Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in the shortgrass steppe

Jack A. Morgan*[†], Daniel G. Milchunas[‡], Daniel R. LeCain*, Mark West[§], and Arvin R. Mosier[¶]

*Rangeland Resources Research Unit and [§]Northern Plains Area, Agricultural Research Service, United States Department of Agriculture, Fort Collins, CO 80526; [‡]Department of Forest, Rangeland, and Watershed Stewardship and Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, CO 80523; and [¶]Soil Plant Nutrient Research Unit, Agricultural Research Service, United States Department of Agriculture, Fort Collins, CO 80526

A hypothesis has been advanced that the incursion of woody plants into world grasslands over the past two centuries has been driven in part by increasing carbon dioxide concentration, $[CO_2]$, in Earth's atmosphere. Unlike the warm season forage grasses they are displacing, woody plants have a photosynthetic metabolism and carbon allocation patterns that are responsive to CO_2, and many have tap roots that are more effective than grasses for reaching deep soil water stores that can be enhanced under elevated CO_2. However, this commonly cited hypothesis has little direct support from manipulative experimentation and competes with more traditional theories of shrub encroachment involving climate change, management, and fire. Here, we show that, although doubling $[CO_2]$ over the Colorado shortgrass steppe had little impact on plant species diversity, it resulted in an increasingly dissimilar plant community over the 5-year experiment compared with plots maintained at present-day $[CO_2]$. Growth at the doubled $[CO_2]$ resulted in an ≈40-fold increase in aboveground biomass and a 20-fold increase in plant cover of *Artemisia frigida* Willd, a common subshrub of some North American and Asian grasslands. This CO_2-induced enhancement of plant growth, among the highest yet reported, provides evidence from a native grassland suggesting that rising atmospheric $[CO_2]$ may be contributing to the shrubland expansions of the past 200 years. Encroachment of shrubs into grasslands is an important problem facing rangeland managers and ranchers; this process replaces grasses, the preferred forage of domestic livestock, with species that are unsuitable for domestic livestock grazing.

C_3 | C_4 | functional group | global change | semiarid grassland

Although atmospheric carbon dioxide concentrations ($[CO_2]$) have increased from ≈280 volumetric ppm in preindustrial times to ≈380 ppm today and are projected to exceed 600 ppm by the end of this century, it is perhaps more important to point out that CO_2 levels are higher today than they have been for at least 650,000 years (1). Furthermore, levels of atmospheric CO_2 for the past half million years have tended to stay closer to the lowest glacial levels of ≈180 ppm compared with the ≈280–300 ppm of interglacial periods. These recent abrupt changes in atmospheric CO_2 have tremendous implications for the adaptation and evolution of relatively modern ecosystems, such as C_4 grasslands, that have evolved under relatively low atmospheric $[CO_2]$ by today's standards. This report focuses on the responses of vegetation in a Colorado semiarid grassland to growth at variable $[CO_2]$, but our report has implications for other rangelands around the world.

Rangelands comprise >40% of Earth's terrestrial surface (2). Although these lands are characteristically water-limited and unsuitable for intensive agriculture, they support one of the world's most extensive agricultural practices, domestic livestock grazing (3–5). Rangelands are important not only for the plant and animal products they provide but also as regions in which distinct pastoral cultures and societies have developed. Rising atmospheric $[CO_2]$ and predicted global change are expected to have an especially strong impact on water-limited regions like rangelands (6, 7), with potential consequences for long-established grazing practices. For instance, although grassland plant production often increases with rising atmospheric CO_2, forage quality can decline because of lower N concentrations (8–11) or because of an increased abundance of lower quality plant species (11).

The alteration of plant community dynamics because of differential plant species or to functional group sensitivities to rising atmospheric CO_2 is of particular concern for native ecosystems, including rangelands, in which the economic value of the land depends in large part on the species composition of the plant community. Species sensitivities to CO_2 are driven in large part by different photosynthetic metabolisms. There is abundant evidence that productivity of plants with the C_3 photosynthetic metabolism responds more to CO_2 than C_4 plants (12–14) because the photosynthetic metabolism of the former is not CO_2-saturated at present-day atmospheric concentrations as it is in C_4 plants (12). However, this trend can be complicated by other plant responses to CO_2, like improved water use efficiency (7) or seedling recruitment (10), both of which are not simply related to species differences in the photosynthetic pathway. The performance of species (and presumably functional groups like photosynthetic class) depends on interactions of the CO_2 responses with soil resources and interspecific plant competition, greatly complicating the predictions of species/plant community responses (14).

