

Effects of experimental warming on herbivory and pathogen loads on subalpine grass species *Festuca thurberi*, *Poa pratensis*, and *Achnatherum lettermanii*

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Independent Research and Course
Summer 2015

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 metabolic rates; pathogen damage may increase as well. We predict that damage by herbivores and pathogens on subalpine grass species *Festuca thurberi*, *Poa pratensis*, and *Achnatherum lettermanii* will increase with warming. Comparisons of estimated percent herbivory on these species in a meadow containing plots subject to experimental warming by infrared heaters and alternating ambient control plots revealed some evidence of increasing herbivory with warming and, thus, increased vulnerability of plants to the indirect effect of global warming of rising herbivore activity.

Introduction

The approximate 0.6°C increase in global mean surface temperatures in the last century is the highest 100-year increase in the past 1000 years (Houghton et al. 2001). As the climate warms, species' ranges may shift to maintain biotic and abiotic conditions that satisfy their niches and, thus, altering community dynamics (Lenoir et al. 2008).

Plant-herbivore interactions are especially of interest for both their importance in agriculture as well as and their involvement in managing nutrient levels and carbon fluxes in ecosystems (Adler et al. 2007). For plants, attack by natural enemies, such as herbivores, is predicted to increase in intensity as global temperatures increase because the season for growth and reproduction is extended and the metabolic rates of generalist herbivores and pathogens increase with warmer temperatures (Roy et al. 2004, Berggren et al. 2009, Bale et al. 2002, Brown 1995, Pollard & Yates 1993).

Data on the effects of warming on plant-herbivore and plant-pathogen interactions, especially regarding alpine species, are limited (Ayres 1993, Malmstrom and Raffa 2000). Moreover, studies examining potential effects of grass species would be advantageous as grasses dominate alpine and subalpine meadows, serving critical ecological roles (Barker et al. 2001). Post and Pedersen (2008) suggest that the role of herbivores play an essential role in maintaining community stability; plant communities that responded to experimental warming with increased biomass response, however, grazing by mammal herbivores reduced arctic plant community compositions to the amount of ambient plots after five years. Similarly, warming has been linked to shifts in marine food web structure and total standing biomass, in which increased herbivore metabolic rates increase consumption of plants (O'Connor et al. 2009).

Because high elevation ecosystems experience temperature restrictions on biological process, these systems are particularly vulnerable to climate change. Studies in a warming experiment established in 1991 in a subalpine meadow in the Rocky Mountains of Colorado reveal variation in grass abundance in time and across treatments (Rudgers et al. 2014) as well as the absence of a definite correlation between aphid density and treatment with regards to aphid-sagebrush interactions (Adler et al. 2007).

If warming shifts niches and introduces species to altered biotic interactions—including increased rates of herbivory and pathogen loads—then alpine grass species could be threatened with extinction. By estimating percent herbivory and pathogen loads on three dominate subalpine grass species, *Festuca thurberi*, *Poa pratensis*, and *Achnatherum lettermanii*, thriving in the aforementioned warming meadow, we observed some variation in predation between treatments.

Methods

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 alternating plots (10x3 m each) in the meadow have been warming by infrared heaters since 6 January 1991, increasing soil temperature to ~2°C; five controlled—not subject to heaters—plots alternate with warmed plots (Figure 1) (Rudgers et al., 2014).

Experimental design

I visually estimated percent herbivory and pathogen loads every two weeks for three marked leaves each from six plants of each species in each plot. Estimates were taken on the same leaves each time. Plants and leaves were selected randomly.

Furthermore, I visually estimated and categorized levels of herbivory and pathogen loads on approximately twenty leaves on each marked plant and measured the volume (cm³) of each plant. For *F. thurberi* and *A. lettermanii*, I measured the length, width, and height of the plant; for *P. pratensis*, I estimated percent cover and measured height.

We modeled percent herbivore or percent pathogen damage in the warming and controlled plots as the dependent variables and time (days) as the independent variable. In addition, we calculated the potential for plant size to be a correlate to herbivory. Data were transformed to fit a normal distribution and were analyzed by a general linear mixed model in the program SAS.

