

# Assessing the stability and uncertainty of predicted vegetation growth under climatic variability: northern mixed grass prairie

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Received 9 February 2000; received in revised form 14 August 2000; accepted 28 November 2000

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## Abstract

Ecosystem models which include both variability of driving variables as an input, and uncertainty and/or stability in their predictions are rare, especially outside of forest and cropland applications. Our objective is to investigate the stability of productivity levels and temporal patterns in a northern mixed grass prairie site using scenarios of varying levels of climate variability. Predictions of annual net primary productivity (NPP) are compared under a variety of global change and management scenarios. Specifically, we investigate the relative responses of  $C_3$  and  $C_4$  vegetation functional groups as a diagnostic of changes in resource availability. Scenarios of gradual temperature increase over 200 years demonstrate that warming will have different effects depending partially on the seasonal timing of that warming, but mostly on the concurrent changes in moisture availability. We propose that stability of vegetation communities may be more important than simply predicting levels of productivity for answering many questions related to the impacts of global change. This is demonstrated using frequencies of consecutive years with low productivity. Moderate increase in precipitation variability without increases to average rainfall can increase productivity and apparently increase stability. Further increase in precipitation variability decreases stability. The uncertainty in NPP predictions can be quantified by repeated simulations using stochastic variations in driving climate variables. Uncertainty in NPP predictions is found to be at the order of 20 g/m<sup>2</sup>/year, or about 25% of long-term averages. This lets us qualify our conclusions and shows that further research can reduce this uncertainty by better predictions of moisture availability, which can be obtained using finer spatial and temporal resolution representations. © 2001 Elsevier Science B.V. All rights reserved.

*Keywords:* Ecosystem models; Uncertainty; Net primary productivity; Grasslands; Stability; Temporal variability; Climate change

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## 1. Introduction

Ecosystem management at the practical level poses big challenges for a number of reasons, including limitations to our understanding of ecosystem functioning, the range of scales over

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which they operate, and restrictions on the scales over and the extent to which we can account for their driving factors. This incomplete understanding causes uncertainty in predicting how an ecosystem will respond to a future change in factors such as land use or climate. This uncertainty is reduced as we gain knowledge from ecosystem-level research.

It is difficult to predict management and climate change effects on ecosystem dynamics across regions through field experimentation alone, because of the inherently short time periods of most experiments compared to the period of environmental processes, and the difficulties of manipulating experiments without changing the system being studied (Thornley and Cannell, 1997). Environmental models offer an alternative, in that they can be used repeatedly, at various scales, and without any disturbance to the study area. However, the choice of an appropriate model for the system under study is not always obvious. Different representations of space and time can alter or mask processes of interest, and the assumptions used in model development may not hold in all potential application areas. To choose a modelling strategy for answering research questions in a given area, one must first determine that a model developed elsewhere will make sensible predictions at all, knowing that often parameter changes will exceed thresholds in a new environment such that the model will completely fail to be representative. Once suitability has been established, it is useful to estimate levels of uncertainty of model predictions.

Our research seeks to identify the major controls on, and therefore modelling strategies for, regional grassland productivity in the northern mixed prairie. Globally, grasslands play an important role in the carbon cycle, covering  $\approx 20\%$  of the Earth's surface and containing about 30% of global carbon stocks (Ojima et al., 1996; Parton et al., 1996). They are also economically important, containing much of the grain growing capacity of the world (Burke et al., 1989). The grassland biome is largely defined by moisture availability (Aber and Melillo, 1991); most natural grasslands (excluding areas maintained by heavy grazing pressure) are in areas with constrained or highly

variable precipitation, making them potentially sensitive to climate change. Effects of climate change on grassland biogeochemistry and carbon stocks have received less attention than in forests, but grasslands are likely to remain roughly constant or even expand in areas under predicted modified climate (Ojima et al., 1996).

Specifically, the aims of the study reported here are to

- evaluate sensitivity of a particular model's (CENTURY) productivity predictions to driving variables in the C<sub>3</sub>/C<sub>4</sub> functional groups of the northern mixed prairie,
- evaluate the model's ability to predict responses of ecosystem productivity and stability to changes in these inputs under climate change scenarios,
- identify major sources of uncertainty in these predictions, quantifying the uncertainty where possible, and
- suggest strategies for reducing uncertainty in predictions that address the research questions relevant to management of this ecosystem.

The northern mixed grass prairie takes up a large portion of the North American Great Plains, bounded by the Fescue prairies and Aspen Parkland of Alberta and Saskatchewan in the north, the Rocky mountain range to the west, the Nebraska sandhills to the south, and tall grass prairie to the east (Coupland, 1992). Dominant vegetation varies with temperature and moisture conditions. Climate is dry-subhumid to semi-arid, with a tendency for dry years to be grouped together, as well as for severe droughts. Mean annual temperature ranges southward through the region from 1 to 18°C mostly caused by a large range of winter temperatures in the north (Coupland, 1992). Mature vegetation communities in the Canadian portion of the mixed grasslands are dominantly *Stipa-Agropyron*, *Stipa-Bouteloua*, *Stipa-Bouteloua-Agropyron*, *Agropyron-Koeleria*, and *Bouteloua-Agropyron* (Coupland, 1992).

We are currently concentrating our research in the northern portion of the mixed prairie, in Grasslands National Park (GNP; see Section 1.2 below for details); this is a particularly interesting region because it contains the northern edge of the continental distribution of vegetation that uses

the  $C_4$  photosynthetic pathway. The two functional groups ( $C_3$  and  $C_4$ ) have important differences in adaptive strategy and competitive abilities, and consequently distinct relative potential productivity for given temperature and moisture combinations. It is important to determine relative affinities of  $C_3$  and  $C_4$  plants to expected climate and atmospheric changes, in order to evaluate potential impacts on species distributions, and global carbon and nitrogen budgets (Peat, 1997). Such work helps answer questions about functional group dynamics across large regions such as the North American prairies as a whole, as well as addressing important issues specific to regions experiencing changes to vegetation communities. Therefore, we are using a variety of techniques to measure and predict productivity patterns of  $C_3$  and  $C_4$  vegetation, starting with a region of protected grasslands in southern Saskatchewan. This includes some “traditional”, plot-based studies of observed productivity and diversity in the park, but is supplemented by working with remotely sensed imagery and environmental models. These tools give us the ability to conduct repeated, frequent, non-destructive and non-disturbing monitoring and experiments, allowing us to address questions at spatial and temporal scales that are not possible with the plot-based work.

### *1.1. Survey of grasslands productivity models*

A number of research projects have looked at various aspects of our stated objectives in other locations. It is beyond the scope of this paper to fully review this work, but it is important to determine which conclusions from experiments at other sites and scales may help us in our study region.

At one end of the spectrum, there are studies that look in great detail (Wu and Levin, 1994; Pachepsky and Acock, 1996; Ryel and Caldwell, 1998) at parts of the ecosystem we want to study, such as species level responses and competition for resources. These share features with plot level field experiments which provide insight into ecological processes by observing dynamics in managed plots of vegetation (Tilman and Pacala,

1993; Wedin and Tilman, 1996 on relationships between species richness, stability, and carbon and nitrogen cycling), but they both also suffer from scaling difficulties. Extrapolation of their results can be problematic, because of the small plot size compared to regional questions, and the fact that they are normally carried out over a relatively short time-period. Therefore, using relationships developed at these scales across regions can lead to significant bias, unless corrections are developed from understanding specific scaling effects (Rastetter et al., 1992; Lammers, 1998; Wirtz, 2000).

A similar problem comes from the use of models that deal with photosynthesis in a lot of detail. Such models can be excellent tools for testing hypotheses about the processes involved, and to answer research questions that require a detailed treatment of different physiological responses. However, extra detail in the modelling of processes requires extra computing resources and normally increases the number of parameters. Both of these can be problematic when trying to address management questions over large regions, either due to limits on computing resources, or the uncertainty involved in the estimation of large numbers of parameters and their variation across space. Sala and Tenhunen (1996) present one example of such a model, predicting photosynthesis at the leaf level and then aggregating up to the canopy – they note that validation became a problem because the complexity of the terrain at their site provided a wide variety of conditions. Battaglia and Sands (1998) and Wegehenkel (2000) are two recent examples examining the effects of varying the level of detail in productivity models on their generality and uncertainty.

Other modelling efforts are designed to be applicable across a more aggregated notion of space. For example, Thornley and Cannell (1997) used the Hurley Pasture model to predict transient and equilibrium effects of increases in temperature and  $CO_2$  concentration for two grassland sites in Scotland, as well as changes to the equilibrium values under scenarios which altered grazing regimes, precipitation, photosynthetically-active radiation, windspeed, and relative humidity. However, these grasslands have significantly more

moisture than much of the North American prairie, are probably kept as grasslands through grazing rather than moisture limitation, and thus are expected to have quite different dynamics than our site.

