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Variation in Fine Root Characteristics and Nutrient Dynamics Across Alaskan Ecosystems

Lindsay A. McCulloch,[1]* Heather Kropp,[2] Alexander Kholodov,[3] Catherine L. Cardelús,[4] Susan M. Natali,[5] and Michael M. Loranty[6]

[1]*Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island, USA;* [2]*Environmental Studies Program, Hamilton College, Clinton, New York, USA;* [3]*Geophysical Institute, University of Alaska Fairbanks, Fairbanks, Alaska, USA;* [4]*Department of Biology, Colgate University, Hamilton, New York, USA;* [5]*Woodwell Climate Research Center, Falmouth, Massachusetts, USA;* [6]*Department of Geography, Colgate University, Hamilton, New York, USA*

Abstract

Carbon cycle perturbations in high-latitude ecosystems associated with rapid warming can have implications for the global climate. Belowground biomass is an important component of the carbon cycle in these ecosystems, with, on average, significantly more vegetation biomass belowground than aboveground. Large quantities of dead root biomass are also in these ecosystems owing to slow decomposition rates. Current understanding of how live and dead root biomass carbon pools vary across high-latitude ecosystems and the environmental conditions associated with this variation is limited due to the labor- and time-intensive nature of data collection. To that end, we examined patterns and factors (abiotic and biotic) associated with the variation in live and dead fine root biomass (FRB) and FRB carbon (C), nitrogen (N) and phosphorus concentrations for 23 sites across a latitudinal gradient in Alaska, spanning both boreal forest and tundra biomes. We found no difference in the live or dead FRB variables between these biomes, despite large differences in predominant vegetation types, except for significantly higher live FRB C:N ratios in boreal sites. Soil C:N ratio, moisture, and temperature, along with moss cover, explained a substantial portion of the dead:live FRB ratio variability across sites. We find all these factors have negative relationships with dead FRB, while having positive or no relationship with live FRB. This work demonstrates that FRB does not necessarily correlate with aboveground vegetation characteristics, and it highlights the need for finer-scale measurements of abiotic and biotic factors to understand FRB landscape variability now and into the future.

Key words: Fine roots; Boreal; Tundra; Belowground biomass; Decomposition; Carbon.

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Highlights

- Site-level characterization of live and dead fine root biomass.

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Author Contributions L.A.M and M.M.L. conceived of the study. L.A.M., H.K., A.K., C.L.C.,S.M.N., and M.M.L performed the research. L.A.M. analyzed the data and wrote the manuscript. All authors contributed to editing and reviewing the manuscript.

**Corresponding author; e-mail:* Lindsay_McCulloch@brown.edu

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- Sampling across a gradient of ecosystems and climate conditions.
- Microenvironment explains fine root biomass dynamics better than biome type.

Introduction

The Arctic is experiencing amplified climate warming that is likely to continue into the future (Chapin and others 2005; Serreze and Barry 2011; Graham and others 2017; Box and others 2019). The resulting changes in ecosystem carbon (C) cycling can impact the global C cycle, potentially creating a positive feedback to climate change (Abbott and others 2016). C stored in soils is particularly important, as it constitutes a substantial portion of total ecosystem C stocks in high-latitude ecosystems. Nearly 50% of the global soil organic C (SOC) pool is found in Arctic tundra and boreal forest ecosystems (Hobbie and Chapin 1998; Jackson and others 2017), where it is held in perennially frozen permafrost soils (Hugelius and others 2014) and seasonally thawed surficial soil layers (that is, active layer). The fate of SOC in the active layer with continued climate warming remains unresolved, owing largely to uncertainties surrounding belowground biomass dynamics (Iversen and others 2015; Blume-Werry and others 2016).

Belowground biomass contributes to the integrity of active layer SOC stocks and comprises about 80% of vegetative biomass in tundra ecosystems (Iversen and others 2015; Blume-Werry and others 2017b). As such, belowground biomass will play an important role in determining the strength of Arctic carbon cycle perturbations with climate warming. Despite this, the majority of research focused on vegetation influence on changing regional C dynamics has dealt primarily with the effects of aboveground vegetation change, particularly associated with northward tree and shrub expansion (Beck and Goetz 2011; Beck and others 2011; Raynolds and others 2012; Pearson and others 2013; Berner and others 2018). Changes in aboveground vegetation do not always reflect changes in belowground vegetation, with documented differences in phenology, growth, decomposition, and biomass (Iversen and others 2015; Blume-Werry and others 2016, 2017b, 2017a; Sloan and others 2016; McLaren and others 2017).

Root biomass in tundra and boreal ecosystems has the potential to act as a C source and/or sink depending on ecological and climatic conditions that influence the ratio of dead to live root biomass (Segal and Sullivan 2014; Iversen and others 2015). Increases in root growth with deeper seasonally thawed active layers, and warmer, longer growing seasons enhance belowground biomass C pools (Kane and others 1991; Rustad and others 2001; Blume-Werry and others 2016). However, belowground biomass interacts with the organic soil layer, composed of organic material from dead plants and/or animals in varying states of decomposition. In these ecosystems, dead plant biomass can remain in the soil for long time periods since decomposition rates are slow, storing C in the organic layer (Robinson and others 1999; Tarnocai and others 2009; Freschet and others 2013; Segal and Sullivan 2014). Climate warming will alter root biomass contributions to SOC, but this may vary with biome, as these biomes vary in turnover time and decomposition rates (Wookey and others 2009; Blume-Werry and others 2016). Decomposition rates are expected to generally increase, as microbial activity and growing season length increase with warming (Mack and others 2004). Increased decomposition will act as a C source (Rustad and others 2001), and the encroachment of shrub and/or trees into graminoid-dominated tundra can prime the decomposition of old SOM, leading to the release of C (Hartley and others 2012; Parker and others 2015; Street and others 2020). Both of these processes may or may not be offset by vegetation growth (Rustad and others 2001; Hartley and others 2012; Parker and others 2015; Street and others 2020). Therefore, understanding differences in dead and live root biomass dynamics between boreal and tundra biomes, and how they vary across the landscape is necessary to understand how ecological change will affect regional C cycling (Nadelhoffer and others 2002).

Both boreal and tundra biomes store a significant portion of the global SOC stock (Hobbie and Chapin 1998; Jackson and others 2017). However, these biomes are composed of vastly different vegetation types with large differences in aboveground biomass and C:N ratios driven by differences in woody biomass (Thompson and others 2004). Understanding SOC now and into the future is further complicated by different plant functional types even within these biome types (deciduous versus evergreen boreal forests or shrub versus graminoid tundra; Welp and others 2007; Laganière and others 2013; Chadburn and others 2017). North American boreal forests are dominated by trees with relatively deep rooting zones, whereas tundra vegetation is comprised largely of graminoids and low shrubs with shallower root zones and greater vegetation seasonality (Bonan and others 1995; Jackson and others 1996). These dis-

tinctions in aboveground biomass and vegetation structure drive differences in ecosystem function, such as surface energy exchange, overall vegetative biomass, litter input amounts and composition, and decomposition rates, between these two biomes (Apps and others 1993; Bonan and others 1995; Sloan and others 2013, 2016). Comprehensive site-level belowground sampling across large spatial scales is difficult because it is both time and labor intensive (Metcalfe and others 2007; Sloan and others 2013; Iversen and others 2015). This has limited our ability to determine (1) whether there are significant differences in fine root biomass and root characteristics between boreal and tundra biomes and (2) whether those differences contribute to variability in belowground processes between these biomes.

Fine root biomass (roots 2 mm or less in diameter) dynamics are particularly influential to understanding belowground processes because fine roots are relatively fast growing and more reflective of climate than longer-lived coarse roots with slower turnover times (Blume-Werry and others 2017b). Fine roots are centers for nutrient and water absorption and may experience fast turnover rates (Silver and Miya 2001; Rasse and others 2005; Clemmensen and others 2013). Fine roots are associated with higher respiration rates and lower concentrations of total non-structural carbohydrates and cellulose (Matamala and others 2003; Makita and others 2012; McCormack and others 2015), creating the potential of fine roots to significantly contribute to decomposition and C cycle dynamics. The relatively high degree of uncertainty surrounding root biomass responses to climatic change is largely driven by challenges associated with collecting data in these remote regions and the subsequent paucity of data (Iversen and others 2015).

Root biomass contributes to a larger proportion of the overall vegetation biomass in Arctic ecosystems in comparison with temperate and tropical ecosystems (Blume-Werry and others 2016). Despite their outsized role, there are few robust estimates of the proportion of this root biomass that is alive and functioning (Iversen and others 2015). The dead:live root biomass ratio gives estimates not only of what portion of the root mass is functioning (live) but also provides insight into how quickly roots decompose relative to how quickly roots are growing. Previous estimates from high-latitude ecosystems suggest lower turnover rates in roots (0.10–0.20 $year^{-1}$) compared to leaf turnover rates (0.55–0.90 $year^{-1}$; Sloan and others 2013). This relative decomposition to growth rate estimate provides insight to whether this C pool could become an overall C source (high decomposition rates) or C sink (high growth rates). Root biomass can influence northern high-latitude terrestrial C dynamics and associated climate feedbacks, but the patterns of geographic variation in root biomass across biomes are relatively poorly understood, especially in comparison with aboveground biomass. However, there is evidence that root biomass increases linearly with leaf area index (leaf area per unit of ground area) up to LAI = 1 m^2 m^{-2} in some high-latitude ecosystems (Sloan and others 2013).

