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Brian J. Wilsey · Samuel J. McNaughton
James S. Coleman

Will increases in atmospheric CO₂ affect regrowth following grazing in C₄ grasses from tropical grasslands? A test with *Sporobolus kentrophyllus*

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Abstract We grew a C₄ grass from the Serengeti ecosystem under ambient (370 ppm) and elevated (700 ppm) CO₂, and under clipped and unclipped conditions to test whether regrowth following grazing would be affected by elevated CO₂. Above-ground productivity was slightly decreased under elevated CO₂, and was similar between clipped and unclipped plants. Regrowth (clipping off-take) following clipping was similar in the two CO₂ treatments, and there was no CO₂ by clipping interaction on biomass, productivity, or leaf nutrient concentrations. Based on this evidence, we suggest that C₄ grasses from the Serengeti will show little direct response to future increases in atmospheric CO₂.

Key words Africa · Grazing · Global change
Grasslands · Herbivory

Introduction

Concentrations of CO₂ in the atmosphere, which have been steadily increasing since the beginning of the Industrial Age, are expected to reach levels as high as 700 ppm during the next century (Conway et al. 1988; Wigley and Raper 1992). Although numerous studies have been conducted on the response of plants to elevated CO₂, relatively few studies have assessed the role that elevated CO₂ will have on plant-animal interactions. The role of elevated CO₂ on the ability of plants to regrow following grazing by large mammals has yet to be addressed.

The objective of this study was to determine whether plant regrowth following grazing (simulated by clipping) of C₄ grasses from the Serengeti will be affected by increases in atmospheric CO₂. The effects of elevated CO₂ on plant allocation patterns and nutrient concentrations

were also measured. A plant from the Serengeti National Park was used because the park contains one of the few remaining large concentrations of wild grazing mammals in the world.

Materials and methods

Sporobolus kentrophyllus (a C₄ stoloniferous perennial) was grown in chambers at Syracuse University under ambient (370 ppm in Syracuse) and elevated (700 ppm) atmospheric CO₂. All plants were propagated vegetatively from a clone that had been under cultivation in the Syracuse University greenhouse. Plants were arranged in a randomized block, split-plot design, with block (blocking on trial – see below) and CO₂ main effect terms in the main plot (with block×CO₂ as the error term), and clipping, harvest date (day 14, 28, 42) and interaction terms in the sub-plot (with three replicates in each treatment). Initial biomass ($n = 3$) was not significantly different between CO₂ treatments ($P > 0.46$). Plants in the clipped treatments were clipped to 5 cm once per week (beginning on day 7) throughout the experiment. White canopy “collars”, which were placed at the top of the canopy in clipped and unclipped plants, were utilized to simulate canopy shading as described by McNaughton (1992).

After the plants were harvested on day 42, the CO₂ treatments were switched between the two chambers and the entire experiment was repeated with a new group of plants. Thus, two trials were conducted (to account for the chamber effect), and these trials were used as the block term in the randomized block design. Hence, not counting the plants harvested on day 0, a total of 72 plants were used in the experiment (2 trials×2 CO₂ treatments×2 clipping treatments×3 harvest dates×3 replicates).

Plants were grown in calcined clay in tall, column-shaped pots (53.3 cm tall and 10 cm in diameter). Each pot received 100 ml of water each afternoon during the acclimation period and through to day 10 (to insure that they survived the transfer into calcined clay), and 60 ml thereafter. Plants received 890 μ E of light at the top of the canopy during the first trial and 725 μ E during the second trial. All plants received 75 ml of whole strength Hoaglands solution (2 g/m² N) weekly and on the same day that plants were clipped. Plants were accidentally fertilized with 75 ml of double strength Hoaglands on day 0, 7 and 21 during the first trial. However, there was no significant interaction between block and CO₂ for any biomass variable ($P > 0.05$).

