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Urea additions and defoliation affect plant responses to elevated CO_2 in a C_3 grass from Yellowstone National Park

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Abstract A common grass from Yellowstone National Park, *Stipa occidentalis*, was grown in a factorial experiment to determine if its response to the direct effects of elevated CO_2 would be affected by defoliation, and urea additions simulating the N in a urine hit. Plants were grown in tall pots (to mimic rooting depth in the field) in growth chambers under elevated (700 ppm) and ambient (370 ppm) CO_2, were defoliated or left undefoliated, and given N-supply rates based on field mineralization rates (untreated) or with an additional 40 g N/m^2. Growth increases in response to elevated CO_2 were largest when plants remained unclipped and received urea additions, and were found primarily in crowns and roots (storage organs). Aboveground biomass, which is the part of the plant consumed by grazing mammals, was not affected by elevated CO_2. The elevated CO_2 treatment caused a reduction in leaf percent N. However, there was a significant interaction between the CO_2 and urea treatments, resulting in a larger difference in leaf percent N between urea-treated and control plants under elevated than under ambient CO_2. Hence, elevations in atmospheric CO_2 may cause an increase in the amount of urine-hit-induced spatial variability in temperate grasslands. Since food quantity remained largely unchanged in response to elevated CO_2, and forage N content went down, grazing mammals may be negatively affected by increases in atmospheric CO_2.

Key words CO_2 enrichment · Grazing · Herbivory · Global change · Grasslands

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Introduction

Atmospheric CO_2 levels are increasing globally and are expected to rise to as high as 700 ppm, approximately double current levels, by the mid- to late 21st century (Conway et al. 1988; Houghton et al. 1990; Wigley and Raper 1992). Elevated CO_2 is expected to cause increases in primary productivity, decreases in litter decomposition, and changes in plant species composition in many temperate and tropical ecosystems (reviewed in Bazzaz 1990; Mooney et al. 1991). However, these responses are expected to vary considerably among plant species and among ecosystems (Bazzaz 1990; Mooney et al. 1991; Poorter 1993; Wilsey 1996).

Most research on plant responses to elevated CO_2 has centered on plant processes in isolation from effects of higher trophic levels. Research centered on how herbivores will be affected by increasing levels of atmospheric CO_2, and how they will affect plant responses to elevated CO_2, remains important for understanding how ecosystems will respond to global change. Insects feeding on plant tissue grown under elevated CO_2 have slower growth rates and increased consumption rates (Lincoln et al. 1986, 1993; Fajer et al. 1989), primarily because of CO_2-induced reductions in tissue N concentration (Ayres 1993; Lincoln et al. 1993).

In grasslands, which covered approximately 25% of the world land surface in precolonial times (Shantz 1954), the principal herbivore species are usually large mammals. Little is known about how grazing by mammals will affect plant responses to elevated CO_2 and how plant responses to elevated CO_2 will affect grazing mammals. Simulated insect defoliation did not affect the response of *Plantago lanceolata* to elevated CO_2 (Fajer et al. 1991). Wilsey et al. (1994) found that simulated mammal defoliation had no effect on how a C_4 grass from Serengeti National Park (Tanzania) responded to elevated CO_2, and there was no effect of elevated CO_2 on forage quality. They concluded that plant-grazer interactions in this ecosystem are not likely to be affected by elevated CO_2. However, since C_3 plants usually

show a larger growth response than C_4 plants to elevated CO_2 (Wong 1979; Curtis et al. 1989a; but see Owensby et al. 1993), other grasses, especially temperate zone C_3 species, may show a different response to elevated CO_2.