Here, we characterize patterns variation in root biomass and associated environmental conditions for 23 sites across a latitudinal gradient in Alaska using observations of fine root biomass (FRB) along with key abiotic and biotic factors. We ask: (1) how do FRB characteristics (mass and nutrient concentrations) vary across and within two Alaskan biomes—tundra and boreal forest? (2) What abiotic and/or biotic factors explain variability in FRB? Given the overall larger vegetation biomass values in boreal forests, we predict higher FRB in this biome compared to the tundra. We hypothesized that the C:N ratio of both live and dead FRB would be higher in boreal forest because of the higher proportion of woody biomass in boreal forests compared to the tundra. As such, we expected higher variation in FRB characteristics between biomes than within biomes, and that variability in abiotic and biotic conditions that were likely to influence decomposition and growth rates of FRB (temperature, soil moisture, vegetation type, thaw depth, and so on) would explain within biome variability. For example, higher aboveground biomass and warmer soils may be associated with higher live FRB, whereas observations of water limitation in tundra ecosystems (Eugster and others 2000) suggest that soil moisture may limit live FRB abundance and decomposition of dead FRB.

Methods

Study Sites

We collected soils at 23 sites along a latitudinal gradient throughout Interior Alaska, the Arctic North Slope and Coastal Western Alaska (Figure 1) during July and August 2015 to quantify FRB in tundra and boreal forest biomes of Alaska (Table 1). To have access to soil temperature data, the sites were selected based on the location of existing permafrost boreholes across Alaska (GTN-P 2015). Several sites were located in close proximity, which controlled for geological and climatic differences

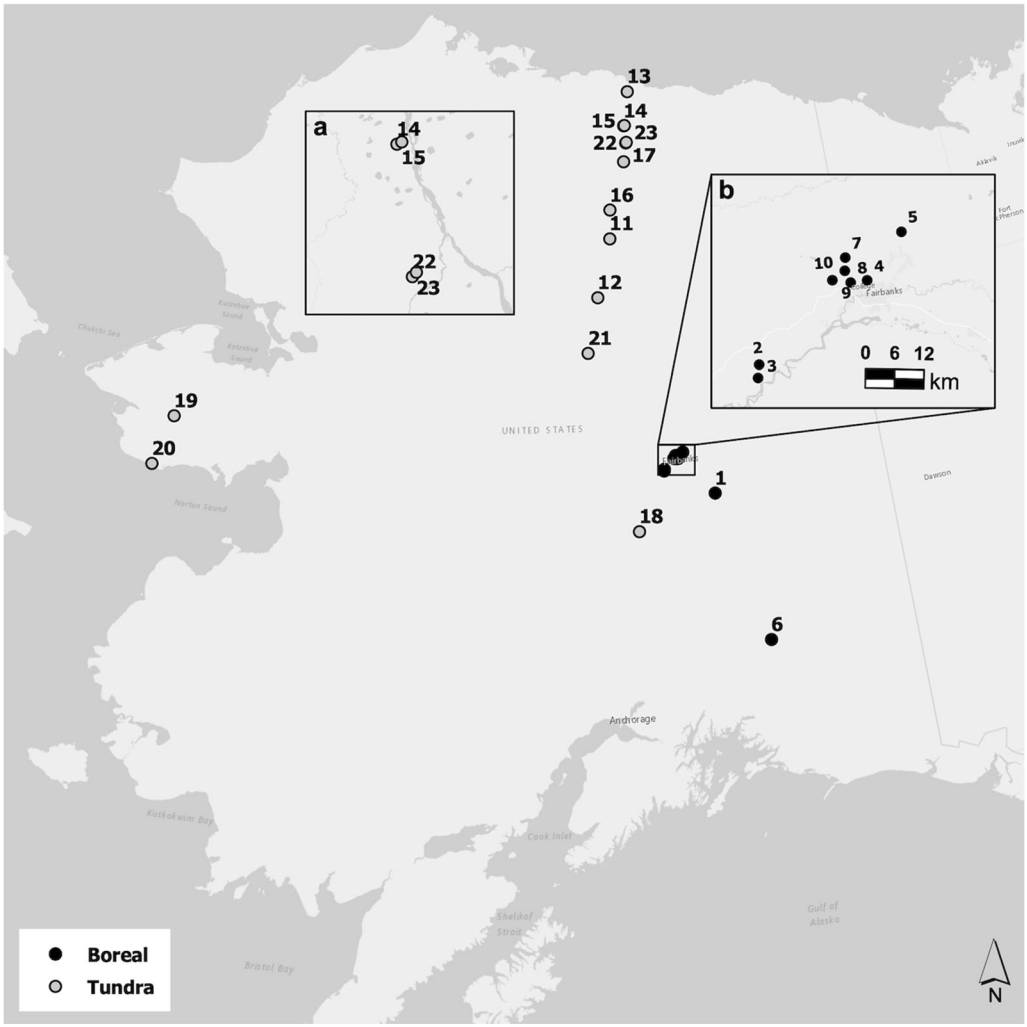

Figure 1. Map of 23 sites in interior, northern, and coastal Alaska. Black circles denote boreal forest sites, and gray circles denote tundra sites. Tundra sites in the inset (**A**) overlap significantly and were slightly jittered for visual purposes.

among sites, allowing differences in vegetation biomass and type to be attributed to the proximal ecosystem characteristics.

Field Sampling

Three organic soil samples were taken from each of the 23 sites ($n = 69$ total cores) along a 28 m transect that was laid with the borehole located near the center of the transect. Sampling began at the 0 m mark and moved 14 m to the east for each additional sample. Soil samples were cut from the ground to an approximate size of 10 cm × 10 cm using a serrated knife. We collected soils to the depth of frozen ground at the time of sampling (20.6 ± 6.6 cm), which was not the full active layer depth (20.7 ± 8.7 cm) and does not represent total FRB but rather FRB at peak growing season from early July to mid-August. Tundra sites were generally sampled later in the growing season with the exception of four boreal sites (sites 1–3 and 6; Table 1). Root biomass was normalized to 10 cm depth to compare across sites. We removed all green living plant biomass, such as mosses, from the sample. Samples that could not be processed immediately were frozen.

Other site variables used in this study include aboveground vegetation cover and biomass, organic layer depth, thaw depth, soil temperature, organic soil moisture, and soil C:N ratio. Visual estimates of aboveground vegetation cover by functional type (moss, shrub, herbaceous, lichen) were made using a 1 m^2 quadrat at the soil sampling location. Vegetation within these plots was collected and dried at 60 °C for at least 48 h for aboveground biomass estimates (Natali and Kholodov 2016). We recorded the sampling depth of

Table 1. Site Descriptions Including Site Name, Date of Sample Collection, Latitude, Longitude, Biome Classification, a Site Description, and Mean Annual Air Temperature (°C)

Site	Name	Date	Lat	Long	Biome	Site description	Temperature (°C)
1	Birch Lake	8/4/15	64.32	146.69	Boreal	Black spruce-dominated forest with Labrador tea, tussocks, and moss	− 3.4
2	Bonanza burned	8/2/15	64.71	148.29	Boreal	Black spruce and birch dominated with Labrador tea understory. Some dense regeneration and lots of woody debris	− 3.2
3	Bonanza unburned	8/2/15	64.71	148.29	Boreal	Black spruce forest with sphagnum, rubus, and Labrador tea understory. Few larix	− 3.2
4	College	7/5/15	64.87	147.86	Boreal	Sparse forest of larix and black spruce with betula, ledum, rubus, alnus, wet sphagnum and tussocks	− 2.9
5	Fox	7/24/15	64.95	147.62	Boreal	Spruce- and birch-dominated site with salix, equisetum, sphagnum, and rubus with no tussocks	− 3.9
6	Gulkana	8/5/15	62.17	145.47	Boreal	Willow- and herb-dominated wet site with few spruce trees	− 3.1
7	Smith Lake 1	7/3/15	64.87	147.86	Boreal	Spruce-dominated forest with *Rosa* sp., ledum, Cornus canadensis understory	− 2.8
8	Smith Lake 2	7/4/15	64.87	147.86	Boreal	Mostly stunted spruce with eriophorum, betula, ledum, vaccinium, sphagnum, rubus, and tussocks	− 2.8
9	Smith Lake 3	7/4/15	64.87	147.86	Boreal	Black spruce-dominated with lots of moss groundcover, ledum, vaccinium, and betula	− 2.8
10	Smith Lake 4	7/3/15	64.87	147.86	Boreal	Sparse spruce-dominated canopy with tussocks, sphagnum, birch, alder, and willow	− 2.8
11	Chandalar	7/8/15	68.07	149.58	Tundra	Betula- and tussock-dominated tundra, eriophorum. Mountains to the east	− 11.6
12	Coldfoot	7/7/15	67.24	150.16	Tundra	Tussocky with betula, ledum, carex, reindeer lichen, snow lichen, eriophorum, and few spruce trees	− 7.7
13	Dead Horse	7/16/15	70.16	148.47	Tundra	Graminoid dominated. Few tussocks and salix shrubs. Frost boils	− 11.1
14	Franklin Bluff-Dry	7/17/15	69.67	148.72	Tundra	Carex, eriophorum, willow, tussock site	− 10.6
15	Franklin Bluff-Wet	7/17/15	69.67	148.72	Tundra	Carex, eriophorum, willow tundra. Ephemerally wet. Little distinction between wet and dry sites	− 10.6
16	Galbraith Lake	7/10/15	68.48	149.5	Tundra	Carex and eriophorum tundra with the Brooks Range to the S, E, W	− 11.4
17	Happy Valley	7/11/15	69.16	148.84	Tundra	Tussock filled with birch, moss, salix, and ledum. Slight slope to the east. South of the Brooks Range	− 10.5
18	Healy	8/8/15	63.88	149.25	Tundra	Tussock-dominated site with few birch and vaccinium	− 4.1
19	Kutizin	7/30/15	65.23	164.83	Tundra	Slightly tussocky site with large betula. Possible pingo to the north	NA

