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Biomass production in a nitrogen-fertilized, tallgrass prairie ecosystem exposed to ambient and elevated levels of CO_2

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Abstract

Increased biomass production in terrestrial ecosystems with elevated atmospheric CO_2 may be constrained by nutrient limitations as a result of increased requirement or reduced availability caused by reduced turnover rates of nutrients. To determine the short-term impact of nitrogen (N) fertilization on plant biomass production under elevated CO_2, we compared the response of N-fertilized tallgrass prairie at ambient and twice-ambient CO_2 levels over a 2-year period. Native tallgrass prairie plots (4.5 m diameter) were exposed continuously (24 h) to ambient and twice-ambient CO_2 from 1 April to 26 October. We compared our results to an unfertilized companion experiment on the same research site. Above- and belowground biomass production and leaf area of fertilized plots were greater with elevated than ambient CO_2 in both years. The increase in biomass at high CO_2 occurred mainly aboveground in 1991, a dry year, and belowground in 1990, a wet year. Nitrogen concentration was lower in plants exposed to elevated CO;!, but total standing crop N was greater at high CO_2. Increased root biomass under elevated CO_2 apparently increased N uptake. The biomass production response to elevated CO_2 was much greater on N-fertilized than unfertilized prairie, particularly in the dry year. We conclude that biomass production response to elevated CO_2 was suppressed by N limitation in years with below-normal precipitation. Reduced N concentration in above- and belowground biomass could slow microbial degradation of soil organic matter and surface litter, thereby exacerbating N limitation in the long term.

Introduction

Atmospheric carbon dioxide concentration is increasing (Boden et al., 1990) and is expected to double by the middle of the next century. Ecosystem-level experiments in natural terrestrial systems are limited, and Mooney et al. (1991) emphasized the need for additional research on terrestrial ecosystem response to elevated CO_2. Responses of individual plants and assemblages of plants to elevated CO_2 in controlled-environment studies have been summarized by various authors (Bazzaz, 1990; Newton, 1991; Strain and Cure, 1985). Productivity responses to CO_2 enrichment at the single plant level in controlled environments usually have been dependent on photosynthetic pathway. Carbon fixation rates in plants with the C_3 pathway generally show a greater response to increasing CO_2 levels than rates in C_4 plants (Kimball, 1983; Nijs et al., 1988; Reichers and Strain, 1988; Wray and Strain, 1986).

The response of natural ecosystems to CO_2 enrichment has been researched for estuarine saltmarsh communities (Curtis et al., 1989a), an Arctic tundra tussock sedge ecosystem (Oechel and Strain, 1985), and a tallgrass prairie ecosystem (Owensby et al., 1993a,b). Curtis et al. (1989a) concluded that communities dominated by *Scirpus olneyi* (C_3) had greater productivity, and that senescence was delayed at high compared to ambient CO_2. Production in *Spartina patens* (C_4) communities was not increased with CO_2 enrichment. Oechel and Strain (1985) reported that an Arctic tundra tussock sedge ecosystem initially responded to CO_2 enrichment with increased productivity, but the increase disappeared within the first year. They reasoned that an acclimation response had occurred in the photosynthetic mechanism. Owensby et al. (1993a) concluded

that tallgrass prairie productivity was enhanced with twice-ambient CO_2 primarily through increased water-use efficiency of the C_4 perennial grass dominants.

Productivity in most temperate terrestrial ecosystems usually is limited by moisture and/or nutrient availability. Increased water-use efficiency under elevated CO_2 has been documented, but effects of supplemental N in natural systems have not been studied. Because essentially all nutrients are cycled within the ecosystem and nutrient supplies in natural systems are relatively constant, increased productivity indicates an increased* nutrient-use efficiency. Curtis et al. (1989a) and Owensby et al. (1993a) reported increased productivity for natural plant communities under elevated CO_2 with the same nutrient resources as communities with ambient CO_2 after 4 and 3 years, respectively. In those natural ecosystems, CO_2 enrichment reduced N concentration for both C_3 and C_4 species, regardless of biomass production response (Curtis et al., 1989b; Owensby et al., 1993b). However, nutrient limitations may negate any long-term increase in productivity in elevated-CO_2 environments.

We assessed effects of ambient and elevated (double ambient) atmospheric CO_2 concentrations on above- and belowground biomass production, leaf area, and N concentration of above- and belowground biomass in a N-fertilized, tallgrass prairie. Effects of CO_2 enrichment on fertilized and unfertilized prairie were compared to test the prediction that increased biomass production was limited by N on CO_2-enriched tallgrass prairie.

