

Real and experimental ecosystem warming: interacting effects on snowmelt, plant community composition and carbon storage in a Rocky Mountain subalpine meadow

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Abstract

A 22 year warming experiment at Rocky Mountain Biological Laboratory has elucidated short term (15 year) responses in plant community and soil organic carbon to artificial warming. This summer's research evaluates long-term (>15 year) changes and, because of recent climate change effects, the relevance of experimental data for predicting real world effects. Ten long-term plots, half heated by 22 W/m² of warming, were tested for changes in soil carbon using soil cores and in plant community composition using aerial coverage measurements converted into biomass. Long term changes in the heated plots showed that soil carbon, which was initially reduced, could recover to previous levels. Carbon is strongly controlled by shrub and forb biomass, which are in turn controlled by melt date. Heated plots were generally predictive of changes due to climate in the controls, with the exception of changes in soil carbon and shrub cover. Responses to real-world warming in control plots have shown a more gradual change and has not yet shown a state change towards SOC recovery. This suggests that this and similar studies are useful for projecting the impacts of global warming, but also shows that short term and long term projections may be very different.

Introduction

Global climate change is a worldwide threat that will impact our biosphere in the next hundred years (Solomon, et al., 2007). Even as early impacts of climate change become visible, however, much long-term information about this phenomenon remains unknown, complicating scientific projections. One critical factor is the potential for warming-induced release of carbon into the atmosphere, a positive feedback effect which could drastically alter predicted climate outcomes (Berthelot, Friedlingstein, Ciais, DuFresne, & Monfray, 2005).

Soil is an important sink for organic carbon, containing as much as 2000 Pg C worldwide (Dixon & Turner, 1991). Carbon is sequestered in the soil through litter deposition by surface plant communities, and lost through heterotrophic respiration and leaching (Figure 1) (Strain, 1985). Climate change can impact soil organic carbon (SOC) accumulation in these soils by increasing or decreasing carbon input and output. Litter deposition can be altered by climate change through changed net primary productivity, which in turn can be influenced by climate both directly and via shifting community structure (Strain, 1985). Decomposition can be affected by plant chemistry, such as different lignin, carbon, and nitrogen ratios and by increased heterotrophy respiration in response to warming conditions (Rustad, et al., 2001) (Kirschbaum, 2000) (Harte, Saleska, & Shih, 2006). Where climate change induces increased precipitation, rainfall can also cause SOC leaching (Kirschbaum, 2000). A meta-analysis of 32 ecosystems across four different biomes suggested that warming would increase soil respiration and above-ground productivity, but that these effects might be transient: these experiments were all between 4 and 9 years long (Rustad, et al., 2001). In order to tease apart potential impacts of warming on carbon flux, longer term warming experiments are required.

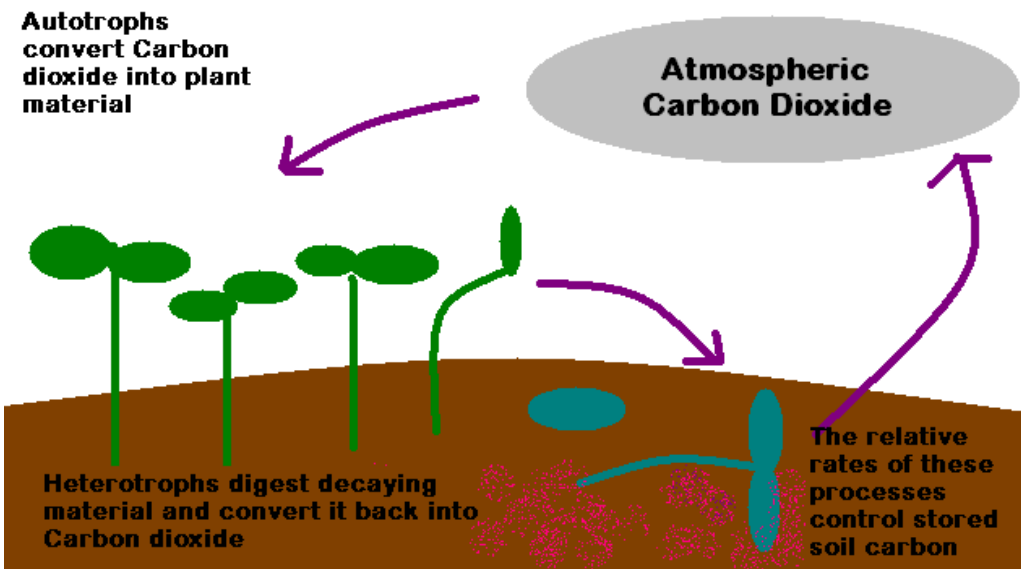


Figure 1 The terrestrial carbon cycle

A long-term warming experiment by John Harte at Rocky Mountain Biological Laboratories has been artificially heating five experimental plots and observing snow melt date, SOC, and plant community structure for the past twenty-one years. A 2002 study used the first ten years of experimental warming to demonstrate decreasing forb cover and increasing shrub cover, as well as an 8% decrease in soil carbon as compared to control plots (Saleska, et al., 2002). Leaching was not the cause, due to the low and decreased soil moisture in the plots. Increased heterotroph respiration due to higher temperatures is another frequently assumed explanation for carbon loss (Cox, Betts, Chris, Spall, & Totterdell, 2000) (Smith & Shugart, 1993). However, studies of soil respiration under different temperature and moisture conditions and field CO₂ measurements showed that while temperature increased, moisture decreased, resulting in insignificant differences in respiration rates across the plots (Saleska, et al., 2002). Therefore, it was suggested that the decreased carbon might be caused by a shift from forb to shrub-dominated plant communities. This shift, from leafy to woody plants, reduced litter input into the system and caused an overall loss of SOC. However, it was believed that with time, the higher lignin ratios in the shrubs would lead to slower decomposition (reduced carbon output), and soil carbon would increase again (Saleska, et al., 2002) (Harte, Saleska, & Shih, 2006). Fifteen years into the warming experiment, although SOC seemed to be recovering somewhat in the warming plots, a four year drought affected both plot treatments, increasing shrub biomass and reducing that of forb even further, and somewhat reducing SOC.

