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Arctic rooting depth distribution influences modelled carbon emissions but cannot be inferred from aboveground vegetation type

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Summary

- The distribution of roots throughout the soil drives depth-dependent plant–soil interactions and ecosystem processes, particularly in arctic tundra where plant biomass is predominantly belowground. Vegetation is usually classified from aboveground, but it is unclear whether such classifications are suitable to estimate belowground attributes and their consequences, such as rooting depth distribution and its influence on carbon cycling.
- We performed a meta-analysis of 55 published arctic rooting depth profiles, testing for differences both between distributions based on aboveground vegetation types (Graminoid, Wetland, Erect-shrub, and Prostrate-shrub tundra) and between ‘Root Profile Types’ for which we defined three representative and contrasting clusters. We further analyzed potential impacts of these different rooting depth distributions on rhizosphere priming-induced carbon losses from tundra soils.
- Rooting depth distribution hardly differed between aboveground vegetation types but varied between Root Profile Types. Accordingly, modelled priming-induced carbon emissions were similar between aboveground vegetation types when they were applied to the entire tundra, but ranged from 7.2 to 17.6 Pg C cumulative emissions until 2100 between individual Root Profile Types.
- Variations in rooting depth distribution are important for the circumpolar tundra carbon-climate feedback but can currently not be inferred adequately from aboveground vegetation type classifications.

Introduction

Plant roots are responsible for the exploration and acquisition of soil resources, such as water and nutrients, but are also key players in carbon dynamics (e.g. Boone et al., 1998; Jobbágy & Jackson, 2001). The amount of carbon that is transferred belowground through root production, turnover, and exudation strongly influences biogeochemical cycling (e.g. Jobbágy & Jackson, 2000). Not only how much plant biomass is present and produced belowground, but also how this biomass is distributed over the soil profile, is important for understanding these processes, as the location of roots relative to the vertical layering of resources and other organisms in the soil profile determines the spatial patterning of depth-dependent interactions between plants and their environment. As such, vegetation affects the distribution of key nutrients and soil organic carbon over the soil profile via its rooting depth distribution (Jobbágy & Jackson, 2000, 2001).

Understanding rooting depth distribution is particularly important in arctic tundra, where above 80% of plant biomass is situated belowground (Mokany et al., 2006; Iversen et al., 2015). Root production is also a large portion of net primary production in arctic tundra, making up 30–90% in sedge-dominated and 10–60% in shrub-dominated tundra (Iversen et al., 2015). At the same time, the Arctic is a system undergoing rapid change, warming three times as fast as the global average (IPCC, 2021). This warming not only leads to accelerating permafrost thaw and increased soil organic matter decomposition, but also stimulates primary production and induces widespread shifts in plant community composition. All these changes may feedback to root- and rhizosphere processes, or themselves be influenced by them.
for example, through changes in rooting depth or root turnover (Keuper et al., 2017; Blume-Werry et al., 2019). Through their strong influence on tundra carbon cycling (Loya et al., 2002, 2004), roots and their depth distribution also lay the foundation for climate feedbacks from tundra soils, which store more than twice as much carbon as is currently in the atmosphere (Hugielus et al., 2014). Despite this importance, a comprehensive understanding of roots and variation in patterns of their vertical distribution in the relatively inaccessible arctic soils is missing.

Being the conduit for carbon fluxes belowground, and through their interactions with soil microbial communities, plant roots influence the stabilization and formation of soil carbon (Clemmensen et al., 2013; Sokol & Bradford, 2019). However, if decomposition is limited by available energy sources, the presence of roots and their exudates can also strongly stimulate the decomposition of soil organic matter, a process called the rhizosphere priming effect (Kuzyakov, 2002; Fontaine et al., 2007). Depending on the distribution of roots throughout the soil profile, plants will interact with a varying amount and quality of soil at different depths (Iversen, 2010; Poirer et al., 2018). Thus, which part and how much of the soil will potentially be subjected to the rhizosphere priming effect depends on rooting depth distribution. It is therefore important to understand the magnitude and drivers of variation in rooting depth distribution and to accurately represent it in models of soil biogeochemistry. Despite this, and although modelling different rooting depths can have stronger effects on biogeochemical pools than increases in temperature or precipitation (Daly et al., 2000), root representation in models remains rudimentary (Smithwick et al., 2014; Warren et al., 2015). This is because roots are notoriously difficult to study and root data, such as depth distribution of root biomass, thus remains scarce.