Shrub encroachment into many world native grasslands over the past 200 years is a well documented species shift that has been attributed in part to this differential species sensitivity to CO_2 (12, 15), with predominantly C_3 woody vegetation displacing C_4 grasses. Bond and Midgley (16) proposed that differences in plant carbon allocation strategies between woody and herbaceous plants in addition to differences in photosynthetic metabolism are involved in woody plant encroachment. However, no direct evidence of this theory has yet been reported, leading some to question the importance of CO_2 in this phenomenon (17, 18).

We are embarking on a period in which plant community dynamics in many of Earth's ecosystems may be subject to relatively rapid changes due to increased atmospheric CO_2 levels and altered climate. These changes may affect not only the traditional goods and services we have come to expect from these lands but may alter their biodiversity as well. Our group previously evaluated the production responses of native Colorado shortgrass steppe vegetation to 5 years of growth (1997–2001) at elevated [CO_2] by using large open-top chambers (OTCs) (10). Here, we use data from this same experiment (http://sgslter.colostate.edu/data/acquisitionplcy.htm) to examine how a doubling of CO_2 concentration for 5 years with OTCs placed over a native shortgrass steppe altered the botanical structure of this important semiarid grassland on the western edge of the North American Great Plains. Indices of diversity and a plant community association index were used to evaluate plant community structure. Analyses of functional plant group responses expand the discussion into plant mechanisms involved in the CO_2 responses and consequences of botanical changes on rangeland agriculture.

Results and Discussion

A total of 34 different plant species were observed in our nine experimental plots during the July species harvests over the 5 years of the CO_2 enrichment experiment (1997–2001). However, the bulk of the aboveground plant biomass (81% averaged across years and CO_2 treatments) was contributed by just three perennial grass species: *Bouteloua gracilis* (C_4 photosynthetic pathway), *Pascopyrum smithii* (C_3 photosynthetic pathway), and *Stipa comata* (C_3). Biomass from other species included a 7% contribution of a sedge, *Carex eleocharis* Bailey; 4% contributed by the subshrub *Artemisia frigida* Willd; and a 7% contribution of the remaining 29 species, a variety of grasses and herbaceous dicots.

The Shannon diversity index (H') was used to evaluate how growth at the two [CO_2] values affected diversity of aboveground plant biomass among the 34 species. Diversity has both evenness (J') and richness (species number) components, and Wilsey *et al.* (19) suggest that all three indices are needed to adequately describe diversity in grassland ecosystems. None of these indices distinguishes contributions or associations of particular species; instead, they rely on species numbers and abundance rankings (20). However, none was significantly affected by CO_2 treatment (Fig. 1 *A*, *C*, and *E*), although small but significant responses due to year were observed (Fig. 1 *B*, *D*, and *F*) and an apparent chamber effect was noted for richness (Fig. 1*A*). Thus, doubling CO_2 for 5 years had very little impact on these common measures of plant species diversity.

Whittaker's (21) community association index was used as a community-wide dissimilarity metric for comparing differences in plant species composition between the elevated and ambient CO_2 plots. Values range from 0 to 1, with 0 indicating identical communities and 1 indicating dissimilar communities with no species in common. In contrast to the diversity indices, a clear and significant ($P = 0.04$) linear trend was observed in the index, indicating increasing dissimilarity in the association of species between the ambient and elevated CO_2 plant communities over time, with the index increasing from 0.17 in the year before CO_2 fumigation to 0.33 by 2001 (Fig. 2). No significant change was observed for Whittaker's index in a comparison between ambient CO_2 and nonchambered control plots, which was conducted to evaluate possible chamber effects on plant species associations (data not shown).

