Long-term exposure to elevated CO_2 enhances plant community stability by suppressing dominant plant species in a mixed-grass prairie

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Climate controls vegetation distribution across the globe, and some vegetation types are more vulnerable to climate change, whereas others are more resistant. Because resistance and resilience can influence ecosystem stability and determine how communities and ecosystems respond to climate change, we need to evaluate the potential for resistance as we predict future ecosystem function. In a mixed-grass prairie in the northern Great Plains, we used a large field experiment to test the effects of elevated CO_2, warming, and summer irrigation on plant community structure and productivity, linking changes in both to stability in plant community composition and biomass production. We show that the independent effects of CO_2 and warming on community composition and productivity depend on interannual variation in precipitation and that the effects of elevated CO_2 are not limited to water saving because they differ from those of irrigation. We also show that this mixed-grass prairie ecosystem is not only relatively resistant to interannual variation in precipitation, but also rendered more stable under elevated CO_2 conditions. This increase in production stability is the result of altered community dominance patterns: Community evenness increases as dominant species decrease in biomass under elevated CO_2. In many grasslands that serve as rangelands, the economic value of the ecosystem is largely dependent on plant community composition and the relative abundance of key forage species. Thus, our results have implications for how we manage native grasslands in the face of changing climate.

climate change | elevated carbon dioxide | grassland | community stability | warming

Ecologists have long recognized the importance of climate in shaping plant communities across spatial and temporal scales (1). Together, precipitation and temperature characterize the distribution of terrestrial biomes across the globe. As climate changes, some biomes will be more vulnerable to temperature increase (2) or altered precipitation (3), whereas others will be more resistant (4–6). Ecological stability, the maintenance of community structure and function despite climatic fluctuation or disturbance (7–9), includes two components: resistance [lack of change despite perturbation (9)] and resilience [return to a previous state following a perturbation (10–13)]. Diversity (14) and productivity (11, 15) can both influence community stability (16) and dampen responses to environmental perturbation (5, 9, 17, 18). What remains unclear is how stability and resistance respond to predicted changes in climate.

Multiple climate change factors simultaneously impact plant performance, community structure, and productivity (4, 19, 20). For example, elevated CO_2 can improve water use efficiency and increase plant productivity (21–23), but warming can reduce it, counteracting the positive water-saving effects of elevated CO_2 (24). In addition, plant species and functional groups that differ in photosynthetic pathway often have contrasting responses to elevated CO_2, warming, and altered precipitation. Furthermore, the effects of individual climate change factors may be additive (25, 26), subadditive (4, 24, 27), or antagonistic (27, 28). As a result, the performance of a given species or functional group depends on interactions among CO_2, temperature, and soil characteristics that influence plant water availability at the community level.

Globally, both elevated CO_2 and warming are expected to lead to pronounced changes in vegetation distribution and structure (25, 29, 30). In North American grasslands, warming is expected to promote C_4 dominance, dampening the ability of these areas to show large responses to elevated CO_2 (25). Because responses to climate change differ among individual plant species and depend on community context (31–33), the resultant community dynamics are difficult to predict. In addition, plant responses to climate manipulations can shift over time. Our earlier work in a mixed-grass prairie shows that in the first 3 y of the Prairie Heating and CO_2 Enrichment (PHACE) experiment, both C_3 and C_4 grass production benefited from elevated CO_2 conditions (34). However, long-term studies of CO_2 enrichment show that plant responses can diminish over time (22, 35), including the responses of dominant grass species in our mixed-grass prairie (36). To accurately characterize the trajectory of species responses and predict the interacting impacts of global climate change on plant community structure and function, long-term experiments are necessary.

Grasslands in the northern Great Plains are experiencing rapid climate change, with average annual temperatures increasing by 2.6 °C over the last century and winter and spring temperatures increasing more rapidly than summer temperatures (37). Grasslands

Significance

Evaluating ecological responses to climate change is essential to predict ecosystem function under future climate scenarios. In a mixed-grass prairie, we use a multifactor field experiment to show that the effects of elevated CO_2 and warming on plant community structure and productivity depend on interannual variation in precipitation. We also show that shifts in plant dominance patterns driven by elevated CO_2 in a mixed-grass prairie ecosystem promoted biomass and compositional stability and resistance to interannual variation in precipitation. The economic value of grasslands is largely dependent on the relative abundance of key forage species. Thus, our results have implications for how we manage native grasslands in the face of changing climate.

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Table 1. Site annual temperature and precipitation data from 2006 to 2013

Q:20 ■■■	30-y mean	2006	2007	2008	2009	2010	2011	2012	2013
Mean annual temperature, °C	8.0	8.55	7.6	7.7	6.3	7.6	6.4	8.8	7.7
Growing season temperature, °C	13.2	13.7	13.3	11.6	12	12.2	11.7	15.1	12.0
Spring precipitation, mm	124	112	127	81	129	200	204	46	69
Total growing season precipitation, mm	178	152	179	147	328	287	286	161	155
Annual precipitation, mm	388	*438*	405	385	510	379	494	241	461