The limited available data on rooting depth distribution have been synthesized globally by Schenk & Jackson (2002), who showed that rooting depth is generally very shallow in arctic tundra compared with other ecosystems: On average, 50% of root biomass is located in the upper 9 cm in tundra, and 95% in the upper 29 cm. One key factor that differentiates arctic tundra from other biomes and contributes to these shallow rooting depths is the presence of perennially frozen ground, permafrost. Permafrost acts as a physical barrier at depth and restricts roots to the active layer, the upper part of the soil column that thaws each summer. However, even if the active layer is relatively thick, for example, at the southern permafrost border, many tundra plants have shallow rooting systems and do not use all the available soil volume (Keuper et al., 2017; Blume-Werry et al., 2019). In addition to abiotic conditions, differing rooting depths between species and plant functional types are a way to avoid competition for scarce belowground resources (de Kroon et al., 2012; Guderle et al., 2018), for example, through uptake of nitrogen at different depth (McKane et al., 2002; Wang et al., 2018; Blume-Werry et al., 2019). The realized rooting depth distribution throughout the soil profile is thus likely a combination of plant species presence and site conditions.

Site observations consistently suggest that graminoids have more roots deeper down in the soil profile than shrubs (Shaver & Cutler, 1979; Miller et al., 1982; McKane et al., 2002; Sullivan et al., 2007; Wang et al., 2016; Blume-Werry et al., 2019; Hewitt et al., 2019). If this is true on a biome scale, changes in the distribution and dominance of different plant community types may modify biogeochemical cycling in the tundra via changes in rooting depth distribution and thus feedback to the climate system. Indeed, a shift from sedgedominated to shrub-dominated tundra following long-term fertilization resulted in a shallower rooting depth distribution leading to losses of deep soil carbon (Sullivan et al., 2007). However, commonly used (aboveground) vegetation classifications are often rather broad and comprise many different species that potentially differ in belowground attributes. We therefore need to understand whether and how commonly used plant community types control rooting depth distribution in arctic tundra, and the degree to which climatic or soil properties contribute as well. Establishing predictive relationships between biotic or abiotic drivers and rooting depth distribution would allow us to incorporate the depth distribution of root-soil interactions into models, which would improve projections of carbon, water, and nutrient cycling in a warming Arctic.

Since the benchmark review of Schenk & Jackson (2002) with 20 arctic root profiles was published, there has been a renewed interest in arctic roots and thus an increase in publications, but there has been no comparative analysis of rooting depth distribution. Here, we present a meta-analysis of published rooting depth profiles of arctic tundra vegetation on permafrost soils, now almost tripling the number of arctic profiles analyzed in Schenk & Jackson (2002). We first assessed the magnitude of variation in root profiles across the arctic tundra and tested whether this variation could be linked to vegetation types, as presented in the Circumpolar Arctic Vegetation Map (CAVM) (Walker et al., 2005), or summarized into Root Profile Types irrespective of aboveground classification, and whether rooting depth distribution could be linked to abiotic factors, such as temperature. Here, we (1) hypothesized that (aboveground) vegetation types would have distinct rooting depth profiles, with shrub-dominated, especially prostrate shrub, tundra to have a more shallow and steeply declining rooting depth distribution than graminoid or wetland tundra. Second, we assessed the influence of rooting depth distribution on modelled carbon fluxes from permafrost-affected soils through rhizosphere priming under baseline (2010) and future climatic conditions (2100; Representative Concentration Pathways 4.5 and 8.5) through a modification of the PrimeSCale model (Keuper et al., 2020). As we assumed distinct differences between vegetation types in rooting depth distributions, we (2) hypothesized strong differences in overall priming-induced carbon emissions between CAVM vegetation types, with highest losses for vegetation that has the majority of root mass in shallow soil layers, where microbial activity is often highest.

