CO_2 enrichment and soil type additively regulate grassland productivity

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Summary

- Atmospheric CO_2 enrichment usually increases the aboveground net primary productivity (ANPP) of grassland vegetation, but the magnitude of the ANPP–CO_2 response differs among ecosystems. Soil properties affect ANPP via multiple mechanisms and vary over topographic to geographic gradients, but have received little attention as potential modifiers of the ANPP–CO_2 response.

- We assessed the effects of three soil types, sandy loam, silty clay and clay, on the ANPP response of perennial C_3/C_4 grassland communities to a subambient to elevated CO_2 gradient over 10 yr in Texas, USA. We predicted an interactive, rather than additive, effect of CO_2 and soil type on ANPP.

- Contrary to prediction, CO_2 and soil additively influenced grassland ANPP. Increasing CO_2 by $250 \, \mu l \, l^{-1}$ increased ANPP by $170 \, g \, m^{-2}$ across soil types. Increased clay content from 10% to 50% among soils reduced ANPP by $50 \, g \, m^{-2}$. CO_2 enrichment increased ANPP via a predominant direct effect, accompanied by a smaller indirect effect mediated by a successional shift to increased dominance of the C_4 tallgrass *Sorghastrum nutans*.

- Our results indicate a large, positive influence of CO_2 enrichment on grassland productivity that resulted from the direct physiological benefits of CO_2 augmented by species succession, and was expressed similarly across soils of differing physical properties.

Introduction

The development of a predictive understanding of how atmospheric CO_2 enrichment is affecting the primary productivity of the terrestrial biosphere is among the most pressing of ecological challenges. The terrestrial biosphere absorbs *c.* 25% of anthropogenic carbon (C) emissions (Le Quéré *et al.*, 2018). Uncertainty in CO_2 effects on ecosystem C uptake is a major constraint in the prediction of C cycling and the provisioning of productivity-related ecosystem services.

Grasslands cover *c.* 25% of the terrestrial area and are an important contributor to the global C balance (Sala *et al.*, 1996). CO_2 enrichment stimulates the aboveground net primary productivity (ANPP) of most water-limited grasslands by increasing plant water use efficiency (WUE; productivity per unit of transpiration; Morgan *et al.*, 2004; Nowak *et al.*, 2004; Fatichi *et al.*, 2016), but grassland ANPP, as other ecosystem functions, is determined by drivers in addition to water availability which act simultaneously and often interactively with CO_2 (Polley *et al.*,

2011). CO_2 enrichment usually shows greater stimulation of plant productivity when nitrogen (N) availability is relatively high (Owensby *et al.*, 1994; Reich & Hobbie, 2013; Mueller *et al.*, 2016), for example. Other drivers include precipitation timing (Hovenden *et al.*, 2014), disturbance regimes (Newton *et al.*, 2014), plant species composition (Langley & Megonigal, 2010; Fay *et al.*, 2012; Polley *et al.*, 2012) and soil properties (Epstein *et al.*, 1997, 1998), including soil texture, which influences water availability to plants (Tor-Ngern *et al.*, 2017).

Soils have received little attention as potential mediators of the ANPP–CO_2 response, apart from the role of soil properties in influencing N and water availability to plants. Spatial variation in soil N is common (García-Palacios *et al.*, 2012), with possible feedbacks on the composition, productivity and CO_2 response of plant assemblages (Owensby *et al.*, 1994; Niklaus & Körner, 2004; Langley & Megonigal, 2010; Reich & Hobbie, 2013; Mueller *et al.*, 2016). Water availability varies across gradients in soil physical and related hydrological properties at spatial scales over which precipitation is similar. CO_2 enrichment typically

shows greater enhancement of productivity in drier years or at drier localities, the result of increased WUE (Owensby *et al.*, 1999; Morgan *et al.*, 2004; Nowak *et al.*, 2004; Fatichi *et al.*, 2016). A similar mechanism may contribute to soil differences in the productivity response to CO_2 enrichment. By increasing WUE, CO_2 enrichment could lead to a greater increase in plant productivity on fine- than coarse-textured soils, because soil water availability to plants (soil water potential) at a given level of extractable soil water is usually lower in fine- than coarse-textured soils (Tor-Ngern *et al.*, 2017).

Soils can also mediate the ANPP–CO_2 response by altering the plant species composition or abundance (Polley *et al.*, 2011; Fay *et al.*, 2015a). Soils with a high percentage of sand content favor productive C_4 tall grasses (Epstein *et al.*, 1998), which may experience greater benefits from CO_2 enrichment relative to shorter statured grasses, for example (Fay *et al.*, 2012; Polley *et al.*, 2012).

The response of ANPP to CO_2 enrichment is likely to differ among soil types when soil effects on productivity are tightly coupled with soil differences in resource (e.g. water, N) availability. Soil-specific responses to CO_2 enrichment are indicated statistically by a soil type $\times$ CO_2 interaction. However, soil physical properties may affect the ANPP–CO_2 response via mechanisms that are independent of, or weakly correlated with, soil differences in resource availability. Plant growth and species abundances are sensitive to variation in soil strength or compaction (Masle & Passioura, 1987; Wallace, 1987; Schrama *et al.*, 2013), for example. In these cases, soil and CO_2 effects on productivity may be additive, the sum of their separate effects, rather than interactive (Zavaleta *et al.*, 2003). Additive effects are evidenced by the absence of a statistical $CO_2 \times$ soil interaction.

We assessed the effects of soil type and CO_2 on the ANPP of perennial grassland communities during a 10-yr field experiment on three soil types in Texas, USA (Polley *et al.*, 2008; Fay *et al.*, 2009). Identical assemblages of C_3 forbs and C_4 grasses were established on three soil types (clay, sandy loam, silty clay), representative of the variation in soil texture and associated hydrological properties in the Blackland Prairie region of Texas. Communities on each soil type were grown along a continuous CO_2 gradient from the pre-industrial concentration ($250 \, \mu l \, l^{-1}$) to a level expected this century ($500 \, \mu l \, l^{-1}$).

