

# Response of grassland biomass production to simulated climate change and clipping along an elevation gradient

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**Abstract** Changes in rainfall and temperature regimes are altering plant productivity in grasslands worldwide, and these climate change factors are likely to interact with grassland disturbances, particularly grazing. Understanding how plant production responds to both climate change and defoliation, and how this response varies among grassland types, is important for the long-term sustainability of grasslands. For 4 years, we manipulated temperature [ambient and increased using open-top chambers (OTC)], water (ambient, reduced using rainout shelters and increased using hand watering) and defoliation (clipped, and unclipped) in three grassland types along an elevation gradient. We monitored plant cover and biomass and found that OTC reduced biomass by 15 %, but clipping and water treatments interacted with each other and their effects varied in different grassland types. For example, total biomass did not decline in the higher elevation grasslands due to clipping, and water addition mitigated the effects of clipping on subordinate grasses in the lower grasslands.

The response of total biomass was driven by dominant plant species while subordinate grasses and forbs showed more variable responses. Overall, our results demonstrate that biomass in the highest elevation grassland was least effected by the treatments and the response of biomass tended to be dependent on interactions between climate change treatments and defoliation. Together, the results suggest that ecosystem function of these grasslands under altered climate patterns will be dependent on site-specific management.

**Keywords** Bunchgrass grasslands · Drought · Grazing · Open-top chambers · Rainout shelters

## Introduction

Global climate change is already impacting many ecosystems around the world (Walther et al. 2002; Rosenzweig et al. 2008), and increasing atmospheric carbon dioxide concentrations will continue to alter the climate (Intergovernmental Panel on Climate Change 2007). Grazing, a disturbance common in the majority of the world's grasslands, will likely interact with climate change to alter ecosystem function in unforeseen ways (Hulme 2005; Koerner et al. 2013), but will also not likely affect all grasslands in the same way or to the same extent (Grime et al. 2000; Rustad et al. 2001; Walker et al. 2006; Heisler-White et al. 2009; Bernhardt-Römermann et al. 2011). Changes in these interactions along gradients are under-studied (Smith et al. 2009) even though gradient studies are an advantageous approach for addressing ecological questions (Keddy 1991) and the effects of climate change on plant communities (Dunne et al. 2004; Etterson 2004).

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Temperature and precipitation patterns are being altered globally, and these changes have already or are predicted to impact ecosystem function (Cramer et al. 2001), global primary production (Zhao and Running 2010) and plant dominance relationships (Kardol et al. 2010). Water availability is likely to have the greatest impact on plant communities in arid environments (Brown et al. 1997; Weltzin et al. 2003). Experimental changes in both the amount and seasonality of water availability can reduce plant productivity (Swemmer et al. 2007; Wu et al. 2010) but responses are highly variable across experiments (White et al. 2012). Natural and experimental warming tends to increase productivity in plant communities (Hudson and Henry 2009; Wu et al. 2010) and can alter species interactions (Klanderud 2005; Tylianski and Didham 2008).

Grazing, a disturbance that can also reduce productivity, is one of the most widespread land uses; although estimates vary, 25 % (Asner et al. 2004) to >50 % (Havstad et al. 2008) of the world's terrestrial land mass is grazed. Interactions between climate change and disturbance are important because they can increase (Voight et al. 2007), mitigate (Klein et al. 2004; Post and Pedersen 2008) or even reverse (Suttle et al. 2007) biomass response to climate change. Therefore, understanding the interacting effects of climate change and grazing on ecosystems is crucial for the maintenance of ecosystem function and global patterns of productivity.

To manage and conserve ecosystems effectively it is imperative that the least resistant systems be identified to minimize the impact of climate change and grazing because not all systems will respond to these processes in the same way (Connell 1978; Grime 2001). We selected bunchgrass grasslands along an elevation gradient in the Southern Interior of British Columbia, Canada. These grasslands represent the northern range of many grassland species (Tisdale 1947). Bunchgrass grasslands are listed as endangered ecosystems in British Columbia (BC Conservation Data Centre 2011), and while they cover <1 % of the province's land area, they are habitat for approximately 30 % of the province's endangered species (Gayton 2004). Additionally, these grasslands are an important source of forage for both wildlife and cattle. The grasslands occur along an elevation gradient which is associated with changes in precipitation, temperature, productivity and plant community type over relatively short distances (<10 km), presenting an ideal system to test how climate change and defoliation affect different plant communities. Temperature in the region is expected to increase by up to 4 °C over the next 100 years, but precipitation patterns are predicted to become more variable and the amount of precipitation may increase or decrease (Canadian Climate Change Scenarios Network 2011). Therefore, to study the effects of defoliation and climate change we used open-top chambers (OTC) to increase

