

Effects of experimental warming on herbivory and fungal pathogen load on subalpine grasses

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Abstract

Rising global temperatures are predicted to alter community dynamics by shifting species ranges and altering biotic interactions. Herbivory is expected to increase with prolonged growing seasons and heightened animal metabolic rates; pathogen damage may increase as well. Thus, we investigated whether damage by herbivores and pathogens on subalpine grass species would increase with warming. We compared percentage aboveground herbivory and foliar pathogen loads on three grass species (*Festuca thurberi*, *Poa pratensis*, and *Achnatherum lettermanii*) using a long-term experimental warming treatment in which plots subjected to experimental warming by infrared heaters alternated with ambient control plots. Within our warming plots there was an increase in the magnitude of herbivory for two of the three subalpine grass species observed. This increase in herbivory suggests that with global warming the damage from insects on grasses will can increase, but may be species specific.

Introduction

Our planet's climate is changing. The IPCC estimates that global mean temperature will continue to rise about 2°C over the 21st century (IPCC 2013). As global warming continues, the increase in temperature can shift species' phenology and demography, and has led to altered species abundance and biodiversity (Lovejoy et al. 2005, Parmesan 2006). However, it is important to understand both direct and indirect effects of climate change as these effects can interact synergistically, impacting biodiversity and ecosystem processes (Lovejoy and Hannah 2005). While it is usually easier to observe the direct effects of climate change by monitoring temperature, rainfall, atmospheric CO₂, etc., observing and understanding the indirect effects are more complicated but equally important for future ecological predictions. Notably, changes in species phenology and demography can lead to mismatched species interactions, an indirect effect of climate change that ultimately weakens the fitness of both species and reduces their populations (Araújo and Luoto 2007, Schweiger et al. 2008, Cunze et al. 2013).

Host-parasite interactions have been shown to be affected by global warming and these imbalances have major consequences for their respective ecosystems (Traill 2010). More specifically, plant-herbivore and plant-pathogen interactions are predicted to increase in intensity as global temperatures rise due to a lengthened growing season, higher insect abundance, as well as increases in the metabolic rates of generalist herbivores and pathogens (Bale et al. 2002, Roy et al. 2004, Stefansson et al. 2013, Rudgers et al. 2014). Some studies suggest that with an increase in abiotic stress, damage levels will increase due to plants' inability to defend against attack (Hanson et al. 2000), while other studies show a decrease in attack with stress (Larsson 1989). This inconsistency may be due to species specific interactions and how well they are able to tolerate abiotic stressors (Larsson 1989). This lack of knowledge limits our ability to predict

how variation in abiotic stress and herbivory regimes will change in future climates (Maron et al. 2014).

We used a long-term (since 1991) warming experiment at the Rocky Mountain Biological Laboratories in Gothic, CO to assess plant pathogen and plant herbivore damage on three species of subalpine grasses. Of the ten plots, five have been manipulated with infrared heaters for 25 years. The benefit of this long-term experiment is that the grasses as well as the herbivores and fungi that affect them have had plenty of time to adjust to the temperature and temperature induced physiological changes in the hosts (Roy et al. 2004). Specifically, we expect to see an increase in herbivory and fungal pathogen load within our warming plots as compared with our non-warming control plots.

Methods

The grass family consists of 10,000 species, many of which are ecologically and economically important (Barker et al. 2001). Furthermore, grasses and grasslands cover more than one-fifth of land area on Earth (Shantz 1954) yet, data on the effects of warming on plant-herbivore and plant-pathogen interactions, especially for alpine and sub-alpine species, are limited (Ayres 1993, Malmstrom and Raffa 2000).

Study site

We collected data from a subalpine meadow at the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado, USA (38°57' N, 106°59' W; elevation 2920 m). Five plots (10m x 3m each) in the meadow have been warming by infrared heaters since the 6th of January 1991, increasing soil temperature to ~2°C; five controlled—not subject to heaters—plots alternate with warmed plots (Rudgers et al., 2014).

