

Arctic plant-soil interactions

Effects and underlying mechanisms of how vegetation shifts affect soil carbon cycling in permafrost soils

Rica Wegner



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Abstract

The ongoing rise in temperature caused by climate change has already increased the vegetation coverage and altered the vegetation composition at higher latitudes. To date, it is unclear how these changes influence the large carbon stocks in permafrost soils. This PhD thesis focuses on whether a vegetation shift among spruce trees, tussock-forming graminoids, birch, and alder shrubs could affect soil carbon cycling in permafrost soils through plant litter and root exudation. This was achieved by analyzing 1) properties of plant litter, bulk soils and soil organic matter (SOM) fractions, 2) root exudate composition and release rates, 3) concentration-dependent effects of exuded organic acids on soil carbon and nutrient cycling, 4) turnover of photosynthates in different soil horizons.

The results suggest that particularly shifts between alder shrubs and graminoids can affect SOM properties and stability by differences in litter composition, and that biomass production and soil physical properties may also be important contributing factors. Under alder shrubs most carbon was stored as easily degradable particulate organic matter and thus SOM under alder shrubs may be particularly vulnerable to microbial decomposition. The analysis of root exudates showed that Arctic shrubs and graminoids have a distinctly different root exudate metabolome, despite having similar exudation rates of primary metabolites. Therefore, identification of secondary metabolites and their impact on SOM decomposition is required for a better understanding of how plant shifts affect soil carbon cycling in permafrost soils through root exudation. In addition, the comparison of measured root exudation with previous laboratory soil incubations, where root exudates were simulated by e.g. glucose additions, uncovered that in most studies simulated root exudation corresponded to root exudation by living plants of several growing seasons. Comparing the effects of organic acids in soils at such high concentrations with lower and realistic additions revealed that the use of too high concentrations overemphasized soil carbon losses and artificially increased microbial nutrient demand. Furthermore, carbon allocation was plant- and depth-specific with alder shrubs allocating less carbon into O horizons than birch shrubs. Considering temporal and spatial variation in root exudation could therefore improve model predictions on plant-mediated carbon losses.

All in all, this thesis demonstrated that a shift in plant types has the potential to alter soil carbon cycling through plant litter and root exudates but that not all effects will result in soil carbon losses.

Keywords: *rhizosphere priming, permafrost, carbon cycling, Arctic ecosystems, MAOM, root exudates, plant litter, stable isotopes, SOM decomposition.*

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Stockholm
University

Department of Environmental Science

Stockholm University, 106 91 Stockholm

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Cover photo of comparing the tussock-forming graminoid and birch shrub site by Rica Wegner

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The complexity of soils is infinite,
and so too is my curiosity.

Abstract

The ongoing rise in temperature caused by climate change has already increased the vegetation coverage and altered the vegetation composition at higher latitudes. To date, it is unclear how these changes influence the large carbon stocks in permafrost soils. This PhD thesis focuses on whether a vegetation shift among spruce trees, tussock-forming graminoids, birch, and alder shrubs could affect soil carbon cycling in permafrost soils through plant litter and root exudation. This was achieved by analyzing 1) properties of plant litter, bulk soils and soil organic matter (SOM) fractions, 2) root exudate composition and release rates, 3) concentration-dependent effects of exuded organic acids on soil carbon and nutrient cycling, 4) turnover of photosynthates in different soil horizons.

The results suggest that particularly shifts between alder shrubs and graminoids can affect SOM properties and stability by differences in litter composition, and that biomass production and soil physical properties may also be important contributing factors. Under alder shrubs most carbon was stored as easily degradable particulate organic matter and thus SOM under alder shrubs may be particularly vulnerable to microbial decomposition. The analysis of root exudates showed that Arctic shrubs and graminoids have a distinctly different root exudate metabolome, despite having similar exudation rates of primary metabolites. Therefore, identification of secondary metabolites and their impact on SOM decomposition is required for a better understanding of how plant shifts affect soil carbon cycling in permafrost soils through root exudation. In addition, the comparison of measured root exudation with previous laboratory soil incubations, where root exudates were simulated by e.g. glucose additions, uncovered that in most studies simulated root exudation corresponded to root exudation by living plants of several growing seasons. Comparing the effects of organic acids in soils at such high concentrations with lower and realistic additions revealed that the use of too high concentrations overemphasized soil carbon losses and artificially increased microbial nutrient demand. Furthermore, carbon allocation was plant- and depth-specific with alder shrubs allocating less carbon into O horizons than birch shrubs. Considering temporal and spatial variation in root exudation could therefore improve model predictions on plant-mediated carbon losses.

All in all, this thesis demonstrated that a shift in plant types has the potential to alter soil carbon cycling through plant litter and root exudates but that not all effects will result in soil carbon losses.

Sammanfattning

Den långvariga temperaturökningen till följd av klimatförändringarna har redan lett till en ökad växtlighet och en förändring av växtsammansättningen i Arktis. Hur dessa förändringar påverkar Arktis permafrostjordar och deras kollagringskapacitet är däremot fortfarande oklart. Denna doktorsavhandling undersöker hur förändringar i vegetationen mellan gran, starr, björk och al kan påverka kolcykeln genom dött växtmaterial och rotexudat. Följande aspekter undersöktes: 1) egenskaper hos döda växtblad, jordar och fraktioner av organiskt material i jorden, 2) sammansättning och frisättning av rotexudat, 3) koncentrationsberoende effekter av utsöndrade organiska syror på kol- och näringskretsloppet i marken, och 4) omvandling av fotosyntater i olika jordhorisonter.

Resultaten tyder på att särskilt övergångar mellan albuskar och gräsväxter kan påverka egenskaperna hos den organiska jordmassan och dess stabilitet genom skillnader i sammansättningen av det nedfallna lövverket, och att biomassaproduktionen och jordens fysikaliska egenskaper också kan vara viktiga bidragande faktorer. Under alar påträffades mer kol i den lättnedbrytbara partikelfractionen, vilket gör den särskilt känslig för mikrobiell nedbrytning. Analys av rotexudat visade också att sammansättningen skiljer sig avsevärt mellan björk, al och starr, även om utsöndringen av primära växtmetaboliter var liknande. Detta illustrerar att utsöndringen av sekundära växtföreningar, i synnerhet, kan ge insikter i hur vegetationstyper påverkar kolcykeln i Arktisk permafrost. Jämförelsen mellan uppmätta rotutsöndringshastigheter och tidigare laboratorieexperiment, där rotutsöndring i jorden exempelvis simulerades genom tillsats av glukos, visade att rotutsöndring motsvarande flera växtsäsonger av levande växter simulerades i många studier. Vid jämförelse av effekterna av organiska syror i marken vid så höga koncentrationer med lägre och mer realistiska tillsatser framgår att användningen av alltför höga koncentrationer ökar frisättningen av markkol och höjer mikroorganismernas näringsbehov. Resultaten visar dessutom att överföringen av fotosyntetiska produkter är växt- och djupspecifik, där albuskar överförde mindre kol till O-horisonterna än björkbuskar. Att ta hänsyn till tidsmässiga och rumsliga variationer i rotutsöndringen skulle därför kunna förbättra modellprognoserna för växtrelaterade kolförluster.

