Effects of Global Change Factors on Sensitive Alpine Plant and Microbial Communities

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ABSTRACT

Global climate changes have greatly changed microbial-plant interactions within sensitive alpine ecosystems. Global climate changes such as temperature increase, elevated levels of snow deposition, and increased nitrogen deposition are being artificially imposed in the moist alpine ecosystem at Niwot Ridge, Colorado as part of a broader study. We used International Tundra Experiment (ITEX) warming chambers, snow fences, and direct nitrogen additions to impose the three global change factors (GCFs). I studied and measured the effects of these global change factors on plant and associated microbial communities by the (a) plant nitrogen exchange, (b) plant productivity, (c) species composition, (d) microbial biomass, (e) N-mineralization rate. Specifically, we addressed (1) if plants and microbes respond similarly to the same GCFs and (2) if GCFs act independently or in combination to affect the overall ecosystem. There was not a single treatment that was consistently significant across all measures. Implication of multiple global change factors resulted in a slight exponential effect regarding plant composition response. This experiment will give insight into the conditions of plant and microbial communities under stress, and will inform us of possible occurrences in other, less sensitive biomes that respond slower to environmental changes.

KEYWORDS

Nutrient cycling, nitrogen cycling, warming snow deposition, alpine tundra, moist meadow

Colorado Rockies

INTRODUCTION

Global climate changes have resulted in great fluctuations in the distribution of precipitation, temperature and nutrient cycling in sensitive terrestrial ecosystems (Vitousek et al. 2002, Chapin et al. 1993, Bowman 1996). The alpine tundra, which has a naturally low buffering capacity resulting from its poor soils and overall low biological productivity, is particularly sensitive to variations in the environment (Galloway 1995). Changes in the alpine tundra include slower rates of nutrient cycling, acidification of soil, and shifts in the interactions of plant communities with microbes (Norby et al. 2000**).** Compared with other biomes, alpine ecosystems are considered relatively untouched by direct anthropogenic impacts, making them excellent indicators of the of climate change effects (Bowman 2001). The most important climatic changes predicted for the next century in the alpine ecosystem are the rise in mean annual temperature, increase of nitrogen deposition, and higher levels of snowpack (IPCC 2007), but the direction and severity these impacts on the alpine communities are unclear.

Global Change Factors (GCFs) are defined as the length growing seasons, rate of nitrogen cycling, and also the amount of snow cover (Bowman 2001) and these factors can act independently or in combination to influence plant growth and nutrient cycling rates by microbes. For example, warmer temperatures lead to a longer growing season, allowing plants to reach higher rates of photosynthesis and biomass accumulation, ultimately affecting and changing the community composition (Norby et al. 2000). A warmer environment also changes microbial decomposition rates, ultimately affecting the diversity of sensitive alpine plants communities (Na et al. 2011). Microbes that are productive in warmer soils will most likely outcompete those that are more sensitive to temperature changes; decreased diversity in microbes decreases the changes of an ecosystem to survive environmental changes (Norby el al.2000). Warming is also the result of excess anthropogenic nitrogen inputs from human activities such as nutrient runoff and fossil fuel combustion (Welker et al. 2001, Bowman 2006). Nitrogen sequestered in snowpack is also released from the snowmelt as temperatures rise in the late spring, providing a significant source of N to moist meadow communities (Bowman 1996). Nitrogen additions depress microbial activities making a plant more sensitive to harsh weather (Vitousek et al. 2002). Warmer temperatures lead to more precipitation that is deposited as snow during the winter (Vitousek et al. 2002), Snowpack creates well-insulated environments that allow continuous microbial

activity throughout the winter (Schimel et al. 2004). Ultimately, the distribution of snow is a key factor influencing the length of the growing season, soil temperature (Walker et al., 2001), decay rates (O'Lear and Seastedt, 1994), soil moisture, plant productivity (Walker et al., 2001), species diversity (Litaor et al., 2008). The complex effects of single and interacting GCFs to the alpine system can be studied from a microbial perspective in the access of nutrients, a perspective that is often ignored in global change research.

Monitoring microbial response to levels GCFs is crucial because under favorable conditions, plant roots often attract mutualistic microbes, such as fungi and bacteria, to increase the root's accessibility to nutrients and to promote overall plant growth (Norby et al. 2000). Plant community composition and microbial nutrient cycling changes as inorganic nitrogen becomes more abundant (Fisk et al. 2001). Although microbial activity decreases with increasing single GCFs (Suding et al. 2008), it is still unclear how they will react to the combinations of these GCFs (D. Gonzalez 2010, undergraduate thesis). Moreover, one limitation to previous work in the moist alpine system is that only microbial biomass was measured without measuring N-mineralization rates (Norby et al. 2000). With additional information of microbial N-mineralization rates performed by microbes, a more complete picture of microbe activity can be used to compare the total mass of microbes to their rate of decomposition activity to made inorganic nitrogen available to plants, and the effects of combinations of GFCs can be evaluated.