The ANPP–CO_2 response differed among soils during the initial 5 yr of this experiment (Fay *et al.*, 2012; Polley *et al.*, 2012). CO_2 enrichment directly increased ANPP on all soil types during at least one of the first 5 yr, probably by increasing leaf photosynthesis rates and leaf-level photosynthetic WUE (Fay *et al.*, 2012). CO_2 effects differed among soils during these initial years because CO_2 feedbacks on productivity through changes in the soil water potential (Fay *et al.*, 2012) and relative abundance of a productive C_4 grass, *Sorghastrum nutans* (Fay *et al.*, 2012; Polley *et al.*, 2012), differed in magnitude among soils. It remains unresolved as to whether the processes that contributed initially to interactive soil $\times$ CO_2 effects on productivity are sustained over longer time periods. N availability did not differ among soils initially (Fay *et al.*, 2012), but longer term changes in N availability (Reich *et al.*, 2018) could alter the relative roles of species abundances,

soil water and N in mediating soil effects on the ANPP–CO_2 response.

We predicted that [CO_2] effects on ANPP would continue to differ among soil types over 10 yr of CO_2 enrichment. Specifically, we predicted first that CO_2 enrichment would elicit the largest absolute increase in ANPP on soils for which mean ANPP was greatest, consistent with evidence that CO_2 leads to a greater stimulation of plant productivity when N availability is high rather than low (Owensby *et al.*, 1994; Reich & Hobbie, 2013; Mueller *et al.*, 2016). Second, we predicted that CO_2 enrichment would elicit the largest proportional increase in ANPP on the soil with the lowest mean water potential, consistent with evidence that CO_2 leads to a greater stimulation of plant productivity when plant growth is water limited (Morgan *et al.*, 2004; Nowak *et al.*, 2004; Fatichi *et al.*, 2016). Third, we predicted that initial, soil-specific responses to CO_2 would be amplified over time as the result of a progressive increase in soil differences in *Sorghastrum* dominance at elevated CO_2. Progressive CO_2 effects on soil resource levels (Luo *et al.*, 2004; Reich & Hobbie, 2013) or plant composition or functioning (Niklaus *et al.*, 2001; Hungate *et al.*, 2004) may reinforce interactive controls on the productivity–CO_2 response. However, the initial soil $\times$ CO_2 interaction for ANPP could be weakened or even eliminated if changes in N mineralization rates (Reich *et al.*, 2018) or climatic variation (Zhu *et al.*, 2016) reverse progressive CO_2 effects that reinforce soil-specific ANPP–CO_2 responses. Answers to questions as to whether or how soil type influences the CO_2 response of productivity will improve our understanding and modeling of grassland responses to the historical and anticipated rise in CO_2 concentration across edaphically variable landscapes.

Materials and Methods

Facility

We used the Lysimeter CO_2 Gradient (LYCOG) facility located outdoors in central Texas, USA to expose grassland communities to a continuous gradient in CO_2 spanning pre-industrial to elevated concentrations ($250–500 \, \mu l \, l^{-1}$) each growing season for a decade (2006–2015) (Supporting Information Fig. S1; Johnson *et al.*, 2000; Polley *et al.*, 2008; Fay *et al.*, 2009, 2015b). LYCOG consists of two transparent, tunnel-shaped chambers, aligned parallel along a north–south axis. Each chamber is divided into 10 consecutive compartments, each 5 m long and 1.2 m wide. The aerial portion of each compartment was built atop a 5-m-long steel container that had been buried to a depth of 1.2 m. The aerial growth of the chambered vegetation was enclosed in a transparent polyethylene film. The desired [CO_2] gradients were maintained by automatically varying the rate of air flow through the chambers in response to changes in photosynthesis (daylight) or respiration (night) rates. Night-time [CO_2] was regulated at $130–150 \, \mu l \, l^{-1}$ above daytime values along each chamber. Air temperature in the chambers was regulated with the goal of matching ambient values by cooling (and dehumidifying) air at 5-m intervals along the chambers. This goal was achieved most consistently during the cooler spring and

autumn months. The chamber air temperature was $1.87 \pm 0.33°C$ cooler than the ambient temperature on average across the full growing season. The air temperature, dew point and $[CO_2]$ were measured at the air entrance and exit of each 5-m compartment at 20-min intervals. CO_2 treatments were maintained each growing season (2006–2015) from March/April through mid-November.

Plant communities

Communities of grassland species were grown in intact soil monoliths (each 1 m × 1 m × 1.5 m deep). Monoliths of three soil types were collected in the Texas Blackland Prairie region (Austin silty clay, $n = 32$; Houston Black clay, $n = 32$; Bastsil sandy loam, $n = 16$). Monoliths were collected by pressing open-ended steel boxes into the soil. Steel-encased monoliths were placed in containers beneath 5-m-long compartments. Each compartment contained two monoliths of each of two of the three soil types. The monolith order within compartments was assigned randomly. Monoliths of the sandy loam soil were included in the second of each consecutive pair of compartments along the chambers. Seedlings of seven perennial species, including four C_4 grasses, two C_3 forbs and one herbaceous legume, were transplanted into each monolith 3 yr before CO_2 treatment. All species are native to central Texas (Diggs *et al.*, 1999) and present in the Texas Blackland Prairie. Eventual community dominants included the C_4 grasses *Bouteloua curtipendula* (Michx.) Torr. and *Sorghastrum nutans* (L.) Nash, and the forb species *Solidago canadensis* L. No fertilizer was applied. Grubs (Coleoptera: Scarabaeidae) killed most transplants in 20 of the total of 80 monoliths (eight silty clay, 12 clay) during the first year of CO_2 treatment. These monoliths were replanted in spring 2007 as *Panicum virgatum* L. (switchgrass) monocultures that were well watered and fertilized for the duration of the experiment to facilitate CO_2 regulation by increasing the photosynthetic sink. Sixty monoliths of species mixtures remained (silty clay, $n = 24$; clay, $n = 20$; sandy loam, $n = 16$). We excluded data from one silty clay monolith on which most vegetation died following year 3 of CO_2 regulation.

Implementation

We surface irrigated each monolith with the equivalent of the growing season (April–October) average of precipitation at our site (560 mm) during each season. We varied the fraction of growing season irrigation that was added in spring vs summer among years to create interannual differences in seasonal water availability, whilst holding the annual irrigation amount constant. All monoliths were subjected to the same irrigation schedule each year. The spring (mid-April through mid-June) fraction of total irrigation that was applied to each of the 60 monoliths with species mixtures was varied interannually between 19 and 43%, the latter being the long-term mean for the site (range = 10–80%; 100-yr record; Fig. S2). Interannual differences in the seasonality of irrigation combined with soil

hydrological differences and seasonal or interannual variation in plant transpiration to create variation in plant-available soil water.

