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Feedback from plant species change amplifies CO_2 enhancement of grassland productivity

H. WAYNE POLLEY*, VIRGINIA L. JIN*† and PHILIP A. FAY*

*Grassland, Soil & Water Research Laboratory, US Department of Agriculture, Agricultural Research Service, Temple, Texas 76502, USA, †Agroecosystem Management Research Unit, US Department of Agriculture, Agricultural Research Service, Lincoln, Nebraska 68583, USA

Abstract

Dynamic global vegetation models simulate feedbacks of vegetation change on ecosystem processes, but direct, experimental evidence for feedbacks that result from atmospheric CO_2 enrichment is rare. We hypothesized that feedbacks from species change would amplify the initial CO_2 stimulation of aboveground net primary productivity (ANPP) of tallgrass prairie communities. Communities of perennial forb and C_4 grass species were grown for 5 years along a field CO_2 gradient (250–500 μL L^{-1}) in central Texas USA on each of three soil types, including upland and lowland clay soils and a sandy soil. CO_2 enrichment increased community ANPP by 0–117% among years and soils and increased the contribution of the tallgrass species *Sorghastrum nutans* (Indian grass) to community ANPP on each of the three soil types. CO_2-induced changes in ANPP and *Sorghastrum* abundance were linked. The slope of ANPP-CO_2 regressions increased between initial and final years on the two clay soils because of a positive feedback from the increase in *Sorghastrum* fraction. This feedback accounted for 30–60% of the CO_2-mediated increase in ANPP on the upland and lowland clay soils during the final 3 years and 1 year of the experiment, respectively. By contrast, species change had little influence on the ANPP-CO_2 response on the sandy soil, possibly because *Sorghastrum* increased largely at the expense of a functionally similar C_4 grass species. By favoring a mesic C_4 tall grass, CO_2 enrichment approximately doubled the initial enhancement of community ANPP on two clay soils. The CO_2-stimulation of grassland productivity may be significantly underestimated if feedbacks from plant community change are not considered.

Keywords: aboveground net primary productivity, C_4 grasses, plant species composition, soil texture, soil water content, subambient CO_2, tallgrass prairie

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Introduction

Experimental enrichment of atmospheric CO_2 usually increases the productivity of grassland and other herbaceous vegetation (Morgan *et al*., 2004b). Rarely is the initial stimulation of growth maintained, however. Growth responses to CO_2 may diminish with time for a variety of reasons, ranging from down-regulation of photosynthetic capacity (Crous *et al*., 2010) to a progressive decrease in N recycling that leads to greater N limitation of growth (Luo *et al*., 2004; Reich *et al*., 2006). Less frequently, community growth responses to CO_2 increase with time (Stöcklin *et al*., 1998). The CO_2 sensitivity of productivity changes because plant responses to CO_2 are regulated by a set of biotic and abiotic variables that are sensitive to feedbacks from CO_2 effects on plant growth (Polley *et al*., 2011b). These variables, which include soil resource supply and the functional composition of plant communities, interact dynamically with ecosystem processes to determine the sensitivity of community productivity to CO_2. Feedbacks from CO_2- and climate-caused changes usually dampen CO_2 effects on community productivity (Leuzinger *et al*., 2011; Polley *et al*., 2011b). Positive feedbacks on CO_2 or climate responses are fewer, but may occur most frequently when mediated through changes in plant species composition or relative abundances (defined herein as 'species change'). For example, a shift to greater C_4 dominance enhanced the positive effects of warming on aboveground net primary productivity (ANPP) of tallgrass prairie by increasing growth per unit of plant N (Niu *et al*., 2010).

There is ample evidence that CO_2 enrichment alters species contributions to grassland productivity (Leadley *et al*., 1999; Edwards *et al*., 2001; Niklaus *et al*., 2001; Polley *et al*., 2003; Morgan *et al*., 2004a), but little documentation that species change enhances the community ANPP-CO_2 response. Why? We suggest five general

Correspondence: H. Wayne Polley, tel. + 254 770 6629, fax + 254 770 6561, e-mail: wayne.polley@ars.usda.gov

reasons. First, feedbacks from species change simply may not have been considered when analyzing experimental data. Second, experiments may have been terminated before species feedbacks were fully expressed. Species change and any resulting feedbacks on the community ANPP-CO_2 response may not be evident in short-term, even multi-year, experiments in which CO_2 effects on resource levels develop slowly. Changes in N cycling that lead ultimately to a change in the ANPP-CO_2 response may require years to manifest (Gill *et al.*, 2002, 2006; Hungate *et al.*, 2004; Jin & Evans, 2007), as would species feedbacks on community ANPP, for example. Third, responsive species may not have been present in plant communities either because the plant species pool was limited or species change was inhibited by management activities or other factors. Fourth, species feedbacks will be difficult to detect when the ANPP-CO_2 relationship differs widely among years because of variation in other factors that regulate plant growth or CO_2 response. Year-to-year variability in environmental factors, such as the amount of photosynthetically active radiation and precipitation (Owensby *et al.*, 1999; Morgan *et al.*, 2004b; Kubiske *et al.*, 2006), could mask species effects on the ANPP-CO_2 relationship. Fifth, species change at elevated CO_2 simply may not have become large enough to significantly affect the ANPP-CO_2 relationship. How large must the shift in species be? The answer depends partly on the magnitude of functional differences among co-occurring species and on whether species shifts result from opposing changes in the productivity of dominant species or simply an increase in productivity of one or more species. The greater the differences in response to CO_2 or CO_2-caused changes in water and N availability among species, the greater, likely, will be the change in ANPP-CO_2 response per unit of change in species relative abundances.

A positive feedback of species change on the ANPP-CO_2 response implies that the increase in community productivity per unit of increase in CO_2 will be greater following species change than before it. We have shown that increasing CO_2 from subambient to elevated concentrations increased the contribution of the tallgrass species *Sorghastrum nutans* (L.) Nash (Indian grass) to ANPP of tallgrass prairie assemblages grown on three soil types of strongly contrasting texture (Polley *et al.*, 2012). The shift to greater *Sorghastrum* abundance during the first 4 years of CO_2 treatment resulted from a CO_2-caused increase in soil water content and was most strongly expressed on the two soils on which the per-unit effect of CO_2 on soil water was greatest. Herein, we test the prediction that the increase in *Sorghastrum* fraction amplified the amount by which CO_2 stimulated ANPP during 5 years of treatment. We hypothesized that feedback effects of *Sorghastrum* on ANPP, like the magnitude of species change, would be greatest for the soils for which the water-savings effect of CO_2 enrichment was greatest. We assumed that *Sorghastrum* is more productive than species that declined in relative abundance under the wetter conditions at high CO_2.

