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Simulating Carbon Dioxide Effects on Range Plant Growth and Water Use with GPFARM-Range Model

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ABSTRACT

Steadily rising carbon dioxide (CO_2) in the Earth's atmosphere has the potential to increase plant biomass production and reduce plant transpiration in semiarid rangelands. Incorporating results from field CO_2-enrichment experiments into process-based simulation models enhances our ability to project climate change impacts on these rangelands. In this study, we added algorithms for computing changes in plant biomass growth and stomatal resistance under elevated [CO_2] to the GPFARM-Range (Great Plains Framework for Agricultural Resource Management in Rangelands) model, a newly developed stand-alone software package for rangeland management. The GPFARM-Range model was tested against 5 yr (1997–2001) of soil water and plant biomass data from CO_2-enrichment (720 ppm) field experiments conducted in shortgrass steppe in northern Colorado. Simulated results for both peak standing crop biomass and soil water for both ambient and elevated [CO_2] treatments had a percent bias within ± 10%, Nash-Sutcliffe efficiency ≥ 0.5, and index of agreement > 0.70. The model also captured the observed trend of increased C_3 grass biomass and reduced plant transpiration under elevated [CO_2]. The model was used to evaluate the separate effectiveness of elevated [CO_2] on plant growth rate (C_3 grasses only) and stomatal resistance (both C_3 and C_4 grasses). Two separate simulations showed that increased growth rate and stomatal resistance due to elevated [CO_2] enhanced total plant biomass gain ($C_3 + C_4$) by 22% and 17%, respectively. The results indicate the algorithms used to simulate the impacts of elevated [CO_2] on range plant growth and water use are reliable and can be used to evaluate rangeland production for predicted increases in [CO_2]. However, further studies are necessary because the reduction in plant transpiration under elevated [CO_2] was underestimated, and increase in nitrogen use efficiency due to elevated [CO_2] is not included.

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Introduction

Increases in atmospheric [CO_2] have been found to enhance plant photosynthesis for C_3 grasses, forbs, and woody vegetation and to reduce plant transpiration (Morgan et al., 2004a, 2007; Owensby et al., 1999; Polley et al., 2003). The positive effect of increasing [CO_2] on photosynthesis is nearly exclusive to C_3 plant species because their photosynthetic apparatus remains unsaturated at present-day [CO_2], while photosynthesis of C_4 species is saturated, or nearly saturated, at present-day [CO_2] (Leakey et al., 2009). Most herbaceous species exhibit declines in leaf stomatal conductance with rising ambient [CO_2], with similar responses in C_3 and C_4 species (Wand et al., 1999). The combinations of both of these responses to increasing CO_2 tend to enhance water use efficiency of plant communities, as well as individual species, in particular under dry conditions (Morgan et al., 2004b, 2011). Although C_3 plants tend to be more sensitive to CO_2 than C_4 plants, both groups can exhibit significant production responses to rising [CO_2] under water-limited conditions (Leakey, 2009; Polley et al., 2003). The species-specific responses to CO_2 are certain to have profound impacts on the ecology of rangelands through shifts in plant species composition, altered forage quality, productivity, and seasonality of growth, all of which have important implications for livestock management.

Simulation models are promising tools for predicting how rising levels of atmospheric CO_2 and associated changes in climate will affect the ecology and productivity of rangelands. If well integrated with field observational investigations, these models could help to predict long-term impacts of climate change (Morgan, 2002). To do this, simulation models capable of describing plant functional group responses to [CO_2] are necessary to evaluate the complex responses of rangelands to climate change. Knowledge of forage growth responses to climate change is important for both tactical (short-term) and strategic (long-term) planning needed in ranch management operations, such as

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anticipating forage production and quality and matching livestock operations accordingly (Derner et al., 2012). Some efforts have examined rangeland forage, and occasionally livestock, production under predicted climate change. For example, Hanson et al. (1993) and Baker et al. (1993) simulated the effect of predicted climate change on forage and livestock in northeastern Colorado and across the United States, respectively, using the Simulation of Production and Utilization of Rangelands model coupled with Colorado Beef Cattle Production Model (SPUR-CBCPM). They reported both forage and animal production were more affected by temperature and precipitation than by elevated [CO_2], and the particular impacts (beneficial and detrimental) varied among regions across the country. Pepper et al. (2005) predicted a sustained C sink under rising [CO_2] in the shortgrass steppe in Colorado as simulated by the Generic Decomposition and Yield Model (G'DAY) and the daily time step version of the Century model (DAYCENT). The DAYCENT model also predicted increased soil water content, plant production, soil respiration, and nutrient mineralization for Colorado shortgrass steppe subjected to twice the present-day concentration of ambient CO_2 (Parton et al., 2007).

The Great Plains Framework for Agricultural Resource Management in Rangelands (GPFARM-Range) model developed by the USDA-Agricultural Research Service is primarily a forage model designed to simulate rangeland forage growth and animal performance in the Great Plains in response to weather, soil, and management to aid in strategic planning (Andales et al., 2005, 2006; Qi et al., 2012). This model is comprehensive in that it considers production and environmental impacts and can be linked to an economic module. The capability of the GPFARM-Range model in simulating rangeland forage growth and livestock development was demonstrated using field data collected near Cheyenne, Wyoming, United States, and Nunn, Colorado, United States (Andales et al., 2005). The GPFARM-Range model simulated the peak standing crop production in exclosure mixed-grass prairie plots with an Index of Agreement (d) value of 0.66 from 1983–2001 at the USDA-ARS High Plains Grasslands Research Station near Cheyenne, Wyoming, United States (Andales et al., 2006). Bryant and Snow (2008) reviewed nine models for pastoral or rangeland farm agro-ecosystems and reported that the GPFARM-Range model showed strengths in predicting forage production of five functional groups (warm-season grasses, cool-season grasses, legumes, shrubs, and forbs) and cow and calf live weights. The model was used to predict sandsage-bluestem production under different stocking rates at the USDA-ARS Southern Plains Experimental Range site near Fort Supply, Oklahoma, United States, with d value of 0.68 for the annual peak standing crop (Adiku et al., 2010). A recent study (Fang et al., 2014) showed that the GPFARM-Range model satisfactorily simulated peak standing crop biomass and stocking rate for a range farm in Wyoming.

Currently, plant and animal responses to [CO_2] are not simulated in the GPFARM-Range model. To address increasing interests in how climate change will affect semiarid rangelands, including the response to [CO_2], algorithms that simulate the direct responses of rangeland vegetation to [CO_2] are needed. Given empirical evidence that semiarid grasslands of the western Great Plains can respond to CO_2 through both photosynthetic and stomatal-induced water relations responses (Morgan et al., 2001, 2004a,b), we modified the plant growth and stomatal conductance processes in the GPFARM-Range model to respond to changes in atmospheric [CO_2]. The objectives of this exercise are to separately model CO_2 effects via plant growth rate and the stomatal or transpirational responses for various functional groups, as well as to evaluate the performance of this new version of GPFARM-Range model against field CO_2 enrichment data. This is important because few rangeland management models have such a function. For example, the SPUR2 model can only simulate CO_2 impacts on plant growth rate but does not take transpirational water use into account. This is an essential way to evaluate the importance of the plant growth response and the indirect water relations response, as well as consequences for C_3 and C_4 plants.