Daytime $[CO_2]$ varied as a linear function of distance along the chambers (Fay *et al.*, 2009). The mean $[CO_2]$ to which each monolith was exposed was calculated using linear regressions of $[CO_2]$ vs distance. Calculated $[CO_2]$ was used as the independent variable in regression analyses with ANPP and species abundances.

Measurements

Volumetric soil water content (vSWC) was measured weekly in the center of each monolith with a neutron probe. Soil water (matric) potential over a depth of 0–50 cm (Ψ_s) was calculated from vSWC using soil-specific Ψ_s–vSWC relationships developed from measurements of Ψ_s with a dewpoint hygrometer (Model WP4T; Decagon Devices, Pullman, WA, USA) (Polley *et al.*, 2016).

Soil N availability was assessed in 2008, 2010, 2013 and 2015 (years 3, 5, 8 and 10 of CO_2 treatment) using ion exchange resins (PRS-probes; Western Ag Innovations, Saskatoon, SK, Canada) to measure NO_3^- and NH_4^+ in soil solution. Resin probes were installed monthly during each of 2 months in both spring (mid-April to mid-June) and summer (mid-July to mid-September) each year. N amounts were measured colorimetrically for probes combined from the two monoliths of a given soil type in each 5-m-long compartment of the CO_2 chambers. Soil N availability per sampling location and year was taken as the monthly average of μg N accumulated per 10 cm^2 of probe surface area.

All vegetation from each monolith was clipped at a height of 5 cm at the end of each growing season following plant senescence. Clipped vegetation was dried (65°C) and weighed by species. Species abundances were calculated as a fraction of total ANPP. Mean ANPP of monoliths was similar in magnitude to the productivity measured in two remnant prairies (clay/silty clay soils) over 5 yr (mean = 309 and 379 g m^{-2} yr^{-1}; Polley *et al.*, 2007), implying no discernible limitation of monolith rooting volume on plant growth.

Data analysis

We used a repeated-measures analysis of covariance (PROCMIXED in SAS 9.4) to model treatment effects on ANPP, fractional contribution of the tall grass *Sorghastrum* to community productivity (fSorg), Ψ_s and soil N:

$$y = \text{intercept} + CO_2 + \text{soil} + \text{monolith(soil)}$$
$$+ \text{compartment(soil)} + \text{chamber(compartment)} + (CO_2$$
$$\times \text{soil}) + \text{year} + (CO_2 \times \text{year}) + (\text{soil} \times \text{year}) + e$$

Eqn 1

where CO_2 was the covariate, soil was a fixed effect, monoliths within soil type (monolith(soil)), soil types within 5-m-long compartments (compartment(soil)) and compartments within

chambers (chambers(compartment)) were random effects, $CO_2 \times$ soil was the soil-specific covariate and e was the random error. Year was a repeated effect fitted using an autoregressive covariance structure. $CO_2 \times$ year and soil $\times$ year terms modeled interannual variation in CO_2 and soil effects on dependent variables.

We also fitted Structural Equation Models (SEMs) to evaluate causal relationships among interacting variables that together affected ANPP (Shipley, 2000; Grace, 2006). Models were fitted using IBM SPSS AMOS 21 software. Our initial (meta) model of predicted ANPP ($\log_e$(ANPP)) included two independent variables, $[CO_2]$ and soil type, the latter represented as the percentage clay content ($\log_e$(% clay)), and three dependent variables, Ψ_s, fSorg and a lagged mediator of fSorg, the *Sorghastrum* fraction of productivity during the previous year (fSorg$_p$). Soil N was not included in the SEM as N did not vary with $[CO_2]$ or soil type and was weakly correlated with ANPP (see Results). SEMs were fitted to a dataset that included measurements from all monoliths, soil types and 10 yr, and separately to data from the first 5 yr or final 5 yr of the experiment. We iteratively removed parameters or pathways from the meta model in order to identify models that yielded the most parsimonious fit among those tested, as indicated by smaller values of the root-mean-square error of approximation (RMSEA) and Akaike's Information Criterion (AIC).

Data accessibility

Data have been deposited in the Dryad Digital Repository doi:10.5061/dryad.1hc582s.

Results

Soil and CO_2 effects on biotic and abiotic variables

Grasses dominated the vegetation on all soils, but species abundances differed among soil types (Fig. 1). C_4 grasses contributed an average of 73%, 84% and 88% of annual productivity on clay, silty clay and sandy loam soils, respectively, over 10 yr. *Sorghastrum nutans* was the dominant grass on the clay and sandy loam soils (32% and 46% of ANPP, respectively) and subdominant to *Bouteloua curtipendula* on the silty clay soil, where *Sorghastrum* contributed 25% of ANPP. *Solidago canadensis* was the dominant C_3 forb, contributing a mean of 9%, 10% and 15% of annual ANPP on the sandy loam, silty clay and clay soils, respectively, over 10 yr. Because grasses dominated communities, ANPP was largely dependent on the growth of these C_4 species.