The total precipitation data include precipitation in the form of rain collected at the PHACE site and snowfall (averaged from the High Plaints Grassland Research Station meteorological station and the National Oceanic and Atmospheric Administration station at the Cheyenne, WY, Airport). Growing season temperature is the mean temperature from March through September annually. Spring precipitation was summed from March through May, a critical time for plant growth in this ecosystem. Growing season precipitation was summed from March through July 20, when the annual biomass harvest occurred. The Q:21 30-y mean data were downloaded from the National Oceanic and Atmospheric Administration Cheyenne Airport meteorological station (www.ncdc.noaa.gov/IPS/lcd/lcd.html). The precipitation data from 2006 (italicized) are partially supplemented with 160 mm of irrigation added to the annual precipitation (278 mm) to yield annual precipitation equivalent to 438 mm.

are extensively grazed, and moisture availability (timing and amount of rainfall) affects grassland productivity to support domestic and native herbivores (3, 38). Compared with other regions, precipitation change is expected to be relatively modest, but there is a general consensus that even if annual precipitation change is small, precipitation timing will become increasingly variable (37) and the number of extreme precipitation events will also increase (39–41). When coupled with rising temperatures, water limitation will increase (42), potentially reducing rangeland productivity (43). Because the timing of water availability regulates grassland productivity and community dynamics (3, 44), variation in background climate may promote or reduce the resistance of grasslands to climate change. The economic value of the ecosystem is largely dependent on the plant community and the relative abundance of key forage grass species (45). Thus, changes in grassland productivity can have clear economic impacts for ranching and managing wildlife (46).

To understand how climate change influences plant community dynamics and stability (namely, resistance to interannual shifts in precipitation), we quantified the impacts of experimentally imposed elevated CO_2, warming, and summer irrigation on plant community composition and aboveground biomass production over 8 y in a northern mixed-grass prairie in southeastern Wyoming. Species that dominate biomass production are expected to respond to changes in climate most directly (47), whereas subdominant species may respond to climate change directly and indirectly through their interactions with the dominant species (6, 48, 49). Thus, we quantified climate change effects on the entire community and on dominant and subdominant community members separately. We addressed three questions: (*i*) Do the effects of climate change on plant community composition and productivity depend on temperature and precipitation variation? (*ii*) Do dominant and subdominant components of the plant community respond differently to climate change? and (*iii*) What is the influence of climate change on community composition and biomass stability?

Results

Relative to the 30-y mean of 8.3 °C, the PHACE experimental site experienced a number of relatively warm and dry years (Table 1). During the same period, there were also a number of wet years, 2009–2011, receiving 25% or more additional annual rainfall relative to the 30-y mean. Spring precipitation, in the form of snow and rain, has a large influence on early season plant growth in the mixed-grass prairie, and spring precipitation varied substantially across the 8-y study (Table 1).

PHACE Treatment Effects on Plant Community Composition and Productivity. The effects of elevated CO_2, warming, and summer irrigation on plant community composition and aboveground biomass production varied between wet and dry years (Table 2 and Fig. S1). Total biomass production increased in wet years and decreased in dry years (34). The effect of elevated CO_2 on plant community composition was significant in the first year of the experiment (when there was no warming treatment in place) and during subsequent relatively dry years, whereas the effect of warming was significant during average and wet years (Table 3). The interaction between elevated CO_2 and warming on composition was significant only in 2013, suggesting that for the majority of the study, their effects were additive rather than antagonistic. Summer irrigation only influenced community composition in 2008 and 2013—years with low spring and summer precipitation—but not in any other year. Effects of summer irrigation on plant community composition did not match those from the equivalent water savings in elevated CO_2 plots, confirming that elevated CO_2 had some direct influence on plant performance.

Responses of Dominant vs. Subdominant Species to Climate Change. Across the 8-y experiment, we found 55 plant species in our plots, but the dominant species *Pascopyrum smithii* and *Boutelua gracilis* together accounted for approximately half of the plot aboveground biomass (mean 57% ±2.8 SE, range 29–71%). Their collective biomass decreased across time from 60% in 2005 to 44.5% in 2013. This decrease in dominants' productivity was largely driven by changes in elevated CO_2 plots (to 29 ± 4% SE in $+CO_2$ and 41 ± 5% SE in $+CO_2$+T in 2013) and not in plots under ambient CO_2 (to 48 ± 4% SE in ambient and 51 ± 4% SE in +T plots in 2013). The ratio of dominant to subdominant biomass decreased under elevated CO_2 over the 8-y study period [analysis of covariance (ANCOVA) $F = 49.7$, $P < 0.0001$; Fig. 1], Q:9 largely because the biomass of the two dominant species

Table 2. Results from two-way permulational ANOVA analyses of the effects of year, warming, elevated CO_2, time, and their interaction on Bray-Curtis plant community composition from 2005 to 2013

Source	df	Pseudo-*F*	$P_{(perm)}$
Year	8	4.9	**0.001**
Elevated CO_2	1	13.9	**0.001**
Warming	1	12.9	**0.001**
Block	1	13.7	**0.001**
Year × CO_2	8	0.4	1
Year × warming	8	0.7	0.9
Warming × CO_2	1	4.5	**0.001**
Year x warming × CO_2	8	0.5	1
Year	8	3.1	**0.001**
Irrigation	1	10.6	**0.001**
Block	1	9.1	**0.001**
Year × irrigation	8	0.5	1

See *Methods* for details. Results from the same analysis performed on irrigated plots are shown separately. Significant effects at $\alpha < 0.05$ are bold.

