

## EXPERIMENTAL WARMING, NOT GRAZING, DECREASES RANGELAND QUALITY ON THE TIBETAN PLATEAU

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**Abstract.** We investigated experimental warming and simulated grazing (clipping) effects on rangeland quality, as indicated by vegetation production and nutritive quality, in winter-grazed meadows and summer-grazed shrublands on the Tibetan Plateau, a rangeland system experiencing climatic and pastoral land use changes. Warming decreased total aboveground net primary productivity (ANPP) by  $40 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  at the meadow habitats and decreased palatable ANPP (total ANPP minus non-palatable forb ANPP) by  $10 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  at both habitats. The decreased production of the medicinal forb *Gentiana straminea* and the increased production of the non-palatable forb *Stellera chamaejasme* with warming also reduced rangeland quality. At the shrubland habitats, warming resulted in less digestible shrubs, whose foliage contains 25% digestible dry matter (DDM), replacing more digestible graminoids, whose foliage contains 60% DDM. This shift from graminoids to shrubs not only results in lower-quality forage, but could also have important consequences for future domestic herd composition. Although warming extended the growing season in non-clipped plots, the reduced rangeland quality due to decreased vegetative production and nutritive quality will likely overwhelm the improved rangeland quality associated with an extended growing season.

Grazing maintained or improved rangeland quality by increasing total ANPP by 20–40  $\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  with no effect on palatable ANPP. Grazing effects on forage nutritive quality, as measured by foliar nitrogen and carbon content and by shifts in plant group ANPP, resulted in improved forage quality. Grazing extended the growing season at both habitats, and it advanced the growing season at the meadows. Synergistic interactions between warming and grazing were present, such that grazing mediated the warming-induced declines in vegetation production and nutritive quality. Moreover, combined treatment effects were nonadditive, suggesting that we cannot predict the combined effect of global changes and human activities from single-factor studies.

Our findings suggest that the rangelands on the Tibetan Plateau, and the pastoralists who depend on them, may be vulnerable to future climate changes. Grazing can mitigate the negative warming effects on rangeland quality. For example, grazing management may be an important tool to keep warming-induced shrub expansion in check. Moreover, flexible and opportunistic grazing management will be required in a warmer future.

**Key words:** climate warming; experimental warming; forage quality; global change; grazing; pastoralism; productivity; rangelands; Tibetan Plateau; tundra.

### INTRODUCTION

Paleoclimate and archeological records indicate that major civilizations have experienced dislocation and state collapse in response to climate change (deMenocal 2001). These historic accounts suggest that contemporary human societies, especially those which have low adaptive capacity and are directly tied to their resource base, may be vulnerable to changes in climate and climate variability. Subsistence-based societies are likely to be more vulnerable to a given climate forcing than

industrially oriented societies, as the former are less buffered from their natural resource base than the latter (Ojima et al. 1994, IPCC Working Group II 2001). Traditional, subsistence-based cultures typically inhabit regions of the world that are currently experiencing the greatest land cover and land use change (Houghton and Ramakrishna 1999). Thus, climate warming, coupled with land use change, may be affecting the ecosystems of the world inhabited by the most vulnerable societies.

In this paper, we investigate the independent and combined effects of experimental warming and grazing on vegetative production and forage nutritive quality on the northeastern Tibetan Plateau. At  $2.5 \times 10^6 \text{ km}^2$ , the rangelands of the Tibetan Plateau are one of the most extensive grazing systems in the world, and support a unique assemblage of wild ungulates (Schaller 1998). Pastoralism has been the main form of subsistence for

Manuscript received 2 May 2005; revised 18 April 2006; accepted 27 June 2006. Corresponding Editor: R. S. Reid.

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the inhabitants of the Plateau for millennia (Miller 1999a); the domestic yak, sheep, and horses rely primarily on the natural vegetation to meet their dietary needs. More than six of Asia's major river systems originate on the Tibetan Plateau and on the order of  $1 \times 10^9$  people live on or downstream of the Tibetan Plateau. This is a region where climate warming has already been observed (Thompson et al. 1993, 2000, French and Wang 1994) and where future warming is predicted to be "greater than average" (Giorgi et al. 2001). Moreover, land use changes associated with privatization and sedentarization are reportedly increasing grazing pressures on the land (Williams 1996, Miller 1999b). Understanding how these changes in climate and pastoral land use may affect rangeland resources on the Tibetan Plateau is important for the future of the pastoralists and others who rely on these resources.

Rangeland quality establishes the bounds within which subsistence-based animal husbandry systems can operate. Two important components of rangeland quality are (1) forage availability and (2) nutritive quality or digestibility of the available forage. These two components are directly related: the amount of forage an animal must ingest to meet a fixed dietary requirement is directly proportional to the losses from digestion and metabolism (Robbins 1993). Total aboveground net primary productivity (ANPP) of the palatable plants represents the available forage. The timing over which live vegetation is available is another important component of forage availability in pastoral systems where supplemental feeding is absent. The chemical constitution of the vegetation represents the availability of nutrients in forage (Van Soest 1994). Since plant growth form groups (i.e., forbs, grasses, sedges, and shrubs, hereafter referred to as "plant groups") and even species within groups differ with respect to their chemical composition and productivity, shifts in the relative proportions of plant groups or species can affect forage quality and quantity.

Experimental warming has been shown to increase or have no net effect on total ANPP; rarely has experimental warming decreased total ANPP (Hobbie and Chapin 1998, Walker et al. 1999, 2006, Rustad et al. 2001, Saleska et al. 2002). Higher temperatures generally advance the growing season through earlier leaf bud burst and green-up (Arft et al. 1999, Schwartz et al. 2006), but have had mixed effects on senescence (Arft et al. 1999, Marchand et al. 2004). Elevated temperatures reportedly decrease forage digestibility by increasing structural and cell wall materials, increasing rates of maturation and lignification and lowering the digestibility of the cell wall contents (Buxton and Fales 1994).

Grazing effects on annual aboveground production has been an intensely researched and debated area of rangeland ecology (Maschinski and Whitham 1989, Vesik and Westoby 1991, Painter and Belsky 1993, McNaughton et al. 1997). In some of these studies, grazing increased ANPP; however, plant defoliation history has

been shown to affect plant ANPP response to defoliation (Turner et al. 1993). Statistical analysis of results from 236 sites around the world found in most studies, grazing negatively affected ANPP (Milchunas and Lauenroth 1993). According to this analysis, the conditions under which grazing increased ANPP include: a long evolutionary history of grazing, low grazing consumption, and low ANPP. Grazing can alter the age structure of leaves and result in chronologically younger leaves, with implications for the photosynthetic capacity of plants (Briske 1991) and growing season length. There is also evidence that grazing can enhance forage quality (Frank and Groffman 1998, Clark et al. 2000).

We examined how experimental warming, simulated grazing, and combined treatments affected forage availability and nutritive content in meadow and shrubland habitats. We examined two aspects of forage availability. The first component, vegetation amount, is represented by total, plant group, and palatable ANPP. Total ANPP is the sum of plant group ANPP, where plant growth form groups are shrub, forb, and graminoid (grass plus sedge). Palatable ANPP refers to total ANPP minus unpalatable forb ANPP. The second component of forage availability, the time over which live vegetation is available, is particularly important for Tibetan pastoralists, as their livestock generally do not receive supplemental feed; rather, they survive on live (more nutritious) and senesced (less nutritious) vegetation throughout the year. We also examined two aspects of forage nutritive content. First, we investigated direct treatment effects on plant nutritive content by measuring warming and clipping effects on foliar chemistry within each plant group. Second, we examined indirect treatment effects on plant nutritive content by measuring the foliar chemical content of the different plant groups to examine how potential shifts in plant group ANPP could affect overall forage quality.

We hypothesized that simulated warming would increase productivity and advance the growing season in this temperature-limited environment, where soil moisture is generally available during the summer monsoon growing season. We hypothesized that simulated grazing would have no effect or increase total productivity, due to a long evolutionary history of grazing in the region, and would extend the time over which live biomass was available. Based on the extant literature, we hypothesized that experimental warming would decrease while experimental grazing would increase forage nutritive content.

There is a prevailing view that Tibetan pastoralists have been mismanaging their resources and overgrazing the rangelands (Yang 1992, Wang et al. 2000). This idea is driving some major grassland policies on the Tibetan Plateau, such as the recent policy which completely eliminates domestic grazing from highly degraded rangelands (Yeh 2006). Others have suggested that climate warming might be responsible for the on-going vegetation changes on the Tibetan Plateau (Chen et al.