Materials and Methods

CO_2 chambers

We used unique, elongated field chambers to expose assemblages of tallgrass prairie species to a continuous gradient in CO_2 spanning pre-industrial to elevated concentrations (Polley *et al.*, 2008; Fay *et al.*, 2009). The Lysimeter CO_2 gradient (LYCOG) facility is located in central Texas, USA (31°05′ N, 97°20′ W) at the Grassland, Soil & Water Research Laboratory. It consists of two transparent, tunnel-shaped chambers each 1.2 m wide and tall and 60 m long, aligned parallel along a north-south axis. Each chamber is divided into 10 consecutive compartments each 5 m long. Aerial growth of chambered vegetation is enclosed in a transparent polyethylene film which transmits >90% of incident irradiance with minimal effects on spectral quality. Chambers depend upon photosynthesis during daylight and upon respiration at night to create CO_2 gradients. Air introduced into chambers during daylight is progressively depleted of CO_2 by photosynthesizing plants as it is moved by blowers toward the outlet of the system. The direction of air flow is reversed at night, and respiration by the enclosed ecosystem progressively increases the CO_2 concentration of chamber air. Desired CO_2 concentration gradients are maintained by automatically varying the rate of air flow through chambers in response to changes to photosynthesis (daylight) or respiration rates (night). During daylight, pure CO_2 is injected into air introduced to the south end of one chamber (elevated chamber) to elevate CO_2 to 500 $\mu L\ L^{-1}$. The CO_2 level is depleted to 370 $\mu L\ L^{-1}$ at the north end of the chamber. Ambient air is introduced into the south end of the second chamber (subambient chamber) to initiate an ambient to subambient CO_2 gradient (370 – 250 $\mu L\ L^{-1}$). Night-time CO_2 levels are regulated at about 130 $\mu L\ L^{-1}$ above daytime values along each chamber. Air temperature and vapor pressure deficit are regulated near ambient values by cooling and dehumidifying air at 5-m intervals along chambers. CO_2 treatments have been maintained each growing season from early April through October since CO_2 control was initiated in 2006.

Soil monoliths

We installed four steel boxes containing intact soil monoliths (each 1 m wide and long × 1.5 m deep) beneath each of the 20 5-m long compartments. Three soil types of contrasting physical and hydrological properties are represented. All are located in the Blackland Prairie region of central Texas. Soils include an upland clay Mollisol from the Austin series (Udorthentic Haplustolls), a lowland clay Vertisol from the Houston Black series (Udic Haplusterts), and a sandy loam Alfisol from the Bastsil (or Bastrop) series (Udic Paleustalfs). Two monoliths of each of two soil types were randomly placed beneath each 5-m long compartment. Twelve compartments contain two monoliths each of the Mollisol and Vertisol (40–45% and 49–55% clay content, respectively; Fay *et al*., 2009). Remaining compartments contain two monoliths of the Alfisol (60–73% sand content, 0–50 cm depth) and two monoliths of either the Mollisol or Vertisol.

Perennial species characteristic of tallgrass prairie in central Texas were transplanted into 60 monoliths in June 2003, 3 years before CO_2 control was initiated. Eight plants of each of four C_4 grass species [*Bouteloua curtipendula* (Michx.) Torr. (side-oats grama), *Schizachyrium scoparium* (Michx.) Nash (little bluestem), *Sorghastrum nutans*, *Tridens albescens* (Vasey) Wooton & Standl. (white tridens)] and three forb species [*Salvia azurea* Michx. Ex Lam. (pitcher sage), *Solidago canadensis* L. (Canada goldenrod), and the legume *Desmanthus illinoensis* (Michx.) MacMill. ex B.L. Rob. & Fernald (Illinois bundleflower)] were transplanted into each monolith (total density = 56 plants m^{-2}; hereafter referenced by genus). Monoliths received ambient precipitation for most of the period prior to CO_2 treatment (Polley *et al*., 2012). We excluded precipitation after initiating CO_2 control in 2006 and irrigated each monolith to simulate the average of growing season precipitation in central Texas (560 mm). Water input was scheduled to mimic the typical seasonal pattern of precipitation during 2007 and 2009, with a maximum during spring and minimum during late summer (August–September). This pattern was reversed in 2008 by adding larger amounts of water in summer than spring. The seasonal total of irrigation was applied in equal monthly increments during 2006. Volumetric soil water content was measured weekly (bi-weekly in 2006) to 0.9 m depth in the center of each monolith with a neutron probe.

ANPP was estimated by clipping vegetation in each monolith to 5 cm height at the end of each growing season, near the time of peak biomass, beginning in 2005 the year prior to CO_2 treatment. Peak biomass provides a reasonable estimate of ANPP in this system because aboveground tissues represent current-year growth only (standing tissues are removed at harvest each year) and all species, with the exception of two minor components of the community, *Desmanthus* and *Tridens* (1.9–8.4% and 0.2–3.3% of peak biomass, respectively), continue growth through autumn. At harvest, plants from each monolith were sorted by species. Harvested tissues were weighed after oven drying for 72 h at 60 °C. Community ANPP was calculated by summing species-specific values of ANPP for each monolith and year. No fertilizer was added. To minimize effects of harvesting on element cycling, harvested material was returned to the monolith from which it was removed prior to the next growing season. Plant material was shredded with a wood chipper to simulate effects of late-season mowing before it was returned.

We used between-year change in the proportional contribution of the dominant species, the grass *Sorghastrum*, to community ANPP (Δ fraction) as an index of vegetation change. Change was calculated for each monolith by subtracting the dominant's contribution to total community production in 1 year from its contribution to production in a preceding year.

The mean CO_2 concentration to which each monolith was exposed was calculated using the linear relationship between CO_2 during daylight and distance along chambers (Fay *et al*., 2009). CO_2 was used as the independent variable in regression analyses with between-year changes in community ANPP, species-specific ANPP, and species fractions.

