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Proportion of fine roots, but not plant biomass allocation below ground, increases with elevation in arctic tundra

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Abstract

Questions: Roots represent a considerable proportion of biomass, primary production and litter input in arctic tundra, and plant allocation of biomass to above- or below-ground tissue in response to climate change is a key factor in the future C balance of these ecosystems. According to optimality theory plants allocate C to the above- or below-ground structure that captures the most limiting resource. We used an elevational gradient to test this theory and as a space-for-time substitution to inform on tundra carbon allocation patterns under a shifting climate, by exploring if increasing elevation was positively related to the root:shoot ratio, as well as a larger plant allocation to adsorptive over storage roots.

Location: Arctic tundra heath dominated by *Empetrum hermaphroditum* close to Abisko, Sweden.

Methods: We measured root:shoot and fine:coarse root ratios of the plant communities along an elevational gradient by sampling above- and below-ground biomass, further separating root biomass into fine (<1 mm) and coarse roots.

Results: Plant biomass was higher at the lower elevations, but the root:shoot ratio did not vary with elevation. Resource allocation to fine relative to coarse roots increased with elevation, resulting in a fine:coarse root ratio that more than doubled with increasing elevation.

Conclusions: Contrary to previous works, the root:shoot ratio along this elevational gradient remained stable. However, communities along our study system were dominated by the same species at each elevation, which suggests that when changes in the root:shoot ratio occur with elevation these changes may be driven by differences in allocation patterns among species and thus turnover in plant community structure. Our results further reveal that the allocation of biomass to fine relative to coarse roots can differ between locations along an elevational gradient, even when overall above- vs below-ground biomass allocation does not. Given the functionally different roles of fine vs coarse roots this could have large implications for below-ground C cycling. Our results highlight the importance of direct effects vs indirect effects (such as changes in plant community composition and nutrient availability) of climate change for future C allocation above and below ground.

1 | INTRODUCTION

More than 80% of plant biomass in arctic tundra is located below ground in the root biomass pool, which is more than in any other biome (Iversen et al., 2015; Mokany, Raison, & Prokushkin, 2006). Roots thus represent a considerable proportion of primary production, biomass turnover and litter input in tundra ecosystems (Iversen et al., 2015). Therefore, tundra plant supply of below-ground biomass to the soil organic matter pool, in combination with the low soil temperatures and decomposition rates in these systems, has been an important contributor to the build-up of large carbon (C) stocks in arctic tundra soils (Tarnocai et al., 2009). The higher than global average warming of arctic tundra with climate change (IPCC 2013) may lead to considerable release of C from these soils (Natali, Schuur, Webb, Pries, & Crummer, 2014). However, whether or not this C release – at least to some extent – is offset by the positive effect of warming on C accumulation via plant growth, is a hotly debated issue (Abbott et al., 2016), and may depend on indirect effects of climate change on plant growth or soil processes via, for instance, climate-driven shifts in nutrient availability or plant community composition (Salmon et al., 2015). Furthermore, while plant growth responses to climate warming may differ above and below ground, the future ecosystem C balance partly depends on the allocation of C to above- and below-ground tissue (Ise, Litton, Giardina, & Ito, 2010). Nevertheless, most current knowledge about how plant biomass in arctic tundra is affected by climate change is based on studies of above-ground plant tissue only, in which roots are overlooked or assumed to respond in a similar way as above-ground tissues (Iversen et al., 2015; Salmon et al., 2015). Determining above- and below-ground plant biomass patterns across communities that have experienced long-term differences in temperature, such as along space-for-time temperature gradients, can inform how C allocation patterns may shift under long-term warming.

A plant root:shoot ratio represents the net outcome of C allocation to its above- and below-ground structures, a process that is in functional equilibrium (Brassard, Chen, & Bergeron, 2009; Brouwer, 1983). According to optimality theory, the root:shoot ratio varies with resource supply and thus plants allocate C to the above- or below-ground structure that captures the most limiting resource (Bloom, Chapin, & Mooney, 1985; Chapin, 1980; Reich et al., 2014). Generally, low temperatures and low N levels lead to higher biomass allocation below ground (Freschet, Swart, & Cornelissen, 2015; Poorter & Nagel, 2000; Poorter et al., 2011), and this pattern is also observed in arctic tundra (Wang et al., 2016). In fact, root:shoot ratios have been shown to increase with increasing latitude or elevation in forests (Girardin et al., 2010; Hertel & Schöling, 2011; Leuschner, Moser, Bertsch, Röderstein, & Hertel, 2007; Mao et al., 2015; Moser et al., 2011; Reich et al., 2014; Zadworny, McCormack, Mucha, Reich, & Oleksyn,

