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Robert R. Blank

Tye Morgan

Lewis H. Ziska

Robert H. White

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Effect of Atmospheric CO_2 Levels on Nutrients in Cheatgrass Tissue

Robert R. Blank[1], Tye Morgan[1], Lewis H. Ziska[2], and Robert H. White[3]

ABSTRACT

*Rising atmospheric CO_2 has resulted in declining tissue nutrient concentrations and leaf biochemicals, which has potential ramifications for animal nutrition, herbivory and litter decomposition rates. We investigated the interacting effects of atmospheric CO_2 concentrations (270, 320, 370, and 420 ppmv), plant age (42, 57, 75, and 87 days), and elevation ecotype (salt desert, sagebrush steppe, and mountain brush) on aboveground tissue nutrient levels and biochemistry of cheatgrass (*Bromus tectorum*), an important range grass in the Great Basin. Most nutrients were affected by significant (*$P < 0.05$*) interactions between CO_2 level and plant age, and plant ecotype and plant age. At 87 days growth, tissue C:N ratios increased significantly and concentrations of P, K, and Mg declined, with rising CO_2 levels suggesting declining forage nutrition. Tissue concentrations of Mn, K, Mg, and Ca increased with plant age and, in general, the low elevation ecotype had greater tissue nutrient concentrations than the high elevation ecotype. Hemicellulose concentration was influenced by a significant CO_2 level by ecotype interaction; overall, the high elevation ecotype had greater concentrations of hemicellulose, which increased with increasing CO_2 levels. The high elevation ecotype had significantly less acid detergent fiber than the low or mid elevation ecotypes. These data suggest that increasing atmospheric CO_2 levels may have a profound effect on the nutritional value of cheatgrass forage, and this effect may differ among elevational ecotypes.*

INTRODUCTION

Plant stoichiometry has been altered by rising atmospheric CO_2 and meta-analysis reveals that, for the important crop plants wheat and rice, tissue concentrations of many nutrients have declined (Loladze 2002). Although growth at elevated CO_2 concentration can decrease tissue nutrient concentrations, enhanced plant growth compensates such that nutrient uptake often increases (Overdieck 1993) For the important nutrient N, most research has documented decreased tissue concentrations with increased atmospheric CO_2 levels (Cotrufo and others 1996). Declining tissue concentrations are not limited to N. Indeed, comparison of nutrient concentrations from a wide variety of herbarium specimens collected during the last 250 years, indicate that recent concentrations of Al, Ca, Cu, Sr, Fe, P, Mg, Mn, K, Na, S, and Zn are invariably lower than earlier collections (Penuelas and Matamala 1993). Atmospheric CO_2 mitigated alteration of plant stoichiometry has potential ramifications for human nutrition (Loladze 2002), animal nutrition (Morgan and others 2004), herbivory (Lindroth and Dearing 2005), litter decomposition rates (Cotrufo and others 1994; Lambers 1993) and vegetation combustibility (Blank and others 2006).

In western North America, the exotic annual grass cheatgrass (*Bromus tectorum*) has aggressively invaded semi-arid to arid plant communities. The resulting increase in wildfires and shortened fire return intervals has promulgated near monocultures of cheatgrass (D'Antonio and Vitousek 1992). The large-scale invasion of the intermountain west by cheatgrass has created a sobering reality; it is now an important and seasonally nutritious forage species for native and non-native grazers (DeFlon 1986; Murray and others 1978). Like many weedy species, growth of cheatgrass is greatly stimulated by rising atmospheric CO_2 (Smith and others 1987; Ziska and others 2005). Our purpose was to determine the interacting effect of atmospheric CO_2 concentrations, plant age, and elevation ecotype on aboveground tissue nutrient levels of cheatgrass. Our working null hypotheses are:

1) Tissue nutrient concentrations will not vary with atmospheric CO_2 concentrations;
2) Tissue nutrient concentrations will not vary with plant age;
3) Tissue nutrient concentrations will not vary with elevational ecotype;
4) Nutrient uptake will not vary with atmospheric CO_2 concentrations