Results

Percent herbivory for all three species changed significantly over time ($p = <0.0002$). Percent herbivory on *F. thurberi* in the warmed and control plots increased from day 0 to day 28 and there was a significant difference in the rates of herbivory on *F. thurberi* in warmed and control plots over time (Figure 2A). Percent herbivory on *P. pratensis* fluctuated in both warmed and control plots and while there is a significant difference in rates in the warmed and control plots, there is no significance of the combined effect of treatment and time (Figure 2B).

There is no significant difference in rates of herbivory on *A. lettermanii* between treatments (Figure 2C).

Percent pathogen damage for all three species changed significantly over time ($p < 0.0001$); however, the combined effects of treatment and time were not significant for any species (Figure 3).

The percent damage on leaves of *F. thurberi* in the warming plots was significantly greater than those in the ambient plots (Figure 4A). The percent damage on leaves of *P. pratensis* in the warming plots was greater than those in ambient plots; however, the data were not significant (Figure 4B). The percent damage on leaves of *A. lettermanii* in the control plots was greater than those in warming plots; the data were not significant (Figure 4C).

Statistical analysis of size as a correlate to herbivory revealed no significant size dependent herbivory on *F. thurberi* ($p = 0.4297$) and *A. lettermani* ($p = 0.7812$). As for *P. pratensis*, the interaction between the effects of size and treatment were significant (Figure 5).

Discussion

The results present some evidence for increased herbivory with warming; data on pathogen damage were inconsistent with original predictions.

As predicted, the estimates of herbivory on *F. thurberi* in warmed and control plots illustrated a significant difference between rates of herbivory that were constant over time; in other words, the amounts of herbivory on *F. thurberi* over time were significantly higher on leaves subject to the warming treatment than those in ambient conditions (Figure 2A), as is consistent with previous studies (Roy et al. 2004). While the difference in rates of herbivory on *P. pratensis* between warmed and control plots was significant, we cannot conclude that this difference is attributable to the contrasting treatments, as predicted (Figure 2B). There is no significant difference between rates of herbivory on *A. lettermanii* between treatments (Figure 2C).

Pathogen damage on all three species of grass was not significantly different between treatments (Figure 3). Furthermore, observed pathogen loads constitute decreasing rate of pathogen damage over time. Perhaps infected leaves continued to grow, decreasing percent damage or we may have mistaken pathogen damage as leaves still growing.

Estimates of amounts of combined herbivore and pathogen damage were consistent with predictions that leaves would be more damaged in warmed plots than in control plots. The percent damage on leaves in warmed plots was significantly greater than that of controlled plots on both *F. thurberi* and *P. pratensis*, though the difference was only significant for *F. thurberi* (Figure 4A, 4B). Similarly to previous studies in which plants in warmed plots generally had more damage than those in ambient plots while some pathogens and herbivores were more active in non-warming plots, percent damage was greater in controlled than in warmed plots for *A. lettermani*—although the data was not significant (Roy et al. 2004).

Contrary to the evidenced Plant Vigor Hypothesis, which suggests increased predation on larger, thriving plants (Inbar et al. 2001, Cornelissen et al. 2008), our data illustrated a negative correlation between *P. pratensis* plant volume and percent damage (Figure 5). Our results do not suggest size dependent herbivory on *F. thurberi* and *A. lettermanii*.

Our study presents some evidence for increased herbivory on some subalpine grass species, thus, suggesting that global warming may make some species vulnerable to climate change indirectly through increased herbivore activity.

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Appendix



Figure 1 GIS Map of warming meadow field site.

