NORDIC JOURNAL OF BOTANY

Check for updates

Research Article

Root biomass distribution in response to increasing active layer thickness across plant communities in a permafrost peatland

Alexandra Werner[1,2], **Lena Muffler**[1,3] and **Gesche Blume-Werry**[4]

[1]Plant Ecology and Ecosystems Research, University of Goettingen, Goettingen, Germany
[2]Ecosystem Management, Department of Environmental Systems Science, Zürich, Switzerland
[3]Ecological-Botanical Garden, University of Bayreuth, Bayreuth, Germany
[4]Climate Impacts Research Centre, Department of Ecology, Environment and Geoscience, Umeå University, Umeå, Sweden

Correspondence: Gesche Blume-Werry (gesche.blume-werry@umu.se)

Nordic Journal of Botany
2026: e05293
doi: 10.1002/njb.05293
Subject Editor: Sylvain Monteux
Editor-in-Chief: Sara Cousins
Accepted 20 August 2026
Published 21 October 2026

In Arctic tundra, the majority of plant biomass is belowground. As temperatures increase and permafrost thaws, new soil volume containing nitrogen becomes available for plant roots, potentially leading to new plant–soil interactions. Whether or not different plant communities adapt their rooting depth distribution in response to increasing active layer thickness, whether roots at depth are similar to shallow ones, and if deep-rooting species potentially redistribute thawed-out nitrogen into more shallow layers remains poorly understood. We studied root biomass, rooting-depth distribution, root dry matter content (RDMC), and ^{15}N natural abundances in a low Arctic peatland. We did this in two plant communities, dominated either by the graminoid *Eriophorum vaginatum* or by various dwarf shrubs, each with either a shallow (51.3 ± 0.9 cm) or a deep (69.4 ± 1.9 cm) active layer. Root biomass declined sharply with depth but did not differ between plant communities or active layer thicknesses, although roots reached the thawfront. RDMC was unaffected by active layer thickness, but was lower in *E. vaginatum* and declined with depth for roots of both functional types. This suggests relatively more acquisitive roots with faster growth and shorter lifespan in deeper soils. Presence of the deep-rooting *E. vaginatum* increased foliar $\delta^{15}N$ ratios of other species, indicating a potential redistribution of nitrogen in the soil column. Our results suggest that, despite the presence of deep-rooting plants and roots down to the thawfront in shallow and deep active layers, rooting depth distribution remains relatively constant. This indicates that an increase in deep roots in response to thawing permafrost is relatively species-specific and might not result in measurable differences in root biomass or its distribution, irrespective of plant community. The decreasing RDMC with depth illustrates that resource strategies vary not only among species but also with soil depth, with implications for carbon and nutrient cycling.

Keywords: dwarf shrubs, peatland, permafrost, root biomass distribution, root dry matter content, rooting depth

NORDIC SOCIETY OIKOS

www.nordicjbotany.org

© 2026 The Author(s). Nordic Journal of Botany published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos.
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

The Arctic is warming at a rate three to four times the global average (IPCC 2021, Rantanen et al. 2022), altering plant community composition and rapidly thawing permafrost (Grosse et al. 2011, Biskaborn et al. 2019). When permafrost thaws, the uppermost, seasonally thawed part of the soil – the so-called 'active layer' – becomes thicker (Åkerman and Johansson 2008, Biskaborn et al. 2019, Strand et al. 2021). This reduces restrictions on rooting depth and results in a larger soil volume which plants can exploit with their roots (Schenk and Jackson 2002, Iversen et al. 2015). About 60–90% of plant biomass in Arctic ecosystems is located belowground (Iversen et al. 2015, Ma et al. 2021), thus, freshly available soil volume might have profound impact on the distribution of roots within the soil profile. Indeed, experimentally increased thaw depth positively stimulated root production and growth (Blume-Werry et al. 2019). With the main portion of plant biomass belowground and roots being a large part of net primary production (Iversen et al. 2015), increased root production or changes in rooting depth distribution in response to permafrost thaw may affect biogeochemical dynamics in northern ecosystems. In addition, roots influence soil carbon (C) and nitrogen (N) cycling via litter input and turnover rates (Clemmensen et al. 2013) and via rhizosphere processes like exudation (Loya et al. 2002, Spitzer et al. 2021), which in turn influence microbial communities (Loya et al. 2002, Spitzer et al. 2021) and can lead to priming (Keuper et al. 2020). This could be particularly important if roots reach newly-thawed soil layers that have not been exposed to rhizosphere processes for hundreds or thousands of years. Changes in the vertical organization of root biomass can therefore result in altered plant–soil interactions, which – at least in modelling studies – have been suggested to affect carbon emissions (Keuper et al. 2020, Blume-Werry et al. 2023). Yet, there is still only limited empirical evidence on how permafrost thawing affects belowground biomass and its depth distribution.

Tundra rooting profiles are generally very shallow, with 50% of roots in the upper 9 cm and 90% of roots in the upper 29 cm (Schenk and Jackson 2002). Yet, as permafrost thaws, large amounts of plant-available N can become available in some newly thawed, deep soil layers, particularly in regions where these horizons contain substantial amounts of N, with up to seven times more N than upper active soil layers (Keuper et al. 2012, Salmon et al. 2016). Plants can generally proliferate roots into N-rich zones and adjust their uptake capacities (Hodge 2004); and, despite the general gap between deep soil N pools released by permafrost thaw and the shallow-rooting profile of most Arctic plants, some species are capable of growing roots deep enough to access deep N pools upon thawing (Keuper et al. 2012, 2017, Blume-Werry et al. 2019), leading to increased biomass production (Keuper et al. 2017). This means that as the active layer is thickening across the Arctic, potentially providing new N pools at depth, rooting depth distribution may change towards more roots deeper down in the soil profile as some plants take advantage of this newly available, relatively N-rich soil volume. Even though a recent meta-analysis indicated that there is no difference in rooting depth distribution between different Arctic plant communities (Blume-Werry et al. 2023), whether and how strongly rooting depth distribution changes in relation to active layer thickness in situ may depend on plant community composition. Many graminoids, like the sedge *Eriophorum vaginatum* (L.) are not only deep-rooting and taking up deep N (Oulehle et al. 2016), but also seem to have a considerable ability to adapt to altered environmental conditions (Wang et al. 2017). In contrast to that, many relatively small-statured dwarf shrubs, such as *Empetrum nigrum* or *Vaccinium uliginosum*, appear to have a comparatively static, shallow rooting system (Blume-Werry et al. 2019) that might not change as active layer thickness increases. Nevertheless, it is still unclear how active layer thickness affects vertical root biomass distribution and whether the magnitude of this effect depends on the plant community. Given that current models that estimate Arctic carbon losses from plant–soil interactions assume different rooting depth distribution between vegetation types and changes therein in response to increasing active layer thickness (Keuper et al. 2020), this information is urgently needed to understand, and correctly model, high-latitude carbon dynamics.

Investing in new, deep roots comes at a cost for the plant, and the amount of resource investment is therefore part of a species' resource allocation strategy (Chapin et al. 1987). The root economics spectrum is a theoretical framework that examines the trade-offs and strategies plant species employ in allocating resources to their root systems (Reich 2014, Roumet et al. 2016). The amount of invested biomass per unit of root length, i.e. tissue density, lines up on a gradient of fast versus slow biomass accumulation which itself is characterized as a resource-conservative versus resource-acquisitive strategy (Kramer-Walter et al. 2016). Growing tissue with lower densities can be a low-cost strategy to explore and access a larger soil volume (Kramer-Walter et al. 2016), but comes at the cost of a shorter lifespan (Ryser 1996), which can be considered an acquisitive trait on the root economics spectrum (Freschet et al. 2010). Generally, the spectrum of conservative versus acquisitive resource allocation strategy is related to gradients of nutrient availability, and most species in nutrient-limited systems, such as Arctic tundra, are associated with conservative strategies (Kramer-Walter et al. 2016). Accordingly, roots of the commonly more resource-conservative dwarf-shrub species tend to display a higher tissue density (Freschet et al. 2010). Yet, the Arctic graminoid *E. vaginatum* displays fast root growth with high turnover rates (Shaver and Billings 1975, Salmon et al. 2016), pointing to a relatively resource-acquisitive strategy. As the deeper parts of the active layer thaw for a shorter period of time than the upper layers, exploring deeper soil depths requires fast growth rates and low tissue densities – i.e. an explorative strategy. There might thus be variation in tissue density between species and plant communities in Arctic tundra, and also along the vertical distribution of roots in the soil profile – both as

17561051, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/njb.05293 by Universitaet Bayreuth, Wiley Online Library on [20/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

rooting depth differs between species, but also between individual plants in response to how long the thawed soil volume is available each season.

Because of its high turnover rates, *E. vaginatum* also leads to high amounts of root litter input, which can largely increase overall root litter input rates, if the species becomes more abundant upon permafrost thaw (Blume-Werry et al. 2019). This high input of fine root litter might be an important N source, as N from root litter is released immediately upon decomposition (Fornara et al. 2009) and plant growth in the tundra is particularly limited by nitrogen availability (van Cleve and Alexander 1981, Veen et al. 2015, Keuper et al. 2017). Root litter input from one species in the community can therefore affect the growth of co-occuring species (Meier et al. 2009). In the nutrient-poor upper soil layers of Arctic ecosystems, N input from root litter could potentially have a fertilizing effect on adjacent shallow-rooting species, especially if it comes from a species with high root turnover and access to an additional N source. This fertilizing effect might be independent from N mineralization, as tundra plants can take up organic forms of nitrogen (Kielland 1994, Schimel and Chapin 1996, Sorensen et al. 2008). Still, little is known about a possible vertical transportation of deep soil N via root litter from the deep-rooting *E. vaginatum*, or whether this redistribution is stronger when the active layer is deeper, and whether it impacts N uptake of adjacent shallow-rooting species.

