

THESIS

CLIMATIC CONSTRAINTS ON HIGH-ELEVATION ABOVEGROUND NET
PRIMARY PRODUCTION

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY AARON B. BERDANIER ENTITLED CLIMATIC CONSTRAINTS ON HIGH-ELEVATION ABOVEGROUND NET PRIMARY PRODUCTION BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

CLIMATIC CONSTRAINTS ON HIGH-ELEVATION ABOVEGROUND NET PRIMARY PRODUCTION

Life in high-elevation ecosystems is hard. Ecosystem functions such as aboveground net primary production (ANPP) are constrained by short growing seasons and patchy resource availability. I quantified ANPP responses to changes in these variables by combining global, regional, and local observations with simple models.

I observed a consistent, linear increase in ANPP with growing season length (4 g/m²/d) at local and regional scales. I also found a nonlinear, asymptotic increase in ANPP with soil moisture across sites, despite variation in space, time, and plant species composition. I hypothesized that this soil moisture limitation may be partially mediated by nitrogen availability based on leaf-level observations from Niwot Ridge, CO. Finally, I compared a set of competing models relating ANPP to growing season length and soil moisture. I found that the combined influence of these variables was modeled best with a cumulative limitation by soil moisture. This model offers a simple basis for predicting the response of high-elevation ANPP to changes in these climatic constraints.

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INTRODUCTION

High-elevation meadows are extreme environments, with mean annual temperatures around 0°C. High-elevation areas in the United States are dominated by winter precipitation, which falls primarily as snow due to temperature constraints (Greenland 1989, Mote et al. 2005, Daly et al. 2007). Low temperatures and high amounts of precipitation as snow make growing seasons short and constrain ecosystem structure and function (Bowman and Seastedt 2001, Körner 2003). Climate in these ecosystems is also highly variable both spatially and temporally (Daly et al. 2007), due to microclimatic topography and vegetation influences on weather patterns (Billings 1973, Ostler et al. 1982, Roe 2004).

Interannual climate variability has profound effects on ecosystem functions such as aboveground net primary production (ANPP) through its influence on key limiting factors such as temperature, water and nutrients (Field et al. 1995, Nemani et al. 2003). Precipitation has an especially strong effect in high-elevation ecosystems. Spatially, the realized snowfall – i.e. the amount of precipitation on the ecosystem as snow (snow depth) and biologically available as spring snowmelt (Taylor and Seastedt 1994) – creates strong gradients in growing season length and soil moisture over small areas (~km²). Temporally, the variability in snow- and rainfall creates changes in growing season length and soil moisture that could exert stress on vegetation and alter ANPP.

Soil moisture and growing season length could constrain high-elevation ANPP, although previous research on high-elevation net primary production has yielded mixed

results. For example, Billings and Bliss (1959) observed that soil moisture and growing season length affected ANPP, but they did not quantify the effects. Knight et al. (1979) found that adding snow in a subalpine meadow decreased ANPP in a wet site, likely due to a shorter growing season length, but increased it in a dry site, due to more moisture and nutrients in the soil. Enquist and Ebersole (1994) observed that adding water during the growing season increased photosynthesis in an alpine forb, while Bowman et al. (1995) found that adding water in a similar study at a different site did not affect ANPP and only marginally increased photosynthesis. With a long-term data set, Walker et al. (1994) identified that ANPP in “snowbed” plant communities was strongly constrained by growing season length, but did not find any strong relationship between production and precipitation or soil moisture. Litaor et al. (2008) emphasized the possibility of a curvilinear response in ANPP along a snowmelt gradient due to the contrasting effects of soil moisture and growing season length. It is difficult to understand the generality of net primary production responses to climate from disparate, and often single-site, studies like these because they do not appear to be directly coherent.

A constraint in understanding limitation in high-elevation ANPP is the issue of scale (Wiens 1989, Levin 1992). An apparent advantage of studying high-elevation ecosystems is the large heterogeneity over small spatial scales (Bowman and Seastedt 2001, Körner 2003). Topography can create local environmental conditions (over $\sim\text{km}^2$) that are as variable as regional averages (Burns and Tonkin 1982, Bowman and Seastedt 2001). This is advantageous for researchers to explore possible hypotheses and conduct experimental manipulations at a single site. However, the ease of studying local heterogeneity as well as the difficulty in accessing many high-elevation areas has created

a tendency for little large-scale or cross-scale work in these ecosystems. An implicit assumption in many site-focused studies is that the knowledge gained at the local scale is relevant at regional, and even global, scales (Walker et al. 1993, Litaor et al. 2008), while this assumption has rarely been examined.

Additionally, simple limitation models based on minimum resource limitation may not be applicable in high-elevation ecosystems, since growing season length and soil moisture, two important abiotic factors in these ecosystems, are not always correlated. While late-melting sites tend to have more moisture than early-melting sites due to the presence of snow (Walker et al. 1994), this relationship can decouple due to changes in topography or physical soil characteristics (Billings 1973). Growing season length could constrain ANPP in all high-elevation ecosystems (because the season length is often < three months) and many of these ecosystems could exhibit periods of low soil moisture even if they have late snowmelt. Thus, there is not a single point where growing season length constraints end and soil moisture constraints begin.

Identifying and quantifying if and how high-elevation ANPP responds to variability in soil moisture and growing season length will increase our knowledge of high-elevation ecosystem functioning. This knowledge can also inform our understanding of the potential impacts of increased atmospheric [CO₂], which include earlier snowmelt, longer growing seasons, and decreased soil moisture in temperate high-elevation ecosystems (Harte et al. 1995, Myneni et al. 1997, Cayan et al. 2001, Christensen et al. 2007). The effect of these changes on high-elevation primary production will depend in large part on the biophysical and biogeochemical responses of the vegetation to key variables like growing season length and soil moisture.

CHAPTER 1: CONSISTENT CROSS-SCALE CONSTRAINTS OF GROWING
SEASON LENGTH ON HIGH-ELEVATION ABOVEGROUND NET PRIMARY
PRODUCTION

ABSTRACT

Growing season length is variable in high-elevation ecosystems globally and strongly influences ecosystem function. However, most high-elevation studies are conducted at single sites, with the assumption that local information is relevant at larger scales. Understanding climatic controls on ecosystem processes requires understanding the relationships between patterns at multiple scales. Here, I ask if local ecosystem responses to growing season length relate to regional and global patterns in high-elevation ecosystems. I collected field data from seven meadows throughout Colorado, USA, for a regional analysis, and from a snow depth gradient at one site for a local analysis. I estimated the local and regional responses of aboveground biomass production and plant species composition to growing season length. Then, I compared the strength of these growing season length responses to global data from the published literature. The upper limit of aboveground biomass increased with growing season length. The strength of this response was approximately $4 \text{ g/m}^2/\text{d}$ at all scales, suggesting similar constraints. Species composition was also strongly related to growing season length at both local and regional scales. The consistent response suggests that it may be possible to use knowledge about the constraints on primary production from local scales

to infer responses at broader, regional scales in high-elevation ecosystems. Moreover, climate-driven changes in growing season length could have important effects on species composition and aboveground biomass production across high-elevation ecosystems at multiple scales.

INTRODUCTION

Over 50% of total annual precipitation occurs during the winter in many high-elevation areas in the western United States and falls primarily as snow (Mote et al. 2005, Daly et al. 2007, USDA-NRCS 2008). Researchers have viewed snow as an important influence on the function and structure of high-elevation ecosystems for over 75 years (Cox 1933, Billings and Bliss 1959, Walker et al. 1994, Litaor et al. 2008). Studies predominantly from single sites, including some on the Eastern edge of the Rocky Mountains, suggest that aboveground biomass production is influenced by winter precipitation primarily because increases in the amount of snow decrease the length of the growing season (Knight et al. 1979, Walker et al. 1994, Litaor et al. 2008). Research on this topic has intensified in recent years due to the potential for climatic changes to alter snowfall and snowmelt patterns, which could advance the initiation of the growing season and extend the length of the growth period (Harte et al. 1995, Mote et al. 2005).

Implicit in these site-specific studies is an assumption that local-scale ecosystem processes are relevant for understanding and predicting broader regional, and even global, responses to changes in climate. While the extrapolation of winter precipitation and growing season length influences on ecosystem processes has been hypothesized and inferred beyond individual sites (Walker et al. 1993, Litaor et al. 2008), we do not know its generality at broader scales. For example, regional differences in winter precipitation

and temperature can cause regional variation in snowmelt date, while factors such as wind and topography can create local variation. Additionally, while it is clear that aboveground biomass can increase with an increase in growing season length when other environmental factors are not limiting, there is little analysis quantifying the response of aboveground biomass production to growing season length, even at local scales (Churkina et al. 2005).

An important step in understanding how climatic conditions control ecosystem processes is to understand the relationship between patterns at local scales and those at larger scales (Walker et al. 1993). Comparing and synthesizing findings from multiple scales of research has been useful for gaining knowledge about high-elevation plant responses to climate change (Dunne et al. 2003). Using information from local-scale studies has also produced reasonable predictions of primary production at regional scales in other grassland ecosystems (Burke et al. 1991). This multi-scale approach can allow us to test the generality of our knowledge and assess the potential for "scaling up" information from local studies to understand regional patterns.

I examined how spatial differences in growing season length influenced local and regional aboveground biomass and plant species composition in Colorado high-elevation meadows. I then compared these data to a global data set compiled from primary literature. The main goals of this study were to understand how local ecosystem processes relate to broader spatial patterns and to estimate the strength of high-elevation aboveground biomass responses to changes in growing season length. Based on previous research, I hypothesized that 1) aboveground biomass and species composition are constrained by growing season length across sites, and 2) local (within site) and regional

(across site) patterns respond similarly to variation in growing season length. This knowledge will inform our understanding of the function of high-elevation ecosystems and how they may change in the future.

METHODS

Regional sampling

In 2007, I identified alpine and subalpine meadow sites throughout Colorado to represent a gradient in growing season length. I chose sites for accessibility, to cover a broad regional area, and to minimize differences in mean annual precipitation, mean annual temperature, slope, and aspect. Access to many high-elevation sites over a regional area is extremely difficult, due to extreme terrain and the distances between locations, which limited the number of sites for this study. I selected seven sites (Figure 1.1, Table 1.1) using 30-year-averaged monthly climate data from the PRISM database (Daly et al. 2007) and a digital elevation model. I chose sites with a southern aspect to control for photoperiod and solar radiation across sites.

PRISM offers spatially-interpolated precipitation and temperature grids at 1 km² resolution that were designed for use in mountainous terrain across the United States (Daly et al. 2007). The PRISM database allowed me to have measurements of precipitation in remote locations without being constrained to sampling at sites with meteorological stations. It has been used to examine the effects of precipitation on ecosystem function in other remote, high-elevation ecosystems (Bowling et al. 2002, Mantgem and Stephenson 2007). I calculated the long-term and 2007 precipitation and temperature averages for each site, as well as the 2007 growing season (June to August) temperature and winter (October to May) precipitation.

I collected aboveground biomass samples and species composition data in the last week of July and the first week of August 2007, around the time of peak biomass in the region (May and Webber 1982). At each site, I collected between three and four subsamples that were averaged to represent a “site” sample. Averaging was done to avoid pseudoreplication at the site level and to account for small-scale heterogeneity within the site. I situated plots in a line perpendicular to the hill slope and spaced each plot 10 m apart to capture within-site heterogeneity.

I quantified plant species composition using a modified point-frame method (Walker et al. 2006) in a 1×1 m frame with a 100-point grid. All plant species present at each point were recorded. Directly adjacent to each species composition plot, I estimated aboveground biomass production by clipping a 0.5×0.5 m quadrat of aboveground biomass, while excluding previous years' dead material. Although plant production calculations can be influenced by the presence of perennial vegetation (Walker et al. 1994), I used the aboveground biomass harvests as an estimate of aboveground net primary production, assuming that the initial biomass was negligible (May and Webber 1982). I dried biomass samples at 60°C for at least 24 hours in a drying oven and weighed them for dry weight.

To examine other variables at the site, I also collected soil samples to measure soil texture and organic matter. Beneath each biomass quadrat I collected two to three 2.5×15 cm soil cores. I sieved air-dried soil samples with a 2mm sieve and removed all root material. I then collected 40 g subsamples for textural analysis, and 4 g subsamples for soil organic matter analysis. Soil texture was determined with a modified hydrometer method for particle size analysis (Gee and Or 2002). Soil organic matter was estimated

with loss-on-ignition (Nelson and Sommers 2002). The organic-matter subsamples were dried at 105°C overnight, weighed, ignited in a muffle furnace at 550°C for two hours, and reweighed. Organic matter was calculated as the fraction lost from the initial weighing.

Local sampling

In 2008, I collected samples from an alpine meadow at the Niwot Ridge LTER site (Figure 1.1; 3500 m; 40° 03' N, 105° 36' W). Plots were situated along a gradient of snow depth created by a snowfence that was established in 1993 (Williams et al. 1998, Walker et al. 1999). Within three years of the snowfence treatment, species turnover and community change was observed (Walker et al. 1999), with the current species composition resembling communities that occur along natural snow depth gradients at Niwot Ridge. The snowfence is situated in the “saddle” research area and is within 200m of the 2007 Niwot Ridge sampling site for the regional analysis.

I chose four replicate plots that were situated in rows moving away from the snowfence, at distances of 10, 25, 45, and 75 m. These 16 plots represented the variability of snow depths within the Niwot Ridge site. This stratification has been used in the past to characterize vegetation responses to snow at the site (Walker et al. 1999). I quantified plant species composition and aboveground biomass in the plots with similar procedures to the ones I used in 2007, but I clipped aboveground biomass in early-August to coincide with the end of the growing season and for consistency with other studies at the site. I restricted clipping to one 0.25 × 0.5 m quadrat per plot to minimize disturbance to the long-term research area.

Global data set

I compiled eight published data sets based on the availability of growing season length and aboveground biomass data (Table 1.2). The studies spanned a 50-year range and were spatially diverse. The data were all published in the original articles, except for growing season length data for Wang et al. (2008), which was obtained with snow presence data at the site from Y. Tang (unpublished data). I used data only from control plots in the study that involved experimental treatments (Harte et al. 1995).

Growing season length estimates

Growing season length is dynamic in high-elevation ecosystems. It is defined as the time when vegetation is actively growing, from when growth begins in the spring to when growth ceases and senescence begins in the fall. The start of the growing season in high-elevation ecosystems often initiates after snowmelt, except for in extremely wind-blown sites or in sites where a discernable snowpack does not accumulate, and can range from late May until late July in the Northern Hemisphere (Körner 2003). At broad spatial scales, changes in average winter precipitation create regional differences in snow free date (Mote et al. 2005). However, within a single site at a local scale, snowmelt can vary greatly over small areas ($< 1 \text{ km}^2$) due to redistribution of snow and accumulation of snowdrifts (Billings 1973, Walker et al. 1994). In contrast to the broad variability in the start of the growing season, the end of the growing season may be controlled more by factors other than the temperature at the end of the growing season (Arft et al. 1999). High-elevation plants may complete growth activity before temperature cues in the fall as an adaptation to the possibility for an anomalously early snowfall (Körner 2003). Instead, the end of the growing season in high-elevation ecosystems may be more

strongly related to photoperiod and the long-term mean annual temperature (Prock and Körner 1996).

I estimated the start of the growing season for the regional data set by quantifying the relationship between the snow free date and winter (October to May) precipitation with snow records from a network of regional SNOTEL (Snow Telemetry) meteorological sites (USDA-NRCS 2008). I obtained 10 years of data from 10 high-elevation SNOTEL sites around Colorado (Figure 1.1) that were chosen to represent the spatial variability in winter precipitation throughout the region. I estimated the snow free date for each site based on the winter precipitation values. I confirmed that these estimates were reasonable with observations from other studies (Walker et al. 1994, Price and Waser 1998). For the local data set, I observed and recorded the snow free date for each plot. All of the studies included in the global data set reported the snow free date.

Based on previous work (Prock and Körner 1996, Arft et al. 1999), I assumed that the end of the growing season was less variable across sites than the beginning of the growing season. I tested this assumption by examining unpublished phenological data at different subalpine sites near the Rocky Mountain Biological Laboratory (RMBL; J. Dunne and K. Taylor, unpubl. data). Across the elevation gradient at RMBL, the end of the growing season (defined by the date of fruit dehiscing pooled across species and years) differed by only one day, despite a greater than 10-day difference in the start of the growing season (indicated by snowmelt date; see Appendix 1 for details). This is consistent with observations in alpine ecosystems (Holway and Ward 1965), reinforcing the hypothesis that the end of the growing season is less sensitive to climate variability than the beginning of the growing season.