2016), as well as in alpine plant communities (Körner & Renhardt, 1987; Ma et al., 2010) – a pattern that supports the optimality theory. Given these results, climate change-induced increases in temperature or nutrient availability in arctic tundra could change plant allocation patterns. However, the experimental evidence to date is inconclusive, showing both increasing (Björk, Majdi, Klemedtsson, Lewis-Jonsson, & Molau, 2007; Sullivan, Arens, Chimner, & Welker, 2008; Sullivan et al., 2007; van Wijk, Williams, Gough, Hobbie, & Shaver, 2003), decreasing (Björk et al., 2007; Clemmensen et al., 2006; McGraw & Chapin, 1989; Sullivan et al., 2008) or unchanged (Clemmensen et al., 2006; Hollister & Flaherty, 2010) root:shoot ratios in arctic tundra in response to fertilization or warming.

Roots differ widely in their forms and functions, thus even plant allocation patterns within the root system can change in response to changing environmental conditions (McCormack et al., 2015; Zadworny et al., 2016). In general, fine roots are responsible for water and nutrient absorption while coarse roots transport and store nutrients and C, even though sizes of adsorptive and transport roots vary between species (Freschet & Roumet, 2017; McCormack et al., 2015). Studies on trees and alpine herbaceous plants have revealed a proportionally lower presence of fine roots under increased resource availability and decreased environmental harshness, such as under long-term changes in environmental conditions or along natural gradients (Körner & Renhardt, 1987; Moser et al., 2011; Zadworny et al., 2016). Not only do fine roots have a higher absorptive capacity than coarse roots, they also have higher respiration rates and N concentrations, as well as shorter life spans and lower concentrations of total non-structural carbohydrates and cellulose (Makita et al., 2012; Matamala, Gonzalez-Meler, Jastrow, Norby, & Schlesinger, 2003; McCormack et al., 2015). Thus, changes within root allocation patterns between fine and coarse roots can have important implications for decomposition rates and soil C sequestration (Goebel et al., 2011; McCormack et al., 2015; Zhang & Wang, 2015). Clearly, evidence that climate change may alter plant biomass allocation above and below ground, as well as between fine and coarse roots, is mounting from other ecosystems (Mao et al., 2015; Moser et al., 2011; Reich et al., 2014); yet, these changes remain poorly understood in arctic tundra. Further, as experiments tend to be short term we lack understanding of how long-term increases in temperature and associated changes influence tundra plant C allocation patterns.

Here, we use an established sub-arctic elevational gradient (e.g. Milbau, Shevtsova, Osler, Mooshammer, & Graae, 2013; Sundqvist, Wardle, Vincent, & Giesler, 2014; Sundqvist, Giesler, Graae, et al., 2011; Vincent, Sundqvist, Wardle, & Giesler, 2014) to better understand the direct and indirect (via changes in plant community composition and nutrient availability) effects of long-term differences in temperature on plant biomass allocation patterns in arctic tundra

heath vegetation. Increasing elevation along this gradient was associated with a decline in air temperature, soil phosphate concentrations, litter decomposition rates, as well as a low turnover of species within heath communities (Sundqvist, Giesler, Graae, et al., 2011; Sundqvist et al., 2014; Veen, Sundqvist, & Wardle, 2015; Vincent et al., 2014). Green foliar tissues had higher concentrations of lignin and plant defence compounds at high elevations relative to low elevations (de Long, Sundqvist, Gundale, Giesler, & Wardle, 2016) – a pattern that suggests increased environmental stress with increasing elevation. Hence, this study system provides the opportunity to test how elevation and associated shifts in temperature and environmental conditions influence plant allocation patterns to above- and below-ground tissues in heath communities across a sub-arctic tundra landscape. Specifically, we use this study system to test the following two hypotheses:

1. Similar to other ecosystems, increasing elevation is negatively related to overall plant biomass, but positively related to the root:shoot ratio (Girardin et al., 2010; Moser et al., 2011).
2. Increasing elevation is positively associated with the ratio of fine to coarse roots because lower nutrient availability favours adsorptive roots over storage roots (Poorter et al., 2011; Reich et al., 2014).

Our results will contribute to future C budget scenarios for arctic tundra ecosystems that incorporate both above- and below-ground ecosystem components, and their potentially different responses to climate change (Iversen et al., 2015; Smithwick, Lucash, McCormack, & Sivandran, 2014; Warren et al., 2015).