To further evaluate plant community changes over time, we partitioned the 34 species observed at our site into four functional groups based on photosynthetic pathway and morphology (13, 14): C_3 grasses (composed of six grass species and one sedge), C_4 grasses (four species), herbaceous forbs (22 minor, mostly C_3 species), and a single woody subshrub species (*A.*
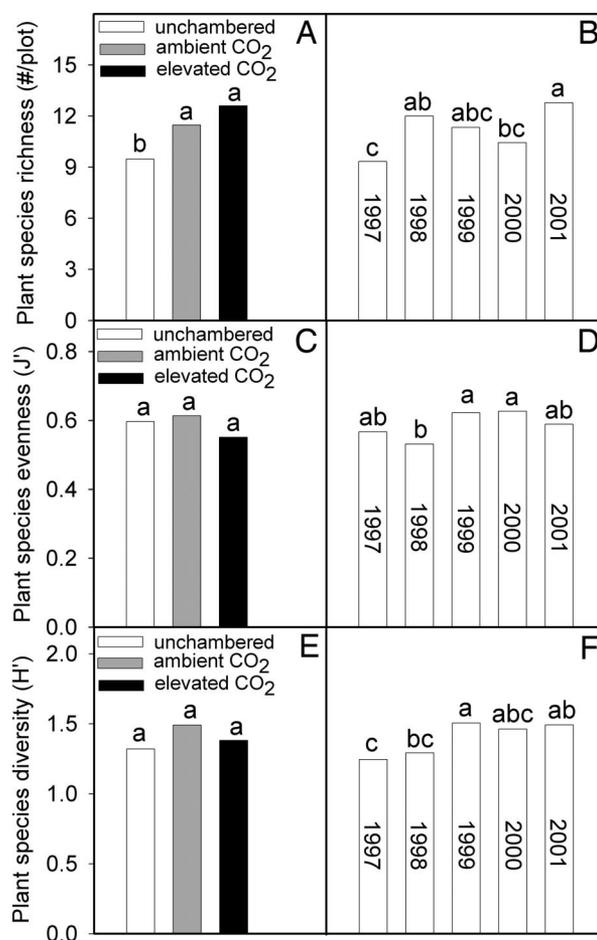

Fig. 1. Plant species richness (*A* and B); evenness (J') (*C* and *D*); and diversity (H') (*E* and *F*) determined from ambient (360 ppm CO_2) and elevated (720 ppm CO_2) OTC plots, plus unchambered plots (*A*, *C*, and *E*), and as affected by years (*B*, *D*, and *F*) on the shortgrass steppe of eastern Colorado. Unchambered plots were included in the experiment as a control to determine whether the chamber had any effect on plant community dynamics, which, for the most part, did not. ANOVA detected significant treatment effects ($P < 0.01$) for richness only and year ($P < 0.01$) effects for all indices. Data are averaged across years (*A*, *C*, and *E*) and across treatments (*B*, *D*, and *F*). Mean differences among treatments and years were determined using a least squares difference test ($P < 0.05$) and are indicated by different letters.

frigida). We examined how peak aboveground biomass was affected by CO_2. ANOVA (Table 1) detected significant treatment effects for C_3 grasses ($P = 0.002$), significant ($P < 0.05$) year effects for all groups but subshrub ($P = 0.06$), and significant or strong trends for all treatment by year interactions (P ranged from 0.03 to 0.11); means comparison tests therefore were determined among treatments within each year.

For most of the years of the experiment, C_3 grasses experienced significantly greater productivity under elevated CO_2, whereas C_4 grasses and forbs were unresponsive to CO_2 (Fig. 3 *A–C*). Although the differences between C_3 and C_4 grasses were predicted based on differences in photosynthetic pathway, greater seedling recruitment of *S. comata*, a dominant C_3 grass and the only grass species to respond to CO_2, was likely an important aspect of the C_3 reaction to CO_2 (10). Low growing season precipitation in 2000 (Fig. 3*D*) and lack of soil water recharge in 2001 resulted in consistently low soil water content in the final 2 years of the experiment (22), which likely was an important factor in the correspondingly low productivity of C_3 grasses in 2000 and 2001 (Fig. 3*A*). Forb species appeared too
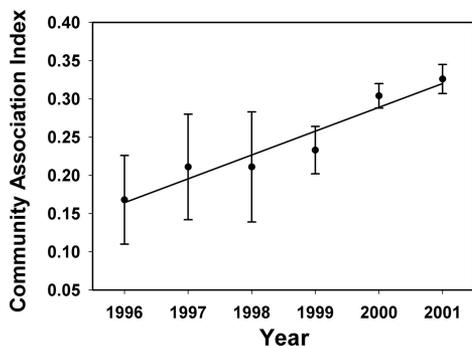
ECOLOGY

