



Carbon budgets for soil and plants respond to long-term warming in an Alaskan boreal forest

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Abstract The potential consequences of global warming for ecosystem carbon stocks are a major concern, particularly in high-latitude regions where soil carbon pools are especially large. Research on soil and plant carbon responses to warming are often based on short-term (< 10 year) warming experiments. Furthermore, carbon budgets from boreal forests, which contain at least 10–20% of the global soil carbon pool, have shown mixed responses to warming. In this study, we measured carbon and nitrogen budgets (i.e., soil and understory vegetation carbon and nitrogen stocks) from a 13-year greenhouse warming experiment in an Alaskan boreal forest. Although there were no differences in total aboveground + belowground pools, the carbon in the moss biomass and in the soil organic layer significantly

decreased with the warming treatment (– 88.3% and – 19.1%, respectively). Declines in moss biomass carbon may be a consequence of warming-associated drying, while shifts in the soil microbial community could be responsible for the decrease in carbon in the soil organic layer. Moreover, in response to warming, aboveground plant biomass carbon tended to increase while root biomass carbon tended to decrease, so carbon allocation may shift aboveground with warming. Overall these results suggest that permafrost-free boreal forests are susceptible to soil carbon loss with warming.

Keywords Boreal forest · Carbon budget · Field experimental warming · Global climate change · Nitrogen budget

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Introduction

Global warming is expected to alter the amount of carbon stored in soils and plants; however, it is unclear whether warming will lead to a net loss or gain of carbon (C) (Crowther et al. 2016; van Gestel et al. 2018). Soil C stocks are the balance of inputs and outputs (Melillo et al. 2011; Lu et al. 2013). The effect of warming on soil C stocks, especially in high-latitude areas (above 60°N) with large C pools (Dixon et al. 1994; Hobbie et al. 2000), depends on the

magnitude of change associated with these C fluxes and on their temperature sensitivity (Knorr et al. 2005; Sistla et al. 2013). Soil carbon losses can occur due to increased microbial and enzyme activity (Schimel et al. 2004; Davidson and Janssens 2006). On the other hand, soil C may increase with warming through increased litter inputs and root production (Majdi and Ohrvik 2004; Rinnan et al. 2008). Further complicating predictions of C gain or loss under warming are changes in soil moisture (Lavelle et al. 1993; Davidson et al. 2000; Saleska et al. 2002; Xu et al. 2015). For example, while warming may stimulate decomposition and plant production, warming-associated drying may decrease decomposition and plant growth. This type of interaction complicates predictions of net C gains and losses (van Gestel et al. 2018).

Determining how boreal forests will respond to warming, and associated drying, is of particular interest. Boreal forests contain at least 10–20% of global soil C (Jobbagy and Jackson 2000; Allison and Treseder 2011; Pan et al. 2011), and their high latitude distribution makes them especially vulnerable to climate change since warming in these regions is expected to occur faster (Chapin et al. 2000; Shukla et al. 2019). Here, we took advantage of a 13-year greenhouse warming experiment in an Alaskan boreal forest to examine aboveground and belowground C and N budgets. Previous studies at this site have shown that, when compared to control plots, warmed plots have reduced fungal abundance and increased fungal diversity (Allison and Treseder 2008; Treseder et al. 2016). Fungal decomposers tend to dominate under warming and drying because of their drought-resistant growth forms (Barnard et al. 2013; Treseder and Lennon 2015) and their ability to decompose recalcitrant compounds (e.g., cellulose and lignin), which may become more abundant with warming due to changes in the plant community (Mcguire et al. 2010; Fontaine et al. 2011; Xiong et al. 2014). Fungi tend to specialize on recalcitrant compounds that may have higher temperature sensitivities for decomposition, thus conferring an advantage over bacteria which tend not to target recalcitrant compounds (Romero-Olivares et al. 2017). Warmed plots at this site were also found to have slower litter decomposition (Romero-Olivares et al. 2017), increased cellulose- and starch-degrading enzyme production (German and Allison 2015), and lowered respiration rates (German and Allison 2015). However, no studies have determined

whether any of these changes in decomposition dynamics have elicited measurable changes in soil and plant C and N pools. A fuller understanding of the relationship between aboveground and belowground C and N dynamics will provide better insight into whether or not ecosystem C gains or losses should be expected with warming in this critical ecosystem.

