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Growing Season Length and Soil Moisture Interactively Constrain High Elevation Aboveground Net Primary Production

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ABSTRACT

Although high elevation meadows are often considered to be primarily temperature-limited, aboveground net primary production (ANPP) is influenced by both growing season length (GSL) and soil moisture (SM). Progress in understanding these responses comes from studies at individual sites that are often focused on single abiotic drivers, so little is known about how climatic constraints relate to one another and limit ANPP at larger scales. We examined the independent and combined effects of these two key climate drivers (GSL and SM) across a suite of high elevation meadows from two continents. We also sampled gradients of each variable at a single site to explore mechanisms for SM and GSL limitations. Here, we show that high elevation meadows are limited by both GSL and SM levels. GSL constrained maximum ANPP by approximately 4 g m^{-2} d^{-1} whereas average daily ANPP beneath this constraint was significantly influenced by SM. Carbon isotope and plant/soil nitrogen data suggest that SM influenced ANPP through its impact on nitrogen availability. Increases in GSL can increase ANPP unless those increases are accompanied by SM decreases. These interactive effects can produce distinct ecological patterns and must be considered when predicting high elevation meadow responses to future climate changes.

Key words: high-elevation; production; growing season length; soil moisture; alpine; subalpine.

INTRODUCTION

Ecosystem responses to changes in climate are complex because multiple factors can affect biological processes simultaneously. Changes in growing season length (GSL) (Myneni and others 1997; White and others 1999) and soil moisture (SM) availability (Angert and others 2005; Ciais and others 2005) both limit primary production globally, with divergent spatial and temporal patterns depending on which constraining factors are strongest (Nemani and others 2003; Zhao and Running 2010). Predicting how an ecosystem will respond to changes in climate requires an understanding of how these constraints relate to one another and limit ecosystem functions.

High elevation meadow ecosystems are constrained strongly by their abiotic environment.

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They are characterized by cold temperatures, which cause short growing seasons, and spatially variable moisture availability related to precipitation and topography (Taylor and Seastedt 1994). Global analyses of primary production trends over time classify high elevation systems as primarily temperature limited (Zhao and Running 2010). However, studies in high elevation meadows have recognized the importance of both GSL (Billings and Bliss 1959; Knight and others 1979; Walker and others 1994; Litaor and others 2008) and SM (Billings and Bliss 1959; Ehleringer and Miller 1975; Enquist and Ebersole 1994) for primary production. These studies have highlighted that delayed snowmelt and cool spring temperatures can restrict aboveground net primary production (ANPP) (Walker and others 1994), whereas drought stress can occur in dry years or in areas with relatively long growing seasons and little snowmelt runoff (Billings and Bliss 1959; Bowman and others 1995). Similar patterns are also observed in high latitude ecosystems (Piao and others 2007; Morgner and others 2010). Although a few studies have examined the response patterns of ANPP to these variables (Walker and others 1994; Jonas and others 2008; Litaor and others 2008), these studies tend to focus on one high elevation site or region; none of these studies has examined the independent and combined effects of key climate drivers across a suite of relatively diverse high elevation sites. Consequently, little is known about the degree of limitation by either variable or how they may interact to influence high elevation ANPP across sites.

Examining mechanisms behind the climatic influences on ecosystem properties can offer insight into how ecosystems function, improve process-based understanding, and facilitate better predictions of future conditions (Clark and others 2001). Progress in understanding the response of high elevation vegetation to climatic changes is demonstrated in studies which emphasize the temporal constraint imposed by GSL (for example, Jonas and others 2008; Cooper and others 2011). Moisture availability is also predicted to change in temperate high elevation ecosystems (Mote and others 2005; Christensen and others 2007). Identifying how ANPP responds to changes in SM is more difficult, though, due to contrasting hypotheses for limitation of high elevation ANPP by moisture (Körner 2003). Decreased SM could induce biophysical drought stress if plants cannot maintain turgor, thereby reducing primary productivity through stomatal closure. Alternatively, decreased SM could reduce mass flow of nutrients in the soil and microbial activity, decreasing nitrogen mineralization and availability, and therefore reducing primary production. Körner (2003) suggests 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. Although both provide a possible explanation for moisture limitation of ANPP, they may have different consequences for how high elevation ecosystems respond to environmental change.

The aims of this study were to (1) identify whether GSL and/or SM constrain ANPP independently and in combination across geographically diverse high elevation sites; and (2) explore the potential mechanisms involved in any SM limitations to primary productivity. We used two primary datasets in this study. We first compiled available data from high elevation meadows across the globe to analyze bi-continental patterns of aboveground biomass responses to GSL and SM. We also collected data from two gradients at a single site (Niwot Ridge, CO) to examine more localized patterns and examine the potential mechanisms that influence the patterns that we observed across sites. We hypothesized that GSL and SM interactively limit high elevation ANPP and that many high elevation meadows are limited by both variables. Specifically, we hypothesized that GSL provides an upper constraint on ANPP by restricting the growth period (Jonas and others 2008), whereas SM limits ANPP beneath this constraint by reducing plant nitrogen uptake, growth, and production processes (Körner 2003). We found that GSL limited high elevation ANPP across sites, but that this pattern was influenced by the availability of SM and nitrogen, which constrained daily ANPP, suggesting a biogeochemical rather than a biophysical constraint to production.