Experimental design

Every two weeks, starting with the first observation on June 8th 2016 and ending with our last observation on September 30th 2016, we visually estimated percent herbivory and fungal pathogen loads, as well as herbivory and fungal type by describing generalized visible characteristics. These observations were made for three tillers marked with colored cable ties from six individual plants of each species in each plot. Estimates were taken on the same tillers by the same observer each time. We attempted to select each individual within the treatment's range (1m from the center of the infrared heaters on each side). Some of these individuals fell outside of this range and will be accounted for in future studies.

Data analysis

Percentage herbivore and pathogen damage were our dependent variables. Warming treatment, plant species identity and their interaction were fixed independent variables and time (in days after first observation) was a continuous independent variable. Data were analyzed using general linear mixed effects models to account for the random effect of plot (nested in warming treatment), as we had multiple observations of each individual and species in each plot. Our data followed a Poisson distribution which we accounted for within our models. We measured the

relative quality of all 80 statistical models using Akaike information criterion statistic (AICc) and chose the best fit for our particular data set and question.

Results

While we saw the percentage of herbivory damage increase over time ($P = < 0.0001$) the effect of warming on each species was not the same. Instead, we saw percent herbivory increase for two of the three species (*P. pratensis* & *F. thurberi*) within our warming plots (Fig. 1). For both *P. pratensis* and *F. thurberi* warming had a significant effect on the herbivory damage observed on individual tillers ($P = 0.0002$ & $P = 0.0168$ respectively). For *A. lettermanii* there was a significant interaction between warming and standardized days ($P = 0.0013$) but this didn't result in an overall increase in herbivory for the warming plots.

Although we did see an increase in fungal pathogen load over time ($P = < 2.2e-16$), damage between our warming plots and control plots were opposite of our prediction, with little to no difference between fungal pathogen load for *A. lettermanii* and *F. thurberi* and a reduction within our warming plots for *P. pratensis* (Fig. 2).

Discussion

Our results lend partial support for increased herbivory with warming while fungal pathogen load with warming was inconsistent for two species and opposite to our predictions for one species.

We expected to see an increase in herbivory within our warming plots as compared with our non-warming control plots across all species. Although we did see a magnitude increase in herbivory, it wasn't consistent across all species (Fig. 1). Instead, what we observed was an increase in damage for two of our three species, one being the bunch grass *Festuca thurberi* and the other being the rhizomatous *Poa pratensis*. *Achnatherum lettermanii*, another bunch grass, showed decreased herbivory within the warming plots for the first two observations which then increased to about the same amount as the control plots with the following two observations (Fig. 1). The increasing herbivory damage for *A. lettermanii* within the warming plot may continue, eventually showing more damage for warming than the ambient control. More observations are needed to see if this pattern is continues or not.

For fungal pathogen loads we also expected to see an increase in damage within our warming plots as compared with our non-warming control plots across all species. This was far from the case. Two species showed almost no difference in magnitude of pathogen loads between warming and control while *P. pratensis* showed a reduced amount of damage from pathogens within the warming plot (Fig. 2). Lessor fungal pathogen load within our warming plots for *P. pratensis* may be due to the pathogens being pushed outside of their habitable range. Since atmospheric moisture is generally the single most important environmental factor influencing the incidence and severity of fungal diseases on plants (Talley et al 2002), it is possible this is why we saw a reduction in pathogen load within our warming plots for *P. pratensis*. In order to

further investigate this relationship for our plots, atmospheric moisture data is needed.

