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1

Abstract

26 The potential consequences of global warming for ecosystem carbon stocks
27 are a major concern, particularly in high-latitude regions where soil carbon
28 pools are especially large. Research on soil and plant carbon responses to
29 warming are often based on short-term (<10 year) warming experiments.
30 Furthermore, carbon budgets from boreal forests, which contain at least 10-
31 20% of the global soil carbon pool, have shown mixed responses to warming.
32 In this study, we measured carbon and nitrogen budgets (i.e., soil and
33 understory vegetation carbon and nitrogen stocks) from a 13-year
34 greenhouse warming experiment in an Alaskan boreal forest. Although there
35 were no differences in total aboveground + belowground pools, the carbon in
36 the moss biomass and in the soil organic layer significantly decreased with
37 the warming treatment (-88.3% and -19.1%, respectively). Declines in moss
38 biomass carbon may be a consequence of warming-associated drying, while
39 shifts in the soil microbial community could be responsible for the decrease
40 in carbon in the soil organic layer. Moreover, in response to warming,
41 aboveground plant biomass carbon tended to increase while root biomass
42 carbon tended to decrease, so carbon allocation may shift aboveground with
43 warming. Overall these results suggest that permafrost-free boreal forests
44 are susceptible to soil carbon loss with warming.

45

3

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). 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

4

69 occur faster (Chapin et al. 2000; Shukla et al. 2019). Here, we took

70 advantage of a 13-year greenhouse warming experiment in an Alaskan

71 boreal forest to examine aboveground and belowground C and N budgets.

72 Previous studies at this site have shown that, when compared to control

73 plots, warmed plots have reduced fungal abundance and increased fungal

74 diversity (Allison and Treseder 2008; Treseder et al. 2016). Fungal

75 decomposers tend to dominate under warming and drying because of their

76 drought-resistant growth forms (Barnard et al. 2013; Treseder and Lennon

77 2015) and their ability to decompose recalcitrant compounds (e.g., cellulose

78 and lignin), which may become more abundant with warming due to changes

79 in the plant community (Mcguire et al. 2010; Fontaine et al. 2011; Xiong et

80 al. 2014). Fungi tend to specialize on recalcitrant compounds that may have

81 higher temperature sensitivities for decomposition, thus conferring an

82 advantage over bacteria which tend not to target recalcitrant compounds

83 (Romero-Olivares et al. 2017). Warmed plots at this site were also found to

84 have slower litter decomposition (Romero-Olivares et al. 2017), increased

85 cellulose- and starch-degrading enzyme production (German and Allison

86 2015), and lowered respiration rates (German and Allison 2015). However,

87 no studies have determined whether any of these changes in decomposition

88 dynamics have elicited measurable changes in soil and plant C and N pools.

89 A fuller understanding of the relationship between aboveground and

90 belowground C and N dynamics will provide better insight into whether or

5

91 not ecosystem C gains or losses should be expected with warming in this
92 critical ecosystem.

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

107

108 **Methods**

109   Our study site is located in a mature black spruce (*Picea mariana*)
110 boreal forest on the Fort Greely military base near Delta Junction, Alaska,
111 USA (63˚55'N, 145˚44'W). The understory vegetation is dominated by
112 mosses, lichens, and shrubs (*Vaccinium uliginosum*, V. *vitis-idaea*, *Ledum*
113 *groenlandicum*, *Empetrum nigrum*, and *Betula glandulosa*) (Treseder et al.

6

114   2004). The soil is an Inceptisol, with an average organic horizon of 9.8 cm

115   (King et al. 2002) and pH of 4.9 (Hanson et al. 2008).