In this study, I examine the influence of the three GFCs on plant and microbial communities of the moist meadow alpine ecosystem in Niwot Ridge, Colorado. I test the rate of microbial N-mineralization and determine the total microbial biomass. Plant biomass of the two dominant plants, *Geum rossii* and *Deschampsia caespitosa,* were collected to assess the competitive nature of these two species to different environmental stresses. Past analyses have shown that high N plots consistently had lower microbial activities (Welker 2001), and in this study I determine if there is a correlation of plant productivity to the metabolic capabilities of soil bacterial communities by studying N-mineralization rates. I hypothesize that (1) plant biomass will increase with individual elevated levels of GFC, and (2) plant biomass will decrease with combination of GFCs. I also predict that there will be (3) a correlation between plant biomass, N-mineralization rates, and microbial biomass, and (4) an increase in the diversity of plant species composition with an increase in the rate of N-mineralization.

METHODS

Site description

I conducted my experiment in the University of Colorado's Mountain Research Station at Niwot Ridge. Niwot Ridge is in the Colorado Front Range of the Rocky Mountains (40° 30' N, 105° 35' W, elevation of ~3450 m), and has a mean annual temperature of -4.1°C and annual average precipitation of about 100 cm each year (Marr 1961). The dominant plant species in this meadow are *Geum rossii* and *Deschampsia caespitosa*, which had relative equal abundance when the experience first started in 2006. The soil pH is approximately 5.0 (Fisk and Schmidt 1995) and the organic matter content is approximately 27% (May and Webber 1982).

Research design

I worked in an established global change experiment in the moist-meadow tundra at Niwot Ridge. The global change experiment was established in 2006 with forty-eight 1-m^2 plots organized into 3 blocks, with sixteen plots in each block and each plot representing a GCF (Fig. 1). Each of the 3 blocks contains sixteen treatment plots (D. Gonzalez, 2010). Since the beginning of 2006, each block has been continually exposed to elevated summer temperatures, increased level of snowpack, and nitrogen additions in all factorial combinations with 6 replicates per treatment (D. Gonzalez, undergraduate thesis, UC Davis).

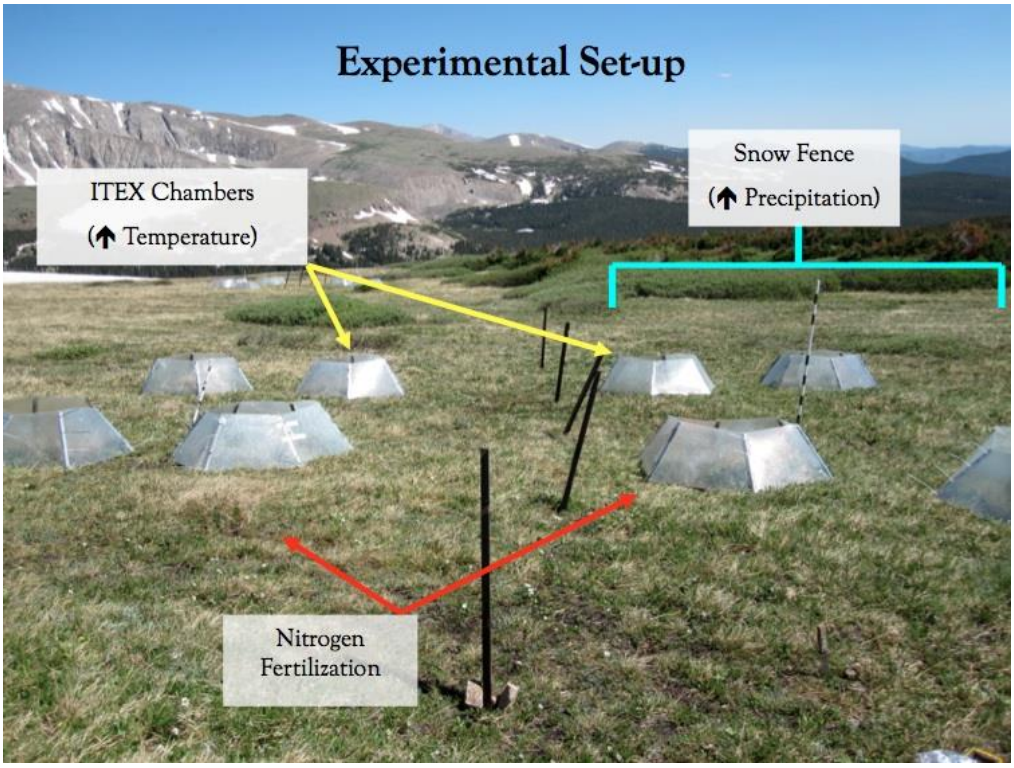

Fig 1. Global Change Treatments set up, Plastic ITEX champers act as miniature green houses, the left over of a snow fence is in the center , nitrogen is directly added with fertilizer.

