

REVIEW PAPER

Impacts of climate change drivers on C₄ grassland productivity: scaling driver effects through the plant community

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Received 2 October 2013; Revised 2 December 2013; Accepted 17 December 2013

Abstract

Climate change drivers affect plant community productivity via three pathways: (i) direct effects of drivers on plants; (ii) the response of species abundances to drivers (community response); and (iii) the feedback effect of community change on productivity (community effect). The contribution of each pathway to driver–productivity relationships depends on functional traits of dominant species. We used data from three experiments in Texas, USA, to assess the role of community dynamics in the aboveground net primary productivity (ANPP) response of C₄ grasslands to two climate drivers applied singly: atmospheric CO₂ enrichment and augmented summer precipitation. The ANPP–driver response differed among experiments because community responses and effects differed. ANPP increased by 80–120 g m⁻² per 100 µl l⁻¹ rise in CO₂ in separate experiments with pasture and tallgrass prairie assemblages. Augmenting ambient precipitation by 128 mm during one summer month each year increased ANPP more in native than in exotic communities in a third experiment. The community effect accounted for 21–38% of the ANPP CO₂ response in the prairie experiment but little of the response in the pasture experiment. The community response to CO₂ was linked to species traits associated with greater soil water from reduced transpiration (e.g. greater height). Community effects on the ANPP CO₂ response and the greater ANPP response of native than exotic communities to augmented precipitation depended on species differences in transpiration efficiency. These results indicate that feedbacks from community change influenced ANPP–driver responses. However, the species traits that regulated community effects on ANPP differed from the traits that determined how communities responded to drivers.

Key words: Atmospheric CO₂ concentration, C₄ perennial grassland, evapotranspiration, exotic plants, plant community composition, pasture, precipitation, tallgrass prairie, transpiration efficiency, water-use efficiency.

Introduction

Boosting primary productivity is a must if we are to feed and secure the energy requirements of an expanding and increasingly affluent human population. Several of the papers in this special issue attest to progress in genetically modifying plants

to increase productivity. It is important to recognize, however, that the selection pressures under which many species evolved resulted in relatively low productivity. Species in many natural and semi-natural ecosystems, including C₄-dominated

Abbreviations: A, net photosynthesis; ANPP, aboveground net primary productivity; ET, evapotranspiration; g_s, stomatal conductance; SE, standard error; SEM, structural equation modelling; TE, transpiration efficiency; WUE, water-use efficiency.

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grasslands, were and are subject to selection pressures, such as resource (e.g. water) limitation and frequent disturbances (Osborne and Sack, 2012; Scheiter *et al.*, 2012). These selection pressures often favour plants that use resources conservatively, are short-statured, or allocate a relatively large fraction of plant carbon (C) to root systems, all of which may limit maximum aboveground growth rate.

Grassland plants increasingly also are subject to physiological and environmental modifications associated with climate change drivers (Polley *et al.*, 2013). The influence of climate change drivers on aboveground net primary productivity (ANPP), as on other ecosystem processes, includes at least three components: (i) the direct, often physiological, responses of plants to drivers, termed ‘direct ecosystem responses’ (Smith *et al.*, 2009); (ii) the impact of climate drivers on plant community composition; and (iii) feedback effects of community change on ecosystem processes (Suding *et al.*, 2008). Direct, physiological responses of plants to climate drivers, such as changes in photosynthesis, typically occur rapidly, depend on plant functional traits, and can accrue to affect plant growth and ANPP. Net ecosystem C uptake increased more following a 1–2 d increase in CO₂ in C₃- than C₄-dominated vegetation, for example (Polley *et al.*, 2007). Drivers also may influence ANPP by shifting the relative abundances, composition, richness, or functional diversity of species in plant communities (collectively, community composition) (Reich *et al.*, 2004; Smith *et al.*, 2009; Polley *et al.*, 2012a; Wu *et al.*, 2012). This indirect link between drivers and ANPP involves both a response of community composition to drivers as reflected in a change in the diversity, relative abundances, or species composition of communities, termed ‘community response’, and feedback effects of the change in community composition on ANPP, termed ‘community effects’ (Suding *et al.*, 2008). The response of community composition to climate drivers often involves inter-related processes. Community change may result if direct effects of drivers differ among species, drivers shift interspecific interactions by altering abiotic conditions such as soil water content, drivers differentially affect species fecundity, regeneration, or dispersal, or as the result of some combination of these processes. Effects of the changed community on ANPP (community effect), by contrast, reflect the impact of shifts in the relative abundances, diversity, or expression of plant traits that regulate productivity (e.g. resource-use efficiency). Community change can augment or reduce the net effect of climate change drivers on ANPP, depending on the functional traits of favoured species. For instance, a shift to greater C₄ dominance (community response) enhanced the positive effects of warming on ANPP of tallgrass prairie (community effect) by increasing biomass production per unit of plant nitrogen (N) (Niu *et al.*, 2010).

Considerable effort has been devoted to categorizing species into groups that respond similarly to climate change drivers. However, species groupings useful for predicting physiological responses to drivers may not forecast changes in community composition (community response) partly because drivers may shift values of abiotic variations (e.g. water availability) that affect community response (e.g. Blumenthal *et al.*, 2013).

Furthermore, species groupings useful for predicting community responses to drivers may not predict feedback effects of community change on ANPP and other processes because community response and community effect may depend on different functional traits (Suding *et al.*, 2008). For example, community response to climate change drivers may be linked to traits related to seed production or seedling recruitment (Jackson *et al.*, 1995; Edwards *et al.*, 2001), whereas feedbacks of community change (community effect) on ANPP may depend predominantly on plant size or traits related to resource-use efficiency (Fay *et al.*, 2012).

Here, we review interactions among climate change drivers (CO₂ enrichment; augmented precipitation), community composition, and ANPP using data from three experiments in C₄-dominated perennial grasslands. Atmospheric CO₂ concentration has increased by about 40% since industrialization (Petit *et al.*, 1999; Keeling *et al.*, 2009) and is anticipated to reach double the pre-industrial concentration during this century (Intergovernmental Panel on Climate Change, 2007). Increased biospheric warming associated with elevated concentrations of CO₂ and other ‘greenhouse gases’ is projected to modify the amount and distribution of annual precipitation (Hoerling and Kumar, 2003; McCabe and Clark, 2006). Precipitation in the southern Great Plains of North America has increased by 8% since 1991 relative to precipitation for the period 1901–1960 (McRoberts and Nielsen-Gammon, 2011). The amount of annual precipitation falling as very heavy events has increased by an even greater percentage (Karl *et al.*, 2009). Summer pulses in precipitation in the southern Plains are predicted to result from an increase in tropical storm activity (Allan and Soden, 2008).