Fig. 2. Whittaker's community association index for contrasts of ambient vs. elevated chambered plots for the pre-CO_2 fumigation year (1996) and the following 5 years of CO_2 enrichment (1997–2001). An index value of 0 indicates both treatments having all species in common and in the same proportions, and a value of 1 indicates no species in common. Regression analyses indicated significant relationships between year and the index calculated for all 34 species ($P = 0.04$); bars indicate SEM.

sporadically among the different study years and experimental plots for a robust test of their CO_2 responsiveness (Fig. 3C). However, biomass of the subshrub *A. frigida* showed a temporal trend of increasing productivity in elevated CO_2 plots compared with ambient and control plots that became significant in the final year of the experiment, when biomass in elevated CO_2 plots exceeded ambient plots by ≈9-fold (Fig. 3D). Compared with the first year of CO_2 enrichment, 1997, biomass increased 40-fold from 0.72 g·m^{-2} in 1997 to 28.7 g·m^{-2} in 2001 in the elevated CO_2 plots.

Measurements of plant cover when averaged over seven or eight time periods during each growing season showed patterns similar to the biomass data. Cover is a different metric of plant growth than biomass because it incorporates the extent to which a species or a group of plants occupies the aerial environment. Trends emerged within most years, suggesting greater cover of C_3 grasses and forbs and less cover of C_4 grasses under elevated CO_2 (Fig. 4 A–C). However, no significant temporal trends (changing cover with time) were observed for C_3 grasses for any treatment, and forb cover increased only slightly with years in unchambered plots. Cover of C_4 grasses in chambers maintained at both ambient and elevated [CO_2] declined similarly from 1997

Table 1. Numerator (Num) and denominator (Den) degrees of freedom (df), F values, and probabilities (Pr > F) for year, CO_2 treatment, and year by CO_2 treatment effects on aboveground biomass of four plant functional groups

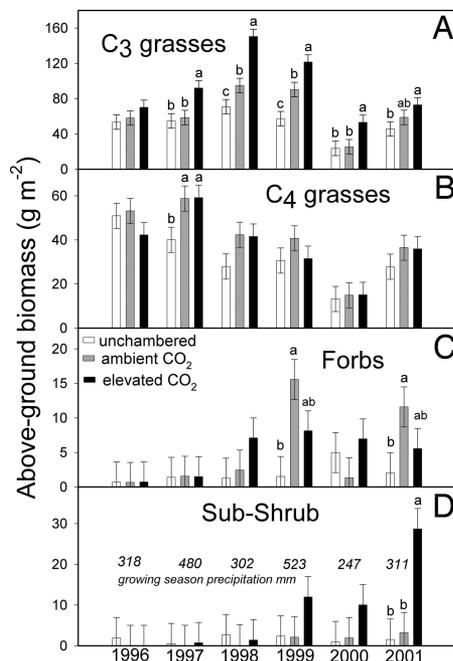| Source of variation	Num df	Den df	F value	Pr > F
C_3 grasses				
Year	5	21	32	<0.0001
Treatment	2	6.0	20	0.0023
Year × treatment	10	21	2.7	0.0278
C_4 grasses				
Year	5	23	26	<0.0001
Treatment	2	6.1	1.2	0.3691
Year × treatment	10	23	1.9	0.0972
Forbs				
Year	5	21	3.1	0.0294
Treatment	2	5.8	1.5	0.3006
Year × treatment	10	21	2.2	0.0586
Subshrub				
Year	5	18	2.6	0.0585
Treatment	2	3.9	2.7	0.1881
Year × treatment	10	19	1.9	0.1113

Fig. 3. Within-year comparisons of aboveground biomass of functional groups C_3 grasses, C_4 grasses, herbaceous forbs, and subshrub (*A. frigida*) as affected by growth in ambient (360 ppm CO_2) and elevated (720 ppm CO_2) OTC plots and nonchambered control plots conducted across 6 years, a baseline year (1996) before treatments, and 5 years of treatments (1997–2001). Means comparison tests were determined among treatments within each year based on a least squares difference test ($P < 0.05$); differences are indicated by different letters, and standard error bars are given.

through 2001 (Fig. 4B), and cover of the subshrub increased for all treatments (Fig. 4D). The temporal decline in C_4 cover was likely due to low soil water content in the final 2 years of the experiment (22) and may reflect a commonly observed drought escape strategy of the system C_4-dominant *B. gracilis* to shed its leaves during prolonged drought. Increased cover of the subshrub *A. frigida* over the same period suggests greater competitive ability of this tap-rooted subshrub for deeper soil water, especially under elevated CO_2. Only *A. frigida* exhibited clear treatment differences, with plant cover under elevated CO_2 increasing significantly faster from 1997 through 2001 compared with both ambient ($P = 0.006$) and unchambered ($P = 0.001$) plots (Fig. 4D). Although the absolute changes in *A. frigida* cover under elevated CO_2 were small, from 0.2% to 4.1%, they represent a >20-fold increase and movement over the course of the experiment out of the minor species category, representing ≈10% of the total community plant cover by the final year of the experiment.

