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The response of four subalpine forbs to supplemental nitrogen within two soil moisture environments near Gothic, CO

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Abstract

Anthropogenic environmental change currently threatens to alter resource availability across the planet, likely driving responses by plant species. In the Colorado Rocky Mountains, climate change is expected to decrease soil moisture availability and increased nitrogen deposition is expected to increase nitrogen availability. This study investigated the resource limitations of *Erigeron speciosus*, *Heliomeris multiflora*, *Lathyrus leucanthus*, and *Lupinus spp.* near the Rocky Mountain Biological Lab in Gothic, CO to provide a better understanding of what resources limit subalpine forbs and to supply evidence to help predict how subalpine forbs might respond to climate change and increased nitrogen deposition. In addition, a functional group level study was conducted to provide insights into how functional group responses could drive changes to biodiversity and ecosystem function. Growth rates and physiological responses were recorded and compared between plants receiving nitrogen and control plants as well as between different soil moisture conditions to investigate whether soil moisture availability might limit the response of subalpine plants to supplemental nitrogen. Results from this study suggest that the growth rate of *Erigeron* is limited by nitrogen and soil moisture, with soil moisture as the more important limiting factor. The growth rate of *Heliomeris* displayed a marginal response to both nitrogen and soil moisture, with soil moisture as the more important, marginally limiting factor. These two results suggest that decreased soil moisture due to climate change could limit the growth rate of *Erigeron* and *Heliomeris*. *Lupine* and *Lathyrus* did not significantly respond to nitrogen or soil moisture, suggesting that soil moisture and nitrogen are not important limiting factors for *Lupine* and *Lathyrus*. This study supports the hypothesis that changes in resource availability can drive plant responses and provides evidence to predict the response of subalpine forbs to anthropogenic environmental change. Ultimately, this research hopes to build on the body of knowledge addressing changes in plant biodiversity and ecosystem function driven by anthropogenic environmental change.

Introduction

Anthropogenic environmental change currently threatens to alter ecosystem resource availability across the planet (IPCC 2007, Katzenburger 2006, De Valpine and Harte 2001, Fay et al. 2002, Vitousek 1997). Climate change is expected to alter soil moisture availability and increase nitrogen mineralization rates (Harte et al. 1995, Katzenburger 2006) while industrial fertilizer use continues to increase global soil nitrogen concentrations (Vitousek et al. 1997). Because soil moisture and nitrogen are two important limiting resources among subalpine plants, changes to the availability of these resources could drive species level plant responses influencing changes in plant biodiversity and ecosystem function (Dunne et al. 2003, Lavorel and Garnier 2002). Understanding how plants will respond to altered resource limitations also helps inform possible future climate change feedback scenarios and is critical to developing ecological management and mitigation strategies (Woodwell and Mackenzie 1995, Ojima et al. 1991).

Investigating plant responses to altered soil moisture and soil nitrogen availability begins with assessing how the availability of these resources is changing (Dunne et al. 2003, De Valpine and Harte 2001). Future soil moisture availability in subalpine ecosystems of the Colorado Rocky Mountains will likely depend on how local climates warm and to what extent local precipitation regimes become altered, while the rate that soil nitrogen concentrations increase depends on

local land-use, local landscapes, and future action taken to curb nitrogen inputs (Fay et al. 2002, Vitousek 1997). Understanding how anthropogenic environmental change will alter the future availability of soil moisture and nitrogen provides a framework for interpreting how resource limitations of specific plant species may ultimately drive the response of those species to climate change and increased nitrogen deposition (Dunne et al. 2004, De Valpine and Harte 2001).

To assess climate change, climate models are used to predict possible future climates (IPCC 2007, Katzenburger 2006, Houghton 2001). Climate model predictions produced by the Intergovernmental Panel on Climate Change (IPCC) estimate a global surface temperature increase between 2°C and 4.5°C by 2100 (IPCC 2007). In 2006, The Aspen Global Change Institute (AGCI) produced a climate change impact assessment for the area near Aspen, CO., predicting a temperature increase of 3.6°C near the town of Aspen by 2030 (Katzenburger 2006). As the climate warms, soil moisture could decrease due to increased evaporation (Harte et al. 1995, De Valpine and Harte 2001). An ongoing experiment being conducted at the Rocky Mountain Biological Laboratory (RMBL) uses infrared heat lamps to simulate a 3°C increase in temperature on experimental plots (Harte et al. 1995, De Valpine and Harte 2001). One result from this long term warming experiment suggests that an increased temperature of 3°C reduces soil moisture by up to 25%, possibly driving plant responses (Harte et al. 1995, De Valpine and Harte 2001). One such response is the loss of shallow rooted species because they are more susceptible to the effects of drought (Cross and Harte 2007).

Although models used to predict future precipitation regimes are not as clear as most temperature predictions, changes in precipitation regimes will likely alter soil moisture availability along with climate warming, possibly decreasing soil moisture further in areas receiving less precipitation (Fay et al. 2002, Katzenburg 2006). One AGCI model predicts that precipitation regimes near Aspen, CO are expected to change, predicting a decrease in total precipitation during the summer growing season by 2030 (Katzenburger 2006). Also by 2030, winter snowpack is predicted to begin building at the base of Aspen Mountain (2422 m) between 1.5 and 4.5 weeks later, and snowmelt date is predicted to occur between 2.5 and 5 weeks earlier than currently (Katzenburger 2006). With respect to soil moisture, decreasing summer rainfall, shortening the duration that the snowpack is on the ground, and decreasing the amount of total snowpack decreases overall available soil moisture, and could increase the importance of soil moisture as a limiting factor (Katzenburger 2006, Fay et al. 2002).