Sammanfattningsvis visar denna doktorsavhandling att förändringar i växtsammansättningen visserligen kan leda till förändringar i kolcykeln via avdött växtmaterial och rotexudat, men att inte alla effekter nödvändigtvis leder till kolförluster i marken.

Zusammenfassung

Der langanhaltende Anstieg der Temperaturen durch den Klimawandel hat bereits zu einer erhöhten Pflanzenbedeckung sowie zu einer Veränderung der Pflanzenzusammensetzung in der Arktis geführt. Nichtsdestotrotz ist es bis heute unklar, wie sich diese Veränderungen auf die Kohlenstoffspeicher von Permafrostböden auswirken. Diese Doktorarbeit fokussiert sich speziell darauf, inwiefern ein Vegetationswechsel zwischen Fichten, Seggen, Birken und Erlen den Kohlenstoffkreis durch abgestorbenes Pflanzenmaterial und Wurzelexsudation beeinflussen kann. Dafür wurden folgende Aspekte untersucht: 1) Eigenschaften abgestorbener Pflanzenblätter, Böden und Fraktionen der organischen Bodensubstanz, 2) Zusammensetzung und Freisetzung von Wurzelexsudaten 3) Konzentrationsabhängigkeit der Effekte von exsudierten organischen Säuren auf Kohlenstoff- und Stickstoffprozesse, 4) Umsatz von Photosynthaten in unterschiedlichen Bodenhorizonten.

Die Ergebnisse zeigen, dass eine Veränderungen der Pflanzenzusammensetzung insbesondere zwischen Erlen und Seggen Eigenschaften und Stabilität der organischen Bodensubstanz beeinflussen können, aber das auch Biomassenproduktion sowie bodenphysikalische Eigenschaften eine Rolle spielen. Unter Erlen wurde mehr Kohlenstoff in der leichtabbaubaren partikulären Fraktion gefunden, wodurch dieser besonders anfällig ist für mikrobielle Zersetzung. Die Analyse der Wurzelexsudate ergab zudem, dass sich die Zusammensetzung zwischen Birken, Erlen und Seggen stark unterscheidet, auch wenn die Exsudation von primären Pflanzenmetaboliten identisch war. Das verdeutlicht, dass insbesondere die Exsudation von sekundären Pflanzenstoffen Aufschluss darüber geben könnte, wie sich ein Pflanzenwechsel auf den Kohlenstoffkreislauf auswirkt. Der Vergleich von gemessenen Wurzelexsudationsraten mit früheren Laborexperimenten, in denen Wurzelexsudate beispielsweise durch Glukosezugaben im Boden simuliert wurden, zeigte, dass in vielen Studien eine Wurzelexsudation von mehreren Vegetationsperioden simuliert wurde. Bei dem Vergleich der Effekte von organischer Säuren im Boden bei derart hohen Konzentrationen mit niedrigeren und realistischeren Zugaben stellt sich heraus, dass die Anwendung von zu hohen Konzentrationen die Freisetzung von Bodenkohlenstoff erhöht und den mikrobiellen Nährstoffbedarf steigert. Zusätzlich zeigen die Ergebnisse, dass die Verlagerung von Photosynthaten pflanzen- und tiefenspezifisch ist, wobei Erlensträucher weniger Kohlenstoff in O-Horizonte verlagerten als Birkensträucher. Die Berücksichtigung zeitlicher und räumlicher Variationen von Wurzelexsudation könnte daher die Modellvorhersagen für pflanzenbedingte Kohlenstoffverluste verbessern.

Zusammenfassend hat diese Doktorarbeit gezeigt, dass Veränderungen in der Pflanzenzusammensetzung zwar über abgestorbenes Pflanzenmaterial und Wurzelexsudate zu Veränderungen im Kohlenstoffkreislauf führen können, dass jedoch nicht alle Effekte zwangsläufig zu Kohlenstoffverlusten im Boden führen.

List of papers

Paper I

Shrub expansion alters soil organic matter cycling in the low Arctic tundra.
Sauerland, L., **Wegner, R.**, Moise, A., Kohl., A. Gil, J., and Wild, B., *Bio-geochemistry* (168), doi: 10.1007/s10533-025-01294-9, 2025.

Paper II

Back to the roots: Characterizing root exudates of dominant tundra plants to improve the understanding of plant-soil interactions in a changing arctic.
Wegner, R., Plassmann, M., Sauerland, L., Carter, A., Monteux, S., Oburger, E., and Wild, B., *Soil Biology and Biochemistry* (209), 109897, doi: 10.1016/j.soilbio.2025.109897, 2025.

Paper III

Organic acid exudation by expanding Arctic shrubs can increase carbon storage in permafrost soils.
Wegner, R., Sauerland, L., Gaita, S. M., Mikutta, R., Monteux, S., Manzoni, S., Andreas Richer and Wild, B., submitted to *Soil Biology and Biochemistry*.

Paper IV

Belowground transformations of fresh carbon are species-dependent for common plants encroaching the Canadian tundra.
Rijkers, **R.**, **Wegner, R.**, Galery Käser, E. A., Horsten, B., Sauerland, L., Frey, L., and Wild, B., submitted to *Journal of Ecology*.

Contribution to papers

I, Rica Wegner have contributed to the below listed papers as follows:

Paper I

I was extensively involved in the conceptualization, organization and conduction of the field work and independently developed laboratory methods for the manuscript. I assisted the main author with data validation and interpretation. The manuscript was drafted by the main author and I contributed to the writing processes prior to submission.

Paper II

The study was primarily conceptualized by me with support of my main supervisor. I organized and led the field sampling and conducted it together with our research group. I coordinated and carried out method development and laboratory analyses with support of co-authors. I autonomously performed data validation, interpretation and analyses as well as the writing of the first manuscript draft with guidance of my supervisor.

Paper III

The study was primary conceptualized by me with support of my two supervisors. I was extensively involved in the conceptualization, organization and conduction of the field work which was carried out together with our research group. I independently coordinated and executed method development and laboratory analyses with support of co-authors. I autonomously performed data validation, interpretation and analyses as well as the writing of the first manuscript draft with guidance of my supervisor and co-authors.

Paper IV

The study was conceptualized by the main author, me and my main supervisor. I was extensively involved in the conceptualization, organization and conduction of the field work. I assisted the main author with data validation and interpretation. The manuscript was drafted by the main author and I contributed to the writing processes prior to submission.

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1. Introduction

1.1. Arctic plant-soil climate feedbacks

About 13 to 18% of the northern hemisphere are covered with permafrost soils (Zhang et al., 2000) which store twice as much carbon as the atmosphere (Canadell et al., 2021). Higher latitudes are especially affected by global warming as the increase in temperature is four times higher than the global average (Rantanen et al., 2022). The consequent thaw of permafrost exposes previously frozen organic matter to microbial decomposition which releases carbon dioxide (CO₂) and other greenhouse gases. By that, permafrost thaw will induce a positive feedback process accelerating global warming (Schaefer et al., 2014).

