

**Research Article****SPECIAL ISSUE: Scaling Effects Regulating Plant Response to Global Change****Dominant plant taxa predict plant productivity responses to CO<sub>2</sub> enrichment across precipitation and soil gradients**Philip A. Fay<sup>1\*</sup>, Beth A. Newingham<sup>2,6</sup>, H. Wayne Polley<sup>1</sup>, Jack A. Morgan<sup>3</sup>, Daniel R. LeCain<sup>3</sup>, Robert S. Nowak<sup>4</sup> and Stanley D. Smith<sup>5</sup><sup>1</sup> Grassland, Soil, and Water Laboratory, USDA-ARS, 808 E Blackland Rd., Temple, TX 76502, USA<sup>2</sup> College of Natural Resources, University of Idaho, PO Box 441133, Moscow, ID 83844, USA<sup>3</sup> Rangeland Resources Research Unit, USDA-ARS, 1701 Centre Avenue, Fort Collins, CO 80526, USA<sup>4</sup> Department of Natural Resources and Environmental Science/MS 186, University of Nevada Reno, 1664 North Virginia, Reno, NV 89557, USA<sup>5</sup> School of Life Sciences, University of Nevada, Las Vegas, 4505 S. Maryland Parkway, Las Vegas, NV 89154, USA<sup>6</sup> Present address: Great Basin Rangelands Research, USDA-ARS, 920 Valley Rd., Reno, NV 89512, USA**Received:** 1 October 2014; **Accepted:** 13 March 2015; **Published:** 30 March 2015**Guest Editor:** Elise S. Gornish**Citation:** Fay PA, Newingham BA, Polley HW, Morgan JA, LeCain DR, Nowak RS, Smith SD. 2015. Dominant plant taxa predict plant productivity responses to CO<sub>2</sub> enrichment across precipitation and soil gradients. *AoB PLANTS* 7: plv027; doi:10.1093/aobpla/plv027

**Abstract.** The Earth's atmosphere will continue to be enriched with carbon dioxide (CO<sub>2</sub>) over the coming century. Carbon dioxide enrichment often reduces leaf transpiration, which in water-limited ecosystems may increase soil water content, change species abundances and increase the productivity of plant communities. The effect of increased soil water on community productivity and community change may be greater in ecosystems with lower precipitation, or on coarser-textured soils, but responses are likely absent in deserts. We tested correlations among yearly increases in soil water content, community change and community plant productivity responses to CO<sub>2</sub> enrichment in experiments in a mesic grassland with fine- to coarse-textured soils, a semi-arid grassland and a xeric shrubland. We found no correlation between CO<sub>2</sub>-caused changes in soil water content and changes in biomass of dominant plant taxa or total community aboveground biomass in either grassland type or on any soil in the mesic grassland ( $P > 0.60$ ). Instead, increases in dominant taxa biomass explained up to 85 % of the increases in total community biomass under CO<sub>2</sub> enrichment. The effect of community change on community productivity was stronger in the semi-arid grassland than in the mesic grassland, where community biomass change on one soil was not correlated with the change in either the soil water content or the dominant taxa. No sustained increases in soil water content or community productivity and no change in dominant plant taxa occurred in the xeric shrubland. Thus, community change was a crucial driver of community productivity responses to CO<sub>2</sub> enrichment in the grasslands, but effects of soil water change on productivity were not evident in yearly responses to CO<sub>2</sub> enrichment. Future research is necessary to isolate and clarify the mechanisms controlling the temporal and spatial variations in the linkages among soil water, community change and plant productivity responses to CO<sub>2</sub> enrichment.

**Keywords:** Central Plains grasslands; climate change; community change; Mojave Desert; primary productivity; rangelands; threshold responses.

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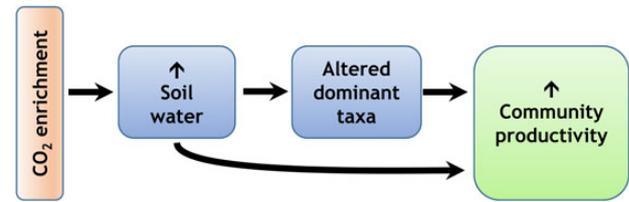
## Introduction

Continued enrichment of the Earth's atmosphere with carbon dioxide (CO<sub>2</sub>) is certain through the coming century and is expected to alter climate and terrestrial ecosystem structure and function. In water-limited ecosystems, one major mechanism by which CO<sub>2</sub> enrichment may cause ecosystem change is by increasing soil water (Morgan et al. 2004b; Nowak et al. 2004a). CO<sub>2</sub> enrichment can increase soil water by reducing stomatal conductance and leaf- and canopy-scale transpiration in both C<sub>3</sub> and C<sub>4</sub> species (Nowak et al. 2004b; Ainsworth and Long 2005). Lower stomatal conductance and plant transpiration under CO<sub>2</sub> enrichment in turn decreases soil water depletion, which results in higher soil water and potentially reduced water limitation of ecosystem processes compared with ambient CO<sub>2</sub>.

