

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

Edited by Harold A. Mooney, Stanford University, Stanford, CA, and approved July 25, 2007 (received for review April 13, 2007)

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, [CO₂], 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 CO₂, and many have tap roots that are more effective than grasses for reaching deep soil water stores that can be enhanced under elevated CO₂. 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 [CO₂] 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 [CO₂]. Growth at the doubled [CO₂] 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 CO₂-induced enhancement of plant growth, among the highest yet reported, provides evidence from a native grassland suggesting that rising atmospheric [CO₂] 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.

C₃ | C₄ | functional group | global change | semiarid grassland

Although atmospheric carbon dioxide concentrations ([CO₂]) 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 CO₂ levels are higher today than they have been for at least 650,000 years (1). Furthermore, levels of atmospheric CO₂ 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 CO₂ have tremendous implications for the adaptation and evolution of relatively modern ecosystems, such as C₄ grasslands, that have evolved under relatively low atmospheric [CO₂] by today's standards. This report focuses on the responses of vegetation in a Colorado semiarid grassland to growth at variable [CO₂], 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 [CO₂] 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 CO₂, 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 CO₂ 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 CO₂ are driven in large part by different photosynthetic metabolisms. There is abundant evidence that productivity of plants with the C₃ photosynthetic metabolism responds more to CO₂ than C₄ plants (12–14) because the photosynthetic metabolism of the former is not CO₂-saturated at present-day atmospheric concentrations as it is in C₄ plants (12). However, this trend can be complicated by other plant responses to CO₂, 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 CO₂ 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 CO₂ (12, 15), with predominantly C₃ woody vegetation displacing C₄ 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 CO₂ in this phenomenon (17, 18).

Author contributions: J.A.M., D.G.M., and A.R.M. designed research; J.A.M., D.G.M., D.R.L., and A.R.M. performed research; J.A.M., D.G.M., D.R.L., and M.W. analyzed data; and J.A.M. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

Abbreviation: OTC, open-top chamber.

[†]To whom correspondence may be addressed at: USDA-ARS, RRRU, CRL, 1701 Centre Avenue, Fort Collins, CO 80526. E-mail: jack.morgan@ars.usda.gov.

© 2007 by The National Academy of Sciences of the USA

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 CO₂ 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 [CO₂] by using large open-top chambers (OTCs) (10). Here, we use data from this same experiment (<http://sgslter.colostate.edu/data/acquisitionp1cy.htm>) to examine how a doubling of CO₂ 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 CO₂ 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 CO₂ enrichment experiment (1997–2001). However, the bulk of the aboveground plant biomass (81% averaged across years and CO₂ treatments) was contributed by just three perennial grass species: *Bouteloua gracilis* (C₄ photosynthetic pathway), *Pascopyrum smithii* (C₃ photosynthetic pathway), and *Stipa comata* (C₃). 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 [CO₂] 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 CO₂ treatment (Fig. 1A, C, and E), although small but significant responses due to year were observed (Fig. 1B, D, and F) and an apparent chamber effect was noted for richness (Fig. 1A). Thus, doubling CO₂ 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 CO₂ 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 CO₂ plant communities over time, with the index increasing from 0.17 in the year before CO₂ fumigation to 0.33 by 2001 (Fig. 2). No significant change was observed for Whittaker's index in a comparison between ambient CO₂ 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): C₃ grasses (composed of six grass species and one sedge), C₄ grasses (four species), herbaceous forbs (22 minor, mostly C₃ species), and a single woody subshrub species (*A.*