Anthropogenic alterations to the global nitrogen cycle are dramatic and continue to occur (Vitousek 1997, E&S Environmental Chemistry Inc. 2008). Due mainly to industrial fertilizers, nitrogen inputs to the terrestrial nitrogen cycle have approximately doubled since 1940, with the majority of the inputs occurring after 1980, suggesting that the rate of anthropogenic inputs has been increasing as global demand for fertilizer has increased (Vitousek et al. 1997). In addition, results from the RMBL suggest warmer temperatures will increase soil nitrogen mineralization, further exacerbating the rate of increasing nitrogen input into the global nitrogen cycle (Harte et al. 1995). Although nitrogen deposition and inputs from fertilizers have increased nitrogen concentrations worldwide, the western slope of the Colorado Rockies has not experienced the intense levels of anthropogenic nitrogen inputs compared to Eastern Colorado and other

agricultural landscapes throughout the world making subalpine meadows near the RMBL a good control for nitrogen research (CASTNET).

With consensus among scientists that the climate is warming, that precipitation regimes will likely decreased precipitation for the Colorado Rocky Mountains, and that global soil nitrogen levels are increasing, subalpine meadows of the Rocky Mountains will likely experience decreased available soil moisture and increased levels of soil nitrogen in the future (IPCC 2007, Katzenbutger 2006). Understanding how plants will respond to changing resource limitations and the implications associated with those responses is important because the responses of individual species to altered resource availability will likely drive changes to plant biodiversity and ecological function, producing climate change feed back scenarios (Woodwell and Mackensie 1995, Ojima et al. 1991, De Valpine and Harte 2001).

In general, subalpine plants of the Rocky Mountains grow in soils where levels of nitrogen or low levels of soil moisture overshadow other resources as a limiting factor (E&S Environmental Chemistry Inc. 2008). Increased nitrogen deposition can cause growth responses in specific plants by placing more importance on limitations of other resources (E&S Environmental Chemistry Inc. 2008, Vitousek et al. 1997). Results from Fenn et al. (2003) suggest that increased soil nitrogen availability can cause soil nitrogen saturation. Characterized by a loss in biodiversity and decreased soil nitrogen retention, soil nitrogen saturation can create changes in ecosystem composition and disruptions in nutrient cycling (Bowman et al., 2006 Fenn et al 2003). If nitrogen availability increases, the response of plant species could be driven by other resource limitations such as soil moisture availability. (De Valpine and Harte 2001).

Research conducted at the Rocky Mountain Biological Lab by De Valpine and Harte investigated whether nitrogen or soil moisture limitations were driving the response of *Erigeron speciosus* and *Helianthella quinquenervis* in their warming experiment. *Erigeron* biomass significantly increased with the addition of water, supporting the hypothesis that *Erigeron* biomass decreased in the warming experiment as a result of water limitation (De Valpine and Harte 2001). *Helianthella* responded with increased flower production to both nitrogen and water, but the results remained statistically unclear as to whether nitrogen or water were limiting, suggesting a possibly contrasting effect of warming on *Helianthella* (De Valpine and Harte 2001). These results provide evidence that changes to resource limitations can elicit species level responses by subalpine plants and suggest that soil moisture limitations may be driving the response of *Erigeron* to warming.

Experimental evidence also suggests that plants within functional groups can respond similarly to altered resource limitations, possibly driving changes of plant biodiversity (West et al. 2005, Harte and Shaw 1995, Luscher et al. 2000). For example, warming experiments at the RMBL showed an overall decrease in forb biomass and an increase in shrub biomass on warmed plots (Harte and Shaw 1995). Shallow rooted forbs likely cannot compete for moisture resources with the deeper root systems of shrubs demonstrating how altered resource limitations can alter plant biodiversity. Luscher et al. (2000) suggest that legumes increase biomass in response to elevated temperature significantly more than plants that are unable to fix nitrogen, suggesting that plants that have the ability to fix nitrogen may respond more favorably to climate warming. One hypothesis to explain this conclusion predicts that legumes would benefit from increased

available soil nitrogen more than other forbs because legumes can “turn off” the bacterial symbiosis that provides legumes with fixed nitrogen in exchange for carbon, therefore availing all carbon sources for the legume to utilize. If plants within the same functional group respond to altered resource limitations similarly, anthropogenic environmental change could drive changes of plant biodiversity and ecosystem function (Harte and Shaw 1995, Zak et al. 2000, Lavorel and Garnier 2002, E&S Environmental Chemistry Inc. 2008).

To build on the understanding of how subalpine plant species of the Rocky Mountains could respond to altered soil moisture and soil nitrogen limitations, four subalpine Rocky Mountain plant species; *Erigeron speciosus*, *Helimeris multiflora*, *Lathyrus leucanthus*, and *Lupinus spp.* were studied near Gothic, CO in the summer of 2009. Studying how plants respond to supplemental nitrogen while growing in different soil moisture conditions provides insights regarding whether soil moisture might limit the nitrogen response of these plants. These findings attempt to shed light on what might drive subalpine plant responses to climate change and increased nitrogen deposition and to provide a framework for understanding how plant biodiversity and ecosystem function may change. In addition to investigating species level responses, the response between legumes and forbs was investigated as a functional group level study. This aspect of the study will provide insight into whether plants within the legume and forb functional groups might respond similarly to altered resource limitations due to climate change, in turn driving changes of plant biodiversity and ecosystem function.