Materials and Methods

Data extraction from the literature

We collected rooting depth distribution data from arctic and subarctic tundra systems within the northern permafrost area from...
published literature, extending the studies included in Schenk & Jackson (2002) with an extensive search in both Web of Science and Google Scholar, resulting in coverage across the circumpolar Arctic (Fig. 1). We included studies when they reported root data from at least three soil depths, permafrost was present, and information on active layer thickness at the site could be found. Most studies report whole-vegetation rooting depth distributions which is why we focused on those. If data from all species present in the community individually were reported (< 5% of profiles), we summed up the individual species data to make whole-community root biomass depth profiles for the respective site. Whenever different root types were reported, we used the smallest diameter ones, as those are generally more important for plant–soil interactions (Pregitzer, 2002; McCormack et al., 2015). If the original data were not publicly available, we extracted them from figures or tables from the manuscripts using the program PLOTDIGITIZER. As amounts of roots or root mass was reported in different ways and units (see Supporting Information Table S1), and also differed between sites, we further standardized root data for each profile by ‘total root mass’ for all subsequent analyses and therefore these data represent proportional and not absolute biomass of roots by depth.

We added information on organic layer depth, if this was reported in site descriptions, latitude, as well as derived climate and other soil data from databases based on study locations (Table S1). The climate data were average annual temperature, maximum temperature of the warmest month, and minimum temperature of the coldest month, all derived from CHELSA (Karger et al., 2017, 2021) as well as average precipitation which we derived from WORLDCLIM (Fick & Hijmans, 2017) due to an overestimation of precipitation from CHELSA at our study sites. Furthermore, we added total nitrogen, pH bulk density of the fine earth fraction, cation exchange capacity of the soil, and organic carbon density from SOILGRID (Poggio et al., 2021) as soil variables that might potentially influence rooting depth profiles. We did not add the timing of sampling into our analysis, as this was not specified for > 40% of the profiles. For those where sampling time were specified, most had been taken in August, followed by July and then September.

Fitting rooting depth distribution curves

Following the work of Schenk & Jackson (2002), we fitted logistic dose–response functions for each rooting depth profile:

\[
r(D) = \frac{100}{1 + \left(\frac{D_{50}}{D}\right)^c},
\]

Eqn 1

where \(r(D)\) is the observed cumulative percentage of root biomass from the surface to above depth \(D\), and the parameters \(D_{50}\) (representing the depth above which 50% of the root biomass is located) and \(c\) (a dimensionless shape parameter) are estimated from the data. As permafrost presents an obvious limit for rooting depth in arctic tundra (Schenk & Jackson, 2002; Blumewerry et al., 2019) and active layer thickness can vary greatly across the Arctic, we fitted this model in two ways: expressing \(D\) either as absolute (measured) depth, or as a fraction of active layer thickness. This latter measure eases comparisons between sites with different active layer thicknesses. For a small number of root profiles, we used the smallest diameter ones, as those are generally more important for plant–soil interactions (Pregitzer, 2002; McCormack et al., 2015). If the original data were not publicly available, we extracted them from figures or tables from the manuscripts using the program PLOTDIGITIZER. As amounts of roots or root mass was reported in different ways and units (see Supporting Information Table S1), and also differed between sites, we further standardized root data for each profile by ‘total root mass’ for all subsequent analyses and therefore these data represent proportional and not absolute biomass of roots by depth.

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profiles, the nonlinear regression routine did not converge, usually because of insufficient data points. These profiles were excluded from subsequent analyses resulting in a total of 55 root profiles from 21 individual studies, almost tripling tundra root profile observations compared with the previous study of Schenk & Jackson (2002), which had 20 profiles from seven studies.

Grouping of rooting depth profiles

The rooting depth profiles were further classified into four vegetation following the classification of the Circumpolar Arctic Vegetation Map (CAVM, Walker et al., 2005): Graminoid tundra (dominated by e.g. Carex aquatilis Wahlenb., Carex ensifolia Turcz. ex Gorodkov, Dupontia fisheri R. Br.), Erect-shrub tundra (dominated by e.g. Betula nana L., Salix glauca L., Vaccinium vitis-idaea L.), Prostrate-shrub tundra (dominated by e.g. Dryas octopetala L., Salix arctica Pall., Salix phlebophylla Andersson), and Wetland tundra (dominated by e.g. Carex aquatilis, Dupontia fisheri, Eriophorum angustifolium Honck.). We classified profiles based on the site description and species presence that were reported in the original papers. As a readily available and spatially explicit product, the CAVM vegetation classes are widely used for upscaling purposes in the northern permafrost region as they allow for a spatial representation of current and future vegetation distribution also in combination with other data products such as soil organic carbon content, gross primary production, and active layer thickness (Bartsch et al., 2016) and thus are relevant for comparison in this study.