Modelling studies in other parts of the world with similar conditions to our study region exist, but we also wish to pay attention to relative amounts of effort needed for parameter estimation. For example, MAGE (Gao et al., 1996) was a possibility for our site given its treatment of processes and the environment it was developed in, but parameterization would require extensive field measurements. On the other hand, we have noted that the CENTURY model (Parton et al., 1987; Metherell et al., 1993) (see Section 1.3 below for model description) is used very frequently for productivity and nutrient dynamics in this region. It lies between models with detailed physiology (such as the Hurley Pasture model) and simple empirical models, and allows very long-term predictions, which makes it good for experiments on long term soil dynamics (e.g. Mikhailova et al., 2000) or climate change (examples discussed below). These characteristics make it attractive for management questions in a regional context, and there is a wide range of prior experiments, with published parameterizations, for sites across the North American prairies. Therefore, we have decided to focus our initial investigations on this model.

Burke et al. (1991) used CENTURY across the Great Plains, partitioning the region into relatively homogeneous units with respect to climate and soils. This study examined relative impacts of climate variability and management options, and found that relatively short-term climatic variations caused significant reductions in carbon storage. However, they also suggested that land management decisions may be more important controls on the carbon balance. The purpose of their study, however, was to extrapolate site research to larger regions (the central Great Plains in this case), and specific conclusions are not necessarily good characterizations of any particular sub-region.

Other modelling projects such as VEMAP seek to model all continental biomes, and include large

regional predictions from a variety of models, including CENTURY (Members, 1995). While the scale of their work does not give us specific predictions for any particular area within the prairies, some of the conclusions they are developing will be valuable for all related prediction projects. For example, Schimel et al. (1997) found that net primary productivity (NPP) and carbon storage predictions from all of the models were sensitive to disturbance, and calls for spatial data and techniques to describe disturbance regimes, and improved treatment of disturbance in ecosystem modelling. It is also important to note that many of the models being used in this and similar projects were developed to predict productivity in specific biomes (usually forests) and have been extended into new realms, such as grasslands. While many of the processes are shared across biomes (e.g. the same submodels, such as Farquhar's daily photosynthesis model, are used in many larger modelling projects), we should have much less confidence in the parameterizations for these new biomes.

At a more regional level, Parton et al. (1996) used CENTURY and GRASS (Coughenour et al., 1984) models to simulate shortgrass productivity patterns in a Colorado, USA and a Kenyan site. GRASS is a more detailed, physiologically based model using a daily time step. Above-ground productivity and peak live biomass estimates from CENTURY corresponded reasonably well with measurements, with errors generally less than  $\pm 25\%$  of observed values. Perhaps more importantly, the two models behaved similarly for a number of predicted properties, such as seasonal monthly live biomass, annual NPP, and peak live biomass. CENTURY was also more successful than empirical site-specific regression equations developed for the sites to predict production and peak biomass.

Ojima et al. (1996) sought to determine grassland ecosystem sensitivity to climate change and increasing CO<sub>2</sub> using the same two models across a broad range of sites. In their North American mixed-grass sites (Central Plains experimental range), the climate scenarios they used predicted  $\approx 4^\circ\text{C}$  warming and 2–15 cm increase of precipitation, depending on the source of the prediction.

Decomposition was increased, as was plant production. NPP predictions were correlated with increased N mineralization, which was itself correlated with the increased precipitation. Increased concentrations of CO<sub>2</sub> caused a small increase in production, and a 30% increase in decomposition. Discrepancies between model predictions for the two climate scenarios they used were mostly attributable to differences in the precipitation projections. They found that 1% and 16% changes in soil C and plant productivity, respectively, were needed over 25 years to observe statistically detectable changes in their 25 year averages under climate change scenarios. This emphasizes the degree of natural variability in climate and productivity, and suggests that predicting stability of ecosystems over numerous seasons may be more important than individual annual productivity predictions.

Thus previous work has addressed aspects of our questions in other parts of the prairies and over larger regions or specific plots. However, differences in scale, future scenarios, physical environment, and vegetation communities make conclusions from these studies either generalities or potentially misleading for our study region. Predicting vegetation dynamics in this area requires us to find an appropriate level of prediction and data support to capture the dominant behaviour of this ecosystem.

We are also interested in the uncertainty involved in our predictions using different methods and assumptions, an analysis that is largely missing from many previous approaches. The first step in this quest is reported in this paper, using the well-known model CENTURY. It fits our purpose at this point largely because it is widely used, and was originally developed for this ecosystem. Therefore, in comparison to other productivity models, it includes phenomena critical to grassland dynamics, such as the tight coupling of soil and vegetation dynamics in the shallow soil layers, and interactions with grazers. This study seeks to test which of our requirements can be met with a 'standard', non-spatial model, and with what level of uncertainty.

## 1.2. Study area

Grasslands National Park is near Val Marie, Saskatchewan (49°15'N, 107°W), currently occupying ≈ 900 km<sup>2</sup> of the Canadian mixed-grass prairie along part of the Saskatchewan–Montana international border. Its management plan, facilities and programs are still under development, and additional lands are being acquired. It was created to provide for the preservation of Canadian native northern mixed grass prairie.

The GNP region is drier than its surroundings; precipitation peaks in the summer, but even this amount is very low, and most of it is evaporated. Winters are usually long, cold, and dry. Variability of the region's climate (with a tendency towards drought) is its key characteristic, however (Loveridge and Potyondi, 1983). The vegetation is dominated by the *Stipa–Bouteloua–Agropyron* community type on sandy loams (Coupland, 1961), but vegetation distribution in this area follows the highly variable climate. After drought it is characteristic of a *Stipa–Bouteloua* community, while after several years of above-average precipitation it shifts to the structure of the *Stipa–Agropyron* type (Coupland, 1992). This is because the C<sub>4</sub> grass *Bouteloua gracilis* is drought resistant yet at the northern limit of its range, and is thus highly sensitive to changes in temperature and moisture availability. The most common grasses are *Stipa comata* (C<sub>3</sub>), *Agropyron* spp. (C<sub>3</sub>), and *B. gracilis* (C<sub>4</sub>); C<sub>4</sub> species make up ≈ 11% of the park's flora according to analysis (Davidson, unpublished data) of a 1993 vegetation inventory (Michalsky and Ellis, 1994), and between 10% and 15% of areal coverage (Davidson, pers. comm.; Davidson and Csillag, 2001; Peat, 1997).

The climatic conditions (Table 1), as well as the underlying soils and the forage quality of the resultant grass, have limited the uses for much of the land in this region; native use was limited because the area was considered a neutral zone for much of its history, it was not attractive for fur traders, and farmers did not arrive until the 1880s. The instability of the climate and questionable government policies early in the century have limited agricultural development ever since (Love-

ridge and Potyondi, 1983). Grazing is one of the key issues being contemplated for the park management plan. The area was largely used for ranching in the past, but starting in 1980, as land parcels were purchased, all grazing by domesticated animals was eliminated. There are no bison left in the area, so any remaining grazing is restricted to that done by deer, antelope, small mammals, and insects. In specific areas of the park, prairie dog grazing is a dominant local control.

### 1.3. CENTURY model – description

CENTURY is a lumped-parameter ecosystem model with a monthly time step and aggregated plant and soil organic dynamics, simulating carbon and nitrogen cycling aboveground and within the top 20 cm of the soil. It concentrates on the biogeochemistry of carbon, nitrogen, phosphorus, and sulphur. It has been used successfully to simulate carbon dynamics, especially in soil organic matter (SOM), across a variety of land use and climate types, and is particularly good in grass and crop ecosystems (Kelly et al., 1997).

The main driving data for the model are (Metherell et al., 1993):

- monthly average maximum and minimum air temperature,
- monthly precipitation,
- lignin content of plant material,
- plant N, S, and P content,
- soil texture,
- atmospheric and soil N inputs, and
- initial soil N, S, and P levels.

The main CENTURY submodels, for the purposes of this study, control SOM, simplified water budget, nitrogen flows, and plant production. The SOM model divides SOM dynamics and matter into three pools with different potential decomposition rates (active, slow, and passive), above- and belowground litter pools, and a surface microbial pool. The pools and flows of carbon through this model are summarized in Fig. 1.

The water budget calculates monthly evaporation and transpiration losses, water content in a user-definable number of soil layers, saturated flow between these layers, and snow water content. A detailed investigation into the hydrology in CENTURY was not performed in this study, but it is an important issue due to the sensitivity of grassland vegetation to moisture availability.