Temperature

To stimulate an environment of elevated temperatures, I set up hexagonal open-top chambers (OTCs) to surround each plot (Fig 1, ITEX chambers). I used six 1m by 1m plastic panels, and anchored them with steel rods to surround 1-m^2 plots and act like miniature greenhouses to effectively alter plot temperature while limiting unwanted ecological effects such as chambers overheating, altered light, moisture and wind (Marion et al 1997).

Snow

To stimulate an environment of increased snowfall, snow fences were erected at the end of the growing season each August. These fences (approximately 1.8 meters tall and 9 meters wide) act as windbreakers and decrease wind velocity resulting in an increase in snow deposition and settling of small particles. These snow fences, made of metal strips that leave space to allow wind to pass, are raised in the middle of each block, separating 16 plots by into halves. These

fences allow for the alteration of snow into two treatments, ambient snowfall and a snow addition.

Nitrogen

To simulate an environment of increased anthropogenic nitrogen deposition, I added nitrogen directly to soil with fertilizer at the beginning of the growing season. The equivalent of 13.4g $m^{-2}yr^{-1}$ (36.7 mg $m^{-2}day^{-1}$) of nitrogen was sprinkled on top in the form of water-soluble pellets called Osmocotes (The Scotts Company, Ohio). These pellets are a source of slow release nitrogen that is steadily released over the span of one year.

Data Collection

Plant nitrogen exchange (plant available nitrogen)

To study the rate of plant nitrogen exchange, I followed similar methods to D. Gonzalez (D. Gonzalee, 2010) and placed two resin bags to record nitrogen exchange in each plot at a depth of 15 cm below soil surface. To minimize the disturbance made to each plot, I placed resin bags in the same holes every year, the lower right and upper left corner. After digging up the resin bags, I made sure to refill the hole with dirt. Resin bags, enclosed by permeable nylon mesh, recorded the plants nitrogen exchange by measuring the difference of available ions within each bag at the end of the growing season (Amer et al. 1955, Olsen et al. 1983, Sibessen1978).

To process the resin bags, I rinsed the resin bags with water after twenty-five days and placed them in 50 ml of 2N KCL solution. I placed the solutions on a shaker at 200 rpm for an hour and then filtered them with Watman No.1 filter paper (Watman Company, Singapore). I sent the samples to the Kiowa Environmental Chemistry Lab at INSTAAR (University of Colorado, Boulder) to quantify inorganic nitrogen (NH4 and NO3 mg N/L).

Plant productivity

Within each sample plot, plant productivity is quantified as the aboveground living plant biomass in a random 20 cm by 20 cm square. The plastic square quadrant was randomly placed within each 1-m^2 plot.

I randomized the location of each1-m^2 plot in which we clipped the above-ground weighed it after oven drying at 60°C for 3 days.

Species composition

I used the point-intercept method of 10 cm pacing to quantify the species richness, species diversity, and ground coverage of each plant. I noted 100 points, with a long probe to tally the plants of the highest growth, in each 1-m^2 plot.

Microbial biomass

I used chloroform to fumigate soil microbes to measure microbial biomass in terms of nitrogen. I let the fumigated chamber sit in the dark for 5 days, to prevent the chloroform from break down, which enables the microbes to continuous to lyse, releasing nitrogen into the soil environment. I put the soil samples in a desiccator chamber containing boiling chips, allowing chloroform to boil under lower pressure to killing all microbes. After I vented the chloroform from the desiccator, the 5-day period rest is to make sure all the microbes were killed. I measured the microbial biomass nitrogen as the difference of weight between fumigated and non-fumigated soil samples. Microbes are unable to respire with chloroform and will release stored Nitrogen. I will calculate the difference in weight, presenting microbial biomass killed during the fumigation period.

N-mineralization rate

To measure the microbial rate of N-mineralization, I used the buried bag technique to study the rate of microbial N-mineralization (Amer et al. 1955). I took one soil core (8 cm in diameter, 15cm deep) from each plot then split into two longwise. I brought back half of the soil core to the lab and extracted immediately for nitrogen and reburied the other half for 28 days in a

sealed with gas permeable polyethylene bag. The buried bag technique allows time for microbes to recycle Nitrogen. By comparing the initial nitrogen to of the first half the soil core that was brought back to the lab to the second half of the soil core that was buried, I calculated the rate of microbial cycling of nitrogen by averaging the difference in nitrogen levels over the number of days in the growing season.

Statistical Analysis

To study the effects of GCFs on plant biomass and plant community composition, and microbial activity such as microbial biomass and N-mineralization rates, I used a three-way analysis of variance (ANOVA) with the statistical software R. ANOVAS will be used to compare both single and interactive effects of GCFs (nitrogen, snow and temperature) and their relation to plant biomass, microbial biomass and N-mineralization rates.