Increased soil water with CO<sub>2</sub> enrichment generally increases the productivity of water-limited plant communities. Greater productivity increases often occur with lower precipitation across precipitation levels typical of grassland ecosystems (Owensby et al. 1996; Morgan et al. 2004b; Nowak et al. 2004b; Körner 2006; Polley et al. 2011), because the increased soil water under CO<sub>2</sub> enrichment is more likely to relieve water limitation (Nowak et al. 2004b). However, in severely water-limited systems such as deserts, CO<sub>2</sub> enrichment may not increase productivity if reduced leaf transpiration is offset by increased leaf area because soil water may not increase. In addition, slow growth rates in drought-adapted desert plants limit the potential to increase community productivity in the short-term (Nowak et al. 2004b; Newingham et al. 2013).

Plant community change is another mechanism by which CO<sub>2</sub> enrichment may increase community productivity (Bradley and Pregitzer 2007; Gornish and Tylianakis 2013). Community change is most likely to alter community productivity when change involves the dominant plant taxa (Smith and Knapp 2003). Smith et al. (2009) suggested that altered resource availability drives the ecosystem change primarily by causing community change. If true, increased soil water with CO<sub>2</sub> enrichment would result in changes in dominant taxa abundance, which would in turn increase productivity. However, increased soil water alone can also result in community productivity increases (Fig. 1).

The contributions of increased soil water and community change to increased community productivity with CO<sub>2</sub> enrichment are also expected to differ with soil texture. At precipitation levels typical of grasslands, soil water will be lower on coarse-textured than fine-textured soils, increasing water limitation of community productivity, and thus the importance of soil water increases in



**Figure 1.** Model by which increased soil water resulting from atmospheric CO<sub>2</sub> enrichment may increase plant community productivity in water-limited ecosystems. The increase in soil water may predict the increase in community productivity, or the effect of soil water increase may be mediated by change in the abundance of dominant plant taxa, which in turn predicts the increase in community productivity.

regulating productivity. For example, over 4 years of CO<sub>2</sub> enrichment, the increase in plant aboveground biomass was best predicted by soil water on a coarse-textured soil, but increases in biomass were best predicted by the abundance of a dominant grass species on a fine-textured soil (Fay et al. 2012), which accounted for up to 60 % of the effect of CO<sub>2</sub> enrichment (Polley et al. 2012b).

To investigate how water-limited plant communities respond to CO<sub>2</sub> enrichment across varying precipitation amounts and soils, we examined soil water, plant community change and plant productivity responses to CO<sub>2</sub> enrichment in five multi-year CO<sub>2</sub> enrichment experiments from mesic and semi-arid grasslands and in a xeric shrubland in the central and western USA. The experiments span a 6-fold range of mean annual precipitation (MAP), which provides a test of variation in CO<sub>2</sub> responses with precipitation. The mesic grassland experiment contained fine and coarse-textured soils, providing a test of texture effects on CO<sub>2</sub> responses. Interannual variability in precipitation is often high in water-limited systems, and so yearly community productivity increases from CO<sub>2</sub> enrichment were correlated with increases in soil water and community change.

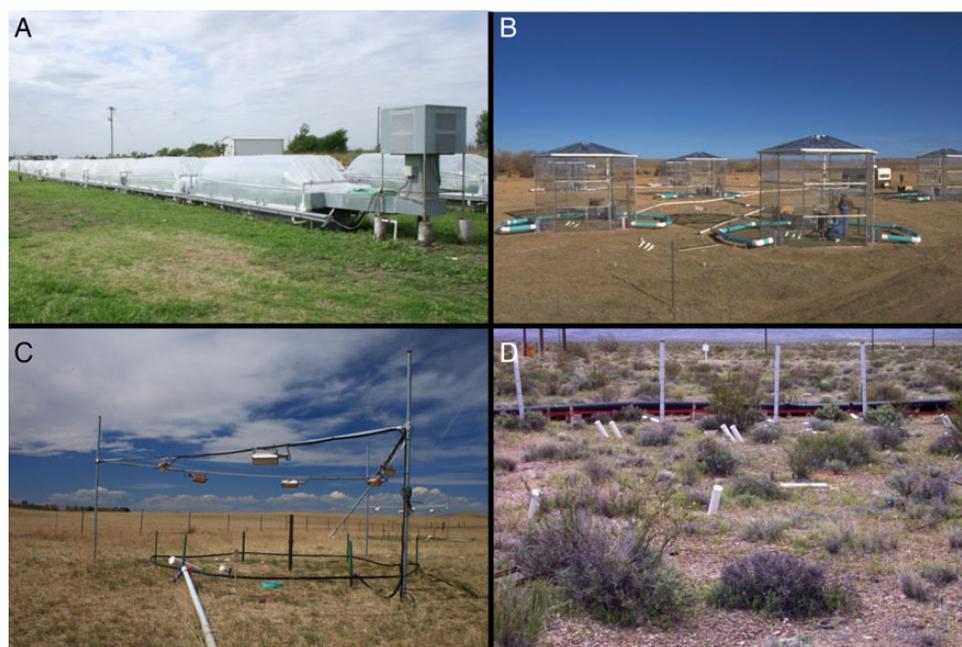
## Methods

### Sites and experiments

**Mesic grassland.** Two CO<sub>2</sub> enrichment experiments were conducted at Temple, TX, USA, in the southern portion of the North American tallgrass prairie, a region of humid subtropical climate with warm summers and abundant precipitation (Table 1). The Prairie CO<sub>2</sub> Gradient (PCG, Fig. 2A, Johnson et al. 2000) experiment manipulated CO<sub>2</sub> using two chambers (1 m tall, 1 m wide and 60 m long) placed on an intact formerly grazed pasture. The C<sub>4</sub> perennial grass *Bothriochloa ischaemum* accounted for 51 % of aboveground biomass, accompanied by C<sub>3</sub> perennial forbs, primarily *Solanum dimidiatum* and *Ratibida columnaris* (Polley et al. 2003). In one chamber,

