Projected ecosystem impact of the Prairie Heating and CO_2 Enrichment experiment

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Summary

- The Prairie Heating and CO_2 Enrichment (PHACE) experiment has been initiated at a site in southern Wyoming (USA) to simulate the impact of warming and elevated atmospheric CO_2 on ecosystem dynamics for semiarid grassland ecosystems.
- The DAYCENT ecosystem model was parametrized to simulate the impact of elevated CO_2 at the open-top chamber (OTC) experiment in north-eastern Colorado (1996–2001), and was also used to simulate the projected ecosystem impact of the PHACE experiments during the next 10 yr.
- Model results suggest that soil water content, plant production, soil respiration, and nutrient mineralization will increase for the high-CO_2 treatment. Soil water content will decrease for all years, while nitrogen mineralization, soil respiration, and plant production will both decrease and increase under warming depending on yearly differences in water stress. Net primary production (NPP) will be greatest under combined warming and elevated CO_2 during wet years.
- Model results are consistent with empirical field data suggesting that water and nitrogen will be critical drivers of the semiarid grassland response to global change.

Key words: carbon dioxide, DAYCENT, global change, grassland, modeling, nitrogen, warming, water.

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Introduction

Global change experiments are challenging both in their implementation and in their explanation. Designing and carrying out experiments that manipulate ambient concentrations of CO_2, temperature, precipitation, or nitrogen (N) deposition in a realistic field environment present a multitude of logistical challenges which make these types of projects expensive to undertake, and therefore limited in scope. The vast majority of such experiments have focused on one, or occasionally two, global change factors (Norby & Luo, 2004), and have been conducted under limited environmental conditions and vegetation, leaving many gaps in our direct knowledge of how combined global change factors will affect natural and agro-ecosystems. A notable exception is the Jasper Ridge Global Change Experiment (Dukes *et al.*, 2005), in which four global change factors (CO_2, warming, precipitation, and N addition) are varied in a full factorial design. While the duration of some global change experiments can be as long as 5–10 yr, sufficient to understand primary responses of plants and some soil processes to experimental perturbations, we know that the time-constants of other processes, such as nutrient cycling, are longer, requiring decades or centuries to reach new equilibria after experimental perturbations, such as doubling of ambient CO_2 concentration (Morgan, 2002). Ecosystems are sensitive to rates of change, underscoring that instantaneous step changes in global change attributes may not induce the same reactions as more incremental changes which are predicted in global circulation models. All of this begs the question of how we can best use our empirical knowledge gained from relatively short-term and limited experiments involving step changes in environmental attributes to predict the long-term responses of natural and agro-ecosystems to the gradual global changes that are underway.

One approach is to use well-integrated modeling and observational investigations (Morgan, 2002; Luo *et al.*, 2004; Norby & Luo, 2004; Pendall *et al.*, 2004). Observational experiments can provide the fundamental knowledge of critical system processes, while modeling fills in knowledge gaps, and evaluates the limitations of our knowledge base that result from inadequate spatial and temporal scaling of our experiments. Such modeling exercises are not uncommon, but they are typically developed near the end or after the conclusion of experiments. This greatly limits their usefulness as feedback tools for refining our research questions, and for developing more useful models to be used in tandem with our empirical investigations.

Our interest is in the semiarid grasslands of the western Great Plains in eastern Colorado and Wyoming. In a CO_2 enrichment experiment conducted in open-top chambers (OTC) on the shortgrass steppe in northern Colorado from 1996 to 2001, we observed that doubling the ambient CO_2 concentration caused strong and consistent increases in plant productivity (Morgan *et al.*, 2004a), attributable in large part to improved plant water relations, particularly higher water-use efficiency (LeCain *et al.*, 2003; Morgan *et al.*, 2004b; Nelson *et al.*, 2004). However, we also observed a decline in forage quality under elevated CO_2 as a result of declining forage concentrations of N (Milchunas *et al.*, 2005) and a shift in species composition towards less nutritious grasses (Morgan *et al.*, 2004a; Milchunas *et al.*, 2005). The dilution of plant N seemed to be mostly a result of the inability of soil N release to keep pace with the higher N demand of faster growing plants under elevated CO_2.

Declining forage quality in native grasslands, such as occurred in the shortgrass steppe under elevated CO_2 concentrations, is an important matter not only for domesticated livestock, but also for the native ungulates that have grazed these systems for thousands of years. We have little information on how warmer ambient temperatures might affect this reaction to CO_2. While increased temperature speeds mineralization (Pendall *et al.*, 2004), long-term exposure to elevated CO_2 may induce a progressive N limitation to primary productivity (Hungate *et al.*, 2003; Luo *et al.*, 2004). There is little direct information on the combined effects of elevated CO_2 and warmer temperatures on soil nutrient cycling, as few experiments have considered more than one global change factor (Norby & Luo, 2004). Further, the long-term consequences of rising CO_2 and warming temperatures cannot easily be gleaned from relatively short-duration field experiments of just a few years. A combined modeling/experimental approach is needed to understand how rising CO_2, plus warmer temperature and altered precipitation patterns, will impact plant community dynamics, vegetation productivity, and forage quality (Norby & Luo, 2004). These matters are of importance for predicting critical ecological and economic outcomes of global change on semiarid grasslands of the Great Plains.

This paper will show how experimental results from a 5-yr-long Colorado elevated CO_2 experiment in Colorado using OTCs (Morgan *et al.*, 2004a) were used to parametrize CO_2 impacts in the DAYCENT (Parton *et al.*, 2001) ecosystem model. We will show how the DAYCENT model has been used to predict the ecosystem impact of the new Prairie Heating and CO_2 Enrichment (PHACE) experiment, which includes the separate and combined treatments of elevated atmospheric CO_2 and warming in semiarid grasslands in south-eastern Wyoming. The two semiarid grassland sites in Wyoming and Colorado are within 34 km of each other and are composed of similar vegetation, making modeled, as well as empirical, comparisons ideal. DAYCENT model results are used to project the impact of the global change experiment over the next 10 yr and to formulate a set of hypotheses about the ecosystem impact of warming and elevated CO_2 concentrations, which will be tested using the extensive field data collected at the PHACE. Data sets to be collected as part of PHACE were selected because of experience gained from the previous elevated CO_2 chamber experiment (Morgan *et al.*, 2004a) and the need for the data to test DAYCENT model predictions. We believe this is one of the first documented modeling exercises that projects ecosystem impacts at the outset of a field experiment.

Description

The Prairie Heating and CO_2 Enrichment experiment

The PHACE experiment was initiated in spring 2006 on semiarid grasslands near Cheyenne, Wyoming. The PHACE experiment is using Free Air CO_2 Enrichment (FACE) technology (Miglietta *et al.*, 2001) to elevate ambient CO_2 concentration, plus a ceramic heater system using a proportional-integral-derivative (PID) feed-back loop (Kimball, 2005) to raise day and night temperatures in 3-m-diameter plots established in a northern mixed-grass prairie. The experimental design consists of five replications each of four factorial combinations of two CO_2 treatments (the control ambient CO_2 treatment of *c.* 375 $\mu l\ l^{-1}$ CO_2, and the elevated CO_2 treatment of 600 $\mu l\ l^{-1}$ CO_2), and two temperature treatments (ambient temperatures and elevated day:night temperatures of 1.5 : 3°C), for a total of 20 experimental plots. As water is viewed as the primary driver of semiarid grassland responses to CO_2 (Morgan *et al.*, 2004b), and also because warming will have important water relation consequences, an important feature in this experiment is the monitoring of plant and soil water relations, leaf and canopy gas exchange, and peak season above-ground biomass and N content by species as an estimate of above-ground net primary production (ANPP). Minirhizotron technology and root in-growth areas are being used to evaluate root growth. Additionally, a suite of soil C