Furthermore, to detect possible patterns in root profile shapes across the dataset without reference to aboveground vegetation type, we calculated Fréchet distances (Alt & Godau, 1995) for all pairwise combinations of root profiles in the dataset with the SIMILARITYMeasures package (Toohey, 2015). The Fréchet distance metric quantifies the similarity in shape between lines defined by sets of points, and thus allows assessment of similarity and dissimilarity between different rooting depth curves. Both cumulative root biomass and root depth were standardized (divided by maximum observed value) before computing distances to remove the influence on the similarity estimation of variation in total biomass or maximum depth. The resulting matrix of Fréchet distances was used as input for a cluster analysis (hierarchical clustering with complete linkage, Paradis & Schliep, 2019). Silhouette analysis (Rousseeuw, 1987) of clustering arrangements obtained with between 2 and 10 classes identified 2 as the optimal number of clusters, but further graphical inspection revealed no clear discontinuity between rooting profiles (see Fig. S1). We therefore proceeded with three representative profile types in order to check how sensitive model estimates of plant–soil interactions are to variation in root profiles on the scale we observe in our dataset. Three clusters were chosen to cover much of the range observed in the field but without focusing on extreme observations, as could have happened with picking the outermost observed profiles instead of summary clusters. These clusters are thus not clearly distinct groups in the field but represent the variation that is present in arctic plant communities. Once clusters, aka Root Profile Types, were defined, distributions of D50 and c parameters per cluster were estimated using Bayesian multivariate linear models (as described below).

Statistical analysis

Differences in rooting depth distribution between vegetation types were tested by fitting Bayesian multivariate linear models in the brms package (Bürkner, 2017, 2018, 2021), a front-end to the Stan probabilistic programming language (Stan Development Team, 2023). As the shape of the estimated root profile curves is fully determined by the two parameters c and D50, this was done with D50 and c as (potentially correlated) response variables and vegetation classification as predictor variable. All brms models fitted used the default priors (brms v.2.16.2) and three chains, each running 3000 iterations (1000 warmup). Convergence of chains was confirmed with the Rhat statistic. Differences between vegetation types in 50% and 90% rooting depth (the latter computed from estimated values of the D50 and c parameters) were tested by generating a posterior distribution of the pairwise differences in parameters between vegetation classification group. We considered vegetation types to be significantly different when the 95% credible interval for the pairwise difference in parameters excluded zero. The matrix resulting of Fréchet distances from the cluster analysis (as mentioned in the previous section) was used as input for ordination analysis with the vegan package (Oksanen et al., 2020). Principle components analysis (PCoA) was used to produce unconstrained ordinations, and distance-based redundancy analysis (dbRDA) was performed in combination with permutational ANOVA to test the correlation of the variation in rooting profile shapes with the abiotic factors detailed above. Graphical illustrations were done with R packages ggplot2 (Wickham et al., 2016) and cowplot (Wilke, 2020).

Quantifying the importance of rooting depth distributions for root–soil interactions and soil carbon losses

To quantify the impact of differences in rooting depth distributions on root–soil interactions, such as the rhizosphere priming effect, we ran a modified version of the PrimeSCale model (Keuper et al., 2020). In brief, the PrimeSCale model was developed to quantify current (year 2010), future (year 2100), and cumulative (2010–2100) soil organic carbon losses from the terrestrial northern circumpolar permafrost area induced by the rhizosphere priming effect, under the Representative Concentration Pathways (RCPs) scenarios 4.5 and 8.5. The model considers projected changes in active layer thickness, gross primary production, vegetation distribution, and growing season length (see Figs S2, S3; Keuper et al., 2020 for details). In our modified version, we focused on the tundra area alone, leaving out the boreal permafrost zone. We assessed differences in rhizosphere priming effect between the different CAVM vegetation types and between the different Root Profile Types representing the variation in published rooting depth profiles as identified in the cluster analysis (i.e. a belowground classification, as mentioned in the previous section). We did this by assuming that the entire tundra biome would be rooted according to either a single vegetation type or...
single Root Profile Type and comparing the carbon losses between these rooting depth distribution types. The resulting analysis therefore gives an indication of the potential sensitivity of arctic soil carbon emissions to variation in rooting depth distributions on the scale of that observed in our dataset. Hereby, we used two different future scenarios for rooting depth distribution: ‘stay-where-they-are’ and ‘adapt-to-new-frontiers’ (Fig. 2). The first scenario assumes the same absolute rooting depth distribution even as active layer thickness increases, that is, plants rooting in the same distance to the soil surface thus representing rooting depth distribution as a static trait. The latter scenario, by contrast, assumes a change in rooting depth distribution as active layer thickness increases, that is we scaled the rooting depth distribution to active layer thickness, such that roots occupy the same relative proportion of the active layer, thereby simulating rooting depth distribution as a plastic trait where roots use the newly available soil volume.