METHODS

Bi-continental Data

We searched for published studies from diverse high elevation meadow sites to include in the analysis, but only included those studies that had both SM and GSL data along with ANPP values. Many studies reported only one of these environmental variables and could not be included. We compiled data from eight published studies that met these criteria (Table 1; Billings and Bliss 1959; Bliss 1966; Kuramoto and Bliss 1970; Knight and others 1979; Rikhari and others 1992; Walker and others 1994; Harte and others 1995; Wang and others 2008). These studies were spatially diverse.

Table 1. Sources and Site Information for the Bi-continental Data Set, Ordered by Year of Study (*Numbers* Indicate References)

Site	Location (lat., lon.)	Elevation (m)	Summer air T (°C)	Avg. snow free date (day of year)	Range of GSL (day)	Range of SM (%)	Years
1. Snowy Range, WY, USA (a)	41.3°, −106.3°	3,353	9.7	183	35–56	21–136	1955
2. Mt. Washington, NH, USA (a)	44.3°, −71.3°	1,800	8.1	158	58–76	17–71	1957–1962
3. Olympic Mountains, WA, USA (sa)	48°, −123.3°	1,530	–	157	71–102	16–37	1967
4. Medicine Bow Mountains, WY, USA (sa)	41.3°, −106°	3,082	–	163	50–69	39–69	1977
5. Baideni-Ali, Himalaya Mountains, India (a)	41.3°, 71.6°	3,425	–	100	90–150	42–50	1989
6. Niwot Ridge, CO, USA (a)	40°, −105.6°	3,528	7.2	169	17–83	27–147	1982–1989
7. Gothic, CO, USA (sa)	39°, −107°	2,920	9.7	118	93–122	26–43	1992
8. Qinghai-Tibetan Plateau, China (a)	37.6°, 101.3°	3,240	8.7	113	126–134	33–76	2002–2004

Locations are rounded to the nearest 1/3 of a degree.
(a) = alpine meadow, (sa) = subalpine meadow. 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 and others (1979), (5) Rikhari and others (1992), (6) Walker and others (1994), (7) Harte and others (1995), and (8) Wang and others (2008).

For example, in the United States, the sites include an east–west, longitudinal and transcontinental gradient across several different mountain ranges as well as a smaller north–south gradient within the Rocky Mountains. The sites also include bi-continental coverage of high elevation sites in North America and Asia, specifically the Indian Himalaya and Tibetan Plateau. Although all sites are either sub-alpine or alpine, they span a 2,000 m elevation range. The sites had zero to minimal livestock grazing except for Rikhari and others (1992), where fences were constructed to exclude grazers from the study area.

The data we use in this analysis were all published in the original articles, except for GSL data for Wang and others (2008), which was obtained with snow presence data at the site from Y. Tang (unpublished data). All GSL estimates were based on the difference between the snow free date and the sampling date at the onset of senescence. This value was either reported in the original article or calculated based on reported data. Using the snow free date could overestimate GSL in windswept areas if spring temperatures are too cool for plant growth (Odland 2011) and could underestimate GSL in snowbed areas where plant growth can begin before snowmelt (Bjork and Molau 2007). We did not have sufficient air or soil temperature data to assess this possibility and uncertainty around our GSL estimates could explain some residual variation in our analysis. However, we consider our estimates to be a good approximation of GSL across sites because they are comparable to the range of values commonly reported for high elevation ecosystems (Körner 2003; Odland 2011).

Biomass samples for all studies were collected at or near peak production. Although we could not account for within-year death of vegetation, we assumed that biomass samples approximated ANPP. Our bi-continental analysis largely examined spatial variation in production among meadows and sites although some of the studies included multiple years of data. Because we examined multiple sites, there were species composition differences across many meadows. Consequently, our results represent responses across species as well as across environmental conditions. When multiple years of data were presented, we used each value as an individual data point to include all available information on GSL and SM responses as has been done previously in large-scale analyses (Huxman and others 2004; Walker and others 2006). We consider these values to be independent because high elevation meadows have minimal initial biomass (Billings and Bliss 1959; Bliss 1966) and respond strongly to environmental conditions in the current year (Walker and others 1994). Restricting the data set to a single year from each study did not change the significance of our conclusions, but reduced the range of observations for calculating production responses.

Niwot Ridge Data

We collected samples in 2008 from an artificial GSL gradient and a natural SM gradient in two meadows at the Niwot Ridge LTER site, CO (Table 1).

