

BIPLABI BHATTARAI

Soil warming effect on belowground
dynamics in subarctic grasslands:
responses of roots, rhizomes,
and rhizobiomes



BIPLABI BHATTARAI

Soil warming effect on belowground
dynamics in subarctic grasslands:
responses of roots, rhizomes, and rhizobiomes



UNIVERSITY OF TARTU
Press

Department of Geography, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

Dissertation was accepted for the commencement of the degree of *Doctor Philosophiae* in Landscape Ecology and Environment Protection at the University of Tartu on 05.05.2025 by the Scientific Council of the Institute of Ecology and Earth Sciences, University of Tartu.

Supervisors: Prof. Ivika Ostonen, University of Tartu, Estonia
Prof. Boris Rewald, Mendel University in Brno, Brno, Czech Republic
Prof. Marika Truu, University of Tartu, Estonia

Opponent: Dr. Lorna Street, The University of Edinburgh, Scotland

Commencement: Senate Hall, University of Tartu Main Building, Ülikooli 18, Tartu, on 25th of August 2025, at 14.15.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu.

ISSN 1406-1295 (print)
ISBN 978-9916-27-917-5 (print)
ISSN 2806-2302 (pdf)
ISBN 978-9916-27-918-2 (pdf)

Copyright: Biplabi Bhattacharai, 2025

University of Tartu Press
www.tyk.ee

TABLE OF CONTENTS

LIST OF ORIGINAL PUBLICATIONS	7
LIST OF TERMS AND ABBREVIATIONS	8
1. INTRODUCTION.....	9
1.1. Climate change and its impact on subarctic ecosystems.....	9
1.2. Warming and belowground plant communities	9
1.3. Use of natural gradients to understand the ecosystem's response to warming	12
1.4. Aims of this thesis.....	13
2. MATERIAL AND METHODS	15
2.1. Description of study sites.....	15
2.2. Experimental setup.....	16
2.3. Measurement of belowground plant biomass (I)	18
2.4. Measurement of soluble sugars, carbon (C) and nitrogen (N) in fine roots and rhizomes (I and III)	19
2.5. Measurement of root length (IV)	20
2.6. Measurement of soil's chemical and physical parameters (I and III) .	20
2.7. Plant species abundance and aboveground biomass (I and III)	21
2.8. Soil microbiome measurements (II).....	21
2.9. Data analysis	22
3. RESULTS	24
3.1. Belowground biomass stocks in subarctic grasslands (Article I and III).....	24
3.2. Effect of soil warming magnitude and duration.....	26
3.2.1. Belowground plant biomass and C, N and soluble sugar pools in biomass (Articles I and III)	26
3.2.2. Plant-root-microbe interactions (Article II)	28
3.2.3. C, N concentrations, and the C:N ratio in fine roots and rhizomes (Article I).....	28
3.2.4. Root growth dynamics: depth- and time-dependent responses (Article IV)	28
3.3. Medium-term vs. long-term soil warming response (Article I, III, IV)	29
3.4. Soluble sugars in dominating species (Article III).....	33
4. DISCUSSION	35
4.1. Belowground biomass stocks in subarctic grasslands (Articles I and IV).....	35
4.2. The influence of soil warming on belowground biomass and associated carbon, nitrogen, and sugar pools (Articles I and III).....	36

4.3. Differentiating fine roots and rhizomes from total biomass: A way forward to understanding effects of warming on short-living and long-living biomass as well as influence on microbial community (Articles I, II and III)	37
4.4. C, N, and sugar pools in fine roots and rhizomes: an adaptation mechanism for subarctic plant communities in long-warmed soil (Articles I and III)	40
4.5. Soluble sugars in fine roots and rhizomes of dominating species (Article III).....	42
4.6. Warming effects on root growth dynamics: influence of soil depth and seasonality (Article IV)	44
4.7. Need for long-term warming experiments to understand the ecosystem's response (Article I–IV)	45
5. CONCLUSION	47
REFERENCES.....	49
SUMMARY	65
EESTIKEELNE KOKKUVÕTE	68
ACKNOWLEDGEMENTS	73
PUBLICATIONS	75
CURRICULUM VITAE	150
ELULOOKIRJELDUS.....	152

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following Publications that are referred to in the text by Roman numerals:

- I Bhattarai, B.,** Sigurdsson, B.D., Sigurdsson, P., Leblans, N., Janssens, I., Meynzer, W., Devarajan, A.K., Truu, J., Truu, M. and Ostonen, I., 2023. Soil warming duration and magnitude affect the dynamics of fine roots and rhizomes and associated C and N pools in subarctic grasslands. *Annals of Botany*, 132(2), pp.269–279. <https://doi.org/10.1093/aob/mcad102>
- II Metze, D.,** Schneckner, J., de Carlan, C.L.N., **Bhattarai, B.,** Verbruggen, E., Ostonen, I., Janssens, I.A., Sigurdsson, B.D., Hausmann, B., Kaiser, C. and Richter, A., 2024. Soil warming increases the number of growing bacterial taxa but not their growth rates. *Science Advances*, 10(8), p.eadk6295. <https://doi.org/10.1126/sciadv.adk6295>
- III Bhattarai, B.,** Richter, A., Metze, D., Sigurdsson, B.D., Sigurdsson, P., Leblans, N., Janssens, I. and Ostonen, I., 2024. Influence of soil warming magnitude and duration on soluble sugar pool in fine roots and rhizomes of subarctic grasslands: Differences at species and plant community level adaptation. *Plant Stress*, 11, p.100406. <https://doi.org/10.1016/j.stress.2024.100406>
- IV Bhattarai, B.,** Baykalov, P., de Carlan, C.L.N., Sigurdsson, B.D., Sigurdsson, P., Janssens, I., Rewald, B., and Ostonen, I., 202x. Effect of soil warming magnitude and duration on root growth dynamics in subarctic grasslands: depth- and time-dependent responses. (manuscript)

Published papers are reproduced with permission from the publishers.

Author's contribution to each paper:

- I** The author contributed to the experimental setup and field data collection, performed laboratory measurements and data analysis, and was the lead author in writing the article.
- II** The author contributed to the experimental setup, field data collection, and interpretation of results.
- III** The author contributed to the experimental setup and field data collection, performed laboratory measurements and data analysis, and was the lead author in writing the article.
- IV** The author developed the study idea, contributed to the experimental setup and field data collection, developed the data analysis approach, analysed the data, and was the lead author in writing the article.

LIST OF TERMS AND ABBREVIATIONS

C	= carbon
N	= nitrogen
BPB	= belowground plant biomass (g m^{-2})
AGB	= aboveground plant biomass (g m^{-2})
FRB	= fine root biomass (g m^{-2})
RHB	= rhizome biomass (g m^{-2})
MTW	= medium-term warming
LTW	= long-term warming
MAP	= mean annual precipitation (mm)
MAT	= mean annual temperature ($^{\circ}\text{C}$)
GLM	= generalised linear model
RDA	= redundancy analysis
SRA	= specific root area ($\text{m}^2 \text{kg}^{-1}$)
SRL	= specific root length (m g^{-1})
T_s	= soil temperature ($^{\circ}\text{C}$)
O-layer ^{thickness}	= organic layer thickness (cm)
BD	= soil bulk density (g cm^{-3})
DNA	= deoxyribonucleic acid
qSIP	= quantitative stable isotope probing
PCR	= polymerase chain reaction

1. INTRODUCTION

1.1. Climate change and its impact on subarctic ecosystems

Climate warming in the northern latitudes, including the Arctic and the subarctic regions, is occurring faster than the global average, making these ecosystems among the most vulnerable (IPCC, 2022). Studies report that the Arctic has warmed at rates approximately twice (Walsh, 2014; Yu et al., 2021; Zhang, 2005), more than twice (Jansen et al., 2020; Rosenstock et al., 2019), or even up to four times (Rantanen et al., 2022) faster than the global average. Regardless of the exact rate, one fact remains clear: climate warming in the high northern latitudes is accelerating, driving significant changes in the carbon (C) dynamics of northern ecosystems (Melillo et al., 2002; Myers-Smith et al., 2020; Verbrugghe et al., 2022b).

Grasslands cover approximately 40% of the global terrestrial area and 25% of the land area in northern latitudes (Chapin et al., 2011). Grasslands are significant carbon reservoirs (Soussana et al., 2007; Sui & Zhou, 2013) that stores about one-third of the global soil organic carbon (White, 2000). Northern latitude ecosystems store a large portion of the global carbon pool (Tarnocai et al., 2009), and have a higher proportion of their biomass in below ground (Mokany et al., 2006; Shaver & Chapin III, 1991), reflecting significant carbon allocation and storage in belowground plant organs. Grassland ecosystems, in particular, exhibit some of the highest root-shoot ratios (Jackson et al., 1996), further highlighting the importance of belowground biomass in their carbon storage. The combination of substantial belowground biomass coupled with the low temperatures in northern latitudes slows the decomposition of soil organic matter (SOM) and results in a huge carbon sink capacity for northern ecosystems (Aerts, 2006; Davidson & Janssens, 2006; Soussana et al., 2007). However, future climate change predictions for northern regions suggest the potential for these ecosystems to shift from being carbon sinks to sources because climate warming is associated with accelerated decomposition and carbon release from the soil (Conant et al., 2011; Craine et al., 2010; Davidson & Janssens, 2006).

1.2. Warming and belowground plant communities

In grasslands, the vegetation composition is variable, and belowground plant organs consist of fine roots and rhizomes with distinct functions and lifespans (Klimešová et al., 2011). Fine roots absorb water and mineral nutrients, while the rhizomes are storage organs that ensure vegetative propagation, anchorage, lateral spread, seasonal regrowth, sharing of resources between ramets, and clonal growth (Callaghan & Emanuelsson, 1985; Freschet & Roumet, 2017; Harris et al., 2023; Jónsdóttir et al., 1996; Klimešová et al., 2018). Among belowground plant organs, fine roots exhibit higher metabolic activity, nutrient content, tissue-level nitrogen (N) concentration, respiration rate (Trocha et al., 2017), microbial stimulation capacity, and turnover rates associated with a shorter lifespan (Gill et al., 2002;

Iversen et al., 2015). Fine roots also respond quickly to changes in temperature, nutrient availability, and water supply through modifications in their biomass, morphology, or associated microbial communities (Majdi, 2001; Ostonen et al., 2011; Parts et al., 2019; Pregitzer & King, 2005; Truu et al., 2017). In contrast, rhizomes, which are longer-lived and more resilient, provide stability under stressful environmental conditions (Čížková et al., 1998). Vegetative reproduction through rhizomes is common in Arctic ecosystems (Billings & Mooney, 1968), where harsh environmental conditions, such as cold temperatures and short growing seasons, make vegetative reproduction through rhizomes a crucial survival strategy (Webber & May, 1977). All belowground organs of plants are expected to serve also as storage organs, and fine roots and rhizomes are often not distinguished when analysing, for example, the storage of sugars in the belowground part of the plant community along the environmental gradients (Chlumská et al., 2022). As rhizomes are specialised belowground organs that function as carbon reserves (Chapin et al., 1990; Ohtake et al., 2006), they are expected to have higher sugar concentrations than fine roots.

Temperature is a key factor that shapes ecosystem processes, influencing plant productivity (Rustad et al., 2001), biomass allocation, and growth (Pregitzer & King, 2005). Soil warming is shown to increase (Leppälammi-Kujansuu et al., 2013) or decrease fine root biomass (Dawes et al., 2015; Melillo et al., 2011), whereas responses of rhizomes are less studied. Warming is shown to shift the plant community composition (Hu et al., 2021; Lin et al., 2010; Xu et al., 2011), and plants' functional type is shown to determine the growth dynamics of belowground plant organs (Malhotra et al., 2020). This could impact the balance of rhizomatous and non-rhizomatous plant species in an ecosystem and change the proportion of fine roots and rhizomes within total belowground plant biomass. Warming could also influence the plants to prioritise their carbon allocation between storage (increasing production of rhizomes) and resource acquisition (increasing production of fine roots). Additionally, warming-induced extensions of the growing season (Leblans, Sigurdsson, Vicca, et al., 2017; Menzel & Fabian, 1999) may allow rhizomatous plants more time to grow and expand, further impacting this balance. Warming is shown to influence the belowground plant biomass (Dawes et al., 2015; Leppälammi-Kujansuu et al., 2013; Melillo et al., 2011) and soluble sugar levels in plant organs (Martínez-Vilalta et al., 2016), indicating a potential warming-driven change in carbon and sugar partitioning in biomass pools of fine roots and rhizomes.

The root-to-rhizome biomass ratio is suggested to better understand plant functions in the belowground (Mokany et al., 2006). Also, it is suggested that belowground growth allocation be calculated separately for fine roots and rhizomes in studying net primary production (NPP) in an ecosystem (Freschet et al., 2021). Studies of C budgets at the ecosystem scale consider belowground plant biomass (BPB) < 2 mm in diameter with the aim of including the most dynamic and short-lived fine roots. However, this diameter-based categorisation fails to account for the functional distinctions between short-lived fine roots and long-lived rhizomes. Thus, we lack an understanding of how C, N, and sugar pools are distributed across the biomass pools of fine roots and rhizomes. At geo-

thermally warmed subarctic grasslands, studies showed that belowground biomass decreased in sites warmed for 5–6 years compared to those warmed for over 50 years (Leblans, 2016; Verbrugghe et al., 2022b; Walker et al., 2020). However, since these studies did not distinguish between fine roots and rhizomes as separate components, it remains unclear how each responded individually to warming. Addressing this gap is particularly important when investigating warming responses, as warming-induced changes in species composition and phenology can alter the relative proportions of fine roots and rhizomes, further complicating predictions of the ecosystem's carbon and nutrient dynamics.

Fine root exudates are a key carbon source for root-associated microbes, supporting their metabolism and growth (Canarini et al., 2019). Therefore, fine root biomass is crucial in shaping root-associated microbial communities by determining the surface area available for exudate release. Anatomical and morphological differences between fine roots and rhizomes (Chapin et al., 1990; Ohtake et al., 2006), particularly the fact that rhizomes are belowground shoots (Klimešová et al., 2018), suggests that they may not exude carbon compounds into the soil, or not in the same amount as fine roots. However, key aspects such as their epidermal characteristics (e.g., presence of root hairs, cuticle thickness) and permeability, which influence exudation and microbial interactions, remain largely unknown. Thus, we can only speculate that fine roots and rhizomes may support distinct microbial communities. Furthermore, since roots serve as an essential carbon source for microbes through litter deposition and exudates, any warming-induced changes in their biomass, carbon (C), nitrogen (N), and sugar content could significantly influence the microbiomes they support.

Microbial communities and their activities decide the fate of soil organic carbon (SOC) (Allison et al., 2010; Bardgett & van der Putten, 2014; Tao et al., 2023) and play a vital role in the ecosystem's carbon cycle. In high-latitude northern ecosystems, where soil microbial growth is particularly temperature-limited, they show a pronounced metabolic and growth response to warming (Karhu et al., 2014; Rijkers et al., 2023). Root-associated microbes may experience a warming effect mediated by plant roots, further influencing their responses. Therefore, it is necessary to study microbial responses to warming, especially considering the effects mediated by plant roots. Furthermore, warming-driven shifts in key physiological plant processes like the start and end of the growing period (phenology) (Leblans, Sigurdsson, Vicca, et al., 2017; Menzel & Fabian, 1999; Richardson et al., 2013) also indicate changes in the seasonality in biomass, productivity, and exudation that will affect the community composition and activity of plant-associated microbes (Walker et al., 2018). Thus, understanding these complex plant-microbe interactions in warming conditions is essential for predicting the consequences of climate change on carbon dynamics in northern ecosystems.

Phenological studies until now have focused on aboveground components, while belowground phenology remains largely overlooked (Abramoff & Finzi, 2015; Piao et al., 2019; Radville et al., 2016). This is because studying belowground growth dynamics has some methodological challenges, as root systems are hidden belowground, making their assessment destructive, labour-intensive and time-consuming (Chen & Brassard, 2013; McCormack & Guo, 2014). Studies have pointed out mismatches between aboveground and belowground phenology

(Abramoff & Finzi, 2015; Liu et al., 2022); thus, overlooking belowground growth dynamics increases the uncertainty in predicting carbon fluxes. It remains unclear whether warming effects are consistent across soil depths, given the significant differences in nutrient content, moisture, organic matter, and microbial communities from topsoil to subsoil (Aguado-Norese et al., 2023; Kätterer et al., 2014). Soil warming stimulates root growth, particularly in the topsoil, where root density and microbial activity are high (Gill & Jackson, 2000). However, these responses may differ in the subsoil due to differences in thermal and nutrient conditions (Gill et al., 2002; Jobbágy & Jackson, 2000). In this case, minirhizotron imaging provides a powerful solution by enabling non-destructive, repeated root growth measurements at different soil depths (Johnson et al., 2001). In the context of climate warming, minirhizotron imaging is particularly valuable for detecting depth-specific responses to temperature changes, offering new insights into how root systems adapt to warming across seasons (Brunner et al., 2013).

1.3. Use of natural gradients to understand the ecosystem's response to warming

Ecosystem responses to climate warming have been studied using various temperature manipulation experiments that use heating cables (Kimball et al., 2018; Melillo et al., 2002), infrared heaters and lamps (Aronson & McNulty, 2009), or open-top chambers (Marion et al., 1997), which have provided valuable insights into global climate warming, but are limited by logistical and financial constraints, resulting in short durations and restricted treatment levels. These limitations can result in an overestimation of response when the ecosystem responds in a logarithmic or overshoot manner, and underestimate them in the case of delayed responses (Beier et al., 2012; De Boeck et al., 2015).

Our current understanding of the effects of warming on belowground plant organs, their C and N pools, and their physiological processes is based mainly on short-term experiments. However, short-term studies may not fully capture long-term acclimation responses (Melillo et al., 2017; Romero-Olivares et al., 2017) and limit the study of slow structural changes, such as shifts in community composition and soil structure (Leblans, 2016). Global meta-analyses have emphasised the importance of long-term studies as ecosystems respond differently to short-term versus long-term warming (Govaert et al., 2021; Hollister et al., 2005; Walker et al., 2020).

To overcome these limitations, natural gradients such as 'Space for time' substitutions and geothermal gradients offer long-term, cost-effective, and experimentally realistic conditions with gradual warming and allow studying a wide range of warming levels and equilibrium responses (Leblans, 2016). Geothermal gradients in soil temperature offer a large temperature variation over small spatial scales, keeping climate, bedrock, elevation, and other confounding environmental factors reasonably constant (Leblans, 2016). Geothermal soil warming gradients enable the study of temperature responses across the full spectrum of climate change predictions, with temperatures ranging from ambient to over 50 °C (where

the geothermal channel is closest to the surface) (O’Gorman et al., 2014). These gradients offer an opportunity to explore underlying mechanisms, identify thresholds in physiological, community, and biogeochemical dynamics, and allow detailed analysis of temperature response curves under extreme warming conditions (Bahn et al., 2014; Kayler et al., 2015).

Geothermal sites must be carefully selected for climate change studies due to potential contamination from magma degassing and high mineral concentrations, which can alter biological, chemical, and physical processes (Guo, 2012; Hernández et al., 2012). Volcanic soils in geothermal areas (Andosol) have unique properties, such as high carbon content and water-holding capacity, which may affect ecological responses (Arnalds, 2004; Óskarsson et al., 2004). Additionally, geothermal sites are not representative of all ecosystems, limiting the generalizability of findings. The small spatial scale of these gradients, while helpful in reducing environmental variability, also restricts the size of the “warm islands,” potentially limiting the scope of biodiversity responses (Leblans, 2016). Geothermal warming also leads to asymmetrical temperature effects, with elevated soil temperatures but limited air warming, restricting the study of air temperature-dependent processes. Despite these limitations, geothermal gradients remain valuable for studying global warming consequences (De Boeck et al., 2015; O’Gorman et al., 2014; Sigurdsson et al., 2016).

In this thesis, I took advantage of geothermal gradients in subarctic grasslands to investigate the dynamics of belowground biomass, focusing specifically on fine roots and rhizomes. I analysed their contribution to the C, N, and sugar pools in the belowground plant biomass in response to the varying duration and magnitude of soil warming. Additionally, I explored the belowground adaptation mechanisms of plant communities together with changes in soil chemistry and the shift in the functional composition of subarctic grassland plant communities. Community-level soluble sugar concentrations and pools provide valuable insights into ecosystem-level responses, but do not fully capture the species-specific physiological responses. To address this, I analysed soluble sugars in fine roots and rhizomes of three dominating species — *Anthoxanthum odoratum*, *Equisetum* spp., and *Ranunculus acris*, together with their response to medium- and long-term soil warming. Furthermore, we studied the growth response of individual populations of active bacteria and archaea to long-term soil warming, particularly considering warming effects mediated by roots. Additionally, I assessed the effects of medium- and long-term geothermal soil warming on the seasonal root growth dynamics in both topsoil and subsoil layers.

1.4. Aims of this thesis

This doctoral thesis aimed to understand how soil warming affects belowground plant biomass, its carbon (C), nitrogen (N), and soluble sugar pools, along with root growth dynamics and microbial growth in subarctic grasslands. I sought to better understand the contribution of these pools and processes to the C balance of the subarctic’s belowground ecosystem as a response to soil warming. To achieve this, I moved beyond the conventional < 2 mm diameter classification

and adopted a functional approach where I separated fine roots and rhizomes. For microbial studies, we advanced beyond community-aggregated measurements to identify active bacterial and archaeal taxa and study how their growth rates are affected by the presence of plant roots. To study root growth dynamics, I employed a non-destructive minirhizotron imaging technique in combination with the automatic root segmentation tool RS_SAG to annotate roots (Baykalov, 2025). The annotated images were used to train a model for automated root detection in the images, and I used that model to assess the effects of medium- and long-term soil warming on root growth dynamics in both topsoil and subsoil layers.

The specific aims of this thesis were as follows:

- 1) To analyse the effect of soil warming magnitude and duration on belowground biomass dynamics of fine roots and rhizomes and their contribution to the C and N pools in the belowground plant biomass (**I**).
- 2) To investigate how growth rates of active populations of bacteria and archaea are influenced by the presence of plant roots (**II**).
- 3) To analyse the effect of soil warming duration and magnitude on soluble sugars in long-lived and short-lived biomass pools (**III**).
- 4) To study the effect of soil warming duration and magnitude on the seasonal root growth dynamics in the topsoil and subsoil (**IV**).

The hypotheses were the following:

- 1) Medium-term soil warming (MTW, 11 years) decreases belowground plant biomass (BPB), fine root biomass (FRB), and rhizome biomass (RHB), whereas under long-term warming (>60 years, LTW) BPB returns to levels similar to non-warming plots. In LTW, the initial decline in carbon and nitrogen pools recovers with stable biomass, changes in root and rhizome chemistry, and shifts in plant community composition (**I**).
- 2) The presence of roots advances bacterial and archaeal growth in soil, but root-microbe interactions are shifted by soil warming, leading to either positive or negative effects on root-associated bacterial and archaeal growth (**II**).
- 3) Soluble sugar concentration in fine roots and rhizomes increases with soil warming at both the plant community and species level. Thus, the soluble sugar pool in fine roots remains stable in warmer soils due to higher sugar concentration, offsetting the decrease in fine root biomass (**III**).
- 4) Soil warming effects on seasonal root growth dynamics in the topsoil and subsoil differ between warming magnitudes and warming durations (**IV**).

2. MATERIAL AND METHODS

2.1. Description of study sites

The study was conducted at two geothermally warmed subarctic grassland sites located 2.5 km apart within the ForHot research area near Hveragerði village, Iceland (64.008°N, 21.178°W; 83–168 m altitude) (Fig. 1; Sigurdsson et al., 2016; www.forhot.is). One site represents medium-term warming (MTW) caused by geothermal activity affecting previously unwarmed soils after a 2008 earthquake and thus had been exposed to 11–14 years of warming during the study period (2019–2022). The other site represents long-term warming (LTW), which has been ongoing for at least 60 years. Both grassland sites are unmanaged, treeless, and dominated by vascular perennial plant species, such as *Anthoxanthum odoratum*, *Ranunculus acris*, *Equisetum pratense*, *Agrostis capillaris*, and *Galium boreale* (Marañón-Jiménez et al., 2018; Sigurdsson et al., 2016). The soil type in both grassland sites is Silandic Andosol, which is characterised by a silt loamy texture (Arnalds, 2004). Climate data from the nearest synoptic station (Icelandic Meteorological Office, 2016) shows a long-term (2003–2015) mean annual air temperature (MAT) of 5.2 °C, mean annual precipitation (MAP) of 1457 mm, and mean wind speed of 6.6 m/s (Icelandic Meteorological Office, 2016). The mean monthly precipitation during May–July was 75 mm, and 135 mm for the rest of the months; the MAT of the coldest and warmest months (December and July) was –0.1 °C and 12.2 °C, respectively (Icelandic Meteorological Office, 2016). The growing season in unwarmed plots begins in late May and ends in late September (Leblans, Sigurdsson, Vicca, et al., 2017; Sigurdsson et al., 2016). A detailed description of the study area is described in Sigurdsson et al. (2016).

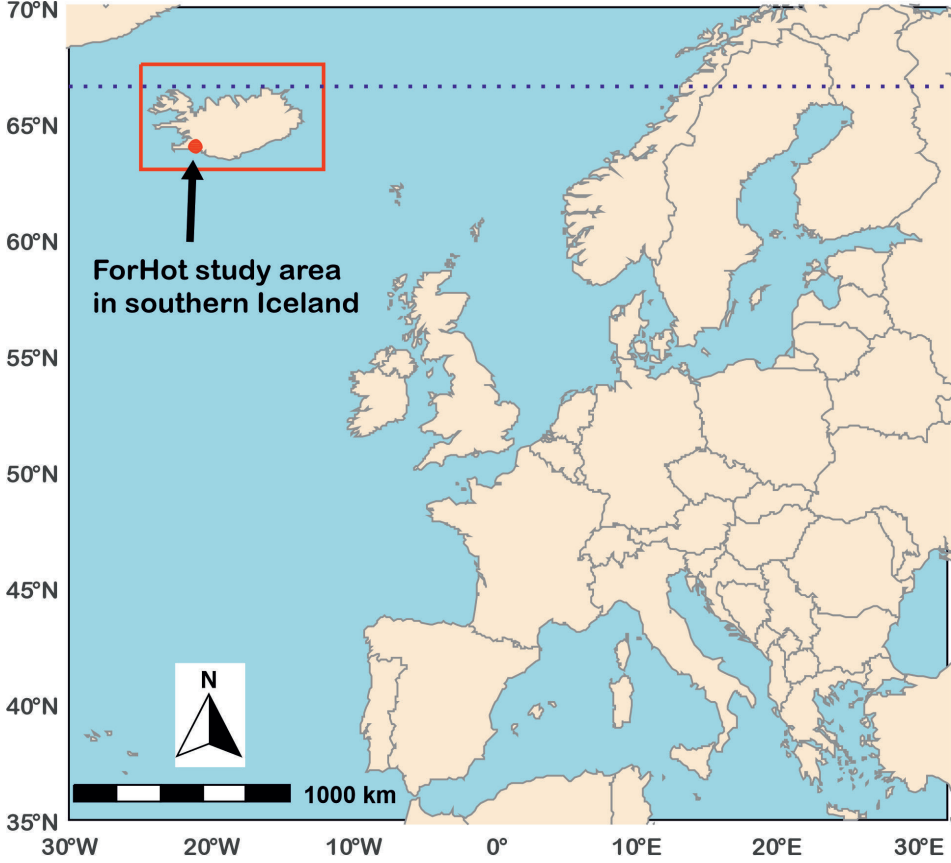


Fig. 1 Location of the ForHot study area in southern Iceland (64.008°N, 21.178°W), marked with a red dot within a red bounding box outlining Iceland on the map of Europe. The dotted blue lines indicate the Arctic Circle. The scale bar provides an approximate spatial reference.

2.2. Experimental setup

The experimental site followed a full factorial design, with five 2×2 m permanent sampling plots located in each of 10 (ca. 50 m long) replicate transects (5 on each MTW and LTW grassland) established in 2013 (Fig. 2; Sigurdsson et al., 2016). The plots were placed perpendicular to the soil temperature (T_s) gradients, with T_s ranging from ambient to $\sim +10$ °C. The T_s in each plot were measured hourly at a depth of 10 cm using a HOBO TidbiT v2 Water Temperature Data Logger (Onset Computer Corporation, USA). The 7-year (2013–2019) average ambient T_s in the plots in both grasslands was 6.1 °C. Despite seasonal and daily fluctuations, the increase in T_s above ambient temperature in warmed plots remained the same throughout the year (Sigurdsson et al., 2016).