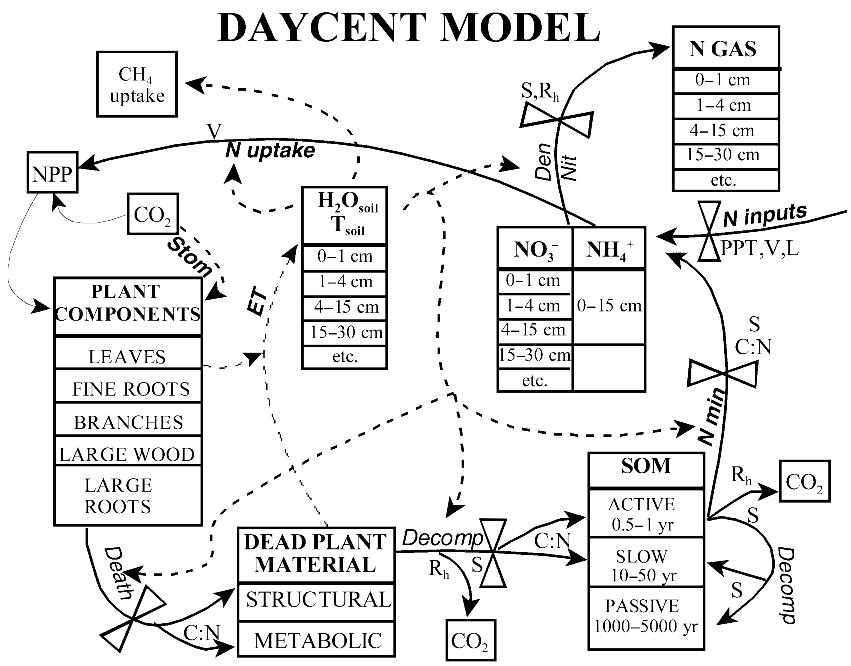

Fig. 1 Diagram for the DAYCENT ecosystem model showing the important carbon (C) and nitrogen (N) flows and the controls for them. ⟶, C and N flows; - - ➤, feedbacks and information flows; ▷◁, control on process; H_2O_{soil}, soil water content; T_{soil}, soil temperature; S, soil texture; C:N, C:N ratio of material; V, vegetation type; SOM, soil organic matter; L, land use; R_h, heterotrophic respiration; N GAS, N_2O, NO_x and N_2; NPP, net primary production; PPT, precipitation. Processes are designated by italics: *Stom*, stomatal conductance; *Death*, plant component death; *Decomp*, decomposition; *N inputs*, N fixation, deposition, and fertilization; *Nit*, nitrification; *Den*, denitrification; *N min*, N mineralization; *ET*, evapotranspiration. Data are from Parton *et al*. (1998), Kelly *et al*. (2000) and Del Grosso *et al*. (2001a,b).

and N, plus trace gas measurements (CH_4, N_2O, NO_x, and CO_2), will document how combined CO_2 enrichment and warming affect system nutrient cycling, and ultimately feedback on primary ecosystem responses to the global change treatments.

DAYCENT model description

The DAYCENT model has been used extensively to simulate ecosystem dynamics for grasslands, forests, and cropping systems in the USA (Kelly *et al.*, 2000; Del Grosso *et al.*, 2001a; Parton *et al.*, 2001). The model has been employed to simulate the impact of agricultural management practices (Del Grosso *et al.*, 2001b, 2002a, 2005) on crop yields, soil carbon (C) contents, and trace gas fluxes (N_2O, NO_x, and CH_4) from US agricultural systems at the site, and at regional and national levels. The grassland version of the DAYCENT model has been tested with data from different grassland sites (Kelly *et al.*, 2000; Pepper *et al.*, 2005; Del Grosso *et al.*, unpublished) and used to project the ecosystem impact of enhanced N deposition, changing CO_2 concentrations, and future potential climatic changes (Pepper *et al.*, 2005). The DAYCENT model simulates the dynamics of soil nutrients (N and phosphorus (P)), soil organic matter (C, N, and P), plant production, soil water and temperature, and trace gas fluxes (N_2O, NO_x, N_2, and CH_4). Figure 1 shows the major components of the DAYCENT model and state variables that control important ecosystem processes. The DAYCENT model is a daily time step version of the CENTURY model (Parton *et al.*, 1987). The goal was to develop an ecosystem model that simulates the dynamics of all of the important greenhouse gases (CO_2, N_2O, and CH_4), and is capable of responding to changes in atmospheric CO_2 concentrations, nutrient deposition, climatic conditions and important ecosystem management practices.

The plant production model simulates the growth of grasses, crops, and trees, and can simulate competition between trees and grasses in savanna systems. The key processes included in the plant production model include growth of different plant parts, plant death, plant phenology, and uptake of soil nutrients. The major factors that control plant growth include soil water and temperature, solar radiation, area of live leaves, and soil nutrients available for plant growth. A detailed description of the plant growth model is presented by Kelly *et al.* (2000), and recent changes to the model have been documented by Del Grosso *et al.* (2001a).

The soil water and temperature submodels simulate daily soil water content and temperature for different soil layers. A detailed description of the soil temperature model is presented by Eitzinger *et al.* (2000), while the soil water model is described by Parton *et al.* (1998). Key processes within the soil water model include saturated and unsaturated water flow, surface runoff, and water flow below the plant rooting zone. A numerical solution of the Darcy water flow equations is used to simulate water flow between soil layers using a half-hour time step. The model can simulate anaerobic conditions resulting from the melting of snow into frozen soils. The soil temperature model simulates daily maximum, minimum, and average soil temperatures at 5-cm depth increments using an analytical solution to soil heat flow equations. The soil water and temperature models have been extensively tested using observed soil water and temperature data sets from many different sites and soil textures (Frolking *et al.*, 1998; Eitzinger *et al.*, 2000; Del Grosso *et al.*, 2001a; Möllerstöm, 2004).

Model parametrizations and verification

The DAYCENT model was set up to represent the experimentally observed ambient control and elevated CO_2 conditions from our previous CO_2 enrichment experiment conducted in eastern Colorado (Morgan *et al.*, 2004a; Mosier *et al.*, 2002). The experiment was conducted at the United States Department of Agriculture-Agricultural Research Service (USDA-ARS) Central Plains Experimental Range (CPER), *c.* 44 km south of Cheyenne, Wyoming, near Nunn, Colorado (lat. 40°50′N, long. 104°42′W), in a pasture dominated by the C_3 grasses *Pascopyrm smithii* and *Stipa comata*, and the C_4 grass *Bouteloua gracilis*. Elevation at the CPER is 1650 m, and long-term average annual precipitation is 320 mm. The experiment used OTCs and had three nonchambered control plots, three chambered control plots maintained at ambient CO_2, and three chambers exposed to elevated (twice ambient, *c.* 720 µl l^{-1}) CO_2 concentrations. The plant growth parameters for the shortgrass steppe (Kelly *et al.*, 2000) were adjusted to represent the growth of plants in the experimental CO_2 chambers. The parameters controlling minimum and maximum C:N ratios were increased to match the observed plant production for the elevated CO_2 experiment, and plant transpiration rates were adjusted to match observed decreases caused by elevated atmospheric CO_2 concentrations. There are extensive data supporting the simulated increase in the plant C:N ratio (Luo *et al.*, 2004) and the decrease in plant transpiration as atmospheric CO_2 concentrations increase (Morgan *et al.*, 2004b). Plant C allocation is dynamic in the DAYCENT model and accounts for water and nutrient stress impacts on C allocation (not adjusted in this application of DAYCENT). Increasing air temperature impacts the system by increasing the vapor pressure deficit over the live leaves, resulting in increased plant transpiration rates. Increasing CO_2 concentrations increases stomatal resistance and thus reduces the negative impact of elevated air temperatures by reducing the temperature-driven potential increases in plant transpirations rates.