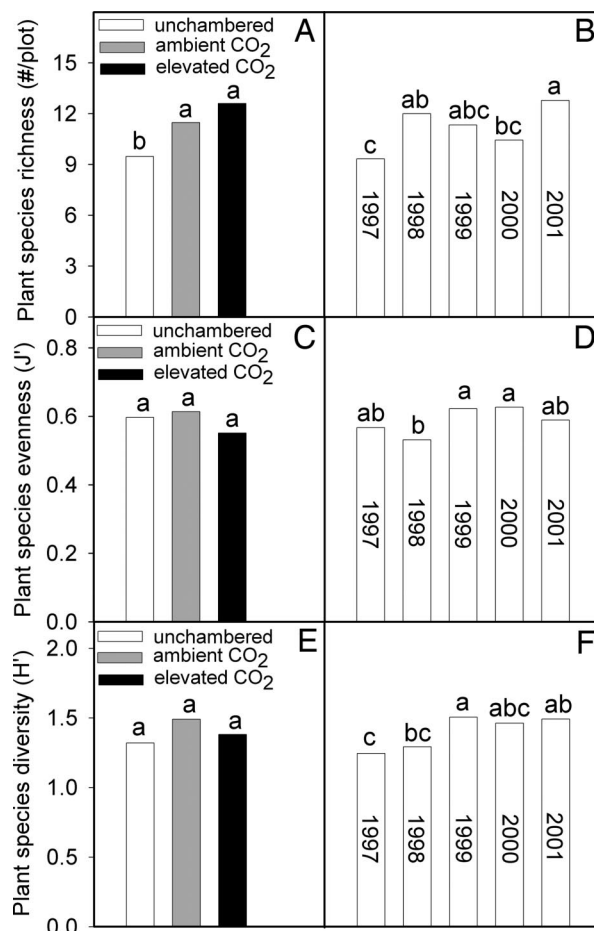


Fig. 1. Plant species richness (A and B); evenness (J') (C and D); and diversity (H') (E and F) determined from ambient (360 ppm CO₂) and elevated (720 ppm CO₂) OTC plots, plus unchambered plots (A, C, and E), and as affected by years (B, D, and F) on the shortgrass steppe of eastern Colorado. Unchambered 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 CO₂. ANOVA (Table 1) detected significant treatment effects for C₃ 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, C₃ grasses experienced significantly greater productivity under elevated CO₂, whereas C₄ grasses and forbs were unresponsive to CO₂ (Fig. 3A–C). Although the differences between C₃ and C₄ grasses were predicted based on differences in photosynthetic pathway, greater seedling recruitment of *S. comata*, a dominant C₃ grass and the only grass species to respond to CO₂, was likely an important aspect of the C₃ reaction to CO₂ (10). Low growing season precipitation in 2000 (Fig. 3D) 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 C₃ grasses in 2000 and 2001 (Fig. 3A). Forb species appeared too

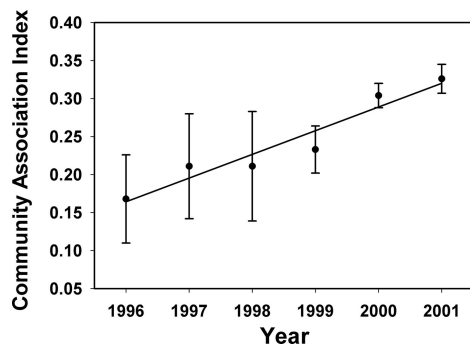


Fig. 2. Whittaker's community association index for contrasts of ambient vs. elevated chambered plots for the pre- CO_2 fumigation year (1996) and the following 5 years of CO_2 enrichment (1997–2001). An index value of 0 indicates both treatments having all species in common and in the same proportions, 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 $0.72 \text{ g}\cdot\text{m}^{-2}$ in 1997 to $28.7 \text{ g}\cdot\text{m}^{-2}$ 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. 4A–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 $[\text{CO}_2]$ declined similarly from 1997

Table 1. Numerator (Num) and denominator (Den) degrees of freedom (df), F values, and probabilities ($\text{Pr} > F$) 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 | $\text{Pr} > F$ |
|--|--------|--------|-----------|-----------------|
| C_3 grasses | | | | |
| Year | 5 | 21 | 32 | <0.0001 |
| Treatment | 2 | 6.0 | 20 | 0.0023 |
| Year \times 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 \times treatment | 10 | 23 | 1.9 | 0.0972 |
| Forbs | | | | |
| Year | 5 | 21 | 3.1 | 0.0294 |
| Treatment | 2 | 5.8 | 1.5 | 0.3006 |
| Year \times treatment | 10 | 21 | 2.2 | 0.0586 |
| Subshrub | | | | |
| Year | 5 | 18 | 2.6 | 0.0585 |
| Treatment | 2 | 3.9 | 2.7 | 0.1881 |
| Year \times treatment | 10 | 19 | 1.9 | 0.1113 |