temperature, manipulated water with rainout shelters or hand watering, and hand clipped vegetation to simulate grazing. The objectives of this study were (1) to test the interactive effects of climate change (warming, and water availability) and defoliation (clipping) on above ground productivity, and (2) to test how these effects change along a natural elevation gradient.

## Materials and methods

### Site description

We conducted our study in Lac du Bois Grassland Provincial Park (Universal Transverse Mercator zone 10; 0680737 E, 5625980 N) within the bunchgrass grasslands of the interior of British Columbia, Canada, and north of the city of Kamloops. The region is semi-arid with an average annual precipitation of 279 mm (CV 1951–2006 = 0.2), 75.5 mm of which is snowfall. The average annual temperature for the region is 8.9 °C, the warmest month is July (21.0 °C) and the coldest is January (−4.2 °C) (Environment Canada 2009).

The grasslands have been categorized as three types: Lower Grasslands (LG), Middle Grasslands (MG) and Upper Grasslands (UG), and are associated with different elevation, temperature, rainfall, soil, plant biomass and vegetation types (van Ryswyk et al. 1964; Table 1). Grasslands at higher elevation are more productive. This is likely due to an increase in the ratio of precipitation to evaporation—rainfall increases with elevation while temperature decreases. The LG are dominated by *Pseudoroegneria spicata* (Pursh) A. Love (bluebunch wheatgrass) and the shrub *Artemisia tridentata* Nutt. (big sagebrush), with *Poa secunda* J.S. Presl (Sandberg's bluegrass) and *Vulpia octiflora* (Walter) Rydb. (six-week fescue) as other common species. The MG are also dominated by *P. spicata*, but *A. tridentata* is less dense; other common species in the MG are *Koeleria macrantha* (Ledeb.) Schult. (June grass), *Achillea millefolium* L. (yarrow) and *Astragalus collinus* Douglas ex G. Don (hillside milkvetch). The UG are mostly devoid of shrubs and dominated by *Festuca campestris* L. (rough fescue), while *P. pratensis* L. (Kentucky bluegrass) and *Juncus balticus* Willd. (Baltic rush) are the next most common species.

### Site data

To describe the different grassland types we harvested standing live biomass and litter, in July 2005, from six 0.25-m<sup>2</sup> plots at each site that were not part of the experiment. This material was dried at 65 °C for 48 h then weighed. Rainfall and ambient temperature were recorded using a

**Table 1** Site characteristics of three grassland types used in the experiment

Grassland type	Mean rainfall (mm)	Mean temperature (°C)	Elevation (m a.s.l.)	Species richness [no./0.25 m <sup>2</sup> (SE)]	Standing biomass [g/m <sup>2</sup> (SE)]	Litter [g/m <sup>2</sup> (SE)]	Soil carbon [% (SE)]	Soil nitrogen [% (SE)]
Upper Grassland	145	15.4	888	5.4 (0.2) b	222.0 (21.6) b	436.8 (83.6) a	9.18 (0.58) a	0.80 (0.04) a
			860	5.3 (0.3) b	250.8 (36.0) a	588.0 (110.0) a	9.09 (0.25) a	0.79 (0.01) a
Middle Grassland	112.4	17.5	761	6.9 (0.3) a	86.8 (21.6) d	96.0 (42.4) b	2.47 (0.11) b	0.23 (0.01) b
			731	5.4 (0.3) b	116.8 (16.4) c	133.6 (13.6) b	2.70 (0.09) b	0.25 (0.01) b
Lower Grassland	95.8	19.3	630	5.6 (0.2) b	94.8 (15.6) d	66.8 (16.4) b	2.02 (0.12) c	0.20 (0.01) c
			581	3.2 (0.2) c	73.2 (13.6) e	41.2 (10.4) c	2.00 (0.22) c	0.19 (0.02) c