Simultaneously, rising temperatures have increased the vegetation cover (Elmendorf et al., 2012) and changed the vegetation composition (Heijmans et al., 2022) in Arctic regions. In particular an increase in woody low and tall growing shrubs like birches and alders, but also of spruce trees, has been observed in the low tundra area (Davis et al., 2021; Fraser et al., 2014; Harsch et al., 2009; Nill et al., 2022). For example, in northwestern Canada near the Arctic Ocean, the coverage in tall shrubs increased about 55% within 33 years (Moffat et al., 2016). However, in regions with high permafrost ice content, shrubs were spatially replaced by graminoids after abrupt permafrost thaw due to an increase in soil moisture (Heijmans et al., 2022). These changes in vegetation types are expected to further intensify with ongoing warming, and predictions suggest that by the end of the century half of the vegetated Arctic will change in its physiognomic class (Pearson et al., 2013).

How a higher plant abundance and a shift of vegetation types impact permafrost carbon stocks are however not well understood. On the one hand, plants can act as a CO₂ sink by fixing atmospheric CO₂ in plant biomass and subsequently transferring carbon as dead plant material into soils (Mekonnen et al., 2018; Mekonnen et al., 2021). On the other hand, plants secrete parts of the photosynthesized carbon as root exudates into the soil which can counteract carbon sequestration (Mekonnen et al., 2021). This is because root exudates contain easily degradable compounds that can stimulate microbial decomposition of soil organic matter (SOM) and thus induce soil carbon losses as CO₂ (Jones et al., 2009; Wild et al., 2014). This process is known as the “rhizosphere priming effect”. Variation in plant carbon uptake (Mekonnen et al., 2018), plant litter decomposability (Vozzo et al., 2025) as well as root exudation between Arctic plant types might lead to different soil

carbon feedbacks under further warming, but are not well explored. Additionally, plants influence soil physical properties, such as soil temperature and moisture, through shading or snow trapping, which could further affect SOM decomposition (Mekonnen et al., 2021). Unresolved plant-specific differences in these complex interactions, and the uncertain magnitude of their carbon sink and source potential, reduce confidence in current climate projections.

1.2. Plant-specific impacts on carbon cycling through root exudation

One focus of this PhD thesis is on achieving a better understanding of rhizosphere priming and whether vegetation shifts among common high-latitude plants, including spruce trees, tussock-forming graminoids, birch and alder shrubs, could affect soil carbon cycling through differences in root exudation. These plant types follow distinct nutrient acquisition strategies which are reflected in their root traits. Spruce trees, birch and alder shrubs have dense root networks with coarse and fine woody roots within the topsoil (Iversen et al., 2015). Together with ectomycorrhizal symbionts, they can explore the soil efficiently for nutrients (Bergmann et al., 2020; Chen et al., 2016). Alder shrubs additionally associate with nitrogen fixing bacteria (Iversen et al., 2015) to fulfil their nutrient demand. By contrast, tussock-forming graminoids do not have dense complex root networks, usually do not build symbioses, but root straight down to the permafrost table where a higher dissolved nitrogen availability occurs (Blume-Werry et al., 2019; Iversen et al., 2015; Keuper et al., 2012). In particular in systems with a generally low nitrogen availability, like the Arctic (Fiencke et al., 2022), rhizosphere priming might support the degradation of nitrogen-rich organic matter and by that might be an important mechanism to support plant growth (Dijkstra et al., 2020; Hicks et al., 2020). Since these plant types follow such distinct nutrient acquisition strategies, it can be hypothesized that they induce different priming responses through differences in root exudate composition and release rates. For instance, through the fixation of atmospheric nitrogen, alder shrubs are less nitrogen-limited and thus their exudates could contain more nitrogen-rich amino acids (Lesuffleur et al., 2007). Amino acids were found in some permafrost soils to cause stronger priming effects than carbohydrates (Na et al., 2022; Wild et al., 2014). Other plants could be more successful in acquiring nitrogen by exuding higher amounts of organic acids. Besides providing labile energy to microorganisms, organic acids contribute abiotically to mineral weathering and release SOM from mineral surfaces (MAOM) (Jilling et al., 2018) which is otherwise not accessible for microbial decomposition (Kleber et al., 2021; Totsche et al., 2018). Since most nitrogen is stored as MAOM in soils (Jilling et al., 2018) targeted breakdown of MAOM through root exudation could alleviate plant and mi-

crobial nitrogen limitation. In addition, plants with different nutrient acquisition strategies might allocate photosynthesized carbon into different plant tissues or exude carbon into different soil horizons depending on their root distribution and soil nutrient availability (Rosling et al., 2004). In particular, insights into depth-specific root exudation are crucial since mineral soil horizons were found to be substantially more susceptible to priming than organic horizons (Wild et al., 2014). Therefore, the overall priming response could be stronger even under lower exudation rates. In order to close these knowledge gaps and to improve model predictions on priming induced carbon losses, such as in Keuper et al. (2020), a fine-scale, plant-specific understanding of plant-soil processes is inevitable. One step in this direction is the characterization and spatial allocation of root exudates.

1.3. Contradictory findings of previous research limit understanding

Data from studies conducted with living Arctic plants in the field are scarce due to the challenges involved by working in remote locations during short growing seasons with plants with slow growth. Therefore, our knowledge on rhizosphere priming largely rests on soil incubation studies adding various concentrations of different primary metabolites to soils (Hicks et al., 2020; Pegoraro et al., 2019; Wild et al., 2014). Substrate additions are usually adjusted to different soil organic or microbial carbon concentrations, but it remains unclear how well this represents field conditions.

So far, studies with artificial substrate additions to permafrost soils contradict each other. For example, during an in-situ experiment, glucose additions into organic horizons beneath birches and tussock-forming graminoids did not induce priming (Lynch et al., 2018), whereas laboratory incubations of organic horizons ranged between negative (Rousk et al., 2016), neutral (Pegoraro et al., 2019; Wild et al., 2014) and positive (Hartley et al., 2010; Hicks et al., 2020; Na et al., 2022) priming effects after glucose additions. A meta-analysis of agricultural plants and soils further reported that gross nitrogen mineralization was only accelerated in experiments conducted with living plants, but not in soil incubations with artificial substrate additions. Rhizosphere priming is a well-known but poorly understood process. To date, it is not possible to accurately predict priming due to the large variability of published research (Huo et al., 2017). These contradicting findings of the past decades highlight that in order to fully understand the mechanisms behind priming, new research directions are needed. So far, it has not been assessed whether the observed discrepancies are related to plant-soil mechanisms or whether they are methodological artefacts. For that, more observational data from living Arctic plants is required.