RESULTS

Plant nitrogen exchange

Temperature ($P<0.05$), Snow with Temperature (Insignificant) decreased $N4^{+}$ level by 30% when compared with the ambient (Figure 1) Nitrogen treatment insignificantly accounted for 15% of increase in total summer inorganic nitrogen when compared with the control (Table 1.2).

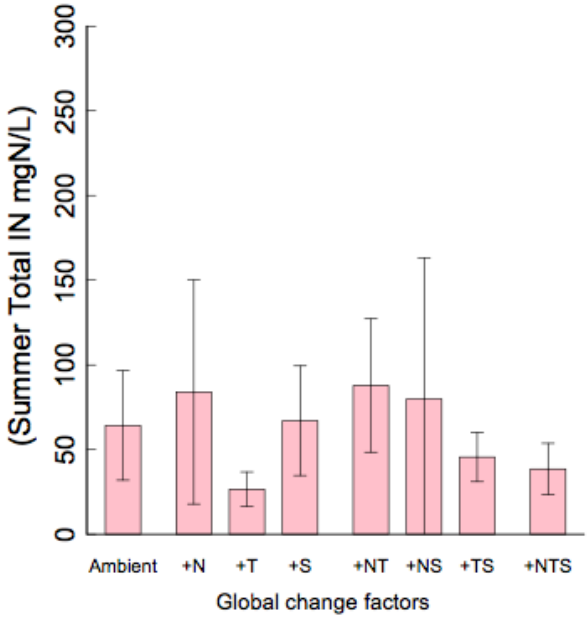

Figure 1. Inorganic nitrogen in single and multiple GCFs. (n=5, see Table 1.2 for *F*-value and *P*-value of significance, determined by ANOVA tests, see table 1.1 for treatment key).

Table 1.1 Treatment key, Imposed GCF treatment and the symbol used in figures

Imposed GCF treatment(s)	Symbol used in figures
Nitrogen	+N
Temperature	+T
Snow	+S
Nitrogen with Temperature	+NT
Nitrogen with Snow	+NS
Temperature with Snow	+TS
Nitrogen with Temperature with Snow	+NTS

Table 1.2 Significant *F*-value and *P*-value found in each community measurements using ANOVA tests (n=5).

Community Measurements	F-value	P-value

Plant nitrogen exchange	S	7.085907	< 0.05
	S:T	3.564144	0.0671*
Plant productivity	N:S	6.50189	< 0.05
Species composition	N	7.085907	< 0.05
Microbial biomass (stratified by one way vs. multiway)	All plots	No significance	No significance
Microbial biomass (stratified by one way vs. mutiway)	1way1 vs. multiway1	6.80789	< 0.05
Microbial biomass (stratified by one way vs. mutiway)	2way1 vs. multiway2	6.05509	< 0.05
Nitrogen mineralization	N	4.357408	0.8934

Df=35 for all treatment except snow

Plant productivity

Plant productivity, characterized by above ground biomass, increase significantly in nitrogen and snow treatment plots across single and multiple GCFs. Plant productivity increased the most in nitrogen and snow plots (Figure 1, Table 1).

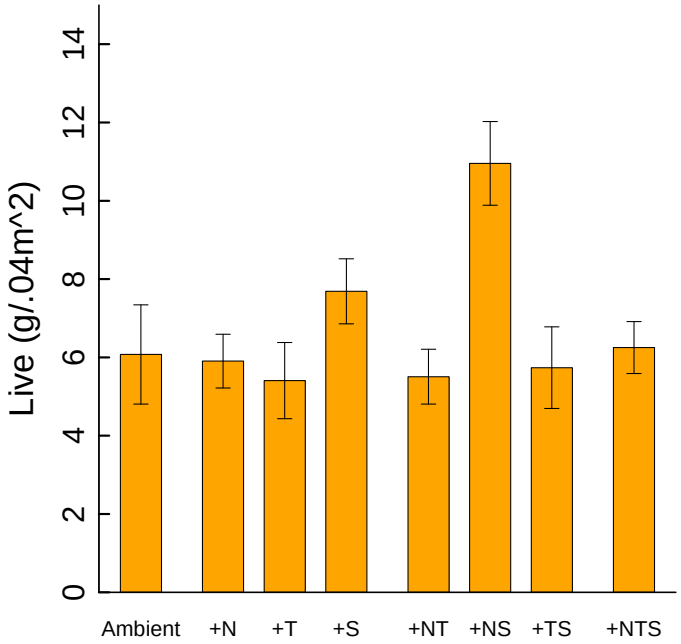

Figure 1. **Above ground live biomass production to single and combination of GCFs.** GCFs n=7, total plots n=36 including control,(see Table 1.2 for *F*-value and significance determined by ANOVA tests, see table 1.1 for treatment key*)*

Species composition

Under treatments of single and combinations of GCFs, there was significant change (P< 0.05) in the growth of the two dominant moist-meadow alpine plants (*Deschampsia cespitosa and Geum Rossii*). The number of *Geum rossii* increased by 4%,in the ambient and treatment plots with increased temperature, in contrast the*, Deschampsia cespitosa* which decreased by 300%, in ambient and treatment plots with increased temperature alone. There is an evident inversely related relationship of growth between *Geum rossi* and *Deschampsia cespitosa* (Figure 5, Table 1).