2 | METHODS

2.1 | Study system

This study was conducted along the northern slope of Mt. Suorooaivi, approximately 20 km southeast of Abisko, Sweden (68°21′N, 18°49′E; Figure S1 in Appendix S1) in sub-arctic heath dominated by *Empetrum hermaphroditum* Hagerup, which is representative of a circumpolar, common vegetation type (Tybirk et al., 2000). Previous work at this study site showed that air temperature and soil nutrient availability, particularly plant available soil phosphate concentrations, declined with increasing elevation (Sundqvist, Giesler, Graae, et al., 2011; Sundqvist et al., 2014; Vincent et al., 2014), and that leaf tissue N:P ratios increased with increasing elevation (Sundqvist, Giesler, & Wardle, 2011).

A set of long-term study sites along this elevational gradient were established in Aug 2015 with eight replicate plots at each of six elevations: 480, 580, 680, 780, 880 and 980 m a.s.l. (elevational range of 500 m; Figure S1 in Appendix S1). The sites were selected to represent the elevational range of treeless sub-arctic tundra heath vegetation along the northeast slope of the study system, starting at the lowest elevation (480 m), using an altimeter to locate elevations at every 100 m above it. At each elevation, the study plots (1 m × 1 m) were randomly selected within heath vegetation of similar slope and aspect, with a minimum distance of 5 m and a maximum distance of 100 m between plots. The previously measured decline in air temperature with elevation along the gradient (e.g. Sundqvist, Giesler, Graae, et al., 2011) was confirmed by air temperature measurements using loggers mounted on plastic sticks, with a plastic reflective sheet for water protection and sunshield, at 10 cm above the ground surface level in three plots per elevation (iButton, Maxim Integrated, San Jose, CA, US) between 28 Aug and 26 Sept 2015 (Figure S2 in Appendix S1). During this time, the highest and lowest elevation differed by 2.5°C in their mean temperatures, and the average difference between elevations was 0.5°C. All sites were dominated by the evergreen dwarf shrub *E. hermaphroditum*, and to a lesser extent by the deciduous shrub *Betula nana* (Figure S3 in Appendix S1). The presence and cover of the evergreen *Vaccinium vitis-idaea* and other deciduous shrubs (*V. uliginosum*, *Arctostaphylos alpinus*, *Cassiope tetragona*, *Salix* spp.), forbs (*Bistorta vivipara*, *Rubus chamaemorus*) and graminoids (*Carex bigelowii*, *Calamagrostis lapponica*) varied among elevations (Figure S3 in Appendix S1).

2.2 | Above-ground vegetation cover

Between 19 and 31 Aug 2015, plant species cover (%) for each vascular species in each plot (1 m²) was visually estimated by two observers and the mean percentage cover of each of the two estimates was recorded to represent the cover of each vascular plant species in each plot.

2.3 | Above- and below-ground biomass sampling

We destructively harvested above- and below-ground biomass between 9–15 Sept 2015, in heath vegetation directly (10–20 cm) outside the long-term vegetation monitoring plots (1 m²) where vegetation cover was estimated. Both above- and below-ground biomass was sampled using a corer with a diameter of 12.2 cm. The corer was placed on top of vegetation representative of the vegetation within each 1-m² plot, and all above-ground biomass within the area of the corer was sampled. Above-ground biomass was clipped at the corers edge when needed, and a soil core for root sampling was taken with the corresponding above-ground biomass still attached to the core. Thus, the same corer was used to sample above- and below-ground biomass at exactly the same location. We sampled soils until bedrock, or to a maximum depth of 15.5 cm (which occurred in a total of three samples; at 480, 580 and 780 m, respectively), as this depth contains the majority of the living root biomass in tundra heath and represents the maximum rooting depth of the dominating plant species *E. hermaphroditum* (Iversen et al., 2015). For plots in which the bedrock was shallower, samples were taken to the maximum depth possible and the depth of the sample was recorded. For all samples, the depth of the organic layer was measured. Samples were brought back to the laboratory on the same day and stored at 5°C until further processing.