1.4. Research objectives

The aim of this PhD thesis is to advance current knowledge of how shifts in vegetation among spruce trees, tussock-forming graminoids, birch and alder shrubs influence soil carbon cycling through litter deposition and root exudation. Thereby the generated data is intended to improve the approximation of laboratory experiments to in-situ processes. Research objectives were addressed by combining multiple experimental approaches and laboratory analyses. More specifically, ...

...in Paper I, aboveground litter and SOM properties as well as SOM pools below different Arctic plant types were characterized using density fractionation, elemental analysis and lignin biomarker to understand whether shifts in plant types can affect SOM properties and stability by litter deposition.

...in Paper II, root exudate composition and release rates of different Arctic plants were examined using targeted and non-targeted liquid chromatography - mass spectrometry (LC-MS) to investigate whether plants could induce different priming responses by differences in root exudation. Results were utilized to validate previous attempts of simulating rhizosphere priming in laboratory soil incubations with artificial substrate additions.

...in Paper III, abiotic and biotic effects of exuded organic acids on carbon and nutrient cycling were tested in soil incubations at two concentrations to determine whether the choice of substrate concentration can bias the mechanistic understanding of plant-soil interactions. The research design was adapted to cover substrate concentrations of previous studies and of root exudation rates of living Arctic plants based on Paper II.

...in Paper IV, an in-situ $^{13}\text{CO}_2$ labeling experiment with different plant types was conducted to understand whether plant types differ in carbon allocation and whether the turnover of ^{13}C -photosynthates is plant-specific and differs along the soil profile.

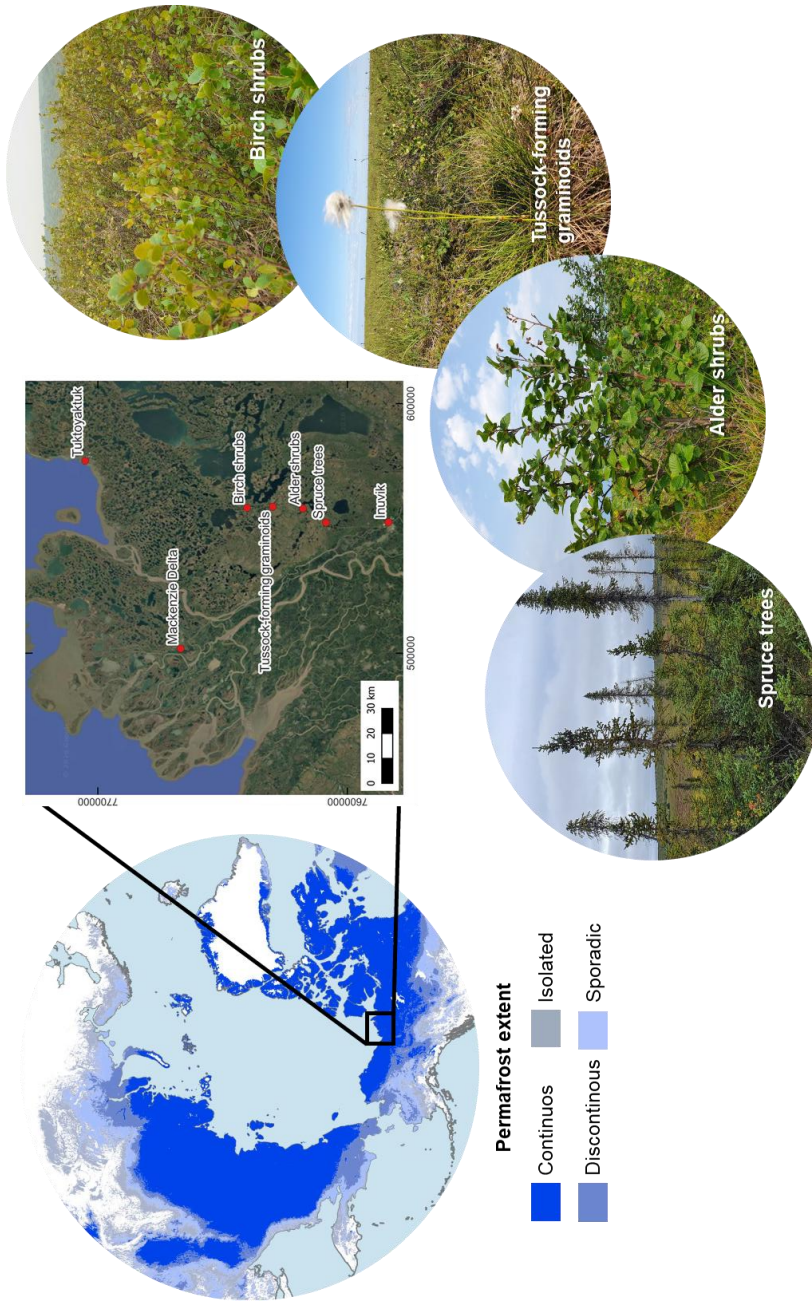


Figure 1: Overview of research sites. Permafrost extent map was created based on Obu et al. (2019). The satellite image originates from Google satellite (XYZ tile, no year). Both maps were created with QGIS (Vers. 3.26.2).

2. Material and methods

2.1. Research area and sites

Fieldwork was conducted within the growing seasons of 2022 and 2023 in northwestern Canada between 25 and 55 km north of Inuvik (68° 19'N and 133° 37'W) on four different sites (Figure 1). The study area was chosen for this thesis project as it is underlain by continuous permafrost and lies within a transition zone of different tundra vegetation types growing on mineral soils. The mean annual air temperature between 1991 and 2020 was between – 11.2 and – 2.8 °C and annual precipitation was on average 238 mm (Government of Canada, 2024). The four selected sites were dominated by the specific plant types: Spruce trees (*Picea mariana*), tussock-forming graminoids (*Eriophorum vaginatum* and *Carex* ssp.), birch shrubs (*Betula glandulosa*) and alder shrubs (*Alnus alnobetula*). Understorey species at all sites were *Vaccinium* ssp., *Rhododendron tomentosum*, *Rubus chamaemorus*, and other graminoids at low and varying abundance. All samples were taken and in-situ experiments were conducted at these sites.

To identify the impact of different plant types on soil carbon cycling and to minimize the influence of varying soil properties, sites and plots with comparable parent material, active layer thickness and topographic position on the top or flanks of ridges were chosen. Soils under all vegetation types were classified as Stagnic Turbic Cryosols (FAO, 2014) (Figure 2) and all sites can be characterized by a medium to well drained hummocky terrain. Soil parent material was described as clayey to loamy textured till with moderate carbonate content. Soil horizons varied in depth but included organic O horizons (Oi, Oe, Oa), followed by consistently small or absent Ah horizons, thick aggregated mineral Bw@ horizons and stagnic coherent mineral Bg@ horizons. Soil texture at all sites and in all mineral horizons was classified as silt loam according to the World Reference Base for Soil Resources (WRB) (FAO, 2014) (Paper I). Nevertheless, soils at the tussock-forming graminoid site were particularly water-saturated, and had in 2022 also partly a lower soil temperature (Paper II).