In grazing ecosystems, nutrients cycle through the grazing rather than through the detrital food web (McNaughton 1985). Thus, nutrients enter the soil organic matter pool through urine and feces, which are in readily degradable forms, rather than through litter. Grass on urine patches has higher rates of productivity and leaf percent N (McNaughton et al. 1988; Day and Detling 1990; Jaramillo and Detling 1992a). These urine patches make up a small percentage of the overall area but a larger proportion of the productivity (Day and Detling 1990) and, therefore, grasslands often show much spatial variability. Since numerous studies have found that the plant response to elevated CO_2 varies with N availability, with fertilized plants showing larger increases in response to elevated CO_2 than unfertilized plants (reviewed in Bazzaz 1990), grasses in urea patches may show a larger response than adjacent vegetation to elevated CO_2. Thus, increases in atmospheric CO_2 may lead to enhanced spatial variability.

The objectives of this study were threefold. First, I wanted to determine if a common C_3 grass, *Stipa occidentalis*, from an important grazing ecosystem would show, under elevated CO_2, predicted increases in growth and decreases in forage quality (indexed with leaf percent N). Second, I wanted to assess how plant responses to elevated CO_2 were affected by simulated grazing (clipping), and third, I wanted to determine if responses would be affected by urine hits, which represent large pulses of N, and are common on grazing lands.

Materials and methods

The plant used in this study, *S. occidentalis*, was collected in October 1993 from Hayden Valley in Yellowstone National Park, Wyoming, USA. Hayden Valley is used as summer range by elk (*Cervus elaphus*) and has a large population of resident bison (*Bison bison*). Plants were put through a dormancy treatment that simulated the daylengths and temperatures of Yellowstone National Park in late fall (down to 5°C), and were then stored in a cold room. After 1 month, the plants were placed back in growth chambers, and daylengths and temperatures were increased to bring them out of dormancy. From one genotype of *S. occidentalis*, 35 clones were propagated for the experiment ($n = 4$ for each CO_2, defoliation, and urea treatment, except $n = 3$ for the urea-clipped-ambient CO_2 treatment because 1 plant died of transplant stress) in the growth chamber with temperatures simulating a summer day in Yellowstone: 23°C during the day and 11°C during the night. This was also the temperature regime used in the experiment. Plants appeared to be morphologically similar to field plants.

Plants were potted in tall (25 cm high) cylindrical pots (10 cm diameter) using rinsed sand as the substrate. Tall pots were used to simulate the rooting depth available to plants in the field; most (82–84%) roots are in the top 20 cm of the soil in Yellowstone National Park (Frank et al. 1994). White collars were used to simulate canopy shading as described by McNaughton (1992). Sand was used in order to be able to control fully nutrient levels in the pots. All pots received 100 ml of water every 3 days throughout the experiment.

Elevated CO_2, 700 ppm, was applied to two separate chambers on day 0; defoliation and urea treatments were begun after an 11-day acclimation period. Ambient CO_2 chambers ($n = 2$) were kept at 370 ppm. CO_2 concentrations inside chambers (Sherer-Gillet Model CEL 37-14) were monitered every 3 min with an automatic CO_2 control system (computer-assisted IRGA), which was calibrated with reference CO_2 every day. CO_2 concentrations were double verified with a second IRGA twice during the experiment. Temperatures were similar in all four chambers; thus, only the direct effects of elevated CO_2 were studied in this experiment. Light levels in growth chambers averaged 615 μE at canopy level (range 603–621). This level was only one-third of full sunlight, but was high in comparison with many growth chamber experiments. Light was provided from a combination of fluorescent and incandescent lamps. Since there were few plants in each chamber ($n = 8$), I could place them away from the middle (relatively well lit) and corners (relatively less lit) of the chambers. Thus, all plants received comparable light levels inside the chambers. Vapour pressure deficit was not controlled inside the chambers. The experiment ran approximately 3 months (86 days) to simulate a growing season in the field.