I estimated two dates for the end of the growing season based on the distinction between alpine and subalpine ecosystems. This estimation was necessary because I collected site-level aboveground biomass samples near the time of peak biomass, which is not necessarily the end of the growing season (Rikhari et al. 1992). While there could be small differences in the end of the growing season between sites within these two ecosystem types, I did not have sufficient data to make a further distinction. However, my estimates should be reasonable, given the consistency observed near RMBL (Appendix 1) and the small variation in slope and aspect among the sites (Table 1.1). I used the average date of fruit dehiscing (subalpine) or petal shed (alpine) to define the end of the growing season. I calculated these dates with unpublished phenology data from RMBL to represent the subalpine sites (J. Dunne and K. Taylor, unpubl. data) and from Niwot Ridge to represent the alpine sites (M. Walker, data online at <http://culter.colorado.edu/exe/.extracttoolA?itexphen.mw>) and confirmed these estimates with published values (Billings and Bliss 1959, Holway and Ward 1965, Price and Waser 1998). For the local and regional data sets, I calculated the length of the growing season as the difference between the end of the growing season and the snow free date. For the global data set, I calculated growing season length as the number of days between snowmelt and aboveground biomass sampling. This calculation could slightly underestimate growing season length but should not affect my conclusions.

Statistical analyses

All statistical tests and analyses were performed in the R program for statistical computing version 2.6.2 (R Development Core Team 2008).

I analyzed plant species composition and its relation to environmental variables with non-metric multidimensional scaling (NMDS) analysis (Kenkel and Orloci 1986) with the "vegan" Community Ecology Package in R. I chose NMDS because it has been considered better than other metric ordination methods due to fewer assumptions about the structure of the data (Minchin 1987). I conducted separate ordinations for local and regional data sets to examine how broad environmental variables, including growing season length, related to plant species composition at the regional scale and how growing season length related to plant species composition at the local scale. I used the Bray-Curtis dissimilarity index, and optimized the ordinations by running multiple random-start runs until the solutions converged to prevent inaccurate local optimum. For the regional analysis, I correlated environmental variables to the ordination axes to assess the goodness of fit of each variable.

To test the response of aboveground biomass to growing season length, I used both least squares and quantile regression. A quantile regression approach has been recommended for examining ecological responses to limiting factors (Cade et al. 1999). This method assumes that the limiting variable of interest (in this case, growing season length) creates an upper constraint on the response variable (aboveground biomass), and that the distribution of the response variable below this constraint is controlled by other factors (Cade et al. 1999).

I used the R package "quantreg" to conduct quantile regressions. For the local and regional data sets, I independently fit the 90th quantile of the linear regression. Setting the quantile to this level allowed me to assess the slope near the top of the distribution (where growing season length is hypothesized to be limiting), but to ensure

that I was not over-fitting the data, in case there was an erroneously-high point (due to small sample sizes). Performing the regression at other quantile levels did not change the results. For the global data set, I fit the 90th quantile for statistical analysis and comparison with the other regressions and I fit the 99th quantile to estimate the maximum global limit on aboveground biomass production.

For each quantile regression, I tested the null hypothesis that the slope was equal to zero with a one-sample t-test. Confidence intervals for the local and regional data sets were estimated with an xy-pair bootstrapping method because of small sample size (Efron and Tibshirani 1986, Cade et al. 1999). Without bootstrapping, I could not generate confidence intervals or consistent standard errors. After producing the independent quantile regressions, I compared the slopes with a one-way ANOVA to examine the hypothesis that they were not significantly different from one another.

RESULTS

The sites for the regional analysis covered a large gradient of winter precipitation (Table 1.1), and represented a broad range of growing season lengths, although there was substantial variation at the local level. Comparing the alpine and subalpine sites, the growing season (June to August) temperature in 2007 was not significantly different ($t = 1.30$, $df = 6$, $P = 0.234$). However, there were differences in soil characteristics (Table 1.1) and plant species composition (Figure 1.2A) between alpine and subalpine sites.

The NMDS ordination for the regional data set clearly separated alpine and subalpine plant communities (Figure 1.2A). While there were differences among sites in species composition, all of the communities were meadows dominated by herbaceous plant species and had similar functional composition. Of the environmental variables

analyzed, growing season length provided the best fit to the ordination, followed by elevation and mean annual temperature (Table 1.3). Similar to the regional scale, local plant species composition was strongly stratified by growing season length (Figure 1.2B).

The local, regional, and global scales all produced positive responses to growing season length at the upper limit of aboveground biomass (Figure 1.3). The slopes of the 90th quantile regressions were significantly greater than zero for the local ($t = 4.76$, $df = 15$, $P = 0.001$), regional ($t = 4.40$, $df = 6$, $P = 0.005$), and global ($t = 5.69$, $df = 83$, $P < 0.001$) data sets, indicating a significant relationship between growing season length and aboveground biomass close to its upper limits across scales. Aboveground biomass increased significantly with growing season length in a least squares regression across the regional ($F_{1,5} = 22.89$, $P = 0.005$, $R^2 = 0.82$) and global ($F_{1,82} = 65.75$, $P < 0.001$, $R^2 = 0.45$) data sets, but not across the local data set ($F_{1,14} = 2.12$, $P = 0.167$, $R^2 = 0.13$).

The quantile regression from the local data set estimated a slope of 4.05 ± 0.85 (mean \pm SE) and the quantile regression from the regional data set estimated a slope of 4.10 ± 0.93 . The global slope was estimated at 3.31 ± 0.58 for the 90th quantile and 3.94 ± 0.84 for the 99th quantile. The slopes of the three 90th quantile regressions were not significantly different from one another ($F_{2,104} = 0.19$, $P = 0.826$). The slope from the regional least squares regression (5.95 ± 1.24) was greater than the slopes from both the local and regional upper quantile regressions. The intercepts of all quantile regressions were not significantly different from zero, suggesting that the upper limit of aboveground biomass production approaches zero as growing season length approaches zero.

DISCUSSION

Regionally, aboveground biomass increased with an increase in growing season length (Figure 1.3). Previous site-based studies in high-elevation ecosystems show similar results. High-elevation aboveground biomass generally increases with a decrease in snow depth (Billings and Bliss 1959, Weaver and Collins 1977, Ostler et al. 1982, Walker et al. 1994). This local pattern is often attributed to increases in growing season length, based on the relationship between snow depth and the snow free date (Liston 1999, Mote et al. 2005); as snow depth decreases, snowmelt occurs earlier, advancing the onset of the growing season. My analysis suggests that a similar phenomenon could occur at regional scales. Across the regional gradient, the alpine sites had less aboveground biomass than the subalpine sites. This could be due to differences in growing season length or other factors like high winds above treeline, soil characteristics, or plant species composition.

At the local scale, I observed a positive relationship between growing season length and aboveground biomass that was similar to the regional data in the short growing season plots, but not in the longer growing season plots (Figure 1.3). This pattern has been found in other observational and experimental high-elevation studies. At the Niwot Ridge site, researchers have reported a curvilinear response in aboveground biomass to growing season length, with short growing season plots appearing to be constrained directly by growing season length and long growing season plots appearing to be constrained by other factors (Walker et al. 1994, Litaor et al. 2008). Similarly, an experimental snow removal in a subalpine meadow showed that aboveground biomass increased with an advance in snowmelt in a mesic site, but

decreased with an advance in snowmelt in a dry site (Knight et al. 1979). This pattern of variation beneath the upper limit was also seen in the plot data from the global data set (Figure 1.3). Decreases below the potential aboveground biomass (defined by growing season length) could be caused by other local variables like soil nutrient resources (Williams et al. 1998) or soil moisture (Litaor et al. 2008). Analyzing the effect of these factors on the location of points below a growing season length constraint was not the goal or within the scope of this study.

Consistent growing season length constraints

Overall, aboveground biomass was constrained at the upper limit by growing season length, regardless of scale. The upper bound of aboveground biomass in response to growing season length was surprisingly similar between the regional and local scales, with only slight variation in the predicted slopes and intercepts (Figure 1.3). Additionally, these regression limits are consistent with the maximum identified with the global data; eighty-eight percent of the aboveground biomass values from the global data set were below the local and regional quantile regressions. The global 99th quantile regression represents my best estimate of the maximum aboveground biomass production for a given growing season length across high-elevation meadows.

The similarity of the independently derived quantile regressions suggests that similar constraints on aboveground biomass exist at the local and regional scale, and that these constraints are consistent across sites in high-elevation meadows. At the local scale, topography, wind, and vegetation cause variation in snow deposition, which creates a broad range of growing season lengths. The range of growing season length values within a site shape the position of the site-level average at the regional scale. The

specific location of a site-averaged point beneath the growing season length constraint will depend on the importance of other limiting factors and the range of snow depth levels at the site.

Previous studies have suggested that the structure of plant communities can influence how ecosystem functions respond to changes in environmental conditions (Bowman 2000). I could not separate whether aboveground biomass responses along the gradients were due directly to the physical constraint of growing season length or indirectly to changes in species composition. Although there was variation in plant species composition across and within sites (Figure 1.2), there were no major changes in plant life forms in this study (Billings 1973, Walker et al. 1994). The similarity of the vegetation structure across the sites could explain why growing season length constraints on the function of these ecosystems are similar within and across sites.

The differences in plant species composition that I observed were best explained by changes in growing season length (Table 1.3). Gradients of species composition in relation to growing season length have been heavily studied in high-elevation ecosystems (Bliss 1966, Kuramoto and Bliss 1970, Komárková and Webber 1978, Litaor et al. 2008). These patterns have been explained largely by phenological responses to the timing of snowmelt (Holway and Ward 1965, Dunne et al. 2003). For example, species that require a relatively long growing season to complete their life cycle may be unsuccessful in areas where snowmelt occurs very late (Walker et al. 1999). Species composition in high-elevation ecosystems can turnover in response to directional environmental changes within three to four years (Harte and Shaw 1995, Walker et al. 1999, Walker et al. 2006). However, analyzing the implications of changes in growing season length with versus

without changes in species composition will require further research. Since I found overlap in growing season length estimates between alpine and subalpine sites (Figure 1.3), other factors, such as soil characteristics (Table 1.1), also likely contribute to ecosystem differences in species composition in high-elevation meadows.

Regional gradient analyses in other ecosystems have produced similar trends to the responses that I observed in aboveground biomass, although most studies have used remote sensing and modeling. Spatially, aboveground biomass appears to increase across sites with temperature, a proxy for growing season length, in high-latitude ecosystems (Epstein et al. 2008). Primary production also appears to have increased regionally in these high-latitude ecosystems in recent decades with a temperature-driven increase in growing season length, as inferred from NDVI observations (Tucker et al. 2001) and modeling studies of primary production (Randerson et al. 1999, White et al. 1999).

The effect of this temporal change in growing season length on net primary production was estimated in a modeling study to be approximately $7.7 \text{ gC/m}^2/\text{d}$ in high-latitude aspen (*Populus tremuloides*) stands and $3.9 \text{ gC/m}^2/\text{d}$ in high-latitude white spruce (*Picea glauca*) stands (Keyser et al. 2000). In another modeling study, the effect of growing season length was estimated with a least squares regression to be approximately $3.5 \pm 2.7 \text{ gC/m}^2/\text{d}$ in high-latitude tundra ecosystems (Piao et al. 2007). Assuming that biomass production is approximately 50% carbon, and that 50% of this production is aboveground, my estimates from field observations generally overlap with these model estimates. The greater response in aspen (*P. tremuloides*) stands could be due to greater leaf nitrogen content (Keyser et al. 2000), or possibly other species-specific factors, emphasizing the need for caution in extrapolating this response to other structurally-

different vegetation types. However, the similarity between my estimates and previous tundra estimates (Piao et al. 2007) suggest that these structurally-similar vegetation types may respond similarly to changes in growing season length.

Conclusion

The observed consistency on the growing season length constraint on high-elevation aboveground biomass production across scales reinforces the estimates made independently at each scale. Perhaps more interestingly, though, the similar responses suggest that it may be possible to use knowledge about the constraints on primary production processes at local scales to infer responses at broader scales in high-elevation ecosystems. Much of the research conducted in high-elevation ecosystems is restricted to a few, relatively accessible and well-studied research sites (e.g. Niwot Ridge LTER, CO, USA; Station Alpine Joseph Fourier, France). The similarity of responses across scales reinforces the value of the production mechanisms that are identified at these sites to possibly be applicable at broader scales.

My estimates of an approximately $4 \text{ g/m}^2/\text{d}$ response in aboveground biomass to changes in growing season length in high-elevation ecosystems provide an initial basis for quantifying the potential effects of climate variability and change on these ecosystems at multiple scales. The strong response in aboveground biomass to growing season length suggests a broad potential for these ecosystems to respond positively to advances in spring snowmelt (White et al. 1999, Tucker et al. 2001). This potential is tempered by the likelihood of other factors limiting biomass production below the upper limit, as I observed at the local and global scales (Figure 1.3). A similar restricted response to growing season length has been observed in other ecosystems (Barber et al. 2000, Angert

et al. 2005), emphasizing the need to understand and quantify how other factors, such as soil moisture, also influence biomass production in these ecosystems.

Table 1.1. Characteristics of study sites, with locations separated by ecosystem type (subalpine or alpine) and arranged by winter precipitation amounts during 2007.

Site ^a	Location (lat, lon)	Elev. (m)	MAT ^b (°C)	MAP ^b (mm)	2007 Winter ^b (mm)	Nearest met. station 2007 Winter (mm) and distance to site ^c	GSL (d)	Slope (%)	Soil texture ^d	SOM ^e (%)
1. WRNF	39°40', -107°14'	3139	1.8	927	583	739 (14.9 km)	90	14	Clay Loam	9.7
2. RMBL	38°58', -106°59'	2904	1.4	893	592	386 (7.4 km)	89	13	Clay	8.5
3. SINP	38°06', -105°38'	3495	-1.3	849	680	734 (16.7 km)	83	26	Clay Loam	11.1
4. SBB	37°55', -107°43'	3435	1.0	1051	825	856 (15.1 km)	76	13	Clay Loam	14.7
5. ME	39°36', -105°38'	3876	-3.3	806	614	638 (6.1 km)	68	24	Sandy Loam	17.9
6. SINP	39°37', -105°37'	3670	-1.5	920	686	734 (17.4 km)	63	27	Sandy Loam	15.7
7. NWT	40°03', -105°35'	3504	-1.4	943	737	630 (3.9 km)	60	12	Sandy Loam	18.1

^a Site names: WRNF = White River National Forest, RMBL = Rocky Mountain Biological Laboratory, SINP = San Isabel National Forest, SBB = Senator Beck Basin, ME = Mount Evans, SINP = San Isabel National Forest, NWT = Niwot Ridge LTER.

^b Data were collected from PRISM (Daily et al. 2007). Means were 30 year averages. Winter was defined as October to May.

^c Meteorological data from SNOTEL (USDA-NRCS 2008).

^d Soil texture characterized by the USDA soil texture classification (USDA-NRCS 2008) and determined gravimetrically (Gee and Or 2002).

^e Soil organic matter determined by loss on ignition at 550°C (Nelson and Sommers 2002).

Table 1.2. Sources for the global data set, ordered by year of study (numbers indicate references below). Locations are rounded to the nearest 1/3 of a degree.

Site	Location (lat, lon)	Elev. (m)	Years
Snowy Range, WY, USA (1) Alpine meadow	41.3°, -106.3°	3,353	1955
Mt. Washington, NH, USA (2) Alpine meadow	44.3°, -71.3°	1,800	1957-1962
Olympic Mountains, WA, USA (3) Subalpine meadow	48°, -123.3°	1,530	1967
Medicine Bow Mountains, WY, USA (4) Subalpine meadow	41.3°, -106°	3,082	1977
Niwot Ridge, CO, USA (5) Alpine meadow	40°, -105.6°	3,528	1982-1989
Baideni-Ali, Himalaya Mountains, India (6) Alpine meadow	41.3°, 71.6°	3,425	1989
Gothic, CO, USA (7) Subalpine meadow	39°, -107°	2,920	1992
Qinghai-Tibetan Plateau, China (8) Alpine meadow	37.6°, 101.3°	3,240	2002-2004

Further information about site locations or vegetation types can be found in the publications: (1) Billings and Bliss 1959, (2) Bliss 1966, (3) Kuramoto and Bliss 1970, (4) Knight et al. 1979, (5) Rikhari et al. 1992, (6) Walker et al. 1994, (7) Harte et al. 1995, (8) Wang et al. 2008.