The CO_2 response of community ANPP is regulated by multiple, often inter-correlated, factors (Polley *et al*., 2011b). We used a statistical modeling approach, structural equation modeling (SEM), to evaluate causal relationships among interacting variables that together affected ANPP (Shipley, 2000; Grace, 2006). SEM with observed variables (path modeling) was used to partition the net effect of CO_2 on ANPP into a direct effect and indirect effects mediated through changes in soil water content and the S*orghastrum* fraction of community ANPP for each soil type (Supporting Information, Fig. S1). The SEM model included direct paths from each variable to ANPP and indirect paths from CO_2 to ANPP through soil water content and the *Sorghastrum* fraction. Bivariate relationships between modeled variables were linear to slightly curvilinear. The ln-transformation of variables rarely improved the linearity of these relationships and did not alter the general relationships among variables that were derived using SEM. We used AMOS 4.0 software (SmallWaters Corp., Chicago, IL, USA) to fit the SEM model to data from each year and soil type. Each path coefficient was divided by its standard error to assess significance. Coefficients with $P < 0.10$ were considered significant. To obtain a significant fit to data for the different soil types, we used a slightly different SEM model for the sandy soil vs. clay soils (Fig. S1). Non-significant paths in the models used for each soil type were retained in final models. Significance in most statistical tests of treatment effects is demonstrated by rejecting a null hypothesis. The reverse is true when testing the adequacy of the full SEM (Shipley, 2000). The hypothesized relationship among variables in the SEM is considered to be consistent with data when the probability level of the statistical test (chi-squared statistic) is greater than the chosen significance level (typically, $P = 0.05$).

Results

Temporal trends in ANPP and Sorghastrum relative abundance

CO_2 enrichment increased both community ANPP (Fig. 1) and the contribution of *Sorghastrum* to community productivity on all three soil types (Fig. 2). Linear increases in community ANPP ranged from 0 (not significant) to 173 g m^{-2} per 100 $\mu L\ L^{-1}$ rise in CO_2 among soils and years, and were larger following 3–5 years of CO_2 exposure than during the initial 2 years of treatment for all soil types (Table 1). At these rates of ANPP increase, community ANPP rose by 45–117%

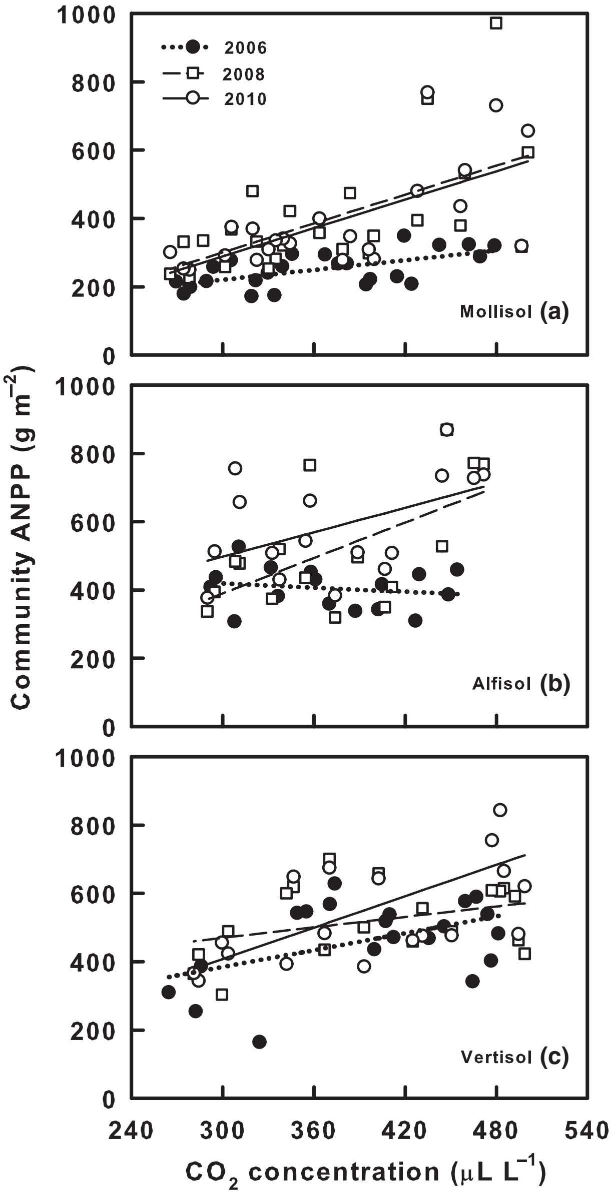

Fig. 1 Relationships between the ANPP of prairie communities (community ANPP) and CO$_2$ concentration for each of three soil types for the first, third, and fifth years of treatment (2006, 2008, 2010). Lines are linear regression fits. See Table 1 for regression statistics.

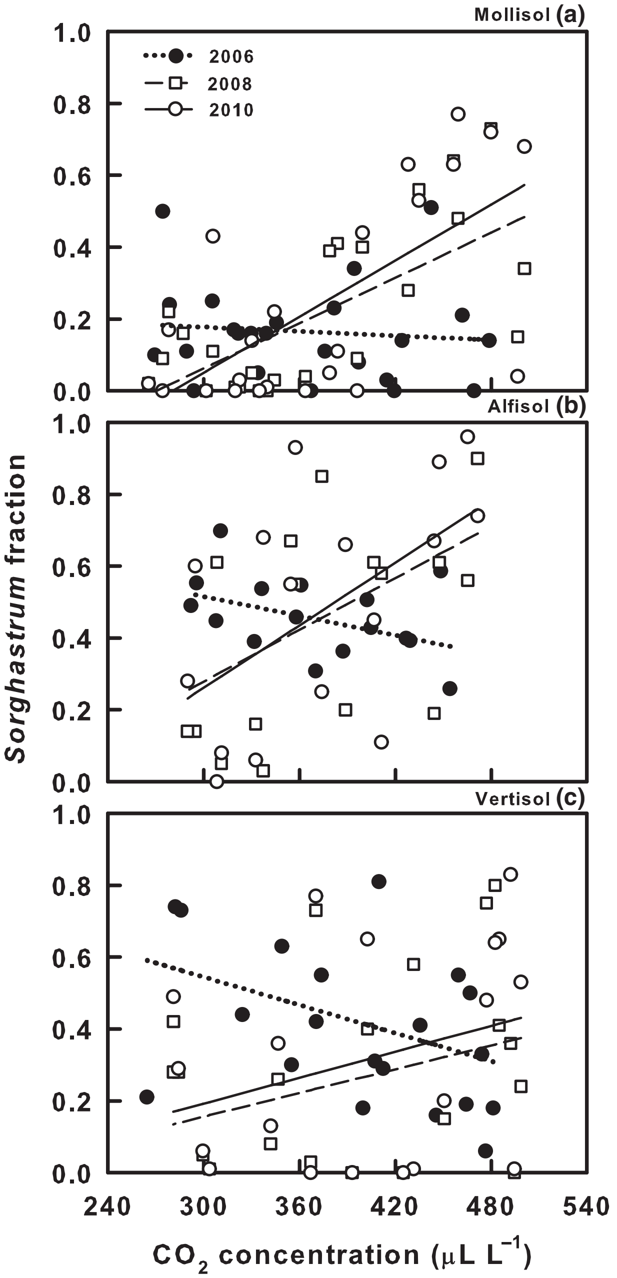

Fig. 2 Relationships between the fractional contribution of *Sorghastrum* to ANPP of prairie communities and CO$_2$ concentration for each of three soil types for the first, third, and fifth years of treatment (2006, 2008, 2010). Lines are linear regression fits. See Table 1 for regression statistics.