2.2. Field methods

2.2.1. Soil, plant and plant litter sampling

The same soil samples were used for Paper I, II and III. Soils were sampled in August and September 2022. At each site, soils from different horizons were collected in four spatial replicates by excavating soil profiles at the center of hummock tops. Soil sampling for Paper IV was conducted in 2023 at the same sites but is described separately in chapter 2.2.2. However, all collected soil samples of both years were root picked and frozen before transport to Stockholm. For Paper I, leaf litter from each plant was additionally collected from the soil surface of each profile and dried at 60 °C for 72 h. In addition, for the root exudate collection in Paper II, individual plants were excavated and transported to the field laboratory with intact soil columns attached (Figure 3a). Roots were kept dark during transport, while the aboveground biomass was exposed to sunlight (Figure 3b).

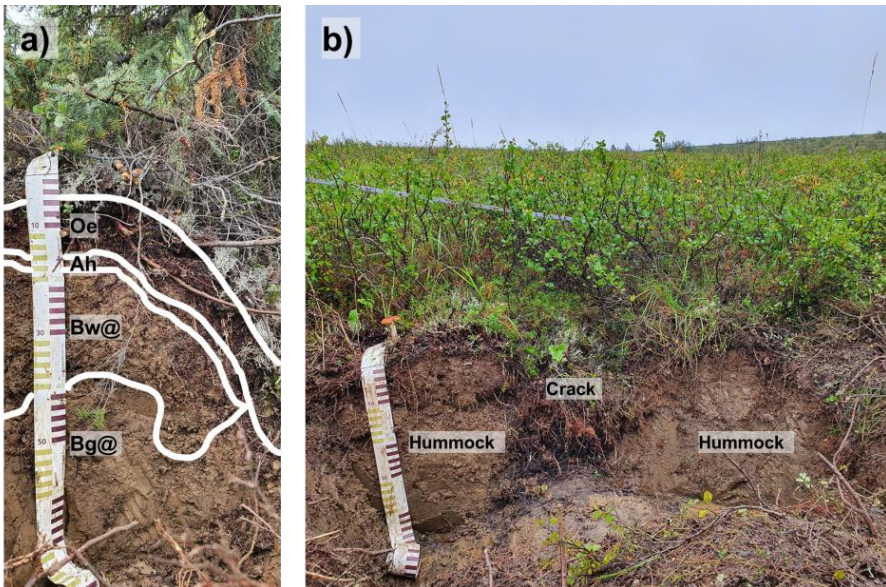


Figure 2: Photos of a Stagnic Turbic Cryosol (left) and a hummock cross section (right).

2.2.2. $^{13}\text{CO}_2$ pulse-chase experiment

In 2023, four replicates of spruce trees, birch and alder shrubs at the corresponding sites were labeled with $^{13}\text{CO}_2$ to trace carbon allocation and compare the turnover of photosynthates of different plants in different soil horizons. A detailed description of the procedure and data processing can be

found in Paper IV. In preparation, 48 h before the labeling understory was removed to avoid uptake of $^{13}\text{CO}_2$ by other plant types. During the labeling, a ventilated transparent polycarbonate-chamber with polypropylene skirt was placed over the plants with a height adjustable frame (Figure 4a). The $^{13}\text{CO}_2$ was injected through air tight septa into the chamber in different intervals over a period of 3 h (Figure 4b). To minimize leakage of inserted $^{13}\text{CO}_2$, the skirt was tightened at the ground surface by covering it with frequently rewetted soil. Leakage was determined by a single propane injection prior to the first $^{13}\text{CO}_2$ addition. Chamber $^{13}\text{CO}_2$ and propane concentrations were monitored during the labeling by frequently taking gas samples which were stored in double wadded glass exetainers (Labco, UK) until further analysis. Photosynthetic uptake was later calculated by the differences in the chamber $^{13}\text{CO}_2$ for given timepoints and was corrected by propane leakage.

To trace down the fate of photosynthesized carbon in different soil depths **1)** soil pore gas, **2)** soil gas surface effluxes and **3)** soils were sampled 1, 5, 10 and 20 days after the labeling event. Samples were taken as follows:

1) Soil pore gas samples were taken at 5, 15, and 25 cm increments with a hollow steel rod (Figure 4c). Depth intervals were chosen to align with the soil horizons O, Bw@ and Bg@, respectively.

2) Surface effluxes from ^{13}C labeled CO_2 were measured by taking gas samples in ca. 50 ppm intervals from dark chambers (Figure 4d). Due to contamination in gas chambers, $^{13}\text{CO}_2$ effluxes could not be estimated by Keeling plots. Instead, $^{13}\text{CO}_2$ effluxes were calculated based on the total CO_2 surface efflux and ^{13}C enrichment of the soil pore gas sample from 25 cm depth. This depth was chosen since it is least affected by atmospheric disturbance. However, there were no significant differences in $\delta^{13}\text{C}$ values of pore space CO_2 with soil depth.

3) To estimate the release of $^{13}\text{CO}_2$ by heterotrophic respiration alone, soils of the different horizons were sampled with a split-tube corer near the plant (Figure 4e) and were later aerobically incubated at 8 °C for 47 days in Stockholm.

Recovered $^{13}\text{CO}_2$ in soil pore gas, surface effluxes and soil incubations were normalized by the amount of $^{13}\text{CO}_2$ photosynthesized.

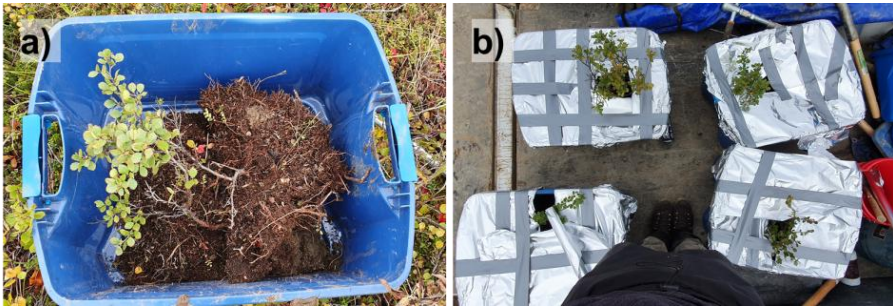


Figure 3: Plant sampling for root exudate collection. a) Collection of plant individuals, b) plant transport.