Here, we investigated the effects of differences in active layer thickness on root biomass, rooting-depth distribution, and plant nitrogen availability in two different low Arctic plant communities, dominated either by the graminoid *E. vaginatum* or by a mix of tundra dwarf shrubs. Specifically, we hypothesized that:

1) active-layer thickness affects root biomass and rooting-depth distribution differently in the two plant communities, where rooting-depth distribution of dwarf shrub-dominated plant communities is independent of active layer thickness, whereas *E. vaginatum*-dominated plant communities shift a greater proportion of roots in deeper soil layers when the active layer is deeper.
2) roots further down in the soil profile belong to resource-acquisitive plants and have a lower root dry matter content (RDMC), as they have a shorter period of time for growth.
3) presence of the deep-rooting *E. vaginatum* promotes the uptake and subsequent re-distribution of permafrost-released nitrogen, more strongly so when the active layer is deeper, thereby allowing access to permafrost-nitrogen for shallow-rooting species.

To test our hypotheses, we measured root biomass distribution and RDMC in 10 cm depth increments down to the permafrost thawfront under plant communities dominated either by *E. vaginatum* or by a mixture of common dwarf shrubs. For each plant community type, we selected areas with either a more shallow active layer (around 50 cm), or a deeper active layer (around 70 cm), across a permafrost peatland in northern Sweden, and separated roots from *E. vaginatum* and all dwarf shrubs. Additionally, we harvested leaves of the six most common vascular plant species and analysed them for natural abundance of $\delta^{15}N$.

Material and methods

Study site

To assess the influence of increasing active layer thickness on plants' belowground biomass production and nutrient uptake strategies, peat cores were sampled. Our study site was an ombrotrophic peatland underlain by permafrost located near Abisko, northern Sweden ('Storflaket', 68°20′50.1″N, 18°58′28.4″E; Supporting information). Climatic conditions at the site are characterized as low Arctic with a mean annual air temperature of 0.5°C (1991–2020) and a mean annual precipitation of 348 mm (1991–2020) (Swedish Meteorological and Hydrological Institute [SMHI]; www.smhi.se). Soil properties are characterized by an organic matter content of 96% in the active layer and 34% in the permafrost (Väisänen et al. 2020). Dissolved organic nitrogen amounts to 0.02 mg g^{-1} SOM in the active layer (Väisänen et al. 2020).

The vegetation is dominated by the peatmoss *Sphagnum fuscum* (Schimp.) H. Klingg. and the vascular vegetation consists of dwarf shrub-dominated patches including the species *Empetrum nigrum* spp. *hermaphroditum* ((Hagerup) Böcher), *Betula nana* (L.), *Andromeda polifolia* (L.), and *Vaccinium uliginosum* (L.). Additionally, there are patches dominated by the graminoid *Eriophorum vaginatum* (L.) with the above dwarf-shrub species occasionally proliferating into those patches. Both dwarf shrub- and *E. vaginatum*-dominated patches have the forb *Rubus chamaemorus* (L.) interspersed, which shares many commonalities with dwarf shrubs, such as low stature and clonal growth. The majority of the species present very shallow roots, only reaching 10–30 cm as maximum rooting depth, whereas *E. vaginatum* and *R. chamaemorus* are relatively deep-rooting (Iversen et al. 2015).

Experimental design

Sampling was conducted in plots in a fully crossed two-factorial design, with either shallow or deep active layer thickness (averaging 51.3 ± 0.9 cm (mean ± SE) and 69.4 ± 1.9 cm, respectively; Supporting information) and being dominated either by the graminoid *E. vaginatum* or by dwarf-shrub species. The total number of plots was 24, with six replicates in each treatment combination. It was ensured that each plot contained a high percentage of vegetation cover. Sampling took place from mid- to late September 2021, at the time of maximum thawing depth of the active layer (up to 90 cm depth).

Vertical distribution of root biomass

To analyse the vertical root biomass distribution, one root sample was taken in each plot with a rectangular stainless steel soil auger made for peatland soils (size 5.5 × 5.0 cm, length

17561051, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/njb.05293 by Universitaet Bayreuth, Wiley Online Library on [20/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

1.0 m), between mid- and late September 2021. Before coring, active layer thickness was measured in each plot with a steel probe (1 cm diameter steel rod). To avoid compression of the topsoil layers in the core due to friction, the first 10 to 15 cm of soil were cut with a breadknife into rectangular shapes with the approximate size 10 × 10 cm. The soil core was then manually driven into the active layer for subsequent soil layers until it reached the permafrost table. After lifting the corer, peat which protruded past the edges of the corer was cut with a bread knife to fit the size of the core. Previously cut topsoil layers were then added to the soil core to produce the actual soil profile. The core was divided into depth increments every 10 cm. The soil core subsamples were then transferred into a plastic bag and stored in a refrigerator at +5°C until further processing.

Root washing and sorting was carried out by washing the samples free of organic soil in several trays filled with deionized water, and dead roots were discarded. The distinction between living and dead roots was based on root colour and elasticity. To make the process more efficient, samples were processed for a standardized amount of time as recommended by Freschet et al. (2021). Processing time standardization was set according to the depth of the attended subsample. Topsoil was defined as the upper 40 cm of soil and these samples were processed for 60 min, whereas medium soil layers of 40 to 60 cm depth were attended to for a maximum of 45 min and samples from deeper soil layers (> 60 cm depth) were washed for a maximum of 30 min. Root samples were processed in a randomized manner, but as samples were taken week by week, the length of time between sampling and processing was maintained. All washed roots were then removed from the tray, dried off, and placed on a paper towel. Roots were sorted according to morphological features and grouped into *E. vaginatum* roots – which are easily identified as they are white, thicker, and less branched than roots of the other species present (Proctor and He 2017) – and all other, dwarf-shrub species roots (including *R. chamaemorus*). Immediately after sorting, fresh weight was analysed on a scale. Root biomass was subsequently oven dried for 72 h at 70°C and dry root biomass was weighed. Root mass density per depth increment was estimated as gram (g) of dry root biomass per litre (l) calculated from the volume of the soil sample(5.5 × 5.0 × 10.0 cm). Maximum rooting depth as the maximum depth at which roots occur (Freschet et al. 2021) was estimated for root types in the depth distribution of the respective treatments.

Root dry matter content

Assessing morphological root traits can serve to gain a better understanding of roots' belowground nutrient allocation strategies. In accordance with Birouste et al. (2014), RDMC was used as a proxy for root tissue density to describe plants' resource acquisition strategies. RDMC is the ratio between dry root biomass and fresh root biomass and was therefore calculated from the biomass data.

Abiotic parameters

We measured C:N ratio over depth as an indicator of nitrogen mineralization and therefore nitrogen availability (Hobbie et al. 2002). Organic matter was manually collected from each of the peat core samples in 10 cm depth increments for elementary analysis. Samples were oven dried at 70°C for 72 h and weighed before and after drying. Samples were subsequently ground and approximately 20 mg of soil was weighed into tin cups. Carbon and nitrogen content was estimated with an elementary analyser (Vario EL III, Elementar, Langenselbold, Germany) where acetanilide was used as a standard.

Natural abundance of ^{15}N stable isotopes in foliar tissue and soil samples

To assess differences in nitrogen uptake capacities between shallow- and deep-rooting species, foliar biomass for the analysis of the natural abundance of ^{15}N was collected. Natural abundance of ^{15}N was described as:

$$\delta^{15}N = \left(\frac{R_{sample} - R_{standard}}{R_{standard}} \right) \times 1000$$

where R is the ratio between ^{15}N and ^{14}N in the soil sample and in atmospheric air, which is used as standard (Robinson 2001). Higher (positive) values of $\delta^{15}N$ suggest an enrichment in the heavier ^{15}N isotope, while lower (negative) values suggest the sample to be ^{15}N-depleted.

Sampling of foliar biomass took place between 9 and 12 September 2021. Leaves were collected in a circle of approximately 20 cm diameter around the position where the soil core was taken. A minimum of 20 leaves of each of the following species were sampled to achieve a minimum of 20–30 mg of dry biomass per sample: *E. vaginatum*, *E. nigrum* spp. *hermaphroditum*, *B. nana*, *A. polifolia*, *R. chamaemorus*, and *V. uliginosum*. Organic matter for the analysis of soil $\delta^{15}N$ was manually collected from the peat core samples in 10 cm depth increments. Prior to grinding, leaves and soil were oven-dried at 70°C for 72 h. We transferred 2–3 mg of the ground foliar material and approximately 5 mg of ground soil into tin cups, folded them into small balls, and put them on a 96 well culture tray. Foliar and soil $\delta^{15}N$ was then analysed with an isotopic mass spectrometer (Delta XP Thermo Electron, Bremen Germany) with Conflo IV interface (Thermo Electron, Bremen Germany) and an elementary analyser (Flash EA 1112 Thermo-Electron, Rodano, Milano, Italy) with acetanilide used as a standard.

Statistical analysis

Statistical analyses were performed in R ver. 4.5.2 (www.r-project.org) and the RStudio interface (Posit team 2026). To determine whether the deep and shallow active layer treatments differed in active layer thickness, a Welch-two-sample t-test with the measured actual active layer thickness was performed. Shapiro–Wilk and Levene tests were performed to test for normal distributions and equality of variances of the data.