Plant biomass was separated into above- and below-ground biomass, which was removed from the soil and washed to remove soil particles. Berries and flowers were included when present, and leaf and root litter (visually estimated) were excluded. Below-ground
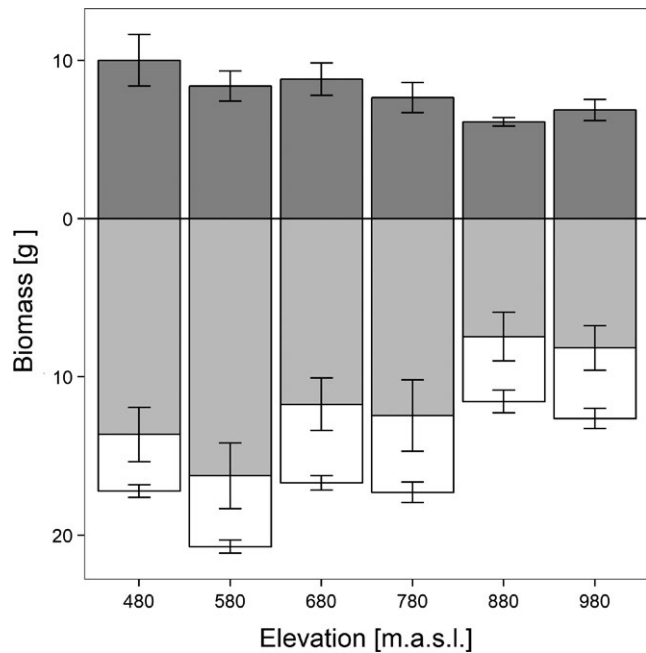
FIGURE 1 Above-ground plant biomass (dark grey, upwards bars) and below-ground biomass (downward bars), further separated into coarse (light grey bars) and fine (white bars) root biomass, along the elevational gradient. Bars show mean ± *SE*, *n* = 8

biomass was further separated by diameter (Mao et al., 2015; Moser et al., 2011) into fine (≤1 mm diameter) and coarse (>1 mm diameter) roots. While some have suggested using root order instead of root diameter when inferring root function (e.g. McCormack et al., 2015), it was not feasible to use such an approach in our study as root systems of dwarf shrub heaths are very difficult to excavate intact, very complex and have high amounts of root biomass. However, as the whole gradient was dominated by the same species, which also have very similar root systems, we are confident that sorting by diameter gave a consistent separation into the same functional groups of roots (Freschet & Roumet, 2017). Above-ground biomass, fine root and coarse root biomass were dried at 70°C for 48 hr and weighed. We then calculated total root:shoot and fine:coarse root ratios from the measured biomass.

2.4 | Soil abiotic properties

Samples for measurement of soil abiotic properties were taken on the 15 Sept 2015. One core of 4.4 cm in diameter was collected in each plot in close proximity and to the same depth as the respective root cores. Samples were brought back to the laboratory on the same day and stored at 5°C overnight. In the lab, subsamples for analysis of soil moisture and bulk density were taken. The volume and fresh weight of each subsample was recorded, and samples were dried at 105°C for 48 hr before measuring dry weight. From the remaining soil of each sample, dead and live plant biomass and stones were removed, and samples were subsequently homogenized (2-mm sieve). A total of 5 g fresh soil was weighed into Greiner tubes and soil mineral N (NH_4^+, NO_2^-, NO_3^-) extracted in 40 ml distilled water; tubes were shaken at

250 rpm on an orbital shaker for a total of 5 h and centrifuged at 1200 *g* for 2 min, after which solutions were filtered to remove solid particles. The filtration product was stored at −15°C until determination of NH_4^+ and NO_2^-/NO_3^- and concentrations with a Flow Injection Analyzer (FIAstar 5000; FOSS NIRSystems, Hllerød, Denmark). One extreme value at 680 m a.s.l. (the same for each ammonium and nitrate) was excluded from analysis after performing Grubb's test for outliers (G = 2.4240, *p* < 0.0001; see Figures S4 and S5 in Appendix S1).

2.5 | Statistical analyses

Elevational gradients can inform on how communities and ecosystem processes vary with temperature and associated climatic factors that change with elevation, whenever careful consideration of other environmental factors that may vary with elevation are taken into account (Körner, 2007). To explore the direct effect of elevation-associated changes in temperature on the different biomass groups (total plant biomass, above-ground biomass as well as fine, coarse and total root biomass), root:shoot ratio and fine:coarse root ratio we used one-way ANCOVA models, with elevation as a categorical variable, and percentage cover of the two most dominant plant species across the gradient (i.e. *E. hermaphroditum* and *B. nana*) as well as soil nutrient concentrations, core depth and soil moisture content as covariates. As there were no significant interactions between the response variables and covariates, we excluded interactions from the final models. Whenever there was a significant effect of a covariate, linear regression was performed to explore any linear relationship between the covariate and the response variable. ANCOVAs were performed on both the measured root:shoot ratios and root biomass values, as well as on values where all root biomass samples were standardized for soil volume (if soils were shallower than standard sampling depth) but in this latter case not including core depth as a covariate. Both sets of variables revealed qualitatively similar results, and here we report unstandardized values in the main text, and standardized values and results in the supplementary material. Differences between elevations for covariates were tested with one-way ANOVAs followed by Tukey's HSD post-hoc tests. When required, data were log-transformed (unstandardized total biomass, standardized root:shoot ratio, fine:coarse root ratio, nitrate concentrations and above-ground biomass) to conform to the assumptions of parametric models. All statistical analyses were performed in R, v 3.1.1 (R Foundation for Statistical Computing, Vienna, Austria).

