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EFFECTS OF ELEVATED CO_2 AND DEFOLIATION ON GRASSES: A COMPARATIVE ECOSYSTEM APPROACH

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Abstract. Three plant species from each of three grassland ecosystems were grown under elevated (700 mL/m³) and ambient (350 mL/m³) CO_2 and were defoliated or left undefoliated to test whether species response to elevated CO_2 and grazing is related to evolutionary grazing history or to mode of photosynthesis. The three ecosystems represented a tropical grassland dominated by C_4 species (the Serengeti of Africa), a temperate grassland dominated by a mixture of C_3 and C_4 species (Flooding Pampa of South America), and a northern temperate grassland dominated by C_3 species (Yellowstone National Park of North America). Plants were grown in growth chambers under common conditions to compare relative responses to grazing and elevated CO_2.

Elevated CO_2 caused an increase in total biomass and total productivity (biomass + clippings) only in Yellowstone species, and increases in growth occurred primarily in crowns and roots (storage organs). There were no significant CO_2 effects on biomass or productivity in Serengeti or Flooding Pampa species, and no CO_2 effects on aboveground biomass or productivity (aboveground biomass + clippings) in species from any of the three ecosystems. Since aboveground plant parts are the portions that are available to grazing mammals, this suggests that increased atmospheric CO_2 may not affect food quantity in these three grasslands. There was no interaction between CO_2 and defoliation for any species; thus, it appears that herbivores will not affect how grasses respond to elevated CO_2 (at least under average nutrient conditions). Elevated CO_2 caused a reduction in leaf percentage of N in species from Yellowstone and Flooding Pampa (especially the C_3 species, *Briza subaristata*), but not in Serengeti species. Because the quantity of food was unaffected by the CO_2 treatments and forage N was reduced, grazing mammals in Yellowstone (elk, *Cervus elaphus,* and bison, *Bison bison*) and the Flooding Pampa (cattle) may be negatively affected.

Responses to defoliation were fairly consistent among ecosystems in aboveground productivity, which did not differ between defoliated and undefoliated plants, and in leaf water potentials and percentage of N, both of which increased in response to defoliation. However, differences among ecosystems were found for crown and root biomass in response to defoliation: Serengeti species, on average, had higher crown and similar root biomasses after defoliation, whereas defoliated species from the other two ecosystems had reduced crown and root biomass. We suggest that the lower intensity and increased temporal variance in grazing pressure in Yellowstone vs. the Serengeti, selected for plants that shift allocation away from roots and crowns in order to compensate for aboveground herbivory.

Key words: CO_2 enrichment; global change; grasslands; grazing; herbivory.

INTRODUCTION

Atmospheric levels of carbon dioxide are increasing and are expected to be double the current levels by the mid-to-late 21st century (Conway et al. 1988, Houghton et al. 1990, 1992, Wigley and Raper 1992). The effects of elevated CO_2 on vegetation vary among ecosystems, with some ecosystems demonstrating large increases in primary productivity, changes in species composition, and reduction in tissue N concentration (Curtis et al. 1989*a, b,* Bazzaz 1990, Mooney et al. 1991), and others (e.g., tundra) showing little or no change (Oberbauer et al. 1986, Oechel et al. 1994).

Many functional characteristics vary among ecosystems, including nutrient, water, light, and temperature availability, the predominant mode of photosynthesis (C_3, C_4, or CAM) in dominant plant species, and types and rates of herbivory (Whittaker 1975, McNaughton et al. 1989, 1991). All of these factors are probably important in how ecosystems will respond to elevated CO_2 (Bazzaz 1990, Mooney et al. 1991, Poorter 1993). Determining whether responses to elevated CO_2 are consistent across ecosystems is important for predicting plant response at the global level (Wilsey 1996*a*). If relative responses to elevated CO_2 are consistent across ecosystems within each biome, then broader and stronger predictions can be made at the biome level. If responses are not consistent across ecosystems, then functional characteristics that correlate with the inconsistencies can be identified (Wilsey 1996*a*).

Most experiments on the effects of elevated CO_2

have studied one or a few species from a single eco-system, and have not considered the effects of higher trophic levels on plant responses to elevated CO_2. Studies on the effects of elevated CO_2 on plant–herbivore interactions have been done mostly with insect herbivores (reviewed in Lincoln et al. 1993). Based on previous research on plant responses to elevated CO_2 under simulated ungulate grazing (Wilsey et al. 1994, Wilsey 1996*b*), it appears that differential responses may be found among grasses from different ecosystems. For example, productivity of a temperate C_3 grass, *Stipa occidentalis,* increased in response to elevated CO_2, but only when plants received urea (high N) and were not clipped, and leaf percentage of N declined by the end of the experiment (Wilsey 1996*b*). However, a tropical C_4 grass, *Sporobolus kentrophyllus,* had similar biomass and tissue nutrient concentrations when grown under elevated and ambient CO_2 (Wilsey et al. 1994). If these results are consistent among species within these two ecosystems, it may mean that different grassland ecosystems have the potential to show different responses to elevated CO_2, and that these responses may be dependent on the relative abundance of C_3 and C_4 plants.