Standing biomass and litter were collected in June 2005 from plots that were not used in the experiment. Mean rainfall and temperature were recorded from May to October in 2007 and 2008, except for rainfall in the Upper Grassland, which are 2007 data only (because of a logger malfunction in 2008). Soil carbon and nitrogen were sampled in control plots in 2008 ( $n = 3$ ). Values are means (SE);  $n = 6$  per site, except as noted. *Different letters* indicate significant differences among sites (Tukey test,  $P = 0.05$ )

rain gauge and temperature logger from May to October 2007 and 2008 (model RG3-M; Onset Computer, Bourne, MA). Soil carbon and nitrogen were sampled in control plots in July 2008 using four pooled 2-cm diameter, 10-cm-deep cores from each plot ( $n = 3$ ). Soil carbon and nitrogen were estimated using an elemental analyzer (model CE-440; Exeter Analytical, North Chelmsford, MA).

#### Experimental design

Five 30-year-old fenced exclosures, two each in the LG and MG and one in the UG, were selected in May 2005. The exclosures in the LG and MG were approximately 20 × 30 m and the exclosure in the UG was approximately 20 × 50 m. The exclosures, created with approximately 1-m-high three-strand barbed wire fence, were originally constructed as part of a long-term cattle grazing experiment. The exclosures keep out cattle, but were open to small mammals and could have been entered by deer. We established one site in each of the two LG and two MG exclosures, and two sites in the UG exclosure. The two sites in the UG exclosure were separated based on their position on a slope. At each site, 36 plots were arranged in a 6 × 6 grid and randomly assigned a treatment within the constraints of a pseudo-Latin square design so that each treatment occurred within every two rows or columns. Each plot was at least 1 m away from adjacent plots and shrubs. OTC were used to increase temperature, with the treatment either at ambient or increased (no OTC, OTC). Water was at ambient, decreased using rainout shelters or increased by hand watering (ambient, rainout shelter and addition) and plots were either clipped or unclipped. Thus, using a factorial design there were 12 treatment combinations each of which was replicated three times at each site for a total of 216 plots. The experiment was run for 4 years, from 2005 to 2008. Treatments were in place from April to October of each year, except in 2005 when they began in May.

The OTC used in this study were similar to the plastic tent design originally described in Marion et al. (1997). The OTC had a square base with each side 1.5 m long. The plastic was secured to a wooden stake driven into the ground, angled so that the top opening was square, 1 m on a side and 40 cm above the soil surface. The plastic (Tufflite IV, 6 mm, 0.152-mm thick; Tyco Plastics and Agricultural Films, Monroe, LA) has high transmission of photosynthetically active radiation and can repel dust from its surface. Soil temperature was measured at 5 cm depth in a subset of plots in the MG; OTC ( $19.6 \pm 1.7^\circ\text{C}$ ) increased temperature above that of the control plots ( $19.3 \pm 1.8^\circ\text{C}$ ); this is a small difference but the magnitude of difference was larger during different environmental conditions and different times of the year (Carlyle et al. 2011).

Rainout shelters were constructed as described in Köchy and Wilson (2004). They comprised a 1-m<sup>2</sup> plastic sheet, the same material used in the OTC, attached to a pole 1 m high at one corner and anchored at the remaining three corners such that they were each 30 cm above the soil surface to allow airflow. The sheet was oriented to block rain from the dominant wind directions during the growing season. Water availability was also manipulated by hand watering plots weekly from May up to and including October of each year. Once per week each plot received water to increase the monthly 30-year rainfall average by 30 %. The 30-year average (1970–2000) monthly rainfall for the months May up to and including September were 24.4, 35.2, 29.5, and 29.1 and 28 mm, respectively (Environment Canada 2005); thus, we added 1.8, 2.6, 2.2, 2.2 and 2.1 mm of rainfall equivalent per week to the plots in each month. Plots were hand-watered slowly to ensure minimal runoff; locally collected rainwater was used for the watering. Grasses respond to the reduction in water availability under the rainout shelters (Fraser et al. 2009) and their environmental effects have been described (Carlyle et al. 2011). Water treatments altered soil volumetric water content (%)

VWC) (ambient plots  $11 \% \text{ VWC} \pm 1.6$ ; rainout shelters,  $8 \% \text{ VWC} \pm 1.1$ , water addition  $13 \% \text{ VWC} \pm 1.8$ ). The effects of both rainout shelters and OTC change over time on daily and seasonal cycles; the structures interact and do not act independently on the intended target variable (water availability and temperature) and alter environmental variability; however, the devices do produce realistic environmental changes (Carlyle et al. 2011).