Table 1. continued

Site	Name	Date	Lat	Long	Biome	Site description	Temperature (°C)
20	Nome	7/28/15	64.51	165.3	Tundra	Carex-, vaccinium-, betula-, and lichen-dominated site	NA
21	Old Man	7/6/15	66.45	150.62	Tundra	Ledum, betula, rubus, dried sphagnum. Lots of reindeer lichen	− 6.5
22	Sag MAT	7/13/15	69.43	148.7	Tundra	Tussock-filled site with a slight slope of the N. Salix, betula, eriophorum, and bistort	− 10.7
23	Sag MNT	7/13/15	69.43	148.67	Tundra	Salix, equisetum, lupinus, poppy, and bistort tundra with few tussocks	− 10.7

each soil sample to characterize localized thawed organic layer depth at time of sampling. Soil temperature data presented in this study are the mean annual temperature from June 2014 to June 2015, collected in the upper 10 cm at established boreholes at each site (GTN-P 2015). We also used site averaged variables of aboveground biomass, organic volumetric soil moisture, soil C:N, organic layer depth and thaw depth data and sampling methods that provided on the Arctic Data Center (Natali and others 2016a, b) for this study's analyses.

Determining Live or Dead Status

In the laboratory, each soil sample was weighed and washed using a sieve (0.25 mm) to remove all the soil from the roots. We then separated the roots into dead and live roots using well-established visual and tensile cues (Hayes and Seastedt 1987; Joslin and Henderson 1987). We characterized live roots by their high tensile strength and bright appearance with a white cortex (Figure S1). Live roots were 'plump' and retained fine branches. We categorized dead roots by low tensile strength and dull coloration with a brown or gray cortex. Dead roots were also flat and/or flabby with few intact fine branches (Figure S1). We further separated live and dead roots into fine (< 2 mm) and coarse (> 2 mm) samples (Mack and others 2004). Once sorted, we dried root samples at 60 °C for at least 48 h before weighing. In this study, we did not use coarse roots in the analyses of boreal ecosystems. The 10 cm by 10 cm soil samples were not likely to capture the 'rare' but large coarse roots found in some boreal forest sites that may disproportionally contribute to belowground biomass estimates. However, a 10 cm by 10 cm soil sample was sufficient for tundra sites and coarse roots were measured. We included coarse roots in calculations of below- to aboveground biomass in our tundra sites, but did not for boreal forest sites.

Biomass Nutrient Analysis

We ground live and dead roots separately in a Wiley mill through a #40 screen before being analyzed on a Costech Analytical Elemental Analyzer for C and nitrogen (N) content and C:N. Phosphorus (P) concentrations were determined using an ash digestion (Jones and Case 1996) followed by colorimetric analysis of ortho-phosphorate on an Astoria Pacific colorimetric autoanalyzer.

Statistical Analyses

We explored three main fine root biomass (FRB) response variables (all standardized to 10 cm depth): live FRB (kg m^{-2} of soil), dead FRB (kg m^{-2} of soil) and dead:live FRB. To determine differences between biome types, we performed nested *T* test analyses using the lme function in lme4, with site nested within biome type. We tested for normality and homoscedasticity assumptions for *T* test analysis using Shapiro–Wilk test and the Levene test, respectively.

We used abiotic (soil C:N ratio, soil temperature to 10 cm, organic soil moisture, organic layer depth, thawed organic layer depth (T-OLD) at time of sampling, and thaw depth) and biotic (vegetation cover type and biomass) parameters measured at each site to explain observed variability in these three FRB response variables. We performed multivariate linear regressions for each of the three main FRB response variables (live FRB, dead FRB, dead:live FRB) variables using the previously mentioned abiotic and biotic parameters (vegetation cover and biomass, soil C:N ratio, moisture and temperature, and biome type) to test if these explanatory variables explain variation in FRB within biomes. We also included T-OLD in each

model to characterize the organic layer depth conditions during peak growing season when these samples were taken. We report both *P* values for each variable, along with *P* values and adjusted R^2 values for each model. We compared C:N ratio and *P* content of live and dead FRB. We calculated below- to aboveground biomass ratio in only tundra sites using FRB values and aboveground biomass measurements. All statistical analyses were performed in R 3.6.2. with tidyverse (1.3.0), ggplot2 (3.3.0), and lme4 (1.1-23) packages (Bates and others 2015; Wickham 2016; Wickham and others 2019; R Development Core Team 2020). Code used for these analyses is publicly archived on GitHub and Zenodo (McCulloch 2020) and data produced in this project are available and archived on the Arctic Data Center (McCulloch and others 2020).

Table 2. Statistical Results from Nested *T* Test Analyses, with Site Nested within Biome Type (Boreal vs. Tundra) for Each Measured Variable [Dead FRB (kg m^{-2} of Soil), Live FRB (kg m^{-2} of Soil), Dead:Live FRB, Dead FRB C:N Ratio, Live FRB C:N Ratio, Dead FRB %P, and Live FRB %P]

Dependent variable	df	*t* value	*P* value
Dead FRB	21	0.633	0.544
Live FRB	21	− 1.446	0.163
Dead:live FRB	21	1.627	0.119
Dead FRB C:N ratio	21	− 1.362	0.188
Live FRB C:N ratio	21	− 2.269	**0.034**
Dead FRB %P	21	− 0.656	0.519
Live FRB %P	21	0.261	0.797

P values less than 0 are bolded.

Results

FRB Variability Between Biomes

Live and dead FRB did not significantly differ between boreal forest and tundra ($P = 0.89$, $P = 0.40$, respectively, Table 2). In both biome types, dead FRB was at least four times greater than live FRB, with mean and standard error values for dead FRB of 0.27 (± 0.053) kg m^{-2} (boreal forests) and 0.31 (± 0.040) kg m^{-2} (tundra), compared to live FRB in boreal forests (0.058 ± 0.013 kg m^{-2}) and tundra (0.040 ± 0.004 kg m^{-2}) ecosystems, respectively (Figure 2). The ratio of dead:live FRB between biome types was also not significantly different ($P = 0.148$, Table 2). The mean below- to aboveground biomass ratio in tundra was 3.7 ± 3.07. However, if we remove dead belowground biomass from these calculated below- to aboveground ratios, the mean ratio is almost eight times less (0.46 ± 0.33) in tundra sites.

Despite congruence in FRB measurements between biome types, we observed large variability in

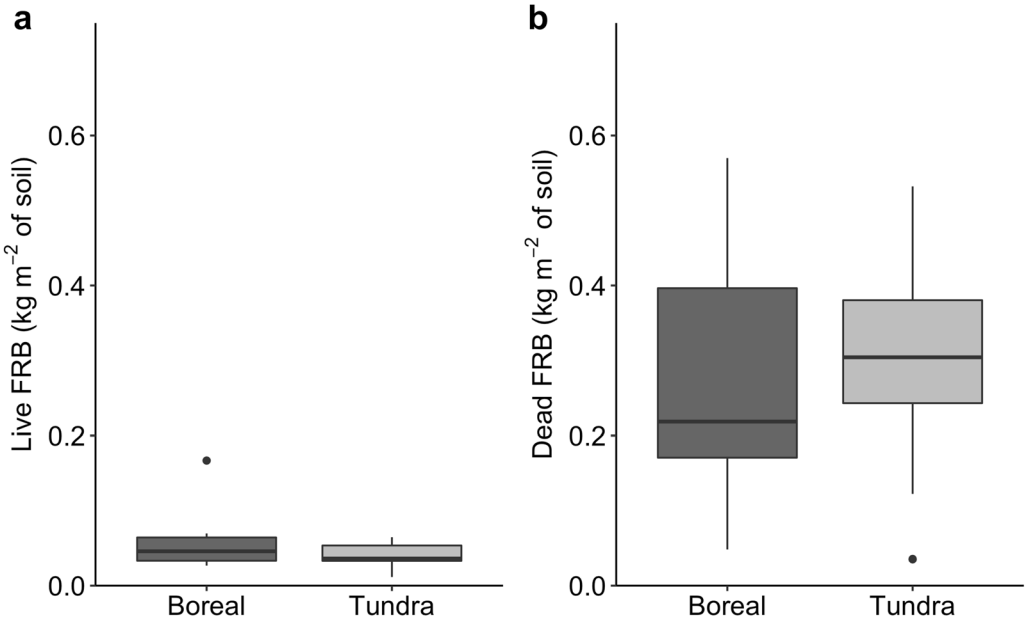

Figure 2. **A** Live and **B** dead FRB (kg m^{-2} of soil, normalized to 10 cm depth) by biome. Boxes represent the interquartile range, the line is the median, and the whiskers are the lowest or highest value within 1.5 times the interquartile range. All points are beyond 1.5 × the interquartile range. Dark gray indicates boreal forest, and light gray indicates tundra.