Materials and methods

Study site

The experimental site was located in pristine tallgrass prairie north of Manhattan, KS, USA (39.12°N, 96.35°W, 324 m above mean sea level). Vegetation on the site was a mixture of C_3 and C_4 species, dominated by the C_4 grasses, ***Andropogon gerardii*** Vitman and ***Sorghastrum nutans*** (L.) Nash. Subdominants included ***Poa pratensis*** L. (C_3), ***Bouteloua*** *curtipendula* (Michx.) Torr. (C_4), and ***Sporobolus*** *asper* var. *asper* (Michx.) Kunth (C_4). Members of the sedge family (C_3) made up 5–10% of the composition. Principal forbs (all C_3) included *Vernonia* ***baldwinii var. interior*** (Small) Schub., ***Ambrosia psilostachya*** DC., ***Artemesia ludoviciana*** Nutt., and ***Psoralea*** *tenuiflora* ***var.*** *floribunda* (Nutt.) Rydb.. Average peak aboveground biomass (dry wt.) of 425 g m^{-2} occurs in early August, of which 35 g m^{-2} is from forbs (Owensby and Anderson, 1967). Soils in the area are transitional from Ustolls to Udolls (Tully series: tine, mixed, mesic, montmorillonitic, Pachic Argiustolls). Slope on the area is 5%. Fire has occurred 2-3 times in 10 years. Past history has included primarily winter grazing by cow-calf pairs. The 30-year average annual precipitation is 840 mm, with 520 mm occurring during the growing season.

Fumigation chambers were placed over the natural vegetation in late March, 1990 and retained on the same area for 2 years. Twice-replicated treatments consisted of ambient CO_2 plus N (AN), chamber plus ambient CO_2 plus N **(CAN),** and chamber plus CO:!-enriched plus N **(CEN).** CO_2-enriched treatments received approximately twice the ambient concentration. N was applied as ammonium nitrate at 56 kg ha-' in late March of both years. Data from an unfertilized companion experiment (Owensby et al., 1993a) with the same CO_2 treatments **(A, CA, CE)** were used to compare the interaction of N with plant response to CO_2.

Fumigation chambers

Each open-top chamber (4.5 m in diameter by 3.25 m in height) had a cone-top baffle that reduced the top opening to 3 m. The baffle added 0.75 m to the height Of the chamber for a total height of 4 m. An aluminum structural framework was covered by 0.15 mm thick, UV-resistant, polyethylene film. The cone-top baffle reduced the opening by 54%, thereby restricting the precipitation that entered the chamber. Within 24 hours following each rainfall event, water equal to 54% of the rainfall amount for an unchambered plot was added using a rotating sprinkler adjusted to cover the diameter of the chamber. Aluminum edging was placed around the upslope bottom edge of the chamber to prevent runoff from entering the chamber. No edging was placed on the lower half of the chamber. One half of each plot was used to estimate biomass production and nutrient concentrations, and the remaining half was grazed by esophageally fistulated sheep to determine forage quality differences among treatments. Data on forage quality are not reported here.

CO_2 treatment

Mass flow controllers, interfaced to a computer, were used to regulate CO_2 flow rate into the enriched cham-

bers based on real-time measurement of CO_2 in the chambers. CO_2-enrichment began on 1 April in both 1990 and 1991. Carbon dioxide enrichment and environmental data acquisition were continuous until late October of each year. The polyethylene film covering the chambers was removed in late October and replaced in late March. During periods of high photosynthetic activity, CO_2 concentrations in the nonenriched treatments (A, CA, AN, CAN) measured at 1 m above the soil surface were 330-340 $\mu L\ L^{-1}$, but during nighttime hours, CO_2 levels reached 400+ $\mu L\ L^{-1}$. At the beginning of the sampling period for each chamber or unchambered plot, a delay of 20 seconds allowed for the IRGA and sample lines to be purged of previous gasses. Ten readings were then taken for all measured parameters and discarded. A paired-t comparison was made on the next 10 readings of CO_2 concentration and the mean of those readings was accepted if the data fell within a 5% confidence interval. Otherwise, readings in sets of 10 were tested until they did not differ. CO_2 concentration was determined using an infra-red CO_2 analyser (LCA-2, Analytic Development Co., Hoddesdon, UK.) which was calibrated initially and following three samplings of the 6 plots using a high resolution CO2 zero gas (300 $\mu L\ L^{-1}$) and span gas (800 $\mu L\ L^{-1}$) (Scott Specialty Gases, Inc., Troy, Ml, USA - $\pm$ 1% accuracy). Following each 6-plot sampling period, a baseline gas was sampled and used to correct for instrument drift during the previous sampling periods. The coefficient of variation for the CO_2 measurement was always $\leqq$ 0.2%. Each plot was sampled once per hour.