CO_2 enrichment increased aboveground productivity across soil types (Table S1; Fig. 2). The $[CO_2]$ effect on ANPP did not differ significantly among soils (analysis of covariance; $CO_2 \times$ soil, $P = 0.12$) (Table S1), but varied among years. The slopes of ANPP–CO_2 relationships were significantly smaller in 2011 and 2013 (years 6 and 8) than in the remaining years (50.8 vs 114.0 g m^{-2} increase in ANPP per 100 μl l^{-1} increase in $[CO_2]$; not shown).
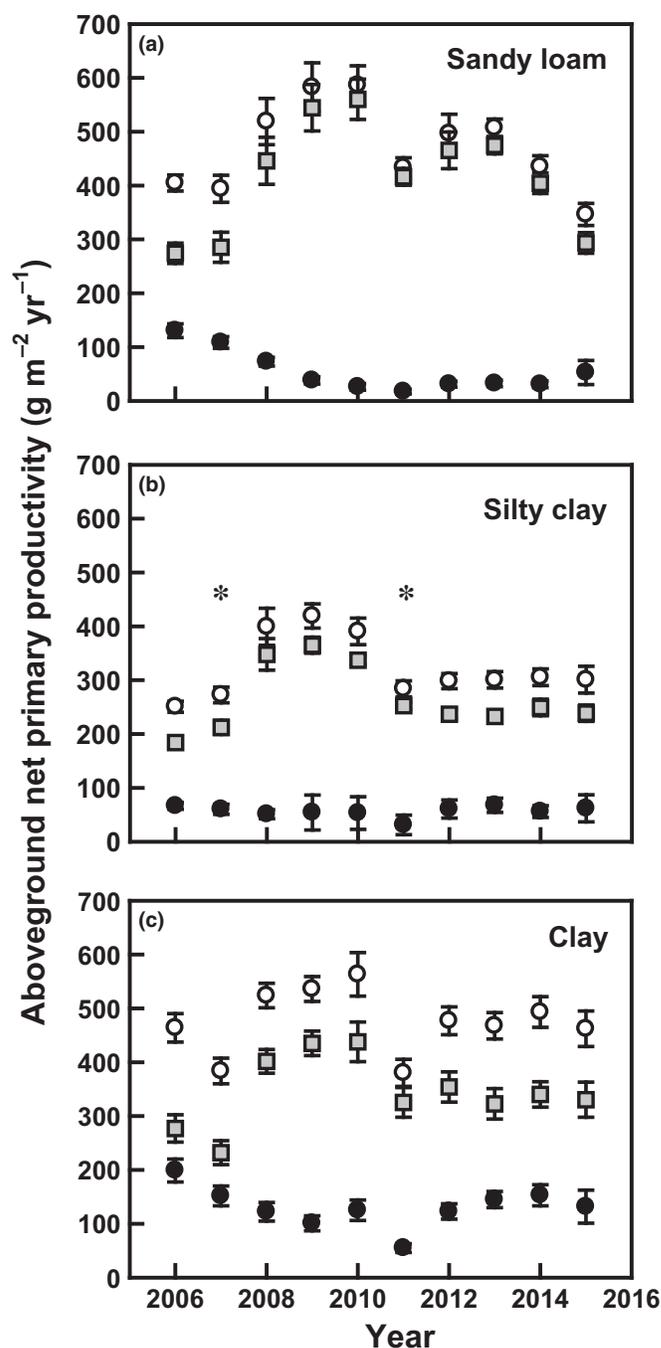
Fig. 1 Mean ($\pm$ SE) values of aboveground net primary productivity (ANPP) for grassland communities (white circles) and component C_4 grasses (gray squares) and C_3 forb species (closed circles) for each of three soil types and year of CO_2 treatment. Values are averaged across $[CO_2]$ treatments for each year and soil ($n = 16$–23). *in (b) indicates years in which ANPP was not significantly lower for the silty clay than clay and sandy loam soils.

ANPP was greater for communities grown on clay and sandy loam soils than on silty clay soil over 10 yr (Fig. 1; mean = 478, 462 and 331 g m^{-2} yr^{-1}, respectively), although soil differences in ANPP varied among years (Table S1). ANPP was smaller on the silty clay than on both the clay and sandy loam soils in all but
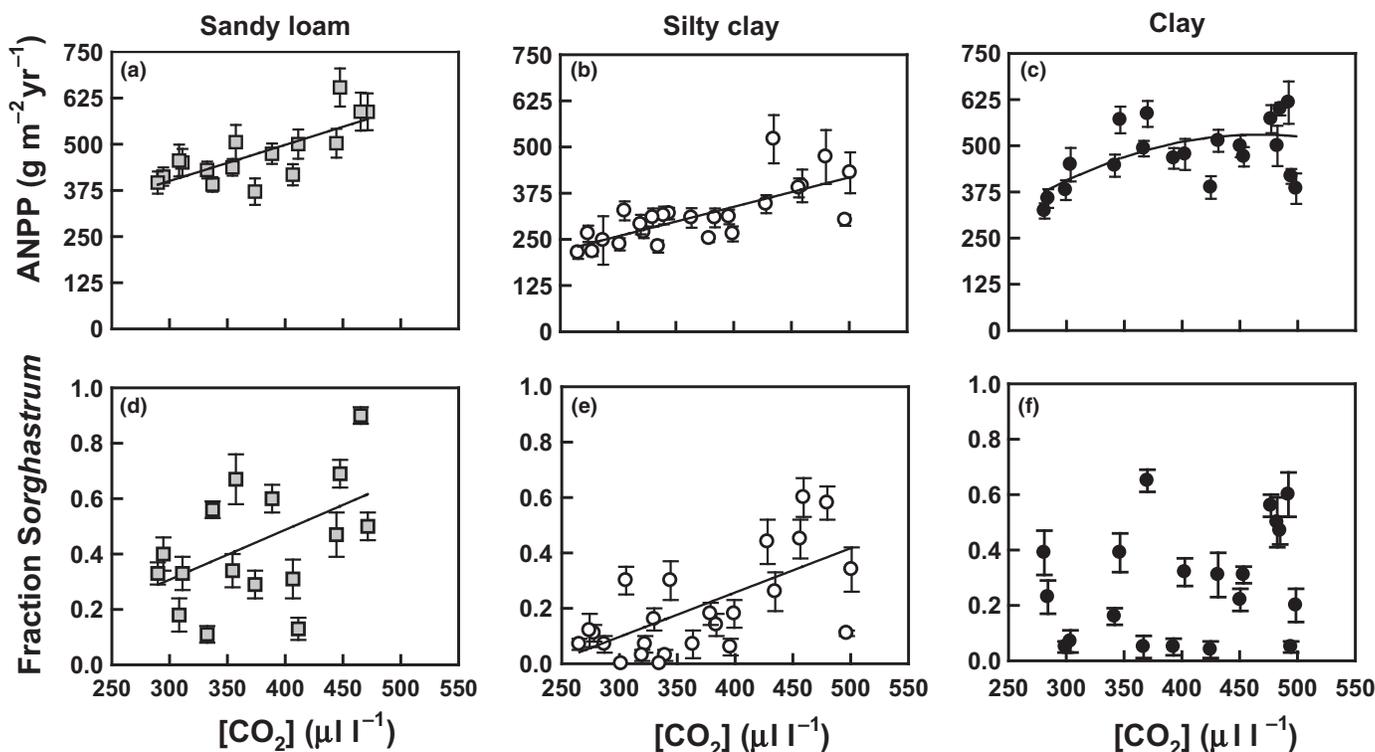
Fig. 2 Mean ($\pm$ SE) responses for total aboveground net primary productivity (ANPP) of communities and the contribution of the tall grass *Sorghastrum* to community productivity (fraction *Sorghastrum*) along a [CO_2] gradient for each of three soil types over a decade of CO_2 treatment. Lines show fits of linear or quadratic regressions to 10-yr averages per monolith for sandy loam (shaded squares; adj. $r^2 = 0.53$ (a) and 0.19 (d); $P < 0.05$), silty clay (open circles; adj. $r^2 = 0.53$ (b) and 0.39 (e); $P < 0.0007$) and clay soils (closed circles, adj. $r^2 = 0.36$, $P = 0.02$ (c) and not significant (f)).

two (2007, 2011) of the first 8 yr, and on both the silty clay and sandy loam soils than on the clay soil during the final year (Fig. 1).