The nitrogen submodel has the same structure as the SOM model, with N flows following C flows according to C:N ratios. These ratios are

Table 1  
Monthly summaries of daily data from Environment Canada Climate Station (# 4038400) 1939–1996<sup>a</sup>

Month	Average total pptn (mm)	S.D. (average total pptn)	Average $T_{\text{mean}}$ (°C)	S.D. ( $T_{\text{mean}}$ )	Average $T_{\text{max}}$ (°C)	Average $T_{\text{min}}$ (°C)
January	16.17	15.79	−13.35	5.09	6.06	−35.28
February	12.72	8.57	−10.82	4.83	8.24	−32.36
March	17.37	11.62	−4.25	3.80	14.57	−25.11
April	24.42	18.66	4.50	2.42	23.50	−12.86
May	41.46	29.53	10.87	1.78	29.30	−5.53
June	58.73	37.54	15.40	1.78	32.90	0.61
July	48.20	43.64	18.79	1.41	34.85	3.59
August	31.58	28.00	17.82	1.67	34.79	1.43
September	26.04	24.94	11.73	1.91	31.32	−6.17
October	16.25	12.85	5.26	1.74	24.97	−13.06
November	15.45	12.12	−4.65	3.98	14.35	−24.46
December	16.10	10.33	−10.54	4.44	7.66	−33.22
Total	324.49					

<sup>a</sup> S.D. = standard deviation, pptn = precipitation,  $T_{\text{min}}$  = minimum daily temperature,  $T_{\text{max}}$  = maximum daily temperature,  $T_{\text{mean}}$  = daily average temperature.

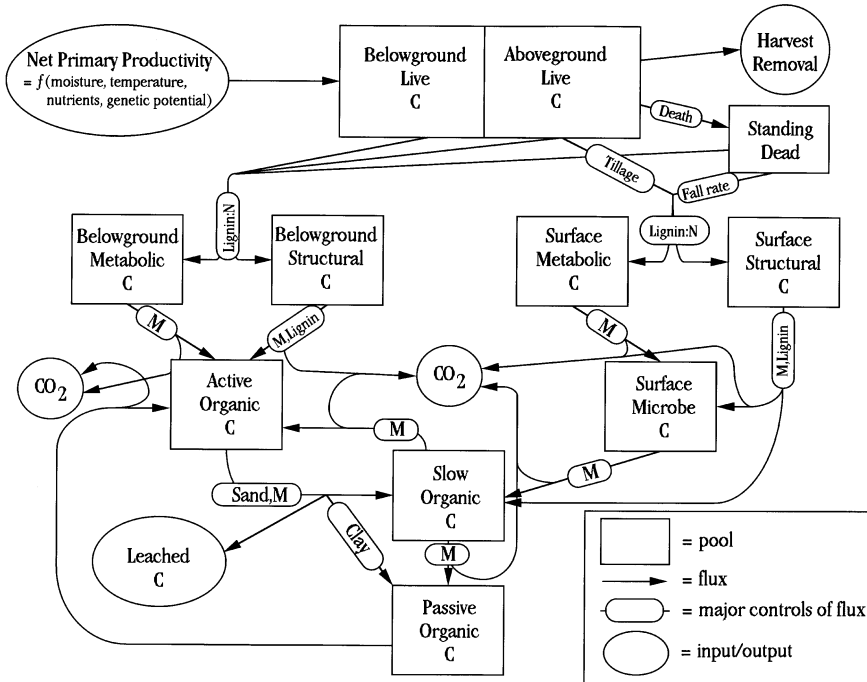


Fig. 1. Carbon flows in the CENTURY SOM model. M stands for a flux multiplier based on the effects of moisture, temperature, and cultivation. Adapted from (Metherell et al., 1993).

fixed in the structural pools, while the metabolic pool ratios vary as a function of N content in incoming residue. Simple equations estimate N deposition and fixation inputs, and losses due to leaching are a function of soil texture and water flow. Losses through mineralization, nitrification, denitrification, volatilization, crop removal, burning, animal transfers and soil erosion are all tracked. Sulfur and phosphorus are also optionally modelled, but were not investigated in this study.

Plant production is modelled assuming that monthly maximum productivity is controlled by moisture and temperature, with reductions if insufficient nutrients are available. The pools and flows of the grass/crop model are presented in Fig. 2.

## 2. Methods

### 2.1. Field measurements

Measurements of productivity and diversity were

made in GNP in 1995, 1996, and 1998. These results provided detailed familiarity with the operation of this ecosystem, which assisted in model parameterization and verification. Soil bulk density cylinders were also taken at each of the biotic sampling sites, in order to sample surface soil texture. Two climate stations immediately adjacent to the park provided hourly data on temperature, precipitation, wind conditions, and relative humidity.

### 2.2. Model setup

Unless otherwise noted, all climate scenario tests used Century 4.0 as currently distributed from the Colorado State University FTP archive (Metherell et al., 1993, [ftp://ftp.nrel.colostate.edu/CENT/century4.0/CENTX/UNIX\\_VERSION/century.tar.Z](ftp://ftp.nrel.colostate.edu/CENT/century4.0/CENTX/UNIX_VERSION/century.tar.Z), 11/11/98), with slight modifications to the source code to permit easy runtime adjustments to long-term climate statistics. Stochastic climate runs used

a 30-year climate record from the study area to define monthly minimum and maximum temperatures, as well as monthly averages and standard deviations of precipitation (Table 1). Records for runs using “actual” climate files were a combination of a 30-year record (1967–1996) of climate station observations from an Environment Canada station at Val Marie (Climate Information Branch, 1996), measurements taken at a newer station at the South-west corner of the park from 1996 to present, and the same system for stochastic climate generation described above for all other years. Soil characteristics were defined using spot measurements taken at our field sites, and the park’s soil survey (Saskatchewan Institute of Pedology, 1992). Soil texture classes were defined as in Clapp and Hornberger (1978).

Vegetation parameters were estimated based on productivity patterns measured in other studies at this site wherever possible. When measurements were not available, example parameters from other sites where CENTURY has been tested were used as a basis, and adjusted as necessary to fit GNP. The most important deviation from the

procedure most users might take given the guidance in the CENTURY documentation concerned the concept of vegetation mixes. The usual procedure is to estimate one set of parameters based on the mix of vegetation at a site, whereas we developed two separate parameterizations, each assuming 100% coverage of  $C_3$  or  $C_4$  vegetation.

For example, CENTURY uses a Poisson density function to empirically fit this relationship:

$$P = \exp_{b_1} \left\{ \frac{b_1}{b_2} \left( 1 - \left( \frac{T_{\max} - T_{\text{soil}}}{T_{\max} - T_{\text{opt}}} \right)^{b_2} \right) \right\} \cdot \left( \frac{T_{\max} - T_{\text{soil}}}{T_{\max} - T_{\text{opt}}} \right)$$

where  $P$  = potential production,  $T_{\text{opt}}$  and  $T_{\max}$  are optimum and maximum temperature for photosynthesis, respectively,  $b_1$  and  $b_2$  are empirical “curve shape” parameters, and  $T_{\text{soil}}$  is soil temperature, estimated from air temperature. The four curve parameters are included in each crop definition (i.e. grass species or mix of species). Normally, these are chosen to represent the aggregated behaviour of a species mix. Since we wished to investigate relative productivity of  $C_3$

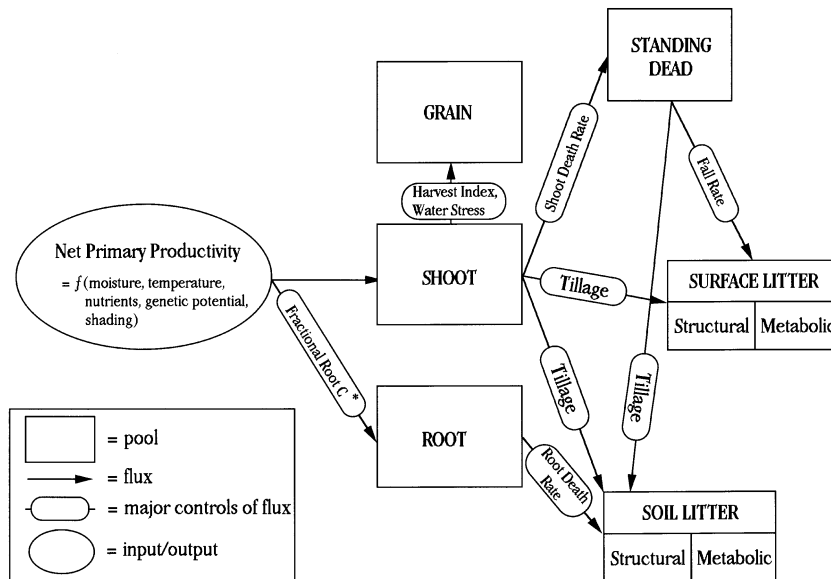


Fig. 2. Grass/crop submodel in CENTURY. Adapted from (Metherell et al., 1993).