We hypothesized that the greenhouse warming treatment would reduce soil C storage owing to greater activity of recalcitrant C decomposers and decrease above- and below-ground plant biomass owing to water limitation (Hypothesis 1; Fig. 1a). Warming-associated drying could also increase soil C storage by inhibiting decomposer activity, while the warming itself could augment above- and below-ground plant biomass by alleviating temperature or nutrient limitation of plants (Hypothesis 2; Fig. 1a). Alternatively, if decomposer activity and plant biomass inputs simultaneously increase or decrease, or if previously reported changes at our site are ephemeral, soil C storage would remain the same (Null Hypothesis). To test these hypotheses, we compared changes in understory aboveground and belowground C and N pools from greenhouse warmed and control plots in order to better understand boreal forest ecosystem response to long-term warming treatment.

Methods

Our study site is located in a mature black spruce (*Picea mariana*) boreal forest on the Fort Greely military base near Delta Junction, Alaska, USA (63°55'N, 145°44'W). The understory vegetation is dominated by mosses, lichens, and shrubs (*Vaccinium uliginosum*, *V. vitis-idaea*, *Ledum groenlandicum*, *Empetrum nigrum*, and *Betula glandulosa*) (Treseder et al. 2004). The soil is an Inceptisol (German and Allison 2015), with an average organic horizon of 9.8 cm (King et al. 2002) and pH of 4.9 (Hanson et al. 2008).

In 2005, a greenhouse warming experiment was established with five pairs of 2.5 × 2.5 m plots within a 1 km² area in the open canopy forest, as described in Allison and Treseder (2008). In each pair, one plot was covered with a wood frame structure covered in greenhouse plastic film in order to warm the plots. Gaps between the frame and the plastic allowed air to circulate, and gutters and tubing allowed water to flow

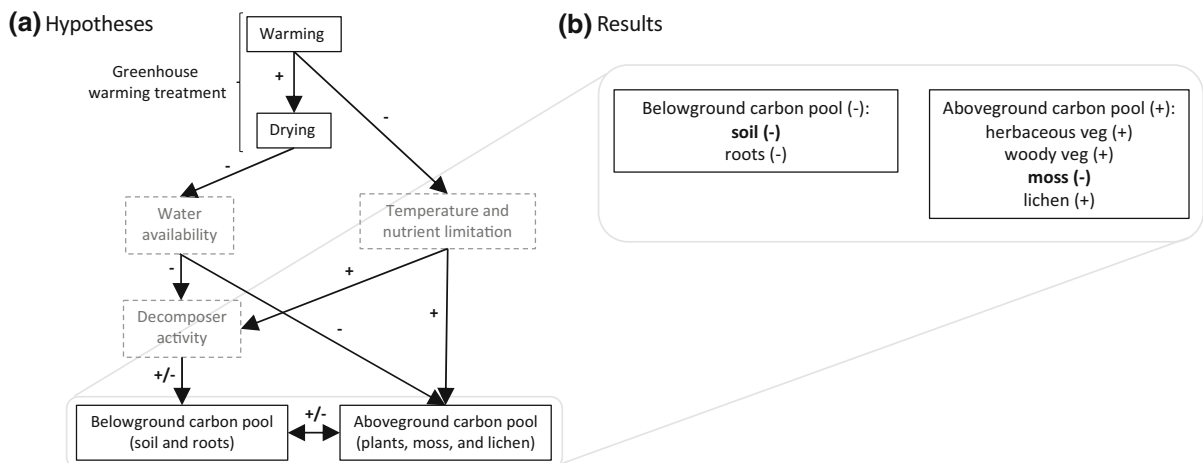


Fig. 1 **a** Hypothesized positive and negative effects of the greenhouse warming treatment on aboveground and belowground C pools in a permafrost-free boreal forest. In this experiment, we measured aboveground and belowground carbon pools (black, solid-lined boxes). Grey, dashed boxes indicate mechanisms that were not measured in this experiment but were observed in prior experiments at our study site (Allison and Treseder 2008; German and Allison 2015; Treseder et al.