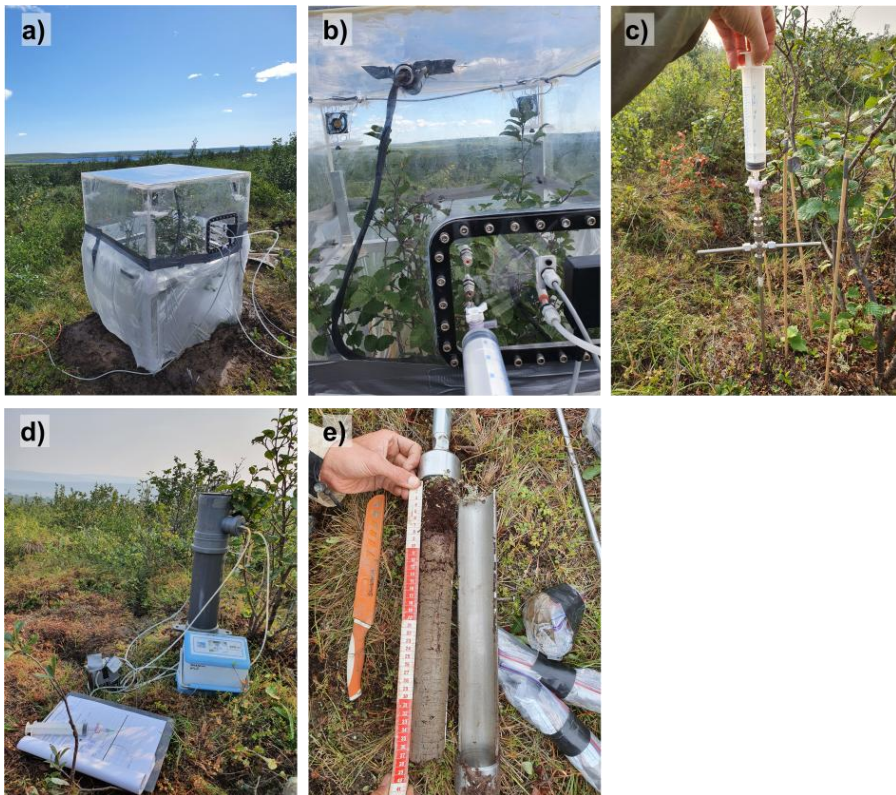


Figure 4: Overview of the $^{13}\text{CO}_2$ pulse-chase experiment in 2023. a) Labeling chamber with tightened skirt, b) injection of $^{13}\text{CO}_2$ into the labeling chamber, c) soil pore gas sampling, d) surface efflux sampling, e) soil sampling with a soil corer.

2.3. Laboratory methods

2.3.1. Soil organic matter fractionation

For Paper I and III, bulk soils from 2022 were fractionated into mineral associated organic matter (MAOM) and particulate organic matter (POM) (Figure 5). In Paper I, soil was fractionated via density fractionation with sodium polytungstate (1.6 g cm^{-3}) (Liebmann et al., 2023). POM was differentiated between free floating POM (fPOM) and in aggregates occluded POM (oPOM). In Paper III, soil was physically fractionated into the mineral fraction by wet sieving ($\leq 20 \mu\text{m}$). Here, only the MAOM fraction was of interest and the POM fraction was discarded. Different fractionation methods were chosen as for Paper III remnants of polytungstate could negatively affect the subsequent soil incubation experiment. During both fractionations, soil was disaggregated using a sonicator (VCX 500, Sonics & Materials inc, USA) at 75% amplitude and a total energy input of 60 J ml^{-1} . Detailed method descriptions can be found in Papers I and III.

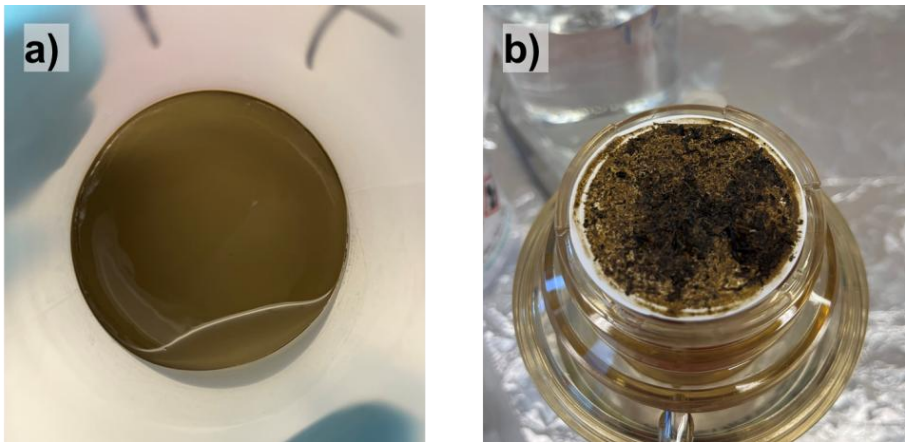


Figure 5: Visual comparison of soil organic matter fractions. a) Mineral associated organic matter (MAOM), b) free floating particulate organic matter (fPOM).

2.3.2. Root exudate sampling

For Paper II, root exudates of field grown tussock-forming graminoids, birch and alder shrubs were collected hydroponically from the described corresponding sites. A detailed method description can be found in Paper II. After plants were transported to the field laboratory, roots were washed free from soil with tap water (Figure 6a). Afterwards belowground tissues were dipped once into ultrapure water and then immersed three times for 5 min

in a sterile Micropur solution to limit transfer of microorganisms and metabolites potentially released upon root damage or cell death into the final sample. The Micropur solution was created by adding 5 mg l⁻¹ Micropur 10.000P (Katadyn Group, Switzerland) (Otxandorena-Ieregi et al., 2024) to ultrapure water at least 24 h before usage. Birch shrubs had rhizomes and graminoids contained dead roots. Removing those would have caused additional damage to the plant, therefore the root tissues were included during the root exudate collection. However, coarse woody roots and dead graminoid roots were not considered during a normalization of root exudation rates per fine-root surface area (FRSA, roots with ≤ 2 mm diameter). This normalization was chosen as coarse woody roots contribute to a lesser extent to root exudation than a normalization by dry weight or total root surface area would emphasize (McDougall and Rovira, 1970; Proctor and He, 2017).

After dipping, the belowground tissues were finally incubated in a fresh Micropur solution for 2 h (Figure 6b). At all times, belowground tissues were protected from light while the aboveground biomass was exposed to sun light. Blanks were produced by incubating the Micropur solution without a plant. The solution of incubated plants and blanks were filtered through 0.2 μm cellulose-acetate syringe filters (OE 66, Whatman, UK) and frozen until further analysis. For the normalization of root exudation rates, belowground tissues were stored in 50% ethanol, later scanned on a flatbed scanner (Epson Expression 10000XL, Seiko Epson, Japan) and FRSA was analyzed with the RhizoVision Explorer software (Seethepalli and York, 2020). Collected root exudates and blanks were analyzed for total organic carbon, organic acids, amino acids and carbohydrates (chapter 2.3.3 and 2.3.7). After the collection of root exudates, leaves and roots were sampled, dried and analyzed for total carbon and nitrogen (chapter 2.3.5).



Figure 6: Root exudate sampling. a) Washing roots with tap water, b) incubating roots in the final Micropur solution.