We have focused on the poorly studied role of plant community change (community response and community effect) in mediating the ANPP response of grassland to CO₂ enrichment and augmented summer precipitation. We assessed the role of ‘community change’ in driver–ANPP interactions using two approaches: (i) experiments in which the response of mixed communities to CO₂ was followed through time; and (ii) an experiment in which community differences (native vs exotic species) were established experimentally at the outset. In addition to quantifying the contribution of community change to the ANPP–driver response, we asked: do the plant traits important in determining temporal shifts in community composition or that differ in experimental communities of native versus exotic species also regulate effects of community change on ANPP? Little information exists to address this question. For example, CO₂ enrichment has long been predicted to favour C₃ over C₄ species by preferentially increasing C₃ photosynthesis and, it is presumed, growth (e.g. Strain and Bazzaz, 1983). However, CO₂ effects on both C₃ and C₄ plants have been shown to vary (Wand *et al.*, 1999; Nowak *et al.*, 2004), and possible feedback effects of C₃–C₄ shifts on community ANPP remain largely undefined (but see Langley and Megonigal, 2010).

Because grassland ANPP and community dynamics are frequently regulated by water availability (Sala *et al.*, 1988; Huxman *et al.*, 2004; Ponce Campos *et al.*, 2013), we emphasize the role of community evapotranspiration (ET) and

water-use efficiency (WUE; ANPP per unit of ET) in driver–community–ANPP interactions. ANPP is the product of ET and WUE (Fig. 1). CO₂ enrichment may modify ANPP by: (i) increasing species-level photosynthetic WUE [or, transpiration efficiency (TE)=net photosynthesis (*A*)/transpiration or stomatal conductance (*g_s*)] and, in aggregate, WUE; or (ii) slowing transpiration with a possible decline in seasonal ET (Owensby *et al.*, 1999; Morgan *et al.*, 2001, 2004; Fay *et al.*, 2012) (Fig. 2). Conversely, augmenting precipitation would be anticipated to increase ANPP by increasing ET. The magnitude of shifts in ET and WUE, in turn, both influence and are influenced by community composition with possible feedback effects on ANPP. We consider CO₂ effects on ANPP to be ‘indirect’ if mediated through change in species relative abundances, the net result of community response and community effect. We deem the remaining CO₂ effects on ANPP to be ‘direct’ but distinguish effects mediated through differences in ET (ET_d) from effects that remain (CO_{2d}). Similarly, we consider differences in the ANPP responses of native and exotic assemblages to augmented precipitation to be the indirect result of community differences.

We anticipated that CO₂ enrichment and augmented precipitation would shift community composition (community response) by increasing soil water content or reducing ET. Specifically, we hypothesized that CO₂ enrichment and augmented summer precipitation would increase soil water content to favour species that responded with a large increase in leaf photosynthesis, as a possible surrogate for growth rate, or that were tall at maturity relative to other members of the community regardless of photosynthetic pathway. Augmented summer precipitation was expected to favour C₄ species, as has been shown for other grasslands (Skinner

et al., 2002; Von Fischer *et al.*, 2008). By contrast, we predicted that the ‘community effect’ on ANPP in the periodically water-limited herbaceous ecosystems we studied would be determined by the aggregate influence of favoured species on WUE.

Materials and methods

CO₂ experiments

We report results from two experiments in which elongated field chambers were used to expose vegetation to a continuous gradient of CO₂ spanning pre-industrial to elevated concentrations. In 1997–2000, we studied CO₂ effects on previously grazed C₃–C₄ grassland (hereafter, pasture) using the Prairie CO₂ Gradient (PCG) facility (Johnson *et al.*, 2000). In 2006–2010, we evaluated CO₂ effects on assemblages of tallgrass prairie species grown in soils of three types using the Lysimeter CO₂ gradient (LYCOG) facility (Fay *et al.*, 2009). Both facilities were located in central Texas, USA (31°05′ N, 97°20′ W) and consisted of two tunnel-shaped chambers, aligned parallel along a north–south axis. Each chamber was divided into ten consecutive compartments, each 5 m long and 1.0 m (PCG) or 1.2 m (LYCOG) wide and tall. Aerial growth of chambered vegetation was enclosed in a transparent polyethylene film. We used photosynthesis during daylight and respiration at night to create CO₂ gradients. The desired CO₂ concentration gradients were maintained by automatically varying the rate of air flow through chambers in response to changes to photosynthesis (daylight) or respiration rates (night). Daytime CO₂ gradients ranged from 560 and 500 μl l⁻¹ to 200 and 250 μl l⁻¹ (PCG and LYCOG, respectively). Night-time CO₂ concentrations were regulated at 130–150 μl l⁻¹ above daytime values along each chamber. Air temperature and vapour pressure deficit were regulated near ambient values by cooling and dehumidifying the air at 5 m intervals along the chambers. CO₂ treatments were maintained during each growing season (April–October).

The CO₂ concentration and dew point of air were measured every 20 min at air entry and exit points of each 5 m compartment