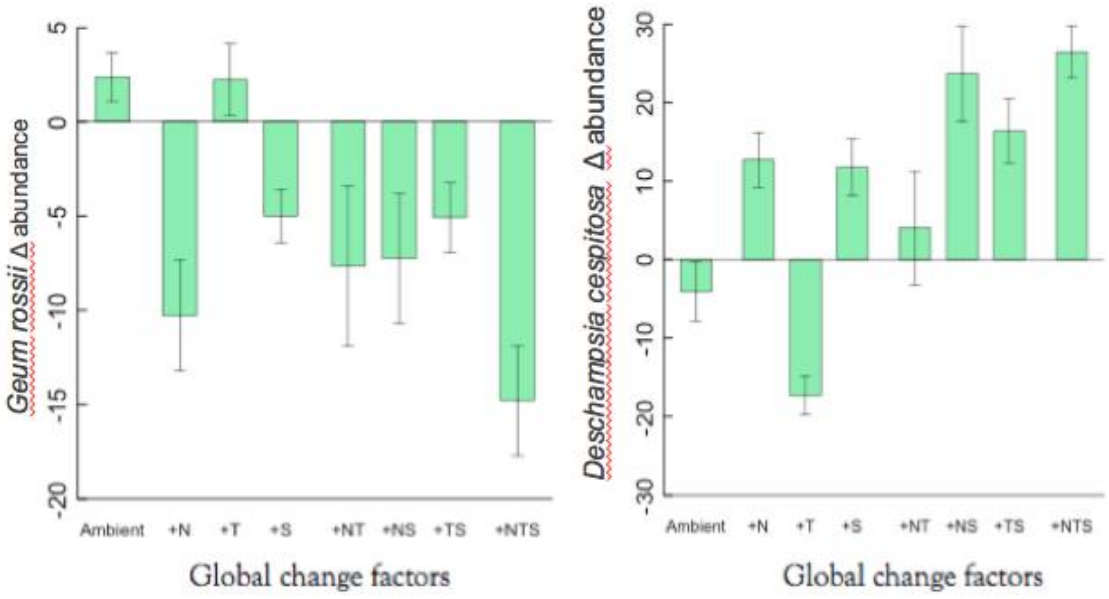

Figure 3. Community composition variance of *Geum rossii* and *Deschampsia cespitosa.* For each GCFs n=5, total plots n=36 including control,(see Table 1.2 for *F*-value and significance determined by ANOVA tests, see table 1.1 for treatment key***)***

Microbial biomass

There was no significant difference in microbial carbon measurements when treatment under single and multiple GCFs were compared across two years, 2010 and 2012. However there was a significance difference between microbial carbon measurements when treatments were grouped together into single and multiple treatments ($P<0.05$, Table 1) and compared to the ambient. Single treatments in 2010 (1way1) and in 2012 (1way2) were compared to multiple treatments in 2010 (Multiway1) and in 2012 (Multiway 2, Figure 4).

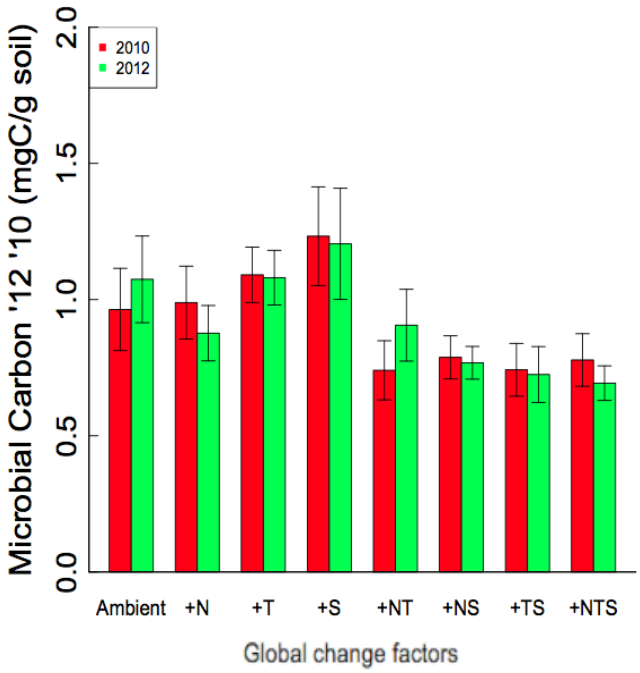

Figure 4. Microbial carbon biomass in single and multiple GCF treatment compared individually between 2010 to 2012. (GCF treatment n=7, see Table 1.2 for *F*-value and significance determined by ANOVA tests, see table 1.1 for treatment key).