We used linear mixed-effects models (LMMs) combined with an analysis of variance (ANOVA) with soil $\delta^{15}N$ [‰],

17561051, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/njb.05293 by Universitaet Bayreuth, Wiley Online Library on [20/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

soil CN ratio, foliar $\delta^{15}N$ [‰], root biomass distribution (g l^{-1}), and RDMC as the response variables in the respective models. Active layer thickness (grouped into type shallow and type deep), plant community composition, soil depth (except for foliar $\delta^{15}N$), and their interactions were used as fixed factors. Plot was used as random factor in all LMMS to account for the dependence of leaf or soil samples in the same plot (from different species or depth increments). All LMMs were fitted with the 'lme4' package (Bates et al. 2015). We additionally analysed root biomass distribution in a subset of *E. vaginatum*-dominated plots to determine whether there were differences in rooting depth distribution between shallow and deep active layer treatments for this specific species.

By design, maximum possible sampling depths differed between active layer types as we did not sample permafrost soil. To enable statistically balanced comparisons, we restricted depth-explicit analyses to subsets only including soil depth to 50 cm depth, which was present in both shallow and deep active layer plots. We further used complementary analysis of response variables integrated over the whole soil profile (total root biomass, and averages of soil CN ratio, soil $\delta^{15}N$, and RDMC) to evaluate whole-profile responses down to the permafrost, with linear models.

Our linear mixed-effects model ANOVA for RDMC was performed with a dataset that distinguished between dwarf-shrub (incl. *R. chamaemorus*) and *E. vaginatum* roots. Consequently, root type – i.e. roots from either dwarf shrubs or *E. vaginatum* – instead of plant community composition was used as fixed factor for this model. Foliar $\delta^{15}N$ was measured from leaves of single species, thus the LMM model used active layer type, plant community composition, and species as fixed factors. To assess whether plant-available nitrogen is vertically redistributed by *E. vaginatum*, differences in foliar $\delta^{15}N$ content between plant communities were analysed separately for the five shrub species in a subset excluding *E. vaginatum*. As soil ^{15}N showed a unimodal vertical depth pattern, we modelled depth with a quadratic term.

All models were reviewed for normality and homogeneity of residual variances as well as checked for zero-inflation and overdispersion. Model analysis was performed with the 'DHARMa' package (Hartig 2024). Log-transformation was performed for the variable root biomass [g l^{-1}] and rank-transformation was performed for the variables RDMC, C:N ratio, and foliar $\delta^{15}N$ to ensure that model assumptions were met. Post hoc testing was performed by obtaining the estimated marginal means, formerly known as least-squares means, with the 'EMMEANS' package (ver. 2.0.2, Lenth and Piaskowski 2026). Additionally, the following packages were used: 'TIDYVERSE' (Wickham et al. 2019), 'CAR' (Fox and Weisberg 2019), 'RMISC' (ver. 1.5.1 Hope 2022), 'GGTHEMES' (Arnold 2025) and 'LMERTEST' (Kuznetsova et al. 2017). Graphical visualizations were obtained using 'GGPLOT2' (Wickham 2016) and 'SJPLOT' (ver. 2.8.15; Lüdecke 2023).

Results

Active layer thickness

The average active layer thickness in plots in the 'shallow' category was 51.3 ± 0.9 cm (mean ± SE), whereas the mean active layer thickness in 'deep' plots was 69.4 ± 1.9 cm and the experimental design with treatments 'shallow' and 'deep' active layer categories could therefore be validated ($t = 8.56$, $df = 15.63$, $p < 0.001$). Maximum active layer thickness observed in the shallow active layer category was 60 cm and up to 90 cm depth in the deep active layer category.

Vertical distribution of root biomass

Generally, root biomass within the upper 50 cm displayed a significant decrease with depth ($F = 274.7$, $p < 0.001$; Fig. 1; Supporting information), with average root biomass in the uppermost 10 cm being 5.1 ± 0.4 g l^{-1} and 0.3 ± 0.06 g l^{-1} in the 50 cm depth increment. However, root biomass did not vary between the shallow and deep active layer categories ($F = 0.3$, $p = 0.600$) and the decline with depth did also not differ between active layer thickness (active layer type × depth, $F = 0.0$, $p = 0.860$). Root biomass did also not differ between the aboveground dominant plant communities ($F = 0.1$, $p = 0.713$), nor by the interaction of active layer thickness and plant community ($F = 0.3$, $p = 0.609$). This means that, within the first 50 cm of peat, neither active layer thickness nor plant community affected the amount of root biomass, in any combination. Similarly, the decline of root biomass with depth did not differ between the two different plant communities (plant community × depth, $F = 0.0$, $p = 0.913$), and overall, patterns of depth distribution of root biomass were consistent between all treatment combinations (active layer type × plant community × depth, $F = 0.3$, $p = 0.576$). These patterns were consistent when we analysed the total amount of biomass integrated over the whole active layer thickness (not just the first 50 cm): neither active layer thickness ($F = 0.3$, $p = 0.582$), nor plant community type ($F = 0.0$, $p = 0.871$), or their interaction ($F = 0.3$, $p = 0.582$) led to different amounts of root biomass.

When analysing *E. vaginatum*-dominated plots alone, we detected a similar pattern as for overall root biomass. Root biomass strongly declined with depth ($F = 207.4$, $p < 0.001$; Fig. 1; Supporting information), being just 1.5% at −70 cm depth of the amount we found at −10 cm depth. Root biomass also did not differ significantly between shallow and deep active layer categories ($F = 0.0$, $p = 0.991$). Similarly, the root biomass distribution with depth did not differ in shallow and deep active layer thickness (active layer type × depth, $F = 0.4$, $p = 0.527$), meaning that root biomass distribution in *E. vaginatum*-dominated plant communities is consistent across different active layer thickness within this low Arctic peatland. Again, there was also no difference in root biomass between shallow and deep active layers when we tested the whole biomass integrated over the whole active layer ($F = 0.9$, $p = 0.361$).

Even though we did not find differences between active layer thicknesses in root biomass or its distribution, we did

17561051, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/njb.05293 by Universitaet Bayreuth, Wiley Online Library on [20/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

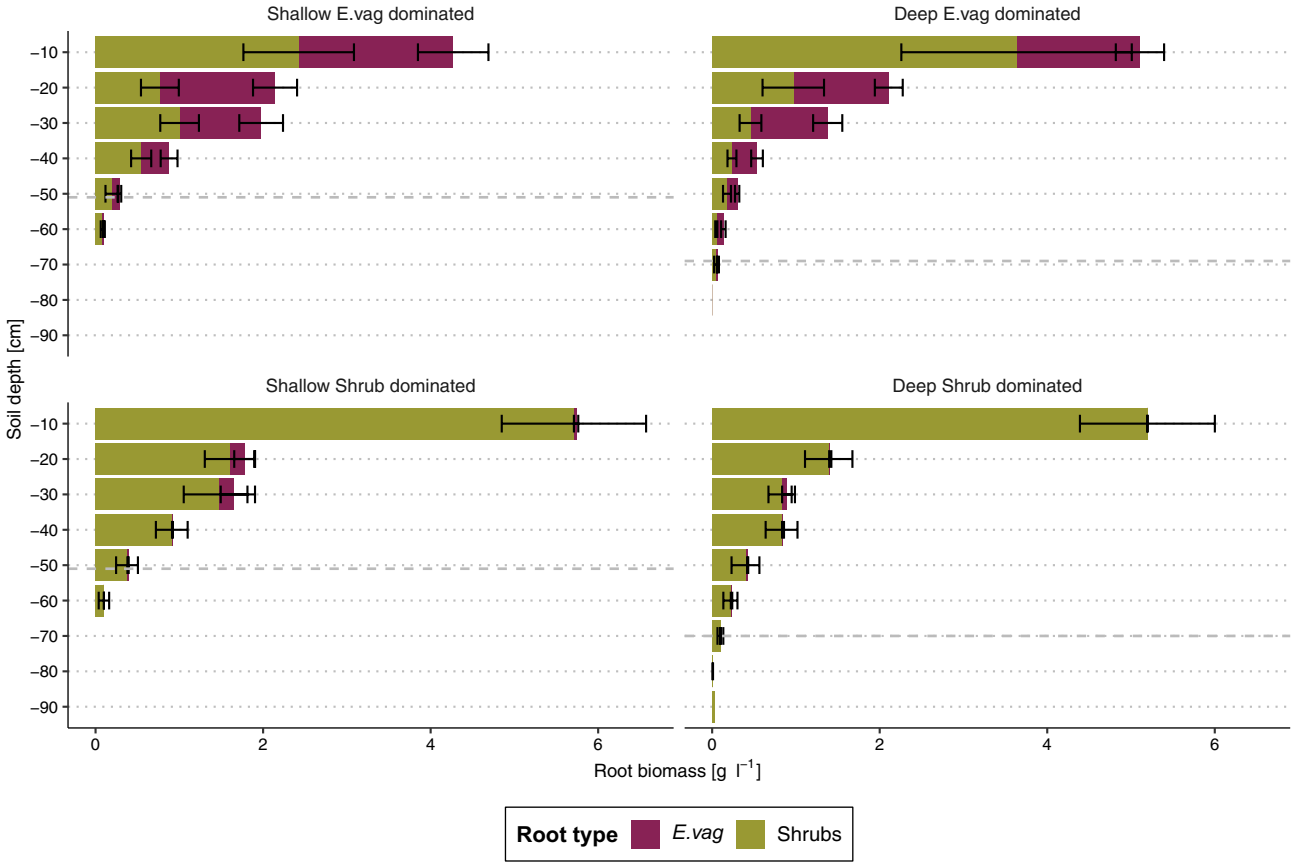


Figure 1. Vertical root biomass distribution of root types per active layer category and plant community type. Stacked bargraphs represent mean root biomass in g l^{-1} for *Eriophorum vaginatum* and dwarf shrubs per depth increment. Error bars display the standard error, n = 6. Dotted lines represent mean active layer thickness per category.

detect roots further down in the soil profile. In both plant communities, the maximum rooting depth was 60 cm in shallow active layer plots (9 out of 12 plots reached a depth of 60 cm; Fig. 1), whereas the pattern was less consistent in deep active layer plots. Within *E. vaginatum*-dominated deep active layer plots, roots proliferated to a maximum depth of 70 cm (6 out of 6 plots), while roots in dwarf shrub-dominated plots reached a maximum depth of 90 cm in deep active layer plots (1 out of 6 plots; Fig. 1). Overall, there was a higher amount of root biomass in dwarf shrub-dominated plots below a depth of 60 cm onwards in deep active layer plots.