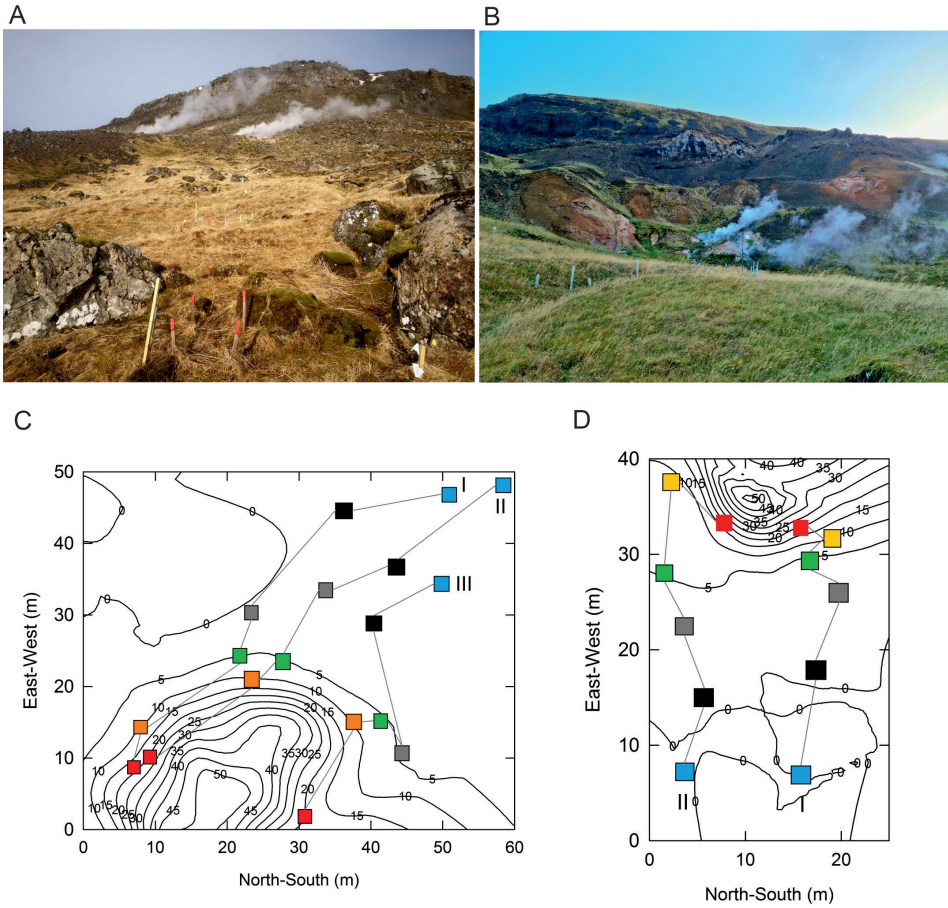


Fig. 2 (A) Picture of medium-term warmed (MTW) subarctic grassland site. (B) Picture of the long-term warmed (LTW) subarctic grassland site. (C) Three transects of the MTW and (D) two transects of the LTW sites in spring 2014 (The lines in C and D represent elevation contours). Each transect has different soil warming levels: $+0^{\circ}\text{C}$ (ambient; blue), $< +2^{\circ}\text{C}$ (black and grey) and $+2^{\circ}\text{C}$ to $+20^{\circ}\text{C}$ (green, orange, and red). Source (C and D): Sigurdsson et al., 2016.

For studies **I**, **III**, and **IV**, three of the five replicate transects in each grassland (transects 1, 2, and 4 in MTW, and transects 2, 3, and 4 in LTW) were selected. Each transect contained five permanent sampling plots, resulting in a total of 30 plots ($n = 30$). However, the long-term T_s (7–9 year average) varied among the corresponding plots along the replicate transects that were initially targeted for the same T_s . Thus, plot-level averages of increases in T_s relative to the ambient temperature were used to analyse the response of belowground plant organs to soil warming. To ensure that the variation in T_s and plant community composition in our study area was captured and that the results were generalisable, the plots of both MTW and LTW grasslands were categorised into three categories with different warming magnitudes: ambient ($n = 3$), $< +2$ °C ($n = 6$) and $> +2$ °C ($n = 6$) (Table 1). This categorisation resembles the risks and impacts in the sub-arctic and arctic regions, which are medium to high, with a mean surface temperature increase of < 2 °C and > 2 °C, according to the IPCC (2022). Details about the range of soil temperature (T_s) in ambient and warmed plots in both medium-term warmed (MTW) and long-term warmed (LTW) grasslands are described in **I**.

For study **II**, we selected four transects (transects 1, 2, 3 and 4) in LTW and collected samples from plots along the gradients that experienced soil warming of $+6$ °C on average and their corresponding control plots at ambient temperatures. We installed two types of metal cores: one with a 1 mm mesh size, allowing both roots and microorganisms to enter, and another with a 30 μ m mesh size, which excluded roots while permitting microorganisms. Additionally, we sampled fresh soil samples (undisturbed soil cores) from the top 10 cm in an area adjacent to the permanent plots where metal cores were installed. This setup resulted in 24 samples representing two warming levels and three core types: undisturbed, root ingrowth, and root exclusion.

2.3. Measurement of belowground plant biomass (I)

Belowground plant biomass was measured at the plot level. We collected a total of 30 soil cores by sampling one core from a randomly selected corner of each of five permanent plots within each of three transects in both MTW and LTW grassland sites (5 plots $\times$ 3 transects $\times$ 2 sites). Each core was taken to a depth of 30 cm, including the organic layer, using a soil corer with a diameter of 4.8 cm. The samples were classified into topsoil (0–10 cm) and subsoil (10–30 cm). Samples from both soil depths were thoroughly washed in the laboratory using a 1-mm sieve over white plastic boxes to ensure that no belowground plant organs were lost during the washing process. All belowground plant organs were examined under a dissecting microscope, cleaned for soil particles, and divided into living and dead materials, considering texture, consistency, and colour (Aerts et al., 1989). Only the living components were included in the further analysis. The morphology and anatomy of the belowground plant organs were inspected visually and under the dissecting microscope, and they were classified as fine

roots and rhizomes. The samples were dried at 50 °C for 96 h to achieve a constant dry weight. Fine root biomass (FRB) and rhizome biomass (RHB) were calculated per ground surface area (g m^{-2}). The sum of FRB and RHB was considered as belowground plant biomass (BPB).

2.4. Measurement of soluble sugars, carbon (C), and nitrogen (N) in fine roots and rhizomes (I and III)

Soluble sugars, C, and N in fine roots and rhizomes were measured at the plot and species levels. For the plot-level analysis, measurements were conducted on plot-level fine roots and rhizomes samples collected in study I. For the species-level study, individuals of three dominating species: *Anthoxanthum odoratum* ($n = 21$), *Equisetum* spp. ($n = 24$) and *Ranunculus acris* ($n = 24$) were sampled along the geothermal gradient of the MTW and LTW sites. Plants were carefully extracted using a small shovel from areas adjacent to the permanent sampling plots to avoid disturbance to the plant community composition in the permanent plots. We extracted a 10×10 cm soil block to a depth of 20 cm, with each plant positioned at the centre. The plants' individual root systems were packed in plastic bags and transported to the laboratory. Fine roots and rhizomes were separated and oven-dried using the previously described procedure for plot-level measurements. Only fine roots and rhizomes attached to the aboveground part were taken as the final sample to ensure accuracy in species identification. The method section of III describes details about determining the soil temperature and warming at the location of plant sampling.

Dry fine roots and rhizomes from plots were ground into a powder using a mortar and pestle, followed by a ball mill (RETSCH MM200, Retsch, Haan, Germany). The concentrations of C and N were measured using an isotope ratio mass spectrometer (IRMS, Delta V Plus + Flash HT + Conflo IV). For measuring soluble sugars, forty mg of finely ground fine root and rhizome powder from plots as well as species was weighed into 2 ml reaction vials with screw caps and suspended using a vortex in 1 ml of Milli Q (deionized) water until the powder was entirely suspended. Vials were put into an 85 °C water bath for 30 minutes, cooled down, and centrifuged at 10,000 g for 2 minutes. The supernatant was frozen until further use. After necessary dilutions, the supernatants were analysed by a High-Performance Liquid Chromatography (HPLC). The soluble sugars (fructose, glucose, and sucrose) were identified and quantified by comparing their retention times and peak areas with standards. The concentration of soluble sugars was expressed as mg g^{-1} DW. The total soluble sugar (TSS) concentration was calculated as the sum of fructose, glucose, and sucrose concentrations. At the plant community level, C, N, and soluble sugar pools in fine roots and rhizomes were calculated by multiplying the sugar, C, and N concentration with the total fine root and rhizome biomass derived from permanent plots and presented as g m^{-2} .

2.5. Measurement of root length (IV)

After soil cores were collected for study **I**, thirty minirhizotron tubes (50 cm long, 5 cm inner diameter) were installed at the exact cored locations in each of five permanent plots within each of three transects in both MTW and LTW (transects 1, 2, and 4 in MTW, and transects 2, 3, and 4 in LTW). The tubes were inserted at an angle of approximately 40–45°, with 40 cm of the tube inserted into the grassland soil. This corresponded to a vertical soil depth of approximately 30 cm, which was used to divide the soil depths into the topsoil and subsoil. We avoided rocks and bedrock and used tape and a cap on the exposed part of each tube to prevent light entry into the tube.

Regular minirhizotron observations started 7 months later, thus allowing recolonisation of the roots in the soil adjacent to the tubes. The tubes were imaged at 16 time points between May 2020 and August 2022. At each time point, two profiles of each tube were imaged—one from the right side and one from the left. Images were captured at 26 locations along the soil depth for each tube profile. Throughout the study, a total of 24,960 images were collected. The image size used in the study was 480×640 pixels (13.5×18 mm). From this collection, 239 images representing different soil temperatures were manually annotated for roots using the RS_SAG tool (Baykalov, 2025). These manual annotations were then used to train a model capable of predicting the presence of roots in other images. It does not combine all types of image quality presented in the whole dataset, but the most frequent and better-quality ones. The software automatically recorded essential parameters, such as the length and surface area of the roots. We used the same minirhizotron camera throughout the study, ensuring that all collected images had the same image window dimensions. It should be noted that the length and projection area analysed in our study are length (mm) and projection area (mm^2) per window of the minirhizotron images. A detailed description of image processing and automatic root segmentation is described in **IV**.

2.6. Measurement of soil's chemical and physical parameters (I and III)

Additional soil samples were taken from all plots to determine the chemical parameters of soil (Table S1 in **I** and **III**): calcium (Ca, mg kg^{-1} DW), phosphorous (P, mg kg^{-1} DW), potassium (K, mg kg^{-1} DW), magnesium (Mg, mg kg^{-1} DW), sodium (Na, mg kg^{-1} DW), sulphur (S, mg kg^{-1} DW), total nitrogen (N_{tot}, mg kg^{-1} DW), dissolved nitrogen and carbon (DN and DC, mg kg^{-1}), dissolved organic carbon (DOC, mg kg^{-1}), total carbon (TC, %), leached carbon (C leached, %; DC/TC), C:N (ratio), and pH. Dissolved nitrogen and carbon were determined using H₂O as an extractant. The thickness of the organic layer (O-layer thickness, cm) in each plot was measured using a ruler. Soil bulk density (BD, g cm^{-3}) and stoniness index (%) of the plots were taken from previous studies (Leblans, 2016; Sigurdsson et al., 2016; Verbrigghe et al., 2022b; Table S1 in **I** and **III**).

2.7. Plant species abundance and aboveground biomass (I and III)

The abundance of plant species in each plot of MTW and LTW grasslands has been described in a previous study (Meynzer, 2016). The data were used to calculate the diversity indices [Shannon's diversity index (H), species richness, and evenness] and functional composition of grassland species, such as ferns, grasses, forbs, non-rhizomatous species and abundances of *Anthoxanthum odoratum*, *Equisetum* spp. and *Ranunculus acris* in this study (Table S1 in **I** and **III**). Plant species were grouped into functional groups using the CLO-PLA database (Klimešová & Bello, 2009). Aboveground biomass (AGB, g m⁻²) in the plots were taken from previous studies (Leblans, 2016; Sigurdsson et al., 2016; Verbrugghe et al., 2022b; Table S1 in **I** and **III**). The root-shoot ratio (R:S) was calculated by dividing AGB by BPB.

2.8. Soil microbiome measurements (II)

In October 2019, we installed stainless steel root ingrowth (mesh size: 1 mm) and root exclusion cores (mesh size: 30 µm) adjacent to each other along the four temperature gradients. Soil was extracted and transferred into cores (cylindrical meshed compartments, length: 10 cm, diameter: 3.5 cm) in the field after manually removing roots and stones. Cores were retracted after 10 months of in situ incubation at peak vegetation season in August 2020. Along with the pre-installed cores, fresh soil samples (undisturbed soil cores) were collected from the top 10 cm in an area adjacent to the permanently monitored warming plots where metal cores were installed. These samples were taken to assess the warming effect on the soil microbiome without previous disturbance.

Soil samples were incubated with ¹⁸O-enriched water vapor at temperatures measured in the field while sampling (ambient ~10.7 °C and warmed ~16.7 °C) for five days. For quantitative stable isotope probing (qSIP), samples were incubated via the ¹⁸O water vapor equilibration method with water enriched in ¹⁸O and water at its natural abundance (Canarini et al., 2020). This process maintained original soil moisture. Growing bacteria and archaea incorporate ¹⁸O into their DNA during replication, increasing its density. After incubation, DNA was extracted and ¹⁸O isotopic composition of the bulk DNA was analysed using a thermochemical elemental analyser (TC/EA, Thermo Fisher Scientific) coupled via a Conflo III open split system (Thermo Fisher Scientific) to an IRMS (Delta V Advantage, Thermo Fisher Scientific). Microbial growth at the community-level (including microbes such as fungi) was calculated based on the difference in ¹⁸O abundance between labeled and natural abundance bulk DNA samples. Microbial community growth rates were derived by integrating DNA production, microbial biomass carbon, and total DNA content. Mass-specific growth or relative community growth was calculated as the rate of microbial community growth per unit of microbial biomass carbon.

To estimate the growth rates of individual bacterial and archaeal taxa, DNA was separated into 24 fractions based on its density via ultracentrifugation in a cesium chloride density gradient. On each fraction, we performed 16S rRNA gene amplicon sequencing and quantified 16S rRNA gene copies via digital droplet PCR. To estimate taxon-specific relative growth rates, we used publicly available code to perform qSIP calculations [https://bitbucket.org/QuantitativeSIP/qsip_repo, <https://github.com/bramstone/qsip>, <https://doi.org/10.5281/zenodo.8109566>; (Metze et al., 2023)]. Taxon-specific ^{18}O enrichment (APE ^{18}O) served as a proxy for bacterial and archaeal growth, which was determined based on the relationships between ^{18}O incorporation, DNA density, Guanine, Cytosine (GC) content, and DNA molecular weight as described in Hungate et al. 2015. A taxon was considered growing if its APE ^{18}O was > 0 , both at the replicate (no bootstrapping resampling) and at the treatment-level (bootstrap resampling). Taxon-specific relative growth rates per day were then calculated, also accounting for incubation period and average soil water ^{18}O enrichment. Taxa that exclusively showed detectable growth in root-ingrowth cores were considered to be putative root-associated taxa. Detailed methodology regarding quantitative stable isotope probing via ^{18}O water vapor equilibration (vapor-qSIP), including bacterial community profiling and taxon-specific growth calculations, is described in **II**.

2.9. Data analysis

For statistical analysis, R version 4.1.0 (R Core Team, 2022) and STATISTICA 7.1 (StatSoft Inc., USA) were used. Data visualisation was performed using the ‘ggplot’ package (Wickham, 2007) and SigmaPlot software (Systat Software, Inc., USA). Statistical significance was determined at $p < 0.05$. Normality was tested using the Shapiro–Wilk and Kolmogorov–Smirnov tests. Comparisons of FRB, RHB, BPB, C:N ratio, C and N pools, and soluble sugar concentration and pool between fine roots and rhizomes and between MTW and LTW were made using ANOVA (for normal distribution), and the Kruskal–Wallis test (for non-normal distribution), and pairwise comparisons were performed using post hoc tests: Tukey HSD test and Dunn’s test (package ‘rstatix’). Data are presented as mean $\pm$ standard error (SE) throughout the manuscript.

Simple regression models were used to analyse the relationships between biomass, soluble sugar concentration, and pool in fine roots and rhizomes with the magnitude of increase in T_s in the plots (an average of 7 years, 2013–2019). Generalised linear models [GLM, type III sum of squares (SS)] were used to assess the effects of soil warming duration (categorical factor) and magnitude (continuous predictor) on biomass, C, N, and soluble sugar concentrations and pools in fine roots and rhizomes (response variables). Each plot was treated as an individual sample. Forward stepwise multiple regression was performed on log-transformed biomass and soluble sugar concentration to determine the most significant variable describing the majority of the TSS pool variance. Initially, it was

tested whether biomass (FRB and RHB) or TSS concentration describes TSS pool variation. Then, the contribution of sucrose, fructose, and glucose was tested, and only the variable that first entered the model was presented.

Redundancy analysis (RDA) (ter Braak & Šmilauer, 2002) was used to explore and test the contribution of the environmental variables: T_s , soil chemical and physical characteristics, the functional structure of the plant community, AGB and R:S ratio and C, N, and C:N in fine roots and rhizomes (Table S1 in **I** and **III**) to explain the variation in the FRB, RHB, C, N and soluble sugar concentration and pools in fine roots and rhizomes in MTW and LTW. We tested all the explanatory factors in each dataset with a forward selection, and significant explanatory factors ($p < 0.05$) were selected, used as a matrix for RDA, and presented as a biplot. Data were log-transformed. The significance of the RDA results was tested using a permutation test [Monte Carlo test (999)]. For a detailed redundancy analysis method, datasets, and number of variables used, see the methods sections **I** and **III**.

Two-way ANOVA with the factors warming (ambient vs. +6 °C) and core type (undisturbed, root ingrowth, root exclusion), followed by Tukey post hoc tests, was used to analyse differences in growing taxa richness, size of the growing community, and mean taxon-specific growth rates. We focused on differences in mean taxon-specific growth rates (calculated per replicate) to avoid pseudo-replication. Mean growth rates of taxa shared between treatments (e.g., warmed vs. ambient) were compared using Student's t-tests. We also employed three-way ANOVA to test whether taxa growing in either distinct or multiple treatments showed different responses in their mean growth rates to warming and root presence. Kruskal-Wallis tests were used to examine shifts in the number of growing taxa within major phyla/families due to warming. Detailed steps for qSIP and statistical analyses used for microbial data are described in **II**.

The Repeated measures ANOVA was used to analyse the duration, magnitude, soil depth, and season effects (categorical factors) on root length and projection area (repeated measures factor was nine) and relative change in length and area (repeated measures factor was eight). Comparisons of root length, root area, and change in root length and area between seasons, warming magnitudes, warming durations, and soil depths were made using ANOVA followed by Tukey's Honest Significant Difference test. Detailed steps for the analysis of root length data are described in **IV**.

3. RESULTS

3.1. Belowground biomass stocks in subarctic grasslands (Article I and III)

In the unwarmed plots of subarctic grasslands, belowground plant biomass (BPB) up to a depth of 30 cm was, on average, approximately 1150 g m^{-2} and above-ground biomass was, on average, $\sim 130 \text{ g m}^{-2}$. Based on our estimates, fine roots constituted a substantial portion (67%) of total BPB, while the remaining biomass consisted of rhizomes. Coarse roots ($>2 \text{ mm}$ in diameter) were minimal, being detected in only one sampling plot. The majority of the BPB in the subarctic grassland was distributed in the topsoil (74% in 0–10 cm; Table S2 in **I**). The bulk density of the soil in the studied subarctic grasslands was 0.65 g cm^{-3} (Table S1 in **I** and **II**; Verbrigghe et al., 2022b), and the organic layer had an average thickness of 4.3 cm (Table S1 in **I**). Under unwarmed conditions, the below-ground plant biomass contained an estimated carbon (C) pool of $\sim 500 \text{ g m}^{-2}$ and a nitrogen (N) pool of approximately 9 g m^{-2} among which 65% of the C pool and 73% of the N pool was in fine root biomass (Table 1).

Table 1: Belowground plant biomass (BPB), fine root biomass (FRB) and rhizome biomass (RHB) and carbon (C) and nitrogen (N) and total soluble sugar (TSS) pools in BPB, FRB and RHB in the whole studied soil depth (0–30 cm) in three soil warming classes (+0 °C, < +2 °C, > +2 °C) and two durations of warming: medium-term warming (MTW) and long-term warming (LTW) presented as mean ± SE. Comparisons between two soil warming durations in the same warming classes are presented as letters X and Y, and between warming classes in the same warming duration are presented as letters a and b. Only significant differences ($p < 0.05$) are presented in the table with letters following the numbers. The underlined letters show a trend ($p < 0.1$) in comparison. Adapted from paper **I** and paper **III**.

Soil warming duration	Soil warming classes	Biomass (g m ⁻²)			Carbon pool (g m ⁻²)			Nitrogen pool (g m ⁻²)			Total soluble sugar pool (g m ⁻²)		
		BPB	FRB	RHB	BPB	FRB	RHB	BPB	FRB	RHB	BPB	FRB	RHB
MTW	+0 °C	1091 ± 173	738 ± 138	353 ± 49	475 ± 78	320 ± 64	154 ± 21	8.4 ± 2.0	6.2 ± 1.3	2.1 ± 0.6	14.2 ± 3.3	6.3 ± 3.2 bX	7.9 ± 1.4
	< +2 °C	1175 ± 288	641 ± 207	535 ± 122	495 ± 124	269 ± 89	227 ± 51	6.4 ± 1.7	4.1 ± 1.4	2.3 ± 0.6	11.6 ± 3.1 X	2.3 ± 1.0 abX	9.3 ± 3.5
	> +2 °C	563 ± 166 X	235 ± 64 X	328 ± 166	244 ± 73 X	101 ± 29 X	143 ± 74	4.1 ± 1.3 X	1.9 ± 0.5 X	2.2 ± 1.3	8.6 ± 1.9 X	1.1 ± 0.3 aX	7.5 ± 2.8 X
LTW	+0 °C	1220 ± 53	796 ± 60	424 ± 65	531 ± 23	341 ± 29	190 ± 29	9.1 ± 0.9	6.6 ± 0.4	2.5 ± 0.6	46.6 ± 12.2	30.8 ± 8.5 Y	15.9 ± 8.9
	< +2 °C	1212 ± 174	853 ± 148	358 ± 62	520 ± 71	368 ± 60	153 ± 26	10.1 ± 1.4	7.0 ± 1.3	3.1 ± 0.5	44.1 ± 8.6 Y	25.3 ± 11.1 Y	18.9 ± 4.6
	> +2 °C	1134 ± 141 Y	589 ± 76 Y	545 ± 76	492 ± 62 Y	254 ± 33 Y	238 ± 33	10.3 ± 1.4 Y	5.6 ± 0.7 Y	4.7 ± 0.8	42.4 ± 2.8 Y	11.6 ± 2.3 Y	30.9 ± 3.5 Y

3.2. Effect of soil warming magnitude and duration

3.2.1. Belowground plant biomass and C, N, and soluble sugar pools in biomass (Articles I and III)

The total belowground plant biomass (BPB) was significantly influenced by the soil warming magnitude (Table 2 in I), and the total BPB decreased exponentially towards higher T_s in MTW, whereas in LTW grassland, a decreasing trend was observed (Fig. 3 A).

The C and N pools in total BPB were reduced by half when soil warming exceeded $+2^\circ\text{C}$ in MTW, while in LTW grassland, these pools remained stable across all warming levels (Table 1; Fig. 7). Furthermore, these pools were significantly lower in MTW compared to LTW grasslands under similar soil warming of $> +2^\circ\text{C}$ (Table 1). Under long-term soil warming, the stable BPB and C and N pools in BPB (Table 1) were related to a higher plant species diversity (Fig. 5).

Fine root biomass (FRB) exhibited greater sensitivity to soil warming than rhizome biomass (RHB) (Fig. 3 B and 3 C). FRB declined exponentially with increasing T_s under both MTW and LTW (Fig. 3 B), with a significantly steeper decline in MTW than in LTW ($p < 0.05$, difference test). In contrast, rhizome biomass (RHB) showed no significant response to soil warming (Table 1 and Fig. 3 C). As FRB declined, the proportion of rhizomes in total BPB increased, particularly under LTW conditions (Fig. 4).

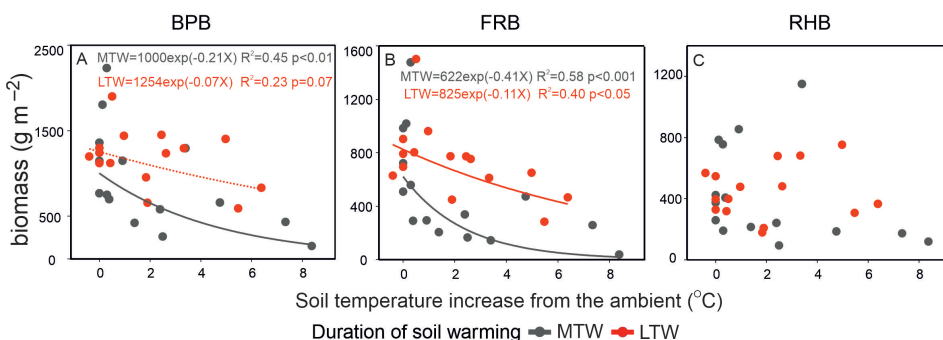


Fig. 3 Belowground plant biomass (BPB; A), fine root biomass (FRB; B) and rhizome biomass (RHB; C) over the whole studied soil depth (0–30 cm) along a soil temperature increase from ambient in medium-term warmed (MTW; grey) and long-term warmed (LTW; red) grasslands. An exponential model was used to describe the decline in biomass along the soil temperature increase from ambient. The solid lines show a relationship at a significance level of $p < 0.05$, and the dashed lines show a trend ($p < 0.1$, one-tailed test). Adapted from paper I Fig 1.

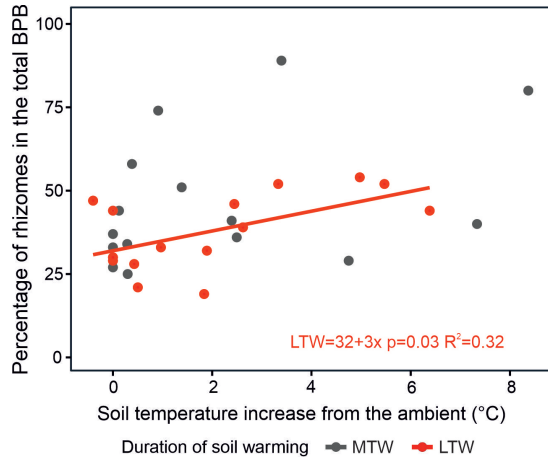


Fig. 4 Percentage of rhizomes in the total belowground plant biomass in the whole studied soil depth (0–30cm) along soil temperature increase from the ambient in medium-term warmed (MTW; grey) and long-term warmed (LTW; red) grassland. A linear regression model was used to describe the increase in the percentage of rhizomes along soil temperature increase from the ambient. The solid lines show a relationship at the significance level of $p < 0.05$. Adapted from paper I Fig. 2.

The C and N pools in FRB were affected by both the duration and magnitude of soil warming, whereas C and N pools in RHB remained unaffected (Table 3 in I). Under the ambient conditions of both MTW and LTW grasslands, C and N pools in fine roots were higher than in rhizomes ($p < 0.05$; Table 1). However, in highly warmed MTW plots, C and N pools in fine roots showed a declining trend, resulting in similar contributions from both fine roots and rhizomes to belowground C and N pools ($p > 0.05$; Table 1).

