

THESIS

TIMING IS IMPORTANT: SEASONALITY OF PRECIPITATION INFLUENCES  
ECOSYSTEM PROPERTIES AND RESPONSE TO GRAZING

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## ABSTRACT

### TIMING IS IMPORTANT: SEASONALITY OF PRECIPITATION INFLUENCES ECOSYSTEM PROPERTIES AND RESPONSE TO GRAZING

Water availability and grazing are both strong drivers of grassland community structure and function. We know that water limited ecosystems, can be very sensitive to temporal changes in precipitation, influencing important properties including primary production, carbon and nutrient cycling and plant and microbial species composition. However, little is known about how the timing of water availability interacts with grazing. I conducted a global meta-analysis to investigate the importance of precipitation seasonality in determining broad-scale patterns of plant community response to grazing. I focused on the relative importance of climatic factors compared with grazing variables in influencing the effects of grazing on plant species composition and primary production. Locations with more summer precipitation experienced greater grazing-induced changes in species composition. Species composition was more responsive to grazing covariates, whereas production was more responsive to climatic variables, particularly the length of the growing season. I explored potential mechanisms for this pattern by conducting a trait study at a climate change experiment on the Tibetan Plateau. Shifting the timing of water availability toward the winter altered community-level plant traits associated with grazing avoidance and tolerance, and grazing sometimes acted as a feedback. Together, these results provide compelling evidence that the timing of precipitation can interact with grazing to drive changes in plant community structure and function. In light of climate changes that may shift the timing of precipitation in many systems worldwide, these effects are increasingly important to understand.

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# 1. HOW DOES THE TIMING OF PRECIPITATION AFFECT ECOSYSTEM PROCESSES IN ARID AND SEMI-ARID GRASSLANDS?

## INTRODUCTION

Precipitation is a strong driver of ecosystem structure and function among all terrestrial biomes. Grassland systems, particularly those that are water-limited, can be very sensitive to temporal changes in precipitation as well (Knapp and Smith 2001), and the distribution of precipitation in relation to growing season temperatures may determine some distinguishing ecosystem properties (Prentice et al. 1992). While mean annual precipitation is most often used to describe ecosystem water relations, it is becoming increasingly clear that the temporal dynamics of precipitation, such as seasonal distribution and the size and frequency of events can significantly modify ecosystem response to total precipitation quantity (Swemmer et al. 2007). I will review the differences between ecosystem properties under climates characterized by primarily summer precipitation (coupled temperature and precipitation) versus climates characterized by dry summers and wet winters (decoupled), and will also explore how climate change will potentially alter ecosystem processes under future predicted precipitation regimes.

Future climate models unanimously report changes in the temporal distribution of precipitation worldwide, although there is great uncertainty surrounding the direction of these changes (Christensen et al. 2007). Nonetheless, it is expected that in many places these changes will take the form of increases in extreme events and time between events, as well as shifts in the seasonality of precipitation. In arid and semi-arid environments, temporal changes in precipitation may result in more dramatic changes in ecosystem functioning than both increasing

temperature and increasing CO<sub>2</sub> levels, and is expected to interact with these factors as well (Weltzin et al. 2003). Therefore, there is some urgency in synthesizing how the temporal distribution of precipitation affects ecosystem processes, which has been the subject of much recent research.

Although precipitation most directly influences soil moisture, the indirect effects on plant and microbial communities may be more relevant (Heisler and Weltzin 2006). The timing of precipitation can directly influence abiotic soil processes such as drainage, infiltration, evaporation, soil temperature, and water availability for uptake by plants (Austin et al. 2004). These processes in turn affect the biotic processes of production, carbon and nutrient cycling, decomposition and microbial, plant, and animal species composition. This paper will specifically focus on the effects of precipitation timing on biotic processes in arid and semi-arid grassland ecosystems.

## REVIEW

### **Primary Production**

It is a well-established relationship that at regional scales aboveground net primary productivity (ANPP) increases with precipitation quantity (Sala et al. 1988). However, much variation in ANPP cannot be explained by variation in precipitation quantity alone. Temporal variation in ANPP is linked with precipitation variability, but is also constrained by production potential (Knapp and Smith 2001). On global scales total precipitation and therefore production potential tends to be inversely correlated with variability in precipitation inputs (as measured by CV). The highest ANPP variability occurs in grassland biomes because they generally have intermediate production and intermediate precipitation variability. ANPP

variability in very arid biomes is constrained by low production potential, whereas ANPP variability in mesic biomes tends to be low because there is relatively low precipitation variability. Grasslands are therefore the most responsive to changes in precipitation inputs, though they tend to be more responsive to increases rather than deficits in precipitation. This may be due to drought adaptations in many grassland species. Regression models of grassland ANPP are greatly improved by including precipitation variability measures as explanatory variables in addition to precipitation amount (Nippert et al. 2006).

At the local level, these broad-scale relationships are often weaker. Even among sites with the same dominant species, interannual variation in ANPP can be explained by different mechanisms (Swemmer et al. 2007). ANPP variation at mesic sites tends to be more dependent on the length of time between precipitation events, indicating low tolerance for drought stress. Meanwhile, ANPP at arid sites can be more constrained by event size and number. In these sites water is likely limiting, and increases in event size and number can increase production up to a saturating point over which the precipitation cannot be converted into new growth. Therefore, mean soil water content is insufficient to explain annual and seasonal variation in ANPP, which is often more responsive to temporal soil moisture availability (Knapp et al. 2002).

As climate changes, precipitation event sizes and time between events are expected to increase outside of the range of historic variability, and examining records for ANPP and precipitation relationships may not allow for extrapolations to future precipitation regimes (Nippert et al. 2006). Experimentally increasing the variability in precipitation of grasslands outside of the historic range tends to decrease ANPP, though not in all systems (Knapp et al. 2002, Fay et al. 2003, Nippert et al. 2006). In one study, reduction in ANPP due to increasing



variability was found to be roughly equal to results obtained from a 30% reduction in annual precipitation (Fay et al. 2003). This could be related to decoupling the water supply and evaporative demand, putting more stress on the plants and decreasing root activity. However, increased variability has been shown to increase root to shoot ratios meaning that total production might remain constant while allocation is shifted belowground.

Time lags in production response to variation in precipitation inputs add further complexity, and can occur on both monthly and annual time scales (Ma et al. 2010). Monthly aboveground production is related to both precipitation and temperature of the preceding months, whereas interannual variations in ANPP are correlated with the previous-year precipitation, the effects of which can be stronger if certain conditions such as drought persist for multiple years. Seasonally, this means that higher winter and spring precipitation will result in more productive early growing seasons with dry summers and falls decreasing late growing season production.

Production can also vary depending on the seasonality of precipitation. Systems whose temperature and precipitation peaks are temporally decoupled (decoupled systems) tend to be responsive to different inputs than systems whose precipitation inputs peak during the summer (coupled systems). Production in decoupled arid systems, such as the Colorado Plateau, has been found to be more sensitive to winter drought than summer drought, probably because plants there rely on winter precipitation for the majority of their ANPP and do not appear to use summer water inputs (Schwinning et al. 2005b). Summer monsoon rainfall is not as consistent as winter precipitation, so plants in decoupled arid climates may not have adapted to use these growing-season inputs. However, in some less arid systems the previous year's summer precipitation is a greater driver of early season production than winter precipitation (Morecroft et al. 2004), meaning that a decoupling of precipitation and temperature patterns could result in

overall decreases in annual productivity if the decreases in late season biomass production are not equally compensated by increases in early season production.

The seasonality of precipitation can also affect how much water is lost from the system. Systems with decoupled precipitation and temperature regimes tend to have lower evapotranspiration rates than coupled systems because there is less evaporative demand during the wet season. Site-level differences in ANPP response to precipitation inputs may be attributed to differences in soil characteristics. For example, in arid grassland systems, soils with a coarser texture tend to lose less water to evapotranspiration due to deeper penetration, and thus have higher ANPP (Sala et al. 1988, Austin et al. 2004). However, as systems become more mesic this relationship reverses, and coarser soils actually lose more water to leaching.

### **Carbon Cycling**

In addition to production and the implications that this has for carbon (C) sequestration, the timing of water inputs can also have great effects on respiration and decomposition, with significant consequences for ecosystem C cycling. Since decomposition is fostered by coinciding warm and wet conditions, systems whose temperature and precipitation patterns are coupled tend to experience faster rates of decomposition. In turn, shifts in precipitation that create sufficiently warm and wet conditions for a greater proportion of the year are likely to result in increasing decomposition rates and loss of terrestrial soil organic carbon (SOC) stores (Aanderud et al. 2010). However, in systems that are naturally coupled, adding winter moisture tends to have a greater impact on CO<sub>2</sub> flux than adding summer precipitation, causing a net C gain with increased winter precipitation (Chimner et al. 2010). This result indicates that changes in the quantity of dry-season precipitation can have greater effects than changes in the amount of wet-season or total precipitation. If winter precipitation takes the form

of snow, insulating effects on soil temperatures may increase CO<sub>2</sub> loss due to increased microbial respiration (Walker et al. 1999), though this has not been found to be significant in all systems (Chimner and Welker 2005).

There may also be a lagged effect of seasonal variation in precipitation on C flux. For example, increasing winter moisture in the mixed grass prairie of WY resulted in greater CO<sub>2</sub> flux during midsummer (Chimner and Welker 2005). This is likely due to increases in soil moisture and gross photosynthesis, and this result is enhanced following summer droughts (Chimner et al. 2010). In contrast, in arid systems, drought in the previous wet season can *decrease* CO<sub>2</sub> flux after a rewetting event, resulting in a net accumulation of C in the system (Potts et al. 2006). This is due to an increase in the efficiency with which the system uses this water pulse. In these particularly arid climates, decreased substrate and soil nitrogen availability following drought likely constrain microbial activity after a rewetting pulse. Although primary production is also constrained by drought, at the ecosystem level the decrease in microbial respiration seems to be greater than the decrease in photosynthesis. This suggests that plant and microbial communities have differing responses to rainfall variability.

In coupled systems, with mostly summer precipitation, CO<sub>2</sub> fluxes tend to be largest during the early summer, though increased variability of precipitation significantly reduces flux during this time of year (Harper et al. 2005). In decoupled systems, with relatively dry summers, early season respiration is mostly attributed to plant growth, and once the soils dry down respiration stops until pulses of precipitation stimulate large increases in heterotrophic respiration and ecosystem C loss (Xu et al. 2004). Large increases in microbial respiration after rewetting could be due to soil aggregates breaking up and releasing more available labile C (Harper et al. 2005). Indeed, sites with higher labile organic C, such as high production sites and

those with fine-grained soil, tend to be more sensitive to water pulses, resulting in increased C losses due to heterotrophic respiration (Austin et al. 2004, Xu et al. 2004). However, after several subsequent rain events this respiration pulse has been shown to decline, indicating that all labile substrates may have been exposed during the preceding events (Zhang et al. 2010).

The size of the respiration pulse after rewetting is dependent on species composition (Norton et al. 2008), how dry the soil is initially, and the size of the rain event (Xu et al. 2004). The size of the rain event is generally positively correlated with soil moisture and CO<sub>2</sub> exchange (St Clair et al. 2009), and small pulses may be too small to affect soil moisture or stimulate physiological activity in the form of CO<sub>2</sub> flux and primary production. The minimum threshold amount of rainfall to stimulate activity can vary throughout the growing season. A case study in Mongolia (Hao et al. 2009) determined that during the early season, when the canopy was not as filled in, small events (<5mm) could stimulate production, but once leaf area index (LAI) increased later in the season, events smaller than 5mm did not penetrate deeply in the soil, and could only stimulate CO<sub>2</sub> loss through microbial respiration. However, this threshold differs among systems, and can be influenced by the decoupling of nutrient supply and demand as well as rooting depth of plants.

Less frequent events tend to increase cumulative CO<sub>2</sub> loss significantly more than more frequent events of the same size (Zhang et al. 2010). In fact, a high frequency of rainfall events can actually increase C storage in the system. Microbial biomass responds inversely to the frequency of rain events, possibly contributing to greater C loss during infrequent rewetting events. Nonetheless, experimentally increasing rainfall variability, creating more extreme but less frequent events, has been shown to result in significant net decreases in annual CO<sub>2</sub> flux (Harper et al. 2005). This is probably because decreases in CO<sub>2</sub> flux during prolonged dry

periods outweigh the temporary increases after rewetting. Respiration responses are related most strongly to surface soil moisture (Qi et al. 2010), so the drying of the top layer during dry intervals, and the deeper percolation of larger events will cause a much lower mean surface soil moisture during the growing season.

Reductions in respiration and CO<sub>2</sub> uptake by plants are both greater in response to variability in soil moisture than to mean soil water content, indicating that precipitation variability may be more important than total precipitation in terms of ecosystem C exchange (Knapp et al. 2002). However, total annual precipitation does modify the magnitude of both respiration and photosynthesis responses, with lower precipitation systems showing greater sensitivity to soil drying (St Clair et al. 2009). Decreases in C flux are likely mediated by plant responses, with lower root mass, root respiration, and root exudation under more variable rainfall regimes, which in turn reduce C inputs into the rhizosphere (Harper et al. 2005). Interestingly, it has been shown that soils experiencing increased variability in precipitation were less sensitive to temperature than under ambient rainfall conditions, meaning that the timing of precipitation may be important in modifying effects of warming.

### **Nutrient Cycling and Microbial Community**

Because nitrogen (N) availability is tightly coupled with soil moisture, changes to water inputs can have strong effects on N cycling, and many of these effects can be attributed to changes in microbial communities and populations. During extended dry periods, N tends to build up in the system due to decreased diffusion and increases in low C:N substrates from microbial deaths (Norton et al. 2008). Rewetting therefore leads to a pulse of available N to plants. Phosphorus can also become more available after a water pulse. Snow can impact N cycling as well, increasing rates of N mineralization and net nitrification (Walker et al. 1999).

Water pulses lead to increased N fluxes with more losses due to volatilization and leaching, as well as higher rates of mineralization due to increased microbial activity (Austin et al. 2004). This mechanism is supported by observed increases in microbial biomass during the first 8 hours after a water pulse, after which it declines (Norton et al. 2008). Plant species composition seems to mediate different rates of decline following the initial microbial growth period. Plant species composition can affect soil nitrification processes as well, with certain species accelerating nitrification rates and gaseous N<sub>2</sub>O emissions following water pulses. Mineralization pulses are especially large in finer textured soils with larger labile C and N pools. Coarser textured soils on the other hand tend to lose more N due to leaching, so the mineralization pulses are not as large. When precipitation falls primarily during the winter, nutrient supply and plant demand are decoupled, causing even greater N losses due to leaching (Austin et al. 2004).

The timing of precipitation may affect microbial community composition. Although much remains unknown about this, we do know that different environmental conditions, particularly with regard to soil moisture, can favor different types of soil microbes. Fungi are more tolerant of desiccation and have higher N-use efficiency than bacteria, and thus, tend to be more abundant during the dry season, which can lead to slower rates of N mineralization (Austin et al. 2004). However, summer droughts and winter warming have been shown to affect mycorrhizal fungal associations and result in increased colonization of plant roots, but decreased hyphal densities (Staddon et al. 2003). While the decline in hyphal density is likely a direct effect of decreased water availability, the other effects may be indirect effects of changes in plant species composition caused by drought and warming.

## **Plant Community Composition**

Changes in precipitation regimes may affect plant diversity and species ranges, as well as alter competitive dynamics between species. While the effect of changes in competitive abilities depends on how strongly competition is affected, as well as the sensitivity of the species in question (Levine et al. 2010), if competitive advantages change along with climate, rapid shifts in community structure and function could occur. Furthermore, changes in precipitation may interact with other climatic changes such as increasing temperatures and atmospheric CO<sub>2</sub> concentrations to further drive changes in species composition (Tietjen et al. 2009). This could have dramatic effects on biodiversity of animals as well as plants, if habitat or forage quality is decreased, and may also feedback to affect local and regional climate if albedo and evapotranspiration are altered significantly (Weltzin et al. 2003). Alterations in community structure that increase the abundance of woody species may result in cascading effects on ecosystem processes such as nutrient and carbon cycles and vegetation dynamics. Increases in shrubs can result in much higher resource heterogeneity in the landscape, with resources accumulating beneath the woody plants, and the spaces between losing nutrients rapidly, causing resource islands around the shrubs (Reynolds et al. 1999).