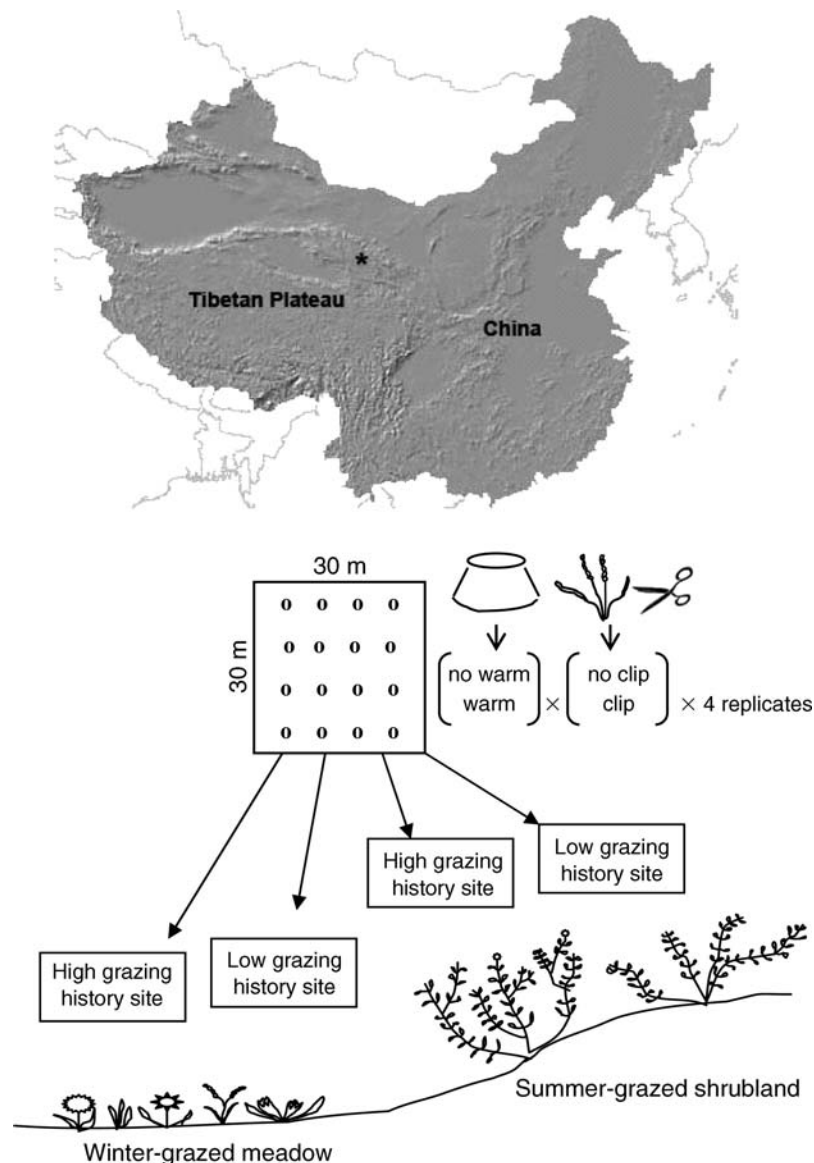


FIG. 1. Top panel: study site region. The star indicates the approximate location of the experiment. Bottom panel: experimental design. We conducted this study in summer-grazed shrubland and winter-grazed meadow. Within each habitat, we identified sites with “low” and “high” grazing intensity history, for a total of four study sites. In each site, we fenced a  $30 \times 30$  m area, within which we established a fully factorial experimental design, with warming by open-top chambers (OTC) and clipping as our main treatments. We had four replicates per treatment.

1998). This is the first study that explicitly examines the independent and combined effects of experimental warming and grazing on the rangelands of the Tibetan Plateau. Therefore, the results of this study can augment the science surrounding this debate and help elucidate warming versus grazing effects on the rangelands, with important policy and management implications.

#### METHODS

##### *Study region and site description*

We conducted our research at the Haibei Alpine Research Station (HARS), a facility run by the

Northwest Plateau Institute of Biology, Chinese Academy of Sciences. HARS is situated at  $37^{\circ}37' \text{ N}$ ,  $101^{\circ}12' \text{ E}$  (Fig. 1, Plate 1). Mean annual temperature is  $-2^{\circ}\text{C}$ , mean annual precipitation is 600 mm, over 80% of which falls during the summer monsoon season. Mean elevation of the valley bottom is 3200m. A detailed site description can be found in Zhao and Zhou (1999).

There are two main habitats in the region: winter-grazed meadow situated along the valley floor, and summer-grazed shrubland situated on the higher slopes encircling the valleys. The meadow is dominated by an assemblage of forbs and graminoids; the shrubland is



PLATE 1. Experimental plots at one of the meadow sites at the Haibei Research Station, located in the northeastern region of the Tibetan Plateau. Yak and sheep graze in the background. Photo credit: J. Klein.

dominated by a deciduous shrub, *Potentilla fruticosa*. The specific vegetative assemblages depend on habitat and grazing history. The alpine meadow and shrub vegetation which occur in this region comprise approximately 35% of the area of the Tibetan Plateau (Zhao and Zhou 1999). In  $75 \times 75$  cm plots, there average 30 plant species, most of which are  $C_3$ , perennial plants. Soils are described as Mat-Cryic Cambisols at the meadows and Mollic-Cryic Cambisols at the shrublands (Gu et al. 2005, Zhao et al. 2005).

We established our experiment in both meadow and shrubland habitats. While all of our study sites were characterized by a long evolutionary history of grazing, we identified sites within each habitat which had “low” and “high” recent grazing intensity histories for the fifteen years prior to our study. Previous work has demonstrated that recent grazing history affects how plants respond to grazing (Turner et al. 1993). Therefore, by including sites with different recent grazing histories, we can evaluate which results are robust, despite differences in recent grazing history. We refer to our four study sites as high grazing intensity history meadow site (HG meadow), low grazing intensity history meadow site (LG meadow), high grazing intensity history shrubland site (HG shrubland), and low grazing intensity history shrubland site (LG shrubland). At the shrubland sites, there had been a 15-year

controlled grazing experiment prior to the establishment of our study (Zhou et al. 2004). At the meadow sites, we established the grazing history by interviewing local herders regarding their use of the rangelands, and by consulting with scientists who had conducted long-term research in the study area. Both the grazing intensity and grazing duration differed among grazing history sites. Within each habitat, the low and high grazing history sites were similar in other features, such as slope, aspect, soil type, and distance to the river. Mean daily air temperature averaged across the growing season (measured 10 cm above the soil surface) was  $0.9^\circ\text{C}$  higher at the meadow than at the shrubland site (at the low graze history sites with no differences at the high graze history sites). Growing-season-averaged mean daily soil temperature (measured 12 cm below the soil surface) was  $2.0^\circ\text{C}$  higher at the meadow sites than at the shrubland sites. The meadow sites were 3% drier than the shrubland sites on a gravimetric mass basis (Klein et al. 2005).

The meadow sites had more total ANPP than the shrubland sites (meadows,  $316 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ; shrublands,  $226 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ; this excludes woody shrub growth) but less peak standing biomass than the shrubland sites (meadows,  $316 \text{ g}/\text{m}^2$ ; shrublands,  $852 \text{ g}/\text{m}^2$ ; this includes woody biomass). The meadows also had more palatable, forb, and graminoid ANPP than the shrubland sites. Shrubs were absent at the meadow sites, but present at

the shrubland sites. Within both habitats, the LG history sites had more palatable ANPP and less forb ANPP than the HG history sites. Within the meadows, the LG site had more total and graminoid ANPP than the HG history sites. Within the shrublands, the LG site had more shrub foliar ANPP, but less graminoid ANPP than the HG sites. Vegetation characteristics at each site are described in detail in Appendix A.

#### Experimental design

Within each of the four 30 × 30 m sites, we laid out 16 plots (for a total of 64 plots). Within each site, we established a complete factorial experimental design where we simulated warming using open top chambers (OTCs) and the defoliation effects of grazing through selective clipping (Fig. 1). We placed the conical OTCs on the plots in September 1997. The OTCs, which were 1.5 m in diameter at the base, 0.75 m diameter at the top and 0.40 m high, remained on the plots year-round. We sampled vegetative properties in a 75 × 75 cm area centered in the plot (the approximate area of the top chamber opening) in order to avoid chamber “edge effects.” The chambers did not exclude precipitation from the 75 × 75 cm area. Moreover, the vegetative canopy, including that of the shrubs, was less than 40 cm in height. OTCs are used by the International Tundra Experiment and are commonly employed to study the effects of climate warming on ecosystems (Marion et al. 1997, Arft et al. 1999, Walker et al. 2006).

The OTCs consistently elevated growing-season-averaged mean daily air temperature at 10 cm above the soil surface by 1.0–2.0°C, maximum daily air temperature by 2.1–7.3°C, and the diurnal air temperature range by 1.9–6.5°C. By contrast, OTCs had few effects on minimum daily air temperature, mean daily soil temperature and moisture; soil properties were monitored 12 cm below the soil surface. OTCs did, however, elevate soil temperature by approximately 1.0°C early in the growing season. Klein et al. (2005) provide a detailed account of OTC and clipping effects on microclimate at these sites.