Within each chamber, defoliation and urea treatments were applied in a 2 × 2 factorial treatment arrangement. Control pots received Hoagland's solution at a rate (0.82 g/m^2 per week N) that furnished plants with N levels comparable to June mineralization levels in Hayden Valley (at the same site from which the plants were collected; Tracy, unpublished data). Urea pots received control levels plus liquid urea at a rate of 40 g/m^2 on day 11. Control plants received an equivalent amount of water on day 11. Urea was added to plants instead of simulated bovine urine (Stillwell 1983; Day and Detling 1990), which contains many other compounds in addition to urea, and this resulted in a loss of realism. However, I used urea rather than simulated urine to prevent the confounding effects of N and other compounds. A few days after the urea treatment, concentrations of NO_3 and NH_4 in soil cores from urea-treated pots were much higher than in control pots, i.e., the urea had broken down into inorganic forms of N (KCl extractions were run on a Latchet autoanalyzer). Plants were clipped to a height of 5 cm on days 11, 36, and 57 to approximate defoliation rates on the summer range of Yellowstone National Park (corresponding to a defoliation rate of 30.2–32.9%) Hence, plants had 27 days to recover from the final defoliation event (Oesterheld and McNaughton 1988).

On days 21, 42, 63, and 86, tillers were counted on each plant. On days 25, 43, 64, and 87, two or three of the first fully expanded leaves were collected and mid-day water potential was measured with a pressure bomb (on day 3 of the watering cycle). Leaves were then cut finely with scissors and leaf percent N was measured with a Carlo Erba (N1500). Leaf collections for N analysis were made on days 26, 64, and 87.

Leaf percent N was used as an index of forage quality because it usually covaries with other nutrients, such as P, Mg, Ca, Cu, Na, and Zn (McNaughton 1990; Ayres 1993), and is usually positively correlated with digestibility (Mattson 1980, and references therein). Hence, if all of these variables covary, then measurement of one (N) gives an indication of how the other variables important to nutrition are being influenced. I also used N as an index of forage quality because of its direct importance to herbivore nutrition (Mattson 1980; Robbins 1983; McNaughton 1990).

On day 87 (harvest), plants were sorted into crowns, leaf blades and other aboveground biomass, roots, and litter. All plant parts were dried and weighed.

Biomass data were analyzed with an ANOVA as a split-plot design, with CO_2 treatment applied to the main plot (chambers), and defoliation and urea treatments applied to the subplot. Thus, the replicate chamber (CO_2) term was used as the error term for the CO_2 main effect and the residual error term was used for defoliation and urea effects. Tiller number and mid-day water potential data were analyzed with repeated-measures analysis of variance, split in time with univariate F-tests. Variables were either ln-transformed or arcsine-transformed (leaf N) before analysis; data were back-transformed for presentation in tables and figures.