It has been proposed that species from different grassland ecosystems differ in their response to grazing, depending on the ecosystem's evolutionary grazing history (Mack and Tettleton 1982, Milchunas et al. 1988). For example, *Agropyron desertorum,* a species introduced into the Great Basin from Eurasia, had evolved in the presence of larger populations of grazing mammals than in the Great Basin (Caldwell et al. 1981), and showed increased root growth in high-nutrient microsites (as might be found in a urine patch), whereas a native species, *Agropyron spicatum,* showed no response (Jackson and Caldwell 1989). *A. desertorum* was also better able to tolerate heavy defoliation than was *A. spicatum* (Caldwell et al. 1981). Evolution under high grazing pressure has also been used to explain the increase in African grasses over South American grasses in heavily (cattle) grazed savannas: in an experiment by Simoes and Baruch (1991), clipped *Hyparrhenia rufa* had higher tillering rates than unclipped plants, whereas there was no increase in tillering rates in *Trachypogon plumosus,* a South American species. However, another study showed a similar amount of compensation for clipping between several African and South American species (Klink 1994). Clearly, there is need for further work on whether plant response to grazing varies among ecosystems.

The objective of this experiment was to compare the responses of several plant species from three different ecosystems (on three continents) to elevated CO_2 and simulated ungulate grazing, and to address the following questions. (1) Are relative responses to elevated CO_2 similar among plant species from each of these ecosystems, and, if not, is mode of photosynthesis a useful predictor of plant response? (2) Are compen-satory responses to simulated grazing similar among plant species from each of these ecosystems, and, if not, is it related to the ecosystem's evolutionary grazing history?

Study Areas

Plants were collected from (1) Yellowstone National Park, United States, North America; (2) Flooding Pampa of Buenos Aires Province, Argentina, South America; and (3) Serengeti Ecosystem, Tanzania, Africa. The three ecosystems included a representative of northern-temperate grasslands, which are exclusively C_3 species (Yellowstone); temperate-mixed grasslands dominated by a mixture of C_3 and C_4 species (Flooding Pampa); and tropical grasslands, which are exclusively C_4 species (Serengeti).

Yellowstone National Park, which occupies 9000 km^2 between 44° and 45°N, is located mostly in north-western Wyoming, United States (detailed descriptions in Houston 1982). The park contains $\approx 20\,000$ elk (*Cervus elaphus*) and 500 bison (*Bison bison*) (Frank and McNaughton 1992). Other ungulates include pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*).

Although 80% of the Park is forested (mostly lodgepole pine, *Pinus contorta*), elk and bison preferentially select grassland habitats (Frank and McNaughton 1992). Elk and bison migrate, following spring greening, from low-elevation winter range sites in the northern part of the park to higher elevation sites in the southern part, and outside of the park (Frank and Mc-Naughton 1992). Two of the plant species used in this study are common grasses in the winter range, *Festuca idahoensis* and *Stipa occidentalis* (Mueggler 1967, Frank et al. 1994), and one is common in grasslands of the summer range, *Agropyron caninum* (Despain 1990:68).

The Flooding Pampa of Argentina ($\approx 35°$S) is located in the Salado River Basin (58 000 km^2) in Buenos Aires Province, Argentina (Sala et al. 1981, Soriano et al. 1991). Most of the river basin (80%) is used for cattle production (Sala et al. 1981, Oesterheld et al. 1992). During pre-Columbian times, the principal herbivore species were pampas deer (*Ozotoceros bezoarticus*) and Rheas (*Rhea americana,* ñandu) (Soriano et al. 1991). The area is very flat and often contains standing water in the early spring, but can encounter drought in the summer because of shallow soils (Sala et al. 1981). The three species used in this study were common, native grasses established from seeds collected inside cattle exclosures (erected in 1977) at Las Chilcas, Buenos Aires Province, Argentina (Sala et al. 1981, Oesterheld and Sala 1990). These species were chosen to represent grasses with each mode of photosynthesis: *Briza subaristata* (C_3), *Panicum millioides* (C_3/C_4 intermediate; Wilson et al. 1983), and *Paspalum dilatum* (C_4).

The Serengeti ecosystem, which is defined by the movement of migratory wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), and eland (*Taurotragus oryx*) (see Sinclair and Norton-Griffiths 1979, McNaughton 1983, 1985, and Sinclair and Arcese 1995 for descriptions of the study area), consists of the Serengeti National Park and adjoining game reserves, and is located between 1° and 3°30′ S. It falls along a rainfall and counterfertility gradient, with tallgrass regions having the highest rainfall and lowest fertility, and shortgrass regions having the lowest rainfall and highest fertility. It contains very large populations of ungulates, including 1.3×10^6 wildebeests, 200 000 zebra, 440 000 Thomson's gazelles (*Gazella thomsonii*), and large populations of resident herbivores, including impala (*Aepyceros melampus*), buffalo (*Syncerus caffer*), and topi (*Damaliscus korrigum*) (Sinclair and Arcese 1995). The grass species that were used in this experiment, all of which had C_4 photosynthesis, were common to tall- and midgrass (*Themeda triandra*), short- and midgrass (*Digitaria macroblephara*), and shortgrass locations (*Sporobolus kentrophyllus*) (McNaughton 1983).