This study’s experimental approach investigated whether the focal plants responded to supplemental nitrogen and whether those responses are constrained by soil moisture availability. Plants were treated with supplemental nitrogen while growing in two naturally occurring soil moisture environments and in experimental plots receiving supplemental water. Integrating experimental data with data collected from a naturally occurring environment is a strong method to compare the response of plants within experimental plots to the response of the same plants in naturally occurring environmental conditions (Dunne et al. 2004). For example, the majority of subalpine forbs near Gothic, CO are perennials with the ability to store resources for use during a favorable growth year. This may delay a plant’s response to a manipulation for several years, making it difficult to attribute plant responses to a specific treatment. In theory, research that takes place within a naturally occurring environment addresses this problem by investigating plants that have adapted to similar resource availability over many years. This integrative approach can strengthen conclusions describing the response of plants to altered soil moisture and soil nitrogen limitations and help inform how those responses may affect plant biodiversity and ecosystem function. This study attempts to build on the body of knowledge addressing how anthropogenic alterations to nitrogen and soil moisture resource limitations will drive species and functional group level plant responses of subalpine forbs growing near the RMBL.

Methods

Study Site

The response of four perennial forbs to supplemental nitrogen growing in two naturally occurring soil moisture environments was studied in a meadow east of the “Bellview Bench” parking area, ¼ mile south of Emerald Lake on Gothic road near the RMBL. It is a relatively treeless area with a large diversity of perennial forbs set in a relatively high elevation. This

elevation experiences a later snowmelt than lower elevations and allows treatments beginning in late June to still affect the majority of the growing season. This environment has wetter soils near the stream and below the large expanse of exposed rock, and drier soils above the exposed rock and further from the stream, providing two soil moisture environments.

To study the response of subalpine forbs to supplemental nitrogen and growing in experimental plots receiving water, Zac German's Judd Falls research site was used. This site near the RMBL is located in an open subalpine meadow and consists of five blocks each containing eight 2 x 2 m experimental plots receiving different treatments. Four plots from each block receiving supplemental water, supplemental nitrogen, water + nitrogen, and control were used in this study. These plots have been receiving nitrogen for four seasons and began receiving water in 2009.

Data Collection

At Bellview Bench, two soil moisture sites (wet and dry) were chosen using a digital soil moisture meter (TDR Campbell Scientific). Soil moisture readings of 20% and higher at the beginning of the experiment were considered "wet" and readings below 15% were considered "dry". Twenty individuals of each of the four focal plants; *Erigeron speciosus*, *Heliomeris multiflora*, *Lathyrus leucanthus*, and *Lupinus ssp.*, were chosen haphazardly in both the "wet" and "dry" soil moisture sites totaling 160 individuals. Ten control plants and ten nitrogen plants were designated from the twenty individuals of each species in both the "wet" and "dry" sites with care taken to match similar plant sizes for each control and nitrogen pair. The research individuals were flagged and tagged with respect to individual number, species type, moisture environment, and nitrogen or control. Soil moisture data was taken twice during the research project to document the integrity of the natural soil moisture difference between the two sites.

Supplemental nitrogen was added to a 0.5 x 0.5 m area surrounding each treatment individual at Bellview Bench in the form of ammonium nitrate (NH_4NO_3) mixed with water (H_2O). In order to apply 9g/m^2 of nitrogen (N) to 80 0.25m^2 sites over the study's duration, 128.57g of NH_4NO_3 was dissolved in 20L of H_2O on four separate occasions and 250mL of this solution was added to each treatment individual. 9g/m^2 of nitrogen was chosen as a supplemental amount to ensure a high level of nitrogen was available to each treated plant and to match the amount of nitrogen being added at the Judd Falls research site. The water used to apply the supplemental nitrogen will be considered negligible, because it is equivalent to 1mm of precipitation. Low ambient humidity and frequent rainfall events during 2009 also helped to negate the weekly addition of 1mm of water.

At Judd Falls, up to three individual *Erigeron*, *Heliomeris*, and *Lathyrus* plants (*Lupine* was not present at Judd Falls) were selected from each focal plot. These plants were flagged and tagged with respect to individual number, block number, and plot number. Nitrogen was added in the same amounts used at Bellview Bench except it was added to the entire plot receiving supplemental nitrogen not individual plants. Supplemental water was applied by pumping water through an irrigation hose and using a flow gauge attached to a garden sprayer. Ten Gallons, equivalent to approximately 1cm of precipitation, was added to each 2 x 32 m treatment plot during each irrigation session, at intervals of two to five days as needed to maintain a high level of soil moisture.

Plant species response was determined by comparing treatment plants to control plants and comparing plants within the different soil moisture environments. Legume response was compared to forb response at Bellview Bench by combining the response data of *Erigeron* with *Heliomeris* as the forb response and *Lupine* with *Lathyrus* as the legume response. The growth response of *Erigeron*, *Heliomeris*, and *Lupine* was recorded by counting the number of stems and measuring three representative stem heights for each individual. The growth response of *Lathyrus* was recorded by counting the number of leaves and the height of the single stem. Plant size was calculated by multiplying the number of stems or number of leaves by the mean stem height for that date. Plant growth rate was calculated by standardizing plant sizes to an initial mean plant size measured on June 28, 2009. Physiological response was recorded by measuring stomatal conductance ($\text{mmol/m}^2\text{s}$) and chlorophyll fluorescence ratios (F_v/F_m). These physiological measures help determine the response of individuals with respect to levels of drought stress and their capacity to capture light energy for photosynthesis. A reproductive phenology index documented the timing of reproduction among study individuals and total reproductive success was documented by calculating the ratio of total flowers produced to total stems.

The results of this research were statistically analyzed using a repeated measures analysis of variance, with replicate plants nested within soil moisture environment. The goal of this analysis was to determine the response of the four focal species and the response of legumes compared to forbs to nitrogen within different soil moisture environments and to compare results from Bellview Bench to results at Judd Falls.