CO_2 enrichment increased ANPP partly by favoring the dominant grass species. Increased [CO_2] boosted the *Sorghastrum* fraction of ANPP (fSorg) (Table S1; Fig. 2). Increased relative abundance of *Sorghastrum*, in turn, increased ANPP across years for each soil type (Fig. 3). fSorg explained 24% of the variance in ANPP across soils and years (ANPP (g m^{-2}) = 332.2 + 274.1 × fSorg; $P < 0.0001$). The CO_2 effect on fSorg changed with time. The contribution of *Sorghastrum* to community ANPP was greater when averaged across elevated [CO_2] than subambient [CO_2] beginning in 2007, year 2 ((fSorg (E-S) > 0); Fig. 4), especially on silty clay and sandy loam soils. The strong initial response of *Sorghastrum* to CO_2 was transient. fSorg(E-S) declined on all three soils beginning in 2010–2011 (years 5–6), with the largest declines in 2012–2013 (years 7–8). The *Sorghastrum* fraction of ANPP (fSorg) did not differ significantly among soils (Table S1); however, nor did soil influence the [CO_2] effect on fSorg.

[CO_2] and soil effects on soil water potential exerted minor feedback on ANPP. CO_2 enrichment increased Ψ_s to 50 cm depth, most strongly for the clay soil, by 0.4 MPa per 100 μl l^{-1} rise in [CO_2] (Fig. 5; CO_2 × soil, $P = 0.02$; Table S1). Ψ_s differed among soils ($P < 0.0001$). Soil water availability was highest for the sandy loam, intermediate for the silty clay and lowest for

the clay (-0.27, -0.73 and -1.76 MPa, respectively). Ψ_s differed among soils because soils differed in hydrological properties that influenced relationships between Ψ_s and vSWC. The range in vSWC created by irrigation treatments and plant transpiration traversed a portion of the Ψ_s vs vSWC curve over which the variation in Ψ_s was relatively large in the clay soil. Conversely, annual means of vSWC did not decline to levels at which Ψ_s responded greatly to the change in water content in the sandy loam soil. Soil differences in Ψ_s vs vSWC relationships are consistent with differences expected from soil variation in texture (% clay content = 9.4%, 43.1% and 52.6% for the sandy loam, silty clay and clay soils, respectively). Over the range of Ψ_s encountered, water potential alone explained little (< 1%) of the variance in ANPP across data from soils and years combined (ANPP = 397.0 − 17.0 × Ψ_s; $P = 0.08$; Fig. 3).

Resin-available soil N, by contrast, did not vary with [CO_2] or differ among soil types over 4 yr of N measurements (Table S1). Soil N declined from 8.3 ± 0.3 μg N 10 cm^{-2} of probe area month^{-1} in 2008 (year 3) to 3.0 ± 0.3 μg N 10 cm^{-2} month^{-1} in 2010 (year 5), when ANPP was near maximal on all soils (Fig. 1), and remained low thereafter (2.3 ± 0.1 and 1.4 ± 0.1 μg N 10 cm^{-2} month^{-1} in years 8 and 10, respectively). Neither fSorg nor Ψ_s was correlated with soil N ($P = 0.94$ and 0.11, respectively). ANPP was a weak positive function of resin-available N across years, soils and [CO_2] (not shown; adj. $r^2 = 0.03$; $P = 0.03$), but was not significantly correlated with the
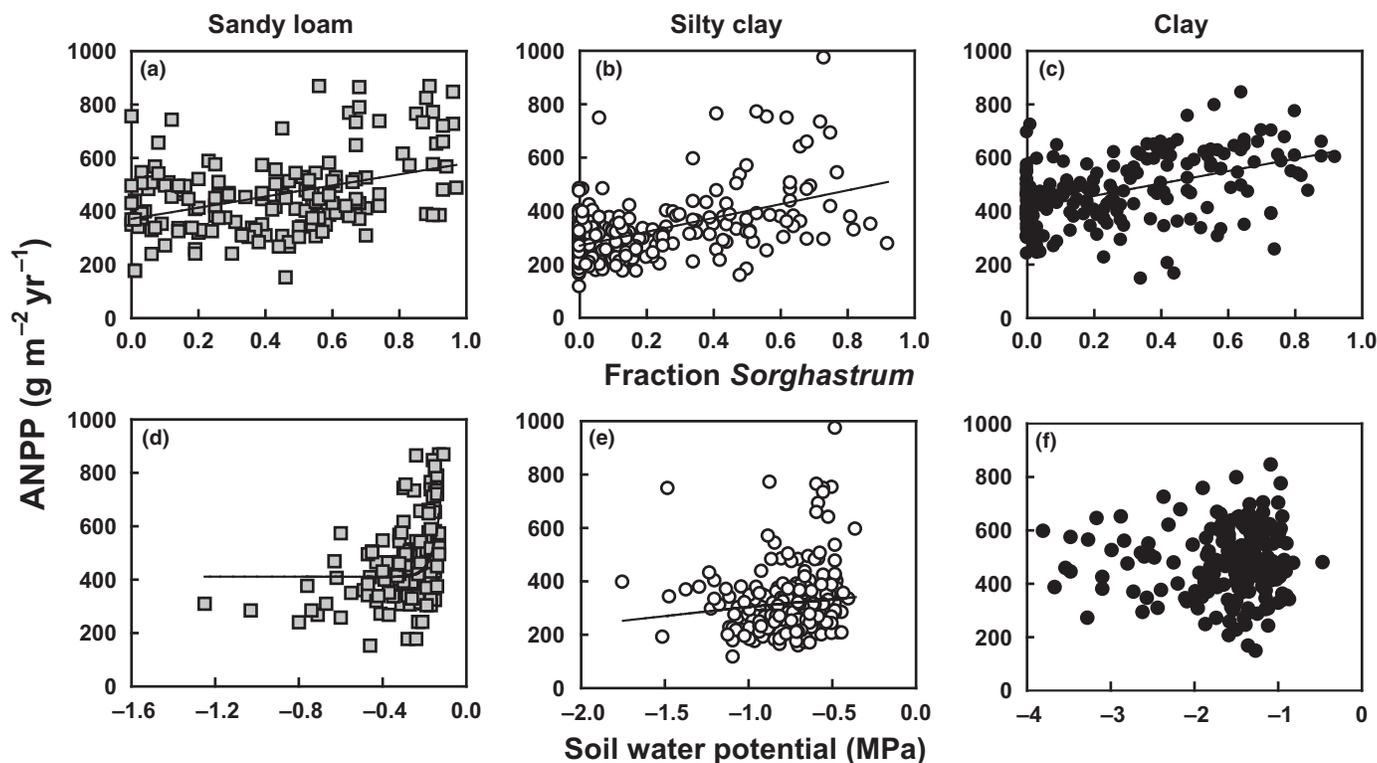
Fig. 3 Relationships between aboveground net primary productivity (ANPP) of grassland communities and (a–c) the contribution of the tall grass *Sorghastrum* to community productivity (fraction *Sorghastrum*) and (d–f) the growing season mean of the soil water potential to 50 cm depth for each of three soil types over a decade of CO_2 treatment. Lines show fits of linear (a–c, e) or exponential (d) regressions to the data from all CO_2 treatments, monoliths and years for sandy loam (shaded squares; adj. $r^2 = 0.15$ and 0.21, $P < 0.0001$, $n = 160$ (a, d)), silty clay (open circles; adj. $r^2 = 0.24$ and 0.01, $P < 0.0001$ and 0.06, $n = 230$ (b, e)) and clay soils (closed circles, adj. $r^2 = 0.20$, $P < 0.0001$ and $P = 0.52$, $n = 200$ (c, f)). The scale of the x-axis differs among panels (d)–(f).
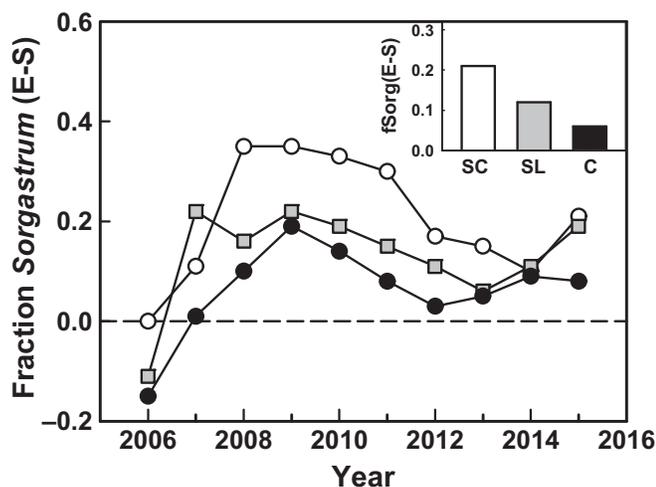