Table 1.3. Pearson correlations and goodness of fit values for the axes of the non-metric multidimensional scaling ordination of species composition and key environmental variables from the regional data set, organized by goodness of fit.

	NMDS1	NMDS2	R ²
GSL	-0.998	0.064	0.816
Elevation	0.961	0.277	0.532
MAT	0.994	0.108	0.485
2007 Winter	-0.621	-0.784	0.278
Slope	-0.926	-0.377	0.020
MAP	-0.126	-0.992	0.001

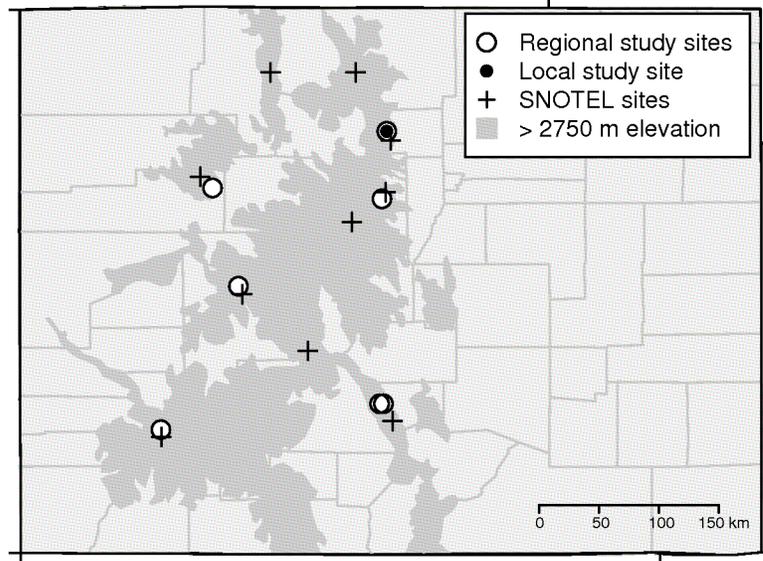


Figure 1.1. Map of study sites in Colorado. Circles are sites in the regional data set, the filled circle is the site of the local data set (Niwot Ridge, CO), and the plus signs are SNOTEL sites used for estimating growing season length.

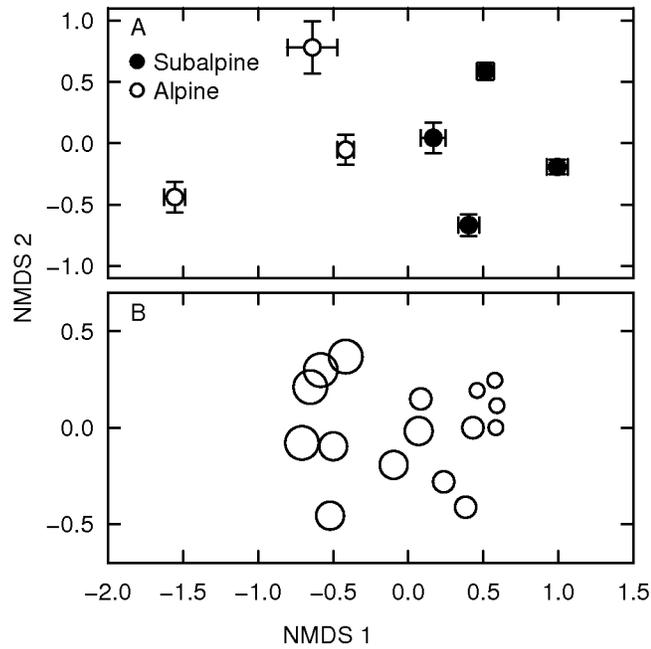


Figure 1.2. Non-metric multidimensional scaling ordination for plant species composition for (A) the regional data set and (B) the local data set. For the regional data set, scores are the average ordination point for the site \pm SE. For the local data set, each point is an individual plot and the size of the points are scaled to the growing season length, ranging from 78 days to 34 days.

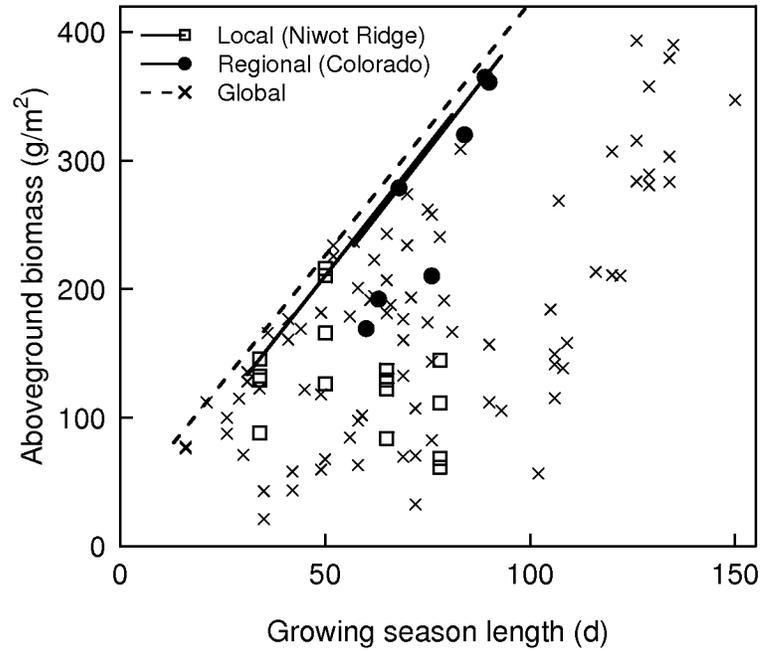


Figure 1.3. Aboveground biomass responses to growing season length. Local data are open squares, regional data are filled points, and data from the global data set are crosshatches. The solid lines are the local and regional quantile regressions (90th quantile), and the dashed line is the maximum global quantile regression (99th quantile).

CHAPTER 2: SOIL MOISTURE LIMITATION OF HIGH-ELEVATION ABOVEGROUND NET PRIMARY PRODUCTIVITY

ABSTRACT

Moisture availability is variable in high-elevation ecosystems and influences their structure and function. But, moisture constraints on high-elevation primary productivity have never been demonstrated at broad scales. I compiled data from a global set of high-elevation studies to examine if and when aboveground net primary productivity (ANPP) is limited by soil moisture. My results show that soil moisture limits ANPP globally and that this pattern is represented best with a non-linear asymptotic model. ANPP responded consistently across studies, despite variation in space, time, and plant communities. I examined possible causes behind this pattern with observational data at one site. I found strong connections between soil moisture, soil nitrogen availability, and plant nitrogen content, suggesting that nitrogen availability may partially mediate the response of high-elevation ANPP to soil moisture. These findings have consequences for high-elevation ecosystem responses to climate variability and change.

INTRODUCTION

High-elevation meadow ecosystem processes are strongly constrained by climatic gradients. Moisture availability in these ecosystems is highly variable in both space and time due to topography, presence or absence of trees, and variability in interannual precipitation (Taylor and Seastedt 1994, Mote et al. 2005). While substantial research

has been conducted on plant ecophysiological responses to moisture in high-elevation ecosystems (Oberbauer and Billings 1981, Enquist and Ebersole 1994, Bowman et al. 1995), little information on broad patterns is available. Consequently, moisture limitation of primary productivity in high-elevation meadows has been qualitatively inferred (Billings and Bliss 1959, Walker et al. 1994) but not demonstrated quantitatively at a large scale (Bowman et al. 1995). Changes in primary productivity influence carbon inputs to ecosystems from the atmosphere (Schimel et al. 2001) and could alter carbon storage in high-elevation ecosystems (Neff et al. 2002). Knowing if and when primary productivity responds to soil moisture availability will increase understanding of interannual and spatial dynamics in ecosystem processes. Additionally, knowledge of the shape and degree of moisture limitation on primary productivity is essential for predicting the impacts of changes in climate on these ecosystems (Harte et al. 1995, Weltzin et al. 2003, Fischlin et al. 2007).

Two mechanisms for moisture limitation have been proposed in high-elevation ecosystems, caused by either biophysical or biogeochemical responses (Körner 2003). Decreased soil moisture could induce biophysical drought stress if plants cannot maintain turgor, thereby reducing primary productivity through stomatal closure. Alternatively, decreased soil moisture could reduce mass flow of nutrients in the soil and microbial activity, decreasing nitrogen mineralization and availability. Decreased nitrogen availability due to decreased soil moisture could reduce primary productivity. Körner (2003) suggested that the second mechanism is more likely in high-elevation ecosystems because the stomata of high-elevation plants are rarely restricted by vapor loss and low leaf water potentials. This idea is anecdotally reinforced with observational research

(Oberbauer and Billings 1981, Körner et al. 1986). While both provide a possible explanation for moisture limitation of primary productivity, they may have different consequences for how high-elevation ecosystems respond to environmental change.

I tested whether high-elevation aboveground net primary productivity (ANPP) was limited by soil moisture by synthesizing data from nine temporally and spatially distinct studies, including observational data that I collected (Table 2.1). The sites represent a broad, global-scale gradient in soil moisture levels in alpine and subalpine meadow ecosystems. I considered linear and non-linear responses to soil moisture and compared these models to a null model (Figure 2.1). I predicted that ANPP would increase significantly with soil moisture. I then examined the contrasting biophysical and biogeochemical limitation hypotheses with leaf samples of *Polygonum viviparum*, a globally common alpine forb, at one site (Niwot Ridge, CO) along a gradient of soil moisture. I measured leaf carbon isotope discrimination ($\delta^{13}\text{C}$) to estimate stomatal closure and measured soil and plant nitrogen to estimate nitrogen limitation. Based on previous research, I predicted that the biogeochemical response to soil moisture would be stronger than the biophysical response.

METHODS

Global patterns

I searched for published studies from diverse sites to include in this analysis, but only included those studies that had both soil moisture and growing season length data along with aboveground net primary production values. Many studies reported only one of these environmental variables, and could not be included. I compiled data from eight published studies that met this criteria (Billings and Bliss 1959, Bliss 1966, Kuramoto

and Bliss 1970, Knight et al. 1979, Rikhari et al. 1992, Walker et al. 1994, Harte et al. 1995, Wang et al. 2008) and collected samples from a natural soil moisture gradient at the Niwot Ridge LTER site, CO (Table 2.1). The analysis largely examined spatial variation in ANPP, although some of the studies included multiple years of data, which added a temporal gradient as well.

I chose observational plots in a dry meadow at Niwot Ridge to control for growing season length, species composition, slope, and aspect. Twelve plots were situated over a 2500 m² area on a shallow, north-facing slope. Soil moisture was monitored in each plot with a Decagon Devices 10HS soil moisture sensor (Decagon Devices, Pullman, WA, USA) and recorded daily with a Campbell Scientific datalogger (Campbell Scientific, Logan, UT, USA). The sensors integrate volumetric water content for an 1100 cm³ area. I converted these values to gravimetric values for comparison with the other studies. I multiplied the volumetric water content (g water/cm³) by the inverse of the bulk density of each plot (cm³/g soil) to estimate the gravimetric soil moisture (g water/g soil) in each plot. All other studies reported soil moisture as gravimetric values. When repeated soil moisture measures were reported (Billings and Bliss 1959, Kuramoto and Bliss 1970), I calculated an average growing season soil moisture value. Gravimetric measures can exceed 100% soil moisture, especially in high-elevation ecosystems, because the measure is by weight. Soil organic matter can be high in these ecosystems (Neff et al. 2002) and can cause bulk density to be lower than the weight of water in soils with extremely high organic content.

All average daily ANPP values were calculated by dividing ANPP (g/m²/y) by growing season length (d/y; calculated as the difference between snow free date and

harvest date). ANPP was estimated by end-of-season aboveground biomass harvests, or regressions based on aboveground cover values (Harte et al. 1995), with the assumption that initial biomass is small and negligible in high-elevation ecosystems (May and Webber 1982). Growing season length confounds primary production values in these ecosystems because it is variable and is a strong driver of plant growth (Körner 2003). In the data set, growing season length varied by a factor of 5 (see Appendix 2).

Normalizing ANPP for growing season length allowed me to control for this factor and focus on the relationship between soil moisture and ANPP. I used data only from control plots in the study that involved experimental warming treatments (Harte et al. 1995).

When multiple years were reported, each year was included as an individual point.

I excluded data points that had growing season lengths < 30 d ($n = 6$; 6% of the initial data set) because the species that inhabit these "snowbed" communities are specifically adapted for short growing seasons (Körner 2003). I expected these ecosystems to exhibit exceptionally high productivity values because they are adapted to complete their life cycle in an extremely short period of time (Walker et al. 1994, Björk and Molau 2007). Additionally, soil moisture and nitrogen levels are often highest immediately after snowmelt in high-elevation ecosystems, providing an important source of soil resources for alpine plants (Bilbrough et al. 2000). The pulse of moisture and nitrogen in the soil after snowmelt can lead to decoupling between soil moisture, nitrogen mineralization, and nitrogen availability when growing seasons are extremely short (Brooks et al. 1998). I confirmed the anomalously high productivity in these points after accounting for soil moisture by examining a plot of soil moisture-normalized ANPP (ANPP/SM) versus growing season length (see Appendix 2, Figure A2.2). All of the

points with growing season lengths < 30 d were over 2 SD above the average values when excluding these points, suggesting that soil moisture constraints were outweighed by other factors in these communities.

Observational gradient analysis

Along the observational gradient at Niwot Ridge, I measured soil nitrogen availability, plant nitrogen content, and carbon isotope discrimination. Inorganic soil nitrogen availability was measured in each plot at Niwot Ridge with Western Ag Innovations, Inc. "PRS" ion-exchange resin probes with a unit of $\mu\text{g NH}_4\text{NO}_3/10 \text{ cm}^2$ of resin membrane (Saskatoon, Saskatchewan, S7N 4L8, Canada). These ion-exchange probes are appropriate for assessing soil nitrogen that is available for plant uptake and ecosystem processes because they integrate soil nitrogen availability over the entire installation period and they compare well with other methods of soil nitrogen availability (Qian and Schoenau 1994, Johnson et al. 2005). While many alpine plants are capable of directly taking up organic forms of soil nitrogen (eg. amino acids) in the absence of inorganic soil nitrogen (Lipson and Näsholm 2001), I considered this measure of inorganic soil nitrogen to be an appropriate index of plant-available soil nitrogen. No research has been done in the field to determine whether plants would preferentially take up organic over inorganic soil nitrogen, and field observations have shown that levels of organic soil nitrogen are strongly correlated with both soil moisture and inorganic soil nitrogen at Niwot Ridge, CO (Miller and Bowman 2003). The ability of plants to directly take up organic forms of nitrogen in the soil should not affect my results. I installed all of the probes within a day after snowmelt and removed them when I sampled the vegetation at the end of the growing season. I returned the probes to Western Ag

Innovations, Inc. for analysis, where they were extracted with 17.5 mL of 0.5 M HCl for one hour in a zip lock bag and analyzed for NH_4^+ and NO_3^- with a Technicon autoanalyzer (Bran and Lubbe, Inc., Buffalo, NY).

I collected leaf samples of *Polygonum viviparum*, a globally common alpine forb, for leaf tissue $\delta^{13}\text{C}$ and nitrogen concentration analysis. Carbon isotope discrimination is used widely as an indicator of stomatal conductance relative to photosynthesis over the entire growing season (Farquhar et al. 1989, Bowman et al. 1995, Dawson et al. 2002), while aboveground plant nitrogen uptake and leaf nitrogen concentration per unit mass are strongly related to photosynthetic capacity (Evans 1989, Reich et al. 1997). I harvested samples at the peak of the growing season (first week of August 2008) to ensure that the majority of representative production was complete (for $\delta^{13}\text{C}$ analysis) and that belowground vegetative structures were not reabsorbing nitrogen from the leaves (Körner 2003). I chose leaves of equal size and with similar canopy position to ensure homogeneity in age and sun exposure (Reich et al. 1997).