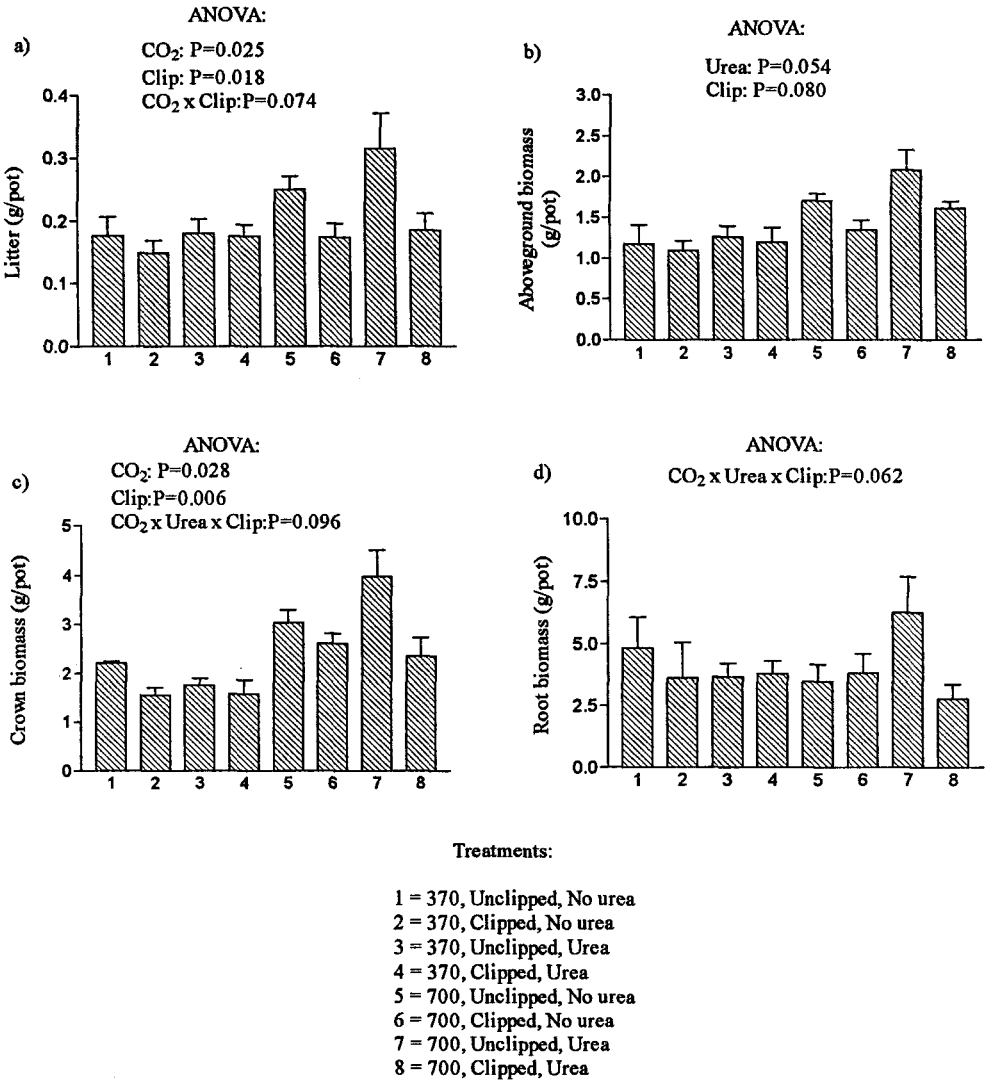

Fig. 1 Mean litter (**a**), aboveground (**b**), crown (**c**), and root (**d**) biomass response to elevated CO_2, clipping, and urea additions (to simulate the N in a urine hit by a large mammal). Data are nontransformed means and *SE*s, and ANOVA effects are presented if *P* values were <0.1

Results

Biomass response

Elevated CO_2 treatments caused significant increases in crown biomass and litter (CO_2 main effect, 1,2 *df*: crown, $P = 0.028$; litter, $P = 0.025$; Fig. 1), but increases in other biomass components were only significant if plants were not clipped and received urea. Aboveground biomass and productivity (biomass + clippings), i.e., the part of the plant consumed by grazing mammals, was not affected by elevated CO_2 (CO_2 effect and interactions, $Ps > 0.155$). Therefore, the quantity of food available to grazing mammals did not change significantly.

Clipping caused a decrease in crown biomass (clipping effect, 1,21 *df*, $P = 0.006$) and litter (clipping main effect, $P = 0.018$; CO_2 × clipping, $P = 0.074$; Fig. 1), a marginally significant decrease in aboveground ($P = 0.080$) and total biomass ($P = 0.064$) (Fig. 1), and an increase in aboveground productivity (aboveground biomass + clippings, $P = 0.008$; Fig. 2). There was no significant effect of clipping on root biomass or total productivity (aboveground + crown + root biomass + clippings) (main effect and CO_2 × clipping interaction, $Ps > 0.136$, Fig. 2).

In general, plants showed little or no biomass response to urea additions. There was no significant difference in crowns, roots, and litter (urea main effect, 1,21 *df*, $Ps > 0.268$; interactions, $Ps > 0.370$; Fig. 1). There were small, only marginally significant, increases in aboveground biomass (14%, $P = 0.054$, Fig. 1) and aboveground productivity (13%, $P = 0.071$, Fig. 2). Total biomass and total productivity were not affected by urea additions ($Ps > 0.534$).