Now, twenty-two years into the experiment, it was predicted that SOC in the experimental plots should be recovering from both initial experimental warming and from the drought. Additionally, the control plots have begun to show a downward trend in melt date, forb cover, and carbon that real world global warming was affecting the plots. This provides an opportunity to both test the model for carbon flux in the experimental plots and to examine how well conditions in the experimental plots predict real-world changes in the controls.

This long-term data also had the potential to test another hypothesis; that shrub AGB might affect melt date. The dark winter leaves and bark of sagebrush (*Artemisia tridentata*) emerging from under snow has a high albedo which, in dense mats, might be able to effect the time of snow melt in some plots. This could create a positive feedback in plots as temperatures rise and sagebrush becomes more dominant.

The purpose of this summer project is to show long term effects of warming on plant communities and soil carbon loss in order to evaluate the relative importance of the above factors in soil carbon flux. These effects will be compared to changes in control plots caused by gradual actual global warming. It will also investigate possible additional effects such as the ability of sagebrush to reciprocally impact melt date. This research project will observe above-ground biomass and compare warming effects on shrub and forb densities to changes in soil carbon. This year's above-ground biomass data as well as accumulated data from the past twenty years will be analyzed to show how well current models predict long term impacts of climate shift on plant communities and soil carbon.

Methods

Ten 3x10 meter research plots were established on an ungrazed south facing slope at 38°57'N, 106°59'W, elevation 2920 m, in Gothic, Colorado in 1991 (Saleska, et al., 2002) (Harte, Saleska, & Shih, 2006) (Harte J. , 2005). These plots represent a broad diversity of indigenous montane plants, and have a soil horizon of approximately 50 cm deep. At five of these plots, suspended radiant heaters are active day and night, year-round.

In 1991 and 1992, the heaters emitted $\sim 15 \text{ W m}^{-2}$. Post 1992 through 2012, these heaters emitted 22 W m^{-2} at soil surface. Temperature probes in these plots record temperature and moisture every two hours year-round. The first annual snow melt date, defined as the time when below ground temperature first reaches above 2°C , is calculated using these probes and used as the temperature comparison across plots. Soil carbon content is measured twice yearly, on June 1 and August 1, by collecting 8-15 cm deep, 1.7 cm diameter soil cores and measuring carbon content in the lab as 50% loss on combustion at 430°C . Above ground biomass and relative densities of shrub and forb within the plots was measured each growing season between 1992 and 2008. This year's plant biomass assessment was the first assessment in three years. Comparable data from 1991-2008 were also analyzed.

Biomass was calculated by placing a 75x75 cm quadrat divided into a 15x15 grid 35 cm above the plot. The grid was placed with the upper left corner of the grid 120 cm from the top of the plot and 70 cm from the left edge of the plot. Within each grid square, ground cover type was categorized into either sagebrush, holly, forb, graminoid, soil, rock, litter, or gopher esker. Percentage cover was converted into aboveground biomass using conversion factors developed in previous years by direct harvest and weighing in external plots. Shrub percent cover was converted to total shrub AGB by multiplying by 2.14. Forb total cover was converted to total forb AGB by multiplying by 1.24. Data was collected from each of the five control and five experimental plots three times on July 18th-19th, June 25th, July 2nd, July 9th, July 16th-17th, and July 23rd. Plots were measured sequentially, with measurements begun at alternating sides of the row for each set. The week's count with the greatest above ground biomass for the season was used as that year's single data point, consistent with the way the 1991-2008 data were recorded. The three measurements were averaged to ensure accurate estimation, and the five plots of each treatment will be considered near replicates (a slight curve to the hillside alters sun exposure, making replication not exact).

This summer's work also synthesized the more than twenty years of data already collected. Changes across melt date, average SOC, forb AGB, shrub AGB, total AGB, and SOC, as well as differences between control and heated plots were analyzed using R. Effects were examined by treatment and by plot across years.

The predictability of control plots by experimental plots will be examined by comparing the slopes of change over time in control and heated plots for all factors.

Shrub effect on melt date, on forb, and on other shrubs will be examined by testing for effects of previous years of shrub growth on melt date, and also by looking for a change in the slope and effect size of these relationships as shrub biomass increases.

Results

Average yearly melt date in heated plots but not controls has become significantly earlier over time (C: slope: -0.7414, $p < 0.114$, $n = 22$; H: slope: -1.2448 $p < 0.00093$, $n = 22$) (Figure 2). When data from every plot was considered, melt date plot by plot has become significantly earlier over time in both control and heated plots (C: slope: -0.7414, $p < 0.000824$, $n = 110$; H: slope: -1.245, $p < 1.23e-07$, $n = 110$) (Figure 4). There was no significant difference in slope melt date over time between control and heated plots (one way Welch's t-test: $p < 0.184$). Control and heated plots differ by an average factor of by an average factor of 15.9 ± 7.9 days.

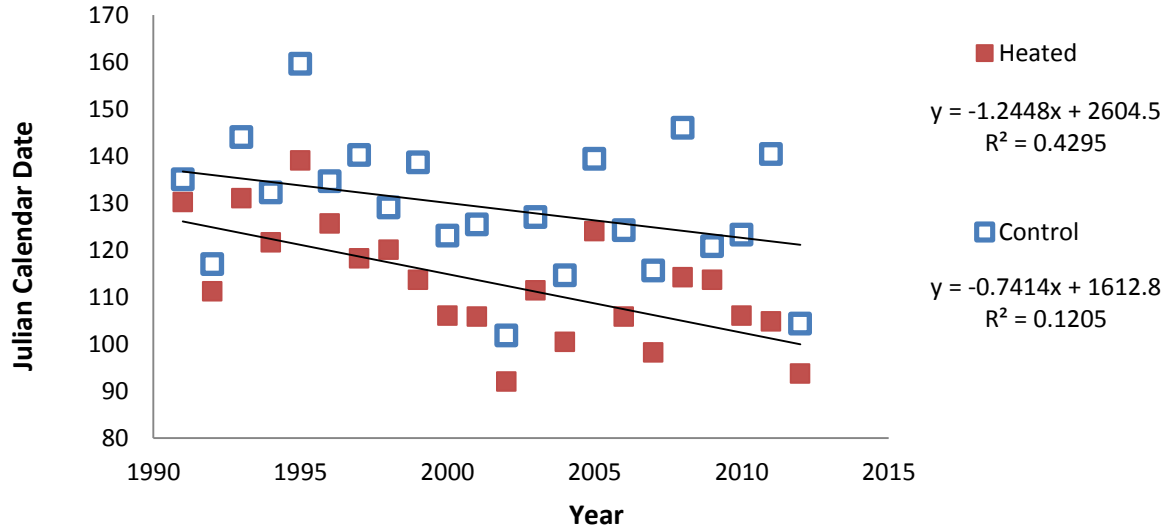


Figure 2 Change over time of day of first melt in control and heated plots, including baseline datapoints 1991 and 1992 which were not included in analysis of slope and p -values.