Chamber environment

Air (T,) and soil (T,) temperatures, air dew point temperature (T_{dp}), and photosynthetic photon flux density (PPFD) were measured an average of once per hour during each day of the growing season. Soil water content was measured weekly using a CPN - 503 DR Hydroprobe (Campbell Pacific Nuclear Corp., Martinez, CA 94553). PPFD was reduced by approximately 11% inside the chambers as determined by quantum sensors (LI-COR, Lincoln, NE, USA; Model L1-190SB) mounted 1 m above the soil surface within and outside a chamber. Soil temperature was measured at -10 cm, and air temperature at 30 cm, 100 cm, and 300 cm from the soil surface. No difference ($p < 0.10$) occurred in soil temperature (-10 cm) between chambered and unchambered plots. Likewise, the temperatures at 30 cm were similar in all plots. At 100 cm, the temperature inside chambers was slightly more than 2°C higher than that in unchambered plots on the hottest days for the period 1000 h to 1500 hr CST ($p < 0.10$). Also on the hottest days, the maximum temperature at 300 cm was some 5°C higher in chambered than in unchambered plots from 0800 hr to 1500 hr CST ($p < 0.10$). The air delivery system for chambered plots kept temperatures at plant canopy height approximately equal to ambient conditions. T_{dp} averaged 1 °C higher in chambered plots than in unchambered plots from 1200 hr to 1500 hr CST ($p < 0.10$). Even though that difference was slight, higher humidities inside the chambers may have reduced evapotranspiration and indirectly affected soil water content (Owensby et al. 1993a). Soil water content, measured at 20, 30, 40, 50, 60, 80, 100, 120, 140, 160, 180, and 200 cm below the soil surface, was significantly higher in chambered plots than in unchambered plots from mid June to late August in both years ($p < 0.10$). CEN plots had higher soil moisture levels than CAN plots under drought conditions during the sampling period ($p < 0.10$).

Meteorological conditions

Precipitation was slightly below normal in 1990 except in August, and temperatures averaged slightly above normal during the growing season (Table 1). Precipitation in 1991 was much below normal during June through October, and temperatures were above normal.

Aboveground biomass sampling

In 1990, sampling began on 14 May and continued at 2-week intervals until 23 July and then at 4-week intervals until 15 October. Samples were clipped to ground level from two, 0.2 x 0.5 m plots randomly located in the ungrazed half of each plot. In 1991, peak live biomass was estimated by clipping two, 0.25 m^2 plots randomly located in the ungrazed half of each plot on 8 August. Peak biomass in tallgrass prairie normally occurs in early August. All biomass sample plots that had been previously clipped were excluded from the randomization for the following sample dates. Clipped samples were placed in an ice chest and transported to the laboratory where they were refrigerated until separation into the following components: *A. gerardii,* other C_4 grasses, *l? pratensis,* other C_3 grasses, grass-like plants (including *Carex* and *Cyperus*) and forbs. Immediately after separation of the samples, leaf area was estimated for each species or species group using a leaf area meter (LI-COR, Lincoln, NE, USA; Mod-

Table 1. Monthly precipitation (mm) and average daily maximum temperatures (C) and deviation from normal for the study site

Month	1990				1991			
	Ppt. (mm)	Dev. (mm)	Temp (C)	Dev. (C)	Ppt. (mm)	Dev. (mm)	Temp (C)	Dev. (C)
Jan	27	6	11.3	8.2	34	13	2.4	-0.7
Feb	22	-2	10.4	3.5	1	-23	14.3	7.4
Mar	105	52	15.5	3	35	-18	18.2	5.7
Apr	23	-48	19.3	-0.6	107	36	21.1	1.1
May	100	-14	22.8	-2.4	130	16	26.9	1.7
Jun	124	-10	32. I	1.9	51	-83	31.8	1.7
Jul	79	-22	33.2	0.1	47	-54	35.5	2.3
Aug	180	100	31.7	-0.8	56	-25	33.7	1.3
Sep	20	-83	30.7	3.1	44	-59	28.9	1.3
Oct	27	-46	23.1	1.4	33	-40	23.6	1.8
Nov	52	14	17.9	5.3	83	46	8.7	-3.9
Dec	26	3	5.4	-0.8	48	25	8.1	1.9
Total	785	-50			669	-166		

el LI-3100). After leaf area determination, samples were dried in a forced-air oven for 72 hr at 55°C, and weighed directly from the oven. In 1991, 20 tillers of *A. gerardii* and *P. pratensis* were collected and dried as above starting on 15 May and continuing at 2-week intervals until 24 July and then at 4-week intervals until 16 October for determination of N concentration.

