities of plant species in the Great Plains of the United States. Plant Ecology 134:173-195.

Epstein, H.E., R.A. Gill, J.M. Paruelo, W.K. Lauenroth, G.J. Jia, and I.C. Burke. 2002. The relative abundance of three plant functional types in temperate grasslands and shrublands of North and South America: effects of projected climate change. Journal of Biogeography 29:875-888.

ESWG. 1996. A national ecological framework for Canada. Ecological Stratification Working Group. Agriculture and Agri-Food Canada and Environment Canada.

Fay, P.A., A.K. Knapp, J.M Blair, J.D. Carlisle, B.T. Danner, and J.K. McCarron. 2003. Rainfall timing, soil moisture dynamics, and plant responses in a mesic tallgrass prairie ecosystem. pp. 147-163 in Changing Precipitation Regimes and Terrestrial Ecosystems: a North American Perspective (J.F. Weltzin and G.R. McPherson, editors). University of Arizona Press, Tucson.

George, T.L., A.C. Fowler, R.L Knight, and L.C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. Ecological Applications 2:275-284.

Gray, S.T., Betancourt, J.L., Jackson, S.T., and Eddy, R.B. 2006. Role of multidecadal climate variability in a range extension of pinyon pine. Ecology 87(5): 1124-1130.

Haddad, N.M., D. Tilman and J.M.H. Knops. 2002. Long-term oscillations in grassland production induced by drought. Ecology Letters 5: 110-120.

Hawkins, B.A. and M. Holyoak. 1998. Transcontinental crashes of insect populations? American Naturalist 152: 480-484.

Heitschmidt, R.K., M.R. Haferkamp, M.G. Karl, and A.L. Hild. 1999. Drought and grazing: I. Effects on quantity of forage produced. Journal of Range Management 52:440-446.

Heitschmidt, R.K., K.D. Klement, and M.R. Haferkamp. 2005. Interactive effects of drought and grazing on Northern Great Plains rangelands. Rangeland Ecology and Management 58:11-19.

Heitschmidt, R.K. and L.T. Vermeire. 2006. Can abundant summer precipitation counter losses in herbage production caused by spring drought? Rangeland Ecology & Management 59: 392-399.

Hellmann, J.J., J.E. Byers, B.G. Bierwagen, and J.S. Dukes. 2008. Five potential consequences of climate change for invasive species. Conservation Biology 22:534-543.

Hogg, E.H. 1994. Climate and the southern limit of the western Canadian boreal forest. Canadian Journal of Forest Research 24:1835-1845.

Hogg, E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agricultural and Forest Meteorology 84:115-122.

Hogg, E.H., and P.A. Hurdle. 1995. The aspen parkland in western Canada: a dry-climate analogue for the future boreal forest? Water, Air and Soil Pollution 82:391-400.

Hogg, E.H., J.P. Brandt, and B. Kochtubajda. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. Canadian Journal of Forest Research 35:610-622.

Hogg, E., J. Brandt, and M. Michaelian. 2008. Impacts of a regional drought on the production, dieback, and biomass of western Canadian aspen forests. Canadian Journal of Forest Research 38:1373-1384.

Igl, L., and D. Johnson. 1997. Changes in breeding bird populations in North Dakota: 1967 to 1992-93. The Auk 114:74-92)

Ives, W.G.H. 1981. Environmental factors affecting 21 forest insect defoliators in Manitoba and Saskatchewan, 1945-69. Canadian Forestry Service, Northern Forest Research Centre, Information Report NOR-X-233.

Jackson, S.T., J.L. Betancourt, R.K. Booth, and S.T. Gray. 2009. Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. PNAS Early Edition. www.pnas.org/cgi/coi/10.1073/pnas.0901644106.

Johnson, D.L. 1993. Insects and climate change: prospects for population changes and implications for environmental quality. pp. 94-98 in Proceedings of the 3rd Prairie Conservation and Endangered Species Workshop. Edited by G.L. Holroyd, H.L. Dickson, M. Regnier, and H.C. Smith. Provincial Museum of Alberta, Natural History Occasional Paper No. 19.