On each harvest date, above- (leaf blades, and culms and leaf sheaths) and below-ground biomass, and plant macro- (ERBA C:N analyzer) and micro-nutrient concentrations (inductively coupled argon plasma mass spectrometer, McNaughton 1988) were measured. Plant leaf tissue was ground through a Wiley mill prior to

B.J. Wilsey (✉) · S.J. McNaughton · J.S. Coleman
Department of Biology, Syracuse University,
Biological Research Laboratories, 110 College Place,
Syracuse, NY 13244, USA

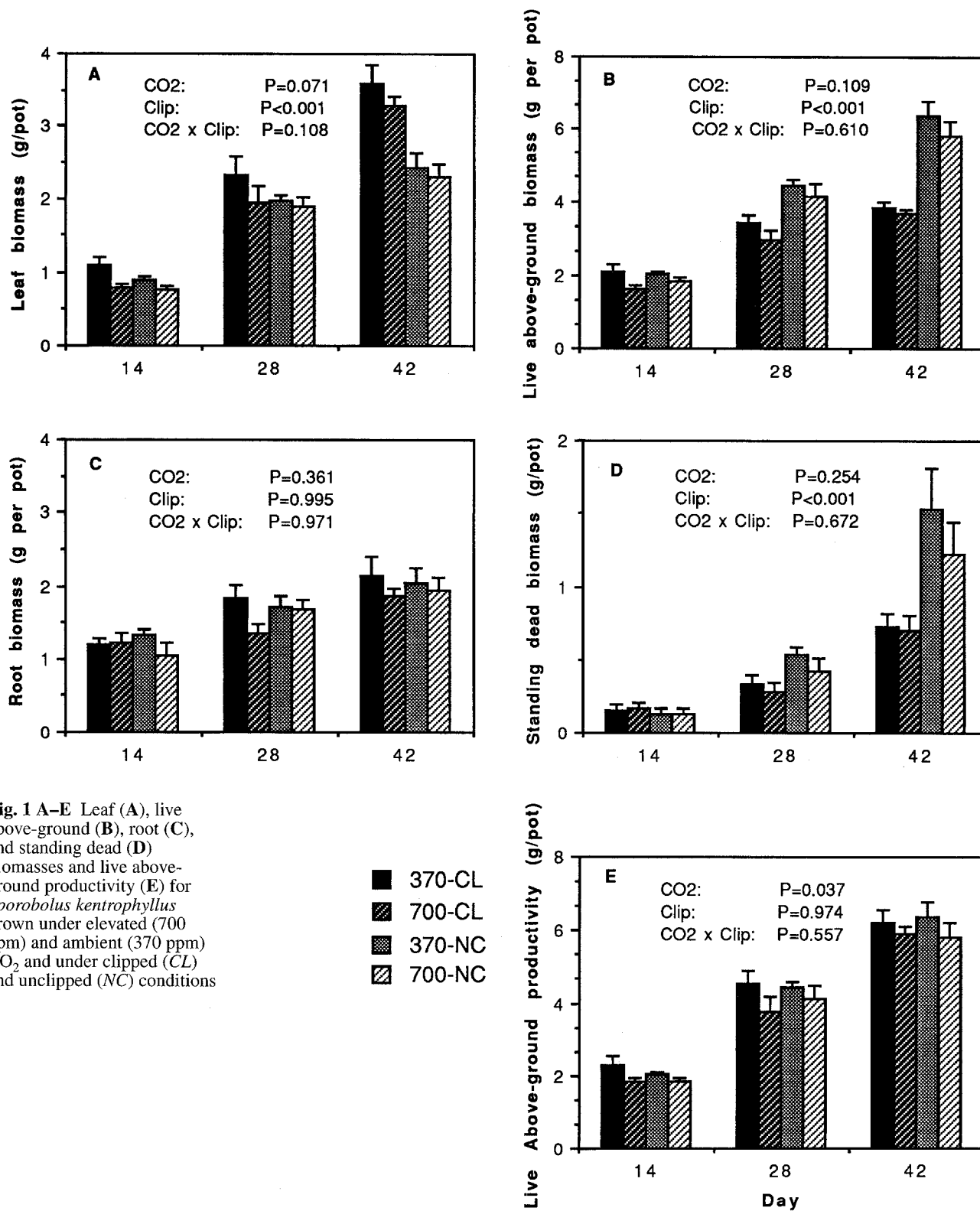


Fig. 1 A-E Leaf (A), live above-ground (B), root (C), and standing dead (D) biomasses and live above-ground productivity (E) for *Sporobolus kentrophyllus* grown under elevated (700 ppm) and ambient (370 ppm) CO₂ and under clipped (CL) and unclipped (NC) conditions

■ 370-CL
▨ 700-CL
▤ 370-NC
▧ 700-NC

nutrient analyses. All variables were natural-log transformed before statistical analysis.