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Table 3. Results from a two-way permutational analysis of the main and interactive effects of warming, elevated CO_2, and year on plant community composition, presenting the pseudo *F* ratio and permuted *P* values within years 2007–2013

	Year (precipitation)															
	2006 (dry)		2007 (average)		2008 (dry)		2009 (wet)		2010 (wet)		2011 (wet)		2012 (dry)		2013 (dry)	
Q:22 ■■■	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Whole community																
$+CO_2$	2.7	**0.005**	1.9	**0.03**	2.4	**0.02**	1.5	0.15	1.5	0.2	1.4	0.2	2.1	**0.03**	0.8	0.7
+T			2.4	**0.03**	1.4	0.2	2.1	**0.03**	1.7	0.08	1.9	**0.05**	2.2	**0.02**	2.5	**0.01**
$+T \times CO_2$			0.5	0.9	0.5	0.9	0.8	0.7	1.1	0.4	1.2	0.3	1.2	0.3	1.9	**0.05**
Water			1.5	0.2	2	**0.03**	2.2	0.2	1.3	0.3	1.3	0.2	1.1	0.3	2	**0.03**
Subdominant community																
$+CO_2$	1.2	0.3	0.7	0.7	1.1	0.4	1	0.5	1.1	0.4	0.6	0.8	1.5	0.2	0.3	1
+T			2.3	0.07	1.4	0.2	2.9	**0.01**	2.7	**0.02**	1.4	0.2	2.4	**0.03**	3	**0.01**
$+T \times CO_2$			0.3	0.9	0.3	0.9	0.7	0.7	1	0.5	0.5	0.8	1.1	0.4	2.1	**0.04**
Water			0.8	0.6	1.2	0.3	2	**0.05**	1.4	0.2	1	0.5	1.7	0.1	1.8	0.08

$+CO_2$, elevated CO_2; +T, warming. In 2006, only the elevated CO_2 treatment was in place. The effects of irrigation were evaluated separately because the irrigation additions were not crossed with the other treatments. Significant treatment effects at the $\alpha < 0.05$ are bold. Growing season precipitation (relative to the 30-y site mean) is noted.

decreased over time, whereas subdominant biomass remained stable or slightly increased. Summer irrigation increased soil water content to nearly the same level as in the elevated CO_2 treatments (50) but had no overall effect on the dominant:subdominant biomass ratio across time (ANCOVA $F = 1.2$, $P = 0.3$), suggesting that the effects of elevated CO_2 were not similar to those of irrigation. There was a marginally significant positive effect of warming on the dominant:subdominant biomass (ANCOVA $F = 3.2$ $P = 0.07$; Fig. 1).

Across the entire plant community, elevated CO_2 and, to a lesser extent, irrigation significantly influenced community composition in dry years, and warming significantly influenced community composition in wet years. However, subdominant plant community composition responded largely to warming (Table 3). The marginally significant effect of irrigation on subdominant community composition in the wet year 2009 could be explained by the late-summer timing of irrigation relative to the timing of precipitation (Table 1). Overall shifts in plant community composition across the 8-y study (Table S1) were mostly driven by changes in the biomass of five species: *B. gracilis* (a C_4 gramonoid); the C_3 gramonoids *Hesperostipa comata, P. smithii*, and *Koeleria macrantha*; and the subshrub *Artemisia frigida* (40% average dissimilarity between 2005 and 2013), with an increase in *A. frigida* and *K. cristata* biomass and a decrease in the other species. Together, CO_2 and warming independently led to divergence in plant community composition, with dominant and subdominant components of the plant community differing in their responses (Table S1). These differential responses reduced community dominance and promoted community evenness and diversity (Fig. S2).

Community Stability Under Climate Change. Compositional and biomass stability (i.e., productivity) varied among treatments ($F_{4,7} = 9.4$, $P < 0.0001$ and $F_{4,24} = 3.5$, $P = 0.03$, respectively). Elevated CO_2, especially in combination with warming, influenced annual plant compositional change (i.e., plot turnover; Fig. 2), maintaining low annual plot turnover for most of the 8-y CO_2 enrichment experiment and conferring compositional stability across time. Similarly, biomass stability was highest in irrigated and elevated CO_2 plots and lowest in ambient and heated plots (Fig. 3). High stability in elevated CO_2 and irrigated plots indicates that productivity remained unchanged across wet and dry years, whereas productivity in ambient and warmed plots was more variable, decreasing in dry years and increasing in wet years (34). Furthermore, the slopes of the relationship between mean aboveground biomass and temporal SD across the 8-y study varied among the PHACE treatments ($F_{4,24} = 3.7$, $P = 0.03$), and productivity was more sensitive to variation in climate (evidenced by high SD) under ambient conditions than in plots under elevated CO_2 (Fig. 3). Community biomass stability in our study was unrelated to species richness or diversity, but positively related to species evenness ($F = 6.7$, $P = 0.02$; Fig. S2), illustrating the importance of the subdominant community in stabilizing plant productivity across dry years. Together, our results illustrate that elevated CO_2 increases community biomass stability in the face of interannual shifts in precipitation, overcoming the negative effects of warming by increasing plant community evenness.