Root, total biomass, and total productivity (total biomass + clippings) responses to elevated CO_2 depended on whether plants received urea hits and whether they were clipped (Fig. 1, 2; CO_2 × urea × clip interaction, 1,21 *df*; (a) *ln*-transformed data: root, $P = 0.062$, total biomass, $P = 0.073$; total productivity, $P = 0.075$; crown, $P = 0.096$; (b) untransformed data: root, $P = 0.055$; total biomass, $P = 0.041$; total productivity, $P = 0.042$; crown, $P = 0.078$; other variables, $Ps > 0.423$). The largest response to CO_2 enrichment was found if the plants had re-

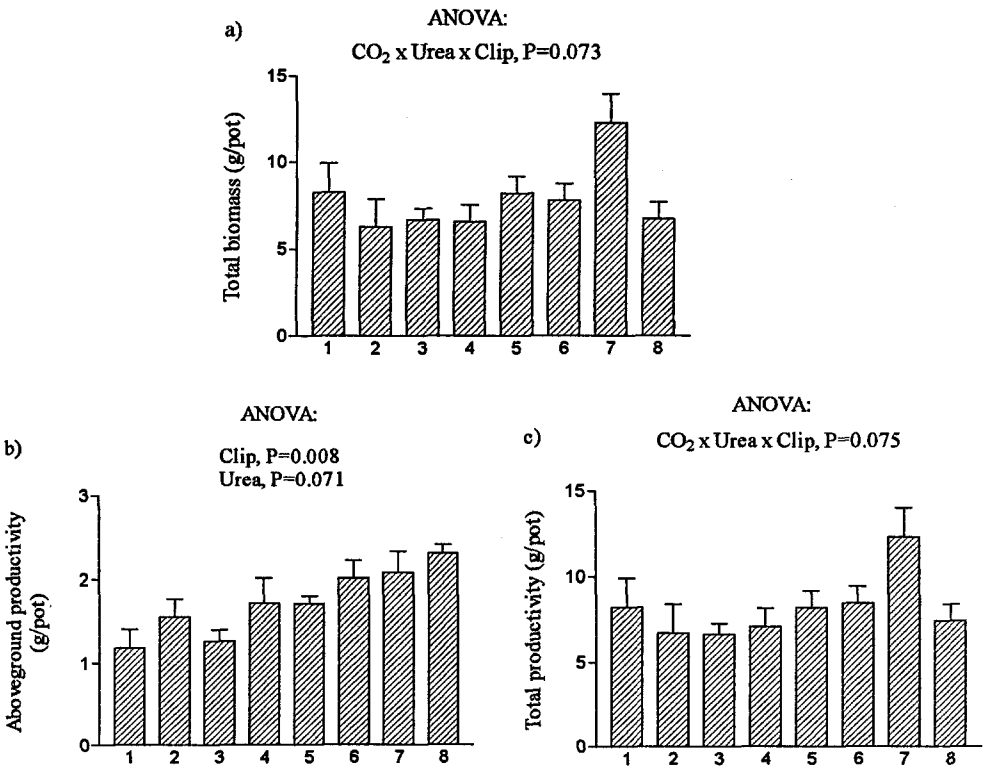

Fig. 2 Responses in mean total biomass (aboveground + crown + root, **a**), aboveground productivity (aboveground biomass + clippings, **b**), and total productivity (total biomass + clippings, **c**) to elevated CO_2, clipping, and urea additions (to simulate the N in a urine hit by a large mammal). Data are non-transformed means and *SE*s, and ANOVA effects are presented if *P* values were <0.1

ceived urea and were not clipped. Plants showed a smaller response to elevated CO_2 if they were clipped or if they did not receive urea. Plants that were clipped and received urea hits had total biomass levels similar to controls. Thus, the plant response to elevated CO_2 appeared to be dampened by simulated mammal-grazing effects.