Plant allocation patterns were tested with allometric regression techniques (Shipley and Peters 1990). Clipped material was added to unclipped material before allocation was calculated.

Results and discussion

Plants under elevated CO_2 tended to have less above-ground biomass and had slightly lower levels of above-ground productivity than did plants growing under ambient conditions (Fig. 1). Root and standing dead biomass were similar between the two CO_2 treatments. Yield to grazers (amount of tissue clipped weekly) also did not differ between CO_2 treatments ($P = 0.86$, data not shown).

Since tropical grasses have the C_4 photosynthetic pathway, in which CO_2 is concentrated within the bundle sheath cells before being fixed, they often respond less to elevated CO_2 than do C_3 plants (see review by Bazzaz 1990, Poorter 1993). However, large responses to elevated CO_2 have been found in a Great Basin C_4 grass and in several C_4 old field herbs (reviewed by Poorter 1993). The growth responses in our study fall within the lower part of the range for C_4 plants found by Poorter (1993). The lower productivity values for plants under elevated CO_2 were evident by day 14, and the difference in plants between CO_2 treatments did not increase during the rest of the experiment (all $\text{CO}_2 \times$ harvest date interactions $P > 0.10$). Although the mechanism for this response is not known, we hypothesize that this difference was an acclimation effect, and that after the plants acclimated to the elevated CO_2 , growth was unaffected.

Although live above-ground biomass was consistently higher in the unclipped treatments, total above-ground productivity (biomass+clippings) was similar among clipped and unclipped plants (Fig. 1). Furthermore, much of the above-ground biomass was standing dead in the unclipped treatments, whereas the clipped plants had less standing dead biomass. There was no significant difference in root biomass between clipped and unclipped plants. The high rate of clipping (64% of the above-ground production was removed by clipping), and short recovery time (7 days; see Oosterheld and McNaughton 1991) that we applied was designed to simulate the high rates of grazing on the short grass plains (McNaughton 1985). However, it is important to note that grazing mammals have effects (trampling, organic depositions, etc.) on vegetation that we did not simulate with clipping.

Elevated CO_2 had little effect on plant allocation patterns. There was no difference in allocation to leaves or roots in response to elevated CO_2 (Fig. 2), and no significant shifts in allocation to (or from) roots in response to clipping. Clipped plants allocated more biomass to leaves than did unclipped plants (Fig. 2), and this effect was especially evident with larger plant sizes. Since leaves have higher nutrient concentrations and photosynthetic rates than does non-leaf tissue (Reekie and Bazzaz 1987; Ruess 1988), a large increase in nutrient availability (to grazers) and whole-plant photosynthesis would result from this shift in allocation to leaves, regardless of levels per unit leaf area. Thus, this shift is one important mechanism in which grasses compensate for the heavy