The major inputs required to run the model included the observed soil physical properties, observed daily precipitation, minimum and maximum daily air temperatures (1949–2002), and land use history of the Colorado site. Observed soil texture (sand, silt, and clay content) data as a function of soil depth were used to characterize soil horizons, while field capacity, wilting point, soil bulk density, and saturated soil hydrologic conductivity were estimated as a function of observed soil texture (Saxton *et al.*, 1986) and adjusted when observed data were available. Observed soil water data were used to adjust field capacity and wilting point. The initial soil C and N, and plant C and N contents, before the start of the experiment (1996) were determined by running the model for a 2000-yr spin-up simulation where we assumed current climate and atmospheric CO_2 concentrations.

We simulated the 5-yr CPER field experiments with the effects of different CO_2 concentrations and chamber effects represented in the model runs. The chamber effects were simulated by scaling down the potential evapotranspiration rate (PET) of the system based on observed chamber PET data and results from Owensby *et al.* (1993) using similar chambers in eastern Kansas. The grassland was defoliated twice each year (half defoliation in late July; full defoliation after plant senescence in October) to simulate the vegetation removed under recommended grazing practice (Morgan *et al.*, 2004a). Simulated above-ground plant production and soil water data (0–10 and 10–40 cm depths) were compared with the observed plant clipped and soil water content data for the 5-yr experiment.

Model projections of PHACE

Next, DAYCENT was used to project the impacts of the PHACE CO_2 and climatic manipulation experiments on critical ecosystem variables for the 10 yr after the experiment began. The PHACE experiment is being conducted on a native semiarid grassland at the USDA-ARS High Plains Grasslands Research Station (lat. 41°11′N, long. 104°54′W) near Cheyenne, Wyoming. Species composition at this site is similar to that of the previous OTC experiment, but cooler temperatures as a result of a higher altitude (1930 m) and slightly higher annual precipitation (38.4 cm) result in a more productive semiarid grassland in most years compared with the nearby shortgrass steppe site. The daily weather data (daily maximum and minimum temperatures and total precipitation) taken from the Cheyenne, Wyoming weather station from 1916 to 2005 were used to drive the model for the 1916–2005 time period, and the daily weather data from 1953 to 1962 were used to project the climate from 2006 to 2015. Data from 1953 to 1962 were selected because the year-to-year variations in weather patterns are typical of the Cheyenne site (combination of dry and wet years). Equilibrium soil C and N contents were derived by running the model for a 2000-yr spin up using the observed weather data from 1916 to 2005 (repeated use of the 1916–2005 weather data for 2000 yr) and the observed soil texture at the site.

The warming manipulation was simulated by increasing both the daily maximum and minimum temperatures by 2°C instead of the 1.5 : 3.0°C conditions of the experiment. This was necessary as differentially altering the maximum and minimum air temperatures in accordance with the experiment would have reduced water stress from that expected in the actual experiment. The variable day:night temperatures decrease the diurnal range of temperature and result in reduced potential evapotranspiration rates because of the DAYCENT assumption that diurnal temperature range is correlated to water vapor pressure, with higher water vapor pressure being associated with a lower diurnal temperature range. In the actual field experiment, the water vapor pressure is not increased as a result of the warming treatment. The major ecosystem impacts of the warming treatment in DAYCENT will be to increase the

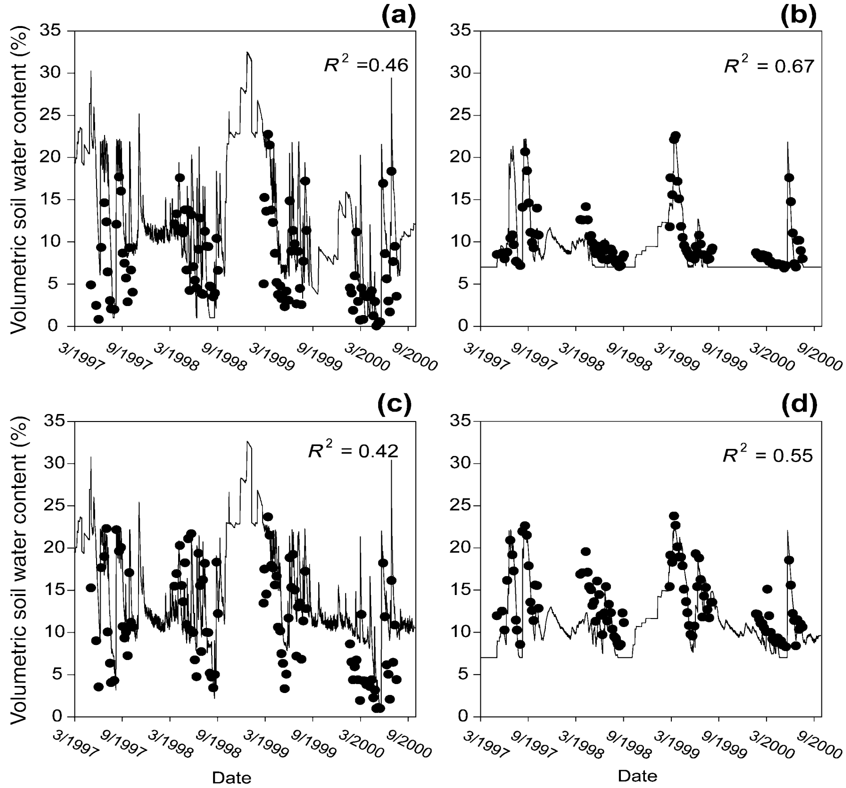

Fig. 2 Simulated (line) and observed (closed circles) soil water content in (a, b) the control chamber treatment for (a) the 0–10 cm and (b) the 10–40 cm layers, and (c, d) the CO_2 elevated treatment for (c) the 0–10 cm and the (d) the 10–40 cm layers in the shortgrass steppe open-top chamber (OTC) project.

time period when plant growth can occur in the spring and fall and to increase the potential evapotranspiration rate (higher air temperatures result in higher vapor pressure deficits). Plant growth in DAYCENT occurs when air temperatures are greater than the critical temperatures for plant growth (longer time period for the warming treatment) and water stress does not limit plant growth.

We did not consider the impact of species shift or altered plant phenology in these model runs. Differential species response to elevated CO_2 can be important in the shortgrass steppe, where productivity responses among major species to CO_2 were found to be limited to a common C_3 grass, *S. comata* (Morgan *et al.*, 2004a). Further, warmer temperatures may favor C_4 grasses over C_3 grasses (Terri & Stowe, 1976), and are certain to enhance phenological development (Dunne *et al.*, 2004; Jolly *et al.*, 2005). We are working on a separate modeling exercise to evaluate the long-term impact of species shift on ecosystem biogeochemistry, including effects on forage quality and animal performance.

A major problem in infrared warming experiments is the artificial drying caused by the heaters. Such experimental warming increases the vapor pressure gradient between leaves and the atmosphere over what would develop if warming occurred everywhere and relative humidity remained constant (Kimball, 2005), as predicted by climate change models. Kimball (2005) has suggested that infrared warming treatments should consider daily water additions which correct for this experimental artifact, but the logistics of adding small water amounts evenly and accurately over field plots could be difficult. Additionally, there will likely be consequences of increasing the number of water pulse events on microbial processes and nutrient cycling. We used DAYCENT to investigate the impact of increasing the precipitation (25%) on days when precipitation occurs, thus eliminating the impact of increasing microbial activity associated with increasing the number of precipitation events. The approach of enhancing precipitation events is a standard methodology for simulating increased precipitation (Dukes *et al.*, 2005), and seemed appropriate as a method for countering the desiccation associated with artificial warming. The model run will evaluate whether increasing precipitation when natural precipitation occurs will increase soil water content enough to compensate for the artificial drying caused by the heaters.