Results

The response of *Erigeron speciosus*, *Heliomeris multiflora*, *Lathyrus leucanthus*, and *Lupinus spp.* to supplemental nitrogen was studied within two soil moisture environments at Bellview Bench and in experimental plots receiving irrigation at Judd Falls. This experimental approach investigate whether nitrogen and soil moisture availability are limiting these focal plant species. Comparing the response of plants receiving nitrogen to control plants tests for nitrogen limitation in these focal species while interpreting that response between different soil moisture environments attempts to address whether soil moisture is limiting the response to supplemental nitrogen. Comparing results at Bellview Bench to results at Judd Falls attempts to integrate the response of the focal species to supplemental nitrogen growing in a two naturally occurring soil moisture environments with results from plants growing in experimental plots receiving water. Growth rate was used as the main response variable while physiological responses were used as additional tools to further interpret how the focal plants may have been responding in the study. Comparing data recorded for legumes with data recorded for forbs attempts to provide insights into whether the functional group level response of the focal plant species in the study was limited by nitrogen and soil moisture availability providing conclusions about what resource limitations could drive changes in plant biodiversity leading to changes in ecosystem function.

Results from Bellview Bench suggest that nitrogen and soil moisture limit the growth rate of *Erigeron*, with a stronger link to soil moisture as the more important limiting factor (Fig 1). *Erigeron* responded to nitrogen in the wet environment with an increased growth rate ($p=0.012$)

compared to control plants suggesting that the growth rate of *Erigeron* is limited by nitrogen when soil moisture is abundant. *Erigeron* control plants in the wet environment responded with an increased growth rate compared to control plants in the dry environment ($p=0.017$) suggesting that the growth rate of *Erigeron* is also limited by soil moisture availability. However, *Erigeron* did not significantly respond to nitrogen in the wet environment compared to the dry environment suggesting that although *Erigeron* appears to be limited by both nitrogen and soil moisture, the more important factor limiting *Erigeron* in this study is soil moisture availability. *Erigeron* responded to nitrogen at Bellview Bench by exhibiting increased photosynthetic capacity ($p=0.01$) in the wet environment compared to control suggesting that nitrogen may limit the photosynthetic capacity of *Erigeron* when soil moisture is abundant (Fig 2). *Erigeron* also responded to nitrogen in the dry environment by exhibiting increased photosynthetic capacity ($p=0.028$) suggesting that nitrogen may limit the photosynthetic capacity regardless of soil moisture availability. This conclusion is supported by the lack of a response by *Erigeron* control plants in the wet environment compared to control plants in the dry environment and by the lack of response by nitrogen plants in the wet environment compared to nitrogen plants in the dry environment, suggesting that the importance of nitrogen overshadows the importance of soil moisture as a limiting factor for photosynthetic capacity. Photosynthetic capacity also increased later in the growing season compared to earlier in the season ($p<0.001$) regardless of nitrogen or soil moisture availability, suggesting that the progression of the growing season influences photosynthetic capacity.

Erigeron stomatal conductance did not respond to nitrogen at Bellview bench, but did show increased conductance in the wet environment compared to the dry illustrating the ability of stomatal conductance data to measure drought stress and supporting the presence of a wet and a dry research site at Bellview Bench.

Results from Bellview Bench suggest that the growth rate (Fig 3) and photosynthetic capacity (fig 4) of *Heliomeris* is limited marginally by soil moisture and nitrogen. *Heliomeris* displayed a slight response to nitrogen in the wet environment with an increased growth rate ($p=0.16$), emphasizing soil moisture as a marginally important limiting factor. *Heliomeris* also responded marginally to nitrogen at Bellview Bench with increased photosynthetic capacity in the dry environment ($p=0.0957$) and in the wet environment ($p=.0647$) compared to control plants, suggesting that nitrogen is an important factor limiting the photosynthetic capacity of *Heliomeris*. High rates of insect herbivory compared to the other focal plants species may have contributed to the lack of a significant response by *Heliomeris* at Bellview Bench. Photosynthetic capacity also increased later in the growing season in the wet environment compared to earlier in the season ($p=0.02$) supporting the conclusion that the progression of the growing season influences photosynthetic capacity.

Heliomeris stomatal conductance did not respond to nitrogen or soil moisture at Bellview Bench.

Lathyrus and *Lupine* did not respond to nitrogen or soil moisture with increased growth rate, photosynthetic capacity, or stomatal conductance at Bellview Bench.

Erigeron at Judd Falls displayed a pattern of increased growth rate (Fig 5) in response to supplemental nitrogen and water, however, this observation could not be explained with

statistical analysis. *Erigeron* photosynthetic capacity and stomatal conductance did not respond to nitrogen or soil moisture at Judd Falls.

Heliomeris at Judd Falls responded to nitrogen with a decreased growth rate (Fig 6) compared to plants in control, water, and water + nitrogen plots suggesting other factors were limiting the growth rate of *Heliomeris* at Judd Falls. *Heliomeris* photosynthetic capacity and stomatal conductance did not respond to nitrogen or soil moisture at Judd Falls.

Lathyrus did not respond to nitrogen or water at Judd Falls with a growth rate or physiological response and all individuals failed to flower.

Nitrogen and soil moisture had no effect on reproductive phenology or flower production at Bellview bench or Judd falls for any of the focal species.

When combining *Heliomeris* with *Erigeron* as forbs and *Lupine* with *Lathyrus* as legumes, there was no difference in growth rate between forbs and legumes. Legume and Forb photosynthetic capacity and stomatal conductance did not respond differently to nitrogen or soil moisture on a functional group level.