The lack of detectable changes in diversity due to variable [CO_2] indicates no important alterations in the number and abundance structure of plant species, and the decreasing similarity between plant communities exposed to elevated and ambient [CO_2] suggests shifts in species composition and their relative contributions to the plant community. Whittaker's community association index is apparently able to detect CO_2-induced changes in community structure because of its reliance on the relative contributions of particular species, whereas diversity, evenness, and richness, which are species-blind, may change more slowly. Increases in Whittaker's index were no doubt partially due to enhanced growth of *S. comata* (10) and *A. frigida* (Fig. 3D) but also were likely influenced by a number of other species that collectively became more dissimilar over time
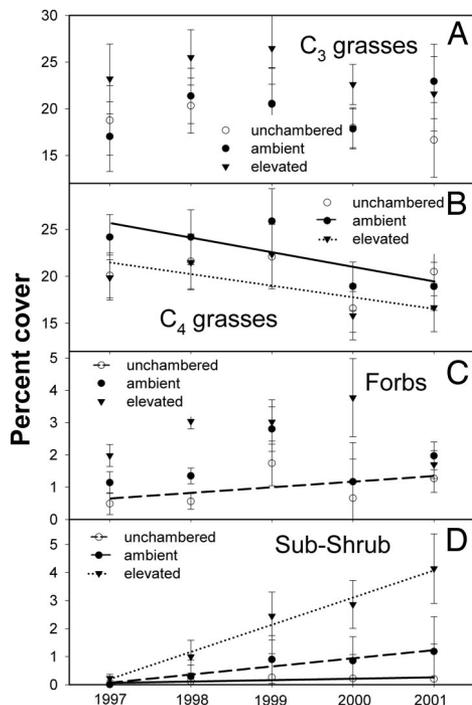
Fig. 4. Evaluations for changes in vegetative cover over 5 years of CO_2 enrichment among four functional groups: C_3 grasses (*A*), C_4 grasses (*B*), herbaceous forbs (*C*), and one subshrub species [*A. frigida* (*D*)]. For each functional group, the annual mean percentage of vegetative cover was regressed on year to evaluate differences in temporal trends for plants grown under elevated (720 ppm CO_2) and ambient (360 ppm CO_2) [CO_2] and the unchambered control conditions in native shortgrass steppe from 1997 to 2001. Only significant ($P < 0.10$) regressions are plotted, which include ambient ($P = 0.03$) and elevated ($P = 0.08$) C_4 grasses, unchambered forbs ($P = 0.04$), and all subshrub treatments ($P < 0.0001$ for elevated and ambient plots; $P = 0.05$ for unchambered plots). For the subshrub, slope of the elevated CO_2 line was significantly greater than slopes of the ambient CO_2 ($P = 0.006$) and unchambered ($P = 0.001$) lines. Each data point represents annual means from measurements taken six or seven times within each growing season; bars indicate SE.

but when assayed individually did not display significant responses to CO_2.

The progressively enhanced biomass and cover of the subshrub *A. frigida* under elevated CO_2 provide evidence from a native grassland that supports the notion that rising atmospheric [CO_2] may be contributing to shrubland expansions of the past 100–200 years (12, 15, 16). The increased proportion of woody plants has reduced significantly the available forage in many world grasslands and, without proactive management measures like burning, has rendered these lands less suitable for livestock grazing. It has long been argued that livestock grazing, fire suppression, and climate change have been responsible for this shrub encroachment, but sorting out the relative importance of these competing forces from the CO_2-induced invasion is challenging (18). No field experiment has confirmed the CO_2-induced shrub expansion hypothesis, and, consequently, the role of CO_2 in shrubland expansion has been questioned (17).