Average forb cover has significantly decreased over time in heated but not control plots (C: slope: -1.226, $p < 0.305$, $n = 18$; H: -2.184, $p < 0.0379$, $n = 18$) (Figure 4). When data from every plot was considered, forb cover plot by plot has significantly decreased in heated plots, but was only marginally significant in control plots (C: slope: -1.757, $p < 0.0734$, $n = 90$; H: slope: -2.732, $p < 0.00383$,

n=90). There was no significant difference between the forb cover over time between control and heated plots (one way Welch's t-test: $p < 0.470$). Control and heated plots differ by an average factor of $27.5 \pm 19.5 \text{ g/m}^2$.

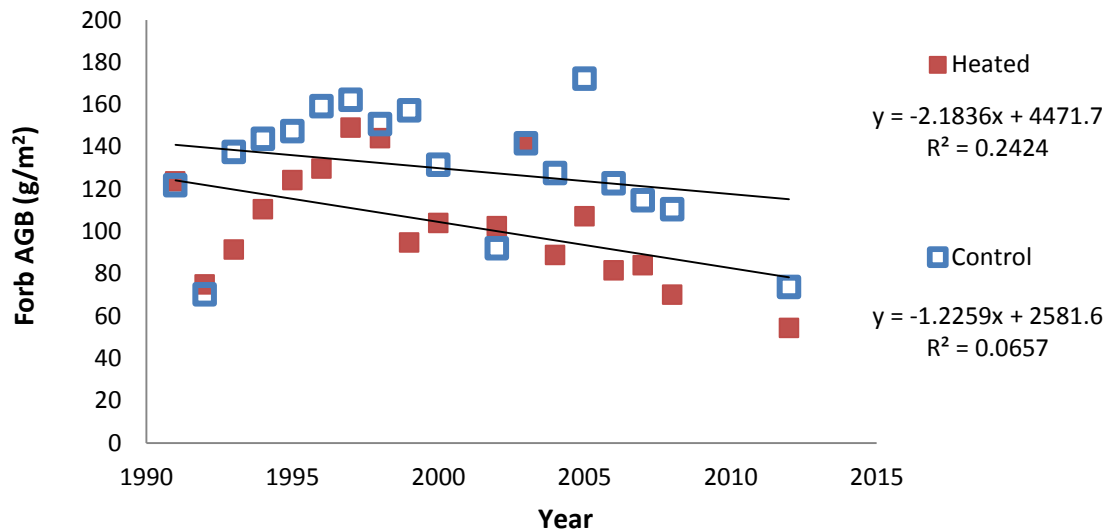


Figure 3 Change over time of forb AGB in control and heated plots, including baseline datapoints 1991 and 1992 which were not included in analysis of slope and p -values.

Average shrub cover has increased significantly in both control and heated plots (C: slope: 1.968, $p < 0.0130$, $n=17$; H: slope: 6.279 $p < 0.00001$, $n=17$) (Figure 5). When data from every plot was considered, shrub cover plot by plot has significantly increased in heated plots, but was only marginally significant in control plots (C: slope: 1.968, $p < 0.0578$, $n=85$; H: slope: 6.279 $p < 3.64e-05$, $n=85$). The slope of shrub cover over time slope was significantly steeper in heated plots than control plots (Welch's one way t-test: $p < 0.0002$).

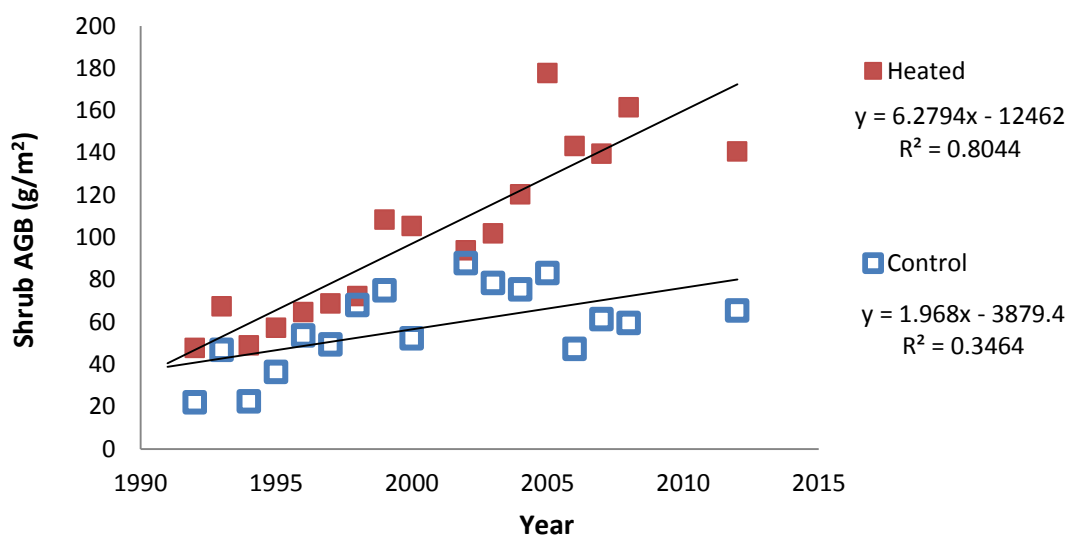


Figure 4 Change over time of shrub AGB in control and heated plots, including baseline datapoints 1991 and 1992 which were not included in analysis of slope and p -values.

Average total AGB has increased significantly in heated but not control plots (C: slope: 0.2186, $p < 0.892$, $n=17$; H: slope: 3.847, $p < 0.00507$, $n=17$) (Figure 6). When data from every plot was considered, total AGB cover plot by plot has significantly decreased in heated plots, but was not significant in control plots (C: slope: 0.1797, $p < 0.867$, $n=85$; H: slope: 3.847, $p < 0.000429$, $n=85$). The slope of total AGB over time was significantly steeper in heated plots than control plots ($p < 0.0359$).