MATERIALS AND METHODS

Hypothesis testing began by collecting seeds from three elevation ecotypes of cheatgrass (*Bromus tectorum* L.) from northern Nevada, U.S.A. The low elevation site (low) was at 1,120 m (4,000 feet) at Poker Brown flat just west of Rye Patch Reservoir, NV (40.28° N, 118.19° W). This site receives about 16 cm (6.3 inches) of annual precipitation and is a salt desert community dominated by *Atriplex confertifolia* Torr. and Frém. S. Watson (shadscale). This site is representative of the most recent invasion by cheatgrass, which occurred in the early 1980s. In 1999, a cheatgrass-fueled wildfire consumed this site. Seeds were collected in 2000. The middle elevation site (mid) is at

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[1]Robert R. Blank and Tye Morgan, USDA-ARS, Exotic and Invasive Weed Research Unit, Reno, NV.
[2]Lewis H. Ziska, USDA-ARS, Crop Systems and Global Change Lab, Beltsville, MD.
[3]Robert H. White, USDA-FS, Forest Products Lab, Madison, WI

1,585 m (5,200 feet) near Emigrant Pass, NV (40.38° N, 116.18° W) and receives on average 30 cm (11.8 inches) of yearly precipitation. This site has historically been dominated by *Artemisia tridentata* ssp. *vaseyana* Nutt. (mountain big sagebrush) and perennial bunchgrasses and is typical of areas where cheatgrass invasion has fostered immense landscape wildfires so detrimental to sagebrush ecosystems. This site burned in 1999 and seeds of cheatgrass were collected in 2000. The high elevation site (high) is at 2,170 m (7,120 feet) at Fox Mountain, NV (41.00° N, 119.33° W). This high elevation community receives on average about 40 cm (15.7 inches) annual precipitation and is dominated by *A. tridentata* ssp. *vaseyana*, *Psuedoroegneria spicata* (Pursh A. Love (bluebunch wheatgrass) and *Cercocarpus ledifolium* Nutt. (curl-leaf mountain mahogany). These high elevation communities are somewhat resistant to cheatgrass invasion. Seeds were collected in 2000.

Seed lots were shipped to Dr. Lewis Ziska's CO_2 controlled environment facility at USDA-ARS, Beltsville MD. More detail on experimental protocols can be found in Ziska and others (2005). Briefly, two to three seeds were sown in pots filled with a 1:1 mixture of sand and vermiculite and thinned to one seedling 4 to 6 days after emergence. A pot volume of 22.1 L was used. For each CO_2 treatment, pots were watered to the drip point daily with a complete nutrient solution containing 14.5 mM m^{-3} nitrogen. Plants were grown at four different CO_2 concentrations (270, 320, 370 and 420 ppmv) for 24 h per day. For all chambers temperature was altered in a diurnal fashion from an overnight low of 15°C to a maximum afternoon value of 25°C, with an average daily (24 h) value of 18.3°C. Similarly photosynthetically active radiation (PAR) was also altered concurrently with temperature, with the highest PAR value (900 to 1000 :mol m^2 s^{-1}) occurring during the afternoon (1200 to 1500). Replicated plants were destructively harvested at 42, 57, 75, and 87 DAS (days after sowing).

Following harvest, aboveground tissue was dried to 60°C and weight recorded. Samples were shipped to the Reno, NV, USDA-ARS plant and soils laboratory for further processing. Tissue was milled separately using a 1-mm sieve opening. A portion of the milled tissue was dried for 48 hours in a desiccator and analyzed for the following. Quantification of tissue C used the Walkley-Black procedure (Walkley and Black 1947), which consists of digestion with acidified $K_2Cr_2O_7$ with supplemental heating to 180°C and back titration of unreacted dichromate with $FeSO_4$. Tissue N was determined using micro-kjeldahl method of catalyzed oxidation in sulfuric acid and H_2O_2 (Isaac and Johnson 1976). Ammonium released was quantified using the total N module on the Lachat autoanalyzer (Salicylate method). Ashing at 550°C followed by solubilization in 1N HCl was used to measure tissue P, K, Ca, Mg, and Na (Campbell and Plank 1998). Ortho-P was quantified using a total P module (vanomolybdate chemistry) for the Lachat autoanalyzer system. Calcium, Mg, Fe, and Mn were quantified using atomic absorption spectrophotometry. Sodium and K were quantified using atomic emission spectroscopy.