FRB across and within these 23 sites (Figure 3; Table S1). Further, we found no significant explanatory relationship between the dead:live FRB ratio and latitude ($P = 0.452$). The dead:live FRB was highly variable across these sites, with coefficient of variation (CV) of 62.7% and similar variation within sites (CV = 58.1%). Boreal sites had higher dead FRB variability (CV = 82.5%) compared to tundra sites (CV = 56.8%). Live FRB values were overall less consistent (CV = 74.4%) across sites compared to the dead FRB values (67.4%), largely driven by higher CV (81.4%) in boreal sites compared to tundra sites (CV = 55.8%). However, the within-site variability in boreal and tundra sites did not vary substantially for live (CV = 45.8%, CV = 49.6%, respectively, Figure 3A) or dead FRB (CV = 52.6%, CV = 48.8%, respectively, Figure 3B).

We found no significant difference in dead FRB C:N ratio between boreal forests and tundra ecosystems ($P = 0.188$, Table 2). However, the live FRB C:N ratio was significantly higher in the boreal forest sites compared to the tundra sites ($P = 0.034$, Table 2), as the percent N content of the live FRB was approximately 13% higher in the tundra sites with similar values in live FRB percent C content between biome types. The percent N content of live and dead FRB was significantly positively correlated with one another ($P < 0.001$, $R^2 = 0.37$).

Despite differences in percent N in live FRB of these ecosystems, there were no significant differences between biomes for FRB P concentrations of live or dead FRB ($P = 0.809$, $P = 0.523$, respectively, Table 2). However, the FRB P concentrations of live and dead FRB were also positively correlated with one another ($P < 0.001$, $R^2 = 0.40$).

FRB Variability Within Biomes

Though there was great variability in FRB within biomes, some abiotic and biotic factors were correlated with FRB across sites (Figure 4). We did not find any relationship between FRB variables and site average organic layer depth or thaw depth (Table S2). We chose to focus on the relationships between the FRB variables and a combination of abiotic and biotic factors including soil C:N ratio, organic soil moisture, soil temperature, and moss cover that explained a significant amount of variation in dead:live FRB ratio, live FRB, and dead FRB (Table 3).

Specifically, these four factors and T-OLD explained 72% of the observed variation in live FRB ($P = 0.022$, $R^2 = 0.72$; Figure 4E–H; Table 3). Within this model, live FRB had significant positive relationship with the soil C:N ratio ($P = 0.014$, Figure 4E). Although live FRB had no relationships with different vegetation types percent cover

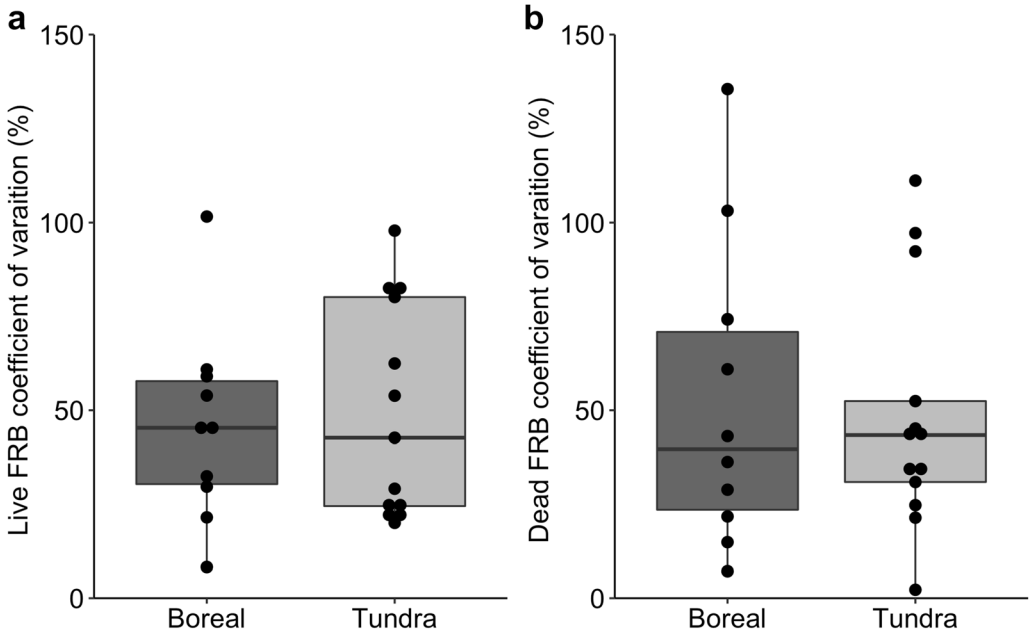

Figure 3. Coefficient of variation (%) for **A** live FRB and **B** dead FRB for each biome. Boxes represent the interquartile range, the line is the median, and the whiskers are the lowest or highest value within 1.5 times the interquartile range. Individual points represent the coefficient of variation for each of the 23 sites. Dark gray indicates boreal forest, and light gray indicates tundra.

Table 3. Multivariate Linear Regression Model Results for Response Variables [Dead:Live FRB, Dead FRB (kg m^{-2} of Soil), and Live FRB (kg m^{-2} of Soil)]

	Estimate	SE	*t* value	*P* value	Adjusted R^2
Dead:Live FRB				**0.028**	0.6961
Soil C:N ratio	− 0.06	0.092	− 0.65	0.538	
Organic moisture	− 0.01	0.004	− 3.22	**0.182**	
Moss cover	− 0.09	0.033	− 2.66	**0.038**	
Soil temperature	− 0.06	0.530	− 1.05	0.334	
T-OLD	0.32	0.100	3.17	**0.019**	
Biome	− 3.27	1.577	− 2.07	0.084	
Dead FRB				0.056	0.6042
Soil C:N ratio	1.10E−02	5.00E−03	2.06	0.085	
Organic moisture	− 8.00E−04	2.10E−04	− 3.85	**0.008**	
Moss cover	− 3.60E−03	1.90E−03	− 1.86	0.112	
Soil temperature	− 6.12E−02	3.12E−02	− 1.96	0.097	
T-OLD	2.44E−02	6.00E−03	4.104	**0.006**	
Biome	− 1.36E−01	9.28E−02	− 1.469	0.192	
Live FRB				**0.022**	0.7187
Soil C:N ratio	1.92E−03	5.59E−04	3.44	**0.014**	
Organic moisture	− 3.00E−05	2.18E−05	− 1.43	0.204	
Moss cover	− 2.86E−05	2.01E−04	− 0.14	0.891	
Soil temperature	− 5.51E−03	3.23E−03	− 1.71	0.139	
T-OLD	2.17E−03	6.14E−04	3.53	**0.012**	
Biome	− 3.12E−03	2.18E−05	− 1.43	0.204	

Significant P values are bolded. Models for each variable included six explanatory variables [soil C:N ratio, organic soil moisture (cm^3 water cm^{-3} soil), moss cover (%), averaged soil temperature to 10 cm (°C), organic layer depth (cm), and biome (boreal vs. tundra)].

(Table S3), we did find about half the variation in live FRB C:N ratio was explained by herbaceous and shrub percent cover ($P < 0.001$, $R^2 = 0.56$). Percent N content in live FRB increased ,whereas percent C content decreased with higher herbaceous cover ($P = 0.002$, $P < 0.001$, respectively), while live FRB percent N content had no relationship with shrub cover and percent C content increased with higher percent shrub cover ($P = 0.70$, $P = 0.001$, respectively). However, the high P content in dead and live FRB was associated with higher percent shrub cover ($P = 0.029$, $R^2 = 0.17$; $P < 0.001$, $R^2 = 0.30$, respectively).

Dead FRB was less well explained by these abiotic and biotic variables ($P = 0.056$, $R^2 = 0.60$; Figure 4A–D; Table 3). Dead FRB was negatively correlated with organic soil moisture ($P = 0.008$; Figure 4B). This combination of abiotic and biotic factors did significantly explain the variability in the dead:live FRB ($P = 0.028$, $R^2 = 0.70$; Figure 4I–L). Moss cover had a negative relationship with dead:live FRB ($P = 0.038$, Figure 4L). Aside from moss cover, we found no significant relationships between aboveground characteristics (biomass and vegetation type) and dead:live, live or dead FRB ($P > 0.05$ for all; Table S3).

Discussion

In our study, the variation in FRB characteristics within tundra or boreal biomes was greater than the variation between these two biomes. In fact, we found no significant difference in FRB between the biomes or across a latitudinal gradient with the exception of live FRB C:N ratio (Table 2; Figure 2). The significantly higher live FRB C:N ratio in boreal forest sites may have been driven by differences in primary vegetation types and soil nutrient cycling dynamics in boreal forests versus tundra ecosystems. Boreal forests sites had a larger proportion of woody vegetation (trees and shrubs) compared to tundra sites, and the high C:N ratio of woody belowground vegetation compared to herbaceous vegetation (Graves and others 2006) likely contributed to this observed difference in live FRB C:N ratios.