2.3.3. Liquid chromatography – mass spectrometry (LC-MS) analysis to characterize root exudates

To characterize the collected root exudate solutions from tussock-forming graminoids, birch and alder shrubs, seven different organic acids, 14 amino acids and nine carbohydrates as primary metabolites were measured by targeted LC-MS analyses with a Dionex Ultimate 3000+ LC coupled to a TSQ Quantiva triple quadrupole MS (Thermo Fisher Scientific, USA). Due to the low concentrations of amino acids and carbohydrates, root exudate solutions were concentrated by combining freeze-drying and N₂ evaporation. Matrix effects and compound losses during concentration procedure were determined by spiking additional selected samples with a standard mix. Due to compound specific recoveries, presented rates of different organic acids can be confidently considered as different if they are at least higher or lower by a factor of 1.2. To compare different amino acids or carbohydrate exudation rates a factor of 2.3 must be considered.

In addition, differences in the overall root exudate metabolome were determined with a Dionex Ultimate 3000+ LC coupled to a QExactive HF Orbitrap (Thermo Fisher Scientific, USA). To that end, a full scan at a resolution of 120,000 FWHM (full width at half maximum) @ 200 Da using the same LC methods as for amino acids (positive mode, scan range of 70–400 Da) and carbohydrates (negative mode, scan range of 100–600 Da) was conducted. The data was analyzed with the Compound Discoverer software (Version 3.3.3.200, Thermo Fisher Scientific, USA). Only masses which met defined quality criteria and which had a hit in the KEGG or PlantCyc databases were considered for plant-specific comparison.

Detailed LC-MS settings and full list of all analyzed compounds are given in Paper II.

2.3.4. Concentration-dependent effects of exuded organic acids on soil carbon and nutrients in soil incubations

In Paper III, the concentration dependence of abiotic and biotic organic acid effects on soil carbon and nutrient cycling was investigated by adding two concentrations of organic acids to soil incubations: 1) A high organic acid concentration of 1% of average soil organic carbon (SOC) (6.5 mg C ml⁻¹) which aligns with previous incubation studies (Keiluweit et al., 2015; Wild et al., 2014) and 2) a 18.5-fold lower concentration (0.35 mg C ml⁻¹, 0.054% of average SOC) simulating 7 days of root exudation into the rhizosphere based on the measured organic acid exudation from birch shrubs in Paper II. To that end, a fully ¹³C labeled organic acid mixture of the four organic acids that were most abundant in birch shrub exudates was prepared and consisted of citric (54%), malic (22%), oxalic (16%) and fumaric acid

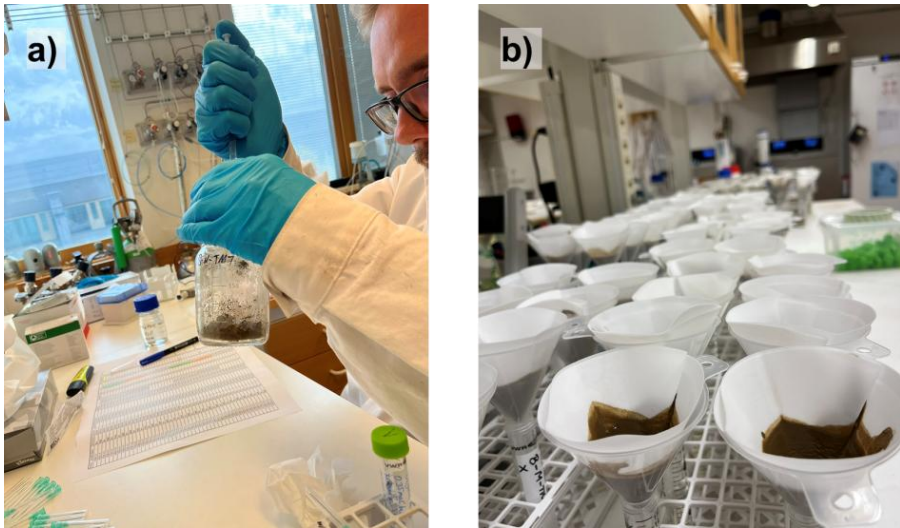


Figure 7: Laboratory work for Paper III. a) Acid addition to soil incubation jars, b) soil extraction for dissolved carbon and nutrient analyses.

(9%) (Merck, Germany). Both acid concentrations were added to (1) sterilized bulk Bw@ and Bg@ horizons, and (2) sterilized and re-inoculated bulk Bw@ and Bg@ horizons, allowing to differentiate pure abiotic effects of organic acids and the combination of abiotic and biotic effects on soils. For a better mechanistic understanding of abiotic mineral substrate-interactions, both acid concentrations were additionally added to (3) sterilized MAOM fractions of Bw@ and Bg@ horizons. Corresponding control treatments were prepared for sterile bulk soils and MAOM fractions as well as for inoculated bulk soils by adding sterile water (Invitrogen, Thermo Fisher Scientific, USA) instead of acids. The inoculum was extracted from a mixture of all four Bw@ horizon replicates. Sterilization was performed using gamma radiation at 50-55 kGy. After a pre-incubation phase of 14 days at 10 °C which enabled establishment of the microbial communities, the ^{13}C labeled organic acid mixture was added (Figure 7a). Over a course of additional 14 days, cumulative SOM respiration and substrate respiration were monitored and dissolved organic carbon and nitrogen, ammonium, nitrate and phosphate were measured before and at the end of the experiment (chapter 2.3.7) (Figure 7b). Acid effects were determined by comparing acid treatments with the control.

In addition, the recovery of added ^{13}C -labeled organic acids in different carbon pools was investigated. Organic acids which were recovered as DOC were classified as weakly bound and dissolved carbon. Incorporation of organic acids into microbial biomass was estimated by assuming a carbon use

efficiency of 0.3, as reported previously for organic acid additions comparable or higher to the high-acid treatments (Brown and Jones, 2024; Jones et al., 2018; Qiao et al., 2019). All carbon which was not respired as CO₂, or recovered as DOC and microbial carbon was considered strongly bound to mineral surfaces (Jones and Edwards, 1998; Jones et al., 2018). To assess whether the addition of organic acids had an overall positive or negative effect on soil carbon, total respired carbon (CO₂SOM and CO₂ from acids) was compared to additionally stabilized or destabilized carbon in inoculated bulk soil treatments.

Furthermore, based on microbial substrate incorporation, the potential stoichiometric microbial nitrogen and phosphate demand was calculated using the global molar soil microbial biomass ratio of 42:6:1 (C:N:P) (Xu et al., 2013). Details are given in Paper III.

Details on the experiment and data evaluation are given in Paper III.

2.3.5. Elementary and isotopic ¹³C composition of gases, soils, plant litter and tissues

Dried soil, SOM fractions, plant litter and tissues were homogenized with a ball mill and analyzed for total carbon and nitrogen with either an EA IsoLink–Delta V Plus system (Thermo Fisher Scientific, USA) or a Flash EA 1112–Delta XP Plus system (Thermo Finnigan, Germany). Carbonate content of soils was tested by comparing soil samples acidified with 1 M HCl with non-acidified samples. Performance details can be found in Papers I, II and III.