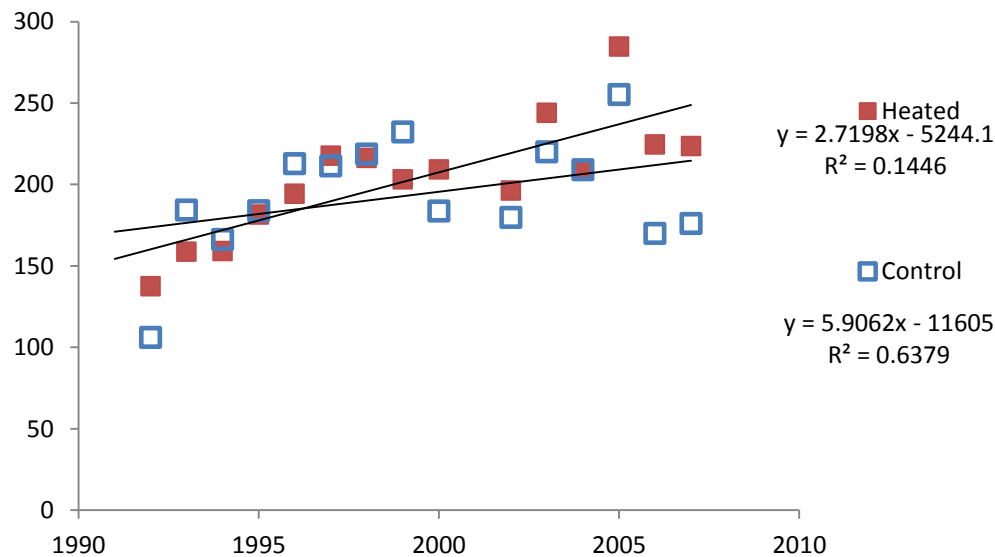


Figure 5 Change over time of day of total forb and shrub AGB in control and heated plots, including baseline datapoints 1991 and 1992 which were not included in analysis of slope and p -values.

Average SOC over time in control plots was significant (C: slope: -0.06723, $p < 0.00301$, $n=21$)(Figure 7). When data from every plot was considered, SOC plot by plot exhibited only a marginally significant effect for control plots (C: slope: -0.03110, $p < 0.0246$, $n=105$;). Differences in slopes for control and heated plots were not tested, as the slope of the heated plots was not significant. The slope of the heated control plots was best described as a sudden loss of carbon and then gradual recovery. The recovery of heated plots (SOC 1994-2012) was a statistically significant positive slope (slope: 0.04196, $p < 0.00902$). Control plot trend during this time was (slope: -0.03823, $p < 0.0527$).

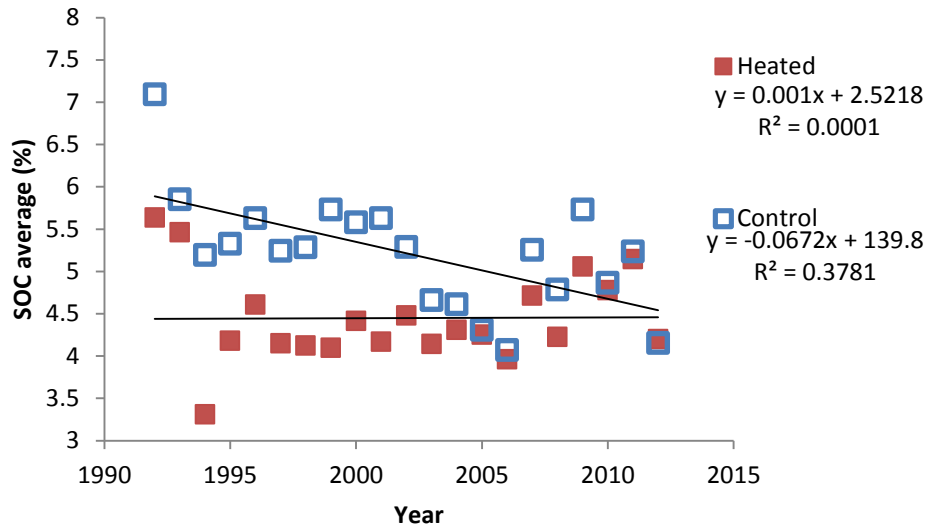


Figure 6 Change over time of % SOC in control and heated plots, including baseline datapoints 1991 and 1992 which were not included in analysis of slope and p<values. Recovery of the heated plots is shown as a dashed trendline.

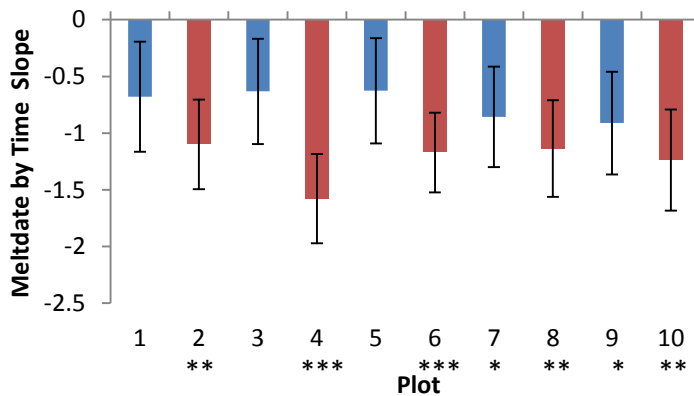


Figure 7 The slopes of melt date over time in each of the 10 plots with standard error. Asterisks indicate significant slopes, *: $p < 0.10$, **: $p < 0.05$, ***: $p < 0.01$.

Considered plot by plot, the slopes and effect size of melt date over time in plots 2, 4, and 6-10 were statistically significant (2: $p < 0.01155$; 4: $p < 0.00070$; 6: $p < 0.00328$; 7: $p < 0.0671$; 8: $p < 0.0148$; 9: $p < 0.0578$; 10: $p < 0.01180$)(Figure 8).