3 | RESULTS

3.1 | Above- and below-ground biomass

Total plant biomass varied across elevations, with higher elevations generally having less total plant biomass. The highest mean value of 29.1 g was found at 580 m and the lowest value of 17.7 g at 880 m (Figure 1, Table 1). Above-ground biomass did not vary significantly among elevations, but showed a trend (*p* = 0.06) of lower values towards the higher elevations (Figure 1, Table 1). Total root biomass varied among elevations and showed a pattern that was similar to overall

TABLE 1 Effect of elevation, as well as the covariates soil NO_2^-/NO_3^- and NH_4^+ concentrations, gravimetric soil moisture content, core depth and percentage cover of *E. hermaphroditum* and *B. nana*, on coarse root biomass, fine root biomass and total root biomass, as well as root:shoot ratio and fine:coarse root ratio. Significant differences are shown in bold, $n = 8$

Source of variation	Total biomass[a]				Above-ground biomass[a]				Total root biomass				Coarse root biomass			
	df	SS	F	p	df	SS	F	p	df	SS	F	p	df	SS	F	p
Elevation	5	1.65	5.0	**0.001**	5	1.11	2.3	0.063	5	461.8	3.8	**0.008**	5	430.3	4.2	**0.005**
NO_2^-/NO_3^-	1	0.001	0.01	0.908	1	0.00	0.0	0.997	1	0.2	0.0	0.936	1	0.5	0.0	0.880
NH_4^+	1	0.95	14.6	**<0.001**	1	0.43	4.5	**0.041**	1	287.6	11.7	**0.002**	1	242.8	11.8	**0.002**
Soil moisture	1	0.02	0.3	0.568	1	0.02	0.2	0.656	1	4.0	0.2	0.687	1	15.2	0.7	0.396
B. nana	1	0.007	0.1	0.753	1	0.09	1.0	0.328	1	0.1	0.0	0.949	1	2.2	0.1	0.743
E. hermaph roditum	1	0.07	1.0	0.324	1	0.006	0.1	0.798	1	11.8	0.5	0.511	1	1.6	0.1	0.784
Core depth	1	0.17	2.8	0.106	1	0.053	0.6	0.459	1	102.8	4.2	**0.048**	1	62.2	3.0	0.091
Residuals	33	2.15			33	3.14			33	808.3			33	678.2		

Source of variation	Fine root biomass				Total root:shoot ratio				Fine:coarse root ratio[a]			
	df	SS	F	p	df	SS	F	p	df	SS	F	p
Elevation	5	10.58	1.2	0.315	5	2.637	0.7	0.612	5	4.271	2.8	**0.032**
NO_2^-/NO_3^-	1	0.08	0.0	0.827	1	0.012	0.0	0.898	1	0.001	0.0	0.957
NH_4^+	1	1.9	1.1	0.300	1	0.422	0.6	0.453	1	1.410	4.6	**0.039**
Soil moisture	1	34.89	20.4	**<0.001**	1	0.518	0.7	0.406	1	2.289	7.5	**0.010**
B. nana	1	3.30	1.9	0.175	1	1.259	1.7	0.198	1	0.066	0.2	0.643
E. hermaph roditum	1	45.78	2.8	0.105	1	0.061	0.1	0.775	1	0.019	0.1	0.804
Core depth	1	5.07	3.0	0.095	1	0.422	0.6	0.453	1	0.008	0.0	0.870
Residuals	33	56.57			33	24.11			33	10.02		

[a]log transformed.
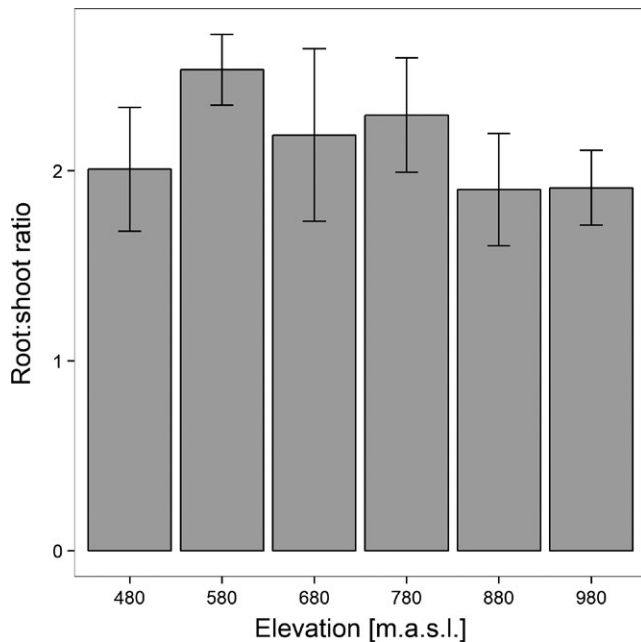
FIGURE 2 Root:shoot ratios along the elevational gradient. Bars show mean ± *SE*, *n* = 8