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Tables and Figures

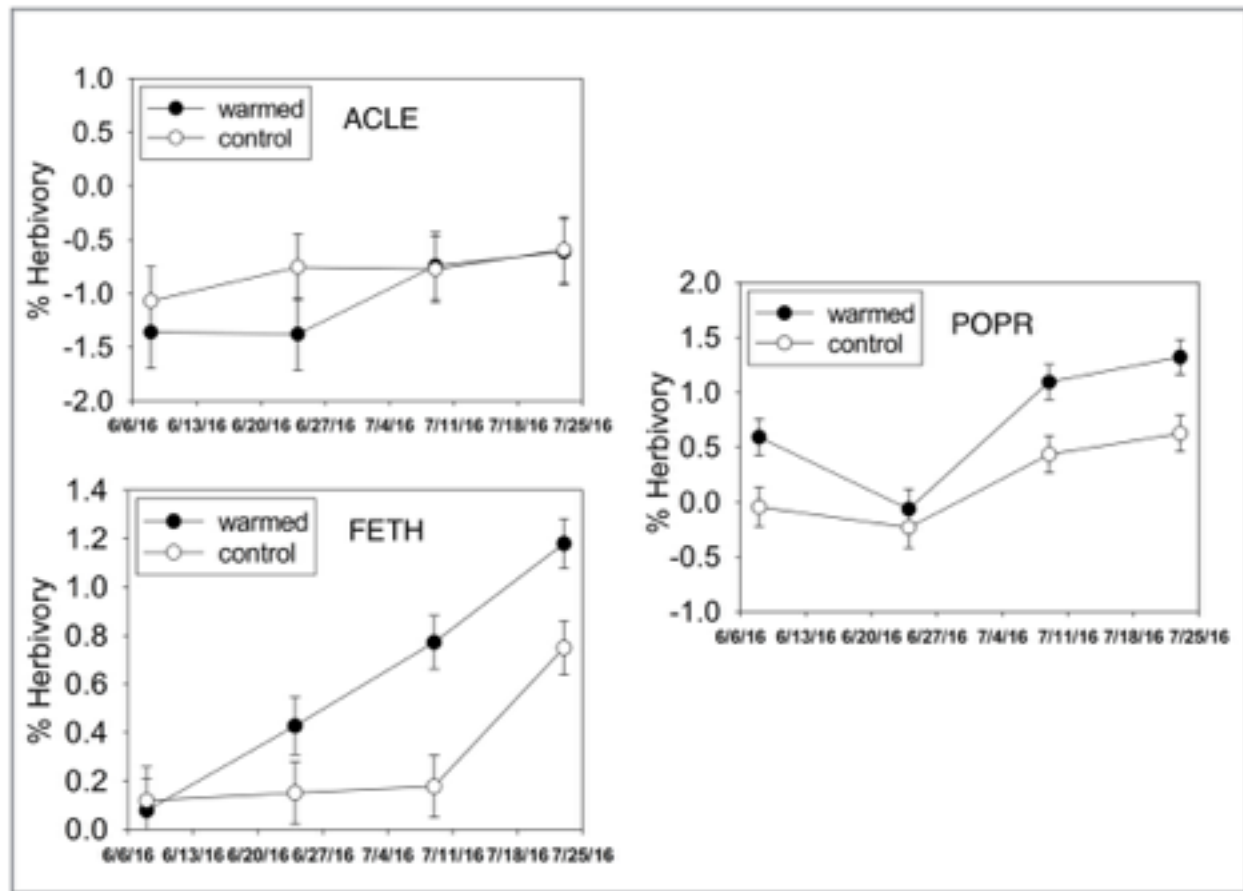


Figure 1. Percent of herbivory over 44-day period on (ACLE) *A. lettermanii* (treatment x days: $p = 0.1444$), (POPR) *P. pratensis* (treatment x days: $p < 0.0001$), and (FETH) *F. thurberi* (treatment x days: $p = 0.0013$) in warmed and control plots. Data are least square means $\pm$ SE ($n = 2,164$).