We began the defoliation treatments in the spring of 1998. In the meadows, traditionally grazed during the winter months, we clipped the plots prior to initiation of growth in the early spring. In the shrublands, traditionally grazed during the summer months, we clipped the plots in mid-July. We clipped plots to approximately 3 cm in height, which is the height of the vegetation outside of the fenced plots in the sites with a high grazing history. We removed approximately 30% of total live peak aboveground (AG) biomass in the shrubland sites and 15% of total peak AG biomass in the meadows, plucking the shrub leaves and stem tips to simulate sheep browsing. We did not clip plants that yak and sheep do not consume (such as *Oxytropis* spp., and *Stellera chamaejasme*). We dried, and weighed the clipped vegetation and added this biomass to the clipped plot ANPP estimates.

To examine how well clipping simulated the effects of actual grazing, in 2000 we established four replicated “grazing control” (GC) plots situated outside of the fenced areas in all four sites. We established these plots more than 5 m but less than 15 m away from the fence to eliminate any “fence” effect but to be representative of the plots within the fenced area. Pairs of GC plots were approximately 2 m apart from each other.

#### Response variables

We used a non-destructive sampling method to estimate ANPP. Within each plot, we sampled a 75 × 75 cm quadrat divided into 400 (20 × 20) 3.75 × 3.75 cm squares. Within each of the 400 squares, we recorded the dominant (>50% coverage) plant group as viewed down onto the top of the vegetative canopy. We also conducted this process off-plot, after which we harvested, dried, separated, and weighed the vegetation for which we had recorded coverage. We then constructed regression relationships between the coverage estimate and dry weight biomass. This is a modified version of the sampling method used by Harte and Shaw (1995) and Dunne (2000). This sampling method yielded the strongest regression relationships (highest  $R^2$  and lowest  $P$  values) to off-plot harvested biomass as compared to leaf area index (LAI), or measuring specific dimensions of the vegetation.

From 1999 to 2001, we measured the biomass of forb species *Morina chinensis*, *Gentiana straminea*, *Saussurea superba*, *Aster flaccidus*, and *Polygonum viviparum* separately because, at least in one site, they comprised a relatively large proportion of the biomass. Some of these species, such as *Saussurea superba*, also had unique morphologies and therefore required separate coverage-biomass regression equations. We also measured some forb species separately because they have important medicinal value, such as *Gentiana straminea*, or because they are non-palatable species, such as *Stellera chamaejasme*. We determined which plants were non-palatable based on conversations with local herders. Non-palatable plants species are those which the livestock avoid. The average adjusted  $R^2$  for all 13 regression models (this includes the plant group biomass regressions as well as the individual forb species' regressions) was 0.96 and the average  $P$  value was 0.0005. The poorest fit model had an adjusted  $R^2$  of 0.91. All equations and more details on this sampling method are in Appendix B.

We conducted the non-destructive biomass estimation once every four weeks throughout the growing season, from approximately May through October from 1998 to 2001. In this system, peak aboveground live biomass is a good approximation of ANPP. All live aboveground biomass is from the current season's growth (there is no new growth carry-over from the previous year). The majority of the standing dead and litter are from the previous years' growth; death in the current year is negligible. We may have slightly underestimated forb

ANPP due to the few early blooming species, whose peak biomass is achieved earlier than the time at which the vast majority of the 85 forb species reach peak biomass. Moreover, we did not measure annual growth increments to shrub woody biomass. Our measurements of shrub ANPP therefore represent foliar production only. Wood production does not directly contribute to forage production; therefore, this is not an important omission. We do, however, estimate standing shrub biomass (which is an estimate of both foliar and woody biomass). Our productivity numbers represent conservative estimates of ANPP and are appropriate for comparing ANPP among sites, treatments and years. Moreover, when we discuss monthly vegetation effects, we refer to biomass rather than production.

To assess treatment effects on forage nutritive quality, we conducted two analyses. For the first analysis, we examined the direct warming and clipping effects on foliar quality by measuring percentage carbon (C) and percentage nitrogen (N) in leaf tissue for each plant group within all of the 64 plots. Percentage N content is related to crude protein content while the C:N ratio is an overall proxy for forage quality. C represents the fibrous components of the vegetation, whereas N represents the easily digestible protein in the forage. Therefore, a higher C:N ratio represents a lower forage quality (Walsh et al. 1997). For this analysis, we collected leaf blades of vegetation at the same level of maturity and at full sun exposure in August of 1998 and 2001. We measured total carbon and nitrogen on a Carlo Erba NC2100 (CE Elantech, Lakewood, New Jersey, USA).

For the second analysis, we examined the indirect warming and clipping effects on forage nutritive quality by comparing foliar quality among the different plant groups at each of the four sites (off-plot) using the Van Soest detergent fiber analysis method (Van Soest 1963, Goering and Van Soest 1970). This allowed us to infer treatment effects on forage quality due to changes in plant group ANPP. For this analysis, we collected leaves of each plant group at peak standing biomass in August 2000 off plot, but within each of the four fenced sites. The Wildlife Habitat and Nutrition Lab at Washington State University, in Pullman, Washington, USA conducted the sequential fiber analysis (Van Soest 1963, Goering and Van Soest 1970). They determined the percentage of neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), and acid insoluble ash (AIA). From the above measurements, we calculated an index of digestibility that has been highly correlated with in vitro digestion studies (Goering and Van Soest 1970): digestible dry matter or DDM (%) =  $0.98S + (NDF)Dc - M$ .  $S$  represents the cell contents, with an average digestibility of 98%.  $Dc$  is the cell wall digestion coefficient  $147.3 - 78.9 \log_{10}([\text{lignin}/\text{ADF}]100)$ .  $M$  represents the estimated fecal losses (we used a standard 12.9 units of digestibility). We did not use the Van Soest analysis to measure direct treatment effects on foliar chemistry within the 64 experimental

plots since this analysis required more leaf tissue than we were willing to harvest from the experimental plots.

Both forage quality analyses were conducted on one “representative species” for each plant group. These species were: forb, *Gentiana straminea*; grass, *Stipa purpurea*; sedge, *Kobresia humilis*; and shrub, *Potentilla fruticosa* (only present at the shrubland sites). The grass and sedge species were chosen because they are the most abundant graminoids in all sites. The forb species was chosen because it was present at all four sites. The shrub was chosen because it was the only shrub species present.

### Data analysis

We conducted a split plot, repeated-measures ANOVA using SAS 9.1 (SAS Institute 2002) to examine treatment and year effects. The whole plot component consisted of habitat (and grazing history nested within habitat), the split plot component consisted of the individual plots within each site, and the repeated measure was year. We used a first order autoregressive covariance structure for the repeated measure model. We nested grazing history within habitat so that we had replicates of habitat ( $n = 2$ ). Since these habitat replicates were chosen to represent distinct recent grazing intensity histories (rather than chosen at random with respect to grazing intensity history), these replicates exhibit more within-habitat variability than if we had chosen them at random. Therefore, significant results should be considered relatively robust across factors such as recent grazing history, despite the low replication. By nesting grazing history within habitat, we are not able to statistically evaluate how recent grazing history modifies treatment effects. To analyze treatment effects on live biomass availability throughout the growing season, we used data from 2000 in a split plot repeated measures design similar to the repeated measures analysis described above. However, for this analysis, “month,” rather than “year” was the repeated measure. To meet normality assumptions, we log-transformed the monthly biomass data. To assess treatment effects on vegetation properties that only occurred within the shrubland sites (e.g., shrub foliar ANPP), we conducted a repeated measures ANOVA and grouped all plots within the shrubland sites.