FIGURE 3 Fine:coarse root ratios along the elevational gradient. Bars show mean ± *SE*, *n* = 8
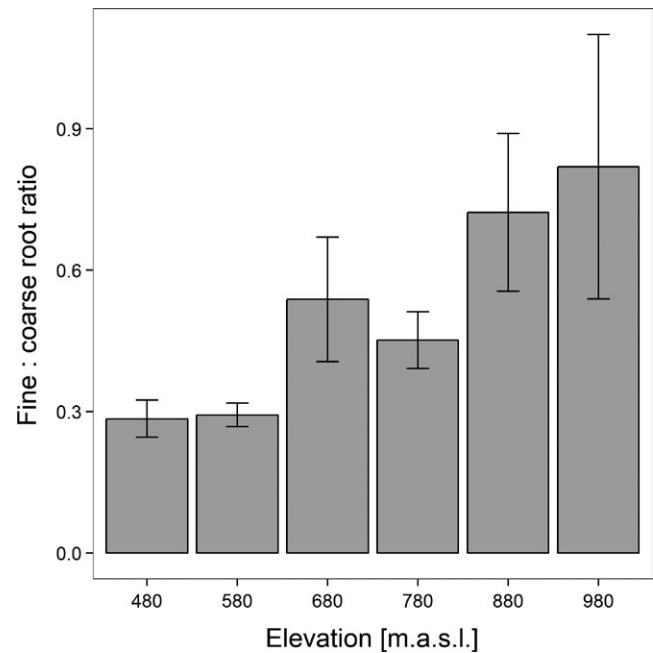
plant biomass, with generally lower values of root biomass at higher elevations. The highest mean root biomass of 20.7 g was observed at 580 m, while the lowest (11.6 g) was observed at 880 m (Figure 1, Table 1). Coarse and fine root fractions differed in their response to elevation. Specifically, coarse root biomass, which made up most of the overall root biomass, was similar to total root biomass – lower at higher elevation. Fine root biomass, on the other hand, did not systematically vary among elevations (Figure 1, Table 1). When standardized for sampled soil volume, total below-ground biomass, coarse and fine root biomass did not vary systematically with elevation (Figure S6, Table S1 in Appendix S1).

3.2 | Root:shoot ratio and fine:coarse root ratio

The root:shoot ratio, which was on average 2.1, did not differ across elevations (Figure 2, Table 1). The decreasing coarse root biomass and stable fine root biomass with elevation (Figure 1) resulted in a significant positive effect of elevation on fine:coarse root ratio, which more than doubled from the two lowest to the two highest elevations (Figure 3, Table 1). When standardized for sampled soil volume, the root:shoot ratio was, on average, 1.8. It followed the same pattern with elevation as unstandardized values (Figure S7, Table S1 in Appendix S1; fine:coarse root ratio identical to unstandardized).

3.3 | Influence of soil N concentrations, core depth, soil moisture content and cover of dominant shrub species

Soil ammonium and nitrate concentrations varied among elevations (Table S2 in Appendix S1), but not systematically (Figures S4 and S5 in Appendix S1). Mean core depth was highest at 580 m and lowest at

880 m (Table S2 in Appendix S1). Soil moisture and percentage cover of *B. nana* did not differ significantly among elevations. Percentage cover of *E. hermaphroditum* was significantly lower at the high relative to low elevation, similar to total vascular plant cover (Table S2 in Appendix S1); and plant communities were dominated by the same species at all elevations (Figure S3 in Appendix S1).

Several of our response variables, for both biomass and allocation, were influenced by one or two covariates (Table 1). However, subsequent regressions between the respective response parameters and the covariates often showed no linear relationships, with soil moisture and core depth as the two exceptions, which were significantly positively related to fine root biomass and total root biomass, respectively (Table S3 in Appendix S1). Similarly, for data standardized by soil volume, several response variables were identified as significant in the ANCOVA (Table S1 in Appendix S1). Subsequent analyses revealed that ammonium concentrations had positive, though weak, effects on total plant biomass and total root biomass, and soil moisture was weakly, but positively related to fine root biomass (Table S4 in Appendix S1).