Vegetation was removed from plots ( $1 \text{ m}^2$ , plus a 0.25-m border) that received the clipping treatment. These plots were non-selectively hand clipped with scissors annually in early July, at the peak of vegetative growth, to a height of 5 cm in 2005, 2006 and 2007.

In July 2008, the final year of the experiment, the vegetation in the center  $0.25 \text{ m}^2$  of all plots, those that had received the clipping treatment in previous years and those which had not, were clipped at ground level. Because this system has a distinct growing period this biomass sample represents the majority of annual plant productivity. All biomass samples were dried for at least 48 h at  $65^\circ \text{C}$  and then weighed. In order to compare all clipped and unclipped plots during the experiment we used total visual percent cover as a proxy for biomass that was estimated, by species, each year by a single observer immediately prior to clipping.

#### Species functional groups

One of two bunchgrasses dominated our study sites. *P. spicata* was dominant in the LG and MG, while *F. campestris* was dominant in the UG. To examine the response of the remainder of the community we divided species into functional groups: dominants, subordinate graminoids, and forbs. *Dominants* included only *F. campestris* or *P. spicata*. Subordinate graminoids included all graminoids except the two dominants. The graminoid group was primarily grasses; but also included the rush *J. balticus* and the sedge *Carex petisata*. The forb group included all non-graminoid and non-woody species except for the cactus *Opuntia fragilis*, which was excluded because it occurred infrequently and it is the only non-C3 species in our study sites.

#### Data analysis

We analyzed the differences among site biomass, litter, soil carbon and soil nitrogen with ANOVA. The relationship between percent cover and total live biomass in 2008 was examined with a simple linear regression. Change in cover over time was analyzed with a repeated-measures ANOVA in which OTC, water, clipping, grassland type and year were fixed effects and site was a random effect. Differences between treatments, within a year, were tested with either a *t*-test or ANOVA. The effect of treatments and

grassland type on biomass and functional group mass was analyzed with a four-way ANOVA in which site was a random effect. All ANOVA were followed with a Tukey test. All variables were  $\log(x + 1)$  transformed, with the exception of forb biomass which was analyzed using single factor Mann–Whitney *U*-test because the variable could not be normalized. All presented errors are SEs. We used R (R Core Team 2012) for all statistical analyses.

#### Results

Our examination of site characteristics of the grassland types shows that, as expected, they differ significantly in species richness ( $F_{5,29} = 7.8$ ,  $P = 0.002$ ), biomass ( $F_{5,29} = 20.2$ ,  $P < 0.001$ ), litter ( $F_{5,29} = 57.4$ ,  $P < 0.001$ ), soil carbon ( $F_{5,11} = 169.1$ ,  $P < 0.001$ ), and soil nitrogen ( $F_{5,11} = 221.0$ ,  $P < 0.001$ ) (Table 1). In 2008, percent cover correlated with total biomass (simple linear regression:  $r^2 = 0.70$ ,  $F_{1,214} = 510.6$ ,  $P < 0.001$ ), so we have used percent cover as an estimate of biomass.

Repeated-measures analysis over the 4 years shows that cover changed over time in all three grassland types (Table 2; Fig. 1). A three-way interaction between year, grassland type and clipping (Table 2; Fig. 1a) shows that clipping reduced cover in all three grassland types by the second year; however, the difference was less pronounced in the UG where there was no difference in 2007 and a slight increase in the final year. There was also a water  $\times$  year interaction (Fig. 1b) in which the differences among water treatments was not apparent until the third year. In 2007, ambient conditions had lower cover than both rainout shelter and water-addition plots, but in 2008 the difference between plots changed so that rainout shelter plots had the highest cover, water-addition plots were intermediate, and ambient plots still had the least cover.