Root dry matter content

RDMC differed between dwarf-shrub and *E. vaginatum* roots, with *E. vaginatum* generally having a 2.4 times lower RDMC than dwarf shrubs ($F = 6.2$, $p < 0.014$; Fig. 2; Supporting information). Interestingly, both *E. vaginatum* and dwarf shrubs had a lower RDMC with increasing depth (depth $F = 36.7$, $p < 0.001$; root type × depth, $F = 0.2$, $p = 0.650$). RDMC ranged from 0.17 ± 0.01 for *E. vaginatum* roots and 0.38 ± 0.01 for dwarf-shrub roots at 10 cm depth to 0.12 ± 0.02 (*E. vaginatum*) and 0.25 ± 0.02 (dwarf shrubs), respectively, at 50 cm depth. RDMC did not differ between active layer thickness ($F = 0.8$, $p = 0.378$), and responses of the different plant community types to active layer thickness did not differ (root type × active layer type, $F = 2.1$ $p = 0.151$), and above that, RDMC was more similar between root types in deeper depths of shallow active layer plots than deep ones there (root type × active layer type × depth, $F = 4.3$, $p = 0.040$).

Again, integrating RDMC over the entire available depths (not just the first 50 cm), showed a similar pattern: differences between root types ($F = 107.1$, $p < 0.001$), but not between active layer thicknesses ($F = 1.3$, $p = 0.264$), or their interaction ($F = 0.8$, $p = 0.386$).

C:N ratio in the depth profile

The C:N ratio decreased significantly in the depth profile ($F = 129.1$, $p < 0.001$; Supporting information), with a mean of 55.4 ± 3.2 in the upper 10 cm and a mean of 25.4 ± 1.0 at 50 cm depth across all treatments, validating our assumption that plant-available nitrogen increases with depth when using C:N ratio as a proxy. C:N ratio was not distinct between active layer thickness ($F = 1.2$, $p = 0.261$), or between active layer thickness within the different depth increments (active layer type × depth, $F = 1.1$, $p = 0.299$), and neither between plant communities (dwarf shrub- or *E. vaginatum*-dominated,

17561051, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/njb.05293 by Universitaet Bayreuth, Wiley Online Library on [20/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

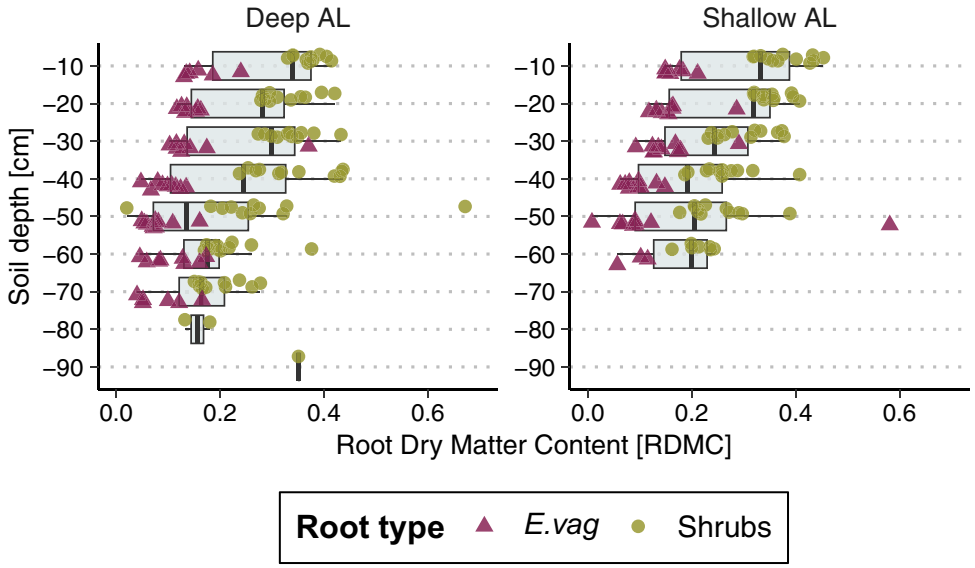


Figure 2. Root dry matter content of *Eriophorum vaginatum* and shrub roots in both plant community types, in either shallow or deep active layer. Box- and whisker plots display first quartile (25th percentile), median, and third quartile (75th percentile). Whiskers extend to 1.5× IQR; each datapoint for both *E. vaginatum* and dwarf-shrub root types is displayed, n = 12.

F = 1.1, p = 0.293) nor any of its interactions (active layer type × plant community, F = 0.1, p = 0.803; plant community × depth, F = 1.4, p = 0.235; active layer type × plant community × depth, F = 0.6, p = 0.454).

When we analysed average C:N ratio over the whole available active layer thickness there was a trend towards a lower C:N ratio in the deep than in the shallow active layer thickness (F = 3.2, p = 0.088), but no difference between plant communities (F = 0.1, p = 0.772) or its interaction with active layer thickness (F = 0.2, p = 0.693).

Natural abundance of $\delta^{15}N$ in soil

$\delta^{15}N$ ratios showed a strong, hump-shaped pattern with depth (depth: F = 59.5, $p < 0.001$, depth^2 F = 55.9, $p < 0.001$; Fig. 3; Supporting information) with an average of 0.9 ± 0.3‰ in the upper (10 cm) to 2.9 ± 0.3‰ at 30 cm and 1.0 ± 0.3‰ in the lower (50 cm) depth increments. None of the other factors, plant communities (F = 2.4, p = 0.121) and active layer thickness (F = 0.7, p = 0.404; Supporting information), nor their interactions affected soil $\delta^{15}N$ ratios (AL type × plant community, F = 0.3, p = 0.564; active layer type × depth, F = 1.9, p = 0.173; plant community × depth, F = 0.8, p = 0.383; active layer type × plant community × depth, F = 1.0, p = 0.325). There was a trend of a change in vertical shape depending on active layer thickness (active layer type × depth^2, F = 3.9, p = 0.051), reflecting that the peak of the hump shape shifted to a slightly lower soil depth in deep active layer plots.

Natural $\delta^{15}N$ abundance in foliar biomass

Overall, the six studied species *E. vaginatum*, *E. nigrum* spp. *hermaphroditum*, *B. nana*, *A. polifolia*, *R. chamaemorus*, and *V. uliginosum* differed significantly in their foliar $\delta^{15}N$ ratios (F = 80.7, $p < 0.001$; Fig. 4; Supporting information). In fact, each species showed individual foliar $\delta^{15}N$ ratio ranges. Among these individual ranges, *E. vaginatum* and *R. chamaemorus* on average displayed higher values than the remaining dwarf-shrub species, with a $\delta^{15}N$ ratio of 0.6 ± 0.7 and 1.5 ± 0.4, respectively. *Andromeda polifolia* on average displayed the lowest values with a $\delta^{15}N$ ratio of −8.2 ± 0.4. Foliar $\delta^{15}N$ ratio did not only differ between species, but also between plant communities (F = 7.8, p = 0.007). Across all species, foliar $\delta^{15}N$ ratios were higher in *E. vaginatum*-dominated plots with, on average, −2.4 ± 0.5 in *E. vaginatum*-dominated plots and −4.4 ± 0.5 in dwarf shrub-dominated plots. Despite these overall higher values, the species-specific pattern stayed similar (plant community × species, F = 0.4, p = 0.780). Active layer thickness did not influence the $\delta^{15}N$ ratio (F = 0.1, p = 0.738), and neither was the species-specific pattern changed by active layer thickness (active layer type × species, F = 0.1, p = 0.996). While not statistically significant, we observed a trend of plant community $\delta^{15}N$ ratio responding to active layer thickness (active layer type × plant community, F = 3.0, p = 0.089), indicating that the influence of different active layer thickness might not be consistent across plant communities.

When focusing only on the five dwarf-shrub species, we again found the same patterns with species-specificity in $\delta^{15}N$ ratios (species, F = 91.3, $p < 0.001$), as well as a significant effect of plant community composition (F = 9.1, p = 0.007), as all dwarf-shrub species displayed the highest foliar $\delta^{15}N$ ratios in their respective ranges in *E. vaginatum*-dominated plots. There was no effect of active layer thickness (F = 0.0, p = 0.912), and this was consistent across plant community types (AL type × plant community, F = 2.8, p = 0.112).