4 | DISCUSSION

We explored plant biomass allocation patterns in response to changes in temperature and associated environmental variables along an elevational gradient in arctic tundra heath. Surprisingly, even with an elevation-related decrease in air temperature of 2.5°C and a span in average total plant biomass from 29.1 to 17.7 g, total above- and below-ground allocation patterns of plant biomass remained stable along the elevational gradient. However, we found that plant communities at higher elevations allocated proportionally

more biomass to fine than to coarse roots compared to the communities at lower elevations – a subtle, yet functionally important, difference.

4.1 | Decreasing plant biomass, but unchanged biomass allocation above and below ground, with increasing elevation

As expected, there was more overall plant biomass at lower elevations. However, contrary to our hypothesis, the root:shoot ratio was unresponsive to elevation. These findings contradict theory (Brouwer, 1983; Poorter et al., 2011), experimental evidence (e.g. Freschet et al., 2015; Poorter et al., 2011), global patterns of root:shoot ratios (Mokany et al., 2006; Reich et al., 2014), as well as observations across arctic sites of root:shoot ratios being responsive to a much larger variation in temperature than in our study system through changes in above-ground biomass (Wang et al., 2016). They are also inconsistent with findings from previous studies conducted along other elevational gradients (e.g. Girardin et al., 2010; Körner & Renhardt, 1987; Leuschner et al., 2007; Moser et al., 2011). One notable difference between our study and these previous studies of root:shoot ratios along environmental gradients is that species composition was largely consistent along our study system, while communities along the gradients in previous studies had extensive, or complete, species turnover. Our study system was consistently dominated by the evergreen dwarf shrub *E. hermaphroditum*, which maintained a high relative abundance across the elevational gradient. Ecosystem functioning can be largely determined by its dominant species (Grime, 1998), and our results may thus suggest that if above- vs below-ground biomass allocation in a dominating species, such as *E. hermaphroditum*, is only weakly responsive or unresponsive to environmental variation it could potentially have a stabilizing effect on the community root:shoot ratio in response to changes in climatic conditions. Furthermore, the previously observed changes in biomass allocation as a response to changing environmental harshness might represent inherent differences in allocation of different plant species growing at different locations rather than direct, plastic responses of those plants to environmental conditions. Similarly, variation in results from experiments in arctic tundra exploring allocation patterns in response to warming or fertilization (e.g. Björk et al., 2007; Hollister & Flaherty, 2010; Sullivan et al., 2008; van Wijk et al., 2003) may relate to variation in plant turnover rates and community shifts across treatments and studies. Plant species turnover rates and plant community responses to changes in climate may thus be important determinants of plant biomass allocation patterns in the future.

4.2 | Relative increase in biomass allocation to fine roots with increasing elevation

As we predicted, resource allocation to fine roots relative to coarse roots increased with increasing elevation in our study system. The fine:coarse root ratio more than doubled with increasing elevation, a

pattern that resulted from declining coarse root biomass with increasing elevation. These results support previous studies along elevational gradients in tropical forests (Moser et al., 2011), for herbaceous plants in the Alps (Körner & Renhardt, 1987) and on the Tibetan plateau (Ma et al., 2010). These fine:coarse root ratio changes could be directly related to plants responding to shifting environmental conditions with elevation. Alternatively, allocation within the root system could be inherent rather than induced by environmental factors. For example, local adaptations can result in individuals of the same species, but from different provenances, having stable but different allocation patterns between adsorptive and transport roots when grown under similar climatic conditions (Zadworny et al., 2016). However, compared to our study system the different provenances studied by Zadworny et al. (2016) spanned a much larger gradient (15° latitude). Thus, while we cannot exclude local adaptation, the communities occurring at different elevations across our study systems are unlikely to represent different provenances, and our findings of a relative increase in allocation to adsorptive, fine roots with increasing elevation is likely to rather reflect a direct response to decreasing temperature and associated environmental conditions that change with elevation.