Soluble sugar pool in FRB of subarctic grassland plant communities decreased with soil warming under both MTW and LTW (Fig. 6 A and 6 B), while in rhizomes, it remained unaffected (Fig. 4 in III). However, the driving factors differed in MTW and LTW (Fig. 6 C). Stepwise regression revealed that under MTW, changes in fine root biomass explained 70% of the variation in the total soluble sugar (TSS) pool in fine roots (Fig. 6 C). Under LTW, the concentration of soluble sugars explained 74% of the variation in the TSS pool in fine roots (Fig. 6 C). Considering the contribution of specific soluble sugar compounds, the change in sucrose concentration was the main driver of TSS pool variation in LTW (Fig. 6 C). Also, in LTW, a positive relationship was observed between sucrose concentration in fine roots and the abundance of grass species *A. odoratum*, which declined with soil warming (Fig. 5 A in III). Additionally, in LTW, an abundance of grass species *A. odoratum* alone explained 14% of the variation in the soluble sugars in fine roots and rhizomes (Fig. 5 A in III).

3.2.2. Plant-root-microbe interactions (Article II)

At ambient conditions, the mean relative growth rates of bacteria and archaea in root-ingrowth cores were, on average, about 2.3 times higher compared to those in root-exclusion cores (Fig. 5 A in **II**). However, with long-term warming, relative growth rates in root inclusion cores significantly decreased, and the positive effect of roots on bacterial and archaeal growth was no longer observed (Fig. 5 A in **II**). Specifically, relative growth rates of putative root-associated taxa were lower in long-warmed plots (Fig. S7 B in **II**). Root ingrowth cores showed larger and more diverse growing communities under long-term warming (Fig. S10 A, B in **II**), whereas the diversity and size of growing communities in root exclusion cores remained unchanged. The growth of several taxa was influenced by the presence or absence of roots (Fig. S11 A in **II**). However, only *Chitinophagaceae* and *Streptomyetaceae* members seemed to consistently profit from the presence of roots, exhibiting higher contributions to the total community's growth when roots were present (Fig. 6 in **II**).

3.2.3. C, N concentrations, and the C:N ratio in fine roots and rhizomes (Article I)

Soil warming significantly affected the C and N concentrations in fine roots and rhizomes (Table 3 in **I**), resulting in changes in the C:N ratio (Fig. 3 in **I**). The N concentration in rhizomes was significantly higher in both soil warming classes under long-term warming (LTW) compared to ambient conditions (Supplementary Data Table S3 in **I**). Consequently, the C:N ratio in rhizomes decreased in both warming classes under LTW, becoming similar to that of fine roots ($p = 1$ and $p = 0.08$, respectively; Fig. 3 A and 3 B in **I**). Additionally, the C:N ratio in LTW was lower compared to the corresponding warming classes under medium-term warming (MTW) (Fig. 3 B in **I**).

3.2.4. Root growth dynamics: depth- and time-dependent responses (Article IV)

Our results show that in subarctic grasslands under ambient conditions, root length and root projection area were concentrated in the topsoil throughout the sampling seasons. On average, $63 \pm 1.3\%$ of root length and $65 \pm 1.3\%$ of root projection area were in the topsoil. Seasonal variation was observed, with the percentage of topsoil root length ranging from $71 \pm 2.5\%$ in the first summer to $59 \pm 2.8\%$ in the third summer and the percentage of topsoil root area ranging from $73 \pm 4.4\%$ in the first summer to $60 \pm 3.0\%$ in the third summer. When analysed separately for medium-term warming (MTW) and long-term warming (LTW), a similar seasonal pattern was observed, with the highest proportion of topsoil root length and area in the first summer and the lowest in the third summer (**IV**).

The repeated measure analysis of variance showed that soil depth and season were the most significant factors affecting root length and projection area (Table 1 in **IV**). Interestingly, soil depth did not affect the change in length or the projection area of roots from the previous season (Table 1 in **IV**). Season had a highly significant effect on all measured root traits – length, projection area, change in length, and projection area (Table 1 in **IV**). Specifically, the interactions between season and warming duration (season $\times$ D), season and warming magnitude (season $\times$ M), and season and soil depth were all significant for all measured root traits.

Our results showed differences in root length, area, and vertical root distribution in response to long-term soil warming. Under ambient conditions, root length and area were consistently higher in the topsoil across all sampling seasons ($p < 0.05$). The effect of soil warming magnitude was more pronounced in the subsoil (Fig. 2 and Fig. 3 in **IV**). Particularly, soil warming of $> +2$ °C in LTW increased root length and area in the subsoil across seasons ($p < 0.05$), while in the topsoil, they remained unchanged ($p > 0.05$), resulting in a similar root length and projection area between the top- and subsoil ($p > 0.05$).

3.3. Medium-term vs. long-term soil warming response (Article I, III, IV)

We observed that ecosystem responses to soil warming vary between medium and long time scales. In the ordination plot (Fig. 5), closer grouping of ambient plots suggested similar pre-warming conditions, whereas varied warming response in different time scales was observed as warmed plots in medium-term warming (MTW) and long-term warming (LTW) formed distinct groups. The greater distance between ambient and warmed plots in MTW indicates a stronger response to medium-term compared to long-term soil warming (Fig. 5). Redundancy analysis (RDA) further identified key determinants of these responses, with functional structure, diversity of the plant community, mean aboveground biomass (AGB), and root-shoot ratio (R:S) explaining 52% of the variation in biomass, C and N concentrations, and pools in fine roots and rhizomes. In the ordination plot, the N concentration and C:N ratio of fine roots and rhizomes exhibited strong correlations with the second axis, which was related to soil temperature (Fig. 5).

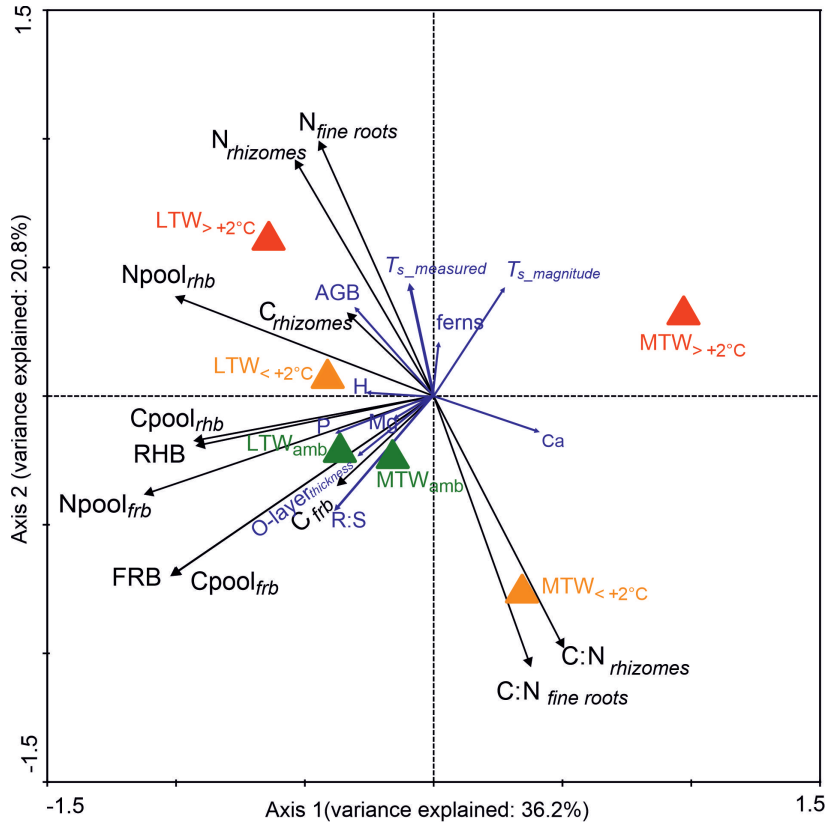


Fig. 5 Ordination biplot based on redundancy analysis (RDA) of the fine root biomass (FRB), rhizome biomass (RHB), and C and N concentration and pools in fine roots and rhizomes (black arrows) in relation to the duration and magnitude of soil warming [MTW and LTW; ambient (green), < +2 °C (orange) and > +2 °C (red) triangles], soil temperature [magnitude of soil temperature increase from ambient ($T_{s_magnitude}$) and measured temperature while sampling ($T_{s_measured}$)], soil chemistry (Mg, P, Ca), soil characteristics such as the thickness of the organic layer ($O-layer_{thickness}$) and plant community characteristics [abundance of ferns and Shannon's diversity index (H)], and mean aboveground biomass (AGB) and root-shoot ratio (R:S; blue arrows). In total, the model described 78.3% of the variation in FRB, RHB, and C and N concentrations and pools in fine roots and rhizomes (999 Monte Carlo permutation test, $P = 0.001$). Adapted from paper I Fig. 5.

In MTW, the decline in fine root biomass (FRB) and its C and N pools, particularly in plots where soil temperature exceeded +2 °C (Fig. 5; Supplementary Data Table S1 in **I**), was related to increased proportional abundance of ferns and a reduced R:S ratio (Fig 5). This decline in FRB was the primary driving factor for the decline in total BPB, C, and N pool in BPB (Table 1 and Fig. 3) and total soluble sugar pool in fine roots under MTW (Fig. 6 C).

In LTW, a lower C:N ratio in fine roots and rhizomes corresponded to higher N concentration and increased AGB. Species diversity (H) showed a positive relationship with stable C and N pools in BPB under LTW. In LTW, the decline in the sugar pool in fine roots was driven by soluble sugar concentration (Fig. 6 C). Aboveground biomass (AGB), the C:N ratio in rhizomes and seven-year average soil temperature ($T_{s_7\text{years}}$), abundance of the grass species *A. odoratum*, and soil bulk density (BD) collectively explained 49% of the variation in sugar concentration in LTW. Notably, sucrose (which accounted for the majority of the soluble sugar) concentration in fine roots positively correlated with the abundance of *A. odoratum* ($r = 0.7$, $p < 0.05$), and both declined as soil temperature and bulk density increased under LTW (Fig. 5 A in **III**).

Medium-term warming responses were characterised by a decline in fine root biomass and its C and N pools that drove the decline in biomass and pools in total BPB and a decrease in the R:S ratio that was related to a decrease in species diversity, belowground-aboveground (R:S) ratio and increase in abundance of ferns towards higher soil temperature (Fig. 7). In contrast, long-term responses were characterised by stabilisation in BPB and its C and N pools driven by an increase in the proportion of rhizomes in the total biomass (Fig. 4) along with higher nitrogen (N) concentration and a decreased carbon-nitrogen (C:N) ratio in rhizomes (Fig. 5 and Fig. 7). Additionally, there was a reduction in total soluble sugar (TSS) pool in FRB which was driven by decrease in sucrose concentration and was related to a decrease in abundance of *A. odoratum*, and increase in AGB and bulk density of soil in LTW (Fig. 5 A in **III**). Additionally, the increase in root length and projection area in the subsoil was observed only under > +2 °C of long-term warming (LTW), highlighting a distinct effect of warming duration on root growth dynamics (**IV**).

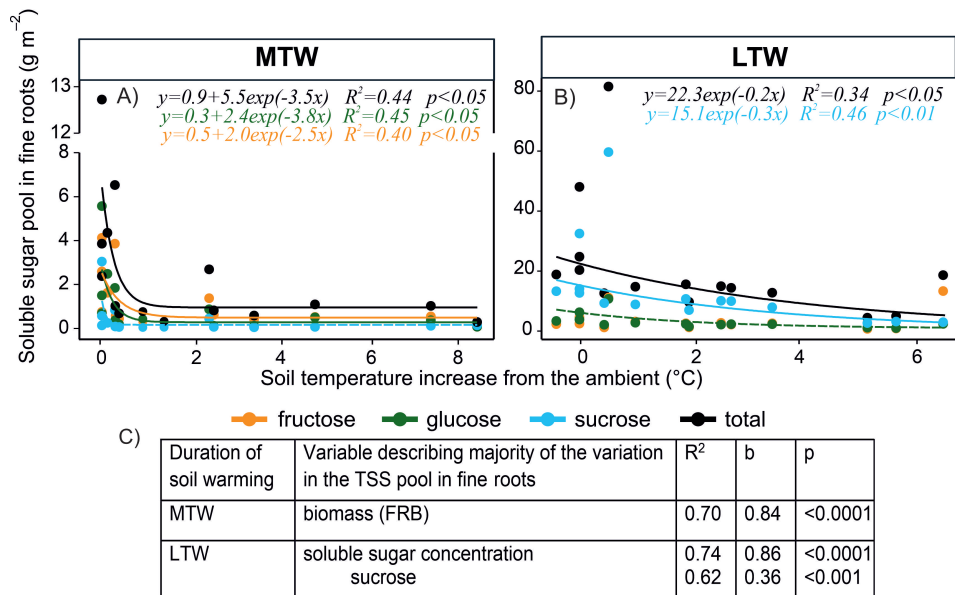


Fig. 6 The total soluble sugar, fructose, glucose, and sucrose pool in fine roots along soil temperature increase from the ambient in medium-term warmed (A; MTW) and long-term warmed (B; LTW) grasslands. An exponential model was used to describe the decline in the sugar pool in response to an increase in soil temperature from the ambient. The solid lines show a relationship at a significance level of $p < 0.05$, and the dashed lines show a trend ($p < 0.1$, one-tailed test). The variable that described the majority of the variation in the TSS pool in fine roots in medium-term warmed (MTW) and long-term warmed (LTW) grasslands [C; results of forward stepwise multiple regression]. Adapted from paper III Fig. 4 and Table 3.

3.4. Soluble sugars in dominating species (Article III)

We observed **species-specific differences** in soluble sugar concentration between the three studied species. Under ambient conditions, the total soluble sugar (TSS) concentration in fine roots and rhizomes of *A. odoratum* were, on average, $10.0 \pm 1.0 \text{ mg g}^{-1} \text{ DW}$ and $20.0 \pm 2.5 \text{ mg g}^{-1} \text{ DW}$, respectively. The TSS concentration in fine roots and rhizomes of *Equisetum* spp. were, on average, $5.0 \pm 1.7 \text{ mg g}^{-1} \text{ DW}$ and $39.0 \pm 3.0 \text{ mg g}^{-1} \text{ DW}$, respectively. On average, the TSS concentration in fine roots and rhizomes of *R. acris* were $96.0 \pm 6.0 \text{ mg g}^{-1} \text{ DW}$ and $69.0 \pm 10.0 \text{ mg g}^{-1} \text{ DW}$, respectively. In all three species, sucrose was the major contributor to total soluble sugar in both fine roots and rhizomes, constituting 47–65% of the total, except in fine roots of *Equisetum* spp., where fructose, glucose, and sucrose had similar contributions in the TSS.

Fine roots and rhizomes of forb *R. acris* had higher total soluble sugar (TSS) concentrations compared to fern *Equisetum* spp. and grass *A. odoratum*. While TSS concentration in fine roots of *A. odoratum* and *Equisetum* spp. were similar ($p > 0.05$), the TSS in rhizomes differed between all three species ($p < 0.05$, highest in *R. acris* followed by *Equisetum* spp. and *A. odoratum*).

We observed a significantly higher TSS concentration in rhizomes compared to fine roots in *A. odoratum* and *Equisetum* spp. (Fig. 1 in **III**), where in *Equisetum* spp., rhizomes contained eight times higher TSS concentration than fine roots ($p < 0.0001$). However, in *R. acris*, the TSS concentration was higher in fine roots than in rhizomes ($p < 0.001$; Fig. 1 in **III**).

The effect of soil warming duration and magnitude on soluble sugar concentration varied among the three plant species and their fine roots and rhizomes. In our study, soil warming did not affect TSS in *Equisetum* spp. and *R. acris*, while in *A. odoratum*, both the duration and magnitude of soil warming and their interaction had a significant effect (Table 1 in **III**). We found that for each degree rise in soil temperature in MTW, TSS concentration in *A. odoratum*'s fine roots increased by $1 \text{ mg g}^{-1} \text{ DW}$ (0.6 mg g^{-1} sucrose, 0.3 mg g^{-1} glucose, and 0.1 mg g^{-1} fructose) and in its rhizomes by $0.6 \text{ mg g}^{-1} \text{ DW}$ (0.4 mg g^{-1} sucrose and 0.2 mg g^{-1} glucose). For each degree of rise in soil temperature in LTW, the TSS in fine roots of *A. odoratum* increased by $2.3 \text{ mg g}^{-1} \text{ DW}$ (1.9 mg g^{-1} sucrose).

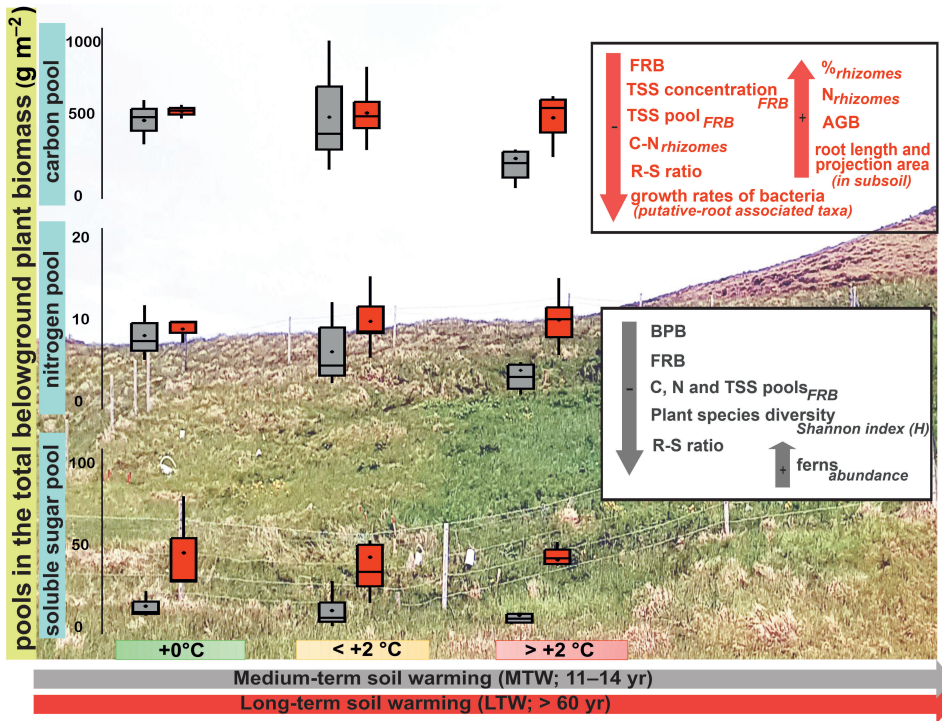


Fig. 7 Graphical summary of thesis results showing the effect of soil warming duration [(medium-term warming (11–14 years; MTW; grey) and long-term warming (> 60 years; LTW; red)] and magnitude (+0 °C, < +2 °C, > +2 °C) on carbon, nitrogen, and total soluble sugar pools in total belowground plant biomass (BPB). In boxplots, means are shown as dots and medians as horizontal lines within each box. Upward arrows (↑) indicate a significant increase, while downward arrows (↓) show a significant decrease in measured variables. The following abbreviations are used: carbon (C), nitrogen (N), total soluble sugar (TSS), fine root biomass (FRB), carbon-nitrogen ratio (C:N), root-shoot ratio (R:S), and aboveground biomass (AGB).

4. DISCUSSION

4.1. Belowground biomass stocks in subarctic grasslands (Articles I and IV)

Grasslands are reported to have some of the highest belowground-aboveground (root-shoot) ratios (Jackson et al., 1996), reflecting significant carbon allocation to belowground plant organs. In this study, belowground parts accounted for nine times more biomass than aboveground, emphasising the importance of studying the belowground responses of subarctic grassland ecosystems, particularly in the context of climate warming. The total root biomass estimated in our study was similar to the one reported for tundra (1200 g m^{-2} ; Jackson et al., 1996). However, the belowground-aboveground plant biomass ratio in the tundra is reported to be 4:1 (Iversen et al., 2015; Mokany et al., 2006), which is substantially lower than the ratio of 9:1 that I estimated in this study for the subarctic grassland. Moreover, BPB in subarctic grassland was found to be notably higher than in other ecosystems like alpine (330 g m^{-2} ; Zhang et al., 2020) and desert grasslands (301 g m^{-2} ; Ma et al., 2008), while it was much lower than in boreal (2900 g m^{-2}) and temperate and tropical forests (4400 g m^{-2} ; Jackson et al., 1996).

Grasslands are known for their diverse vegetation composition, including grasses, forbs, and sedges, as well as a high diversity of belowground plant organs such as fine roots and rhizomes (Klimešová et al., 2011). At the ecosystem level, the functional composition of plant communities determines root characteristics and traits (Bessler et al., 2012; Maestre et al., 2006; Siebenkäs & Roscher, 2016), including belowground biomass (Mueller et al., 2013) and growth dynamics (Malhotra et al., 2020). Particularly in grassland, the functional structure of plant communities potentially determines the proportion of belowground organs, as different plant functional types exhibit distinct belowground structures. For example, grasses usually have short rhizomes (Tilman & Wedin, 1991), forbs have relatively less extensive belowground structures (Dwire, 2001), and sedges develop long, extensive networks of rhizomes (Bernard et al., 1990). Based on our estimates, a substantial portion (67%) of total BPB was from fine roots, while the remaining biomass consists of rhizomes, highlighting structural diversity in plant organs within belowground plant communities in subarctic grassland ecosystems. The vertical distribution of belowground plant biomass (BPB) within the soil depth was also notable in this study. A significant majority of the biomass (74%), length (63%), and projection area (65%) of belowground plant organs were concentrated in the topsoil (0–10 cm), which was much higher than the globally averaged topsoil root distribution in temperate grassland (44%) and for all ecosystems combined (30%) (Jackson et al., 1996). This suggests a unique rooting strategy by plant communities in subarctic grasslands, potentially shaped by a combination of factors, including the distinct soil characteristics of brown andosols (Arnalds, 2005) interacting with environmental conditions and plant community dynamics in the studied subarctic grassland (Sigurdsson et al., 2016).

4.2. The influence of soil warming on belowground biomass and associated carbon, nitrogen, and sugar pools (Articles I and III)

The observed decline in BPB was consistent with the findings of Walker et al. (2020), who reported a reduction in belowground plant biomass after 5–8 years of warming. However, our study found that this decline persisted for even until 11 years, with BPB, C, N, and soluble sugar pool in biomass reduced approximately by half, following a +4.8 °C temperature increase from ambient conditions. After more than 60 years of soil warming, the decline in BPB was less pronounced, showing only a trend rather than a significant reduction, whereas the C, N, and soluble sugar pools in BPB were comparable to non-warmed conditions. Belowground plant biomass (BPB) plays a crucial role in retaining the C pool in soils (Högberg & Read, 2006; Pollierer et al., 2007) as root-derived C remains in the soil longer than C from aboveground plant litter (Clemmensen et al., 2013; Verbruggen et al., 2016). Particularly in grasslands, belowground litter from fine roots (< 2 mm in diameter) represents approximately 33% of annual litter inputs (Freschet et al., 2013), making BPB a key source of soil organic matter (Crow et al., 2009; Rasse et al., 2005). The decline in SOC previously observed in subarctic grassland (Verbrigghe et al., 2022b) may be linked to the reduction in BPB, which decreased the input of root-derived carbon, which is a crucial component for SOC stabilisation. Also, in other ecosystems, belowground plant biomass significantly influenced SOC accumulation (Yao et al., 2023), and enhanced belowground biomass growth helped offset SOC loss (Song et al., 2025). In addition to biomass, root distribution patterns in the soil depth regulate the accumulation of SOC with deeper-rooted plants, promoting long-term storage of SOC (Jobbágy & Jackson, 2000; Lorenz & Lal, 2005). Notably, the substantial loss of SOC in the topsoil could be attributed to the large proportion (up to 86%) of plant biomass located in the topsoil, indicating large litter and exudate input in topsoil, which, combined with warming-induced acceleration in decomposition rates (Berbeco et al., 2012; Davidson & Janssens, 2006), might have further exacerbated SOC loss in the topsoil (Verbrigghe et al., 2022b). Interestingly, a higher proportion of total plant input from belowground and aboveground litter is found in the topsoil, but proportionately more SOC accumulates at the deeper soil surface (Jobbágy & Jackson, 2000). Faster microbial decomposition of fresh litter at the surface soil layers, leaching of carbon compounds into deeper layers, longer turnover times, and increased chemical recalcitrance of soil organic matter (SOM) in the deeper layers contribute to the stabilisation of SOC (Jobbágy & Jackson, 2000; Lorenz & Lal, 2005).

At the ecosystem level, the functional composition of plant communities influences belowground plant biomass (Furey & Tilman, 2021; Mueller et al., 2013; Podzikowski et al., 2023; Yang et al., 2019) and belowground growth dynamics (Malhotra et al., 2020). The observed decline in biomass was likely related to a shift in the functional composition of plant communities towards a higher

abundance of pioneer species (e.g., ferns such as *Equisetum* spp.). This shift might be linked to decreased plant species richness with soil warming, as reported at the same site (Meynzer, 2016). Warming may favour stress-tolerant and pioneer plant species while reducing overall species richness, which in turn negatively impacts the belowground biomass stocks, as a loss in species diversity has been shown to affect belowground plant biomass (Cowles et al., 2016).

4.3. Differentiating fine roots and rhizomes from total biomass: A way forward to understanding effects of warming on short-living and long-living biomass as well as influence on microbial community (Articles I, II and III)

Our novel, function-based approach of classifying BPB into fine roots and rhizomes revealed that fine roots were more sensitive to soil warming compared to rhizomes (I). Fine roots that are known for their high sensitivity to changes in soil temperature (Bonanomi et al., 2021; Parts et al., 2019; Poorter et al., 2012) showed an exponential decline in biomass in response to increasing T_s under both medium- and long-term warming (I), suggesting that the temperature sensitivity of fine roots is not just a transient response. However, short-term phenotypic responses, such as modifications in growth and traits in response to environmental changes, are commonly observed in fine roots (Arnold et al., 2019; Encinas-Valero et al., 2022; Valdés et al., 2019).

The root system functions as an integrated network of roots, symbiotic fungi, and bacteria (Freschet et al., 2021; Ostonen et al., 2017), with fine roots having an essential functional role due to their higher metabolic rates and microbial stimulation capacity (Iversen et al., 2015; Trocha et al., 2017). Thus, changes in fine root traits, biomass, production, and turnover rates are key indicators of the potential change in C available for microbial communities (Soong et al., 2020). Fine root biomass is particularly important for root-associated taxa since it determines the root surface where exudates are released, and fine root exudates, including sugars, are used by root-associated microbes to maintain their metabolism and growth (Canarini et al., 2019; Dijkstra et al., 2022; Fan et al., 2022). Supporting this, a recent experiment in a temperate forest showed that although warming did not affect the fine root exudation rate, an increased FRB led to a higher overall root exudation under warming conditions (Heinzle et al., 2023). In addition to the biomass, sugar concentration in fine roots is also important for root-associated microbial taxa, as a positive linear relationship between sugar concentrations in fine roots and exudation rates of organic C is reported (Hermans et al., 2006). A warming-induced decrease in fine root biomass (I), soluble sugar concentration and pool in fine roots (III), and fine root production (Fang et al., 2023) suggests decreased carbon inputs in below ground with long-term warming. Thus, reduced growth rates of root-associated bacterial and archaeal taxa in long-warmed plots (II) likely resulted from an inadequate supply of carbon from fine

roots exacerbated by increased metabolic and respiratory costs related to warming (Dijkstra et al., 2022; Maraňón-Jiménez et al., 2018; Schindlbacher et al., 2011). Studies have shown that plant roots have a strong effect on soil bacterial community structure (Santoyo, 2022). In our study, the presence of roots influenced the growth of several bacterial and archaeal taxa (**II**). Similarly, a study in temperate forests also showed an increased diversity of root-associated bacterial communities in response to long-term warming (Kengdo et al., 2022).

The decline in fine root biomass (FRB) had a steeper slope in MTW than in LTW grassland, suggesting that in MTW, there is a greater reduction in the fine root surface where exudates are released. Given that fine root exudates are a key carbon source for root-associated microbial communities (Canarini et al., 2019), this steeper decline may lead to a faster decrease in carbon available for microbial metabolism and growth (Soong et al., 2020) along the soil warming gradient in MTW. This was reflected in the earlier decline in bacterial and fungal biomass at a lower soil warming threshold of +3–7 °C in MTW compared to LTW, where the microbial composition was stable up to +9 °C (Radujković et al., 2018). Furthermore, another study showed that the soil metabolome shifted from primary to secondary metabolites at a higher soil temperature ($T_s \geq +5$ °C) in LTW grassland, compared to a lower threshold (+1–3 °C) in MTW grassland (Gargallo-Garriga et al., 2017). The functional composition of plant communities influences root traits (Freschet et al., 2017; Maestre et al., 2006), biomass (Mueller et al., 2013), and growth dynamics (Malhotra et al., 2020) that in turn also affect microbial communities (Cantarel et al., 2015). Soil metabolome in grasslands depends upon root traits (Williams et al., 2022), and the shift in metabolites from primary to secondary indicates stress in the plant and a change in microbial communities (Gargallo-Garriga et al., 2018). Given this connection, I infer that the plant community's functional composition influences plant and microbial responses to soil warming through changes in root traits, biomass, and growth response. Based on our results, I suggest that the observed steeper decline in fine root FRB (**I**) and the shift in species composition toward a higher abundance of pioneer species (**I**) may be linked to the earlier decline in microbial biomass (Radujković et al., 2018) and an early shift in soil metabolome (Gargallo-Garriga et al., 2017), both at a lower threshold in MTW compared to LTW.