We conducted stratified random sampling to capture variation in GSL and SM while minimizing differences in other variables. The GSL gradient was created by a snowfence that was established in 1993 (Williams and others 1998). Within 3 years of the snowfence treatment species turnover and community change was observed, with the current species composition resembling communities that occur along natural snow depth gradients at Niwot Ridge. We sampled at distances of 10, 25, 45, and 75 m from the snowfence to obtain a range of GSLs between 34 and 78 days (approximately 2-week intervals between each band), with four plot replicates within each GSL band. We estimated GSL by the number of days between snowmelt and peak aboveground biomass (Berdanier 2010).

Twelve SM gradient plots were identified over a 2500 m^2 area in a dry meadow near the GSL gradient. The plots had similar plant communities and were on a shallow north-facing slope. SM differences existed among plots due to differences in soil water-holding capacity (Berdanier 2010). GSL differences between plots were minimal; the snowmelt date in all plots was within 4 days. SM was monitored in each plot with a Decagon Devices 10HS SM 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 cm^3 area. We converted these values to gravimetric values with bulk density measures from each plot for comparison with the other studies. For all studies we calculated average growing season SM values. Gravimetric measures can exceed 100% SM, especially in high-elevation ecosystems, because the measure is by weight. Soil organic matter can be high in these ecosystems (Neff and others 2002) and can cause bulk density to be lower than the weight of water in soils with extremely high organic content.

For all the studies (bi-continental and Niwot Ridge data sets) ANPP values were obtained with peak aboveground biomass harvests. In the observational plots at Niwot Ridge, we clipped 0.25 × 0.5 m quadrats of aboveground biomass per plot and excluded previous years' dead material. Samples were collected in early August before the onset of senescence. Although plant production calculations can be influenced by the presence of perennial vegetation (Walker and others 1994), these values approximate ANPP with an assumption that initial biomass is small and negligible in high-elevation meadows (Klein and others 2007).

Growing Season Length Influence

To test the response of ANPP to GSL, we used both least squares and quantile regressions. We examined the influence of site on the response to GSL with a linear analysis of covariance. We also examined the quantile response to test the limiting effect of GSL. Quantile regression has been recommended for examining ecological responses to limiting factors (Cade and others 1999). The method assumes that the limiting variable of interest (in this case, GSL) creates an upper constraint on the response variable (ANPP), and that the distribution of the response variable below this constraint is controlled by other factors (Cade and others 1999). We used the R package ''quantreg'' for quantile regressions and fit the 90th quantile of the linear regression to assess the slope near the top of the distribution (where GSL is hypothesized to be limiting), but to ensure that we were not overfitting the model to the data. Confidence intervals were estimated with an *xy*-pair bootstrapping method because of small sample size.

Soil Moisture Influence

We estimated average daily ANPP ($g\ m^{-2}\ d^{-1}$) to analyze the direct influence of SM because GSL variability confounds primary production values in these ecosystems (Körner 2003). GSL varied by a factor of five in the bi-continental data set. Normalizing ANPP by GSL allowed us to control for this factor and focus on the relationship between SM and ANPP. We examined the response of average daily ANPP to SM by fitting linear and nonlinear models to the overall data set. Similar to the GSL analysis, we examined the influence of site on the SM response with a linear analysis of covariance. The nonlinear model was a modification of the asymptotic Michaelis–Menten equation,

$$\mathrm{ANPP} = \frac{\alpha(\mathrm{SM} - c)}{\alpha/\gamma + (\mathrm{SM} - c)},$$

where c is the SM level when no growth occurs, α is the asymptote of daily ANPP, and γ is the slope of the productivity response at low SM. We excluded data points that had GSLs less than 30 days ($n = 6$ or 6% of the initial data set) because the species that inhabit these ''snowbed'' communities are specifically adapted to complete their life cycle in an extremely short period of time (Walker and others 1994; Bjork and Molau 2007); their daily productivity rates are approximately twice those of other high elevation communities in this analysis (Berdanier 2010).

To investigate the relative importance of the hypothesized mechanisms behind SM limitations at

Niwot Ridge, we measured soil nitrogen availability, plant nitrogen content, and carbon isotope discrimination. Inorganic soil nitrogen availability was estimated in each plot at Niwot Ridge with Western Ag Innovations, Inc. ''PRS'' ion-exchange resin probes (Saskatoon, Saskatchewan, S7 N 4L8, Canada). These ion-exchange probes provide a useful and independent measure of soil nitrogen availability for plant uptake because they indicate cumulative soil nitrogen concentrations over the entire installation period and represent the nitrogen that would be available to plant roots (Johnson and others 2005). We installed the probes within a day after snowmelt and removed them when we sampled the vegetation at the end of the growing season. The probes were extracted with 17.5 ml of 0.5 M HCl and analyzed for NH_4^+ and NO_3^- with a Technicon autoanalyzer (Bran and Lubbe, Inc., Buffalo, NY).