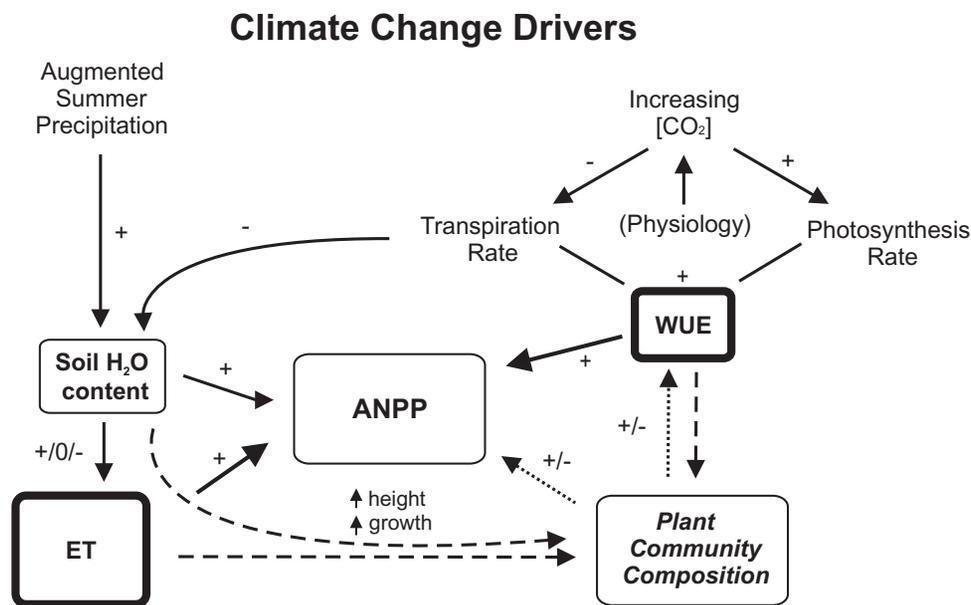


Fig. 1. A conceptual representation of the influence of two climate change drivers, increasing CO₂ and augmented summer precipitation, on ANPP of periodically water-limited communities of grassland plants. Drivers may influence ANPP by altering community WUE or ET, both considered direct effects of CO₂ enrichment (bold lines), or by altering plant community composition (community response; dashed lines) with possible feedback of community change on ANPP (community effect; dotted lines). Driver effects on ANPP are considered to be ‘indirect’ if mediated through change in plant community composition (the net result of community response and community effect). The anticipated sign of driver effects and feedbacks on ANPP is indicated (+, 0, -). Environmental regulators of physiology and ET, such as air temperature and the leaf-to-air vapour pressure deficit, are not shown for simplicity.

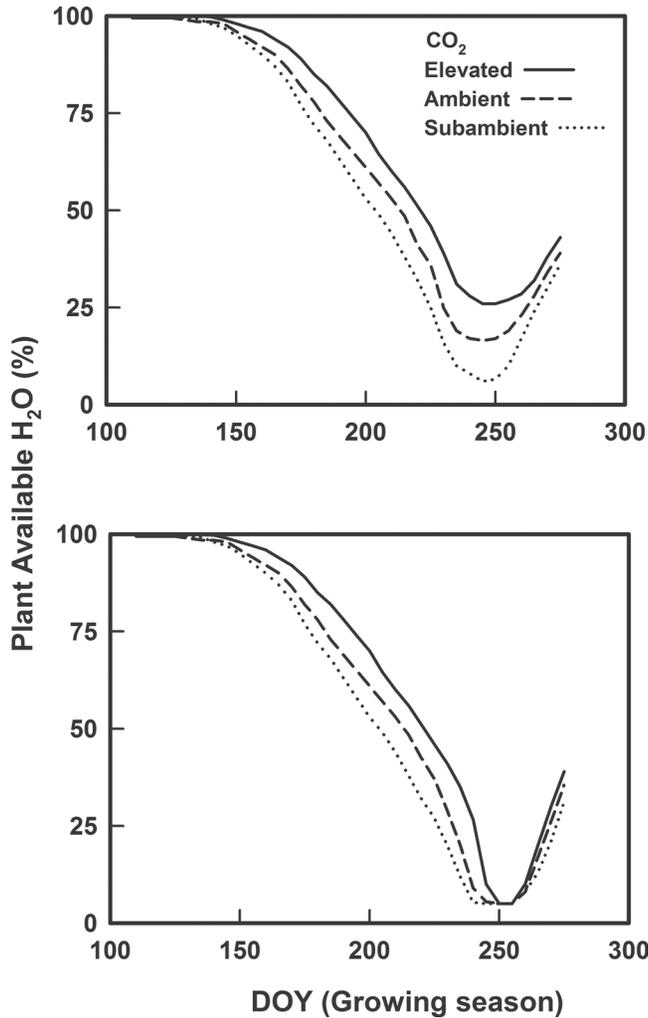


Fig. 2. A conceptual representation of how CO₂ enrichment may affect soil water content (plant-available H₂O) and, under a given precipitation regime, community ET. As has been frequently demonstrated, CO₂ enrichment may slow the decline in soil water content during periods between major precipitation events by reducing transpiration rate. A slight decrease in transpiration and ET may occur in systems or years in which soil water content remains above the level to which plants may extract water (upper panel). Alternatively, CO₂ may have little effect on ET, as measured by the maximum amount by which plants deplete soil water, in systems or years in which water content declines to a threshold level below which plants cannot extract water (lower panel). Trends are indicated by solid lines for elevated CO₂, dashed lines for ambient CO₂, and dotted lines for subambient CO₂.

along the chambers using infrared gas analysers (Li 6262; LiCor Biosciences, Lincoln, Nebraska, USA). CO₂ concentration at the air entrance and exit of each chamber was measured at 2 min intervals (Johnson et al., 2000; Polley et al., 2008; Fay et al., 2009). Air temperatures at the southern and northern extremes of each compartment were measured every 15 s with fine-wire (0.5 mm) thermocouples. The temperature, CO₂ concentration, and dew-point temperature of air at each sampling location were averaged over each daytime and night-time period of CO₂ regulation. The growing season mean of CO₂ concentration during both daylight and night-time varied as a linear function of distance along the chambers (Johnson et al., 2000; Fay et al., 2009). Overall, 90% of the daily mean values of CO₂ concentration along chambers fell within 20–50 μl l⁻¹ of the growing season mean for the location (Johnson et al., 2000; Fay et al., 2009).

The PCG facility was constructed on pasture dominated by the exotic C₄ perennial grass *Bothriochloa ischaemum* (L.) Keng (King Ranch bluestem) and C₃ perennial forbs *Solanum dimidiatum* Raf. (Western horse-nettle) and *Ratibida columnaris* (Sims) D. Don (Mexican hat) (hereafter referenced by genus). The site had been grazed for at least 50 years prior to construction. The soil is a silty clay mollisol from the Austin series (Udorthentic Haplustolls), the surface 0.4 m of which is composed mostly (35–40%) of clay. The soil beneath the chambers was separated from the surrounding soil to a depth of 0.9 m with a rubber-coated fabric. The LYCOG facility was constructed above 5 m long × 1.2 m wide × 1.6 m deep steel containers that were buried to a depth of 1.2 m. Four intact soil monoliths (each 1 × 1 × 1.5 m deep) were placed into each of the 20 5 m long containers. Three soil types of contrasting physical and hydrological properties were included. These include the silty clay mollisol on which the PCG facility was constructed and a clay vertisol from the Houston Black series (Udic Haplusters; 45–55% clay to a depth of 1.5 m) and sandy loam alfisol from the Bastil (Bastrop) series (Udic Paleustalfs; 60–73% sand in the upper 0.5 m). Two monoliths of each of two soil types were randomly placed into each 5 m long container. Monoliths with intact soil structure were collected by using hydraulic pressure to press the open-ended steel boxes into the soil (Polley et al., 2008). Perennial species characteristic of tallgrass prairie in central Texas were transplanted into 60 monoliths in June 2003, 3 years before CO₂ treatment was initiated. Eight plants of each of four C₄ grass species [*Bouteloua curtipendula* (Michx.) Torr. (side-oats grama), *Schizachyrium scoparium* (Michx.) Nash (little bluestem), *Sorghastrum nutans* (L.) Nash (Indian grass), *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 *Desmodium 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).