I analyzed $\delta^{13}\text{C}$ and nitrogen concentration in the leaves with a Carlo Erba NA1500 (Milano, IT) elemental analyzer connected to a VG Isochrom continuous flow isotope ratio mass spectrometer (Isoprime Inc., Manchester, UK) at the Stable Isotope Laboratory, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO. The integrated thermal conductivity detector allows seamless analysis of nitrogen concentrations from the elemental analyzer and ^{13}C isotope discrimination from the mass spectrometer on each sample. The analytical precision of each isotopic measurement was $\pm 0.2\text{‰}$. I estimated aboveground plant nitrogen content by multiplying *Polygonum viviparum* leaf nitrogen concentration (% N) and total

aboveground net primary production ($\text{g/m}^2/\text{y}$) as an index of the mass of nitrogen (g N/m^2) taken up by the aboveground vegetation during the year. Forbs made up over 75% of the ANPP in the plots, and *Polygonum viviparum* composed approximately 15% of the total plant cover.

Statistical analysis

I developed all models and performed all statistical tests in the R program for statistical computing, version 2.6.2 (R Development Core Team 2008). I tested four models:

1. a null model of no response, $ANPP = b$,
2. a linear model, $ANPP = m \times SM + b$,
3. a linear model with a zero intercept, $ANPP = m \times SM + 0$, and
4. a non-linear, Michaelis-Menten model, $ANPP = \frac{\alpha(SM - c)}{\left[\frac{\alpha}{\gamma} + (SM - c)\right]}$.

In all models, ANPP is average daily aboveground net primary productivity, SM is soil moisture, m is the slope of the response, and b is the intercept. The linear model with a zero intercept assumes that ANPP approaches zero as soil moisture approaches zero. In the Michaelis-Menten model, α is the productivity asymptote, γ is the slope of the response at low soil moisture levels, and c is the soil moisture compensation point (SM level when productivity = 0). I estimated parameter values and calculated model likelihoods (Burnham and Anderson 2003, Hobbs and Hilborn 2006) with the "bbmle" R package. This process optimizes parameter values by maximizing the negative log-likelihood in the multi-dimensional parameter space. I used a corrected Akaike's Information Criterion (AIC_c ; Akaike 1973, Burnham and Anderson 2004) to assess model fit, and I compared the different models with AIC_c differences (ΔAIC_c) and AIC_c

weights (w_i ; Burnham and Anderson 2003; see Appendix 2). The w_i is the relative probability that a model is the best of the candidate set. Models with $\Delta AIC_c > 10$ are generally removed from the set as unlikely candidates (Burnham and Anderson 2003).

I performed all linear regressions in R with least-squares linear models. To assess the power of a non-significant regression, I conducted an *a posteriori* power analysis with a pre-specified effect size and the observed variance (Thomas 1997). The pre-specified effect size was the maximum possible effect, calculated as the range of observed parameter values divided by the range of observed soil moisture values. I also calculated the minimum detectible effect size with a power of 0.80 and the observed variance (see Appendix 2).

RESULTS

Average daily ANPP increased with increasing soil moisture (Figure 2.2). The best model was a non-linear, Michaelis-Menten function (Table 2.2), which represented an asymptotic response to soil moisture. There was a 99% probability that this model fit the data best out of the candidate set, although there was some evidence that a linear regression also fit the data (1%). A linear regression of average daily ANPP versus soil moisture was highly significant ($F_{1,88} = 151.4$, $P < 0.001$, $R^2 = 0.63$). Performing a linear regression with the data source as a covariate showed that there were significant differences in the intercepts among studies ($F_{8,72} = 4.3$, $P < 0.001$). However, after accounting for differences in the data source covariate, the linear soil moisture response was still highly significant ($F_{1,72} = 54.2$, $P < 0.001$). Additionally, there was no significant interaction between soil moisture and data source ($F_{8,72} = 1.9$, $P = 0.074$), suggesting only weak differences among the individual slopes. I consider the non-linear

model to be the best fit of the set but I present both the linear and non-linear models as possible candidates. The linear, zero-intercept model and the null model of no response were both rejected due to their high AIC_c values (Table 2.2).

The asymptote and slope of the non-linear response curve offer insight into when soil moisture may become particularly limiting to high-elevation ANPP. I estimated when "limitation" may be prominent in the data set with the half-saturation constant – the soil moisture level when productivity is 1/2 of a maximum value. This is a novel approach to estimate the effect of soil moisture on ANPP, although it has been used widely to examine nutrient limitation in algal growth (e.g. Tilman 1981). This constant could be a valuable benchmark for comparison with future studies. The curve has an asymptote of 6.35 ± 1.39 g/m²/d (mean \pm SD), although productivity only reaches 72% of this value in the data set. Using the asymptote of the curve as the theoretical maximum potential productivity, I obtained a limitation value of approximately 87% soil moisture (Figure 2.2). Using the maximum observed value in the data set as the maximum potential productivity, I estimated a value of 51% soil moisture (95% CI: 19.5-105%). This second value provides a more conservative, and possibly more reliable, "limitation" estimate than the theoretical value calculated with the model parameterized asymptote.

In the gradient at Niwot Ridge, I was able to explore the biophysical and biogeochemical hypotheses for moisture limitation of ANPP with leaf samples of *Polygonum viviparum*. The soil moisture gradient covered 32% of the soil moisture values in the global data set and extended below the half-saturation constant "limitation" values. I found that $\delta^{13}\text{C}$ was not significantly related to soil moisture (Figure 2.3A; $F_{1,10} = 0.14$, $P = 0.71$, $R^2 = 0.01$) and that the observed soil moisture effect was very small (m

= -0.007). The estimated power for detection of the maximum possible effect along the gradient was 0.97, and the minimum effect that would be significant with a power of 0.80 was $m = -0.063$ (almost 10 times the observed effect). The point with the second lowest soil moisture level along the gradient had an unexplained lower discrimination (higher $\delta^{13}\text{C}$) than the other points.

In contrast to the $\delta^{13}\text{C}$ results, growing season inorganic soil nitrogen (NH_4NO_3) availability increased significantly with soil moisture (Figure 2.3B; $F_{1,10} = 8.2$, $P = 0.017$, $R^2 = 0.45$). This response was also reflected in aboveground plant nitrogen uptake. Estimated aboveground plant nitrogen content (g N/m^2 ; Figure 2.3C; $F_{1,10} = 6.5$, $P = 0.028$, $R^2 = 0.40$) and leaf nitrogen concentrations ($\text{mg N/g leaf tissue}$; Figure 2.3D; $F_{1,10} = 5.3$, $P = 0.044$, $R^2 = 0.59$) both increased significantly with inorganic soil nitrogen across the gradient.

DISCUSSION

Global patterns

High-elevation ANPP was limited by soil moisture across sites, after accounting for differences in growing season length (Figure 2.2). I observed a consistent, significant response across space, time, and vegetative communities, suggesting that the pattern is robust and generalizable throughout high-elevation meadow ecosystems. The relationship was best fit with a non-linear, asymptotic Michaelis-Menten model, which was 99 times more likely to be the best model than the others (Table 2.2). This model characterizes the enzymatic limitation of biochemical reactions, and has been used to represent the limitation of primary productivity to soil resources in other ecosystems (Rastetter et al. 1991, Pacala et al. 1996).

My estimate of "limitation" at 87% soil moisture, based on the half-saturation constant, covers over 3/4 of the observations. However, the alternative "limitation" estimate of 51% soil moisture, based on the maximum observed productivity, may provide a more reliable benchmark, given uncertainty in estimating the asymptote of the curve. Still, over 1/2 of the observations were beneath this value, suggesting that many high-elevation ecosystems are at least partially-limited by soil moisture.

Previous experimental research on resource limitation in high-elevation ecosystems has produced mixed results. Theoretically, ecosystems with long growing seasons and low snowpack should exhibit seasonal drought, especially in years with low growing season precipitation (Taylor and Seastedt 1994). But, evidence for effects of precipitation on productivity is limited (Bowman et al. 1995, Walker et al. 1994). Experimental watering increased photosynthetic rates in an alpine forb in one study, which was attributed to a combination of increased leaf water potential, stomatal conductance, and leaf nitrogen concentrations (Enquist and Ebersole 1994). In contrast, another experimental study at Niwot Ridge, CO found no response in photosynthetic rates or ANPP with a water addition, but an increase in both with a nitrogen addition (Bowman et al. 1995). This discrepancy could be due to topographic influences on soil moisture distribution. An alternative explanation could be an insensitivity of soil moisture levels to variation in water inputs in some alpine ecosystems, due to high soil organic matter and water holding capacity (Appendix 3). Neither experimental study reported soil moisture levels so direct attribution of the results (both positive and negative) to moisture could not be made.

Ecosystem responses to manipulations of nitrogen availability (eg. Bowman et al. 1995) are informative with my results if soil moisture influences nitrogen availability and uptake by plants. There is a strong correlation between soil moisture and nitrogen mineralization across early- and late-melting alpine meadows at Niwot Ridge, CO (Fisk et al. 1998), and in a subalpine meadow at Gothic, CO (Shaw and Harte 2001). At Niwot Ridge, seasonal patterns of microbial activity and nitrogen transformations are positively related to soil moisture, which affects inorganic nitrogen availability for ecosystem processes (Fisk et al. 1998). Additionally, soil moisture explained rates of decomposition in another study at Niwot Ridge, CO (Bryant et al. 1998), providing a link between soil moisture, decomposition processes, and microbial nitrogen transformations. However, these relationships could become decoupled in the future if other factors, like soil temperature, also exert a strong control on nitrogen mineralization, as was found in a warming experiment in a subalpine meadow (Shaw and Harte 2001).

Possible mechanisms

The observational data from Niwot Ridge covered a large range of soil moisture levels in the middle of the global data set, where moisture appeared to be particularly limiting. This gradient allowed me to explore two possible mechanisms behind the observed soil moisture limitation. My observation of no response in $\delta^{13}\text{C}$ (Figure 2.3A) suggests that stomatal closure may not be the only factor limiting ANPP with a decrease in soil moisture over the range of measurements (when soil moisture is greater than 25%). If stomatal conductance decreased with photosynthesis at low soil moisture levels, I would expect less discrimination of ^{13}C (higher $\delta^{13}\text{C}$) in plant tissues. The minimum effect that I could detect along the gradient was much smaller than that observed in leaf

$\delta^{13}\text{C}$ studies in other ecosystems (Garten and Taylor 1992) and the estimated power was high, suggesting that there was little chance of making a Type II error.

Other studies reinforce the conclusion that high-elevation vegetation is not primarily limited by stomatal closure with low soil moisture, except at extremely low leaf water potential levels (Oberbauer and Billings 1981, Körner 2003). Stomata may be less responsive to soil moisture and leaf water potential at high elevations if their conductance is controlled by other environmental factors. High-elevation plants generally have greater stomatal conductances and higher transpiration rates than lower-elevation plants (Körner et al. 1989), which could be influenced more by solar radiation than by soil moisture (Körner et al. 1986). Generally higher solar radiation at high elevations may increase demand for plants to keep stomata open despite low soil moisture levels to maintain photosynthesis and to avoid light damage (Lambers et al. 2008).

Stress by low soil nutrient availability could also partially explain why I found no response in leaf $\delta^{13}\text{C}$ to soil moisture. The mobility of nutrients in the soil is a strong determinant of root nutrient acquisition (Clarkson 1985). A decrease in soil nitrogen availability (Figure 2.3B), diffusion, and mass flow when soil moisture is low should reduce plant nitrogen uptake (Figures 2.3C and 2.3D), decreasing nitrogen availability for the production of photosynthetic enzymes like Rubisco (Lambers et al. 2008). The resulting drop in photosynthetic capacity along with minor reductions in stomatal conductance could balance the supply and demand of CO_2 for primary production, resulting in nearly constant internal CO_2 concentrations (Tezara et al. 1999) and, subsequently, $\delta^{13}\text{C}$ values. Deciphering whether this pattern is widespread throughout high-elevation ecosystems will require further research.

A limitation of my results is that I examined only one abundant species at a single site. Experimental data from a nitrogen and moisture manipulation in a subalpine meadow suggested the possibility of differential, species-specific responses to resource availability, with some species appearing to be limited more by moisture and others appearing to be limited more by nitrogen (de Valpine and Harte 2001). While this research emphasizes the value of examining community-specific responses to resource availability, the strong relationship that I observed at the ecosystem level across vegetative types (Figure 2.2) is reinforced by previous research demonstrating broadly-consistent plant physiological responses to functional traits like leaf nutrient status (Reich et al. 1997).

Conclusions

The global relationship between soil moisture and average daily ANPP (Figure 2.2) and the observed connections between soil moisture, available soil nitrogen, and plant nitrogen uptake at Niwot Ridge (Figure 2.3) are relevant for understanding high-elevation ecosystem responses to interannual climate variability and directional climate changes (Walker et al. 1994, Fischlin et al. 2007). Experimental soil warming of 3 °C in a subalpine meadow decreased soil moisture by 25% (Harte et al. 1995). An equivalent decrease in soil moisture could decrease daily ANPP between 0.3 and 1.2 g/m²/d in this data set based on the best model (0.62 g/m²/d average), resulting in an 8-64% reduction in daily ANPP in this study, depending on initial soil moisture levels (22% average). A potential ANPP decrease of this amount, in addition to the coincident decrease in leaf nitrogen concentrations, could decrease carbon uptake through photosynthesis and also potentially decrease both the quantity and the quality of litter entering the system.

A decrease in soil moisture and ANPP could feedback to decrease the release of carbon through decomposition, thereby slowing carbon cycling in high-elevation ecosystems. However, my results from Niwot Ridge suggest that the specific response to a change of this magnitude could depend on whether soil nitrogen availability changes with soil moisture availability (Fisk et al. 1998), or whether warming could increase nitrogen mineralization despite a decrease in soil moisture (Shaw and Harte 2001). Additionally, whether this feedback could balance the decrease in inputs to maintain the source/sink status of high-elevation ecosystems will require further research. But, my results offer the first quantitative estimate of the degree of moisture limitation in high-elevation ANPP globally. These findings can be used to develop and test high-elevation ecosystem carbon-cycle models.

Table 2.1. Locations, site ecosystem types, elevations, years, and coordinates for the studies included in my analysis, ordered by year of study.

Site	Elev. (m)	Years	Coordinates	SM range (%)	N
1. Snowy Range, WY, USA (<i>a</i>)	3353	1955	41.3N, 106.3W	21-136	8
2. Mt. Washington, NH, USA (<i>a</i>)	1800	1957-1962	44.3N, 71.3W	17-71	12
3. Olympic Mountains, WA, USA (<i>sa</i>)	1530	1967	47.9N, 123.4W	16-37	3
4. Medicine Bow Mountains, WY, USA (<i>sa</i>)	3082	1977	41.4N, 106.2W	39-69	4
5. Himalaya Mountains, Baiden-Ali, India (<i>a</i>)	3425	1989	30.2N, 79.7E	42-50	6
6. Niwot Ridge, CO, USA (<i>a</i>)	3528	1982-1989	40.1N, 105.6W	27-146	26
7. Gothic, CO, USA (<i>sa</i>)	2920	1992	39.0N, 107.0W	26-43	10
8. Qinghai-Tibetan Plateau, China (<i>a</i>)	3240	2002-2004	37.6N, 101.3E	33-76	9
9. Niwot Ridge, CO, USA (<i>a</i>)	3528	2008	40.1N, 105.6W	24-66	12

(*a*) = alpine, (*sa*) = subalpine

Sources: 1. Billings and Bliss (1959), 2. Bliss (1966), 3. Kuramoto and Bliss (1970), 4. Knight et al. (1979), 5. Rikhari et al. (1992), 6. Walker et al. (1994), 7. Harte et al. (1995), 8. Wang et al. (2008), 9. Berdanier, unpubl. data.

Table 2.2. Comparison of competing models from information theoretic analysis, ordered by model probability (w_i). R^2 values are the coefficients of determination for observed versus predicted regressions (Appendix 2, Figure A2.3). Model numbers refer to corresponding numbers in Figure 2.1.