We observed high within-site variation in FRB characteristics that were likely controlled by and interacted with a complex set of abiotic and biotic conditions. For these sites, it appeared that localized soil conditions (C:N ratio, temperature, and organic soil moisture) and percent moss cover better explained the observed variability in FRB characteristics than broader geographic variation in

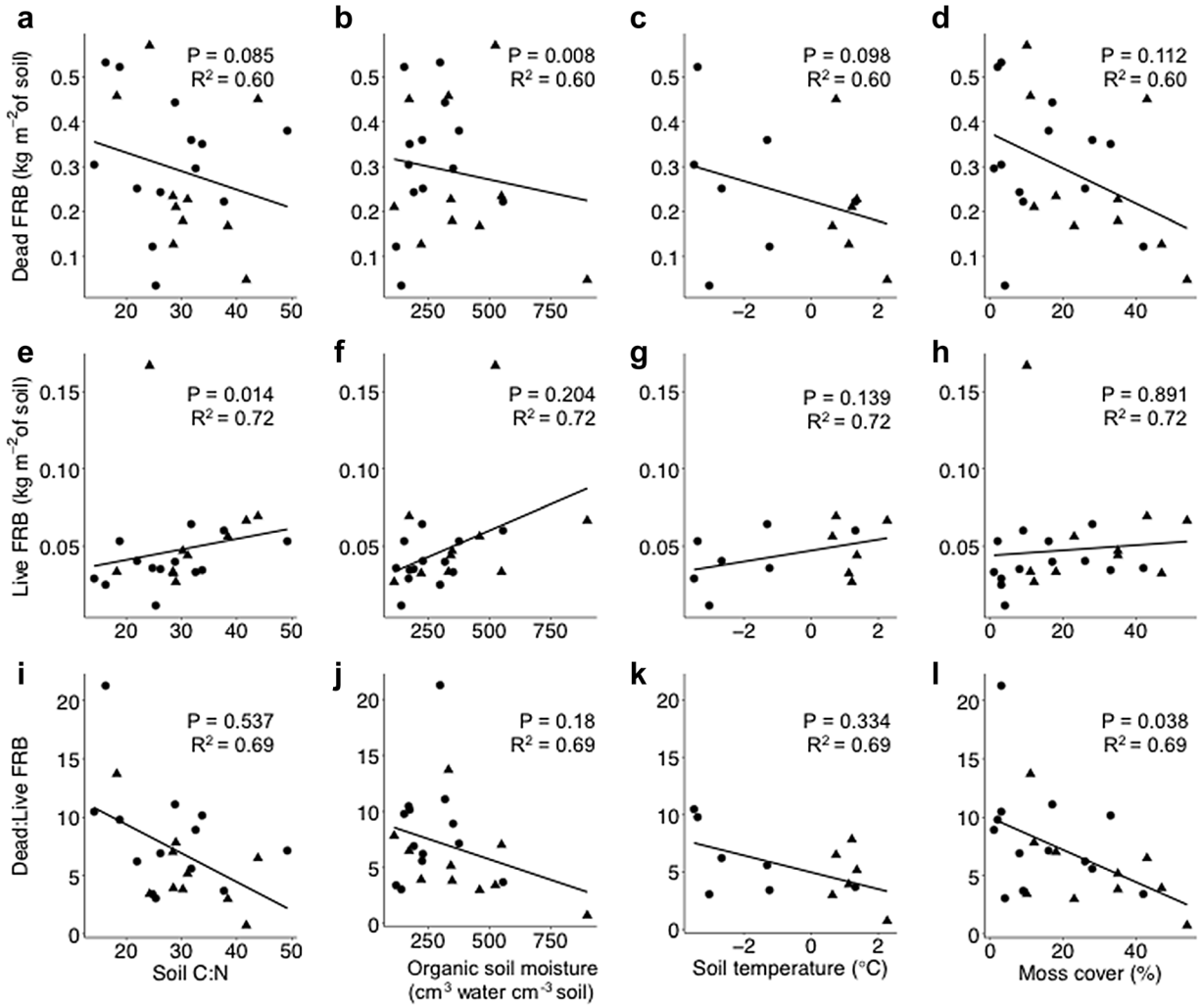

Figure 4. Bivariate relationships of the linear relationships derived from the multivariate linear regressions models with abiotic (soil C:N ratio, soil temperature to 10 cm, organic soil moisture) and biotic (moss percent cover) factors and dead FRB (**A–D**, respectively), live FRB (**E–H**, respectively), and dead:live FRB ratio (**I–L**, respectively). *P* values and adjusted R^2 values are provided for factors from multivariate models that include all four of these abiotic and biotic factors, along with biome type (boreal versus tundra) and T-OLD for each of three response variables (dead FRB, live FRB, and dead:live FRB). Triangles denote boreal sites, and circles denote tundra sites.

climate or biome type (Lantz and others 2010; Evgrafova and others 2018).

Variation in FRB Characteristics

Despite no significant differences in live and dead FRB between biomes, our data align with other studies that show high below- to aboveground biomass ratios in high-latitude ecosystems compared to more temperate systems (Dennis and Johnson 1970; Jonasson 1992; Hobbie and Chapin 1998; Jonasson and others 1999). This holds true in this study, even when only live FRB was explicitly considered, though excluding dead FRB led to an almost eightfold decrease in mean below- to aboveground ratio. Unlike what we would expect based on whole plant economic spectrum theory (Reich 2014) or what has been seen in previous studies (Reich and others 1998; Sloan and others 2013; Shen and others 2019), aboveground vegetation variables (percent cover and biomass) were not overall good predictors of FRB dynamics. This may be because we used a community-level sampling method, where other studies quantified above- and belowground characteristics for individual plants (expect for Sloan and others 2013) and sampling at the community-level may be too coarse to capture the coordination between traits. Sloan and others (2013) found a strong relationship between LAI and fine root biomass; however, they

only included FRB less than 1 mm, whereas we included FRB less than 2 mm. In the absence of LAI data we cannot directly determine whether a similar pattern exists at our sites, and note that differences in the definition of FRB may explain this potentially conflicting result.

This relatively high live FRB in high-latitude ecosystems may be the result of continued FRB growth for several weeks after the beginning of aboveground senescence. Blume-werry and others (2016) showed a 50% longer growing season for belowground biomass compared to aboveground biomass in northern Sweden. Continued FRB growth could be critical for nutrient acquisition, as late growing season experiences high decomposition rates, while aboveground growth conditions may be too harsh or light limited (Blume-Werry and others 2016). As temperatures warm, the pattern of high belowground biomass compared to aboveground biomass may continue as increased decomposition rates release nutrients from organic matter later into the season promoting root growth (Blume-Werry and others 2016). An observed eightfold decrease in below- to aboveground ratio estimates when only live biomass is considered suggests that caution should be taken when interpreting belowground biomass estimates without live and dead distinctions (Iversen and others 2015).

We observed significantly higher live FRB C:N ratio in the boreal forest biome compared to tundra (Table 2). This variability in live FRB C:N ratio was largely driven by higher N content in live FRB tundra ecosystems with different vegetation types (mainly herbaceous and shrub). More than half the variability in live FRB C:N ratio was explained by shrub and herbaceous cover, likely a result of differences in C concentrations in FRB associated with these vegetation types (Iversen and others 2015). Non-woody vegetation cover (herbaceous cover) was associated with lower live FRB C:N ratios. However, neither of these factors were associated with live FRB amounts, suggesting no change in overall amount of live FRB but rather changes in FRB elemental composition.

The P and N contents of both live and dead biomass samples were positively correlated with each other, similar to previous studies, indicating little resorption of nutrients before senescence (Gordon and Jackson 2000) and/or slow FRB decomposition rates (Freschet and others 2013). It is difficult to disentangle what drove the observed variability in the elemental composition of live and dead FRB between sites. Soil P availability conditions at each site could have contributed to differences in FRB P concentrations between sites, as vegetation P concentration can be plastic to soil P availability (Chapin and others 1986). Although we do not have soil P availability measurements at these sites to confirm this hypothesis, we did find a relationship with plant functional group, as a significant portion of P content variability in live and dead FRB was explained by percent shrub cover.

Abiotic and Biotic Conditions and FRB Variation

Moss cover, soil temperature, soil organic moisture, and soil C:N ratio all explained observed variability in FRB. These factors varied in their relationship with FRB, as some factors only correlated with dead:live FRB, dead FRB or live FRB (Table 3; Figure 4). Further, all of these factors can vary substantially in relatively small spatial scales, potentially explaining the large heterogeneity observed in FRB characteristics within sites. Soil conditions, such as temperature, moisture, and C:N ratio, can all influence microbial activity and therefore decomposition rates (Mack and others 2004; Campbell and others 2010; Demarco and others 2011; Lavoie and others 2011). Decomposition rates not only affect stocks of dead FRB, but may influence soil nutrient availability that may up- or down-regulate live FRB growth. Vegetation cover can also have implications on these soil characteristics. For example, moss cover has been found to keep soil temperatures cooler for longer into the growing season and retain water (Gornall and others 2007).

Dead FRB was negatively related to moss cover and organic soil moisture, which are often highly correlated with each other. In this study we only found a weak correlation between moss cover and organic soil moisture, though our instantaneous measurements may not reflect long-term site-level patterns. High soil moisture can slow decomposition rates, allowing for dead FRB to accumulate, but we found low dead FRB associated with higher organic soil moisture and high moss cover. It is possible even the soils with the highest soil moisture were not wet enough to saturate the soil to significantly inhibit microbial activity. This sampling does not provide information on potential moisture dynamics of drying and wetting of these soils, which can create pulses of microbial activity to could diminish stocks of dead FRB (Xiang and others 2008).

Live FRB was lower in sites with colder temperatures. Warmer temperatures may be correlated with specific vegetation types, such as shrubs and

trees that are observed to be expanding under climate change (Raynolds and others 2006; Frost and Epstein 2014; Myers-Smith and others 2015), which could drive higher FRB. Aside from moss percent cover, the measured vegetation types (shrubs, herbaceous, lichen, and other) do not explain variability in measured FRB amounts. This suggests observed differences in FRB between individual species may not necessarily lead to community-level differences (Shaver and Cutler 1979; Chapin and others 1980). However, soil temperature data largely fall out into the two biome types (colder temperatures associated with tundra ecosystems), suggesting FRB dynamics may be driven by complex interactions between community composition and temperature that are difficult to resolve (Figure 4G).