17561051, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/njb.05293 by Universitaet Bayreuth, Wiley Online Library on [20/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

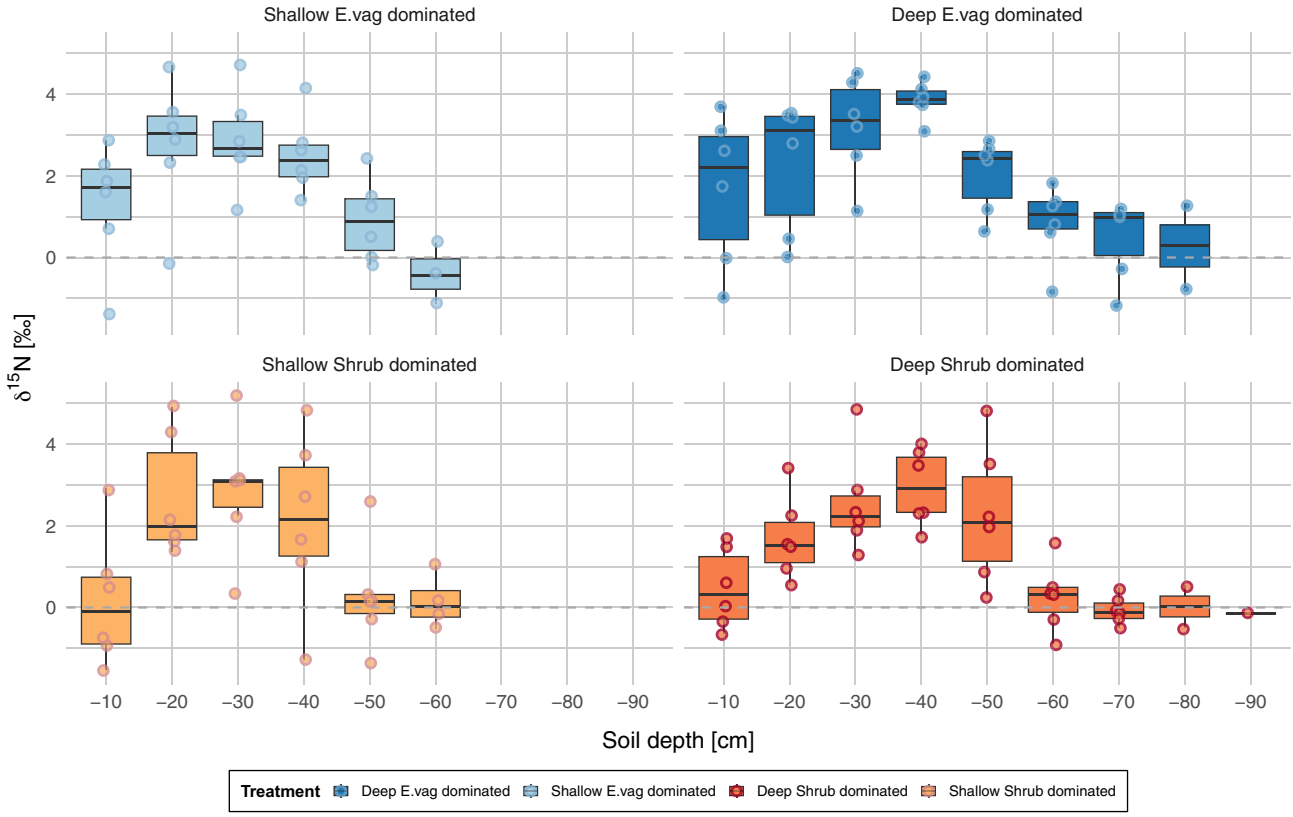


Figure 3. Vertical distribution of soil $\delta^{15}N$ [‰] per active layer category and plant community type. Box- and whisker plots display first quartile (25th percentile), median, and third quartile (75th percentile). Whiskers extend to 1.5× IQR; each datapoint is displayed, n = 6.

Discussion

We studied how permafrost thaw depth affects the depth distribution of root mass and RDMC in a low Arctic peatland. Root biomass declined strongly with depth in both *E. vaginatum*- and dwarf shrub-dominated communities, but was neither influenced by active layer thickness nor plant community. RDMC was not only lower in *E. vaginatum* than in dwarf-shrub roots but also declined with depth, indicating less investment and shorter-lived roots further down in the soil profile.

No differences in vertical root biomass distribution between plant communities and active layer thickness

Dwarfshrubs are generally known to have shallow rooting systems in the Arctic, whereas some sedges, such as *E. vaginatum*, can be deep-rooting (Iversen et al. 2015). As permafrost is thawing and releasing plant-available nitrogen in the generally nutrient-limited tundra (Keuper et al. 2012, Salmon et al. 2016), deep-rooting species might adapt their rooting distribution and grow more roots in deeper soil layers to take advantage of released nitrogen (Keuper et al. 2017, Blume-Werry et al. 2019). We thus initially hypothesized that *E. vaginatum*-dominated plant communities would have more roots deeper down in the soil profile than dwarfshrub-dominated plant communities, and that *E. vaginatum* – but not dwarfshrubs – would increase root biomass at depth in areas with deeper active layers. Yet, rooting depth distribution in the upper 50 cm did not differ between plant communities or active layer thicknesses. Both *E. vaginatum*- and dwarf-shrub-dominated communities displayed a rather similar vertical root biomass distribution in both deep and shallow active layer scenarios. In all treatment combinations, most root biomass was in the uppermost soil layer with a steep decline throughout the active layer. This suggests that there is no difference in rooting depth distribution between the studied plant communities, even though the dominant plant in one, *E. vaginatum*, is known for being deep-rooting (Proctor and He 2019). It is important to note that even though rooting depth distribution did not differ between active layer thickness within the upper 50 cm, and total amounts of root biomass across the whole respective profile did not differ, roots of *E. vaginatum* and other roots were present down to the thawfront even in deep active layer plots (Fig. 1). Based on morphological appearance (Rewald et al. 2012), we assume that the non-*E. vaginatum* roots at the thawfront all belonged to the same species: *Rubus chamaemorus*. Indeed, previous studies have also observed *R. chamaemorus* roots at the thaw front (Keuper et al. 2017, Hewitt et al. 2019) or have shown that they can take up N from the thaw front (Keuper et al. 2017, Blume-Werry et al. 2019). Although the abundance of *R. chamaemorus* was low compared to the other species, it still seems likely that the non-*E. vaginatum* deep roots mainly

17561051, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/njb.05293 by Universitaet Bayreuth, Wiley Online Library on [20/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

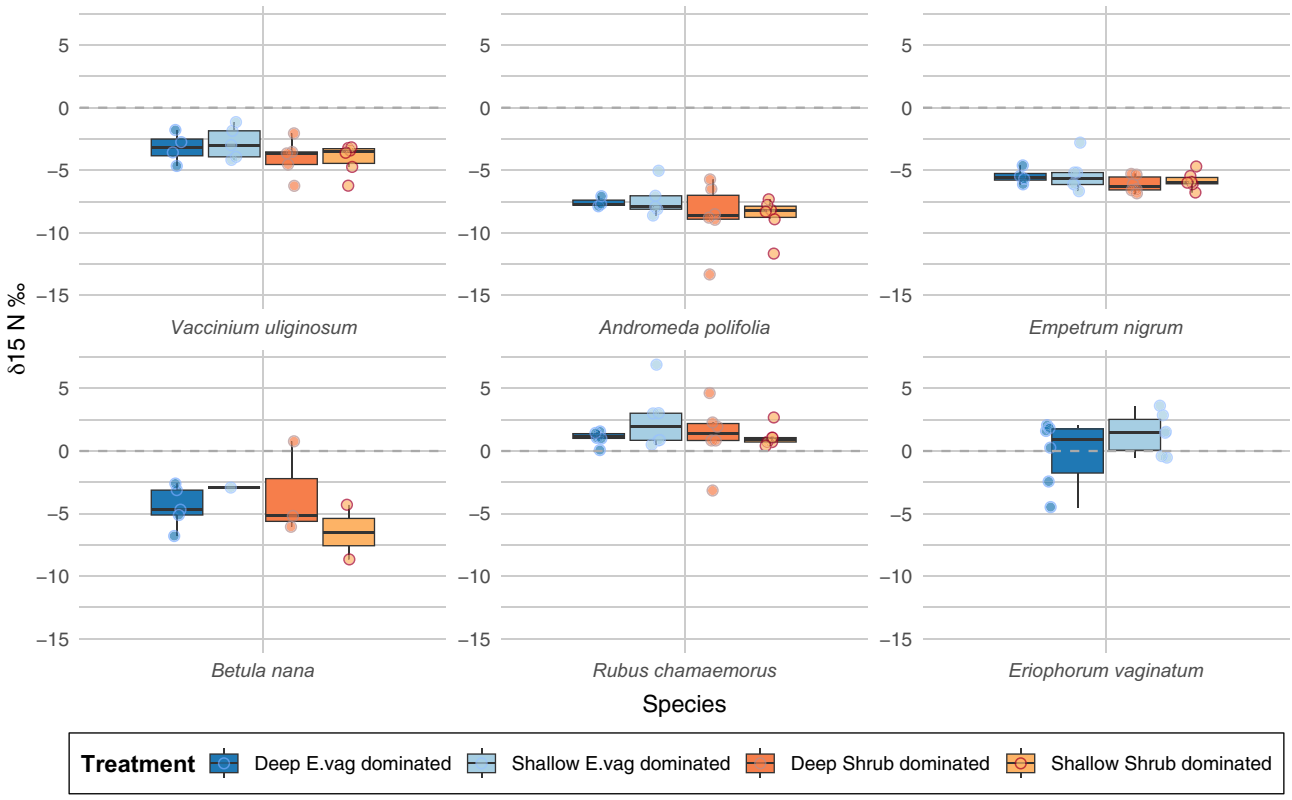


Figure 4. Foliar $\delta^{15}N$ [‰] for each species per active layer category and plant community type. Box- and whisker plots display first quartile (25th percentile), median, and third quartile (75th percentile). Whiskers extend to 1.5× IQR, but each datapoint is displayed, n = 6 plots, but not all species were present in all plots.

or only belonged to *R. chamaemorus*, due to its previously demonstrated presence at the thawfront, whereas all the other (dwarf-shrub) species only rooted shallowly (Shaver and Cutler 1979, Keuper et al. 2017, Blume-Werry et al. 2019). Thus, even if we did not detect any overall changes in biomass or its distribution in response to permafrost thaw, the presence of deep roots down to the thawfront – even if only a few – may have important ecological implications as they may contribute to aeration of the soil or stimulate microbial activity via root litter and exudation (Määttä and Malhotra 2024, Friggens et al. 2025, Mollenkopf et al. 2026). Taken together, this means that plant communities with varying abundance of dwarf-shrub and graminoid species can show similar root mass and depth distribution, if at least one deep-rooting species, such as *E. vaginatum* or *R. chamaemorus*, is present in each.