In contrast, rhizomes did not respond to soil warming, and their proportion in total belowground plant biomass (BPB) increased as fine roots declined, particularly under long-term warming (LTW; **I**). The C, N and soluble sugar pools in rhizomes remained unaffected in both MTW and LTW (**I** and **III**). This suggests that rhizomes are more resilient to environmental stresses, as previously reported (Čížková et al., 1998; Itogawa & Harada, 2020; Zhou et al., 2014), which may contribute to their survival in changing environments. A higher proportion of rhizomes indicates a greater flow of assimilates into rhizomes or a shift in plant community composition (Michielsen, 2014) towards rhizomatous species. However, the C and N derived from rhizomes may not be directly available to soil microbes based on anatomical and physiological distinctions between fine roots and rhizomes. A higher share of long-living biomass in total BPB (Klimešová

et al., 2018) potentially mitigates faster carbon and nitrogen loss. However, our understanding turnover and decomposition rates of rhizomes, particularly in response to warming, remain entirely unknown and requires further investigation. Although it has been reported that in grasslands, rhizome lifespan averages between 5 and over 8 years, with a mean decomposition time ranging from one growing season to 7 years (Wildova et al., 2007), while root turnover rates are significantly faster, averaging about 1–2 times per growing season (Amato & Giménez, 2022).

Plant productivity in high-latitude ecosystems like the Arctic and tundra is nutrient-limited (Demarco et al., 2014; Shaver & Chapin III, 1991). This limitation would decrease the biomass allocation to aboveground and increase it to fine root biomass for better nutrient acquisition (Marschner, 1996). However, warming shifted the biomass allocation to aboveground parts in tundra ecosystems (Wang et al., 2017). In this study, medium-term soil warming of $> +2$ °C reduced biomass allocation to fine roots without changing aboveground allocation (**I**), suggesting that nutrient availability does not strongly limit plant growth in the subarctic or that nutrient availability increases with increasing temperatures. However, in the same study site, nitrogen content in soil decreased with warming (Marañón-Jiménez et al., 2019), which suggests that resource acquisition became more efficient due to changed fine root traits and improved root-soil contact (Löhmus et al., 1989). This effect is particularly relevant at the MTW site, where a decline in FRB (**I**) coincided with an increase in fine root specific root area (Fang et al., 2023). High specific root area (SRA) in response to warming is also reported in other studies (Kengdo et al., 2022; Parts et al., 2019) and could imply a warming-driven shift at community level towards more acquisitive plant strategies (Reich, 2014) in sites like wet tundra (Bjorkman et al., 2018) and also in studied subarctic grassland site where water limitation is not an issue (Sigurdsson et al., 2016). High SRA in fine roots might also indicate an alternative resource acquisition strategy by maximizing soil exploration instead of relying on colonisation by mycorrhiza (Bergmann et al., 2020).

These findings of changed aboveground and belowground biomass allocation patterns indicate a potential shift in litter input dynamics from aboveground and belowground plant organs in a warmer subarctic future. However, I must acknowledge that in this study, I focused on standing belowground biomass, which consists of fine root and rhizome biomass. This biomass is a pool, constituting a balance between fine root and rhizome production and losses due to mortality (Gill & Jackson, 2000; Sullivan et al., 2008). It is important to carefully interpret these results, as the interpretation often confuses biomass production with standing biomass pools, especially in belowground studies. This study was also based on one-time measurements. We were able to get some valuable and interesting insights through this study; however, seasonal experiments that capture the seasonal dynamics of grassland vegetation and its effect on biomass, soluble sugars, and microbial responses will give a better understanding of the warming responses of these ecosystems.

Furthermore, species-specific responses to warming, particularly in terms of belowground biomass, remain poorly understood. At the community level, warming-induced changes in belowground biomass often mask the potential species-specific responses. Enhanced root growth by a single grass species, *Anthoxanthum odoratum*, which was also among the dominant species in our study sites, drove overyielding in species mixtures (Mommer et al., 2010). Specifically, in high-latitude ecosystems like the tundra and the Arctic, some species have shown a substantial increase or decrease in biomass (Hobbie & Chapin III, 1998), while others showed no change at all (Hollister & Flaherty, 2010; Ma et al., 2022). These species-specific responses in biomass (whether increase, decrease, or neutral) may offset one another and result in minimal net changes in biomass at the community level. To better understand the impacts of warming on high-latitude ecosystems, future studies should focus on species-specific responses in belowground biomass and analyse how contrasting biomass changes contribute to belowground community dynamics and changes in belowground C and N stocks.

4.4. C, N, and sugar pools in fine roots and rhizomes: an adaptation mechanism for subarctic plant communities in long-warmed soil (Articles I and III)

Warming is reported to induce changes in the chemistry of the belowground organs of plants (Li et al., 2021; Malhotra et al., 2020). Long-term soil warming increased rhizomes' N concentration, decreasing its C:N ratio (I). A higher N concentration might indicate an increased nutrient uptake efficiency, either due to rhizobionts that are stable and adapted to a higher soil temperature (Radujković et al., 2018; Verbrugghe et al., 2022a; Walker et al., 2018), higher metabolic activity and respiration (Roumet et al., 2016) or higher turnover and decreased longevity (Eissenstat et al., 2000; Tjoelker et al., 2005) of rhizomes in long-warmed soils. Roots with high nitrogen content also indicate a rapid resource uptake and growth (Roumet et al., 2016; Weemstra et al., 2016).

Furthermore, the C:N ratio in rhizomes decreased and became similar to that of fine roots (Fig. 3 B in I), indicating a change in their chemical quality and decomposability (Amougou et al., 2011). Warming-induced reductions in root C:N ratios were linked to enhanced nitrogen mineralization and increased soil nitrogen availability, leading to an increase in root nitrogen content (Salazar et al., 2020). Warming is shown to change the quality of different functional types of plant litter by changing the concentrations of lignin and N, thus affecting the decomposition process (Lu et al., 2017). As warming and litter quality are the major drivers regulating the litter decomposition rate (Amougou et al., 2011; Berbeco et al., 2012), I suggest that long-term warming modifies the chemical properties of BPB, with significant implications for nutrient cycling in the rhizosphere. Traits like higher N concentration in fine roots and rhizomes were related to an increasing mean AGB, indicating higher nutrient uptake efficiency

related to an increase in N content (**I**) that potentially increased the aboveground biomass under long-term warming (**I**).

Thus, the difference between C and N pools of 11- and 60-year warmed grasslands was the greatest in fine root biomass but not in rhizome biomass. In unwarmed conditions of both MTW and LTW, fine roots had higher C and N pools than rhizomes (**I**). However, soil warming duration and magnitude altered this balance; while fine root pools declined in highly warmed MTW plots, rhizome pools remained stable, leading to equal contributions from both components to belowground C and N pools (**I**). This shift coincided with the proportional abundance of ferns increasing and the R:S ratio decreasing with high soil warming in the MTW grassland (**I**). This shift in C and N pools from short-living fine roots biomass to long-living rhizome biomass may alter the balance of carbon and nitrogen stocks in belowground pools, contributing to a complex feedback loop in the subarctic ecosystem's carbon and nitrogen cycles.

Most importantly, the stability of BPB, C, N, and sugar pools under long-term warming may suggest a new equilibrium in the plant-soil system reached after prolonged exposure to warming; it must be noted that this stability is driven largely by rhizomes whose proportion increased in long-warmed soils as fine roots declined (Fig. 4). This means, majority of the C, N, and soluble sugar pools in belowground are in rhizome biomass. However, soluble sugars are dynamic and can be used by the plant for metabolism, growth, and defence, and their presence in rhizomes does not necessarily mean they are being stored long-term as a reserve (Prescott et al., 2020). Plants use carbon compounds as a substrate for their metabolism and to build structural biomass (Martínez-Vilalta et al., 2016). In high-elevation ecosystems, a higher soluble sugar concentration in plant tissue indicates an oversupply of carbon from a disproportionate decline in structural growth relative to photosynthesis (Hoch et al., 2003; Hoch & Körner, 2012). Particularly in subarctic grasslands, warming is reported to increase annual photosynthesis and extend the length of the growing season (Leblans et al., 2017). This increase, combined with no change in aboveground carbon demand (indicated by no change in AGB) and decreased carbon demand for belowground organs (indicated by a decrease in BPB), led to a surplus carbon accumulation as soluble sugars in rhizomes in medium-term warmed subarctic grassland (**III**). Given that, the functional structure and diversity of plant communities described a substantial proportion (40%) of the variation in fine roots' and rhizomes' sugar concentration in MTW (**III**), we could also speculate that sugar concentration at the plant community-level reflects species-specific differences in sugar concentration and their response to soil temperature.

4.5. Soluble sugars in fine roots and rhizomes of dominating species (Article III)

All belowground organs of plants are assumed to serve also as storage organs, and roots and rhizomes are often not distinguished when analysing, for example, the storage of sugars in the belowground part of the plant community along the environmental gradients (Chlumská et al., 2022). However, this approach overlooks the functional distinctions between these organs, as emerging research highlights considerable variability in sugar concentrations among different plant tissues (Janeček et al., 2011; Martínez-Vilalta et al., 2016; Montague et al., 2022).

Organ-specific differences in soluble sugar concentration were observed in our study between the three studied species (III). Levels of sugars in plant cells and their storage strongly depend on plant organs (Lemoine et al., 2013). Since rhizomes are specialised belowground structures functioning as carbon reserves (Chapin et al., 1990; Ohtake et al., 2006), they were expected to exhibit higher sugar concentrations than fine roots as observed in *A. odoratum* and *Equisetum* spp., where rhizomes had significantly higher total soluble sugar (TSS) concentrations—up to eight times higher than fine roots in *Equisetum* spp. However, in *Ranunculus acris*, the opposite pattern was observed, with higher TSS concentrations in fine roots than in rhizomes. These results challenge the general assumption that rhizomes contain higher soluble sugar concentrations than fine roots.

Species-specific differences in soluble sugar concentration that were observed between the three studied species (III) align with other studies (Diaz-Toribio & Putz, 2021; Hiltbrunner et al., 2021), likely due to species-specific variations in physiological processes, including respiration and photosynthesis. For instance, a higher carbohydrate concentration was observed in forb *Psoralea tenuiflora* compared to grasses *Panicum virgatum*, *Andropogon scoparius*, and *Sorghastrum nutans* (Fick & Nolte, 1986). Similarly, in the current study, fine roots and rhizomes of forb *R. acris* had higher total soluble sugar (TSS) concentrations compared to fern *Equisetum* spp. and grass *A. odoratum*.

The concentration of soluble sugars within plant tissues depends upon the balance between carbon supply (i.e., photosynthesis) and carbon demand (i.e., respiration and growth) (Michelot et al., 2012). Soil warming has been shown to increase photosynthesis (Tang et al., 2016), plant respiration, and growth (Dietze et al., 2014). Previous research has reported both an increase (Galiano et al., 2017; Rogiers et al., 2011) and a decrease in belowground sugar concentrations under environmental stressors such as drought and warming (Galiano et al., 2017; Xiong et al., 2018). **Species-specific response to soil warming** in terms of soluble sugars (III) was observed in this study, where soil warming did not affect soluble sugars in *Equisetum* spp. and *R. acris*, while soluble sugars in *A. odoratum* showed a significant response to soil warming (III). Specifically, the negative correlation between soluble sugar concentrations and root respiration is reported (Ryhti et al., 2022). Soil warming is shown to increase root respiration, which consumes sugars such as sucrose, and if the supply does not meet the

consumption, soluble sugars in roots decrease. Fine roots of *A. odoratum* particularly exhibited a clear temperature-dependent response, with total soluble sugar (TSS) concentrations increasing under both long-term warming (LTW) and medium-term warming (MTW). These findings may be associated with species-specific responses and differences in root growth and respiration demands with warming (Ryhti et al., 2022) and the highest root plasticity in grasses as they respond quickly to changing environments (Sotillo et al., 2024). Temperature-dependent processes such as fast spring flushing through remobilisation of stored soluble sugars and the new root and rhizome formation or regeneration during the growing period can be supported by the consumption of non-structural carbon stored in the belowground organs (Hiltbrunner et al., 2021; Lubbe et al., 2021). While soluble sugars in belowground organs generally reflect carbon reserves available for resprouting (Moreira et al., 2012), grasses primarily rely on recent photosynthates for seed germination (Janeček et al., 2011). Therefore, the increased sugar accumulation in *A. odoratum* under soil warming could indicate surplus carbon stored after fulfilling growth and respiration demands or reflect an adaptive shift toward enhanced carbon storage under warming conditions. However, contrasting findings by Prescott et al. (2020) suggest that the production of photosynthates, including non-structural carbohydrates (NSCs) and secondary metabolites, tends to increase under lower temperatures. Notably, for each degree of rise in soil temperature, the TSS concentration increased twice in LTW compared to MTW, suggesting a potential physiological change that was more pronounced under long-term warming. In the same study site, *R. acris* showed decreased leaf-level photosynthetic capacity in warmed plots, indicating reduced assimilation of photosynthates by *R. acris* under soil warming (Callebaut, 2022). Surprisingly, in this study, changes in soluble sugar concentration in fine roots and rhizomes of *R. acris* were not observed in response to soil warming. Given that *R. acris* exhibited higher soluble sugar concentrations compared to other studied species, we can speculate that although C assimilation decreased with warming, the cost of respiration was still met, leading to no decrease in soluble sugars in *R. acris*, likely due to species-specific variations in physiological processes, including respiration and photosynthesis.

However, it must be acknowledged that the present study lacks data on non-soluble non-structural carbohydrates (NSCs) compounds such as starch. Starch is a major storage carbohydrate in many plant species (Dietze et al., 2014; Dong & Beckles, 2019; Hartmann & Trumbore, 2016) and is broken down into soluble sugars to support metabolic activities, growth, and stress responses (Smith & Zeeman, 2020) and remains interconvertible with soluble sugars (Zeeman et al., 2004). Starch plays a dual role: acting as a ‘sugar source’ when carbon is in demand and as a ‘sugar sink’ when sugars are in excess, ensuring optimal carbon reserve utilisation (MacNeill et al., 2017). Thus, there is an opportunity for future studies to incorporate starch dynamics into investigations of fine root and rhizome responses to warming.

4.6. Warming effects on root growth dynamics: influence of soil depth and seasonality (Article IV)

Warming influences root dynamics directly by stimulating its growth or indirectly through enhancing belowground C allocation (Bai et al., 2010). Warming-induced changes in root growth patterns have been documented across various ecosystems, with results suggesting that warming can either stimulate or inhibit root growth (Leppälammi-Kujansuu et al., 2013; Melillo et al., 2011) and the effects may potentially depend on factors such as soil depth, season, and warming magnitude and duration. In our study, soil depth and season were the most significant factors influencing root length and projection area (**IV**). Under ambient conditions, the proportion of root length and area was consistently higher in the topsoil than in the subsoil throughout the seasons. Particularly, shallow rooting is observed in high-latitude ecosystems like the Tundra (Jackson et al., 1996) and subarctic grasslands (Bhattarai et al., 2023), resulting in higher nutrient availability, higher microbial activity and higher root decomposition rate in upper soil layers (Gill et al., 2002). However, as soil warming progresses, deeper soil layers become suitable for root growth, and root development may increase in the deep layers (Kaspar & Bland, 1992). However, under elevated CO₂, deeper rooting is a common response in forest ecosystems, while grasslands tend to exhibit shallower rooting (Iversen, 2010).

In the high-warmed plots of the LTW, we observed a shift in root distribution patterns, with root length and area increased in the subsoil, leading to similar root lengths and areas between the topsoil and subsoil. This suggests that prolonged exposure to warming altered root distribution patterns, potentially due to changes in soil nutrient availability (Marañón-Jiménez et al., 2019), prompting a shift in biomass allocation to deeper layers, as the proliferation of new roots into deeper layers can stimulate the mineralisation of older organic matter (Dijkstra et al., 2022). This, in turn, might have influenced microbial community and activity in the long-warmed soils (Walker et al., 2018) as changes in root growth and distribution influence soil microbial communities and nutrient cycling processes (Bardgett & van der Putten, 2014). Rooting depth is also functionally determined by species and ecosystem type (Jackson et al., 1996). Thus, in an ecosystem, warming-induced shifts in species composition (Hoeppepner & Dukes, 2012; Hu et al., 2021; Lin et al., 2010) would also impact the rooting depth.

The vertical distribution of organic matter and nutrients in the soil is closely linked to rooting patterns (Jobbágy & Jackson, 2000). Deeper root systems may enhance plant access to water and nutrients in subsoil layers, potentially increasing plant resilience to climatic variability (Tariq et al., 2024). However, shifts in root biomass distribution can also affect soil carbon dynamics, as root-derived carbon inputs are a major contributor to soil organic matter formation (Verbruggen et al., 2016). Thus, the increased root proliferation at deeper soil depths under warming may affect previously stable soil organic matter pools. The inputs of root exudates (De Graaff et al., 2007) or litter from root turnover (Iversen et al., 2008) could further stimulate the decomposition of old C in the

deeper soil (Fontaine et al., 2007). Studies have shown that subsoil carbon pools are more sensitive to warming in the long term, potentially leading to accelerated carbon loss (Hicks Pries et al., 2017; Jia et al., 2019; Soong et al., 2021). This would be true if deep roots turnover and decomposition rate increased under increased temperatures. However, our findings showed that soil depth did not affect changes in root length and projection area from the previous season, indicating that root growth and mortality rates could be similar across depths. This result is particularly interesting in our study, where we examined root responses to geothermal soil warming, which is more intense in the subsoil.

Our results indicated that the effects of warming duration, warming magnitude, and soil depth on root growth are dependent on season, supporting the general idea that root growth is dynamic and time-dependent. Previous research has shown that warming effects on root dynamics vary with seasonal shifts in soil moisture, temperature, and microbial activity (Abramoff & Finzi, 2015; Piao et al., 2019). While previous research suggests that warming extends the above-ground growing season at the same site (Leblans, Sigurdsson, Aerts, et al., 2017), our findings hint at earlier growth in warmed plots, as evidenced by higher root length and area in the first spring. However, this higher growth could also reflect a warming-induced stimulation of growth rather than an earlier start, as in grasslands, root phenology is generally more resistant to warming-induced shifts compared to aboveground phenology (Gill & Jackson, 2000; Möhl et al., 2022).

In the studied subarctic grassland, the high species diversity, with approximately 50 species, resulted in roots exhibiting a wide range of colours and shapes. While colour and morphological changes are commonly used as indicators of root senescence, this approach was not applicable to our study due to the substantial variation in root traits. Consequently, I could not distinguish between newly grown, pre-existing, and dead roots, meaning that my measurements reflected both root growth and mortality occurring between sampling sessions. Thus, a key limitation of our study was that, in analysing root images, I could only measure root length and area at each sampling session without tracking individual roots throughout the seasons and determining root turnover rates. Future research could overcome this limitation by integrating advanced imaging techniques with computational models that enable the tracking of individual roots over time in diverse ecosystems like those in the subarctic.

4.7. Need for long-term warming experiments to understand the ecosystem's response (Article I-IV)

Ecosystems have been reported to exhibit varying medium- and long-term warming responses (Hollister et al., 2005; Melillo et al., 2017; Romero-Olivares et al., 2017), with subarctic ecosystems particularly showing a less extreme long-term response compared to short-term (Walker et al., 2020). In our study, the ordination plot showed a distinct grouping of warmed plots in MTW and LTW, indicating varying medium- and long-term responses. Additionally, a greater

distance between ambient and warmed plots in MTW compared to LTW reflected a stronger response to medium-term soil warming (I).

Under long-term soil warming, BPB and C and N pools in BPB remained stable and were related to stable species diversity compared to MTW (I). Furthermore, the C and N sugar pools in BPB were significantly lower in MTW compared to LTW grasslands under similar soil warming of $> +2\text{ }^{\circ}\text{C}$ (I), suggesting differences in ecosystem responses to warming over different time scales. The different driving factors for the decline in soluble sugar pool in fine roots in MTW and LTW grassland (biomass in MTW and sugar concentration in LTW; III) indirectly indicate that plant communities have undergone physiological and biochemical adaptation in long-warmed soil. It could also indicate that plant community structure has changed with long-term exposure to soil warming, as soluble sugar concentration depends on species. We observed a positive relationship between sucrose concentration (the major soluble sugar) in fine roots and the abundance of grass species *A. odoratum* that declined with long-term soil warming. Additionally, an abundance of grass species *A. odoratum* alone explained 14% of the variation in the soluble sugars in fine roots and rhizomes (III). This relationship suggests that changes in the composition of the grassland plant community induced by soil warming can affect the storage of soluble sugars in the belowground biomass pool. Increased root length and area in the subsoil, alongside acclimation of root growth in the topsoil of LTW (IV), suggest a redistribution of root growth that was potentially driven by changes in nutrient availability, resource acquisition strategies, or shifts in plant community composition. Our microbial results highlight the necessity of long-term warming experiments, as the direction of plant-microbe interactions shifted from positive to neutral under long-term warming (II). All these patterns that were observed in our studies underscore the critical importance of long-term warming studies for understanding the impacts of warming on key belowground processes and microbial response in subarctic environments.

In adaptation over time, changes in the belowground biomass of a plant community are primary, and declines in biomass are characteristic of many plant species, while physiological and biogeochemical processes take time to adapt, including long-term processes such as shifts in functional plant community structure and changes in soil chemistry. These findings suggest that the changes observed in the soluble sugar pool and its drivers reflect both biogeochemical and physiological adaptations or shifts in the plant community over different time scales. Soluble sugar pools are shown to relate positively with belowground plant biomass, even for plants with extremely low sugar concentrations (Diaz-Toribio & Putz, 2021). Considering the challenges and labour involved in sampling plants' belowground organs in their entirety, studies predict the sugar pool from sugar concentration. Our study showed that considering only a change in biomass or concentration can lead to a misleading assumption of the corresponding change in the sugar pool (III).

5. CONCLUSION

My thesis investigated the medium- and long-term effects of soil warming on belowground processes in subarctic grasslands, focusing on plant biomass, plant-microbe interactions, and root growth dynamics. Belowground plant biomass was further categorised into fine root biomass (FRB) and rhizome biomass (RHB) to assess the carbon (C), nitrogen (N), and total soluble sugar (TSS) pools within their biomass. By analysing the effects of soil temperature increases up to +2 °C and exceeding +2 °C (projected increase up to 8.4 °C under the IPCC's RCP8.5 scenario), we identified key patterns in belowground plant and microbial community responses, shifts in biomass composition, changes in phenological, physiological and biochemical responses over time. Our findings highlight the importance of an organ-based approach in understanding long-term adaptation mechanisms to warming, as fine roots and rhizomes exhibited distinct sensitivity as well as physiological and biochemical responses to soil warming.

- **Fine root biomass was the key driver of medium-term responses, whereas rhizomes played a crucial role in long-term adaptation.** FRB declined with both medium- and long-term soil warming, with a steeper decline under medium-term warming, while rhizomes showed no significant response.
- **The decrease in FRB drove the decline in total belowground plant biomass and its C, N, and sugar pools under medium-term warming** and was related to a shift in the plant community composition towards an increase in the abundance of pioneers (e.g., ferns).
- **The adaptation of BPB and its associated C, N, and soluble sugar pools to soil warming was a long and gradual process. However, in the new equilibrium state that was attained after prolonged warming, biomass composition and quality were shifted** as the proportion and N content of rhizomes increased and their C:N ratio decreased. This suggests a change in the balance of C, N, and sugar pools between short-lived fine roots and long-lived rhizomes and the decomposability of rhizomes under long-term warming. These results indicate significant implications for microbial communities and soil nutrient cycling, potentially influencing future climate change trajectories. However, to better understand the impact of global warming on belowground carbon and nitrogen dynamics, further research is needed on the turnover rates of fine roots and, especially, rhizomes under warming conditions.
- **Warming disrupted plant-microbe interactions, shifting them from positive to neutral.** The presence of plant roots promoted higher microbial growth rates at ambient temperatures, but this effect diminished with prolonged warming, leading to a shift in plant-microbe interactions from positive to neutral. Our result suggests that long-term warming disrupts plant-microbe interactions by reducing putative root-associated microbial growth.

- **Changes in the soluble sugar pool are dependent on plant community dynamics.** While warming increased soluble sugars in fine roots and rhizomes of specific grass species such as *A. odoratum*, the overall fine root sugar pool declined at the community level. This decline was attributed to differences in biomass-driven changes in MTW and concentration-driven changes in LTW. These findings suggest that biomass fluctuations govern medium-term responses, while long-term ecosystem responses involve physiological and biochemical adaptations, including altered sugar allocation strategies within belowground organs.
- Contrary to the general hypothesis that rhizomes store more sugars than fine roots, our results show that **in forbs like *R. acris*, fine roots contain higher sugar concentrations than rhizomes**, highlighting the complexity of belowground carbon allocation among plant functional groups and their organs.
- Our results highlight that root growth in the topsoil acclimated to long-term soil warming, while increased root length and projection area in the subsoil suggested a redistribution of biomass, potentially due to changes in nutrient availability and resource acquisition strategies or shifts in plant community composition towards deep-rooted species. These findings emphasise the potential implications of warming on belowground carbon dynamics for sub-arctic ecosystems under prolonged warming.
- Our findings indicate **the need for long-term warming** studies to fully capture ecosystem shifts, as short- and medium-term experiments may not reflect the equilibrium states of plant-soil-microbe interactions attained after long-term exposure to warming.