Belowground biomass sampling

An estimate of relative belowground biomass production was obtained using buried root ingrowth bags (Lund et al., 1970). In early June 1990, four, 5-cm diameter soil cores were removed to a depth of 15 cm from the center of each plot. Fine-mesh nylon bags, filled with a mixture of fine and coarse sand to a volume equal to the soil core, were placed in the core holes. Eight bags were placed in new holes in each plot in late March, 199 1. Root ingrowth bags were removed from the soil in early November of each year. Roots that had grown into the bags were removed, dried for 72 hr at 55°C, and weighed.

Chemical determinations

Root and shoot tissues from the biomass sampling were ground to pass a screen with 1 mm diameter holes and digested with sulfuric acid/hydrogen peroxide solution (Linder and Harley, 1942). N concentrations were colorimetrically determined (Technicon, 1977). Average total standing-crop N was determined by multiplying N concentration by standing biomass.

Data analysis

Data for each year were analyzed separately using ANOVA (SAS 6.06.01, SAS Inst., Cary, NC, USA) as a randomized complete block design. The model included replication and CO_2 treatment, and, when applicable, date and the date x CO_2 treatment interaction were included. Relative values (%) were analyzed following an arc sine transformation. Statistical significance for the F test was at $p < 0.10$. Means were separated using Duncan's Multiple Range Test ($p < 0.10$). Statistical analysis indicated no sampling date x CO_2 treatment interaction for aboveground biomass in 1990 and N concentration in 1990 and 199 1; therefore, seasonal means are reported.

Results

Aboveground biomass and leaf area

In 1990, *A. gerardii* biomass (bm) and leaf area (la) averaged over all clipping dates were greater for **CEN** plots than for CAN and AN plots (bm, $p = 0.0001$; la, $p = 0.0001$) (Fig. 1). *P. pratensis* biomass and leaf

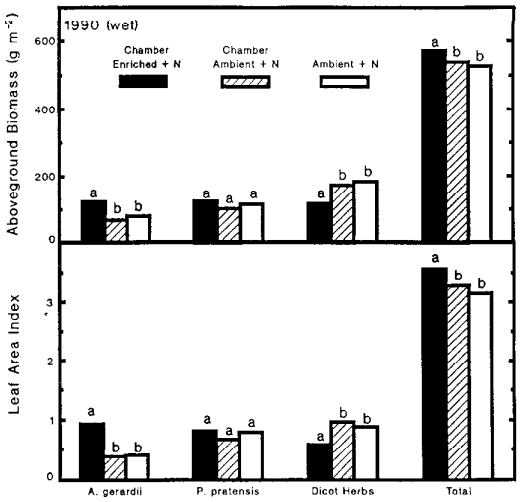

Fig. 1. Mean aboveground biomass (g m^{-2}) and leaf area index for indicated species and species groups averaged over nine growing season sampling dates in 1990 for native tallgrass prairie exposed to twice-ambient and ambient CO_2 concentrations and with 56 kg ha-' added as ammonium nitrate. Means within species or species groups with a common letter do not differ [Duncan's Multiple Range Test, $p < 0.101$.

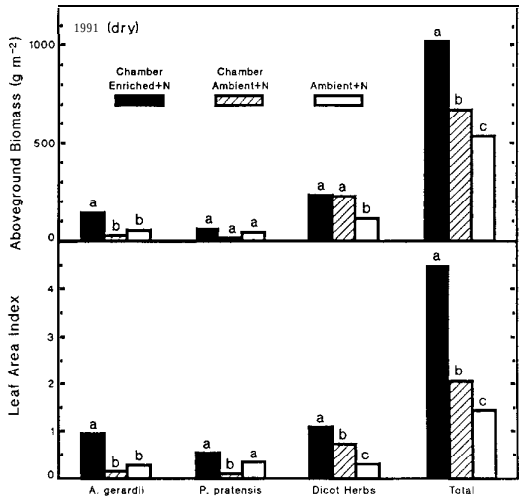

Fig. 2. Mean aboveground biomass (g m^{-2}) and leaf area index for indicated species and species groups in early August, 1991 for native tallgrass prairie exposed to twice-ambient and ambient CO_2 concentrations and with 56 kg ha-' added as ammonium nitrate. Means within species or species groups with a common letter do not differ [Duncan's Multiple Range Test, $p < 0.10$].

area averaged over all clipping dates did not differ among treatments (bm, $p = 0.3630$; la, $p = 0.1186$). Forb biomass and leaf area averaged over all clipping dates were significantly greater in CAN and A plots than in CEN plots (bm, $p = 0.1830$; la, $p = 0.1987$). Total biomass and leaf area for all species groups combined averaged over all clipping dates were significantly greater in CEN plots than in CAN and A plots (bm, $p = 0.0011$; la, $p = 0.0001$).