Model	AIC_c (df)	ΔAIC_c	w_i	R^2
4. Non-linear	36.4 (4)	0.0	0.990	0.68
2. Linear	45.6 (3)	9.2	0.010	0.63
3. Linear-zero	58.1 (2)	21.8	< 0.001	0.63
1. Null	132.0 (2)	95.6	< 0.001	0.00

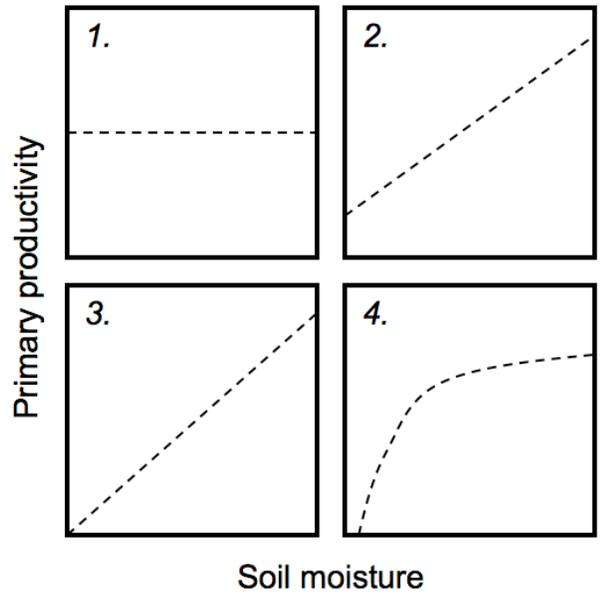


Figure 2.1. Hypothetical models for the influence of soil moisture on aboveground net primary productivity: 1. Null, 2. Linear, 3. Linear-zero intercept, 4. Non-linear.

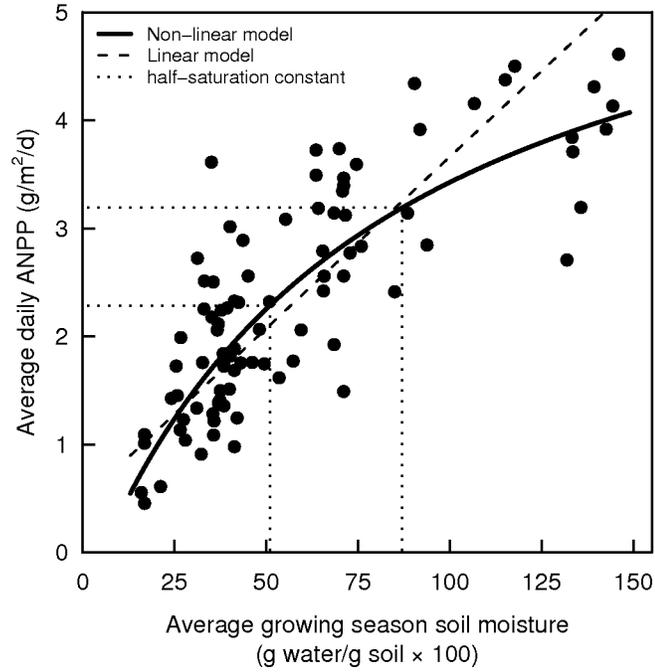


Figure 2.2. Response of average daily aboveground net primary productivity (ANPP) to average growing season soil moisture in the nine, high-elevation studies from Table 2.1. The solid, bold line is the non-linear model and the dotted intersections are the half-saturation constant estimates (maximum \times 0.5; see text for details). The dashed linear regression was highly significant (ANPP = 0.025 \times soil moisture + 0.941; $R^2 = 0.63$; $P < 0.001$) but was not chosen as the best model (Table 2.2).

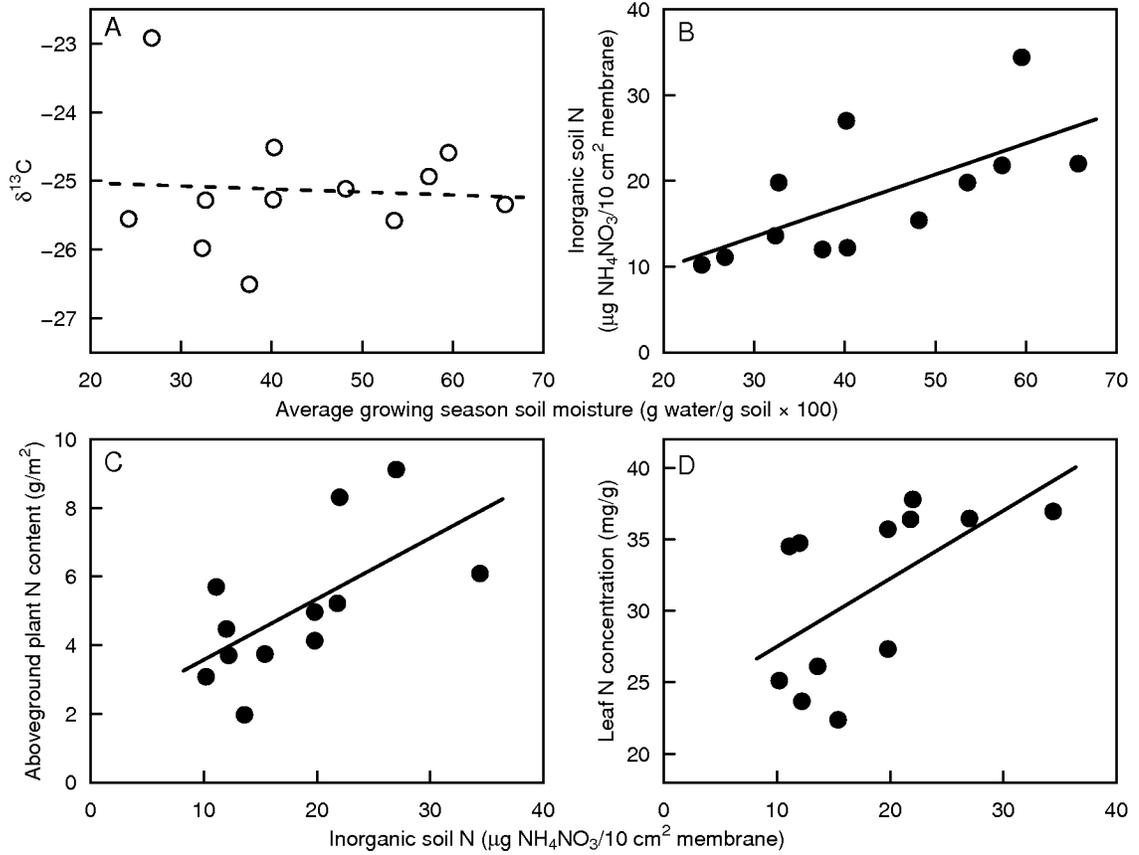


Figure 2.3. Links between soil moisture, soil inorganic nitrogen, and plant nitrogen from the gradient at Niwot Ridge, CO. A. Carbon isotope discrimination ($\delta^{13}\text{C}$) in leaf samples of *Polygonum viviparum* did not change significantly with soil moisture ($R^2 = 0.01$, $P = 0.71$). B. Inorganic soil nitrogen increased significantly with soil moisture ($R^2 = 0.45$, $P = 0.02$). C and D. Aboveground plant nitrogen content ($R^2 = 0.40$, $P = 0.03$) and leaf nitrogen concentrations ($R^2 = 0.59$, $P = 0.04$) both increased significantly with inorganic soil nitrogen.

CHAPTER 3: CUMULATIVE CLIMATIC LIMITATION OF HIGH-ELEVATION
ABOVEGROUND NET PRIMARY PRODUCTION

ABSTRACT

Climatic limitations of net primary production are a central focus of ecological research, but model predictions are highly variable, reflecting uncertainties in our understanding. Generally, soil moisture and growing season length strongly shape aboveground net primary production (ANPP). However, basic relationships may not accurately capture interactions between these climatic variables and ANPP may be inaccurately predicted in ecosystems where these factors are weakly correlated, like high-elevation meadows. I developed a set of competing models based on soil moisture and growing season length responses and tested them with data from a global set of high-elevation meadow studies. I tested the hypotheses that soil moisture and growing season length were both necessary to accurately predict high-elevation ANPP and that this limitation was cumulative. The best model predicted ANPP with high accuracy ($R^2 = 0.76$) and represented a cumulative limitation by both growing season length and soil moisture. This finding has implications for high-elevation ecosystem responses to changes in climate. Increases in temperature could increase ANPP due to an extended growing season but could decrease ANPP if this response is accompanied by a decrease in soil moisture.

INTRODUCTION

Climatic limitations of net primary production are a central focus of ecological research (Whittaker and Likens 1973, Nemani et al. 2003). Previously, I have shown that aboveground net primary production (ANPP) in high-elevation ecosystems increases with both growing season length (Chapter 1) and soil moisture (Chapter 2). These relationships provide descriptions that can be used to predict ANPP in response to changes in either variable independently. The connections between climatic conditions, environmental variables, and ANPP are reinforced by research in other ecosystems. These studies demonstrate how temperature and precipitation can influence ANPP through growing season length (Myneni et al. 1997, Randerson et al. 1999) and soil moisture (Knapp et al. 2002, Angert et al. 2005, Ciais et al. 2005, Arnone et al. 2008). Yet globally, model predictions of ANPP responses to changes in climate are highly variable due to different formulations of influential processes, reflecting uncertainties in our knowledge and complexity across systems (Cramer et al. 1999).

High-elevation ecosystem responses to growing season length and soil moisture may be distinct from corresponding low-elevation ecosystems because these factors are highly variable in space and time and are not always correlated. In high-elevation meadows, growing season length is influenced by snowfall amounts, topography, wind, and vegetation structure while soil moisture is often controlled by snowmelt patterns, temperature, soil properties, and rainfall amounts (Billings 1973, Körner 2003). Local gradients in topography and soil characteristics can cause soil moisture to be variable across a range of growing season lengths, and regional gradients in temperature can cause these patterns to be different among sites. In contrast, growing season length and soil

moisture are often negatively correlated in temperate ecosystems (Churkina and Running 1998), where many ANPP models are developed and parameterized (Bonan 1993, Parton et al. 1993, Scurlock and Olson 2002).

Both growing season length and soil moisture are recognized as influential variables. But making accurate predictions depends on representing realistic connections between the predictive relationships and questioning whether both variables are necessary. There are multiple models that could be used to predict ANPP, based on the primary relationships that I presented previously (a linear growing season length response and a non-linear soil moisture response) and different combinations among them. Combined models can represent limitation either simply as the minimum of the two variables or as a cumulative limitation. While it is not clear which representation is more accurate, a minimum resource limitation model could overestimate high-elevation ANPP with short growing seasons and low soil moisture because of unrepresented cumulative effects. Conversely, ANPP may be underestimated in this type of model with relatively longer growing seasons and lower soil moisture, common predicted responses of many high-elevation ecosystems to increases in temperature (Harte et al. 1995, Cayan et al. 2001, Christensen et al. 2007).

I developed multiple models to predict ANPP in response to growing season length and soil moisture to identify how high-elevation meadow ecosystems may respond to changes in these variables. I synthesized observational data from eight temporally and spatially distinct studies to estimate model parameters and compared the competing models with information criteria analyses. Based on previous research, I tested the hypotheses that 1) soil moisture and growing season length are both necessary to predict

ANPP accurately, and 2) soil moisture modulates the response of ANPP to growing season length to produce cumulative effects, as opposed to a minimum resource limitation.

METHODS

Models

I developed seven models to predict ANPP with different combinations of growing season length and soil moisture influences. First I explain the three independent models and their biological connection and then I describe how they were integrated into four models with combined influences. I developed and analyzed all of the models in the R statistical computing platform, version 2.6.2 (R Development Core Team 2008).

Plant growth increases with growing season length as a temporal constraint. In the simplest formulation, I represented the response of ANPP to growing season length with a linear function (Figure 3.1A),

$$ANPP = m_{gsl} \times GSL + B_o, \quad (1)$$

where m_{gsl} is the slope of the response, GSL is the growing season length, and B_o is the biomass when $GSL = 0$. I assumed that B_o would not be zero because high-elevation ecosystems are dominated by perennial plant species that maintain vegetative biomass for multiple years (Körner 2003). This simple model could represent the response of ANPP to growing season length better than a more complex function, depending on the data and characteristics of the ecosystems. For example, fast-growing vegetation may exhibit a linear response at the beginning of the growing season.

Alternatively, plant growth may be more accurately represented with a sigmoid function, which can represent more detailed biological responses. At the start of the

growing season biomass is small but plant growth is rapid, causing plant growth to appear exponential until the growth rate slows and ANPP reaches an asymptote (Figure 3.1B). A longer growing season due to temperature changes can advance the start of the growing season (Randerson et al. 1999) and allow plants to approach the maximum. Researchers have used a Gompertz growth function to represent plant growth through time (Erickson 1976, Haefner 2005). I used the Gompertz equation,

$$ANPP = K \times e^{-\left[\log\left(\frac{B_0}{K}\right)\right]} \times e^{(-\beta \times GSL)}, \quad (2)$$

where K is the maximum ANPP, β is the rate of decline in productivity, and B_0 is the biomass when $GSL = 0$. I assumed that initial biomass at the beginning of the growing season was constant across ecosystems and that changes in growing season length did not affect K . For both growing season length models, I assumed that B_0 was equal to the minimum value in the data set (21 g/m²/y). Using this constant value allowed quicker computation and ensured that ANPP in all ecosystems was positive.

In contrast to growing season length constraints, average growing season soil moisture is a resource-based limitation that can produce nonlinear and saturating responses in vegetation (Figure 3.1C, Haefner 2005). The Michaelis-Menten model is an asymptotic function that has been used to model plant growth in response to soil resources (Rastetter et al. 1991, Pacala et al. 1996). It models plant growth as a saturating function of soil moisture and is frequently related to enzyme activity in biochemical reactions like photosynthesis. I used the equation,

$$ANPP = \frac{\alpha(SM - c)}{\left[\frac{\alpha}{\gamma} + (SM - c)\right]}, \quad (3)$$

where SM is soil moisture, c is the soil moisture level when no growth occurs, α is the asymptote of ANPP, and γ is the slope of the ANPP response at low soil moisture. The variables were parameterized to a fixed value. I assumed that a soil moisture compensation point, c , existed but I did not constrain it in the models.

Models for the combined influences of growing season length and soil moisture considered the independent effects of these factors on ANPP. The first two combined models were based on Liebig's "law of the minimum" (Figures 3.1D and 3.1E), where ANPP is limited by either growing season length or soil moisture, with the equation,

$$ANPP = \min[f(GSL), f(SM)] , \quad (4)$$

where $f(GSL)$ is the growth response to growing season length and $f(SM)$ is the growth response to soil moisture. I ran separate models with the linear (Equation 1) and nonlinear (Equation 2) growing season length functions to compare these different formulations. The second two combined models defined growing season length as a maximum constraint on ANPP (Figures 3.1F and 3.1G). Soil moisture modulated growth as a proportion of the maximum potential,

$$\rho = \frac{(SM - c)}{\left[\frac{1}{\gamma} + (SM - c)\right]} . \quad (5)$$

The soil moisture constraint in this model (Figure 3.1F) is identical to Equation 3, but α has been substituted with one, making ρ a proportional scalar. I then modeled ANPP with the equation,

$$ANPP = f(GSL) \times \rho , \quad (6)$$

where $f(GSL)$ is the growing season length response in equations 1 (Figure 3.1F) or 2 (Figure 3.1G). Because growing season length is not directly a resource-based constraint,

ANPP could approach the maximum potential with "optimal" resources. Decreased soil moisture would decrease the ANPP response beneath this constraint. I assumed that the soil moisture response parameters were constant regardless of growing season length. The combined models produce unique predictions and have different implications for the processes that control ANPP, whether it is a response to the minimum limiting factor or a cumulative response.

Data collection

I compiled eight published data sets based on the availability of soil moisture, growing season length, and ANPP data (Table 3.1). The studies spanned a 50-year range and were spatially diverse. The data were all published in the original articles, except for growing season length data for Wang et al. (2008), which was obtained with snow presence data at the site from Y. Tang (unpublished data). I used data only from control plots in the study that involved experimental treatments (Harte et al. 1995). Growing season length was quantified as the number of days between snowmelt and ANPP sampling for each ecosystem. In some cases soil moisture was greater than 100% because it was calculated gravimetrically (g water/g soil). All values are represented as the average soil moisture throughout the growing season. Soil moisture for Billings and Bliss (1959) was averaged from repeated measures reported in the study. All ANPP values were reported as $\text{g/m}^2/\text{y}$, and were collected with aboveground biomass harvests, or with regressions based on aboveground cover values (Harte et al. 1995), after peak production at the end of the growing season.