116   In 2005, a greenhouse warming experiment was established with five

117   pairs of 2.5 x 2.5 m plots within a 1 km^2 area in the open canopy forest, as

118   described in Allison and Treseder (2008). In each pair, one plot was covered

119   with a wood frame structure covered in greenhouse plastic film in order to

120   warm the plots. Gaps between the frame and the plastic allowed air to

121   circulate, and gutters and tubing allowed water to flow in; the other plot was

122   left unmanipulated as a control (Allison and Treseder 2008). All plots

123   excluded large trees. Air temperature increased by an average of 1.6°C and

124   Onset HOBO data loggers recorded an average of 0.5°C increase in soil

125   temperature at 5 cm depth (Table S1; Allison and Treseder 2008). As a result

126   of the greenhouse warming treatment, soil moisture also decreased by an

127   average of 22% in the warmed plots (Table S1; Allison and Treseder 2008).

128   Passive warming approaches, such as this one, not only warm and dry but

129   can also alter temperature variation, light intensity, CO_2 concentration, wind

130   speed, snow cover, and herbivory (Kennedy 1995; Aronson and McNulty

131   2009; Bokhorst et al. 2011). However, in remote areas where line power is

132   not available, greenhouse warming is a practical and cost-efficient way to

133   elevate temperature. Passive warming treatments are also good at

134   minimizing soil disturbance compared to other approaches like heated cables

135   (Aronson and McNulty 2009). Here, when we refer to the *warming treatment,*

136 we are referring to the collective change in the microclimate which includes,

137 but is not limited to, warming and drying.

138   In July 2017, two 0.6 x 0.6 m subsamples of aboveground biomass

139 were collected from each plot. The two subsamples were combined in the

140 field and the contents were sorted into different bags by moss and plant

141 type. Two soil cores (7 cm in diameter × 12 cm in depth) were taken from

142 each plot and divided into three fractions: lichens, O (organic) horizon, and A

143 (mineral) horizon. Depth of the soil organic layer is reported in the

144 supplement (Table S2). We then combined fractions of the same type in the

145 field. Samples were kept cool during transportation and subsequently stored

146 at -20°C until processing at the University of California, Irvine. In the lab, we

147 separated the vegetation samples into herbaceous (leaves and stems) and

148 woody biomass (see Table S3 for list of plant species and for how plant types

149 were categorized). The O and A soil horizons were sieved and separated

150 manually into root biomass, soil, and other organic matter biomass

151 components. We estimated bulk density of the soil horizons by calculating

152 soil volumes and dry weights. We separated the lichen fraction into lichen

153 biomass, litter, and soil components (see Table S4 for approximate

154 percentages). However, since it was difficult to disentangle these

155 components precisely, the lichen fraction was treated as a single unit in

156 subsequent analyses. After final partitioning of each of the plant, moss, and

157 soil samples, all samples were dried at 60°C, weighed for biomass, and

158 subsamples were finely ground using a ball mill. The subsamples were then

8

159 combusted for C:N using a Thermo Scientific FlashEA 1112 Nitrogen and

160 Carbon analyzer. Pool size for each aboveground and belowground

161 component was estimated using the biomass, bulk density (when

162 applicable), and elemental analysis data. It was not possible to estimate pool

163 size for the mineral horizon because, unlike the organic horizon, we did not

164 sample the entire horizon.

165   Data were tested for normality and log-transformed if needed. Two-

166 tailed, paired t-tests at $\alpha<0.05$ were conducted to test for differences

167 between the paired control and warmed plots. We also used a generalized

168 linear model, weighted by mass, to check for differences in plant community

169 composition in the plots and treatments in R version 3.4.1 (R Core Team

170 2017). Correlations were tested (also in R) to identify relationships between

171 the aboveground and belowground variables measured. Because our sample

172 size was relatively small (five pairs of plots), we conducted a power analysis

173 in G*Power (Erdfelder et al. 2009) to determine the sample size needed to

174 achieve a power of 0.80.