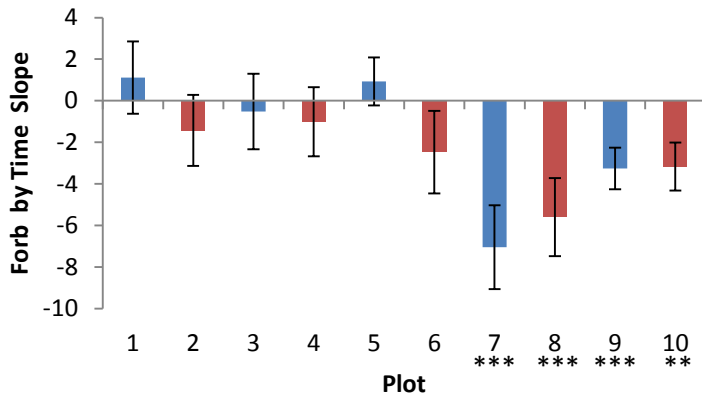


Figure 8 The slopes of forb AGB over time in each of the 10 plots with standard error. Asterisks indicate significant slopes, *: $p < 0.10$, **: $p < 0.05$, *: $p < 0.01$.**

Considered plot by plot, the slopes of forb over time in plots 7, 8, 9, and 10 were statistically significant (7: $p < 0.00302$; 8: $p < 0.00883$; 9: $p < 0.00516$; 10: $p < 0.01414$) (Figure 9).

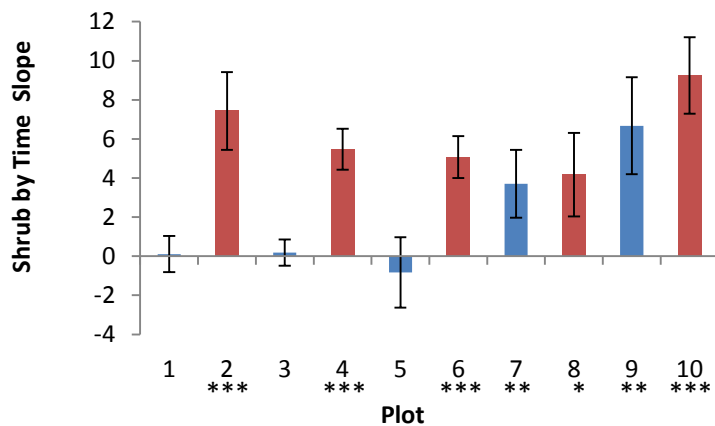


Figure 92 The slopes of shrub AGB over time in each of the 10 plots with standard error. Asterisks indicate significant slopes, *: $p < 0.10$, **: $p < 0.05$, *: $p < 0.01$.**

Considered plot by plot, the slopes of shrub AGB over time in plots 2, 4, and 6-10 were statistically significant (2: $p < 0.00199$; 4: $p < 0.00011$; 6: $p < 0.00027$; 7: $p < 0.04952$; 8: $p < 0.07029$; 9: $p < 0.01670$; 10: $p < 0.00026$) (Figure 10).

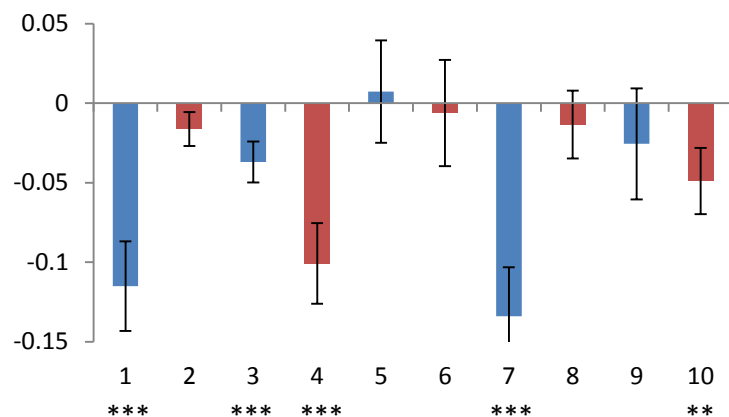


Figure 10 The slopes of carbon over time in each of the 10 plots with standard error. Asterisks indicate significant slopes, *: $p < 0.10$, **: $p < 0.05$, ***: $p < 0.01$.

Considered plot by plot, the slopes of carbon over time in plots 1 and 7 were statistically significant (1: $p < 0.00715$, 7: $p < 0.00031$) (Figure 11).

To separate out causal relationships between these factors, plausible relationships were examined with the causal factor from the same year, one year prior, two years prior, and three years prior.

Melt date 0-3 years prior had no significant correlation with soil organic carbon in either control or heated plots (Table 1). However, control shrub from one year prior had a significant negative relationship to control plot soil organic carbon, and heated shrub from 2 and 3 years prior had a significant positive relationship to carbon (CS1: slope: -0.01602, $p < 0.00948$; HS2: slope: 0.00570, $p < 0.02028$; HS3: slope: 0.00426, $p < 0.04660$)(Table 2). Control forb from the same year and heated forb from 3 years previous had a significant negative relationship with carbon (CF0: slope: 1.295895, $p < 0.002646988$; HF3: slope: -0.008852, $p < 0.0413$)(Table 2).

Carbon	Control		Heated	
	P value	Slope	P value	Slope
MD0	0.74511	0.003619	0.87935	-0.001578
MD1	0.3181	0.01190	0.91891	-0.001074
MD2	0.0996	0.01547	0.61265	0.004789
MD3	0.0603	0.017091	0.0895	-0.013647

Table 1 Relationship between soil organic carbon and melt date from the same and previous years

Carbon	Control		Heated	
	P value	Slope	P value	Slope
S0	0.052	-0.018016	0.458	-0.002542
S1	0.0095	-0.016919	0.834	0.0006688
S2	0.124	-0.01004	0.0225	0.005466
S3	0.0467	-0.012549	0.0182	0.005093 0
F0	0.609	-0.003269	0.284	-0.005400
F1	0.432	-0.005417	0.393	-0.005040
F2	0.277	0.005455	0.756	0.001566
F3	0.432	0.003741	0.00733	-0.01103

Table 2 Relationships between soil organic carbon and shrub and forb AGB from the same and prior years.