METHODS

Plants were propagated from a single genotype within each species. Yellowstone and Serengeti plants were vegetatively propagated from plants collected from the field, whereas plants from the Flooding Pampa were propagated from plants that had been grown from seed. Yellowstone plants, which were dormant when collected in October, were brought out of dormancy by gradually increasing light and temperature levels up to spring-like conditions. Serengeti grasses were propagated from plants that had been under cultivation in the Syracuse University, New York greenhouse since the 1970s.

Plants were trimmed to similar sizes (e.g., all roots were 10 cm long) and were planted in cylindrical pots (10 cm diameter and 25 cm tall) that contained a 50:50 mixture of sand and calcined clay. Tall pots were used to simulate the natural rooting volume for grasses in these ecosystems: in Yellowstone, 82–84% of the roots are in the top 20 cm of soil (Frank et al. 1994); in the Flooding Pampa, 65% of the roots are above a depth of 10 cm and 85% are above 30 cm (Soriano et al. 1991); in the Serengeti, an average of short-, mid-, and tallgrass sites had 71% in the top 20 cm (S. J. McNaughton, *unpublished data*). Four plants per treatment per species were propagated, for a total of 144 plants (three species × three ecosystems × two CO_2 treatments × two clipping treatments × four replicates). However, several *Themeda triandra, Stipa occidentalis,* and *Briza subarastata* plants died due to transplantation shock, so the number of samples was three in some treatments.

All plants received the same amounts of fertilizer and water during the experiment. Plants received Hoag-

land's solution every 3 d, providing nitrogen at a rate of 1 g·m⁻²·wk⁻¹, which roughly corresponds to nitrogen availability in the Serengeti (B. J. Wilsey and S. J. McNaughton, *unpublished data*), and is slightly more N than plants in the Summer range of Yellowstone receive in June (0.75g·m⁻²·wk⁻¹; Tracy 1996). Plants were given 150 mL of water every 3 d during the experiment.

Temperatures in the chambers were 25°C during the day and 13°C at night, which roughly corresponds to an average late-spring day in Argentina, when maximum overlap of growth occurs in C_3 and C_4 grasses (Sala et al. 1981). The average high temperatures in the Serengeti are 28°C during the day and 14°C at night (McNaughton et al. 1983), and the average high temperatures in July in Yellowstone are 27°C during the day and 8°C at night (National Oceanic and Atmospheric Administration monthly climatological data).

In two growth chambers, CO_2 was increased to 700 mL/m³ after an 18-d acclimation period; CO_2 levels in two ambient CO_2 chambers were kept at 350 mL/m³. Light levels in chambers averaged 794 μmol of photons (range: 775–809 μmol), only half the level of full sunlight, but high for a growth chamber experiment. Within each chamber, plants were clipped by removing all tissue above the height of 5 cm on days 15, 36, and 64, and white collars were used to simulate canopy shading, as described in McNaughton (1992). This type of defoliation was meant to simulate grazing by large, relatively unselective mammals (e.g., bison, cattle, and wildebeest).

Measurements of midday leaf water potential were made on day 71, at the end of the watering cycle. On day 50, three of the first fully expanded leaves were collected from each plant, dried, chopped with scissors, and run through a Carlo Erba N1500 (Fisons Instruments, 20090 Rodano MI, Italy) to measure leaf N. Leaf percentage of N was used as an index of forage quality because it covaries with other important nutrients and digestibility (Mattson 1980, McNaughton 1990, Ayres 1993), and because of its direct importance to mammal nutrition (Mattson 1980, Robbins 1983, McNaughton 1990).

At harvest, separate root collections were made from the top and bottom half of pots to determine if "pot binding" existed. However, total biomass per pot was used for comparisons between CO_2 and defoliation treatments.

Data were analyzed as a split-plot design, with the CO_2 main effect in the main plot and clipping and species effects and their interactions in the subplot. Thus, the chamber (CO_2) effect was used as the error term for the CO_2 main effect and the residual error term for other tests. Within the subplot, nested ANOVA was used on species nested within ecosystem, with ecosystem and species as fixed effects (Neter et al. 1985). A priori contrasts were made between CO_2 treatments within each ecosystem. Biomass variables were

TABLE 1. Probability values from ANOVA of biomass (grams per pot) for nine species from three grassland ecosystems (Serengeti, Yellowstone National Park, Flooding Pampa), grown under elevated (700 mL/m^3) and ambient (350 mL/m^3) CO_2 and under clipped and unclipped conditions.