**Table 1.** Location, climate and CO<sub>2</sub> treatments for the four experiments. MAP, mean annual precipitation; MAT, mean annual temperature.

Experiment	CO <sub>2</sub> treatments ( $\mu\text{mol mol}^{-1}$ )	Location, lat., long.	Elevation (m)	MAP (mm)	MAT (max, °C)	MAT (min, °C)
PCG	200–550	Texas, USA; 31°05', –97°20'	186	914	35	3
LYCOG	250–500	Texas, USA; 31°05', –97°20'	186	914	35	3
OTC	360 and 720	Colorado, USA; 40°40', –104°45'	1555	320	16	0.5
PHACE	385 and 600	Wyoming, USA; 41°11', –104°54'	1930	384	18	–3
NDDF	375 and 550	Nevada, USA; 36°46', –115°57'	970	148	38	–5

**Figure 2.** CO<sub>2</sub> manipulation experiments included in the study. (A) Carbon dioxide gradient chambers used in PCG and LYCOG experiments in mesic grassland (Photo: P. Fay, USDA-ARS). (B) Open-top chambers used in short-grass steppe experiment (Photo: S. Cox, USDA-ARS). (C) Free-air CO<sub>2</sub> enrichment technology used in mixed-grass prairie PHACE experiment (Photo: S. Cox, USDA-ARS). (D) FACE plot used in xeric shrubland experiment (L. Fenstermaker, Desert Research Institute).

CO<sub>2</sub>-enriched air was introduced at the chamber entrance, and photosynthesis by the enclosed vegetation depleted the air of CO<sub>2</sub> as it transited the length of the chamber. Air flow rates were controlled to create a 550–350  $\mu\text{mol mol}^{-1}$  gradient in CO<sub>2</sub>. Similarly, ambient air was supplied to the second chamber, which was controlled to create a 365–200  $\mu\text{mol mol}^{-1}$  gradient. The chambers were divided into 5 m sections, and air was cooled and dehumidified in each section to maintain air temperature and vapour pressure deficit near ambient conditions. The CO<sub>2</sub> gradients were maintained during the growing seasons of 1997–2000.

The Lysimeter CO<sub>2</sub> Gradient (LYCOG) experiment was the successor to the PCG experiment and adapted the PCG chambers to enclose 60 intact soil monoliths (1.5 m<sup>3</sup>) from a silty clay, a sandy loam and a heavy

clay soil, arranged in a stratified random design along the two chambers (Fig. 2A; Polley et al. 2008; Fay et al. 2009). The monoliths supported well-established, constructed communities of native prairie. The C<sub>4</sub> grasses *Sorghastrum nutans*, *Bouteloua curtipendula*, *Schizachyrium scoparium* and *Tridens albescens* accounted for 80 % of total aboveground biomass. The remainder was C<sub>3</sub> forbs (*Solidago canadensis*, *Salvia azurea*) and one legume (*Desmanthus illinoensis*; Fay et al. 2012; Polley et al. 2012a). Other species were regularly removed by hand or selective glyphosate application. Air temperature and vapour pressure deficit were controlled as for PCG; CO<sub>2</sub> concentration was maintained at 500–380 and 380–250  $\mu\text{mol mol}^{-1}$  during 2006–10. In both experiments, irrigation regimes were representative of average growing season precipitation for the site.

**Semi-arid grassland.** Two CO<sub>2</sub> enrichment experiments were conducted in a cold semi-arid steppe region of northeastern Colorado and southeastern Wyoming, characterized by cooler summers than the other sites (Table 1). Semi-arid grasslands are more water-limited than mesic grasslands, are dominated by a different, more drought tolerant assemblage of species and are predicted to be more responsive in plant productivity to CO<sub>2</sub> enrichment than mesic grasslands (Morgan et al. 2004b). An open-top chamber (OTC, Fig. 2B) experiment was conducted during 1996–2001 in short-grass steppe near Fort Collins, Colorado. Basal cover of the vegetation was ~25%. Two perennial C<sub>3</sub> grasses *Pascopyrum smithii* and *Hesperostipa comata* accounted for 60% of aboveground biomass, accompanied by a C<sub>4</sub> grass, *Bouteloua gracilis*, and forbs (Morgan et al. 2001, 2004a). Six circular plots of 15.5 m<sup>2</sup> were fitted with OTCs which were randomly assigned to maintain an ambient CO<sub>2</sub> level of 360 μmol mol<sup>-1</sup> or an elevated CO<sub>2</sub> level of 720 μmol mol<sup>-1</sup> during the growing season.