Leaf water potential and tillering rates

Mid-day leaf water potential was consistently less negative in the elevated CO_2 treatment (CO_2 effect, 1,2 *df*, $P = 0.014$; all interactions with CO_2, $P > 0.115$, Table 1), and thus plants growing under elevated CO_2 were less water-stressed than control plants. Plants in the urea treatments had less negative water potentials early in the experiment and more negative water potentials later in the experiment than control plants (time × urea, 3,63 *df*, $P = 0.056$; other interactions with urea, $P > 0.104$). Leaf water potentials were not significantly different between clipped and unclipped plants (clip, 1,21 *df*, $P = 0.209$; time × clip, 3,63 *df*, $P = 0.084$).

Tillering rates were not affected by the CO_2 treatment and, thus, increases in biomass due to CO_2 were from increases in expansion of existing shoots (mostly in crowns) rather than in production of new ones (CO_2 main effect and interactions, $P > 0.121$, Table 1). Under low N conditions (controls), clipped plants had consistently more tillers than unclipped plants; under high N (urea plants), clipped plants had fewer tillers early in the experiment and more tillers later in the experiment than unclipped plants (time × urea × clip, 3,63 *df*, $P = 0.008$).

Forage N content

Plants from the elevated CO_2 treatment had lower leaf percent nitrogen than those from the ambient CO_2 treatment (CO_2 main effect, 1,2 *df*, $P = 0.001$; Table 1, Fig. 3). This difference between treatments increased as the experiment progressed, with a 23.3% difference between CO_2 treatments by the end of the experiment (time × CO_2, 2,42 *df*, $P = 0.001$). Leaf percent N decreased significantly during the experiment for both treatments, but the rate of decrease was much higher for plants in the elevated CO_2 treatment (Fig. 3). The CO_2 response also depended on whether or not plants received urea: later in the experiment, plants that had received urea showed a smaller decrease in leaf percent N under elevated CO_2 treatments than did control plants (CO_2 × urea, 1,21 *df*, $P = 0.058$; time × CO_2 × urea, 2,42 *df*, $P = 0.031$).

In contrast to the biomass response, which differed little between plants that had received urea hits and controls, leaf percent N was 27% higher in urea treatments (Fig. 3); the difference was highest early in the experiment, but a significant difference persisted through the end of the experiment. There was no significant difference between clipped and non clipped plants in leaf percent N (clip effect, $P = 0.189$; all interactions, $P > 0.106$).

The combined response of leaf percent N to urea and CO_2 treatments led to a larger difference between urea and control plants in elevated than in ambient CO_2 plots (Fig. 3). For example, by the end of the experiment, there was a 33% difference between urea and control plants in the elevated CO_2 treatment and only a 17% dif-

Table 1 Number of tillers, leaf water potential, and leaf percent N in plants grown under ambient (370 ppm) and elevated (700 ppm) CO_2, with and without urea additions, and under clipped and non-clipped conditions (mean, *SE* in parentheses)