At the end of the experiment, the total biomass was altered by temperature, water and clipping, and was subject to interactions (Table 3). Clipping reduced biomass in the LG and MG, but not in the UG (Fig. 2a). Clipping also interacted with the water treatments such that total biomass declined with clipping under the rainout shelter and ambient treatments, but not with water additions (Fig. 2b). OTC reduced total biomass from  $133.9 \pm 9 \text{ g/m}^2$  to  $114.2 \pm 8.0 \text{ g/m}^2$ . On average ambient water plots had the lowest biomass ( $106.6 \pm 10 \text{ g/m}^2$ ), followed by water addition ( $126.1 \pm 10 \text{ g/m}^2$ ) and rainout shelter plots ( $139.5 \pm 11 \text{ g/m}^2$ ). Clipping reduced mean biomass by a third from  $148.2 \pm 9 \text{ g/m}^2$  to  $99.9 \pm 8 \text{ g/m}^2$ .

Dominant grass species, which comprise 73, 78 and 92 % of the control plot biomass in the LG, MG and UG, respectively, responded similarly to that of total biomass (Table 3). Dominant grasses declined with clipping in the LG and MG,

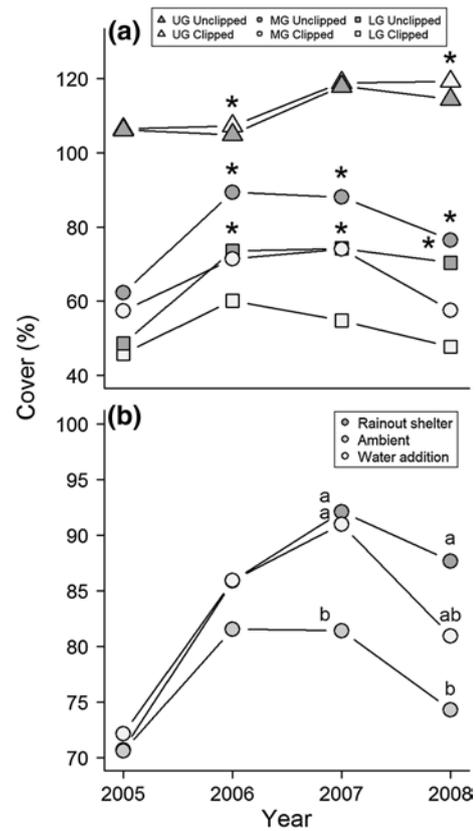
**Table 2** Results of a repeated-measures ANOVA testing the effects of open-top chambers (OTC), water addition or rainout shelters (W), clipping (C) and year (Y) in the three grassland types (T) on total percent cover

	<i>df</i>	<i>F</i> -value
<b>Between</b>		
Type	2	143.10***
OTC	1	0.01
Water	2	4.21*
Clipping	1	17.40***
Year	1	5.03*
T × O	2	0.32
T × W	4	1.59
O × W	2	0.32
T × C	2	6.19**
O × C	1	0.58
W × C	2	0.67
T × O × W	4	0.38
T × O × C	2	0.77
T × W × C	4	0.13
O × W × C	2	0.58
T × O × W × C	4	1.06
Residuals	179	
<b>Within</b>		
Year	3	40.89***
T × Y	6	9.30***
O × Y	3	1.02
W × Y	6	4.05***
C × Y	3	7.23***
T × O × Y	6	0.89
T × W × Y	12	1.76
O × W × Y	6	1.19
T × C × Y	6	2.89**
O × C × Y	3	0.68
W × C × Y	6	0.99
T × O × W × Y	12	1.31
T × O × C × Y	6	1.19
T × W × C × Y	12	0.58
O × W × C × Y	6	0.54
T × O × W × C × Y	12	0.91
Residuals	539	

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ; significant values ( $P < 0.05$ ) are in *italic*

but not the UG (Fig. 3a). The plants also responded positively to rainout shelter in the LG, but showed no response to watering treatments in the MG and UG (Fig. 3b). OTC had no significant effect on the dominants.