We collected leaf samples of *Bistorta vivipara*, a common alpine forb, for leaf tissue $\delta^{13}C$ and nitrogen concentration analysis. Carbon isotope discrimination is used widely as an indicator of stomatal conductance relative to photosynthesis over the entire growing season (Bowman and others 1995; Dawson and others 2002), whereas aboveground plant nitrogen uptake and leaf nitrogen concentration per unit mass are strongly related to photosynthetic capacity (Evans 1989; Reich and others 1997). We harvested samples at the peak of the growing season to ensure that the majority of representative production was complete (for $\delta^{13}C$ analysis) and that belowground vegetative structures were not reabsorbing nitrogen from the leaves (Körner 2003). We chose leaves of equal size and with similar canopy position to ensure homogeneity in age and sun exposure (Reich and others 1997). We analyzed $\delta^{13}C$ 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). We estimated aboveground plant nitrogen content by multiplying *Bistorta vivipara* leaf nitrogen concentration (% N) and total aboveground biomass ($g\ m^{-2}$) as an index of the mass of nitrogen ($g\ N\ m^{-2}$) taken up by the aboveground vegetation during the year. Forbs comprise over 75% of the aboveground biomass in the plots, and approximately 15% of the total plant cover was *Bistorta vivipara*.

Interactions Between GSL and SM

We fit the bi-continental data set with four models to examine how GSL and SM independently and interactively influence ANPP,

1. GSL only,
2. SM only,
3. GSL or SM, and
4. GSL and SM,

and we compared them with Akaike's Information Criterion (AIC, Akaike 1973). The local Niwot Ridge data could not be included in this analysis because we did not measure both GSL and SM across the two gradients. The influence of GSL was modeled with a linear equation, whereas the influence of SM was modeled with the modified Michaelis–Menten equation. The first interaction model was based on Liebig's ''law of the minimum,'' where aboveground biomass production was limited by either GSL or SM and was estimated with the minimum prediction of both models. For example, if GSL was long and SM was low, ANPP was calculated from the SM response; if GSL was short and SM was high, ANPP was calculated from the GSL response. For the second interaction model, we defined GSL as an upper constraint on aboveground biomass production, like the quantile regression, and modeled the influence of SM beneath this constraint with the Michaelis–Menten equation adjusted to be a proportion by setting the asymptote (α) to 1. We used maximum likelihood to estimate the parameters for each model and calculate confidence intervals (Burnham and Anderson 2002) with the ''bbmle'' R package. We used a corrected AIC (AIC_c) to insure against sample size influences and compared the different models with AIC_c differences (ΔAIC_c) and AIC_c weights (w_i; Burnham and Anderson 2002).

RESULTS

Growing Season Length Influence

ANPP increased with GSL (Figure 1). Performing a linear regression with each site as a covariate, we found a significant influence of different sites on the response to GSL ($F = 4.39$, df = 8, $P < 0.001$). Accounting for these differences, ANPP still increased significantly with GSL ($F = 5.86$, df = 1, $P = 0.02$). However, we found a significant interaction between the GSL response and site ($F = 5.56$, df = 8, $P < 0.001$), indicating that the response to GSL was different across sites. To highlight these differences, we present a comparison between the overall regression and the Niwot Ridge GSL gradient (Figure 1). The least squares response was significant overall ($F_{1,82} = 67.33$, $P < 0.001$, $R^2 = 0.40$) but not significant for the Niwot Ridge GSL gradient ($F_{1,14} = 2.12$, $P = 0.17$, $R^2 = 0.13$). Despite differences in the least squares

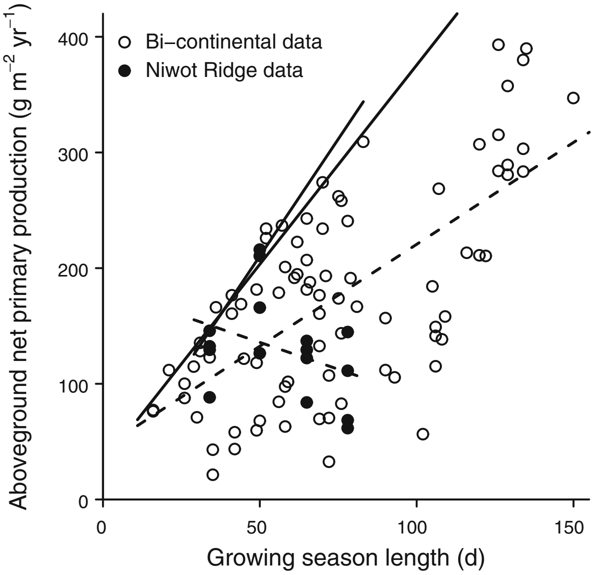

Figure 1. Aboveground net primary production responses to GSL. *Solid lines* are 90th quantile regressions and *dashed lines* are least-squares regressions. Data from the Niwot Ridge GSL gradient are highlighted to emphasize differences in least-squares regressions despite insignificant differences in the quantile regressions across sites.