To appropriately propagate uncertainty from estimation of root profile differences between vegetation type or Root Profile Type, we used the Monte Carlo method with the PrimeSCale model. These uncertainty estimates are based on the overall PrimeSCale model parameters, and not only rooting depth distribution, which was run with 1000 parameter sets drawn from the input data from Keuper et al. (2020) and posterior distributions of the Bayesian models described above.

Results

Rooting depth distribution in different aboveground tundra vegetation types

The shape of rooting depth distribution did not differ between the tundra vegetation types defined by CAVM (i.e. Graminoid tundra, Erect-shrub tundra, Prostrate-shrub tundra, and Wetland tundra): all pairwise comparisons of root-depth distribution parameters D50 and c were nonsignificant ($P > 0.05$; Figs 3, 4). This was the case both when rooting depth profiles were summarized according to absolute (measured) soil depth and when summarized relative to the active layer thickness, which varied between sites and ranged from 25 to 70 cm (average 35 ± 1.6 cm SE).

While the shape of rooting depth distribution (fully determined by D50 and c) did not differ between CAVM vegetation classes, there were slight differences in the modelled depth above which 90% of roots occur, likely because small differences get amplified further down the curve (Fig. 4). Vegetation in Graminoid tundra thus rooted deeper than in Wetland tundra (absolute depth; Graminoid tundra on average 28.5, 23.5–33.3 cm highest probability density, Wetland tundra 18.0, 12.2–23.3 cm highest probability density), and also used a higher fraction of the active layer (on average 0.70, 0.61–0.79 highest probability density) than roots in Wetland tundra (0.53, 0.43–0.64 highest probability density).

Root Profile Types

While we did not find any obvious grouping according to the (aboveground) CAVM classes, rooting depth profiles present in the dataset did show variation. We thus summarized these different rooting strategies into three cluster types (Fig. 5) to cover much of the range observed in the field but without focusing on extreme observations. These Root Profile Types were determined without references to CAVM class and obtained through a cluster analysis. While we arbitrarily chose the amount of clusters, they do represent the rooting variation present in arctic tundra and clearly illustrate different rooting strategies, with: (1) a Root Profile Type where the majority of root biomass is in the uppermost part of the active layer and then sharply declines toward the permafrost (‘shallow’, 50% of root biomass in the upper 19% of the

Fig. 2 Conceptual presentation of how different vegetation types, as well as different adaptations to increasing soil volume at depth, may lead to varying amounts of soil subjected to the priming effect at different depths. These conceptual scenarios have been implemented within the PrimeSCale model to estimate rhizosphere priming-induced carbon losses (see Table 1).
Factors that influence rooting depth distribution

(Dis)similarities between rooting depth distributions were primarily driven by maximum observed depth, as shown with nonmetric multidimensional scaling (Figs 6a, S4). That is, across the arctic tundra biome, maximum observed rooting depth was the main determinant of differences and similarities between rooting depth profiles, rather than a different shape of the profile. When we thus further standardized the profiles by the depth to which they were sampled, there were no clear patterns visible and, as expected by their similar shape among CAVM vegetation classes, as described above, (still) no clustering by the CAVM classes (Fig. 6b). This indicates that other factors than (aboveground) vegetation classes are driving differences and similarities between rooting depth distributions in arctic ecosystems. However, of the environmental factors that we included in our analysis, only active layer thickness, minimum temperature of the coldest month and cation exchange capacity of the soil were significantly correlated with the ordination (permutational ANOVA, \( P < 0.05 \), when standardized by sampling depth). Latitude, organic layer depth, average temperature, maximum temperature of the warmest month, and average precipitation did not influence rooting depth distribution (all \( P > 0.05 \)).