Johnson, W.C., B.V. Millett, T. Gilmanov, R.A. Voldseth, G.R. Guntenspergen and D.E. Naugle. 2005. Vulnerability of northern prairie wetlands to climate change. BioScience 55:863-872.

Johnson, W.C., B. Werner, G.R. Guntenspergen, R.A. Voldseth, B. Millett, D.E. Naugle, M. Tulbure, R.W.H. Carroll, J. Tracy, and C. Olawsky. 2010. Prairie wetland compexes as landscape functional units in a changing climate. BioScience 60:128-140.

Kelly, A.E., and M.L. Goulden. 2008. Rapid shifts in plant distribution with recent climate change. PNAS 105:11823-11826.

Kharin, V.V., and F.W. Zwiers. 2000. Changes in the extremes in an ensemble of transient climate simulation with a coupled atmosphere-ocean GCM. Journal of Climate 13:3760-3788.

Kharin, V.V., and F.W. Zwiers. 2005. Estimating extremes in transient climate change simulations. Journal of Climate 18:1156-1173.

Kirchner, T.B. 1977. The effects of resource enrichment on the diversity of plants and arthropods in a shortgrass prairie. Ecology 58:1334-1344.

Kittel, T.B.F., Rosenbloom, N.A., Painter, T.H., and Schimel, D.S. 1995. The VEMAP integrated database for modelling United States ecosystem/vegetation sensitivity to climate change. Journal of Biogeography 22: 857-862.

Knapp, A.K., and M.D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291:481-484.

Kochy, M., and S.D. Wilson. 2004. Semiarid grassland responses to short-term variation in water availability. Plant Ecology 174:197-203.

Kreyling, J., C. Bierkuhnlein, L. Ellis and A. Jentsch. 2008. Invasibility of grassland and heath communities exposed to extreme weather events – additive effects of diversity resistance and fluctuating physical environment. Oikos 117: 1542-1554.

Kuchler, A.W. 1964. Potential natural vegetation of the conterminous United States. American Geographical Society. Special Publication No. 36. Map at 1:3,168,000 and accompanying manual.

Larson, D.L. 1995. Effects of Climate on Numbers of Northern Prairie Wetlands. Climatic Change 30: 169-180.

Lauenroth, W.K., and O.E. Sala. 1992. Lon-term forage production of North American shortgrass steppe. Ecological Applications 2:397-403.

Lenihan, J.M., and R.P. Neilson. 1995. Canadian vegetation sensitivity to projected climatic change at three organizational levels. Climatic Change 30:27-56.

Long, S.P., and P.R. Hutchin. 1991. Primary production in grasslands and coniferous forests with climate change: an overview. Ecological Applications, 1: 139-156.

Lucash, M.S., B. Farnsworth, and W.E. Winner. 2005. Response of sagebrush steppe species to CO_2 and soil temperature. Western North American Naturalist 65:80-86.

Malcolm, J.R., and L.F. Pitelka. 2000. Ecosystems and global climate change: a review of potential impacts on U.S. terrestrial ecosystems and biodiversity. Pew Center on Global Change.

Martinez-Meyer, E., A.P. Peterson, and W.W. Hargrove. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography 4:305-314.

Mattson, W.J., and R.A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. BioScience 37:110-118.

McCarty, J.P. 2001. Ecological consequences of recent climate change. Conservation Biology 15:320-331.

McCune, B., J.B. Grace and D.L. Urban. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McGinn, S.M., A. Shepherd, and O.O. Akinremi. 2001. Assessment of climate change and impacts on soil moisture and drought on the Prairies. Final Report for the Climate Change Action Fund (CCAF) Science, Impacts and Adaptation. Agriculture and Agri-Food Canada, Lethbridge, AB.

McMenamin, S.K., E.A. Hadly, and C.K. Wright. 2008. Climate change and wetland desiccation cause amphibian decline in Yellowston National Park. Proceedings of the National Academy of Sciences of the United States of America 105:16988-16993.