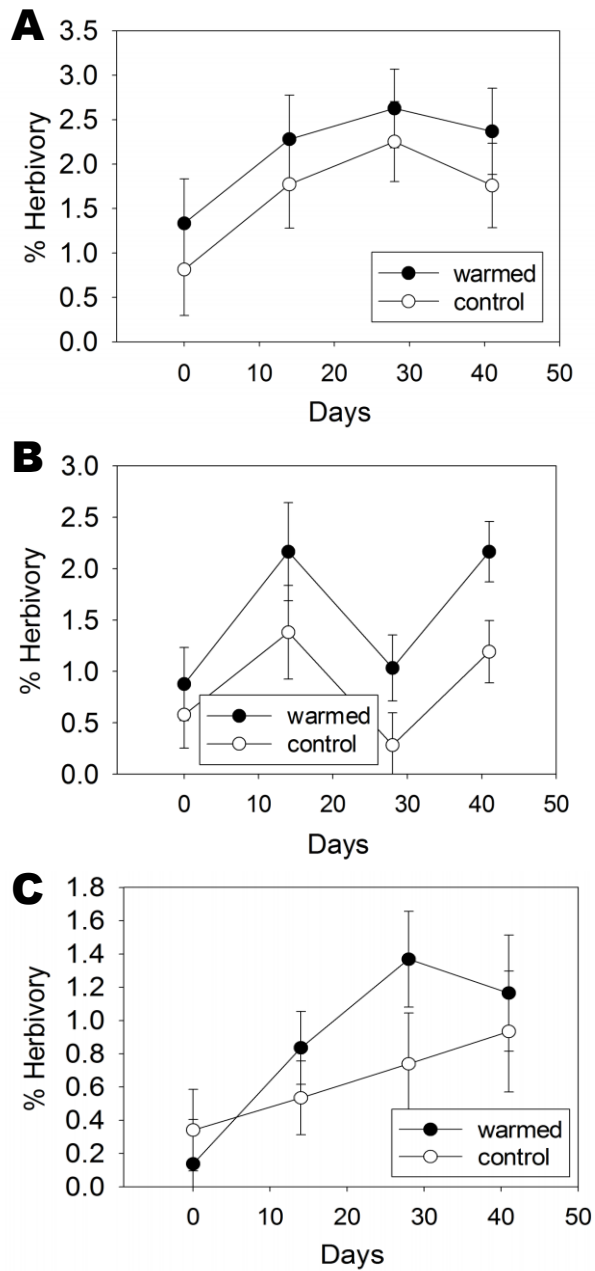


Figure 2 Rates of herbivory over 41-day period on (A) *F. thurberi* (treatment x days: $p=0.0061$), (B) *P. pratensis* (treatment: $p=0.0704$), and (C) *A. lettermanii* (treatment x days: $p=0.3459$) in warmed and control plots. Data are means $\pm$ SE ($n=720$).