Nitrogen mineralization

With the buried bag technique there was no significance difference of nitrogen mineralization rate of plants to different GCFs (Figure 6, Table 1). There was an absence of significant relationships across plots. There were no trends in N-mineralization across sites (Figure 6, Table 1).

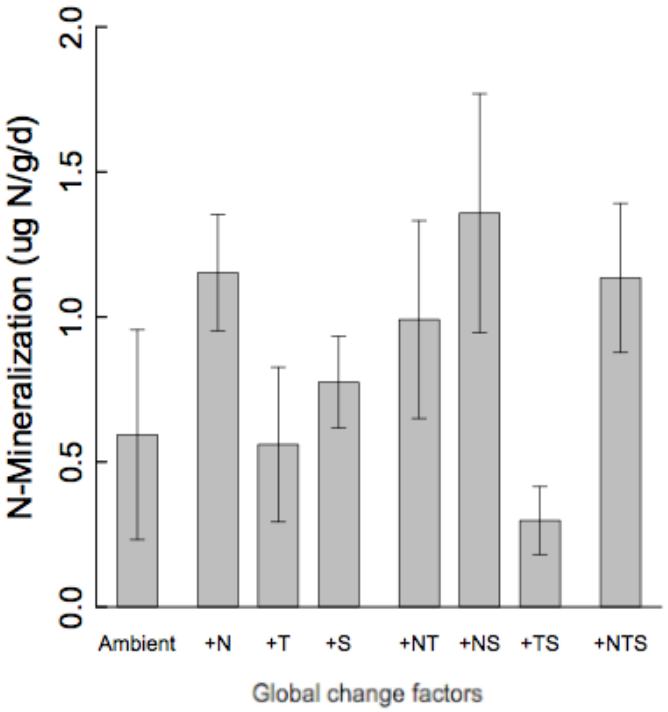

Figure 6. Plant nitrogen mineralization rates in single and multiple GCF treatments. (see Table 1.2 for *F*-value and significance determined by ANOVA tests. see table 1.1 for treatment key).

DISCUSSION

Plant nitrogen exchange, plant productivity, species composition, microbial biomass and nitrogen mineralization are measured for single and combination of GCFs (nitrogen, temperature and warming). Although significant treatments measurements were not consistently significance across different aspect of community measurement, nevertheless, these data give us important insights to how plants and microbes respond to global change: There was no single treatment that was found to be significant in both plant and microbial responses. Implication of multiple GCFs resulted in a slight exponential and interaction effect regarding plant and microbial responses due to the overall stress of the ecosystem.

Plant nitrogen exchange

Uptake of inorganic nitrogen significance in snow only is contrary to previous studies in the literature which showed significance in nitrogen (Chapin 1980, Gutschick 1981). The unexpected decrease in plants nitrogen uptake in nitrogen addition plots suggests there are other pools of nitrogen we have not measured and other aspects of the unknown ecosystem budget system may be involved in plant nitrogen uptake. Plant's nitrogen exchange rates did not correspond to the quantity of nitrogen available. Nitrogen cycling is critical to the plant's growth (Odum 1969, Vitousek and Reiners 1975), function (Vitousek 1982) and even the response to environmental disturbance (Vitousek et al. 1979). Long-term comparisons may also produce different trends in comparison to the results from this study or simply our resin bags were faulty. Nutrient exchange is a key component in forecasting the rate of plant growth.

Plant productivity

Aboveground plant biomass (live) demonstrates the health of a plant, is significantly increased by N:S (nitrogen with snow). The significant growth in nitrogen and snow suggest a favored environment of increase moisture and winter soil surface temperatures from snow, resulting in higher growth when nutrients is supplemented with moisture. The litter increase for N:S treatment also suggests a higher rates of decomposition (Webber et al. 1976). The significant results of the decreased above ground live biomass associated with a temperature increase showed suggest the drying out of soil. This demonstrates the possibility of the canceling effect of treatment, also observed by Price and Waser (2000), is demonstrated through nitrogen and temperature treatment plots. Nitrogen may increase productivity while increase temperature decreases productivity. By directing our focus to study plant productivity of the dominant species, we can gain a better idea of the effects of GCFs on a more individual level than the whole spectrum of population interactions.

Species composition

There is an inverse relationship of species abundance between *Deschampsia cespitosa* and *Geum rossii*, the same treatments that caused an increase in growth for *Geum rossii* lead to a decrease in growth for *Deschampsia cespitosa.* The stronger the niche differentiation between focal species and the rest of the community, the weaker the potential indirect effects of climate will be (Callaway et al 2002). *Deschampsia cespitosa* and *Geum rossii* have very different

competitive niches, demonstrating a change in abundance caused by a direct change to GCFs instead of indirect effects such as species interactions (Michalet et al 2006). The change in plant species abundance above ground is caused by a change in microbial interactions below ground. A good way to gauge the health and diversity of plants is by its associated microbial community.