In 1991, biomass and leaf area were sampled only in early August. Biomass and leaf area of *A. gerurdii* (bm, $p = 0.0717$; la, $p = 0.0130$) and all species combined (bm, $p = 0.0721$; la, $p = 0.0010$) were greater in CEN plots than in CAN and AN plots (Fig. 2). *P. pratensis* biomass and leaf area did not differ among the treatments (bm, $p = 0.2128$; la, $p = 0.2330$). *P. pratensis* peak biomass and leaf area occurred in early June, so the August sampling date does not reflect an estimate of peak biomass, but should indicate relative treatment responses. Forb biomass was greater in chambered than unchambered plots (bm, $p = 0.7398$; la, $p = 0.6138$).

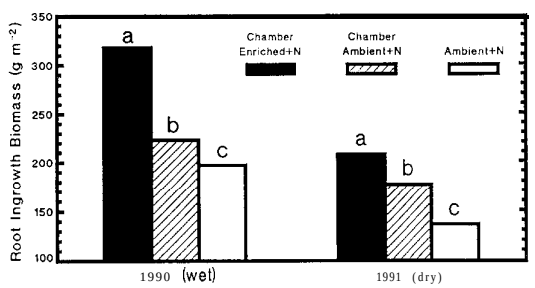

Fig. 3. Root biomass in ingrowth bags to a 15-cm depth in tallgrass prairie exposed to twice ambient and ambient CO_2 concentrations and with 56 kg ha-' added as ammonium nitrate. Data are means of four bags per plot in 1990 and eight bags per plot in 1991 replicated three times. Means with a common letter within year do not differ [Duncan's Multiple Range Test, $p < 0.10$].

Root ingrowth biomass

In 1990, root ingrowth biomass, measured in nylon bags, was essentially doubled in CEN plots compared to CAN and AN plots ($p = 0.0001$) (Fig. 3). In 1991, CEN plots also had greater root ingrowth biomass than CAN plots, which had greater biomass than AN plots ($p = 0.0536$).

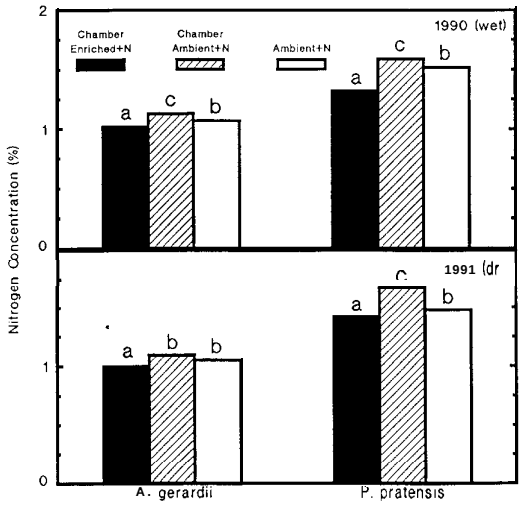

Fig. 4. Nitrogen concentration (%) for aboveground biomass of *Andropogon gerardii* and *Poa pratensis* averaged over nine sampling dates in 1990 and 1991 for native tallgrass prairie exposed to twice-ambient and ambient CO_2 concentrations with 56 kg ha^{-1} N added as ammonium nitrate. Means within species or species groups with a common letter do not differ [Duncan's Multiple Range Test, $p < 0.10$].

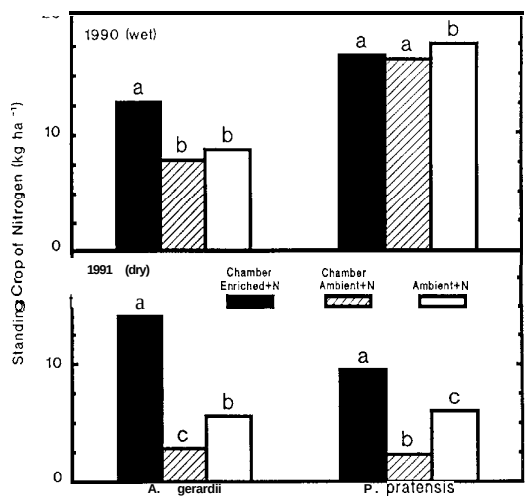

Fig. 5. Standing crop total *N* (kg ha^{-1}) of *Andropogon gerardii* and *Poa pratensis* averaged over nine sampling dates in 1990 and 1991 for native tallgrass prairie exposed to twice-ambient and ambient CO_2 concentrations with 56 kg ha^{-1} N added as ammonium nitrate. Means within species or species groups with a common letter do not differ [Duncan's Multiple Range Test, $p < 0.10$].