Table 2  
Key parameter differences between C<sub>3</sub> and C<sub>4</sub> vegetation predictions

CENTURY variable name	Description	C <sub>3</sub> value	C <sub>4</sub> value
PRDX(1)	Potential aboveground monthly crop production (g C/m <sup>2</sup> )	250.0	325.0
PPDF(1)	Optimal temperature for production – parameterizes Poisson probability density function (PPDF) to simulate temperature effect on production	15.0	28.0
PPDF(2)	Maximum temperature for production, second parameter for above PPDF	35.0	45.0
PPDF(3)	Left curve shape for above PPDF	2.5	1.0
PPDF(4)	Right curve shape for above PPDF	1.9	2.5
PRAMN(1,1)	Minimum C:N with no biomass	20.0	30.0
PRAMN(1,2)	Minimum C:N with biomass ≥ biomax	30.0	90.0
PRAMX(1,1)	Maximum C:N with no biomass	30.0	35.0
PRAMX(1,2)	Maximum C:N with biomass ≥ biomax	40.0	95.0
CRPRTF(1)	Fraction of N retranslocated from leaves at death	0.3	0.4

and C<sub>4</sub> vegetation, two separate “extreme” parameterizations were developed, representing 100% coverage of each functional group. This allows for the ability to change the mix of vegetation over time in future studies, and the use of lab-derived values for parameterizing specific plants or functional groups. The key parameters that differentiated C<sub>3</sub> and C<sub>4</sub> productivity are summarized in Table 2.

Most SOM submodel initializations used empirical methods developed for the North American prairie. All model runs, unless otherwise noted, were from the year 1 to 2130; the first 1900 years are “spin-up” time to ensure stability in the pools and fluxes, and output was only examined from 1900 to 2130.

### 2.3. Controls on productivity

#### 2.3.1. Sensitivity: prescribed climate scenarios

Initial runs were performed with climate records from 1967 to 1998, and stochastically generated climate based on long-term averages for all other years. This was first used to drive separate predictions for C<sub>3</sub> and C<sub>4</sub> vegetation under the base climate, then constant absolute additions to monthly temperatures were forced into the model as climate warming scenarios. This was our first and simplest test of the effects of climate change (subsequent experiments, below, use a completely stochastic climate setup to provide a more flexible method to test long-term climate

change scenarios). Investigations into the effects of grazing and increasing CO<sub>2</sub> concentrations were also done using this prescribed climate setup.

CENTURY allows for increasing concentrations of CO<sub>2</sub> over time using a linear ramp between two dates and concentrations. We increased atmospheric CO<sub>2</sub> from 350 to 700 ppm between 1900 and 2100. The increases to photosynthetic rate are generally much more for C<sub>3</sub> species, and these are parameterized separately. CO<sub>2</sub> fertilization can be modelled by the equation:

$$NPP_e = NPP_0(1 + \beta \ln(CO_2_e / CO_2_0))$$

where the subscripts e and 0 refer to the enriched and control CO<sub>2</sub> environments, respectively, and  $\beta$  is an empirical parameter ranging between 0 and 0.7 (Metherell et al., 1993). CENTURY transforms this equation to allow for separate treatment and parameterization for the effects of increased CO<sub>2</sub> on relative production, reductions in transpiration, ranges of C to element ratios, and shoot:root C allocation ratios.

#### 2.3.2. Sensitivity: stochastic climate scenarios

In order to further test the effects of climate change scenarios, CENTURY was modified to allow simple linear changes to average and standard deviation of monthly precipitation, as well as minimum and maximum monthly temperatures, over a given time period. All runs presented here used a time-period of 200 years for this transient climate change, from 1900 to 2100. Combinations

of temperature and precipitation changes that were used are presented in Table 3. All model runs from here on used this climate setup.

Specific climate change scenarios were chosen, to a large degree, to evaluate which combinations would have large effects on the uncertainty of productivity predictions. The magnitudes of increases in mean temperature are in line with the range of predictions for the Canadian prairie region by the Canadian Centre for Climate Modelling and Analysis (Herrington et al., 1997). Predicted changes to mean precipitation range in this area from decreases of 15% to increases of 50% depending on the season and which climate model is used (Herrington et al., 1997). The changes to variability of precipitation are important tests of the CENTURY predictions, but it is very difficult to estimate how likely these scenarios are. There is general agreement in climate modelling work predicting more extreme temperatures and higher frequency of drought in the northern mid-continental areas, but predictions related to climate variability and extremes are still plagued by errors and limitations in simulating climate at regional scales (Meehl et al., 2000). Timing of climate change is also critical in scenario development; most climate model predictions in the literature make predictions for a given atmospheric CO<sub>2</sub>, and the timing of this level depends largely on future anthropogenic emissions. We have elected to create scenarios that simply change temperature and precipitation a certain amount per century to avoid this complexity.

Table 3  
Climate change scenario permutations used for CENTURY predictions

Minimum and maximum temperature	Additions of 0, +1, +2, +4, +6, +8, +10 each month, as well as +4 and +8 April–June only (°C)
Average precipitation	Additions of -8, -4, -2, -1, 0, +1, +2, +4, and +8 to total monthly precipitation (cm)
Standard deviation precipitation	-8, -4, -2, 0, +2, +4, +8 to standard deviations of monthly precipitation (cm)

## 2.4. Stability

Productivity alone does not describe whether or not a plant community is ‘doing well’. Since CENTURY deals with an aggregate concept of vegetation, comparing individual mortalities or recruitment of areas is impossible, and our modelling setup can not directly address the issue of how species diversity and productivity are related. The nature of this relationship in grasslands, as in other ecosystems, still exhibits apparently conflicting results depending on experimental setup, and the scales of observation (e.g. Tilman and Pacala, 1993; Tilman et al., 1996; Wedin and Tilman, 1996; Rusch and Oesterheld, 1997; Austin, 1999; Waide et al., 1999; McCann, 2000). However, we can get some information on how well functional groups are doing by modelling their growth separately, and looking at variability of productivity as an index of stability. To accomplish this, we have defined a low productivity year as one in which the productivity falls below the first quartile of predicted NPP in the “base climate” (i.e. based on observed long-term averages) scenario. With this threshold defined (< 83.7 g/m<sup>2</sup>/years for C<sub>3</sub> vegetation, and < 92.7 g/m<sup>2</sup>/years for C<sub>4</sub>), we calculated frequencies of productivity shortfalls in individual years, as well as for 2 and 3 years in a row, for various climate scenarios.

## 2.5. Uncertainty

CENTURY uses a stochastic precipitation generator to simulate monthly precipitation distributions based on summary statistics. This sub-model was modified to allow the generation of independent model runs with unique realizations of the precipitation time series, while all other parameters were held constant. Using this modification, a simplified Monte-Carlo setup was used on a number of the above scenarios. For each scenario, 50 independent realizations of the potential precipitation regime were generated, and CENTURY predicted the resulting productivity and nutrient dynamics; the distribution of predicted probability was collected from the outputs of these runs. The variability of productivity provides an estimate of the uncertainty in model output caused

Table 4  
 Predicted and measured biomass, Grasslands National Park<sup>a</sup>

Date	CENTURY biomass (g/m <sup>2</sup> )	Measured biomass (g/m <sup>2</sup> )
30 March 95	0.0	
30 April 95	36.1	
14 May 95		10.4
31 May 95	40.9	
4 June 95		27.0
30 June 95	51.1	
4 July 95		45.7
30 July 95	42.3	
7 August 95		47.6
31 August 95	44.9	

<sup>a</sup> Predictions are CENTURY monthly predictions of above-ground live biomass for 1995, using the C3 parameterization described in text. Values are converted from g C to g of dry biomass using average carbon content measured by Peat (1997). Measured values are averages of clipping data reported by Peat (1997) for the same year, including all grasses and forbs.

by variability of monthly average precipitation. Larger numbers of runs (up to 150) were experimented with but did not significantly change the average or variability of the predicted productivity.

### 3. Results and discussion

#### 3.1. Controls on productivity: prescribed climate scenarios

Using climate records and parameters derived for a specific site at GNP, CENTURY predicted annual NPP dynamics which compared well with annual NPP estimates based on field observations (Peat, 1997), and with general trends reported by Tieszen et al. (1997). Intra-seasonal patterns of productivity and responses to moisture availability did not match measurements and expected patterns as well; within individual years CENTURY tended to predict an earlier and more vigorous green-up than was observed (Table 4). Since the annual productivity compared well, and since there was high uncertainty in both the measured biomass and the aggregate parameterization used for the CENTURY prediction, this was considered an acceptable deviation.

The base grazing scenario was designed to mimic the area's history, with moderate grazing (defined in CENTURY as having a linear effect on productivity) from 1900 to 1979, and low grazing thereafter. Scenarios which changed the grazing history at only specific times in the model run had little effect on long-term dynamics. Manipulating the grazing intensity throughout the model runs did have an effect, as shown in Fig. 3, but it is relatively small compared to the uncertainty caused by other inputs. Changes to the grazing regime in this area are most important in terms of productivity because of the effects on moisture availability. We suspect that a more sophisticated model of hydrology is needed to study this phenomenon well. More significant effects of grazing on ecosystem function can be seen in predictions of accumulations of standing dead plant material and net carbon accumulation. These pools are important in terms of links to global change cycles, species diversity within the park, and the ability to monitor park vegetation with satellite imagery, however they were beyond the scope of this study.