Milchunas, D.G., and W.K. Lauenroth. 1995. Inertia in plant community structure: state changes after cessation of nutrient-enrichment stress. Ecological Applications 5:452-458.

Morgan, J.A., A.R. Mosier, D.G. Milchunas, D.R. LeCain, J.A. Nelson, and W.J. Parton. 2004. CO_2 enhances production but alters species composition and reduces forage quality in the Colorado shortgrass steppe. Ecological Applications. 14: 208 – 219

Murphy-Klassen, H.M., T.J. Underwood, S.G. Sealy, and A.A. Czyrnyj. 2005. Long-term trends in spring arrival dates of migrant birds at Delta Marsh, Manitoba, in relation to climate change. The Auk 122:1130-1148.

Neilson, R.P. 2003 The importance of precipitation seasonability in controlling vegetation distribution. pp. 47-74 in Changing Precipitation Regimes and Terrestrial Ecosystems: a North American Perspective (J.F. Weltzin and G.R. McPherson, editors). University of Arizona Press, Tucson.

Neilson, R.P., L.F. Pitelka, A.M. Solomon, R. Nathan, G.F. Midgley, J.M.V. Fragoso, H. Lischke, and K. Thompson. 2005. Forecasting regional to global plant migration in response to climate change. BioScience 55(9):749-759.

Nie, D., M.B. Kirkham, L.K. Ballou, D.J. Lawlor, and E.T. Kanemasu. 1992. Changes in prairie vegetation under elevated carbon dioxide levels and two soil moisture regimes. Journal of Vegetation Science 3:673-678.

Niemuth, N.D., J.W. Solberg, and T.L. Shafer. 2008. Influence of moisture on density and distribution of grassland birds in North Dakota. The Condor 110:211-222.

Nyirfa, W.N., and B. Harron. 2002. Assessment of climate change on the agricultural resources of the Canadian Prairies. Agriculture and Agri-Food Canada, Prairie Farm Rehabilitation Administration, Regina, SK.

Ojima, D.S., W.J. Parton, M.B. Coughenour, J.M.O. Scurlock, T.B. Kirchner, T.G.F. Kittel, D.O. Hall, D.S. Schimel, E. Garcia Moya, T.G. Gilmanov, T.R. Seastedt, Apinan Kamnalrut, J.I. Kinyamario, S.P. Long, J-C. Menaut, O.E. Sala, R.J. Scholes, and J.A. van Veen. 1996. Impact of climate and atmospheric carbon dioxide changes on grasslands of the world. Pp. 271-311 in: Breymeyer, A.I., D.O. Hall, J.M. Melillo, and G.I. Agren (eds.). Global change: effects on coniferous forests and grasslands. John Wiley and Sons, Chichester.

Opdam, P. and D. Wascher. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation 117: 285-297.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology and Systematics 37:637-669.

Parmesan, C., T.L. Root and M.R. Willig. 2000. Impacts of extreme weather and climate on terrestrial biota. Bulletin of the American Meteorological Society 81: 443-450.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.

Parmesan, C., S. Gaines, L. Gonzalez, D.M. Kaufman, J. Kingsolver, A.T. Peterson, and R. Sagarin. 2005. Empirical perspectives on species borders: from traditional biogeography to global change. Oikos 108:58-75.

Parton, W.J., D.S. Ojima, and D.S. Schimel. 1994. Environmental Change in Grasslands: Assessment Using Models. Climatic Change, 28:111-141.

Parton, W.J., M.B. Coughenour, J.M.O. Scurlock, D.S. Ojima, T.G. Gilmanov, R.J. Scholes, D.S. Schimel, T.B. Kirchner, J.-C. Menaut, T.R. Seastedt, E. Garcia Moya, Apinan Kamnalrut, J.I. Kinyamario, and D.O. Hall. 1996. Grassland ecosystem modeling: development and test of ecosystems models for grassland systems. Pp. 229-267 in: Breymeyer, A.I., D.O. Hall, J.M. Melillo, and G.I. Agren (eds.). Global change: effects on coniferous forests and grasslands. John Wiley and Sons, Chichester.