Results

Model vs open-top chamber data comparison

Once the DAYCENT model was parametrized to simulate the OTC CO_2 experiment, model results were compared with the observed data. A detailed model vs data comparison (Fig. 2) for the control and elevated CO_2 treatments shows that the model correctly simulated the dynamic changes in soil water content following rainfall events (0–10 and 10–40 cm depths)

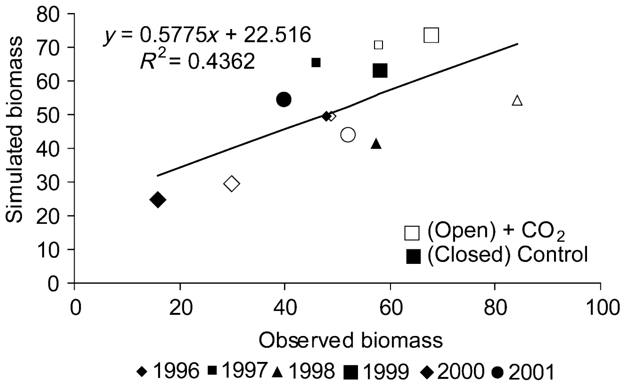

Fig. 3 Comparison of observed above-ground plant production (July clipping data) for the chamber control and elevated CO_2 treatments in the shortgrass steppe open-top chamber (OTC) project from 1996 to 2001.

and movement of soil water down to deeper soil depths (10–40 cm depth) for both treatments and that the increase in soil water content for the elevated CO_2 treatment tends to be higher at the lower soil depth (look at data from 1998 to 1999). The R^2 for the model vs data comparison ranges from 0.42 to 0.67, with a general trend for the 10–40 cm depth to have higher R^2 values for both treatments. A comparison of the observed and simulated soil water results for the control and elevated CO_2 treatments shows that the soil water content is similar when the soil is wet and very dry, but that the soil stays wetter longer during the dry down periods following rain events.

The elevated CO_2 treatment plant biomass (July clipping) data show a consistent 17–88% increase in above-ground plant biomass for all of the experimental years compared with controlled ambient conditions (Morgan *et al.*, 2004a,b). Comparison of the model results with the observed data shows that the model predicted the major year-to-year variations in yields (high yields in 1999 (wet year) vs low yields in 2000 (dry year)) and the observed increases in plant production for the elevated CO_2 treatment (Fig. 3). The R^2 of linear regression of model predictions vs observed data ranges from 0.43 for the control chamber to 0.47 for the CO_2 chamber. The simulated average annual increase in July biomass for the elevated CO_2 treatment is 35% vs 12% for the observed data, thus showing that the model tends to underestimate CO_2-induced increases in plant biomass. The simulated annual ANPP for the elevated CO_2 treatment is 27% greater than the control and ANPP is higher for each of the 5 years. The likely reason for the underestimate in biomass for the elevated CO_2 treatment is that there was a species shift toward the C_3 grass *S. comata*. An important aspect of that shift was greater seedling recruitment of *S. comata*. Further, *S. comata* has a substantially higher C to N ratio for live plant biomass compared with the other dominant species (King *et al.*, 2004; Milchunas *et al.*, 2005). Neither of these phenomena was represented in the model run, and their absence would tend to underestimate the community response. The other major discrepancy was an underestimate of plant biomass for the year 1998 in both treatments. DAYCENT model results show increased plant N uptake, soil respiration rates, and N mineralization for the elevated CO_2 treatment resulting from wetter soil water conditions in the elevated CO_2 treatment.

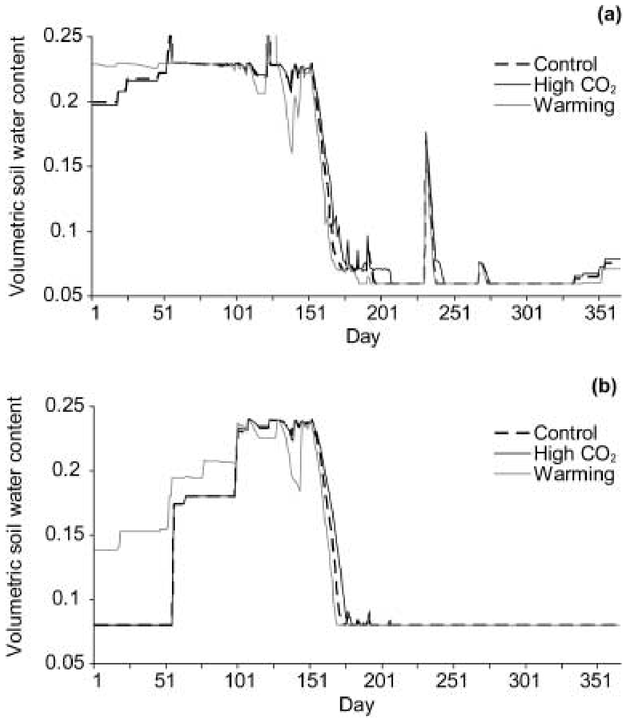

Fig. 4 Simulated soil water content for the control, elevated CO_2, and warming treatments at the Prairie Heating and CO_2 Enrichment (PHACE) experiment for (a) 4–15 cm soil depth and (b) 15–30 cm soil depth, projected for 2008.

Projected PHACE modeling results

An example of results (Fig. 4) from one of the 10 simulation years (2008) shows how the warming treatment of the PHACE generally predicts a decrease of soil water content (4–15 cm and 15–30 cm layers) during the growing season, and a slight increase (4–15 cm layer) during the winter and spring when warming increases snow melt. Results for the elevated CO_2 run (Fig. 4) predict that soil water content will be higher for both soil layers with elevated CO_2 during the dry down periods and similar when it is very wet or dry. These results are consistent with the observed impact of elevated CO_2 from the OTC experiment in Colorado. Combining the warming treatment with the elevated CO_2 treatment generally results in a decrease in soil water content compared with the elevated CO_2 results (data not shown).

The simulated warming experiment causes soil respiration (Fig. 5a) to increase in two of the years and to decrease in another two of the years, with a general trend for a slight

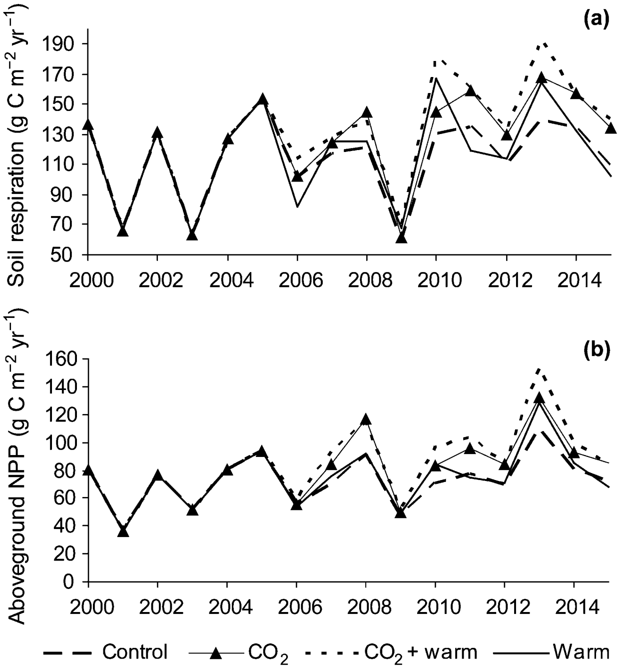

Fig. 5 Simulated annual soil respiration (a) and above-ground net primary production (ANPP) (b) for the Prairie Heating and CO_2 Enrichment (PHACE) experiment during the next 10 yr for the control, elevated CO_2, warming, and combined elevated CO_2 and warming experiments.

increase in soil respiration during most years. The simulated decrease in soil respiration occurs as a result of drying of the soil associated with warming, while the increases in soil respiration are a response to the increased soil temperatures (soil heterotrophic respiration rates are higher at higher soil temperatures). Overall there is a slight positive impact of soil warming on soil respiration rates. The elevated CO_2 treatments consistently cause an increase in soil heterotrophic respiration (except in years 2006 and 2009) as a result of the higher soil water content (Fig. 4). Combining warming with the elevated CO_2 treatments slightly increases soil respiration rates for most years and results in substantial increases in soil respiration during two years (years 2010 and 2013, which were wetter years).