Meltdate from heated plots 1, 2, and 3 years prior had a significant negative relationship to shrub AGB (HM1: slope: -2.1109, $p < 0.00345$; HM2: slope: -1.7113, $p < 0.02764$; HM3: slope: -1.9305, $p < 0.01535$). Melt date from control plots of the same year and heated plots of 2 years prior had a significant positive relationship to forb AGB (CM0: slope: 1.2959, $p < 0.00265$; HM0: slope: 1.048989, $p < 0.02861548$; HM2: slope: 1.091864, $p < 0.04400608$).

Shrub	Control		Heated	
	Slope	P value	Slope	P value
MD0	-0.3786799	0.24570787	-1.380751	0.075855185
MD1	-0.6492151	0.067532103	-2.110872	0.0034473776
MD2	-0.2421494	0.49928995	-1.711347	0.027640501
MD3	-0.1507025	0.6764079	-1.930454	0.015354075

Table 3 Relationship between shrub AGB and melt date from the same and prior years.

Forb	Control		Heated	
	Slope	P value	Slope	P value

MD0	1.295895	0.002646988	1.048989	0.02861548
MD1	-0.01382021	0.98092653	0.4573443	0.4070104
MD2	0.8049936	0.1195290	1.091864	0.04400608
MD3	0.02542278	0.9633228	0.6384515	0.2991512

Table 4 Relationship between forb AGB and melt date from the same and prior years.

Total AGB 2 years prior had a negative effect on soil carbon in heated plots (HA2: slope:-0.006165, $p<0.0247$). Shrub growth from the 1, 2, and 3 years previous had a significant negative relationship with forb growth in heated plots (HS1: slope: -0.38747, $p<0.02133$; HS2: slope: -0.45624, $p<0.004025$; HS3: slope: -0.48574, $p<0.01328$).

Carbon	Control		Heated	
	Slope	P value	Slope	P value
A0	-0.006507	0.215	-0.005899	0.131
A1	-0.007673	0.0551	-0.001934	0.594
A2	9.088e-05	0.982	0.006165	0.0247
A3	-0.001730	0.66	0.001771	0.512

Table 5 Relationship between soil organic carbon and total forb and shrub AGB from the same and prior years.

Forb	Control		Heated	
	Slope	P value	Slope	P value
S0	0.1909065	0.6350309577	-0.3222179	0.05137936
S1	-0.1153438	6.460857e-01	-0.3874713	0.02132789
S2	-0.3162283	3.337045e-01	-0.4562431	0.004024504
S3	-0.5047766	1.180963e-01	-0.485748	0.01327533
Shrub	Control		Heated	
	Slope	P value	Slope	P value
S0	0.08071015	0.63503096	-0.7139658	0.0513793588
S1	-0.03396900	0.86177977	-0.5403992	0.25862946
S2	0.2445599	0.1980116	0.1608656	0.7532677
S3	0.1658338	0.4086319	0.2212471	0.7062144

Table 6 Relationship between forb and shrub AGB from the same and prior years.

Shrub growth from 1 year previous had a significant negative relationship with melt date in both control and heated plots (CS1: slope: -0.3144, $p < 0.0384$; HS1: slope: -0.17819, $p < 0.00611$; HS2: slope: -0.1586017, $p < 0.02946604$).

Meltdate	Control		Heated	
	Slope	P value	Slope	P value
S0	-0.2341654	2.457079e-01	-0.1413273	7.585518e-02
S1	-0.3144302	3.836288e-02	-0.1781899	6.113342e-03
S2	-0.2991896	9.491291e-02	-0.1586017	2.946604e-02
S3	-0.2543970	1.523055e-01	-0.1271991	7.702892e-02

Table 7 Relationship of meltdate to shrub AGB from the same and prior years

This method of examining previous year's relationships to a current factor is supported generally by the lack of a strong relationship between data from previous years and current years within a factor. A significant year to year relationship existed only for shrub, total AGB, and melt date data. Heated melt date data from two years prior had a positive relationship with current melt date (HM2: slope: 0.55334, $p < 0.0146$). Shrub AGB had a significant positive relationship to previous year's growth in control plots (CS1: slope: 0.46526, $p < 0.02941$). Shrub AGB had a positive relationship between shrub AGB one, two, and three years previous in heated plots (HS1: slope: 0.88014, $p < 0.00012$; TS2: slope: 0.81947, $p < 0.00226$; HS3: slope: 0.77112, $p < 0.00754$). Total AGB had a positive relationship between total AGB one and two years previous in heated plots (HA1: slope: 0.50120, $p < 0.03146$; HA2: slope: 0.53227, $p < 0.00758$).

	Control		Heated	
	Slope	P-value	Slope	P- value
S1	0.7251	0.0294	0.8210	0.000118
S2	0.5743	0.0868	0.7164	0.00226
S3	0.7069	0.106	0.6830	0.00754
F1	0.2361	0.4321	0.3273	0.2008
F2	0.1946	0.5815	0.2724	0.3501
F3	-0.5251	0.142813	-0.1578	0.547563
M1	-0.1301	0.542	0.3809	0.08352
M2	0.3607	0.08876	0.5210	0.0146
M3	0.04982	0.830571	0.2719	0.27245
C1	0.5697	0.0358	0.1390	0.61309
C2	0.4856	0.1075	-0.3015	0.340507
C3	0.05738	0.85782	-0.03094	0.9396
A1	0.2967	0.448	0.6597	0.0315
A2	0.3720	0.342	0.9235	0.00758
A3	-0.4334	0.31509	0.5762	0.205

Table 6 Relationship of the variables shrub AGB, forb AGB, meltdate, and carbon to the same variable 1, 2, and 3 years prior.