Paruelo, J.M., and W.K. Lauenroth. 1996. Relative abundance of plant functional types in grasslands and shrublands of North America. Ecological Applications 6:212-1224.

Pearson, R.G., and T.P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology & Biogeography 12: 361-371.

Peters, R.L. 1992. Conservation of biological diversity in the face of climate change. Pp. 15-30 in R.L. Peters and T.E. Lovejoy (eds.). Global warming and biological diversity. Yale University Press.

Peterson, A.T. 2003. Projected climate change effects on Rocky Mountain and Great Plains birds: generalities of biodiversity consequences. Global Change Biology 9:647-655.

Polley, H.W. 1997. Implications of rising atmospheric carbon dioxide concentration for rangelands. Journal of Range Management 50:562-577.

Powell, L.R., A.A. Berg, D.L. Johnson, and J.S. Warland. 2007. Relationships of pest grasshopper populations in Alberta, Canada to soil moisture and climate variables. Agricultural and Forest Meteorology 144:73-84.

Reading, C.J. 2007. Linking global warming to amphibian declines through its effects on female body condition and survivorship. Oecologia 151:125-131.

Rehfeldt, G.E., C.C. Ying, D.L. Spittlehouse, and D.A. Hamilton, Jr. 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. Ecological Monographs 69:375-407.

Rehfeldt, G.E., D.E. Ferguson, and N.L. Crookston. 2009. Aspen, climate, and sudden decline in western USA. Forest Ecology and Management 258:2353-2364.

Ricketts, T.H., et al. 1999. Terrestrial ecoregions of North America: a conservation assessment. World Wildlife Fund—United States and Canada. Island Press, Washington, DC.

Riley, J. L., S.E. Green, and K.E. Brodribb. 2007. A conservation blueprint for Canada's prairies and parklands. Nature Conservancy of Canada, Toronto, ON.

Risser, P.G., E.C. Birney, H.D. Blocker, S.W. May, W.J. Parton, J.A. Wiens. 1981. The true prairie ecosystem. US/IBP Synthesis Series 16. Hutchinson Ross Publishing Company, Stroudsburg, PA.

Rodriguez Iglesias, R.M., and Kothmann, M.M. 1997. Structure and causes of vegetation change in state and transition model applications. Journal of Range Management 50: 399-408.

Root, T.L. 1988. Environmental factors associated with avian distributional limits. Journal of Biogeography 15: 489-505.

Root, T.L., J.T. Price, K.R. Hall, S.H. Schneider, C. Rosenzweig and A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 1-4.

Rotenberry, J.T. 1980. Dietary relationships among shrubsteppe passerine birds: competition or opportunism in a variable environment. Ecological Monographs 50:93-110.

Rotenberry, J.T., and J.A. Wiens. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. Ecology 72:1325-1335.

Running, S.W., and L.S. Mills. 2009. Terrestrial ecosystem adaptation. Resources for the Future Report.

Sala, O.E., W.J. Parton, L.A. Joyce, and W.K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40-45.

Sauchyn, D., and S. Kennedy. 2005. The potential for land degradation under climate change in the vicinity of six rural communities in Saskatchewan. Prairie Forum 30:173-186.

Sauchyn, D., E. Barrow, X. Fang, N. Henderson, M. Johnston, J. Pomeroy, J. Thorpe, E. Wheaton, and B. Williams. 2009. Saskatchewan's natural capital in a changing climate: an assessment of impacts and adaptation. Report to Saskatchewan Ministry of Environment from the Prairie Adaptation Research Collaborative, 167 pp.

Schimel, D.S., T.G.F. Kittel, and W.J. Parton. 1991. Terrestrial biogeochemical cycles: global interactions with the atmosphere and hydrology. Tellus 43AB:188-203.