Materials and Methods

GPFAR-Range Model Overview

The Great Plains Framework for Agricultural Resource Management (GPFARM) decision support software was released by USDA-ARS in the early 2000s for strategic planning and to evaluate alternative management for farms and ranches in the U.S. Northern Great Plain area (Ascough et al., 2002). The stand-alone GPFARM-Range model was initially developed in Fortran to simulate forage growth and cow-calf production on native rangelands and later converted to a component-based modular model in Java, under the Object Modeling System (OMS) framework at the USDA-ARS. Infiltration from rainfall or snow melt is computed by the Green-Ampt approach, and water redistribution in the soil profile is simulated by Darcy's law. The upper boundaries, potential soil evaporation and plant transpiration, are estimated by the double layer model of Shuttleworth and Wallace (1985), an enhancement of the Penman-Monteith equation (Farahani & Ahuja, 1996). The forage module is phenology based, driven by heat units (growing degree days) for five functional groups of plant species: warm-season grasses, cool-season grasses, legumes, shrubs, and forbs. The weight gain or loss of cows and calves is calculated by their demand for forage, availability of forage and supplements, and forage intake. The forage and animal modules are described in detail in Andales et al. (2005; 2006).

Recently a carbon-nitrogen cycle module from the N Leaching and Environmental Analysis Package (NLEAP) was added into the GPFARM-Range model (Qi et al., 2012). Potential nitrogen uptake was computed by predicted daily shoot and root growth and CN ratios. Actual N uptake is limited by the total available NH_4-N and NO_3-N in each soil layer. Because water and temperature are the major limiting stress factors for the growth of native range plants, and in most cases rangeland soil nitrogen release is a function of soil moisture, the model assumes nitrogen availability does not affect plant growth in this model.

Modeling [CO_2] Impact on Plant Growth

The Michaelis-Menton–based empirical approach has been successfully used in crop models like the DSSAT-CERES to simulate the effect of CO_2 on growth of C_3 plants (Allen et al., 1987; Ko et al., 2010; Peart et al., 1989). To simulate CO_2 effects on grass biomass, we used the equation:

$$V[CO_2] = \frac{V_{max} \times [CO_2]}{K_m + [CO_2]} \quad (1)$$

where [CO_2] is the CO_2 concentration in the air (ppm); V[CO_2] is the biomass growth rate (kg·d^{-1}) as function of the concentration of [CO_2]; V_{max} is the maximum potential biomass growth rate (kg·d^{-1}); and K_m (ppm) is the value of [CO_2] at which the $V = 0.5\ V_{max}$.

From the FACE experiments at two CO_2 concentrations for fully irrigated spring wheat at Maricopa, Arizona from 1992–1993 to 1996–1997, average of six values over four seasons, it is found that (Ko et al., 2010):

$$V(550ppm) = 1.119V(370ppm) \quad (2)$$

Solving Eqs. (1) and (2), we can obtain $K_m = 178.1$. We assume that this value of K_m for spring wheat, a C_3 grass, also applies to C_3 grass species in the rangelands. In our study, the baseline [CO_2] concentration was 360 ppm; therefore [CO_2] scalar on relative growth rate (ELEVCO2_Growth) under elevated concentration can be expressed as:

$$ELEVCO2_Growth = \frac{V[CO_2]}{V(360)} = \frac{[CO_2]}{360} \times \frac{178.1 + 360}{178.1 + [CO_2]} \quad (3)$$

The plant growth component of the GPFARM-Range model was documented in Andales et al. (2006). Daily biomass accumulation of five

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functional groups (C_4 grasses, C_3 graminoids, forbs, legumes, and shrubs) in the GPFARM-Range model is computed by the product of potential growth rate, current live biomass, environmental fitness factors including temperature and soil water, and a mass effect parameter determined by community structure and animal intake. The effect of elevated [CO_2] on plant growth (ELEVCO2_Growth) for C_3 grasses and forbs was incorporated into the growth rate through:

$$\frac{dW}{dt} = GrRate \times W \times EVP \times MassEffect \times ELEVCO2_Growth \quad (4)$$

where *dW* is the daily change in above-ground biomass (kg·ha^{-1}), *dt* is the calculation time step (d), *GrRate* is the potential relative growth rate (kg·kg^{-1}·d^{-1}), *W* is above-ground live biomass (kg·ha^{-1}), *EVP* is the environmental fitness factor (0–1), and *ELEVCO2_Growth* is the growth factor impacted by elevated [CO_2]. The environmental factor is the product of water (EWP) and temperature (ETP) stresses for range plant growth. The EWP is a threshold response curve as a function of the ratio of actual evapotranspiration to potential evapotranspiration. The ETP function is an empirical bell-shaped function using variables of minimum, maximum, and optimum temperatures. *MassEffect* is a factor to reflect the impact of community structure and animal intake on plant growth:

$$massEffect = 1 - \frac{net\ Prim\ Prod + sForDietIn}{1.092 \times (forgeMax \times pop\ \ Prop)} \quad (5)$$

where *netPrimProd* is the net primary production (kg·ha^{-1}) and *sFortDietIn* is the total biomass intake by different group of animals (kg·ha^{-1}). *ForageMax* is an estimated potential total biomass of all five functional groups under optimum condition (kg·ha^{-1}), and *popProp* is the population proportion of each functional groups (0–1).

Modeling [CO_2] Impact on Stomatal Resistance

Leaf conductance of 80 data sets for a wide range of plant species was examined by Morison (1987) at [CO_2] ranging from 330–660 ppm. The basic finding from the study was that leaf conductance at 660 ppm was reduced by 40% when compared with 330 ppm. Furthermore, this relationship was found to be linear between 330 and 660 ppm and apparently does not differ between C_3 and C_4 grasses (Morison & Gifford, 1983). Although not tested, we assumed the linear relationship was still valid when [CO_2] exceeded 660 ppm. Noting that stomatal resistance is the inverse of leaf conductance, the [CO_2] scalar on stomatal resistance for all functional groups can be rewritten from Eq. (16) by Stockle et al. (1992), which was proposed to modify the Environmental Policy and Integrated Model (EPIC) model (Williams et al., 1989):