2016; Romero-Olivares et al. 2017). Depending on which mechanisms dominate, we predicted different responses for aboveground and belowground C pools. **b** Inlay of changes to aboveground and belowground C pools found in our experiment. Positive and negative signs indicate increases and decreases in pool size with the greenhouse warming treatment. Bolded text (soil and moss) specifies significance ($P \leq 0.05$)

in; the other plot was left unmanipulated as a control (Allison and Treseder 2008). All plots excluded large trees. Air temperature increased by an average of 1.6 °C and Onset HOBO data loggers recorded an average of 0.5 °C increase in soil temperature at 5 cm depth (Table S1; Allison and Treseder 2008). As a result of the greenhouse warming treatment, soil moisture also decreased by an average of 22% in the warmed plots (Table S1; Allison and Treseder 2008). Passive warming approaches, such as this one, not only warm and dry but can also alter temperature variation, light intensity, CO₂ concentration, wind speed, snow cover, and herbivory (Kennedy 1995; Aronson and McNulty 2009; Bokhorst et al. 2011). However, in remote areas where line power is not available, greenhouse warming is a practical and cost-efficient way to elevate temperature. Passive warming treatments are also good at minimizing soil disturbance compared to other approaches like heated cables (Aronson and McNulty 2009). Here, when we refer to the *warming treatment*, we are referring to the collective change in the microclimate which includes, but is not limited to, warming and drying.

In July 2017, two 0.6 × 0.6 m subsamples of aboveground biomass were collected from each plot. The two subsamples were combined in the field and

the contents were sorted into different bags by moss and plant type. Two soil cores (7 cm in diameter × 12 cm in depth) were taken from each plot and divided into three fractions: lichens, O (organic) horizon, and A (mineral) horizon. Depth of the soil organic layer is reported in the supplement (Table S2). We then combined fractions of the same type in the field. Samples were kept cool during transportation and subsequently stored at − 20 °C until processing at the University of California, Irvine. In the lab, we separated the vegetation samples into herbaceous (leaves and stems) and woody biomass (see Table S3 for list of plant species and for how plant types were categorized). The O and A soil horizons were sieved and separated manually into root biomass, soil, and other organic matter biomass components. We estimated bulk density of the soil horizons by calculating soil volumes and dry weights. We separated the lichen fraction into lichen biomass, litter, and soil components (see Table S4 for approximate percentages). However, since it was difficult to disentangle these components precisely, the lichen fraction was treated as a single unit in subsequent analyses. After final partitioning of each of the plant, moss, and soil samples, all samples were dried at 60 °C, weighed for biomass, and subsamples were finely ground using a

ball mill. The subsamples were then combusted for C:N using a Thermo Scientific FlashEA 1112 Nitrogen and Carbon analyzer. Pool size for each aboveground and belowground component was estimated using the biomass, bulk density (when applicable), and elemental analysis data. It was not possible to estimate pool size for the mineral horizon because, unlike the organic horizon, we did not sample the entire horizon.

Data were tested for normality and log-transformed if needed. Two-tailed, paired *t*-tests at $\alpha < 0.05$ were conducted to test for differences between the paired control and warmed plots. We also used a generalized linear model, weighted by mass, to check for differences in plant community composition in the plots and treatments in R version 3.4.1 (R Core Team 2017). Correlations were tested (also in R) to identify relationships between the aboveground and belowground variables measured. Because our sample size was relatively small (five pairs of plots), we conducted a power analysis in G*Power (Erdfeiler et al. 2009) to determine the sample size needed to achieve a power of 0.80.