Supplementary watering during winter and summer has revealed the differing effects of seasonality of precipitation on plant communities (Robertson et al. 2010). In systems with naturally coupled temperature and precipitation patterns, increases in winter precipitation may facilitate increases in diversity and shifts in species composition, as winter precipitation is most important for recruitment. However, in systems with naturally decoupled precipitation and temperature, native perennial species rely most strongly on winter precipitation, which can moderate the impact of summer drought on species composition (Morecroft et al. 2004). Summer

precipitation on the other hand tends to increase growth and density of existing species, suggesting that it may have a more stabilizing effect on productivity. The response of individual species to changes in precipitation patterns is not always predictable, as the response to any given change is determined by a complex interplay among functional growth form, reproductive strategy, photosynthetic pathway, phenology, and competition.

Competition plays an important role in differentiating species niches, and in environments with high soil moisture variability there are several adaptations that species can employ to differentiate themselves from competitors. These different strategies combined with high levels of inter-annual water variability may be what allows arid and semi-arid systems to maintain surprising levels of species diversity (Chesson et al. 2004), as the annual timing of resource availability can determine which strategy may be favored during a given year. There are two components to competition in a variable water environment, as outlined by the two-phase resource dynamics hypothesis (Goldberg and Novoplansky 1997). These are the pulse period, in which species that are able to most quickly extract soil water will be favored, and the interpulse period, which is the dry period in which drought tolerance traits become most important to survival. The strategy that a plant uses may be geared toward one or another of these phases, and include phenological adaptations such as setting seed early before dying (annuals), becoming dormant (perennials), and timing germination to make use of early resources; they also include physiological adaptations such as minimizing water loss through storage and C4 or CAM photosynthetic pathways, or tolerating drought through utilizing more stable water sources (Chesson et al. 2004).

Partitioning of resources can occur both spatially and temporally, though the two may be strongly correlated. For instance, the two-layer model suggesting that grasses and woody



species use water sources from different vertical soil layers (Walter 1971) also implies that they utilize water from different temporal precipitation events (Golluscio et al. 1998). Shrubs, trees, and other deep-rooted species tend to make use of deeper water sources, which are recharged during winter precipitation events. Meanwhile, shallow rooted grass species generally make use of water in the top layers of soil that falls during the growing season (Kulmatiski et al. 2010). While it has been verified that grasses and woody species do not often compete strongly for water (Golluscio et al. 1998), isotopic analysis has shown that their water use can sometimes overlap significantly (Schwinning et al. 2005a, Kulmatiski et al. 2010), and shrubs in particular can be very flexible in their vertical use of water resources (Dodd et al. 1998).

The size of the precipitation event can also affect which species are able to utilize the water. Unless there is a particularly large event, summer precipitation tends to only penetrate into the top layer of soil where it is either taken up by plants or evaporated (Golluscio et al. 1998). Although grasses are always able to respond to large rainfall events during the growing season, they cannot use all of the water when it percolates deeper than their roots. Shrubs on the other hand are only able to respond to large rainfall events when the soil is already dry at their rooting depth, otherwise their growth is not water-limited, and it is only during particularly dry seasons that this condition would coincide with phenologically active periods. Because of this, in decoupled environments deeper-rooted shrubs tend to be the most drought-adapted species (Morecroft et al. 2004, Golluscio et al. 2009).

There is evidence that there is a tradeoff between the dependence on winter precipitation of deeper-rooted plants, and the ability to use summer precipitation of the more shallow rooted plants, indicating that the latter group may be more opportunistic in their water use (Golluscio et al. 2009). Interestingly, this means that even in quite arid environments plants

are not necessarily able to make use of large increases in annual precipitation if it occurs during the summer months. Because summer monsoon rains in arid systems tend to be much more uncertain than winter precipitation, species in decoupled climates may not have evolved adaptations to increase summer rain use efficiency (Schwinning et al. 2005b). This means that deeper rooted species such as shrubs are relatively insensitive to pulses or temporary increases in water supply, while grasses can have greater growth responses (Kochy and Wilson 2004). Moreover, grasses in stands of shrubs also exhibit a lack of response to increasing water availability, implying that shrubs may serve to stabilize water supply for other species. This may be due to hydraulic lift, in which water from deeper sources is relocated to surface soil via the root system of shrubs, where it can then be utilized by other plants (Caldwell et al. 1998).

Increasing winter precipitation tends to have the expected effect of favoring deeper-rooted, cool-season plants both observationally (Snyder and Tartowski 2006) and experimentally (Chimner et al. 2010), while summer droughts result in decreases in perennial grass cover (Morecroft et al. 2004). In some arid decoupled systems, however, herbaceous species actually respond negatively to shifting precipitation toward the summer, with decreases in biomass, cover, and density (Bates et al. 2006). Shrubs on the other hand do not respond strongly in terms of cover or density, but instead can produce more reproductive structures with later water availability. This effect is likely due to the early phenology common to places with very dry summers (Bates et al. 2006). Species in arid systems tend to enter dormancy early in the season and do not use summer precipitation to support the next year's growth (Schwinning et al. 2005b). Therefore, shifting timing of precipitation toward the summer essentially causes winter drought, which decoupled systems tend to be much more sensitive to than summer drought.

Some species, however, have adapted a flexible phenology that can take advantage of water inputs when they become available (Reynolds et al. 1999).

Resource partitioning among different growth forms may differ depending on life stage. In savanna systems, for example, trees use different depths of water during different life stages (Weltzin and McPherson 1997). During the recruitment phase, tree seedlings utilize even shallower water than grasses, which may increase recruitment rates within established grassy areas. As they mature, tree seedlings increasingly reach to deeper water sources, until after around two years of age their depth surpasses that of grasses. Shrubs show a similar change in resource partitioning in which the growth of shrubs is much more closely linked to fluctuations in water inputs during the early stages of development, after which it become more insensitive (Reynolds et al. 1999). This means that shifts in the timing of precipitation and therefore the depth of soil water sources, may impact species differently during different life stages, and could alter the stability of the coexistence between grasses and woody species.

Although decoupled systems tend to favor woodier species, coupled systems tend to favor C4 (warm season) grasses and CAM plants (Winslow et al. 2003). This is because these photosynthetic pathways have better water-use efficiency at high temperatures than C3 (cool-season) species (Amundson et al. 1994). When precipitation and temperatures are coupled, both C3 and C4 grass phenologies tend to be linked closely with water availability (Niu et al. 2005). However when precipitation and temperature are decoupled, C3 plants are more active and show the greatest response to water inputs during the fall, while C4 plants are more active and more responsive to water inputs during the mid-summer. This may be due to seasonal differences in whether water or temperature is the limiting factor to growth. C4 plants in general are not as

affected by interspecific competition as C3 plants, indicating that C4 plants might be better competitors for water due to higher water-use efficiency (Niu et al. 2005).

Plant species diversity has been shown to increase in response to more variable precipitation (Knapp et al. 2002). Communities tend to shift toward more drought tolerant composition because increased variability in precipitation generally leads to more drought stress due to the top layer of soil drying during longer intervals between events. Meanwhile, more extreme events may lead to greater soil recharge in the deeper water layers and less overall evaporative water loss (Tietjen et al. 2009). Indeed, deeper-rooted forbs tend to increase production in response to larger precipitation events, while grasses tend to favor more frequent small events (Robertson et al. 2009).

More extreme but less frequent rainfall events can also differentially affect the response of C3 and C4 plants at the physiological level (Fay et al. 2002). C3 forbs tend to be more responsive to soil moisture, with stomatal conductance and photosynthetic efficiency increasing with soil moisture. C4 grasses on the other hand do not respond as much to soil moisture, possibly because of a higher innate water use efficiency and drought tolerance. Fay et al. (2003) found the dominant species in their system to be even less responsive than other C4 graminoid species. Coupled systems that receive most of their precipitation during summer monsoons tend to have more variable precipitation patterns in general, thus, tolerance of high variability may be what gives these dominant grass species a competitive edge.

Altering the timing and distribution of precipitation events has also been shown to impact the spread of invasive species, which may be conferred competitive advantages over native species by utilizing soil water from different depths or at different times during the

growing season (Kulmatiski et al. 2006). For example, though increasing winter precipitation in an already decoupled system did not result in strong responses from native species, *Bromus tectorum*, an invasive annual plant, did respond positively to this treatment (Bates et al. 2006). A similar experiment in a coupled system found that increases in snow aided recruitment of the invasive taprooted forbs *Centaurea diffusa*, *Gypsophila paniculata*, and *Linaria dalmatica*, without response from native species (Blumenthal et al. 2008). These same invaders were seldom seen without the addition of snow.

Isotopic analysis of water use by exotic and native plants show that increasing invasion under altered rainfall is likely due to the different timing of water extraction by the exotic invaders (Kulmatiski et al. 2006). Exotic annual grasses tend to use water early in the growing season preempting the activity of native plants, while forbs with deep taproots are able to use deep soil water after the native plants have already senesced in the later part of the growing season. The presence of invasive species such as *B. tectorum* can also act as a feedback in the ecosystem, accelerating rates of carbon and nitrogen cycling, and thereby creating conditions more favorable for its own growth (Norton et al. 2008). These consequences are more pronounced when there are frequent summer rain events, and under these conditions the changes in ecosystem properties can be quite significant.

## DISCUSSION

Precipitation and its effects on soil moisture mediate most ecosystem processes, and differences in precipitation regimes globally are responsible for many of the ecosystem features that distinguish biomes from one another (Prentice et al. 1992). The timing and distribution of precipitation is an important factor in driving these differences, although it is only relatively recently that the effects of precipitation timing have been explored in a mechanistic

way. Since precipitation regimes are expected to experience changes worldwide, it is important that the implications of these changes on ecosystem processes are incorporated into models, yet there are still gaps in our understanding. This is partly due to extreme complexity, as water plays a role in nearly all aspects of ecosystem functioning. This makes predicting the effects of precipitation changes quite challenging. Nonetheless, there are still some important avenues of research that will greatly improve our understanding of the subject. I will discuss some potential directions for future studies, as well as the strengths and limitations of the main approaches used to investigate these questions.

While some notable multi-factor climate studies have been conducted, the interactions between timing of precipitation and other global change processes are still relatively unknown. Warming, CO<sub>2</sub> increases, grazing, land-use change, changes in fire regimes and nutrient deposition will all likely interact with precipitation timing, and should be investigated further through cross-site observation, multi-factor experimentation, and modeling. One potential interaction between warming and precipitation timing is that more winter precipitation may fall as rain rather than snow. Some studies suggest that the form of precipitation can be important, though the effects are unclear (Walker et al. 1999). Isotopic analysis may be an important tool in distinguishing the effects of rain versus snow by tracking the flow of water from each form through the ecosystem.

There is also a dearth of information regarding belowground processes. Very few studies investigate how microbial communities will respond to shifts in precipitation timing, though the importance of these communities in mediating ecosystem processes is becoming increasingly apparent. I suggest that future studies include measurements of microbial populations and community composition, as well as decomposition dynamics. While it is known

that edaphic differences affect response to precipitation inputs, there is still little beyond the inverse texture hypothesis in the way of elucidating these effects. More needs to be known about how soil properties interact with precipitation timing, as well as how precipitation timing can feed back to alter these soil properties.

There are four main approaches used by scientists to investigate the effects of the timing of precipitation on ecosystems:

1. *Observational studies that compare ecosystem properties across climatic gradients.* These studies are useful in identifying broad patterns that can be better generalized across systems, particularly when they are global in scope. However, while this method can be effective for understanding intrinsic differences between systems with differing precipitation regimes, it cannot provide much insight into how these systems might respond to changes in precipitation.
2. *Observational studies that compare ecosystem responses to natural seasonal and annual variability in precipitation.* These studies can be an elegant way of investigating short-term ecosystem responses to precipitation inputs, but are not as useful for looking at effects of sustained shifts in precipitation. They are also constrained by only looking at the historic range of variability in precipitation, which climate models predict will be surpassed in many systems.
3. *Experiments that manipulate water availability through supplemental watering, snow fences, or rainout shelters, and investigate the response of ecosystem processes to these treatments.* These studies are quite useful in identifying the mechanistic basis of ecosystem responses, however, the nature of these experiments is that they are usually single-system investigations, and are often only in place for a few years due to time and money constraints. I suggest that more coordinated efforts be established to investigate long-term, multi-system

responses to certain precipitation manipulations with a uniform experimental design. Because precipitation change is expected to interact with other simultaneously occurring global changes, multi-factor climate experiments will be necessary to understand these interactive effects.

4. *Ecosystem models that incorporate hydrological and vegetation responses to altered precipitation.* In general, these models can be very useful tools and will only improve as mechanistic knowledge is gained through experimentation and observation. However, models that fail to incorporate the hydrological differences associated with temporal precipitation patterns, and simply use mean annual precipitation as a black box for water availability may be drastically oversimplifying a key ecosystem driver that affects almost all ecosystem processes either directly or indirectly. Models may also be improved by including feedbacks that large-scale vegetation shifts may have on climate.

## CONCLUSION

The timing of precipitation affects belowground microbial communities as well as net photosynthesis, which together determine decomposition dynamics, C and N cycling, and productivity. As precipitation regimes shift due to climate change, altering these processes alone could result in changes to ecosystem functioning, but in concert with expected changes in vegetation could cause system flips and rapid restructuring of ecosystems. The implications of altered precipitation regimes can be quite complex and difficult to predict because these processes can have cascading effects on species interactions, soil properties, production, climate, fire regime, and nutrient cycling. Improvements in our understanding of these complexities will be gained through coordinated efforts in experimentation and synthesis.



## 2. SIZE ISN'T EVERYTHING, TIMING IS ALSO IMPORTANT: CLIMATIC INFLUENCES ON VEGETATION RESPONSE TO GRAZING

### INTRODUCTION

Although in geographic extent grazing is the largest land-use on earth (Asner et al. 2004), there is still a good deal of uncertainty about why certain ecosystems are more sensitive to the effects of grazing than others. Water availability and grazing are both strong drivers of rangeland community structure and production (Milchunas et al. 1988, Williams et al. 1996, Olf and Ritchie 1998), and though we know that rangeland communities, particularly those that are water limited, can be very sensitive to temporal changes in precipitation (Knapp and Smith 2001, Austin et al. 2004), little is known about how the timing of water availability interacts with grazing (Milchunas et al. 1994, Veblen 2008). Nonetheless, systems whose precipitation falls primarily during the growing season and those whose precipitation falls primarily during the winter have notable differences that are likely to influence their response to grazing.

Climate change scenarios predict that many coupled systems will experience shifts in precipitation regimes, causing peaks in temperature and precipitation to become temporally decoupled, and vice versa (Christensen et al. 2007). Growing season length is another variable that is expected to change under future climates, with earlier springs and later summers due to warming (IPCC 2007). To understand the implications of these shifts, it is important to assess how plant community response to grazing depends on the seasonality of water availability and the length of the growing season.

Among terrestrial rangeland systems, some are able to sustain populations of grazing animals while maintaining a stable-state of vegetation (Biondini et al. 1998, Stohlgren et al. 1999, Arevalo et al. 2011), whereas others have undergone irreversible changes as a result of grazing, some of which degrade the system to the point where they can no longer support grazers (Asner et al. 2004). Changes can include encroachment by shrubs (Austin and Urness 1998, Roques et al. 2001) or exotic plant species (DiTomaso 2000), extirpation of native plant species (Olf and Ritchie 1998), and erosion of soil. Some changes due to grazing may be reversible, such as shifts in abundance of species (Chase et al. 2000, Fuhlendorf et al. 2001) and traits (Diaz et al. 2007), or changes in production (Milchunas et al. 1994, Castro and Freitas 2009), soil characteristics (Fernandez-Lugo et al. 2009), and nutrient availability (Augustine and McNaughton 2006). However, reversible changes could potentially compound upon each other to tip the ecosystem past thresholds (Sasaki et al. 2008), and many of these grazing effects also have the potential to interact strongly with shifts in the timing of precipitation and other climatic changes (Fuhlendorf et al. 2001, Weltzin et al. 2003, Austin et al. 2004).

Results of previous meta-analyses and syntheses have identified several key drivers that may be responsible for certain systems being more sensitive to grazing (Milchunas and Lauenroth 1993, Proulx and Mazumder 1998, Chase et al. 2000), but there remains a large amount of unexplained variation. In particular, productivity and evolutionary history of grazing have been identified as two of the most influential factors, and have formed the basis of certain classic conceptual models regarding how systems respond to grazing (Milchunas et al. 1988). I included these variables in my model, and hypothesized that the timing of annual precipitation and the duration of the growing season would also contribute to grazing response.