$$ELEVCO2_Rs = \frac{1}{\left(1.4 - 0.4 \times \frac{C}{330}\right)} \quad (6)$$

where *ELEVCO2_Rs* is the impact factor of [CO_2] on stomatal resistance (unitless) and *C* is the [CO_2] in the air (ppm). We subsequently added this impact factor *ELEVCO2_Rs* into the Shuttleworth and Wallace equation (1985) to compute potential plant transpiration in the GPFARM-Range model:

$$\lambda PT = \frac{\Delta[(R_n - G) - R_{nsub}] + \rho c_p (VPD_0)/r_a^c \times f}{\Delta + \gamma[1 + (r_a^c \times ELVCO2_Rs)/r_a^c]} \quad (7)$$

where λPT is the latent heat of potential plant transpiration (MJ·m^{-2}·d^{-1}), Δ is the slope of saturation vapor pressure curve at air temperature (kPa·°C^{-1}), R_n is net solar radiation above the canopy (MJ·m^{-2}·d^{-1}), *G* is the soil heat flux (MJ·m^{-2}·d^{-1}), R_{nsub} is the net solar radiation below the canopy (MJ·m^{-2}·d^{-1}), ρc_p is the volumetric heat capacity of air (MJ·m^{-3}·°C^{-1}), VPD_0 is air vapor pressure deficit at the mean canopy height (kPa), r_a^c is the bulk boundary layer resistance of the canopy (s·m^{-1}), r_s^c is the bulk stomatal resistance of the canopy (s·m^{-1}), γ is the psychrometric constant (kPa·°C^{-1}), *f* is time conversion constant (1.1574×10^{-5} d·s^{-1}), and *ELEVCO2_Rs* is the impact factor of [CO_2] on canopy stomatal resistance. λPT was subsequently converted to PT by multiplying a conversion factor of 0.408 mm MJ^{-1}·m^2 and partitioned into each soil layer in accordance to root distribution. Transpirational water efflux was partitioned among different soil layers and given a weight based on root distribution:

$$AT_i = \begin{cases} PT_i & PT_i \le AW_i \\ AW_i & PT_i > AW_i \end{cases} \quad (8)$$

where AT_i is the actual transpirational water use in ith soil layer (mm·d^{-1}), PT_i is the potential plant transpiration partitioned into *i*th layer (mm·d^{-1}), and AW_i is plant available water in the *i*th soil layer(mm). Plant available water is defined as:

$$AW_i = \begin{cases} 0 & S_e < 0 \\ \left(\theta - \theta_{wp}\right) d_i & S_e \ge 0.5 \\ \left(\theta - \theta_{wp}\right)(2S_e) d_i & S_e < 0.5 \end{cases} \quad (9)$$

$$S_e = \frac{\theta - \theta_{wp}}{\theta_{fc} - \theta_{wp}} \quad (10)$$

where θ is the soil water content (cm^3·cm^{-3}), θ_{wp} is the permanent wilting point (cm^3·cm^{-3}), d_i is the depth of the *i*th soil layer, θ_{fc} is the field capacity (cm^3·cm^{-3}), and S_e is relative soil water content. Total AT is the summation of AT_i. The rooting depth is a user-defined value for each functional group, and available water is difference between current volumetric water content and permanent wilting point for each soil layer.

Field Experiment Data Set

A field study designed to investigate the effect of atmospheric [CO_2] on plant growth in Open Top Chambers (OTC) was conducted at the Central Plains Experimental Range (CPER) at Nunn, Colorado, United States (40°50′N, 104°43′W, 1 650 m elevation) from 1997–2001 (Morgan et al., 2001, 2004a). A randomized complete block design with three blocks based on vegetation composition and two CO_2 treatments per block was used. The OTC were 3.8 m high and 4.5 m in diameter, with the elevated treatment maintained at a daytime [CO_2] of 720 ± 15 ppm and the ambient treatment maintained at a daytime ambient [CO_2] of approximately 360 ppm. The plant community was dominated by C_3 grasses. During the growing season, soil moisture in the chambers was monitored weekly using Time Domain Reflectometry for the top 0–15 cm and Neutron probe (Troxler Model 4301) for 15–100 cm. The neutron probes were calibrated for the Remmit fine sandy loam at this site. Above-ground live biomass was sampled in late July each year, the approximate time of peak standing biomass, to estimate net primary production of above-ground plant biomass (Morgan et al., 2007). Cool season grasses (C_3) found in this site were *Pascopyrum smithii* and *Stipa comata,* and warm season grass (C_4) was mainly *Bouteloua gracilis*. Weather data, including daily precipitation, air temperature, solar radiation, wind speed, and relative humidity were measured at the site. Leaf gas exchange was measured for the three dominant species listed earlier on selected dates during the growth period in each year. The measurements included leaf-level transpiration, stomatal resistance, and the ratio of leaf internal to external [CO_2]. Further details of this field study can be found in Morgan et al. (2001; 2004a).

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Modeling Procedure

The modified GPFARM-Range model was tested for C_3 and C_4 grasses only in this study. Forbs, which comprise about 12% biomass of site vegetation, are a diverse number of species whose representation varies considerably among years and about which we have less knowledge regarding their physiological responses to [CO_2]; they were therefore not included in the analysis. Most plant growth parameters, such as maximum, optimum, and minimum temperature (°C) for growth; growing degree-days (GDDs) for emergence, maturity, and senescence; and maximum growth rate were adopted from studies conducted by Andales et al. (2006) and Qi et al. (2012) (Table 1). The average stomatal resistance (r_s^c) for plants under ambient [CO_2] (360 ppm) was set equal to the average measured stomatal resistance for all C_3 and C_4 plants (r_s; 149 s·m^{-1}) at this site. Saturated soil hydraulic conductivity, saturated water content, and residual water content were from Rawls et al. (1982, Table 2) according to the measured soil texture. The soil at this experiment site is a Remmit fine sandy loam (Ustollic camborthids). Parameters adjusted in this study were maximum total forage production of all functional groups *(forageMax)*, proportion of each functional group in the total population *(propPop)*, and Brooks and Corey (1964) soil hydraulic parameters.

Modeling was conducted with a typical two-stage procedure: calibration and validation. For the model calibration and validation, some modelers use one treatment for calibration and the rest for validation, and some use all treatments in 1 yr as calibration and other years for validation (Ma et al., 2012). In our case, there were only two treatments; therefore using the former strategy would give a larger data set for calibration. Data from all 5 yr of the ambient [CO_2] treatment were used for model calibration, and data from the elevated [CO_2] treatment were used to validate the model. For the calibration, the observed weather data were used and the [CO_2] was set to 360 ppm. All plant growth parameters except for *forageMax* and *propPop* were adopted from Andales et al. (2006) and Qi et al. (2012). The trial-error method was used to estimate *forageMax* and *propPop* based on the model evaluation statistics listed below to determine the smallest difference between simulated and observed annual peak standing crop biomass in each year. This resulted in an estimated *forageMax* of 1 900 kg·ha^{-1} for all C_3 and C_4 grasses. The proportions of C_3 and C_4 grasses were calibrated to 0.73 and 0.27, respectively, to get the best fit of the combined biomass for all grasses. Major plant growth parameters are given in Table 1.