Our treatments were T(control), no OTC, no clip; T(warm), +OTC, no clip; T(clip), no OTC, +clip; T(warm  $\times$  clip), +OTC, +clip. If a warm  $\times$  clip interaction was absent, we refer to an overall “warm effect” of  $([T(\text{warm}) + T(\text{warm} \times \text{clip})]/2 - [T(\text{control}) + T(\text{clip})]/2)$ . This describes the average effects of warming, in both the presence and absence of clipping. If, however, a warm  $\times$  clip interaction was present, we describe the effects of “warm (no clip)” =  $[T(\text{warm}) - T(\text{control})]$  and “warm (+clip)” =  $[T(\text{warm} \times \text{clip}) - T(\text{clip})]$  separately. We follow the same convention for the clipping effects. The combined effects of warming and clipping =  $[T(\text{warm} \times \text{clip}) - T(\text{control})]$ . If no warm  $\times$  clip interaction was present, the combined

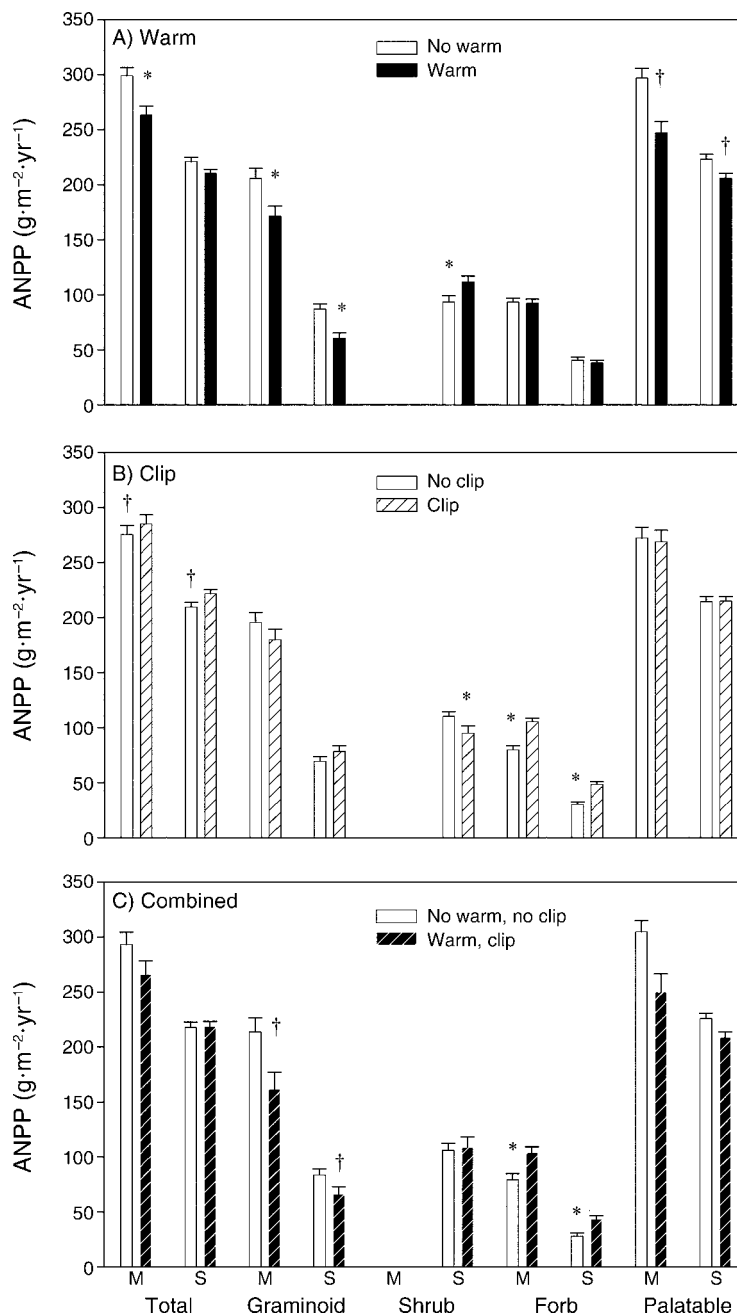


FIG. 2. (A) Warming, (B) clipping, and (C) combined treatment effects on total vegetative aboveground net primary productivity (ANPP), graminoid ANPP, shrub foliar ANPP, forb ANPP, and palatable ANPP (total ANPP minus non-palatable forb ANPP) at both meadow and shrubland sites. Bars represent mean ( $\pm$ SE) values from 1998–2001 from meadow habitat (M) and shrubland habitat (S). The open bars in (A), (B), and (C) do not represent the same plots. The “no warm” plots in (A) are the T(control) + T(clip) plots ( $n = 8$ ); the “no clip” plots in (B) are the T(control) + T(warm) plots ( $n = 8$ ). For (C), the white bars represent the T(control) plots ( $n = 4$ ); see *Methods*. Significance levels are indicated for significant treatment effects, either by habitat or averaged over habitat. For shrub foliar ANPP, we depict a significant clipping effect, although this effect was only significant in 2000 and 2001 (not averaged over all years). For forb ANPP, there was a habitat  $\times$  warm  $\times$  clip interaction such that at the meadows, the warm (no clip) treatment decreased forb ANPP. Results from the repeated-measure, split-plot ANOVAs are presented in Appendix C (Table C1).

\*  $P < 0.05$ ; †  $0.05 < P \leq 0.1$ .

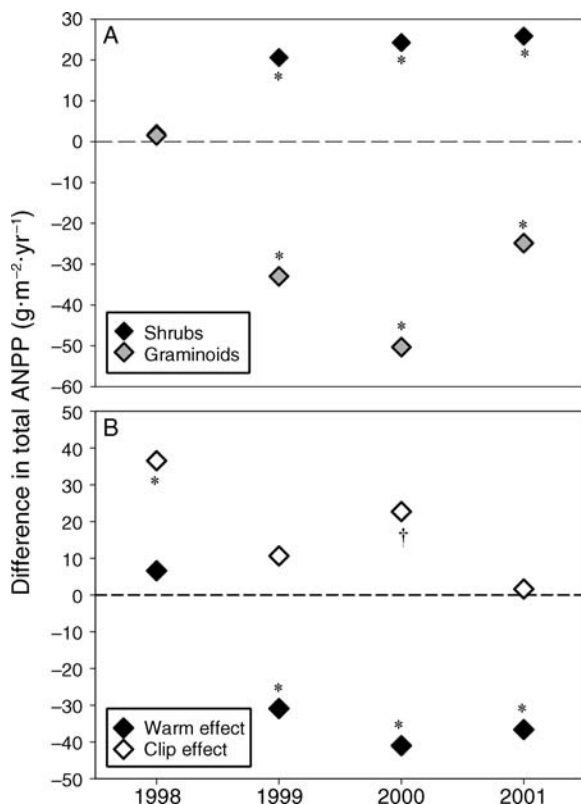


FIG. 3. (A) Mean warming effect (warmed plots minus non-warmed plots) for shrub foliar ANPP (black diamonds) and graminoid ANPP (gray diamonds) at the shrubland sites from 1998 to 2001. In 1998, the symbol for the graminoid warming is superimposed on the shrub warming effect. (B) Mean difference in total ANPP due to warming (black diamonds) and clipping (open diamonds) averaged over all sites from 1998 to 2001.

\*  $P \leq 0.05$ ; †  $0.05 < P \leq 0.1$ .

treatments are strictly additive, where  $[T(\text{warm} \times \text{clip}) - T(\text{control})] = ([T(\text{warm}) - T(\text{control})] + [T(\text{clip}) - T(\text{control})])$ . That is, the combined treatment effect will equal the sum of the separate warm (no clip) and clip (no warm) effects. If an interaction was present, then  $[T(\text{warm} \times \text{clip}) - T(\text{control})] = ([T(\text{warm}) - T(\text{control})] + [T(\text{clip}) - T(\text{control})] + \text{interaction effect})$ . Here, the combination of warm and clip interact to create an effect which cannot be represented simply by the sum of the individual warm (no clip) and clip (no warm) effects. Rather, the combined effect and the strictly additive effect differ by the sign and magnitude of the interaction effect. For all analyses, reported results are significant at  $P \leq 0.05$ , unless we state otherwise in the text. This is an on-going study, although the data we present in this paper are from 1998–2001.

## RESULTS

### Warming and clipping effects on aboveground vegetative productivity

For most of the vegetation responses to experimental warming described in this section, there was no effect in

1998, with significant effects in subsequent years. All ANOVA results are presented in Appendix C.

Experimental warming decreased total ANPP by  $40 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  at the meadow sites, with no effect on total ANPP at the shrubland sites (Fig. 2A). The different warming effect on total ANPP at the meadow habitats as compared to the warming effect on total ANPP at the shrubland habitats is explained by changes in plant group ANPP. Warming decreased graminoid ANPP, which was present at both habitats, but increased shrub foliar production, which was present only at the shrubland sites. At both habitats, warming decreased graminoid ANPP by  $36\text{--}50 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ , while at the shrubland habitats, warming increased shrub foliar ANPP by  $20\text{--}25 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  from 1999 to 2001 (this excludes shrub woody production) and increased total aboveground peak standing biomass by  $72 \text{ g} \cdot \text{m}^{-2}$  in 2000 ( $P = 0.1$ ) and  $102 \text{ g} \cdot \text{m}^{-2}$  in 2001 (this includes shrub woody biomass). At the shrubland sites, the increase in shrub foliar ANPP countered the decrease in graminoid ANPP, resulting in no net change in total ANPP (Fig. 3A). At the meadows, the decrease in graminoid ANPP in response to warming resulted in a decline in total ANPP.

Warming had no effect on overall forb ANPP due to an individualistic forb species response to warming (Fig. 2A). Forb ANPP responses to warming were species dependent, varied in the presence or absence of clipping, and were generally more pronounced over time (Appendix C: Table C2). Changes to important forb species were observed (Fig. 4). For example, warm (no clip) decreased the ANPP of the medicinal plant, *Gentiana straminea*, while warm (+clip) had no significant effect on *Gentiana straminea* ANPP. In contrast, warming increased the non-palatable plant *Stellera chamaejasme*, regardless of the presence/absence of clipping. Warm (no clip) had no effect on the non-palatable plant, *Oxytropis* spp., while warm (+clip) decreased *Oxytropis* spp.