175

176 **Results**

177   After 13 years of the greenhouse warming treatment, soil C in the

178 organic layer decreased by 19.1% in the warmed treatment (Table 1; $P =$

179 0.048), while understory aboveground biomass trended towards C stocks

180 increasing by 1.5- to 4-fold (except for moss). Total aboveground biomass C

181 was higher under the warmed plots, but the difference was not statistically

9

182 significant (Table 1; P = 0.236). However, separating the data by vegetation

183 type, we observed that moss decreased by 88.3% with greenhouse warming

184 (Table 1; P = 0.034). In contrast, the C biomass of herbaceous vegetation,

185 woody vegetation, and lichen increased with the warming treatment,

186 although these trends are only marginally significant at most (P = 0.166, P =

187 0.069, and P = 0.285, respectively). Based on the power analysis, we

188 suspect that we may have detected significance with a larger sample size

189 (Table S5). In terms of aboveground biomass of individual plant species,

190 there were no significant differences between the treatments (Table S6). In

191 addition, soil organic horizon depth did not change with the warming

192 treatment (P = 0.922).

193   The greenhouse warming treatment increased allocation of

194 aboveground vegetative C by 13%. Root biomass decreased in the warming

195 treatment by nearly a third, albeit non-significantly (P = 0.595), while total

196 aboveground vegetation increased (Table 1). There was also a positive

197 relationship between root biomass C and moss biomass C (R = 0.698; P =

198 0.025; Table S7). However, no other significant relationships between

199 aboveground and belowground C pools were evident (Table S7).

200   Percent C was higher for herbaceous and woody vegetation in the

201 greenhouse warmed plots, but this trend was not statistically significant

202 (Table 2; P = 0.270 and P = 0.108, respectively). Percent N was significantly

203 lower in warmed plots for both herbaceous and woody vegetation (Table 2; P

204 = 0.044 and P = 0.028, respectively), resulting in higher C:N ratios in the

10

205 warmed plots (Table 2; herbaceous $P = 0.055$; woody $P = 0.118$). Percent C

206 and %N in the soil layers did not change significantly with the warming

207 treatment (Table 2).

208

209 **Discussion**

210   To our knowledge, this work is the first to directly measure how C and

211 N pools respond to long-term warming in an Alaskan, permafrost-free boreal

212 forest. We found that the long-term greenhouse warming treatment

213 significantly reduced soil C in the organic layer and moss biomass C (Figure

214 1B). At the same time, aboveground plant biomass C tended to increase

215 while root C tended to decrease. Altogether, the distribution of C stocks

216 within this ecosystem tended to shift from belowground to aboveground in

217 response to the warming treatment.

218   These results are important because permafrost-free boreal forests are

219 understudied, yet represent approximately 45-60% of all boreal forests

220 (Allison and Treseder 2011). Forests cover over 30% of Earth's land surface,

221 with more than a third of that coming from boreal forests (Bonan 2008).

222 Understanding the uncertainties associated with these systems' responses

223 provides greater clarity for biogeochemical model parameterization. These

224 findings also corroborate other permafrost-free boreal forest studies (Niinisto

225 et al. 2004; Bronson et al. 2008), which find that CO_2 fluxes from boreal

226 forest soils increase with warming. Altogether, these results suggest that

227 warming can alter C pools in boreal forests lacking permafrost.

11

228   We found that the soil organic layer experienced a 19.1% reduction in

229   C with the warming treatment, supporting Hypothesis 1. Declines in soil C

230   are consistent with results of a prior study at this site predicting soil C loss

231   with warming due to shifts in the fungal community, which could improve

232   breakdown of recalcitrant C (Treseder et al. 2016). In contrast, other studies

233   from this site found that warming and drying during the growing season

234   suppressed microbial activity and decomposition (Allison and Treseder 2008;

235   Romero-Olivares et al. 2017), suggesting a delay in soil C loss. However, in

236   the context of our results, this suppression of microbial activity may be

237   reflective of only the short-term or seasonal response (Schmidt et al. 2007).

238   This could be due to the relatively quick successional changes of the

239   microbial community (Schmidt et al. 2007; Voriskova and Baldrian 2013) or

240   depletion of the labile organic matter (Knorr et al. 2005). Microbial activity

241   may return to pre-disturbance levels or increase once the community is

242   adapted to the new environmental conditions (Allison et al. 2010; Karhu et

243   al. 2014). Since aboveground C biomass increased with the warming

244   treatment, it is unlikely that lower aboveground litter production was

245   responsible for the decline in soil C.