Discussion

Our 8-y study included years with substantial climate variation, and plant biomass production varied twofold between the wettest

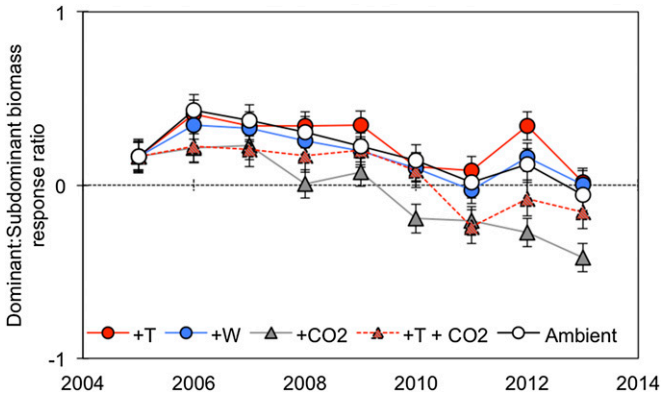

Fig. 1. The effects of the PHACE climate-change treatments on the dominant:subdominant biomass response ratio, calculated as the ratio of dominant species *P. smitthii* and *B. gracilis* to the subdominant species across time. Elevated CO_2 treatments were initiated in 2006 and warming and summer irrigation in 2007. +T indicates warmed plots, +W indicates irrigated plots, $+CO_2$ indicates plots under elevated CO_2, and $+T+CO_2$ indicates plots under both warming and elevated CO_2. Biomass is represented as the least-square means of the ANCOVA model that accounts for baseline differences in biomass in 2005. Error bars are ±1 SEM ($n = 5$ per treatment). A shift to greater abundance of dominant species is indicated by +1, and a shift to greater abundance of subdominant species is indicated by −1.

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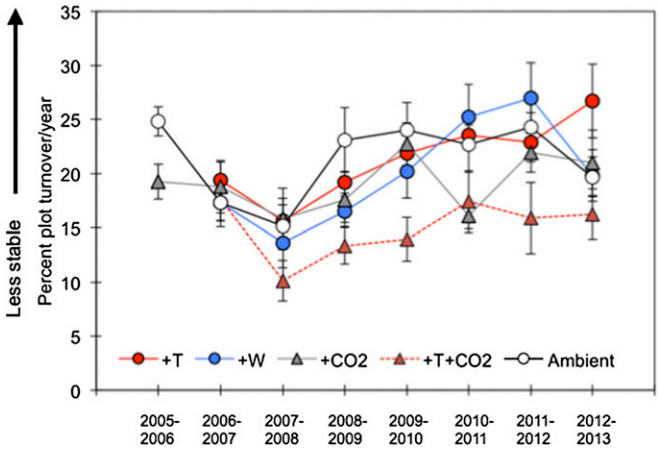

Fig. 2. The effects of the PHACE climate change treatments on annual community compositional turnover. Plot turnover (i.e., dissimilarity) is the inverse of the square-root–transformed Bray Curtis similarity index, and annual turnover was calculated per plot. Elevated CO_2 treatments were initiated in 2006 and warming and summer irrigation in 2007. +T indicates warmed plots, +W indicates irrigated plots, +CO_2 indicates plots under elevated CO_2, and +T+CO_2 indicates plots under both warming and elevated CO_2. Turnover initially decreases, suggesting that plant communities are relatively stable from year to year, but increases from 2009 to 2013, more so in the ambient, warmed, and irrigated but not elevated CO_2 plots, indicating that those plots are experiencing more turnover in community composition from year to year and, thus, are less resistant to changes in climate. Error bars are ±1 SEM (n = 5 per treatment).

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and driest years. However, despite large variation in biomass across time, plant community production was more stable under "future ~ elevated CO_2 + warming" climate conditions than under current climate in our study system. Warming had little effect on biomass stability, which was low compared with biomass stability under elevated CO_2. However, plant communities experiencing both elevated CO_2 and warming did not differ from plant communities under elevated CO_2 alone, and at least in terms of biomass production, elevated CO_2 was a strong stabilizing force. Although summer irrigation did not appear to influence community compositional stability or the biomass ratio of dominant to subdominant species, it did stabilize overall aboveground biomass production across dry years, and its effect on biomass stability was similar to that of elevated CO_2. Our findings corroborate the importance of water availability in driving most measures of ecosystem function, including plant productivity, in arid ecosystems (38, 51).

In contrast to the increase in overall productivity under elevated CO_2 conditions we observed in the first 3 y of the PHACE experiment (34), elevated CO_2 reduced biomass production of dominant species, particularly in later years. When extended over the 8-y duration of the PHACE experiment, we found that elevated CO_2 and warming have differential effects on plant community composition, productivity, and stability. Although we saw a consistent difference between "present ~ ambient" and "future ~ elevated CO_2 + warming" plant community composition, the isolated effects of elevated CO_2 and warming depended on precipitation, in agreement with findings from other grassland studies (30). The effect of elevated CO_2 and irrigation on plant community composition was evident in dry years and the effect of warming in wet years, but there was no interaction between elevated CO_2 and warming, and their combined effects were additive rather than antagonistic. The findings we report from a mixed-grass prairie, however, are not necessarily generalizable to all other grassland systems, where the effects of elevated CO_2, warming, and irrigation can vary along an aridity gradient and be contingent on land management (52).