Influence of rooting depth distribution on root–soil interactions and soil carbon losses

When we tested whether estimates of plant–soil interactions are sensitive to rooting depth distribution, the PrimeSCale model showed that even assuming such extreme scenarios as the whole tundra being rooted according to each of the individual CAVM vegetation classes resulted in remarkable similar amounts of carbon emissions due to the rhizosphere priming effect. Emissions ranged from 0.07 to 0.08 Pg C in different vegetation types under present-day conditions (Table 1a). This similarity did also not change in the future when active layer thickness increases, neither in the ‘stay-where-they-are’-scenario (0.10–0.11 in 2100

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**Table S2** for average values of D50, D90, and c for each of the Root Profile Types.
under RCP4.5; and 0.20–0.23 under RCP8.5) nor in the ‘adapt-to-new-frontiers’-scenario (0.06–0.08 in 2100 under RCP4.5; and 0.07–0.08 under RCP8.5). That is, even if all tundra would change from one vegetation type to another, this would result in a virtually identical rhizosphere priming effect because of their similar range of rooting depth distribution. All CAVM classes showed the same trajectory of priming-induced carbon emissions until 2100, with increasing emissions only under the ‘stay-where-they-are’-scenario (roughly a tripling of C losses), whereas the ‘adapt-to-new-frontiers’-scenario had very small or no effects with future warming in all four tundra vegetation types. In other words, if plants root deeper as active layer thickness increases and thus keep using the same fraction of the active layer, carbon losses remained constant also in the future scenarios.

When we implemented the three different Root Profile Types instead of the a priori aboveground classifications, we found strong differences in priming-induced carbon emissions. Under present-day conditions, assuming that all of tundra would be rooted according to the ‘shallow’ Root Profile Type induced the highest rhizosphere priming effect with 0.10 Pg C yr$^{-1}$, which is twice as much as for the ‘intermediate’ Root Profile Type (0.05 Pg C yr$^{-1}$) and three times as much as for ‘deep’ Root Profile Type (0.03 Pg C yr$^{-1}$, Table 1). Similar to the analysis with CAVM vegetation classes, warming also roughly tripled carbon losses due to the rhizosphere priming effect in the ‘stay-where-they-are’-scenario but not in the ‘adapt-to-new-frontiers’ scenario, while the strong relative differences between the Root Profile Types remained similar in both scenarios. The modelled processes were thus very sensitive to the observed differences in rooting depth profiles in our database. The main difference between the aboveground vegetation classification and the belowground identification of Root Profile Types is how strongly the amount of modelled carbon emissions differ between the
individual classifications. That is, emissions under the ‘shallow’ Root Profile Type of the belowground classification were almost three times as large as under the ‘deep’ Root Profile Type, while the different aboveground classifications showed virtually no difference.

Discussion

Aboveground vegetation classes hardly differ in rooting depth distributions

Contrary to our expectations, the shape of rooting depth distribution did not differ between the commonly used, aboveground vegetation types of the Circumpolar Arctic Vegetation Map (CAVM). This is illustrated by the similar shape parameter $c$ of the depth distribution curves and similar depths above which 50% of roots are located, as well as the lack of correlation between clustering of rooting depth profiles based on their shapes (Fréchet distance) and the CAVM tundra types. Only the estimated depths above which 90% of roots are located differed between Graminoid tundra and Wetland tundra, both in terms of absolute depth (28.5 vs 18.0 cm) and relative to the active layer thickness (0.7 vs 0.53 fraction used). The CAVM classes of Graminoid and Wetland tundra share many plant species and tend to be dominated by graminoids. Instead, these vegetation types mainly differ in wetness, suggesting that despite the fact that many tundra species can build aerenchyma to root in anoxic conditions (Iversen et al., 2015), the deepest rooting distributions in wetlands may be restricted by waterlogged conditions in deeper soils rather than by species composition as such. Overall, the similar rooting depth distribution among vegetation types suggests that even a complete restructuring of the tundra biome from one CAVM vegetation type to another would hardly change rooting depth distribution, since even such dissimilar vegetation types as Prostrate-shrub tundra and Graminoid tundra had similar rooting depth distributions.