The Prairie Heating and CO<sub>2</sub> Experiment (PHACE, Fig. 2C) was conducted in a northern mixed prairie near Cheyenne, Wyoming (Parton et al. 2007). Cool-season C<sub>3</sub> grasses, mostly *P. smithii* and *H. comata*, account for 75% of aboveground biomass. C<sub>4</sub> grasses, almost exclusively *B. gracilis*, and sedges, forbs and small shrubs account for the rest (Morgan et al. 2011). PHACE treatments were factorial combinations of two levels of CO<sub>2</sub>; ambient = 385 μmol mol<sup>-1</sup> and elevated = 600 μmol mol<sup>-1</sup> achieved using Free-Air CO<sub>2</sub> Enrichment (FACE) technology, and ambient or warmed temperature regimes (+1.5/3.0 day/night), with five replications each. Treatments were randomly assigned to twenty 3.3 m diameter circular plots. Here we consider data from 2006 to 2009 from ambient temperature treatments.

**Xeric shrubland.** The Nevada Desert FACE Facility (NDFF, Fig. 2D) was located in the Mojave Desert in southern Nevada, USA, on the Nevada National Security Site, formerly the Nevada Test Site. The climate is mid-latitude desert with the lowest annual precipitation of the sites (Table 1) and was thus predicted to be the least responsive to CO<sub>2</sub> enrichment due to severe water limitation. Most precipitation occurs during the winter. The NDFF used the FACE technology with three ambient plots averaging 375 μmol mol<sup>-1</sup>, three elevated plots averaging 550 μmol mol<sup>-1</sup> CO<sub>2</sub> and three non-blower control plots without FACE infrastructure; all plots were 23 m in diameter. The NDFF experiment was conducted from April 1997 to June 2007. Experimental plots were in a *Larrea tridentata*—*Ambrosia dumosa* desert scrub community, which consisted of C<sub>3</sub> shrubs, forbs, annuals and a C<sub>4</sub> bunchgrass (Jordan et al. 1999).

## Sampling and data analysis

We used previously published data on soil water content, and dominant taxa and total community aboveground biomass to estimate soil water change, community change and community productivity change in each year of CO<sub>2</sub> enrichment. All sites measured vertical profiles of volumetric soil water content (Nelson et al. 2004; Nowak et al. 2004a; Parton et al. 2007; Fay et al. 2009). In LYCOG soil water potential was calculated from soil water content using soil water characteristic curves for each soil (Fay et al. 2012). At the grassland sites, dominant taxa and community biomass were estimated annually from the dry mass of current-year standing aboveground biomass. Aboveground biomass in the xeric shrubland experiment was determined by a single harvest of standing aboveground biomass after 10 years of CO<sub>2</sub> enrichment (Newingham et al. 2013), and responses of dominant species were determined as in Newingham et al. (2014).

The response ratio  $\beta$  (Amthor and Koch 1996; eq. 1) was computed from the dominant taxa biomass, community biomass, and growing season mean volumetric soil water content at enriched (C<sub>E</sub>) and ambient (C<sub>A</sub>) CO<sub>2</sub> each year.

$$\beta = \frac{(Y_E/Y_A) - 1}{\ln(C_E/C_A)} \quad (1)$$

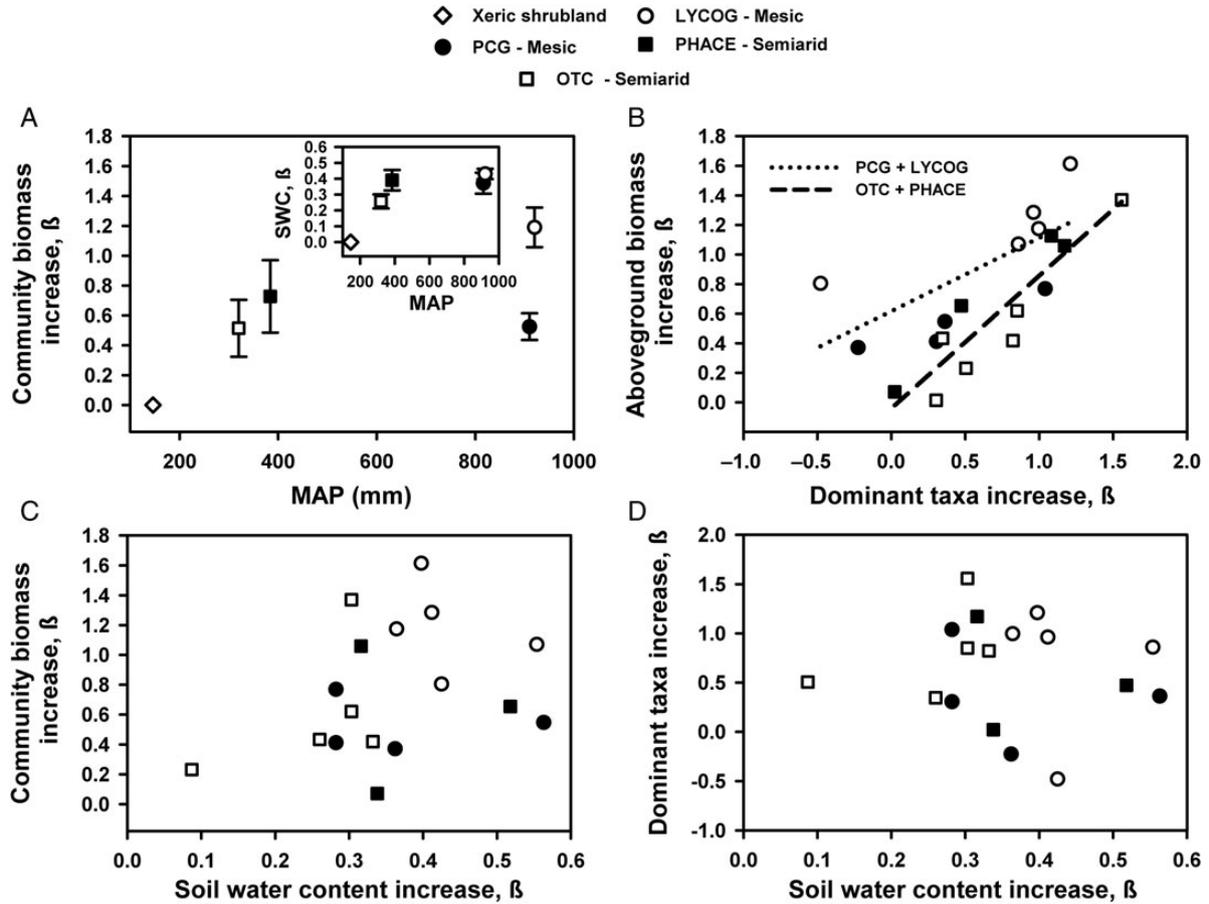
The calculation of  $\beta$  standardizes the responses for different levels of CO<sub>2</sub> used among the experiments.