Microbial biomass

While microbial carbon biomass data did not show any differences of treatments when compared individual GCF across the two years, multiple treatments of GCFs (multiway) were consistently lower than single treatment plots (1way). Single factor treatment showed a consistently benefit to increased the amount of microbial carbon concentrations, while multiple factors decreased the microbial carbon measurements, possibly due stress of the system. Lower amounts of microbes suggest a stressed system that hinders microbes to function and reproduce. This is consistent with previous data, which have shown that an increase in nitrogen leads to a decrease in microbial diversity **(**Ramirez et al 2010**).** Microbes are the key actor in nitrogen mineralization, which is the break down of inorganic nitrogen to organic nitrogen for its uptake by plants.

Nitrogen mineralization

There seems to be a lag in microbial response to GCFs as microbial nitrogen mineralization rates differ drastically from microbial biomass. Nitrogen immobilization can create a nitrogen deficit for plants resulting in a decrease of plant biomass (Chen et al 2008, Fisk 1994). An accumulation of mineralized nitrogen can be stored under the winter snowpack, which can be available for plants to produce spring roots (Billings et al 1978, Kummerow et al 1983).

Limitation

It is difficult to determine if associations are casual, as treatment significance was not found to be consistent across all measurements such as nitrogen plant exchange and plant productivity. There are many possibilities of confounders contributing to both hide or falsely present data relationships and significance across microbial and plant relationships. Resin bags used to measure plant nitrogen exchange were not very consistent as many resins fell out during the dirt washing stage. PVC pipes that were used to hold resin were not homogenized, which may mask the potential effects. The inconsistency of these significant treatments across different

measurements shows that GCFs treatments may not be the only causal factors to plant and microbial interactions.

The importance of snow treatments could have possibly been masked by its low degree of freedom. In my study design there are only 2 treatments of snow (ambient and additional snow). Additional moisture or snow treatments can help gauge another environmental aspect of ecosystem dynamics when there is an over flush of precipitation.

Future Directions

It is essential to continue this study over a long-term period due to the buffering abilities of soil. As the study continues, experimental methods should be kept consistent to minimize bias. Long-term green house experiments could be done with greater number of controlled environmental factors to study interactions between microbial and plant competition for nutrients. Future experiments can create multiple treatments of snow or moisture to increase the degree of freedom of snow and to unmask the effects of snow to plant and microbial communities. Soil cores used to determine microbial biomass can also be measured in the winter and compared to that measured in the summer.

Broader Implication and Conclusion

The effect of GCFs to the sensitive moist-meadow alpine plant and microbial interactions is dramatic. Studying this ecosystem gives insight to what will occur in other less sensitive plant ecosystem in relation to the rise of climate change. The nitrogen flow cycles does not only give insights to ecosystem dynamics but also can be possibly describe the effects of nutrients washout to nearby and downhill reservoirs. Future studies need to be consistent to observe the potential change of GCFs to the ecosystem.

Currently, there are wide variations in the results of plant ecological climate change research in the alpine system, making long-term data even more essential to establish a consistent finding. For example Fisk (1994) found an increase in microbial biomass with increase nitrogen throughout different seasons, while Ramirez et al (2010) found nitrogen addition decreased microbial biomass by 35% over a yearlong incubation period. The slight trend of nitrogen in the 2010 measurements of my study agreed with the study by Fisk and Schmidt

(1994) while those of the 2012 measurements agreed with Ramirez et al (2010). Although my data of a single growing season of 2012 may not present a lot of insight into plant microbial interactions by itself, they are still essential pieces to the continuation measurements to the buffering and threshold of these systems.

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REFERENCES

Billings, W.D., Peterson, K.M., Shaver, G.R., 1978. Growth, turnover, and respiration rates of roots and tillers in tundra graminoids. In: Tieszen, L.T., (Ed.), Vegetation and Production Ecology of an Alaskan Arctic Tundra, Springer, New York, pp. 415–434.

Bowman, W.D., J.C. Schardt, and S.K. Schmidt. 1996. Symbiotic N2-fixation in alpine tundra: ecosystem input and variation in fixation rates among communities. Oecologia 108: 345-350.

Bowman, W.D. 2001. Introduction: Historical perspective and significance of alpine ecosystem studies. Pages 3–12 in W. D. Bowman and T. R. Seastedt, editors. Structure and function of an alpine ecosystem: Niwot Ridge, Colorado. Oxford University Press, New York, New York, USA

Bowman, W.D., J.R. Gartner, K. Holland, and M. Wiedermann. 2006. Nitrogen critical loads for alpine vegetation and terrestrial ecosystem response: Are we there yet? Ecological Applications 16: 1183–1193.