(Mollisol), 0–98% (Alfisol), and 0–81% (Vertisol) from 280 to 480 μL L^{-1}. The *Sorghastrum* fraction varied widely among monoliths along the CO$_2$ gradient in a given year (Fig. 2), but slopes of fraction-CO$_2$ regression relationships were greater following 2–3 years of exposure than during the initial year of treatment for Mollisol and Alfisol soils (Table 1). The *Sorghastrum* fraction was a significant positive function of CO$_2$ for the Vertisol in 2009 only, but was negatively correlated to CO$_2$ following the first year of treatment (2006). Consequently, CO$_2$ enrichment increased the contribution of *Sorghastrum* to community ANPP between the pretreatment year and fifth year of CO$_2$ exposure on all soils (Fig. S2).

CO$_2$ enrichment increased the *Sorghastrum* fraction of community productivity by increasing *Sorghastrum* ANPP and, on the Alfisol soil, reducing the amount by

Table 1 Linear regressions relating community ANPP and the *Sorghastrum* fraction of ANPP to CO_2 concentration for each of three soil types and each year of CO_2 treatment. Regression slopes represent the change in ANPP or *Sorghastrum* fraction per 100 μL L^{-1} increase in CO_2 concentration

	ANPP (g m^{-2})				*Sorghastrum* fraction				
Soil/Year	Intercept	Slope	r^2	P-value	Intercept	Slope	r^2	P-value	n
Mollisol									
2006	77.95	47.52	0.34	0.002	0.237	−0.021	0	0.65	24
2007	3.70	72.68	0.52	<0.0001	−0.219	0.089	0.28	0.006	24
2008	−122.31	140.93	0.33	0.002	−0.568	0.212	0.46	0.0002	24
2009	−172.87	158.51	0.51	<0.0001	−0.803	0.268	0.56	<0.0001	23
2010	−126.78	138.49	0.43	0.0004	−0.730	0.261	0.42	0.0005	23
Alfisol									
2006	478.64	−19.98	0	0.51	0.785	−0.088	0.12	0.1	16
2007	−80.94	126.76	0.53	0.0008	−0.656	0.282	0.32	0.01	16
2008	−130.47	173.33	0.31	0.01	−0.442	0.241	0.22	0.04	16
2009	−26.95	170.38	0.47	0.003	−0.383	0.239	0.22	0.04	16
2010	139.04	119.41	0.19	0.05	−0.609	0.294	0.26	0.03	16
Vertisol									
2006	137.32	82.31	0.18	0.04	0.934	−0.135	0.14	0.06	20
2007	116.82	66.10	0.16	0.04	0.036	0.048	0	0.44	20
2008	316.00	51.15	0.08	0.12	−0.175	0.114	0.05	0.17	19
2009	370.71	42.70	0.04	0.2	−0.413	0.178	0.22	0.03	19
2010	−50.91	152.96	0.35	0.005	−0.168	0.122	0.05	0.19	19

which the combined ANPP of remaining species increased between the pretreatment (2005) year and fifth year of exposure (Fig. 3). CO_2 enrichment reduced the 5-year change in the combined ANPP of all species other than *Sorghastrum* on the Alfisol largely by reducing the increase in ANPP of two subdominant grasses, *Bouteloua* and *Schizachyrium* (Table S2). CO_2 enrichment also reduced the amount by which *Bouteloua* ANPP increased during 5 years on the Mollisol, but the combined ANPP of all species other than the dominant *Sorghastrum* was not affected by CO_2 on this upland clay soil (Fig. 3). Together, *Sorghastrum* and *Bouteloua* accounted for an average of 0.60 and 0.73 of community productivity on the clay Mollisol and Vertisol soils, respectively, following 5 years of CO_2 treatment. By contrast, *Sorghastrum* and *Schizachyrium* together accounted for a mean 0.89 of ANPP on the sandy Alfisol after 5 years.

The shared tendency for ANPP and the *Sorghastrum* fraction to increase more with time at elevated than subambient CO_2 resulted in a positive correlation between changes in ANPP and the *Sorghastrum* fraction for each soil type (Fig. 4). These correlations between cumulative changes in community properties imply a direct causal linkage between the *Sorghastrum* fraction and ANPP sensitivity to CO_2. However, both ANPP and the *Sorghastrum* fraction varied with CO_2 (Table 1), evidence that ANPP was regulated directly and indirectly by CO_2, the indirect effect mediated partly through among-year change in the *Sorghastrum* fraction (i.e., Δ fraction = *Sorghastrum* fraction$_{(t)}$ − *Sorghastrum* fraction$_{(t\text{-}1\ldots n)}$). In addition, community ANPP during any given year likely was sensitive to the current *Sorghastrum* fraction, as determined partly by the initial composition of vegetation, rather than to CO_2-mediated change in the fraction only. We used structural equation modeling to determine the contribution of CO_2-caused shifts in both the *Sorghastrum* fraction and soil water content to the response of community ANPP to CO_2.

Structural equation models

SEM models adequately fit data from each year of CO_2 treatment and soil type (${\chi^2}_3 = 0.2$–6.3, $P = 0.97$–0.10) and explained 36–54%, 3–56%, and 9–38% of the variance in ANPP for the Mollisol, Alfisol, and Vertisol soils, respectively.