Elevated CO_2 concentrations (Fig. 5b) consistently increase above-ground plant production (except in 2006 and 2009) with an average increase of 30%. Years 2006 and 2009 are years when elevated CO_2 concentrations have little impact on plant production. The warming treatment increases plant production in two years, and has a minimal effect during the other years. The years when warming has a positive impact on plant production are the years when warming causes an increase in soil heterotrophic respiration rates, while warming-induced decreases in soil respiration (in years 2006, 2011, and 2015) are associated with slight decreases in ANPP. Combining the elevated CO_2 and warming treatments results in slight increases in ANPP for most years and large increases in ANPP for the 2 years when warming alone causes large increases in soil respiration rates (years 2010 and 2013). Figure 6(a) shows that there is a positive correlation of elevated CO_2 concentrations and warming-induced changes in ANPP to changes in soil respiration rates ($R^2 = 0.80$). Figure 6(b,c) show that annual ANPP and heterotrophic soil respiration are positively correlated ($R^2 > 0.85$) to the annual average climatic decomposition index (CDI; the average annual value of the combined temperature/water index that controls decomposition rates of the soil organic matter pools). These results suggest that the major factor controlling annual changes and treatment differences in ANPP and soil respiration rates is the change in CDI. Thus, when elevated CO_2 or warming treatments result in an increase in CDI, there will be a corresponding increase in ANPP, soil respiration, and soil N mineralization.

Exposure to elevated CO_2 results in a predicted gradual decline in soil organic C over the 10-yr simulation (Fig. 7). Soil N follows a similar pattern in the long run, but exhibits an initially brief increase during the first year (2006). The simulated decrease in soil C contents with elevated CO_2 concentrations is primarily a result of increased soil decomposition rates caused by increased soil water content, as soil C inputs to the soil have increased with elevated CO_2 concentrations. Soil warming results in a slight increase in soil C and N contents; combining the warming and elevated CO_2 treatments shows little impact of warming, with the results of the combined treatment similar to those for the elevated CO_2 run. The warming treatment shows interesting year-to-year changes, with simulated increases in soil C and N associated with the decreased soil respiration rates in 2006 and decreased soil C contents associated with the warming-induced high soil respiration rates simulated in years 2010 and 2013. The long-term impact of these treatments on the soil C and N contents is difficult to predict as there are substantial year-to-year differences in soil C and N contents for the different treatments.

Results of the modeled water additions, which were carried out to compensate for the excessive soil drying associated with current warming experiments (Kimball, 2005), show (Fig. 8) that increasing precipitation events by 25% in the warming treatment increases soil water content to similar values to those modeled for the control run. Higher soil water contents associated with adding precipitation causes the ANPP to be increased by 18% relative to the warming treatment, and by 27% relative to the control treatment, and completely eliminates the negative impact that warming had on plant production for selected years when soil drying reduced plant production (Fig. 5b).

Discussion

Ecosystem computer models have been used extensively to help interpret field experiments. This paper demonstrates the use of the DAYCENT model to simulate the responses to

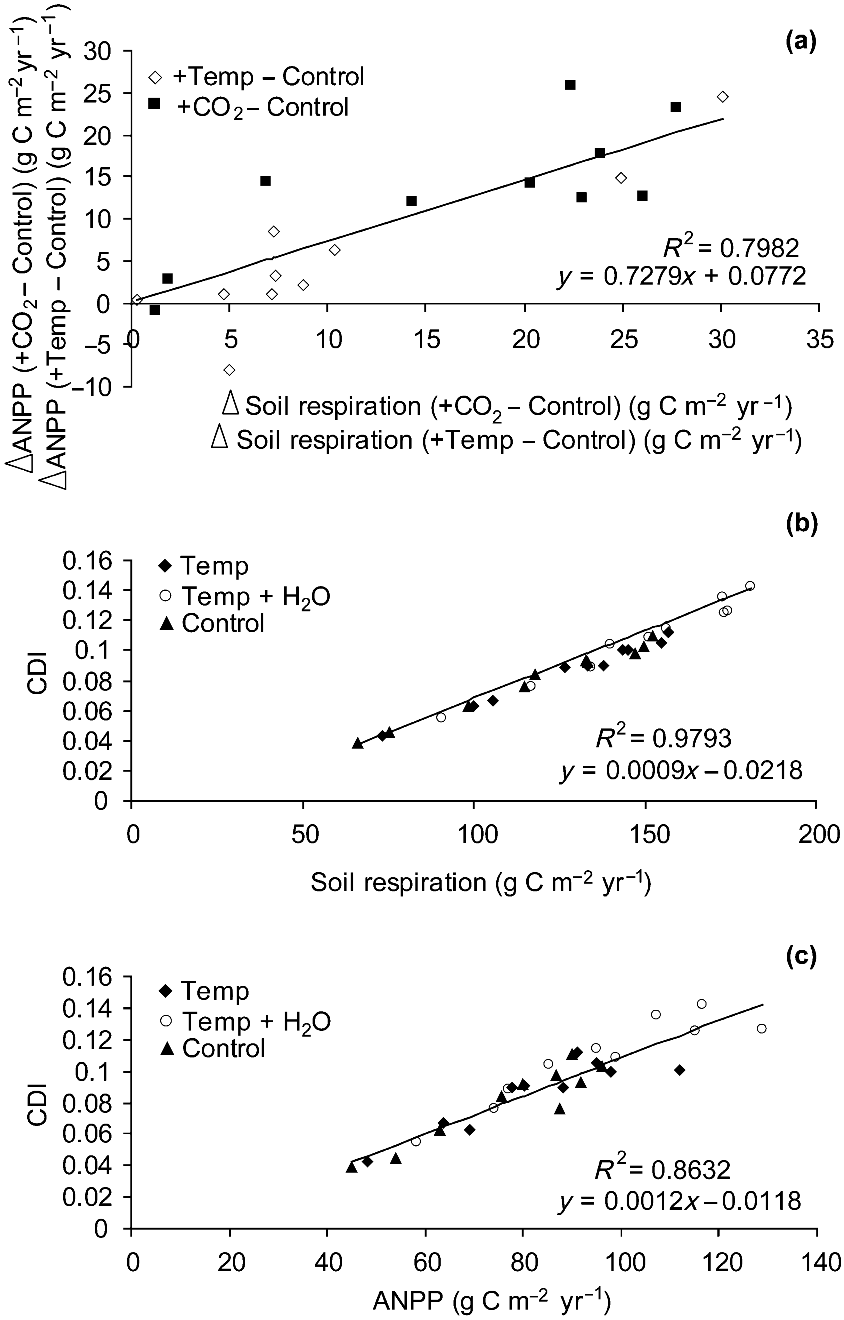

Fig. 6 (a) Comparison of the simulated differences in above-ground net primary production (ANPP) between the elevated CO_2 and the control treatments with the simulated annual soil respiration differences between the elevated CO_2 and the control treatments (2006–2015) along with the same patterns for the warmed treatment minus control model results. (b) Comparison of the simulated ANPP with the annual average climatic decomposition index (CDI). (c) Comparison of simulated annual soil respiration rates with CDI for the 2006–2015 time period.

elevated CO_2 in a previous OTC experiment in eastern Colorado, predicts the projected ecosystem impact of the PHACE field experiments during the next 10 yr, and suggests how field measurements will be used to test model-derived hypotheses about the impact of PHACE experiments on semiarid grassland ecosystems. Comparison of field data and model results for the OTC experiment showed that the model represented the major seasonal and year-to-year changes of the control and elevated CO_2 treatments, with the model correctly showing greater soil water content (Fig. 2) and above-ground plant production (Fig. 3) under elevated CO_2. The model results tended to underestimate the observed increase in plant production for the elevated CO_2 treatment. The likely cause for this discrepancy is the observed shift in plant species toward a species that has much higher C to N ratios for live plant biomass. This shift was not explicitly represented in the model parametrization. DAYCENT also predicted greater heterotrophic soil respiration and plant N uptake (data not shown), results that are consistent with some field study results reported by Pendall *et al.* (2004, 2005) and King *et al.* (2004).