Through a relative increase in fine root biomass, plants multiply the amount of root surface area and thus their capacity for water and nutrient uptake (McCormack et al., 2015). This pattern should be especially beneficial in cold environments with strong seasonality (Freschet et al., 2017) and low nutrient content in the soil (Körner & Renhardt, 1987). Yet, soil N content and soil moisture did not show a unidirectional response to elevation in our study, and even though these factors influenced plant biomass and fine:coarse root ratio (Table 1), only soil moisture showed a (weak) positive linear relationship with fine root biomass. Numerous measurements in heath vegetation confirm that elevation is associated with declining soil P concentrations in our study system (Sundqvist, Giesler, Graae, et al., 2011; Sundqvist et al., 2014; Vincent et al., 2014). Additionally, previous results from this system show increasing foliar C:P and N:P ratios towards higher elevation (de Long et al., 2016; Sundqvist, Giesler, & Wardle, 2011), further indicative of declining P availability towards the higher elevations. While N is considered the primary limiting nutrient in high-latitude ecosystems such as arctic tundra (Aerts & Chapin, 2000; Tamm, 1991), our findings of relatively more fine, adsorptive roots at high elevations may thus be caused by decreasing P availability with elevation. Increases in P availability may thus influence allocation patterns within the root system (Hermans, Hammond, White, & Verbruggen, 2006) and potentially lead to fewer fine roots in this tundra system.

Fine roots are generally responsible for the uptake of short-lived and spatially variable resources, and therefore turn over relatively more quickly than coarse roots (McCormack et al., 2015). Moreover, fine roots have higher respiration and exudation rates as well as lower concentrations of total non-structural carbohydrates and cellulose than coarse roots (McCormack et al., 2015; Yuan & Chen, 2010; Zhang & Wang, 2015). Accordingly, the increased relative allocation to fine vs coarse roots we observe in response to elevation-associated changes in temperature could influence decomposition rates of root biomass

and soil organic matter, and ultimately soil C cycling (Goebel et al., 2011; McCormack et al., 2015; Zhang & Wang, 2015).

Root:shoot ratios are widely used as an estimate of C allocation dynamics in plant communities, both among ecosystem types and among vegetation types within the same ecosystem (Mokany et al., 2006). These are generally based on few measurements of below-ground biomass in relation to above-ground biomass, and are subsequently used as conversion factors to infer root biomass, for example for total plant biomass or C stocks, as well as C allocation of different plant communities in ecosystem models (Mokany et al., 2006; Smithwick et al., 2014; Warren et al., 2015). However, while these fixed conversion factors may be modelled according to optimal allocation theory at a global scale, they do not allow for direct responses of roots to environmental conditions (Smithwick et al., 2014). The very specific pattern of fine root dynamics observed here was not detected in the overall root:shoot ratio, because fine roots only contribute a relatively small fraction of total plant biomass. Compared to their biomass, however, fine roots are disproportionally important in ecosystem processes (Finzi et al., 2015; Zhang & Wang, 2015). Thus, by only measuring the overall root:shoot ratio, essential patterns of resource allocation might easily be overlooked. However, given the different functional roles of fine vs coarse roots, we argue that studies separating roots of different diameter or – even better – different function in measurements of biomass allocation responses to environmental change, are important in providing information allowing more accurate model predictions of the future C cycle.

5 | CONCLUSIONS

We have shown that above- and below-ground plant biomass allocation remained consistent along an elevational gradient in arctic tundra heath vegetation, while relatively more biomass was allocated to fine roots as opposed to coarse roots towards higher elevations. Thus, we propose that changes in root:shoot ratio in-situ, as previously observed along other environmental gradients, might be largely driven by differences among species that have evolved in response to particular climates, rather than plastic, within-species responses to varying environmental conditions. Indirect effects of climate change, such as changes in plant community composition, may thus be more important than direct influences of temperature in determining future C allocation above and below ground. In contrast, our results imply that changes in allocation patterns between coarse and fine roots may be more strongly driven by environmental conditions. We further highlight how a stable root:shoot ratio can be associated with shifts in allocation patterns within roots, which may be an important driver of plant function and ecosystem processes, such as C cycling, across the same environmental gradient.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1

Figure S1 Location of the elevational gradient on Mt. Suorooaivi near Abisko, northern Sweden

Figure S2 Daily mean air temperature at each elevation between 28 Aug and 26 Sept 2015

Figure S3 Percentage cover of six 6 most dominant plant species, as well as all graminoids and all other vascular plants together at each of the elevational sites

Figure S4 Ammonium concentration in the soil along the elevational gradient

Figure S5 Nitrate concentration in the soil along the elevational gradient

Figure S6 Above-ground, coarse and fine root biomass (standardized per sample volume) along the elevational gradient.

Figure S7 Root:shoot ratio (standardized per sample volume) along the elevational gradient

Table S1 ANCOVA results for all root variables standardized per samples volume

Table S2 Plant cover, soil moisture, soil core depth and inorganic nitrogen concentrations along the elevational gradient.

Table S3 Linear relationships of significant covariates to the response variables

Table S4 Linear relationships of significant covariates to the response variables (root biomass standardised for sampled soil volume)