Increased CO<sub>2</sub> concentrations had relatively little effect (< 5% change) on average annual C<sub>3</sub> productivity in most years unless precipitation was increased as well. In wet years there was a pronounced increase (Fig. 4) for both types of plants, and C<sub>4</sub> vegetation, which already has higher water efficiency, lost much of its advantage. Although C<sub>3</sub> theoretically has the potential for much more of a productivity gain than C<sub>4</sub>, it is not realized in this ecosystem unless a lot more water is available. This is consistent with results of Ojima et al. (1996) and Riedo et al. (2000), which also looked at effects of climate change and CO<sub>2</sub> increases in a grassland setting, with the CENTURY and PaSim models, respectively. Their conclusions included the general statement that in many environments there will be other limiting factors that interfere with the potential for CO<sub>2</sub> fertilization, including interactions between grazing, moisture status, temperature, and carbon fertilization. This interaction of factors amplifies the uncertainty in overall predictions, particularly when the model is especially sensitive to one of the interacting factors, and means that

scenario- and site-specific predictions are necessary.

Manipulations of temperature records demonstrated that seasonal temperature trends do have strong impacts on patterns and relative magnitudes of productivity of  $C_3$  and  $C_4$  grasses through the season. However, temperature alone cannot explain productivity patterns. This can be demonstrated by examining intra-seasonal production patterns in years with contrasting climates. The 1995–1998 series is useful for this purpose, containing a wet year (1995), a moderate year with a heavy late summer rains (1996), a wet Spring (1997), and a year with a very dry Winter and Spring (1998). Fig. 5 presents the  $C_3$  and  $C_4$

productivity predictions during this period, under the base climate and three warming scenarios. The wet summer of 1995 was by far the most productive in this time-period.  $C_4$  vegetation fixed almost  $20 \text{ g/m}^2$  higher than  $C_3$  production under the base climate, but when  $2^\circ\text{C}$  were added to the monthly average minimum and maximum temperatures (Fig. 5a),  $C_3$  vegetation got an early start with the plentiful moisture in the Spring, and the total annual productivities ended up approximately equal. In 1996, the pattern is similar, but the effect of increased temperature on moisture stress is seen, as neither vegetation type met the productivity level of  $C_4$  vegetation under the base climate. In 1998, the severe drought drastically

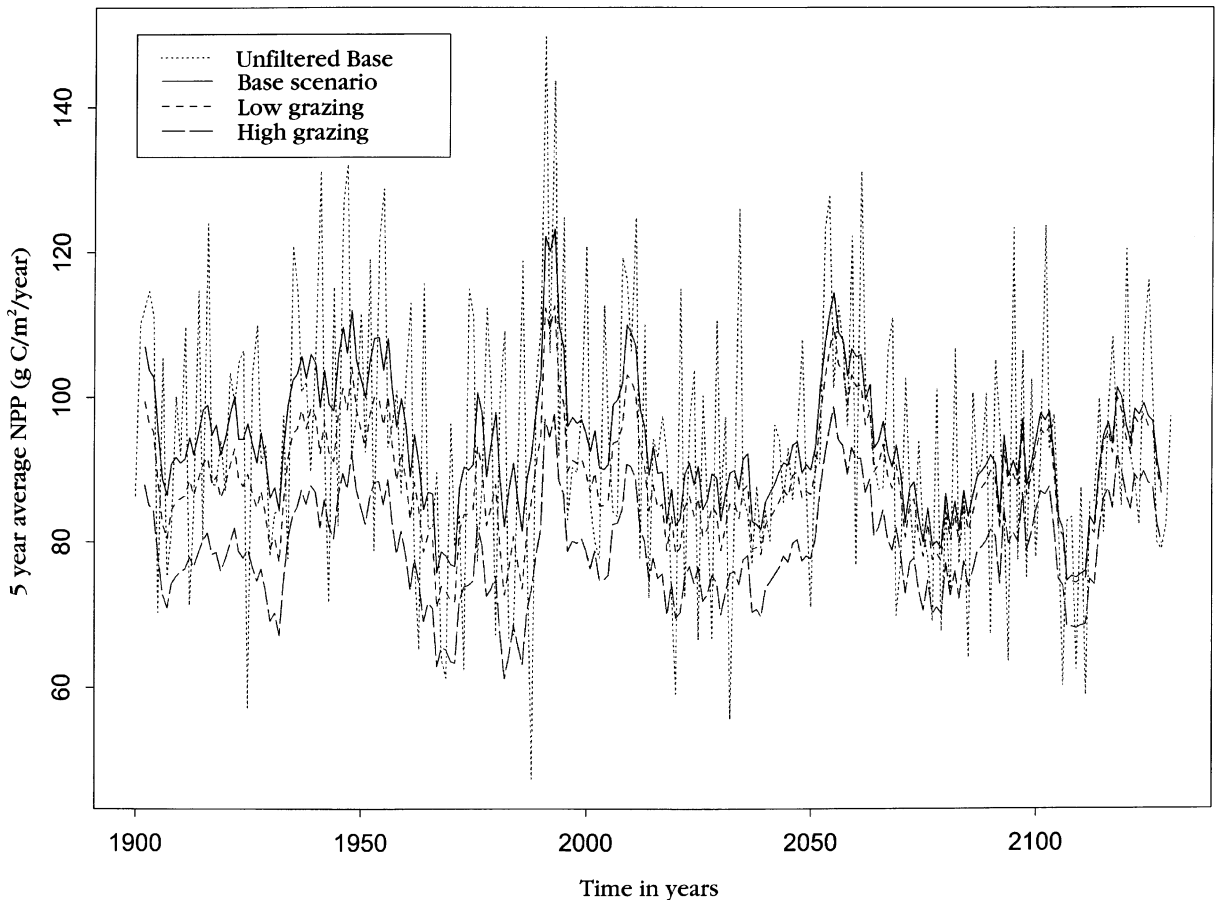


Fig. 3. Effect of grazing regime on NPP predicted NPP. Grey line (“Unfiltered base”) shows unfiltered annual predictions under the base scenario, to indicate degree of variability. All other (darker) lines are 5 year moving averages of predicted NPP. Details of grazing scenarios provided in text.

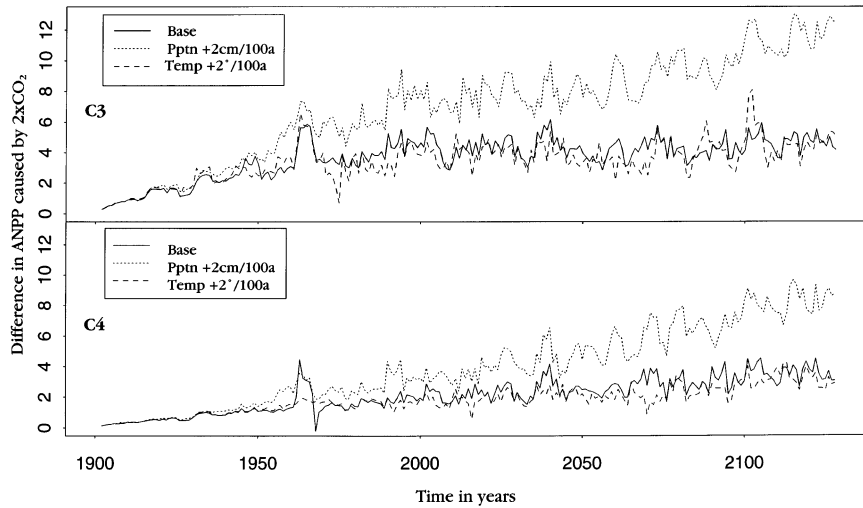


Fig. 4. Effects of doubling atmospheric CO<sub>2</sub> concentrations from 1900 to 2100, on 5 year running average of annual NPP (ANPP) predictions.

