Impacts of climate change drivers on C\textsubscript{4} grassland productivity: scaling driver effects through the plant community

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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 C\textsubscript{4} grasslands to two climate drivers applied singly: atmospheric CO\textsubscript{2} 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\textsuperscript{-2} per 100 \mu l l\textsuperscript{-1} rise in CO\textsubscript{2} 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 CO\textsubscript{2} response in the prairie experiment but little of the response in the pasture experiment. The community response to CO\textsubscript{2} was linked to species traits associated with greater soil water from reduced transpiration (e.g. greater height). Community effects on the ANPP CO\textsubscript{2} 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 CO\textsubscript{2} concentration, C\textsubscript{4} 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 C\textsubscript{4}-dominated...
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 C₃-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 Megenigal, 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 (gₛ)] 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 (ETₐ) from effects that remain (CO₂₂d). 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 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 C₄–C₃ 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.

**Climate Change Drivers**

![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.](https://academic.oup.com/jxb/article-abstract/65/13/3415/2877465)
along the chambers using infrared gas analysers (Li 6262; LiCor Biosciences, Lincoln, Nebraska, USA). CO\textsubscript{2} 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, CO\textsubscript{2} concentration, and dew-point temperature of air at each sampling location were averaged over each daytime and night-time period of CO\textsubscript{2} regulation. The growing season mean of CO\textsubscript{2} 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 CO\textsubscript{2} concentration along chambers fell within 20–50 µl l\textsuperscript{-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 C\textsubscript{4} perennial grass Bothriochloa ischaemum (L.) Keng (King Ranch bluestem) and C\textsubscript{3} 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 soil 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 Hapludalfs; 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 containers 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 CO\textsubscript{2} treatment was initiated. Eight plants of each of four C\textsubscript{4} grass species [Bothelolova curtipendula (Michx.) Torr. (side-oats grama), Schizachyrium scoparium (Michx.) Nash (little bluestem), Sorghastrum nutans (L.) Nash (Indian grass), Tridens albenscens (Vasey) Wooton & Standl. (white tridens)] and three forb species [Salvia azurea Michx. Ex Lam. (pitcher sage), Solidago canadensis L. (Canada goldenrod), and the legume Desmanthus illinoisensis (Michx.) MacMill. ex B.L. Rob & Fernald (Illinois bumbleflower)] were transplanted into each monolith (total density=56 plants m\textsuperscript{-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\textsuperscript{-1} CO\textsubscript{2} and was not correlated with ANPP on any soil type (Fay et al., 2012). Similarly, CO\textsubscript{2} 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 CO\textsubscript{2} 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; Wisley 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. 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). 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 the season. Drainage below the rooting zone of plants was also small. For example, drainage through Lycog grass 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; r²=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 r²=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 (ETᵣ) and effects that remained (CO₂ᵣ), 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 (χ² 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 μl⁻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 μl⁻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 gₛ, and increasing A and TE efficiencies (Aᵣ, gₛ) 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 C₃ 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×CO₂), whereas ANPP of the dominant C₃ grass, Bothriochloa, decreased as CO₂ rose during the experiment (change in ANPP=195.32–0.99×CO₂; Fig. 4).

We used SEM to determine the contributions of direct CO₂ effects (CO₂ᵣ, ETᵣ) 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
a change in ET (CO\textsubscript{2}; Fig. 6) that was probably linked to the CO\textsubscript{2}-caused increase in TE of the dominant species (Fig. 1) and a negative, direct effect mediated through a CO\textsubscript{2}-caused decrease in ET (ET\textsubscript{d}; Figs. 5 and 6). A change in community composition (composition), as reflected in a change in the contribution of the C\textsubscript{4} grass Bothriochloa to the community, also affected ANPP (Fig. 5). CO\textsubscript{2} enrichment increased ANPP (community effect) by reducing the Bothriochloa fraction (community response), the latter a result of the CO\textsubscript{2}-caused decline in ET. The pathway linking CO\textsubscript{2} directly to composition was not significant, and therefore was not included in the final SEM model. CO\textsubscript{2} enrichment increased the abundance of C\textsubscript{3} forbs at the expense of the initially dominant C\textsubscript{4} grass to increase community ANPP by 15% of the magnitude of CO\textsubscript{2} (Fig. 6).

Prairie assemblages (LYCOG experiment)

CO\textsubscript{2} enrichment increased ANPP of prairie communities on three soil types by an average of 79–122 g m\textsuperscript{-2} per 100 µL L\textsuperscript{-1} rise in CO\textsubscript{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\textsubscript{2} for Sorghastrum than for Bouteloua because CO\textsubscript{2} enrichment preferentially increased photosynthesis of Sorghastrum.

Prairie assemblages on each soil type became strongly dominated by C\textsubscript{4} grasses at the expense of C\textsubscript{3} forbs. The grass fraction of ANPP increased with time across CO\textsubscript{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\textsubscript{2}. The CO\textsubscript{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 µL L\textsuperscript{-1} CO\textsubscript{2} (Polley et al., 2012a).