Effect	df	Root	Crown	Litter	Above†	Total	Above Prod.†	Total Prod.†
CO_2	1	0.066	0.086	0.304	0.467	0.122	0.397	0.127
Error	2							
Ecosystem	2	0.662	0.001	0.001	0.001	0.074	0.001	0.005
Species (E)‡	6	0.001	0.001	0.001	0.001	0.001	0.001	0.001
E × CO_2	2	0.168	0.209	0.423	0.469	0.049	0.687	0.089
CO_2 × Species (E)‡	6	0.121	0.799	0.979	0.754	0.170	0.624	0.195
Clipping	1	0.001	0.044	0.001	0.001	0.001	0.172	0.005
C × CO_2	1	0.510	0.180	0.481	0.411	0.569	0.703	0.511
C × E	2	0.056	0.001	0.496	0.002	0.054	0.374	0.219
C × Species (E)‡	6	0.337	0.054	0.007	0.001	0.012	0.001	0.248
C × CO_2 × E	2	0.883	0.126	0.432	0.894	0.570	0.984	0.738
C × CO_2 × Species (E)‡	6	0.943	0.778	0.440	0.622	0.915	0.636	0.920
Error	95							

Note: Abbreviations are E, Ecosystem; C, Clipping.

† ''Above'' refers to aboveground biomass; ''prod.'' refers to productivity (biomass + clippings).

‡ Nested tests for variation among species within ecosystems and for interactions between treatments and species within ecosystems.

ln-transformed and leaf percentage of N was arcsine-transformed before analysis to improve normality and to homogenize variances (Steel and Torrie 1980).

RESULTS

Biomass and productivity

Elevated CO_2 caused an increase in total biomass and total productivity (above + root + clippings) only in grass species from Yellowstone National Park (Table 1, Figs. 1 and 3; contrasts, elevated vs. ambient CO_2 for Yellowstone species: both $P < 0.01$). There was no effect of CO_2 treatment on total productivity of plants from the Flooding Pampa or the Serengeti (contrasts: Pampa, $P = 0.65$ and 0.53; Serengeti, $P = 0.55$ and 0.42). Plants from all three ecosystems had marginally significantly higher root and crown biomasses under elevated CO_2 than under ambient CO_2 (Table 1). However, there was some indication of a CO_2 × ecosystem interaction, with the largest responses occurring in Yellowstone species (Table 1, Fig. 1). There was no significant difference in litter between plants grown under ambient vs. elevated CO_2.

Aboveground biomass and productivity (biomass + clippings), which are the portions of the plant consumed by grazing mammals, were not significantly different between the two CO_2 treatments in any of the three ecosystems (Table 1, Fig. 1). Furthermore, there was no significant effect on mass of the clippings in response to elevated CO_2. Thus, the quantity of food available for grazing mammals was not changed by increases in CO_2.

Aboveground biomass was much lower in clipped plants than in unclipped plants, because clipped plants had only 9 d to recover from the final defoliation event
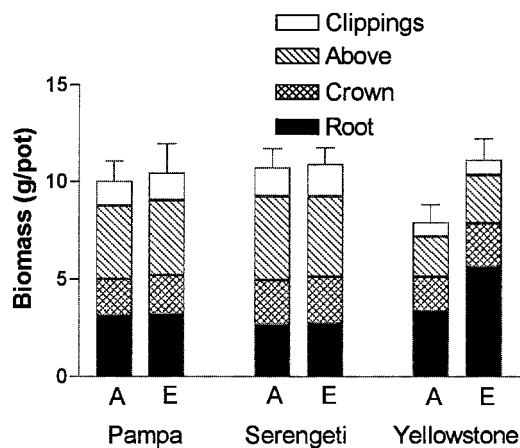

FIG. 1. Biomass (mean + 1 SE) in grasses from three separate grassland ecosystems, averaged across defoliation treatments, when grown under elevated (E, 700 mL/m^3) vs. ambient (A, 350 mL/m^3) CO_2. In the key, above refers to aboveground biomass.
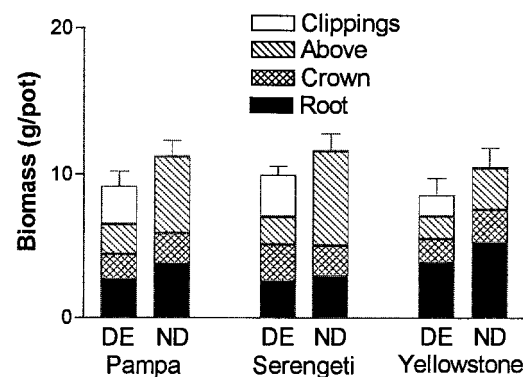