Results

After 13 years of the greenhouse warming treatment, soil C in the organic layer decreased by 19.1% in the warmed treatment (Table 1; $P = 0.048$), while understory aboveground biomass trended towards C stocks increasing by 1.5- to 4-fold (except for moss). Total aboveground biomass C was higher under the warmed plots, but the difference was not statistically significant (Table 1; $P = 0.236$). However, separating the data by vegetation type, we observed that moss decreased by 88.3% with greenhouse warming (Table 1; $P = 0.034$). In contrast, the C biomass of herbaceous vegetation, woody vegetation, and lichen increased with the warming treatment, although these trends are only marginally significant at most ($P = 0.166$, $P = 0.069$, and $P = 0.285$, respectively). Based on the power analysis, we suspect that we may have detected significance with a larger sample size (Table S5). In terms of aboveground biomass of individual plant species, there were no significant differences between the treatments (Table S6). In addition, soil organic horizon depth did not change with the warming treatment ($P = 0.922$).

Table 1 Effects of greenhouse warming on boreal forest carbon and nitrogen pools after 13 years of treatment ± 1 standard error

	C (g m^{-2})		<i>P</i>	N (g m^{-2})		<i>P</i>
	Control	Greenhouse		Control	Greenhouse	
Herbaceous vegetation	19.96 $\pm$ 6.83	77.32 $\pm$ 38.75	0.166	0.50 $\pm$ 0.19	1.34 $\pm$ 0.59	0.259
Woody vegetation	33.63 $\pm$ 20.00	97.05 $\pm$ 32.77	0.069	0.37 $\pm$ 0.23	0.53 $\pm$ 0.18	0.511
Moss	66.50 $\pm$ 25.01	7.78 $\pm$ 6.07	0.034	1.23 $\pm$ 0.45	0.34 $\pm$ 0.30	0.142
Lichen fraction	193.64 $\pm$ 74.77	301.83 $\pm$ 67.57	0.285	2.09 $\pm$ 0.74	2.55 $\pm$ 0.48	0.687
Sum aboveground	313.73 $\pm$ 59.94	483.97 $\pm$ 122.25	0.236	4.19 $\pm$ 1.25	4.76 $\pm$ 1.15	0.773
Organic soil horizon						
Roots	407.85 $\pm$ 132.86	290.10 $\pm$ 97.8	0.595	6.13 $\pm$ 2.40	6.00 $\pm$ 1.45	0.957
Soil	679.02 $\pm$ 84.03	549.47 $\pm$ 36.95	0.048	25.25 $\pm$ 3.74	20.83 $\pm$ 1.54	0.287
Other	15.76 $\pm$ 13.11	46.92 $\pm$ 31.50	0.276	0.17 $\pm$ 0.14	0.57 $\pm$ 0.34	0.307
Sum belowground	1102.63 $\pm$ 179.03	886.50 $\pm$ 148.75	0.115	31.55 $\pm$ 4.83	27.40 $\pm$ 2.44	0.350
Total above and belowground	1416.36 $\pm$ 181.49	1370.47 $\pm$ 255.38	0.810	35.74 $\pm$ 4.56	32.17 $\pm$ 2.99	0.376

Bold indicates significance ($P \leq 0.05$)

The greenhouse warming treatment increased allocation of aboveground vegetative C by 13%. Root biomass decreased in the warming treatment by nearly a third, albeit non-significantly ($P = 0.595$), while total aboveground vegetation increased (Table 1). There was also a positive relationship between root biomass C and moss biomass C ($R = 0.698$; $P = 0.025$; Table S7). However, no other significant relationships between aboveground and belowground C pools were evident (Table S7).

Percent C was higher for herbaceous and woody vegetation in the greenhouse warmed plots, but this trend was not statistically significant (Table 2; $P = 0.270$ and $P = 0.108$, respectively). Percent N was significantly lower in warmed plots for both herbaceous and woody vegetation (Table 2; $P = 0.044$ and $P = 0.028$, respectively), resulting in higher C:N ratios in the warmed plots (Table 2; herbaceous $P = 0.055$; woody $P = 0.118$). Percent C and %N in the soil layers did not change significantly with the warming treatment (Table 2).