	Tiller number	Leaf water potential	Leaf percent N
Day 21			
370-NC-NUR	18.3 (2.2)	−3.1 (0.3)	3.31 (0.26)
370-CL-NUR	21.3 (2.2)	−3.2 (0.3)	3.65 (0.26)
370-NC-UR	23.3 (2.2)	−3.5 (0.3)	5.05 (0.26)
370-CL-UR	22.5 (2.6)	−3.0 (0.3)	4.82 (0.30)
700-NC-NUR	18.5 (2.2)	−2.3 (0.3)	3.18 (0.26)
700-CL-NUR	18.3 (2.2)	−2.5 (0.3)	3.55 (0.26)
700-NC-UR	27.0 (2.2)	−2.3 (0.3)	4.62 (0.26)
700-CL-UR	22.3 (2.2)	−2.0 (0.3)	4.89 (0.26)
Day 42			
370-NC-NUR	27.5 (3.5)	−3.4 (0.2)	
370-CL-NUR	31.0 (3.5)	−3.5 (0.2)	
370-NC-UR	29.8 (3.5)	−3.5 (0.2)	
370-CL-UR	28.0 (4.1)	−3.1 (0.2)	
700-NC-NUR	29.8 (3.5)	−2.8 (0.2)	
700-CL-NUR	36.3 (3.5)	−2.5 (0.2)	
700-NC-UR	28.3 (3.5)	−2.6 (0.2)	
700-CL-UR	28.3(3.5)	−2.2(0.2)	
Day 63			
370-NC-NUR	35.5 (3.5)	−3.4 (0.2)	3.42 (0.17)
370-CL-NUR	43.3 (3.5)	−3.6 (0.2)	3.15 (0.17)
370-NC-UR	35.8 (3.5)	−3.4 (0.2)	3.95 (0.17)
370-CL-UR	34.7 (4.1)	−3.9 (0.3)	3.67 (0.19)
700-NC-NUR	38.8 (3.5)	−2.2 (0.2)	2.15 (0.17)
700-CL-NUR	45.8 (3.5)	−2.5 (0.2)	2.45 (0.17)
700-NC-UR	45.0 (3.5)	−2.3 (0.2)	3.49 (0.17)
700-CL-UR	42.0 (3.5)	−2.4 (0.2)	3.81 (0.17)
Day 87			
370-NC-NUR	47.0 (3.7)	−2.9 (0.1)	2.47 (0.20)
370-CL-NUR	55.3 (3.9)	−2.8 (0.1)	2.89 (0.20)
370-NC-UR	54.3 (6.0)	−3.6 (0.2)	3.24 (0.20)
370-CL-UR	57.3 (4.8)	−3.5 (0.6)	3.22 (0.23)
700-NC-NUR	51.0 (4.1)	−2.4 (0.1)	1.52 (0.20)
700–CL-NUR	55.5 (3.6)	−2.4 (0.2)	2.11 (0.20)
700–NC-UR	51.5 (1.7)	−2.8 (0.1)	2.82 (0.20)
700–CL-UR	74.8 (9.2)	−2.3 (0.2)	2.63 (0.20)

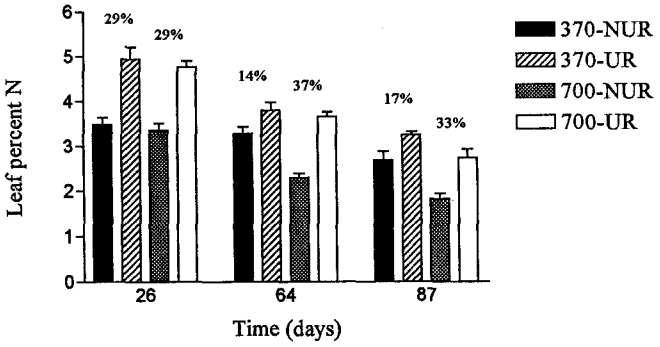

Fig. 3 Mean leaf percent N, averaged across clipping treatments, in plants grown under elevated (700 ppm) and ambient CO_2 (370 ppm) with and without urea additions (to simulate the N in a urine hit by a large mammal). Percentages denote differences between urea treatments

ference in the ambient CO_2 treatment. This indicates that under elevated CO_2, there would be greater spatial variability in the field.

Discussion

Overall, the total biomass response of *S. occidentalis* to elevated CO_2 was similar (a mean 18% increase in biomass) to the response found for other grassland species (Poorter 1993; Wilsey 1996). However, the increase in total biomass in response to elevated CO_2 was dependent on plants not being clipped and receiving urea treatments (i.e., having high N conditions). Many other studies have shown that plants show a larger response to elevated CO_2 when they are well-fertilized (Wong 1979; Patterson and Flint 1982; Zangerl and Bazzaz 1984; Brown and Higgenbotham 1986; Larigauderie et al. 1988). Most growth chamber studies have been conducted under high nutrient conditions and without clipping treatments and, thus, have somewhat overestimated plant response to elevated CO_2 compared to natural environments, where nutrients are commonly limiting to growth and yield. However, the plant response to elevated CO_2 reported here was still greater than the response found in tropical C_4 grasses (Wilsey et al. 1994; Wilsey 1995).