Irrigation equivalent to precipitation was applied to the pasture in the PCG facility on the day following the precipitation events (Polley et al., 2002). During each growing season, monoliths in the LYCOG facility were irrigated with the equivalent of the average of growing season precipitation in central Texas (560 mm; Polley et al., 2011). Monoliths were irrigated twice weekly. Each monolith was equipped with a dedicated system for collecting water that drained through soil into reservoirs located beneath the steel boxes encasing the monoliths (Polley et al., 2008). Drainage water was removed from the collection reservoirs using a vacuum pump and weighed.

The concentration of total N in soil declined with depth in all soil types but was greater by a factor of two over the 0–10 cm depth increment in the clay and silty clay than in the sandy loam soils studied in the LYCOG experiment (0.21, 0.15, and 0.08%, respectively; Fay et al., 2009). Nevertheless, resin-available soil N was similar among the soil types during the LYCOG experiment, decreased by only about 15% from 280 to 480 μl l⁻¹ CO₂, and was not correlated with ANPP on any soil type (Fay et al., 2012). Similarly, CO₂ enrichment did not consistently affect the N concentration of aboveground tissues in the PCG experiment (Polley et al., 2003), apparently because a negative effect of CO₂ on N mineralization rates (Gill et al., 2002) was counterbalanced by a net transfer of N from soil organic matter to plants (Gill et al., 2006).

Augmented summer precipitation experiment

An irrigation treatment was applied to species mixtures included in the Maintenance of Exotic versus Native Diversity experiment (MEND; Wilsey et al., 2009, 2011). MEND is a common garden experiment located in the same previously grazed grassland (pasture) as the PCG experiment. Nine-species mixtures (communities) of either all exotic or all native species were planted in 1 × 1 m plots from which pasture vegetation had been removed with herbicide. Plots were established using equal-mass transplants from a pool of 18 native and 18 exotic perennial species. Included in each plot were

four C₄ grasses, four C₃ forb species, and one C₃ grass species. The species origin and a summer irrigation treatment were randomly assigned to plots using a two-way factorial arrangement. Random draws were used to vary the composition of species mixtures. Plots were established in two blocks, one planted in October 2007 and one in March 2008. Four draws of mixture composition were included within each of the two blocks (×2 origin×2 irrigation treatments), each with two replicates, for a total of 32 mixtures per block. Rainfall has been predicted to increase during warm periods of the year (Allan and Soden, 2008), and consequently the irrigation treatment was imposed during the warmest period of the year (July–August). The irrigation treatment was designed to simulate the average difference between precipitation received during the 10% of wettest summers (July–August) in the historical record (1913–2007) for the site and the mean of summer precipitation (difference=130 mm). Irrigated plots were hand watered from mid-July to mid-August at a rate of 128 mm per month in eight equal increments.

Sampling and data analysis

Each week during CO₂ experiments, we measured the volumetric soil water content in the centre of each 5 m compartment of the chambers (pasture) or each monolith (prairie assemblages) with a neutron probe. Neutron attenuation was measured at 0.15–0.3 m increments to a depth of 1.35 m (pasture) or 1.5 m (prairie assemblages). We calculated the growing season maximum of soil water depletion for each chamber compartment or monolith as an index of differences in ET among CO₂ treatments. In these experiments, the same amount of water was applied to each chamber or monolith during a given year, runoff was prevented, and the vegetative canopy was closed during most of season. Drainage below the rooting zone of plants was also small. For example, drainage through LYCOG monoliths during the 2008 growing season accounted for 0.4, 1.9, and 4.6% of the 560 mm of irrigation water applied to clay, sandy loam, and silty clay monoliths, respectively. CO₂ did not affect drainage on the sandy loam or silty clay soils ($P=0.16$ and 0.08 , respectively), but drainage increased exponentially with CO₂ on the clay soil, albeit by a small absolute amount (from <0.1 to 0.9% of irrigation; $r^2=0.31$, $P=0.007$). ET was estimated by subtracting the growing season minimum of water content, defined as the minimum water content derived by averaging consecutive weekly values, from the water content averaged over the first two measurements of the growing season when soil water content was maximal. We consider the maximum of growing season water depletion to be a more biologically relevant index of differences in ET in these experiments than the net change in soil water content over the full growing season. Soil water content typically reaches a minimum late in the season (September–October; Polley *et al.*, 2002). Much of the growing season recharge of the profile thus occurs during the period when plant activity is declining.

ANPP in CO₂ experiments was determined by clipping vegetation in each chamber compartment or monolith to a height of 5 cm at the end of each growing season. Plants were sorted by species at harvest. Harvested tissues were weighed after oven drying for 72 h at 60° C. Aboveground biomass and species composition in the irrigation experiment were determined twice per year (late June and October) in each plot with point intercept techniques. Biomass per plot (g m⁻²) was calculated from point intercept data (25 grid points per plot) using regression relationships between number of hits per species and biomass (mean $r^2=0.89$).

We used the between-year change in the proportional contribution of dominant species or species groups to ANPP as an index of vegetation change. Change was calculated for each chamber compartment or monolith by subtracting the dominant's contribution to production in one year from its contribution to ANPP in the following year.

Structural equation modelling (SEM) with observed variables (path modelling) was used to partition the influence of CO₂ on ANPP into direct effects, segregated into effects mediated through differences in ET (ET_d) and effects that remained (CO_{2d}), and an

indirect effect mediated through change in community composition, as represented by shifts in the contribution of dominant species to community ANPP (Shipley, 2000; Grace, 2006). The indirect effect of CO₂ on ANPP through community change represents the net effect of 'community response' to CO₂ and feedbacks of community change on the ANPP-CO₂ response, the 'community effect'. SEM is based on patterns of covariation between variables with the goal of minimizing differences between observed and predicted patterns of covariation. By contrast, the goal in typical least-squared regression analysis is to minimize the squared differences between observed and predicted values of individual observations (Shipley, 2000). The bivariate relationships between the variables we modelled were linear. The SEM model was fitted using IBM SPSS AMOS 21 software. The hypothesized relationship among variables in a SEM is considered to be consistent with data when the probability level of the statistical test (χ^2 statistic) is greater than the significance level ($P=0.05$; Shipley, 2000). Standardized coefficients were derived by analysing values for each variable that were standardized by subtracting the mean and dividing by the standard deviation.