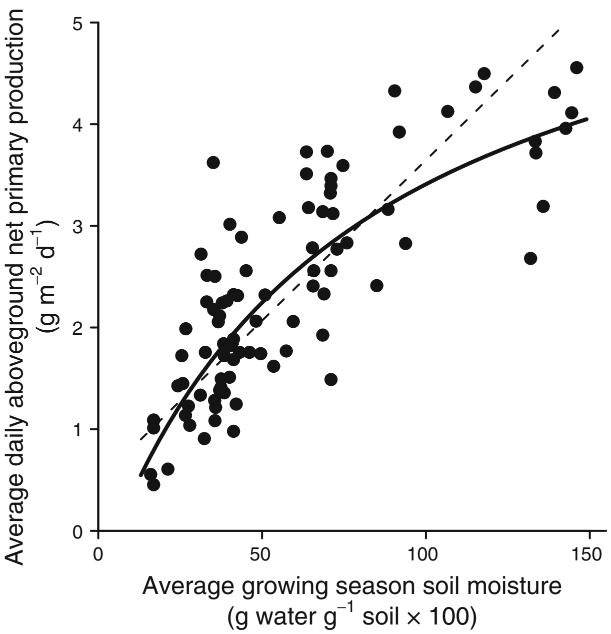

Figure 2. Response of average daily aboveground net primary production to average growing season SM. The *solid, bold line* is the non-linear model. The *dashed* linear regression was highly significant (ANPP = 0.025 × SM + 0.941; $R^2 = 0.63$; $P < 0.001$) but was not chosen as the best model (see text for details).

regressions, the slopes of the 90th quantile regressions for this comparison were both significantly greater than zero and were not significantly different from one another ($t = 0.69$, df = 29.25, $P = 0.50$), suggesting similar responses to GSL at the upper limit.

The slopes of these responses provide an estimate for the influence of GSL on ANPP. For the quantile regressions, the slope indicates maximum daily ANPP. We estimated an overall slope of 3.31 ± 0.58 g m^{-2} d^{-1} (mean ± SE). The slope of the least squares regression was 1.68 ± 0.22 g m^{-2} d^{-1}, which approximates the average daily ANPP across sites.

Soil Moisture Influence

Average daily ANPP also increased with increasing SM (Figure 2). The nonlinear model ($\mathrm{AIC_c} = 36.4$, $w_i = 0.990$) fit the data better than a linear model ($\mathrm{AIC_c} = 45.6$, $\Delta\mathrm{AIC_c} = 9.2$, $w_i = 0.010$), although both models outperformed a flat response of no effect ($\mathrm{AIC_c} = 132.0$, $\Delta\mathrm{AIC_c} = 95.6$, $w_i < 0.001$). The linear regression of average daily ANPP versus SM was highly significant ($F_{1,88} = 151.4$, $P < 0.001$, $R^2 = 0.63$). When we considered a site covariate, there was a significant influence of site on the response to SM ($F = 3.79$, df = 8, $P < 0.001$). However, there was no significant interaction between SM and site ($F = 1.34$, df = 8, $P = 0.24$), suggesting insignificant differences among the slopes of the responses across sites. Additionally, after accounting for differences in the site covariate, the linear SM response was still highly significant ($F = 23.18$, df = 1, $P < 0.001$). We consider the nonlinear model to be a better fit than the linear regression, but present both as possible responses.

In the SM gradient at Niwot Ridge, we examined potential causes for moisture limitation of ANPP. The Niwot Ridge SM gradient covered 32% of the SM values in the bi-continental data set and spanned over the lower half of observations. We found that *Bistorta vivipara* leaf δ^{13}C was not significantly related to SM (Figure 3A; $F_{1,10} = 0.14$, $P = 0.71$, $R^2 = 0.01$) and that the observed SM effect was very small (slope = −0.007). To assess the power of the non-significant regression, we conducted an a posteriori power analysis with a prespecified effect size and the observed variance and calculated the minimum detectible effect size with a power of 0.80 and the observed variance (Thomas 1997). The estimated power for detection of the maximum possible effect along the gradient was 0.97 and the minimum effect that would be