Soil water content  $\beta$  was calculated for the soil depth that best predicted aboveground biomass: 0–135 cm (PCG), 0–40 cm (LYCOG), 70–100 cm (OTC) and 5–25 cm (PHACE). We calculated  $\beta$  in the mesic grassland CO<sub>2</sub> gradients from values of biomass and soil water content at 500 and 390 μL L<sup>-1</sup> CO<sub>2</sub>. These values were estimated from linear regressions of biomass and soil water content against CO<sub>2</sub> for each year. In LYCOG, regressions were fit across all three soils and for each soil separately. The  $\beta$  values were not calculated for the xeric shrubland because there were no responses to CO<sub>2</sub> enrichment in growing season soil water content and no on-going responses in total or dominant taxa aboveground biomass. Correlations among the  $\beta$  for community biomass, soil water content and dominant taxa were tested with linear regression analysis. The magnitude of community biomass  $\beta$  with no community change was estimated from the y-intercept of community biomass  $\beta$ /dominant taxa  $\beta$  regressions.

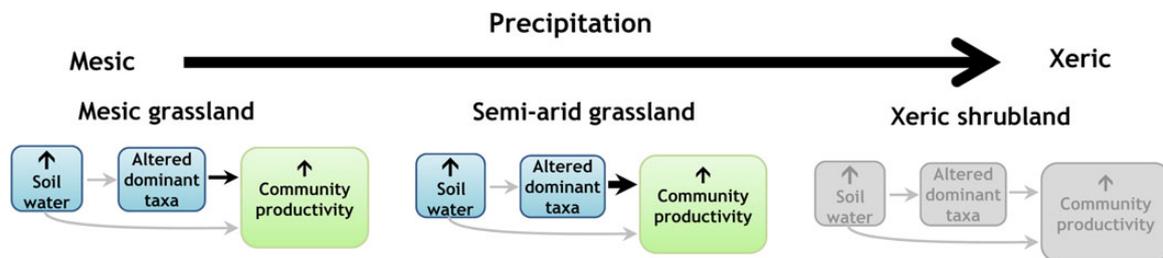
## Results

### Precipitation gradient

**Mesic grassland.** Mean community biomass  $\beta$  was 0.52 in PCG and 1.19 in LYCOG (Fig. 3A), corresponding to



**Figure 3.** Relationships among community aboveground biomass, MAP, dominant plant taxa biomass and soil water content (SWC) responses to CO<sub>2</sub> enrichment in xeric shrubland, mesic grassland and semi-arid grassland CO<sub>2</sub> enrichment experiments. (A) Community biomass  $\beta$ , mean  $\pm$  SE across all years of CO<sub>2</sub> manipulation for each experiment, plotted by site MAP. Inset is the corresponding mean  $\pm$  SE soil water content  $\beta$ . (B) Relationship between annual values of  $\beta$  for community biomass and dominant plant taxa, with linear regressions fit separately to mesic grassland and semi-arid grassland experiments. (C and D) Relationships of community biomass  $\beta$  and dominant plant taxa  $\beta$  to soil water content  $\beta$ .



