Title: How deep should we go to understand roots at the top of the world?

A commentary on "Arctic rooting depth distribution influences modelled carbon emissions but cannot be inferred from aboveground vegetation type" by Gesche Blume-Werry *et al.* 2023

Quote from text: "...we have limited understanding of how plant-soil-climate linkages may change over space and time. Thus the ability to understand and predict the dynamics and distribution of the hidden belowground world across the vast and remote northern high-latitudes has been somewhat of a 'holy grail' for … belowground ecologists"

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Rooted in a Unique Environment at the Top of the World

The harsh environmental conditions and short summers of northern, high-latitude biomes impose unique constraints on the plants that make their living in the Arctic tundra and the boreal forest. To escape the harsh aboveground environment and to facilitate nutrient acquisition, plants at the top of the world often allocate a large portion of their biomass belowground. In turn, the close proximity of living plant roots to vast stores of sequestered soil carbon in these biomes means that shifts in rooting depth distribution and the size of the root-soil interface have a large potential to influence ongoing climate change. While we have a hard-won understanding of the distribution of plant communities across the Arctic tundra and the boreal forest from boots-on-the-ground observations scaled to the landscape level using climate-informed mapping techniques (i.e., the Circumpolar Arctic Vegetation Map (CAVM); Walker *et al.*, 2005), these vegetation maps are only the tip of the iceberg (Iversen *et al*., 2015). Root form and function remain hidden beneath the land surface. An article recently published in this issue of *New Phytologist*, Blume-Werry *et al*. (pp. 000-000) asked whether rooting depth distribution could be inferred from commonly-used vegetation mapping classifications across the pan-Arctic – an important question to guide our understanding, mapping, and prediction of belowground characteristics and ecosystem feedbacks at the top of the world. Unfortunately, they found that the answer was 'not quite'. If we are unable to predict belowground rooting depth distributions across large spatial scales by leveraging aboveground vegetation community distributions, how then should belowground researchers proceed?

The Holy Grail of Belowground Ecology: Predicting Hidden Changes in Vegetation Form and Function across Environmental Gradients

In much of the North, plant roots are constrained by permanently frozen soil to a shallow 'active layer' of soil that thaws progressively over the course of each growing season. Furthermore, underlying, impervious permafrost – or in turn, deep depressions caused by scouring from past glaciation – can lead to flooded or saturated soils (Fig. 1). This waterlogging can limit root distribution to surface, oxic soils, and can lead to a thick layer of poorly-decomposed, organic peat at the soil surface with different characteristics from mineral soils (Walker *et al.*, 2003). Northern landscapes are often colonized by plant communities with special belowground adaptations, including a perennial growth habit, mycorrhizal associations, and aerenchymous roots (Chapin *et al.*, 1996; Spasojevic & Suding, 2012). Ironically, these uniquely-adapted plant communities are experiencing some of the most rapid environmental change in the world, as the high-latitudes are warming at a rate three- to four times faster than the rest of the globe (Rantanen *et al.*, 2022). However, we have limited understanding of how plant-soil-climate linkages may change over space and time. Thus the ability to understand and predict the dynamics and distribution of the hidden belowground world across the vast and remote northern high-latitudes has been somewhat of a 'holy grail' for the broader community of belowground ecologists (Iversen *et al.*, 2015, 2018).

Informed by maps that characterize vegetation distribution across high-latitude landscapes, terrestrial biosphere models are a tool that can be used to predict changes in the composition and function of vegetation – above- and belowground – across the land surface in response to changing environmental conditions. However, terrestrial biosphere models represent vegetation characteristics at a finer grain than mapped vegetation communities, grouping plant species that colonize high-latitude biomes by their functional trait variation into plant functional types (PFTs) that characterize the impacts of plant species on, and their response to changes in, their surrounding abiotic and biotic environment. Indeed, while Blume-Werry *et al.* (2023) did not find that mapped aboveground vegetation was a good predictor of community rooting depth, they did find that they could successfully cluster their rooting depth observations into 'Root Profile Types'. This indicates that while vegetation mapping units that broadly incorporate multiple plant species and functional types are too coarse or encompass too much biological variation to fully capture predictable belowground plant trait variation, model PFTs may be a useful tool to characterize above- and belowground linkages across high-latitude environments.

Ranging from root-less mosses and plant-like lichens to vascular graminoids and shrubs and deciduous and evergreen trees, PFTs inhabiting the Arctic tundra and boreal forest vary in their rooting depth distributions, their interactions with soil microbiota, and their ratio of belowground to aboveground tissues (e.g., root/shoot ratio; Chapin *et al.*, 1996). However, terrestrial biosphere models have often neglected the unique characteristics of the species that colonize high-latitude biomes, especially belowground (Iversen *et al.*, 2015, 2018). While progress has been made in recent years to incorporate plant traits that represent tundra and boreal vegetation into at least one land surface model (Shi *et al.*, 2021; Sulman *et al.*, 2021), the representation of important root traits such as rooting depth distribution remains coarse and often disconnected to surrounding soil characteristics (Drewniak, 2019).