The two most abundant species in the plots, *P. smithii* and *B. gracilis*, decreased in dominance under elevated CO_2 plots, whereas total plot biomass remained relatively unchanged or increased slightly during the 8-y study, suggesting that subdominant community biomass increased. Indeed, there is evidence that as subdominants play an increasingly large role in communities, stability can increase (47, 53). Because subdominant community composition did not change under elevated CO_2, species already present in the community were likely increasing their productivity. In contrast, subdominant biomass production remained unchanged in warmed plots, but community composition shifted, suggesting that some subdominant species increased and some decreased production and that subdominants may differ in their sensitivity to warmer conditions. Further, shifts in subdominant community composition in response to warming did not result in overall change in production, likely because the increase in production of particular subdominant species was counteracted by the decline in production of other subdominant species. The differential responses of dominant and subdominant species to climate change factors provide some evidence that the subdominant community responding not only to the climate change treatments directly but also to the changes in dominant biomass (6, 54).

The dominance hypothesis postulates that dominant species use the majority of resources and have disproportionally large community impacts (55). As a result, the responses of these species to climate change can determine the rate at which other species can respond (47). However, grassland subdominants often thrive under unstable ecological or climate conditions, including across wet and dry years (56), and in the mixed-grass prairie, can show strong responses to elevated CO_2 (36). Indeed, enhanced subdominant graminoid production under elevated CO_2 stabilized overall biomass production across dry years. Together, the differential effects of elevated CO_2 and warming on co-occurring dominant and subdominant plant species in the PHACE experiment led to a decrease in dominance and an increases in evenness, driven by shifts in the subdominant community. Our results provide an important counterexample to situations in which global changes increase dominance and reduce diversity [e.g., N deposition (57)]. Other studies report

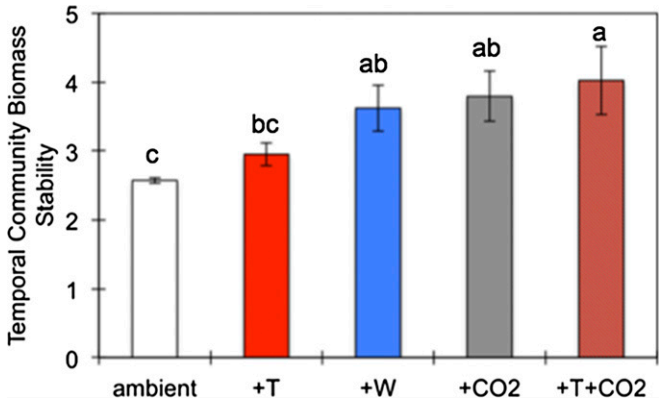

Fig. 3. Temporal biomass stability across the 8-y PHACE experiment. Temporal stability calculations are provided in *Methods*. Treatments are indicated on the x axis, where +T indicates warmed plots, +W indicates irrigated plots, +CO_2 indicates plots under elevated CO_2, and +T+CO_2 indicates plots under both warming and elevated CO_2. The results from a one-way ANOVA, with Tukey's honestly significant difference means separation test (α = 0.05), are presented. Different letters indicate statistically significant differences at α = 0.05, and all other comparisons are not statistically significantly different. Error bars are ±1 SEM (n = 5 per treatment).

a positive relationship between stability and species richness or diversity (15, 24, 26), but biomass stability in our study was only positively associated with species evenness, further illustrating the importance of the subdominant community in stabilizing plant productivity across dry years. The relationship between community evenness and biomass stability was especially strong in the plots representative of future climate conditions (namely, plots that received both elevated CO_2 and warming treatments).

Globally, grasslands cover up to 1/3 of the terrestrial surface and provide important ecosystem services, including carbon sequestration and forage for livestock. Over the past two centuries, many grasslands across the globe have been transformed by agriculture, grazing, fire, and invasive species. Anthropogenic influences are expected to intensify to keep pace with a growing global population that relies heavily on grassland production. In addition to land use, climate impacts most aspects of grassland function (51, 58). In rangelands, the economic value of livestock operations relies on stable production of key forage grass species (45, 59). Others have noted that the dominant species in our plots, *P. smithii* and *B. gracilis*, as well as the subdominants *H. comata*, *C. eleocharis*, *A. frigida*, *S. coccinea*, and *K. macrantha*, are relatively drought- and disturbance-tolerant (60–63), and our findings generally agree. Although the dominance patterns in ambient mixed-grass prairie plots shifted slightly over the 8-y study, the transition from *P. smithii*- and *B. gracilis*-dominated communities to the subdominants occurred gradually. Despite the general shift in dominance in ambient plots, overall plant community biomass and composition remained relatively stable, but rendered more stable under elevated CO_2. As climate becomes increasingly variable (30, 64), with longer and more pronounced droughts in the future, elevated CO_2 appears to further stabilize this mixed-grass prairie community against shifts in precipitation. Thus, our results suggest that production can be maintained under elevated CO_2 conditions, but with subdominant plant species contributing more to total production and perhaps increasing in dominance. Such shifts in species composition can have important implications for rangeland quality and should be considered in future management plans for mixed-grass prairie ecosystems.