Because grazing has been in practice longer than most scientific experiments, the majority of studies on the effects of grazing, including the present study, use grazing exclusion to compare grazed and ungrazed vegetation. These studies do not strictly test the effects of grazing on species composition, but rather test the effects of grazing removal. This is a subtle yet important difference.

It is tempting to conclude that communities that show greater changes in species composition after grazing removal are more sensitive to grazing, because there are greater differences between the grazed and ungrazed vegetation. This may be a misguided conclusion, because the ability to recover after a disturbance can be an indication of resilience (Cingolani et al. 2005) and elasticity of the system, whereas inability to change or recover can indicate that irreversible changes have already occurred, or that the system has crossed a threshold to an alternate state, and may not have the ability to return to previous conditions (May 1977). Unfortunately, the nature of grazing exclusion studies does not allow us to discern whether changes in species composition due to grazing represent a return to a previous state or a transition to an alternate state.

The successional rangeland equilibrium model (Ellis and Swift 1988) assumes that changes in species composition after grazing removal represent a directional change toward the original vegetation, prior to the introduction of grazing, implying that the system has strong internal regulation. However, this is not necessarily the case. On the other extreme, vegetation can move toward new or alternate stable states, with climatic drivers maintaining the system in non-equilibrium through irreversible transitions (Westoby et al. 1989). It is likely that both equilibrium processes and non-equilibrium processes are at work in any given system, but the relative strength of these processes can be influenced by various drivers, both internal and

external, and can vary based on spatial or temporal scale as well (Huston 1979, Ellis and Swift 1988). Therefore, when grazing is removed, climatic factors may modulate and impose destabilizing forces on the associated directional response of the plant species composition (Briske et al. 2003).

Meta-regressions can be extremely useful in identifying broad patterns, and the drivers that act as main contributors to these patterns. In this analysis I sought to identify the relative importance of various climatic factors and grazing variables in determining the effect of grazing on changes in species composition and primary production. We particularly focused on the contributions of precipitation seasonality and growing season length, which have not been investigated in previous studies of this nature. In order to do this I assembled a global dataset of grazing exclusion studies along with associated climate data, and applied a Bayesian hierarchical meta-regression model to assess what the most important factors are in determining sensitivity to grazing. Results from this model allow us to identify which systems may be more sensitive to grazing, as well as which areas may become more sensitive in the future due to changes in precipitation patterns and climate warming. Because of the nature of this analysis I was also able to determine which types of vegetation communities are more sensitive to different drivers.

## METHODS

### **Literature Search**

Data were obtained from herbivore exclusion studies globally from a variety of sources, including other meta-analyses, articles on the ISI Web of Knowledge (<http://apps.isiknowledge.com>) database, and to avoid publication bias I solicited unpublished data from scientists and networks of scientists who I knew were conducting grazing studies. I

limited the studies to those that were concerned with the effects of large, mammalian herbivores in terrestrial rangeland systems.

Because Milchunas and Lauenroth (1993) had similar requirements for their meta-analysis, I used applicable data from their study (n=157 comparisons), and conducted a literature search for studies that had been published since 1990. The search in Web of Science was done with the following inquiry in November, 2011, and yielded 1093 articles:

```
((TS=((graz* OR herbiv* OR enclosure*) AND (plant or vegetat* OR tree* OR shrub* OR grass* OR forest* OR forb* OR herb* OR savanna*) AND (communit* OR species OR composition OR richness OR divers*) NOT (tropic* OR marine OR aquatic OR freshwater OR rodent* OR insect* OR lagomorph* OR arthropod* OR "small mammal"* OR paleo* or plankton* or tidal* or intertidal* or sea* or alga* or fish* or bird* or larva* or nematod* or fossil* or invertebrate* or predat*)) AND TI=(graz* OR herbiv* OR exclos* OR ungraz*)))) AND Document Types=(Article)
```

Refined by: Web of Science Categories=( ECOLOGY )

Timespan=1990-2011. Databases=SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH.

Lemmatization=On

The following criteria were used to determine inclusion in the dataset:

- (1) Studies that compared ungrazed plots with grazed plots in close proximity, during the same year. Treatments must have been in effect for at least 4 years. Studies that compared the same plot before and after grazing abandonment were not included due to the confounding temporal factor, and those that compared different grazing regimes or intensities but did not have an ungrazed treatment were not included.
- (2) Articles must have reported data for cover, biomass, abundance or density at the species level for the two different treatments. Sampling must have occurred while the treatment was still in effect (i.e. grazing treatments must still be grazed, ungrazed treatments must not be currently grazed).

- (3) Grazing was performed by ungulates or livestock such as goats, sheep, or cattle. Small mammal (i.e. rodent, lagomorph) or invertebrate grazers were not included. Grazing treatments that simulated grazing by mowing or clipping were not included.
- (4) Studies were not included if the grazed treatments were grazed during only the winter months in order to keep the seasonality of grazing relatively consistent.
- (5) Locations must be temperate climates that are arid to sub-humid. Because tropical locations do not have strong seasonality, and in these places the growing season is entirely determined by precipitation, locations whose mean monthly temperature is never below 5°C were excluded from the analysis. I further limited the data to studies that occurred in naturally occurring rangelands, with mean annual precipitation no higher than 1200mm, and no transplanting, burning, or mowing occurring to maintain the vegetation type.
- (6) Studies were not included if there were other major confounding factors (i.e. one plot was mowed and one was not, or burned or with differing climates, communities or land-use histories aside from grazing).

### **Data Extraction**

We found a total of 80 studies representing 93 locations with n=222 grazing comparisons, including data from Milchunas and Lauenroth (1993) that met the criteria. Among these comparisons, grasslands were most heavily represented (n=138), followed by shrublands (n=57), and then woodlands (n=27). Most studies were fencing studies, in which a section of long-term grazed area was fenced off from use by herbivores.

The impact of grazing on species composition was assessed by comparing the relative abundances of species between each pair of grazed and ungrazed treatments at a given site. These data were obtained by extracting cover, biomass, abundance, or density data from

tables or graphs of published articles, or in some cases directly from the authors. When multiple forms of abundance data were available, areal cover was used. When available, the total aboveground net primary productivity (ANPP) was also obtained for each treatment. Each study was categorized based on its dominant vegetation type as grassland, shrubland, or woodland. Experimental variables unique to each study, such as the duration of grazing exclusion and the qualitative or quantitative (if available) intensity of grazing were obtained, and the latitude and longitude coordinates for each site were determined as closely as possible based on reading the article.

For each separate location, 30 year mean climate data were obtained to the nearest ten minutes from the Climatic Research Unit, University of East Anglia (New et al. 2002). From this dataset I used mean monthly temperature and mean monthly precipitation, as well as CV for monthly precipitation. Following the format from Milchunas and Lauenroth (1993), each location was also ranked based on history of grazing.

### **Effect Size**

For an indicator of grazing effect size on species composition, I used a species dissimilarity index ( $D$ ), which I calculated by taking the complement of Whittaker's (1952) association index, comparing species composition data from the grazed and ungrazed plots of each individual site. For studies in which there were multiple grazing treatments (i.e. different intensities),  $D$  was calculated as a separate data point for each grazed treatment. This was calculated by taking half the sum of the absolute difference in relative cover between the grazed (g) and ungrazed (u) treatments for all species ( $j$ ) (Equation 1).

$$D(g,u) = \frac{1}{2} \sum_j \left| \frac{y_{gj}}{\sum_j y_{gj}} - \frac{y_{uj}}{\sum_j y_{uj}} \right| \quad (1)$$

In this equation,  $y_{gj}$  represents the absolute abundance (cover, biomass, or density) of species  $j$  in the grazed treatment and  $y_{uj}$  represents the absolute abundance of species  $j$  in the ungrazed treatment. I also calculated the production effect ( $E$ ) as the proportional change in ANPP in grazed versus ungrazed treatments (Equation 2).

$$E(g,u) = \frac{(ANPP_g - ANPP_u)}{ANPP_u} \quad (2)$$

### Model Construction

We used a Bayesian meta-regression approach to analyze the relative effect of various climate and grazing covariates on grazing effect size, using species dissimilarity ( $D$ ) and production effect ( $E$ ) as dependent variables. The meta-regression approach is similar to multiple regression in that it allows determination of how multiple factors affect the dependent variable, and compare the relative importance of each factor in determining effect size. This approach is a more quantitative way of conducting meta-analyses than vote counting, and provides a way of accounting for potential confounding factors and dissimilarities in study design (Gurevitch and Mengersen 2010).

All independent variables were centered and standardized by subtracting the mean from each data point and dividing by the standard deviation so that regression coefficients could be directly compared with one another. I used a hierarchical model, allowing each regression coefficient to vary depending on community type, as well as a pooled model of data from all



communities. All of the variables included in the models were selected a priori as factors that I thought would be important in determining grazing effect. Thereby I avoided model selection, data dredging, and over-parameterization (Thompson and Higgins 2002).

The variables I chose are described in detail below:

- *Community Type (c)*: Each data point was classified by vegetation community type, as grassland, shrubland, or woodland, depending on the dominant vegetation. Grassland communities included some meadows, wetlands, and alpine sites. Woodland communities included savanna, forest, and pinyon-juniper vegetation types.

Experimental covariates

- *Duration of Grazing Exclusion ( $X_1$ )*: The number of years the grazing exclusion treatments were in effect before sampling. If the site was never known to have been grazed, a maximum of 100 years was assigned.
- *Grazing Intensity ( $X_2$ )*: When available, this number was given as a percentage of ANPP consumed by grazers. When stocking rates were supplied, an estimate of consumption was calculated based on a standard animal unit consuming 12 kg/day. For each community type, sites with both qualitative (Light, Medium, Heavy, Very Heavy) and quantitative (% Consumption) data for grazing intensity were used to estimate the average consumption for each qualitative level of grazing. These average values for each community type were then applied to sites in which only a qualitative assessment of grazing intensity was available. When neither qualitative nor quantitative estimates of grazing intensity were available, the average consumption level for that community type was applied.

Location-level variables

- *Seasonality of precipitation ( $X_3$ ):* This metric was calculated as the mean monthly precipitation (mm) during the growing season divided by the mean monthly precipitation during the winter (see definition of growing season below). Therefore values greater than 1 imply that summer precipitation is greater per unit time than winter precipitation. Values less than 1 imply that there is more precipitation per unit time during the winter than during the growing season.
- *Growing season length ( $X_4$ ):* The number of months in which mean temperatures are greater than 5 °C.
- *Mean Annual Precipitation ( $X_5$ ):* The mean yearly precipitation.
- *Evolutionary History of Grazing ( $X_6$ ):* Milchunas and Lauenroth (1993) used an expert ranking system to quantify evolutionary history of grazing, between 1 and 4 (short to long). When available for a given location, the rank that they assigned was used. When unavailable, sites were categorized as Short, Medium, or Long history of grazing, based on literature and sites nearby. A coarse estimate of the rank was then applied, where sites characterized as Short were given a rank of 1.5, sites characterized as Medium were given a rank of 2.5 and sites characterized as Long were given a rank of 3.5.

We applied a Bayesian hierarchical linear regression model (Equation 3), as well as a simple Bayesian linear regression model, to estimate the effect of each covariate ( $\check{X}=X_{1,\dots,6}$ ) on grazing effect size ( $Y$ ).  $Y$  can represent either the effect of grazing on species composition ( $D$ ) or the effect on production ( $E$ ) as the dependent variable. In the hierarchical model the regression coefficients ( $\check{B}=B_{1,\dots,6}$ ) for each covariate were allowed to vary for the three different community types ( $c$ ), but were estimated from a common distribution, whose means and standard deviations are represented by the vectors  $\check{\mu}$  and  $\check{\sigma}$  respectively (Equation 3). I separated by community type

because different types of vegetation have been found to respond differently to different drivers, and I wished to discern the relative importance of each covariate to the different communities. In the simple Bayesian model I pooled the data from all community types to find single estimates of each regression coefficient.

$$\begin{aligned}
P(Bo, \vec{B}_c, \tau | Y, \vec{X}) \propto & \\
& \prod_i P(Y_i | \hat{Y}_i, \tau) \cdot P(\hat{Y}_i | Bo_i, \vec{B}_{c_i}, \vec{X}_i) \cdot P(Bo_i | \beta_0, \beta_{1_l}, \beta_{2_s}) \\
& \times \prod_c P(\vec{B}_c | \vec{\mu}, \vec{\sigma}) \times \prod_l P(\beta_{1_l} | \mu_{o_1}, \sigma_{o_1}) \times \prod_s P(\beta_{2_s} | \mu_{o_2}, \sigma_{o_2}) \\
& \times P(\tau) \cdot P(\vec{\mu}) \cdot P(\vec{\sigma}) \cdot P(\beta_0) \cdot P(\mu_{o_1}) \cdot P(\sigma_{o_1}) \cdot P(\mu_{o_2}) \cdot P(\sigma_{o_2})
\end{aligned} \tag{3}$$

The intercept ( $Bo$ ) of both the pooled model and the hierarchical model was allowed to vary based on location ( $l$ ) and study ( $s$ ), in order to address potential pseudo-replication as a result of multiple data points coming from some locations, and also multiple locations being represented by some studies. The intercept was not allowed to vary by community type. Because multiple regression coefficients were varying by community type, a Wishart distribution was used to directly model the correlation matrix among the covariates (Gelman and Hill 2007).

Since  $D$  is distributed between 0 and 1, I used a probit function to constrain the output of the regression model to that interval, and a beta distribution was used to match the model output with the data (Equation 4). When modeling  $E$  as the dependent variable, the probit function was unnecessary, and I used a normal distribution for the data model (Equation 5).

$$\hat{D}_i = \text{probit}^{-1}(Bo_i + \vec{B}_{c_i} \cdot \vec{X}_i) \quad D_i \sim \text{beta}(\hat{D}_i, \tau) \tag{4}$$

$$\hat{E}_i = Bo_i + \vec{B}_{c_i} \cdot \vec{X}_i \quad E_i \sim \text{normal}(\hat{E}_i, \tau) \tag{5}$$

The standard deviation for the process and data models were combined into one parameter for all of the data points. I chose not to use a weighted regression model because the sampling error was not known for many of the studies. Although weighting by sampling error is a standard practice for meta-analyses (Gurevitch and Hedges 1999), it has been found that unweighted regression can actually be more robust in cases where the sampling error would require estimation and could potentially introduce misleading information (Fletcher and Dixon 2012).

The analysis was conducted using R (R Development Core Team 2012). I estimated the parameters of the model using Markov chain Monte Carlo (MCMC) with a Gibbs sampling step, by running JAGS (Just Another Gibbs Sampler) through the rjags package (Plummer 2011) within R. Gelman and Heidel diagnostics were used to verify that the MCMC chains had converged. I also calculated one-way p-values, to provide a more familiar metric, as the proportion of the posterior distribution of  $B$  that lies on the opposite side of zero from the mean. When  $p < 0.10$ , I considered the effect of the corresponding covariate to be weakly significant, and when  $p < 0.05$  I considered the effect to be significant, and when  $p < 0.001$  I considered the effect to be strongly significant.

### **Model Checking**

I conducted posterior predictive checks by sampling from the posterior distribution to assess how well the model fit the data (Gelman 2003). If the model is a reasonable fit, I would expect the data simulated from the posterior distribution to appear similar to the observed data. I compared the model residuals, mean, and coefficient of variation (CV) between the data and the data simulated from the posterior distribution, calculating p-values for these metrics based on the

proportion of cases that the simulated values exceeded the values calculated from the observed data.

## RESULTS

### Spread of data

There were some differences in grazing implementation based on community type. Of the studies included in my dataset, the duration of grazing exclusion tended to be shorter in woodland sites (Figure 2.1a). The intensity of grazing, as measured by the percent of ANPP consumed was higher on average in shrublands compared with woodlands and grasslands (Figure 2.1b).