Results

CO₂ enrichment

Pasture (PCG experiment)

ANPP of pasture increased by an average of 110 g m⁻² per 100 $\mu\text{l l}^{-1}$ rise in CO₂ during the final 3 years of 4 years of treatment (Polley *et al.*, 2003). ANPP was 30% greater on average across CO₂ treatments during the final 3 years than the initial year of the experiment (1060 vs 737 g m⁻²). Consequently, the relative increase in ANPP over the 200–560 $\mu\text{l l}^{-1}$ CO₂ gradient declined during the 4 years of CO₂ treatment, from 57% during year 1 to 46, 37, and 0% (no significant CO₂ effect) during years 2–4, respectively.

The increase in community ANPP along the subambient to enriched CO₂ gradient was associated with declining g_s and increasing A and TE efficiencies (A/g_s) of two dominant species, the C₄ grass *Bothriochloa* and C₃ perennial forb *Solanum* (Anderson *et al.*, 2001; Maherali *et al.*, 2002). TE was greater at subambient CO₂ for *Bothriochloa* than for *Solanum* and increased more per unit of increase in CO₂ for the C₄ grass than for the C₃ forb species.

CO₂ reduced the seasonal maximum of soil water depletion over the full 1.35 m profile during each of the first 3 years (Polley *et al.*, 2002) and at a depth of 0.9–1.35 m during each of the final 3 years (Fig. 3). Water depletion was greatest during 1998, a year with a mid-season drought.

Plant communities shifted from dominance by C₄ grasses across the CO₂ gradient to co-dominance by C₄ grasses and C₃ perennial forbs, predominantly *Ratibida*, *Solanum*, and *Solidago*, at elevated CO₂ (Polley *et al.*, 2003). The ANPP of forbs increased as a function of CO₂ during the experiment (change in ANPP= $-170.94+1.24\times\text{CO}_2$), whereas ANPP of the dominant C₄ grass, *Bothriochloa*, decreased as CO₂ rose during the experiment (change in ANPP= $195.32-0.99\times\text{CO}_2$; Fig. 4).

We used SEM to determine the contributions of direct CO₂ effects (CO_{2d}, ET_d) and an indirect effect linked to shifts in community composition (community effect and response) to the ANPP-CO₂ response (Fig. 5). The CO₂ effect on ANPP included a large and positive direct effect not associated with

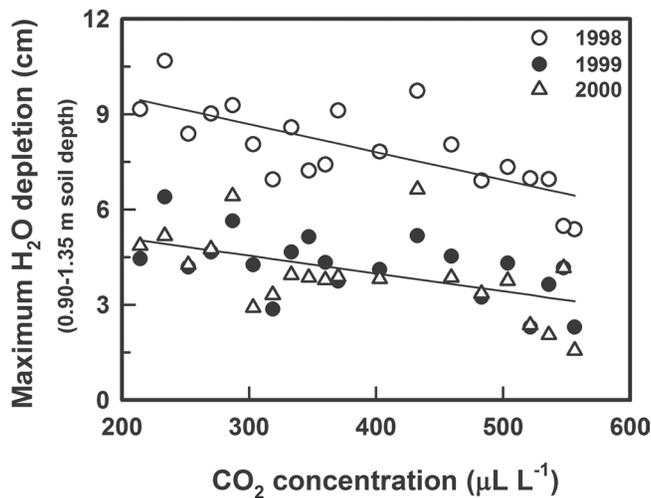


Fig. 3. Relationship between the seasonal maximum of soil water depletion (0.90–1.35 m depth increment) and CO_2 concentration for C_3 – C_4 pasture (PCG experiment). Lines are linear regression fits [$r^2=0.50$ and 0.27 ; $n=20$ and 40 for data from 1998 (open circle) and 1999 (closed circle), 2000 (open triangle) combined, respectively, $P=0.0003$].

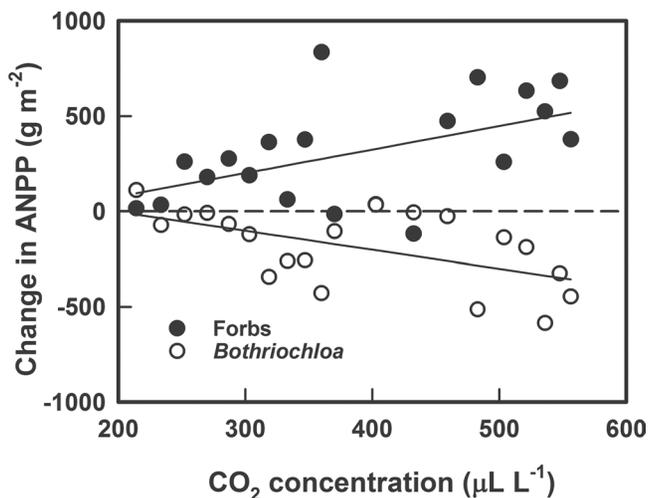


Fig. 4. Relationships between the change in ANPP of the C_4 grass *Bothriochloa* (open circle) and of C_3 perennial forb species (closed circle) between the first season of treatment and years 3 and 4 (averaged) of the PCG experiment ($n=20$) and CO_2 concentration. Lines are linear regression fits for *Bothriochloa* ($r^2=0.28$, $P=0.01$) and forbs ($r^2=0.22$, $P=0.02$).

a change in ET (CO_{2d} ; Fig. 6) that was probably linked to the CO_2 -caused increase in TE of the dominant species (Fig. 1) and a negative, direct effect mediated through a CO_2 -caused decrease in ET (ET_d ; Figs. 5 and 6). A change in community composition (composition), as reflected in a change in the contribution of the C_4 grass *Bothriochloa* to the community, also affected ANPP (Fig. 5). CO_2 enrichment increased ANPP (community effect) by reducing the *Bothriochloa* fraction (community response), the latter a result of the CO_2 -caused decline in ET. The pathway linking CO_2 directly to composition was not significant, and therefore was not included in the final SEM model. CO_2 enrichment increased the abundance of C_3 forbs at the expense of the initially dominant C_4 grass to increase community ANPP by 15% of the magnitude of CO_{2d} (Fig. 6).