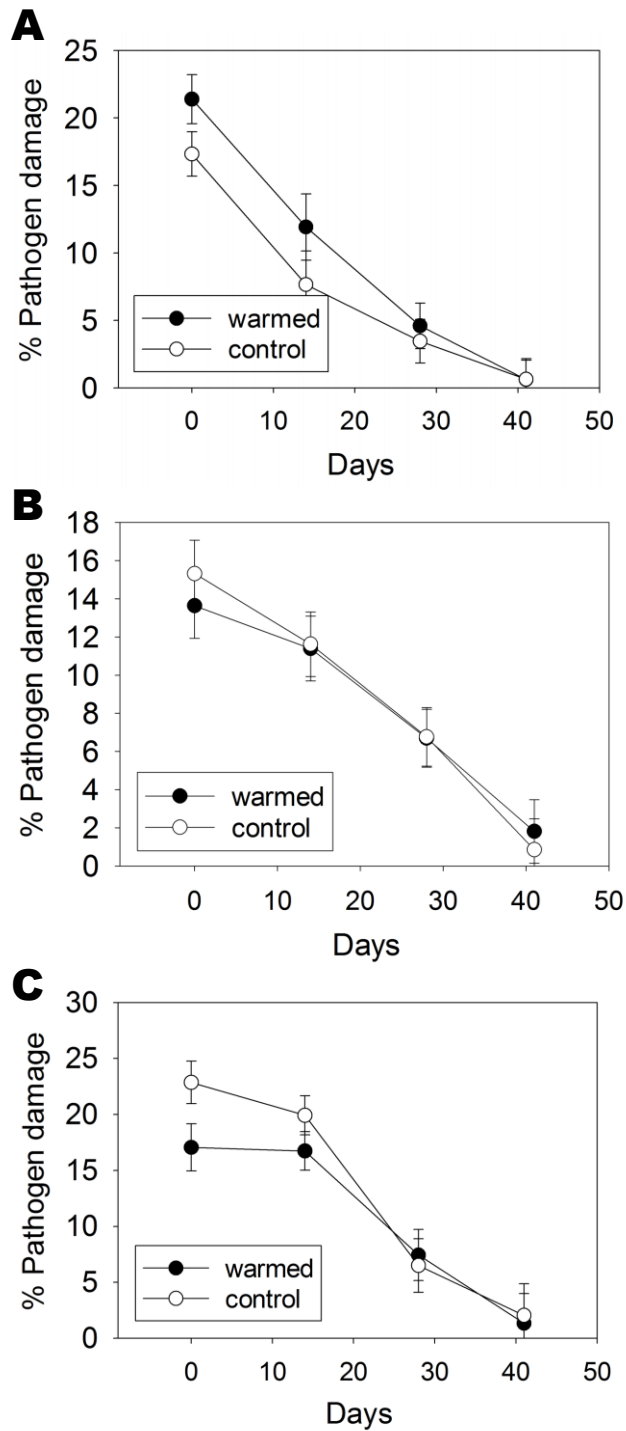


Figure 3 Rates of pathogen damage over 41-day period on (A) *F. thurberi* (treatment x days: $p=6564$), (B) *P. pratensis* (treatment x days: $p=0.289$), and (C) *A. lettermanii* (treatment x days: $p=0.9913$) in warmed and control plots. Data are means $\pm$ SE ($n=720$).

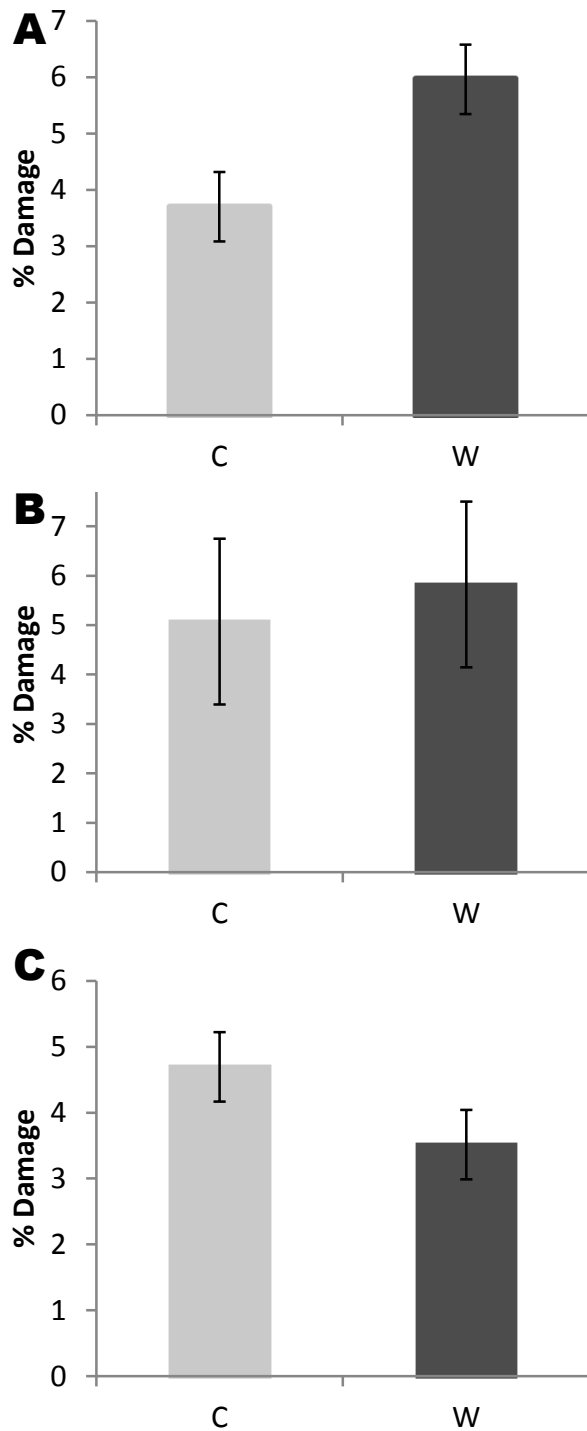


Figure 4 Proportion of damage on leaves of (A) *F. thurberi* ($p=0.0426$), (B) *P. pratensis* ($p=0.6183$), and (C) *A. lettermanii* ($p=0.1039$) in control (C) and warmed plots (W). Data are means $\pm$ SE ($n \sim 1,200$).