With increasing active layer thickness, the root system architecture of deep-rooting plants may enable them to tap new nitrogen sources (Doussan et al. 2009, Nacry et al. 2013), which could impact plant community composition. *Eriophorum vaginatum*, for example, has been shown to respond to a deepening of the active layer with increasing rooting depth (Wang et al. 2016, Blume-Werry et al. 2019, Ma et al. 2022), whereas evergreen and deciduous dwarf-shrubs species in the Arctic, such as *E. nigrum, B. nana*, *V. uliginosum*, and *A. polifolia* have shown non-plastic responses towards a deepening of the active layer (Keuper et al. 2017, Blume-Werry et al. 2019, Hewitt et al. 2019). However, while we did find *E. vaginatum* roots to a depth of 70 cm, the relative rooting depth distribution pattern of the entire plant community – and even *E. vaginatum* alone – did not change with increasing active layer thickness, nor did total biomass. Our results thus indicate that increasing the abundance of deep roots as a response to increasing active layer thickness is rather species-specific than community- or plant functional type- specific, and might not result in measurable differences in root biomass distribution – at least not in response to naturally varying active layer thickness as present here (where the difference between our 'shallow' and 'deep' ALT categories was approximately 18 cm). Corresponding with our results, Blume-Werry et al. (2023) found no differences in vertical root biomass distribution between aboveground vegetation types in a meta-analysis. However, our data suggest that this lack of difference might hinge on single plant species, such as *R. chamaemorus* or *E. vaginatum*, being present or absent in the community. Further, as our results are different to others that have shown varying rooting depth distribution between graminoid- or shrub- dominated communities (Wang et al. 2016, Keuper et al. 2017, Blume-Werry et al. 2019), it is important to identify when and in which plant communities the spatial distribution of root biomass is prone to shift. This is particularly important as current modelling efforts are based on presumed differences in rooting depth distribution between plant communities and in response to varying

17561051, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/njb.05293 by Universitaet Bayreuth, Wiley Online Library on [20/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

active layer thickness. For example, in the PrimeSCale model (Keuper et al. 2020), increasing active layer thickness leads to decreasing amounts of roots in shallow soil layers as roots are distributed over a larger soil volume. If the lack of difference in response to active layer thickness and plant community type observed here is common on a larger circumpolar scale, this would mean that such modelling assumptions would have to be reconsidered. More empirical data allowing generalization of root responses in different plant communities is thus essential for predicting ecosystem responses to thawing permafrost.

Root dry matter content decreases with depth

RDMC is a functional trait that is used as an inexpensive and easy-to-use proxy for root tissue density (Shipley and Vu 2002, Birouste et al. 2014), illustrating the economics behind resource use strategies: both lower RDMC and lower root tissue density are characteristic of a resource-acquisitive strategy and linked to a higher nutrient uptake rate (Ryser and Lambers 1995, Wahl and Ryser 2000), fast growth, and short life-span; whereas a higher RDMC indicates a more conservative plant growth strategy (Ryser and Lambers 1995, Ryser 1996, Wahl and Ryser 2000, Hummel et al. 2007, Birouste et al. 2014). Here, we observed clear differences in RDMC between root types (*E. vaginatum* versus dwarf-shrub roots). *Eriophorum vaginatum* had a lower RDMC than dwarf shrubs, which fits to its known fast root turnover and growth rates (Salmon et al. 2016), especially compared to Arctic dwarf shrubs. These RDMC patterns are consistent with the root economic spectrum, contrasting 'cheap' low carbon input, fast-growing, explorative roots with slow-growing, long-lived roots with a high tissue density (Freschet et al. 2010, Rehling et al. 2021). The root traits observed in *E. vaginatum* could therefore be classified as relatively more resource-acquisitive, while the RDMC found in dwarf shrubs indicates a relatively more resource-conservative strategy, on the spectrum we observed here. Dwarf shrubs tend to display trait characteristics from the conservative end of the plant economic spectrum in aboveground organs as well (Dorrepaal et al. 2005, Freschet et al. 2010), and the lower tissue density might enable *E. vaginatum* to be deep-rooting and explore freshly thawed permafrost soil quickly and without substantial carbon investment compared to the usually more shallow-rooting dwarf shrubs.

We did not only observe differences in RDMC between roots of dwarf shrubs and *E. vaginatum* but also a decreasing RDMC with depth in both root types. It is likely that because the deeper soil is only thawed and thus available for a shorter period of time during the already short Arctic summer season, only roots with low RDMC are worth growing that deep. Underlying reasons could be that the same species has a lower RDMC in deeper roots, as was the case for *E. vaginatum*, or that only those species with a low RDMC root that deep, i.e. a change in species composition of our pooled dwarf-shrub root samples. For example, tree species with a lower root density are able to proliferate deeper into the soil (Kramer-Walter et al. 2016). Assessing whether RDMC changes within the same species with depth due to adaption to environmental conditions, or whether only species with a low RDMC root deeply, might therefore be an important area for future research.

Increased foliar $\delta^{15}N$ ratios of dwarf shrubs in the presence of *E. vaginatum*

Previous studies of nitrogen dynamics in low Arctic tundra suggested that nitrogen from the permafrost thawfront, taken up by deep-rooting plants, might be vertically redistributed within the active layer over time, becoming available to shallow-rooting plants (Hewitt et al. 2019, 2020, Pedersen et al. 2020). Among processes driving this hypothetical mechanism are increased leaf and root litter input due to a higher nitrogen availability (Hewitt et al. 2019), increased decomposition of (plant and fungal) biomass and exudates from roots (Pedersen et al. 2020). Here, we presumed that this potential redistribution of nitrogen by deeper-rooting plants might be mirrored in natural abundances of foliar and soil $\delta^{15}N$. In our assessment of soil $\delta^{15}N$, we observed patterns of $\delta^{15}N$ with depth, with the highest natural ^{15}N abundance at about 20 (shallow ALT) to 40 (deep ALT) cm depth and the lowest ^{15}N abundance both closest to the surface and at the thawfront. As higher $\delta^{15}N$ can be indicative of greater mineralization, this difference in depth for the peak between the two active layer thicknesses, even if only marginally significant, may therefore indicate a depth-shift in microbial activity, diversity, or abundance (Groß-Schmölders et al. 2020). This could be an interesting avenue for future research targeted at shifting hotspots of microbial communities and activity related to permafrost thaw. Besides microbial activity, varying hydrological history and status could be another factor explaining the observed patterns in soil $\delta^{15}N$ (Groß-Schmölders et al. 2020). However, we did not detect differences in $\delta^{15}N$ between soils under *E. vaginatum*- and dwarf shrub-dominated communities, nor between different active layer types. This could indicate that, as of now, there has been no substantial redistribution of permafrost nitrogen, which may in any case take a long time to be visible. Accordingly, an assessment of N dynamics in a permafrost thaw gradient in Alaska revealed that changes in N dynamics manifested only over years to centuries (Finger et al. 2016).

Our survey of foliar $\delta^{15}N$ ratios of the six vascular plant species present in the studied low Arctic peatland revealed highly species-specific ranges of $\delta^{15}N$, also seen in previous studies, e.g. for *E. vaginatum*, *V. uliginosum*, *E. nigrum*, and *B. nana* (Michelsen et al. 1996, Nadelhoffer et al. 1996). These species-specific values could be indicative of different individual nutrient uptake strategies (Nadelhoffer et al. 1996, Kahmen et al. 2008), such as mycorrhizal associations (Michelsen et al. 1996, Hobbie et al. 2005, 2009) or may mirror N uptake from different soil depths and hence different rooting depths (Oulehle et al. 2016, Hewitt et al. 2019, Pedersen et al. 2020). While these species-specific ratios are not surprising and their underlying causes not the aim of this study, we did observe another interesting pattern: $\delta^{15}N$ ratios varied between vegetation communities, with all species having their highest $\delta^{15}N$ ratios in plots dominated by *E. vaginatum*. Thus, even though soil $\delta^{15}N$ ratios did not differ between

17561051, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/njb.05293 by Universitaet Bayreuth, Wiley Online Library on [20/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

vegetation communities, it seems the presence of *E. vaginatum* might indeed induce a redistribution of nitrogen that is available to neighbouring plants, or stimulate activity of different microbial communities, leading to a change in $\delta^{15}N$ signature, or lead to a shift in the type of nitrogen taken up from different parts of the soil column, e.g. a different niche-partitioning within the community (McKane et al. 2002). This hypothesis is in line with the findings of our assessment of vertical root biomass distribution, where we showed that *E. vaginatum* has relatively more roots at the depth with the highest $\delta^{15}N$ ratios than woody dwarf shrubs do.