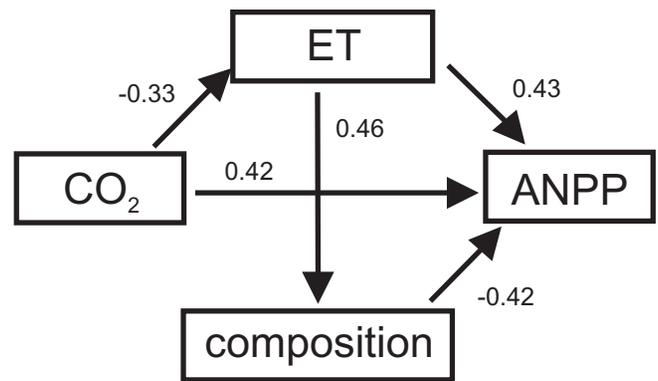


Fig. 5. A SEM describing CO_2 effects on ANPP of pasture communities over the final 3 years of 4 years of treatment (PCG experiment). Maximum likelihood techniques were used to calculate path coefficients that minimize the difference between the calculated covariance matrix and the covariance matrix present in the data. Standardized coefficients for each variable are calculated by subtracting the variable mean and dividing by its standard deviation. Standardized coefficients are listed beside each path. CO_2 effects on ANPP were considered to be ‘direct’ unless mediated through a CO_2 -caused shift in community composition, as reflected in the *Bothriochloa* fraction of ANPP (composition). Pathways linking CO_2 to ANPP through composition include two components, the community compositional response to CO_2 and the community effect on ANPP.

Prairie assemblages (LYCOG experiment)

CO_2 enrichment increased ANPP of prairie communities on three soil types by an average of 79–122 g m^{-2} per 100 $\mu\text{L l}^{-1}$ rise in CO_2 over the first 5 years of treatment (Polley et al., 2012b). The increase in ANPP was associated with an approximate doubling of leaf TE in the two dominant grass species, the tallgrass *Sorghastrum* and the mid-grass species *Bouteloua* (Fay et al., 2012). However, TE was greater at ambient and elevated CO_2 for *Sorghastrum* than for *Bouteloua* because CO_2 enrichment preferentially increased photosynthesis of *Sorghastrum*.

Prairie assemblages on each soil type became strongly dominated by C_4 grasses at the expense of C_3 forbs. The grass fraction of ANPP increased with time across CO_2 treatments (grass fraction in year 4 was 0.81, 0.87, and 0.93 for the clay, silty clay, and sandy loam soils, respectively; Polley et al., 2012a). The contribution of the tallgrass *Sorghastrum* to ANPP increased at elevated CO_2 . The CO_2 -caused increase in *Sorghastrum* was accompanied by an offsetting decline in production of the mid-grass *Bouteloua*. The *Bouteloua* fraction of ANPP decreased from 0.75 to 0.15 (silty clay) and from 0.25 to 0.0 (sandy loam), whereas the *Sorghastrum* fraction rose from 0.08 to ~0.45 (silty clay, clay) and from 0.25 to 0.75 (sandy loam) from 280 to 480 $\mu\text{L l}^{-1}$ CO_2 (Polley et al., 2012a).

CO_2 increased the contribution of *Sorghastrum* to community ANPP partly by reducing canopy-level transpiration rates (Polley et al., 2008) and increasing soil water content (Fay et al., 2012; Polley et al., 2012a). Maximum water depletion to 1.5 m was a decreasing linear function of CO_2 in two of five growing seasons for the sandy loam soil, but in only one of the five years for the silty clay soil (Table 1). CO_2 did not affect water depletion on the clay soil during any year.

The CO_2 -caused increases in *Sorghastrum* abundance and ANPP of assemblages were correlated (Polley et al., 2012b;

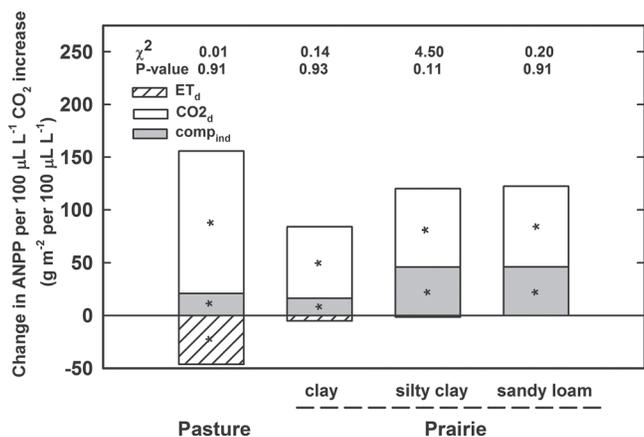


Fig. 6. Components of the CO₂ effect on ANPP of pasture (PCG experiment) and prairie communities grown on each of three soil types (LYCOG experiment). CO₂ effects were partitioned using SEM for data over the final 3 years and first 5 years of the pasture and prairie experiments, respectively (see Figs 5 and 7). Represented are 'direct' CO₂ effects resulting both from a direct linkage between CO₂ and ANPP (CO_{2d}; open) and through change in ET (ET_d; hatched) and an 'indirect' CO₂ effect mediated through shifts in community composition, as reflected in differences in the *Bothriochloa* (pasture) or *Sorghastrum* (prairie) fraction of ANPP along the CO₂ gradient (comp_{ind}; shaded). The latter indirect effect includes two components, the response of community composition to CO₂ (community response) and the effect of community change on ANPP (community effect). Values for each component of the CO₂ effect are expressed as the change in ANPP (g m⁻²) per 100 μl l⁻¹ increase in CO₂ concentration. Significant effects are denoted with an asterisk. χ^2 and *P* values for the full SEM model are listed [degree of freedom=1 (PCG) or 2 (LYCOG)]. The full model is considered to be consistent with data when the *P* value of the χ^2 statistic is >0.05.

Fig. 6). Paths in the SEM models linking CO₂ to ANPP through the *Sorghastrum* fraction (composition) accounted for 38% of the CO₂-caused increase in ANPP on the silty clay and sandy loam soils and 21% of the net CO₂ effect on the clay soil (Fig. 7). The direct effect of CO₂ that was not linked to change in ET (CO_{2d}) predominated on each soil, accounting for 62–79% of the increase in ANPP (Fig. 6). ANPP was positively correlated to ET to a depth of 0.7 m for the clay and sandy loam soils, but paths linking CO₂ to community ANPP through ET were not significant for any soil (Fig. 7).

Augmented summer precipitation (MEND experiment)

Species richness (Fig. 8) and the ratio of C₃ to C₄ biomass declined more rapidly in communities planted with all exotic rather than all native perennial species (Wilsey *et al.*, 2011; Daneshgar *et al.*, 2013). The decline in diversity of exotic communities was reflected in a large increase in relative abundances of C₄ grasses with traits associated with relatively high capture of CO₂ and light (Daneshgar *et al.*, 2013). End-of-season aboveground biomass was greater in exotic than native communities, despite the more equitable C₃–C₄ abundances and greater species diversity of native assemblages (Wilsey *et al.*, 2011). Species diversity and richness were greater in summer-irrigated than in non-irrigated plots.