Our findings contrast with previous site observations where graminoid species often had relatively more roots deeper down in the soil profile than other species – a phenomenon that has been observed in Scandinavian, Alaskan, and Siberian tundra (e.g. Wang et al., 2016; Blume-Werry et al., 2019; Hewitt et al., 2019). It may be that previously observed local rooting patterns, which are representative of a few specific species and not a whole CAVM class, do not hold on the biome scale. Alternatively, the here used CAVM vegetation classes may be too broad to reveal differences in rooting depth distribution. For example, ‘Erect shrub tundra’ covers such differently sized species as Vaccinium vitis-idaea and Salix glauca with maximum rooting depths of 10 and 30 cm, respectively (Iversen et al., 2015). A larger number of community profiles or many profiles from different species or growth forms might have allowed for a finer aboveground classification. At the same time, the broad classifications of the CAVM

![Fig. 5 Root Profile Types, typical rooting depth curves, based on cluster analysis of the 55 rooting depth profiles plotted as cumulative root biomass against depth (relative to active layer thickness). Shown are means and 95% confidence intervals on the mean relationship fitted with local polynomial regression, with the original observations in the background. One Root Profile Type has the roots located in shallow soil layers (green), one with relatively deeper roots (blue), and an intermediate one (dark red). ALT, active layer thickness.](image-url)
are commonly used to scale or model ecosystem processes (Wullschleger et al., 2014; Bartsch et al., 2016; Thomas et al., 2019; Keuper et al., 2020). Our results suggest that such an approach overlooks variation in rooting depth distribution and may thus underestimate variation in root–soil interactions.

Variations in rooting depth distributions are present in tundra

The observed similar rooting depth distributions across the CAVM vegetation classes could suggest that rooting depth
distribution is a static, analogous trait, but we simultaneously show that variation in rooting depth profiles does exist in arctic tundra. We clustered rooting depth distributions into different Root Profile Types within the range of observed rooting profiles, but these Root Profile Types did not correspond to the aboveground CAVM classes. The Root Profile Types ranged from the very shallow and then steeply declining ‘shallow’ to the ‘deep’ Root Profile Type with a more equal distribution of roots over the soil profile. The full range of rooting depth strategies is thus not captured by following established aboveground vegetation classifications. Species associated with the ‘shallow’ Root Profile Type are likely ones that invest into long-lived and rather costly roots with which they capture nutrients for the longest possible period (Bergmann et al., 2020), such as Empetrum nigrum L. or Vaccinium vitis-idaea (Keuper et al., 2017; Hewitt et al., 2019). Plant communities with the ‘deep’ rooting depth distribution could be dominated by species such as Eriophorum vaginatum L., Rubus chamaemorus L., or Carex bigelowii Torr. ex Schwein. (Shaver & Billings, 1975; Keuper et al., 2017; Hewitt et al., 2019), producing rather cheap roots to explore greater soil depths that are only available for a short period of time.

Where roots are located in the soil profile strongly influences plant–soil interactions

Root–soil interactions are at the base of many important ecosystem processes, such as carbon cycling. Root inputs are the main source of soil carbon (Clemmensen et al., 2013; Sokol et al., 2019) but contrasting, the presence of roots and their exudates can also stimulate microbial decomposition of soil organic matter (the rhizosphere priming effect; Fontaine et al., 2003; Street et al., 2020). We tested whether different rooting depth distributions can translate to relevant differences in soil–root interactions by applying the observed contrasting Root Profile Types, as well as the root distributions based on aboveground vegetation types (CAVM), in the PrimeSCale model (Keuper et al., 2020). Due to their similar rooting depth distributions, using different CAVM vegetation types in the PrimeSCale model induced similar rhizosphere priming effects under current and future conditions, suggesting that even broad-scale changes in vegetation would not change priming-induced carbon emissions. However, there were strong differences in priming-induced carbon losses among the Root Profile Types identified here: 0.10 Pg C yr⁻¹ for the ‘shallow’ Root Profile Type vs 0.03 Pg C yr⁻¹ for the ‘deep’ Root Profile Type under present-day (2010) conditions, and 0.29 Pg C yr⁻¹ vs 0.13 Pg C yr⁻¹, respectively, in 2100 under the RCP8.5 scenario. These differences between Root Profile Types are substantial and would amount to differences in cumulative carbon losses until 2100 of 7 Pg C under RCP4.5 (11.2 Pg C for the shallow Root Profile Type, 4.2 for the deep Root Profile Type) or 10.4 Pg C under RCP8.5 (17.6 vs 7.2 Pg C). In the previously published PrimeSCale estimate of c. 40 Pg priming-induced soil carbon losses from the northern permafrost region (including boreal forests) low sensitivity to rooting depth distribution was assumed based on the use of current and future CAVM vegetation classes (Keuper et al., 2020). However, our results indicate that estimates are highly sensitive to the location of roots in the soil profile, but that the CAVM classes do not reflect this variation.