Conclusions

We show that roots are present all the way down to the thawfront, even at 90 cm depth, bringing them into contact with previously frozen soils, which could have important ecological implications. However, root biomass distribution with depth was the same in the first 50 cm of the active layer for both plant communities and under different active layer thicknesses, indicating no strong changes in root biomass or depth distribution in response to deeper active layers. We observed intra-specific changes in RDMC with decreasing dry matter content with increasing depth, which points at a shift towards more acquisitive resource allocation strategies with greater depth. In addition, we detected species-specific $\delta^{15}N$ ratios with the highest intra-specific signatures in communities dominated by *E. vaginatum*. This may be due to either a redistribution of nitrogen from the permafrost table, an altered source of nitrogen uptake, or a sign of differential microbial activity. The thawing of permafrost in low Arctic peatlands in Fennoscandia might therefore ultimately have the potential to directly and indirectly alter plant community composition by favouring deep-rooting species, and their influence on ecosystem C and N cycling.

Acknowledgements – We are thankful for the help of Dietrich Hertel, Paul Hübner, Annegret Kellner, Reinhard Langel, and Uta Nüsse-Hahne in the field and lab.
Funding – GB-W acknowledges funding from the Swedish Research Council (Vetenskapsrådet), grant no. 2022-04089. The Climate Impacts Research Centre (Umeå University), the Abisko Scientific Research Station, and the Plant Ecology and Ecosystems Research group at University of Göttingen all provided facilities and equipment critically contributing to the success of this project.
Conflict of interest – The authors declare no conflict of interest.
Permits – Our study involved only small-scale field observations and sampling that did not cause permanent or significant environmental impact and therefore did not meet the threshold for consultation or permit requirement (according to the Swedish Environmental Code). No protected areas, species, or habitats were affected.

Author contributions

Alexandra Werner: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Visualization (lead); Writing – original draft (equal). **Lena Muffler**: Writing – review and editing (equal). **Gesche Blume-Werry**: Conceptualization (equal); Funding acquisition (lead); Methodology (lead); Project administration (lead); Supervision (lead); Writing – original draft (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.mw6m906cr (Werner et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Åkerman, H. J. and Johansson, M. 2008. Thawing permafrost and thicker active layers in sub-Arctic Sweden. – Permafrost Periglac. Process. 19: 279–292.
Arnold, J. B. 2025. ggthemes: extra themes, scales and geoms for 'ggplot2'. – R package ver. 5.2.0, https://cran.r-project.org/web/packages/ggthemes/index.html.
Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.
Birouste, M., Zamora-Ledezma, E., Bossard, C., Pérez-Ramos, I. M. and Roumet, C. 2014. Measurement of fine root tissue density: a comparison of three methods reveals the potential of root dry matter content. – Plant Soil 374: 299–313.
Biskaborn, B. K. et al. 2019. Permafrost is warming at a global scale. – Nat. Commun. 10: 1–11.
Blume-Werry, G., Milbau, A., Teuber, L. M., Johansson, M. and Dorrepaal, E. 2019. Dwelling in the deep – strongly increased root growth and rooting depth enhance plant interactions with thawing permafrost soil. – New Phytol. 223: 1328–1339.
Blume-Werry, G., Dorrepaal, E., Keuper, F., Kummu, M., Wild, B. and Weedon, J. T. 2023. Arctic rooting depth distribution influences modelled carbon emissions but cannot be inferred from aboveground vegetation type. – New Phytol. 240: 502–514.
Chapin, F. S., Bloom, A. J., Field, C. B. and Waring, R. H. 1987. Plant responses to multiple environmental factors. – BioScience 37: 49–57.
Clemmensen, K. E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R. D., Wardle, D. A. and Lindahl, B. D. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. – Science 339: 1615–1618.
Dorrepaal, E., Cornelissen, J. H. c., Aerts, R., Wallén, B. and Van Logtestijn, R. S. P. 2005. Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? – J. Ecol. 93: 817–828.
Doussan, C., Pagès, L. and Pierret, A. 2009. Soil exploration and resource acquisition by plant roots: an architectural and modelling point of view. – In: Lichtfouse, E., Navarrete, M., Debaeke, P., Souchère, V. and Alberola, C. (eds), Sustainable agriculture. Springer, pp. 583–600.
Finger, R. A., Turetsky, M. R., Kielland, K., Ruess, R. W., Mack, M. C. and Euskirchen, E. S. 2016. Effects of permafrost thaw

17561051, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/njb.05293 by Universitaet Bayreuth, Wiley Online Library on [20/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

on nitrogen availability and plant–soil interactions in a boreal Alaskan lowland. – J. Ecol. 104: 1542–1554.
Fornara, D. A., Tilman, D. and Hobbie, S. E. 2009. Linkages between plant functional composition, fine root processes and potential soil N mineralization rates. – J. Ecol. 97: 48–56.
Fox, J. and Weisberg, S. 2019. An R companion to applied regression. – Sage.
Freschet, G. T., Cornelissen, J. H. C., van Logtestijn, R. S. P. and Aerts, R. 2010. Evidence of the 'plant economics spectrum' in a subarctic flora. – J. Ecol. 98: 362–373.
Freschet, G. T. et al. 2021. A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. – New Phytol. 232: 973–1122.
Friggens, N. L., Hugelius, G., Kokelj, S. V., Murton, J. B., Phoenix, G. K. and Hartley, I. P. 2025. Positive rhizosphere priming accelerates carbon release from permafrost soils. – Nat. Commun. 16: 3576.
Grosse, G., Romanovsky, V., Jorgenson, T., Anthony, K. W., Brown, J. and Overduin, P. P. 2011. Vulnerability and feedbacks of permafrost to climate change. – Eos Trans. AGU 92: 73–74.
Groß-Schmölders, M., von Sengbusch, P., Krüger, J. P., Klein, K., Birkholz, A., Leifeld, J. and Alewell, C. 2020. Switch of fungal to bacterial degradation in natural, drained and rewetted oligotrophic peatlands reflected in $\delta^{15}N$ and fatty acid composition. – Soil 6: 299–313.
Hartig, F. 2024. DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models. – R package ver. 0.5.0, https://cran.r-project.org/web/packages/DHARMa/index.html.
Hewitt, R. E., Taylor, D. L., Genet, H., McGuire, A. D. and Mack, M. C. 2019. Below-ground plant traits influence tundra plant acquisition of newly thawed permafrost nitrogen. – J. Ecol. 107: 950–962.
Hewitt, R. E., DeVan, M. R., Lagutina, I. V., Genet, H., McGuire, A. D., Taylor, D. L. and Mack, M. C. 2020. Mycobiont contribution to tundra plant acquisition of permafrost-derived nitrogen. – New Phytol. 226: 126–141.
Hobbie, E. A., Jumpponen, A. and Trappe, J. 2005. Foliar and fungal ^{15}N:^{14}N ratios reflect development of mycorrhizae and nitrogen supply during primary succession: testing analytical models. – Oecologia 146: 258–68.
Hobbie, J. E., Hobbie, E. A., Drossman, H., Conte, M., Weber, J. C., Shamhart, J. and Weinrobe, M. 2009. Mycorrhizal fungi supply nitrogen to host plants in Arctic tundra and boreal forests: ^{15}N is the key signal. – Can. J. Microbiol. 55: 84–94.
Hobbie, S. E., Nadelhoffer, K. J. and Högberg, P. 2002. A synthesis: the role of nutrients as constraints on carbon balances in boreal and Arctic regions. – Plant Soil 242: 163–170.
Hodge, A. 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. – New Phytol. 162: 9–24.
Hope, R. M. 2022. Rmisc: Ryan miscellaneous. – R package ver. 1.5.1, https://cran.r-project.org/web/packages/Rmisc/index.html.
Hummel, I., Vile, D., Violle, C., Devaux, J., Ricci, B., Blanchard, A., Garnier, É. and Roumet, C. 2007. Relating root structure and anatomy to whole-plant functioning in 14 herbaceous Mediterranean species. – New Phytol. 173: 313–321.
IPCC 2021. Summary for policymakers. – In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M. I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R., Maycock, T. K., Waterfield, T., Yelekçi, O., Yu, R. and Zhou, B. (eds), Climate Change 2021: the physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press, pp. 3–32.
Iversen, C. M., Sloan, V. L., Sullivan, P. F., Euskirchen, E. S., McGuire, A. D., Norby, R. J., Walker, A. P., Warren, J. M. and Wullschleger, S. D. 2015. The unseen iceberg: plant roots in Arctic tundra. – New Phytol. 205: 34–58.
Kahmen, A., Wanek, W. and Buchmann, N. 2008. Foliar $\delta^{15}N$ values characterize soil N cycling and reflect nitrate or ammonium preference of plants along a temperate grassland gradient. – Oecologia 156: 861–870.
Keuper, F., Bodegom, P. M., Dorrepaal, E., Weedon, J. T., Hal, J., Logtestijn, R. S. P. and Aerts, R. 2012. A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands. – Global Change Biol. 18: 1998–2007.
Keuper, F., Dorrepaal, E., van Bodegom, P. M., van Logtestijn, R., Venhuizen, G., van Hal, J. and Aerts, R. 2017. Experimentally increased nutrient availability at the permafrost thaw front selectively enhances biomass production of deep-rooting subarctic peatland species. – Global Change Biol. 23: 4257–4266.
Keuper, F. et al. 2020. Carbon loss from northern circumpolar permafrost soils amplified by rhizosphere priming. – Nat. Geosci. 13: 560–565.
Kielland, K. 1994. Amino acid absorption by Arctic plants: implications for plant nutrition and nitrogen cycling. – Ecology 75: 2373.
Kramer-Walter, K. R., Bellingham, P. J., Millar, T. R., Smissen, R. D., Richardson, S. J. and Laughlin, D. C. 2016. Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. – J. Ecol. 104: 1299–1310.
Kuznetsova, A., Brockhoff, P. B. and Christensen, R. H. B. 2017. lmerTest package: tests in linear mixed effects models. – J. Stat. Softw. 82: 1–26.
Lenth, R. V. and Piaskowski, J. 2026. emmeans: estimated marginal means, aka least-squares means. – R package ver. 2.0.4, https://cran.r-project.org/web/packages/emmeans/index.html.
Loya, W. M., Johnson, L. C., Kling, G. W., King, J. Y., Reeburgh, W. S. and Nadelhoffer, K. J. 2002. Pulse-labeling studies of carbon cycling in Arctic tundra ecosystems: contribution of photosynthates to soil organic matter. – Global Biogeochem. Cycles 16: 1101.
Lüdecke, D. 2023. sjPlot: data visualization for statistics in social science. – R package ver. 2.9.0, https://cran.r-project.org/web/packages/sjPlot/index.html.
Ma, H., Mo, L., Crowther, T. W., Maynard, D. S., van den Hoogen, J., Stocker, B. D., Terrer, C. and Zohner, C. M. 2021. The global distribution and environmental drivers of aboveground versus belowground plant biomass. – Nat. Ecol. Evol. 5: 1110–1122.
Ma, T., Parker, T., Fetcher, N., Unger, S. L., Gewirtzman, J., Moody, M. L. and Tang, J. 2022. Leaf and root phenology and biomass of *Eriophorum vaginatum* in response to warming in the Arctic. – J. Plant Ecol. 15: 1091–1105.
Määttä, T. and Malhotra, A. 2024. The hidden roots of wetland methane emissions. – Global Change Biol. 30: e17127.
McKane, R. B., Johnson, L. C., Shaver, G. R., Nadelhoffer, K. J., Rastetter, E. B., Fry, B., Giblin, A. E., Kielland, K., Kwiatkowski, B. L., Laundre, J. A. and Murray, G. 2002. Resource-based niches provide a basis for plant species diversity and dominance in Arctic tundra. – Nature 415: 68–71.