REFERENCES

- Abramoff, R. Z., & Finzi, A. C. (2015). Are above- and below-ground phenology in sync? *New Phytologist*, 205(3), 1054–1061. <https://doi.org/10.1111/nph.13111>
- Aerts, R. (2006). The freezer defrosting: Global warming and litter decomposition rates in cold biomes. *Journal of Ecology*, 94(4), 713–724. <https://doi.org/10.1111/j.1365-2745.2006.01142.x>
- Aerts, R., Berendse, F., Klerk, N. M., & Bakker, C. (1989). Root production and root turnover in two dominant species of wet heathlands. *Oecologia* 1989 81:3, 81(3), 374–378. <https://doi.org/10.1007/BF00377087>
- Aguado-Norese, C., Cárdenas, V., Gaete, A., Mandakovic, D., Vasquez-Dean, J., Hodar, C., Pfeiffer, M., & Gonzalez, M. (2023). Topsoil and subsoil bacterial community assemblies across different drainage conditions in a mountain environment. *Biological Research*, 56(1), 35. <https://doi.org/10.1186/s40659-023-00445-2>
- Allison, S. D., Wallenstein, M. D., & Bradford, M. A. (2010). Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience*, 3(5), 336–340. <https://doi.org/10.1038/ngeo846>
- Amato, M. T., & Giménez, D. (2022). Quantifying root turnover in grasslands from biomass dynamics: Application of the growth-maintenance respiration paradigm and re-analysis of historical data. *Ecological Modelling*, 467, 109940. <https://doi.org/10.1016/j.ecolmodel.2022.109940>
- Amougou, N., Bertrand, I., Machet, J. M., & Recous, S. (2011). Quality and decomposition in soil of rhizome, root and senescent leaf from *Miscanthus x giganteus*, as affected by harvest date and N fertilization. *Plant and Soil*, 338(1), 83–97. <https://doi.org/10.1007/s11104-010-0443-x>
- Arnalds, O. (2004). Volcanic soils of Iceland. *CATENA*, 56(1–3), 3–20. <https://doi.org/10.1016/j.catena.2003.10.002>
- Arnold, P. A., Kruuk, L. E. B., & Nicotra, A. B. (2019). How to analyse plant phenotypic plasticity in response to a changing climate. *New Phytologist*, 222(3), 1235–1241. <https://doi.org/10.1111/nph.15656>
- Aronson, E. L., & McNulty, S. G. (2009). Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*, 149(11), 1791–1799. <https://doi.org/10.1016/j.agrformet.2009.06.007>
- Bahn, M., Reichstein, M., Dukes, J. S., Smith, M. D., & McDowell, N. G. (2014). Climate–biosphere interactions in a more extreme world. *New Phytologist*, 202(2), 356–359. <https://doi.org/10.1111/nph.12662>
- Bai, W., Wan, S., Niu, S., Liu, W., Chen, Q., Wang, Q., Zhang, W., Han, X., & Li, L. (2010). Increased temperature and precipitation interact to affect root production, mortality, and turnover in a temperate steppe: Implications for ecosystem C cycling. *Global Change Biology*, 16(4), 1306–1316. <https://doi.org/10.1111/j.1365-2486.2009.02019.x>
- Bardgett, R. D., & van der Putten, W. H. (2014). Belowground biodiversity and ecosystem functioning. *Nature*, 515(7528), 505–511. <https://doi.org/10.1038/nature13855>
- Baykalov, P. (2025). *GitHub – dIcarusb/Root-Segmentation_subArctic-Grassland-RS_SAG: Code for automatic root segmentation of images from BARTZ system, from sub-arctic grasslands*. GitHub. https://github.com/dIcarusb/Root-segmentation_subArctic-Grassland-RS_SAG

- Beier, C., Beierkuhnlein, C., Wohlgemuth, T., Penuelas, J., Emmett, B., Körner, C., de Boeck, H., Christensen, J. H., Leuzinger, S., Janssens, I. A., & Hansen, K. (2012). Precipitation manipulation experiments – challenges and recommendations for the future. *Ecology Letters*, 15(8), 899–911.
<https://doi.org/10.1111/j.1461-0248.2012.01793.x>
- Berbeco, M. R., Melillo, J. M., & Orians, C. M. (2012). Soil warming accelerates decomposition of fine woody debris. *Plant and Soil*, 356(1–2), 405–417.
<https://doi.org/10.1007/S11104-012-1130-X>
- Bergmann, J., Weigelt, A., van der Plas, F., Laughlin, D. C., Kuyper, T. W., Guerrero-Ramirez, N., Valverde-Barrantes, O. J., Bruelheide, H., Freschet, G. T., Iversen, C. M., Kattge, J., McCormack, M. L., Meier, I. C., Rillig, M. C., Roumet, C., Semchenko, M., Sweeney, C. J., van Ruijven, J., York, L. M., & Mommer, L. (2020). The fungal collaboration gradient dominates the root economics space in plants. *Science Advances*, 6(27), eaba3756. <https://doi.org/10.1126/sciadv.aba3756>
- Bessler, H., Oelmann, Y., Roscher, C., Buchmann, N., Scherer-Lorenzen, M., Schulze, E.-D., Temperton, V. M., Wilcke, W., & Engels, C. (2012). Nitrogen uptake by grassland communities: Contribution of N₂ fixation, facilitation, complementarity, and species dominance. *Plant and Soil*, 358(1), 301–322.
<https://doi.org/10.1007/s11104-012-1181-z>
- Bhattarai, B., Sigurdsson, B. D., Sigurdsson, P., Leblans, N., Janssens, I., Meynzer, W., Devarajan, A. K., Truu, J., Truu, M., & Ostonen, I. (2023). Soil warming duration and magnitude affect the dynamics of fine roots and rhizomes and associated C and N pools in subarctic grasslands. *Annals of Botany*, 132(2), 269–279.
<https://doi.org/10.1093/aob/mcad102>
- Billings, W. D., & Mooney, H. A. (1968). The Ecology of Arctic and Alpine Plants. *Biological Reviews*, 43(4), 481–529.
<https://doi.org/10.1111/j.1469-185X.1968.tb00968.x>
- Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., HilleRisLambers, J., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., ... Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, 562(7725), 57–62.
<https://doi.org/10.1038/s41586-018-0563-7>
- Bonanomi, G., Idbella, M., Zotti, M., Santorufo, L., Motti, R., Maisto, G., & De Marco, A. (2021). Decomposition and temperature sensitivity of fine root and leaf litter of 43 mediterranean species. *Plant and Soil* 2021 464:1, 464(1), 453–465.
<https://doi.org/10.1007/S11104-021-04974-1>
- Brunner, I., Bakker, M. R., Björk, R. G., Hirano, Y., Lukac, M., Aranda, X., Børja, I., Eldhuset, T. D., Helmisaari, H. S., Jourdan, C., Konôpka, B., López, B. C., Miguel Pérez, C., Persson, H., & Ostonen, I. (2013). Fine-root turnover rates of European forests revisited: An analysis of data from sequential coring and ingrowth cores. *Plant and Soil*, 362(1), 357–372. <https://doi.org/10.1007/s11104-012-1313-5>
- Callaghan, T. V., & Emanuelsson, U. (1985). Population Structure and Processes of Tundra Plants and Vegetation. *The Population Structure of Vegetation*, 399–439.
https://doi.org/10.1007/978-94-009-5500-4_17
- Callebaut, T. (2022). Gas exchange in subarctic grasslands impact of medium-term and long-term soil warming on leaf gas exchange in subarctic *Ranunculus acris* L.

- Canarini, A., Kaiser, C., Merchant, A., Richter, A., & Wanek, W. (2019). Root Exudation of Primary Metabolites: Mechanisms and Their Roles in Plant Responses to Environmental Stimuli. *Frontiers in Plant Science*, 10. <https://doi.org/10.3389/fpls.2019.00157>
- Canarini, A., Wanek, W., Watzka, M., Sandén, T., Spiegel, H., Šantrůček, J., & Schneckner, J. (2020). Quantifying microbial growth and carbon use efficiency in dry soil environments via ^{18}O water vapor equilibration. *Global Change Biology*, 26(9), 5333–5341. <https://doi.org/10.1111/gcb.15168>
- Cantarel, A. A. M., Pommier, T., Desclos-Theveniau, M., Diquélou, S., Dumont, M., Grassein, F., Kastl, E. M., Grigulis, K., Lainé, P., Lavorel, S., Lemauiel-Lavenant, S., Personeni, E., Schloter, M., & Poly, F. (2015). Using plant traits to explain plant-microbe relationships involved in nitrogen acquisition. *Ecology*, 96(3), 788–799. <https://doi.org/10.1890/13-2107.1>
- Chapin, F. S., Matson, P. A., & Vitousek, P. M. (2011). *Principles of Terrestrial Ecosystem Ecology*. Springer. <https://doi.org/10.1007/978-1-4419-9504-9>
- Chapin, F. S., Schulze, E.-D., & Mooney, H. A. (1990). The Ecology and Economics of Storage in Plants. *Annual Review of Ecology and Systematics*, 21, 423–447.
- Chen, H. Y. H., & Brassard, B. W. (2013). Intrinsic and Extrinsic Controls of Fine Root Life Span. *Critical Reviews in Plant Sciences*, 32(3), 151–161. <https://doi.org/10.1080/07352689.2012.734742>
- Chlumská, Z., Liancourt, P., Hartmann, H., Bartoš, M., Altman, J., Dvorský, M., Hubáček, T., Borovec, J., Čapkova, K., Kotlínek, M., & Doležal, J. (2022). Species- and compound-specific dynamics of nonstructural carbohydrates toward the world's upper distribution of vascular plants. *Environmental and Experimental Botany*, 201, 104985. <https://doi.org/10.1016/j.envexpbot.2022.104985>
- Čížková, H., Botany, V. B.-A., & 1998, undefined. (1999). Rhizome respiration of *Phragmites australis*: Effect of rhizome age, temperature, and nutrient status of the habitat. *Elsevier*. <https://doi.org/10.1007/BF02913396>
- Clemmensen, K. E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R. D., Wardle, D. A., & Lindahl, B. D. (2013). Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest. *Science*, 339(6127), 1615–1618. <https://doi.org/10.1126/science.1231923>
- Conant, R. T., Ryan, M. G., Ågren, G. I., Birge, H. E., Davidson, E. A., Eliasson, P. E., Evans, S. E., Frey, S. D., Giardina, C. P., Hopkins, F. M., Hyvönen, R., Kirschbaum, M. U. F., Lavalley, J. M., Leifeld, J., Parton, W. J., Megan Steinweg, J., Wallenstein, M. D., Martin Wetterstedt, J. Å., & Bradford, M. A. (2011). Temperature and soil organic matter decomposition rates – synthesis of current knowledge and a way forward. *Global Change Biology*, 17(11), 3392–3404. <https://doi.org/10.1111/J.1365-2486.2011.02496.X>
- Cowles, J. M., Wragg, P. D., Wright, A. J., Powers, J. S., & Tilman, D. (2016). Shifting grassland plant community structure drives positive interactive effects of warming and diversity on aboveground net primary productivity. *Global Change Biology*, 22(2), 741–749. <https://doi.org/10.1111/gcb.13111>
- Craine, J. M., Fierer, N., & McLauchlan, K. K. (2010). Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nature Geoscience*, 3(12), 854–857.
- Crow, S. E., Lajtha, K., Filley, T. R., Swanston, C. W., Bowden, R. D., & Caldwell, B. A. (2009). Sources of plant-derived carbon and stability of organic matter in soil: Implications for global change. *Global Change Biology*, 15(8), 2003–2019. <https://doi.org/10.1111/j.1365-2486.2009.01850.x>

- Davidson, E. A., & Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 2006 440:7081, 440(7081), 165–173. <https://doi.org/10.1038/nature04514>
- Dawes, M. A., Philipson, C. D., Fonti, P., Bebi, P., Hättenschwiler, S., Hagedorn, F., & Rixen, C. (2015). Soil warming and CO₂ enrichment induce biomass shifts in alpine tree line vegetation. *Global Change Biology*, 21(5), 2005–2021. <https://doi.org/10.1111/gcb.12819>
- De Boeck, H. J., Vicca, S., Roy, J., Nijs, I., Milcu, A., Kreyling, J., Jentsch, A., Chabbi, A., Campioli, M., Callaghan, T., Beierkuhnlein, C., & Beier, C. (2015). Global Change Experiments: Challenges and Opportunities. *BioScience*, 65(9), 922–931. <https://doi.org/10.1093/biosci/biv099>
- De Graaff, M.-A., Six, J., & Van Kessel, C. (2007). Elevated CO₂ increases nitrogen rhizodeposition and microbial immobilization of root-derived nitrogen. *New Phytologist*, 173(4), 778–786. <https://doi.org/10.1111/j.1469-8137.2006.01974.x>
- Demarco, J., MacK, M. C., Bret-Harte, M. S., Burton, M., & Shaver, G. R. (2014). Long-term experimental warming and nutrient additions increase productivity in tall deciduous shrub tundra. *Ecosphere*, 5(6), 1–22. <https://doi.org/10.1890/ES13-00281.1>
- Diaz-Toribio, M. H., & Putz, F. E. (2021). Underground carbohydrate stores and storage organs in fire-maintained longleaf pine savannas in Florida, USA. *American Journal of Botany*, 108(3), 432–442. <https://doi.org/10.1002/ajb2.1620>
- Dietze, M. C., Sala, A., Carbone, M. S., Czimczik, C. I., Mantooth, J. A., Richardson, A. D., & Vargas, R. (2014). Nonstructural carbon in woody plants. *Annual Review of Plant Biology*, 65, 667–687. <https://doi.org/10.1146/annurev-arplant-050213-040054>
- Dijkstra, P., Martinez, A., Thomas, S. C., Seymour, C. O., Wu, W., Dippold, M. A., Megonigal, J. P., Schwartz, E., & Hungate, B. A. (2022). On maintenance and metabolisms in soil microbial communities. *Plant and Soil*, 476(1), 385–396. <https://doi.org/10.1007/s11104-022-05382-9>
- Dong, S., & Beckles, D. M. (2019). Dynamic changes in the starch-sugar interconversion within plant source and sink tissues promote a better abiotic stress response. *Journal of Plant Physiology*, 234–235, 80–93. <https://doi.org/10.1016/j.jplph.2019.01.007>
- Dwire, K. A. (2001). *Relations Among Hydrology, Soils, and Vegetation in Riparian Meadows: Influence on Organic Matter Distribution and Storage*.
- Eissenstat, D. M., Wells, C. E., Yanai, R. D., & Whitbeck, J. L. (2000). Building roots in a changing environment: Implications for root longevity. *New Phytologist*, 147(1), 33–42. <https://doi.org/10.1046/j.1469-8137.2000.00686.x>
- Encinas-Valero, M., Esteban, R., Hereş, A.-M., Vivas, M., Fakhret, D., Aranjuelo, I., Solla, A., Moreno, G., & Curiel Yuste, J. (2022). Holm oak decline is determined by shifts in fine root phenotypic plasticity in response to belowground stress. *New Phytologist*, 235(6), 2237–2251. <https://doi.org/10.1111/nph.18182>
- Fan, K., Holland-Moritz, H., Walsh, C., Guo, X., Wang, D., Bai, Y., Zhu, Y., Fierer, N., & Chu, H. (2022). Identification of the rhizosphere microbes that actively consume plant-derived carbon. *Soil Biology and Biochemistry*, 166, 108577. <https://doi.org/10.1016/j.soilbio.2022.108577>
- Fang, C., Verbrugghe, N., Sigurdsson, B. D., Ostonen, I., Leblans, N. I. W., Marañón-Jiménez, S., Fuchslueger, L., Sigurðsson, P., Meeran, K., Portillo-Estrada, M., Verbruggen, E., Richter, A., Sardans, J., Peñuelas, J., Bahn, M., Vicca, S., & Janssens, I. A. (2023). Decadal soil warming decreased vascular plant above and belowground production in a subarctic grassland by inducing nitrogen limitation. *New Phytologist*, 240(2), 565–576. <https://doi.org/10.1111/nph.19177>

- Fick, W. H., & Nolte, D. L. (1986). Field Collection Techniques for Total Nonstructural Carbohydrate Analysis of Plant Storage Organs. *Transactions of the Kansas Academy of Science* (1903-), 89(1/2), 40. <https://doi.org/10.2307/3627730>
- Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., & Rumpel, C. (2007). Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature*, 450(7167), 277–280. <https://doi.org/10.1038/nature06275>
- Freschet, G. T., Cornwell, W. K., Wardle, D. A., Elumeeva, T. G., Liu, W., Jackson, B. G., Onipchenko, V. G., Soudzilovskaia, N. A., Tao, J., & Cornelissen, J. H. C. (2013). Linking litter decomposition of above- and below-ground organs to plant–soil feedbacks worldwide. *Journal of Ecology*, 101(4), 943–952. <https://doi.org/10.1111/1365-2745.12092>
- Freschet, G. T., Pagès, L., Iversen, C. M., Comas, L. H., Rewald, B., Roumet, C., Klimešová, J., Zadworny, M., Poorter, H., Postma, J. A., Adams, T. S., Bagniewska-Zadworna, A., Bengough, A. G., Blancaflor, E. B., Brunner, I., Cornelissen, J. H. C., Garnier, E., Gessler, A., Hobbie, S. E., ... McCormack, M. L. (2021). A starting guide to root ecology: Strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. *New Phytologist*, 232(3), 973–1122. <https://doi.org/10.1111/nph.17572>
- Freschet, G. T., & Roumet, C. (2017). Sampling roots to capture plant and soil functions. *Functional Ecology*, 31(8), 1506–1518. <https://doi.org/10.1111/1365-2435.12883>
- Furey, G. N., & Tilman, D. (2021). Plant biodiversity and the regeneration of soil fertility. *Proceedings of the National Academy of Sciences of the United States of America*, 118(49). <https://doi.org/10.1073/PNAS.2111321118>
- Galiano, L., Timofeeva, G., Saurer, M., Siegwolf, R., Martínez-Vilalta, J., Hommel, R., & Gessler, A. (2017). The fate of recently fixed carbon after drought release: Towards unravelling C storage regulation in *Tilia platyphyllos* and *Pinus sylvestris*. *Plant, Cell & Environment*, 40(9), 1711–1724. <https://doi.org/10.1111/pce.12972>
- Gargallo-Garriga, A., Ayala-Roque, M., Sardans, J., Bartrons, M., Granda, V., Sigurdsson, B. D., Leblans, N. I. W., Oravec, M., Urban, O., Janssens, I. A., & Peñuelas, J. (2017). Impact of soil warming on the plant metabolome of Icelandic grasslands. *Metabolites*, 7(3). <https://doi.org/10.3390/metabo7030044>
- Gargallo-Garriga, A., Preece, C., Sardans, J., Oravec, M., Urban, O., & Peñuelas, J. (2018). Root exudate metabolomes change under drought and show limited capacity for recovery. *Scientific Reports* 2018 8:1, 8(1), 1–15. <https://doi.org/10.1038/s41598-018-30150-0>
- Gill, R. A., Burke, I. C., Lauenroth, W. K., & Milchunas, D. G. (2002). Longevity and turnover of roots in the shortgrass steppe: Influence of diameter and depth. *Plant Ecology*, 159(2), 241–251. <https://doi.org/10.1023/A:1015529507670>
- Gill, R. A., & Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. *New Phytologist*, 147(1), 13–31. <https://doi.org/10.1046/j.1469-8137.2000.00681.x>
- Govaert, S., Vangansbeke, P., Blondeel, H., De Lombaerde, E., Verheyen, K., & De Frenne, P. (2021). Forest understorey plant responses to long-term experimental warming, light and nitrogen addition. *Plant Biology*, 23(6), 1051–1062. <https://doi.org/10.1111/plb.13330>
- Guo, Q. (2012). Hydrogeochemistry of high-temperature geothermal systems in China: A review. *Applied Geochemistry*, 27(10), 1887–1898. <https://doi.org/10.1016/j.apgeochem.2012.07.006>

- Harris, T., Klimeš, A., Martínková, J., & Klimešová, J. (2023). Herbs are not just small plants: What biomass allocation to rhizomes tells us about differences between trees and herbs. *American Journal of Botany*, 110(7), e16202. <https://doi.org/10.1002/ajb2.16202>
- Hartmann, H., & Trumbore, S. (2016). Understanding the roles of nonstructural carbohydrates in forest trees – from what we can measure to what we want to know. *New Phytologist*, 211(2), 386–403. <https://doi.org/10.1111/nph.13955>
- Heinzle, J., Liu, X., Tian, Y., Kwatcho Kengdo, S., Heinze, B., Nirschi, A., Borken, W., Inselsbacher, E., Wanek, W., & Schindlbacher, A. (2023). Increase in fine root biomass enhances root exudation by long-term soil warming in a temperate forest. *Frontiers in Forests and Global Change*, 6. <https://doi.org/10.3389/ffgc.2023.1152142>
- Hermans, C., Hammond, J. P., White, P. J., & Verbruggen, N. (2006). How do plants respond to nutrient shortage by biomass allocation? *Trends in Plant Science*, 11(12), 610–617. <https://doi.org/10.1016/j.tplants.2006.10.007>
- Hernández, P. A., Pérez, N. M., Fridriksson, T., Egbert, J., Ilyinskaya, E., Thárhalls-son, A., Ívarsson, G., Gíslason, G., Gunnarsson, I., Jónsson, B., Padrón, E., Melián, G., Mori, T., & Notsu, K. (2012). Diffuse volcanic degassing and thermal energy release from Hengill volcanic system, Iceland. *Bulletin of Volcanology*, 74(10), 2435–2448. <https://doi.org/10.1007/s00445-012-0673-2>
- Hicks Pries, C. E., Castanha, C., Porras, R. C., & Torn, M. S. (2017). The whole-soil carbon flux in response to warming. *Science*, 355(6332). <https://doi.org/10.1126/SCIENCE.AAL1319>
- Hiltbrunner, E., Arnaiz, J., & Körner, · Christian. (2021). Biomass allocation and seasonal non-structural carbohydrate dynamics do not explain the success of tall forbs in short alpine grassland. *Oecologia*, 197, 1063–1077. <https://doi.org/10.1007/s00442-021-04950-7>
- Hobbie, S. E., & Chapin III, F. S. (1998). The Response of Tundra Plant Biomass, Above-ground Production, Nitrogen, and Co2 Flux to Experimental Warming. *Ecology*, 79(5), 1526–1544. [https://doi.org/10.1890/0012-9658\(1998\)079\[1526:TROTPB\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[1526:TROTPB]2.0.CO;2)
- Hoch, G., & Körner, C. (2012). Global patterns of mobile carbon stores in trees at the high-elevation tree line. *Global Ecology and Biogeography*, 21(8), 861–871. <https://doi.org/10.1111/j.1466-8238.2011.00731.x>
- Hoch, G., Richter, A., & Körner, Ch. (2003). Non-structural carbon compounds in temperate forest trees. *Plant, Cell & Environment*, 26(7), 1067–1081. <https://doi.org/10.1046/j.0016-8025.2003.01032.x>
- Hoepfner, S. S., & Dukes, J. S. (2012). Interactive responses of old-field plant growth and composition to warming and precipitation. *Global Change Biology*, 18(5), 1754–1768. <https://doi.org/10.1111/j.1365-2486.2011.02626.x>
- Högberg, P., & Read, D. J. (2006). Towards a more plant physiological perspective on soil ecology. *Trends in Ecology & Evolution*, 21(10), 548–554. <https://doi.org/10.1016/J.TREE.2006.06.004>
- Hollister, R. D., & Flaherty, K. J. (2010). Above- and below-ground plant biomass response to experimental warming in northern Alaska. *Applied Vegetation Science*, 13(3), 378–387. <https://doi.org/10.1111/j.1654-109X.2010.01079.x>
- Hollister, R. D., Webber, P. J., & Tweedie, C. E. (2005). The response of Alaskan arctic tundra to experimental warming: Differences between short- and long-term responses. *Global Change Biology*, 11(4), 525–536. <https://doi.org/10.1111/j.1365-2486.2005.00926.x>

- Hu, X., Zhou, W., Li, X., Niklas, K. J., & Sun, S. (2021). Changes in Community Composition Induced by Experimental Warming in an Alpine Meadow: Beyond Plant Functional Type. *Frontiers in Ecology and Evolution*, 9. <https://doi.org/10.3389/fevo.2021.569422>
- IPCC. (2022). *Climate Change 2022 – Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (1st ed.). Cambridge University Press. <https://doi.org/10.1017/9781009325844>
- Itogawa, H., & Harada, T. (2020). Anoxia tolerance of the rhizomes of three Japanese Iris species with different habitat. *Aquatic Botany*, 167, 103276. <https://doi.org/10.1016/J.AQUABOT.2020.103276>
- Iversen, C. M. (2010). Digging deeper: Fine-root responses to rising atmospheric CO₂ concentration in forested ecosystems. *New Phytologist*, 186(2), 346–357. <https://doi.org/10.1111/j.1469-8137.2009.03122.x>
- Iversen, C. M., Ledford, J., & Norby, R. J. (2008). CO₂ enrichment increases carbon and nitrogen input from fine roots in a deciduous forest. *New Phytologist*, 179(3), 837–847. <https://doi.org/10.1111/j.1469-8137.2008.02516.x>
- Iversen, C. M., Sloan, V. L., Sullivan, P. F., Euskirchen, E. S., McGuire, A. D., Norby, R. J., Walker, A. P., Warren, J. M., & Wullschlegel, S. D. (2015). The unseen iceberg: Plant roots in arctic tundra. *New Phytologist*, 205(1), 34–58. <https://doi.org/10.1111/nph.13003>
- Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E., & Schulze, E. D. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia*, 108(3), 389–411. <https://doi.org/10.1007/BF00333714>
- Janeček, Š., Lanta, V., Klimešová, J., & Doležal, J. (2011). Effect of abandonment and plant classification on carbohydrate reserves of meadow plants. *Plant Biology*, 13(2), 243–251. <https://doi.org/10.1111/J.1438-8677.2010.00352.X>
- Jansen, E., Christensen, J. H., Dokken, T., Nisancioglu, K. H., Vinther, B. M., Capron, E., Guo, C., Jensen, M. F., Langen, P. L., Pedersen, R. A., Yang, S., Bentsen, M., Kjær, H. A., Sadatzki, H., Sessford, E., & Stendel, M. (2020). Past perspectives on the present era of abrupt Arctic climate change. *Nature Climate Change*, 10(8), 714–721. <https://doi.org/10.1038/s41558-020-0860-7>
- Jia, J., Cao, Z., Liu, C., Zhang, Z., Lin, L., Wang, Y., Haghipour, N., Wacker, L., Bao, H., Dittmar, T., Simpson, M. J., Yang, H., Crowther, T. W., Eglinton, T. I., He, J.-S., & Feng, X. (2019). Climate warming alters subsoil but not topsoil carbon dynamics in alpine grassland. *Global Change Biology*, 25(12), 4383–4393. <https://doi.org/10.1111/gcb.14823>
- Jobbágy, E. G., & Jackson, R. B. (2000). THE VERTICAL DISTRIBUTION OF SOIL ORGANIC CARBON AND ITS RELATION TO CLIMATE AND VEGETATION. *Ecological Applications*, 10(2), 423–436. [https://doi.org/10.1890/1051-0761\(2000\)010\[0423:TVDOSO\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2)
- Johnson, M. G., Tingey, D. T., Phillips, D. L., & Storm, M. J. (2001). Advancing fine root research with minirhizotrons. *Environmental and Experimental Botany*, 45(3), 263–289. [https://doi.org/10.1016/S0098-8472\(01\)00077-6](https://doi.org/10.1016/S0098-8472(01)00077-6)
- Jónsdóttir, I. S., Callaghan, T. V., & Headley, A. D. (1996). Resource dynamics within arctic clonal plants. *Ecological Bulletins*, 45, 53–64.
- Karhu, K., Auffret, M. D., Dungait, J. A. J., Hopkins, D. W., Prosser, J. I., Singh, B. K., Subke, J.-A., Wookey, P. A., Ågren, G. I., Sebastià, M.-T., Gourevau, F., Bergkvist, G., Meir, P., Nottingham, A. T., Salinas, N., & Hartley, I. P. (2014). Temperature

- sensitivity of soil respiration rates enhanced by microbial community response. *Nature*, 513(7516), 81–84. <https://doi.org/10.1038/nature13604>
- Kaspar, T. C., & Bland, W. L. (1992). Soil temperature and root growth. *Soil Science*, 154(4), 290.
- Kätterer, T., Börjesson, G., & Kirchmann, H. (2014). Changes in organic carbon in topsoil and subsoil and microbial community composition caused by repeated additions of organic amendments and N fertilisation in a long-term field experiment in Sweden. *Agriculture, Ecosystems & Environment*, 189, 110–118. <https://doi.org/10.1016/j.agee.2014.03.025>
- Kayler, Z. E., De Boeck, H. J., Fatichi, S., Grünzweig, J. M., Merbold, L., Beier, C., McDowell, N., & Dukes, J. S. (2015). Experiments to confront the environmental extremes of climate change. *Frontiers in Ecology and the Environment*, 13(4), 219–225. <https://doi.org/10.1890/140174>
- Kengdo, S. K., Peršoh, D., Schindlbacher, A., Heinzle, J., Tian, Y., Wanek, W., & Borken, J. Werner. (2022). Long-term soil warming alters fine root dynamics and morphology, and their ectomycorrhizal fungal community in a temperate forest soil. *Global Change Biology*, 00, 1–18. <https://doi.org/10.1111/GCB.16155>
- Kimball, B. A., Alonso-Rodríguez, A. M., Cavaleri, M. A., Reed, S. C., González, G., & Wood, T. E. (2018). Infrared heater system for warming tropical forest understory plants and soils. *Ecology and Evolution*, 8(4), 1932–1944. <https://doi.org/10.1002/ece3.3780>
- Klimešová, J., & Bello, F. (2009). CLO-PLA: The database of clonal and bud bank traits of Central European flora. *Journal of Vegetation Science*, 20(3), 511–516. <https://doi.org/10.1111/j.1654-1103.2009.01050.x>
- Klimešová, J., Doležal, J., Dvorský, M., de Bello, F., & Klimeš, L. (2011). Clonal Growth Forms in Eastern Ladakh, Western Himalayas: Classification and Habitat Preferences. *Folia Geobotanica*, 46(2–3), 191–217. <https://doi.org/10.1007/S12224-010-9076-3>
- Klimešová, J., Martínková, J., & Ottaviani, G. (2018). Belowground plant functional ecology: Towards an integrated perspective. *Functional Ecology*, 32(9), 2115–2126. <https://doi.org/10.1111/1365-2435.13145>
- Leblans, N. I. W. (2016). *Natural gradients in temperature and nitrogen: Iceland represents a unique environment to clarify long-term global change effects on carbon dynamics*.
- Leblans, N. I. W., Sigurdsson, B. D., Aerts, R., Vicca, S., Magnússon, B., & Janssens, I. A. (2017). Icelandic grasslands as long-term C sinks under elevated organic N inputs. *Biogeochemistry*, 134(3), 279–299. <https://doi.org/10.1007/s10533-017-0362-5>
- Leblans, N. I. W., Sigurdsson, B. D., Vicca, S., Fu, Y., Penuelas, J., & Janssens, I. A. (2017). Phenological responses of Icelandic subarctic grasslands to short-term and long-term natural soil warming. *Global Change Biology*, 23(11), 4932–4945. <https://doi.org/10.1111/gcb.13749>
- Lemoine, R., La Camera, S., Atanassova, R., Dédaldéchamp, F., Allario, T., Pourtau, N., Bonnemain, J.-L., Laloi, M., Coutos-Thévenot, P., Maurousset, L., Faucher, M., Grousse, C., Lemonnier, P., Parrilla, J., & Durand, M. (2013). Source-to-sink transport of sugar and regulation by environmental factors. *Frontiers in Plant Science*, 4. <https://doi.org/10.3389/fpls.2013.00272>
- Leppälammi-Kujansuu, J., Salemaa, M., Kleja, D. B., Linder, S., & Helmisaari, H.-S. (2013). Fine root turnover and litter production of Norway spruce in a long-term temperature and nutrient manipulation experiment. *Plant and Soil* 2013 374:1, 374(1), 73–88. <https://doi.org/10.1007/S11104-013-1853-3>