The Brooks-Corey hydraulic parameters of air-entry pressure (h_e) and pore size distribution index (λ) were also calibrated using the trial-error method by comparing simulated soil water storage with measured values from the ambient [CO_2] treatment. Because soil moisture and biomass interacted, during calibration the *forageMax* and Brooks-Corey parameters were adjusted in several iterations. Calibrated Brooks-Corey parameters, along with measured texture and other soil hydraulic parameters from Rawls et al. (1982), are listed in Table 2. Calibrated pore size distribution index (λ) values were high but within the range given by Rawls et al. (1982) due to high sand content in the soil (66–79%).

Model validation used the elevated [CO_2] (720 ppm) data and all parameter values estimated from the calibration procedure except for initial soil water content. The simulated results in peak standing crop biomass and soil water content under elevated [CO_2] were compared with field observed data.

Table 1
Plant growth parameters used for calibrating the ambient [CO_2] (360 ppm) treatment.

Parameter	Definition	C_4 grasses	C_3 grasses
forageMax (kg·ha^{-1})[1]	Maximum forage production	1 900[3]	
RST (s·m^{-1})[2]	Mean stomatal resistance	149[4]	
propPop[1]	Proportion of population from each functional group	0.27	0.73
MaxGrowthRate (kg · kg^{-1}·day^{-1})	Maximum relative growth rate of shoot	0.22A[5]	0.19[1]
Tmax (°C)	Maximum temperature for growth	45A	36A
Topt (°C)	Optimum temperature for growth	30A	20A
Tmin (°C)	Minimum temperature for growth	5A	0A
matureGDD (°Cday)	Growing degree-days to maturity	1500Q	2500Q
SenGDD (°Cday)	Day senescence begins	1400Q	1800Q

[1] Calibrated.
[2] Measured.
[3] Total maximum forage production biomass (C_3 + C_4 grasses).
[4] Average stomatal resistance was 149 s·m^{-1} for both C_3 and C_4 grasses.
[5] Parameters denoted with "A" are from Andales et al. (2006) and those from "Q" are from Qi et al. (2012).

Statistics

Ma et al. (2012) listed a number of model evaluation statistics, and in this study we used percent bias (PBIAS), Nash-Sutcliffe efficiency (NSE), index of agreement (D), and root mean squared deviation (RMSD):

$$PBIAS = \frac{\sum_{i=1}^{n}(P_i - O_i) \times 100}{\sum_{i=1}^{n} O_i} \quad (11)$$

$$NSE = 1 - \frac{\sum_{i=1}^{n}(O_i - P_i)^2}{\sum_{i=1}^{n}\left(O_i - \overline{O}\right)^2} \quad (12)$$

$$D = 1 - \frac{\sum_{i=1}^{n}(O_i - P_i)^2}{\sum_{i=1}^{n}\left(|O_i - \overline{O}| + |P_t - \overline{O}|\right)^2} \quad (13)$$

$$RMSD = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(P_i - O_i)^2} \quad (14)$$

where O_i is the ith observed value, P_i is the ith simulated value; $\overline{O}$ is the mean of observed values, and n is the total number of observations. Model performance was considered "acceptable" when the PBIAS was within ± 15%, NSE ≥ 0.50, and D ≥ 0.70 (Ma et al., 2012; Moriasi et al., 2007).

Results and Discussion

Calibration Results Using Data from Ambient [CO_2]

Calibration results of peak standing crop biomass using the ambient [CO_2] treatment data were considered acceptable for all model statistics (Fig. 1). The 5-yr mean simulated peak standing crop biomass of all grasses (i.e., C_3 + C_4) was within ± 5% error (PBIAS) of the 5-yr mean observed biomass (1 022 vs. 1 053 kg·ha^{-1}, respectively), with PBIAS = −2.9%, NSE = 0.68, and D = 0.89 (Fig. 1c). RMSD was 196 kg·ha^{-1}, about 19% of the observed average and within ± 1 mean standard deviation of observed biomass. The 5-yr mean simulated peak standing crop biomass was within ± 5% error of the 5-yr mean observed biomass for C_3 grasses (653 simulated vs. 666 observed kg·ha^{-1}, Fig. 1a) and C_4 grasses (378 simulated vs. 388 observed kg·ha^{-1}; Fig. 1b). The model simulated C_3 grass production (PBIAS = −1.9%, NSE = 0.78, and D = 0.93, Fig. 1a) slightly better than C_4 grasses (PBIAS = 5.0%, NSE = 0.57, and D = 0.79; Fig. 1b). This was partly attributed to the annual variance in plant community structure. For unknown reasons, in 1997 the observed C_4 grasses comprised 50% of the total biomass, while in other years C_4 grasses only accounted for 31% to 38% of the

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Table 2
Soil hydraulic parameters used in the GPFARM-Range model.

Depth	Bulk density	Clay	Sand	Saturated hydraulic conductivity	Saturated water content	Residual water content[1]	Air-entry pressure[2]	Pore size distribution index
cm	$g \cdot cm^{-3}$	%	%	$cm \cdot h^{-1}$	$cm^3 \cdot cm^{-3}$	$cm^3 \cdot cm^{-3}$	cm	
0–5	1.45	9.0	78.0	5.00	0.437	0.035	25	0.85
5–15	1.40	10.3	77.0	5.00	0.437	0.035	25	0.80
15–30	1.40	10.7	74.0	5.00	0.453	0.033	20	0.80
30–45	1.40	11.3	79.0	2.59	0.453	0.033	20	0.80
45–60	1.35	16.7	75.0	2.59	0.453	0.033	20	0.80
60–90	1.35	20.3	66.0	1.32	0.453	0.033	20	0.70
90–100	1.35	20.3	66.0	1.32	0.453	0.033	20	0.70

Note: Bulk density and clay and sand content were site-specifically measured means; saturated hydraulic conductivity, saturated water content, and residual water content were from Rawls et al. (1982). Air-entry pressure and pore size distribution index for Brooks-Corey equation were calibrated using observed soil water data.
[1] Water content at which the gradient of soil water change with respect to pressure becomes zero.
[2] Pressure at which the soil starts draining.