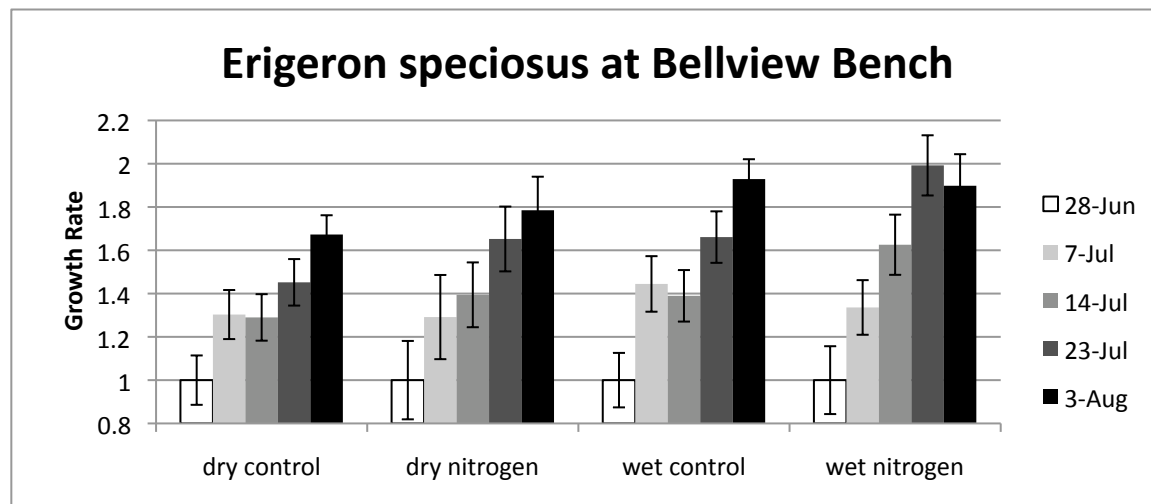


Fig. 1 *Erigeron* responded to nitrogen and soil moisture availability with increased growth rate at Bellview Bench ($p=0.0123$). Growth rate is calculated by standardizing individual plant sizes to the initial mean on June 28.

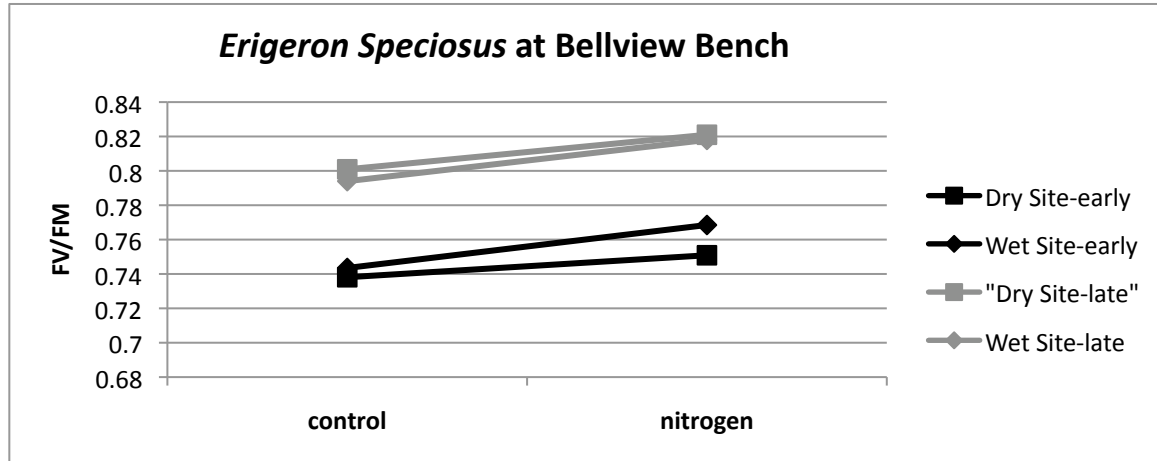


Fig. 2 *Erigeron* responded to nitrogen with an increased photosynthetic capacity in both the wet environment ($p=0.008$) and the dry environment ($p=0.0278$) at Bellview Bench. *Erigeron* also responded later in the growing season with increased photosynthetic capacity compared to earlier in the season. FV/FM represents the ratio of chlorophyll fluorescence with higher percentages equaling higher photosynthetic capacity.

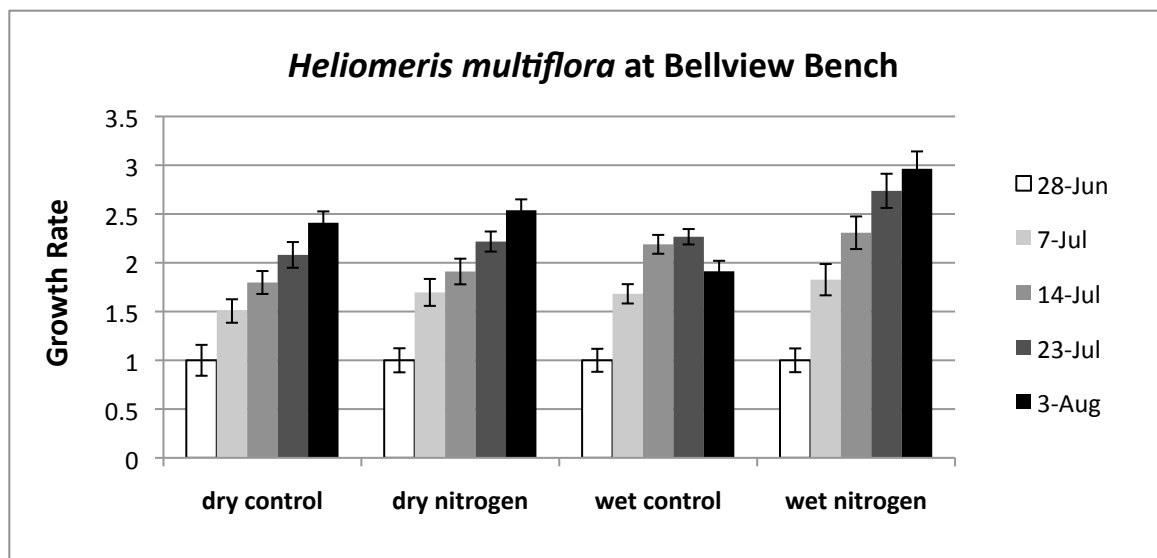


Fig 3. *Heliomeris* displayed a slight response to nitrogen in the wet environment at Bellview Bench ($p=0.16$).