Variation in live FRB was significantly explained by the soil C:N ratio. When the soil C:N ratio is higher, N may be less available for plant use and as a result live FRB may increase to explore more of the soil profile (Salmon and others 2016, 2018; Iversen and others 2017; Hewitt and others 2019). Lower soil C:N ratio values were associated with lower live FRB. It is possible that warmer temperatures, and therefore faster decomposition rates, lead to higher nutrient availability (Grogan and Chapin III 2000; Mack and others 2004; Blume-Werry and others 2016; Salmon and others 2016). Less live FRB may have been needed to acquire the necessary soil nutrients when soil nutrient availability was higher. There was a positive correlation between T-OLD and soil temperature at 10 cm (correlation coefficient = 0.49) in these sites, suggesting warmer temperatures increased the soil depth FRB could utilize and altered where FRB are allocated within the soil profile. More detailed sampling of root depth throughout the soil profile is needed to determine this.

Increased N availability has been observed as permafrost thaws (Lavoie and others 2011; Salmon and others 2016, 2018; Keuper and others 2017). This surge of N from permafrost thaw may not necessarily align with peak vegetation growth. Nutrients may be leached out of the system or taken up by microbes before they can be utilized by plants (Jonasson and others 1999; Iversen and others 2015; Keuper and others 2017). The N associated with permafrost thaw is often released deeper in the soil profile (Keuper and others 2017). Therefore, the soil C:N ratio measurements and root systems may not have been deep enough to identify or access this additional source of N. More detailed measurements of soil nutrient stocks and cycling, along with vegetation dynamics throughout the growing season are necessary to identify the mechanisms behind the patterns we observed.

Together, variability in soil characteristics (temperature, C:N ratio, and organic soil moisture) and moss cover strongly correlated with the variability in dead:live FRB (Figure 4). Moss cover significantly explained the amount of variation observed in this FRB ratio, which was mostly driven by high moss cover associated with lower dead FRB (Figure 4D, H, I). A high adjusted R^2 value (0.69) suggests that these four parameters may be influential to and/or interact with root growth, longevity, and/or decomposition and therefore affect the dead:live FRB. Given the generally low decomposition rates in this region, it may be the case that root turnover is longer in soils with greater moss abundance, either due directly to changes in longevity or indirectly due to preferential rooting of species with longer-lived roots. However, it is difficult to disentangle the potential interactions between FRB and these soil conditions given the paucity of data. Manipulations of vegetation cover and soil conditions may help determine the casual mechanism.

T-OLD was the only variable in these models that had a positive significant relationship with all three FRB variables (live, dead and dead:live FRB). These T-OLD values represent the soil depth available for root growth and decomposition at time of sampling (peak growing season). Sites that had experienced greater soil thawing had a larger volume of soil for FRB to grow into while also exposing more of dead FRB stock for sampling. Interestingly, we see no relationship between FRB variables and OLD (taken at the end of the growing season). This suggests that T-OLD at time of sampling is important to account for when trying to understand how FRB varies with other abiotic and biotic factors in the environment. Comprehensive sampling of FRB at the end of the growing season, when OLD has reached its maximum, is needed to know if the observed strong relationship between T-OLD and FRB continues through the end of the growing season.

Implications for Ecosystem Change

Despite large differences in vegetation type and biomass between biomes, we saw no significant difference in FRB between boreal forest and tundra biomes, or even within tundra sites. This implies that regional increases in vegetation productivity (Beck and Goetz 2011), including shrubification and treeline advance (Raynolds and others 2006; Frost and Epstein 2014; Myers-Smith and others

2015) will not necessarily be accompanied by increases in live FRB in surface soil. This disconnect between above- and belowground responses to variable environmental conditions has been previously observed in these ecosystems (Blume-Werry and others 2016, 2017a, b; McLaren and Buckeridge 2019). Consequently, creating landscape-scale predictions of FRB and ecosystem C cycle dynamics based on changes in vegetation communities or biome characterization may be difficult to achieve. This presents a challenge for predicting how changes in high-latitude C dynamics will feedback to global climate change given the high proportion of vegetation C stocks held belowground (that is, roots), in these ecosystems. The lack of correspondence between biome type and dead FRB dynamics means that soil C dynamics may also be difficult to predict based on vegetation shifts, given that dead roots serve as key soil substrate inputs. Overall, these results suggest that ecological controls on plant allocation and decomposition will determine how live and dead FRB, respectively, will contribute to future high-latitude C dynamics.

Variability in FRB was linked primarily to heterogeneity in soil moisture, C:N ratio, temperature, and moss cover that occur at relatively small spatial scales. Covariation in soil temperature and moisture, as well as bryophyte distribution, makes the causal mechanisms difficult to determine. Although soil temperature is governed by climate, it can be modified by snow cover, soil moisture, and canopy shading, among other factors (Loranty and others 2018). Similarly, soil moisture will be modified by climatic changes in precipitation regimes, and perhaps more importantly, on permafrost thaw dynamics that may lead to either the wetting or drying of these landscapes (Andresen and others 2020). Understanding how FRB dynamics will change with climate is challenging because future precipitation regimes as well as the hydrologic consequences of permafrost thaw are both highly uncertain in space and time. Continued efforts to identify the mechanistic underpinnings of relationships between environmental drivers and FRB dynamics will be essential to quantify future C cycle changes across the circumpolar region.

Conclusions

This study provides site-based community estimates for both live and dead FRB dynamics across a large geographic scale that spans a gradient of biome types. This work echoes previous findings of the potential disconnect between above- and belowground dynamics in these Arctic ecosystems, suggesting the need for more belowground studies and cautioning against extrapolating observed aboveground patterns to belowground processes (Grogan and Chapin III 2000; Iversen and others 2015; Blume-Werry and others 2016, 2017a). Aside from live FRB C:N ratio, we see no difference in FRB characteristics between these two biome types. These results indicate the need for finer spatial scale measurements of FRB characteristics and related biotic and abiotic conditions in order to explain the variability we observed within these Alaskan boreal and tundra ecosystems. Our results indicate that factors such as soil C:N, moisture, and temperature may be more important than vegetation biomass or community composition for understanding FRB variability. Consequently, understanding how these soil conditions change with climate, and how they may interact with vegetation changes, is key for predicting future FRB characteristics and associated C cycle implications with continued climate change.

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Code and Data Availability Code used for the analyses and figures are archived in a GitHub repository (https://github.com/lmcculloch/AK2015/blob/master/McCulloch_ViPER_FineRoots_2020.R) and are published on Zenodo (https://doi.org/10.5281/zenodo.3997566). Data are publicly available and archived on the Arctic Data Center (https://arcticdata.io/catalog/view/doi%3A10.18739%2FA2ZS2KD6V).

References

Abbott BW, Jones JB, Schuur EAG, Chapin FS, Bowden WB, Bret-Harte MS, Epstein HE, Flannigan MD, Harms TK, Hollingsworth TN, Mack MC, McGuire AD, Natali SM, Rocha A V., Tank SE, Turetsky MR, Vonk JE, Wickland KP, Aiken GR, Alexander HD, Amon RMW, Benscoter BW, Bergeron Y, Bishop K, Blarquez O, Bond-Lamberty B, Breen AL, Buffam I, Cai Y, Carcaillet C, Carey SK, Chen JM, Chen HYH, Christensen TR, Cooper LW, Cornelissen JHC, De Groot WJ, Deluca TH, Dorrepaal E, Fetcher N, Finlay JC, Forbes BC, French NHF, Gauthier S, Girardin MP, Goetz SJ, Goldammer JG, Gough L, Grogan P, Guo L, Higuera PE, Hinzman L, Hu FS,

Hugelius G, Jafarov EE, Jandt R, Johnstone JF, Karlsson J, Kasischke ES, Kattner G, Kelly R, Keuper F, Kling GW, Kortelainen P, Kouki J, Kuhry P, Laudon H, Laurion I, MacDonald RW, Mann PJ, Martikainen PJ, McClelland JW, Molau U, Oberbauer SF, Olefeldt D, Paré D, Parisien MA, Payette S, Peng C, Pokrovsky OS, Rastetter EB, Raymond PA, Raynolds MK, Rein G, Reynolds JF, Robards M, Rogers BM, Schdel C, Schaefer K, Schmidt IK, Shvidenko A, Sky J, Spencer RGM, Starr G, Striegl RG, Teisserenc R, Tranvik LJ, Virtanen T, et al. 2016. Biomass offsets little or none of permafrost carbon release from soils, streams, and wildfire: An expert assessment. Environ Res Lett 11.

Andresen CG, Lawrence DM, Wilson CJ, David McGuire A, Koven C, Schaefer K, Jafarov E, Peng S, Chen X, Gouttevin I, Burke E, Chadburn S, Ji D, Chen G, Hayes D, Zhang W. 2020. Soil moisture and hydrology projections of the permafrost region—a model intercomparison. Cryosphere 14:445–59.

Apps MJ, Kurz WA, Luxmoore RJ, Nilsson LO, Sedjo RA, Schmidt R, Simpson LG, Vinson TS. 1993. Boreal forests and tundra. Water, Air, Soil Pollut 70:39–53.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48.