Subordinate grass species were reduced from  $7.5 \pm 0.8 \text{ g/m}^2$  to  $6.1 \pm 0.8 \text{ g/m}^2$  by the OTC (Table 3). There was also a three-way interaction between grassland



**Fig. 1** Changes in vegetative cover over 4 years in response to experimental treatments. **a** Response to clipping among three grassland types, **b** response to watering treatments, *small letters* indicate significant differences within years between treatments (Tukey test,  $P < 0.05$ ). *Asterisk* indicates significant difference between clipped (*open symbols*) and unclipped (*filled symbols*) plots within a grassland type for each year (*t*-test,  $P < 0.05$ ). *LG* Lower Grasslands, *MG* Middle Grasslands, *UG* Upper Grasslands

type, watering and clipping (Table 3; Fig. 4). In the LG, the subordinate graminoids tended to be reduced under the water treatments without clipping, but had the least biomass under ambient water availability when clipped. They generally responded positively to clipping in the MG, but not under rainout shelter. In the UG, without clipping they tended to decline with water treatments, but responded positively to the combination of clipping and rainout shelter. Post hoc Tukey tests were not significant.

The biomass of forbs in the LG tended to decline due to the OTC [ $U_{0.1(2), 36, 36} = 791.5$ ,  $P = 0.10$ , OTC  $9.9 \pm 1.6 \text{ g}$ , ambient  $16.4 \pm 2.7 \text{ g}$ ]. In the MG, rainout shelters [ $U_{0.1(2), 24, 24} = 168.5$ ,  $P = 0.01$ ] and water addition [ $U_{0.1(2), 24, 24} = 173$ ,  $P = 0.02$ ] more than doubled the biomass of forbs [ambient  $10.1 \pm 3.1 \text{ g}$ , water addition  $26.6 \pm 5.3 \text{ g}$ , and rainout shelter  $22.9 \pm 5.0 \text{ g}$ ]. In the UG, forbs tended to respond positively to clipping [ $U_{0.1(2), 36, 36} = 503.5$ ,  $P = 0.10$ ] (clipped  $4.5 \pm 1.5 \text{ g}$ , unclipped  $1.8 \pm 1.4 \text{ g}$ ), although they only comprised 1 % of the total biomass.

**Table 3** Results of ANOVA testing the effects of OTC, W, and C on total biomass, and dominant and subordinate graminoid biomass

Factors	df	Total biomass	Dominants	Subordinate graminoids
		<i>F</i> -value	<i>F</i> -value	<i>F</i> -value
Grassland type	2	164.14***	176.96***	54.65***
OTC	1	7.36**	3.61 <sup>·</sup>	5.47*
Water	2	11.88***	7.95***	0.35
Clipping	1	69.20***	87.33***	1.32
Site	3	12.91***	4.53**	0.62
T × O	2	1.30	0.41	1.18
T × W	4	2.00	3.13*	0.82
O × W	2	1.09	0.16	0.25
T × C	2	9.45***	13.32***	1.48
O × C	1	1.70	0.95	1.04
W × C	2	3.31*	0.67	2.27
T × O × W	4	0.77	0.56	1.17
T × O × C	2	1.21	2.80 <sup>·</sup>	0.77
T × W × C	4	1.76	0.74	3.53**
O × W × C	2	1.55	1.07	1.90
T × O × W × C	4	1.60	1.44	0.86

Residual *df* = 177. For abbreviations, see Table 2

*P* < 0.1, \* *P* < 0.05, \*\* *P* < 0.01, \*\*\* *P* < 0.001; significant values (*P* < 0.05) are in *italic*