Parameter estimation and model selection

I used maximum likelihood to estimate the parameters for each model (Burnham and Anderson 2003, Hobbs and Hilborn 2006, Bolker 2008) with the "bbmle" R package. This process optimized parameter values that maximize each models' fit to the ANPP data. I identified values to initiate the optimization with quantile regression, but I did not constrain the range of values. For the best model, I estimated when soil moisture limitation occurred with the half-saturation constant, which is the soil moisture level when ANPP is 50% of the asymptote. This is a novel approach to quantify the effect of soil moisture on ANPP, although it has been used to examine limitation in other settings, for example nutrient limitation of growth by algae (e.g. Tilman 1981) or soil microorganisms (e.g. Lipson et al. 1999). It could be a valuable benchmark for comparison with other studies. I calculated confidence intervals for the parameter estimates of each model and for the half-saturation constant to confirm that the estimates were within the bounds of possible values.

I used Akaike's Information Criterion (AIC; Akaike 1973) to compare the seven models. AIC was calculated with the equation, $AIC = -2L + 2k$, where L is the log-likelihood and k is the number of parameters in the model. I used a corrected AIC (AIC_c) to insure against sample size influences (Burnham and Anderson 2004). The AIC_c decreases as the likelihood increases, but it increases as the number of parameters increases, as a penalty for over-fitting the data and having high complexity. Models with low AIC_c values provide a better fit for the data. I compared the different models with AIC_c differences (ΔAIC_c) and AIC_c weights (w_i ; Burnham and Anderson 2003). ΔAIC_c is the difference between each model's AIC_c and the lowest AIC_c and w_i is a normalized

index of the relative likelihood. Models with $\Delta AIC_c > 10$ are generally removed from the candidate set as unlikely models (Burnham and Anderson 2003). I compared model predictions to observations with least-squared linear regressions, and tested the bivariate fits to a 1:1 regression (Appendix 4).

RESULTS

The linear, cumulative limitation model (Eqs. 1, 5 and 6) had greater support in the data than all alternative models (Table 3.2, Figure 3.2). There was nearly no uncertainty ($w_i > 0.999$) that this model provided the best fit for the data across ecosystems, and it was clearly separated from the other models, based on their high ΔAIC_c values. The nonlinear, cumulative limitation model had the next greatest support, followed by the linear and nonlinear minimum limitation models (Table 3.1). Models with only individual effects performed worse than the combined models and the minimum limitation models performed worse than the cumulative limitation models.

Plotting observed versus predicted ANPP values showed that the cumulative model predictions were closer to the observed values than the other models (Figure 3.2). There were differences among the models in the strengths of the relationships, and some of the comparisons had slopes significantly different from one. The only comparisons that did not differ significantly from a 1:1 regression were the linear, cumulative limitation and the linear growing season length only models (Appendix 4), suggesting that predictions of the other models were slightly biased. Predictions of the linear, cumulative limitation model accounted for 75.9% of the variation in observations across ecosystems, and had a slope closest to one with a linear regression (Figure 3.2).

The parameters estimated for the linear, cumulative limitation model were all significantly greater than zero. Growing season length influenced ANPP by 4.04 ± 0.63 g/m²/d (mean \pm SE). A one percent decrease in soil moisture caused a $3.25 \pm 1.23\%$ decrease in ANPP at low soil moisture levels, but the effect decreased and approached zero as soil moisture levels increased to the maximum. The half-saturation constant estimate for when limitation occurred in the data set was 43% soil moisture, but this value had a broad 95% confidence interval (26-130%) due to variability in predicting the soil moisture response curve (see Appendix 5 for more details).

DISCUSSION

Both growing season length and soil moisture are necessary to accurately predict high-elevation ANPP, emphasizing strong regulation by both factors in these ecosystems. This has been suggested in previous studies (e.g. Billings and Bliss 1959, Sacks et al. 2007), but never explicitly tested before now. ANPP was less closely related to individual factors than in some previous studies (e.g. Lieth 1975, Bonan 1993), possibly because of the variety of abiotic conditions across the data set and a weak relationship between growing season length and soil moisture. However, the poor prediction of ANPP with only one factor is consistent with other studies (Scurlock and Olson 2002, Zheng et al. 2003). As my results and these studies suggest, analyses that consider simple ANPP responses to temperature or precipitation may provide little information in many temperate, high-elevation ecosystems, where these factors can interact to influence environmental variables like growing season length and soil moisture.

Another primary finding is that soil moisture modulated the response of ANPP to growing season length. The combined models that predicted ANPP as the minimum

response to growing season length or soil moisture performed worse than models that employed a cumulative limitation (Table 3.2). This finding reinforces previous research on resource limitation which emphasizes influences from multiple factors (Bloom et al. 1985, Field et al. 1992), and suggests that models that focus on minimum resource limitation (e.g. Lieth 1975) cannot predict high-elevation ANPP as accurately as models where cumulative effects are considered.

In my analysis, models that predicted the influence of growing season length as a linear function performed better than nonlinear models (Table 3.2). Although the linear models had one less parameter than their respective nonlinear models, the differences in ΔAIC_c values between the linear and nonlinear models were sufficiently high to reject the number of parameters as a cause (Burnham and Anderson 2003). Alternatively, it suggests that vegetation growth is particularly fast at the beginning of the growing season in high-elevation ecosystems so that growth is steep, as opposed to shallow, and more similar to a linear than an exponential pattern. High-elevation vegetation, especially “snowbed” vegetation, has particularly fast growth following snowmelt to ensure completion of plant life cycles in the short growing season (Björk and Molau 2007). Also, ANPP did not saturate at the end of the growing season, suggesting that ANPP is still primarily limited by short growing seasons in these ecosystems. I expect that with longer growing seasons than observed in this data set, a nonlinear sigmoid function could represent ANPP better than a linear model.

The linear, cumulative limitation model performed well compared to other ecosystem models in the literature. The variance explained by the predictions based on the coefficient of determination (R^2) was comparable to a global grassland model (Parton

et al. 1993; $R^2 = 0.70$), as well as a model developed for two meadows at a single, alpine research site (Baptist and Choler 2008; $R^2 = 0.89$ and 0.95). While these values cannot be directly compared, due to differences in sample size, it is likely that additional variation is introduced by expanding the scale of observations from a single to multiple sites. The linear, cumulative limitation model explained more of the variance in the observed values ($R^2 = 0.76$) than a minimum resource limitation model fit to a global data set with a similar sample size ($R^2 = 0.44$, $n = 86$, Scurlock and Olson 2002), further emphasizing the need to consider cumulative limitation. The remaining variance in the best model presented here could be due to factors that I did not incorporate, like species composition, or simplifying assumptions that I made in all of the models, like a constant initial biomass value.

The combined effects of growing season length and soil moisture on ANPP are particularly important for predicting ANPP and CO_2 uptake in response to climate variability and change. Previous studies suggested that early season warming advances the start of the growing season and influences ANPP and CO_2 uptake in a broad range of ecosystems (Randerson et al. 1999, White et al. 1999). My results show that advances in the start of the growing season can potentially increase ANPP. My finding of an approximately $4 \text{ g/m}^2/\text{d}$ response in ANPP to growing season length in the absence of soil moisture constraints at a global scale is consistent with my findings at regional and local scales in other high-elevation ecosystems (Chapter 1; Appendix 5). Other studies suggest that drying that accompanies warming can have a negative effect on ANPP (Barber et al. 2000, Angert et al. 2005, Arnone et al. 2008). These studies are consistent with my estimate of an approximately 3% response in ANPP to low soil moisture levels, although

the soil moisture “limitation” estimate of 43% is lower than I estimated in previous analysis (Chapter 2; Appendix 5). This estimate may be lower because it was made with a data set that included ecosystems with short growing seasons, which do not appear to be as limited by soil moisture. Alternatively, it may be lower because the asymptote of the soil moisture curve was constrained by the influence of growing season length, which could be more realistic than the simplified maximum observed value calculation made in the previous analysis (Chapter 2).

The cumulative limitation model captured the dynamics between growing season length and soil moisture to predict high-elevation ANPP with high accuracy. This model reinforces previous studies showing that ecosystem responses to climate change can be complex and contrasting, with implications for carbon dynamics in seasonal ecosystems. Increases in temperature can increase ANPP due to an extended growing season but can decrease ANPP if this response is accompanied by a decrease in soil moisture. My findings also show that complex ecosystem dynamics can be represented with simple models and that these models can be fit with observational data to test our understanding of potential ecosystem responses to climate change.

Table 3.1. Study site characteristics, ordered by year of study (numbers indicate references below).

Site	Location	Elevation	Years
Snowy Range, WY, USA (1) Alpine meadow	106.3°W, 41.3°N	3,353m	1955
Mt. Washington, NH, USA (2) Alpine meadow	71.3°W, 44.3°N	1,800m	1957-1962
Olympic Mountains, WA, USA (3) Subalpine meadow	123.3°W, 48°N	1,530m	1967
Medicine Bow Mountains, WY, USA (4) Subalpine meadow	106°W, 41.3°N	3,082m	1977
Niwot Ridge, CO, USA (5) Alpine meadow	105.6°W, 40°N	3,528m	1982-1989
Baideni-Ali, Himalaya Mountains, India (6) Alpine meadow	71.6°E, 41.3°N	3,425m	1989
Gothic, CO, USA (7) Subalpine meadow	107°W, 39°N	2,920m	1992
Qinghai-Tibetan Plateau, China (8) Alpine meadow	101.3°E, 37.6°N	3,240m	2002-2004

Further information about site locations or vegetation types can be found in the publications: (1) Billings and Bliss 1959, (2) Bliss 1966, (3) Kuramoto and Bliss 1970, (4) Knight et al. 1979, (5) Rikhari et al. 1992, (6) Walker et al. 1994, (7) Harte et al. 1995, (8) Wang et al. 2008.

Table 3.2. Model selection

Model ^a	AIC _c	df	ΔAIC _c	w _i
1. Cumulative, linear	65.2	4	0.0	> 0.999
2. Cumulative, nonlinear	83.9	5	18.7	< 0.001
3. Minimum, linear	104.1	5	38.9	< 0.001
4. Minimum, nonlinear	121.8	6	56.6	< 0.001
5. GSL only, linear	125.7	2	60.5	< 0.001
6. SM only	130.9	4	65.7	< 0.001
7. GSL only, nonlinear	132.3	3	67.1	< 0.001

^a GSL = growing season length; SM = soil moisture

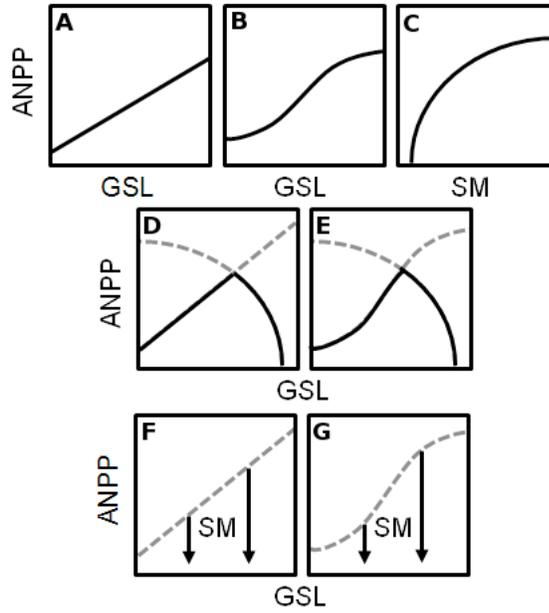


Figure 3.1. Hypothetical models for the influence of growing season length and soil moisture on high-elevation ANPP. The individual models are for A.) the linear and B.) nonlinear influence of growing season length, and C.) the nonlinear influence of soil moisture on ANPP. The multiple resource models show D-E.) minimum limitation, and F-G.) cumulative limitation with linear and nonlinear growing season length influences.

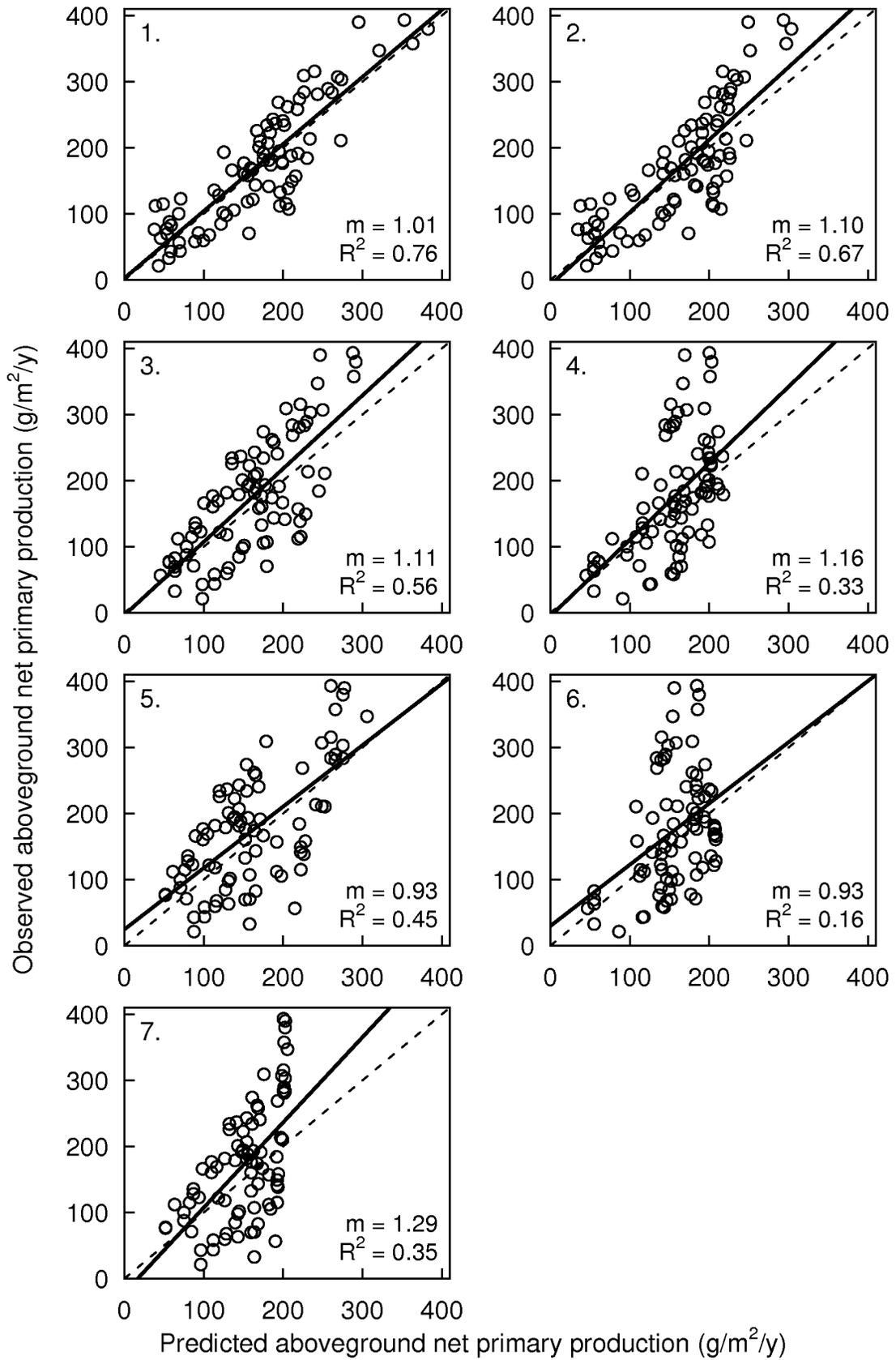


Figure 3.2. Observed versus predicted regressions for the seven models shown in Table 3.2. The solid lines reflect linear regressions, while the dashed lines are 1:1, to show deviations from a perfect relationship. Each panel shows the slope (m) and coefficient of determination (R^2) for the regression.

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APPENDIX 1: ESTIMATING GROWING SEASON LENGTH

I analyzed an unpublished, multi-year phenological data set from three sites near RMBL (J. Dunne and K. Taylor, unpubl. data) to test my assumption that the end of the growing season was invariant across sites. The data set contained phenological records for multiple species at three subalpine meadow sites (low, middle, high) over three years (1996-1998). The sites were within 10 km of each other and were all over 2750 m above sea level. At each site there were 10 plots. The average phenological stage of each species was estimated in each plot throughout the growing season. Seven phenological stages were recorded: 0) plant not yet flowering, 1) unopened buds, 2) open flowers, 3) old flowers, 4) initiated fruit, 5) enlarged fruit, 6) dehisced fruit.