For both the CAVM profiles and the Root Profile Types, priming-induced emissions only increased under future conditions if the rooting depth distribution did not adapt to increasing active layer thickness. Priming-induced soil carbon losses are strongest when the depths of maximum root biomass and soil decomposer activity overlap; simulated deeper rooting depth thus led to a disconnection between high root density and high soil decomposer activity in the shallow soil, which overall reduced the magnitude of priming in the model. However, recent empirical evidence shows that belowground production can be stimulated by warming and a deepened active layer to the extent that both deep and shallow root production increases (Wang et al., 2017; Blume-Werry et al., 2019). In fact, there is evidence both on a global (Song et al., 2019) and tundra biome scale (Kummerow & Ellis, 1984; Chapin III et al., 1988; Blume-Werry et al., 2019), that belowground increases in production can be stronger than aboveground. In that case, priming by new, deeper roots may add to or enhance existing priming in shallower soil layers. We demonstrate here that root distributions have a meaningful impact on ecosystem processes, thus advancing knowledge about changes therein clearly should be a research priority.

Are root functional types the way forward?

One potential way forward for meaningful inclusion of belowground responses to climate change is to move from plant community types based on aboveground criteria to ‘root functional types’. Here, species could be classified according to their root, and not leaf, properties allowing a better understanding of how shifts in production or species composition could influence (belowground) ecosystem processes. These root functional types would ideally include more than depth distribution and allow classifications based on root growth rate, turnover, exudation rate, phenology, or plasticity. In our illustration of the rhizosphere priming effect, for example, the strength of the priming effect may very well differ between species even if they have the same rooting depth distribution due to different exudation quantities and qualities (Vries et al., 2019), or mycorrhizal symbionts (Parker et al., 2021). There is a growing awareness among the scientific community that root dynamics are important but at the moment; the (spatial) data to provide robust belowground traits are often missing, especially from cold biomes. For example, < 1% of trait entries in the global repository for plant traits, the TRY database, are root traits but 10% of all requests from TRY are for maximum rooting depth (Iversen et al., 2017; Kattge et al., 2019).

In conclusion, though rooting depth distributions of circum-polar vegetation varied, they were not related to aboveground vegetation types nor driven by most of the tested abiotic factors. The distribution of roots in the tundra soil profile is important for plant–soil interactions and for the tundra carbon-climate feedback, as indicated by strong variation in potential carbon emissions from the priming effect among Root Profile Types. The question remains what, if not classic plant community
compositions, drives rooting depth distribution in arctic tundra. Given that root responses to environmental conditions tend to be highly variable and are likely influenced by a range of interacting factors, analysis of additional biotic and abiotic factors may be required to quantify drivers and spatial patterns of tundra root-depth distributions. Such data are currently lacking but are essential to increase understanding and prediction of impacts of climate change and permafrost thaw on root biomass distribution and ecosystem processes in arctic tundra.

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Competing interests

None declared.

Author contributions

GB-W conceived the idea. GB-W, ED, FK and BW designed the study and collected the data, JTW led the data analysis. MK lead the model implementation. GB-W wrote the manuscript with contributions from ED, FK, MK, BW and JTW.

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Data availability

Data underlying this article are available at figshare doi: 10.6084/m9.figshare.22698889, code for the PrimeSCale model, including model scripts, complementary function scripts and input data for the model, is available at https://git.bolin.se/bolin/keuper-wild-2020.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Choice of clusters of root profile distances.

**Fig. S2** Schematic overview over PrimeSCale model input sources and combinations.

**Fig. S3** Depth distribution of Root Profile Types modelled depending on active layer thickness.

**Fig. S4** Scores of PCoA (not standardized for maximum rooting depth) plotted against the maximum sampling depth.

**Table S1** Overview of rooting depth profiles included in this meta-analysis.

**Table S2** Average of D50, D90, and $c$ for each Root Profile Type.

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