Mollisol. CO_2 enrichment increased community ANPP on the Mollisol soil during each year of treatment, with linear increases of 48–159 g m^{-2} per 100 μL L^{-1} increase in CO_2 (Fig. 5). The CO_2 effect on community ANPP was 2-fold greater during the final 3 years than first 2 years of treatment because CO_2 increased ANPP by increasing the *Sorghastrum* fraction. The pathway

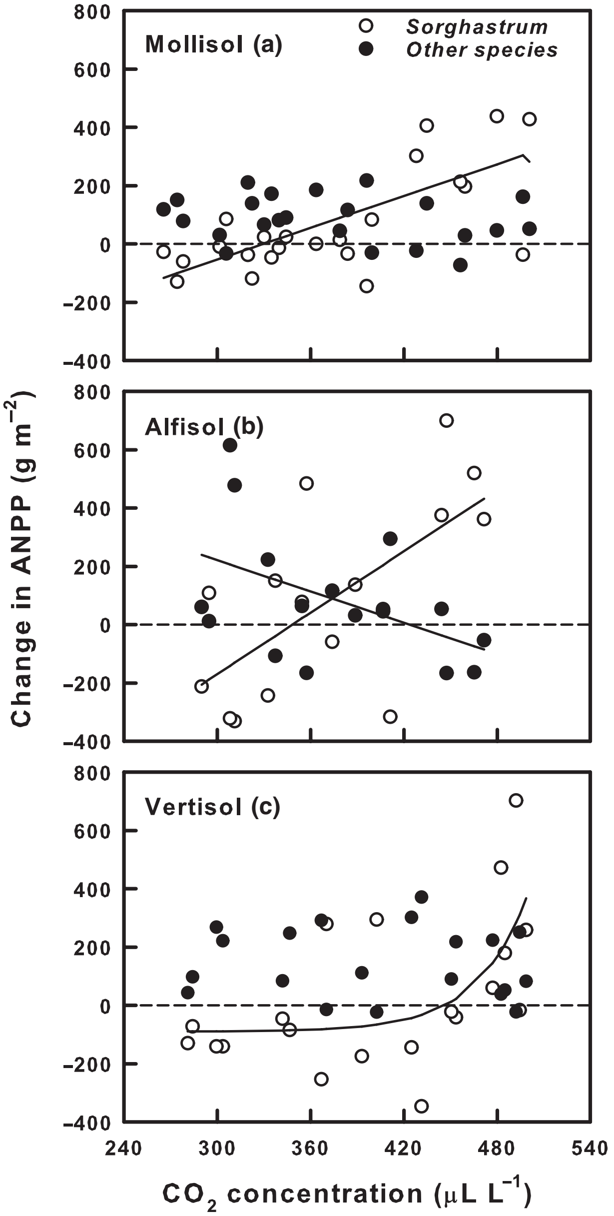

Fig. 3 Relationships between the 5-year change in ANPP of the dominant grass species *Sorghastrum* and of all remaining (other) species in prairie communities combined and CO$_2$ concentration for each of three soil types. Change in ANPP was calculated by subtracting the ANPP for the year prior to CO$_2$ treatment (2005) from ANPP following year 5 of treatment (2010). Lines are significant linear or exponential regression fits to changes in species ANPP for Mollisol (*Sorghastrum*, $r^2 = 0.45$, $P = 0.0003$, $n = 23$), Alfisol (*Sorghastrum*, $r^2 = 0.39$, $P = 0.006$; other species, $r^2 = 0.16$, $P = 0.07$, $n = 16$), and Vertisol soils, respectively (*Sorghastrum*, $r^2 = 0.29$, $P = 0.02$, $n = 20$; $r^2 = 0.17$, $P = 0.09$ following exclusion of a single point for which the change in ANPP > 600 g m^{-2}). The regression model with greatest r^2 value was selected. The change in combined ANPP of species other than *Sorghastrum* was not related to CO$_2$ for the Mollisol ($P = 0.29$) or Vertisol soils ($P = 0.72$), consequently no lines are shown.

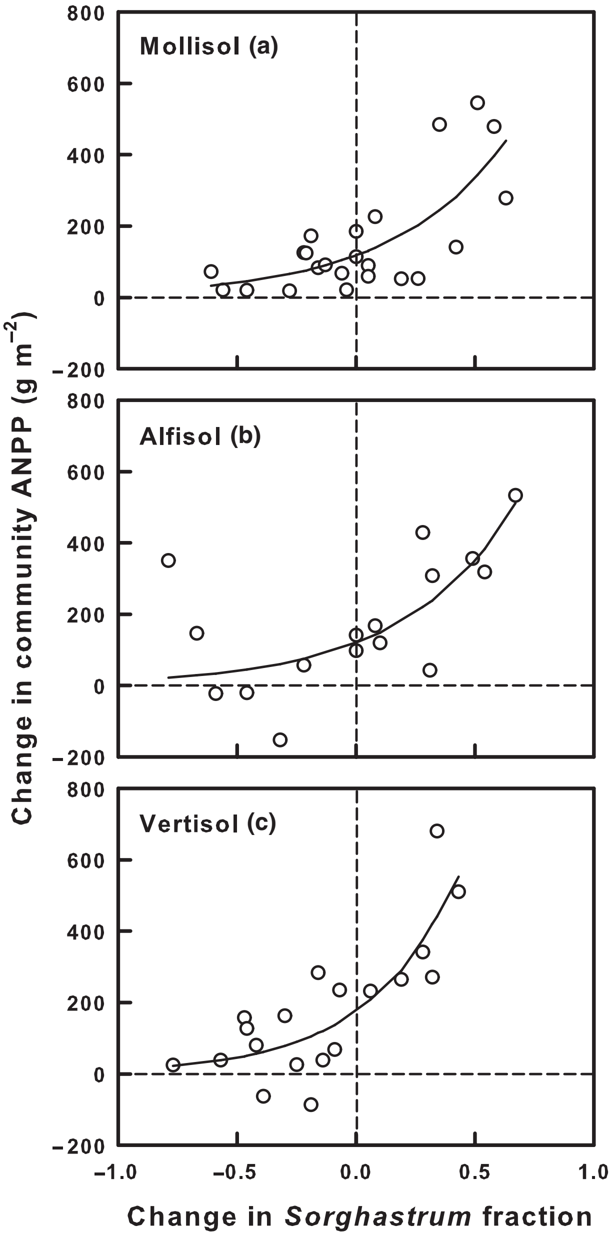

Fig. 4 Relationships between the 5-year change in ANPP of prairie communities and change in the fractional contribution of *Sorghastrum* to community ANPP for each of three soil types. Change in ANPP or *Sorghastrum* fraction was calculated by subtracting values measured the year prior to CO$_2$ treatment (2005) from values measured after 5 years of treatment (2010). Lines are exponential regression fits to changes in community ANPP for Mollisol ($r^2 = 0.53$, $P < 0.0001$, $n = 23$), Alfisol ($r^2 = 0.45$, $P = 0.003$, $n = 16$), and Vertisol soils, respectively ($r^2 = 0.66$, $P < 0.0001$, $n = 19$).