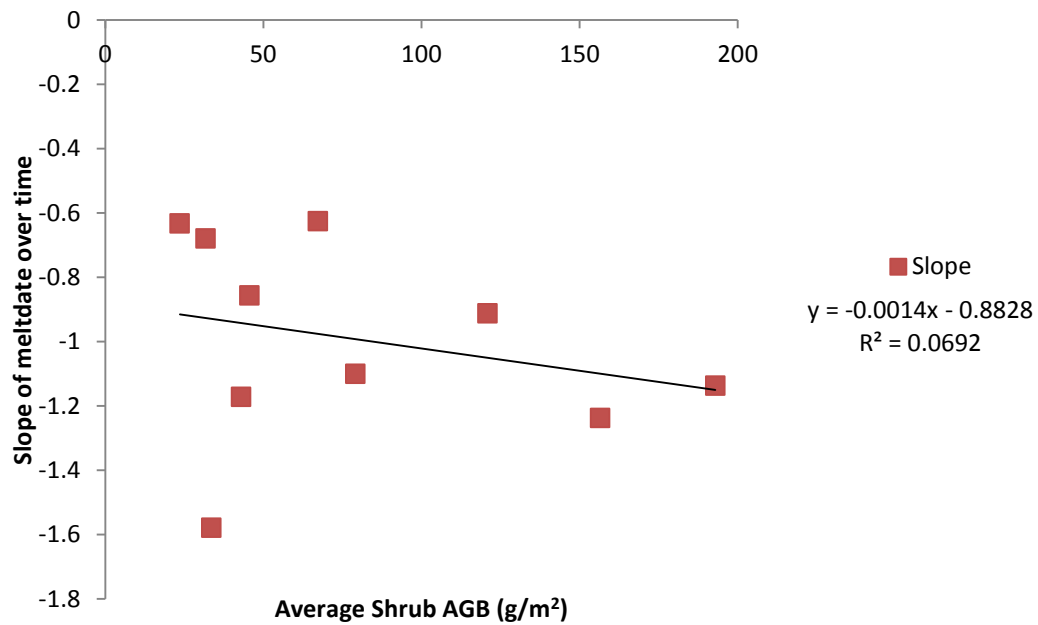


Figure 3 Slopes of melt date change over time as related to the average shrub AGB in that plot.

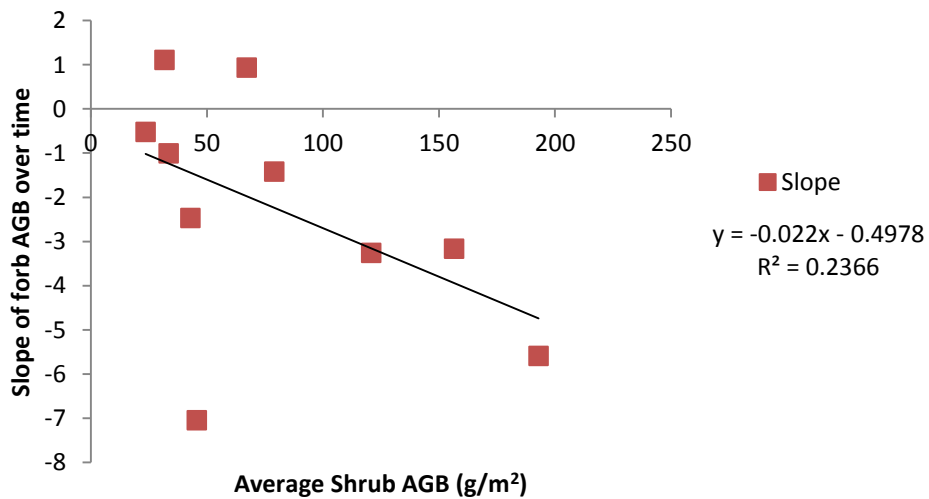


Figure 42 Slopes of forb AGB plotted against the average shrub AGB in that plot.

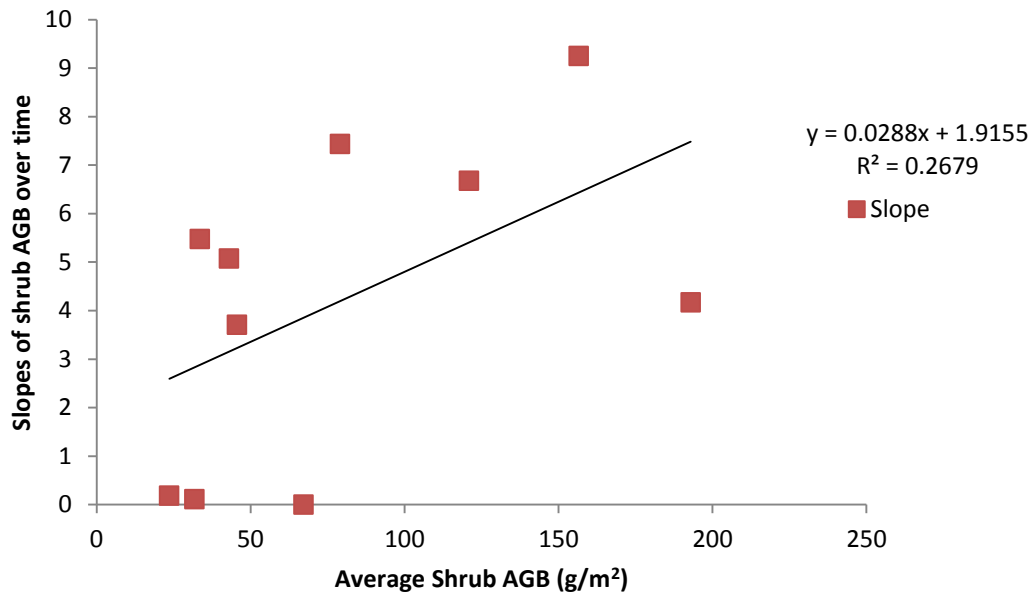


Figure 53 Slopes of shrub AGB plotted against the average shrub AGB in that plot.

Discussion:

Changing melt date: plant communities and carbon loss

Heated plots were found to melt consistently earlier than the control plots, demonstrating that experimental warming did quantifiably alter the plot environments. Additional change was observed; an increasingly early melt date which both plots experienced in parallel, most likely caused by real world global warming effects on the plots. Research at the same location has observed progressive changes in flower phenology, also driven by changing snowmelt (Inouye, 2008). Climate change has also been observed worldwide with global surface temperatures having increased at a rate of 0.2 °C a decade for the past 30 years (Hansen, et al., 2006). Warming appears to affect plots linearly, with no difference in rate of change between experimental and heated plots. This is likely due to melt date being a direct physical consequence of warming in both heated and control plots. This is further supported by the wattage change which occurred in heated plots in 1992. When warming was increased from 15 W/m² to 22 W/m² in the plots, a proportional effect on melt date was observed (Harte, *Personal communication*).