N concentration and standing crop N

The N concentration in aboveground tissues of ***A. gerardii*** and ***P. pratensis,*** averaged over nine sampling dates, was always lower in CEN plots than in CAN and AN plots in both 1990 and 1991 ($p = 0.0001$) (Fig. ***4).*** In 1990, ***P. pratensis*** and ***A. gerardii*** biomass both had higher N concentrations in CAN plots than AN plots; in 1991, ***P. prutensis*** biomass showed the same response, but ***A. gerurdii*** had similar N concentrations in CAN and AN plots ($p = 0.0001$). Average standing crop of ***N*** of ***A. gerurdii*** was greater in CEN plots than in CAN and AN plots in both 1990 and 1991 ($p = 0.0001$) (Fig. 5). Average N standing crop in ***A. gerardii*** was similar in CAN and AN plots in 1990, but was greater in AN than CAN plots in 1991 (0.0001). Average standing crop ***N*** of ***P. pratensis*** during 1990 did not differ in CEN and CAN plots, but was higher in AN plots ($p = 0.0001$). However, in 1991, average N standing crop of ***P. prutensis*** was greater in CEN plots than in CAN and AN plots, with AN values being greater than CAN values ($p = 0.0001$).

Comparison of unfertilized and fertilized response to elevated CO_2

In order to determine whether N availability limited the response of tallgrass prairie to elevated CO_2, we compared relative biomass production response of N-fertilized plots to those from unfertilized plots in a study conducted concurrently on the same site (Owensby et al., 1993a) (Fig. 6). These data show that aboveground biomass production under elevated CO_2 was limited by N availability, particularly in 1991, a dry year. During 1990, the increased aboveground biomass production in CO_2-enriched plots compared to unchambered ambient plots was primarily from the C_4 perennial grasses. Owensby et al. (1993a) showed that the fumigation chamber affected water relations in a manner similar to that of elevated CO_2, and that the effects were not additive. Therefore, we compared the unchambered ambient plots to the CO_2-enriched plots. When fertilized, total biomass production was 24% greater on elevated CO_2 plots than ambient and 16% greater on unfertilized. The primary increase came from ***A. gerurdii.*** However, in 1991 the increase in biomass production from elevated CO_2 with N fertilizer was 90% and 33% on the the unfertilized plots. ***A. gerardii*** biomass production in 1991 under elevated CO_2 compared to ambient was apparently greatly lim-

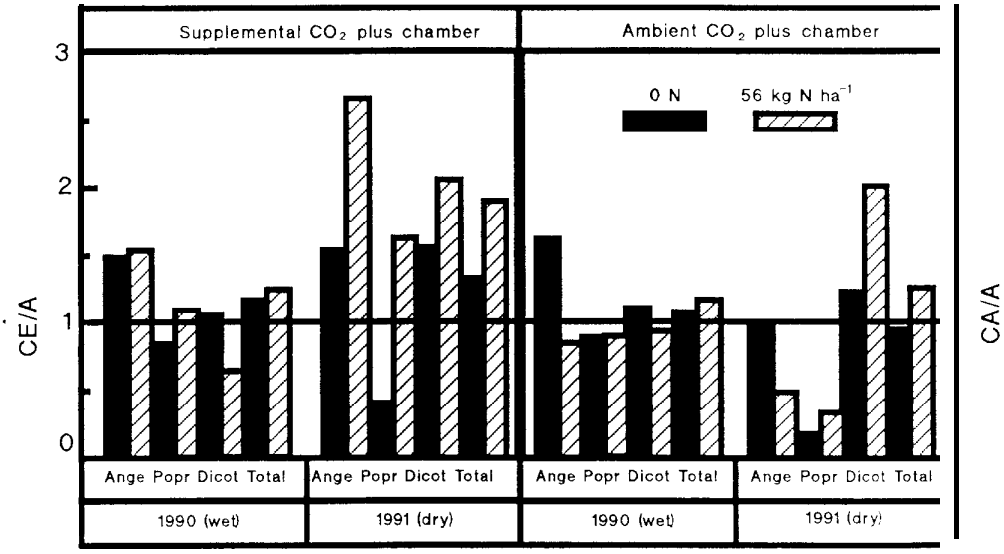

Fig. 6. Relative stimulation of aboveground biomass production by twice-ambient carbon dioxide concentrations compared to unchambered ambient plots with (treatment ratio, CEN/A) and without (CE/A) supplemental nitrogen (left) and by the open-top chamber effect with (CAN/A) and without (CA/A) supplemental nitrogen (right). Treatment abbreviations are defined in the text. Ange= *A. gerardii*, Popr= *P. pratensis*, Dicot= dicot herbs. Unfertilized data from Owensby et al. (1993a).

ited by N availability (a 166% increase in biomass on fertilized plots and a 19% increase on unfertilized). Aboveground biomass production enhancement by supplemental CO_2 in ***P. pratensis,*** and dicot herbs was amplified greatly by N fertilizer in 1991.