## Discussion

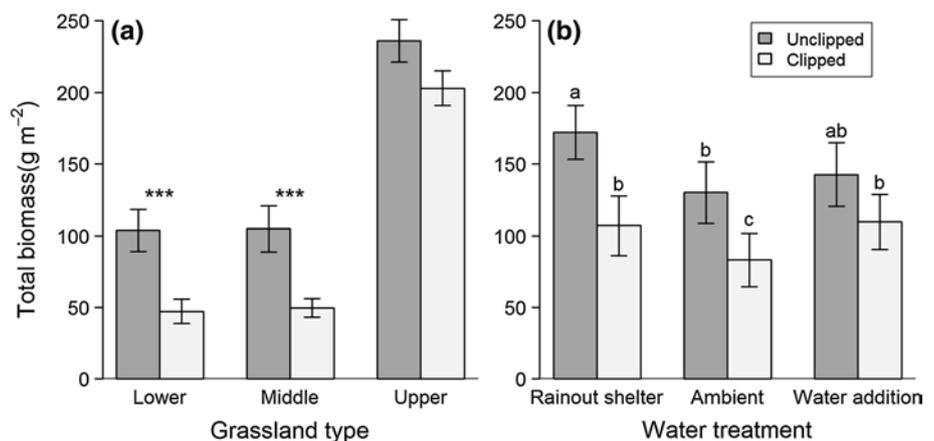
Climate change and grazing have both been recognized as factors controlling plant biomass production. Our results show that interactions between these processes are also important and suggest that changes in plant production due to climate change will be dependent on disturbance, management and location.

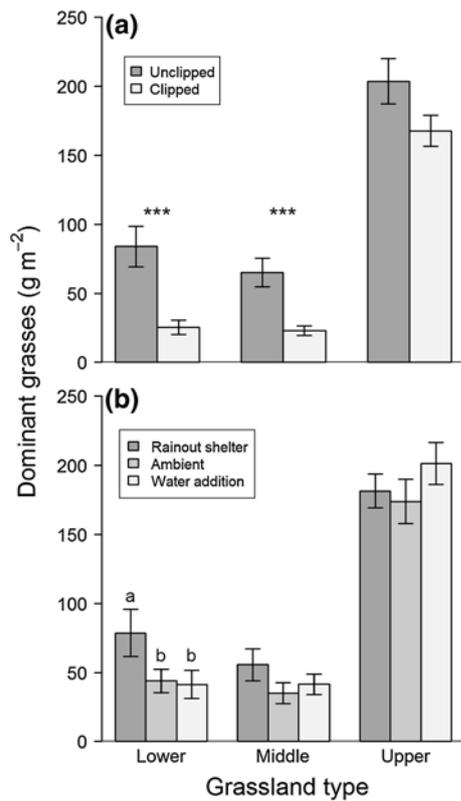
Contrary to most other experiments testing the effects of warming on plant communities (Rustad et al. 2001; Wu et al. 2010), we found that warming reduced plant biomass.

We predicted this response because water, regulated in part by temperature, is most likely a limiting factor in semi-arid grasslands. The majority of warming studies have occurred in the Arctic and other cooler climates, where increased temperature likely increases plant metabolism and extends the growing season without limiting plant resources (Rustad et al. 2001; Walker et al. 2006). On the Tibetan Plateau, Klein et al. (2007) observed that defoliation mitigated the negative effects of warming treatments on productivity. In contrast, we found that clipping reduced productivity in the two grasslands that received the least amount of precipitation, regardless of climate treatments, and we also observed the lowest production, in all three grassland types, in plots that were both warmed and clipped. This suggests that disturbances, such as grazing, may interact with climate change to negatively influence ecosystem function—especially plant production which may have consequences for the sustainability of cattle grazing in these bunchgrass grasslands.

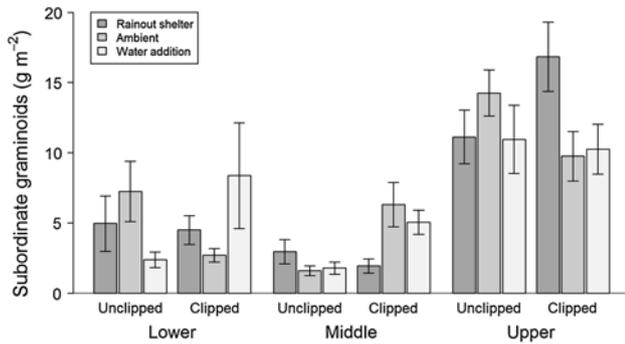
Water treatments also had significant effects suggesting changes in precipitation are also important. However, changes in productivity due to watering treatments were not as expected. Adding water to plots had no effect on biomass production; even though water additions increased soil moisture during the growing season (Carlyle et al. 2011). These plants may be adapted to short growing seasons and unable to take advantage of extended water availability. Water addition did contribute to compositional changes in the grasslands (C. N. Carlyle, unpublished data), so the lack of biomass response may be transient and develop over time as composition shifts towards species adapted to use the increased water availability (Smith et al. 2009). The increase in plant biomass under the rainout shelters, in the LG, was also unexpected and could occur because of plant physiology, trophic interactions or unintended treatment effects, but remains a question for investigation. Other studies have observed slight increases or no reduction in biomass due to rainout shelters. Gilgen and