Increases in growth in response to elevated CO_2 occurred primarily in crowns, which can serve a storage function in grasses. For example, Danckwerts et al. (1991) found that ^{14}C was translocated from crowns to regrowing leaves in *Themeda triandra*, the most common grass in Africa. Thus, under elevated CO_2, plants appeared to store excess carbon instead of producing new leaf tissue (Loehle 1995). Had the experiment been continued into the next growing season, it might have been shown that these storage reserves enabled plants to show a stronger flush of growth during the following spring.

Increases in plant biomass in response to urea treatments were smaller than those observed in plants from other grasslands (Ruess and McNaughton 1988; Day and Detling 1990; Jaramillo and Detling 1992a). In these other ecosystems, which like most grasslands contain grasses that have evolved in the presence of large grazing mammals, plants are able to show a large flush of growth in response to a urine hit. Plants in Yellowstone also evolved in the presence of grazing mammals, but do not exhibit a plastic response to urea treatments. *S. occidentalis*, which was collected from a high-elevation grassland within Yellowstone, could be constrained by the evolution of a slow growth rate (Chapin 1980) and, thus, lack the response to urea. Plants did show a large increase in leaf percent nitrogen in response to urea additions, or "luxury consumption" (Chapin 1980). Further work should be done to determine if plant growth responds to urea additions, and how grazing mammals respond to urine hits (e.g. Jaramillo and Detling 1992b), in the field.

Clipping resulted in increases in aboveground productivity. This observation is consistent with Yellowstone

field studies by Frank and McNaughton (1993): grasses outside exclosures had higher rates of aboveground productivity than grasses protected from grazing by fences. Clipping also caused a decrease in crown biomass, a variable not measured in the field studies of Frank and McNaughton (1993). On the basis of these results, I hypothesize that plants were able to overcompensate aboveground by either breaking down crowns or shifting allocation of resources away from crowns to the aboveground component after being clipped. In a defoliation experiment with two other Yellowstone species, I found that clipped grasses had less crown and root biomass than non clipped grasses (Wilsey 1995).

Since there were no large increases in aboveground biomass in response to elevated CO_2, and this is the portion of the plant consumed by grazing mammals, the quantity of food available to them would be largely unaffected by elevated CO_2. However, plant quality, indexed by leaf percent N, decreased substantially in response to elevated CO_2. Reductions in leaf percent N are often found in temperate grasses (Curtis et al. 1989b; Owensby et al. 1993) but not in tropical grasses (Wilsey et al. 1994; Wilsey 1995). Thus, in temperate grasslands under elevated CO_2, grazing mammals will have the same amount of food available to them, but it will be of lower quality.

Insects feeding on foliage grown under elevated CO_2, and feeding on low-quality foliage in general (Evans 1938; Slansky and Feeny 1977) usually increase their feeding, and may be able to compensate for reduced forage quality by prolonging the time spent feeding (Lincoln et al. 1993). However, grazing mammals spend up to 84% of their day in feeding activity (feeding and ruminating) (Van Soest 1982: 336), and may not be able to prolong feeding activity under elevated CO_2 to gain the required protein. If animals extend the amount of time spent feeding and ruminating, it may be at the expense of resting, reproductive, and predator avoidance activities. Hence, if food quantity remains unchanged by increases in elevated CO_2, and food quality declines, than grazing mammals may be negatively affected.

Previous studies on the effects of urine hits on grasslands found that urine patches have large effects on aboveground productivity and forage quality (Day and Detling 1990; Jaramillo and Detling 1992), and species composition (Steinauer and Collins 1995). Since urea is not evenly distributed around grasslands, grazing mammals usually generate a large increase in spatial heterogeneity. Since differences in leaf percent N between urea-treated plants and controls were higher under elevated CO_2 than under ambient CO_2, these data suggest that grazing-mammal-induced spatial variability in forage quality might be enhanced with increases in atmospheric CO_2 concentrations.

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