- Li, Z., Rubert-Nason, K. F., Jamieson, M. A., Raffa, K. F., & Lindroth, R. L. (2021). Root Secondary Metabolites in *Populus tremuloides*: Effects of Simulated Climate Warming, Defoliation, and Genotype. *Journal of Chemical Ecology*, 47(3), 313–321. <https://doi.org/10.1007/S10886-021-01259-w>
- Lin, D., Xia, J., & Wan, S. (2010). Climate warming and biomass accumulation of terrestrial plants: A meta-analysis. *New Phytologist*, 188(1), 187–198. <https://doi.org/10.1111/j.1469-8137.2010.03347.x>
- Liu, H., Wang, H., Li, N., Shao, J., Zhou, X., van Groenigen, K. J., & Thakur, M. P. (2022). Phenological mismatches between above- and belowground plant responses to climate warming. *Nature Climate Change*, 12(1), 97–102. <https://doi.org/10.1038/s41558-021-01244-x>
- Lõhmus, K., Oja, T., & Lasn, R. (1989). Specific root area: A soil characteristic. *Plant and Soil*, 119(2), 245–249. <https://doi.org/10.1007/BF02370415>
- Lorenz, K., & Lal, R. (2005). The Depth Distribution of Soil Organic Carbon in Relation to Land Use and Management and the Potential of Carbon Sequestration in Subsoil Horizons. *Advances in Agronomy*, 88, 35–66. [https://doi.org/10.1016/S0065-2113\(05\)88002-2](https://doi.org/10.1016/S0065-2113(05)88002-2)
- Lu, W., Liu, N., Zhang, Y., Zhou, J., Guo, Y., & Yang, X. (2017). Impact of vegetation community on litter decomposition: Evidence from a reciprocal transplant study with ¹³C labeled plant litter. *Soil Biology and Biochemistry*, 112, 248–257. <https://doi.org/10.1016/j.soilbio.2017.05.014>
- Lubbe, F. C., Klimešová, J., & Henry, H. A. L. (2021). Winter belowground: Changing winters and the perennating organs of herbaceous plants. *Functional Ecology*, 35(8), 1627–1639. <https://doi.org/10.1111/1365-2435.13858>
- Ma, T., Parker, T., Fetcher, N., Unger, S. L., Gewirtzman, J., Moody, M. L., & Tang, J. (2022). Leaf and root phenology and biomass of *Eriophorum vaginatum* in response to warming in the Arctic. *Journal of Plant Ecology*, 15(5), 1091–1105. <https://doi.org/10.1093/jpe/rtac010>
- MacNeill, G. J., Mehrpouyan, S., Minow, M. A. A., Patterson, J. A., Tetlow, I. J., & Emes, M. J. (2017). Starch as a source, starch as a sink: The bifunctional role of starch in carbon allocation. *Journal of Experimental Botany*, 68(16), 4433–4453. <https://doi.org/10.1093/jxb/erx291>
- Maestre, F. T., Bradford, J., Mark A, Reynolds, &, & James F. (2006). Soil heterogeneity and community composition jointly influence grassland biomass. *Journal of Vegetation Science*, 17(3), 261–270. <https://doi.org/10.1111/J.1654-1103.2006.TB02445.X>
- Majdi, H. (2001). Changes in fine root production and longevity in relation to water and nutrient availability in a Norway spruce stand in northern Sweden. *Tree Physiology*, 21(14), 1057–1061. <https://doi.org/10.1093/treephys/21.14.1057>
- Malhotra, A., Brice, D. J., Childs, J., Graham, J. D., Hobbie, E. A., Vander Stel, H., Feron, S. C., Hanson, P. J., & Iversen, C. M. (2020). Peatland warming strongly increases fine-root growth. *Proceedings of the National Academy of Sciences of the United States of America*, 117(30), 17627–17634. <https://doi.org/10.1073/PNAS.2003361117>
- Marañón-Jiménez, S., Peñuelas, J., Richter, A., Sigurdsson, B. D., Fuchslueger, L., Leblans, N. I. W., & Janssens, I. A. (2019). Coupled carbon and nitrogen losses in response to seven years of chronic warming in subarctic soils. *Soil Biology and Biochemistry*, 134, 152–161. <https://doi.org/10.1016/j.soilbio.2019.03.028>

- Marañón-Jiménez, S., Soong, J. L., Leblans, N. I. W., Sigurdsson, B. D., Peñuelas, J., Richter, A., Asensio, D., Fransen, E., & Janssens, I. A. (2018). Geothermally warmed soils reveal persistent increases in the respiratory costs of soil microbes contributing to substantial C losses. *Biogeochemistry*, 138(3), 245–260.
<https://doi.org/10.1007/s10533-018-0443-0>
- Marion, G. m., Henry, G. h. r., Freckman, D. w., Johnstone, J., Jones, G., Jones, M. h., Lévesque, E., Molau, U., Mølgaard, P., Parsons, A. n., Svoboda, J., & Virginia, R. a. (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, 3(S1), 20–32.
<https://doi.org/10.1111/j.1365-2486.1997.gcb136.x>
- Marschner, C. (1996). H. Marschner Mineral Nutrition of Higher Plants 2nd edition 1995 Academic Press London 889 (ISBN 0-12-473543-6). Price: 29.95 Pound Sterling. *Journal of Plant Physiology*, 148, 765–765.
[https://doi.org/10.1016/S0176-1617\(96\)80382-8](https://doi.org/10.1016/S0176-1617(96)80382-8)
- Martínez-Vilalta, J., Sala, A., Asensio, D., Galiano, L., Hoch, G., Palacio, S., Piper, F. I., & Lloret, F. (2016). Dynamics of non-structural carbohydrates in terrestrial plants: A global synthesis. *Ecological Monographs*, 86(4), 495–516.
<https://doi.org/10.1002/ecm.1231>
- McCormack, M. L., & Guo, D. (2014). Impacts of environmental factors on fine root lifespan. *Frontiers in Plant Science*, 5, 205. <https://doi.org/10.3389/fpls.2014.00205>
- Melillo, J. M., Butler, S., Johnson, J., Mohan, J., Steudler, P., Lux, H., Burrows, E., Bowles, F., Smith, R., Scott, L., Vario, C., Hill, T., Burton, A., Zhou, Y. M., & Tang, J. (2011). Soil warming, carbon-nitrogen interactions, and forest carbon budgets. *Proceedings of the National Academy of Sciences of the United States of America*, 108(23), 9508–9512. <https://doi.org/10.1073/PNAS.1018189108>
- Melillo, J. M., Frey, S. D., DeAngelis, K. M., Werner, W. J., Bernard, M. J., Bowles, F. P., Pold, G., Knorr, M. A., & Grandy, A. S. (2017). Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science*, 358(6359), 101–105. <https://doi.org/10.1126/science.aan2874>
- Melillo, J. M., Steudler, P. A., Aber, J. D., Newkirk, K., Lux, H., Bowles, F. P., Catri-cala, C., Magill, A., Ahrens, T., & Morrisseau, S. (2002). Soil warming and carbon-cycle feedbacks to the climate system. *Science*, 298(5601), 2173–2176.
<https://doi.org/10.1126/SCIENCE.1074153>
- Menzel, A., & Fabian, P. (1999). Growing season extended in Europe. *Nature*, 397(6721), 659–659.
- Metze, D., Schnecker, J., Canarini, A., Fuchslueger, L., Koch, B. J., Stone, B. W., Hungate, B. A., Hausmann, B., Schmidt, H., Schaumberger, A., Bahn, M., Kaiser, C., & Richter, A. (2023). Microbial growth under drought is confined to distinct taxa and modified by potential future climate conditions. *Nature Communications*, 14(1), 5895. <https://doi.org/10.1038/s41467-023-41524-y>
- Meynzer, W. (2016). *The effect of temperature and nitrogen on plant community structure in Icelandic subarctic grassland ecosystems*.
- Michelot, A., Simard, S., Rathgeber, C., Dufrêne, E., & Damesin, C. (2012). Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree Physiology*, 32, 1033–1043.
<https://doi.org/10.1093/treephys/tps052>

- Michielsen, L. (2014). *Plant communities and global change: Adaptation by changes in present species composition or adaptation in plant traits. A case study in Iceland. Of Science in Biology, specialization Ecology and Environment.*
- Möhl, P., von Büren, R. S., & Hiltbrunner, E. (2022). Growth of alpine grassland will start and stop earlier under climate warming. *Nature Communications*, 13(1), 7398. <https://doi.org/10.1038/s41467-022-35194-5>
- Mokany, K., Raison, R. J., & Prokushkin, A. S. (2006). Critical analysis of root: Shoot ratios in terrestrial biomes. *Global Change Biology*, 12(1), 84–96. <https://doi.org/10.1111/j.1365-2486.2005.001043.x>
- Mommer, L., Van Ruijven, J., De Caluwe, H., Smit-Tiekstra, A. E., Wagemaker, C. A. M., Joop Ouborg, N., Bögemann, G. M., Van Der Weerden, G. M., Berendse, F., & De Kroon, H. (2010). Unveiling below-ground species abundance in a biodiversity experiment: A test of vertical niche differentiation among grassland species. *Journal of Ecology*, 98(5), 1117–1127. <https://doi.org/10.1111/j.1365-2745.2010.01702.x>
- Montague, M. S., Landhäusser, S. M., McNickle, G. G., & Jacobs, D. F. (2022). Preferential allocation of carbohydrate reserves belowground supports disturbance-based management of American chestnut (*Castanea dentata*). *Forest Ecology and Management*, 509, 120078. <https://doi.org/10.1016/j.foreco.2022.120078>
- Moreira, B., Tormo, J., & Pausas, J. G. (2012). To resprout or not to resprout: Factors driving intraspecific variability in resprouting. *Oikos*, 121(10), 1577–1584. <https://doi.org/10.1111/j.1600-0706.2011.20258.x>
- Mueller, K. E., Tilman, D., Fornara, D. A., & Hobbie, S. E. (2013). Root depth distribution and the diversity–productivity relationship in a long-term grassland experiment. *Ecology*, 94(4), 787–793. <https://doi.org/10.1890/12-1399.1>
- Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P. S. A., Berner, L. T., Bhatt, U. S., Bjorkman, A. D., Blok, D., Bryn, A., Christiansen, C. T., Cornelissen, J. H. C., Cunliffe, A. M., Elmendorf, S. C., ... Wipf, S. (2020). Complexity revealed in the greening of the Arctic. *Nature Climate Change*, 10(2), 106–117. <https://doi.org/10.1038/s41558-019-0688-1>
- O’Gorman, E. J., Benstead, J. P., Cross, W. F., Friberg, N., Hood, J. M., Johnson, P. W., Sigurdsson, B. D., & Woodward, G. (2014). Climate change and geothermal ecosystems: Natural laboratories, sentinel systems, and future refugia. *Global Change Biology*, 20(11), 3291–3299. <https://doi.org/10.1111/gcb.12602>
- Ohtake, N., Ruamrungsri, S., Ito, S., Sueyoshi, K., Ohyama, T., & Apavatjirut, P. (2006). Effect of nitrogen supply on nitrogen and carbohydrate constituent accumulation in rhizomes and storage roots of *Curcuma alismatifolia* Gagnep. *Soil Science and Plant Nutrition*, 52(6), 711–716. <https://doi.org/10.1111/j.1747-0765.2006.00094.x>
- Óskarsson, H., Arnalds, Ó., Gudmundsson, J., & Gudbergsson, G. (2004). Organic carbon in Icelandic Andosols: Geographical variation and impact of erosion. *CATENA*, 56(1), 225–238. <https://doi.org/10.1016/j.catena.2003.10.013>
- Ostonen, I., Helmisaari, H.-S., Borken, W., Tedersoo, L., Kukumägi, M., Bahram, M., Lindroos, A.-J., Nöjd, P., Uri, V., Merilä, P., Asi, E., & Lõhmus, K. (2011). Fine root foraging strategies in Norway spruce forests across a European climate gradient. *Global Change Biology*, 17(12), 3620–3632. <https://doi.org/10.1111/j.1365-2486.2011.02501.x>
- Ostonen, I., Truu, M., Helmisaari, H.-S., Lukac, M., Borken, W., Vanguelova, E., Godbold, D. L., Lõhmus, K., Zang, U., Tedersoo, L., Preem, J.-K., Rosenvald, K., Aosaar, J., Armolaitis, K., Frey, J., Kabral, N., Kukumägi, M., Leppälamm-

- Kujansuu, J., Lindroos, A.-J., ... Truu, J. (2017). Adaptive root foraging strategies along a boreal-temperate forest gradient. *New Phytologist*, 215(3), 977–991. <https://doi.org/10.1111/nph.14643>
- Parts, K., Tedersoo, L., Schindlbacher, A., Sigurdsson, B. D., Leblans, N. I. W., Oddsdóttir, E. S., Borken, W., & Ostonen, I. (2019). Acclimation of Fine Root Systems to Soil Warming: Comparison of an Experimental Setup and a Natural Soil Temperature Gradient. *Ecosystems*, 22(3), 457–472. <https://doi.org/10.1007/s10021-018-0280-y>
- Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, 25(6), 1922–1940. <https://doi.org/10.1111/gcb.14619>
- Podzikowski, L. Y., Heffernan, M. M., & Bever, J. D. (2023). Plant diversity and grasses increase root biomass in a rainfall and grassland diversity manipulation. *Frontiers in Ecology and Evolution*, 11. <https://doi.org/10.3389/fevo.2023.1259809>
- Pollierer, M. M., Langel, R., Körner, C., Maraun, M., & Scheu, S. (2007). The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecology Letters*, 10(8), 729–736. <https://doi.org/10.1111/J.1461-0248.2007.01064.X>
- Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., & Mommer, L. (2012). Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. *New Phytologist*, 193(1), 30–50. <https://doi.org/10.1111/j.1469-8137.2011.03952.x>
- Pregitzer, K. S., & King, J. S. (2005). Effects of Soil Temperature on Nutrient Uptake. *Nutrient Acquisition by Plants*, 277–310. https://doi.org/10.1007/3-540-27675-0_10
- Prescott, C. E., Grayston, S. J., Helmisaari, H.-S., Kaštovská, E., Körner, C., Lambers, H., Meier, I. C., Millard, P., & Ostonen, I. (2020). Surplus Carbon Drives Allocation and Plant-Soil Interactions. *Trends in Ecology & Evolution*, 35(12). <https://doi.org/10.1016/j.tree.2020.08.007>
- R Core Team. (2022). *R: A Language and Environment for Statistical Computing*.
- Radujković, D., Verbruggen, E., Sigurdsson, B. D., Leblans, N. I. W., Janssens, I. A., Vicca, S., & Weedon, J. T. (2018). Prolonged exposure does not increase soil microbial community compositional response to warming along geothermal gradients. *FEMS Microbiology Ecology*, 94(2). <https://doi.org/10.1093/femsec/fix174>
- Radville, L., McCormack, M. L., Post, E., & Eissenstat, D. M. (2016). Root phenology in a changing climate. *Journal of Experimental Botany*, 67(12), 3617–3628. <https://doi.org/10.1093/jxb/erw062>
- Rantanen, M., Karpechko, A. Y., 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(1), 1–10. <https://doi.org/10.1038/s43247-022-00498-3>
- Rasse, D. P., Rumpel, C., & Dignac, M.-F. (2005). Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil*, 269(1), 341–356. <https://doi.org/10.1007/s11104-004-0907-y>
- Reich, P. B. (2014). The world-wide ‘fast–slow’ plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>
- Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., & Toomey, M. (2013). Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, 169, 156–173. <https://doi.org/10.1016/j.agrformet.2012.09.012>

- Rijkers, R., Dekker, M., Aerts, R., & Weedon, J. T. (2023). Maximum summer temperatures predict the temperature adaptation of Arctic soil bacterial communities. *Bio-geosciences*, 20(4), 767–780. <https://doi.org/10.5194/bg-20-767-2023>
- Romero-Olivares, A. L., Allison, S. D., & Treseder, K. K. (2017). Soil microbes and their response to experimental warming over time: A meta-analysis of field studies. *Soil Biology and Biochemistry*, 107, 32–40. <https://doi.org/10.1016/j.soilbio.2016.12.026>
- Rosenstock, N., Ellström, M., Oddsdóttir, E., Sigurdsson, B. D., & Wallander, H. (2019). Carbon sequestration and community composition of ectomycorrhizal fungi across a geothermal warming gradient in an Icelandic spruce forest. *Fungal Ecology*, 40, 32–42. <https://doi.org/10.1016/j.funeco.2018.05.010>
- Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vrignon-Brenas, S., Cao, K., & Stokes, A. (2016). Root structure–function relationships in 74 species: Evidence of a root economics spectrum related to carbon economy. *New Phytologist*, 210(3), 815–826. <https://doi.org/10.1111/nph.13828>
- Rustad, L. E., Campbell, J. L., Marion, G. M., Norby, R. J., Mitchell, M. J., Hartley, A. E., Cornelissen, J. H. C., Gurevitch, J., Alward, R., Beier, C., Burke, I., Canadell, J., Callaghan, T., Christensen, T. R., Fahnestock, J., Fernandez, I., Harte, J., Hollister, R., John, H., ... Wright, R. (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, 126(4), 543–562. <https://doi.org/10.1007/s004420000544>
- Ryhti, K., Schiestl-Aalto, P., Tang, Y., Rinne-Garmston, K. T., Ding, Y., Pumpanen, J., Biasi, C., Saurer, M., Bäck, J., & Kulmala, L. (2022). Effects of variable temperature and moisture conditions on respiration and nonstructural carbohydrate dynamics of tree roots. *Agricultural and Forest Meteorology*, 323, 109040. <https://doi.org/10.1016/j.agrformet.2022.109040>
- Salazar, A., Rousk, K., Jónsdóttir, I. S., Bellenger, J.-P., & Andr sson,  . S. (2020). Faster nitrogen cycling and more fungal and root biomass in cold ecosystems under experimental warming: A meta-analysis. *Ecology*, 101(2), e02938. <https://doi.org/10.1002/ecy.2938>
- Santoyo, G. (2022). How plants recruit their microbiome? New insights into beneficial interactions. *Journal of Advanced Research*, 40, 45–58. <https://doi.org/10.1016/j.jare.2021.11.020>
- Schindlbacher, A., Rodler, A., Kuffner, M., Kitzler, B., Sessitsch, A., & Zechmeister-Boltenstern, S. (2011). Experimental warming effects on the microbial community of a temperate mountain forest soil. *Soil Biology and Biochemistry*, 43(7), 1417–1425. <https://doi.org/10.1016/j.soilbio.2011.03.005>
- Shaver, G. R., & Chapin III, F. S. (1991). Production: Biomass Relationships and Element Cycling in Contrasting Arctic Vegetation Types. *Ecological Monographs*, 61(1), 1–31. <https://doi.org/10.2307/1942997>
- Siebenk s, A., & Roscher, C. (2016). Functional composition rather than species richness determines root characteristics of experimental grasslands grown at different light and nutrient availability. *Plant and Soil*, 404(1), 399–412. <https://doi.org/10.1007/s11104-016-2853-x>
- Sigurdsson, B. D., Leblans, N. I. W., Dauwe, S., Gudmundsd ttir, E., Gundersen, P., Gunnarsd ttir, G. E., Holmstrup, M., Ilieva-Makulec, K., K tterer, T., Marteinsd ttir, B., Maljanen, M., Oddsd ttir, E. S., Ostonen, I., Pe uelas, J., Poeplau, C., Richter, A., Sigurdsson, P., Van Bodegom, P., Wallander, H., ... Janssens, I. (2016). Geothermal ecosystems as natural climate change experiments: The ForHot research

- site in Iceland as a case study. *Icelandic Agricultural Sciences*, 29(1), 53–71. <https://doi.org/10.16886/IAS.2016.05>
- Smith, A. M., & Zeeman, S. C. (2020). Starch: A Flexible, Adaptable Carbon Store Coupled to Plant Growth. *Annual Review of Plant Biology*, 71(Volume 71, 2020), 217–245. <https://doi.org/10.1146/annurev-arplant-050718-100241>
- Song, H. J., Galgo, S. J. C., Turner, B., Mishra, U., & Kim, P. J. (2025). *Greater Root Biomass Offsets Soil Organic Carbon Loss Under Climate Change in Rice Paddies* (SSRN Scholarly Paper No. 5122814). Social Science Research Network. <https://doi.org/10.2139/ssrn.5122814>
- Soong, J. L., Castanha, C., Hicks Pries, C. E., Ofiti, N., Porras, R. C., Riley, W. J., Schmidt, M. W. I., & Torn, M. S. (2021). Five years of whole-soil warming led to loss of subsoil carbon stocks and increased CO₂ efflux. *Science Advances*, 7(21). <https://doi.org/10.1126/SCIADV.ABD1343>
- Soong, J. L., Fuchslueger, L., Marañón-Jimenez, S., Torn, M. S., Janssens, I. A., Penuelas, J., & Richter, A. (2020). Microbial carbon limitation: The need for integrating microorganisms into our understanding of ecosystem carbon cycling. *Wiley Online Library*, 26(4), 1953–1961. <https://doi.org/10.1111/gcb.14962>
- Sotillo, A., Hardion, L., Chanez, E., Fujiki, K., & Muratet, A. (2024). Plant responses to urban gradients: Extinction, plasticity, adaptation. *Journal of Ecology*, 112(12), 2861–2875. <https://doi.org/10.1111/1365-2745.14427>
- Soussana, J. F., Allard, V., Pilegaard, K., Ambus, P., Amman, C., Campbell, C., Ceschia, E., Clifton-Brown, J., Czobel, S., Domingues, R., Flechard, C., Fuhrer, J., Hensen, A., Horvath, L., Jones, M., Kasper, G., Martin, C., Nagy, Z., Neftel, A., ... Valentini, R. (2007). Full accounting of the greenhouse gas (CO₂, N₂O, CH₄) budget of nine European grassland sites. *Agriculture, Ecosystems & Environment*, 121(1), 121–134. <https://doi.org/10.1016/j.agee.2006.12.022>
- Sui, X., & Zhou, G. (2013). Carbon dynamics of temperate grassland ecosystems in China from 1951 to 2007: An analysis with a process-based biogeochemistry model. *Environmental Earth Sciences*, 68(2), 521–533. <https://doi.org/10.1007/s12665-012-1756-2>
- Sullivan, P. F., Arens, S. J. T., Chimner, R. A., & Welker, J. M. (2008). Temperature and microtopography interact to control carbon cycling in a high arctic fen. *Ecosystems*, 11(1), 61–76. <https://doi.org/10.1007/s10021-007-9107-y>
- Tang, B., Yin, C., Wang, Y., Sun, Y., & Liu, Q. (2016). Positive effects of night warming on physiology of coniferous trees in late growing season: Leaf and root. *Acta Oecologica*, 73, 21–30. <https://doi.org/10.1016/j.actao.2016.02.002>
- Tao, F., Huang, Y., Hungate, B. A., Manzoni, S., Frey, S. D., Schmidt, M. W. I., Reichstein, M., Carvalhais, N., Ciais, P., Jiang, L., Lehmann, J., Wang, Y.-P., Houlton, B. Z., Ahrens, B., Mishra, U., Hugelius, G., Hocking, T. D., Lu, X., Shi, Z., ... Luo, Y. (2023). Microbial carbon use efficiency promotes global soil carbon storage. *Nature*, 618(7967), 981–985. <https://doi.org/10.1038/s41586-023-06042-3>
- Tariq, A., Graciano, C., Sardans, J., Zeng, F., Hughes, A. C., Ahmed, Z., Ullah, A., Ali, S., Gao, Y., & Peñuelas, J. (2024). Plant root mechanisms and their effects on carbon and nutrient accumulation in desert ecosystems under changes in land use and climate. *New Phytologist*, 242(3), 916–934. <https://doi.org/10.1111/nph.19676>
- Tarnocai, C., Canadell, J. G., Schuur, E. a. G., Kuhry, P., Mazhitova, G., & Zimov, S. (2009). Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, 23(2). <https://doi.org/10.1029/2008GB003327>

- ter Braak, C., & Šmilauer, P. (2002). *Canoco reference manual and CanoDraw for Windows user's guide*. 500.
- Tilman, D., & Wedin, D. (1991). Plant Traits and Resource Reduction For Five Grasses Growing on a Nitrogen Gradient. *Ecology*, 72(2), 685–700.
<https://doi.org/10.2307/2937208>
- Tjoelker, M. G., Craine, J. M., Wedin, D., Reich, P. B., Tilman, D., & Tjoelker, M. G. (2005). Linking leaf and root trait syndromes among 39 grassland and savannah species. *Wiley Online Library*, 167(2), 493–508.
<https://doi.org/10.1111/j.1469-8137.2005.01428.x>
- Trocha, L. K., Bułaj, B., Kutczyńska, P., Mucha, J., Rutkowski, P., & Zadworny, M. (2017). The interactive impact of root branch order and soil genetic horizon on root respiration and nitrogen concentration. *Tree Physiology*, 37(8), 1055–1068.
<https://doi.org/10.1093/TREEPHYS/TPX096>
- Truu, M., Ostonen, I., Preem, J.-K., Lõhmus, K., Nõlvak, H., Ligi, T., Rosenvald, K., Parts, K., Kupper, P., & Truu, J. (2017). Elevated Air Humidity Changes Soil Bacterial Community Structure in the Silver Birch Stand. *Frontiers in Microbiology*, 8.
<https://doi.org/10.3389/fmicb.2017.00557>
- Valdés, A., Marteinsdóttir, B., & Ehrlén, J. (2019). A natural heating experiment: Phenotypic and genotypic responses of plant phenology to geothermal soil warming. *Global Change Biology*, 25(3), 954–962. <https://doi.org/10.1111/gcb.14525>
- Verbrugghe, N., Leblans, N. I. W., Sigurdsson, B. D., Vicca, S., Fang, C., Fuchslueger, L., Soong, J. L., Weedon, J. T., Poeplau, C., Ariza-Carricondo, C., Bahn, M., Guenet, B., Gundersen, P., Gunnarsdóttir, G. E., Kätterer, T., Liu, Z., Maljanen, M., Marañón-Jiménez, S., Meeran, K., ... Janssens, I. A. (2022b). Soil carbon loss in warmed subarctic grasslands is rapid and restricted to topsoil. *Biogeosciences*, 19(14), 3381–3393. <https://doi.org/10.5194/bg-19-3381-2022>
- Verbrugghe, N., Meeran, K., Bahn, M., Canarini, A., Fransen, E., Fuchslueger, L., Ingrisch, J., Janssens, I. A., Richter, A., Sigurdsson, B. D., Soong, J. L., & Vicca, S. (2022a). Long-term warming reduced microbial biomass but increased recent plant-derived C in microbes of a subarctic grassland. *Soil Biology and Biochemistry*, 167, 108590. <https://doi.org/10.1016/J.SOILBIO.2022.108590>
- Verbruggen, E., Jansa, J., Hammer, E. C., & Rillig, M. C. (2016). Do arbuscular mycorrhizal fungi stabilize litter-derived carbon in soil? *Journal of Ecology*, 104(1), 261–269. <https://doi.org/10.1111/1365-2745.12496>
- Walker, T. W. N., Janssens, I. A., Weedon, J. T., Sigurdsson, B. D., Richter, A., Peñuelas, J., Leblans, N. I. W., Bahn, M., Bartrons, M., De Jonge, C., Fuchslueger, L., Gargallo-Garriga, A., Gunnarsdóttir, G. E., Marañón-Jiménez, S., Oddsdóttir, E. S., Ostonen, I., Poeplau, C., Prommer, J., Radujković, D., ... Verbruggen, E. (2020). A systemic overreaction to years versus decades of warming in a subarctic grassland ecosystem. *Nature Ecology and Evolution*, 4(1), 101–108.
<https://doi.org/10.1038/s41559-019-1055-3>
- Walker, T. W. N., Kaiser, C., Strasser, F., Herbold, C. W., Leblans, N. I. W., Woebken, D., Janssens, I. A., Sigurdsson, B. D., & Richter, A. (2018). Microbial temperature sensitivity and biomass change explain soil carbon loss with warming. *Nature Climate Change*, 8(10), 885–889. <https://doi.org/10.1038/s41558-018-0259-x>
- Walsh, J. E. (2014). Intensified warming of the Arctic: Causes and impacts on middle latitudes. *Global and Planetary Change*, 117, 52–63.
<https://doi.org/10.1016/j.gloplacha.2014.03.003>