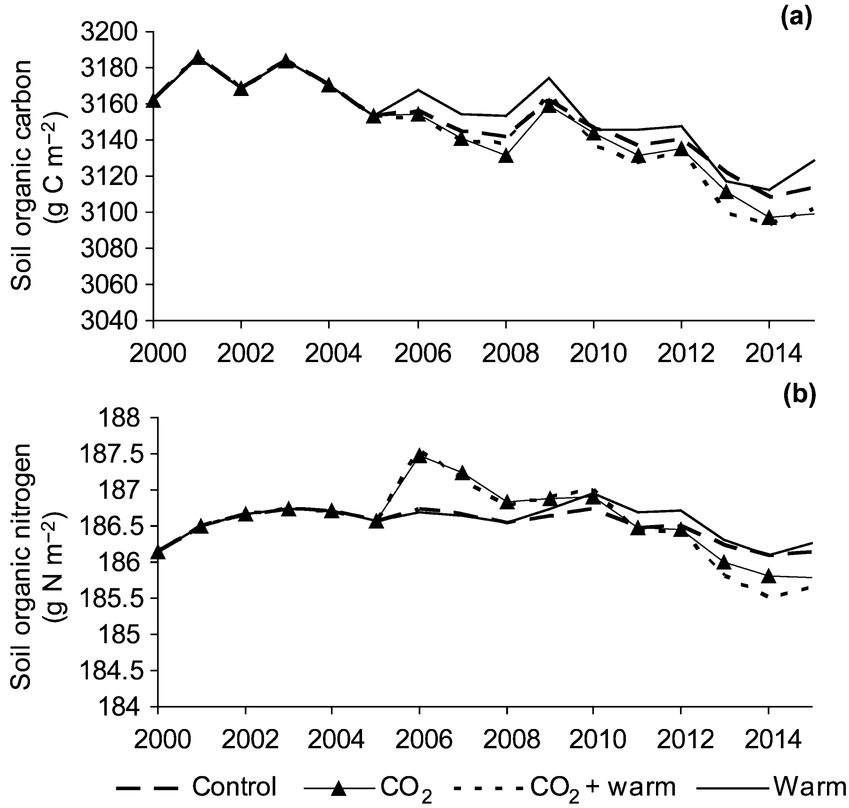

Fig. 7 DAYCENT model simulated soil organic carbon (C; 0–20 cm) (a) and soil organic nitrogen (N; 0–20 cm) (b) for the Prairie Heating and CO_2 Enrichment (PHACE) experiment for the next 10 yr for the control, elevated CO_2, warming, and combined elevated CO_2 and warming experiments.

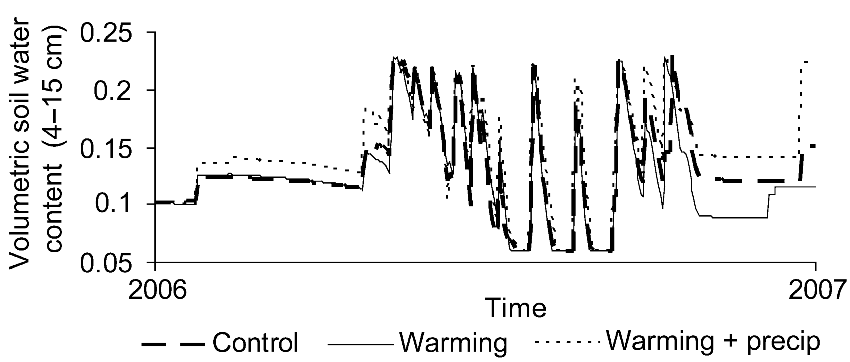

Fig. 8 Model simulated soil water content (4–15 cm depth) for the control, warming, and combined warming plus water addition treatments.

Modeled ANPP tends to be greatest in the combined elevated CO_2 and warming treatment, especially in high-production years. Combined warming and CO_2 enrichment can involve numerous system-level interactions including direct plant, and secondary hydrologic and biogeochemical reactions (Morgan *et al.*, 2004b; Reich *et al.*, 2006). Warming and CO_2 both have the potential to increase plant production through direct effects on plant physiology and soil–plant hydrology, although alterations in nutrient cycling, as a result of increased plant growth and warming-induced desiccation, can slow and reverse those tendencies. In our simulation exercise, combined warming and CO_2 enrichment stimulated plant productivity through the water relations benefits to microbial mineralization and plant growth, thereby meeting CO_2- and temperature-enhanced plant productivity with increased N mineralization. Based on results from the OTC experiment, we previously predicted that combined warming and elevated CO_2 in these semiarid grasslands should result in greater increases in biomass compared with increases in CO_2 alone (Morgan *et al.*, 2001). July above-ground biomass was always greatest in elevated CO_2 chambered plots and smallest in the nonchambered control plots (Morgan *et al.*, 2001, 2004a). Assuming that the main chamber effect was attributable to the average 2.6°C warmer temperature in the chambered plots, we speculated that combined warming and CO_2 enrichment were responsible for the large increases in plant biomass observed in elevated chambers (representing warming and elevated CO_2) compared with the nonchambered controls (present ambient temperature and CO_2). Despite a sequence of both wet and dry years, total harvested above-ground plant biomass was more than double in elevated chambered plots compared with control plots (Morgan *et al.*, 2004a), with no treatment-by-year interactions, suggesting that combined warming and rising CO_2 should result in substantive production increases in most years. An important objective of our new PHACE experiment will be to increase our understanding of the effect of this potential interaction of temperature and CO_2 on soil–plant water relations and the implications for ANPP.

Enhancing rainfall for the warming treatment by 25% during rain days resulted in increased soil water content, plant production, soil heterotrophic respiration, and soil turnover rates, and potentially better represents the projected impact of atmospheric warming in the future. These results show that adding precipitation during existing precipitation events has the potential to simulate the ecosystem impact of future increased water vapor contents. The strong effects of warming on ANPP in wet years are a result of the combined effects of the lengthened growing season and enhanced soil N mineralization (Rustad *et al.*, 2001; Shaw & Harte, 2001; Reich *et al.*, 2006), the latter supporting the warming-induced growth potential with increased soil plant N. A more thorough comparison of different precipitation manipulation experiments needs to be carried out in order to solve the problem of heater-induced desiccation.

Model results from this paper and Pepper *et al.* (2005) show that the two most important direct impacts of elevated CO_2 concentrations on grassland ecosystems are the reduction of plant transpiration rates and the increase in the C to N ratio of live plant material. Pepper *et al.* (2005) used the DAYCENT and G'DAY models to simulate the impact of elevated CO_2 concentrations on the CPER grassland site. DAYCENT results show that the dominant impact of elevated CO_2 is to increase soil water content (as a result of reduced transpiration) which then results in increased potential plant growth, plant N demand, soil decomposition rates, and soil N mineralization. G'DAY model results show a smaller increase in soil water content and decomposition rates, decreased soil N mineralization rates (as a result of higher dead plant C to N ratios), and increased plant production attributable to the higher N-use efficiency. Continuous soil water monitoring and intensive measurements of leaf gas exchange, water potential, seasonal soil respiration, N plant uptake, and ANPP are scheduled for all of the PHACE experiments, which will determine which of the ecosystem models is correct and if the reduced transpiration rates from the CPER chamber experiments are observed in the mini-FACE field elevated CO_2 plots. Long *et al.* (2005) suggest that the observed reduction in transpiration rates and increase in soil water contents in our CPER OTCs tend to overestimate the positive impact of elevated CO_2 concentrations. Litter decay rates and N release data for surface and root litter bags and seasonal soil respiration data will indicate whether increases in soil water content in the elevated CO_2 plots result in increased litter decomposition and soil N mineralization rates. Preliminary data from the first year of the PHACE experiment show that elevated CO_2 concentrations substantially enhance ANPP and increase soil water content, thus supporting DAYCENT predicted model results for the PHACE experiment and negating the predictions of Long *et al.* (2005) about chamber impacts on transpiration water losses.