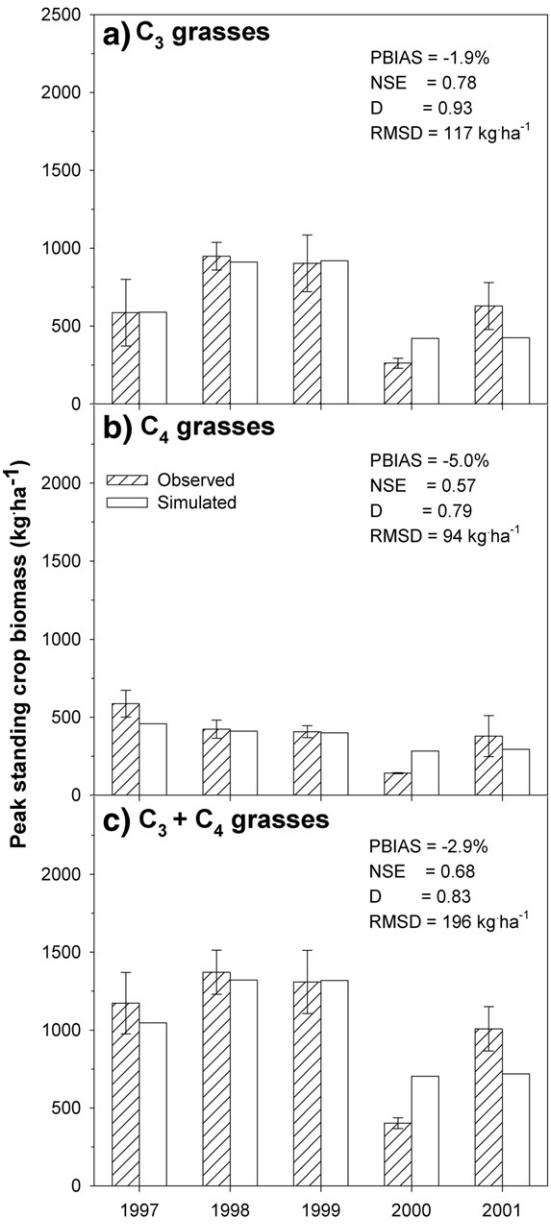

Fig. 1. Calibrated results comparing observed and simulated peak standing crop biomass under ambient [CO_2] (360 ppm) conditions for a) C_3 (cool-season) grasses, b) C_4 (warm-season) grasses, and c) $C_3 + C_4$ grasses. Error bars represent ± 1 standard deviation. D indicates index of agreement; NSE, Nash-Sutcliffe model efficiency; PBIAS, percent bias; RMSD, root mean squared deviation.

total biomass and may partly explain the undersimulation of C_4 and oversimulation of C_3 grass biomass. Simulated peak standing biomass was less accurately simulated in 2000 and 2001 than the other years, with peak standing biomass overestimated for both C_3 and C_4 grasses in 2000 and underestimated in 2001. Both 2000 and 2001 were relatively drier years, with annual precipitation of 349 and 340 mm, respectively, as compared with 504, 422, and 557 mm for 1997, 1998, and 1999, respectively. The higher observed peak standing biomass in 2001 was presumably because more rainfall occurred in July while in 2000 the majority of the rain fell after August. The model does not respond well to late-season rainfall events (Andales et al., 2005). The temperature was similar in both years with total growing degree day (0°C base) of 3 029, and 2 995°C day from 1 March to 31 September in 2000 and 2001, respectively.

Simulated and observed soil water during the growing season in the top 100 cm are presented in Fig. 2. For the ambient [CO_2] treatment (360 ppm), which was used for calibration, soil water was simulated by the GPFARM-Range model satisfactorily with PBIAS = 8%, NSE = 0.50, and D = 0.83. RMSD of the simulation was 2.3 cm, 22% of the average observed. The mean standard deviation of the observed soil water was as low as 0.98 cm, equivalent to 9% of the average observed. The RMSD was within ± 2.5 standard deviation of the observed soil water.

Validation Results Using Data from Elevated [CO_2]

Validation results for peak standing crop biomass used the elevated [CO_2] treatment data (Fig. 3). The 5-yr mean simulated peak standing crop biomass of all grasses (i.e., $C_3 + C_4$) was within ± 5% error of the 5-yr mean observed biomass (1 380 vs. 1 346 $kg \cdot ha^{-1}$, respectively), with PBIAS = 2.6%, NSE = 0.87, and D = 0.96 (Fig. 3c). RMSD was 153 $kg \cdot ha^{-1}$, about 12% of the observed average and within ± 1 mean standard deviation of observed biomass. The 5-yr mean simulated peak standing crop biomass (1 005 $kg \cdot ha^{-1}$) was within ± 5% error of the 5-yr mean observed biomass (980 $kg \cdot ha^{-1}$) for C_3 grasses (Fig. 3a) and for C_4 grasses (376 simulated vs. 366 observed $kg \cdot ha^{-1}$; Fig. 3b). Unlike the calibrated results for ambient [CO_2], the model predicted C_4 grass production (PBIAS = 2.6%, NSE = 0.72, and D = 0.90, Fig. 3b) slightly better under elevated [CO_2] than for C_3 grasses (PBIAS = 2.5%, NSE = 0.70, and D = 0.89; Fig. 3a). Further, simulated biomass for 2000 and 2001 more closely matched the observed biomass in the elevated [CO_2] treatment than was observed in the ambient [CO_2] treatment calibration results. Under elevated [CO_2], simulated results were better in 2000 for both C3 and C4 grasses than in the ambient conditions used in the calibration (i.e., simulated results were within 1 standard deviation [SD] of the observed in the validated results).

Soil water during the growing season for the top 100 cm in the elevated [CO_2] treatment was simulated in an acceptable manner with PBIAS = 3%, NSE = 0.68, and D = 0.88 (Fig. 2). RMSD was 2.0 cm, which was 16% of the observed mean soil water across all years. The ratio of RMSD to average standard deviation for soil water simulated