Methods

The PHACE experiment was initiated in 2005 at the U.S. Department of Agriculture Agricultural Research Service High Plains Grasslands Research Q:11 Q:12 Station, located west of Cheyenne, WY (41° 11′ N latitude, 104° 54′ W longitude). The vegetation at PHACE is a northern mixed-grass prairie and is dominated by C_3 graminoids. C_4 grasses make up 25% of the plant community, and 20% of the plant community consists of sedges, forbs, and small shrubs. Annual precipitation at the site averages 384 mm; mean winter air temperature is −2.5 °C, and mean summer air temperature is 17.5 °C. The site was regularly grazed since 1974, but was fenced to prevent livestock grazing in 2005. The soil at the site is a fine-loamy, mixed, mesic Aridic Argiusoll, pH 7.9. In the north side of the site, the soil is Ascalon series, and the south side soil is Altvan series; as a result of these soil type differences, we blocked the experimental units by soil type and included block as a random effect in the models. In 2005, 25 circular 3.4-m–diameter plots were established with a 60-cm–deep impermeable barrier to prevent lateral inflow. Elevated atmospheric CO_2 was applied starting in 2006 and accomplished by using mini-FACE (The Free Air CO_2 Enrichment) technology [ambient CO_2 ~385 parts per million by volume (ppmv) and elevated CO_2 600 ± Q:13 40 ppmv (65)], using 3.3-m FACE rings. A differential daytime/nighttime warming (1.5/3 °C) treatment was applied by using infrared heaters (66) in full factorial design, with five replicates for each of the four combinations (ambient, +CO_2 and ambient temperature; ambient CO_2 and + temperature; +CO_2 and ambient temperature; and + CO_2 + temperature). Elevated CO_2 treatments were initiated in early spring of 2006, and warming and summer irrigation were started in the spring of 2007. All plots were irrigated by hand in 2006 to facilitate establishment of an associated experiment (20 mm × eight irrigation dates, the equivalent of 160 mm of additional growing-season precipitation). Beginning in 2007, plots were irrigated to match the water saving under elevated CO_2 treatments, receiving an equivalent of 18 mm of precipitation with each irrigation × five irrigation dates in 2007, the equivalent of 90 mm of additional growing-season precipitation. From 2008 to 2011, irrigated plots received an equivalent of 21 mm of precipitation three times during the growing season (equivalent to 63 mm of additional precipitation), and in the dry year of 2012, 65 mm of water was added four times during the growing season (equivalent to 260 mm). In 2013, 24 mm was added before harvest. The site, experimental setup, and treatment performance are described in detail in ref. 34. Annual aboveground production was clipped by species to the crown in 12 subplots of 625 cm^2 in each experimental plot, alternating the location of the clipped area each year. Vegetation was harvested in late July, at the time of peak biomass. All harvested material was sorted to species, dried for 3 d at 55 °C, and weighed. We used species-specific relative biomass in all subsequent statistical analyses.

Analyses. ***Plant community productivity and composition.*** To examine the effects Q:14 of the climate-change treatments over time on plant community composition, we used a two-way permutational analysis of variance (PERMANOVA) on the Bray Curtis similarity index of square-root transformed species-specific relative biomass, with year, elevated CO_2, and warming as the fixed effects in one model, block as a random effect, and year and irrigation in a separate model because the treatment application was not fully factorial (warming and elevated CO_2 were not crossed with irrigations). The same main effects were tested within each year, with the effects of elevated CO_2 only in 2006 because it was the only treatment in place. The PERMANOVA analysis was complimented with permutational analysis of multiple dispersions (PERMDISP), Q:15 a multivariate analysis of dispersion that calculates the centroid of each treatment in multivariate space and calculates the distance of each plot within the treatment from the treatment centroid. We found no significant PERMDISP differences within treatments, indicating that the PERMANOVA results show significant differences among treatments that are not the result of dispersion differences within treatments. A similarity percentage (SIMPER) analysis was performed to quantify the contribution of individual species to compositional differences among treatments and years. The PERMANOVA, PERMDISP, and SIMPER analyses were conducted for the whole community and the subdominant community separately; for the latter, we removed the two dominant species, *P. smithii* and *B. gracilis,* and recalculated the relative biomass of the remaining species. Principle coordinates analysis (PCO) ordination was performed to visualize whole plot composition in a 2D space. The multivariate community analyses PCO, PERMANOVA, and SIMPER analyses were performed by using PRIMER (Version 1.0.3; Plymouth Marine Laboratory).

The multivariate analyses were complimented with a series of univariate analyses. We calculated a biomass response ratio by taking the difference between dominant and subdominant biomass and dividing it by the sum of dominant and subdominant biomass. Changes in the ratio of dominant (*B. gracilis* and *P. smithii*) to subdominant species biomass over time were analyzed by using an ANCOVA, with block as a random effect, plot number nested within treatment, treatment effects and their interaction as well as their interactions with year, and 2005 biomass and its interaction with year included as covariates to account for differences in starting conditions among plots. Least-square means from the ANCOVA model were plotted to illustrate the effects of the climate-change treatments on the biomass response ratio instead of raw biomass measures because ANCOVA model least-square means account for differences in biomass between plots at the start of the experiment.