This matter of N cycling and how it responds to global change may be one of the most important global change issues of ultimate importance to ranchers, their livestock, and the native ungulates that have relied on these native forages for thousands of years. Luo *et al.* (2004) suggest that limited soil N availability will reduce the potential positive impacts of higher CO_2 concentrations on plant production. They also suggest that down-regulation of plant growth as a result of N limitation will not occur if there are increases in N inputs to the system or reductions in N loses. Increased N-use efficiency of plants (grow more on less soil N) can also sustain CO_2-induced increases in plant production; however, this response will be partially compensated for by reduced soil N availability as a result of increased soil N immobilization associated with higher litter C to N ratios. Another mechanism to sustain increased plant production is to increase soil N mineralization available for plant growth because of higher soil decomposition rates. Experimentally observed results from PHACE experiments in the future showing a consistent CO_2-induced increase in total N uptake and plant production along with increased N release from decomposing leaf and root litter would support the hypothesis that increased soil water content causes increases in soil decomposition rates and N release that sustain long-term increases in plant production (DAYCENT predictions). The DAYCENT model predicts that net N release from soil organic matter in the CO_2 treatment is a potential N source for increased N uptake by the plant. Observed results from PHACE experiments showing decreased plant N uptake, increased plant production (higher C to N ratios of live leaves), and decreased N release for decomposing leaf and root litter in elevated CO_2 would support G'DAY model results and N down-regulation of plant production (Luo *et al.*, 2004).

Mosier *et al.* (2003) showed that there was a tendency for lower NO_x gas fluxes for the CPER elevated CO_2 chamber experiments. The DAYCENT simulated model results for the elevated CO_2 experiment show decreased NO_x gas fluxes comparable with the Mosier *et al.* (2003) results. Luo *et al.* (2006) suggest that other N losses are also reduced in elevated CO_2 treatments. The long-term impact (20–100 yr) of lower N losses would be to increase soil N mineralization, organic soil N contents and plant production. In the long term, lower N losses would compensate for the increased N mineralization resulting from the CO_2-induced increase in soil water content. It is very difficult to test these different hypotheses as soil organic N pools are quite large, and we are unable to measure small changes (5–10% changes) in soil organic N pools with sufficient accuracy.

To evaluate responses of N cycling to treatments, we had already planned on using ^{15}N plot applications to help monitor total plant and soil N, plus N pools, in addition to nondestructive (mini-rhizotron) and destructive (root bags) methods to assess root production. We plan to add additional experimental measurements that will specifically test the model predictions that: (a) elevated CO_2 concentrations will increase soil decomposition rates; (b) warming will have both positive and negative impacts on soil decomposition rates depending on the rainfall pattern; and (c) combining warming with elevated CO_2 concentrations will enhance soil decomposition rates during wet years.

DAYCENT model results suggest that plant production responses for all of the treatments are correlated to changes in CDI (Parton *et al.*, 2007). Gholz *et al.* (2000) showed that the CENTURY model CDI index is well correlated to mass loss and N release of decomposing root and leaf litter, and Del Grosso *et al.* (2005) showed that soil respiration rates are well correlated to the CDI index used in DAYCENT. The model results in this paper suggest that mean annual CDI values are positively correlated to annual soil respiration rates, ANPP, soil N mineralization, and N uptake (see Fig. 6). We will use the observed data from Prairie Heating and CO_2 Enrichment (PHACE) experiments to test this hypothesis. The DAYCENT model results suggest that the major impact of the different treatments is to change the CDI value and that ecosystem responses can then be predicted if we know treatment impacts on CDI. Mean annual values of CDI will be calculated using the DAYCENT model and the observed soil water and temperature data and will then be correlated with treatment and yearly observed changes in annual ANPP, soil respiration rates, soil N mineralization, and plant N uptake. The observed PHACE data sets will also be used to test the model predictions that the combined impact of warming and elevated CO_2 treatments can be derived by adding the separate impacts of these treatments (see Fig. 5). This model prediction for a perennial grassland runs counter to observations from a California annual grassland showing that the impacts of CO_2 with other global change factors tended to be nonadditive (Dukes *et al.*, 2005).

Finally, it is worth noting that, in addition to not accounting for species shifts, daycent does not account for interactive effects of animal grazing on N cycling (Allard et al., 2003; Augustine & McNaughton, 2006). By logistical necessity, most field experiments do not consider the interactive effects of global change and defoliation, and most that do are limited in their involvement of the animal response to clipping (Owensby et al., 1999; Teyssonneyre et al., 2002; Morgan et al., 2004a). Although it is not a feasible option to introduce grazing animals in our present PHACE experiment because of its small ring-size, one of our objectives is to evaluate the impacts of grazing on CDI (Augustine & McNaughton, 2006), and to incorporate those dynamics into daycent to adequately describe the interactive effects of CO2 and grazing on C and N dynamics.

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References

Allard V, Newton PCD, Lieffering M, Clark H, Matthew C, Soussana J-F, Gray YS. 2003. Nitrogen cycling in grazed pastures at elevated CO_2: N returns by ruminants. *Global Change Biology* **9**: 1731–1742.

Augustine DJ, McNaughton SJ. 2006. Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems* **9**: 1–16.

Del Grosso SJ, Mosier AR, Parton WJ, Ojima DS. 2005. DAYCENT model analysis of past and contemporary soil N_2O and net greenhouse gas flux for major crops in the USA. *Soil Tillage and Research* **83**: 9–24.

Del Grosso SJ, Ojima DS, Parton WJ, Mosier AR, Peterson GA. 2002a. Regional assessment of net greenhouse gas fluxes from agricultural soils in the USA Great Plains under current and improved management. In: van Ham J, Baede APM, Guicherit R, Williams-Jacobs JGFM, eds. *Proceedings of the Third International Symposium on Non-CO_2 Greenhouse Gases.* Rotterdam, the Netherlands: Millpress, 469–474.

Del Grosso SJ, Parton WJ, Mosier AR, Hartman MD, Brenner J, Ojima DS, Schimel DS. 2001a. Simulated interaction of carbon dynamics and nitrogen trace gas fluxes using the DAYCENT model. In: Schaffer M, Ma L, Hansen S, eds. *Modeling carbon and nitrogen dynamics for soil management.* Boca Raton, FL, USA: CRC Press, 303–332.

Del Grosso SJ, Parton WJ, Mosier AR, Hartman MD, Keough CA, Peterson GA, Ojima DS, Schimel DS. 2001b. Simulated effects of land use, soil texture, and precipitation on N gas emissions using DAYCENT. In: Follett RF, Hatfield JL, eds. *Nitrogen in the environment: sources, problems, and management.* Elsevier Science Publishers, 413–431.

Dukes JS, Chiariello NR, Cleland EE, Moore LA, Shaw MR, Thayer S, Tobeck T, Mooney HA, Field CB. 2005. Responses of grassland production to single and multiple global environmental changes. *PLoS Biology* **3**: e319.

Dunne JA, Saleska SR, Fischer ML, Harte J. 2004. Integrating experimental and gradient methods in ecological climate change research. *Ecology* **85**: 904–916.

Eitzinger J, Parton WJ, Hartman MD. 2000. Improvement and validation of a daily soil temperature submodel for freezing/thawing periods. *Soil Science* **165**: 525–534.