Another portion of cheatgrass tissue was sent to the USDA-FS, Forest Products Lab, Madison WI for analyses of compositional carbohydrates. These analyses were only done on cheatgrass grown for 87 days. The standard method involved hydrolysis in H_2SO_4, purification, separation and quantitation using anion exchange chromatography and pulsed amperometric detection (Davis 1998).

Data structure is as follows: 4 CO_2 treatments x replication in 2 bays x 3 elevation ecotypes x 5 replications = 120 total samples. Most attributes were analyzed using a three-way ANOVA with [CO_2], ecotype, and plant age as the classification variables. Hemicellulose, acid detergent fiber, and compositional carbohydrates were only determined on cheatgrass grown for 87 days and thus were analyzed using a two-way ANOVA with [CO_2] and ecotype as classification variables. Mean comparisons used Tukey's Honest Significant Difference at the $P < 0.05$ level.

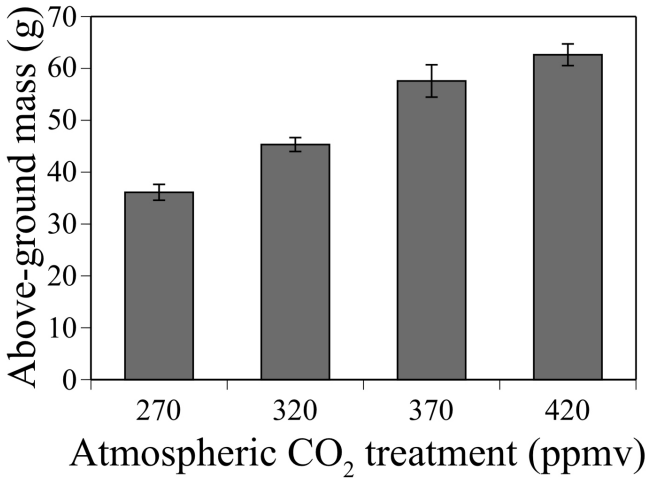


Figure 1—Relationship of above-ground cheatgrass mass with CO_2 treatment. Data are for plants grown to 87 days and pooled over ecotype. For more details, consult Ziska and others 2005.

Table 1—Result of statistical analyses for tissue nutrient concentrations in cheatgrass.

	N	C	C:N	P	K	Mg	Ca	Mn
Ecotype	0.0559	0.3421	<0.0001	<0.0001	0.0192	<0.0001	<0.0001	0.2449
CO_2	0.0094	0.0900	<0.0001	0.5932	0.3004	<0.0001	0.2036	0.6240
Ecotype x CO_2	0.8687	0.3377	0.6600	0.5313	0.9118	0.7119	0.0600	0.5307
Age	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Ecotype x Age	0.1024	0.3416	0.0276	0.0009	0.0004	0.0089	<0.0001	0.0001
CO_2 x Age	0.0087	<0.0001	0.0175	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Ecotype x CO_2 x Age	0.1370	0.1854	0.3784	0.9403	0.2618	0.9878	0.1640	0.2409