Beck P, Horning N, Goetz S, Loranty M, Tape K. 2011. Shrub cover on the North Slope of Alaska: A circa 2000 baseline map. Arctic, Antarct Alp Res 43:355–63.

Beck PSA, Goetz SJ. 2011. Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: Ecological variability and regional differences. Environ Res Lett 7.

Berner LT, Jantz P, Tape KD, Goetz SJ. 2018. Tundra plant above-ground biomass and shrub dominance mapped across the North Slope of Alaska. Environ Res Lett 13.

Blume-Werry G, Jansson R, Milbau A. 2017a. Root phenology unresponsive to earlier snowmelt despite advanced above-ground phenology in two subarctic plant communities. Funct Ecol 31:1493–502.

Blume-Werry G, Lindén E, Andresen L, Classen AT, Sanders NJ, von Oppen J, Sundqvist MK. 2017b. Proportion of fine roots, but not plant biomass allocation belowground, increases with elevation in arctic tundra. J Veg Sci 2018:1–10.

Blume-Werry G, Wilson SD, Kreyling J, Milbau A. 2016. The hidden season: Growing season is 50% longer below than above ground along an arctic elevation gradient. New Phytol 209:978–86.

Bonan GB, Chapin FS, Thompson SL. 1995. Boreal forest and tundra ecosystems as components of the climate system. Clim Change 29:145–67.

Box JE, Colgan WT, Christensen TR, Schmidt NM, Lund M, Parmentier FJW, Brown R, Bhatt US, Euskirchen ES, Romanovsky VE, Walsh JE, Overland JE, Wang M, Corell RW, Meier WN, Wouters B, Mernild S, Mård J, Pawlak J, Olsen MS. 2019. Key indicators of Arctic climate change: 1971–2017. Environ Res Lett 14.

Campbell BJ, Polson SW, Hanson TE, Mack MC, Schuur EAG. 2010. The effect of nutrient deposition on bacterial communities in Arctic tundra soil. Environ Microbiol 12:1842–54.

Chadburn S, Krinner G, Porada P, Bartsch A, Beer C, Belelli Marchesini L, Boike J, Elberling B, Friborg T, Hugelius G, Johansson M, Kuhry P, Kutzbach L, Langer M, Lund M, Parmentier F-J, Peng S, Van Huissteden K, Wang T, Westermann S, Zhu D, Burke E. 2017. Carbon stocks and fluxes in the high latitudes: Using site-level data to evaluate Earth system models. Biogeosciences Discuss: 1–41.

Chapin FS, Johnson DA, Mckendrick JD, Mckendrick JAYD. 1980. Seasonal movement of nutrients in plants of differing growth form in an Alaskan Tundra ecosystem: Implications for herbivory. J Ecol 68:189–209.

Chapin FS, Shaver GR, Kedrowski RA. 1986. Environmental controls over carbon, nitrogen and phosphorus fractions in *Eriophorum vaginatum* in Alaskan Tussock Tundra. J Ecol 74:167–95.

Chapin FS, Sturm M, Serreze MC, McFadden JP, Key JR, Lloyd AH, McGuire AD, Rupp TS, Lynch AH, Schimel JP, Beringer J, Chapman WL, Epstein HE, Euskirchen ES, Hinzman LD, Jia G, Ping CL, Tape KD, Thompson CDC, Walker DA, Welker JM. 2005. Role of land-surface changes in arctic summer warming. Science (80-) 310:657–60.

Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle DA, Lindahl B. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science (80-) 339:1615–9.

Demarco J, Mack MC, Bret-Harte MS. 2011. Availability in three Alaskan arctic plant communities microenvironment, matter quality on N in three Alaskan Arctic plant communities the effects of Sno. Ecosystems 14:804–17.

Dennis JG, Johnson PL. 1970. Shoot and rhizome-root standing crops of Tundra vegetation at Barrow, Alaska. Arct Alp Res 2:253.

Eugster W, Rouse WR, Pielke RA, Mcfadden JP, Baldocchi DD, Kittel TGF, Chapin FS, Liston GE, Vidale PL, Vaganov E, Chambers S. 2000. Land–atmosphere energy exchange in Arctic tundra and boreal forest: Available data and feedbacks to climate. Glob Chang Biol 6:84–115.

Evgrafova A, de la Haye TR, Haase I, Shibistova O, Guggenberger G, Tananaev N, Sauheitl L, Spielvogel S. 2018. Small-scale spatial patterns of soil organic carbon and nitrogen stocks in permafrost-affected soils of northern Siberia. Geoderma 329:91–107. https://doi.org/10.1016/j.geoderma.2018.05.014.

Freschet GT, Cornwell WK, Wardle DA, Elumeeva TG, Liu W, Jackson BG, Onipchenko VG, Soudzilovskaia NA, Tao J, Cornelissen JHC. 2013. Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. J Ecol 101:943–52.

Frost GV, Epstein HE. 2014. Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. Glob Chang Biol 20:1264–77.

Gordon WS, Jackson RB. 2000. Nutrient concentrations in fine roots. Ecology 81:275–80.

Gornall JL, Jónsdóttir IS, Woodin SJ, Van Der Wal R. 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia 153:931–41.

Graham RM, Cohen L, Petty AA, Boisvert LN, Rinke A, Hudson SR, Nicolaus M, Granskog MA. 2017. Increasing frequency and duration of Arctic winter warming events. Geophys Res Lett 44:6974–83.

Graves JH, Peet RK, White PS. 2006. The influence of carbon—nutrient balance on herb and woody plant abundance in temperate forest understories. J Veg Sci 17:217.

Grogan P, Chapin III FS. 2000. Initial effects of experimental warming on above- and belowground components of net ecosystem CO_2 exchange in arctic tundra. Oecologia 125:512–20.

GTN-P. 2015. Global Terrestrial Network for Permafrost metadata for permafrost boreholes (TSP). PANGAEA.

Hartley IP, Garnett MH, Sommerkorn M, Hopkins DW, Fletcher BJ, Sloan VL, Phoenix GK, Wookey PA. 2012. A potential loss of carbon associated with greater plant growth in the European Arctic. Nat Clim Chang 2:875–9.

Hewitt RE, DeVan MR, Lagutina IV, Genet H, McGuire AD, Taylor DL, Mack MC. 2019. Mycobiont contribution to tundra plant acquisition of permafrost-derived nitrogen. New Phytol 226:126–41.

Hobbie SE, Chapin FS. 1998. The response of tundra plant biomass, aboveground production, nitrogen, and CO_2 flux to experimental warming. Ecology 79:1526–44.

Hugelius G, Strauss J, Zubrzycki S, Harden JW, Schuur EAG, Ping CL, Schirrmeister L, Grosse G, Michaelson GJ, Koven CD, O'Donnell JA, Elberling B, Mishra U, Camill P, Yu Z, Palmtag J, Kuhry P. 2014. Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. Biogeosciences 11:6573–93.

Iversen CM, McCormack ML, Powell AS, Blackwood CB, Freschet GT, Kattge J, Roumet C, Stover DB, Soudzilovskaia NA, Valverde-Barrantes OJ, van Bodegom PM, Violle C. 2017. A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. New Phytol 215:15–26.

Iversen CM, Sloan VL, Sullivan PF, Euskirchen ES, Mcguire AD, Norby RJ, Walker AP, Warren JM, Wullschleger SD. 2015. The unseen iceberg: Plant roots in Arctic Tundra. New Phytol 205:34–58.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411.

Jackson RB, Lajtha K, Crow SE, Hugelius G, Kramer MG, Piñeiro G. 2017. The ecology of soil carbon: Pools, vulnerabilities, and biotic and abiotic controls. Annu Rev Ecol Evol Syst 48:419–45.

Jonasson S. 1992. Plant responses to fertilization and species removal in Tundra related to community structure and clonality. Oikos 63:420–9.

Jonasson S, Michelsen A, Schmidt IK. 1999. Coupling of nutrient cycling and carbon dynamics in the Arctic, integration of soil microbial and plant processes. Appl Soil Ecol 11:135–46.

Jones JB, Case BW. 1996. Soil testing and plant analysis no. 3. In: Methods of soil analysis Part 3. pp 389–415.

Kane D, Hinzman LD, Zarling JP. 1991. Thermal response of the active layer to climatic warning in a permafrost environmnet. Cold Reg Sci Techonol 19:111–22.

Keuper F, Dorrepaal E, van Bodegom PM, van Logtestijn R, Venhuizen G, van Hal J, Aerts R. 2017. Experimentally increased nutrient availability at the permafrost thaw front selectively enhances biomass production of deep-rooting subarctic peatland species. Glob Chang Biol 23:4257–66.

Laganière J, Paré D, Bergeron Y, Chen HYH, Brassard BW, Cavard X. 2013. Stability of soil carbon stocks varies with forest composition in the canadian boreal biome. Ecosystems 16:852–65.

Lantz TC, Gergel SE, Kokelj SV. 2010. Spatial heterogeneity in the shrub tundra ecotone in the Mackenzie Delta region, Northwest territories: Implications for Arctic environmental change. Ecosystems 13:194–204.

Lavoie M, Mack MC, Schuur EAG. 2011. Effects of elevated nitrogen and temperature on carbon and nitrogen dynamics in Alaskan arctic and boreal soils. J Geophys Res Biogeosciences 116:1–14.