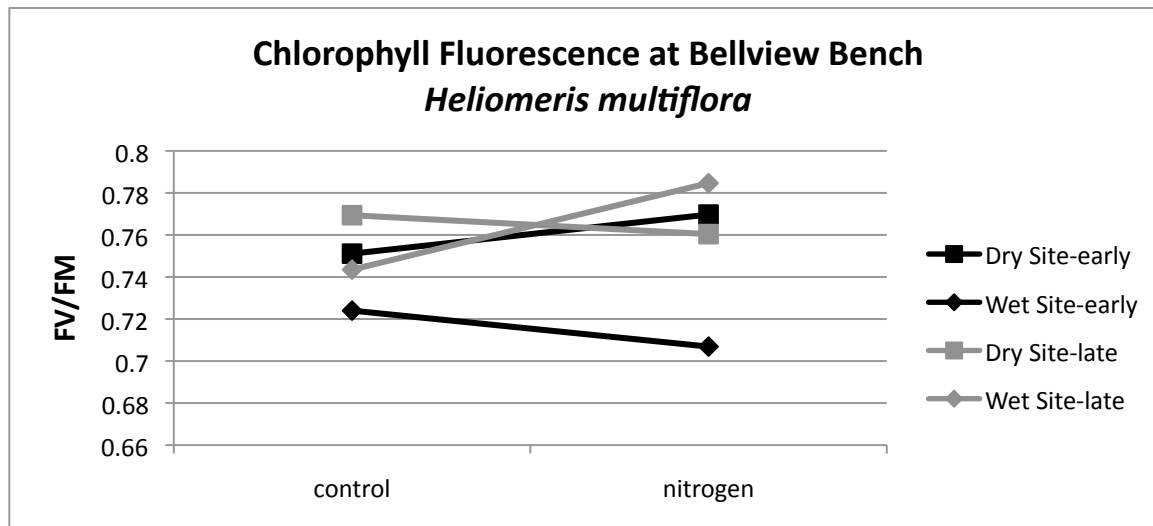


Fig. 4 *Heliomeris* responded marginally to nitrogen with increased photosynthetic capacity in the dry environment early in the season ($p=0.957$) and marginally in the wet environment late in the season when the effect of nitrogen was analyzed with the effect of date ($p=0.0647$). *Erigeron* at Bellview Bench also responded with increased photosynthetic capacity later in the growing season compared to early in the season.

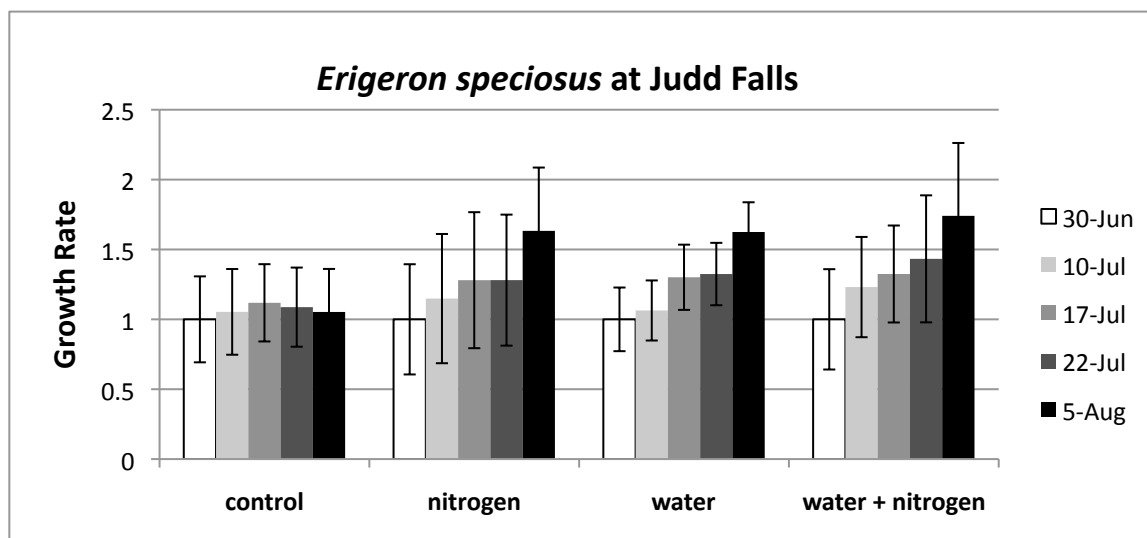


Fig. 5 *Erigeron* at Judd Falls did not respond with statistical significance, but a pattern of increased growth rate is observed with nitrogen, water, and nitrogen + water compared to control.