Next steps: How deep should we go to understand roots at the top of the world?

The capability to predict belowground form and function across the vast expanse of the northern high latitudes is a tangled problem that spans spatial and temporal scales and encompasses a number of biological and environmental considerations. We suggest a few paths forward so that we as a belowground research community might find the connections that unlock our understanding and prediction of belowground processes in a rapidly changing region of the world.

Plant Functional Types. We suggest that the next generation of high-latitude field campaigns emphasize measuring differences in root traits – especially rooting depth distribution and dynamics that drive belowground carbon and nutrient cycling (Blume-Werry *et al.*, 2019, 2023) – and that 'boots-on-the-ground' observations be coupled with vegetation mapping at the species or PFT level (e.g., Yang *et al*., 2023) to inform terrestrial biosphere models. We further propose a PFT-informed framework that explicitly encompasses the plant root traits that are most relevant in northern, highly organic soils (Box 1).

Edaphic constraints. At a coarse scale, vegetation community composition and cover may prove to be a weak predictor of rooting depth distributions across large regions such as the Arctic tundra (e.g., Blume-Werry *et al.* 2023) or the broader expanse of the global north underlain by largely organic soils. However, we may be able to set bounds on 'potential' rooting depth by estimating physical constraints on rooting depth distribution (e.g., active layer thickness, Sulman *et al*., 2021), or water table depth for plant species without aerenchymous roots. However, these bounds reflect only the maximum allowable rooting depth and are insensitive to variable responses in rooting depth distributions among plant species or functional types to deepening active layers or water table depths (e.g., Blume-Werry *et al.*, 2019).

Space and Time. Our ability to understand and predict belowground plant form and function now and in response to changing environmental conditions over the next 50 – 100 years will depend on accurately quantifying baseline values of rooting depth distribution in places like the Arctic tundra and boreal forest (e.g., Iversen *et al.*, 2018; Blume-Werry *et al.*, 2019). However, the northern high latitudes are vast, and can never be fully understood by relying solely on 'boots on the ground' observations. Thus attempts to link belowground processes with ecosystem structure and function observed remotely – as done by Blume-Werry *et al*. (2023) – are key to broadening our understanding of spatial variation at the top of the world. In addition, we must understand the differential responses of plant and soil communities to environmental change and increasingly frequent disturbance events over time, which may result in novel ecosystems with new linkages among vegetation and soils. However, the future can only be accurately projected if we update terrestrial biosphere models to appropriately represent the unique characteristics of plants and soils in high-latitude biomes.

Conclusions

Blume-Werry *et al.* (2023) took on the important and difficult challenge of predicting root form and function in the hidden belowground world from observed aboveground vegetation community composition across the pan-Arctic. They did not find the 'holy grail' of relationships that many belowground ecologists continue to hope for, but they did lay a foundation for cross-disciplinary teams to build upon. We continue to believe that holistic approaches that include remote sensing (Yang *et al.*, 2023; Blume-Werry *et al.*, 2023), mechanistic modeling and machine learning (Langford *et al.*, 2019; Shi *et al.*, 2021; Sulman *et al.*, 2021), and cross-disciplinary collaboration with empirical researchers (Sulman *et al.*, 2021; Blume-Werry *et al.*, 2023) can improve our understanding of above- and belowground linkages across space and over time.

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Literature Cited

Blume-Werry G, Dorrepaal E, Keuper F, Kummu M, Wild B, Weedon JT. **2023**. Arctic rooting depth distribution influences modelled carbon emissions but cannot be inferred from aboveground vegetation type. *The New phytologist*.

Blume-Werry G, Milbau A, Teuber LM, Johansson M, Dorrepaal E. **2019**. Dwelling in the deep - strongly increased root growth and rooting depth enhance plant interactions with thawing permafrost soil. *New Phytologist* **223**: 1328–1339.

Chapin FS III, Bret-Harte MS, Hobbie SE, Zhong H. **1996**. Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of vegetation science: official organ of the International Association for Vegetation Science* **7**: 347–358.

Drewniak BA. **2019**. Simulating dynamic roots in the Energy Exascale Earth System land model. *Journal of Advances in Modeling Earth Systems* **11**: 338–359.