Over the first 5 years of the MEND experiment, irrigation to augment summer precipitation increased ANPP

Table 1. Linear regression analyses for relationships between the seasonal maximum of soil water depletion (0–1.5 m depth) by prairie vegetation and CO₂ concentration for each of three soil types and each of the first 5 years of CO₂ treatment (LYCOG experiment)

Regression slopes represent the change in water depletion (cm) per 100 μl l⁻¹ increase in CO₂ concentration. Also listed are the mean and SE of water depletion across CO₂ treatments for each soil type and year.

Soil/year	Water depletion (cm)						
	Intercept	Slope	r ²	P value	Mean	SE	n
<i>Silty clay</i>							
2006	–	–	–	0.07	3.68	0.41	24
2007	17.25	–2.64	0.46	0.0002	7.35	0.56	24
2008	–	–	–	0.24	9.00	0.98	24
2009	–	–	–	0.93	4.60	0.69	23
2010	–	–	–	0.70	12.83	1.00	23
<i>Sandy loam</i>							
2006	10.07	–1.50	0.25	0.03	4.45	0.42	16
2007	22.87	–3.66	0.33	0.01	9.16	0.91	16
2008	–2.95	2.99	0.24	0.03	8.27	0.85	16
2009	–	–	–	0.50	3.94	0.41	16
2010	–	–	–	0.44	8.98	1.21	16
<i>Clay</i>							
2006	–	–	–	0.28	3.97	0.84	20
2007	–	–	–	0.14	10.13	1.07	20
2008	–	–	–	0.94	11.24	0.72	19
2009	–	–	–	0.70	6.31	0.83	19
2010	–	–	–	0.71	12.06	0.47	19

by an average of 10% in native communities [Fig. 8; from 333.0 to 364.5 g m⁻², standard error (SE)=19.8 g m⁻²], but by only 1% in exotic communities (from 394.4 to 397.7 g m⁻², SE=19.8 g m⁻²; *P*=0.03 for the origin×irrigation interaction). Community type thus mediated the ANPP-irrigation response. We interpret the differing responses of native versus exotic communities to irrigation as evidence that ET, WUE, or both were greater among native than among exotic species.

Discussion

CO₂ enrichment stimulated ANPP of both C₄-dominated pasture (PCG experiment) and tallgrass prairie assemblages (LYCOG experiment) largely via a 'direct' effect (CO_{2d}) that was not associated with a change in ET. CO₂ probably increased ANPP by increasing canopy photosynthesis rate (Mielnick *et al.*, 2001) and WUE (Polley *et al.*, 2002; Fay *et al.*, 2012) and delaying the onset of plant water limitation by slowing transpiration (Jackson *et al.*, 1994; Polley *et al.*, 2008) with a resulting increase in soil water content (Fay *et al.*, 2012; Polley *et al.*, 2012a). CO₂ enrichment 'indirectly' altered ANPP through changes in the C₄ composition of communities, change mediated entirely via CO₂-caused differences in ET in pasture. Feedback from community change increased ANPP by 15% of CO_d in pasture but accounted for 21–38% of the net increase in ANPP in prairie assemblages.

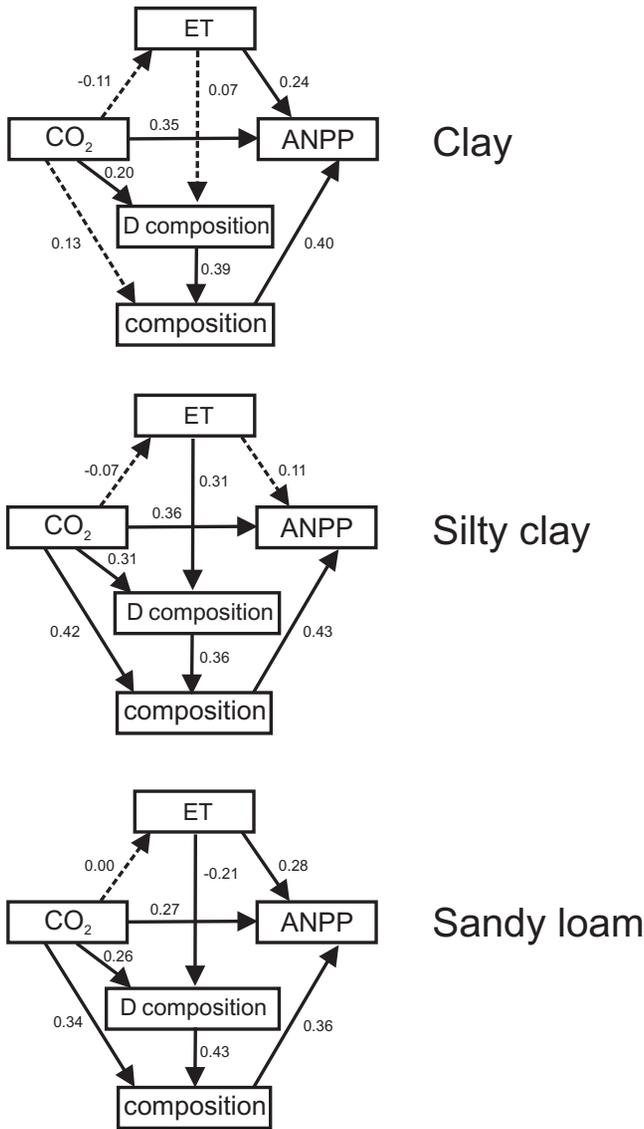


Fig. 7. SEMs describing CO₂ effects on ANPP of prairie communities grown for 5 years on each of three soil types. Non-significant pathways are indicated by dashed lines. Standardized coefficients are listed beside each path. CO₂ effects on ANPP were considered to be ‘direct’ unless mediated through a CO₂-caused shift in community composition, as reflected both in the change in the *Sorghastrum* fraction of community ANPP during a given year (Δ composition) and the current *Sorghastrum* fraction of ANPP (composition). Pathways linking CO₂ to ANPP through composition include two components, the community response to CO₂ and community effect on ANPP. A model is assumed to be consistent with data when $P > 0.05$ for the χ^2 statistic ($P = 0.93, 0.11, \text{ and } 0.91$ for the clay, silty clay, and sandy loam soils, respectively).