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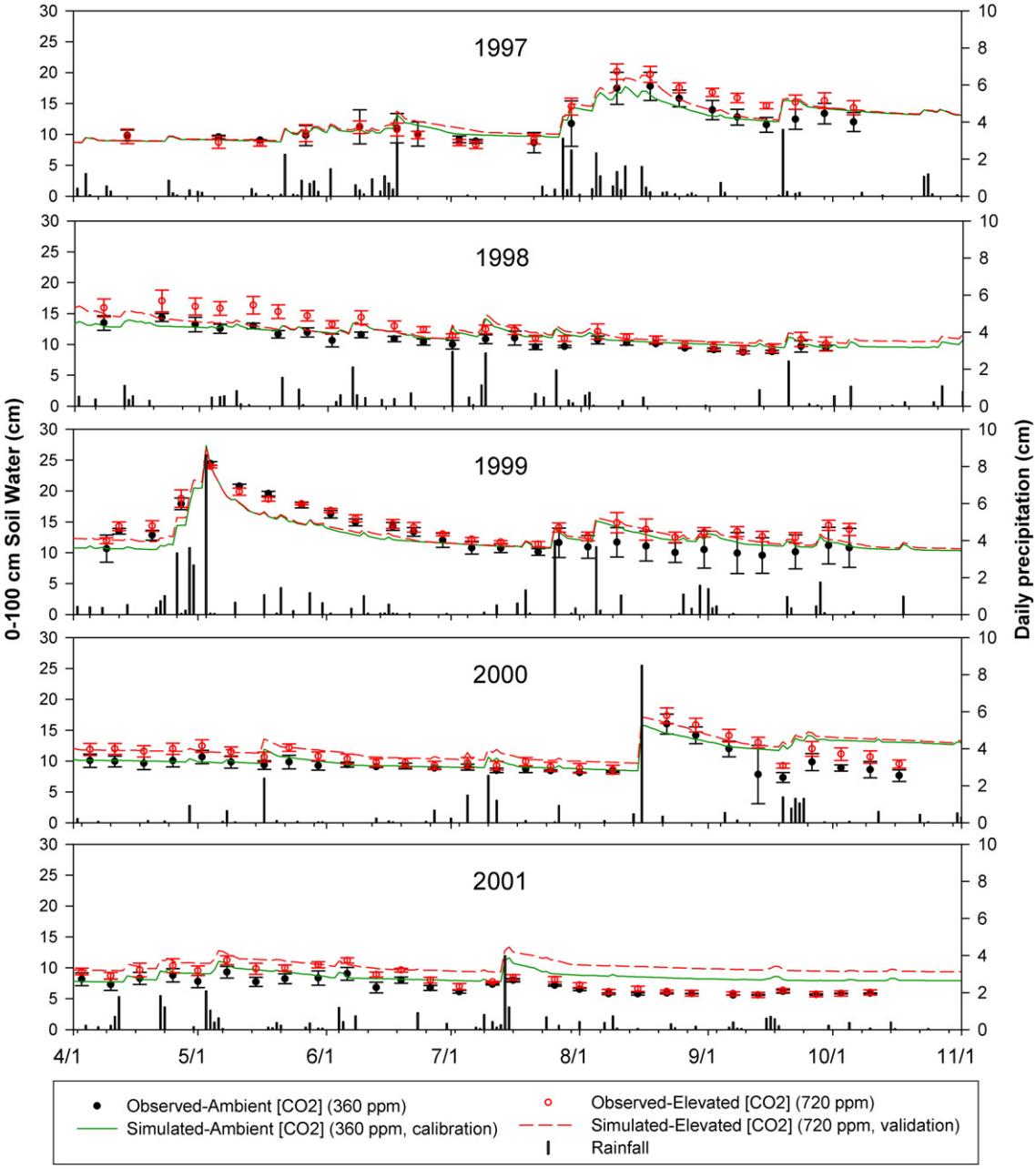

Fig. 2. Observed and simulated soil water storage in 0–100 cm soil for ambient (PBIAS = 8%, NSE = 0.50, D = 0.83, and RMSD = 2.3 cm) and elevated (PBIAS = 3%, NSE = 0.68, D = 0.88, and RMSD = 2.0 cm) [CO_2] conditions. Error bars represent ± 1 standard deviation. D indicates index of agreement; NSE, Nash-Sutcliffe model efficiency; PBIAS, percent bias; RMSD, root mean squared deviation.

in the elevated [CO_2] treatment was 2.5, indicating that RMSD was simulated within ± 2.5 mean standard deviation of observed values.

Evaluation of the [CO_2] Impact Algorithms

The modified model simulated the observed trend of peak standing above-ground biomass well under ambient and elevated [CO_2] treatments. Simulated mean total peak standing crop biomass (C_3 and C_4) over 5 yr increased from 1 062 kg·ha^{-1} under ambient [CO_2] to 1 400 kg·ha^{-1} under elevated [CO_2] treatments, within 4% error from the observed values of 1053 versus 1 346 kg·ha^{-1} for the two [CO_2] treatments, respectively. The percentage of simulated increase in total production of all grasses (C_3 and C_4) with elevated [CO_2] was 32%, close to the observed increase of 28%. The simulated and observed increase in peak standing crop due to elevated CO_2 was 47% versus 49% for C_3 grasses, and −5% versus 1% for C_4 grasses. When increasing [CO_2] from 350 to 650 ppm, McKeon et al. (2009) similarly reported that forage production would increase by about 25% across most arid and semiarid zones in Australia using the GRASP model. In our study, simulated peak standing crop biomass of C_3 grasses increased by 335 kg·ha^{-1} under elevated [CO_2] (720 ppm) compared with ambient [CO_2] (360 ppm), close to the observed difference of 314 kg·ha^{-1}. For C_4 grasses, the model showed a 1% increase (378 kg·ha^{-1} for ambient vs. 381 kg·ha^{-1} for elevated [CO_2]) in peak standing crop biomass due to doubling [CO_2], and the observed data showed 5% reduction (388 vs. 366 kg·ha^{-1}).

Although the modified model simulated soil water in an acceptable manner and successfully duplicated the trend of soil water increase due to elevated [CO_2], simulated difference in soil water storage between elevated and ambient [CO_2] conditions was 36% less than the

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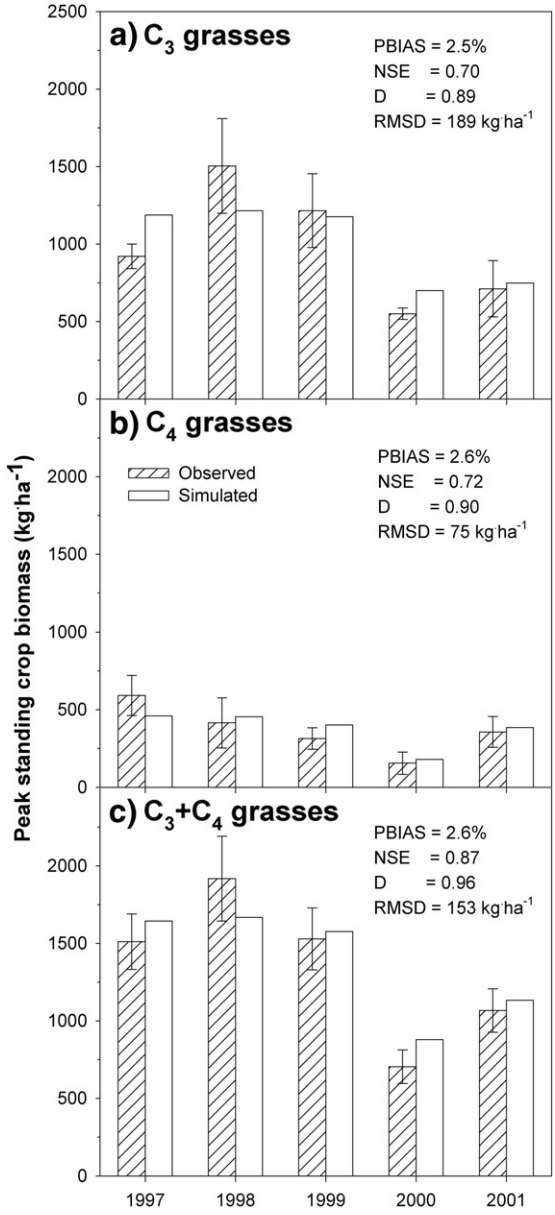