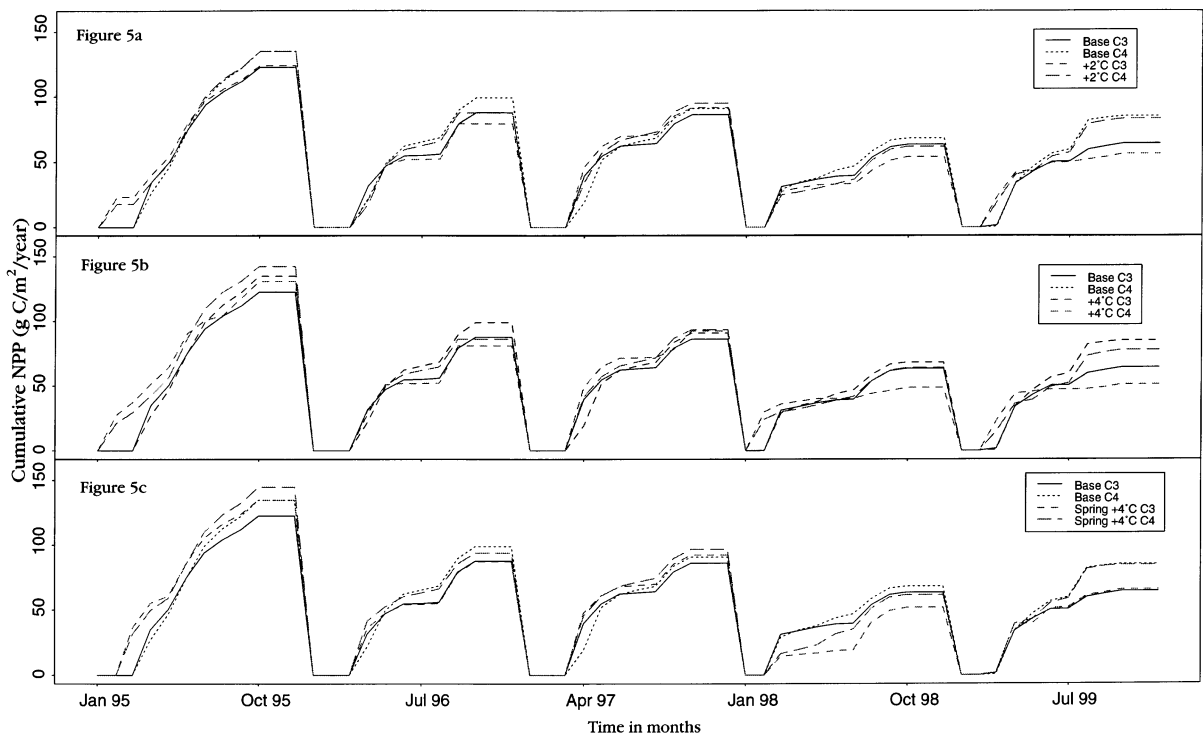


Fig. 5. Details of accumulating annual NPP predictions (monthly time step) for 5 year under base climate and three warming scenarios. Warming scenario magnitudes (e.g. +2°C) refer to absolute changes to average monthly temperatures throughout the scenario, where recorded averages are used from 1967 to 1998, and long-term averages based on this record are used for all other years.

reduced productivity in each scenario, particularly the warm  $C_3$ , which had about  $20 \text{ g/m}^2$  less carbon produced than the base climate. When the warming effect was increased to  $4^\circ\text{C}$  (Fig. 5b), drought conditions were exacerbated, and productivity was further boosted when moisture was sufficient; in 1995 the  $C_3$  boost in the Spring was enough for  $C_3$  to outperform  $C_4$  over the year. In 1998, the drought was amplified by increased temperature, and  $C_4$  production falls closer to base  $C_3$  levels.

A “Spring warming” scenario (Fig. 5c) attempts to predict the effects of concentrating the warming into one part of the year, a scenario which may be occurring in this part of the world (see Myneni et al., 1997). In this case, the warming was only applied from April to June, and  $4^\circ\text{C}$  per century of warming were necessary to produce significant differences from the base climate. Again, in 1995 the spring warming produced a  $C_3$  advantage, since its growth starts earlier in the season; the base summer temperatures decreased moisture stress for the rest of the season as compared to the previous

scenario, resulting in higher overall annual production. This advantage is still lost in drier years, however, due to moisture stress.

The Spring warming scenario results confirm that under some conditions, the hypothesis that  $C_3$  plants could benefit from climatic warming if it is concentrated in the early growing season is feasible. Again, however, the specific annual results are strongly governed by moisture availability, causing high interannual variability in the relative magnitudes of  $C_3$  and  $C_4$  productivity.

### 3.2. Controls on productivity: stochastic climate scenarios

$C_3$  and  $C_4$  grasses clearly have different sensitivities to changes in temperature and precipitation, but these factors can not be separated in the above experiments. Therefore, a series of tests was performed investigating permutations of adjustments to average temperatures, and average and standard deviation of monthly precipitation.

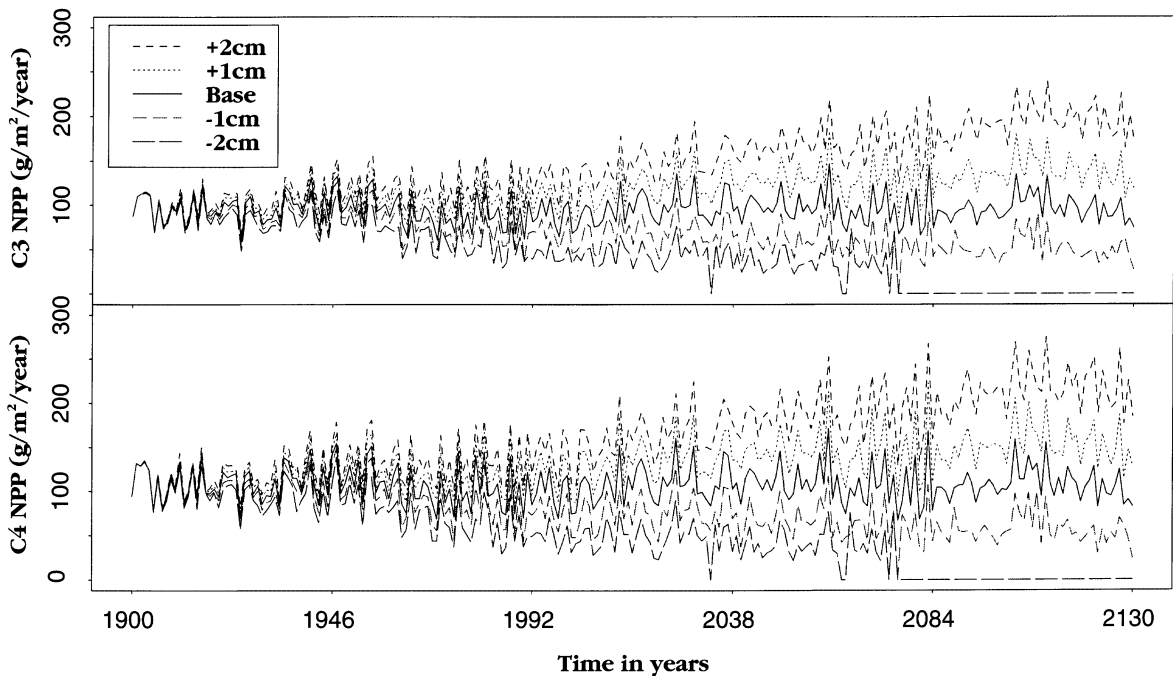


Fig. 6. Effects of changes to average monthly precipitation on predicted NPP, over time. Changes to monthly precipitation (indicated in the legend) refer to linear adjustments of monthly values per 100 years, starting in 1900.

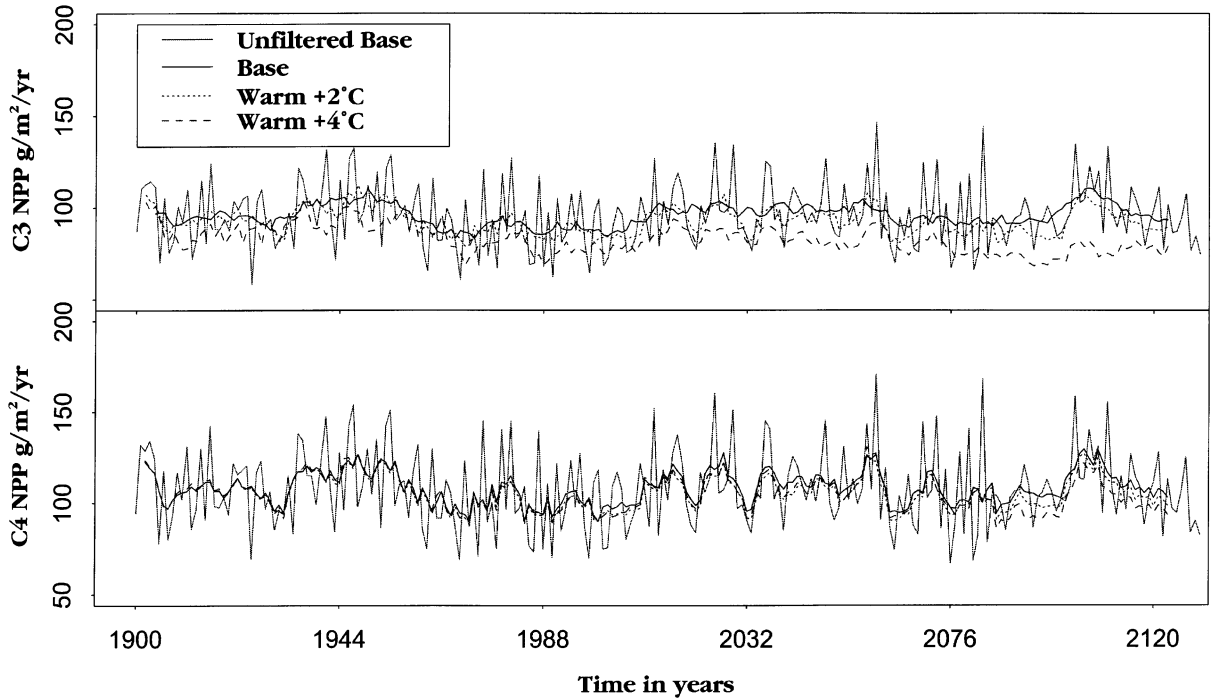


Fig. 7. Effects of changes to monthly average temperature on predicted NPP, over time. Changes to monthly temperatures (indicated in the legend) refer to linear adjustments of monthly values per 100 years starting in 1900. Grey line (“Unfiltered base”) shows unfiltered annual predictions under the base scenario, to indicate degree of variability. All other (darker) lines are 5 year moving averages of predicted NPP.