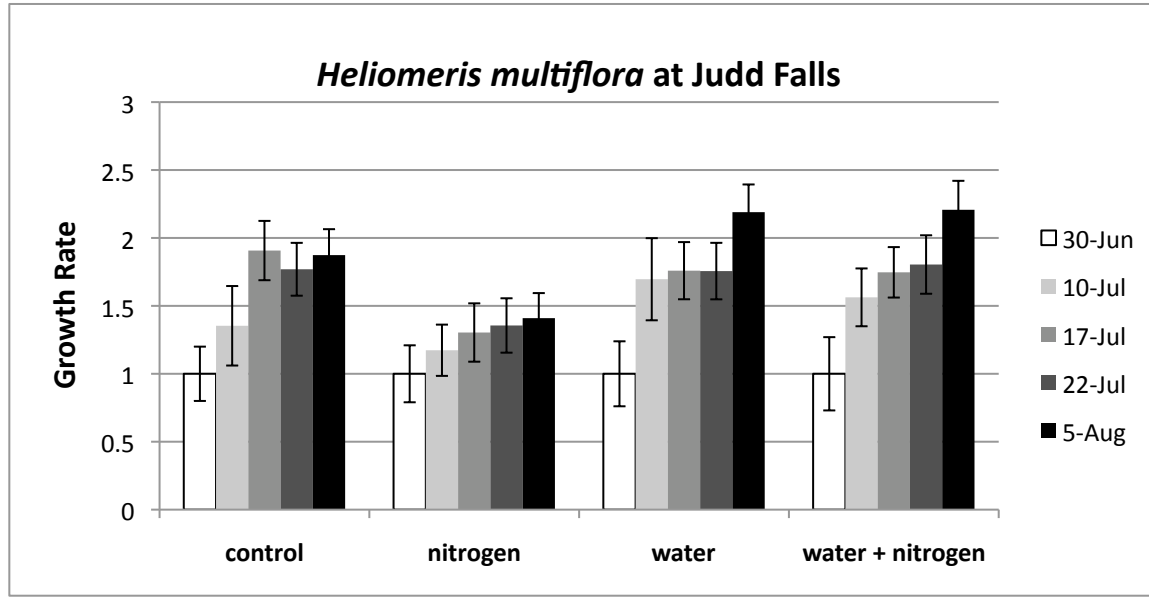


Fig. 6 *Heliomeris* at Judd Falls responded to nitrogen with a decreased growth rate compared to plants in control, water, and water + nitrogen plots suggesting other factors were limiting the growth rate of *Heliomeris* at Judd Falls.

Discussion

Erigeron's growth response to nitrogen and soil moisture at Bellview Bench suggests that *Erigeron* exhibits an increased growth rate when nitrogen and soil moisture are both abundant and when only soil moisture is abundant. The growth response by *Heliomeris* was marginal at Bellview Bench, however, an increase in growth rate was observed in response to nitrogen suggesting that *Heliomeris* is marginally limited by nitrogen and soil moisture availability. One result from a study by DeValpine and Harte (2001) to investigate whether soil moisture or nitrogen availability drove the response of *Erigeron* to warming suggests that soil moisture availability significantly limits the biomass production of *erigeron* and nitrogen marginally limits biomass production. Results from De Valpine and Harte (2001) suggest alterations to nitrogen and soil moisture resource availability due to climate warming drove the response of *Erigeron*. Results from this study at Bellview Bench and Judd Falls provide evidence suggesting soil moisture and nitrogen availability can influence the growth rate of *Erigeron* and *Heliomeris* supporting conclusions by De Valpine and Harte that the growth rate of *Erigeron* is limited by soil moisture and to a lesser degree, nitrogen availability. This implies that climate change, specifically climate warming, may lead to a decrease in abundance of *Erigeron* and *Heliomeris*.

Erigeron significantly increased photosynthetic capacity in response to nitrogen in both the wet and dry environments at Bellview Bench suggesting that nitrogen limits photosynthetic capacity regardless of soil moisture availability. *Heliomeris* marginally increased photosynthetic capacity in response to nitrogen in the dry environment and in the wet environment suggesting that nitrogen limitation marginally constrains the photosynthetic capacity of *Erigeron*. Increased photosynthetic capacity in response to nitrogen can be explained by the role nitrogen plays as a biochemical requirement for photosynthesis. Nitrogen availability can limit the number of

nitrogen containing substrates needed for synthesizing photosynthetic enzymes, thereby limiting photosynthetic capacity (Sims et al. 1998). Results from Heckathorn et al. (1997) suggest nitrogen limitations drove decreased photosynthetic capacity in prairie grasses following a drought by linking a decreases in nitrogen containing enzymes required for photosynthesis in leaves to nitrogen limitations driven by drought.

Erigeron and *Heliomeris* also increased photosynthetic capacity later in the growing season compared to earlier in the season suggesting that leaf maturity or annual physiological leaf cycles limit the photosynthetic capacity of *Erigeron* and *Heliomeris* at specific times throughout the growing season. Increased photosynthetic capacity later in the growing season compared to earlier in the season can be explained by leaf maturity. Soukupov et al. (2008) recorded low, steady levels of chlorophyll fluorescence during winter months in evergreen and broad leaf plants in the temperate zone. Photosynthetic capacity, measured by chlorophyll fluorescence ratios, increased with the onset of spring, remained high throughout the growing season, and decreased with the onset of fall marked by the first frost (Soukupov et al. 2008). Although the plant leaves studied by Soukupov et al. exist for multiple seasons, perennial forbs existing in subalpine meadows could increase photosynthetic capacity as the growing conditions improve from spring to summer just as plants in the temperate zone do during the transition from winter to summer. Research from this study at Bellview Bench provides evidence that the photosynthetic capacity of *Erigeron*, and *Heliomeris* is limited by nitrogen and leaf maturity, supporting previous research.