A. frigida, commonly called fringed sage, is an aromatic, mat-forming perennial shrub, ranging 10–60 cm tall (23). Although small in stature, it is the most widely distributed and abundant *Artemisia* species in the world, occurring from Mexico north through primarily the western United States and Canada to Alaska. Although considered a native to the United States, it also can be found in Siberia, Mongolia, and Kazakhstan. The superior CO_2 response of *A. frigida*, which ranks among the

highest reported in the literature (24, 25), may be attributed to one or more mechanisms. High CO_2 has been hypothesized to speed up recovery of woody plants from fire or grazing (16). Our experiment, which included simulated grazing through alternate year defoliation, posits that the benefit of higher atmospheric CO_2 to woody plants may be extended to improved access to soil water, possibly through increased carbon allocation to its roots. *A. frigida* is not characteristically a deeply rooted plant, but Coupland and Johnson (26) point out that *A. frigida* root systems will adjust to periods of more abundant water supply by developing deeper tap roots. Such conditions may have prevailed in the early years of the experiment, when growing season precipitation was relatively abundant (3-year average of 435 mm for years 1997–1999 compared with a long-term value of 280 mm) (Fig. 3*D*) and soil water content was generally high, especially in the elevated CO_2 treatment (22). Compared with shallow-rooted grasses like the site-dominant *B. gracilis*, the tap-root of *A. frigida* may enhance its ability to extract soil water at depths that can increase under elevated CO_2 (10, 22, 26, 27). Greater access to soil water may have been especially important under the conditions of low soil water content that prevailed in the final 2 years of the experiment (22). Other characteristics that may explain greater CO_2 sensitivity of *A. frigida* are its C_3-photosynthetic metabolism, especially in comparison to the C_4 system-dominant *B. gracilis*; long-lived aboveground woody tissues; and high nitrogen use efficiency, which has been hypothesized to confer greater CO_2 sensitivity in woody plants compared with the less nitrogen use-efficient grasses they are displacing (28).

A. frigida tends to increase under heavy grazing and other disturbances, is unpalatable to livestock, invades deteriorated grasslands, and is considered a weed (23, 29). It is also one of the least desirable *Artemisia* species for wildlife (23, 30), although it may be used by small hoofed mammals, like pronghorn (*Antilocapra americana* Ord.) or elk (*Cervus canadensis* Erxleben), especially in the overwintering months, and can be an important food source for sage-grouse (*Centrocercus urophasianu*). Our results, which indicate that growth of *A. frigida* can be enhanced dramatically simply by increasing ambient [CO_2], suggest that rising atmospheric [CO_2] already may be causing important changes in the ecology of the semiarid grasslands of the western Great Plains. Further research is needed to determine whether these results can be extended to the performance of *A. frigida* in other North American or Asian grasslands or to other major shrub species (12, 15, 16), including other *Artemesia spp.* (31), whose expansion into many world grasslands is already well documented.

The results of this experiment clearly highlight the importance of evaluating ecological changes from several perspectives. Although diversity, evenness, and richness seemed unaffected by 5 years of CO_2 enrichment, Whittaker's index showed a clear trend of community change. However, the only significant species responses to emerge from this experiment were the previously reported greater productivity of the C_3 grass *S. comata* under elevated CO_2 (10) and the finding that growth of *A. frigida* increased more rapidly at elevated CO_2 than at ambient CO_2. Like *A. frigida*, *S. comata* also has potentially negative consequences for forage quality (11). It seems plausible that the gradual increase in atmospheric [CO_2] that has been underway for >200 years may induce important changes in diversity, but documenting such changes in a relatively short-term experiment on small plots is a challenge.

Materials and Methods

Site Description. The experiment was conducted at the United States Department of Agriculture–Agricultural Research Service Central Plains Experimental Range (latitude 40° 50′ N longitude 104° 43′ W) at the northern limit of the shortgrass steppe, a semiarid grassland on the western edge of the North