Discussion

To our knowledge, this work is the first to directly measure how C and N pools respond to long-term warming in an Alaskan, permafrost-free boreal forest. We found that the long-term greenhouse warming treatment significantly reduced soil C in the organic layer and moss biomass C (Fig. 1b). At the same time, aboveground plant biomass C tended to increase while root C tended to decrease. Altogether, the distribution of C stocks within this ecosystem tended to shift from belowground to aboveground in response to the warming treatment.

These results are important because permafrost-free boreal forests are understudied, yet represent approximately 45–60% of all boreal forests (Allison and Treseder 2011). Forests cover over 30% of Earth's land surface, with more than a third of that coming from boreal forests (Bonan 2008). Understanding the uncertainties associated with these systems' responses provides greater clarity for biogeochemical model parameterization. These findings also corroborate other permafrost-free boreal forest studies (Niinistö et al. 2004; Bronson et al. 2008), which find that CO₂ fluxes from boreal forest soils increase with warming.

Table 2 Effects of greenhouse warming on boreal forest percent carbon, percent nitrogen, and C:N ratios after 13 years of treatment ± 1 standard error

	%C			%N			C:N		
	Control	Greenhouse	<i>P</i>	Control	Greenhouse	<i>P</i>	Control	Greenhouse	<i>P</i>
Herbaceous vegetation	49.76 $\pm$ 0.42	50.28 $\pm$ 0.42	0.270	1.15 $\pm$ 0.07	0.92 $\pm$ 0.07	0.044	44.08 $\pm$ 2.77	55.48 $\pm$ 3.91	0.055
Woody vegetation	49.35 $\pm$ 0.43	50.73 $\pm$ 0.36	0.108	0.61 $\pm$ 0.06	0.36 $\pm$ 0.13	0.028	83.63 $\pm$ 8.29	253.57 $\pm$ 91.68	0.118
Moss	44.22 $\pm$ 0.67	44.29 $\pm$ 5.61	0.958	0.87 $\pm$ 0.07	1.05 $\pm$ 0.25	0.523	52.86 $\pm$ 5.56	52.21 $\pm$ 14.89	0.896
Lichen fraction	48.93 $\pm$ 2.39	47.49 $\pm$ 3.56	0.959	0.67 $\pm$ 0.30	0.42 $\pm$ 0.05	0.410	106.44 $\pm$ 23.03	118.95 $\pm$ 14.82	0.275
Organic soil horizon									
Roots	48.97 $\pm$ 1.55	48.21 $\pm$ 3.31	0.868	0.71 $\pm$ 0.10	1.27 $\pm$ 0.39	0.305	74.28 $\pm$ 9.37	50.47 $\pm$ 11.61	0.292
Soil	24.09 $\pm$ 3.89	24.71 $\pm$ 3.57	0.899	0.86 $\pm$ 0.11	0.92 $\pm$ 0.09	0.705	27.46 $\pm$ 1.35	26.58 $\pm$ 1.40	0.663
Mineral soil horizon									
Roots	43.48 $\pm$ 3.49	47.05 $\pm$ 2.33	0.406	1.18 $\pm$ 0.19	1.03 $\pm$ 0.19	0.677	44.64 $\pm$ 13.21	52.13 $\pm$ 10.23	0.730
Soil	9.93 $\pm$ 1.85	8.93 $\pm$ 1.81	0.602	0.37 $\pm$ 0.09	0.35 $\pm$ 0.10	0.655	28.01 $\pm$ 2.79	27.85 $\pm$ 2.51	0.908

Bold indicates significance ($P \leq 0.05$)

Altogether, these results suggest that warming can alter C pools in boreal forests lacking permafrost.