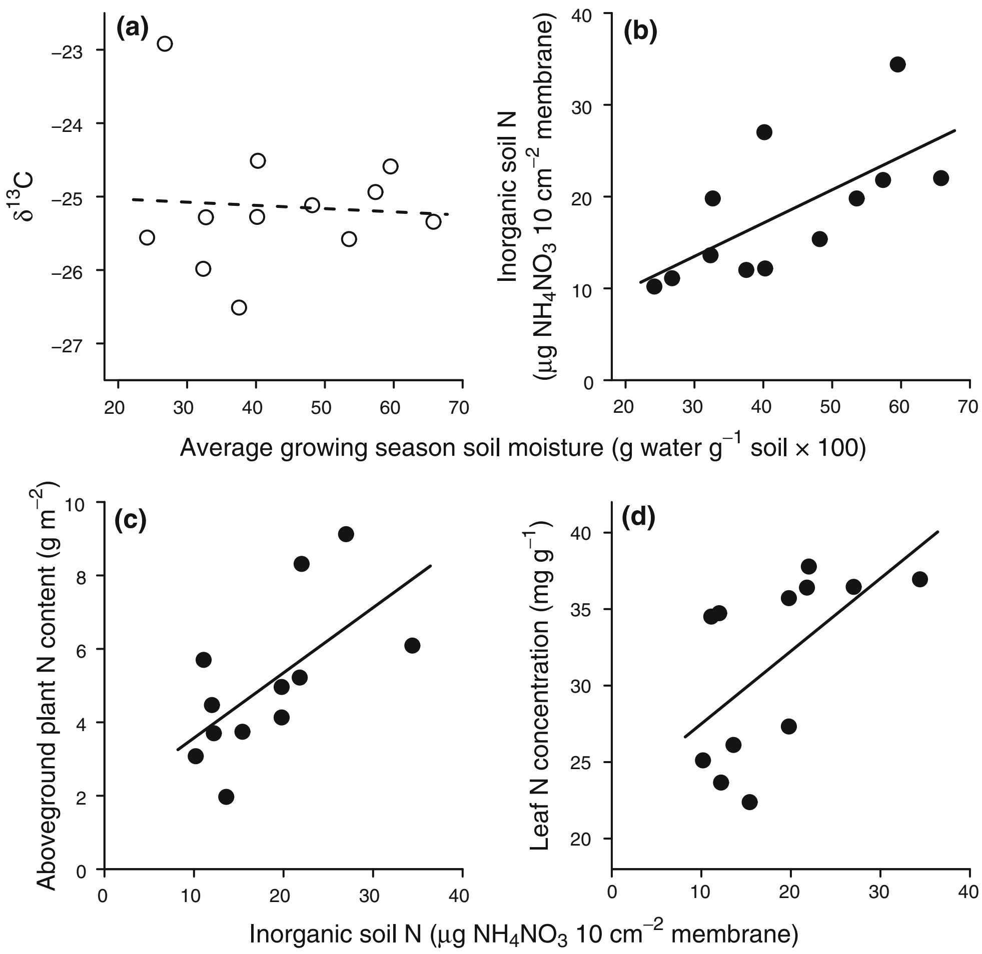

Figure 3. Links among SM, soil inorganic nitrogen, and plant nitrogen from the SM gradient at Niwot Ridge, CO. **A** Carbon isotope discrimination ($\delta^{13}C$) in leaf samples of *Bistorta vivipara* did not change significantly with SM ($R^2 = 0.01$, $P = 0.71$). **B** Inorganic soil nitrogen increased significantly with SM ($R^2 = 0.45$, $P = 0.02$). **C**, **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.

significant was a slope of −0.063 (almost 10 times the observed effect), suggesting that there was little chance of making a Type II error.

In contrast to the $\delta^{13}C$ results, growing season inorganic soil nitrogen (NH_4NO_3) availability increased significantly with SM (Figure 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 3C; $F_{1,10} = 6.5$, $P = 0.028$, $R^2 = 0.40$) and leaf nitrogen concentrations (mg N g^{-1} leaf tissue; Figure 3D; $F_{1,10} = 5.3$, $P = 0.044$, $R^2 = 0.59$) both increased significantly with inorganic soil nitrogen across the gradient.

Interaction Between GSL and SM

Models that included an interaction between GSL and SM outperformed the models with only GSL or SM. The GSL × SM model had greater support in the data than the alternative models (Table 2; Figure 4). There was nearly no uncertainty ($w_i > 0.999$) that this model provided the best fit for the data across sites. It was clearly separated from the other models based on their high ΔAIC_c values.

Plotting observed versus predicted ANPP values showed that the GSL × SM model predictions were closer to the observed values than the other models. Predictions of the GSL × SM model accounted for 75.9% of the variation in observations across sites, and had a slope closest to one with a linear regression (Figure 4), indicating a close fit between predicted and observed values. In the interactive model, GSL influenced ANPP by 4.04 ± 0.63 g m^{-2} d^{-1}. Moreover, a 1% decrease in SM caused a $3.25 \pm 1.23\%$ decrease in daily ANPP at low SM levels, but the effect decreased and approached zero as SM levels increased to the maximum.