FIG. 2. Biomass (mean + 1 SE) in grasses from three grassland ecosystems, averaged across CO_2 treatments, when defoliated (DE) or left nondefoliated (ND).
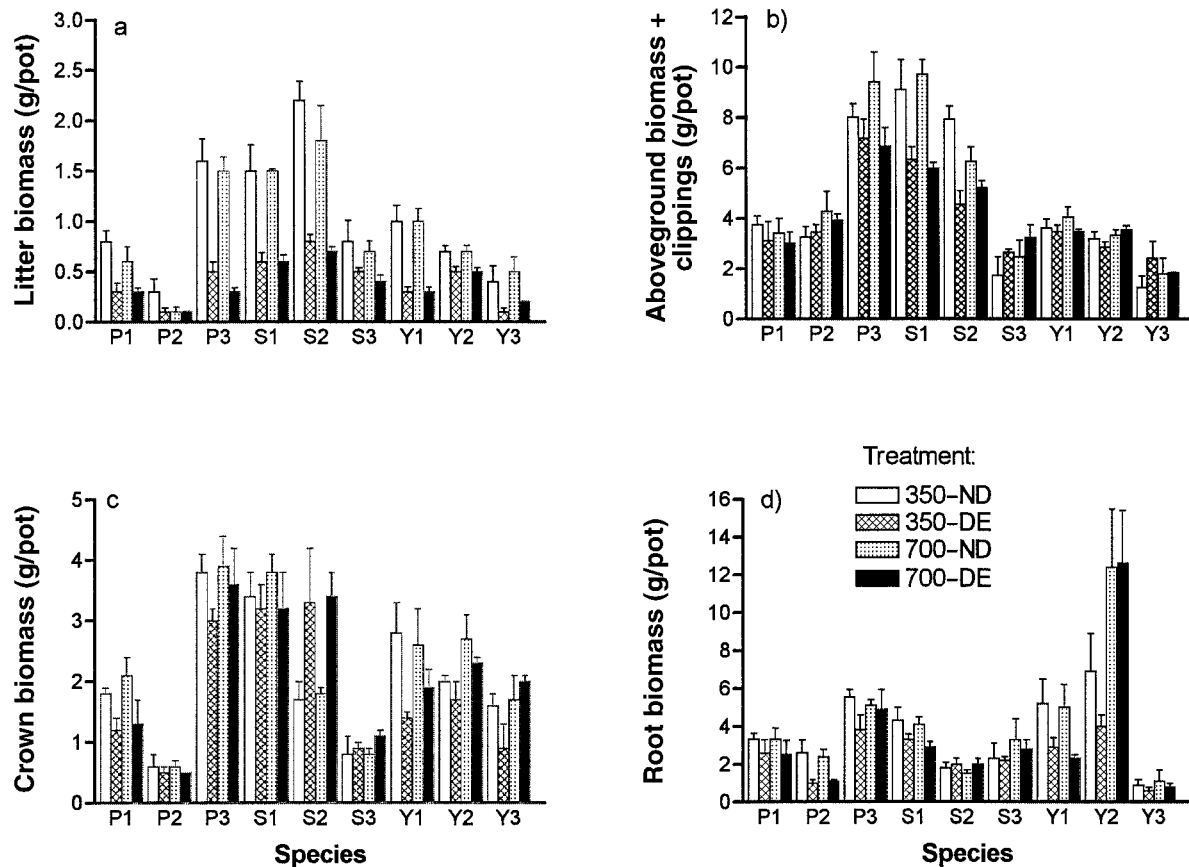
FIG. 3. Litter (a), aboveground biomass + clippings (b), crown (c), and root (d) biomass (mean + 1 SE) in grasses from three grassland ecosystems, when grown under elevated (700 mL/m³) and ambient (350 mL/m³) CO_2 and either defoliated (DE) or left nondefoliated (ND). Species are as follows: P1, *Briza subaristata*; P2, *Panicum millioides*; P3, *Paspalum dilatum*; S1, *Digitaria macroblephara*; S2, *Sporobolus kentrophyllus*; S3, *Themeda triandra*; Y1, *Agropyron caninum*; Y2, *Festuca idahoensis*; and Y3, *Stipa occidentalis*.

before harvest (Oesterheld and McNaughton 1991). This difference was smallest in Yellowstone species. However, aboveground productivity (biomass + clippings) was not significantly different between plants that were clipped vs. plants that remained unclipped, and this relationship was consistent across ecosystems, although there was variation in plant response to clipping among species within ecosystems (Table 1, Fig. 2). Thus, although individual species within ecosystems showed differential responses to clipping, on average, plant species among the three ecosystems showed a similar amount of compensatory response (but no overcompensation) to aboveground clipping.

The response of crowns and roots to clipping, however, did vary among ecosystems (Figs. 2 and 3). Crowns, which often serve a storage function in grasses (Danckwerts et al. 1991), were significantly larger in unclipped than in clipped plants in species from the Flooding Pampa (especially *Briza subarastata*) and Yellowstone National Park (especially *Agropyron caninum*) (Table 1 and Fig. 2). In the Serengeti, which has

a greater grazing pressure, crown biomass was actually higher in clipped than in unclipped plants (especially in *Sporobolus kentrophyllus*)(Table 1 and Fig. 2).

Root biomass response varied among ecosystems in a way that was consistent with the crown biomass data (Table 1). Unclipped plants from the Flooding Pampa and Yellowstone National Park had higher root biomasses than did clipped plants (contrasts: Pampa, $P < 0.01$; Yellowstone, $P < 0.01$). However, in plants from the Serengeti, there was no difference in root biomass between clipped vs. unclipped plants (contrast: $P = 0.81$). This relationship was consistent across species within ecosystems.