Callaway R. M., Brooker R. W., Choler P. et al. (2002) Positive interactions among alpine plants increases with stress. Nature **417**: 844–8.

Chapin, F.S., L. Moilanen, and K. Kielland. 1993. Nutritional controls over nitrogen and phosphorus resorption from Alaska birch leaves. Ecology 72:709–715.

Chapin, F. S., III. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics **11**:233–260.

Chen, W., Y. Wu, N. Wu, and P. Luo. 2008. Effects of snow-cover duration on plants species diversity of alpine meadows on eastern Qinghai-Tibetan Plateau. J.Mt.Sci **5**:327-339.

Fisk, M. C., S. K. Schmidt, 1994. Nitrogen mineralization and microbial biomass nitrogen dynamics in three alpine tundra communities. Soil Science Society of America **59**:1036-1043.

Fisk, M.C. and S.K. Schmidt 1995. Nitrogen mineralization and microbial biomass N dynamics in three alpine tundra communities.*Soil Sci. Soc. Am. J.* 59: 1036-1043.

Galloway, J.N., W.H. Schlesinger, H. Levy II, A. Michales, and J.L. Schnoor. 1995. Nitrogen-fixation: Anthropogenic enhancement-environmental response. Global Biogeochemical Cycles 9:235–252.

Gonzalez, David.2010. Studying global change factors in Colorado's moist meadow. Undergraduate thesis.

Gutschick, V. P. 1981. Evolved strategies in nitrogen acquisition by plants. American Naturalist **118**:607–637.

IPCC 2007. Climate Change 2007: Synthesis Report. 104 Pages. Contribution of Working Groups I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.)], IPCC, Geneva, Switzerland.

Li Na, Wang Genxu, Yang Yan, Gao Yongheng, and Liu Guangsheng. 2011. Plant production, and carbon and nitrogen source pools, are strongly intensified by experimental warming in alpine ecosystems in the Qinghai-Tibet Plateau. Soil Biology & Biochemistry **43**:942-953.

Litaor M. I., M. Williams, and T. R. Seastedt. 2008. Topographic controls on snow distribution, soil moisture, and species diversity of herbaceous alpine vegetation, Niwot Ridge, Colorado. Journal of Geophysical Research-Biogeosciences 113:G02008.

Norby, R.J., T.M. Long, J.S. Hartz-Rubin, and E.G. O'Neill. 2000. Nitrogen resorption in senescing tree leaves in a warmer, CO2-enriched atmosphere. Plant and Soil **224**: 15–29.

Michalet R., Brooker R. W., Cavieres L. A. et al. 2006. Do biotic interactions shape both sides of the humped back model of species richness in plant communities? Ecol. Lett. **9**: 767– 773.

Molau U. 1997. Responses to natural climatic variation and experimental warming in two tundra plant species with contrasting life forms: *Cassiopetetragona* and *Ranunculus nivalis.* Global Change Biology **3**:97-107

Odum, E. P. 1969. The strategy of ecosystem development. Science **164**:262–270

Olear H., T.Seastedt. 1994. Landscape Patterns of Litter Decomposition in Alpine Tundra. Oecologia **99**:95-101.

Price, M.S., and N. M. Waser. 2000. Responses of subalpine meadow vegetation to four years of experimental warming. Ecological Applications **10(3)**: 811-823.

Ramirez KS., Craine JM., Fierer. N 2010. Nitrogen fertilization inhibits soil microbial respiration regardless of the form of nitrogen applied. Soil Biology and Biochemistry **42**: 2336–2338.

Suding, K.N., I.W. Ashton, H. Bechtold, W.D. Bowman, M.L. Mobley, and R. Winkleman. 2008. Plant and microbe contribution to community resilience in a directionally changing environment. Ecological Monographs 78: 313–329.

Kummerow, J., Ellis, B.A., Kummerow, S., Chapin, F.S. III, 1983. Spring growth of shoots and roots in shrubs of an Alaskan muskeg. American Journal of Botany **70**: 1509–1515.

Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. BioScience **25**:376–381.

Vitousek, P. M., J. R. Gosz, C. C. Grier, J. M. Melillo, W. A. Reiners, and R. L. Todd. 1979. Nitrate losses from disturbed ecosystems. Science **204**:469–474.

Vitousek, P. M. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist **119**:553–572.

Vitousek, P.M., S. Hattenschwiler, L. Olander, and S. Allison. 2002. Nitrogen and nature. Ambio 31:97-101.

Welker, J.M., W.D. Bowman, and T.R. Seadstedt. 2001. Environmental Change and Future Directions in Alpine Research. Pages 304-322 in W. D. Bowman and T. R. Seastedt, editors. Structure and function of an alpine ecosystem: Niwot Ridge, Colorado. Oxford University Press, New York, New York, USA.