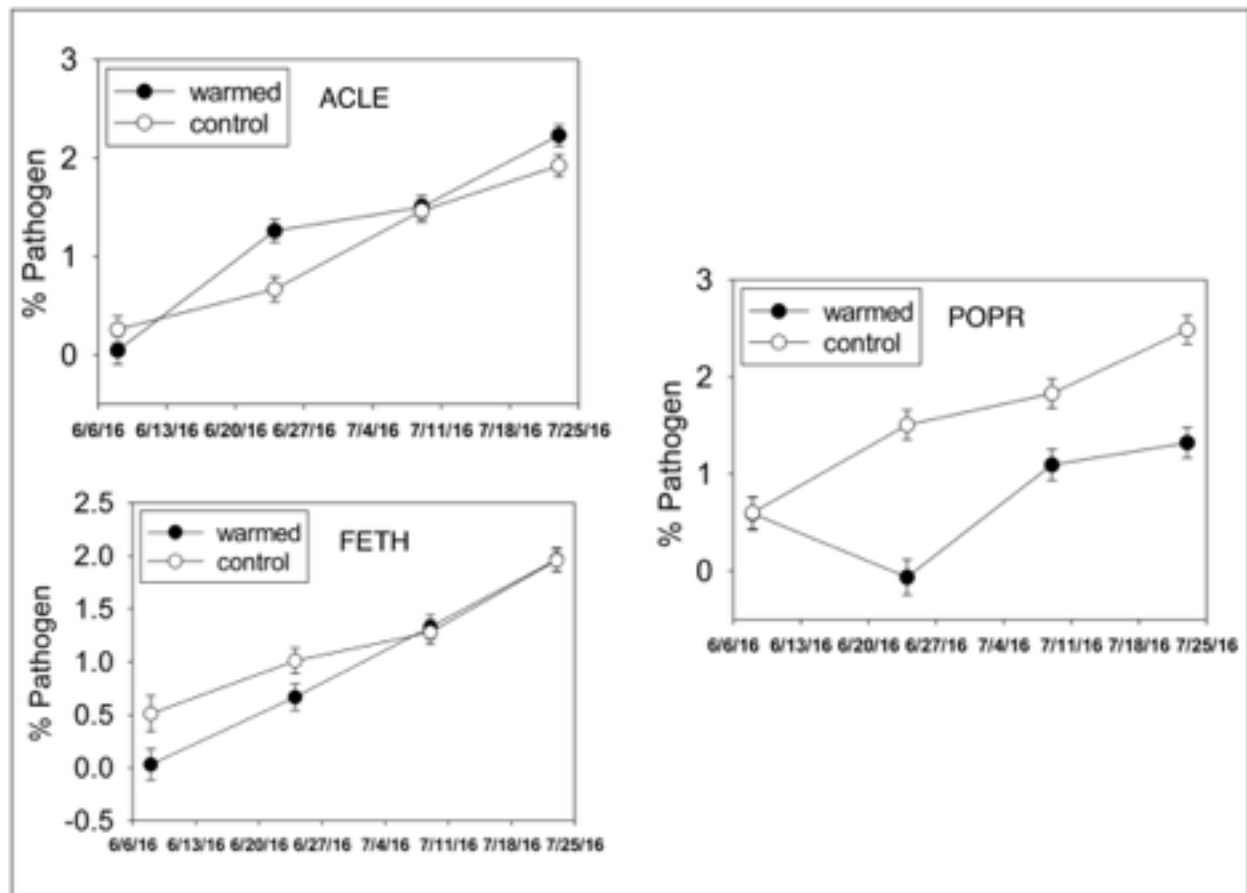


Figure 2. Percent of pathogen load over 44-day period on (ACLE) *A. lettermanii* (treatment x days: $p = 0.0768$), (POPR) *P. pratensis* (treatment x days: $p < 0.0001$), and (FETH) *F. thurberi* (treatment x days: $p = 0.0002$) in warmed and control plots. Data are least square means $\pm$ SE ($n = 2,161$)



Figure 3. GIS Map of warming meadow