Fig. 4 Temporal trends in the CO_2 effect on the relative abundance of the tallgrass species *Sorghastrum* for grassland communities grown on each of three soil types. Shown are the annual values of the elevated vs subambient difference (E-S) in fractional contribution of *Sorghastrum* to community aboveground net primary productivity (ANPP) for silty clay (SC; open circles), sandy loam (SL; gray squares) and clay soils (C; closed circles). The inset shows 10-yr averages of the E-S difference in *Sorghastrum* fraction for each soil type.

locations of 5-m-long compartments along chambers (chamber position) after accounting for effects of variation in $[CO_2]$ and fSorg using a sequential regression analysis ($P > 0.15$).

Structural equation models

SEMs were used to test joint effects of the two independent variables, $[CO_2]$ and $\log_e(\% \text{ clay})$, and three dependent variables, Ψ_s, fSorg and fSorg$_p$, on ANPP ($\log_e(\text{ANPP})$). This model adequately fitted the data from all soils, monoliths and years combined and explained 37% of the variance in ANPP (Fig. 6). Both the $[CO_2]$ and $\log_e(\% \text{ clay})$ effects on ANPP were primarily direct, rather than mediated through changes in fSorg or Ψ_s. The direct CO_2 effect was positive and accounted for 80% of the total CO_2 effect on ANPP. The direct effect of soil type (clay content) on ANPP was negative. CO_2 enrichment indirectly increased ANPP by increasing fSorg, but reduced ANPP by increasing Ψ_s, because mean ANPP was greater for the clay soil with lowest mean Ψ_s than the silty clay soil with higher potential. Indirect effects of greater clay content on ANPP were opposite in sign to those of $[CO_2]$. The total positive effect of CO_2 enrichment was twice the negative effect of clay content. Increasing CO_2 by $100 \mu l \, l^{-1}$ increased ANPP by $85 \, g \, m^{-2}$, whereas increasing the clay content by 10% reduced ANPP by $12 \, g \, m^{-2}$.
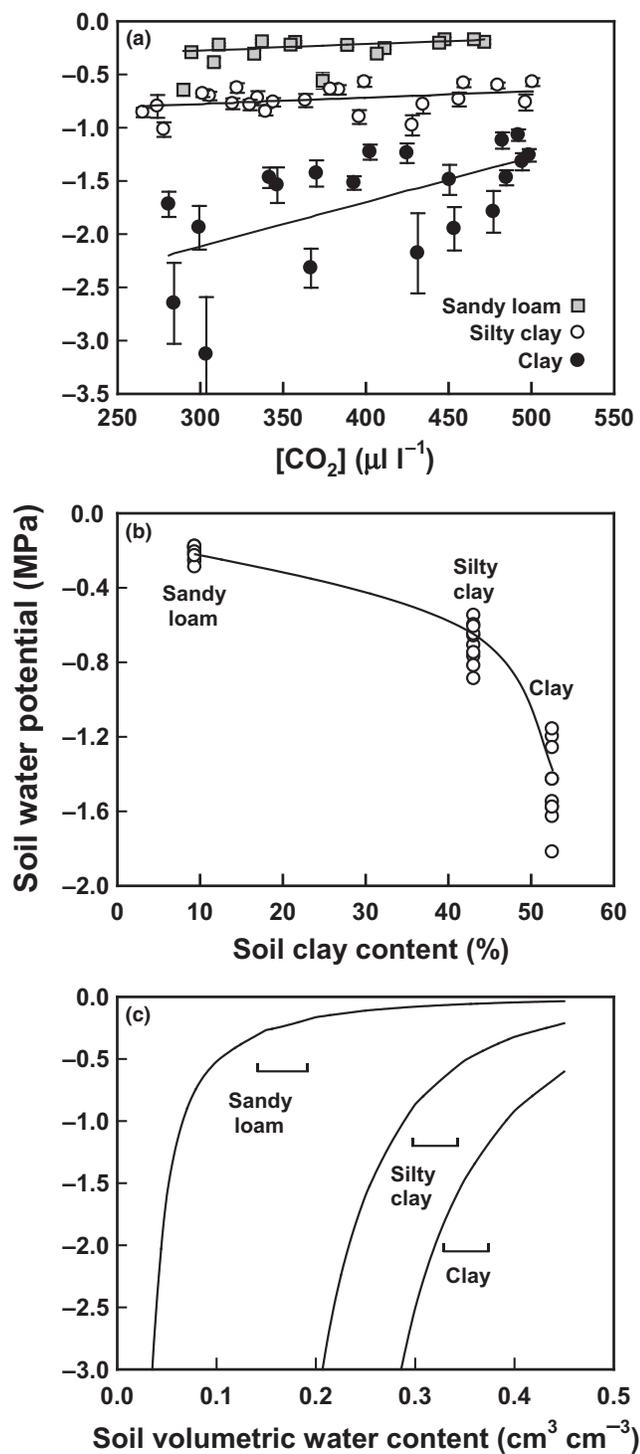
Fig. 5 Relationships between the soil water potential to 50 cm depth (Ψ_s) of three soil types and three variables: atmospheric $[CO_2]$ (a), soil percentage clay content (b) and volumetric water content (vSWC; c). Lines in (a) show linear regression fits to 10-yr averages per monolith ($\pm$ SE) for sandy loam (adj. $r^2 = 0.26$, $P = 0.04$, $n = 14$ after deleting two outlier points), silty clay (adj. $r^2 = 0.10$, $P = 0.08$, $n = 23$) and clay (adj. $r^2 = 0.31$, $P = 0.006$, $n = 20$) soils. Shown in (b) are the growing season means of Ψ_s for each of the 10 yr of CO_2 treatment. Brackets in (c) denote the range in growing season means of vSWC observed for each soil type. Ψ_s was calculated from measurements of vSWC using soil-specific Ψ_s–vSWC relationships developed using a dewpoint hygrometer.