linking CO$_2$ to community ANPP through the *Sorghastrum* fraction (Fig. 6) accounted for 47–63% of the CO$_2$-caused increase in ANPP during 2008–2010 (Fig. 5). Among years, the total effect of CO$_2$ on community

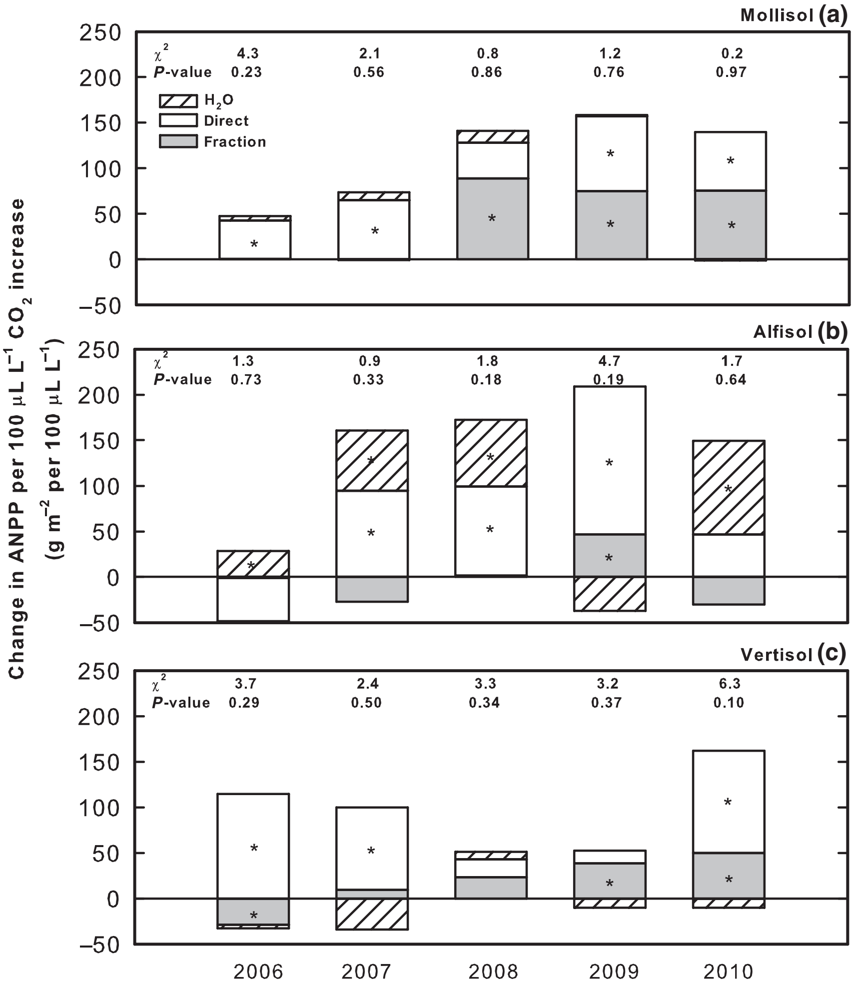

Fig. 5 Direct and indirect components of the CO$_2$ effect on ANPP of prairie communities that were grown on each of three soil types for 5 years. CO$_2$ effects were partitioned using SEM (Table S1, Fig. S1). Indirect effects of CO$_2$ on ANPP were mediated through changes in soil water content (H$_2$O) and the fractional contribution of the dominant C$_4$ grass species *Sorghastrum* to community productivity (fraction). Values for each effect were calculated using unstandardized path coefficients and are expressed as the change in ANPP (g m^{-2}) per 100 μL L^{-1} increase in CO$_2$ concentration. Significant effects are denoted with an asterisk. An indirect effect was considered significant if coefficients for one or more pathways linking CO$_2$ to ANPP were significant. The overall effect of CO$_2$ on ANPP as mediated by species change, for example, represents the sum of the effects derived from paths linking CO$_2$ to ANPP through the *Sorghastrum* fraction. Chi-square (χ^2) and *P*-values for the full SEM model are listed. The full model is considered to be consistent with data when the *P*-value of the chi-squared statistic is >0.05. The df = 3 for all soils except the Alfisol in 2007–2008 for which a simplified version of the SEM was required (df = 1).

ANPP was positively correlated with the magnitude of the indirect effect of CO$_2$ through the increase in *Sorghastrum* fraction ($r^2 = 0.87$; $P = 0.01$). Conversely, paths linking CO$_2$ to ANPP through changes in soil water content were not significant.

Alfisol. CO$_2$ enrichment increased community ANPP on the Alfisol in all but the first year of treatment (Fig. 5). The total CO$_2$ effect included large direct effects in 3 years, depended relatively little on the *Sorghastrum* fraction, and was mediated in 3 of 4 years (2007, 2008, 2010) through an increase in soil water content. The *Sorghastrum* fraction was negatively correlated with CO$_2$ following 2006, the first year of treatment (Fig. 7), apparently because of variability in vegetation that developed during the establishment period. In years 4 and 5 (2009–2010), the coefficient for the pathway linking CO$_2$ and the *Sorghastrum* fraction was positive, indicating that CO$_2$ enrichment increased *Sorghastrum's* contribution to community productivity. Paths linking CO$_2$ to community ANPP through the *Sorghastrum* fraction were significant only for 2009, however. ANPP of prairie communities increased by 46.8 g m^{-2} per 100 μL L^{-1} increase in CO$_2$ as a result

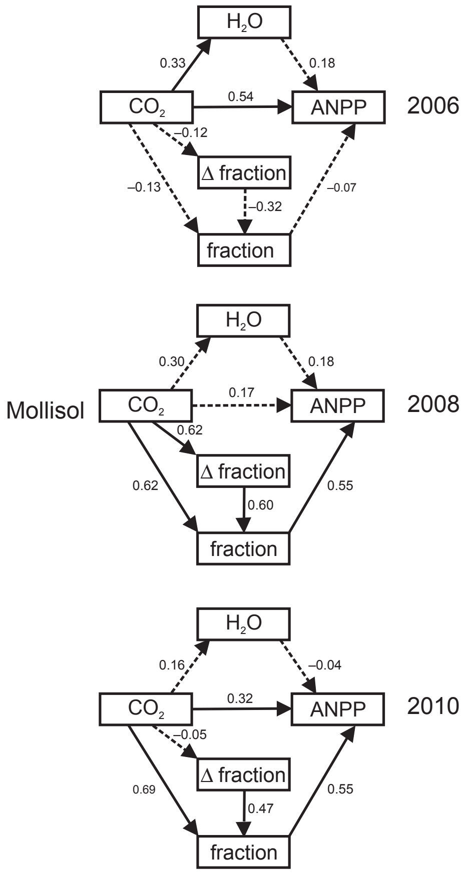

Fig. 6 Structural equation models describing direct and indirect effects of CO_2 on ANPP of prairie communities grown on a Mollisol for the first, third, and fifth years of treatment (2006, 2008, 2010; models for remaining years were omitted for brevity). Maximum likelihood techniques were used to calculate path coefficients that minimize the difference between the calculated covariance matrix and the covariance matrix present in the data. Standardized coefficients are calculated by first standardizing each variable by subtracting its mean and dividing by its standard deviation. Non-significant pathways are indicated by dashed lines. Standardized coefficients are listed beside each path. Modeled are indirect effects of CO_2 through soil water content, change in the *Sorghastrum* fraction of community ANPP during a given year (Δ fraction), and the *Sorghastrum* fraction of ANPP (fraction).