DISCUSSION

Growing Season Length Influence

GSL constrained ANPP near the upper limit across the bi-continental and the local Niwot Ridge datasets. The slopes of these responses, approximately 3–4 g m^{-2} d^{-1}, provide an indication of the

Table 2. Comparison of Models for High Elevation Meadow Aboveground Net Primary Production, with Differences among Models Indicated by ΔAIC_c and Relative Model Probabilities Indicated by w_i

Model	AIC_c	df	ΔAIC_c	w_i
1. GSL and SM	65.2	4	0.0	>0.999
2. GSL or SM	104.1	5	38.9	<0.001
3. GSL only	125.7	2	60.5	<0.001
4. SM only	128.7	3	63.5	<0.001

GSL = growing season length; SM = soil moisture.

influence of GSL on potential biomass production across plant communities. However, despite similarities between the quantile responses, the least squares regressions were dramatically different. At Niwot Ridge, ANPP followed a curvilinear pattern in response to GSL, increasing and then decreasing as GSL increased. This pattern has been found in other studies and is generally attributed to limitation in long growing season plots by environmental variables other than GSL, such as SM (Litaor and others 2008; Wipf and Rixen 2010), emphasizing the value of comparing the quantile responses.

Regional to global scale gradient analyses in other ecosystems have produced relationships that are similar to the quantile responses of ANPP to GSL that we report here, although many studies have used remote sensing and modeling. Spatially, ANPP increases across sites with temperature, a proxy for GSL, in high latitude ecosystems (Epstein and others 2008). Primary production has also increased in these high latitude ecosystems in recent decades with a temperature-driven increase in GSL, as inferred from NDVI observations (Tucker and others 2001) and modeling studies of primary production (White and others 1999). The effect of this temporal change in GSL on net primary production was estimated in a modeling study to be approximately 7.7 gC m^{-2} d^{-1} in high latitude aspen (*Populus tremuloides*) stands and 3.9 gC m^{-2} d^{-1} in high latitude white spruce (*Picea glauca*) stands (Keyser and others 2000). In another modeling study, the effect of GSL was estimated to be approximately 3.5 ± 2.7 gC m^{-2} d^{-1} in high latitude tundra ecosystems (Piao and others 2007). Assuming that biomass production is approximately 50% carbon, and that 50% of this production is aboveground, our 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 and others 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 the estimates reported here and previous arctic tundra estimates (Piao and others 2007) suggest that these structurally similar vegetation types may respond similarly to changes in GSL (Wipf and Rixen 2010).

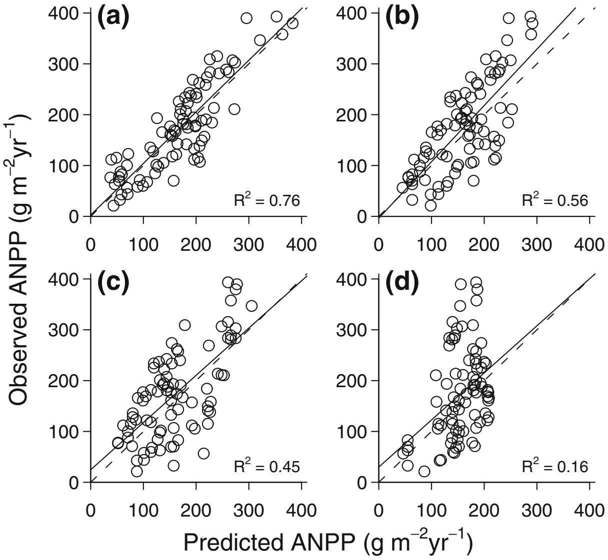

Figure 4. Observed versus predicted regressions for the models shown in Table 2; **A** GSL and SM, **B** GSL or SM, **C** GSL only, and **D** SM only. The *solid lines* reflect linear regressions whereas the dashed lines are 1:1 relationships. Each panel shows the coefficient of determination (R^2) for the linear regression.

Observations of average daily ANPP from site-based, local studies are similar to the average bi-continental response of high elevation ANPP to GSL reported here (1.7 ± 0.2 g m^{-2} d^{-1}). For example, Körner (2003) estimated daily ANPP in alpine ecosystems to be 2.2 ± 0.9 g m^{-2} d^{-1}, which overlaps with and is theoretically equivalent to the average response that we found. These estimates are averages across plant communities and include the influence of other limiting variables such as SM. Consequently, estimates that do not consider multiple environmental influences may underestimate the direct influence of GSL on ANPP patterns.

Soil Moisture Influence

High-elevation daily ANPP was limited by SM across the bi-continental and local datasets after accounting for differences in GSL (Figure 2). We observed a consistent, significant response across space, time, and vegetative communities. The relationship was best fit with a nonlinear, asymptotic model. Ecosystems with long growing seasons and low snowpack should theoretically exhibit seasonal drought, especially in years with low growing season precipitation (Taylor and Seastedt 1994). But, evidence for moisture limitation on high elevation ANPP is limited. 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). 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 and others 1995). Moisture limitation at high elevations may be more pronounced in dry than in wet years (Bowman and others 1995) and correlations between SM and nitrogen availability in alpine and subalpine meadows (Fisk and others 1998; Shaw and Harte 2001) may influence the patterns that we observed. For example, at Niwot Ridge, seasonal patterns of microbial activity and nitrogen transformations are positively related to SM, which affects inorganic nitrogen availability for ecosystem processes (Fisk and others 1998).