Ecosystem resistance/stability. We assessed the effects of the PHACE climate-change treatments on stability using two approaches. To assess community compositional stability, we first quantified community compositional dissimilarity, taking the inverse of the square-root–transformed Bray Curtis similarity index on the sample × species matrix and calculating the annual percentage of community turnover per plot. Small changes in community composition within a plot from year to year represent greater community stability than larger shifts. The effects of the climate-change treatments on indices of community composition for each year were examined by using an ANOVA, with elevated CO_2 and warming as the main effects and block as a random effect, and followed with Tukey–Kramer post hoc comparisons. A separate one-way ANOVA was used to look at the effect of elevated CO_2 in 2006 and irrigation between 2007 and 2012. To assess temporal biomass stability, *S*, we calculated the mean plot productivity per treatment across the study (μ) and divided by the temporal SD over the same time period (σ) (17). Log-transformed temporal biomass stabilities were compared among treatments by using a one-way ANOVA, with post hoc Tukey–Kramer comparisons to distinguish treatment differences. All univariate analyses were performed by using JMP (Version 10.0; SAS Institute).

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Supporting Information

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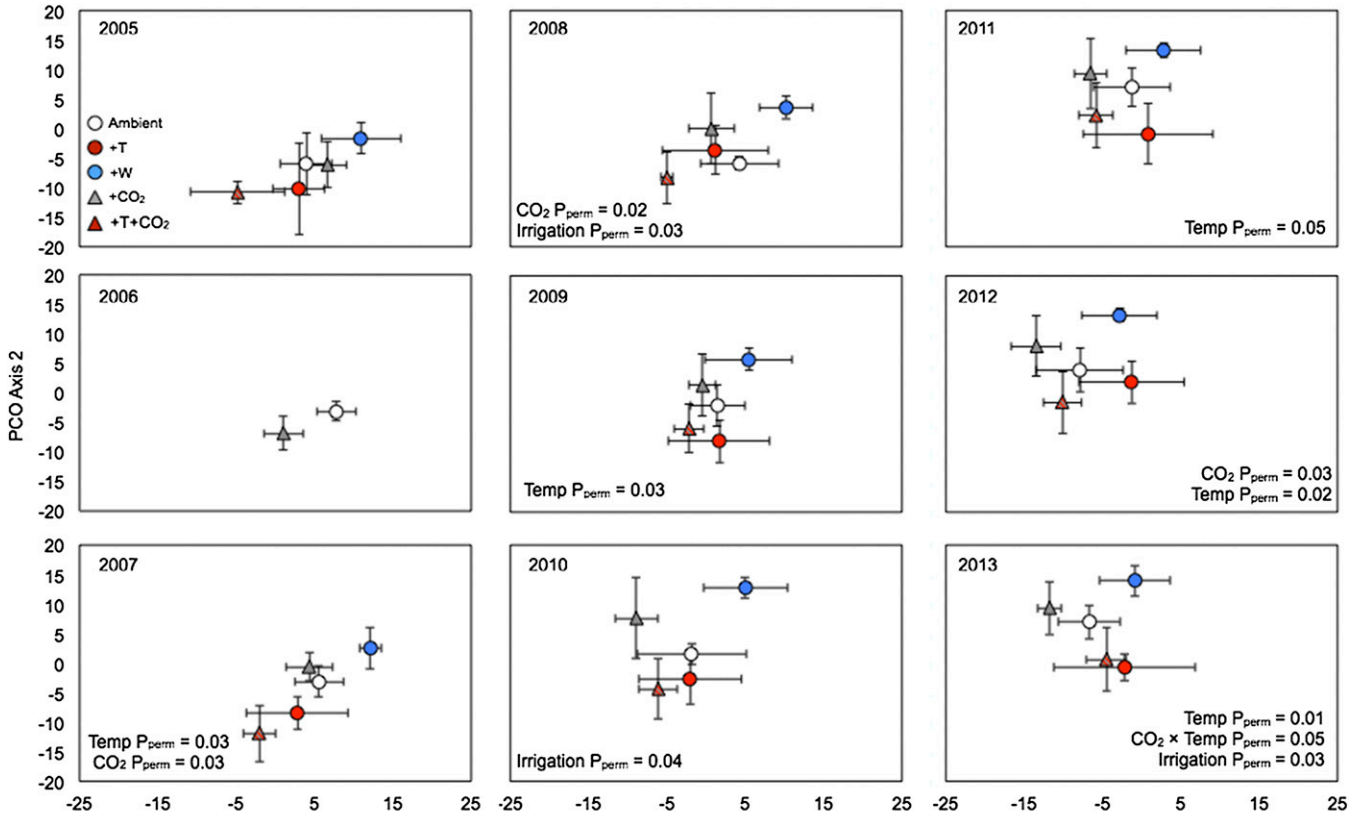

Fig. S1. Species PCO ordination plots, with axis 1 and 2 scores that together explain 37% of the variation. Elevated CO_2 treatments were initiated in 2006 and warming and summer irrigation in 2007. Individual and interacting effects of the PHACE treatments are noted, where significant in the PERMANOVA. +T indicates warmed plots, +W indicates irrigated plots, +CO_2 indicates plots under elevated CO_2, and +T+CO_2 indicates plots under both warming and elevated CO_2. Each point signifies the average of PCO axis 1 and 2 scores across replicates within that treatment (n = 5), and error bars are ±1 SEM.