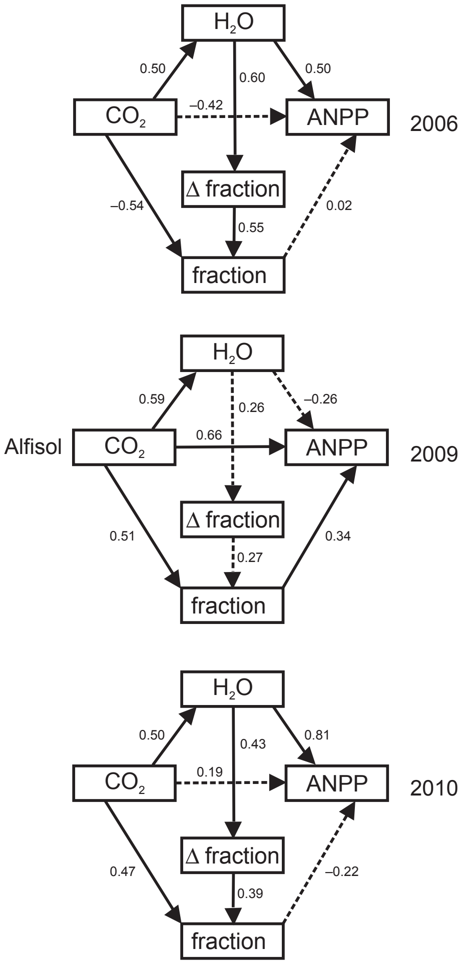

Fig. 7 Structural equation models describing direct and indirect effects of CO_2 on ANPP of prairie communities grown on an Alfisol for the first, fourth, and fifth years of treatment (2006, 2009, 2010; models for remaining years were omitted for brevity). Non-significant pathways are indicated by dashed lines. Standardized coefficients are listed beside each path. Modeled are indirect effects of CO_2 through soil water content, change in the *Sorghastrum* fraction of community ANPP during a given year (Δ fraction), and the *Sorghastrum* fraction of ANPP (fraction).

(Fig. 5). This indirect effect of CO_2 on community ANPP was only 28% of the magnitude of the direct CO_2 effect.

Vertisol. The bivariate community ANPP-CO_2 relationship was positive each year for the Vertisol but was significant in 2006, 2007, and 2010 only (Table 1). The positive effect of CO_2 on ANPP of prairie communities was entirely direct during the first 2 years, but resulted from or included a significant indirect effect mediated through an increase in the *Sorghastrum* fraction in 2010 (as well as in 2009; Fig. 5). Community ANPP was positively correlated with the *Sorghastrum* fraction each year (Fig. 8), in contrast to trends observed for Mollisol and Alfisol soils, with linear increases in ANPP of 199–413 g m^{-2} per unit increase in the *Sorghastrum* fraction (not shown). However, the coefficient for the pathway linking CO_2 and the *Sorghastrum* fraction was negative after year one of treatment (2006), meaning that *Sorghastrum* contributed less to community ANPP at elevated than subambient CO_2. This pattern was reversed in later years. The temporal trend for *Sorghastrum* to increase at elevated CO_2, combined with the strong

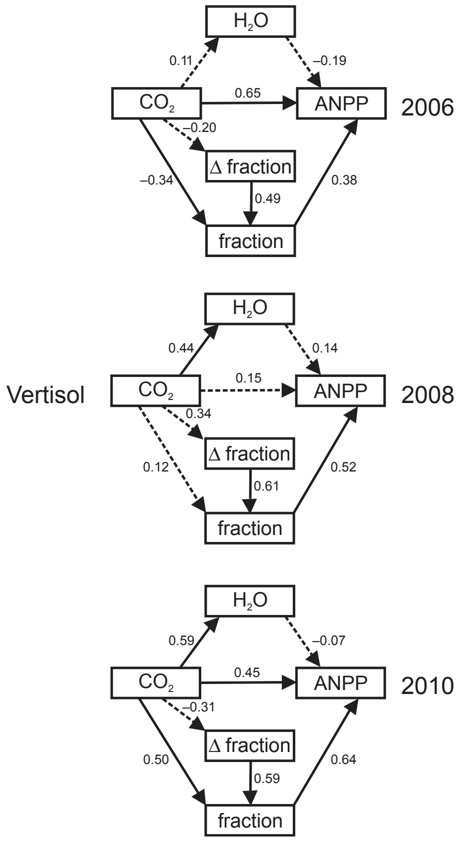

Fig. 8 Structural equation models describing direct and indirect effects of CO_2 on ANPP of prairie communities grown on a Vertisol for the first, third, and fifth years of treatment (2006, 2008, 2010; models for remaining years were omitted for brevity). Non-significant pathways are indicated by dashed lines. Standardized coefficients are listed beside each path. Modeled are indirect effects of CO_2 through soil water content, change in the *Sorghastrum* fraction of community ANPP during a given year (Δ fraction), and the *Sorghastrum* fraction of ANPP (fraction).

positive link between community ANPP and the *Sorghastrum* fraction in all years, caused the net CO_2 effect on ANPP through the *Sorghastrum* fraction to increase from 1 year to the next (Fig. 5). Paths linking CO_2 to community ANPP through changes in soil water content were not significant for the Vertisol, as for the other clay soil.