The predominant pathways via which $[CO_2]$ and soil type influenced ANPP differed between SEMs fitted to the data from the first 5 yr vs final 5 yr of the experiment (Figs S3, S4). The soil effect on ANPP was entirely indirect for the first 5 yr of the experiment (2006–2010; Fig. S3), mediated through fSorg. By contrast, neither $[CO_2]$ nor the percentage clay content influenced the current year *Sorghastrum* fraction (fSorg) via a direct pathway during the final 5 yr of the experiment (2011–2015; Fig. S4).

Discussion

Contrary to our prediction that the ANPP–CO_2 response would differ among soils, we found that atmospheric $[CO_2]$ and soil type additively affected the aboveground productivity of perennial grassland communities. Increasing CO_2 from 280 to 480 $\mu l\, l^{-1}$ increased productivity by *c.* 170 g m^{-2} across soil types, a productivity enhancement comparable with that anticipated from a 290-mm increase in mean annual precipitation (MAP) across grasslands in the North American Central Plains (Sala *et al.*, 1988). Conversely, increasing clay content from 10% (sandy loam soil) to 50% (clay soil) reduced productivity by *c.* 50 g m^{-2}. Also contrary to prediction, CO_2 enrichment did not elicit a larger absolute increase in ANPP on soils with greatest mean ANPP (sandy loam, clay) or a larger relative increase in ANPP on the soil with the lowest mean water potential (clay). Initial soil differences in the ANPP–CO_2 response were also not amplified in later years by continued soil-specific increases in *Sorghastrum* dominance at elevated CO_2. Our results indicate a large positive influence of CO_2 enrichment from subambient to elevated concentrations on grassland productivity which, under the conditions of this experiment, was expressed similarly across soil types that differed in physical and related hydrological properties.