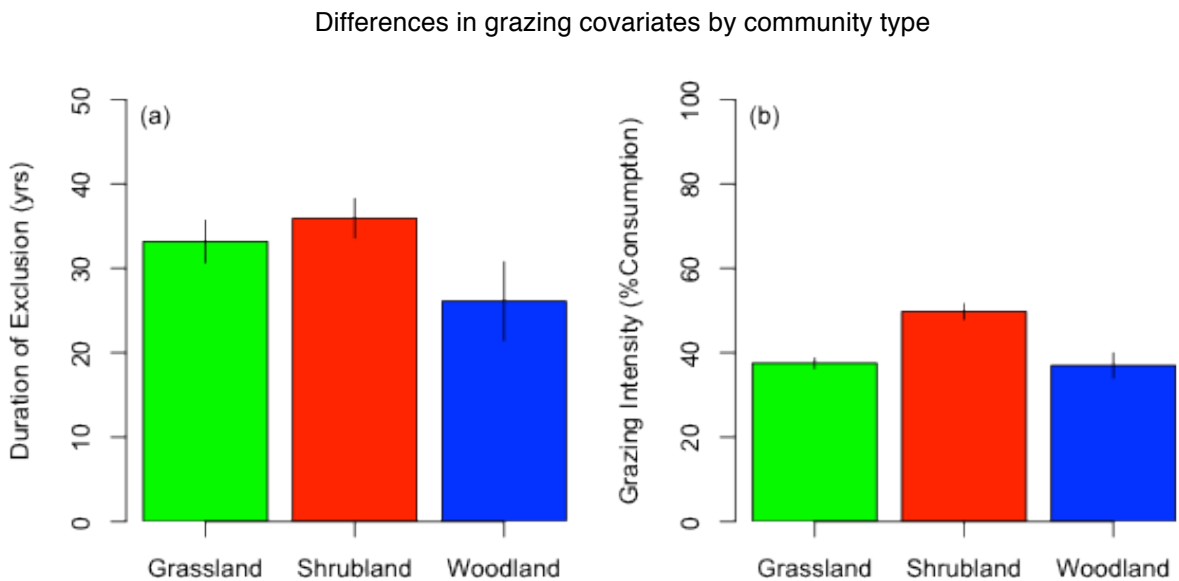


Figure 2.1 Mean values for grazing covariates in each community type (grassland=green, shrubland=red, woodland=blue). The black bars represent standard error of the mean. Panel (a) shows differences in the duration of grazing exclusion and panel (b) shows differences in grazing intensity as measured by percent of ANPP consumed.

### Differences in location covariates by community type

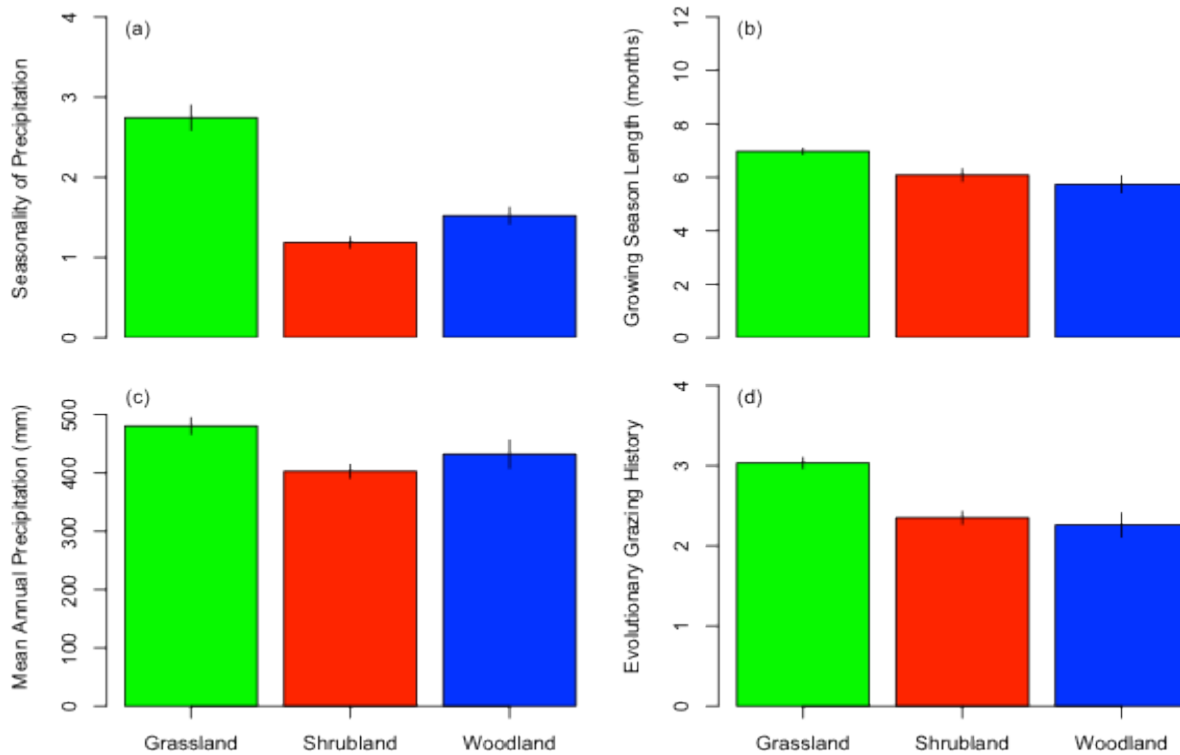


Figure 2.2 Means of location-level covariates based on community type (grassland=green, shrubland=red, woodland=blue). The black bars represent standard error of the mean. Panel (a) shows seasonality of precipitation, with larger values indicating a higher proportion of summer, compared to winter, precipitation. Panel (b) shows growing season length in months, and panel (c) shows mean annual precipitation in mm. Panel (d) shows evolutionary history of grazing, based on a ranking system from 1-4, with 1 being the shortest and 4 being the longest.

There are some inherent patterns in the spread of the location-level data when aggregated by community type, because the dominant vegetation type is to a large extent determined by climatic conditions. Within the dataset, grassland sites on average had more seasonal rainfall patterns skewed toward summer precipitation regimes (Figure 2.2a), slightly longer growing seasons (Figure 2.2b), and an overall higher mean annual precipitation (MAP) than shrublands and woodlands (Figure 2.2c). Shrublands and woodlands had similar climatic means, although shrublands were found in areas with greater amounts of winter precipitation (Figure 2.2a), tended to have slightly longer growing seasons (Figure 2.2b), and have slightly

less MAP (Figure 2.2c) than woodland sites. The average grassland site also had a longer evolutionary history of grazing than shrubland or woodland sites (Figure 2.2d).

There was little difference in mean effect of grazing on species composition for the three different community types (Figure 2.3a). However, woodland sites had a markedly greater production decrease in grazed plots compared with grassland and shrubland sites (Figure 2.3b).

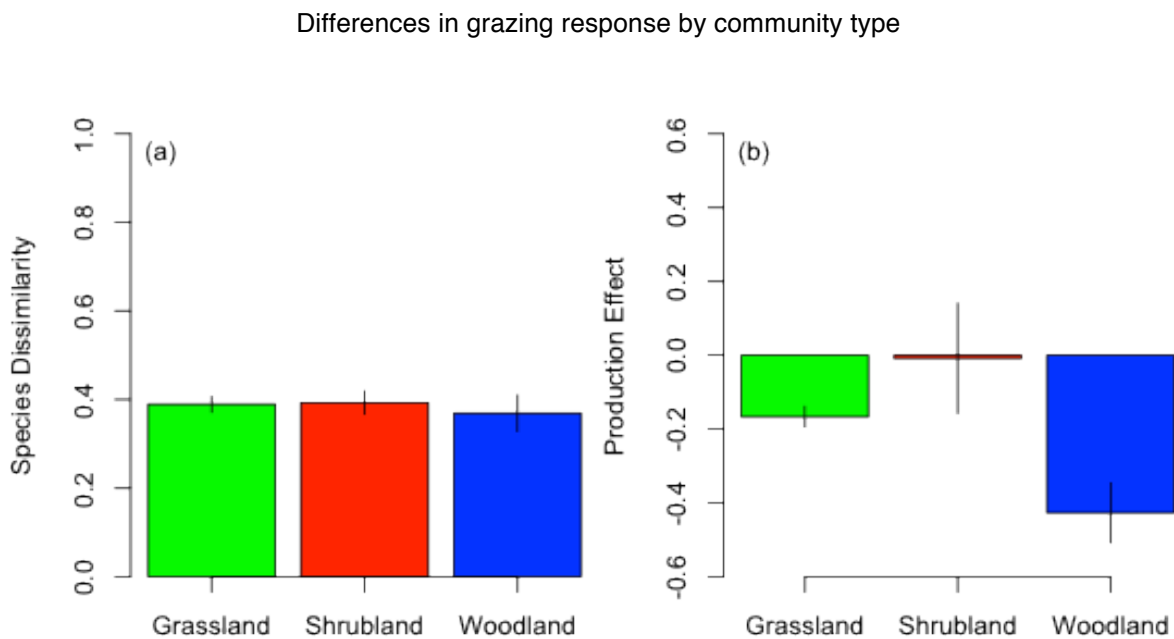


Figure 2.3. The differences in grazing effect size based on community type (grassland=green, shrubland=red, woodland=blue). The black bars represent standard error from the mean. Panel (a) shows the differences in species dissimilarity between grazed and ungrazed plots, and panel (b) shows the change in production in grazed plots compared with ungrazed plots.

### Species Composition

We found grazing intensity and duration of grazing exclusion covariates to be the most strongly influential variables on the species dissimilarity ( $D$ ) between grazed and ungrazed plots in all community types (Table 2.1). Duration of grazing exclusion was slightly more influential than grazing intensity, though both were positively correlated with changes in species

composition due to grazing (Figure 2.4a,b). The effect of duration of grazing exclusion on  $D$  was significant ( $p < 0.05$ ), and the effect of grazing intensity was strongly significant ( $p < 0.001$ ) for the pooled model ( $n = 22$ ), and both were significant for all community types in the hierarchical model ( $p < 0.05$ ).

The influence of experimental covariates on grazing effect size

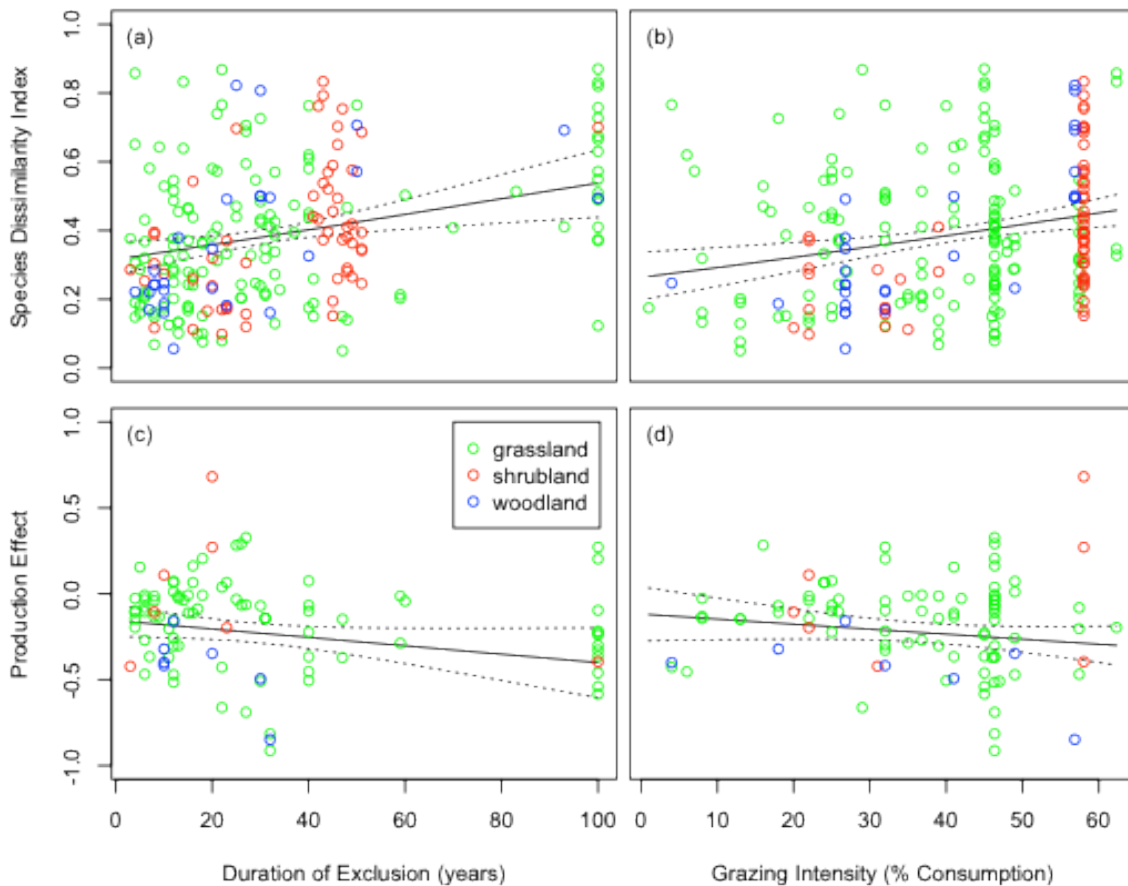


Figure 2.4. The effect of experimental covariates, duration of grazing exclusion (panels (a) and (c)) and grazing intensity (panels (b) and (d)) on species dissimilarity (panels (a) and (b)) and ANPP (panels (c) and (d)). Black lines represent the slope estimated from the pooled model, with data from all community types, and 95% credible intervals are shown with dashed lines. For each plot all other covariates are held at their mean values. The observed data are represented by colored circles (grassland=green, shrubland=red, woodland=blue).

Seasonality of precipitation, though non-significant, had a consistently positive correlation with changes in species composition (Figure 2.5a). This effect was the strongest



climatic influence in shrublands and woodlands, and in shrublands was nearly as strong as the grazing covariates (Table 2.1). It had the weakest influence of any of the climatic factors in grasslands.

Table 2.1. Values of regression coefficients ( $B$ ) representing the effect of each variable on the difference in species composition between grazed and ungrazed plots. The associated Bayesian  $p$ -values are calculated as the proportion of the posterior distribution of  $B$  that falls on the other side of zero. Results are shown for the pooled model as well as the hierarchical model, in which values of  $B$  were allowed to vary by community type. \*\*\* indicates a strongly significant effect ( $p < 0.001$ ); \*\* indicates a significant effect ( $p < 0.05$ ); \* indicates a weakly significant effect ( $p < 0.10$ ).

Variable	Pooled (n=222)		Grassland (n=138)		Shrubland (n=57)		Woodland (n=27)	
	$B$	$p$ -value	$B$	$p$ -value	$B$	$p$ -value	$B$	$p$ -value
<i>Duration of Exclusion</i>	+0.151**	0.001	+0.139**	0.003	+0.164**	0.005	+0.164**	0.008
<i>Grazing Intensity</i>	+0.129***	<0.001	+0.116**	0.003	+0.130**	0.007	+0.144**	0.006
<i>Seasonality of Precipitation</i>	+0.059	0.180	+0.047	0.219	+0.111	0.164	+0.081	0.219
<i>Growing Season Length</i>	-0.063*	0.080	-0.058*	0.084	-0.053	0.108	-0.072*	0.053
<i>Mean Annual Precipitation</i>	+0.086**	0.027	+0.085**	0.033	+0.054	0.179	+0.035	0.257
<i>Evolutionary Grazing History</i>	+0.039	0.250	+0.017	0.378	+0.051	0.257	+0.059	0.231

Growing season length was weakly significant ( $p < 0.10$ ) in all models, and there was a consistently negative correlation between growing season length and changes in species composition (Figure 2.5b). The mean effect of this variable was among the stronger climate effects in both grassland and woodland communities. Mean annual precipitation (MAP) had a significant effect ( $p < 0.05$ ) on  $D$  in the pooled model and in grassland communities ( $n = 138$ ), in which wetter sites had greater changes in species composition due to grazing exclusion (Table

2.1, Figure 2.5c). For shrubland ( $n = 57$ ) and woodland ( $n = 27$ ) communities, MAP was not found to be significant, though the overall relationship was still positive.

Though evolutionary history of grazing had a consistently positive correlation with species dissimilarity (Figure 2.5d), the effect was never close to significant and was the weakest of the covariates in the pooled model. It was also consistently among the weakest of the effects in all community types.