Our observation of no response in δ^{13}C across a SM gradient could indicate that stomatal closure was not the only factor limiting production with a decrease in SM over the range of measurements. If stomatal conductance decreased with photosynthesis at low SM levels, we would have expected less discrimination of ^{13}C (higher δ^{13}C) in plant tissues. The minimum effect that we found along the gradient was much smaller than leaf δ^{13}C changes observed in other ecosystems (Garten and Taylor 1992) and there was enough power to detect a significant difference. Other studies support the conclusion that high-elevation vegetation is not primarily limited by stomatal closure with low SM, except at extremely low leaf water potential levels (Oberbauer and Billings 1981; Körner 2003). Stomata may be less responsive to SM and leaf water potential at high elevations if their conductance is controlled by other environmental factors, such as solar radiation (Körner and others 1986). High solar radiation at high elevations may increase demand for plants to keep stomata open despite low SM levels to maintain photosynthesis and to avoid light damage (Lambers and others 2008).

Stress from low soil nutrient availability could also partially explain why we found no response in leaf δ^{13}C to SM. The mobility of nutrients in the soil is a strong determinant of root nutrient acquisition (Clarkson 1985). A decrease in soil nitrogen availability, diffusion, and mass flow when SM is low should reduce plant nitrogen uptake, decreasing nitrogen availability for the production of photosynthetic enzymes like Rubisco (Lambers and others 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 and others 1999) and, subsequently, δ^{13}C values. Although this research identifies important mechanisms for SM limitations of ANPP for an abundant species at one high elevation site, deciphering whether this pattern is widespread in high-elevation ecosystems will require further research.

Interaction Between GSL and SM

Models that included both GSL and SM influences on ANPP had the greatest predictive ability. GSL constrained ANPP whereas variation in SM limited production beneath this constraint. This model outperformed a model considering limitation by either GSL or SM (depending on which variable is most limiting). We suggest that SM can limit ANPP beneath the constraint from GSL across the range of GSL levels. Regulation of high elevation primary production by these two climatically driven variables (not just one or the other) has been suggested in previous studies (for example, Billings and Bliss 1959; Sacks and others 2007), but never explicitly field tested across a broad array of sites before now.

The responses that we observed with the GSL × SM interaction model reinforce our analyses of each variable independently. Our finding of an approximately 4 g m^{-2} d^{-1} response in ANPP to GSL in the absence of SM constraints is consistent with the results from the GSL analysis. Additionally, examining the influence of SM after accounting for differences in GSL supports our finding that SM can limit daily ANPP regardless of GSL.

We did not explicitly consider temporal responses of an individual ecosystem to changes in either variable, which limits our ability to directly infer responses to climatic change. Many of the sites and plots that we examined had pre-existing differences in plant species composition (Berdanier 2010), and ecosystem responses to changes in climate without species turnover may not be as strong as patterns across vegetative communities (for example, Baptist and others 2010). We encourage future research that tests the strength of these responses within communities over time to examine the importance of variation in species composition. However, our results are consistent with research on ecosystem responses to changes in the environment. For example, early season warming can advance the start of the growing season and influence primary production and CO_2 uptake in a broad range of ecosystems (White and others 1999; Jonas and others 2008) whereas drying that accompanies warming can have a negative effect on primary production (Barber and others 2000; Angert and others 2005).

Conclusion

GSL and SM both limited high elevation ANPP when considered independently and combined across sites on two continents. We predicted high elevation ANPP by considering an interaction between GSL and SM where both variables continuously limit production. Advances in the start of the growing season in high elevation meadows can potentially increase ANPP due to an extended growth period but can decrease ANPP regardless of GSL if this response is accompanied by a decrease in SM.

This finding has consequences for the responses of high elevation ecosystems to changes in climate. For example, an experimental soil warming of 3°C in a subalpine meadow advanced snowmelt by 7 days and decreased SM by 25% (Harte and others 1995). An equivalent decrease in SM could decrease daily ANPP between 0.3 and 1.2 g m^{-2} d^{-1}, depending on initial SM levels (0.6 g m^{-2} d^{-1} average). However, the corresponding increase in GSL could potentially increase ANPP by approximately 28 g m^{-2}. The balance of these two responses, in combination with species composition changes, will determine whether ANPP responds positively, negatively, or neutrally to warming. Consequently, this study demonstrates that, across a diverse set of high elevation sites, the interactive effects of SM and GSL can produce distinct ecological patterns and must be considered to predict high elevation production responses to future changes in climate.

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