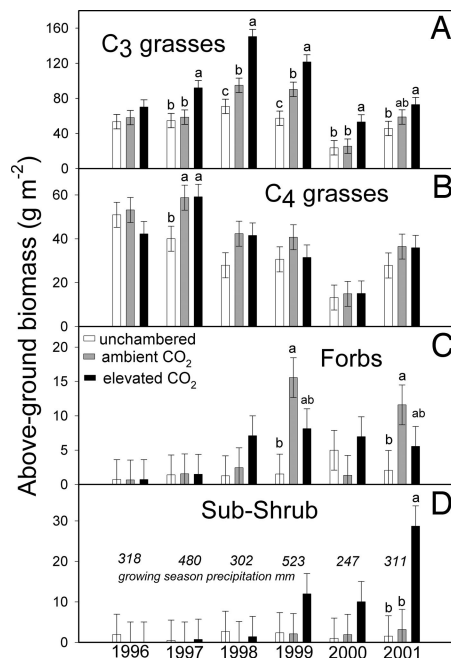


Fig. 3. Within-year comparisons of aboveground biomass of functional groups C_3 grasses, C_4 grasses, herbaceous forbs, and subshrub (*A. frigida*) as affected by growth in ambient (360 ppm CO_2) and elevated (720 ppm CO_2) OTC plots and nonchambered control plots conducted across 6 years, a baseline 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 $\approx 10\%$ of the total community plant cover by the final year of the experiment.

The lack of detectable changes in diversity due to variable $[\text{CO}_2]$ 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 $[\text{CO}_2]$ 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

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 CO₂ on this native ecosystem was investigated using OTCs (4.5 m in diameter, ≈3.8 m in height, enclosing 15.5 m² of ground area or a volume of 60.5 m³). A portion of the pasture initially was divided into three blocks, and three 15.5-m² circular plots per block were randomly selected as the experimental treatment plots: a chambered, ambient CO₂ treatment (360 ± 20 ppm CO₂); a chambered, elevated CO₂ treatment (720 ± 20 ppm CO₂); and an unchambered control plot of equal ground area, which was used to assess the chamber effect. [CO₂] was not controlled at night and was generally <450 ppm of CO₂ in all treatments. The chamber [CO₂] was checked approximately weekly, and the range was generally ±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). CO₂ fumigation proceeded in the elevated chamber CO₂ 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 CO₂ treatments) and from 1997 to 2001 (the years of CO₂ treatments) during the period of peak standing phytomass (late July). A metal wire grid containing 56 quadrats, with each quadrat measuring 40.5 × 15.3 cm (3.46 m² 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 CO₂ 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 × 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 i th 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 i th 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 CO₂ treatment effects 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: C₃ grasses (two dominant perennial grasses, four minor grass species, and one *Carex* species), C₄ grasses (one dominant perennial grass, three minor species), herbaceous dicots (22 minor species, mostly C₃), 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-CO₂ treatment was used as the error term for CO₂ 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, C₃ grasses, C₄ 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.

We thank Mary Ashby, Jeff Thomas, Jim Nelson, Mary Smith, Susan Crookall, Larry Tisue, Stacey Poland, Jennifer King, and David Jensen for technical assistance and Brian Wilsey, Wayne Polley, and two anonymous reviewers for helpful comments on the manuscript. This research was supported in part by National Science Foundation Terrestrial Ecology and Global Change Award IBN-9524068, National Science Foundation Award DEB-9708596, and Shortgrass Steppe Long-Term Ecological Research Project DEB-9350273.

- 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.
- Campbell BD, Stafford-Smith DM, McKeon GM (1997) *Global Change Biol* 3:177–187.
- Noble IR, Gitay H (1996) *J Veg Sci* 7:329–336.
- Squires VR, Sidahmed A (1997) *Ann Arid Zone Res* 36:79–96.
- 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.
- Niklaus PA, Körner C (2004) *Ecol Monogr* 74:491–511.
- 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.
- Gill RA, Polley HW, Johnson HB, Anderson LJ, Mahehall H, Jackson RB (2002) *Nature* 417:279–282.
- 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.
- Morgan JA, Mosier AR, Milchunas DG, LeCain DR, Nelson JA, Parton WJ (2004) *Ecol Appl* 14:208–219.
- Milchunas DG, Mosier AR, Morgan JA, LeCain DR, King JY, Nelson JA (2005) *Agri Ecosyst Environ* 111:166–184.
- Polley HW (1997) *J Range Manage* 50:562–577.
- 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 Theoret 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 McArthur 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.