Changing melt date has been shown to affect both forb and shrub AGB (Saleska, et al., 2002). Warming decreased forb AGB. Forbs in the control plots, responded to same year changes in melt date, while heated plots responded more to melt date from several years previous. The lack of correlation between forb growth and forb growth from previous years further supports that this may represent a differential response across the treatment types. These different rates of change could be due to change in community composition or genetic frequency of certain traits amongst the forbs in those plots. Altered community composition might also introduce novel biotic stresses

which could inhibit plant phenotypic plasticity (Valladares, Gianoli, & Gómez, 2007). It might also be due to different phenotypic plasticity in plants from different long term treatments. Forbs in the heated plots may have exhausted their capacity for short term adaptation and acclimation. Therefore, they would only be able to respond to climate change with longer term shifts in community composition.

Melt date from one and two years prior had a significant effect on heated plot shrub AGB. This may suggest that shrub aboveground biomass changes more slowly, as might be expected from a woody shrub which has more invested in each stage of growth (Perfors, Harte, & Alter, 2003). The lack of response in the control plots may be due to a weaker or simply very delayed shrub response. However, distinguishing between effects of prior and present years of shrub growth is difficult because of the strong correlation between shrub growth from year to year. However, that strong correlation also suggests a slower, less variable shrub response to warming. A delayed shrub response may also explain the different slopes of shrub AGB over time in the control and heated plots. Both slopes start at the same intercept, with shrub growth being similar in both plots. Overtime, shrub growth in heated plots is consistently steeper than in the control plots, rather than changing in synchrony with the control as melt date and forb cover does. This may be because shrub has not adjusted to the higher temperatures in the heated plots. These slopes have continued to diverge, suggesting that the effect of additional warming on shrub AGB has not yet plateaued.

Shrub and forb AGB are in turn associated with changes in the SOC content of the soil. Data from SOC over time in the heated plots suggested that the plots experienced a sharp drop in SOC during the first five years of the experiment but then began to regain that SOC over time. The control plots, however, have experienced a gradual and linear reduction in SOC over time. This may be induced by the way in which shrub biomass contributes to SOC, with a lower rate of litter deposition and decomposition (Saleska, et al., 2002; Hobbie, 1996). Compared to forbs, shrub deposits relatively little litter, and so an increase in shrub represents an immediate reduction in the amount of carbon containing organic matter being added to the soil. However, shrub litter has a higher lignin content than forbs do, meaning that it decomposes more slowly than other litter (Shaw & Harte, 2001). There may exist a threshold where enough lignin containing shrub material has been added to the soil so that increasing shrub biomass is no longer resulting in a loss but a gain of SOC. By contrast, forb growth in the heated plots is either negatively correlated or unrelated to carbon, perhaps because in those plots the more rapid decomposition of forb leaf litter material is more important than the higher rate of litter deposition. In the control plots, this relationship is different and not significant. Similarly in regards to shrub AGB the heated plots have reached a point of state change and so see a positive relationship of shrub with carbon with a long time delay. The control plots, however, experience a negative relationship, because they have not yet reached that point of state change.

The insignificance of other relationships between forb and SOC may show that shrub AGB is the main driver behind changes in SOC. There was also a significant relationship between forb AGB and shrub AGB in the same year, and of shrub on forb one and two years previous in the heated plots. This may be caused by shrub crowding out forbs as they become more dominant, or may simply reflect trends induced by changes due to the shared factor of melt date.

In this system, melt date acts as a primary driver changing forb and shrub biomass in the plots. This driver has increased shrub biomass and decreased shrub biomass in both plots. Overall, AGB has been increasing over time in the heated plots but not control. Forb responds more quickly to changing melt date than does shrub. Shrub and forb both strongly influence SOC. How they respond may be influenced by the relative litter and decomposition rates of the plants.

Comparisons of control and heated plots

Melt date and forb AGB in the control plots closely tracked what was occurring in the heated plots, suggesting that these effects may be easy to project into the future. Shrub, however, was less easy to predict and responded more strongly to heated plot warming than control plot warming. This may be an artifact of the long term nature of the warming experiment. Sagebrush, (*Artemisia tridentata*) is known to increase its growth rate as it grows older. Heated plots may have more older-growth sagebrush extant in the plots, resulting in a more rapid growth rate. There was no clear relationship between plot by plot effect size of shrub growth rate and plots with more sagebrush within them. However, there was some evidence that slopes of change in shrub AGB over time were steepest in plots with more shrub biomass. The high woody investment of shrub growth may mean that response to warming is delayed (Perfors, Harte, & Alter, 2003). Carbon followed a very different trend in control and heated plots, likely influenced by a state change which occurred quickly in the heated plots but has not yet occurred in the control plots. This leaves it yet indeterminate if the future SOC of the control plots could be predicted by data from the experiment.

The effect of increasing shrub growth on melt date and forb

An additional proposed property of shrub growth was the ability of shrub to influence melt date directly, through altered albedo. It was shown that higher shrub AGB one year prior, but not in the same year, was associated with earlier melt date. This suggested that shrub growth was influencing melt date. However, the rate of melt date change over time did not seem to be associated with greater shrub AGB. Additionally, the slope of forb change over time appeared to be greater in plots with more shrub AGB.

Another potential effect of shrub was its ability to negatively impact forb growth through competition. A previous study on site showed competition between *A tridentata* and forb species (Roswell M. , 2010). A relationship between effect size of the melt date forb relationship and shrub AGB suggested that plots with more shrub had the strongest effect on forb change over time. This could be because plots with more shrub are also those with the greatest plant community response overall to heating. However, in comparison effect size of the change in shrub growth over time did not seem to be correlated to shrub biomass. This implies that a competition induced response makes more sense. The slope of forb AGB change over time did seem to be was associated with greater shrub AGB.

In summation

Vegetation is changing in the control plots at a different pace than in the heated plots, mainly driven by the faster rate of change of shrub AGB. Soil carbon is being lost more gradually in the control plots than the heated plots, with no evidence of the vegetation driven recovery which affected the

heated plots. This state change is very important since it turned the heated plots from net carbon sources to sinks which are still regaining carbon. Therefore, it is important to attempt to identify why the control plots have not yet reached this state change and when they might be expected to do so.

Global warming threatens to change plant communities and ecosystems around the world. Predicting specific effects can allow scientists to develop conservation programs and mitigation strategies. Understanding key state changes such as those exhibited in the warming meadow help with those predictions and strategies. In particular, predicting SOC helps predict potential positive feedback mechanisms that could further or reduce warming.

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