Warming significantly decreased palatable ANPP (total ANPP minus non-palatable forb ANPP) at both meadow and shrubland sites (Fig. 2A). Contrary to our predictions, warming decreased the amount of available forage at these sites.

Clipping accurately simulated grazing effects on ANPP. The ANPP values in the grazed (grazing control) and clipped plots were not significantly different, with only one exception: in 2000, clipped plots had  $12 \text{ g} \cdot \text{m}^{-2}$  less forb ANPP than the grazed plots ( $P = 0.06$ ); there were no differences between forb ANPP in clipped and grazed plots in 2001 (Appendix C: Table C3).

Clipping effects on ANPP were often in the opposite direction as warming effects (Fig. 2B). While warming generally decreased total ANPP from 1999 onward, clipping increased or had no effect on total ANPP, depending on year (Fig. 3B). Unlike warming, clipping had no effect on graminoid ANPP. Whereas warming generally increased shrub foliar ANPP, clipping de-



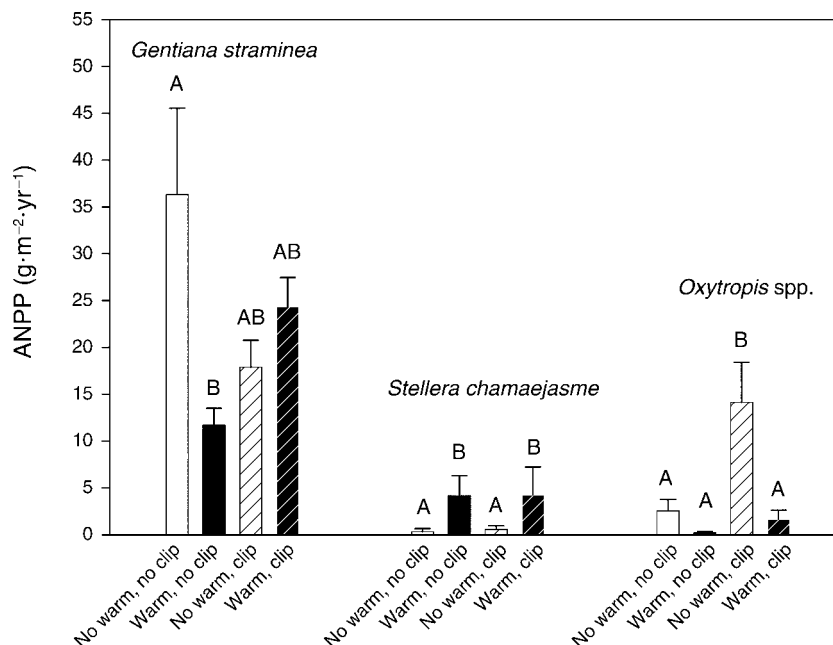


FIG. 4. Mean forb ANPP values for T(control), T(warm), T(clip), and T(warm  $\times$  clip) for the medicinal forb *Gentiana straminea* (left), and the non-palatable forbs *Stellera chamaejasme* (center) and *Oxytropis* spp. (right) in 2001. Since warm  $\times$  clip interactions were present for *Gentiana* and *Oxytropis* (Appendix C: Table C2) we present treatment means separately (rather than averaging over treatment, as in Fig. 2). Bars represent means ( $\pm$ SE);  $n = 4$  replicates. Bars with different letters are significantly different at  $P \leq 0.05$ .

creased shrub foliar ANPP by approximately  $35 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  in 2000 and 2001. Whereas warming generally had no effect on overall forb ANPP, clipping increased forb ANPP. Similar to warming, clipping effects on forb ANPP depended on species and the presence or absence of warming. For example, clip (no warm) had no effect on the non-palatable plant *Stellera chamaejasme*, increased the non-palatable plant *Oxytropis* spp., and had no effect on the medicinal plant *Gentiana straminea*; clip (+warm) had no effect on all three species (Fig. 4). Clipping had no significant effect on palatable ANPP (Fig. 2B). These findings generally support our predictions of ANPP responses to simulated grazing.

While warming decreased total ANPP at the meadows in most years, and clipping increased total ANPP at both habitats in some years, combined treatments had no effect on total ANPP (Fig. 2C). That is, the warming and clipping effects cancelled each other, resulting in no significant effect on total ANPP. Combined treatments similarly cancelled each other, with no effect on palatable ANPP and shrub foliar ANPP. Combined treatments resulted in a  $35 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  ( $P = 0.09$ ) decline in graminoid ANPP, which moderates the larger decline experienced under warming alone. Similar to the clipping alone effect, forb ANPP increased under combined treatments by  $20 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ .

Synergistic interactions between combined warming and clipping occurred, which dampened the ANPP declines experienced under the strictly additive treat-

ment effects. That is, the decline in ANPP under the combined warming and clipping treatments was generally less than the decline in ANPP which resulted from the sum of the independent effects of warming and clipping. For example, in 2001, additive treatments significantly decreased total vegetative ANPP by  $82 \text{ g} \cdot \text{m}^{-2}$ , whereas combined treatments resulted in a nonsignificant decline of  $35 \text{ g} \cdot \text{m}^{-2}$  (Fig. 5). This pattern was also exhibited with respect to the ANPP of palatable vegetation, of the medicinal plant *Gentiana straminea*, of the non-palatable plant *Oxytropis* spp., of *Aster Flaccidus*, *Morina chinensis*, and *Polygonum viviparum*.

Our measurements of total root biomass response to experimental warming and grazing indicate the treatment effects on ANPP described in this section do not result from shifting allocation patterns between the above and belowground pools. Details on root sampling methods and belowground biomass results are presented in Appendix C (Table C4).

#### Warming and clipping effects on aboveground monthly live biomass for 2000

By examining treatment effects on monthly biomass for 2000, we can assess how the warming and clipping treatments affected live biomass availability throughout the growing season. We can also observe important within growing season treatment interactions which were not present when evaluated over the entire growing season.

Contrary to our predictions, warming extended, but did not advance, the time over which live biomass was available (Fig. 6A, B). Moreover, monthly warming effects on live biomass depended on the presence or absence of clipping (Appendix C: Table C5). Early in the growing season, in May, there was no difference in live biomass between non-warmed and warmed plots, regardless of the presence or absence of clipping. However, by the end of the growing season, in October, warming in the absence of clipping increased live biomass by 75 g/m<sup>2</sup>, while warming in the presence of clipping had no effect on live biomass. From June through September, the decline in biomass with warming was generally smaller in the presence than in the absence of clipping.

Consistent with our predictions, clipping extended the time over which live biomass was available at both habitats and advanced the time over which live biomass was available at the meadow sites (Fig. 6C, D). That is, clipping effects on biomass varied by month and also depended on habitat (Appendix C: Table C5). At the meadow sites, clipping increased total biomass both early (May and June) and late (October) in the growing season. By contrast, at the shrubland sites, clipping increased total biomass in October only. Monthly clipping effects on biomass also depended on the presence or absence of warming. For example, while clipping in the presence and absence of warming both increased biomass in October, the increase in the absence of warming was three times larger than the increase in the presence of warming.

Combined warming and clipping both advanced and extended the time over which live biomass was available (Appendix C: Table C5), an important improvement to rangeland quality. Combined treatments increased total live biomass in both May (+20 g/m<sup>2</sup>) and October (+117 g/m<sup>2</sup>), but decreased live biomass in July. The decline in July biomass under combined treatments (−40 g/m<sup>2</sup>) was almost one half the decline in July biomass under the sum of the independent warming and clipping effects (−75 g/m<sup>2</sup>), suggesting that the synergistic interaction of warming and clipping dampened the decline in July biomass due to the strictly additive treatment effects of warming plus clipping.

#### *Warming and clipping effects on foliar nutritive quality*

We hypothesized that warming would decrease forage nutritive quality, but warming effects on foliar N and C:N were mixed and varied by year and plant group (ANOVA results are in Appendix C: Tables C6 and C7). When there was a significant effect, warming tended to decrease forage quality in 1998, but increase forage quality in 2000. Warming decreased (1998) and increased (2000) foliar N in sedges and shrubs (Fig. 7A). In 1998, warming had no effect (sedge) and increased (shrub) foliar C:N ratios; by contrast, warming decreased foliar C:N ratios for both sedges

and shrubs in 2000. Warming had no effect on foliar N and C:N ratios of grasses and forbs (Fig. 7B).

Our prediction that clipping would increase forage foliar quality was generally supported by the foliar N and C:N data (Fig. 7). Clipping increased forb foliar N content regardless of year ( $P = 0.1$ ). Clipping increased grass foliar N content in 1998 (both habitats) and 2000 (shrublands). Clipping also increased sedge foliar N content in 2000 (both habitats) with no effect on shrub foliar N content. Clipping decreased grass foliar C:N ratios (both years), with a larger decline at the shrublands than at the meadow sites. Clipping decreased sedge foliar C:N in 2000 (both habitats) with no effect on forb and shrub foliar C:N.