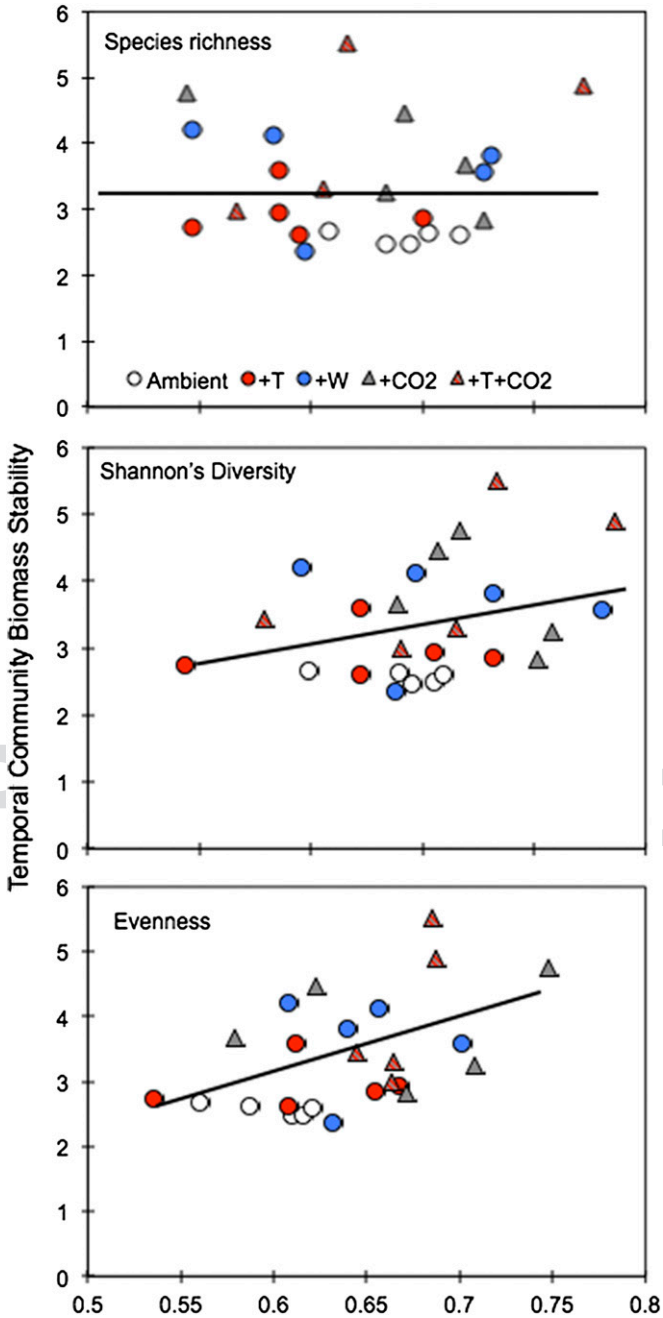

Fig. S2. The linear relationships between species richness (*Top*), Shannon's diversity (*Middle*), and evenness (*Bottom*) and temporal community biomass stability from 2005 to 2012. +T indicates warmed plots, +W indicates irrigated plots, $+CO_2$ indicates plots under elevated CO_2, and +T $+CO_2$ indicates plots under both warming and elevated CO_2.

Table S1. Annual plant community composition turnover, indicated by similarity percentage analysis of square-root–transformed plant community compositional dissimilarity between years

	SIMPER similarity, % (contribution ≥ 9%)															
Whole community																
2005–2006		2006–2007		2007–2008		2008–2009		2009–2010		2010–2011		2011–2012		2012–2013		
H. comata	13.8	*H. comata*	14.9	*H. comata*	17	*H. comata*	14	*H. comata*	12.4	*H. comata*	11.6	*H. comata*	10	*H. comata*	10.3	
B. gracilis	9.6	*P. smitthii*	10	*P. smitthii*	12	*P. smitthii*	10	*K. macrantha*	10	*K. macrantha*	10	*A. frigita*	9	*A. frigita*	9.5	
				K. macrantha	9							*K. macrantha*	9			
Subdominant community																
2005–2006		2006–2007		2007–2008		2008–2009		2009–2010		2010–2011		2011–2012		2012–2013		
H. comata	13	*H. comata*	14.1	*H. comata*	15.4	*H. comata*	12.7	*H. comata*	12.1	*H. comata*	11.9	*H. comata*	10.7	*H. comata*	11.5	
A. frigita	10.7	*A. frigita*	9.5	*K. macrantha*	11.2	*K. macrantha*	10.3	*K. macrantha*	11.3	*K. macrantha*	11	*A. frigita*	10.6	*A. frigita*	11.2	
C. duriuscula	8.5			*C. duriuscula*	11	*C. duriuscula*	9.6			*A. frigita*	9	*K. macrantha*	10.1	*K. macrantha*	10	
				A. frigita	9.4									*C. duriuscula*	9	

The major species contributing to the differences among the whole plant community between years are *Hesoerostipa comata*, *Artemisia frigida*, *Koeleria macrantha*, and *Pascopyrum smithii* and among the subdominant plant community, *H. comata* and *A. frigida* remain important in driving community differentiation and *Carex duriuscula* emerges as important in the subdominant community when *P. smithii* and *B. gracilis* are excluded from the analysis.

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