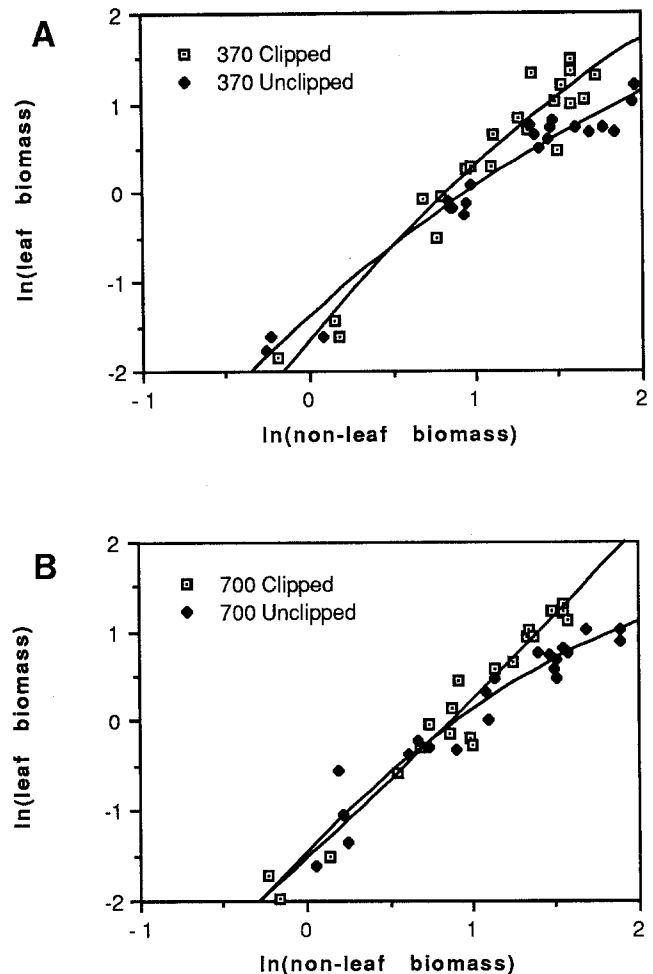


Fig. 2 A, B Allometric plots of leaf tissue versus non-leaf tissue for plants grown under 370 (A) and 700 (B) ppm CO_2 and under weekly clipping or non-clipped conditions. Significant shifts in leaf allocation occurred in response to clipping ($F = 125.89$, $P < 0.01$), whereas there was no response to the CO_2 treatment ($F = 0.04$, not significant).

grazing pressure on the short-grass plains (Oosterheld and McNaughton 1988).

Leaf nutrient concentrations, which generally declined as the experiment progressed (Fe, Mg, Mn, P, Ca, K, and Zn; significant at $P < 0.05$; N, B, Co, Cu, Mo, V, and Na; not significant), were similar between plants under ambient and elevated CO_2 concentrations (all P values > 0.05 , Table 1), and were generally higher in clipped plants than in unclipped plants (Table 1). No interaction was found between CO_2 and clipping for any nutrient.

Our rates of N supply were probably higher than mineralization rates in the field, since percent N was higher (Table 1) in our plants compared to plants from the field (rainy season mean = 2.8, range = 0.9–4.9; McNaughton unpublished data). This should have increased the likelihood of observing an increase in biomass in response to elevated CO_2 (Bazzaz 1990), but decreased the likelihood of observing a N-limited decrease in regrowth following clipping (McNaughton et al. 1983).

Table 1 Leaf nutrient concentrations [mean in mg/kg (SE), harvest dates combined] for plants grown under ambient (370 ppm) and elevated (700 ppm) CO₂ concentrations and under clipped and unclipped conditions. Different super-script letters within an element denote significant differences among treatments

Nutrient	370 ppm CO ₂		700 ppm CO ₂	
	Clipped	Unclipped	Clipped	Unclipped
N	36461(1248) ^a	36317(1645) ^a	34389(776) ^a	36339(544) ^a
K	21512(749) ^a	23482(1176) ^b	21287(557) ^a	24332(1221) ^b
Na	5423(227) ^a	5980(255) ^a	5830(266) ^a	5951(243) ^a
P	3411(112) ^a	3446(135) ^a	3416(127) ^a	3501(168) ^a
Mg	2387(106) ^a	2129(60) ^a	2317(99) ^a	2059(66) ^a
Ca	1940(85) ^a	1810(67) ^a	1884(92) ^a	1798(52) ^a
Fe	582(55) ^a	411(50) ^b	691(86) ^a	472(74) ^b
Mn	57(6) ^a	47(4) ^b	51(4) ^a	45(4) ^b
Zn	16(1) ^a	15(1) ^a	16(1) ^a	15(1) ^a
B	6.0(0.4) ^a	6.8(0.5) ^a	5.7(0.4) ^a	5.9(0.4) ^a
Cu	4.6(0.5) ^a	4.4(0.4) ^a	4.9(0.4) ^a	3.8(0.2) ^a
Co	5.8(3.2) ^a	1.7(0.4) ^a	2.5(0.6) ^a	1.9(0.4) ^a
Mo	0.5(0.1) ^a	0.5(0.1) ^a	0.5(0.1) ^a	0.5(0.1) ^a

In conclusion, regrowth following simulated grazing and plant nutrient concentrations were not affected by elevated CO₂. Thus, we suggest that C₄ grasses from the Serengeti, and perhaps other C₄ grasses from tropical grazing ecosystems, will be largely unaffected by the predicted increases in atmospheric CO₂. Longer-term experiments with a variety of plant species, including both C₃ and C₄ species, should be conducted to test this hypothesis further.

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