Combined warming and clipping treatments increased or had no effect on foliar N and decreased or had no effect on C:N (Fig. 7). Combined warming and clipping treatments generally increased graminoid forage quality, reflecting the clipping effects on forage quality. Combined treatments increased grass foliar N in both years ( $P = 0.09$ ) and sedge foliar N in 2000. This decreased the C:N ratio of sedges, with no effect on grass C:N ratios. Combined treatments had no effects on foliar N and C:N ratios for shrubs and forbs.

Despite the mixed effects of warming on foliar percentage N and C:N reported above, we found that the indirect warming effect on forage quality, through changes to plant growth form composition, are likely to be negative. Specifically, warming results in less digestible shrubs replacing more digestible graminoids. According to the percentage DDM index of digestibility, shrubs were the least digestible, grasses were of intermediate digestibility, and sedges and forbs were most digestible (Fig. 8A). Forbs and shrubs had the highest percent of digestible, non-fibrous compounds. According to the percentage NDF ranking, forb < shrub < sedge < grass. However, of the fibrous compounds present, shrubs had more cellulose, lignin, and silica than other plant groups; grasses also had relatively higher values in this category. Percentage ADF was ranked forb < sedge < grass = shrub and percentage silica ranked forb < sedge = grass < shrub. Shrubs had significantly more lignin (ADL) than all other plant groups, among whom ADL values did not differ (Fig. 8B). Therefore, warming resulted in less palatable shrubs replacing more palatable graminoids, thereby reducing rangeland quality. In contrast, clipping had no effect on the production of the palatable graminoids and reduced the less palatable shrubs, thereby increasing rangeland quality. Combined treatments had mixed effects on rangeland quality by reducing the production of palatable graminoids with no effects on the production of the less palatable shrubs.

#### DISCUSSION

Warming generally decreased rangeland quality by reducing forage availability and forage nutritive content. Warming decreased total ANPP at the meadows, with

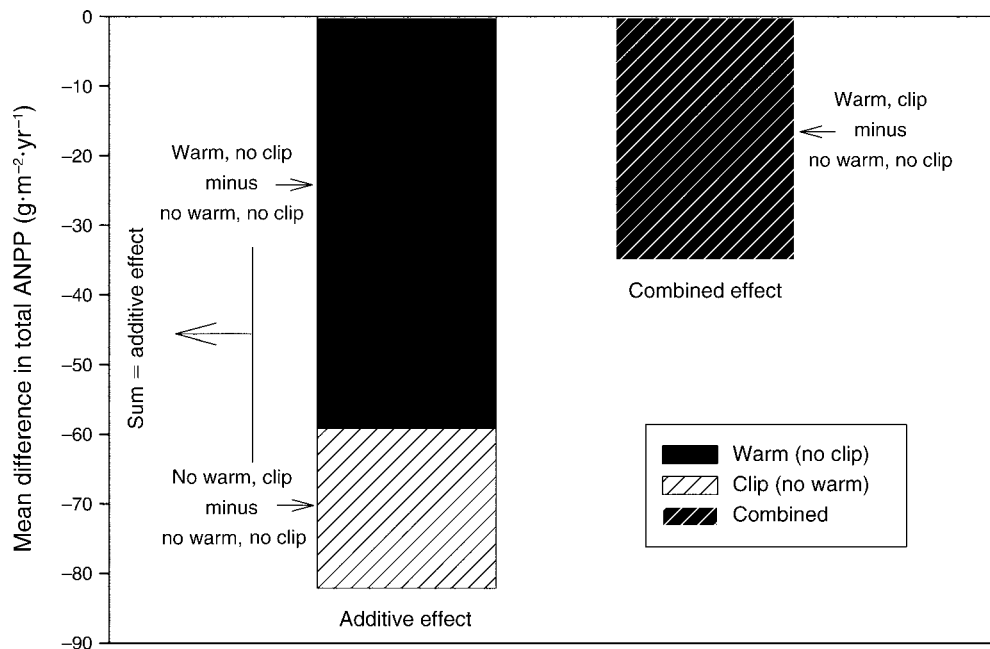


FIG. 5. Mean difference in total ANPP due to additive treatment effects (left side) vs. combined treatment effects (right side) for all sites in 2001. The additive effect consists of the sum of the warm (no clip) and the clip (no warm) effects minus the controls (no warm, no clip). In 2001, both warm (no clip) and clip (no warm) decreased total ANPP relative to controls. While Fig. 3B shows no effect of clipping on total ANPP relative to non-clipped plots in 2001, Fig. 3B represents the average clipping effect both in the absence and presence of warming  $([T(\text{clip}) + T(\text{warm} \times \text{clip})]/2 - [T(\text{control}) + T(\text{warm})]/2)$ . Here, we represent the clip effect in the absence of warming  $[T(\text{clip}) - T(\text{control})]$ . The combined effect is composed of  $T(\text{warm} \times \text{clip})$  plots minus  $T(\text{control})$  plots. Thus, the interaction of warming and clipping dampened the decline in ANPP due to the sum of the independent warm and clip effects.

no effects at the shrublands. At the shrubland sites, the decrease in graminoid ANPP was compensated for by an increase in shrub foliar ANPP. Forb species generally responded individually to warming, such that warming had no effect on total forb ANPP. However, warming did have important effects on non-palatable and medicinal forb species ANPP. Warming decreased palatable forage ANPP at all sites. Warming sometimes extended, but did not advance, the growing season. While warming effects on foliar C and N were mixed, the warming induced shifts in plant group ANPP result in less palatable shrubs replacing more palatable graminoids.

Simulated grazing, whose effects were generally in the opposite direction as warming, maintained or improved rangeland quality by increasing forage availability and forage nutritive content. Clipping generally increased overall ANPP and had no effect on palatable plant ANPP. Clipping consistently extended and sometimes advanced the growing season. Clipping effects on foliar C and N and clipping induced shifts in plant group ANPP resulted in increased forage nutritive quality. Synergistic interactions between warming and clipping were present, such that clipping could mediate the warming induced declines in production and forage nutritive quality.

#### *Warming and clipping effects on aboveground vegetative productivity*

Our findings, that experimental warming decreased total ANPP in an alpine meadow tundra ecosystem, contradict predictions and results from other studies of tundra response to warming. For example, Hobbie and Chapin (1998) predicted increased air temperature would have little direct effect on biomass or production in the tundra. Warming experiments from alpine and arctic tundra sites have reported no net change in total biomass with experimental warming (Harte and Shaw 1995, Hobbie and Chapin 1998). Many tundra sites also report increased growth of tundra plant species with experimental warming (Arft et al. 1999, Hollister et al. 2005, Walker et al. 2006). Saleska et al. (2002) did observe a decrease in plant productivity in response to soil warming in a montane meadow. In a meta-analysis of warming experiments across several ecosystem types, Rustad et al. (2001) found that AG plant productivity increased in 13 out of 20 sites, decreased in two out of 20 sites, and had no effect in five out of 20 sites.

While our results differ from most reported findings, our system is also quite different from all other sites. Of all the sites where experimental warming experiments have been conducted, our temperate alpine site is most similar to the montane and alpine sites in the Rocky Mountains, USA (Harte and Shaw 1995, Walker et al.