### **Production**

Duration of grazing exclusion was again a significant covariate ( $p < 0.05$ ) in the pooled model ( $n = 95$ ), and among the most influential variable ( $B = -0.064$ ) explaining the production effect ( $E$ ), or the proportional difference in ANPP due to grazing (Table 2.2, Figure 2.4c). In the hierarchical model the duration of exclusion was still significant in grasslands ( $n = 81$ ) and shrublands ( $n = 7$ ), but was not as significant in woodlands ( $n = 7$ ). Grazing intensity was not as strongly significant nor influential a covariate on production effect (Figure 2.4d). However, intensity was weakly significant ( $p < 0.1$ ) in the pooled model and for grassland communities. Both duration of exclusion and grazing intensity were negatively correlated with  $E$ .

In the pooled model the length of the growing season was the strongest ( $B = 0.176$ ) and most highly significant variable ( $p < 0.0001$ ) explaining the effect of grazing on production, with longer growing seasons associated with more positive effects on production due to grazing (Figure 2.5f). This relationship was strongly significant ( $p < 0.001$ ) for all grasslands and woodlands in the hierarchical model, and significant for shrublands ( $p < 0.01$ ). Length of growing season was the most influential of all the variables on production effect for both

grassland and woodland communities, and the second most influential variable in shrublands (Table 2.2).

Table 2.2. Values of regression coefficients (*B*) representing the effect of each variable on the production effect, or proportional difference in ANPP between grazed and ungrazed plots. The associated Bayesian *p*-values are calculated as the proportion of the posterior distribution of *B* that falls on the other side of zero. Results are shown for the pooled model as well as the hierarchical model, in which values of *B* were allowed to vary by community type. \*\*\*\* indicates a strongly significant effect ( $p < 0.001$ ); \*\* indicates a significant effect ( $p < 0.05$ ); \* indicates a weakly significant effect ( $p < 0.10$ ).

Variable	Pooled (n=95)		Grassland (n=81)		Shrubland (n=7)		Woodland (n=7)	
	<i>B</i>	<i>p</i> -value	<i>B</i>	<i>p</i> -value	<i>B</i>	<i>p</i> -value	<i>B</i>	<i>p</i> -value
<i>Duration of Exclusion</i>	-0.064**	0.037	-0.057**	0.033	-0.070**	0.044	-0.052	0.102
<i>Grazing Intensity</i>	-0.045*	0.071	-0.040*	0.068	-0.027	0.177	-0.032	0.149
<i>Seasonality of Precipitation</i>	+0.034	0.178	+0.037	0.153	+0.023	0.245	+0.038	0.200
<i>Growing Season Length</i>	+0.176***	<0.001	+0.178***	<0.001	+0.155**	0.012	+0.183***	0.001
<i>Mean Annual Precipitation</i>	-0.061**	0.047	-0.040	0.135	-0.219**	0.013	-0.060	0.216
<i>Evolutionary Grazing History</i>	-0.032	0.213	-0.030	0.216	-0.025	0.262	-0.024	0.266

The most influential variable on production effect in shrubland communities was mean annual precipitation ( $B = -0.219$ ), with greater reductions in production due to grazing at wetter sites (Figure 2.5g). This was a significant relationship. Although MAP ( $B = -0.061$ ), was also significant in the pooled model it was not as influential as length of growing season or duration of grazing exclusion. MAP was not significant in either grasslands or woodlands, although still had a negative correlation with production effect.

The influence of the location-level variables on changes in species composition and production due to grazing

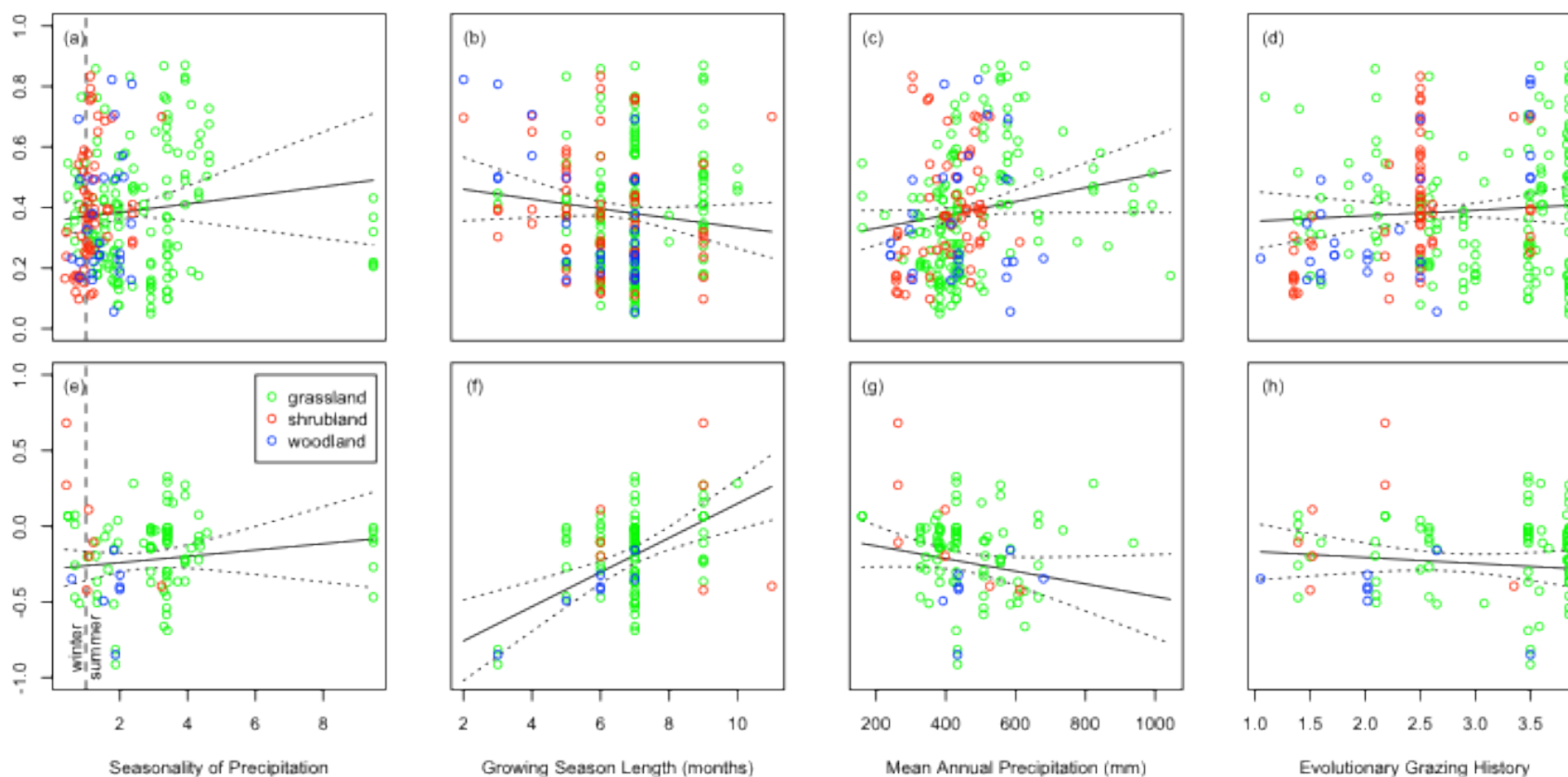


Figure 2.5 Effects of location-level variables (x-axis labels) on species dissimilarity (panels (a)-(d)) and production effect (panels (e)-(h)) as a result of grazing. Shown in black are the slopes (solid lines) with 95% credible intervals (dashed lines) estimated from the pooled model, evaluating all communities at once. In order to obtain the plots, all other covariates were held at their mean values. The observed data is represented by circles, with each community type plotted in a different color (grassland=green, shrubland=red, woodland=blue).

Neither the seasonality of precipitation nor the evolutionary history of grazing had a significant influence on the effect of grazing on production. In both the pooled model and the hierarchical model these were two of the least influential covariates. However, there was a trend towards a positive relationship between seasonality of precipitation and production effect, suggesting that in locations with a higher proportion of summer precipitation, grazing had a more positive influence on production (Figure 2.5e). Evolutionary history of grazing had a nearly equal but negative effect on production, in which the production at sites with a longer history of grazing was more negatively impacted by grazing (Figure 2.5h).

### **Model Checking and Convergence**

The MCMC chains of parameter estimates from both pooled models converged according to all diagnostic tests. MCMC chains from the hierarchical models did not have as conclusive convergence. However, I ensured that for each parameter estimate there was at least one diagnostic test that indicated convergence of the chains. I also ran each model multiple times, and yielded parameter estimates that were within 0.003 of one another each time.

The posterior predictive check indicated that my model was a reasonable fit for the data. Visual inspection of the data simulated from the posterior distribution compared with the observed data did not appear notably different. Furthermore, p-values from the posterior predictive check indicated that there was not a significant difference between the simulated and observed data in either residuals, mean, or CV.

## **DISCUSSION**

My results support the idea that both equilibrium and non-equilibrium processes are at work in these grazing ecosystems. Viewing grazing as an internal regulator, the tight

coupling of the biotic variables, grazing intensity and duration with vegetation dynamics indicates that equilibrium processes may be acting most strongly to affect species composition response to grazing (Ellis and Swift 1988, Briske et al. 2003). However, the external climatic drivers of growing season length, and in shrubland communities, mean annual precipitation, were strongly linked to changes in ANPP due to grazing. This indicates that non-equilibrium processes are acting more strongly on the grazing effect on production.

My results also show that different community types can be differentially responsive to different drivers. Because to some extent vegetation community is determined climatically, including climate variables and community type at different hierarchical levels of the model allowed me to disentangle somewhat the effects due to climate, and those due to dominant vegetation type. I found that climatic factors aside from just quantity of precipitation can be important in determining how sensitive a system is to grazing, as both the seasonality of precipitation and the length of the growing season can have a role in determining the magnitude of the grazing effect. Indeed, I found climatic factors to outweigh the effect of evolutionary history of grazing. Below, I discuss the effects of each variable from the model, and offer possible explanations.

### **Grazing Covariates**

I found the experimental grazing variables to be the strongest and most significant indicators of species dissimilarity between grazed and ungrazed treatments. Increases in the duration of grazing exclusion and grazing intensity were both related to greater changes in species composition. This result, while not surprising, is in contrast to the results of Milchunas and Lauenroth (1993), who found that differences in species composition were more affected by ecosystem-level variables than grazing variables. However, it is important to note that these

changes in composition arise from a different mechanism than those of ecosystem-level factors, and do not have the same implications for elasticity of the system because the drivers are not affecting the system, but rather the parameters of the experiment.

The duration of grazing exclusion had a stronger and more significant effect than grazing intensity on changes in ANPP due to grazing, though both of these variables were negatively correlated with production effect. In contrast to the effect on species dissimilarity, changes in production were more responsive to certain climate variables than they were to changes in grazing variables. This is consistent with results from Milchunas and Lauenroth (1993).

### **Seasonality of Precipitation**

Of the location-level factors, the seasonality of precipitation was the strongest determinant of changes in species composition due to grazing in both shrublands and woodlands. Across the board, I found that locations with a higher proportion of summer precipitation tended to have greater grazing-induced changes in species composition than areas with a greater proportion of winter precipitation. In contrast, I did not find precipitation seasonality to have a strong influence on the effect of grazing on aboveground production.

My results suggests that species composition in systems with summer precipitation regimes may actually be more elastic, or have a greater capacity for change, and that changes due to grazing may be more reversible. I speculate that this could be due to the greater availability of phenological niches in systems with summer precipitation regimes, in which more species are adapted to take advantage of summer water inputs (Schwinning et al. 2005a, Golluscio et al. 2009). This could indicate greater functional response diversity in the

species pool, and more potential for shifts in species composition due to a fluctuating resource environment.

This could be exacerbated by the preference of woody species for climates with winter precipitation regimes (Golluscio et al. 1998). Woody species are relatively insensitive to changes in resource supply (Bates et al. 2006, Golluscio et al. 2009), and can act as buffers to changes in species composition. This could cause these systems to be less elastic, and therefore less resilient to grazing. This is supported by my result that seasonality had a greater effect in shrublands and woodlands compared with grasslands. Woody communities that receive a greater proportion of summer precipitation may contain a relatively greater proportion of graminoid species, and therefore their species composition may have more elasticity.

In addition, locations with a winter precipitation regime tend to be slower cycling systems (Aanderud et al. 2010), and therefore we would expect its species to have more conservative growth strategies and to be better defended against herbivores (Vandermeijden et al. 1988, Herms and Mattson 1992). Summer precipitation regimes tend to foster faster cycling systems with species that are more tolerant of, and also palatable to grazers (Caldwell et al. 1981). Indeed, graminoid species tend to be more palatable than woody species, which favor areas with a higher proportion of winter precipitation due to their deep roots (Snyder and Tartowski 2006, Chimner et al. 2010). Therefore grazed treatments with summer precipitation regimes may have a greater proportion of species being consumed, which could also account for greater changes in species composition due to grazing.



## **Length of Growing Season**

The length of the growing season was negatively correlated with changes in species composition due to grazing, but this driver was not among the most influential climate variables. This negative relationship suggests that in locations with a longer growing season grazed species may have the opportunity to regrow some of the biomass that was consumed (Caldwell et al. 1981, Vandermeijden et al. 1988, Herms and Mattson 1992). Systems with short growing seasons may not have such opportunities for regrowth after consumption.

This could have two different effects, depending on the proportion of species that have the ability to regrow after defoliation. If all species are able to regrow equally, then a longer growing season could minimize changes in species composition by reducing available space for recruitment of different species during the following growing season. Here, we are making the assumption that systems with long growing seasons have not already undergone irreversible changes in species composition due to grazing, and the changes we see represent the original impact that grazing had on species composition.

Alternatively, if only some species are able to regrow after grazing, then longer growing seasons could enable more rapid shifts in species composition toward the species that are able to capitalize on the extra time. In this case, my result could be explained if grazing had already caused systems with long growing seasons to cross thresholds, losing their ability to return to their previous state. In such systems we would again not expect to see large changes in species composition when grazing is removed (Cingolani et al. 2005).

The length of the growing season was the single most important driver of the effect of grazing on aboveground production, with a strongly positive correlation in all

community types. We can also attribute this to the system's ability to regrow after being grazed. If this mechanism were responsible for the pattern I found, we would expect rapid regrowth after defoliation to more often be a successful plant strategy over avoidance of grazing in systems with longer growing seasons. This effect could be enhanced in systems that have a large proportion of annual plants, which tend to favor long growing seasons (Pitt and Heady 1978), as annuals tend to increase aboveground production more than perennials in response to grazing (Milchunas and Lauenroth 1993, Diaz et al. 2007).

### **Mean Annual Precipitation**

Mean annual precipitation, as a proxy for ecosystem productivity, has previously been identified as a main factor in determining sensitivity to grazing (Milchunas and Lauenroth 1993, Chase et al. 2000). My results only partially support this. MAP was a strong driver of species dissimilarity due to grazing in grassland systems, but was not a very important driver in shrublands or woodlands. Its importance in grassland systems likely caused MAP to come out as the most important covariate in the pooled model because a disproportionate majority of my dataset came from grassland systems.

In all community types the quantity of precipitation was positively correlated with changes in species composition due to grazing, which is consistent with prior studies (Chase et al. 2000, Osem et al. 2004). This may be because drought tolerance traits can pre-adapt species to grazing tolerance, whereas species that are well suited to take advantage of larger quantities of water are often tall statured in order to compete for light, and are not well adapted to grazing (Milchunas et al. 1988, Osem et al. 2004, Diaz et al. 2007). Therefore, in areas with higher MAP there may be both resource-capture specialists and grazing-tolerant species present in the species pool, giving these systems the ability to switch species composition depending on conditions

(Cingolani et al. 2005). This relationship may be less pronounced in shrublands and woodlands due to the differing physiology of woody species. Because woody species are usually adapted to take advantage of deeper water supplies, there is not the same tradeoff between resource capture and grazing tolerance, and in fact, woody tissues can be viewed as a defense against herbivory.

On the other hand, MAP strongly influenced the effect of grazing on production in shrublands, even more so than the length of the growing season. This relationship was strongly negatively correlated, with places with higher amounts of precipitation having a stronger negative impact of grazing on production. While MAP still had a negative correlation with production effect in grasslands and woodlands, the relationship was not nearly as evident in these community types. However, MAP was still a significant factor in the pooled model.