RESULTS AND DISCUSSION

Growth of cheatgrass is greatly enhanced with increasing CO_2 levels (figure 1, Ziska and others 2005). Elevated CO_2 and other aspects of global change may confer a competitive advantage to some invasive plants (Dukes and Mooney 1999). Concentration of N and C in leaf tissue of cheatgrass was affected by significant CO_2 treatment by plant age interactions (table 1). Tissue N generally declined with increasing plant age, but more so for the 420 ppmv CO_2 treatment (table 2). Plants harvested on day 57 and day 87, trended lower in tissue N with exposure to greater atmospheric CO_2. Interpretation of these data is problematic in that plants were supplied luxury levels of N in order to express maximum growth. None-the-less, cheatgrass tissue N declined significantly from 4.68 percent at pre-industrial levels to 4.20 at present CO_2 levels. Our data confirms that elevated CO_2 can increase nutrient use efficiency of N (Drake and others 1997), but is affected by plant age and CO_2 level. We suspect that if this experiment were conducted in a soil medium without luxury levels of N availability, the effect may have been more pronounced. Percent C in cheatgrass tissue declined significantly in plants grown for 87 days relative to plants harvested earlier (table 2). Moreover, for plant harvest at 87 days, percent C increased significantly at the 420 ppmv CO_2 treatment compared to the other CO_2 treatments. Carbon to nitrogen ratios were affected by significant CO_2 treatment by plant age and ecotype by plant age interactions (table 1). For plants harvested at 87 days, C:N ratios increased significantly from plants grown at pre-industrial CO_2 levels to plants grown at present and future CO_2 levels (table 2). With increasing atmospheric CO_2, plants often increase tissue C:N ratios (Cotrufo and others 1996), which may reduce palatability and affect plant-herbivore interactions (Bazzaz 1990).

All other nutrients measured in cheatgrass tissue were influenced by significant CO_2 treatment by plant age and ecotype by plant age interactions (table 1). At pre-industrial and present levels of atmospheric CO_2, tissue P increased significantly for plants harvested at 87 days relative to plants harvested earlier (table 3). Tissue P declined significantly with increasing CO_2, but only

Table 2—Tissue Nutrient concentrations of C and N and C:N ratios for cheatgrass tissue.[a]

	Harvest time			
C02	Day 42	Day 57	Day 75	Day 87
Level/ecotype	Tissue N (%)			
270 ppmv	5.0^{a-c}	4.7^{a-b}	4.3^{c-e}	4.8^{a-d}
320 ppmv	5.2^{ab}	4.9^{a-d}	4.3^{c-e}	4.8^{a-d}
370 ppmv	4.5^{b-e}	4.3^{c-e}	4.0^{e}	4.2^{de}
420 ppmv	5.4^{a}	4.2^{de}	4.3^{c-e}	4.2^{de}
	Tissue C (%)			
270 ppmv	34.6^{ab}	34.7^{ab}	34.4^{ab}	31.2^{c}
320 ppmv	33.7^{b}	33.5^{b}	33.9^{b}	33.7^{c}
370 ppmv	34.9^{ab}	35.7^{a}	34.6^{ab}	33.9^{c}
420 ppmv	34.4^{ab}	34.0^{b}	35.2^{ab}	33.6^{b}
	Tissue C:N			
270 ppmv	8.2^{b-e}	8.6^{b-e}	9.2^{a-c}	7.6^{de}
320 ppmv	7.4^{e}	8.0^{de}	9.0^{a-d}	8.0^{ce}
370 ppmv	9.1^{a-d}	9.7^{ab}	10.1^{a}	9.2^{a-c}
420 ppmv	7.6^{de}	9.5^{ab}	9.0^{b-e}	9.2^{a-c}
Low	8.4^{bc}	9.7^{a}	9.7^{a}	9.2^{ab}
Mid	7.9^{c}	8.8^{a-c}	8.7^{a-c}	8.6^{a-c}
High	7.9^{c}	8.3^{bc}	9.6^{a}	7.8^{c}

[a]For each attribute, values with different superscripts are significantly different at the .05 level of probability.

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for plants harvested at 87 days. At 57 days of growth, tissue P concentrations declined from the low elevation to high elevation ecotypes, but trend was not significant. With increasing plant age, concentrations of K in cheatgrass tissue increased for all CO_2 treatments and for all ecotypes (table 3). With increasing CO_2, tissue K declined significantly, but only for plants harvested on day 87. Overall, the high elevation ecotype had significantly less tissue K than the mid or low elevation ecotypes. For harvest times of 57, 75, and 87 days, tissue Mg generally declined with increasing CO_2 concentrations. For plants grown at 270 and 370 ppmv CO_2, tissue Mg generally increased with plant age. Overall, the high elevation ecotype had significantly less tissue Mg than the low or