For each site I pooled data for all plots and years for four common herbaceous species (*Lathyrus lanszwertii*, *Erigeron speciosus*, *Eriogonum subalpinum*, and *Helianthella quinquenervis*) to represent the average site phenology. Then, I regressed the day of the year by phenological stage for each site. I compared the responses with an ANCOVA to test for differences between the sites, and I used Type III Sums of Squares so that the site (*Site*) and phenological stage (*Stage*) variables were entered into the model at the same time. This formulation allows for more accurate testing of an interaction between *Site* and *Stage*.

The three sites had significantly different intercepts (*Site*), and significantly different slopes (*Site* × *Stage*; Table A1.1). This indicates that the beginning of the growing season occurred at different dates (confirmed with snowmelt dates, Dunne et al.

2003) and that phenology progressed at different rates during the growing season across sites. Despite differences among sites in the beginning of the growing season, the differences between sites at the last phenological stage were less than one day (Figure A1.1). This response likely occurs because species increase the duration of their life history more than the advance in spring snowmelt across sites (Steltzer and Post 2009) and is consistent with the hypothesis that high-elevation vegetation is constrained by growing season length. Additionally, the uniformity in the end of the growing season across sites suggests that high-elevation species respond phenologically as predicted (Körner 2003) and that my assumption of a common date for the end of the growing season across sites was acceptable.

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Table A1.1. Analysis of covariance test for differences among site phenology in subalpine meadows near RMBL.

	df	Type III SS	Mean Squares	F-ratio	P-value
Intercept	1	11,741,240	11,741,240	79,227.1	< 0.0001
Stage	1	704,131	704,131	4,751.3	< 0.0001
Site	2	20,790	10,395	70.1	< 0.0001
Stage × Site	2	5,530	2,665	18.7	< 0.0001
Error	2,960	438,664	148		

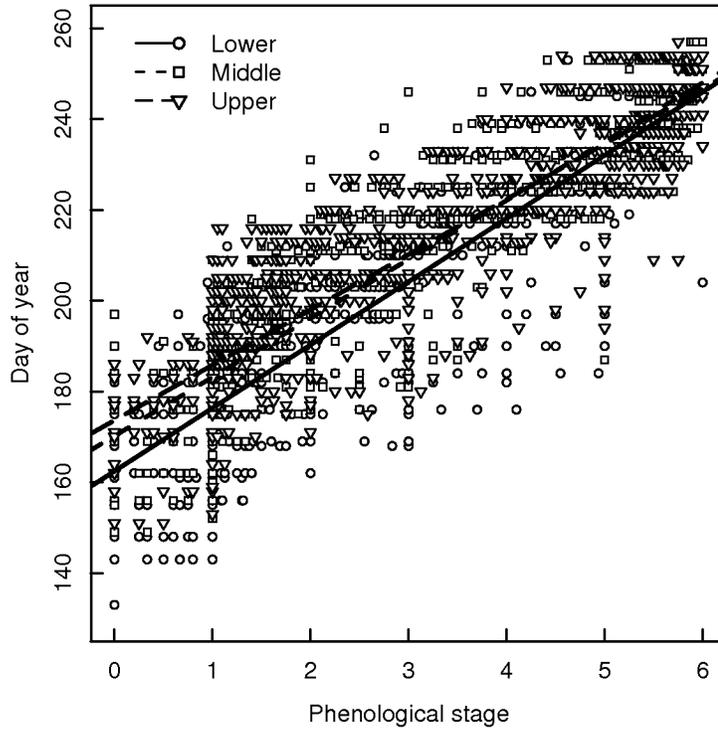


Figure A1.1. Phenological development patterns at three different subalpine meadows near RMBL. The low site has circles and a solid line, the middle site has squares and a short-dashed line, and the high site has triangles and a long-dashed line.

APPENDIX 2: SUPPLEMENTAL METHODS

Growing season length

Growing season length is a confounding factor when trying to understand environmental influences of ANPP in high-elevation ecosystems because it is highly variable spatially. Generally, high-elevation meadows are constrained by short growing seasons, due to low temperatures in winter and the presence of snow. This spatial variability is present across sites, but is also found within a site (see Chapter 1), due to differences in snow deposition patterns. In my data set, growing season length varied from less than one month in late-lying snowbeds to five months in early-melting sites (greater than a factor of 5). The broad distribution caused plots with long growing seasons to have greater ANPP than plots with short growing seasons in my data set (Figure A2.1). To remove this variable as a factor, I divided all aboveground net primary production values by growing season length. The result was average daily rates of aboveground net primary productivity.

In my analysis, I excluded plots that had growing season lengths less than 30 d, based on an assumption that these plots were dominated by “snowbed” species that exhibit rapid growth, regardless of environmental conditions (Walker et al. 1994, Björk and Molau 2007). I tested this assumption by normalizing ANPP values by soil moisture (ANPP/SM). I hypothesized that if these “snowbed” species did not exhibit rapid growth then the environment-normalized ANPP would be approximately equal (with little variance) across plots. I plotted the environment-normalized ANPP versus growing

season length (Figure A2) to see if the six plots with short growing seasons (< 30 d) had high environment-normalized ANPP values. Then, I compared the variance in the data set with and without these six plots.

The plots with short growing seasons had the highest environment-normalized ANPP values (Figure A2.2). The coefficient of variation (mean/SD) of the data set was over 50% greater when I included the six plots with growing seasons shorter than 30 d (0.54 with, 0.34 without). These six plots were over 2 SD greater than the mean that I calculated after excluding them, indicating that they had anomalously-high environment-normalized ANPP values. This finding suggests that ANPP in these plots is influenced by factors other than soil moisture, like evolutionary growth adaptations (Björk and Molau 2007). Excluding these six values allowed me to examine soil moisture influences without the confounding influence of a rapid growth adaptation.

Model analysis

I analyzed my hypothesized models with likelihood and information theory. This approach uses two steps: 1) estimating parameters by maximizing the likelihood of the overall model, and 2) comparing the likelihood of each model to the others to rank and identify the best model(s). Parameter estimation in the “bbmle” package in R is done by minimizing the negative log likelihood for the model. The program scans over a multi-dimensional parameter space (where n is the number of estimated parameters) to find the “optimal” parameter combination (i.e. the lowest negative log likelihood). The negative log likelihood is frequently used because it is computationally easier to identify the minimum negative log likelihood than to identify the maximum likelihood (Bolker 2008).

Model comparison was done by examining goodness of fit from regressions of observed versus predicted values (Figure A2.3) and calculating the AIC for each model. AIC is an information criterion that is frequently used for comparing models (Burnham and Anderson 2003). It was calculated with the equation,

$$AIC = -2L + 2k ,$$

where L is the log-likelihood and k is the number of parameters in the model. In my analysis I used a corrected AIC (AIC_c) to insure against sample size influences. The AIC_c was calculated with the equation,

$$AIC_c = AIC + \frac{2k \times (k + 1)}{n - k - 1} ,$$

where n is the number of observations (Burnham and Anderson 2004). As sample size increases, AIC_c approaches AIC (Burnham and Anderson 2004). The conclusions obtained from AIC_c were not different from those obtained from AIC, however, I reported AIC_c so that sample size would not influence the reported results.

For comparing models, AIC_c decreases as the likelihood increases, but it increases as the number of parameters increases, as a penalty for over-fitting the data and having high complexity. Models with low AIC_c values provide a better fit for the data. I quantitatively compared the models with model differences and model likelihoods (Burnham and Anderson 2003). The model differences (ΔAIC_c) were the difference between each model's AIC_c and the lowest AIC_c in the set. These values allowed me to compare how well the models fit the data relative to each other. The model likelihoods (w_i) were calculated for each model with the equation,

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^N \exp\left(-\frac{1}{2}\Delta_r\right)} ,$$

where Δ is the ΔAIC_c for a given model and N is the number of models. This value is the weight of evidence that a given model is the best model out of the set, and it is considered to be a relative probability (Burnham and Anderson 2003).

Power analysis

A posteriori power analysis has been suggested to statistically assess the potential for making a Type II error in analysis (failing to reject a null hypothesis when it is actually false; Thomas 1997). This calculation allowed me to examine my ability to detect a change in $\delta^{13}C$ values across my data set. I calculated power with a pre-specified effect size (the maximum effect size in the data set), and then I calculated the minimum effect size that I could detect in my dataset with a power of 0.8 (a standard statistical reference point; Thomas 1997). Using the observed variance and a pre-specified effect size allowed me to evaluate whether the sample size was great enough to detect a difference (Thomas 1997). Calculating the minimum effect size allowed me to determine if I could detect a substantial response across my gradient.

I used the method outlined by Thomas (1997). Briefly, power was calculated with the equation,

$$\text{power} = 1 - F_F(F_{\text{crit}} | \nu_1, \nu_2, \lambda),$$

where F_F is the cumulative distribution function for a noncentral F distribution, F_{crit} is the critical value from the F distribution, ν_1 and ν_2 are the degrees of freedom, and λ is a variance parameter (Thomas 1997). I calculated λ with the equation $\lambda = SSH/\sigma^2$, where SSH is the hypothetical slope (effect size) times the sum of squares and σ^2 is the observed variance. To estimate the minimum detectable effect size with power = 0.8, I determined λ and then solved for the effect size.

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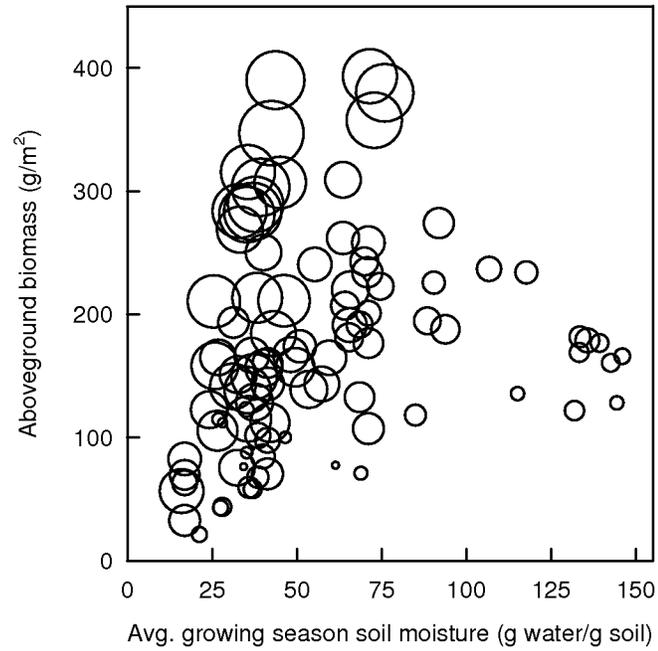


Figure A2.1. Aboveground biomass production versus soil moisture. Point sizes are scaled by the growing season length, with small points having relatively short growing seasons and large points having relatively long growing seasons (range from 16 to 150 d).

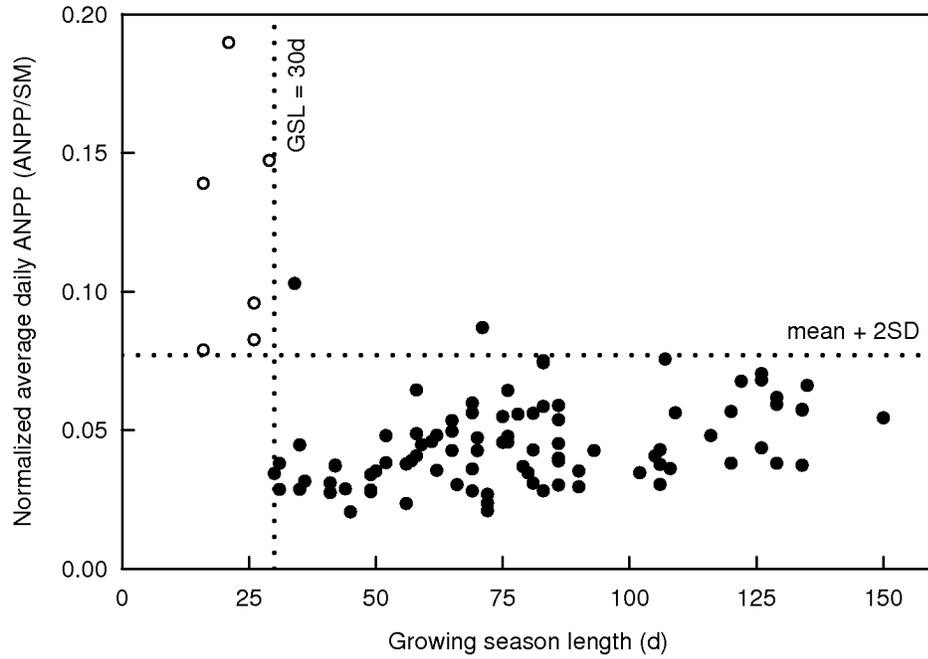


Figure A2.2. Environment-normalized ANPP versus growing season length. Plots excluded from analysis are shown with hollow points. The vertical dotted line is the point where growing season length is 30d, and the horizontal dotted line is the point 2SD above the mean when excluding the six short growing season points.

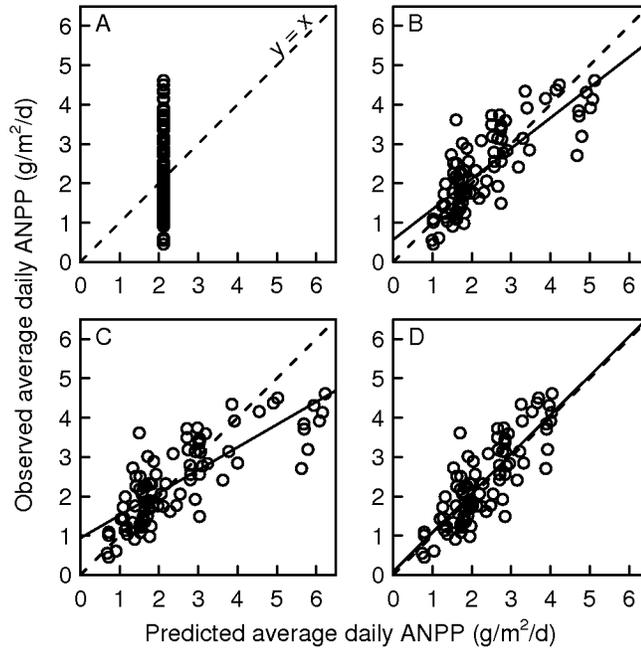


Figure A2.3. Regressions between predicted and observed ANPP values for each model. Panels correspond to models in Figure 2.1 (null, linear, linear-zero, nonlinear).

APPENDIX 3: SOIL MOISTURE AND WATER INPUTS IN AN ALPINE ECOSYSTEM

Soil moisture exhibits high spatial variability in alpine ecosystems, due to influences of topography, dominant snow patterns, physical soil characteristics, and biota (Isard 1986, Taylor and Seastedt 1994). While this variability could have an influence on ecosystem processes (Billings and Bliss 1959, May and Webber 1982, Walker et al. 1994), manipulative experiments have yielded mixed, and possibly conflicting, results (Enquist and Ebersole 1994, Bowman et al. 1995) suggesting that ecosystem function may not be as limited by soil moisture as previous research implies. While the authors in these studies attempted to manipulate soil moisture with water addition, soil moisture levels were not explicitly reported.

Based on this, I asked whether soil moisture is influenced by temporal variability in precipitation. I manipulated growing season precipitation (rainfall) in a dry meadow site at Niwot Ridge to determine if soil moisture in this ecosystem responds to changes in rainfall. The experiment was done in the twelve plots used in the mechanism test (discussed above). In half of the plots, I added 80 mm of rainfall, which I calculated to be just over 1 standard deviation above the long-term average growing season rainfall at the Niwot Ridge site. I considered an increase of this amount to be an above-average deviation.

I calculated the long-term rainfall values with 20 years of precipitation data from the Niwot Ridge LTER program (data available online at

<http://culter.colorado.edu/exec/extracttoolA?sdlpdayv.ml>) and I assumed that precipitation between June and August fell as rain. Average growing season rainfall at the site was 270 ± 77 mm. Ambient rainfall in the 2008 growing season was 234 mm. I added 12.5 L of water to each 1×1.25 m manipulation plot once a week for eight weeks, resulting in 10 mm of additional rainfall per addition. I added water to each plot with a backpack sprayer (Solo, Newport News, VA) over a 15-minute period to encourage absorption into the soil, to prevent runoff, and to replicate a precipitation event.