Schimel, D.S., W.J. Parton, T.G.F. Kittel, D.S. Ojima, and C.V. Cole. 1990. Grassland biogeochemistry: links to atmospheric processes. Climatic Change 17:13-25.

Schneider, R.R., A. Hamann, D. Farr, Xianli Wang, and S. Boutin. 2009. Potential effects of climate change on ecosystem distribution in Alberta. Canadian Journal of Forest Research 39:1001-1010.

Sheffield, J., and E.F. Wood. 2007. Projected changes in drought occurrence under future global warming from multi-model, multi-scenario, IPCC AR4 simulations. Climate Dynamics. DOI 10.1007/s00382-007-0340-z.

Sims, P.L., Singh, J.S., and Lauenroth, W.K. 1978. The structure and function of ten western North American grasslands: I. Abiotic and vegetational characteristics. Journal of Ecology, 66: 251-285.

Singh, T., and E.E. Wheaton. 1991. Boreal forest sensitivity to global warming: implications for forest management in western interior Canada. Forestry Chronicle 67:324-348.

Skelly, D.K., L.N. Joseph, H.P. Possingham, L.K. Freidenburg, T.J. Farrugia, M.T. Kinnison, and A.P. Hendry. 2007. Evolutionary responses to climate change. Conservation Biology 21:1353-1355.

Smoliak, S. 1986. Influence of climatic conditions on production of *Stipa-Bouteloua* prairie over a 50-year period. Journal of Range Management 39:100-103.

Smoliak, S. 1956. Influence of climatic conditions on forage production of shortgrass rangeland. Journal of Range Management 10: 89-91.

Sorenson, L.G., R. Goldberg, T.L. Root, and M.G. Anderson. 1998. Potential effects of global warming on waterfowl populations breeding in the Northern Great Plains. Climatic Change 40:343-369.

Stringham, T.K., W.C. Krueger, and P.L. Shaver. 2003. State and transition modeling: an ecological process approach. Journal of Range Management 56:106–113.

Svejcar, T., J. bates, R. Angell, and R. Miller. 2003. The influence of precipitation timing on the sagebrush steppe ecosystem. pp. 91-106 in Changing Precipitation Regimes and Terrestrial Ecosystems: a North American Perspective (J.F. Weltzin and G.R. McPherson, editors). University of Arizona Press, Tucson.

Sykes, C. 2008. Simulation of the effects of climate change on forage and cattle production in Saskatchewan (PhD thesis), Dept of Animal and Poultry Science, University of Saskatchewan,

Tepedino, V.J., and N.L. Stanton. 1981. Diversity and competition in bee-plant communities on short-grass prairie. Oikos 36:35-44.

Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham,B.F.N. Erasmus, M. Ferreira de Siquelra, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A.T. Peterson, O.L. Phillips, and S.E. Williams. 2004. Extinction risk from climate change. Nature 427:145-148.

Thomson, A.J. 2009. Climate indices and mountain pine beetle-killing temperatures. Forestry Chronicle 85:105-109.

Thorpe, J. 2007a. Saskatchewan Rangeland Ecosystems, Publication 4: Communities on the Loam Ecosite. Saskatchewan Prairie Conservation Action Plan. Saskatchewan Research Council Pub. No. 11881-4E07.

Thorpe, J. 2007b. Impacts of climate change on range site classification in the Canadian Prairies. Saskatchewan Research Council Pub. No. 11929-1E07.

Thorpe, J., B. Houston, and S. Wolfe. 2004. Impacts of climate change on grazing capacity of native grasslands in the Canadian Prairies. Saskatchewan Research Council, Saskatoon, SK, Publication No. 11561-1E04.

Thorpe, J., S.A. Wolfe, and B. Houston. 2008. Potential impacts of climate change on grazing capacity of native grasslands in the Canadian prairies. Canadian Journal of Soil Science 88:595-609.

Tilman, D. and A. El Haddi. 1992. Drought and biodiversity in grasslands. Oecologia 89: 257-264.

Travis, J.M.J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proceedings of the Royal Society of London. Series B, Biological Sciences 270: 467-473.