246   Declines in soil C in the organic layer with long-term warming are

247   common (Kane and Vogel 2009; DeAngelis et al. 2015). However, a recent

248   study from a boreal forest in Eastern Canada contrasts our results. They

249   found no change in soil C stocks with 9 years of warming treatment (Marty et

250   al. 2019). This discrepancy could be due to differences in topography, C

12

251   quality, soil depth, or experimental design between the Eastern Canadian

252   study and ours.

253   Also in support of Hypothesis 1, moss biomass C decreased with

254   warming by 88.3%. This considerable decline in moss could potentially be

255   attributed to greater susceptibility to water loss with warming (Charron and

256   Quatrano 2009) since moisture declined in our warmed plots by 22% (Allison

257   and Treseder 2008). However, in support of Hypothesis 2, the herbaceous

258   and woody vegetation increased with the warming treatment (Figure 1B).

259   This increase in aboveground vegetation could be due to removal of

260   temperature limitations (Hobbie et al. 1999) or the ability to produce deeper

261   roots to acquire water (Comas et al. 2013; Lindh et al. 2014). These

262   increases in aboveground vegetation could also be an unintended

263   consequence of the greenhouse warming treatment, such as decreased

264   herbivory (Aronson and McNulty 2009). In contrast, the greenhouse warming

265   treatment reduced photosynthetic active radiation by 30-40% (Allison and

266   Treseder 2008), yet we found an increase in photosynthetic biomass.

267   Perhaps with a different warming technique, the aboveground C response to

268   warming would be more pronounced. The decrease in moss and increase in

269   herbaceous and woody vegetation may neutralize the effect of the warming

270   treatment on total aboveground C pools.

271   In addition to these changes in aboveground biomass pools, root

272   biomass C declined with the warming treatment, although not significantly

273   (Table 1). Additionally, root and moss biomass C positively correlated (Table

      13

274 S7). These results are surprising given our predictions about moisture

275 structuring the vegetation response. However, since aboveground vegetation

276 %N decreased with the warming treatment (increasing aboveground

277 vegetation C:N), perhaps N limitation plays a role. While warming is typically

278 thought to decrease N limitation owing to increased N mineralization (Rustad

279 et al. 2001), low soil moisture can slow N mineralization (Beier et al. 2008).

280 This mechanism could elicit lower root growth with moisture loss.

281 Alternatively, perhaps warming and drying resulted in a deeper rooting

282 system to acquire water and nitrogen that was not captured in our

283 experiment. Inclusion of deeper soil horizons, and their roots, may provide

284 additional clarity, especially since C and N stocks in boreal forests can be

285 substantial in these deeper layers (Kane et al. 2005; Vogel et al. 2005; Marty

286 et al. 2015, 2017). Additionally, we only measured understory aboveground

287 biomass. Inclusion of trees may further explain the relationship between

288 aboveground and belowground pools in this critical ecosystem.

289   In conclusion, we did not find that warming led to a net loss or gain of

290 C. However, our results suggest that permafrost-free boreal forests are

291 susceptible to C loss from soil and moss with warming. Carbon losses from

292 soil and moss represent approximately 9% and 4% of the total C stock

293 calculated in our experiment, respectively. These changes could contribute

294 to climate change if increases in herbaceous and woody biomass no longer

295 compensate for these losses. Furthermore, if vegetative C continues to

296 transfer from belowground to aboveground, we might expect habitat shifts

14

297 and future changes to C stocks. Aboveground pools may be less stable than

298 belowground pools for storing C (Zhou et al. 2006), so an increase in the

299 proportion of aboveground C could cause additional C losses with

300 disturbance. Knowledge of individual warming responses from different C

301 pools improves mechanistic understanding of ecosystem responses to

302 climate change, which is especially important for this vulnerable forest

303 system.