CO\textsubscript{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\textsubscript{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\textsubscript{2} did not affect water depletion on the clay soil during any year.

The CO\textsubscript{2}-caused increases in Sorghastrum abundance and ANPP of assemblages were correlated (Polley et al., 2012b;
Table 1. Linear regression analyses for relationships between the seasonal maximum of soil water depletion (0–1.5 m depth) by prairie vegetation and CO$_2$ concentration for each of three soil types and each of the first 5 years of CO$_2$ treatment (LYCOG experiment)

Regression slopes represent the change in water depletion (cm) per 100 μl l$^{-1}$ increase in CO$_2$ concentration. Also listed are the mean and SE of water depletion across CO$_2$ treatments for each soil type and year.

<table>
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<th>Soil/year</th>
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<th>Slope</th>
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<th>$P$ value</th>
<th>Mean</th>
<th>SE</th>
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Fig. 6. Components of the CO$_2$ effect on ANPP of pasture (PCG experiment) and prairie communities grown on each of three soil types (LYCOG experiment). CO$_2$ 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’ CO$_2$ effects resulting both from a direct linkage between CO$_2$ and ANPP (CO$_2$-open) and through change in ET (ET$_{CO2}$-hatched) and an ‘indirect’ CO$_2$ effect mediated through shifts in community composition, as reflected in differences in the Bothriochloa (pasture) or Sorghastrum (prairie) fraction of ANPP along the CO$_2$ gradient (comp$_{CO2}$-shaded). The latter indirect effect includes two components, the response of community composition to CO$_2$ (community response) and the effect of community change on ANPP (community effect). Values for each component of the CO$_2$ effect are expressed as the change in ANPP (g m$^{-2}$) per 100 μl l$^{-1}$ increase in CO$_2$ concentration. Significant effects are denoted with an asterisk. $\chi^2$ 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 $\chi^2$ statistic is >0.05.

Augmented summer precipitation (MEND experiment)

Species richness (Fig. 8) and the ratio of C$_4$ to C$_3$ 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 C$_4$ grasses with traits associated with relatively high capture of CO$_2$ and light (Daneshgar et al., 2013). End-of-season aboveground biomass was greater in exotic than native communities, despite the more equitable C$_3$–C$_4$ 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 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

CO$_2$ enrichment stimulated ANPP of both C$_4$-dominated pasture (PCG experiment) and tallgrass prairie assemblages (LYCOG experiment) largely via a ‘direct’ effect (CO$_2$$_{3a}$) that was not associated with a change in ET. CO$_2$ 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). CO$_2$ enrichment ‘indirectly’ altered ANPP through changes in the C$_4$ composition of communities, change mediated entirely via CO$_2$-caused differences in ET in pasture. Feedback from community change increased ANPP by 15% of CO$_2$ in pasture but accounted for 21–38% of the net increase in ANPP in prairie assemblages.
As predicted, ‘community responses’ to increased CO$_2$ were reflected in increased abundances of species with traits that conferred an advantage under higher soil water availability. CO$_2$ favoured C$_3$ perennial forbs over a C$_4$ grass in pasture by reducing ET and favoured a C$_4$ 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. CO$_2$ enrichment amplified the ANPP response of prairie assemblages by favouring a C$_4$ grass with high TE, but apparently limited the ANPP benefit of community change in pasture by favouring C$_3$ forbs. Water ‘saved’ at elevated CO$_2$ in pasture as result of slower transpiration was increasingly diverted from use by the initially dominant C$_4$ grass to the increasingly dominant and taller C$_3$ forbs (Polley et al., 2003), despite the lower TE of the latter (Anderson et al., 2001). Not coincidentally, the ANPP-CO$_2$ response declined with time. The simultaneous decrease in ANPP-CO$_2$ response (Polley et al., 2003) and probable decline in WUE that occurred as less water-use efficient C$_3$ forbs replaced a C$_4$ grass (Anderson et al., 2001) implies that community change limited the CO$_2$ 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.

**Fig. 7.** SEMs describing CO$_2$ 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. CO$_2$ effects on ANPP were considered to be ‘direct’ unless mediated through a CO$_2$-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 CO$_2$ to ANPP through composition include two components, the community response to CO$_2$ 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, and 0.91 for the clay, silty clay, and sandy loam soils, respectively).

**Fig. 8.** Upper graph: temporal trends in plant species richness (species per m$^2$) 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 non-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-irrigation interaction.
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 CO$_2$ treatments, despite CO$_2$- caused variation in the TE of dominant species (Anderson et al., 2001; Fay et al., 2012). CO$_2$ 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. CO$_2$ 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 CO$_2$ 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 CO$_2$ 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 CO$_2$. 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 CO$_2$ were linked to plant traits associated with a positive growth response to greater water availability. By contrast, community effects on the ANPP-CO$_2$ 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.

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