Iversen CM, Childs J, Norby RJ, Ontl TA, Kolka RK, Brice DJ, McFarlane KJ, Hanson PJ. **2018**. Fine-root growth in a forested bog is seasonally dynamic, but shallowly distributed in nutrient-poor peat. *Plant and Soil* **424**: 123–143.

Iversen CM, Sloan VL, Sullivan PF, Euskirchen ES, McGuire AD, Norby RJ, Walker AP, Warren JM, Wullschleger SD. **2015**. The unseen iceberg: plant roots in arctic tundra. *New Phytologist* **205**: 34–58.

Langford ZL, Kumar J, Hoffman FM, Breen AL, Iversen CM. **2019**. Arctic vegetation mapping using unsupervised training datasets and convolutional neural networks. *Remote Sensing* **11**: 69.

Rantanen M, Karpechko AY, Lipponen A, Nordling K, Hyvärinen O, Ruosteenoja K, Vihma T, Laaksonen A. **2022**. The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment* **3**.

Shi X, Ricciuto DM, Thornton PE, Xu X, Yuan F, Norby RJ, Walker AP, Warren JM, Mao J, Hanson PJ, *et al.* 2021. Extending a land-surface model with *Sphagnum* moss to simulate responses of a northern temperate bog to whole ecosystem warming and elevated CO_2. *Biogeosciences* **18**: 467–486.

Spasojevic MJ, Suding KN. **2012**. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology* **100**: 652–661.

Sulman BN, Salmon VG, Iversen CM, Breen AL, Yuan F, Thornton PE. **2021**. Integrating arctic plant functional types in a land surface model using above- and belowground field observations. *Journal of Advances in Modeling Earth Systems* **13**: e2020MS002396.

Walker DA, Jia GJ, Epstein HE, Raynolds MK, Chapin FS III, Copass C, Hinzman LD, Knudson JA, Maier HA, Michaelson GJ, *et al.* 2003. Vegetation-soil-thaw-depth relationships

along a low-arctic bioclimate gradient, Alaska: synthesis of information from the ATLAS studies. *Permafrost and Periglacial Processes* **14**: 103–123.

Walker DA, Raynolds MK, Daniëls FJA, Einarsson E, Elvebakk A, Gould WA, Katenin AE, Kholod SS, Markon CJ, Melnikov ES, *et al.* 2005. The Circumpolar Arctic vegetation map. *Journal of Vegetation Science* **16**: 267–282.

Yang D, Morrison BD, Hanston W, McMahon A, Baskaran L, Hayes DJ, Miller CE, Serbin SP. **2023**. Integrating very-high-resolution UAS data and airborne imaging spectroscopy to map the fractional composition of Arctic plant functional types in Western Alaska. *Remote Sensing of Environment* **286**: 113430.

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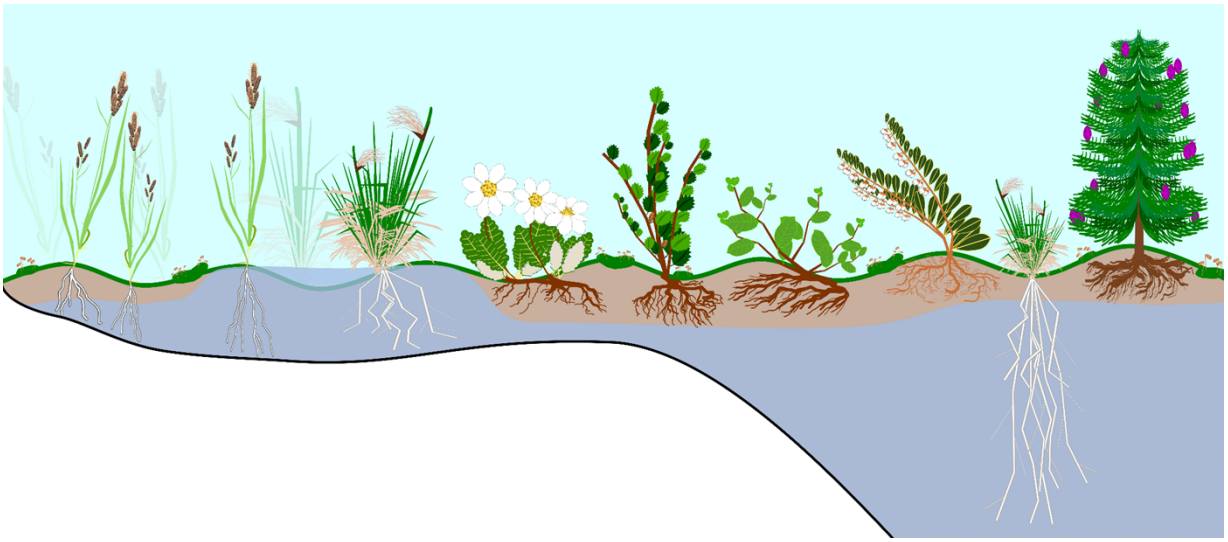