Discussion and conclusions

The primary purpose of this study was to test the hypothesis that the increased biomass production in a tallgrass prairie under elevated CO_2 would be limited by N availability, in both the short and long term. Short-term limitations of seasonal biomass production under elevated CO_2 would be associated with the inherent low availability of N in tallgrass prairie. This hypothesis assumes that other resources are not limiting. In the tallgrass prairie, both water and N have been shown to limit aboveground biomass production (Owensby et al., 1969). In a previous study without supplemental N, Owensby et al. (1993a,b) concluded that the primary impact of elevated CO_2 on biomass production was mediated through improved water-use efficiency. In addition, Knapp et al. (1993) reported that the photosynthetic capacity under optimal conditions of ***A. gerardii*** was greater in a dry year under elevate CO_2. Therefore, we predict that increased water-use efficiency and increased photosynthetic capacity of the dominant C_4 perennial grasses during years of suboptimal precipitation in a CO_2-enriched tallgrass prairie will result in increased above- and belowground production. Owensby et al. (1993a,b) also concluded that increased N uptake occurred because of increased root exploration of the soil mass and that N-use efficiency increased because the N requirement of the plant was reduced. Numerous studies have shown reductions in N concentration for C_3 and C_4 species under elevated CO_2 across a wide range of nitrogen availabilities (Coleman et al., 1991; Hoching and Meyer, 1985; Larigauderie et al., 1988).

If the response of aboveground biomass production to elevated CO_2 results primarily from increased water use efficiency (Owensby et al., 1993a), the N availability may more greatly limit the response of tallgrass prairie to elevated CO_2 in years when higher WUE is expressed as an increase in biomass production. This expectation is supported by data on aboveground biomass production in this study and by similar results for unfertilized prairie. Hunt et al. (1991) modeled ecosystem function with elevated CO_2 (2 x ambient) and their results predicted persistent increase in primary production in spite of what they concluded was N limitation, but nutrient cycles in ecosystems exposed to elevated CO_2 are essentially unstudied. However,

root ingrowth biomass production was greater in 1990, a wet year, than in dry 1991. Since roots do not grow into dry soil, and the root ingrowth bags extended to only 15 cm, this result is not unexpected. Root growth may have been shifted to a greater soil depth in the dry year. Bazzazz (1990) and Newton (1991) reviewed the research dealing with natural ecosystems and concluded that generally root growth increased proportionately more with elevated CO_2 than shoot growth.

The chamber effects determined by plotting the ratios **CAN/A** and **CA/A** (Fig. 6) gave mixed results. Nevertheless, we concluded that presence of the chamber imposed N limitation on biomass productivity. The total aboveground biomass response was due to a large effect on dicot herbs. Owensby and Smith (1979) reported that dicot herb production and population density were increased by N fertilization in tallgrass prairie.

Long-term impacts of the apparent N limitation to growth can be inferred from the effects of elevated CO_2 on N concentration in biomass. Owensby et al. (1993b) reported a general reduction in N concentration of unfertilized tallgrass prairie species subjected to elevated CO_2. Those reductions in N concentration were greater than the reductions found in the current fertilized study. Nevertheless, CO_2 enrichment caused reductions in tissue N concentration even with supplemental N. Reductions in N concentration in above- and belowground biomass could potentially slow N cycling by limiting microbial decomposition rate. Indeed, Rice et al. (1993) measured direct stimulation of microbial activity by adding N to the same plots used in this study. Without added N, CO_2-enriched plots had a greater soil carbon content than ambient CO;? plots, indicating reduced microbial activity or greater C input. They concluded that N limitation under elevated CO_2 would slow nutrient cycling and exacerbate N limitation.

Based on the data presented here and those presented earlier by Owensby et al. (1993a,b), we conclude that the future impact of elevated CO_2 on tallgrass prairie will entail increased biomass production in years with water stress and that N availability will limit the magnitude of the response.

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References

Bazzaz F A 1990 The response of natural ecosystems to the rising global CO_2 levels. Annu Rev. Ecol. Syst. 21,167–196

Boden T A, Kanciruk P and Farrell M P 1990 Trends '90, A compendium of data on global climate change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge TN. 257 p.

Coleman J S, Rochefort L, Bazzaz F A and Woodward F I 1991 Atmospheric CO_2, plant nitrogen status and the susceptibility of plants to an acute increase in temperature. Plant, Cell Environ 14, 667–674.