- Wang, P., Limpens, J., Mommer, L., van Ruijven, J., Nauta, A. L., Berendse, F., Schaepman-Strub, G., Blok, D., Maximov, T. C., & 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. *Journal of Ecology*, 105(4), 947–957. <https://doi.org/10.1111/1365-2745.12718>
- Webber, P. J., & May, D. E. (1977). The Magnitude and Distribution of Belowground Plant Structures in the Alpine Tundra of Niwot Ridge, Colorado*. *Arctic and Alpine Research*, 9(2), 157–174. <https://doi.org/10.1080/00040851.1977.12003911>
- Weemstra, M., Mommer, L., Visser, E. J. W., van Ruijven, J., Kuyper, T. W., Mohren, G. M. J., & Sterck, F. J. (2016). Towards a multidimensional root trait framework: A tree root review. *New Phytologist*, 211(4), 1159–1169. <https://doi.org/10.1111/nph.14003>
- White, R. P. (2000). Grassland ecosystems. *World Resources Institute*, 81. https://www.365lewuyou.com/files/d8/s3fs-public/pdf/page_grasslands.pdf
- Wickham, T. (2007). *The ggplot Package License GPL*. <http://had.co.nz/ggplot/>
- Wildova, R., Wild, J., & Herben, T. (2007). *Fine-scale dynamics of rhizomes in a grassland community*.
- Williams, A., Langridge, H., Straathof, A. L., Muhamadali, H., Hollywood, K. A., Goodacre, R., & de Vries, F. T. (2022). Root functional traits explain root exudation rate and composition across a range of grassland species. *Journal of Ecology*, 110(1), 21–33. <https://doi.org/10.1111/1365-2745.13630>
- Xiong, D., Yang, Z., Chen, G., Liu, X., Lin, W., Huang, J., Bowles, F. P., Lin, C., Xie, J., Li, Y., & Yang, Y. (2018). Interactive effects of warming and nitrogen addition on fine root dynamics of a young subtropical plantation. *Soil Biology and Biochemistry*, 123, 180–189. <https://doi.org/10.1016/j.soilbio.2018.05.009>
- Xu, W., Gu, S., Zhao, X. Q., Xiao, J., Tang, Y., Fang, J., Zhang, J., & Jiang, S. (2011). High positive correlation between soil temperature and NDVI from 1982 to 2006 in alpine meadow of the Three-River Source Region on the Qinghai-Tibetan Plateau. *International Journal of Applied Earth Observation and Geoinformation*, 13(4), 528–535. <https://doi.org/10.1016/J.JAG.2011.02.001>
- Yang, Y., Tilman, D., Furey, G., & Lehman, C. (2019). Soil carbon sequestration accelerated by restoration of grassland biodiversity. *Nature Communications*, 10(1), 718. <https://doi.org/10.1038/s41467-019-08636-w>
- Yao, Y., Dai, Q., Gao, R., Yi, X., Wang, Y., & Hu, Z. (2023). Characteristics and factors influencing soil organic carbon composition by vegetation type in spoil heaps. *Frontiers in Plant Science*, 14. <https://doi.org/10.3389/fpls.2023.1240217>
- Yu, L., Zhong, S., Vihma, T., & Sun, B. (2021). Attribution of late summer early autumn Arctic sea ice decline in recent decades. *Npj Climate and Atmospheric Science*, 4(1), 1–14. <https://doi.org/10.1038/s41612-020-00157-4>
- Zeeman, S. C., Smith, S. M., & Smith, A. M. (2004). The breakdown of starch in leaves. *New Phytologist*, 163(2), 247–261. <https://doi.org/10.1111/j.1469-8137.2004.01101.x>
- Zhang, J. (2005). Warming of the arctic ice-ocean system is faster than the global average since the 1960s. *Geophysical Research Letters*, 32(19). <https://doi.org/10.1029/2005GL024216>
- Zhou, P., An, Y., Wang, Z., Du, H., & Huang, B. (2014). Characterization of gene expression associated with drought avoidance and tolerance traits in a perennial grass species. *PLoS ONE*, 9(8). <https://doi.org/10.1371/JOURNAL.PONE.0103611>

SUMMARY

High-latitude northern ecosystems, including subarctic regions, are warming at an unprecedented rate, surpassing the global average. Warming has significant effects on plant growth, phenology, plant community composition and carbon allocation in plant tissues. Given the strong relationship between temperature and plant physiological, phenological, and biogeochemical processes, climate warming is expected to accelerate temperature-dependent processes such as decomposition and mineralisation. These changes could significantly alter carbon (C) dynamics in northern ecosystems.

The grassland biome covers approximately 40% of the Earth's terrestrial surface and stores about one-third of the global soil organic carbon. In northern biomes, such as the Arctic and tundra, a higher proportion of plant biomass is found belowground, highlighting the importance of belowground plant organs in carbon storage in these biomes. However, the effects of soil warming on belowground plant biomass (BPB) dynamics remain poorly understood, particularly in grasslands where BPB consists of functionally distinct organs, such as short-lived fine roots and long-lived rhizomes. Fine roots have high metabolic activity and are responsible for water and nutrient uptake, whereas rhizomes are storage organs that facilitate vegetative propagation. Most previous studies have classified belowground biomass based on diameter thresholds (e.g., fine roots < 2 mm), which does not differentiate between fine roots and rhizomes, limiting our understanding of carbon, nitrogen, and soluble sugar pools in these different biomass types.

Despite the well-established role of microbial activity in carbon cycling, the impact of warming on root-associated microbial communities remains poorly understood. Root-associated microbes may experience a warming effect mediated by plant roots, further influencing their responses. Thus, a comprehensive understanding of plant-microbe interactions under warming conditions is crucial to predict future carbon dynamics shifts accurately. Furthermore, while significant progress has been made in studying aboveground phenology, belowground growth dynamics have received much less attention. The hidden nature of root systems makes studying them challenging, as most methods for assessing root growth are destructive, labour-intensive, and time-consuming. These methodological challenges contribute to the knowledge gap in belowground processes and increase uncertainty in carbon flux predictions, as mismatches between aboveground and belowground phenology have been observed. While warming is known to stimulate root growth in the topsoil, its impact on root growth in the subsoil, where nutrient and moisture conditions differ, remains largely unknown. This doctoral thesis aimed to understand the effects of soil warming on belowground plant biomass, carbon (C), nitrogen (N), and soluble sugar pools in belowground plant biomass, microbial growth, and belowground growth dynamics in subarctic

grasslands. I sought to better understand the contribution of these pools and processes in the C balance of the subarctic's belowground ecosystem as a response to soil warming.

I adopted a functional approach to better understand belowground biomass dynamics and C, N, and soluble sugar pools in biomass, separating fine roots and rhizomes rather than using a conventional < 2 mm diameter classification. With this approach, I sought to better understand the contribution of these pools and processes in the C balance of the subarctic's belowground ecosystem as a response to soil warming. For microbial studies, we advanced beyond community-aggregated measurements to identify active bacterial and archaeal taxa and study how their growth rates are affected by the presence of plant roots. Community-level soluble sugar concentrations and pools provide valuable insights into ecosystem-level responses but do not fully capture the species-specific physiological responses. To address this, I analysed soluble sugars in fine roots and rhizomes of three dominating species- *Anthoxanthum odoratum*, *Equisetum* spp., and *Ranunculus acris*, together with their response to medium- and long-term soil warming. We utilised a non-destructive minirhizotron imaging technique in combination with the automatic root segmentation tool RS_SAG to annotate roots and train a model for automated root detection in the images (Baykalov, 2025). This approach enabled me to study depth-specific root growth responses across seasons with less effort and time. Unlike short-term warming studies, which do not capture long-term adaptations, I utilised geothermal gradients to investigate the effects of warming duration [medium-term warming (MTW; 11–14 years) and long-term warming (LTW; > 60 years)] and magnitude (0–8.4 °C) that allowed us to see responses in long term up to $+ 2$ °C and exceeding $+ 2$ °C (projected increase up to 8.4 °C under the IPCC's RCP 8.5 scenario).

Total belowground plant biomass declined exponentially with increasing T_s under MTW, fine root biomass decreased under both MTW and LTW, and rhizome biomass proportionally increased under LTW. In MTW, the decline in BPB correlated with an increase in fern abundance, indicating a shift in plant functional composition. Our study revealed the complex interplay between soil warming, plant biomass shifts, and microbial community dynamics in subarctic grasslands. Presence of plant roots promoted higher microbial growth rates at ambient temperatures, but this effect diminished with prolonged warming, leading to a shift in plant-microbe interactions from positive to neutral. Long-term warming reduced putative root-associated taxa as fine root biomass declined, indicating a decline in carbon source for microbes.

Contrary to the general hypothesis that rhizomes store more sugars than fine roots, our results indicate that it is not true for forbs such as *R. acris*, where fine roots had higher sugar concentration, highlighting the complexity of belowground carbon allocation among plant functional groups. Soluble sugar concentrations in fine roots of *A. odoratum* increased with soil warming. At the community level, the TSS pool in fine roots declined with warming in MTW due to biomass reduction, whereas in LTW, the decline was attributed to a decrease in

sucrose concentration. These biochemical changes were linked to plant community composition shifts, particularly the reduced abundance of *A. odoratum* under long-term warming.

Furthermore, the C, N, and sugar pools in BPB were significantly lower in MTW compared to LTW grasslands under similar soil warming of $> +2\text{ }^{\circ}\text{C}$, suggesting differences in ecosystem responses to warming over different time scales. The different driving factors for the decline in soluble sugar pools in fine roots in MTW and LTW grassland (biomass in MTW and sugar concentration in LTW) indirectly indicate that plants have undergone physiological and biochemical adaptation in long-warmed soils. It could also indicate that plant community structure has changed with long-term exposure to soil warming, as soluble sugar concentration depends on species. High long-term soil warming influenced root growth in the soil layers. While root growth in the topsoil acclimated to soil warming, increased root length and area in the subsoil suggested a redistribution of biomass, potentially due to changes in nutrient availability, resource acquisition strategies, or shifts in plant community composition towards deep-rooted species.

Conventional biomass categorisations that do not differentiate between fine roots and rhizomes may overlook critical adaptations in response to long-term warming. Understanding these organ-specific responses is essential for predicting the resilience of plant communities under future climate scenarios. The shift in BPB composition and balance of C and N and sugar pools between fine roots and rhizomes suggests that ecosystems undergo structural changes and physiological and biochemical adaptations over time. The increasing proportion of rhizomes in BPB and changes in their chemistry may influence decomposition rates and microbial activity, with implications for soil carbon and nitrogen dynamics. The observed decline in putative root-associated microbial growth further suggests that warming changes plant-microbe interactions, potentially affecting nutrient cycling. Given that long-term adaptation processes occur gradually, short- and medium-term studies may fail to capture the entire trajectory of ecosystem responses to warming. Therefore, future research should prioritise long-term experiments and focus on the turnover rates of fine roots and rhizomes, particularly rhizomes. A deeper understanding of these dynamics will be crucial for predicting how subarctic grasslands and similar high-latitude ecosystems respond to climate warming.

EESTIKEELNE KOKKUVÕTE

Mulla soojenemise mõju subarktiliste rohumaade taimekoosluste maa-alusele osale: muutused juurte, risoomide ja risobioomide dünaamikas

Kliimamuutuste tagajärjel soojenevad põhjapoolsed, suurtel laiuskraadidel asuvad arktilised ja subarktilised ökosüsteemid enneolematult kiiresti. Arktika soojenemine ületab globaalset keskmist ning sellel on märkimisväärne mõju sealsete taimede kasvule, fenoloogiale, taimekoosluste liigilisele koosseisule, aga ka biomassi ning orgaanilise süsiniku jaotusele taimekooslustes- ja kudedes. Arvestades taime füsioloogiliste, fenoloogiliste ning koosluse biogeokeemiliste protsesside tugevat seost temperatuuriga, eeldatakse temperatuurist sõltuvate protsesside kiirenemist. Temperatuuri tõustes suureneb orgaanilise aine produktioon, aga ka suremus ja lagunemine. Need muutused võivad põhjapoolsetes ökosüsteemides oluliselt muuta kogu süsiniku (C) aineringe dünaamikat.

Rohumaad katavad ligikaudu 40% maismaa pinnast ning talletavad ja säilitavad ligikaudu kolmandiku ülemaailmsest mulla orgaanilisest süsinikust. Arktilistel rohumaadel ning tundras kasvavatel taimedel on suurem osa biomassist maa all, mis näitab kui oluline on nende bioomide maa-aluste taimeorganite kasvu dünaamika ja selle muutused nende ökosüsteemide süsinikuringes. Mulla soojenemise mõju kohta taimede maa-aluse biomassi dünaamikale on endiselt vähe teada, eriti rohumaadel, kus maa-alune biomass koosneb funktsionaalselt erinevatest organitest, milleks on enamasti lühiealised peened juured ja pikaalised risoomid. Juured on metaboolselt aktiivsed ja vastutavad vee ja toitainete omastamise eest, samas kui risoomid on maa-alused varred, mis talitlevad vegetatiivse paljunemise ja säilitusorganitena. Enamus varasemaid taimekoosluste maa-alust osa analüüsivaid uuringuid klassifitseerivad taimede maa-alust biomassi läbimõõdu alusel, näiteks peenjuured, mille läbimõõt on alla 2 mm. Selline lähene mine ei tee paraku vahet talituslikult erinevatel peentel juurtel ja risoomidel. Samas ökosüsteemide ainevarud ja nende dünaamika sõltuvad erineva eluea ja funktsiooniga organite käibest. Lisaks võib talituslikult erinevate organite dünaamika peita endas olulist informatsiooni taimekoosluse kohanemise ja kohastumise võime kohta. Mikroobikoosluste suur roll ning olulisus ökosüsteemide aineringetes on hästi teada, ent oluliselt vähem on teada spetsiifiliste mikroobirühmade, sealhulgas näiteks otseselt juurtega assotsieerunud bakterite ja arhede dünaamikast ning keskkonnamuutuste mõjust erinevatele mikroobirühmadele mulla soojenemisel. Juurtega assotsieerunud mikroobirühmad on otseselt kui ka kaudselt mõjutatud mulla soojenemisest, kaudne mõju on vahendatud juurte reaktsioonist mulla soojenemisele. Seega on süsinikuringe muutuste täpsemaks ennustamiseks oluline paremini mõista taimede ja mikroobide interaktsioone kliima soojenemise tingimustes.

Koos ilmastiku muutumise trendidega, näiteks varasema kevad- või pikema sügissoojusega võib täheldada muutusi taimekoosluste fenoloogias. Kui taimede

maapealse osa fenoloogia muutumise jälgimisel ning mõjude analüüsil on tehtud olulisel edusamme, siis taimede maa-aluse fenoloogia ja kasvudünaamika muutuste kohta soojenevas mullas on endiselt väga vähe andmeid. Juurestike varjatud olemus muudab nende kasvu ja talitlemise uurimise keeruliseks, kuna enamus kasutatavaid meetodeid on destruktiivsed ning väga suure töömahu ja ajakuluga. Metodoloogilised ja tehnilised probleemid maa-aluste protsesside uurimisel on otseselt seotud andmete vähesusega ning väga suure ebamäärasusega taimekoosluste maa-aluse osa hindamisel. Lisaks on arvatud, et soojenemisega kaasneb suurem asünkroonsus maapealsete ja maa-aluste fenoloogiliste protsesside vahel. Kuigi üldjoontes mulla soojenemine stimuleerib juurte kasvu, siis muutused mulla vee- ja toitainete režiimis ning mikroobikoosluste dünaamikas võivad soojenemise mõju muuta. Paraku on sellekohaseid teadmisi erinevate ökosüsteemide kohta ikka veel väga vähe.

Käesoleva doktoritöö eesmärk oli mõista kliimamuutustega kaasneva mulla soojenemise mõju taimekoosluste maa-alustele organitele, juurte ja risoomide biomassile ja süsiniku- ja lämmastikuvarule nendes. Eraldi tähelepanu pöörati muutustele subarktiliste rohumaa maa-aluses fenoloogias ning analüüsiti biokeemilisi muutusi juurtes ja risoomides sisalduvates lahustuvate suhkrute varudes (glükoos, fruktoos, sahharoos) lähtuvalt mullasoojenemise kestusest (11 vs >60 aastat kestnud mullasoojenemine). Kuna juured mullas on alati assotsieerunud mikroobikooslustega risosfääris, mis oluliselt mõjutavad juurte kasvu ja arengut, siis analüüsiti mullasoojenemisega kaasnevaid muutusi juurtega assotsieerunud mikroobide kasvudünaamikas nii koosluse kui liigirühma tasandil. Erakordse võimaluse jälgida mullasoojenemise mõju subarktiliste rohumaa taimekoosluste maa-alusele osale andis Islandil 2008. aastal toimunud maavärin, mille tagajärjel avanesid Hveragerdi küla lähistel laiuvate rohumaa all uued geotermaalsed allikad. Muld soojenes lokaalsetel gradientidel 0–8,4 °C ning proovide kogumise hetkeks 2019. aastal oli mullasoojenemine kestnud 11 aastat, mille nimetasime keskmise kestvusega mulla soojenemisega alaks. Sellele proovialale leiti lähiümbrusest võrdluseks sarnase mulla ja taimekooslusega rohumaa, mille muld oli samaväärselt geotermaalselt soojendatud olnud pikaajaliselt ehk üle 60. aasta. Käesolev doktoritöö analüüsib soojenevate rohumaa koosluste ja taimede maa-aluseid protsesse ja võimalikke muutusi subarktiliste bioomide maa-aluses ainerings. Tulemuste analüüsil võeti eraldi arvesse mulla-soojenemise määr ja kestvus, võrreldi taimekoosluste juurte ja risoomide reaktsioone alla +2 °C tõusu ja üle +2 °C tõusu korral, millest viimane vastaks IPCC RCP 8.5 stsenaariumi järgi 8,4-kraadisele temperatuuri tõusule.

Oma doktoritöös kasutasin, erinevalt konventsionaalsest juurestiku peenemat osa diameetripõhiselt (< 2mm) eristavast lähenemisest, funktsionaalset läheneviisi ning jagasin taimekoosluste maa-aluse biomassi talituslikult erinevatesse rühmadesse ning mõõtsin juuri ja risoomi eraldi. Varasemates uuringutes on risoomid ja juured tihtipeale koondatud ühtseks maa-aluseks biomassiks, mis aga varjutab taimekoosluste funktsionaalseid muutusi ja kohanemist mullas. Risoomid mängivad olulist rolli rohttaimede kasvu ja ellujäämise tagamisel rasketes keskkonnaoludes, nad on pikaealisemad ja kasvukeskkonna varieeruvatele

oludele vastupidavamad. Kui juured on lühiealised ja keskkonnamuutuste suhtes haavatavamad, siis risoomid on maa-alused varred ega talitle juurtena, vaid on nii toitainete säilitamise, transpordi kui ka vegetatiivse paljunemise organid. Talitlusel põhineva klassifikatsiooni kasutamisel oli eesmärgiks paremini mõista taimekoosluse maa-aluste organite kohanemist ja kohastumist mulla soojenedes. Mulla ja risosfääri mikroobikoosluste analüüsil vaatasime mikroobikoosluse tasandi dünaamikast kaugemale ning analüüsisime millised bakterid ja arhed pika-ajaliselt soojemas mullas kasvavad ning kuidas taimede juured ja nende kasv erinevatel mullatemperatuuri tasemetel bakterite kasvukiirust mõjutavad.

Lahustuvate suhkrute varu juurtes ja risoomides on taimedele oluline energia-varu ning selle muutumine vastusena keskkonnamuutustele, antud juhul mulla soojenemisele, indikeerib muutusi taimekoosluse juurestike biokeemilistes protsessides. Samas ei pruugi taimekoosluse tasandil määratud lahustuvate suhkrute varu dünaamika väljendada liigispetsiifilisi reaktsioone, pigem võivad vastasuunalised muutused erinevate taimede juurtes muutusi lahustuvate suhkrute varus isegi peita. Seepärast analüüsisin oma töös Islandi subarktiliste rohumaade kolme domineeriva taimeliigi – lõhnava maarjahein (*Anthoxanthum odoratum*), osi (*Equisetum* spp.) ja kibe tulikas (*Ranunculus acris*) juurte ja risoomide lahustuvate suhkrute sisalduse ja varu dünaamikat kahel, erineva kestvusega mulla-soojendusgradiendil.

Juurte fenoloogia ja sesoonsete muutuste jälgimiseks ja analüüsimiseks soojenevatel rohumaadel kasutasime minirisotrone, millega kogusime 2,5 aasta jooksul ligikaudu 27000 pilti kuni 30 cm sügavusest mullakihist. Pildid analüüsisime automaatse segmenteerimise tööriista RS_SAG abil ning koolitasime masinõppel põhineva programmi piltidelt tuvastama juuri ning mõõtma nende pikkust ja pindala. Masinõppel põhineva meetodika kasutamine võimaldas esmakordselt nii ajamahukaid juurte kasvudünaamika analüüse läbi viia ühe doktoritöö raames ning on oluline samm mitte ainult taimekoosluste maa-aluse fenoloogia mõistmiseks, vaid ka oluline meetodiline edasiarendus. Lisaks analüüsisime koostöös teiste uurimisrühmadega juurtega seotud risosfääri- ja mullabakterite ning arhede kasvureaktsiooni mulla pikaajalisele soojenemisele. Juur-risobioom uuringud vajavad kompetentsi nii taimede ökofüsioloogias kui mullamikrobioloogias, mistõttu juurte ja nendega assotsieerunud risosfääris ning mullas elavate mikroobikoosluste dünaamikat käsitlevaid komplekseid analüüse on vähe. Käesolevast tööst analüüsisime juurte vahendatud mõju soojenevas mullas mikroobikooslustele tervikuna, aga ka spetsiifilistele, just juurtega assotsieerunud mikroobirühmadele risosfääris.

Doktoritöö tulemusena selgus, et subarktiliste rohumaade kogu maa-alune biomass vähenes temperatuuri tõustes eksponentsiaalselt 11 aastat soojenenud mullaga rohumaal, aga juurte biomass vähenes nii keskmiselt kui pikaajaliselt soojenenud mullaga rohumaadel. Samas kui üle 60 aasta geotermaalselt soojendatud rohumaal oli maa-aluses biomassis muutunud juurte ja risoomide suhe: risoomide biomass oli proportsionaalselt suurenenud. 11 aastat soojendatud rohumaal korreleerus kogu maa-aluse biomassi vähenemine osjade ohtruse suurene-

misega, mis näitab taimekoosluse koosseisu funktsionaalse muutuse mõju. Käesoleva doktoritöö tulemused näitavad mulla soojenemise, taimede maa-aluse biomassi funktsionaalse nihke ja mikroobikoosluste dünaamika keerulist koosmõju soojenevatel subarktilistel rohumaadel. Taimede juured soodustavad mikroobide suuremat kasvu kontrolltingimustes, samas kui pikaajaline mulla soojenemine muutis taimede ja mullamikroobide koostoime positiivsest neutraalseks. Pikaajalise mulla soojenemise toimet vähenesid juurtega seotud taksonid, mis on seletatav juurte biomassi kui mikroobidele olulise süsinikuallika olulise vähenemisega.

Vastupidiselt üldlevinud teadmisele, et risoomid kui varuorganid sisaldavad võrreldes juurtega alati rohkem suhkruid, ei õnnestunud meil seda kibeda tulika puhul tõestada. Tulika juurte lahustuvate suhkrute sisaldus oli oluliselt kõrgem, kui vastavad suhkrute kontsentratsioonid risoomides. Lõhnava maarjaheina juurte lahustuvate suhkrute kontsentratsioon suurenes koos mulla soojenemisega, samal ajal kui teistel liikidel oli soojenemise mõju tagasihoidlikum. Seega võivad erinevad liigid mulla soojenemisele subarktiliste rohumaade taimekooslustes erinevalt reageerida, mida koosluse tasandil varjutab paljude taimeliikide vastasuunaline muutus.

Taimekoosluste tasandil vähenes keskmise kestvusega mulla soojenemisel kogu lahustuvate suhkrute varu maa-aluses osas ennekõike juurte biomassi vähenemise tõttu. Samas kui pikaajaliselt soojendatud mullaga rohumaadel oli peamine põhjus sahharoosi kontsentratsiooni langus, mis viitab juba biokeemilistele muutustele maa-aluses biomassis. Tõenäoliselt osutab see juba kohastumuslikele muutustele taimekoosluses, mis tekivad pikaajalise soojenemise tagajärjel. Samas võib oma mõju avaldada ka taimekoosluse koosseisu muutus, sest rohkem kui 2-kraadise mullatemperatuuri tõusuga taimeruutudel vähenes oluliselt lõhnava maarjaheina arvukus.

Kokkuvõttes oli subarktiliste rohumaade süsiniku- ja lämmastikuvary, lahustuvate suhkrute varu 11 aastat kestnud ja rohkem kui kahekraadise mulla-soojenemisega aladel oluliselt madalamad võrreldes rohkem kui kuuskümmend aastat soojendatud mullal kasvanud rohumaadega. See viitab soojenemise ajalise kestvuse olulisusele, aga ka aeganõudvatele kohastumisprotsessidele. Lahustuvate suhkrute varu vähenemist määravad tegurid – vähenev juurte biomass keskmise kestvusega mullasoojenemisel ja lahustuvate suhkrute sisaldus juurtes ja risoomides pikaajaliselt soojenenud mullal kasvanud kooslustes näitab kaudselt, et pikaajaliselt soojendatud mullaga rohumaal on maa-alune biomass saanud kohastuda biokeemiliste ja füsioloogiliste protsesside tasandil. Samas võib oluline roll olla ka muutunud liigilisel koosseisul, kuna selgus, et suhkrute kontsentratsioon ja selle dünaamika on liigispetsiifilised, aga liigispetsiifilisi maa-aluse biomassi muutusi me endiselt veel määrata ei suuda. Pikaajalisel mulla soojenemisel taimekoosluse maa-alune biomass taastus, ent proportsionaalne jaotus juurte ja risoomide vahel nihkus risoomide kasuks.

Töö tulemusena selgus, et talituslikult erinevate juurte ja risoomide mitte eristamine taimekoosluste maa-aluses biomassis võib varjutada olulisi keskkonnamuutustega kohanemise mehhanisme. Lühi- ja pikaajalise biomassi nihe

võib olla oluline rohumaakoosluste aineringe muutuste mõistmisel ning olla vajalik kliimastenaariumite ebamäärasuse vähendamisel. Risoomide suurenev osakaal kogu maa-aluses biomassis ja muutused nende keemias võivad mõjutada lagunemiskiirust ja vähendada mikroobide aktiivsust risosfääris ja mullas, mis omakorda mõjutab mulla süsiniku ja lämmastiku dünaamikat. Juurtega assotsieerunud mikroobide kasvu vähenemine viitab sellele, et soojenemine muudab taimede ja mikroobide koostoimeid, mõjutades omakorda toitainete ringlust mullas. Arvestades, et pikka aega nõudvad kohanemis- ja kohastumisprotsessid toimuvad järk-järgult, võivad lühiajalised ja keskmise kestvusega kliimamuutusi simuleerivad uuringud kergesti üle- või alahinnanguid anda. Seetõttu peaksid tulevased uuringud seadma esikohale pika-ajalised katsed ning keskenduma juurte ja risoomide, eriti risoomide käibe. Maa-aluste organite kasvudünaamika sügavam mõistmine on ülioluline, et ennustada, kuidas subarktilised rohumaad ja sarnased, suurtel laiuskraadidel kasvavad ökosüsteemid reageerivad kliima soojenemisele.