Total biomass, which was lower in unclipped than in clipped plants in all three ecosystems, differed most between clipping treatments in plants from the Flooding Pampa (Table 1, Figs. 2 and 3). There was evidence that Serengeti plants had a smaller reduction in the amount of total productivity in response to clipping (contrasts, clipped vs. unclipped: Pampa, $P < 0.01$; Yellowstone, $P < 0.05$; Serengeti, $P = 0.73$).

TABLE 2. Probability values from ANOVA of leaf percentage of N and leaf water potential (w.p. in MPa) for nine plant species from three grassland ecosystems (Serengeti, Yellowstone National Park, Flooding Pampa) that were grown under elevated (700 mL/m³) and ambient (350 mL/m³) CO_2 and under clipped and unclipped conditions.

Effect	df	Leaf N	Leaf w.p.
CO_2	1	0.162	0.001
Error	2		
Ecosystem	2	0.001	0.001
Species (E)	6	0.002	0.001
E × CO_2	2	0.001	0.031
CO_2 × Species (E)	6	0.737	0.019
Clipping	1	0.001	0.001
C × CO_2	1	0.520	0.329
C × E	2	0.923	0.741
C × Species (E)	6	0.997	0.048
C × CO_2 × E	2	0.321	0.672
C × CO_2 × Species (E)	6	0.749	0.947
Error	95		

Note: Abbreviations are as in Table 1.

Leaf water potential

Plants grown under elevated CO_2 had significantly less negative water potentials, and this difference was found in all three ecosystems (Table 2, Fig. 4). There was highly significant variation in leaf water potential among ecosystems and among species within ecosystems, largely dependent on mode of photosynthesis. Leaf water potentials were low enough to cause fairly low midday water potentials, reflecting the fact that the plants did not receive overly plentiful water supplies. Although plants all received the same amount of water, the C_4 plants had much less negative water potentials than did the C_3 plants.

Clipping also caused an increase in leaf water potential, although the difference was not significant in all species (Fig. 5). A significant increase in water potential in response to clipping occurred in *Briza subarastata, Paspalum dilatum, Themeda triandra, Agropyron caninum,* and *Festuca idahoensis.* A nonsignificant trend was also found in *Panicum millioides, Dig-*

FIG. 5. Midday water potential (mean and 1 SE) in grasses from three grassland ecosystems, averaged across CO_2 treatments, when defoliated or left nondefoliated. See Fig. 3 for species codes.

itaria macroblephara, and *Stipa occidentalis.* However, there was clearly no difference between clipped and unclipped *Sporobolus kentrophyllus.*

Forage N content

Plants in elevated CO_2 treatments had significant reductions in leaf N concentrations only in plants from Yellowstone and the Flooding Pampa (contrasts: Yellowstone, $P < 0.01$; Pampa, $P < 0.02$; Fig. 6, Table 2). There was no difference in leaf percentage of N between CO_2 treatments in any of the species from the Serengeti (contrast: Serengeti, $P = 0.26$). There was no difference among plant species within ecosystems in how they responded to elevated CO_2; thus, a response to elevated CO_2 was found only at the ecosystem level (Table 2). Within the Flooding Pampa, there was some indication that the differences were found in the C_3 species *B. subarastata* and in the C_3/C_4 intermediate *P. millioides,* but not in the C_4 species *P. dilatum.*

There was a large amount of variation in leaf percentage of N, both among ecosystems and among species within ecosystems (Table 2). Leaf N was highest in Yellowstone grasses (2.82%) and lower in grasses
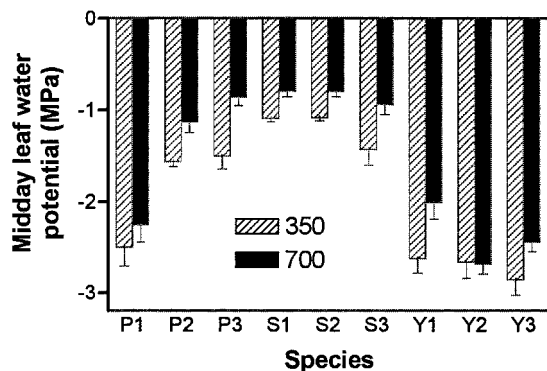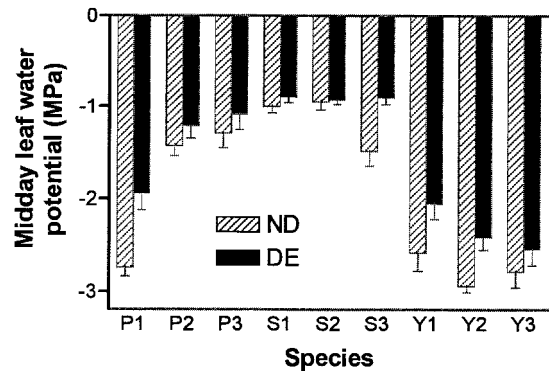