Fig. 3. Validation results comparing observed and simulated peak standing crop biomass under elevated [CO_2] (720 ppm) conditions for a) C_3 (cool-season) grasses, b) C_4 (warm-season) grasses, and c) C_3+C_4 grasses. Error bars represent ± 1 standard deviation. D indicates index of agreement; NSE, Nash-Sutcliffe model efficiency; PBIAS, percent bias; RMSD, root mean squared deviation.

observed difference. The observed increase in soil water under elevated [CO_2] was 1.4 cm over the 5 yr (1997–2001). However, simulated soil water under the elevated [CO_2] was 0.9 cm more than under ambient [CO_2]. The fact that the GPFARM-Range model underestimated the increase in soil water under elevated [CO_2] could be attributed to underestimating the reduction of plant transpiration under elevated [CO_2]. Simulated evaporation and transpiration during the growing season from April to August is listed in Table 3. The simulated actual transpiration under elevated [CO_2] was 12.4 cm in the main growing season, only 6.7% less than under ambient [CO_2]. However, the observed transpiration was reduced by 24% and 20% for the *P. smithii* and *B. gracilis* leaves during 1997–2000 (LeCain et al., 2003). Simulated total potential transpiration for C_3 and C_4 grasses was reduced from 43.3 cm under ambient [CO_2] to 34.6 cm (20%) under elevated [CO_2], while McKeon et al. (2009) reported that the reductions in potential transpiration when doubling [CO_2] from 350–700 ppm were 32% and

Table 3
Simulated evaporation and transpiration for the growing season (April through August) under ambient and elevated [CO_2] conditions.

Year	Rainfall	Ambient [CO_2] (360 ppm)				Elevated [CO_2] (720 ppm)			
		Pot. E	Pot. T	Act. E	Act. T	Pot. E	Pot. T	Act. E	Act. T
	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)	(cm)
1997	37.5	38.2	34.2	15.9	14.8	37.2	27.5	15.2	12.9
1998	27.6	35.9	43.3	14.4	14.5	32.2	37.2	13.5	15.7
1999	45.3	31.2	45.7	13.3	16.1	31.9	34.6	14.5	14.3
2000	17.7	43.9	45.5	8.3	11.0	45.5	35.6	8.9	9.9
2001	26.0	42.5	47.9	12.1	9.9	41.9	38.0	12.6	9.4
Average	30.8	38.4	43.3	12.8	13.3	37.7	34.6	12.9	12.4

Act. E indicates simulated actual evaporation; Act. T, simulated actual transpiration; Pot. E, potential evaporation; Pot. T, potential transpiration.

40% for C_3 and C_4 grasses, respectively, in a simulation for rangeland in Australia.

Underpredicting the reduction in potential plant transpiration indicated that the potential transpiration computed by the Shuttleworth-Wallace equation (Eq. (7)) was not sensitive to stomatal resistance of the canopy under the scenarios in our study. The observed increase in stomatal resistance was approximately 38% and 56% for *P. smithii* and *B. gracilis*, respectively (computed from Table 4 in LeCain et al., 2003), and this led to 24% and 20% reductions in observed actual transpiration. However, using the impact factor in Eq. (6), when stomatal resistance factor for the elevated [CO_2] treatment increased by 83% in comparison with ambient [CO_2] (*ELEVCO2_Rs* = 1.04 for [CO_2] at 360 ppm and 1.90 for [CO_2] at 720 ppm), we only get 20% decrease in simulated potential transpiration and subsequently 6.7% reduction in simulated actual transpiration. It indicates that the Shuttleworth-Wallace equation, or the actual transpiration estimation method (Eqs. (8) and (9)), may need further testing under increasing [CO_2] for computing plant transpiration. Although there are opportunities for improving the GPFARM-Range model in simulating the transpiration response to elevated [CO_2], the newly added algorithms nevertheless captured the differences in range plant growth and the trend of reducing transpiration under elevated [CO_2].

Table 4
Simulation scenarios for separating effects of [CO_2] on plant growth (photosynthesis) and stomatal resistance (water use efficiency).

				Elevated [CO_2] (kg·ha^{-1})		
				Scenario		
Functional group	Yr	Ambient [CO_2] (kg·ha^{-1})	Plant growth component Stomatal resistance component	1[1] ON ON	2 ON OFF	3 OFF ON
C_3 grasses	1997	681		1 190	1 197	971
	1998	929		1 222	1 156	1 082
	1999	940		1 194	1 166	969
	2000	439		728	605	645
	2001	434		765	625	550
	Average	*685*		*1020*	*950*	*843*
		(Baseline)		*49%*	*39%*	*23%*
C_4 grasses	1997	449		460	446	459
	1998	417		454	439	454
	1999	399		399	402	398
	2000	304		203	101	296
	2001	320		387	322	399
	Average	*378*		*381*	*342*	*401*
		(Baseline)		*1%*	*−10%*	*6%*
Total		**1 062**		**1 400**	**1 292**	**1 245**
		(Baseline)		**32%**	**22%**	**17%**

ON indicates the component in the model was turned on; OFF, the component in the model was turned off.

[1] Scenario was the validation run previously presented in Figs. 1 and 3.

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Separated Effects of Growth Rate and Stomatal Resistance

Using the modified GPFARM-Range model, we wanted to assess the proportion of changes in peak standing crop biomass that could be attributed to increased plant biomass growth or reduced stomatal resistance, which resulted in increased water use efficiency. To do this we switched on/off each of these newly added two components in the model (Table 4). For example, turning off the [CO_2] impacts on plant growth in the model but leaving the stomatal resistance algorithms functioning, the simulated change in biomass would be a result of increased water use efficiency. When having both the plant growth and stomatal resistance algorithms turned on (scenario 1, Table 4), the simulated total peak standing crop (sum of C_3 and C_4 grasses) under ambient [CO_2] (1 062 kg·ha^{-1}) was increased by 32% on average under elevated conditions (1 400 kg·ha^{-1}). It suggested that C_3 and C_4 grasses were not evenly favored when doubling [CO_2]. Peak standing crop biomass of C_3 grasses increased by 49%, while biomass of C_4 grasses increased only by 1% (scenario 1 in Table 4). This was because C_3 grasses benefited from both increased biomass accumulation and water use efficiency while C_4 grasses benefited only from increased water use efficiency. In the lowest rainfall year of 2000, the simulated increase of C_3 biomass due to enhanced photosynthesis and water use efficiency under elevated [CO_2] was 289 kg·ha^{-1}, comparable with the increases in 1998, 1999, and 2001 when annual precipitation was approximately 50% to 150% higher than 2000.