ACKNOWLEDGEMENTS

First and foremost, I would like to express my sincere gratitude to my supervisor Ivika Ostonen. Your unwavering support has been the bedrock upon which this thesis stands strong. Your guidance, openness, and availability have been invaluable, both academically and personally. Seeing your passion and dedication, I learned not to hesitate for a moment, to get my hands dirty, endure the rain, wind, and hailstone, and sweat it out in the field all day, digging, sorting, and imaging roots. Your commitment and love towards your work is genuinely inspiring. Special thanks for your support during my maternity leave and throughout the challenges in the visa process while I was navigating my life in a foreign country.

I thank my co-supervisors, Marika Truu and Boris Rewald, for their support throughout my research journey. Although our collaboration was relatively brief, it was a great learning experience. A special thanks to Marika—I vividly remember one of the times we met when she was working with meticulous precision in the lab. I remember asking her how she could be so precise, and she shared a simple yet profound insight: *“When you know what’s important to you, you will make it as precise as possible.”* Over the years, I have internalised this lesson, and it has proven to be true in both my research and personal growth. Thank you for this wisdom. I would also like to thank Jaak Truu for his support during this research period. I want to thank Páll for his support during the experimental setup and sampling. I would also like to thank Heli for her overall support in this journey and for printing countless documents and papers without being annoyed, often at very short notice.

I would like to extend my heartfelt thanks to Maire, whose kindness and warmth made every day a little brighter. From the first day I arrived in office and until today, you continue to greet me with a smile that never fades. Your cheerful “Tere Biplabi!” and “Chao Biplabi!” were small gestures that made a big difference, reminding me that no matter how stressful things got, there was always a moment of kindness waiting for me at the office reception.

A big thank you to my Rootlab colleagues, especially Marili. Our casual conversations about food, movies, plants, and life provided much-needed breaks and helped me get through some of my most difficult writing days. I would also like to thank Arun for his collaboration during this study.

I am incredibly fortunate to have met so many wonderful fellow PhDs from the FutureArctic project. You all are amazing, and I could not have asked for better colleagues. Coline, Dennis, Virginia, and Fabrizzio, you have become more than just friends. Thank you for supporting me like a family and for your kindness and friendship that goes beyond research. Dennis, honestly, a big thanks to you. Thank you for leading that amazing rhizobiome paper, which now also lives as a very important part of my thesis. A big thanks to Pavel, I have genuinely enjoyed working with you.

My deepest thanks go to my best friend, my husband, Bikash. Thank you for being my constant source of strength and motivation. This achievement is as much yours as it is mine. My beautiful daughter Ridhantika, thank you for bringing so much joy and perspective into my life. Thank you for eating well and sleeping well so that I could finish my thesis. I should not forget my parents, sister, and brother, who always wanted me to be happy. I owe so much gratitude to my 90-year-old grandparents, who have eagerly awaited the day I complete this thesis and return home. I would like to thank my father-in-law for his constant encouragement and for his genuine interest in my progress. His good-humoured questions about when I would finally be done were a constant source of both motivation and laughter. I have always felt his support and knowing how proud he is of my work has made me feel seen, appreciated, and encouraged.

My fieldwork in Iceland holds a special place in my heart. It was an experience like no other, demanding yet incredibly rewarding. I was always the slowest as I climbed the valley of Grændalur, trailing behind my colleagues but soaking in every bit of the breathtaking landscape. I still remember pausing often to catch my breath, but in those moments, I could look out at the vast, untouched wilderness stretching endlessly before me. Iceland is even more special to me because I spent long stretches of time there during the COVID pandemic, often in quarantine with Coline, surrounded by nothing but nature and the quiet rhythm of the land. Thanks to our time in Iceland, Coline and I became two anxious buddies—navigating quarantine, the PhD journey, and the endless uncertainties of life. However, those were actually real moments, somehow very peaceful. Thus, Iceland is not just a place I worked, but it is a place I carry within me, a place I will always long to return to.

It feels incredibly serendipitous that I received the call for the interview for this PhD position right as I was backpacking through Eastern Europe and had just arrived in Estonia. Reflecting on my journey, it feels as though I was destined to be here, doing this research while enjoying saunas in the Estonian woods. The joy of living here with my beloved husband and welcoming my beautiful daughter has brought me profound happiness and contentment. For this, I am grateful to Estonia's nature and saunas for providing the positivity and tranquillity that have supported me throughout this research.

This work was supported by European Union's Horizon 2020 framework programme for research and innovation: grant agreement No. 813114, the Estonian Research Council Grant PRG916 and PRG2614 and Center of Excellence for Sustainable Land Use; subproject SLTOM24105 (TK232U3).

PUBLICATIONS

CURRICULUM VITAE

Name: Biplabi Bhattarai
Date of Birth: 25.05.1992
Telephone: 53905166
ORCID: 0000-0003-2199-4537
E-mail: biplabi.bhattarai@ut.ee

Education

2019– PhD student, (sup) Ivika Ostonen-Märtin; Marika Truu; Boris Rewald, University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, University of Tartu
2016–2019 MSc in “Sustainable forests and nature management”, University of Gottingen, Germany and Bangor University, UK (Erasmus Mundus double degree)
2010–2015 BSc in Forestry, Tribhuvan University, Kathmandu, Nepal

Professional Career

2019– University of Tartu, Institute of Ecology and Earth Sciences, Junior research fellow

Research Interest

Belowground ecology of ecosystems, belowground organs of plants – functional partitioning of biomass and carbon between roots and rhizomes, root morphology, root-rhizobiome in soil, image-based analysis of roots, automation of root phenotyping, root-soil microbial interactions

Publications

Bhattarai, Biplabi; Richter, Andreas; Metze, Dennis; Sigurdsson, Bjarni D.; Sigurdsson, Páll; Leblans, Niki; Janssens, Ivan; Ostonen, Ivika (2024). Influence of soil warming magnitude and duration on soluble sugar pool in fine roots and rhizomes of subarctic grasslands: Differences at species and plant community level adaptation. *Plant Stress*, 11, 100406. DOI: 10.1016/j.stress.2024.100406.

Metze, Dennis; Schneckner, Jörg; de Carlan, Coline Le Noir; **Bhattarai, Biplabi**; Verbruggen, Erik; Ostonen, Ivika; Janssens, Ivan A.; Sigurdsson, Bjarni D.; Hausmann, Bela; Kaiser, Christina; Richter, Andreas (2024). Soil warming increases the number of growing bacterial taxa but not their growth rates. *Science Advances*, 10 (8). DOI: 10.1126/sciadv.adk6295.

Söllinger, Andrea; Ahlers, Lauren S; Dahl, Mathilde Borg; Sigurðsson, Páll; de Carlan, Coline Le Noir; **Bhattarai, Biplabi**; Gall, Christoph; Martin, Victoria S; Rottensteiner, Cornelia; Motleleng, Liabo L; Breines, Eva Marie;

- Verbruggen, Erik; Ostonen, Ivika; Sigurdsson, Bjarni D; Richter, Andreas; Tveit, Alexander T (2024). Microorganisms in subarctic soils are depleted of ribosomes under short-, medium-, and long-term warming. *The ISME Journal*, 18 (1), wræ081. DOI: 10.1093/ismejo/wrae081.
- Kharel, Bikash; Rusalepp, Linda; **Bhattarai, Biplabi**; Kaasik, Ants; Kupper, Priit; Lutter, Reimo; Mänd, Pille; Rohula-Okunev, Gristin; Rosenvald, Katrin; Tullus, Arvo (2023). Effects of air humidity and soil moisture on secondary metabolites in the leaves and roots of *Betula pendula* of different competitive status. *Oecologia*, 202, 193–210. DOI: 10.1007/s00442-023-05388-9.
- Bhattarai, B.**; Sigurdsson, B.D.; Sigurdsson, P.; Leblans, N.; Janssens, I.; Meynzer, W.; Devarajan, A.K.; Truu, J.; Truu, M.; Ostonen, I. (2023). Soil warming duration and magnitude affect the dynamics of fine roots and rhizomes and associated C and N pools in subarctic grasslands. *Annals of Botany*, 132 (2), 269–279. DOI: 10.1093/aob/mcad102.

Scholarships and awards

Erasmus Mundus Scholarship 2016-2018 for pursuing MSc in “Sustainable Forest and Nature Management (SUFONAMA).”

Third place at the University of Tartu 3-minutes thesis (3MT) competition, 2022

Other professional activities

- 2022, EGU General Assembly, Austria, Vienna, oral presentation “Soil warming duration and magnitude affects dynamics of fine roots and rhizomes and C and N pools in belowground biomass in subarctic grasslands”.
- 2022, BIOGEOMON 2022, 10th international symposium on Ecosystem Behavior, Tartu, Estonia, poster presentation “Soil warming duration and magnitude affects dynamics of fine roots and rhizomes and related C and N pools in belowground of subarctic grasslands”.
- 2022, New Phytologist next generation scientist 2022, Tartu, Estonia, poster presentation “Soil warming duration and magnitude affect dynamics of fine roots and rhizomes and related C and N pools in belowground of subarctic grasslands”.
- 2022, The FutureArctic/ForHot 2022, Annual Workshop, Reykjavik, Iceland, oral presentation, “Soil warming duration and magnitude affects dynamics of fineroots and rhizomes and related C and N pools, production, turnover and fine root traits in belowground of subarctic grasslands”.
- 2023, EGU General Assembly, Austria, Vienna, poster presentation “Non-structural carbohydrates in fine roots and rhizomes in warmed subarctic grasslands”
- 2023, FutureArctic/FORHOT – 12th formal project meeting 2022, Tartu Estonia, oral presentation “Response of plant belowground organs to soil warming”

ELULOOKIRJELDUS

Nimi: Biplabi Bhattarai
Sünniaeg: 25.05.1992
Telefon: 53905166
ORCID: 0000-0003-2199-4537
E-post: biplabi.bhattarai@ut.ee

Haridustee:

- 2019– doktorantuur, (juhendajad) Ivika Ostonen-Märtn; Marika Truu; Boris Rewald, Loodus- ja täppisteaduste valdkond, Ökoloogia ja maateaduste instituut, Tartu Ülikool
- 2016–2019 magistrantuur “Sustainable forests and nature management”, Göttingeni ülikool, Saksamaa ja Bangori ülikool, Suurbritannia (Erasmus Mundus ühised magistriõppekavad)
- 2010–2015 bakalaureus metsanduse erialal, Tribhuvani ülikool, Katmandu, Nepal

Teenistuskäik

- 2019– Tartu Ülikool, Loodus- ja täppisteaduste valdkond, ökoloogia ja maateaduste instituut, maastikuökoloogia nooremteadur

Uurimisvaldkond

Ökosüsteemide maa-alune ökoloogia, taimede maa-alused organid – biomassi ja süsiniku funktsionaalne jaotumine juurte ja risoomide vahel, juurte morfoloogia, juur-risobioom mullas, juurte pildipõhine analüüs, juurte fenotüüpimise automatiseerimine, juurte ja mulla mikroobide interaktsioonid

Publikatsioonide loetelu

- Bhattarai, Biplabi;** Richter, Andreas; Metze, Dennis; Sigurdsson, Bjarni D.; Sigurdsson, Páll; Leblans, Niki; Janssens, Ivan; Ostonen, Ivika (2024). Influence of soil warming magnitude and duration on soluble sugar pool in fine roots and rhizomes of subarctic grasslands: Differences at species and plant community level adaptation. *Plant Stress*, 11, 100406. DOI: 10.1016/j.stress.2024.100406.
- Metze, Dennis; Schnecker, Jörg; de Carlan, Coline Le Noir; **Bhattarai, Biplabi;** Verbruggen, Erik; Ostonen, Ivika; Janssens, Ivan A.; Sigurdsson, Bjarni D.; Hausmann, Bela; Kaiser, Christina; Richter, Andreas (2024). Soil warming increases the number of growing bacterial taxa but not their growth rates. *Science Advances*, 10 (8). DOI: 10.1126/sciadv.adk6295.
- Söllinger, Andrea; Ahlers, Lauren S; Dahl, Mathilde Borg; Sigurðsson, Páll; de Carlan, Coline Le Noir; **Bhattarai, Biplabi;** Gall, Christoph; Martin,

- Victoria S; Rottensteiner, Cornelia; Motleleng, Liabo L; Breines, Eva Marie; Verbruggen, Erik; Ostonen, Ivika; Sigurdsson, Bjarni D; Richter, Andreas; Tveit, Alexander T (2024). Microorganisms in subarctic soils are depleted of ribosomes under short-, medium-, and long-term warming. *The ISME Journal*, 18 (1), wræ081. DOI: 10.1093/ismejo/wrae081.
- Kharel, Bikash; Rusalepp, Linda; **Bhattarai, Biplabi**; Kaasik, Ants; Kupper, Priit; Lutter, Reimo; Mänd, Pille; Rohula-Okunev, Gristin; Rosenväld, Katrin; Tullus, Arvo (2023). Effects of air humidity and soil moisture on secondary metabolites in the leaves and roots of *Betula pendula* of different competitive status. *Oecologia*, 202, 193–210. DOI: 10.1007/s00442-023-05388-9.
- Bhattarai, B.**; Sigurdsson, B.D.; Sigurdsson, P.; Leblans, N.; Janssens, I.; Meynzer, W.; Devarajan, A.K.; Truu, J.; Truu, M.; Ostonen, I. (2023). Soil warming duration and magnitude affect the dynamics of fine roots and rhizomes and associated C and N pools in subarctic grasslands. *Annals of Botany*, 132 (2), 269–279. DOI: 10.1093/aob/mcad102.

Uurimistoetused ja stipendiumid

Erasmus Mundus stipendium 2016–2018 magistrantuur “Sustainable Forest and Nature Management (SUFONAMA).”

Kolmas koht Tartu Ülikooli konkursil Teadus kolme minutiga, 2022

KonverentsiettekanDED

- 2022, EGU General Assembly, Austria, Viin, suuline ettekanne “Soil warming duration and magnitude affects dynamics of fine roots and rhizomes and C and N pools in belowground biomass in subarctic grasslands”.
- 2022, BIOGEOMON 2022, 10th international symposium on Ecosystem Behavior, Tartu, Eesti, posterettekanne “Soil warming duration and magnitude affects dynamics of fine roots and rhizomes and related C and N pools in belowground of subarctic grasslands”.
- 2022, New Phytologist next generation scientist 2022, Tartu, Eesti, posterettekanne “Soil warming duration and magnitude affect dynamics of fine roots and rhizomes and related C and N pools in belowground of subarctic grasslands”.
- 2022, The FutureArctic/ForHot 2022, Annual Workshop, suuline ettekanne, Reykjavik, Island “Soil warming duration and magnitude affects dynamics of fineroots and rhizomes and related C and N pools, production, turnover and fine root traits in belowground of subarctic grasslands”.
- 2023, EGU General Assembly, Austria, Viin, posterettekanne “Non-structural carbohydrates in fine roots and rhizomes in warmed subarctic grasslands”
- 2023, FutureArctic/FORHOT – 12th formal project meeting 2022, Tartu, Eesti, suuline ettekanne “Response of plant belowground organs to soil warming”

DISSERTATIONES GEOGRAPHICAE UNIVERSITATIS TARTUENSIS

1. **Вийви Руссак.** Солнечная радиация в Тыравере. Тарту, 1991.
2. **Urmäs Peterson.** Studies on Reflectance Factor Dynamics of Forest Communities in Estonia. Tartu, 1993.
3. **Ülo Suursaar.** Soome lahe avaosa ja Eesti rannikumere vee kvaliteedi analüüs. Tartu, 1993.
4. **Kiira Aaviksoo.** Application of Markov Models in Investigation of Vegetation and Land Use Dynamics in Estonian Mire Landscapes. Tartu, 1993.
5. **Kjell Weppling.** On the assessment of feasible liming strategies for acid sulphate waters in Finland. Tartu, 1997.
6. **Hannes Palang.** Landscape changes in Estonia: the past and the future. Tartu, 1998.
7. **Eiki Berg.** Estonia's northeastern periphery in politics: socio-economic and ethnic dimensions. Tartu, 1999.
8. **Valdo Kuusemets.** Nitrogen and phosphorus transformation in riparian buffer zones of agricultural landscapes in Estonia. Tartu, 1999.
9. **Kalev Sepp.** The methodology and applications of agricultural landscape monitoring in Estonia. Tartu, 1999.
10. **Rein Ahas.** Spatial and temporal variability of phenological phases in Estonia. Tartu, 1999.
11. **Эрки Таммиксаар.** Географические аспекты творчества Карла Бэра в 1830–1840 гг. Тарту, 2000.
12. **Garri Raagmaa.** Regional identity and public leaders in regional economic development. Tartu, 2000.
13. **Tiit Tammaru.** Linnastumine ja linnade kasv Eestis nõukogude aastatel. Tartu, 2001.
14. **Tõnu Mauring.** Wastewater treatment wetlands in Estonia: efficiency and landscape analysis. Tartu, 2001.
15. **Ain Kull.** Impact of weather and climatic fluctuations on nutrient flows in rural catchments. Tartu, 2001.
16. **Robert Szava-Kovats.** Assessment of stream sediment contamination by median sum of weighted residuals regression. Tartu, 2001.
17. **Heno Sarv.** Indigenous Europeans east of Moscow. Population and Migration Patterns of the Largest Finno-Ugrian Peoples in Russia from the 18th to the 20th Centuries. Tartu, 2002.
18. **Mart Külvik.** Ecological networks in Estonia — concepts and applications. Tartu, 2002.
19. **Arvo Järvet.** Influence of hydrological factors and human impact on the ecological state of shallow Lake Võrtsjärv in Estonia. Tartu, 2004.
20. **Katrin Pajuste.** Deposition and transformation of air pollutants in coniferous forests. Tartu, 2004.

21. **Helen Sooväli.** *Saaremaa waltz*. Landscape imagery of Saaremaa Island in the 20th century. Tartu, 2004.
22. **Antti Roose.** Optimisation of environmental monitoring network by integrated modelling strategy with geographic information system — an Estonian case. Tartu, 2005.
23. **Anto Aasa.** Changes in phenological time series in Estonia and Central and Eastern Europe 1951–1998. Relationships with air temperature and atmospheric circulation. Tartu, 2005.
24. **Anneli Palo.** Relationships between landscape factors and vegetation site types: case study from Saare county, Estonia. Tartu, 2005.
25. **Mait Sepp.** Influence of atmospheric circulation on environmental variables in Estonia. Tartu, 2005.
26. **Helen Alumäe.** Landscape preferences of local people: considerations for landscape planning in rural areas of Estonia. Tartu, 2006.
27. **Aarne Luud.** Evaluation of moose habitats and forest reclamation in Estonian oil shale mining areas. Tartu, 2006.
28. **Taavi Pae.** Formation of cultural traits in Estonia resulting from historical administrative division. Tartu, 2006.
29. **Anneli Kährik.** Socio-spatial residential segregation in post-socialist cities: the case of Tallinn, Estonia. Tartu, 2006.
30. **Dago Antov.** Road user perception towards road safety in Estonia. Tartu, 2006.
31. **Üllas Ehrlich.** Ecological economics as a tool for resource based nature conservation management in Estonia. Tartu, 2007.
32. **Evelyn Uuemaa.** Indicatory value of landscape metrics for river water quality and landscape pattern. Tartu, 2007.
33. **Raivo Aunap.** The applicability of gis data in detecting and representing changes in landscape: three case studies in Estonia. Tartu, 2007.
34. **Kai Treier.** Trends of air pollutants in precipitation at Estonian monitoring stations. Tartu, 2008.
35. **Kadri Leetmaa.** Residential suburbanisation in the Tallinn metropolitan area. Tartu, 2008.
36. **Mare Remm.** Geographic aspects of enterobiasis in Estonia. Tartu, 2009.
37. **Alar Teemusk.** Temperature and water regime, and runoff water quality of planted roofs. Tartu, 2009.
38. **Kai Kimmel.** Ecosystem services of Estonian wetlands. Tartu, 2009.
39. **Merje Lesta.** Evaluation of regulation functions of rural landscapes for the optimal siting of treatment wetlands and mitigation of greenhouse gas emissions. Tartu, 2009.
40. **Siiri Silm.** The seasonality of social phenomena in Estonia: the location of the population, alcohol consumption and births. Tartu, 2009.
41. **Ene Indermitte.** Exposure to fluorides in drinking water and dental fluorosis risk among the population of Estonia. Tartu, 2010.
42. **Kaido Soosaar.** Greenhouse gas fluxes in rural landscapes of Estonia. Tartu, 2010.

43. **Jaan Pärn.** Landscape factors in material transport from rural catchments in Estonia. Tartu, 2010.
44. **Triin Saue.** Simulated potato crop yield as an indicator of climate variability in Estonia. Tartu, 2011.
45. **Katrin Rosenvald.** Factors affecting EcM roots and rhizosphere in silver birch stands. Tartu, 2011.
46. **Ülle Marksoo.** Long-term unemployment and its regional disparities in Estonia. Tartu, 2011, 163 p.
47. **Hando Hain.** The role of voluntary certification in promoting sustainable natural resource use in transitional economies. Tartu, 2012, 180 p.
48. **Jüri-Ott Salm.** Emission of greenhouse gases CO₂, CH₄, and N₂O from Estonian transitional fens and ombrotrophic bogs: the impact of different land-use practices. Tartu, 2012, 125 p.
49. **Valentina Sagris.** Land Parcel Identification System conceptual model: development of geoinfo community conceptual model. Tartu, 2013, 161 p.
50. **Kristina Sohar.** Oak dendrochronology and climatic signal in Finland and the Baltic States. Tartu, 2013, 129 p.
51. **Riho Marja.** The relationships between farmland birds, land use and landscape structure in Northern Europe. Tartu, 2013, 134 p.
52. **Olle Järv.** Mobile phone based data in human travel behaviour studies: New insights from a longitudinal perspective. Tartu, 2013, 168 p.
53. **Sven-Erik Enno.** Thunderstorm and lightning climatology in the Baltic countries and in northern Europe. Tartu, 2014, 142 p.
54. **Kaupo Mändla.** Southern cyclones in northern Europe and their influence on climate variability. Tartu, 2014, 142 p.
55. **Riina Vaht.** The impact of oil shale mine water on hydrological pathways and regime in northeast Estonia. Tartu, 2014, 111 p.
56. **Jaanus Veemaa.** Reconsidering geography and power: policy ensembles, spatial knowledge, and the quest for consistent imagination. Tartu, 2014, 163 p.
57. **Kristi Anniste.** East-West migration in Europe: The case of Estonia after regaining independence. Tartu, 2014, 151 p.
58. **Piret Pungas-Kohv.** Between maintaining and sustaining heritage in landscape: The examples of Estonian mires and village swings. Tartu, 2015, 210 p.
59. **Mart Reimann.** Formation and assessment of landscape recreational values. Tartu, 2015, 127 p.
60. **Järvi Järveoja.** Fluxes of the greenhouse gases CO₂, CH₄ and N₂O from abandoned peat extraction areas: Impact of bioenergy crop cultivation and peatland restoration. Tartu, 2015, 171 p.
61. **Raili Torga.** The effects of elevated humidity, extreme weather conditions and clear-cut on greenhouse gas emissions in fast growing deciduous forests. Tartu, 2016, 128 p.
62. **Mari Nuga.** Soviet-era summerhouses On homes and planning in post-socialist suburbia. Tartu, 2016, 179 p.

63. **Age Poom.** Spatial aspects of the environmental load of consumption and mobility. Tartu, 2017, 141 p.
64. **Merle Muru.** GIS-based palaeogeographical reconstructions of the Baltic Sea shores in Estonia and adjoining areas during the Stone Age. Tartu, 2017, 132 p.
65. **Ülle Napa.** Heavy metals in Estonian coniferous forests. Tartu, 2017, 129 p.
66. **Liisi Jakobson.** Mutual effects of wind speed, air temperature and sea ice concentration in the Arctic and their teleconnections with climate variability in the eastern Baltic Sea region. Tartu, 2018, 118 p.
67. **Tanel Tamm.** Use of local statistics in remote sensing of grasslands and forests. Tartu, 2018, 106 p.
68. **Enel Pungas.** Differences in Migration Intentions by Ethnicity and Education: The Case of Estonia. Tartu, 2018, 142 p.
69. **Kadi Mägi.** Ethnic residential segregation and integration of the Russian-speaking population in Estonia. Tartu, 2018, 173 p.
70. **Kiira Mõisja.** Thematic accuracy and completeness of topographic maps. Tartu, 2018, 112 p.
71. **Kristiina Kukk.** Understanding the vicious circle of segregation: The role of leisure time activities. Tartu, 2019, 143 p.
72. **Kaie Kriiska.** Variation in annual carbon fluxes affecting the soil organic carbon pool and the dynamics of decomposition in hemiboreal coniferous forests. Tartu, 2019, 146 p.
73. **Pille Metspalu.** The changing role of the planner. Implications of creative pragmatism in Estonian spatial planning. Tartu, 2019, 128 p.
74. **Janika Raun.** Mobile positioning data for tourism destination studies and statistics. Tartu, 2020, 153 p.
75. **Birgit Viru.** Snow cover dynamics and its impact on greenhouse gas fluxes in drained peatlands in Estonia. Tartu, 2020, 123 p.
76. **Iuliia Burdun.** Improving groundwater table monitoring for Northern Hemisphere peatlands using optical and thermal satellite data. Tartu, 2020, 162 p.
77. **Ingmar Pastak.** Gentrification and displacement of long-term residents in post-industrial neighbourhoods of Tallinn. Tartu, 2021, 141 p.
78. **Veronika Mooses.** Towards a more comprehensive understanding of ethnic segregation: activity space and the vicious circle of segregation. Tartu, 2021, 161 p.
79. **Johanna Pirrus.** Contemporary Urban Policies and Planning Measures in Socialist-Era Large Housing Estates. Tartu, 2021, 142 p.
80. **Gert Veber.** Greenhouse gas fluxes in natural and drained peatlands: spatial and temporal dynamics. Tartu, 2021, 210 p.
81. **Anniki Puura.** Relationships between personal social networks and spatial mobility with mobile phone data. Tartu, 2021, 144 p.
82. **Alisa Krasnova.** Greenhouse gas fluxes in hemiboreal forest ecosystems. Tartu, 2022, 185 p.

83. **Tauri Tampuu.** Synthetic Aperture Radar Interferometry as a tool for monitoring the dynamics of peatland surface. Tartu, 2022, 166 p.
84. **Najmeh Mozaffaree Pour.** Urban Expansion in Estonia: Monitoring, Analysis, and Modeling. Tartu, 2022, 169 p.
85. **Bruno Montibeller.** Evaluating human-induced forest degradation in different biomes using spatial analysis of satellite-derived data. Tartu, 2022, 112 p.
86. **Holger Virro.** Geospatial data harmonization and machine learning for large-scale water quality modelling. Tartu, 2022, 138 p.
87. **Azadeh Rezapour.** The impact of climate change on fine root trait responses of deciduous and coniferous trees. Tartu, 2023, 108 p.
88. **Isaac Newton Kwasi Buo.** Multi-scale thermal Remote Sensing, Machine Learning, and Radiative Flux Modeling to Assess Urban Overheating. Tartu, 2023, 116 p.
89. **David Knapp.** The relationship between residential segregation, school segregation and family context. Tartu, 2024, 122 p.
90. **Reti Ranniku.** Impact of environmental conditions and soil microbiome on greenhouse gas fluxes from soil and tree stems in hemiboreal drained peatland forest. Tartu, 2024, 142 pp.
91. **Kalev Koppel.** Advancing urban and agricultural monitoring using Sentinel-1 synthetic aperture radar data. Tartu, 2025, 119 pp.
92. **Sandeep Thayamkottu.** Ecosystem scale modelling of carbon and nitrogen cycles in peatlands. Tartu, 2025, 129 pp.