American Great Plains used extensively for livestock grazing. Long-term annual precipitation and growing season precipitation amounts are 320 and 280 mm, respectively (22). The effect of elevated CO_2 on this native ecosystem was investigated using OTCs (4.5 m in diameter, $\approx$3.8 m in height, enclosing 15.5 m^2 of ground area or a volume of 60.5 m^3). A portion of the pasture initially was divided into three blocks, and three 15.5-m^2 circular plots per block were randomly selected as the experimental treatment plots: a chambered, ambient CO_2 treatment (360 $\pm$ 20 ppm CO_2); a chambered, elevated CO_2 treatment (720 $\pm$ 20 ppm CO_2); and an unchambered control plot of equal ground area, which was used to assess the chamber effect. [CO_2] was not controlled at night and was generally <450 ppm of CO_2 in all treatments. The chamber [CO_2] was checked approximately weekly, and the range was generally $\pm$20 ppm from the target treatment concentrations. From late March until mid-October from 1997 to 2001, the OTCs surrounded two plots in each of the three blocks (for a total of six chambers). CO_2 fumigation proceeded in the elevated chamber CO_2 treatment as soon as the chambers were placed on the plots each spring and was continued until they were removed in the autumn when vegetation was dormant. For more detail, see ref. 10.

Plant Biomass and Plant Cover. Aboveground plant biomass was measured by species in 1996 (the year before CO_2 treatments) and from 1997 to 2001 (the years of CO_2 treatments) during the period of peak standing phytomass (late July). A metal wire grid containing 56 quadrats, with each quadrat measuring 40.5 $\times$ 15.3 cm (3.46 m^2 total), was placed over the southern half of each plot, and vegetation in every other quadrat (28 quadrats) was clipped to the crown, separated by species, dried at 60°C, and weighed. This defoliation protocol removes 50% of the green vegetation and was incorporated into the CO_2 treatment experimental design primarily as a means to represent the nominal grazing conditions for these grasslands (10).

The percentage of plant cover by species was estimated visually monthly from April through October in 10 quadrats, each measuring 10 $\times$ 10 cm, placed within the biomass metal wire sampling grid in each of the OTCs.

Community Measures. From the plant biomass data, we calculated richness as the number of species, the widely used Shannon diversity index (H'), as

$$H' = - \sum_{i=1}^{s} p_i \log p_i$$

where p_i is the proportion of the ith species (s) in the population and evenness (J') is

$$J' = H'/\log s$$

according to Pielou (20).

We used Wittaker's index of community association (21), defined here as A, as a dissimilarity metric and calculated it as

$$A = 0.5 \times \sum_{i=1}^{s} |p_{i(a)} - p_{i(e)}|$$

where $p_{i(a)}$ and $p_{i(e)}$ are the proportions of the ith species (s) in the ambient and elevated plots, respectively. Values range from 0 to 1, with values of 0 indicating identical communities and 1 being dissimilar communities, having no species in common.

Statistical Analyses. We used a linear mixed model with repeated measures (SAS Proc MIXED; SAS Institute, Cary, NC) to analyze for CO_2 treatment affects on richness, species evenness (J'), and species diversity (H'). A linear mixed model (SAS Proc GLIMMIX; SAS Institute) also was used to evaluate aboveground biomass responses among four plant functional groups: C_3 grasses (two dominant perennial grasses, four minor grass species, and one *Carex* species), C_4 grasses (one dominant perennial grass, three minor species), herbaceous dicots (22 minor species, mostly C_3), and one subshrub (*A. frigida*). In both the diversity and functional group analyses, "year" was used as a repeated measure variable, "block" was specified as a random effect (thereby removing the variability due to blocking), and block·CO_2 treatment was used as the error term for CO_2 treatment comparisons. A first-order, autoregressive covariance structure was used for the covariance structure of the aboveground biomass data set.

Whittaker's community association index (21) was analyzed for year effects in contrasts involving ambient vs. elevated plots by regressing year on the index using a repeated measures mixed model.

Temporal trends in plant cover were evaluated by averaging cover of the four functional groups, C_3 grasses, C_4 grasses, herbaceous forbs, and the subshrub, across each year's six or seven sampling dates and then regressing percentage cover on year and treatment by using a repeated measures mixed model for each functional group. A heterogeneous first-order, autoregressive covariance structure was used to account for autocorrelated responses and increasing variance over time. The subshrub was the only functional group in which temporal trends ($P < 0.10$) in plant cover were observed for all three treatments. Estimate statements were added to the Proc MIXED statements to test whether the linear increase in mean percentage cover for the elevated treatment exceeded the same for the ambient treatment and the control treatments of the subshrub group.