When the CO_2 impacts on stomatal resistance algorithms were turned off (scenario 2), the simulated peak standing crop biomass increased by 22% under elevated conditions (i.e., from 1 062 kg·ha^{-1} at 360 ppm to 1 292 kg·ha^{-1} at 720 ppm) due to [CO_2] stimulation of plant growth for C_3 grasses. When the CO_2 impacts on plant growth algorithms were turned off (scenario 3), the simulated peak standing crop biomass increased by 17% under elevated conditions (i.e., from 1 062 kg·ha^{-1} at 360 ppm to 1 245 kg·ha^{-1} at 720 ppm) due to increased water use efficiency under elevated [CO_2] for both C_3 and C_4 grasses. From this analysis, we estimated that stomatal resistance responses and photosynthetic responses influenced the increase in the total peak standing crop biomass to a similar magnitude. The C_4 biomass would have been reduced by 10% if elevated [CO_2] only had favored plant growth of C_3 grasses (scenario 2); however, C_4 biomass would have increased by 6% if [CO_2] had only increased stomatal resistance of C_3 and C_4 leaves (scenario 3). These simulations showed that under elevated [CO_2], the loss of C_4 biomass (presumably due to the competition with C_3 grasses with enhanced growth potential) was offset by increased water use efficiency of C_4 grasses. When the impacts of [CO_2] on plant growth and stomatal resistance were combined (scenario 1), C_4 grasses under increased [CO_2] did not lose biomass as in Scenario 2 but rather had slightly increased biomass by 1% due to the benefit from higher water use efficiency.

Comparison with Other Models

Simulated increase in total biomass under elevated [CO_2] is much higher in our study than that by Hanson et al. (1993). Using the modified SPUR model, Hanson et al. (1993) concluded that increase in total biomass in eastern Colorado was only 4.1% (852.2 vs. 818.3 kg·ha^{-1}) when doubling [CO_2], while in our study the increase would be 32%. There are two major reasons for the inconsistence of these simulations by GPFARM-Range and the SPUR model. Firstly, the structure of plant community in Hanson et al. (1993) was different from our study. It was dominated by C_4 grasses in Hanson et al. (1993) while in our study the majority was C_3 grasses. High proportion of C_4 grass would lead to less total biomass accumulation for the whole community under elevated [CO_2] because C_4 species are nearly CO_2 saturated. Secondly, in the SPUR model, only the impact of [CO_2] on plant growth rate (Eq. (1)) was incorporated—not the stomatal resistance. As we test the separate effects, these two components almost evenly influenced biomass accumulation. The SPUR model may underestimate the increase in biomass accumulation because it neglected the water reserved by the reduced transpiration of plants under elevated [CO_2].

A more recent simulation by Pepper et al. (2005) showed that, under doubled [CO_2], net primary production increase in northeastern Colorado shortgrass steppe would be 19% and 25%, respectively, as simulated by G'DAY and DAYCENT models. Our simulation results were closer to Pepper et al. (2005) than Hanson et al. (1993) because impacts of [CO_2] on both plant growth and transpiration were coded in G'DAY and DAYCENT and our model GPFARM-Range. However, the fact that our simulated increase was still higher than Pepper et al. (2005) was mainly because the dominant plant was C_3 grasses in our study but C_4 grasses in Pepper et al. (2005).

Parton et al. (2007) employed the same data to simulate biomass accumulation using the DAYCENT model. In Parton et al. (2007), the coefficient of determination (R^2) of linear regression of predicted versus observed total biomass was 0.43 for the ambient treatment and 0.47 for the elevated [CO_2] treatment; in our study the R^2 values were 0.70 and 0.91, respectively. DAYCENT generally underestimated biomass for elevated [CO_2] treatment, and the likely reason was that DAYCENT does not separate range plants into different functional groups and thus could not predict the species shift to C_3 grasses (Parton et al., 2007). In our study, the observed proportion of C3 grass increased from 63% under ambient [CO_2] to 73% under elevated [CO_2]; and the GPFARM-Range simulation showed that C3 proportion increased from 64% to 73%. It suggests that this GPFARM-Range model can mimic the shift of warm and cool season grasses.

Limitations of the Model and Data

One of the limitations of the model we found, as discussed earlier, was that the Shuttleworth-Wallace equation could not reflect the magnitude of stomatal resistance impact on plant transpirational water use. Furthermore, in comparison with the Free-Air CO_2 Enrichment (FACE) experiment, the Open Top Chamber (OTC) method may result in a more stable [CO_2] concentration in the air but would lead to reductions in solar radiation and wind speed and increases in temperature, relative humidity, and rainfall due to interception by the walls. Meta-analysis of many past studies suggested that OTC would produce a stronger [CO_2] effect than open-field FACE setting (Macháčová, 2010). In our case, if the experiment were conducted with the FACE approach, the observed reduction in ET may not be as significant as it was. Therefore the less effectiveness of the Shuttle-Wallace equation in predicting ET reduction due to elevated [CO_2] might be true for grasses growing in larger open space. Although there is no comparison of ET between OTC and FACE, we would expect less ET in OTC due to less energy received from the sun.

Five out of the six lessons learned from FACE were applicable to range plants (Leakey et al., 2009). This modified GPFARM-Range model has addressed three of them: under elevated [CO_2], plant growth increases; water use decreases; and photosynthesis for C_4 plant is not stimulated but can be indirectly enhanced under dry conditions. The impact of N use efficiency as affected by CO_2 is not incorporated in the model yet, given the findings that rangeland plant biomass was limited by N as well, in particular under a relatively high level of precipitation (Hooper & Johnson, 1999; LeBauer & Treseder, 2008). In addition, the stomatal resistance should be adjustable for each functional groups, rather than only one average value for all the groups. They will be major considerations for further development of this model.

Management Implications

Algorithms adopted from the SPUR2 and EPIC models to quantify elevated [CO_2] impacts on range plant growth and stomatal resistance were added to the GPFARM-Range model. These approaches were tested against a 5-yr field [CO_2] enrichment data set with elevated [CO_2] of

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720 ppm versus ambient concentration of 360 ppm at a shortgrass steppe site in Colorado. Differences in peak standing crop biomass and soil moisture between elevated and ambient [CO_2] treatments were adequately captured by the model according to our model evaluation statistics. Therefore the algorithms used in this study seem reliable in predicting [CO_2] impacts on range plant biomass accumulation and water use. The GPRARM-Range model can capture the trend of species shift to C_3 grasses. This model can be used to estimate integrated impact of climate change, including changes in precipitation, temperature, and atmospheric CO_2 concentration, on range plant growth and stocking rate. The increasing trend of peak standing crop under elevated CO_2 does not suggest that rangelands in northern Colorado may sustain a higher stocking rate in the future because of the lowest digestibility of the CO_2-induced high biomass species.

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