This negative relationship may arise from the inability of certain highly productive species to tolerate grazing. This could occur when, for instance, the apical meristem is located higher on the stalk and gets nipped off by grazers (Milchunas et al. 1988). These species are also often more palatable, and hence preferentially consumed by herbivores. They then may be replaced by less productive but more well defended species. It is curious, however, that MAP is so much more important in shrubland community types than in grasslands or woodlands. Again, this could be due to the differing growth strategy of shrubs, in which they may allocate more belowground growth upon being defoliated, whereas productive grassland systems can sometimes increase production after grazing due to release from light-limitation. Alternatively, this may be another indication that shrublands are less elastic with regards to species composition, and therefore do not have the species pool required to shift their composition to include more grazing-tolerant species.

## **Evolutionary History of Grazing**

One of the most surprising results from my analysis is the apparent lack of influence of evolutionary history of grazing on either species dissimilarity or production effect. My results did consistently show a positive correlation between length of grazing history and species dissimilarity due to grazing, which is consistent with prior studies (Milchunas and Lauenroth 1993), but this relationship was weak. On production effect, evolutionary history of grazing had a negative effect, with longer histories resulting in greater decreases in production due to grazing. Most previous studies and theories have counted this as one of the most important factors in determining sensitivity to grazing, and yet I did not find it to be strongly influential in any of my models. I offer several possible explanations for this discrepancy.

Firstly, my coarse categorization of grazing history may not have been adequate to capture the relationship. However, if the effect was strong, the correlation should have been clear even given the coarse metric. If the relationship is non-linear, or if it merely modifies the effect of other variables, then it is possible that my model was not appropriate to assess the effect. In the future it would be interesting to include evolutionary history of grazing as a level in a hierarchical model such that it was able to modify the effect of other predictor variables.

Alternatively, evolutionary history of grazing seems to be unavoidably correlated with seasonality of precipitation, such that sites with higher proportion of summer precipitation more often evolved with grazing animals. Since this is the first grazing meta-analysis I know of that explicitly takes seasonality of precipitation into account, it is possible that previous studies had been picking up some of the influence of seasonality in the perceived effect of evolutionary history of grazing. Conversely, it is possible that this correlation within the dataset did not allow the model to distinguish between the two drivers.

Lastly, excluding tropical sites and other sites with year-round growing season temperatures may have removed the data for which evolutionary history of grazing becomes the most important. Although there is not necessarily reason to believe that evolutionary history of grazing is less important in temperate sites, I do not know what the effect of excluding this portion of the available data might have had.

## CONCLUSION

Although these results provide important insight into what factors affect vegetation sensitivity to grazing, they also raise many questions that are outside of the scope of this study to answer. Because there are only single time points represented by the data, and because I did not investigate the nature of shifts in species composition, I am limited in my ability to infer whether greater changes in species composition upon grazing removal represent higher or lower sensitivity to grazing. This would depend on whether grazing removal causes directional recovery of plant communities toward their pre-grazing state, which cannot happen if the community has already crossed thresholds into alternate stable states. It has been suggested by Cingolani et al. (2005) that more resilient systems in this context should be able to change more rapidly, whereas less resilient systems may have undergone irreversible changes such as species extinctions, and changes may take longer or not occur at all. Non-resilient sites would therefore display smaller differences between ungrazed and grazed species composition.

Though we may be unable to determine how sensitive the original vegetation was at the dawn of grazing, this perhaps is no longer a useful question. Furthermore, it is unlikely, and perhaps undesirable, that communities would return to an original pre-grazing composition when grazing is removed. Due to evolutionary time, over the course of which many global changes have occurred, original species compositions may be obsolete. I suggest adopting a

strategy of managing these systems to retain elasticity by maximizing the capacity for change in response to both external and internal drivers. This can be done through identifying thresholds and conditions that have the potential to tip systems past these thresholds. It also involves identifying the important regulators of key processes in a given system.

Our results indicate that drier summers, longer growing seasons, and lower mean annual precipitation may be the climatic factors that decrease the elasticity of systems with regard to the responsiveness of species composition to grazing, particularly in grasslands. However, because it is the species pool that mostly determines the elasticity of species composition, it is difficult to determine how changes in climate will affect elasticity. It may be likely that areas with high elasticity will stay elastic in the face of climate changes, whereas less elastic communities may experience species loss and degradation as they move past thresholds to alternate stable states.

### 3. GRAZING AND CLIMATE CHANGE: DOES THE TIMING OF SEASONAL WATER AVAILABILITY INFLUENCE SENSITIVITY TO YAK GRAZING ON THE TIBETAN PLATEAU?

#### INTRODUCTION

Understanding interactions between climate changes and grazing is imperative, as grasslands cover more than one-third of the Earth's surface and livestock grazing is the most spatially extensive land-use worldwide (Asner et al. 2004). Still, we know little about how grazing interacts with changes in the timing of moisture availability (Milchunas et al. 1994, Veblen 2008). Nonetheless, there are important differences between grassland systems whose precipitation falls primarily during the growing season (coupled climate) and those whose precipitation falls primarily during the winter (decoupled climate) (Figure 3.1) that are likely to interact with grazing.

Climate change scenarios predict that many coupled systems will experience shifts in precipitation regimes, causing peaks in temperature and precipitation to become temporally decoupled (Christensen et al. 2007). In order to fully understand the effects that climate change and the forecasted temporal changes in precipitation (IPCC 2007) will have on grazed grassland communities, it is important to assess how grazing responses differ between coupled and decoupled systems. I used the Tibetan Plateau as my study system to investigate how yak grazing and the timing of soil moisture availability affect plant traits that mediate grazing response.

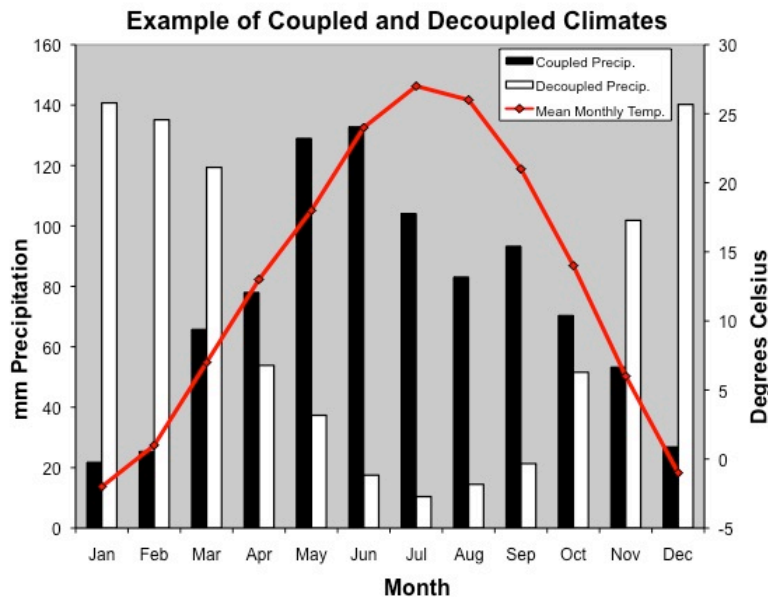


Figure 3.1. Examples of coupled (solid bars) and decoupled (open bars) precipitation regimes with respect to mean monthly temperatures (line).

The Tibetan Plateau is an extensive high elevation rangeland system with a coupled climate whose many pastoral communities are largely reliant on livestock for their livelihoods. This region also strongly influences global climate and regional water supply. Climate projections predict that this area will experience dramatic changes, with increased winter precipitation and decreased summer water availability due to warming (IPCC 2007). It is unclear how these changes will affect the ecology and forage quality of the rangeland, and how grazing will interact with these changes (Klein et al. 2004, 2007), as this region is relatively understudied compared with the rest of the world.

We used a mechanistic, trait-based approach to help further elucidate the role of climate in influencing plant traits that affect grazing response under both coupled and decoupled precipitation regimes. This study will improve our knowledge of how the Tibetan Plateau will respond to changes in climate, and how this will impact rangeland quality and management plans for livestock grazing.



There are two main strategies that plants can use to cope with grazing, regrowth (tolerance) and defense (avoidance), and the preferred strategy may be related to site resource environment (Vandermeijden et al. 1988). Ultimately, the strategy employed often represents a tradeoff between consumption by herbivores and the cost of investing in longer-lived leaves with higher carbon content that make the tissue less digestible to herbivores (Vandermeijden et al. 1988). The avoidance strategy is characterized by traits including higher stem to leaf ratios, short stature, physical defenses such as spines or thorns, thick and/or waxy leaves, and presence of recalcitrant or toxic compounds in tissues. Tolerance strategies involve rapid regrowth from defoliation (Anderson and Briske 1995, Hobbs 1996, Hawkes and Sullivan 2001) and are characterized by allocation to resource acquisition, via photosynthetic tissues and root structures. These resource allocation traits include higher nitrogen (N) content in leaf tissues, higher specific leaf area (SLA), and more allocation to root growth (Caldwell et al. 1981).

Defensive strategies are more often employed in resource limited, slow-cycling systems since the cost of regrowing new tissue after defoliation is higher compared to the payoff in carbon gain (Coley et al. 1985, Vandermeijden et al. 1988, Herms and Mattson 1992). In high resource environments where new tissue is not costly to produce, the extra investment in defenses may be unnecessary and grazing tolerance is usually a more prevalent strategy (Wise and Abrahamson 2007). In these systems, grazing has been known to act as a positive feedback, increasing rates of nutrient cycling and tolerance traits (McNaughton et al. 1988, Cebrian and Lartigue 2004). Even among plants with very similar phenologies and growth forms, leaf economics can play a large role in tolerance to grazing (Caldwell et al. 1981, Wright et al. 2004).

Many recent studies have used trait-based approaches to investigate how grassland plant assemblages respond to grazing by assessing traits corresponding to grazing

avoidance and tolerance strategies (Diaz et al. 2007). Trait based approaches in measuring plant response to grazing have been found to be more informative than simply looking at species responses (Pakeman 2004). This is particularly relevant because communities that favor avoidance strategies tend to have low palatability and forage quality, whereas grazing-tolerant species are usually associated with higher forage quality, since they are more palatable and have higher nutrient content. However, there is not strong consensus about what climatic or historical conditions favor which strategy, and how grazing can cause negative or positive feedbacks (Hobbs 1996, Hawkes and Sullivan 2001). By answering these questions we will be better able to predict ecosystem response to grazing under future climate change scenarios, and manage land for increases rather than reductions in forage production and quality.

Results from a global analysis of grazing exclusion studies (Chapter 2) indicate that grazing induces greater changes in species composition in coupled climates than decoupled climates. One explanation for this pattern is that decoupled systems favor species composition with higher proportion of grazing avoiders than grazing tolerators. Systems in which less palatable plant species are more prevalent may be less responsive to grazing because a smaller proportion of species are being defoliated (Adler et al. 2005).

There are two reasons that decoupled systems are likely to have more avoidance traits than coupled systems. The first reason is that coupled systems, where the majority of annual precipitation occurs during the warm growing season, are characterized by relatively warm, wet conditions, which tend to foster faster rates of nutrient cycling than decoupled systems (Aanderud et al. 2010). Coupled systems also tend to lose more water than decoupled systems due to increased evapotranspiration during the summer, while decoupled systems tend to lose more nitrogen (N) due to the asynchrony between nitrogen supply and demand by plants

(Austin et al. 2004) (Table 3.0). These intrinsic differences result in a slower cycling and more nutrient poor environment in decoupled systems, which I hypothesized would select for a larger proportion of grazing avoidance plant traits.

Coupled	Decoupled
↑ Evapotranspiration	↓ Evapotranspiration
↓ N loss	↑ N Loss
↓ SOC storage	↑ SOC storage
↑ Decomposition	↓ Decomposition
↑ Bacterial community	↑ Fungal community
Shallow rooted plants	Deeper rooted plants
↑ Response to H <sub>2</sub> O inputs	↓ Response to H <sub>2</sub> O inputs

Table 3.0. Some intrinsic differences between coupled and decoupled grassland systems

The second reason that decoupled systems are likely to have more avoidance traits is that increased winter precipitation in the decoupled system results in water reaching greater depths since it is less likely to be immediately evaporated or taken up by plants. Because woody, deeper-rooted species such as shrubs primarily make use of these deep, early season resources (Golluscio et al. 1998), these species thrive in decoupled systems. Shrubs have a relatively high proportion of tissues that are unpalatable to herbivores, and browsers rather than grazers more often consume the palatable parts of woody plants. Shrubs can also be relatively insensitive to changes in growing season precipitation (Bates et al. 2006, Golluscio et al. 2009) and can act as a buffer to resource fluctuations.

I tested the following hypotheses:

*H1: Experimentally decoupling the climate of a coupled system will result in a higher proportion of community-level grazing avoidance traits than the coupled climate.*

I predicted that shifting the precipitation timing of this coupled system toward the winter would favor less palatable plant species such as shrubs and more well defended forbs and legumes.

*H2: Grazing under an experimentally decoupled climate will result in an increase in avoidance traits, while grazing in a coupled climate will result in an increase in tolerance traits.*

I predicted that in both climate treatments grazing would act as a positive feedback to exacerbate the effects of climate on plant traits.

*H3: Coupled climates will experience greater grazing-induced changes in species composition than an experimentally decoupled climate.*

Because of a higher proportion of plants employing avoidance strategies, I predicted that the decoupled treatments will be less responsive to grazing-induced changes in species composition than the ambient (coupled) climate.

## METHODS

### **Study Site**

Nam Tso, Tibet Autonomous Region (N 30°46.44', E 90°59.31', 4820 m) is a high alpine ecosystem in central Tibet. The mean annual temperature of this site is 0 °C and mean annual precipitation is around 300 mm, approximately 80% of which falls during the summer months (Nam Co Annual Report 2008). This region is home to many pastoral

communities, in which livestock are essential to peoples' livelihoods. The rangeland is usually grazed from February to October by yaks, goats, and sheep.

As a high alpine environment, the Tibetan Plateau is expected to be very sensitive to the effects of climate change, particularly warming (Klein et al. 2004, 2007). Moreover, climate models also predict that this area, along with many coupled climate systems, will experience a shift in the timing of precipitation, with wetter winters due to more frequent and extreme snow events, and drier summers due to warming (Christensen et al. 2007).

### **Experimental Design**

I utilized an experimental climate study, which was established in Nam Tso in 2009, and had been in effect for 3 years at the time of data collection in the summer of 2011. In plots grazed and ungrazed by yak (8 m diameter), there were smaller sub-plots (1 m diameter) containing climate treatments. Water manipulations and warming were used to simulate potential climate scenarios and investigate how grazing would interact with the climate treatments. I examined control plots representing the ambient, coupled climate, and treatment plots representing a decoupled climate, both grazed and ungrazed by yak. There were four replicates for each climate and grazing combination, each in a different sampling block. The decoupled climate treatment shifted the timing of water availability toward the winter without significantly altering mean annual soil moisture by using (a) fiberglass open-top warming chambers that decrease summer soil moisture and (b) spring snow additions that add approximately 1.3 m to the ambient snowfall. Yaks were tethered to the center of the grazed plots at four intervals throughout the growing season for 3 days each in accordance with moderate grazing levels for the region. A more detailed description of the experimental design can be referenced in Hu et al. (In review).

The experimental design is unique in its use of live grazers in combination with the water manipulations, and allowed me to investigate how augmenting early season soil moisture and decreasing summer moisture in a naturally coupled climate affected grazing-related plant traits and the sensitivity of the plant community to grazing.

### **Data collection**

To identify mechanisms defining the interaction between grazing and climate, I measured species-level plant traits for grazing avoidance versus tolerance strategies. I focused on seven focal species, which comprised no less than 84% of the cover in all plots. These species were: *Kobresia pygmea*, a sedge, which is the main grazing forage for livestock on the plateau, another sedge species *Carex moorcroftii*, the forbs *Potentilla saundersiana*, *Potentilla bifurca* and *Leontopodium pusillum*, the shrub *Potentilla fruticosa*, and legumes of the genus *Astragalus*. It is suspected that some *Astragalus* species at this site are toxic to herbivores, which is why this species was included even though it was not one of the most abundant species.