Without any statistically significant phenological or reproductive responses by any focal species, this study suggests that nitrogen and soil moisture availability do not influence the timing of reproduction or the amount of reproductive structures produced by *Erigeron*, *Heliomeris*, *Lupine*, and *Lathyrus* within a single growing season. Water and nitrogen may contribute to growth rate and not flowering success, explaining this result. Also, resources could be stored for future seasons and the response from supplemental resources may not be expressed in the same year as the experiment. Integrating research done in naturally occurring environments and experimental plots attempted to address this issue. Responses to warmed plots in at Judd Falls this season in the absence of a measurable warming effect supports the hypothesis that resources are stored by perennial plants, offering one explanation for a lack of a growth response in some species and flowering response for all species German (unpublished data).

When combining the species responses into functional groups, forbs did not exhibit an increased growth rate, suggesting that responses to nitrogen and soil moisture limitations are species specific. The response by *Erigeron* and *Heliomeris* coupled with the lack of a response by *Lathyrus* and *Lupine* would imply that forbs would respond on a functional level compared to legumes. However, this study does not imply that species from the same functional groups will respond similarly to altered nitrogen and soil moisture resource limitations.

Conclusion

Understanding how anthropogenic environmental change will alter local resource availability and investigating the resource limitations of common plant species in a community can help predict future plant responses to climate change and increased nitrogen deposition. This study

supports this hypothesis, at least when investigating the roll of nitrogen and soil moisture as drivers of species level plant responses. Although a functional group level response was not evident in this study, the response of *Erigeron* and *Heliomeris* and the lack of response by *Lupine* and *Lathyrus* implies that the depth of a plant's root system and the ability to fix nitrogen through bacterial symbiosis may provide an advantage to resisting drought and nitrogen limitations. Under future scenarios with decreased soil moisture and increased nitrogen availability, this study, and other previous research suggests that *Erigeron* and *Heliomeris* may decrease in biomass due to soil moisture constraints altered by climate change.

Future directions for study

Only above ground biomass and physiological responses over one growing season were investigated in this study. Understanding how perennial plants store nutrients for favorable growth years and if underground biomass is responding to nitrogen and soil moisture availability would help interpret the results of this study more clearly. If responses to nitrogen and soil moisture availability are expressed with increased root biomass or are being delayed by the plant in favor of storing nutrients for future seasons, then this experimental design would not detect those responses.

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Literature Cited

- Bowman, W. D. et al. 2006. Nitrogen critical loads for alpine vegetation and terrestrial ecosystem response: are we there yet. *Ecological Society of America* 16: 1183-1193.
- Cross, M. S. and J Harte. 2007. Compensatory response to loss of warming sensitive plant species. *Ecology* 88: 740-748
- De Valpine, P. and J. Harte. 2001. Plant responses to experimental warming in a montane meadow. *Ecology* 82: 637-647.
- Dunn, J. A. et al. 2003. Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecological Monographs* 73: 69-86.
- E&S Environmental Chemistry Inc. 2009. Alpine Vegetation Workshop: Response of Alpine and Subalpine Plant Species to Changes in Atmospheric N Deposition
- Fay P. A., et al. 2002. Altered rainfall patterns, gas exchange, and growth in grasses and forbs. *International Journal of Plant Sciences* 163: 549-557.
- Fenn, M. E. et al. 2003. Ecological effects of nitrogen deposition in the western United States. *Bioscience* 4: 404-419.
- Harte, J. et al. 1995. Global warming and soil microclimate: Results from a meadow warming experiment. *Ecological Applications* 5: 132-150.

Harte, J. and R. Shaw 1995. Shifting dominance within a montane vegetation community: results of a climate warming experiment. *Science* 267: 876-880.

Heckathorn, S. A. et al. 1997. The contribution of drought-related decreases in foliar nitrogen concentration to decreases in photosynthetic capacity during and after drought in prairie grass. *Physiologia Plantarum* 101: 173-182.

IPCC, 2007: Summary for Policymakers. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H. L. Miller (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IPCC, 2001: *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* [Houghton, J.T., Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, and C.A. Johnson (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 881 pp.

Katzenberger, J., ed. 2006. Climate change and Aspen: an assessment of impacts and potential responses. A report in the Aspen Global Change Institute Elements of Change series, AGCI.

Lavorel, S. and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the holy grail. *Functional Ecology* 16: 545-556.

Luscher, A. et al. 2000. Direct evidence that symbiotic N-fixation in fertile grasslands is an important trait for a strong response of plants to elevated Atmospheric CO₂. *Global Change Biology* 6: 655-662.

Ojima, D. S. et al. 1991. Critical issues for understanding global change effects on terrestrial ecosystems. *Ecological Applications* 1: 316-325.

Sims D. A., et al. 2002. Comparison of photosynthetic acclimation to elevated CO₂ and limited nitrogen supply in Soybeans. *Plant, Cell and Environment* 21: 945-952.

Soukupov, J. et al. 2008. Annual variation of the steady state chlorophyll fluorescence of evergreen plants in the temperate zone. *Functional plant Biology* 35: 63-76.

Vitousek, P. M. et al. 1997. Human alterations of the global nitrogen cycle: Sources and consequences. *Ecological Applications* 7: 737-750.

West, J. B. et al. 2006. Legume species identity and soil nitrogen supply determine symbiotic nitrogen fixation responses to elevated atmospheric CO₂. *New Phytologist* 167: 523-530.

Woodell, G. M. et al. 1998. Biotic feedbacks in the warming of the Earth. *Climate Change* 40: 495-518.

Zak, D. R. et al. 2000. Atmospheric CO₂ Soil-N availability, and Allocation of biomass and Nitrogen *Populus Tremuloides*. *Ecological Applications* 10: 34-46.