Curtis P S, Drake B G, Leadley P W, Arp W J and Whigham D F 1989a Growth and senescence in plant communities exposed to elevated CO_2 concentrations on an estuarine marsh. Oecologia 78, 20–29.

Curtis P S, Drake B G and Whigham D F 1989b Nitrogen and carbon dynamics in C_3 and C_4 estuarine marsh plants grown under elevated CO_2 in situ. Oecologia 78, 297–301.

Hocking P J and Meyer C P 1985 Responses of noogoora burr (*Xanthium occidentale* Bertol.) to nitrogen supply and carbon dioxide enrichment. Ann. Bot. 55, 835-844.

Hunt H W, Trlica M Z, Redente E F, Moore J C, Detling J K, Kittel T G F, Walter D E, Fowler M C, Klein D A and Elliott E T 199 1 Simulation model for the effects of climate change on temperate grassland ecosystems. Ecol. Mod. 53, 205–246.

Kimball B A 1983 Carbon dioxide and agricultural yield, an assemblage and analysis of 430 prior observations. Agron. J. 75, 779–788.

Knapp A K, Hamerlynck E P and Owensby C E 1993 Photosynthesis and water relations responses to elevated CO_2 in the C_4 grass *Andropogon gerardii*. Int. J. Plant Sci. 154, 459–466.

Larigaudetie A, Hilbert D W and Oechel W C 1988 Effect of CO_2 enrichment and nitrogen availability on resource acquisition and resource allocation in a grass, *Bromus mollis*. Oecologia 77, 544-549.

Linder R C and Harley C P I942 A rapid method for the determination of nitrogen in plant tissue. Science 96, 565-566.

Lund Z F, Pearson R W and Buchanan G A 1970 An implanted soil mass technique to study herbicide effects on root growth. Weed Sci. 18, 279-281.

Mooney H A, Drake B G, Luxmore R J, Oechel W C and Pitelka L F 1991 Predicting ecosystem responses to elevated CO_2 concentrations. Bioscience 41.96104.

Newton P C D 1991 Direct effects of increasing carbon dioxide on pasture plants and communities. N. Z. J. Agric. Res. 34, l-24.

Nijs I, Impens I and Behaeghe T 1988 Effects of rising atmospheric carbon dioxide concentration on gas exchange and growth of perennial ryegrass. Photosynthetica 22, 44–50.

Oechel W C and Strain B R 1985 Native species responses to increased carbon dioxide concentration. In Direct Effects of Increasing Carbon Dioxide on Vegetation. Eds. B R Strain and J D Cure. pp 117-154. U. S. D.O. E., NTIS, Springfield, VA.

Owensby C E and Anderson K L 1967 Yield responses to time of burning in the Kansas Flint Hills. J. Range Manage. 23, 12-16.

Owensby C E, Hyde R M and Anderson K L 1969 Effects of clipping and supplemental nitrogen and water on loamy upland bluestem range. J. Range Manage. 23, 341–346.

Owensby C E and Smith E F 1979 Fertilizing and burning Flint Hills bluestem range. J. Range Manage. 32, 254–258.

Owensby C E, Coyne P I, Ham J M, Auen L M and Knapp A K 1993a. Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated levels of CO_2. Ecol. Appl. 3, 644–653.

Owensby C E, Coyne P I and Auen L M 1993b Nitrogen and phosphorus dynamics of a tallgrass prairie ecosystem exposed to elevated carbon dioxide. Plant, Cell Environ. 16. 843–850.

Reichers G Hand Strain B R 1988 Growth of blue grama (*Bouteloua gracilis*) in response to atmospheric CO_2 enrichment. Can. J. Bot. 66, 1570-1573.

Rice C W, Garcia F 0, Hampton C 0 and Owensby C E 1994. Microbial response in tallgrass prairie to elevated CO_2. Plant and Soil (*In* press).

Strain B R and Cure J D 1985 Direct effect of increasing carbon dioxide on vegetation. Carbon Dioxide Research, State of the Art. US. D.O.E. Washington, DC.

Technicon Industrial Systems 1977 Individual/simultaneous determination of nitrogen and/or phosphorus in BD acid digests. Industrial Method NO. 334-74 WB+.

Tolley L C and Strain B R 1984 Effects of atmospheric CO_2 enrichment and water stress on growth of *Liquidamber styraciflua* L. and *Pinus taeda* L. seedlings. Can J. Bot. 10, 2135-2139.

Wray S M and Strain B R 1986 Response of two old field perennials to interactions of CO_2 enrichment and drought stress. Am. J. Bot. 73, 1486-1491.