17561051, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/njb.05293 by Universitaet Bayreuth, Wiley Online Library on [20/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Meier, C. L., Keyserling, K. and Bowman, W. D. 2009. Fine root inputs to soil reduce growth of a neighbouring plant via distinct mechanisms dependent on root carbon chemistry. – J. Ecol. 97: 941–949.
Michelsen, A., Schmidt, I. K., Jonasson, S., Quarmby, C. and Sleep, D. 1996. Leaf 15 N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non-and arbuscular mycorrhizal species access different sources of soil nitrogen. – Oecologia 105: 53–63.
Mollenkopf, M., Lenge, K., Drabesch, S., Monteux, S., Van Grinsven, S., Joshi, P., Dorrepaal, E., Wild, B., Kappler, A. and Muehe, E. M. 2026. Graminoids increase greenhouse gas emissions from thawed permafrost at the end of the growing season. – Global Change Biol. 32: e70783.
Nacry, P., Bouguyon, E. and Gojon, A. 2013. Nitrogen acquisition by roots: physiological and developmental mechanisms ensuring plant adaptation to a fluctuating resource. – Plant Soil 370: 1–29.
Nadelhoffer, K., Shaver, G., Fry, B., Giblin, A., Johnson, L. and McKane, R. 1996. ^{15}N natural abundances and N use by tundra plants. – Oecologia 107: 386–394.
Oulehle, F., Rowe, E. C., Myška, O., Chuman, T. and Evans, C. D. 2016. Plant functional type affects nitrogen use efficiency in high-Arctic tundra. – Soil Biol. Biochem. 94: 19–28.
Pedersen, E. P., Elberling, B. and Michelsen, A. 2020. Foraging deeply: depth-specific plant nitrogen uptake in response to climate-induced N-release and permafrost thaw in the High Arctic. – Global Change Biol. 26: 6523–6536.
Posit team 2026. RStudio: integrated development environment for R. – Posit Software, PBC, www.posit.co.
Proctor, C. and He, Y. 2017. Quantifying root extracts and exudates of sedge and shrub in relation to root morphology. – Soil Biol. Biochem. 114: 168–180.
Proctor, C. and He, Y. 2019. Quantifying wetland plant vertical root distribution for estimating the Interface with the anoxic zone. – Plant Soil 440: 381–398.
Rantanen, M., Karpechko, A. Yu., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T. and Laaksonen, A. 2022. The Arctic has warmed nearly four times faster than the globe since 1979. – Commun. Earth Environ. 3: 1–10.
Rehling, F., Sandner, T. M. and Matthies, D. 2021. Biomass partitioning in response to intraspecific competition depends on nutrients and species characteristics: a study of 43 plant species. – J. Ecol. 109: 2219–2233.
Reich, P. B. 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. – J. Ecol. 102: 275–301.
Rewald, B., Meinen, C., Trockenbrodt, M., Ephrath, J. E. and Rachmilevitch, S. 2012. Root taxa identification in plant mixtures – current techniques and future challenges. – Plant Soil 359: 165–182.
Robinson, D. 2001. $\delta^{15}N$ as an integrator of the nitrogen cycle. – Trends Ecol. Evol. 16: 153–162.
Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vrignon-Brenas, S., Cao, K.-F. and Stokes, A. 2016. Root structure–function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. – New Phytol. 210: 815–26.
Ryser, P. 1996. The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. – Funct. Ecol. 10: 717–723.
Ryser, P. and Lambers, H. 1995. Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. – Plant Soil 170: 251–265.
Salmon, V. G., Soucy, P., Mauritz, M., Celis, G., Natali, S. M., Mack, M. C. and Schuur, E. A. G. 2016. Nitrogen availability increases in a tundra ecosystem during five years of experimental permafrost thaw. – Global Change Biol. 22: 1927–1941.
Schenk, H. J. and Jackson, R. B. 2002. The global biogeography of roots. – Ecol. Monogr. 72: 311–328.
Schimel, J. P. and Chapin, F. S. 1996. Tundra plant uptake of amino acid and NH 4+ nitrogen in situ: plants complete well for amino acid N. – Ecology 77: 2142–2147.
Shaver, G. R. and Billings, W. D. 1975. Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. – Ecology 56: 401–409.
Shaver, G. R. and Cutler, J. C. 1979. The vertical distribution of live vascular phytomass in cottongrass tussock tundra. – Arct. Antarct. Alp. Res. 11: 335–342.
Shipley, B. and Vu, T.-T. 2002. Dry matter content as a measure of dry matter concentration in plants and their parts. – New Phytol. 153: 359–364.
Sorensen, P. L., Clemmensen, K. E., Michelsen, A., Jonasson, S. and Ström, L. 2008. Plant and microbial uptake and allocation of organic and inorganic nitrogen related to plant growth forms and soil conditions at two subarctic tundra sites in Sweden. – Arct. Antarct. Alp. Res. 40: 171–180.
Spitzer, C. M., Wardle, D. A., Lindahl, B. D., Sundqvist, M. K., Gundale, M. J., Fanin, N. and Kardol, P. 2021. Root traits and soil micro-organisms as drivers of plant–soil feedbacks within the sub-arctic tundra meadow. – J. Ecol. 110: 466–478.
Strand, S. M., Christiansen, H. H., Johansson, M., Åkerman, J. and Humlum, O. 2021. Active layer thickening and controls on interannual variability in the Nordic Arctic compared to the circum-Arctic. – Permafrost Periglac. Process. 32: 47–58.
Väisänen, M., Krab, E. J., Monteux, S., Teuber, L. M., Gavazov, K., Weedon, J. T., Keuper, F. and Dorrepaal, E. 2020. Meshes in mesocosms control solute and biota exchange in soils: a step towards disentangling (a)biotic impacts on the fate of thawing permafrost. – Appl. Soil Ecol. 151: 103537.
van Cleve, K. and Alexander, V. 1981. Nitrogen cycling in tundra and boreal ecosystems. – Ecol. Bull. 33: 375–404.
Veen, G. F., Sundqvist, M. K., Metcalfe, D. and Wilson, S. D. 2015. Above-ground and below-ground plant responses to fertilization in two subarctic ecosystems. – Arct. Antarct. Alp. Res. 47: 693–702.
Wahl, S. and Ryser, P. 2000. Root tissue structure is linked to ecological strategies of grasses. – New Phytol. 148: 459–471.
Wang, P., Heijmans, Monique M. P. D., Mommer, L., van Ruijven, J., Maximov, T. C. and Berendse, F. 2016. Belowground plant biomass allocation in tundra ecosystems and its relationship with temperature. – Environ. Res. Lett. 11: 055003.
Wang, P., Limpens, J., Mommer, L., Ruijven, J., Nauta, A. L., Berendse, F., Schaepman-Strub, G., Blok, D., Maximov, T. C. and Heijmans, M. M. P. D. 2017. Above- and below-ground responses of four tundra plant functional types to deep soil heating and surface soil fertilization. – J. Ecol. 105: 947–957.
Werner, A., Muffler, L. and Gesche Blume-Werry, G. 2026. Data from: Root biomass distribution in response to increasing active layer thickness across plant communities in a permafrost peatland. – Dryad Digital Repository, https://doi.org/10.5061/dryad.mw6m906cr.
Wickham, H. 2016. ggplot2: elegant graphics for data analysis. – Springer.
Wickham, H. et al. 2019. Welcome to the Tidyverse. – J. Open Source Softw. 4: 1686.

17561051, 0, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.1002/njb.05293 by Universitaet Bayreuth, Wiley Online Library on [20/10/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License