**Figure 4.** Summary of correlations among changes in soil water, abundance of dominant plant taxa and plant community biomass increases with CO<sub>2</sub> enrichment in mesic grassland, semi-arid grassland and xeric shrubland. Solid arrows denote positive correlations among variables, and thicker lines denote stronger relationships. Grey boxes indicate no significant CO<sub>2</sub> enrichment effects, and grey lines indicate no correlations.

community biomass increases with CO<sub>2</sub> enrichment of 15 and 29 %, respectively. Mean soil water content  $\beta$  was 0.37 for PCG and 0.43 for LYCOG (Fig. 3A, inset), corresponding to 9–10 % increases in soil water content.

Carbon dioxide enrichment altered the abundance of dominant grasses in both mesic grassland CO<sub>2</sub> experiments. In LYCOG, C<sub>4</sub> grass  $\beta$  ranged from –0.9 to 1.2.

In PCG, C<sub>4</sub> grass  $\beta$  ranged from –0.23 to 1.0 (Fig. 3B), corresponding to –20 to 90 % changes in C<sub>4</sub> grass biomass. Across both experiments, community biomass  $\beta$  increased with the C<sub>4</sub> grass  $\beta$  ( $R^2 = 0.43$ ,  $P = 0.03$ , Fig. 3B). The community biomass  $\beta$  at the y-intercept was 0.6, equating to a 15 % increase in community biomass with CO<sub>2</sub> enrichment in the absence of change in C<sub>4</sub> grass biomass. The values of

$\beta$  for community and C<sub>4</sub> grass biomass were not correlated with soil water content  $\beta$  ( $P > 0.69$ , Fig. 3C and D).

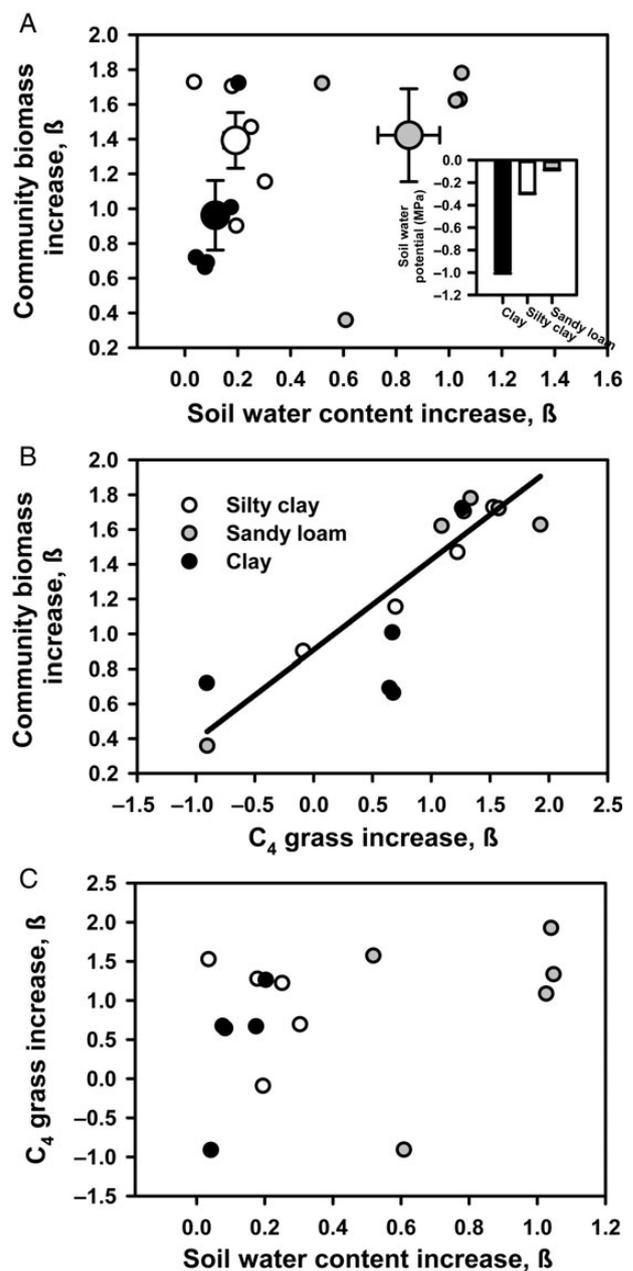
**Semi-arid grassland.** Mean community biomass  $\beta$  was 0.51 in OTC and 0.73 in PHACE (Fig. 3A), corresponding to 31 and 35 % increases, respectively, in community biomass under CO<sub>2</sub> enrichment. Mean soil water content  $\beta$  averaged 0.26 for OTC and 0.39 for PHACE (Fig. 3A, inset), corresponding to 17–18 % increases in soil water content.

Carbon dioxide enrichment increased the abundance of the dominant plant taxa in both semi-arid grassland experiments. C<sub>3</sub> grass  $\beta$  averaged 0.65 in the OTC experiment and 0.30 in the PHACE experiment (Fig. 3B), corresponding to 30–50 % increases with CO<sub>2</sub> enrichment. Community biomass  $\beta$  strongly increased with the C<sub>3</sub> grass  $\beta$  (slope = 0.90,  $R^2 = 0.81$ ,  $P = 0.0002$ , Fig. 3B), with a slope nearly twice that of the community–C<sub>4</sub> grass  $\beta$  relationship for mesic grassland (slope = 0.50, Figs 3B and 4). The community biomass  $\beta$  at the y-intercept was 0, indicating that there was no community biomass increase with CO<sub>2</sub> enrichment in the absence of change in C<sub>3</sub> grass biomass. As in the mesic grassland,  $\beta$  values for community biomass and C<sub>3</sub> grass biomass were not correlated with soil water content  $\beta$  across the two experiments ( $P > 0.59$ , Figs 3C and D and 4).