FIG. 4. Midday water potential (mean and 1 SE) in grasses from three grassland ecosystems, averaged across defoliation treatments, when grown under elevated (700 mL/m³) and ambient (350 mL/m³) CO_2. See Fig. 3 for species codes.
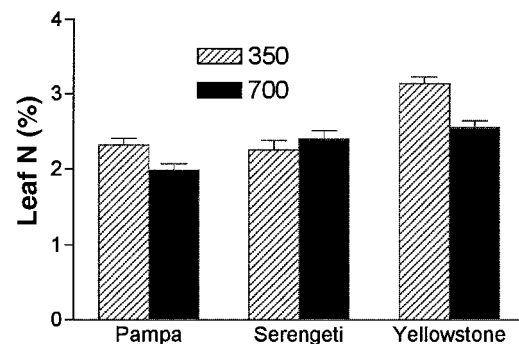

FIG. 6. Leaf percentage of N (mean + 1 SE) in grasses from three grassland ecosystems, averaged across defoliation treatments, when grown under elevated (700 mL/m³) and ambient (350 mL/m³) CO_2.
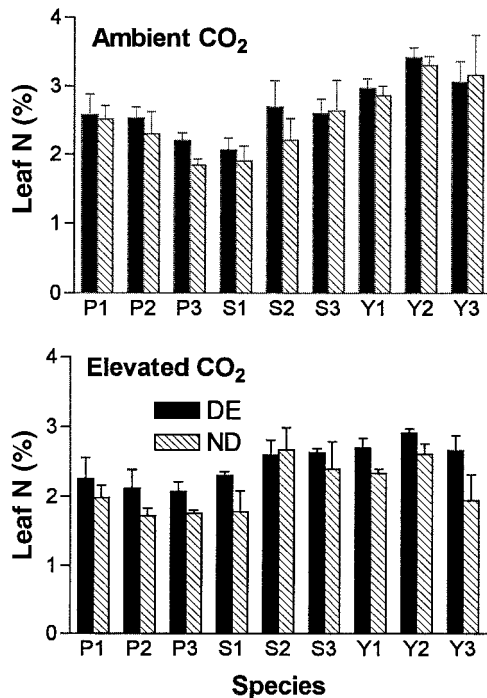
FIG. 7. Leaf percentage of N (mean + 1 SE) in grasses from three grassland ecosystems, when grown under ambient and elevated CO_2 and either defoliated or left nondefoliated. See Fig. 3 for species codes.

from the Serengeti (2.32%) and Flooding Pampa (2.16%).

Clipping resulted in an increase in percentage of N in all nine species (Table 2, Fig. 7). This response was consistent among ecosystems and among species within ecosystems.

DISCUSSION

In this experiment, we grew plants from three diverse ecosystems under common conditions in growth chambers to determine if there were differences in their response to CO_2 enrichment and defoliation. Although an attempt was made to give the plants realistic (in the range of field values) amounts of N, water, and rooting volume, the plants had to be grown under a single temperature and nutrient regime for data to be comparable across species. Because the experimental conditions did not exactly correspond to any of the three ecosystems, and because of the inherent artificial nature of growth chambers (e.g., low light and artificial soils), absolute (quantitative) predictions on how these plants will respond in the field in their respective ecosystems are not possible. However, these data should be useful as measures of relative response to treatments.

The response to elevated CO_2 in grasses from these three ecosystems was largely dependent on mode of photosynthesis, and was consistent with earlier experiments with a C_4 Serengeti species (Wilsey et al. 1994) and a C_3 Yellowstone species (Wilsey (1996b). This

consistency, and the fact that no CO2 $\times$ species (ecosystem) interactions were found, suggest that differences may be found among grassland ecosystems in how they respond to elevated CO_2.

We suggest that the lack of response to CO_2 in C_4 plants and the small aboveground response in C_3 plants were not caused by root restriction, based on two pieces of evidence. First, there was unoccupied rooting space in all pots at the end of the experiment. An overall average of 69% of the roots were in the top half (range across species: 53–86%) and 31% were in the bottom half of pots at harvest; this estimate was highest (86%) in the species (*Festuca idahoensis*) with the greatest root mass. Second, a separate study with *Sporobolus kentrophyllus* (same genotype) growing under plentiful N supplies (two times greater than in this experiment) and in pots twice as large, showed a similar lack of response (Wilsey et al. 1994).

In this experiment, in contrast to an earlier experiment (Wilsey 1996b), there were no interactions between CO_2 and clipping. Thus, plants showed similar responses to elevated CO_2 whether they were clipped or remained unclipped. These results are consistent with those of Fajer et al. (1991), who found no effect of simulated insect herbivory on plant response to elevated CO_2. Based on the data from this experiment and the experiment from Wilsey (1996b), it is likely that grazing mammals will affect plant responses to elevated CO_2 primarily through nutrient cycling rather than through direct defoliation.

Because grazing mammals consume the aboveground portions of grasses, and aboveground biomass and productivity were not affected by elevated CO_2, the amount of food available to them might not change in response to increases in atmospheric CO_2 (see also Wilsey et al. 1994, Wilsey 1996b). However, in Yellowstone and Flooding Pampa grasses, forage quality declined in response to elevated CO_2. Thus, in Yellowstone and, to some extent, in the Flooding Pampa, grazing mammals will have the same amount of food available, but it will be of lower quality. As a result, grazing mammals may be negatively effected by increases in CO_2 (Wilsey 1996b).