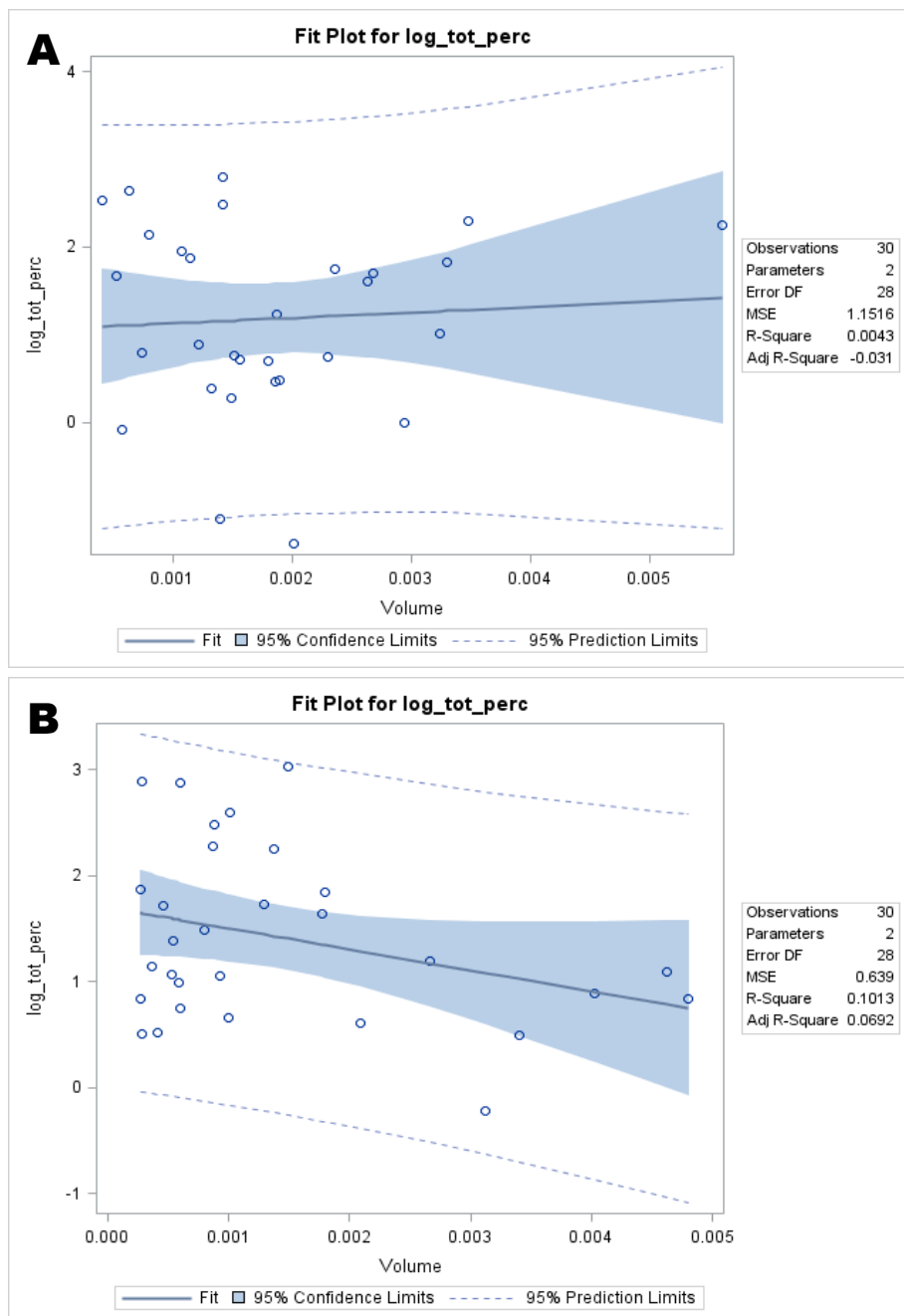


Figure 5 Percent herbivory by *P.pratensis* plant volume varies in (A) control and (B) warming plots ($p=0.005$) ($n=60$).