Loranty MM, Abbott BW, Blok D, Douglas TA, Epstein HE, Forbes BC, Jones BM, Kholodov AL, Kropp H, Malhotra A, Mamet SD, Myers-Smith IH, Natali SM, O'Donnell JA, Phoenix GK, Rocha AV, Sonnentag O, Tape KD, Walker DA. 2018. Reviews and syntheses: Changing ecosystem influences on soil thermal regimes in northern high-latitude permafrost regions. Biogeosciences 15:5287–313.

Mack MC, Schuur EAG, Bret-Harte MS, Shaver GR, Chapin FS. 2004. Ecosystem carbon storage in arctic tundra reduce by long-term nutrient fertilization. Nature 431:440–3.

Makita N, Kosugi Y, Dannoura M, Takanashi S, Niiyama K, Kassim AR, Nik AR. 2012. Patterns of root respiration rates and morphological traits in 13 tree species in a tropical forest. Tree Physiol 32:303–12.

Matamala R, Gonzàlez-Meler MA, Jastrow JD, Norby RJ, Schlesinger WH. 2003. Impacts of Fine Root Turnover on Forest NPP and Soil C Sequestration Potential. Science (80-) 302:1385–7.

McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D, Helmisaari HS, Hobbie EA, Iversen CM, Jackson RB, Leppälammi-Kujansuu J, Norby RJ, Phillips RP, Pregitzer KS, Pritchard SG, Rewald B, Zadworny M. 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. New Phytol 207:505–18.

McCulloch LA. 2020. lmcculloch/AK2015: Variation in fine root characteristics and nutrient dynamics across Alaskan ecosystems. https://doi.org/10.5281/zenodo.3997566.

McCulloch LA, Natali S, Kholodov A, Loranty M. 2020. Fine root biomass and nutrient concentrations from Alaskan borehole sites, 2015 (ViPER project). Arct Data Cent.

McLaren JR, Buckeridge KM. 2019. Decoupled above-and belowground responses to multi-decadal nitrogen and phosphorus amendments in two tundra ecosystems. Ecosphere 10.

McLaren JR, Buckeridge KM, van de Weg MJ, Shaver GR, Schimel JP, Gough L. 2017. Shrub encroachment in Arctic tundra: Betula nana effects on above- and belowground litter decomposition. Ecology 98:1361–76.

Metcalfe DB, Williams M, Aragão LEOC, Da Costa ACL, De Almeida SS, Braga AP, Gonçalves PHL, Silva JDA, Malhi Y, Meir P. 2007. A method for extracting plant roots from soil which facilitates rapid sample processing without compromising measurement accuracy: Methods. New Phytol 174:697–703.

Myers-Smith IH, Elmendorf SC, Beck PSA, Wilmking M, Hallinger M, Blok D, Tape KD, Rayback SA, Macias-Fauria M, Forbes BC, Speed JDM, Boulanger-Lapointe N, Rixen C, Lévesque E, Schmidt NM, Baittinger C, Trant AJ, Hermanutz L, Collier LS, Dawes MA, Lantz TC, Weijers S, JØrgensen RH, Buchwal A, Buras A, Naito AT, Ravolainen V, Schaepman-Strub G, Wheeler JA, Wipf S, Guay KC, Hik DS, Vellend M. 2015. Climate sensitivity of shrub growth across the tundra biome. Nat Clim Chang 5:887–91.

Nadelhoffer KJ, Johnson L, Laundre J, Giblin AE, Shaver GR. 2002. Fine root production and nutrient content in wet and moist arctic tundras as influenced by chronic fertilization. Plant Soil. 242:107–13.

Natali S, Kholodov A. 2016. Understory percent cover by functional group from Alaska borehole sites, 2015 (ViPER project). Arct Data Cent.

Natali S, Kholodov A, Loranty M. 2016a. Active layer soil bulk density, moisture, carbon and nitrogen concentration and stable isotope data from Alaska borehole sites, 2015 (ViPER project). Arct Data Cent.

Natali S, Kholodov A, Loranty M. 2016b. Thaw depth and organic layer depth from Alaska borehole sites, 2015, 2017, 2018 (ViPER Project). Arct Data Cent.

Parker TC, Subke JA, Wookey PA. 2015. Rapid carbon turnover beneath shrub and tree vegetation is associated with low soil carbon stocks at a subarctic treeline. Glob Chang Biol 21:2070–81.

Pearson RG, Phillips SJ, Loranty MM, Beck PSA, Damoulas T, Knight SJ, Goetz SJ. 2013. Shifts in Arctic vegetation and associated feedbacks under climate change. Nat Clim Chang 3:673–7.

R Development Core Team. 2020. A Language and Environment for Statistical Computing. Vienna, Austria. http://www.r-project.org.

Rasse DP, Rumpel C, Dignac M-F. 2005. Is soil carbon mostly root carbon? Mechanism for specific stabilisation. Plant Soil 269:341–56.

Raynolds MK, Walker DA, Epstein HE, Pinzon JE, Tucker CJ. 2012. A new estimate of tundra-biome phytomass from trans-Arctic field data and AVHRR NDVI. Remote Sens Lett 3:403–11.

Raynolds MK, Walker DA, Maier HA. 2006. NDVI patterns and phytomass distribution in the circumpolar Arctic. Remote Sens Environ 102:271–81.

Reich PB. 2014. The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. J Ecol 102:275–301.

Reich PB, Tjoelker MG, Walters MB, Vanderklein DW, Buschena C. 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. Funct Ecol 12:327–38.

Robinson CH, Kirkham JB, Littlewood R. 1999. Decomposition of root mixtures from high arctic plants: A microcosm study. Soil Biol Biochem 31:1101–8.

Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J, Alward R, Beier C, Burke I, Canadell J, Callaghan T, Christensen TR, Fahnestock J, Fernandez I, Harte J, Hollister R, John H, Ineson P, Johnson MG, Jonasson S, John L, Linder S, Lukewille A, Masters G, Melillo J, Mickelsen A, Neill C, Olszyk DM, Press M, Pregitzer K, Robinson C, Rygiewiez PT, Sala O, Schmidt IK, Shaver G, Thompson K, Tingey DT, Verburg P, Wall D, Welker J, Wright R. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–62.

Salmon VG, Schädel C, Bracho R, Pegoraro E, Celis G, Mauritz M, Mack MC, Schuur EAG. 2018. Adding depth to our understanding of nitrogen dynamics in permafrost soils. J Geophys Res Biogeosci 123:2497–512.

Salmon VG, Soucy P, Mauritz M, Celis G, Natali SM, Mack MC, Schuur EAG. 2016. Nitrogen availability increases in a tundra ecosystem during five years of experimental permafrost thaw. Glob Chang Biol 22:1927–41.

Segal AD, Sullivan PF. 2014. Identifying the sources and uncertainties of ecosystem respiration in Arctic tussock tundra. Biogeochemistry 121:489–503.

Serreze MC, Barry RG. 2011. Processes and impacts of Arctic amplification: A research synthesis. Glob Planet Change 77:85–96. https://doi.org/10.1016/j.gloplacha.2011.03.004.

Shaver GR, Cutler JC. 1979. The vertical distribution of live vascular phytomass in cottongrass Tussock Tundra. Arct Alp Res 11:335.

Shen Y, Gilbert GS, Li W, Fang M, Lu H, Yu S. 2019. Linking aboveground traits to root traits and local environment: Implications of the plant economics spectrum. Front Plant Sci 10:1–12.

Silver WL, Miya RK. 2001. Global patterns in root decomposition: Comparisons of climate and litter quality effects. Oecologia 129:407–19.

Sloan VL, Fletcher BJ, Phoenix GK. 2016. Contrasting synchrony in root and leaf phenology across multiple sub-Arctic plant communities. J Ecol 104:239–48.

Sloan VL, Fletcher BJ, Press MC, Williams M, Phoenix GK. 2013. Leaf and fine root carbon stocks and turnover are coupled across Arctic ecosystems. Glob Chang Biol 19:3668–76.

Street LE, Garnett MH, Subke JA, Baxter R, Dean JF, Wookey PA. 2020. Plant carbon allocation drives turnover of old soil organic matter in permafrost tundra soils. Glob Chang Biol 26:4559–71.

Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G, Zimov S. 2009. Soil organic carbon pools in the northern circumpolar permafrost region. Glob Biogeochem Cycles 23:1–11.

Thompson C, Beringer J, Chapin FS, McGuire AD. 2004. Structural complexity and land-surface energy exchange along a gradient from arctic tundra to boreal forest. J Veg Sci 15:397–406.

Welp LR, Randerson JT, Liu HP. 2007. The sensitivity of carbon fluxes to spring warming and summer drought depends on plant functional type in boreal forest ecosystems. Agric For Meteorol 147:172–85.

Wickham H. 2016. ggplot2: Elegant graphics for data analysis. New York: Springer.

Wickham H, Averick M, Bryan J, Chang W, McGowan L, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen T, Miller E, Bache S, Müller K, Ooms J, Robinson D, Seidel D, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H. 2019. Welcome to the Tidyverse. J Open Source Softw 4:1686.

Wookey PA, Aerts R, Bardgett RD, Baptist F, Bråthen K, Cornelissen JHC, Gough L, Hartley IP, Hopkins DW, Lavorel S, Shaver GR. 2009. Ecosystem feedbacks and cascade processes: Understanding their role in the responses of Arctic and alpine ecosystems to environmental change. Glob Chang Biol 15:1153–72.

Xiang SR, Doyle A, Holden PA, Schimel JP. 2008. Drying and rewetting effects on C and N mineralization and microbial activity in surface and subsurface California grassland soils. Soil Biol Biochem 40:2281–9.