Figure 1. Illustration of the changes in active layer thickness (light brown, underlain by permanently frozen soil, white) and water table height (blue) from graminoid to wetland tundra, and then from prostrate- and erect shrub tundra toward the boreal forest (from Northern tundra to more Southerly boreal forest as you move from the left to right). Roots of many plant functional types (PFTs) in these highly organic soils are limited in their downward distribution at various points along this latitudinal gradient by permafrost (white) and high water tables (blue, excepting some graminoid species with aerenchymous roots).

169

Box 1 - Towards a cohesive root functional type framework as suggested by Blume-Werry *et al*. (2023): a guide to improve representation of belowground plant traits in terrestrial biosphere models. Note that these do not include all plant traits represented by terrestrial biosphere models, rather these are the subset of traits that could enable improved understanding or model representation of belowground plant form and function, or in turn, impacts of plant root traits on the belowground environment or soil processes.

1. **Rooting depth distribution** - The aggregate impact of PFT presence and abundance on rooting depth distribution may drive ecosystem carbon and nutrient cycling (Blume-Werry *et al.* 2023), as well as ecosystem responses to warming, thawing permafrost, and elevated CO_2.
2. **Mycorrhizal type** - The type of mycorrhizal fungal partner that high-latitude plants associate with (e.g. ecto- and ericoid mycorrhizal fungi; less often arbuscular or no mycorrhizal association) is a trait that integrates plant architecture, root coarseness, and possibly rooting depth distribution. For example, vegetation types such as evergreen and deciduous shrubs in the Ericaceae family distribute their roots shallowly in high-latitude soils, employing ericoid mycorrhizal fungi to rapidly take up organic forms of nitrogen and phosphorus from litter deposited at the soil surface. Additionally, these symbioses can determine which nutrient resources are functionally available to differing plant species and functional types, influencing vegetative composition and rates of nutrient cycling.
3. **Leaf longevity (e.g. annually deciduous vs. 'evergreen')** - Leaf longevity serves as a coarse heuristic of plant tissue nutrient densities. The longevity of evergreen leaves is in part due to high lignin content, causing evergreen leaves to have higher carbon-to-nitrogen ratio than deciduous leaves. These emergent differences in litter quality thus impact rooting depth distribution via effects on soil carbon and nutrient cycling.
4. **Growth form (e.g. graminoids, forbs, shrubs, trees)** - Growth form differences encompass aspects of belowground structure, including rhizomes (sedges and forbs), belowground woody stems (shrubs), and coarse roots (trees), as well as rooting depth distribution (Blume-Werry *et al.*, 2019). In turn, growth form can predict aboveground impacts on the belowground soil environment, including vegetation shading of soil and surrounding plant communities which cools the soil surface, or in turn, trapping of snow and warming of the soil surface, which could impact nutrient cycling and rooting depth distribution. Note that it may be useful to further partition PFTs according to potential plant height (e.g., dwarf, prostrate, low- and tall shrubs; Sulman *et al.*, 2021).
5. **Allocation -** Plants rooted in the organic soils of the Arctic and boreal regions tend to allocate a large amount of their biomass belowground as roots and rhizomes in

response to limited nutrient availability in cold, acidic, and often waterlogged soils (Iversen *et al*., 2015). While the current generation of terrestrial biosphere models tend to assume a 1:1 allocation of new production to leaf- and fine-root biomass, this does not accurately represent high-latitude biomes (Sulman *et al.*, 2021).

6. **Aerenchyma** - When active layer thickness is not limiting, some graminoids and forbs have deep rooting depth distributions, using aerenchymous root tissue to 'breathe' in saturated conditions – enabling root proliferation beneath the water table level but in turn oxygenating the soils surrounding their roots, impacting microbial nutrient cycling via altered redox conditions and pH. In high-latitude biomes underlain by organic soils, these tissues are often – though not exclusively – observed in sedges (Cyperaceae).
7. **Nitrogen fixation symbiosis** - Tall-shrubs to short trees in the genera *Alnus* and forbs in the Fabaceae family rely on bacterial symbionts (*Frankia* and rhizobia, respectively) housed within their roots to fix nitrogen directly from atmospheric N_2 rather than acquiring organic or mineral forms of nitrogen from the soil itself, and thus limit their soil exploration to shallower soils and altering belowground carbon allocation (Chapin *et al.*, 1996). In turn, this can lead to a patchwork of 'islands' of higher nutrient availability within a broader nutrient-limited landscape.

170