1. Jansen E, Overpeck J, Briffa KR, Duplessy J-C, Joos F, Masson-Delmotte V, Olgao D, Otto-Bliesner B, Peltier WR, Rahmstorf S, *et al.* (2007) in *Climate Change 2007: The Physical Science Basis*, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Avery KB, Tignor M, Miller HL (Cambridge Univ Press, Cambridge, UK), pp 443–497.
2. Campbell BD, Stafford-Smith DM, McKeon GM (1997) *Global Change Biol* 3:177–187.
3. Noble IR, Gitay H (1996) *J Veg Sci* 7:329–336.
4. Squires VR, Sidahmed A (1997) *Ann Arid Zone Res* 36:79–96.
5. Polley HW, Morgan JA, Stafford-Smith M, Campbell B (2000) in *Climate Change and Global Crop Productivity*, eds Reddy KR, Hodges HF (CAB Intl, Oxfordshire, UK), pp 293–314.
6. Niklaus PA, Körner C (2004) *Ecol Monogr* 74:491–511.
7. Morgan JA, Pataki DE, Körner C, Clark H, Del Grosso SJ, Grünzweig JM, Knapp AK, Mosier AR, Newton PCD, Niklaus PA, *et al.* (2004) *Oecologia* 140:11–25.
8. Gill RA, Polley HW, Johnson HB, Anderson LJ, Maherall H, Jackson RB (2002) *Nature* 417:279–282.
9. Owensby CE, Cochran RM, Auen LM (1996) in *Carbon Dioxide, Populations, and Communities*, eds Körner C, Bazzaz F (Academic, San Diego, CA), pp 363–371.
10. Morgan JA, Mosier AR, Milchunas DG, LeCain DR, Nelson JA, Parton WJ (2004) *Ecol Appl* 14:208–219.
11. Milchunas DG, Mosier AR, Morgan JA, LeCain DR, King JY, Nelson JA (2005) *Agri Ecosyst Environ* 111:166–184.
12. Polley HW (1997) *J Range Manage* 50:562–577.
13. Poorter H, Navas M-L (2003) *N Phytol* 157:175–198.

14. Reich PB, Tilman D, Craine J, Ellsworth D, Tjoelker MG, Knops J, Wedin D, Naeem S, Bahauddin D, Goth J, *et al.* (2001) *N Phytol* 150:435.
15. Idso SB (1992) *Climate Change* 22:85–86.
16. Bond WJ, Midgley GF (2000) *Global Change Biol* 6:865–869.
17. Van Auken OW (2000) *Annu Rev Ecol Syst* 31:197–215.
18. Archer S, Schimel DS, Holland EA (1995) *Climate Change* 29:91–99.
19. Wilsey BJ, Chalcraft DR, Bowles CM, Willig MR (2005) *Ecology* 86:1178–1184.
20. Pielou EC (1966) *J Theort Biol* 13:131–144.
21. Whittaker RH (1952) *Ecol Monogr* 22:1–44.
22. Nelson JA, Morgan JA, LeCain DR, Mosier AR, Milchunas DG, Parton BA (2004) *Plant Soil* 259:169–179.
23. United States Department of Agriculture Forest Service (2002) *Wildland Shrubs of the United States and its Territories: Thanmic Description*, General Technical Report IITF-WB-1, ed Francis JK (US Dep of Agric Forest Service, Provo, UT), available at www.fs.fed.us/global/iitf/pdf/shrubs/Artemisia%20frigida.pdf.
24. Ainsworth EA, Long SP (2005) *N Phytol* 165:351.
25. Mohan JE, Ziska LH, Schlesinger WH, Thomas RB, Sicher RC, George K, Clark JS (2006) *Proc Natl Acad Sci USA* 103:9086–9089.
26. Coupland RT, Johnson RE (1965) *J Ecol* 53:475–507.
27. LeCain DR, Morgan JA, Milchunas DG, Mosier AR, Nelson JA, Smith DP (2006) *Plant Soil* 279:219–228.
28. Teyssonneyre F, Picon-Cochard C, Falcimagne R, Soussana J-F (2002) *Global Change Biol* 8:1034–1046.
29. Whitson TD (1997) *Weeds of the West* (Univ of Wyoming, Laramie, WY), pp 1–630.
30. Cooperrider AY, Bailey JA (1984) in *Proceedings–Symposium on the Biology of Artemisia and Chrysothamnus*, General Technical Report INT-200, eds McArthus ED, Welch BL (US Dep Agric For Serv, Ogden, UT), pp 46–54.
31. Knapp PA, Soule PT (1996) *Ann Assoc Am Geographers* 86:387–411.

ECOLOGY