As predicted, ‘community responses’ to increased CO₂ were reflected in increased abundances of species with traits that conferred an advantage under higher soil water availability. CO₂ favoured C₃ perennial forbs over a C₄ grass in pasture by reducing ET and favoured a C₄ tallgrass in prairie assemblages by increasing soil water content. The ‘community effect’ on ANPP depended, at least partly, on the influence of favoured species on WUE. CO₂ enrichment amplified the ANPP response of prairie assemblages by favouring a C₄ grass with high TE, but apparently limited the ANPP benefit of community change in

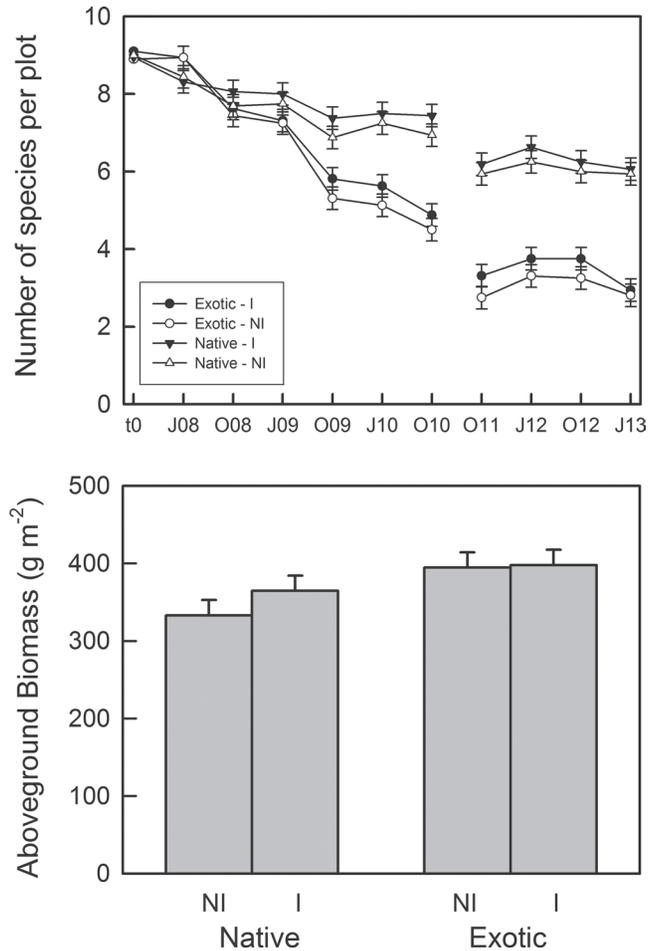


Fig. 8. Upper graph: temporal trends in plant species richness (species per m²) of plots planted to all exotic (circles) or all native perennial species (triangles) that received ambient precipitation only (open symbols) or precipitation augmented by summer irrigation (closed symbols). Plots were not sampled during June in the drought year of 2011. Lower graph: aboveground biomass of not-irrigated (NI; ambient precipitation only) and irrigated (I) assemblages of all native or all exotic species over the first 6 years of treatment. Bars indicate 1 SE. $P = 0.03$ for the origin \times irrigation interaction.

pasture by favouring C₃ forbs. Water ‘saved’ at elevated CO₂ in pasture as result of slower transpiration was increasingly diverted from use by the initially dominant C₄ grass to the increasingly dominant and taller C₃ forbs (Polley et al., 2003), despite the lower TE of the latter (Anderson et al., 2001). Not coincidentally, the ANPP-CO₂ response declined with time. The simultaneous decrease in ANPP-CO₂ response (Polley et al., 2003) and probable decline in WUE that occurred as less water-use efficient C₃ forbs replaced a C₄ grass (Anderson et al., 2001) implies that community change limited the CO₂ effect on ANPP. The ANPP response to supplemental water in the MEND experiment was greater among the more-diverse native than exotic assemblages, reflecting a ‘community effect’ that possibly resulted because of greater TE among native species. In total, our results imply that the response of grassland ANPP to climate change drivers may be significantly miscalculated if feedback effects of community shifts or differences on ANPP are ignored.

Not surprising, ANPP was positively correlated with ‘apparent ET’ in the ecosystems we studied. Summer irrigation increased ANPP of native communities in the MEND experiment (Wilsey *et al.*, 2011), apparently by increasing ET. ANPP was positively correlated to ET as reflected in soil water depletion in pasture communities (PCG experiment) and prairie assemblages on two of three soil types (LYCOG experiment). A difference in ET thus was a significant predictor of productivity difference across CO₂ treatments, despite CO₂-caused variation in the TE of dominant species (Anderson *et al.*, 2001; Fay *et al.*, 2012). CO₂ enrichment increased the seasonal mean of soil water content in both experiments by reducing the rate at which water content declined (Polley *et al.*, 2002; Fay *et al.*, 2012; Polley *et al.*, 2012a), but consistently reduced the maximum of water depletion only in pasture. Soil water content in central Texas grasslands typically declines to a minimum value in late summer/early autumn when the plant canopy is fully developed, precipitation is reduced, and evaporative demand is high. CO₂ enrichment may delay the decline in soil water availability in these ecosystems by reducing transpiration rates to reduce maximum water use in some years and for some communities.

WUE should become an increasingly important determinant of community productivity when water availability declines (Huxman *et al.*, 2004). Differences in WUE that result from CO₂ enrichment or differences in community composition will have the greatest impact on ANPP when water limitation constrains variation in ET among communities. Apparent ET was similar across the CO₂ gradient for prairie assemblages growing on a given soil type. As a consequence, increased abundance of a grass with high TE augmented the ANPP response to CO₂. Similarly, water input and thus apparent ET did not differ between native and exotic communities in the MEND experiment, implying that the greater increase in biomass of native communities resulted partly from greater WUE. The ANPP effect of shifting the abundances of species that differ in TE will thus probably be greatest when water limitation is sufficient to constrain variation in ET among communities.

Community responses to CO₂ were linked to plant traits associated with a positive growth response to greater water availability. By contrast, community effects on the ANPP-CO₂ and ANPP-irrigation response were determined, at least partly, by how favoured or dominant species affected WUE. Our results imply that the species traits favoured by climate change drivers may differ from the traits that most influence feedbacks of community change on ANPP.

Acknowledgements

Chris Kolodziejczyk operated CO₂ chambers. Field and laboratory assistance from Anne Gibson, Katherine Jones, Chris Kolodziejczyk, Alicia Naranjo, Kyle Tiner, and numerous students was invaluable in the MEND and CO₂ experiments. Tim Dickson, Forest Isbell, Parker Knutson, Terri Beth Teaschner, and Anna Loan-Wilsey assisted with weeding and harvests of the MEND experiment. Funding for MEND was provided by a grant from the National Science Foundation (DEB0639417) to BW. RJ acknowledges support from the US Department of Energy (Program in Ecosystem Research #ER64242). Daniel Johnson and Lewis Ziska provided insightful reviews of the manuscript. Mention of trade names or commercial products

does not imply endorsement by the US Department of Agriculture. USDA is an equal opportunity provider and employer.

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