**Fig. 2** Total biomass mean ( $\pm$ SE) in response to interactions between clipping and **a** grassland type, and **b** water treatments after 4 years. \*\*\*Significant difference between clipped and unclipped pairs within grassland types (*P* < 0.001); different letters above bars indicate significant differences between treatment (Tukey test, *P* < 0.05)





**Fig. 3** Dominant grass biomass mean ( $\pm$ SE) in response to **a** clipping and **b** watering treatments in the three grassland types. \*\*\*Significant difference between clipped and unclipped pairs (Tukey test,  $P < 0.001$ ); different letters above bars denote significant treatment differences within grassland types (Tukey test,  $P < 0.05$ )



**Fig. 4** Subordinate graminoid biomass mean ( $\pm$ SE) in response to an interaction between grassland type, clipping and watering treatments

Buchmann (2009) observed a slight increase of biomass at one site due to rainout shelters, despite a decrease in leaf water potential—indicating water stress. Lucas et al. (2008) reported an unexpected increase in population growth rate of *Cryptantha flava* under rainout shelters and attributed the effect to increased temperatures during a cold year. Meta-analyses of water effects on plant productivity are mixed:

one reported no effect of water addition in the Arctic (Dormann and Woodin 2002) and the other reported a positive response of biomass to watering and biomass reduction when precipitation is reduced (Wu et al. 2010), suggesting that the effects of water availability on plant systems are complex and not completely understood. The response in our study appears to be a trend independent of inter-annual environmental conditions as the effects were apparent in the final 2 years of the study. The positive response was mostly attributable to growth of *P. spicata*.

The dominant grasses appear to play a major role in determining the overall response of biomass production. This is most likely due to mass-ratio effects in which the relative abundance of the dominant plant determines the amount of overall community response (Grime 1998). Additionally, Kardol et al. (2010) reported that dominant plants played an important role in determining grassland response to climate change treatments because while dominants respond primarily to environmental change, change of the strength of competitive effects from the dominant has a larger effect on the response of the subordinate species. We saw that subordinate grasses tended to respond positively to clipping where the dominants declined, but while the influence of dominance on community response appears to occur along our study gradient it has not contributed to a consistent response.

Identification of ecosystems susceptible to change is important for conservation and sustainable land use. We found that response of grassland productivity to experimental manipulation of temperature, water and clipping varied by grassland type. Grime et al. (2000) propose four reasons why a plant community may be more resistant to climate change: a history of exposure to climate extremes, succession status, diversity, and functional composition. All of our sites were close to each other, and temperature and rainfall monitoring indicates that they were subject to similar weather patterns. The LG and MG would be more likely to experience climate extremes of heat or drought, yet they showed more response to the treatments. All of our sites were fenced to exclude large grazers, had not experienced fires or other major disturbance for at least 30 years and could all be classified as late-stage successional communities. The different grasslands had similar plot-level diversity (Table 1) so we cannot assess whether diversity confers resistance to change as has often been predicted (McCann 2000; Ives and Carpenter 2007). Grime et al. (2000) reported that low-productivity grasslands were more resistant to climate manipulations than high-productivity sites and functional composition was the likely explanation of resistance. In our experiment, the UG contained a different suite of species than the LG and MG; however, we currently do not have enough information about the functional composition of these grasslands to assess this hypothesis.

## Conclusion

The response of ecosystems to multiple treatments are often complex. We have shown that grassland biomass responds to warming, rainfall, defoliation and interactions between climate change and defoliation, but the response varies among grassland types. Overall, high-elevation grasslands showed the least response to treatments while middle-elevation grasslands were altered the most. The responses we saw were largely driven by dominant species. Regionally, these grasslands are important for cattle and wildlife forage, but these results indicate that defoliation in a warmer, drier environment may not support either of these uses.

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