**Xeric shrubland.** The xeric shrubland responses to CO<sub>2</sub> enrichment were a dramatic departure from those of the mesic and semi-arid grasslands. Carbon dioxide enrichment at the NDFP had no effect on soil water content (Nowak et al. 2004a) or on cumulative total aboveground and belowground biomass (Newingham et al. 2013) and productivity of dominant annual plant taxa (Smith et al. 2014; Fig. 4) following 10 years of CO<sub>2</sub> enrichment. Thus, there was no basis for testing correlations among  $\beta$  values for soil water content, dominant taxa and aboveground biomass in this system.

### Soils gradient

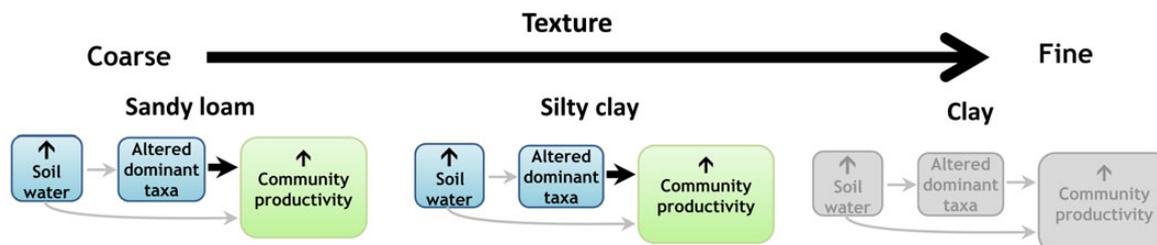
The total community biomass increase resulting from CO<sub>2</sub> enrichment varied considerably among soil types in the LYCOG experiment. Mean community biomass  $\beta$  was 1.0 on the fine-textured clay soil and 1.4 on the silty clay and sandy loam soils (Fig. 5A), corresponding to 23–35 % increases in aboveground biomass with CO<sub>2</sub> enrichment. Soil water content mean  $\beta$  was 0.1–0.2 (range 0.03–0.31) in the clay and silty clay soils, increasing to 0.85 (range 0.50–1.04) on the sandy loam soil (Fig. 5A), which also had the highest mean soil water potential (Fig. 5A, inset). These values of  $\beta$  corresponded to 1–26 % increases in soil water content with CO<sub>2</sub> enrichment. Community biomass  $\beta$  was not correlated with soil water content  $\beta$  on any soil



**Figure 5.** Relationships among community aboveground biomass, dominant plant taxa biomass and soil water content responses to CO<sub>2</sub> enrichment in the three soils in the LYCOG experiment in mesic grassland. (A) Community biomass  $\beta$ , mean  $\pm$  SE across all years of CO<sub>2</sub> manipulation in relation to soil water content  $\beta$ . Large symbols denote means  $\pm$  SEs across years for each soil. Inset is the corresponding mean  $\pm$  SE soil water potential for each soil type. (B) Community biomass  $\beta$  relationship to C<sub>4</sub> grass  $\beta$ , with linear regressions fit to silty clay and sandy loam soils. (C) C<sub>4</sub> grass  $\beta$  relationship to soil water content  $\beta$ .

individually ( $0.06 < P < 0.41$ , Figs 5A and 6) or across all soils ( $P = 0.09$ ).

The value of  $\beta$  for C<sub>4</sub> grasses ranged from  $-1.0$  to  $2.0$  across all soils (Fig. 5B), corresponding to  $-41$  to  $130$  %



**Figure 6.** Summary of correlations among changes in soil water, abundance of dominant plant taxa and plant community biomass increases with CO<sub>2</sub> enrichment on three soils in mesic grassland. Solid arrows denote positive correlations among variables, and thicker lines denote stronger relationships. Grey boxes indicate no significant CO<sub>2</sub> enrichment effects, and grey lines indicate no correlations.

changes in *C*<sub>4</sub> biomass with CO<sub>2</sub> enrichment. The community biomass  $\beta$  increased with *C*<sub>4</sub> grass  $\beta$  on the silty clay and sandy loam soils (slope = 0.52,  $R^2 = 0.90$ ,  $P = <0.0001$ ). The community biomass  $\beta$  on these two soils was 0.9 at the *y*-intercept for *C*<sub>4</sub> grass  $\beta$ , equating to a 2 % increase in community biomass with CO<sub>2</sub> enrichment in the absence of change in *C*<sub>4</sub> grass biomass. Community biomass  $\beta$  was not correlated with *C*<sub>4</sub> grass  $\beta$  on the clay soil ( $P = 0.31$ , Fig. 5B). Dominant grass  $\beta$  was not correlated with soil water content  $\beta$  for any soil ( $0.28 < P < 0.58$ ; Figs 5C and 6).