For each of the key species listed above, in each treatment plot, I sampled a number of traits associated with grazing tolerance and avoidance strategy. Data collection occurred in early August, at peak biomass, in the third year of the experiment. Sampling protocols, including the number of samples taken from each plot to accurately portray heterogeneity, were based on those suggested in Cornelissen et al. (2003). As such, all traits were measured on healthy individuals on fully open leaves with no evident damage. Plot averages were then taken for each species-trait to represent a single data point. Specifically, the traits I measured were:

- *Height*: This was measured using a ruler (For *K. pygmaea* n = 14/plot, for all other species n = 7/plot). Decreased plant height is a common response to grazing, irrespective of climate variation (Diaz et al. 2007), and may be an indication of increased allocation to roots (Evju et al. 2009).
- *Stem to leaf ratio*: I collected whole aboveground portions of individuals (n = 3/plot) to determine stem to leaf ratio. In order to do this the plants were dried in an oven at 60°C for 72 hours and then separated by hand into stem and leaf components and weighed. Petioles were counted as part of the leaf. A higher stem to leaf ratio is indicative of grazing avoidance. This trait was only measured for *P. fruticosa*, *P. bifurca*, and *P. saundersiana* since they were the only species with notable stems.
- *Leaf fiber content*: Leaf tissue samples (1g/plot) were analyzed by the Soil, Water and Plant Testing Laboratory at Colorado State University using the Van Soest detergent fiber analysis method (Vansoest 1963). This method allowed me to determine the percentage of acid detergent fiber (ADF), acid detergent lignin (ADL) and neutral detergent fiber (NDF) in the leaf tissues, which are measurements of the indigestible components of cell walls. These measurements are indicative of digestibility and forage quality (Goering 1970). Increases in forage ADF, ADL, and NDF concentrations decrease digestibility and forage quality. For some plots there was not enough plant material available and individual species were combined within treatment groups for these analyses.
- *Leaf dry matter content (LDMC)*: Wet weight and dry leaf weight (see drying protocol above) were measured (n = 10/plot) to calculate leaf dry matter content (LDMC = dry weight/wet weight). Greater LDMC values represent more conservative growth strategies, and less allocation to resource capture. It can therefore be indicative of grazing avoidance.

- *Specific leaf area (SLA)*: The same leaf samples that were used for LDMC (n = 10/plot) were flattened and photographed in the field at a standardized distance on a white background containing a ruler for reference. Leaf area was determined from the photographs using image area calculation software (WinFolia, Regent Instruments Inc., Quebec City, Canada), and SLA was calculated as  $SLA = \text{Leaf area (m}^2\text{)}/\text{Dry weight (g)}$ . Higher specific leaf areas are associated with greater allocation to light capture, and tolerance of grazing. Due to a dearth of *Astraglaous spp.*, samples were not collected for LDMC or SLA.
- *Standing root biomass*: This was sampled by taking 1.5” diameter soil cores to a depth of 20cm (n = 3/plot) in patches of *K. pygmaea* (the dominant species). Cores from each plot were pooled, frozen (4-5 months), and then washed of soil and debris, retaining as many fine roots as possible. Washed roots from each plot were dried in an oven at 60°C for 72 hours and then weighed. Higher allocation to belowground production allocation can be indicative of grazing tolerance.
- *Areal cover*: A 1m<sup>2</sup> sampling frame was used to determine cover of each species. The frame is divided in a 20x20 grid, and the proportional cover of species in each square was determined to the nearest 1/3, 1/4 or 1/6 depending on the number of species present in each square. Data from all 400 squares were then combined to determine the proportional cover of each species in the sampling plot.

## Data analysis

Using these plot-level trait values for each species, means for each species-trait combination were calculated within the four treatment combinations, which I hereafter call the treatment-level species-trait mean. This metric captures the treatment effects on intraspecific trait variation. I quantified the amount of intraspecific variation for each species-trait as the



coefficient of variation (CV) of the plot-level species-trait values, and the intraspecific variation for each trait as the mean of the CVs for each species. I also calculated an overall trait mean for each species, which I hereafter call the species-trait mean. This metric ignores the effect of treatment on intraspecific trait variation. I determined interspecific variation for each trait by calculating the CV among all treatment-level species means for the given trait. For the rest of the analysis, species-trait means were calculated using log-transformed and standardized plot-level species traits.

In each plot, relative cover was calculated for the focal species. The proportion of total cover represented by the seven focal species was determined for each plot, and the adjusted relative cover for each species was calculated based on this value. For each trait, a community-level mean was calculated for each plot based on weighting the mean species-trait values by the adjusted relative cover of that species. I also calculated this value using treatment-level species-trait means, to assess the treatment effect on community-level traits including intraspecific variation.

I analyzed differences in community-level means for each trait using analyses of variance (ANOVA) with grazing treatment and climate treatment as fixed effects. To test H1, I used pre-planned contrasts to compare community-level grazing avoidance and tolerance traits between the ambient and decoupled climate treatments. To test H2, I compared grazing-induced changes in community-level plant traits in the control and decoupled climate treatments by looking at the interactive effects.

To quantify changes in species composition between treatments, I used a species dissimilarity index, which is the complement of Whittaker's association index (Whittaker 1952),

and is based on the sum of the absolute differences in adjusted relative cover for each species. I calculated the species dissimilarity between pairs of grazed and ungrazed treatments, as well as control and decoupled climate treatments within blocks. To test H3, I used separate analyses of variance (ANOVA) to determine the effect of climate on changes in species composition due to grazing, and the effect of grazing on changes in species composition due to climate.

## RESULTS

Table 3.1. For each trait the intraspecific coefficient of variation (CV) was calculated as the mean of the species-trait CVs of the seven focal species. The interspecific CV was calculated as the CV of the mean species-traits of the seven focal species. Grazing avoidance is indicated by increases in stem to leaf ratio (Stem: Leaf), leaf dry matter content (LDMC), acid detergent lignin (ADL), neutral detergent fiber (NDF), and acid detergent fiber (ADF). Grazing tolerance is indicated by increases in specific leaf area (SLA) and height.

Trait	Intra-specific CV	Inter-specific CV
Stem: Leaf	0.411	1.213
LDMC	0.219	0.143
ADL	0.392	0.347
NDF	0.144	0.216
ADF	0.184	0.143
SLA	0.153	0.361
Height	0.177	0.56

The highest amounts of interspecific variation were in the height and stem to leaf ratio traits (Table 3.1, 3.2). In most traits the interspecific variation exceeded the intraspecific variation. However, this did not hold true for LDMC, ADL, and ADF, which displayed greater intraspecific than interspecific variation (Table 3.1). This suggests that these traits may have more plasticity and sensitivity to environmental conditions and resource environment. Because the general assumption that traits are more similar within species than among species was violated, I focus on the results obtained by using treatment-level species-traits rather than pooling by species.

The greatest change in species cover was a decrease in *K. pygmaea*, the main forage species, under the decoupled climate treatment. Grazing, on the other hand tends to increase *K. pygmaea*, a result that agrees with Klein et al.'s (2004) assertion that grazing can dampen the effects of warming. Though most other species also followed this trend, with grazing induced changes in the opposite direction of the decoupled climate treatment, *Astragalus spp.* had decreases in cover for both treatments, and the shrub, *P. fruticosa*, increased in cover with a decoupled climate (Table 3.2). For both of these species the effect of climate was much greater than the effect of grazing on changes in cover.

Table 3.2. Species-trait means are shown for the seven focal species using untransformed data. The coefficient of variation for each species-trait was calculated over the treatment-level species-trait means and indicates the amount of intra-specific variation. The mean change in relative cover of each species due to adding grazing, and due to the decoupled climate treatment are shown in the last two rows,  $\pm$  the standard error (SE). Grazing avoidance is indicated by increases in stem to leaf ratio (Stem: Leaf), leaf dry matter content (LDMC), acid detergent lignin (ADL), neutral detergent fiber (NDF), and acid detergent fiber (ADF). Grazing tolerance is indicated by increases in specific leaf area (SLA) and height.

Species-Trait	<i>Astragalus spp.</i>	<i>C. moorcroftii</i>	<i>K. pygmaea</i>	<i>L. pusillum</i>	<i>P. bifurca</i>	<i>P. fruticosa</i>	<i>P. saundersiana</i>
Stem: Leaf	NA	NA	NA	NA	0.214	1.929	0.268
LDMC	NA	0.510	0.564	0.420	0.438	0.575	0.426
%ADL	14.613	17.887	24.605	11.679	15.334	28.339	13.109
%NDF	55.170	69.027	75.193	41.934	48.905	51.287	48.275
%ADF	38.193	44.127	48.675	35.515	34.792	43.823	33.950
SLA (mm <sup>2</sup> /g)	NA	0.011	0.014	0.017	0.009	0.006	0.010
Height (mm)	9.310	34.116	13.433	9.098	14.440	18.238	10.857
$\Delta$ Cover due to Grazing	-0.004 $\pm 0.007$	-0.017 $\pm 0.014$	0.029 $\pm 0.059$	-0.006 $\pm 0.020$	0.009 $\pm 0.006$	0.002 $\pm 0.035$	-0.013 $\pm 0.010$
$\Delta$ Cover due to Climate	-0.020 $\pm 0.015$	0.024 $\pm 0.013$	-0.076 $\pm 0.057$	0.004 $\pm 0.021$	-0.003 $\pm 0.006$	0.058 $\pm 0.036$	0.014 $\pm 0.014$

### Effect of Climate and grazing treatments on species traits

We saw significant effects of climate, grazing, and the interaction between climate and grazing on several community-level plant traits (Table 3.3). The decoupled climate

treatment caused increases in height, while grazing caused decreases. LDMC, ADL, and SLA were increased by both climate and grazing treatments. ADF was also increased by climate. This means that both grazing avoidance and tolerance traits were increased by decoupling the climate, because height and SLA are both grazing tolerance traits and LDMC, ADL, and ADF are associated with grazing avoidance. Aside from increasing SLA, a resource-capture trait, grazing mostly increased grazing avoidance traits.

Table 3.3. Results from the ANOVA listing effect size of the decoupled climate treatment and the grazing treatment on community-level traits. For this analysis, log-transformed and standardized data for treatment-level species-traits were used to calculate community-level traits. Significant effects are indicated by asterisks as follows: \*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ . Grazing avoidance is indicated by increases in stem to leaf ratio (Stem: Leaf), leaf dry matter content (LDMC), acid detergent lignin (ADL), neutral detergent fiber (NDF), and acid detergent fiber (ADF). Grazing tolerance is indicated by increases in specific leaf area (SLA) and height.

Trait	Climate Effect	Grazing Effect	Climate*Grazing Effect
Stem: Leaf	0.19308	-0.14948	-0.027149
LDMC	*** 0.4818	*** 0.5228	*** 0.456
ADL	*** 0.29964	*** 0.4594	-0.04944
NDF	-0.06183	-0.06735	* 0.11896
ADF	*** 0.16753	0.012645	*** 0.08001
SLA	*** 0.27079	** 0.1683	-0.04537
Height	** 0.07681	* -0.05512	-0.007736
Root Biomass	-0.018201	-0.06894	0.018412

When I ran the same ANOVA on community-level traits using species-traits pooled by species, the only significant effect was the effect of climate on height ( $p < 0.05$ ), which was also positive, though not as strong as when intraspecific variation was included. That effect can be attributed to changes in species composition. There was also a weakly significant ( $p=0.096$ ) effect of climate on SLA, which decreased with decoupled climate, and is due to changes in species composition rather than trait selection. This is the opposite of the effect when

both intra- and interspecific variations were included. This could imply that a certain species may affect SLA oppositely from the direction of trait selection, and that SLA is not the trait being selected for.

### Climate and grazing interactions

Climate and grazing interaction on LDMC

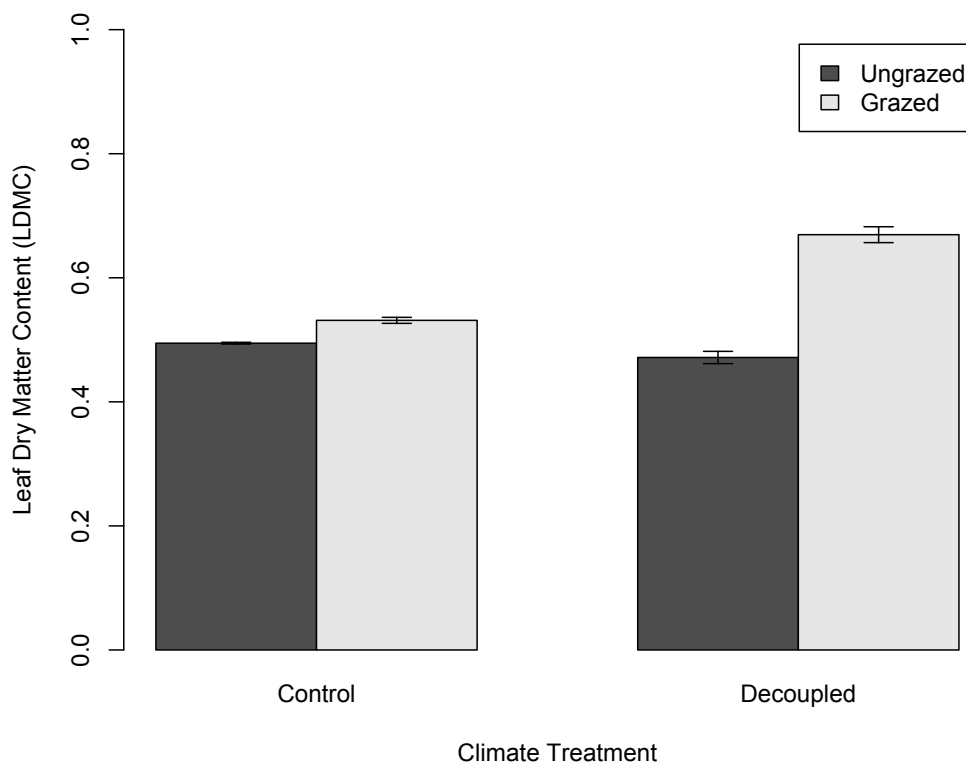


Figure 3.2. This plot shows the interaction between climate and grazing treatments on leaf dry matter content (LDMC). Error bars represent standard deviation of the mean.

There were significant interactions between grazing and climate for LDMC, ADF, and NDF (Table 3.3). In the control climate treatment, grazing only slightly increased LDMC, whereas in the decoupled climate treatment, grazing dramatically increased LDMC, a shift that indicates grazing avoidance. However, in the absence of grazing the climate treatment had only a small effect on LDMC (Figure 3.2).

### Climate and grazing interaction on ADF

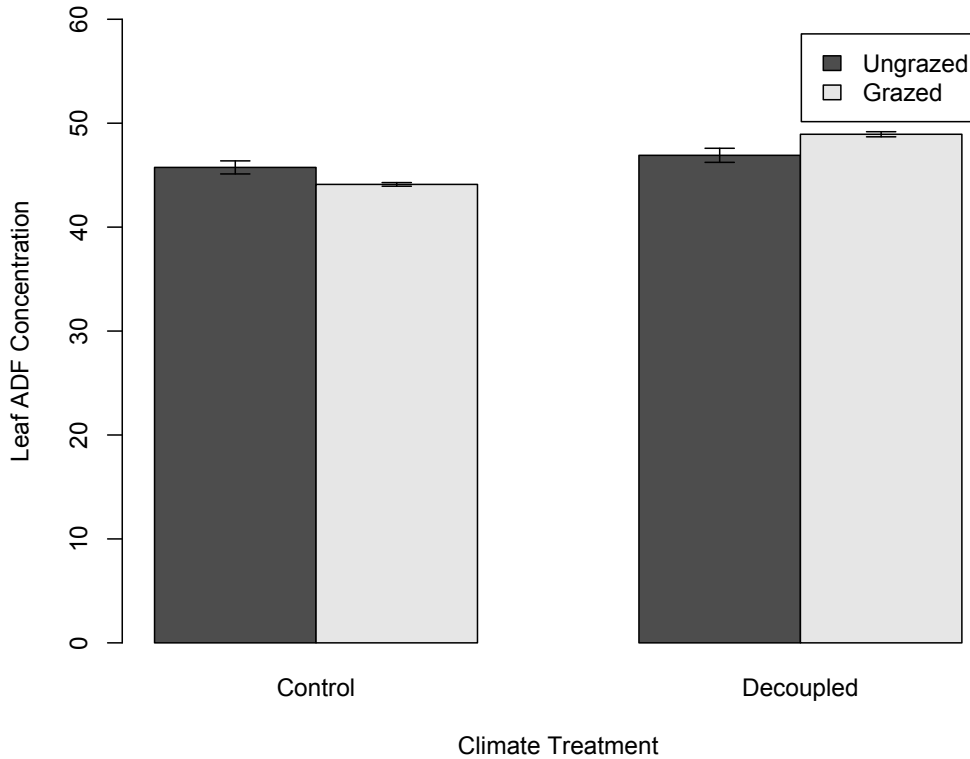


Figure 3.3. This plot shows the interaction between climate and grazing treatments on acid detergent fiber (ADF) concentrations in leaf tissues. Error bars represent standard deviation of the mean.