The dominance of precipitation control on production is clearly demonstrated by changing the average monthly precipitation; Fig. 6 shows that the effects of these scenarios on annual productivity is much greater than any of the other scenarios. A precipitation decrease of 2 cm per century was enough to kill all grass by 2075, whereas increasing precipitation averages by the same amount almost doubled productivity. With temperature increases alone (Fig. 7),  $C_3$  productivity actually drops because of the increased moisture stress, while  $C_4$  vegetation shows little change until about 2085, when the moisture stress becomes high enough to cause a small drop in productivity.

### 3.3. Stability

With no changes in precipitation, there is a

consistent increase in probability of “failure” with warmer temperatures (Fig. 8). When precipitation is close to the base amounts, increasing the variability of monthly precipitation decreases the chance of crop failure. This is because the precipitation is so low to begin with, and more extreme dry months do not change the fact that the vegetation is under severe water stress; when there are wetter months, the grass is able to swiftly take advantage of them, keeping the community alive. If the average precipitation increases by 3 cm per century, however, increased variability of precipitation does increase the chance of low productivity years.  $C_4$  vegetation is more resistant to the stresses created by these scenarios, with lower failure counts in all categories, and extremely low probability of failure years once precipitation is increased.

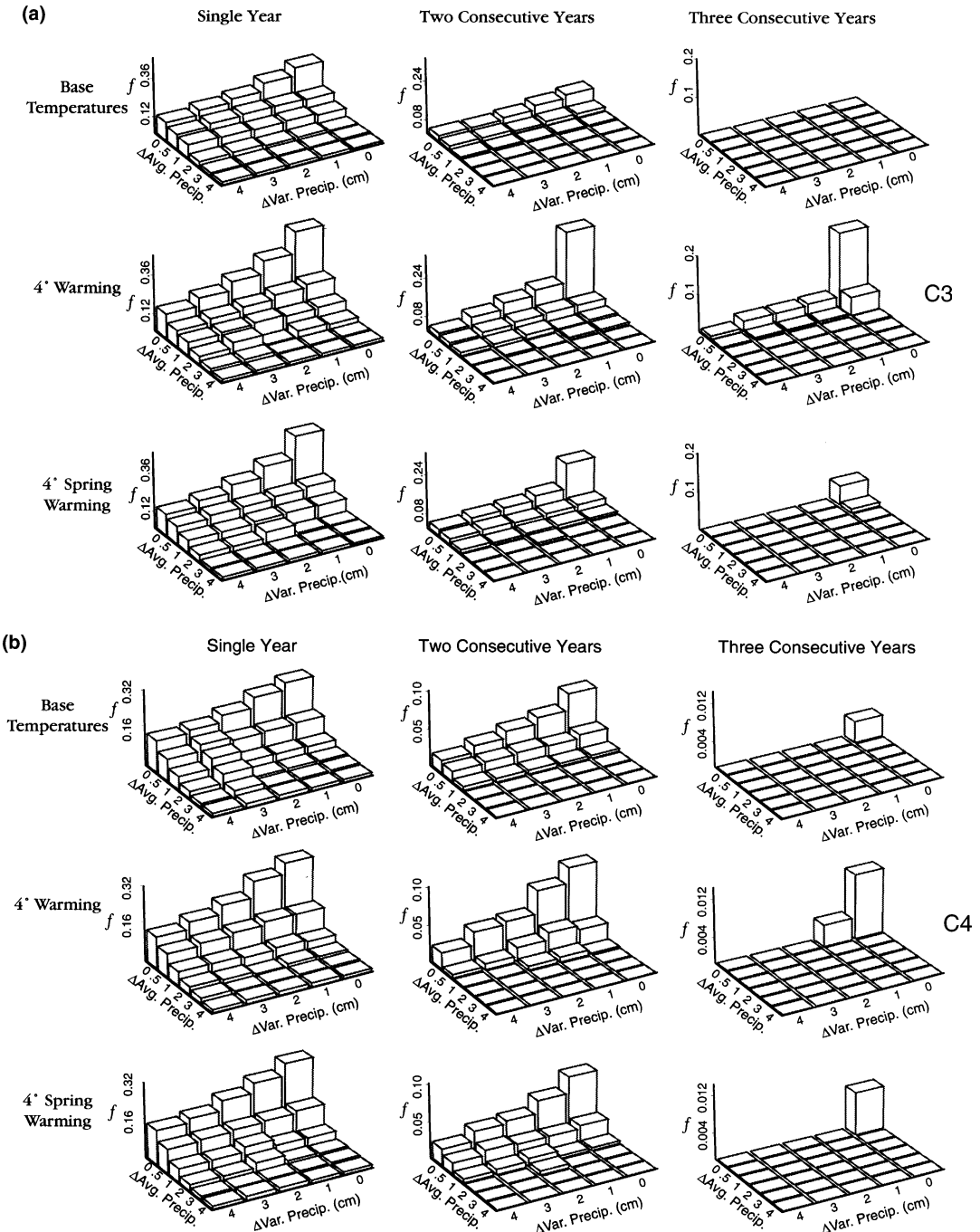


Fig. 8. Stability of productivity in various climate-change scenarios, as shown by calculating frequencies of low productivity years, as well as the frequencies of this occurring in 2 and 3 consecutive years. Height of bars records frequency of low productivity years.  $\Delta$ Avg = changes per century (starting in 1900) to average monthly precipitation in cm.  $\Delta$ var = changes per century to variability of monthly precipitation. Height of bars records frequency of low productivity years. (a)  $C_3$  vegetation, (b)  $C_4$  vegetation.



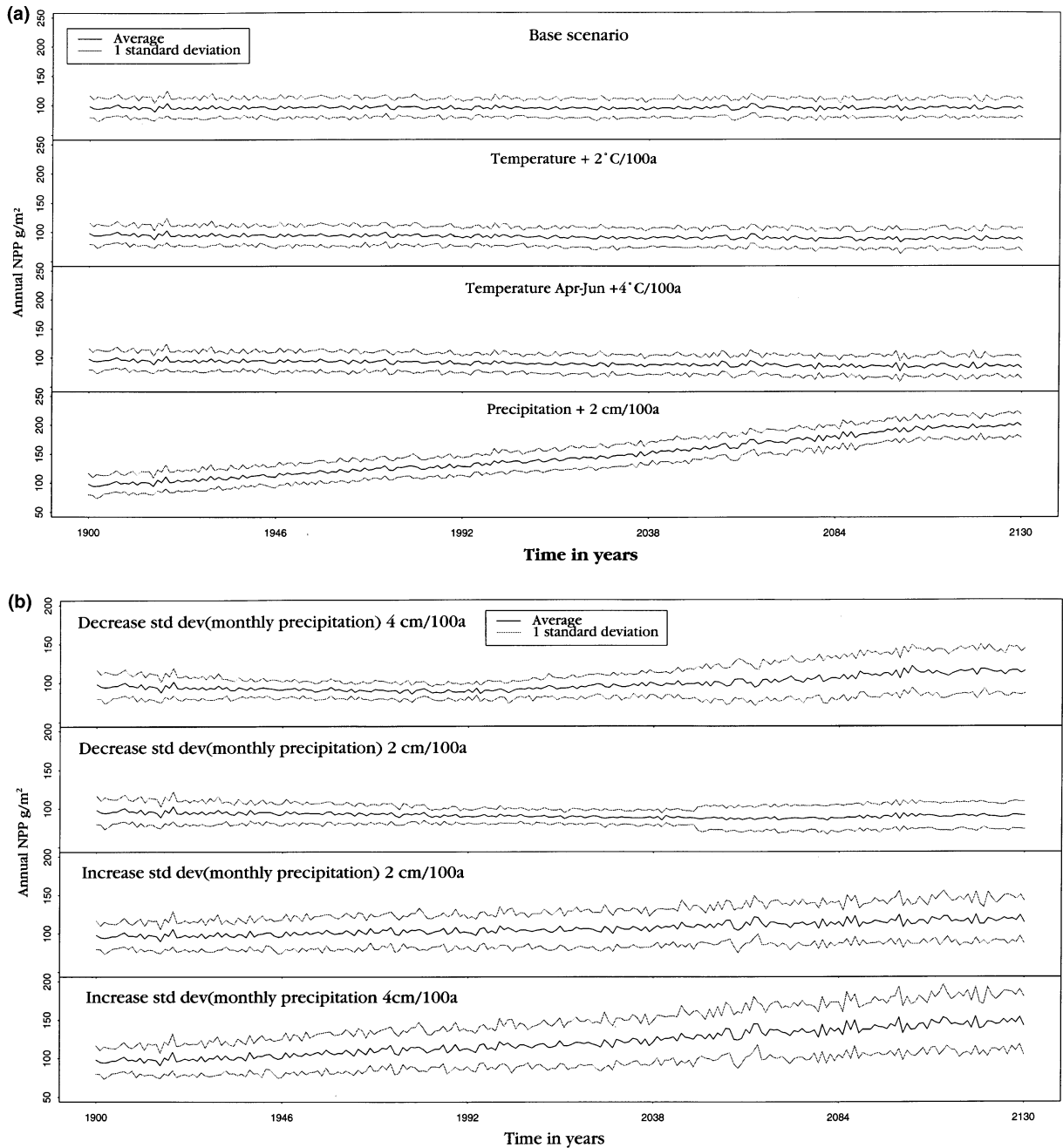


Fig. 9. Uncertainty in NPP predictions over time for various scenarios. Dark lines illustrate the average prediction of 50 model runs with stochastic climate; grey lines indicate one standard deviation of these predictions. (a) Base climate and changes to average climate inputs, (b) changes to variability of precipitation inputs.