Van der Kamp, G., Stolte, W.J., and Clark, R. 1999. Drying out of small prairie wetlands after conversion of their catchments from cultivation to permanent brome grass. Journal of Hydrological Sciences: 387-397.

Vandall, J., N. Henderson, and J. Thorpe. 2006. Suitability and adaptability of current protected area policies under different climate change scenarios: the case of the Prairie Ecozone, Saskatchewan. Saskatchewan Research Council Publication No. 11755-1E06.

Visser, M.E., and C. Both. 2005. Shifts in phenology due to global climate chage: the need for a yardstick. Proceedings of the Royal Society B 272:2561-2569.

Walther, G-R. 2003. Plants in a warmer world. Perspectives in Plant Ecology, Evolution and Systematics 6/3:169-185.

Wang, G. 2005. Agricultural drought in a future climate: results from 15 global climate models participating in the IPCC 4th Assessment. Climate Dynamics 25:739-753.

Watmough, M. D. and M.J. Schmoll. 2007. Environment Canada's Prairie & Northern Habitat Monitoring Program Phase II: recent habitat trends in the PHJV. Environment Canada, Canadian Wildlife Service, Edmonton, AB.

Westoby, M., B.H. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42:266–274.

Wiens, J.A. 1974. Climatic instability and the "ecological saturation" of bird communities in North American grasslands. Condor 65: 385-400.

Willms, W.D., S. Smoliak, and A.W. Bailey. 1986. Herbage production following litter removal on Alberta native grasslands. Journal of Range Management 39:536-540..

Willms, W.D., S.M. McGinn, and J.F. Dormaar. 1993. Influence of litter on herbage production in the mixed prairie. Journal of Range Management 46:320-324.

Winslow, J.C., E.R. Hunt, Jr., and S.C. Piper. 2003. The influence of seasonal water availability on global C_3 versus C_4 grassland biomass and its implications for climate change research. Ecological Modelling 163:153-173.

Wolfe, S., and J. Thorpe. 2005. Shifting sands: climate change impacts on sand hills in the Canadian prairies and implications for land use management. Prairie Forum 30:123-141.

Woodward, F.I. 1987. Climate and plant distribution. Cambridge University Press. 174 pp.

Wroe, R., S. Smoliak, B. Adams, W. Willms, and M.L. Anderson. 1988. Guide to range condition and stocking rates for Alberta grasslands. Alberta Forestry, Lands, and Wildlife, Public Lands.

Ziska, L.H., D.M. Blumenthal, G.B. Runion, E.R. Hunt Jr., and H. Diaz-Soltero. 2011. Invasive species and climate change: an agronomic perspective. Climatic Change 105:13-42.

APPENDIX A. COMMON AND SCIENTIFIC NAMES OF SPECIES MENTIONED IN THE TEXT

Common Name	Scientific Name
Trees:	
balsam fir	*Abies balsamea*
white birch	*Betula papyrifera*
tamarack	*Larix laricina*
white spruce	*Picea glauca*
black spruce	*Picea mariana*
jack pine	*Pinus banksiana*
lodgepole pine	*Pinus contorta*
piñon pine	*Pinus spp.*
balsam poplar	*Populus balsamifera*
trembling aspen	*Populus tremuloides*
bur oak	*Quercus macrocarpa*
Shrubs:	
leadplant	*Amorpha canescens*
silver sagebrush	*Artemisia cana*
big sagebrush	*Artemisia tridentata*
rabbitbrush	*Chrysothamnus spp.*
shrubby cinquefoil	*Dasiphora fruticosa*
wolf-willow	*Elaeagnus commutata*
prairie rose	*Rosa arkansana*
western snowberry	*Symphoricarpos occidentalis*
horsebrush	*Tetradymia canescens*
yucca	*Yucca glauca*
Graminoids:	
Columbia needlegrass	*Achnatherum nelsonii*
Richardson's needlegrass	*Achnatherum richardsonii*
big bluestem	*Andropogon gerardii*
red three-awn	*Aristida purpurea*
side-oats grama	*Bouteloua curtipendula*
blue grama	*Bouteloua gracilis*
hairy grama	*Bouteloua hirsuta*
cheatgrass	*Bromus tectorum*
buffalograss	*Buchloe dactyloides*
plains reedgrass	*Calamagrostis montanensis*
sand reedgrass	*Calamovilfa longifolia*
low sedge	*Carex duriuscula*
thread-leaved sedge	*Carex filifolia*
Parry oatgrass	*Danthona parryi*
timber oatgrass	*Danthonia intermedia*
northern wheatgrass	*Elymus lanceolatus*
awned wheatgrass	*Elymus trachycaulus* ssp. *subsecundus*
foothills rough fescue	*Festuca campestris*