We found that the soil organic layer experienced a 19.1% reduction in C with the warming treatment, supporting Hypothesis 1. Declines in soil C are consistent with results of a prior study at this site predicting soil C loss with warming due to shifts in the fungal community, which could improve breakdown of recalcitrant C (Treseder et al. 2016). In contrast, other studies from this site found that warming and drying during the growing season suppressed microbial activity and decomposition (Allison and Treseder 2008; Romero-Olivares et al. 2017), suggesting a delay in soil C loss. However, in the context of our results, this suppression of microbial activity may be reflective of only the short-term or seasonal response (Schmidt et al. 2007). This could be due to the relatively quick successional changes of the microbial community (Schmidt et al. 2007; Voriskova and Baldrian 2013) or depletion of the labile organic matter (Knorr et al. 2005). Microbial activity may return to pre-disturbance levels or increase once the community is adapted to the new environmental conditions (Allison et al. 2010; Karhu et al. 2014). Since aboveground C biomass increased with the warming treatment, it is unlikely that lower aboveground litter production was responsible for the decline in soil C.

Declines in soil C in the organic layer with long-term warming are common (Kane and Vogel 2009; DeAngelis et al. 2015). However, a recent study from a boreal forest in Eastern Canada contrasts our results. They found no change in soil C stocks with 9 years of warming treatment (Marty et al. 2019). This discrepancy could be due to differences in topography, C quality, soil depth, or experimental design between the Eastern Canadian study and ours.

Also in support of Hypothesis 1, moss biomass C decreased with warming by 88.3%. This considerable decline in moss could potentially be attributed to greater susceptibility to water loss with warming (Charron and Quatrano 2009) since moisture declined in our warmed plots by 22% (Allison and Treseder 2008). However, in support of Hypothesis 2, the herbaceous and woody vegetation increased with the warming treatment (Fig. 1b). This increase in aboveground vegetation could be due to removal of temperature limitations (Hobbie et al. 1999) or the ability to produce deeper roots to acquire water

(Comas et al. 2013; Lindh et al. 2014). These increases in aboveground vegetation could also be an unintended consequence of the greenhouse warming treatment, such as decreased herbivory (Aronson and McNulty 2009). In contrast, the greenhouse warming treatment reduced photosynthetic active radiation by 30–40% (Allison and Treseder 2008), yet we found an increase in photosynthetic biomass. Perhaps with a different warming technique, the aboveground C response to warming would be more pronounced. The decrease in moss and increase in herbaceous and woody vegetation may neutralize the effect of the warming treatment on total aboveground C pools.

In addition to these changes in aboveground biomass pools, root biomass C declined with the warming treatment, although not significantly (Table 1). Furthermore, root and moss biomass C were positively correlated (Table S7). These results are surprising given our predictions about moisture structuring the vegetation response. However, since aboveground vegetation %N decreased with the warming treatment (increasing aboveground vegetation C:N), perhaps N limitation plays a role. While warming is typically thought to decrease N limitation owing to increased N mineralization (Rustad et al. 2001), low soil moisture can slow N mineralization (Beier et al. 2008). Perhaps warming and drying resulted in a deeper rooting system to acquire water and nitrogen that was not captured in our experiment. Inclusion of deeper soil horizons, and their roots, may provide additional clarity, especially since C and N stocks in boreal forests can be substantial in these deeper layers (Kane et al. 2005; Vogel et al. 2005; Marty et al. 2015, 2017). Additionally, we only measured understory aboveground biomass. Inclusion of trees may further explain the relationship between aboveground and belowground pools in this critical ecosystem.

In conclusion, we did not find that warming led to a net loss or gain of C. However, our results suggest that permafrost-free boreal forests are susceptible to C loss from soil and moss with warming. Carbon losses from soil and moss represent approximately 9% and 4% of the total C stock calculated in our experiment, respectively. These changes could contribute to climate change if increases in herbaceous and woody biomass no longer compensate for these losses. Furthermore, if vegetative C continues to transfer from belowground to aboveground, we might expect

habitat shifts and future changes to C stocks. Above-ground pools may be less stable than belowground pools for storing C (Zhou et al. 2006), so an increase in the proportion of aboveground C could cause additional C losses with disturbance. Knowledge of individual warming responses from different C pools improves mechanistic understanding of ecosystem responses to climate change, which is especially important for this vulnerable forest system.

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