304

312

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491 **Table 1.** Effects of greenhouse warming on boreal forest carbon and

492 nitrogen pools after 13 y of treatment ± 1 standard error. Bold indicates

493 significance ($P \le 0.05$).

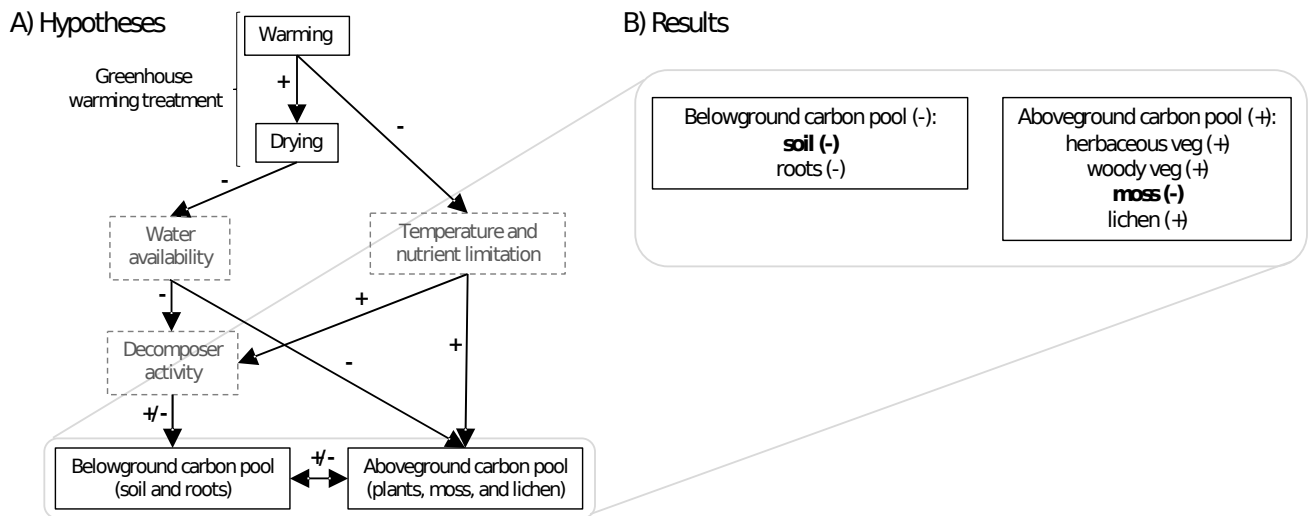|	C (g m^{-2})			N (g m^{-2})		
	Control	Greenhouse	*P*	Control	Greenhouse	*P*
Herbaceous vegetation	19.96 ± 6.83	77.32 ± 38.75	0.166	0.50 ± 0.19	1.34 ± 0.59	0.259
Woody vegetation	33.63 ± 20.00	97.05 ± 32.77	0.069	0.37 ± 0.23	0.53 ± 0.18	0.511
Moss	**66.50 ± 25.01**	**7.78 ± 6.07**	**0.034**	1.23 ±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

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496 **Table 2.** Effects of greenhouse warming on boreal forest percent carbon, percent nitrogen, and C:N ratios

497 after 13 y of treatment ± 1 standard error. Bold indicates significance ($P \leq 0.05$).

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

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A) Hypotheses

Warming

Greenhouse warming treatment

+

Drying

-

-

Water availability

-

Temperature and nutrient limitation

-

+

Decomposer activity

+

-

+/-

Belowground carbon pool (soil and roots)

+/-

Aboveground carbon pool (plants, moss, and lichen)

B) Results

Belowground carbon pool (-):
soil (-)
roots (-)

Aboveground carbon pool (+):
herbaceous veg (+)
woody veg (+)
moss (-)
lichen (+)

500

Figure 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. Bolded text (soil, moss, and the relationship between roots and moss) specifies significance ($P \leq 0.05$).

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