Grazing pressure is higher in the Serengeti than it is in Yellowstone: Serengeti National Park is about three times the size of Yellowstone National Park (15 times larger if only grasslands are included), but contains >100 times the number of migratory ungulates. Although it is not known how much grazing the Flooding Pampa received during pre-Columbian times, it was probably less than in the Serengeti (Sala et al. 1981, Milchunas et al. 1988, Soriano et al. 1991). Because of this differential grazing pressure, Serengeti grasses may be adapted to higher grazing pressures and, as a result, can compensate for grazing without relying on a shift in allocation to aboveground regrowth and away from roots and crowns. This may account for the reduction we saw in root and crown biomass in clipped

plants from Yellowstone and Flooding Pampa, but not from the Serengeti. These data may partially explain why shifts in allocation aboveground are found more often in North American grasses (e.g., Caldwell et al. 1981, Jaramillo and Detling 1988, Holland et al. 1992) than in African grasses (e.g., McNaughton et al. 1983, McNaughton and Chapin 1985, Oesterheld and Mc-Naughton 1988, Wilsey et al. 1994). In African grasses, shifts in allocation in response to clipping primarily occur away from culms and leaf sheaths to leaf blades (Oesterheld and McNaughton 1988, Wilsey et al. 1994).

Another aspect of the grazing regime that differs among these ecosystems, and especially between the Serengeti shortgrass plains and Yellowstone, is the temporal variance in grazing pressure. In the shortgrass plains, herbivory is intense and continuous, with almost all (up to 95%) of the aboveground biomass removed during the growing season (McNaughton 1985). In Yellowstone and in transition areas of the Serengeti (McNaughton et al. 1988), plants usually have several weeks either before migratory grazers arrive (e.g., the summer range in Yellowstone) or after they leave (e.g., the winter range in Yellowstone) to replace crown and root biomass. Thus, a shift in allocation away from crowns to replace aboveground tissue after migrants have left may be beneficial to the plant in order to get a head start on competitors for light. However, on the Serengeti shortgrass plains, a shift in allocation would not necessarily be beneficial to the plant, because the aboveground biomass would again be consumed after the shift took place. A shift in allocation away from crowns to replace aboveground biomass may be an adaptation to infrequent, but intense (temporally variable), grazing pressure. Thus, we suggest that allocational shifts will not occur in grasses that are not adapted to grazing (Caldwell et al. 1981), nor in grasses that have evolved under intense and continuous grazing.

Predictions stemming from our hypothesis are: (1) grass species from the Serengeti shortgrass plains, which receive intense and continuous grazing pressure (McNaughton 1985), would not shift allocation away from roots and crowns in response to grazing; and (2) plants in transition areas with low populations of resident herbivores, which are under infrequent but intense grazing pressure, would shift allocation in response to grazing. Although we cannot test this notion directly with our data, we did find that *Sporobolus kentrophyllus,* one of the codominant plants on the shortgrass plains, increased crown biomass and did not reduce root biomass in response to clipping, whereas the other two species responded more similarly to species from the other two ecosystems.

In conclusion, there were similarities and differences in how nine plant species from three grasslands on three continents responded to elevated CO_2 and clipping. Species in all three ecosystems had less negative midday water potentials and increased root biomass in response to elevated CO_2, although the root biomass response was much larger in Yellowstone species than in the others. Significant increases in other plant parts, mostly in crowns, occurred only in Yellowstone species (all C_3 plants). Thus, higher latitude temperate grasslands, or other grasslands with C_3 species as dominants, may be more heavily impacted by elevated CO_2, with plants showing increased biomass in roots and crowns (storage organs; see Loehle 1995) and reduced leaf N.

We did not find evidence for a $CO_2 \times$ defoliation interaction, but the reductions in tissue N could have important implications for herbivores. Grazing mammals cannot increase the amount of time spent feeding to compensate for low forage quality, as do insects (Slansky and Feeny 1977), and food retention time is inversely correlated with forage N content in ungulates (Van Soest 1982). Because the N content of forage decreased whereas the quantity of food largely remained unchanged, grazing mammals might be negatively affected by increases in atmospheric CO_2 in the Yellowstone and Flooding Pampa, and possibly in other temperate grasslands (Owensby et al. 1993*a, b*, Wilsey 1996*b*). Other grasslands, especially tropical grasslands, that have C_4 species as dominants may be less affected by elevated CO_2 (Wilsey et al. 1994).

Common responses to clipping among ecosystems included less water stress and increased leaf percentage of N in clipped vs. unclipped plants. Plant species from all three ecosystems showed some compensation (but not overcompensation) for clipping, but varied in their response. Yellowstone and Pampa species made large shifts in allocation away from crowns and roots, whereas Serengeti species compensated for clipping without incurring a loss in crown and root biomass.

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