Three factors may explain why initial soil-specific effects on the ANPP–CO_2 response were not maintained over 10 yr. First, CO_2 effects on ANPP were primarily direct rather than mediated by soil differences in CO_2 effects on soil water or N. CO_2 and soil effects on water and N availability were apparently too small to significantly influence the ANPP–CO_2 response. Second, Ψ_s did not consistently regulate productivity across soil types. Water limitation frequently enhances the relative effect of CO_2 enrichment on productivity (Morgan *et al.*, 2004; Nowak *et al.*, 2004; Fatichi *et al.*, 2016), although this result is not universal (Dukes *et al.*, 2005; Hovenden *et al.*, 2014). In this experiment, however, Ψ_s apparently did not decline to levels sufficient to consistently constrain growth across soil types. Third, the progressive increase in *Sorghastrum* abundance at higher CO_2, which amplified soil differences in the ANPP–CO_2 response during the initial 3–5 yr of treatment (Fay *et al.*, 2012), ended following year 6, resulting in only a small *Sorghastrum*-mediated effect of CO_2 enrichment on ANPP over 10 yr. Year 6 (2011) was characterized by the most severe drought in Texas in a record extending to 1895 and was accompanied by elevated temperatures and evaporative demand (Hoerling *et al.*, 2013). Growing season temperatures in CO_2 chambers were higher in 2011 than during the 4 yr that
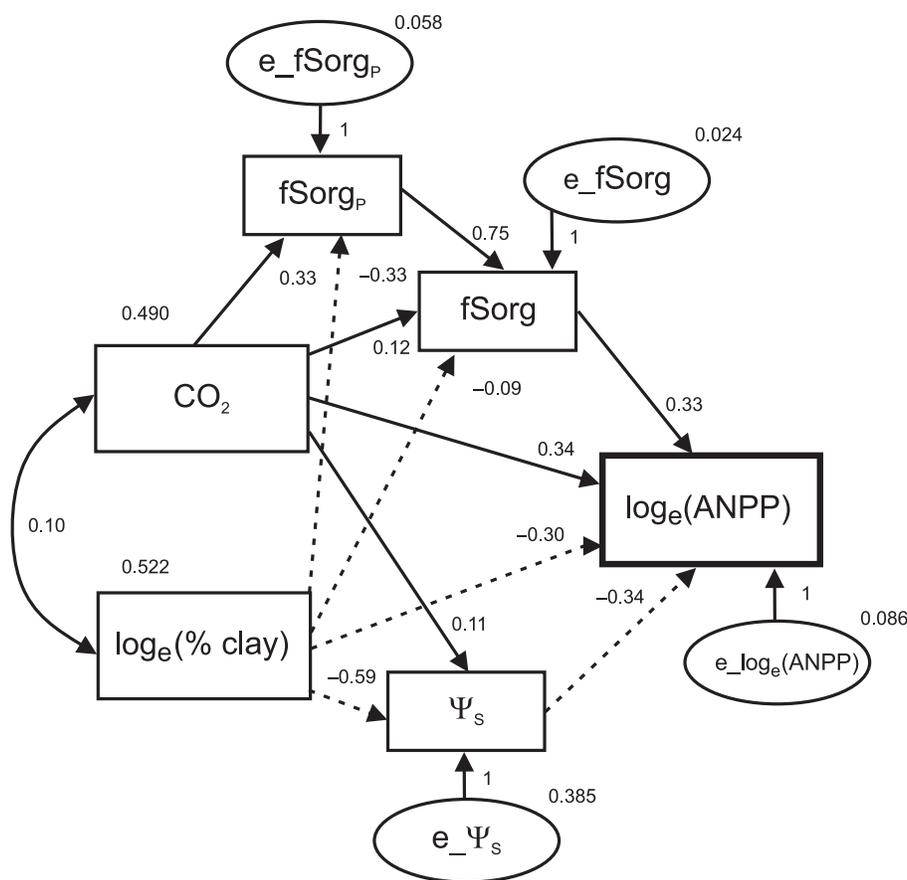
Fig. 6 Structural equation model of variables affecting the annual aboveground net primary productivity [$\log_e$(ANPP)] of grassland communities over a decade ($\chi^2 = 0.61$, df = 3, $P = 0.90$, RMSEA < 0.001, AIC = 48.6, $r^2 = 0.37$, $n = 590$). CO_2 concentration and soil type, the latter represented as $\log_e$(% clay content), are independent variables. The growing season mean of soil water potential to 50 cm depth (Ψ_s), the fractional contribution of the tallgrass *Sorghastrum* to community productivity (fSorg) and fSorg during the previous year (fSorg$_p$) are dependent variables. CO_2 and soil type co-vary, as indicated by the curved line, because the physical placement of monoliths of a given soil type along the Lysimeter CO_2 Gradient (LYCOG) facility was correlated with CO_2 treatment. Standardized coefficients are listed beside the paths linking the variables. Solid lines represent positive correlations. Dashed lines represent negative correlations. Numbers displayed above the boxes for independent variables are estimated variances for [CO_2]/100 or $\log_e$(% clay). Numbers displayed adjacent to the ovals are residual errors for dependent variables (e.g. e_fSorg).

preceded and followed 2011 (Fig. S2). The CO_2 effect on *Sorghastrum* abundance declined on all soils following 2011, possibly because increased evaporative demand disadvantaged this relatively drought-sensitive species (Swemmer *et al.*, 2006). Community change plays an important role in ecosystem response to global change drivers (Langley & Hungate, 2014), as it did in this experiment.

The predominant direct effect of CO_2 on ANPP is probably explained by increased photosynthetic WUE (assimilation rate/transpiration rate) (Fay *et al.*, 2012). Evapotranspiration rates were similar across the CO_2 gradient for prairie assemblages growing on a given soil type (Polley *et al.*, 2014); consequently, the CO_2-caused increase in WUE probably arose from increased canopy-level C assimilation rates. The genesis of the direct effect of soil percentage clay content on ANPP is difficult to discern from the available data, but soil effects were not explained by soil differences in water or N availability. Other mechanisms which may have contributed to a soil effect on productivity include soil differences in aeration, resistance to root penetration (Masle & Passioura, 1987; Wallace, 1987; Schrama *et al.*, 2013) and

limitation of ANPP by elements other than N (Niklaus & Körner, 2004; Polley *et al.*, 2016).

CO_2 and soil effects on ANPP were additive in this study, as initial soil differences in species succession diminished over time. Additive effects of climate change factors on diversity and productivity were also observed during the initial years of the Jasper Ridge Global Change Experiment (Shaw *et al.*, 2002; Zavaleta *et al.*, 2003). The more typical finding is that CO_2 effects on ANPP are conditioned by other productivity-regulating variables (e.g. Reich & Hobbie, 2013; Mueller *et al.*, 2016; Zhu *et al.*, 2016). Whether additive or interactive effects on ANPP prevail across soil types will probably depend on the extent to which growth-limiting resources vary among soils. The greater the range in resource levels among soils, the greater the likelihood that the ANPP–CO_2 response will differ among soils. Under the conditions of this experiment, however, CO_2 enrichment had a large and positive influence on grassland productivity that was expressed similarly across soil types. The initial ANPP–CO_2 response differed among soils because CO_2 effects on Ψ_s and *Sorghastrum* abundance differed among soils. Soil-related differences in CO_2 effects weakened during the

latter half of the experiment and did not influence across-soil responses over the decade-long study. Our results demonstrate a role of species differences and change in mediating soil effects on the ANPP–CO_2 response, but imply that CO_2 effects on productivity can be estimated across soils of different physical properties in some situations.

Author contributions

HWP and PAF supervised LYCOG operation and wrote the initial draft of the manuscript. All authors, including MJA, HPC, AEG, RAG, RBJ, VLJ, ARK and LGR, contributed to data collection, processing and summarization, and aided in writing the final version of the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article:

Fig. S1 Aerial view of the Lysimeter CO$_2$ Gradient (LYCOG) facility.

Fig. S2 Yearly irrigation and temperature in the CO$_2$ gradient experiment.

Fig. S3 Structural equation model of variables affecting the annual aboveground net primary productivity (log$_e$(ANPP)) of grassland communities during the first 5 yr of CO$_2$ treatment, 2006–2010.

Fig. S4 Structural equation model of variables affecting the annual aboveground net primary productivity (log$_e$(ANPP)) of grassland communities during the final 5 yr of CO$_2$ treatment, 2011–2015.

Table S1 Linear, mixed model tests of the responses of productivity, species abundances, and soil water and N to independent variables and variable interactions over a decade-long CO$_2$ enrichment experiment.

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