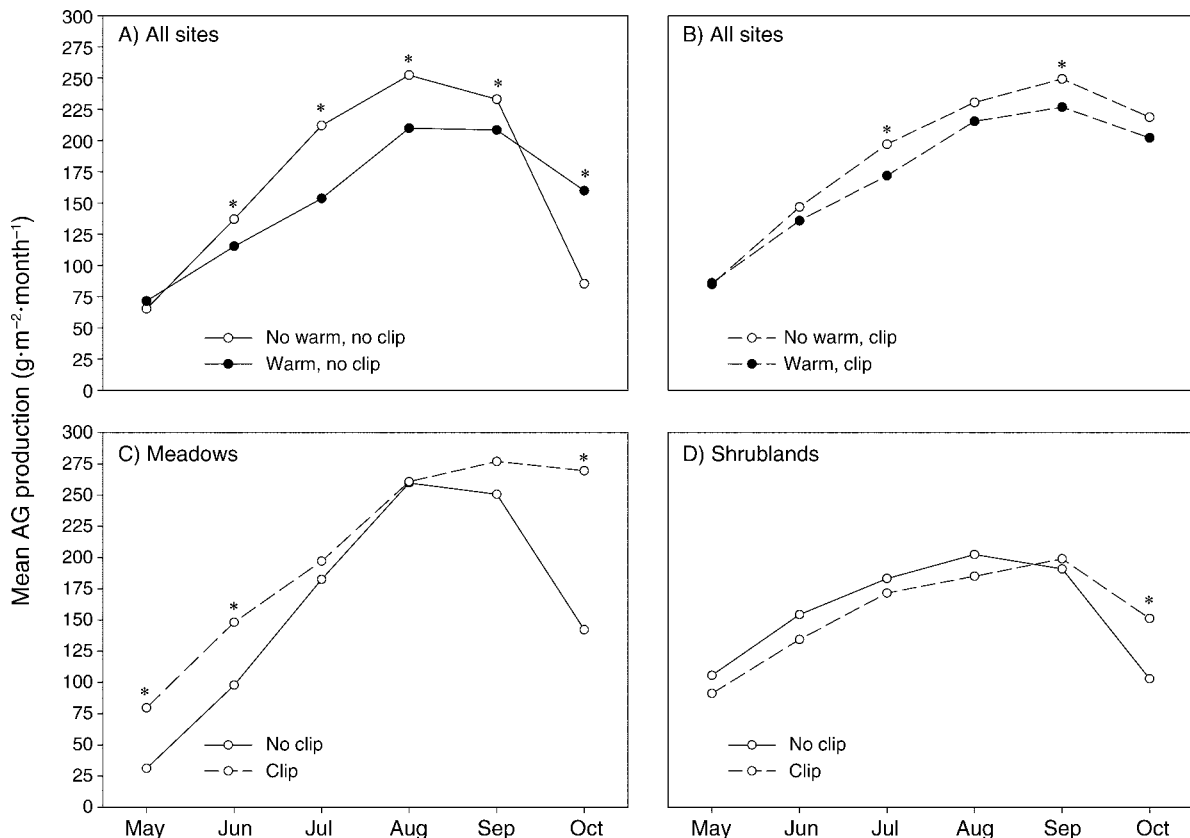


FIG. 6. Monthly averaged mean live aboveground (AG) biomass from May through October in 2000 due to (A) warm (no clip) at all sites; (B) warm (clip) at all sites; (C) clipping at the meadows; and (D) clipping at the shrublands. We separate warming effects based on presence/absence of clipping, but average over habitat for (A) and (B) because there was a warm  $\times$  clip  $\times$  month interaction. We separate clipping effects by habitat, but average over warming for (C) and (D) because there was a clip  $\times$  habitat  $\times$  month interaction (Appendix C: Table C5). The data were analyzed under a log transformation; however, here we present the untransformed mean values.

\*  $P < 0.05$ .

1999), although there are important differences. In particular, in these Rocky Mountain sites, over 80% of precipitation falls in the winter months as snowfall; soils progressively dry out over the growing season. In these sites, soil moisture and snowmelt date have important controls over plant productivity (Harte and Shaw 1995, Fisk et al. 1998, Jones et al. 1998, Williams et al. 1998, Dunne 2000). In contrast, the alpine rangelands of the northeastern Tibetan Plateau receive over 80% precipitation during the summer monsoon growing season. Winters are typically dry with occasional snowfall that melts relatively quickly due to the high solar radiation. Zobel and Singh (1997) have demonstrated that due to the influential role of the unique Asian monsoon climate, many properties of Himalayan forests, such as phenology, physiology, forest structure, and rates of ecosystem processes, cannot be predicted from data collected in other forest regions of the world not subjected to this climatic pattern; our findings suggest this may also be the case with our alpine rangeland sites

of the northeastern Tibetan Plateau. These findings caution against extrapolating results from global change-ecosystem studies to other unstudied regions within the same biome.

In Klein et al. (2004), we describe how high leaf temperatures, extended growing seasons followed by the sudden onset of winter conditions, and increased litter cover could explain decreases in species richness with warming; these physical, physiological and abiotic mechanisms could also explain the ANPP responses to experimental warming. However, while both habitats were vulnerable to significant declines in total vegetation diversity with warming, we observed differential vulnerability of habitats to changes in total ANPP with warming. Specifically, our findings suggest that the winter-grazed meadows may be more vulnerable to warming-induced total ANPP changes than the summer-grazed shrublands.

Our results provide evidence of "overcompensation" of ANPP (Turner et al. 1993) in response to clipping at

these sites. While clipping is different from grazing, our ANPP responses to clipping and actual grazing were similar. The long evolutionary history of grazing and the ample availability of soil moisture during the growing season at these sites may explain these findings, which provide further support for the conditions under which overcompensation occurs. These results were robust across habitat and across sites with different recent grazing intensity histories. These results call into question the prevailing opinion on the Tibetan Plateau, that grazing decreases the productivity of the rangelands.

The synergistic interactions between warming and clipping, where the combined treatments dampened the declines due to the strictly additive treatment effects, suggest that we cannot predict the combined effects of global changes from single factor studies. Moreover, the muted decrease in ANPP that was sometimes achieved with warming in the presence of clipping (as compared to warming in the absence of clipping) suggests that clipping (or grazing) may be an important management tool in mitigating warming effects on vegetative productivity in this region.

*Warming and clipping effects on aboveground productivity by growth form*

Despite no warming effect on total ANPP at the shrubland sites, shrub foliar ANPP increased and graminoid ANPP decreased in response to experimental warming. Warming studies at other sites have similarly observed increasing shrub growth and biomass with experimental warming (Harte and Shaw 1995, Hobbie and Chapin 1998, Arft et al. 1999, Weltzin et al. 2000, Perfors et al. 2003, Walker et al. 2006). These changes in vegetative composition may be more important for rangeland quality than the changes in total forage productivity. The results from the plant group foliar chemistry analysis revealed that shrubs are less digestible than other plant groups. Moreover, in this region, sheep browse the shrub foliage, while yaks and horses do not consume shrub foliage (Cincotta et al. 1991, Wang et al. 2000). Therefore, these vegetative compositional changes could result in herd composition changes whereby sheep are favored over yak and horses. Since yak are the basis of Tibetan culture, identity, and the traditional subsistence-based lifestyle in many regions of the Plateau, vegetation-mediated changes in herd composition could have profound social, economic, political and ecological consequences for the Tibetan pastoralists. Shrub expansion also has important implications for net energy balance and ecosystem carbon storage (Schlesinger et al. 1990, Hibbard et al. 2003, Chapin et al. 2005).

Clipping generally counteracted the warming effects on shrub ANPP. The finding that clipping decreased shrub ANPP is contrary to results from many arid systems, where grazing has been shown to increase shrubs on the landscape (Schlesinger et al. 1990). While grazing-induced increases in shrub density result from

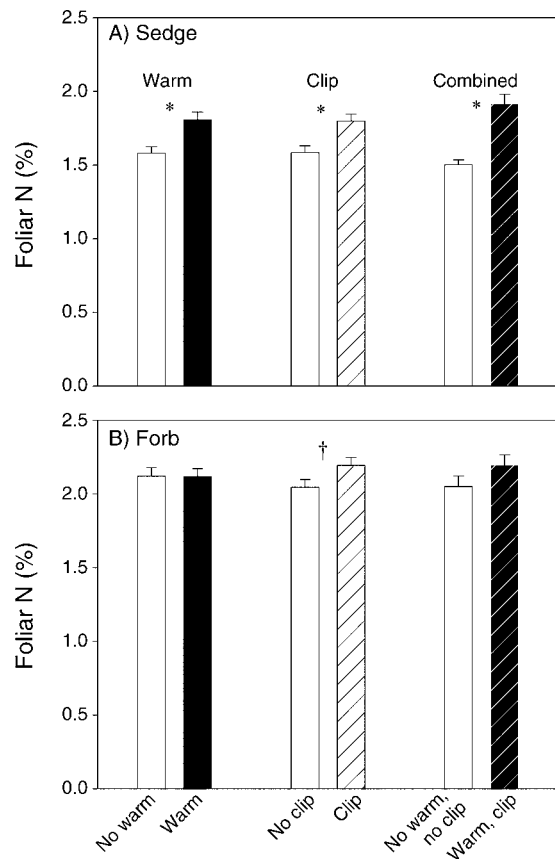


FIG. 7. Percentage of foliar N in 2000 for (A) sedges and (B) forbs. Values are mean + SE. The warming effect, the clipping effect, and the combined treatment effect are presented.