Frolking SE, Mosier AR, Ojima DS, Li C, Parton WJ, Potter CS, Priesack E, Stenger R, Haberbosch C, Dörsch P, Flessa H, Smith KA. 1998. Comparison of N_2O emissions from soils at three temperate agricultural sites: simulations of year round measurements by four models. *Nutrient Cycling in Agroecosystems* **52**: 77–105.

Gholz HL, Wedin D, Smitherman S, Harmon ME, Parton WJ. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: Toward a global model of decomposition. *Global Change Biology* **6**: 751–765.

Hungate BA, Dukes JS, Shaw MR, Luo Y, Field CB. 2003. Nitrogen and climate change. *Science* **302**: 1512–1513.

Jolly WM, Nemani R, Running SW. 2005. A generalized, bioclimatic index to predict foliar phenology in response to climate. *Global Change Biology* **11**: 619–632.

Kelly RH, Parton WJ, Hartman MD, Stretch LK, Ojima DS, Schimel DS. 2000. Intra and interannual variability of ecosystem processes in shortgrass steppe. *Journal of Geophysical Research* **105**: 20 093–20 100.

Kimball BA. 2005. Theory and performance of an infra-red heater for ecosystem warming. *Global Change Biology* **11**: 2041–2056.

King JY, Mosier AR, Morgan JA, LeCain DR, Milchunas DG, Parton WJ. 2004. Plant nitrogen dynamics in shortgrass steppe under elevated at mospheric carbon dioxide. *Ecosystems* **7**: 147–160.

LeCain DR, Morgan JA, Mosier AR, Nelson JA. 2003. Soil and plant water relations, not photosynthetic pathway, primarily influence photosynthetic responses in a semi-arid ecosystem under elevated CO_2. *Annals of Botany* **92**: 41–52.

Long SP, Ainsworth EA, Leakey ADB, Nösberger J, Ort DR. 2006. Food for thought: Lower-than-expected crop yield stimulation with rising CO_2 concentrations. *Science* **312**: 1918–1921.

Luo Y, Hui D, Zhang D. 2006. Elevated CO_2 stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis. *Ecology* **87**: 53–63.

Luo Y, Su B, Currie WS, Dukes JS, Finzi A, Hartwig U, Hungate B, McMurtrie RE, Oren R, Parton WJ, Pataki DE, Shaw MR, Zak DR, Field CB. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience* **54**: 731–739.

Miglietta F, Peressotti A, Vaccari FP, Zaldei A, de Angelis P, Scarascia-Mugnozza G. 2001. Free-air CO_2 enrichment (FACE) of a poplar plantation: the POPFACE fumigation system. *New Phytologist* **150**: 465–476.

Milchunas DG, Mosier AR, Morgan JA, LeCain DR, King JY, Nelson JA. 2005. Elevated CO_2 and defoliation effects on a shortgrass steppe: Forage quality versus quantity for ruminants. *Agriculture, Ecosystems and Environment* **111**: 166–184.

Möllerstöm L. 2004. Modeling soil temperature and soil water availability in semi-arid Sudan: validation and testing. PhD thesis, Lund University, Lund, Sweden.

Morgan JA. 2002. Looking beneath the surface. *Science* **298**: 1903–1904.

Morgan JA, LeCain DR, Mosier AR, Milchunas DG. 2001. Elevated CO_2 enhances water relations and productivity and affects gas exchange in C_3 and C_4 grasses of the Colorado shortgrass steppe. *Global Change Biology* **7**: 451–466.

Morgan JA, Mosier AR, Milchunas DG, LeCain DR, Nelson JA, Parton WJ. 2004a. CO_2 enhances productivity of the shortgrass steppe, alters species composition, and reduces forage digestibility. *Ecological Applications* **14**: 208–219.

Morgan JA, Pataki DE, Körner C, Clark H, Del Grosso SJ, Grünzweig JM, Knapp AK, Mosier AR, Newton PCD, Niklaus PA, Nippert JB, Nowak RS, Parton WJ, Polley HW, Shaw MR. 2004b. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. *Oecologia* **140**: 11–25.

Mosier AR, Morgan JA, King JY, LeCain D, Milchunas DG. 2002. Soil–atmosphere exchange of CH_4, CO_2, NO_x and N_2O in the Colorado shortgrass steppe under elevated CO_2. *Plant and Soil* **240**: 201–211.

Mosier AR, Pendall E, Morgan JA. 2003. Effect of water addition and nitrogen fertilization on the fluxes of CH_4, CO_2, NO_x, and N_2O following five years of elevated CO_2 in the Colorado Shortgrass Steppe. *Atmospheric Chemistry and Physics* **3**: 1703–1708.

Nelson JA, Morgan JA, LeCain DR, Mosier AR, Milchunas DG, Parton WJ. 2004. Elevated CO_2 increases soil moisture and enhances plant water relations in a long-term field study in the semi-arid shortgrass steppe of Northern Colorado. *Plant and Soil* **259**: 169–179.

Norby RJ, Luo Y. 2004. Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multi-factor world. *New Phytologist* **162**: 281–293.

Owensby CE, Coyne PI, Ham JM, Auen LM, Knapp AK. 1993. Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO_2. *Ecological Applications* **3**: 644–653.

Owensby CE, Ham JM, Knapp AK *et al.* 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO_2. *Global Change Biology* **5**: 497–506.

Parton WJ, Hartman M, Ojima DS, Schimel DS. 1998. DAYCENT: Its land surface submodel: description and testing. *Global Planetary Change* **19**: 35–48.

Parton WJ, Holland EA, Del Grosso SJ, Hartman MD, Martin RE, Mosier AR, Ojima DS, Schimel DS. 2001. Generalized model for NO_x and N_2O emissions from soils. *Journal of Geophysical Research* **106**: 17403–17420.

Parton WJ, Schimel DS, Cole CV, Ojima DS. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal* **51**: 1173–1179.

Parton WJ, Silver WL, Burke IC, Grassens L, Harmon ME, Currie WS, King JY, Adair EC, Brandt LA, Hart SC, Fasth B. 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* **315**: 361–364.

Pendall E, Bridgham S, Hanson PJ, Hungate B, Kicklighter DW, Johnson DW, Law BE, Luo Y, Megonigal JP, Olsrud M, Ryan MG, Wan S. 2004. Below-ground process responses to elevated CO_2 and temperature: a discussion of observations, measurement methods, and models. *New Phytologist* **162**: 311–322.

Pendall E, King JY, Mosier AR, Morgan J, Milchunas D. 2005. Stable isotope constraints on net ecosystem production under elevated CO_2. In: Flanagan LB, Ehleriner JR, Pataki DE, eds. *Stable isotopes and biosphere–atmosphere interactions: processes and controls*. San Diego, CA, USA: Elsevier Academic Press, 182–198.

Pepper DA, Del Grosso SJ, McMurtrie RE, Parton WJ. 2005. Simulated carbon sink response of shortgrass steppe, tallgrass prairie and forest ecosystems to rising (CO_2), temperature and nitrogen input. *Global Biogeochemical Cycles* **19**: 1–20.

Reich PB, Hungate BA, Luo Y. 2006. Carbon–nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology and Systematics* **27**: 611–636.

Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* **126**: 43–562.

Saxton KE, Rawls WJ, Romberger JS, Papendick RI. 1986. Estimating generalized soil-water characteristics from texture. *Soil Science Society of America Journal* **50**: 1031–1036.

Shaw MR, Harte J. 2001. Response of nitrogen cycling to simulated climate change: differential responses along a subalpine ecotone. *Global Change Biology* **7**: 193–210.

Terri JA, Stowe LG. 1976. Climatic patterns and the distribution of C_4 grasses in North America. *Oecologia* **23**: 1–12.

Teyssonneyre F, Picon-Cochard C, Falcimagne R, Soussana J-F. 2002. Effects of elevated CO_2 and cutting frequency on plant community structure in a temperate grassland. *Global Change Biology* **8**: 1034–1046.