plains rough fescue	*Festuca hallii*
Idaho fescue	*Festuca idahoensis*

Common Name	**Scientific Name**
Hooker's oatgrass	*Helictotrichon hookeri*
needle-and-thread	*Hesperostipa comata*
western porcupine grass	*Hesperostipa curtiseta*
porcupine grass	*Hesperostipa spartea*
June grass	*Koeleria macrantha*
green needle grass	*Nassella viridula*
switchgrass	*Panicum virgatum*
western wheatgrass	*Pascopyrum smithii*
plains bluegrass	*Poa arida*
Kentucky bluegrass	*Poa pratensis*
Sandberg's bluegrass	*Poa secunda*
bluebunch wheatgrass	*Pseudoroegneria spicata*
little bluestem	*Schizachyrium scoparium*
squirreltail	*Sitanion hystrix*
Indian grass	*Sorghastrum nutans*
prairie cordgrass	*Spartina pectinata*
sand dropseed	*Sporbolus cryptandrus*
prairie dropseed	*Sporobolus heterolepis*

Forbs:

pasture sage	*Artemisia frigida*
prairie sage	*Artemisia ludoviciana*
arrowleaf balsamroot	*Balsamorhiza sagittata*
mouse-ear chickweed	*Cerastrium arvense*
purple prairie-clover	*Dalea purpurea*
hairy prairie-clover	*Dalea villosa var. villosa*
larkspurs	*Delphinium spp.*
horseweed	*Erigeron canadensis*
northern bedstraw	*Galium boreale*
scarlet gaura	*Gaura coccinea*
cranesbill	*Geranium spp.*
broomweed	*Guterrezia sarothrae*
hairy golden-aster	*Heterotheca villosa*
dotted blazing-star	*Liatris punctata*
lupines	*Lupinus spp.*
skeletonweed	*Lygodesmia juncea*
plains prickly-pear	*Opuntia polyacantha*
moss-phlox	*Phlox hoodii*
bahia	*Picradeniopsis oppositifolia*
lance-leaved psoralea	*Psoralea lanceolata*
prairie coneflower	*Ratibida columnifera*
Russian-thistle	*Salsola kali*
scarlet mallow	*Sphaeralcea coccinea*
western spiderwort	*Tradescantia occidentalis*
ironweed	*Vernonia fasciculata*

Common Name	**Scientific Name**
Birds:	
Baird's sparrow	*Ammodramus bairdii*
grasshopper sparrow	*Ammodramus savannarum*
sage sparrow	*Amphispiza belli*
Sprague's pipit	*Anthus spragueii*
burrowing owl	*Athene cunicularia*
lark bunting	*Calamospiza melanocorys*
piping plover	*Charadrius melodus*
horned lark	*Eremophila alpestris*
loggerhead shrike	*Lanius ludovicianus excubitorides*
Brewer's sparrow	*Spizella breweri*
clay-coloured sparrow	*Spizella pallida*
western meadowlark	*Sturnella neglecta*
Herptiles:	
northern prairie skink	*Eumeces septentrionalis*
northern leopard frog	*Lithobates pipiens*
Insects:	
Edith's checkerspot	*Euphydryas editha*
Dakota Skipper	*Hesperia dacotae*
forest tent caterpillar	*Malacasoma disstria*