I monitored daily soil moisture levels in the plots with Decagon Devices 10HS soil moisture probes. I converted these values from volumetric to gravimetric values with soil bulk density measurements (see Methods section for more information). I calculated the "saturated" soil moisture in each plot by finding the maximum soil moisture level throughout the measurement period. This measurement was an approximation of the field water holding capacity. Many high-elevation soils are saturated with water at the beginning of the growing season due to abundant moisture from snowmelt (Billings and Bliss 1959, Taylor and Seastedt 1994, Harte et al. 1995). In all samples, the "saturated" soil moisture was found in the first week of measurement.

I quantified the water holding capacity of soils in each plot with a modified pressure plate apparatus (Dane and Hopmans 2002) at the Natural Resource Ecology Laboratory (Colorado State University, Fort Collins, CO). I used 20 g subsamples from the bulk density cores, which were collected within 0.5 m of the soil moisture probes. I passed each subsample through a 2 mm sieve to homogenize the subsamples and to improve contact with the ceramic plate. I placed the air dry samples in metal sleeves on the pre-soaked ceramic plate. I wetted them with deionized water over 24 hours to ensure

contact with the plate. Then, I sealed the pressure apparatus and applied 1/3 atmosphere of pressure for four days to equilibrate the samples to the simulated field water holding capacity. The laboratory was kept at a constant temperature of 20°C. The samples were removed, weighed (for a wet weight), oven dried at 105°C, and weighed again (for a dry weight) to determine the gravimetric water holding capacity (g water/g soil). Further details about the methods can be found in Dane and Hopmans (2002).

I tested the effect of the rainfall manipulation with an analysis of variance on the average growing season soil moisture values. I performed a correlation between the approximated field water holding capacity ("saturated" soil moisture) and the laboratory-simulated water holding capacity (from the pressure plate apparatus). Then, I tested the effect of water holding capacity on the average growing season soil moisture with a linear regression analysis. All statistical analyses were performed in R (R Development Core Team 2008).

Ambient growing season rainfall at the site was below average in 2008. Average soil moisture in the plots covered a broad range of values, although this range did not appear to be due to differences in precipitation inputs (Figure A3.1). The average soil moisture levels did not respond significantly to the increase in rainfall ($F_{1,10} = 0.40$, $P = 0.54$), due to high within-treatment variability. I hypothesized that this variability could be due to differences among plots in physical soil characteristics, like water holding capacity.

A regression of average growing season soil moisture versus approximated field water holding capacity was highly significant (Figure A3.2; $F_{1,10} = 129.3$, $P < 0.001$, $R^2 = 0.93$), suggesting that the average soil moisture in this ecosystem can be strongly

predicted with the field water holding capacity. Additionally, there was a strong correlation between the approximated field water holding capacity and the laboratory-simulated water holding capacity (Figure A3.2 insert; $r = 0.96$, $P < 0.001$), suggesting that the pressure plate apparatus gave a good approximation of the water holding capacity, as has been found in other studies (Dane and Hopmans 2002, Cresswell et al. 2008), and that the soils were saturated at the beginning of the growing season.

These results reinforce the idea that average soil moisture in this ecosystem is relatively insensitive to changes in growing season rainfall, because the soils are often saturated at the beginning of the growing season (Figure A3.1A) and because of high water holding capacity (Figure A3.2). Soil water holding capacity can be increased by increased soil organic matter (Hudson 1994, Saxton and Rawls 2006), which is generally high in alpine ecosystems (Seastedt and Adams 2001, Neff et al. 2002). The high spatial variability in soil moisture that I observed could be due to spatial variation in soil texture and organic matter content, possibly caused by differences in litter inputs and decomposition or other soil-forming factors (Jenny 1941, Burns and Tonkin 1982). Variation in soil moisture among plots or sites (and within treatments) could outweigh the influence of rainfall on soil moisture levels in this ecosystem. These differences could explain discrepancies between studies in high-elevation ecosystems that have attempted to examine the effects of changes in moisture on ecosystem properties with manipulative experiments (e.g. Bowman et al. 1995).

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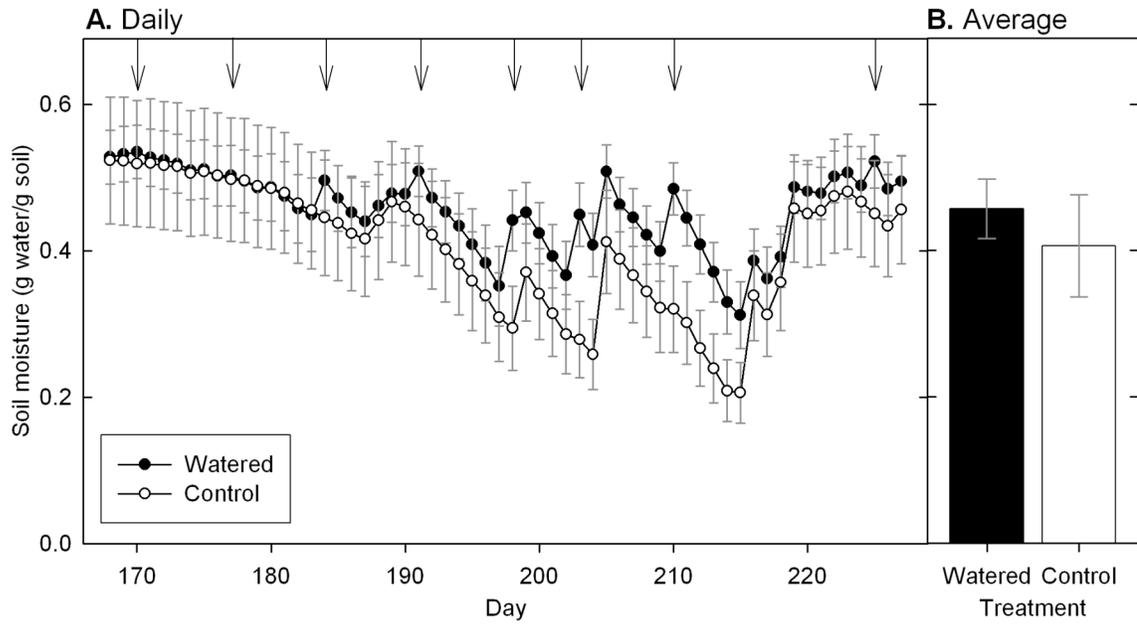


Figure A3.1. Soil moisture response to precipitation manipulation at Niwot Ridge, CO, showing A. daily soil moisture levels, and B. average growing season soil moisture. Arrows indicate when 10mm water additions occurred. All values are means \pm standard errors.

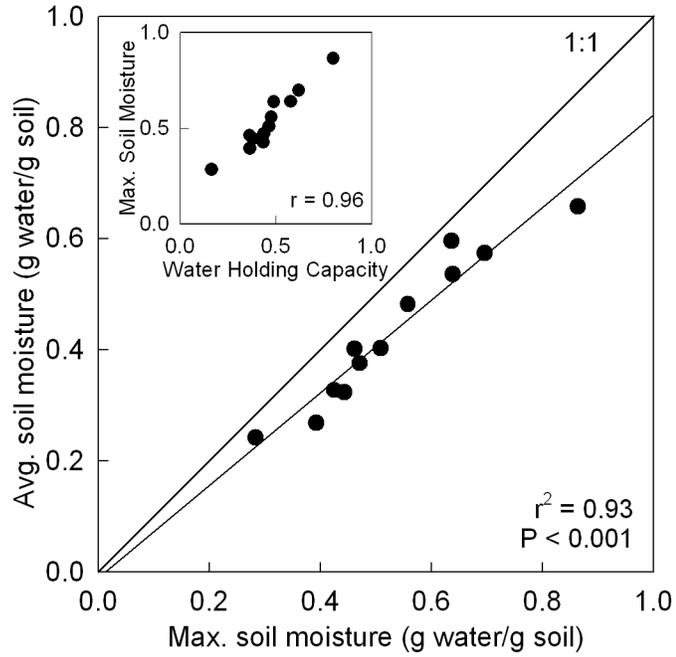


Figure A3.2. Average growing season soil moisture versus maximum recorded soil moisture, an indicator of field water holding capacity. The insert shows a correlation between maximum recorded soil moisture and laboratory-simulated water holding capacity.

APPENDIX 4: TESTING MODEL FIT

Identifying the best model of a candidate set and assessing its ability to predict observations is an essential, yet complex, step in analysis. Statistically rigorous methods, like maximum likelihood analysis (Akaike 1973, Burnham and Anderson 2003), make model selection relatively easy by quantifying both model fit and parsimony into a single index (AIC). But, assessing how well a model predicts observations is more difficult.

The most basic approach is a linear correlation between observed and predicted values, which provides an index of both linearity and tightness (Zar 1999). This can be extended by performing a regression of observed values on predicted values to assess how well the model's predictions can predict observations (coefficient of determination, R^2 ; Haefner 1996). However, this approach does not accurately address the question of goodness of fit to a 1:1 line, which would be expected for a comparison between predictions and observations.

I assessed the fit of comparisons between observed and predicted values with linear regressions that test for deviations from a slope equal to one (Warton et al. 2006). I fixed the intercept of the regressions to zero to test a 1:1 relationship. I performed the regressions in the R program "smatr," which offers methods for drawing inference from bivariate line fits. The regressions tested for a correlation between residuals and fitted values, which would suggest a deviation from the predicted line (Warton et al. 2006).

All of the comparisons except for the linear, multiple-resource limitation model and the linear growing season length model had relationships that deviated from a 1:1

line (Table A4.1). The nonlinear, multiple-resource limitation model and the soil moisture only model differed significantly at $P < 0.10$, and the others deviated at $P < 0.05$. The comparisons suggest that most of the models predicted ANPP with some bias, except for the linear, multiple-resource limitation model and the linear growing season length only model comparisons. This finding reinforces the maximum likelihood model selection, which chose the linear, multiple-resource limitation model as the best model based on model fit and parsimony, by identifying little bias in this model. While there was also little bias in the linear growing season length only model comparison, it was not chosen as a better model possibly because of variability around the relationship (Figure 3.2). In some cases, the slope predictions (Table A4.1) are greater than those from the linear regressions in Figure 2 because the slope test was fit to a 1:1 line with a fixed intercept of zero, while the linear regressions had unconstrained slopes and intercepts. Both fits provide different information about the model fit. The slope test assesses the slope of the relationship only, while the linear regression tests the tightness of the data around the line.

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Table A4.1. Bivariate test for observed versus predicted regressions, fit to a linear regression with a slope (m) equal to one and an intercept equal to zero. Models are arranged by their likelihoods (Table 3.2). The test statistic (r) is the sample correlation between the residuals and the fitted values. Slope predictions (m) correspond to the points in Figure A4.1, and are bound by the upper and lower 95% confidence intervals.

Model	r	m ± CI	P
Cumulative, linear	0.116	1.03 ± 0.05	0.2954
Cumulative, nonlinear	0.202	1.06 ± 0.07	0.0660 #
Minimum, linear	0.250	1.09 ± 0.09	0.0218 *
Minimum, nonlinear	0.271	1.13 ± 0.13	0.0127 *
GSL only, linear	0.156	1.06 ± 0.08	0.1562
SM	0.206	1.11 ± 0.12	0.0604 #
GSL only, nonlinear	0.326	1.16 ± 0.14	0.0025 *

Significance codes: # < 0.10, * < 0.05

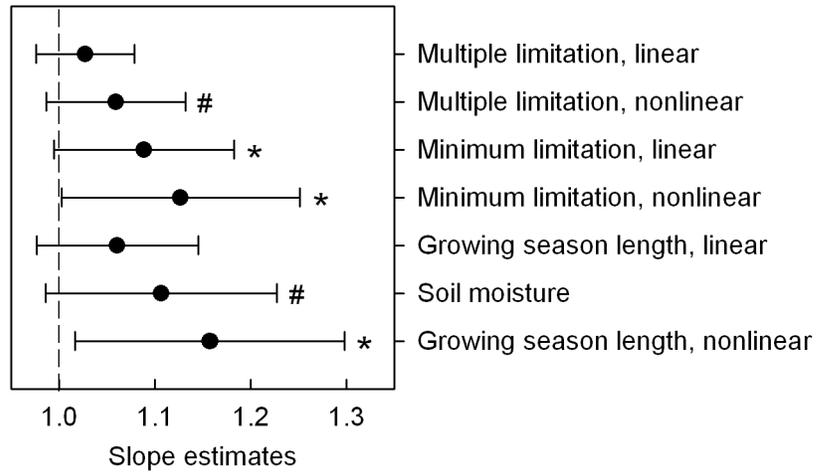


Figure A4.1. Slope estimates from the observed versus predicted comparisons in Table A4.1, showing bias from a slope of one. Values are bound by 95% confidence intervals and are arranged in the same order as Table A4.1. Significance codes are: # < 0.10, * < 0.05.

APPENDIX 5: COMPARISON OF PARAMETER ESTIMATES

I performed a qualitative comparison of parameter estimates from my different analyses to evaluate the effects of growing season length and soil moisture on high-elevation ANPP further. I estimated the growing season length effects (Figure A5.1) with slope estimates from the growing season length regressions at different scales. The local model used the Niwot Ridge data from Chapter 1, the regional model used the Colorado data set from Chapter 1, and the global model used the data from Chapter 3. The local and regional models assumed equal variances for the 95% confidence intervals because they were based on least-squares linear regressions. The confidence interval estimate for the global model has unequal variances around the mean because it was based on the maximum likelihood analysis, which made no assumptions about normality. All three slope estimates are extremely close, and are within the standard errors of one another (Figure A5.1).

I estimated the soil moisture effects with the half-saturation constant (discussed in the methods section). I compared the global estimate from Chapter 2 with the global estimate from this analysis (Figure A5.2). In Chapter 2, I calculated the standard error and 95% confidence interval by propagating errors in the parameter estimates for the Michaelis-Menten curve. I made an assumption that there was no covariance in parameter estimates, to enable easier estimation of the errors around the value. For the estimate from this analysis, the asymptote was fixed at one, and the intercept had little variability ($10.2 \pm 2.2\%$ soil moisture). I calculated the standard error and confidence

interval by calculating the half-saturation constant at the standard error and confidence limits of the slope parameter with the mean of the intercept and the fixed asymptote.

Even with this conservative estimation, the 95% confidence intervals were extremely broad (Figure A5.2). The average values from both analyses overlap with the error estimates, but the value from Chapter 2 is slightly higher, possibly due to the different formulation of the maximum value. The analysis in Chapter 2 used the maximum observed value in the data set, while the analysis from this chapter used the maximum production predicted by the growing season length constraint. Further refinement of the moisture limitation value estimate will require more data. But these estimates provide a range of values for estimation in the future. Additionally, it is clear that soil moisture is limiting in these ecosystems, since the lower end of the 95% confidence intervals are both well above zero (Figure A5.2).

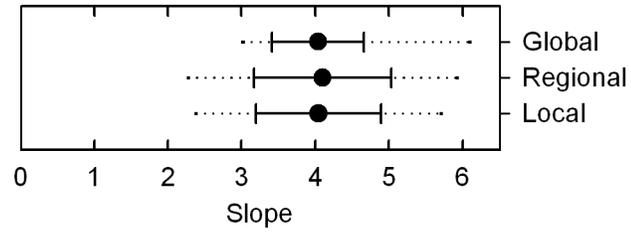


Figure A5.1. Comparison of the influence of growing season length (slope) on high-elevation ANPP. Local and regional estimates are from Chapter 1, and the global estimate is from Chapter 3. Solid lines are standard errors around the mean, and the dotted lines bound 95% confidence intervals.

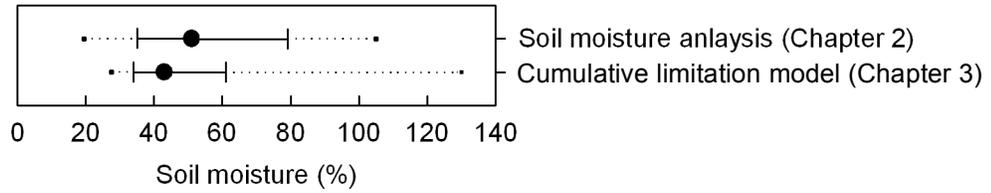


Figure A5.2. Comparison of when soil moisture limitation occurs in high-elevation ANPP globally (estimated with the half-saturation constant) from my two analyses. The solid lines are the standard error around the mean, and the dotted lines bound the 95% confidence intervals.