## Discussion

Carbon dioxide enrichment can increase the productivity of communities solely by increasing soil water or by mediating community change. Soil water increases were expected to cause larger community productivity responses with lower precipitation and on coarser-textured soils in the grasslands, but responses were expected to decline sharply in the extreme aridity of the xeric shrubland. Our findings indicate that in the grasslands, yearly soil water content increases never predicted community change or community productivity. Instead, community change caused a larger community productivity response in semi-arid than that in mesic grasslands, and the predicted sharp decline in responsiveness to CO<sub>2</sub> was supported in the xeric shrubland.

The absence of cumulative increases in community productivity with CO<sub>2</sub> enrichment in the xeric shrubland may be explained by the absence of increased soil water and community change. There was no sustained increase in soil water content (Nowak et al. 2004a) because CO<sub>2</sub> enrichment only increased photosynthesis and water-use efficiency and decreased stomatal conductance in occasional wet years (Nowak et al. 2001; Naumburg et al. 2003; Housman et al. 2006; Aranjuelo et al. 2011). There was also no sustained community change because the dominant perennial species were unaffected by CO<sub>2</sub> enrichment (Newingham et al. 2014), and responses were confined to native and exotic annuals which transiently increased with CO<sub>2</sub> enrichment only during high rainfall years (Smith et al. 2000, 2014).

Thus, the mechanisms proposed as the fundamental drivers of productivity increases with CO<sub>2</sub> enrichment in water-limited ecosystems were largely absent in this arid ecosystem.

In the grasslands, the absent correlations between soil water content change, community change and community productivity increases suggests that effects of increased soil water on plant productivity were not well represented by the growing season mean soil moisture response. Increased soil water content may not always translate into greater plant growth because plant growth exhibits a threshold response to soil water (Lambers et al. 2008). Soil water variability, such as an increased duration or severity of soil water deficit, in current or previous years may lower community productivity (Polley et al. 2002; Fay et al. 2003, 2011; Heisler-White et al. 2008; Hovenden et al. 2014; Reichmann and Sala 2014), and the CO<sub>2</sub> effect on soil water during drought periods may be a better predictor of productivity responses than the mean response in soil water over the growing season.

The lack of correlation between yearly soil water change and community responses differs from previous findings. Averaged over multiple years of CO<sub>2</sub> enrichment, increased community productivity occurred in part because of increased soil water in these grassland experiments (Polley et al. 2003; Nelson et al. 2004; Morgan et al. 2011; Fay et al. 2012). The importance of soil water increases averaged over multiple years but not in any given year suggests that predictors of community change or productivity responses at one temporal scale may not apply at other scales in these grasslands (Peters et al. 2004).

Community change was a stronger predictor of community productivity increases in the drier semi-arid grassland compared with the mesic grassland. The weaker relationship to community change in mesic grassland stemmed from 2 years when CO<sub>2</sub> enrichment increased plant productivity but decreased the dominant taxa (Fig. 3B), indicating that productivity of other species in these mesic grassland communities increased with CO<sub>2</sub> enrichment enough to offset decreases in the dominants. In contrast, the dominant taxa never decreased in the semi-arid grassland. Offsetting responses within

communities may dampen the productivity response to CO<sub>2</sub> in mesic grassland (Hooper et al. 2005), and both dominant and sub-dominant taxa can contribute to community productivity responses to CO<sub>2</sub> enrichment.

Two other factors may have contributed to the stronger community change effect on community productivity increases in the semi-arid grassland. First, lower MAP and higher mean soil water content increases with CO<sub>2</sub> enrichment may have resulted in release from water limitation for all community members in the semi-arid grassland compared with the mesic grassland. Second, in the mesic grassland, there was no community change effect on community productivity on the clay soil. The strong community change/productivity responses occurred on the two soils with high mean soil water potential (Fay et al. 2012), suggesting that the overall availability of soil water, not the increase in soil water content, determines community and productivity responses to CO<sub>2</sub> enrichment.

In the semi-arid grassland during years with no community change, there was no increase in community biomass, suggesting that yearly increases in community productivity were almost completely explained by community change. Although community change was a weaker predictor of community productivity change in mesic grassland, it still predicted ~80 % of the productivity response. These results suggest that, in years with no community change, community productivity increased by 15–22 % from other potential causes, such as direct effects of CO<sub>2</sub> enrichment on carbon gain or plant water status (Ainsworth and Long 2005).

## Conclusions

Community change predicted most of the changes in community productivity in the grasslands and better predicted community productivity responses in the drier grassland and on soils with higher plant availability of soil water in the mesic grassland. The xeric shrubland makes clear that in the absence of increased soil water or community change, increased community productivity is unlikely. The linkage of community change and productivity to yearly changes in soil water with CO<sub>2</sub> enrichment remains unclear, but it may depend more on the temporal variability in soil water than on the size of the increase. Future research needs to isolate and clarify the temporal and spatial mechanisms controlling the linkages among soil water, community change and plant productivity responses to CO<sub>2</sub> enrichment.

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## Contributions by the Authors

P.A.F. and B.A.N. conceived the manuscript and led the writing, P.A.F. analysed the data and the remaining authors contributed data, edited the manuscript and approved the submission.

## Conflict of Interest Statement

None declared.

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