mid-elevation ecotypes. Tissue Ca generally declined with increasing CO_2, but only significantly for plants harvested on days 57 and 75. Levels of Ca in cheatgrass tissue responded erratically with plant age, generally increasing to day 75 then declining. The high elevation ecotype had significantly more tissue Ca (47.7 mmol kg^{-1}) than either the low (57.3) or the mid elevation (53.7) ecotypes. Calcium is known to mitigate salt tolerance in plants (Marschner 1997), which may explain higher levels in the low elevation ecotype taken from a salt-desert environment. With increasing plant age, tissue Mn increased significantly (table 3). Tissue Mn varied inconsistently with CO_2 treatment and increased significantly at 420 ppmv CO_2 only for plants harvested on day 75. The high elevation ecotype had generally lower tissue Mn than the other ecotypes, but only significantly lower for plants harvested on day 87.

Hemicellulose in cheatgrass tissue was affected by a significant interaction between ecotype and CO_2 treatment (table 4). For the high elevation ecotype, hemicellulose declined by increasing CO_2 treatment. A main effect due to ecotype influenced acid detergent fiber (ADF); ADF was significantly less for the high elevation ecotype. Lack of sample size precluded determination of interactive effects for K-lignin and composition carbohydrates. K-lignin concentration in cheatgrass tissue was significantly less for the high elevation ecotype and significantly less when grown at 320 ppmv CO_2 (table 4). Glucan was the major composition carbohydrate in cheatgrass tissue, and was significantly less in the high elevation ecotype and significantly greater in plant growth at present and future levels of CO_2.

SUMMARY AND IMPLICATIONS

Cheatgrass tissue nutrient concentrations were significantly affected by an interaction among atmospheric CO_2 concentration, plant age, and elevational ecotypes thereby refuting working null hypotheses. Our work indicates future projected increases in atmospheric CO_2 concentrations will further increase the maximum growth potential of cheatgrass, will increase its nutrient use efficiency, and alter its biochemical composition. Clearly, ecotypes of cheatgrass will respond differently to rising CO_2. Undoubtedly, the response of cheatgrass to rising CO_2 will alter its competitive profile and interactions with herbivores.

Table 3—Cheatgrass tissue nutrient concentrations of P, K, Mg, Ca, and Mn.[a]