On fiber concentrations (ADF and NDF), the interaction between grazing and climate was similar, where grazing had an opposite effect depending on climate. The decoupled climate treatment caused a significant increase in ADF from the ambient climate values regardless of the presence of grazing. However, grazing led to a decrease in ADF under ambient climate, and an increase in ADF under the decoupled climate treatment (Figure 3.3). This shift also indicates a shift toward avoidance strategies being favored in decoupled climates.

### Climate and grazing interaction on NDF

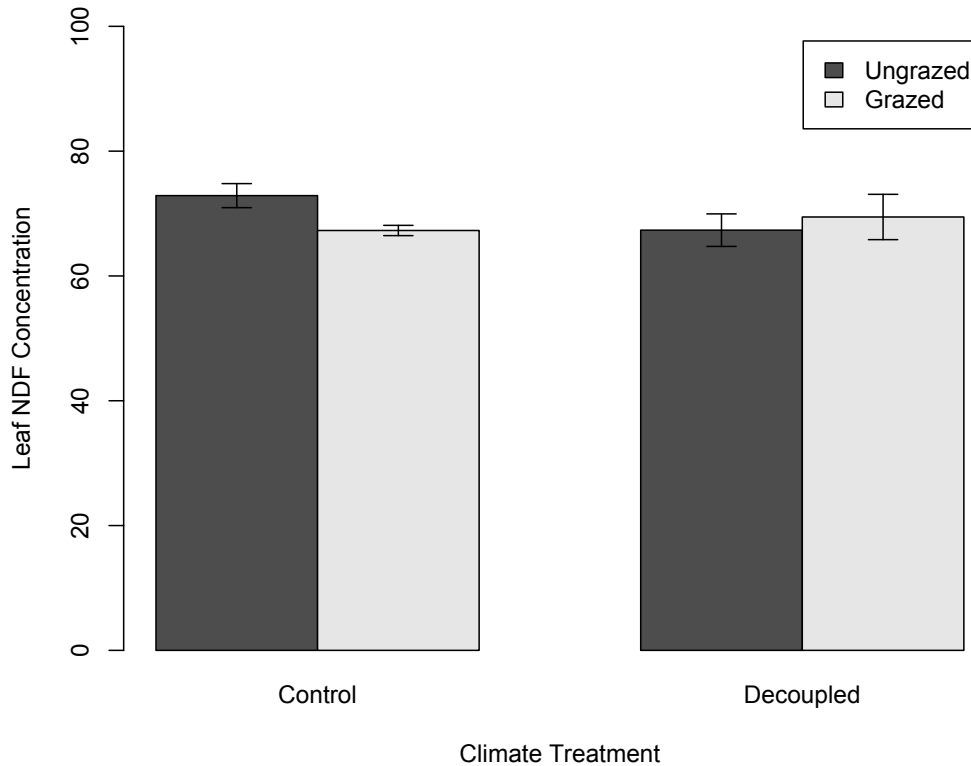


Figure 3.4. This plot shows the interaction between climate and grazing treatments on neutral detergent fiber (NDF) concentrations in leaf tissues. Error bars represent standard deviation of the mean.

Neither grazing nor climate had significant individual effects on NDF, but in the ambient climate, grazing caused a large decrease in NDF, indicating tolerance of grazing. In the decoupled climate grazing had a smaller effect, but caused an overall increase in NDF, indicating more of an avoidance strategy (Figure 3.4).

### Species composition

Grazing-induced changes in species composition were significantly greater in the decoupled climate compared with the ambient climate ( $p=0.0401$ , Figure 3.5). In fact, the dissimilarity indices did not overlap at all; the smallest change in species composition seen in the

decoupled climate treatment was still larger than the largest changes in species composition in the ambient climate.

Although the changes in species composition due to climate were not significantly affected by grazing, there was a trend toward smaller changes in the grazed treatment, and larger climate-induced changes in the ungrazed treatment.

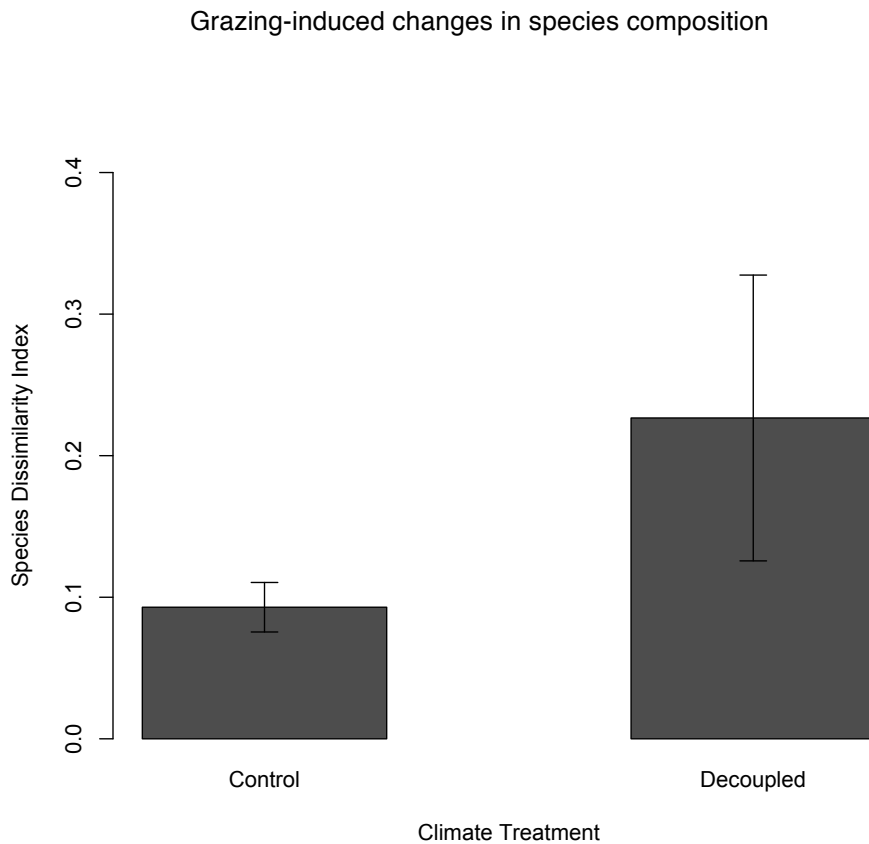


Figure 3.5. This plot shows grazing-induced changes in plant species composition under ambient and decoupled climate treatments. The species dissimilarity index on the y-axis ranges from 0 to 1, with increasing values indicating greater differences between species abundances in grazed versus ungrazed plots. Error bars represent standard deviation of the mean.



## DISCUSSION

Using a trait-based approach allowed me to determine which traits are most strongly influenced by the timing of water availability and grazing, and therefore provided more general insight in how plant assemblages will respond under future climates, and how grazing may interact with climate-induced changes (McGill et al. 2006). While many traits may contribute to performance, I focused on a suite of traits that represent a tradeoff between conservative growth strategies that limit tissue loss, and fast growth strategies that maximize resource acquisition (Wright et al. 2004). Conservative traits are associated with grazing avoidance strategies while resource acquisition traits are associated with grazing tolerance strategies.

One key assumption of trait-based approaches is that trait variation within a species is less than trait variation among species. However, intraspecific differences can account for a significant amount of variation between communities as well (Jung et al. 2010), and this assumption did not hold true for all traits in my dataset. Intraspecific variation can drive both convergence due to habitat filtering and divergence through niche differentiation. I included intraspecific trait variation in my model to help detect and illuminate these processes. Due to the harsh nature of the Tibetan Plateau, I expect that habitat filtering has resulted in strong convergence of traits among species. This may explain why interspecific variation was so low. On the other hand, intraspecific variation allows these species to adapt to fluctuations in resource environment.

### **The effect of climate on community-level traits**

We found the decoupled climate treatment to shift five traits toward avoidance (three significantly) and two traits significantly toward tolerance strategies. NDF changed

somewhat ambiguously (Figure 3.4). Thus, I found H1, that the decoupled climate treatment would increase grazing avoidance traits, to be only partially supported by the data. ADL, ADF, and LDMC of leaf tissues all increased significantly, indicating tougher, more fibrous, and less palatable leaves. Stem to leaf ratio increased and root biomass decreased, which can also indicate avoidance of grazing.

One tolerance trait that increased under the decoupled climate treatment was height. This trait is associated with light competition, and was also significantly affected by changes in species composition. This could indicate that as taller species move in, the other species need to compete more for light. The other tolerance trait that increased under the decoupled climate was SLA, which also indicates higher allocation to photosynthesis and light capture. This effect was entirely due to intraspecific variation, as the effect was the opposite when only interspecific variation was accounted for. All species except for *C. moorcroftii* and *L. pusillum* significantly ( $p < 0.001$ ) increased mean SLA due to the decoupled climate treatment. Changes in species composition due to climate, however, seem to favor species with lower SLA, which may or may not be a causal relationship.

This discrepancy has been seen in previous studies as well, in which grazing caused palatable species to allocate less to resource acquisition, while unpalatable species increased in abundance as well as resource acquisition traits (Chen et al. 2005). This could lead to an increase in community-level acquisition traits (associated with tolerance) while the dominant strategy is still avoidance.

Because the decoupled treatment drove greater changes in intraspecific than interspecific traits, I speculate that this must be due to increases in intraspecific competition. I suggest

that intraspecific competition for water in the decoupled climate treatment drives selection toward resource acquisition traits in the abundant, palatable species while interspecific competition selects for species with more conservative growth strategies, perhaps as palatable, grazing-tolerant species (i.e. *K. pygmaea*) are gradually replaced. A study by Hu et al. (In review) conducted as part of the same experiment, found that plant species partition water from snow events but do not partition water from growing season precipitation. This finding supports this idea that the decoupled climate treatment caused greater intraspecific competition for water.

Light is rarely limiting in the Tibetan Plateau due to the short stature of the plants and the high elevation, but it is possible that the small amount of light reduction due to the warming chambers could be responsible for increases in light-acquisition traits. However, if light were limiting we would expect grazing to interact with this effect as it can release light-limitation, so I find it more plausible that something else is driving this effect.

### **Grazing feedbacks**

There were three significant climate by grazing interactions, which all affected traits indicative of more conservative, avoidance strategies. LDMC and ADF traits both increased due to the decoupled climate treatment alone, whereas NDF was decreased. However, the presence of grazing in the decoupled climate treatment increased all three avoidance traits. This supports H2, and indicates that grazing in a decoupled climate can act as a feedback, enhancing the efficacy of avoidance traits. This was evident as the presence of grazing increased avoidance traits in the decoupled climate while increasing tolerance traits in the ambient climate.

## Changes in species composition due to grazing

Our results indicate that the decoupled climate treatment causes species composition to be more sensitive to the effects of grazing, with significantly greater species dissimilarity between grazed and ungrazed plots. This contradicts H3, which was based on a global meta-analysis (Chapter 2). Although the decoupled climate treatment enhanced changes in species composition due to grazing, I found evidence (though not significant) that grazing can serve to dampen the effects of changes in species composition due to climate. This result is in accordance with previous studies from the Tibetan Plateau (Klein et al. 2004).

Conceptual diagram for changes in community composition due to climate and grazing

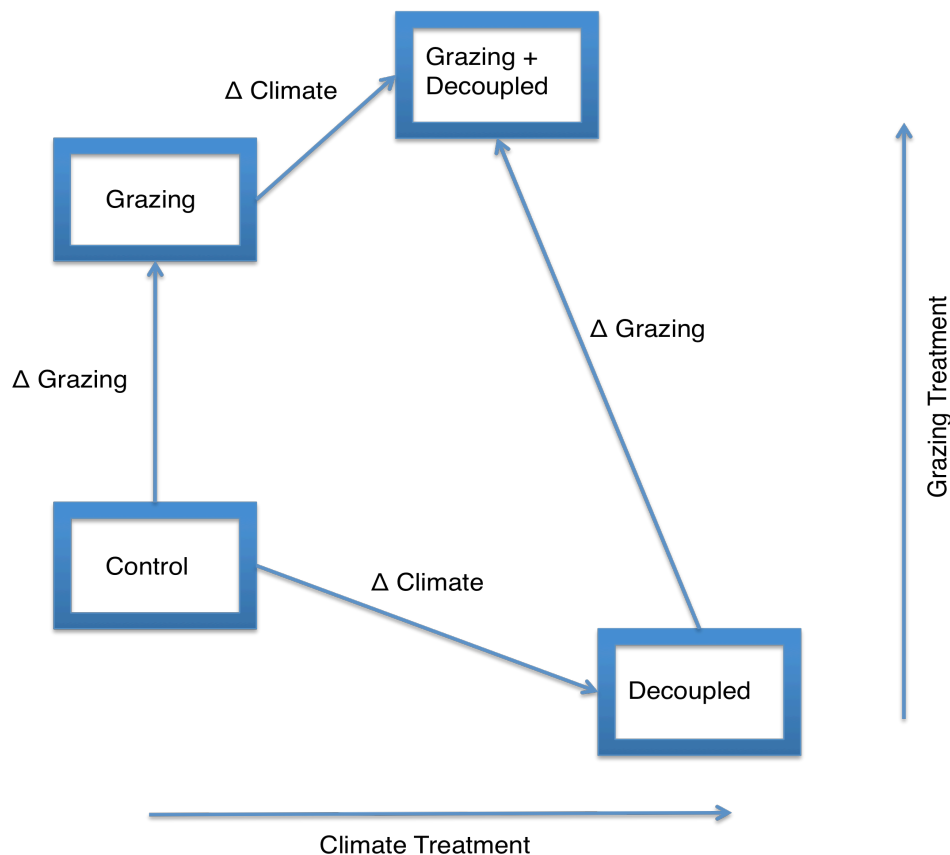


Figure 3.6. A conceptual diagram illustrating how it is possible for grazing to cause convergence of species compositions between control and decoupled climate treatments, while decoupling the climate can cause divergence between grazed and ungrazed species compositions

This phenomenon could occur if grazing caused convergence of species compositions between control and decoupled climate treatments, while decoupling the climate caused divergence between grazed and ungrazed species compositions (Figure 3.6). However, my results show that grazing actually more often caused divergence of species traits. This may mean that grazing causes divergence in intraspecific trait selection while buffering against changes in species composition. This is in accordance with the idea that grazing can have a stabilizing effect on species composition, driving equilibrium processes, and that climate can be more of a non-equilibrium process (Ellis and Swift 1988, Briske et al. 2003). My results also suggest that species well adapted to grazing may respond negatively to a shift in the timing of water availability toward the winter. However, grazing could reverse this effect.

## CONCLUSION

Many studies have shown that the resource environment and climate can mediate the plant response to grazing. This has been attributed to environmental filtering from the regional species pool that selects for a limited set of species that are more suited to certain grazing responses (De Bello et al. 2005). These responses have been particularly linked to annual precipitation and site fertility, and I have shown that the timing of moisture availability can also determine the most effective plant strategy in response to grazing. Furthermore, this response does not necessarily result from a difference in species pool, but rather from the interplay of intraspecific and interspecific trait selection processes that may operate on different time scales and in response to different drivers.

Our results show that on the Tibetan Plateau, forecasted changes in the timing of moisture availability may cause changes in species composition that could be mediated by grazing. Grazing causes divergent selection of intraspecific traits between control and decoupled

climates, possibly allowing these species to survive better under the altered climate, and buffering against changes in species composition. However, because the treatments were only in effect for 3 years, it is possible that the intraspecific trait changes due to grazing merely slow the effect of climate-induced changes in species composition. This could happen if intraspecific selection operates on a faster time-scale than interspecific selection. Longer studies will be needed to fully understand the long-term consequences of shifts in the timing of precipitation.

Our results suggest that a decoupled climate may interact with grazing to cause decreases in forage quality and palatability through increases in grazing avoidance traits. This has the potential to negatively impact many peoples' livelihoods in the Tibetan Plateau. It will be important to conduct studies investigating the role played by intensity of grazing in these responses to better formulate management plans to maximize forage quality.

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