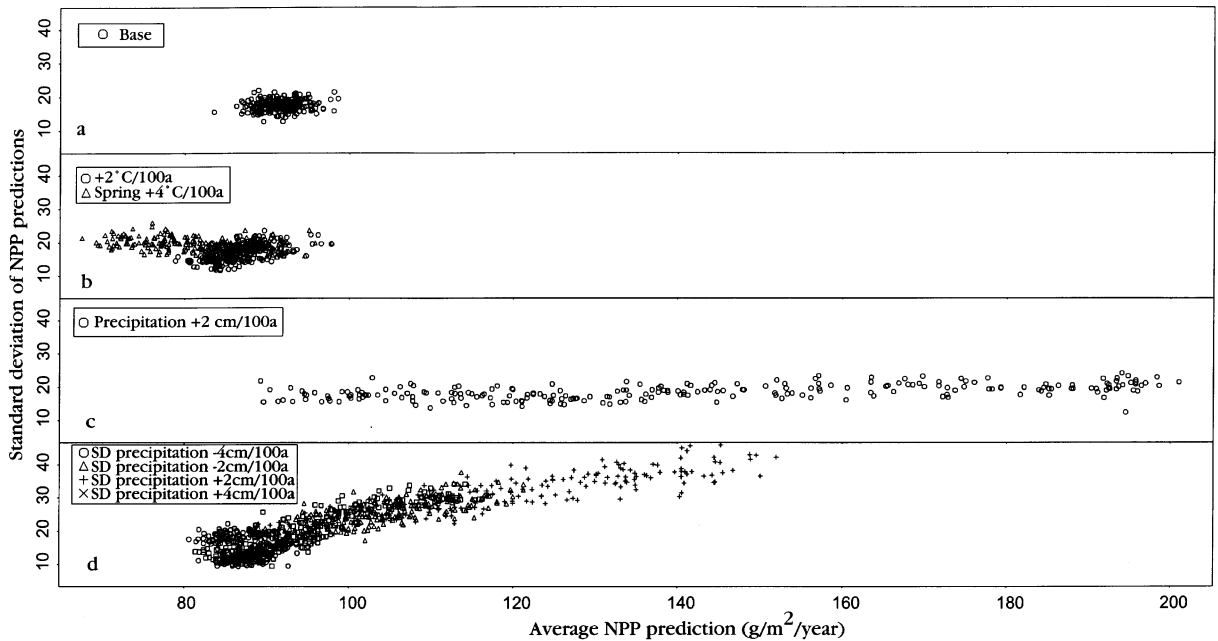


Fig. 10. Uncertainty of NPP predictions as a function of average prediction magnitude, for (a) the base climate, (b) a 2°C per century warming in monthly average temperatures and a 4°C warming in the Spring months only, (c) 2 cm/century of increasing average monthly precipitation, and (d) increases and decreases of 2 and 4 cm per century in the variability of monthly precipitation.

### 3.4. Uncertainty

To study the extent of prediction uncertainty caused by the stochastic precipitation, we examine means and standard deviations of multiple predictions. When averages are changed with constant variance (Fig. 9a), the margin of error remains constant across time, since the variability of monthly precipitation is not altered. Changes in the variability of precipitation across time have a larger effect (Fig. 9b). Apparently, no matter whether this variability is increased or decreased, the overall variability of the predictions gets larger.

There is an uncertainty of at least  $\pm 10$ – $20$   $\text{g}/\text{m}^2/\text{years}$  in the NPP predictions in any scenario, which is an important qualifier to any predictions made with the model. If the variability of monthly average precipitation increases in a changing climate, the consequent uncertainty in our NPP predictions increases to over  $40$   $\text{g}/\text{m}^2/\text{years}$ , or about 35%. Other examples of productivity predictions that provide uncertainty estimates are

fairly rare, however, we have seen similar magnitudes of uncertainty when predicting nitrogen dynamics in a forest ecosystem with PnET (Handcock et al., 1999), and Veldkamp et al. (1996) reported coefficients of variance in Terrestrial Vegetation Model predictions of crop yields of 1.9–16.6% for most crops, and over 600% for two extreme examples.

Since the Monte-Carlo sampling was driven by sampling of climate parameters from a monthly generalization, these results suggest that predictions of productivity dynamics under this scenario may be better served with a model using finer temporal resolution. Many other models have moved to daily time steps for photosynthesis predictions, and Chen et al. (1999) suggests that even a daily time step may miss important diurnal dynamics when predicting photosynthesis.

The uncertainty trends can be seen again in Fig. 10, which plots the standard deviation of each year's prediction versus the average, across the 50 simulations. Scenarios with changes to average temperatures or precipitation (Fig. 10b and c)

showed that these scenarios do not consistently control productivity patterns. The scenarios with decreases in precipitation variability have the lowest consistent uncertainty in NPP predictions, but even there the standard deviation of the prediction is always at least  $\approx 10\%$  of the prediction. As the input variability provided by the scenario increases, NPP uncertainty increases with the magnitude of the prediction, but not in a linear fashion (Fig. 10d); apparently given the level of variability in our inputs, the confidence in predictability of NPP levels off at about  $\pm 20$  g/m<sup>2</sup>/years.

#### 4. Conclusions

We have evaluated the sensitivity of C<sub>3</sub> and C<sub>4</sub> productivity to management and climate factors, including CO<sub>2</sub> concentration, grazing, temperature, and precipitation magnitude and variability. Precipitation variability best explains variability in annual productivity. Major known trends in ecosystem functioning can be reliably and robustly reproduced.

The importance of these inputs were re-assessed under a range of climate change scenarios. The pattern of warming can be important, but variability of precipitation remains the primary control. Examining the stability of production, estimated by sub-threshold NPP and its frequency in consecutive years, provides a perspective on favourable versus unfavourable conditions by functional groups. We think this new perspective can serve as a potential link between productivity and diversity. The frequency of failures, as function of precipitation and precipitation pattern, exhibits a strongly nonlinear response.

The inherent uncertainty of NPP prediction is due to two major factors, in this modelling environment: lumped parameterization of the growth model, and (over) generalization of climate. With a Monte-Carlo simulation study, we quantified the latter, using a climate simulator in which the variability of monthly precipitation was the stochastic component. Under the base scenario, NPP was predicted with 15–25% (10–15 g/m<sup>2</sup>/years) uncertainty. Least reliable results were ob-

tained when both precipitation and its variability increased (25–30% or 40–45 g/m<sup>2</sup>/years). It is important to note for long-term simulations that the confidence intervals change substantially, sometimes non-monotonically, over time. More sophisticated predictions of the area's response to climate change should also take into account the fact that there will likely be different changes to monthly precipitation at different times of year. However, given the uncertainty in our predictions when precipitation variability is altered, at this point we are concentrating on narrowing that uncertainty instead of more realistic climate scenarios.

Reduction of uncertainty calls for two types of immediate refinements: finer representation of spatial and temporal moisture variability. We are currently working on implementing a spatially distributed, daily time step model version. In the longer term, we will investigate linkages of these types of biogeochemical models with biogeographic models of species distribution and interaction.

In summary, this modelling framework is a good diagnostic tool to identify and quantify major controls on, their sensitivity to, and the inherent uncertainty of long-term grassland annual net primary production. There are strong limits on the role of reparameterization of the existing model for reducing prediction uncertainty, but work towards this goal can be stimulated by identifying key controls of ecosystem processes and their sensitivities to driving variables.

#### Acknowledgements

This research was supported by a National Sciences and Engineering Research Council grant to F. Csillag. Facilities and advice were provided by Grasslands National Park and Parks Canada, particularly by P. Fargey and S. McCanny. A. Davidson's field work provided extensive background beyond that possible from the measurements taken specifically for this study, and his suggestions for this paper are most appreciated.

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