CO_2 x Age Interaction					Ecotype x Age Interaction				
CO_2 Level	Day 42	Day 57	Day 75	Day 87	Ecotype	Day 42	Day 57	Day 75	Day 87
Tissue P (mol kg^{-1})									
270 ppmv	0.19^{bc}	0.17^{b-e}	0.18^{b-d}	0.24^{a}	Low	0.18^{a-c}	0.18^{a-c}	0.16^{bc}	0.19^{ab}
320 ppmv	0.19^{bc}	0.194^{b}	0.17^{e}	0.19^{bc}	Mid	0.18^{a-c}	0.17^{bc}	0.17^{c}	0.20^{a}
370 ppmv	0.16^{c-e}	0.15^{de}	0.14^{e}	0.19^{bc}	High	0.18^{a-c}	0.16^{c}	0.16^{c}	0.20^{a}
420 ppmv	0.17^{b-e}	0.16^{b-e}	0.16^{c-e}	0.17^{b-e}					
Tissue K (mol kg^{-1})									
270 ppmv	1.10^{e-g}	1.16^{d-f}	1.28^{b-e}	1.56^{a}	Low	1.02^{f}	1.21^{c-e}	1.22^{cd}	1.50^{a}
320 ppmv	1.19^{d-e}	1.22^{c-f}	1.19^{d-f}	1.40^{ab}	Mid	1.21^{c-e}	1.22^{cd}	1.32^{bc}	1.44^{ab}
370 ppmv	0.96^{g}	1.08^{fg}	1.20^{d-f}	1.39^{a-c}	High	1.06^{ef}	1.03^{f}	1.12^{d-f}	1.32^{bc}
420 ppmv	1.13^{e-g}	1.15^{d-f}	1.21^{d-f}	1.31^{b-d}					
Tissue Mg (mol kg^{-1})									
270 ppmv	0.17^{b-e}	0.20^{ab}	0.20^{ab}	0.23^{a}	Low	0.18^{a-d}	0.18^{a-c}	0.17^{b-d}	0.21^{a}
320 ppmv	0.19^{b-d}	0.20^{a-c}	0.16^{c-e}	0.18^{b-d}	Mid	0.17^{b-d}	0.19^{ab}	0.19^{a-c}	0.18^{a-c}
370 ppmv	0.14^{e}	0.16^{de}	0.17^{d-e}	0.20^{c}	High	0.16^{cd}	0.15^{d}	0.16^{b-d}	0.19^{a-c}
420 ppmv	0.17^{b-e}	0.15^{de}	0.16^{de}	0.16^{c-e}					
Tissue Ca (mmol kg^{-1})									
270 ppmv	50.9^{b-d}	76.9^{a}	68.2^{a}	56.6^{b}	Low	41.6^{e}	62.1^{ab}	61.8^{ab}	64.5^{a}
320 ppmv	42.1^{de}	53.0^{bc}	53.5^{bc}	51.1^{b-d}	Mid	46.0^{de}	62.8^{ab}	58.8^{a-c}	47.8^{de}
370 ppmv	45.1^{c-e}	54.7^{bc}	56.8^{bc}	49.9^{b-d}	High	43.5^{e}	50.6^{c-d}	54.1^{b-d}	44.8^{e}
420 ppmv	36.7^{e}	49.3^{b-d}	54.4^{bc}	52.0^{b-d}					
Tissue Mn (mmol kg^{-1})									
270 ppmv	1.93^{ef}	2.20^{d-f}	2.57^{b-e}	3.17^{ab}	Low	2.01^{f}	2.40^{c-f}	2.59^{c-f}	3.50^{a}
320 ppmv	2.59^{b-d}	3.26^{a}	2.52^{b-e}	3.48^{a}	Mid	2.12^{ef}	2.57^{c-f}	2.85^{b-d}	3.39^{ab}
370 ppmv	1.67^{f}	1.93^{ef}	2.28^{d-f}	3.11^{ab}	High	2.30^{ef}	2.24^{ef}	2.36^{d-f}	2.93^{bc}
420 ppmv	2.39^{c-e}	2.22^{d-f}	3.04^{ab}	3.33^{a}					

[a]For each interaction of each attribute, values with different superscripts are significantly different at the 0.05 level of probability.

Table 4—Results of statistical analyses for tissue biochemical component concentrations.[a]

	Hemicellulose									
	Ecotype			ADF	K-lignin		Glucan		Mannan	
CO_2 ppmv	4000	5200	7120	Ecotype	Ecotype	CO_2	Ecotype	CO_2	Ecotype	CO_2
	----------%----------			%	%	%	%	%	%	%
270	21.3^{b-d}	21.4^{bc}	24.0^{a}	Low 21.2^{a}	Low 7.7^{ab}	270 8.7^{a}	Low 21.9^{a}	270 20.0^{b}	Low 0.12^{b}	270 0.22^{a}
320	22.2^{a-c}	21.2^{b-d}	22.4^{a-c}	Mid 21.3^{a}	Mid 8.8^{a}	320 6.3^{b}	Mid 22.2^{a}	320 20.7^{b}	Mid 0.21^{a}	320 0.10^{b}
370	20.9^{cd}	21.9^{a-c}	21.3^{b-d}	High 18.6^{b}	High 6.6^{b}	370 8.2^{a}	High 20.1^{b}	370 22.6^{a}	High 0.13^{b}	370 0.16^{ab}
420	19.3^{d}	23.2^{ab}	21.9^{a-c}			420 7.7^{a}		420 22.3^{a}		420 0.13^{b}
ANOVA	Ecotype		0.0185	<0.0001	0.0243		0.0158		0.0659	
	CO2		0.4688	0.5832		0.0090		0.0069		0.0085
	Interaction		0.0146	0.7029						

[a]Values determined on cheatgrass tissue after 87 days growth. For K-lignin, glucan, and mannan, insufficient tissue for some samples only allowed comparison of main effects due to ecotype and CO2 concentrations. ADF refers to acid detergent fiber. For each attribute, values with different superscripts are significantly different at the 0.05 level of probability.

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