\*  $P \leq 0.05$ ; †  $0.05 < P \leq 0.1$ .

complex interactions among many factors (not just defoliation as represented by our clipping treatments), the control plots at the LG shrubland site had more shrub ANPP as compared to the control plots at the HG shrubland site. The composition of the LG and HG shrubland control plots result from more than fifteen years of different grazing intensities (Zhou et al. 2004). Thus, the more heavily grazed plots had less shrub ANPP than the lightly grazed plots; these results are consistent with our clipping results. Moreover, we found that the grazing control plots (grazed plots) and the clipped plots were similar with respect to shrub ANPP. Thus, the decrease in shrub ANPP at this site is not likely due to differential grazing vs. clipping effects. Rather, the decrease of shrub ANPP with clipping could be due to other factors, including the relatively high mean annual precipitation in this region (600 mm/yr), properties of this specific deciduous shrub species (which prefers to grow in moister areas), the lack of fire as an important process in this system, and the fact that sheep browse on the shrubs (particularly early in the growing season). By 2000, the combined treatments had no effect

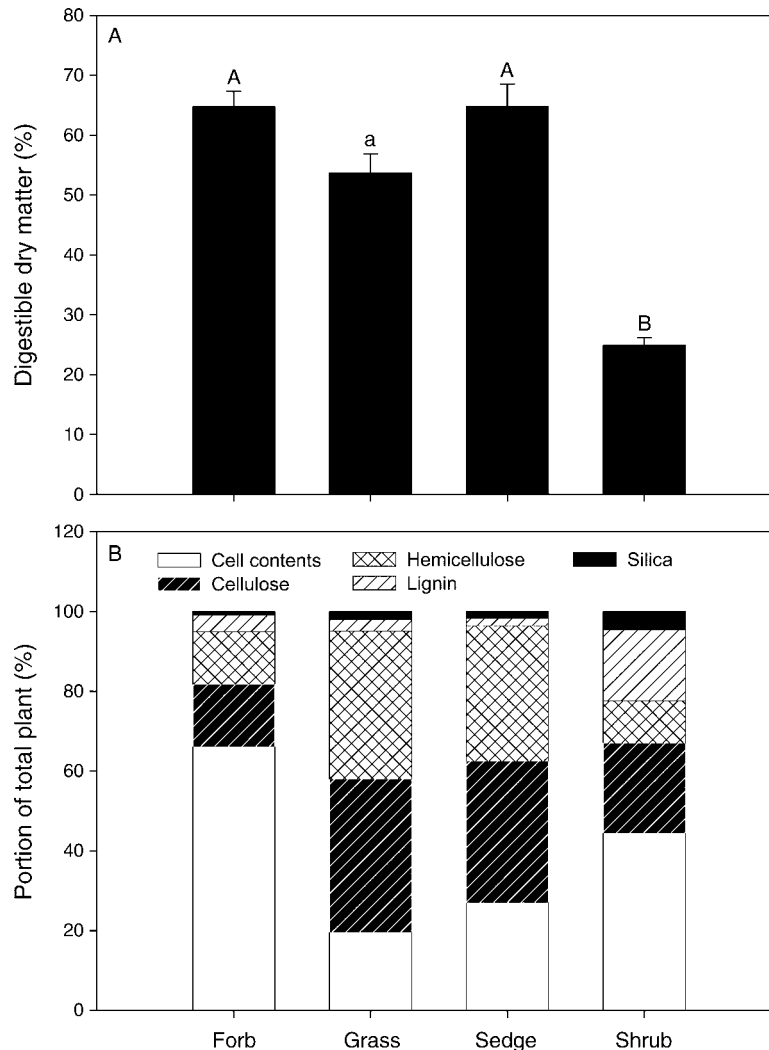


FIG. 8. Plant group comparisons of (A) digestible dry matter (mean + SE) and (B) forage chemical content. In the top figure, bars with different letters are significantly different at  $P \leq 0.05$ . Bars that share the same letter with a different case (i.e., A and a) are different at  $P \leq 0.1$ .

on shrub ANPP; the increase with warming was countered by the decrease with clipping. These findings suggest that in this study region, grazing management may be an important tool to keep warming-induced shrub expansion in check.

In our study, warming decreased graminoid ANPP. Harte and Shaw (1995) and Hobbie and Chapin (1998) found no change in graminoid biomass, while Weltzin et al. (2000) found decreases in graminoid production with experimental warming. Grass species increased with warming in monoculture, but decreased with warming when combined with forbs (Dunnett and Grime 1999); interspecific competition, rather than a direct response to warming, mediated this response. A similar phenomenon could explain the decrease in graminoid ANPP with warming at the shrubland sites. In control plots, we

found a negative correlation between shrub and grass ANPP (Pearson correlation =  $-0.7$ ,  $n = 114$ ). Therefore, at the shrubland sites, decreasing graminoids could result from the warming induced increase in shrubs. At the meadow sites, soil moisture declines with warming (which were present in all warmed plots at the HG meadow site, but only present in the warm (+clip) plots at the LG meadow site; Klein et al. 2005) could be a potential explanation for the graminoid decreases at these sites, in addition to the mechanisms described in Klein et al. (2004).

Our examination of forb species' responses to experimental warming demonstrates an individualistic response. De Valpine and Harte (2001) also found forb species' AG biomass responded differently to warming. The implications for forage quality depend on the net

balance of which forbs did better and which did worse. For example, warming increased the biomass of *Stellera chamaejasme*, a poisonous, non-palatable plant. However, warm (+clip) decreased *Oxytropis* spp., also a non-palatable plant. Warm (no clip) decreased *Gentiana straminea*, a medicinal plant that brings important supplemental income to the pastoralists. These shifts in individual non-palatable and medicinally valuable forb species ANPP may be more important for vegetation quality than the overall response of forbs as a group. Clipping consistently increased forb ANPP. Again, the identity of those forbs is more important than the overall response of forbs as a group. Clipping increased the non-palatable *Oxytropis* spp. ANPP, decreasing the value of the rangeland vegetation.

*Warming and clipping effects on aboveground monthly live biomass for 2000*

The extension of live biomass availability with warming, and the advancement and extension live biomass availability with clipping, can have important implications for pastoralism in this region of the Tibetan Plateau. In winter, domestic herbivores survive on low-quality senesced vegetation and typically lose 50–80% of body weight gained during the warmer part of the year (Zhao and Zhou 1999). Animal mortality is often highest in the spring, when animals are weak, when females are lactating, and when late spring storms are common (Cincotta et al. 1992, Zhao and Zhou 1999). Therefore, advancing and extending the growing season may constitute a substantial improvement to rangeland quality in terms of increasing herd survival and increasing the time over which live vegetation is available, since live vegetation has higher nutritive content than senesced vegetation (Nelson and Moser 1994). The finding that warming can alter the timing of forage availability also has important management implications. Tibetan pastoralists have traditionally used a grazing management system that emphasized mobility and opportunistic, but managed, grazing. Current policies have been restricting this mobility and imposing more rigid policies regulating the timing and locations of movement (Miller 1999b). Our research suggests that under certain circumstances, warming can alter the timing of forage availability in this study region. Therefore, the more rigid grazing system must account for these dynamic changes in forage availability. Our results also suggest that removing grazing from this system would shorten the time over which live vegetation is available.

*Warming and clipping effects on foliar nutritive quality*

The largest change in vegetation quality with warming may occur with the replacement of relatively higher-quality graminoids with lower-quality shrubs. With respect to foliar N and C:N ratios, warming did not consistently increase C:N ratios as we had predicted. For some plant groups, warming actually increased foliar N and decreased the foliar C:N ratio. This may reflect the

warming-induced increase in available nitrogen in the soil (Klein et al. 2004) rather than the direct warming effect on foliar chemistry. This suggests that warming effects on foliar C and N content may be more complex, dynamic or species-specific than previously thought. Clipping decreased shrub ANPP thereby improving nutritive forage quality at the shrubland sites. Both clipping and combined treatments consistently improved plant C and N chemistry, as we had predicted. However, as mentioned previously, the forage quality changes due to plant group shifts could have a larger effect on forage quality than the more subtle and dynamic within plant group shifts in leaf chemistry.

## CONCLUSIONS

Our study provides ecological evidence that remote regions of the world, and the ecosystems on which they depend, may be vulnerable to changes in climate. Local land use patterns can be carefully employed to mitigate these effects. Our findings suggest that the rangelands on the northeastern Tibetan Plateau can respond strongly to changes in temperature. Our findings also demonstrate that grazing can increase productivity and can mitigate the negative warming effects on vegetation production and quality. Thus, the prevailing view—that grazing is decreasing vegetative productivity in the region—may be oversimplifying the processes driving ongoing vegetation changes in the region. Opportunistic grazing management strategies will be required under future climate warming scenarios. This finding calls into question the more rigid and sedentary rangeland policies that are being imposed in this and other pastoral regions of the world.

## ACKNOWLEDGMENTS

We thank the Haibei Research Station staff, E. Betts, J. Hu, S. Kloss, S. Lippert, J. Z. Liu, S. McCarthy, P. Sun, and T. Thundup for assistance in the field. We thank C. D'Antonio, T. Benning, and two anonymous reviewers for their comments on this work. This research was supported by grants to J. A. Klein from the American Alpine Club, Sigma Xi, and the National Science Foundation (INT-9907375).

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#### APPENDIX A

Vegetative properties at the four experimental study sites (*Ecological Archives* A017-019-A1).

#### APPENDIX B

Method for estimating aboveground net primary productivity (*Ecological Archives* A017-019-A2).

#### APPENDIX C

ANOVA results for warming and clipping effects on vegetative properties (*Ecological Archives* A017-019-A3).