Discussion

Increasing CO_2 from subambient to elevated concentrations increased ANPP of perennial prairie communities on each of the three soil types we studied (see also, Fay *et al.*, in press). Linear increases ranged from 0–173 g m^{-2} per 100 $\mu L\ L^{-1}$ increase in CO_2 among soils and years, and were larger following 3–5 years of CO_2 exposure than during the initial 2 years of treatment for all soil types. CO_2 also increased the relative contribution of the tallgrass *Sorghastrum* to community productivity on all three soils by increasing *Sorghastrum* ANPP and, on the alluvial sandy soil (Alfisol), reducing the amount by which the combined ANPP of remaining species increased during the 5-year experiment. Importantly, these two general trends, the increase in community ANPP and increase in the *Sorghastrum* fraction of productivity at elevated CO_2, were positively correlated as predicted on the three soils. The response of community ANPP to CO_2 increased with time on the two clay soils because of a positive feedback from the CO_2-caused increase in the *Sorghastrum* fraction. This feedback accounted for 47–63% of the CO_2-mediated increase in community ANPP on the upland clay soil (Mollisol) during the final 3 years and 33% of the ANPP increase on the lowland clay soil (Vertisol) during the final year. CO_2 also favored *Sorghastrum* on the Alfisol, but species change had little effect on the ANPP-CO_2 response of communities. Rather, CO_2 enrichment increased community ANPP on this sandy soil both directly and through an increase in soil water content that likely resulted from reduced transpiration.

We hypothesized that feedback effects of species change on community ANPP would be greatest for the soils for which the water-savings effect of CO_2 was greatest under the assumption that water savings would favor species that are more productive under wetter conditions. Our hypothesis was only partially supported. Per unit of rise in CO_2, the increase in soil water content was greater by more than a factor of 1.8 and 2.4 on the Alfisol than Mollisol and Vertisol soils, respectively (Polley *et al.*, 2012). Yet, the positive feedback of increased *Sorghastrum* abundance on community ANPP was least on the sandy Alfisol.

Species shifts that involve opposing changes in the productivity of dominant species likely will enhance the sensitivity of community ANPP to CO_2 only when the increase in productivity of the favored species exceeds any decrease in productivity of disadvantaged species. Species change had little effect on the ANPP-CO_2 response of the Alfisol because CO_2 enrichment increased *Sorghastrum* at the expense of other species, including subdominant C_4 grasses. Element or other limitations on community ANPP may lead to offsetting changes in productivity among species.

CO_2 enrichment may change species relative abundances by increasing the production of one or more species without affecting biomass of other dominant and co-dominant species. This 'favored-species' route to species change is the most frequently reported 'mechanism' by which CO_2 affects grassland communities (Leadley *et al.*, 1999; Morgan *et al.*, 2004a). CO_2 increased the contribution of *Stipa comata* to aboveground production of shortgrass steppe but did not affect growth of other dominant grasses (Morgan *et al.*, 2004a), for example. CO_2 increased *Sorghastrum* productivity on the two clay soils (Mollisol and Vertisol), but did not significantly affect the combined ANPP of species other than *Sorghastrum*. The result was a direct correlation between the increase in relative abundance of the tallgrass and increase in community ANPP by year 5 of the experiment.

Our results highlight the obvious, but important role that the presence of productive and CO_2-responsive species play in determining the sensitivity of community ANPP to CO_2, as well as the importance of multiyear CO_2 experiments. Community ANPP was a significant and positive function of the *Sorghastrum* fraction on the Vertisol even early in the experiment when the *Sorghastrum* fraction was negatively correlated to CO_2 (2006). Community response to CO_2 apparently was depressed because less-responsive species usurped growth-limiting resources from *Sorghastrum*. Wang (2007) similarly invoked resource usurpation by weakly responsive species to explain the smaller CO_2 effect on growth of communities than species monocultures. By preferentially increasing *Sorghastrum* productivity, CO_2 contributed to a positive feedback on the ANPP-CO_2 response of prairie communities on the Vertisol. Results for this clay soil also demonstrate that initial responses to CO_2 enrichment may be misleading. Simple bivariate relationships between community ANPP and CO_2 were weaker and generally exhibited smaller slopes for the Vertisol than other soils (see also Fay *et al.*, in press). Interpreted from a physiological perspective, prairie communities on this lowland clay were the least responsive to CO_2. Only with time did it become evident that the ANPP-CO_2 response was regulated largely by a biotic feedback.

Clearly, factors in addition to CO_2 can influence the ANPP-CO_2 relationship by modifying vegetation and its response to CO_2. Disturbances, such as grazing and fire, or N fertilization may alter CO_2 effects on species by facilitating seed dispersal and seedling recruitment (grazing; Newton *et al.*, 2006) or changing competitive interactions among plants (grazing, fire, N fertilization; e.g., Henry *et al.*, 2006). For example, N fertilization initially enhanced the CO_2 stimulation of productivity in herbaceous brackish wetland, but promoted a shift from C_3 to C_4 species that suppressed CO_2 effects on community productivity by the third and fourth years of treatment (Langley & Megonigal, 2010). Because of the vagaries of seed dispersal and disturbance effects, species relative abundances may vary more in space at a given time than over time in response to CO_2, even in a given community type on a given soil. Species effects on the ANPP thus may also be reflected in spatial variation in the ANPP-CO_2 response.

Increasing CO_2 from pre-Industrial to elevated levels contributed to a positive feedback on the ANPP-CO_2 response of prairie communities by favoring a widely distributed tallgrass species. The feedback accounted for 30–60% of the CO_2-mediated increase in community ANPP on two of three soil types during the final 1–3 years of treatment. Feedback effects were smallest for the soil type on which the increase in *Sorghastrum* was largely compensated for by a decline in the productivity and relative abundances of two sub-dominant C_4 grasses. We anticipate that species change will enhance the community ANPP-CO_2 response provided that shifting species exhibit different functional responses to CO_2 and the shift in species abundances is sufficiently large relative to the magnitude of functional differences in species. The smaller are species differences in response to CO_2 or accompanying changes in water and N availability, the greater, likely, must be the change in species abundances to influence the ANPP-CO_2 relationship. Simulations from dynamic global vegetation models indicate that CO_2-caused changes in vegetation will be greatest in grasslands and savannas (Cramer *et al.*, 2001). Our results highlight the importance of accounting for species change and composition when predicting CO_2 effects on community productivity and other aspects of the functioning of these ecosystems (e.g., Polley *et al.*, 2011a).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Description of variables included in structural equation models.

Table S2. Linear regression relationships between the 5-year change in ANPP of sub-dominant perennial grasses and CO_2 concentration for each of three soil types.

Figure S1. The theoretical structural equation model used to explore direct and indirect effects of CO_2 enrichment on ANPP of prairie communities.

Figure S2. Relationships between the 5-year change in the fractional contribution of *Sorghastrum* to ANPP of prairie communities and CO_2 treatment for each of three soil types.