Total CO₂ concentrations in Paper III were analyzed with a gas chromatograph equipped with a flame ionization detector (FID) (SRI 8610C, SRI instruments, USA). Propane concentrations were also measured on a gas chromatograph with FID (7890A GC, Agilent Technologies, USA) to account for leakage during the in-situ ¹³CO₂ labeling experiment in Paper IV. Analysis of the isotopic composition of ¹³CO₂ in Papers III and IV was performed with a Picarro 2201i (Eindhoven, Netherlands) coupled to a SAM autosampler (openautosampler.com, Canada). In Paper IV, also total CO₂ concentrations were measured with the Picarro 2201i.

Details on performances and data evaluation can be found in the corresponding papers.

2.3.6. Lignin phenol extraction and analysis from soils and plant litter

For Paper I, lignin phenols were measured as common biomarker for plant residues in bulk soils, SOM fractions and plant litter. A detailed method description is given in Paper I. First, organic matter was digested by

an alkaline copper oxide oxidation using a microwave. Afterwards, phenolic compounds were extracted using ethyl acetate and quantified using a gas chromatograph coupled to a mass spectrometry system (GC-MS, 7820A, Agilent Technologies, USA). Total lignin was calculated by the sum of syringyl, vanillyl and cinnamyl phenols. Additionally, lignin degradation was proxied by the ratio of vanillic acid over vanillin (Vd/Vl).

2.3.7. Measurements of dissolved carbon and nutrients

For Paper II and III, dissolved organic carbon, total dissolved nitrogen as well as ammonium and nitrate of soil samples were determined by soil extraction with 0.5 M K₂SO₄ (ratio 1:4 w/v). Inorganic phosphate from soils was extracted with 0.5 M NaHCO₃ at a pH of 8.5 (ratio 1:15 w/v). In addition, in Paper II, microbial biomass was estimated by chloroform fumigation with subsequent soil extraction of total dissolved carbon. For all soil extractions, soils were shaken for 30 min at 200 RPM and then filtered through 0.8 µm ash less paper filter (Whatman 40, UK). Ammonium (Kandeler and Gerber, 1988) and nitrate (Miranda et al., 2001) were measured photometrically at 660 and 540 nm, respectively. Total dissolved nitrogen was determined by the alkaline persulfate reaction to nitrate with subsequent photometric analysis of nitrate (Hood-Nowotny et al., 2010). Dissolved organic nitrogen could be then calculated by subtracting ammonium and nitrate from total dissolved nitrogen. Soil phosphorus was also measured photometrically at 882 nm (Murphy and Riley, 1962). Dissolved organic carbon was determined in soil extracts and in root exudates with a total organic carbon analyzer (Shimadzu TNM-L, Shimadzu Corporation, Japan) in Paper II. In Paper III, dissolved organic carbon in soil extracts was analyzed together with δ¹³C values using liquid chromatography-isotope ratio mass spectrometry (Thermo Fisher Scientific, USA).

3. Results and discussion

3.1. Plant type can affect SOM properties and stability

Plants contribute to SOM stabilization through several mechanisms. One pathway is through the uptake of CO₂ and its incorporation into plant biomass which enters the soil as dead plant litter. By differences in litter properties, vegetation shifts could affect SOM properties and thereby its decomposability and persistence time (Mekonnen et al., 2021). Whether differences in aboveground litter properties result in differences in SOM properties and stability was investigated in Paper I by characterizing litter and SOM properties as well as SOM pools below spruce trees, tussock-forming graminoids, birch and alder shrubs. The results reveal that in particular alder and graminoids have a distinct influence on SOM properties and stability.

The comparison of bulk soil and MAOM fraction properties with those of aboveground litter at the alder shrub site suggests a direct impact of litter on SOM. The results show that bulk soils, MAOM fractions, aboveground litter (Paper I) below alder as well as fresh alder leaves and roots (Paper II) exhibited the highest nitrogen content across all plant types. Alder shrubs fix atmospheric nitrogen symbiotically and thus litter collected under alder shrubs was most enriched in nitrogen (Nadelhoffer et al., 1996). In addition, soils below alder shrubs contained more POM than soils from other plant types and thus a larger proportion of carbon and nitrogen was stored as POM below alder shrubs. More POM in soils under alder shrubs might be best explained by the larger size of alder shrubs and their consequent larger litter production. Biomass production might be especially favored by the reduced nutrient limitation through symbiotic nitrogen fixation (Bencke, 1970; Street et al., 2018). Since more carbon and nitrogen are stored as POM, which is more accessible for microorganisms and less resistant to temperature-driven decomposition than MAOM, SOM under alder shrubs is likely more vulnerable to microbial decomposition than SOM at the other sites (Gentsch et al., 2018).

The nitrogen content of POM from alder soils, different from the MAOM fraction, was not particularly rich in nitrogen and instead comparable to other plant types. This is surprising since POM directly derives from plant litter. This could suggest that during the degradation of alder litter nitrogen is leached and adsorbed to mineral surfaces or incorporated into microbial biomass and subsequently adsorbed to mineral surfaces as microbial necromass (Whalen et al., 2022). Direct formation pathways of MAOM are not fully understood yet (Whalen et al., 2022). Besides litter composition, greater litter production of alder shrubs might additionally contribute to the

higher nitrogen content in the MAOM fractions below alder shrubs. However, whether alder shrubs contribute on the long-term to stable MAOM formation by increased litter production needs further clarification.

The effect of litter composition on bulk soil properties was also visible at the tussock-forming graminoid site. Graminoid litter was especially characterized by low nitrogen and high lignin content (Figure 8b) and the same pattern was observed in bulk soils and SOM fractions. Higher lignin and simultaneously lower nitrogen content in graminoid litter, can lower SOM decomposability in particular in the early state of decomposition (Bonanomi et al., 2023). Accordingly, bulk soils as well as POM and MAOM fractions from graminoid soils exhibited the highest C/N ratio, indicating lower degradation of SOM. Additionally, in contrast to soils below other plant types, lignin degradation in soils below graminoids did not increase with depth and was further not different between POM and MAOM fractions (Figure 8c). Since soils at the site with tussock-forming graminoids were strongly water-saturated and additionally had the lowest soil temperature, lignin degradation, and likely also of other SOM, were further reduced by lower microbial activity (Dao et al., 2022). High abundance of tussock-forming graminoids, such as *E. vaginatum*, is commonly observed at sites with high water saturation as they are best adapted to these conditions (Heijmans et al., 2022; Iversen et al., 2015). The low degradability of SOM under these conditions could reduce carbon losses under climate warming.

For both sites it is more likely that at lower depths root litter rather than leaf litter affected bulk soils properties. Properties of deeper horizons might be also related to a previous vegetation cover, but similar patterns in the deep and shallow soils suggest rather an influence of current vegetation. Overall, the results indicate that plant litter composition influences bulk soil properties and stability, and that biomass production and soil physical properties may also be important contributing factors. In particular alder shrubs and tussock-forming graminoids have a distinct impact and shifts between these plant types could affect the vulnerability of SOM to decomposition under rising temperatures.

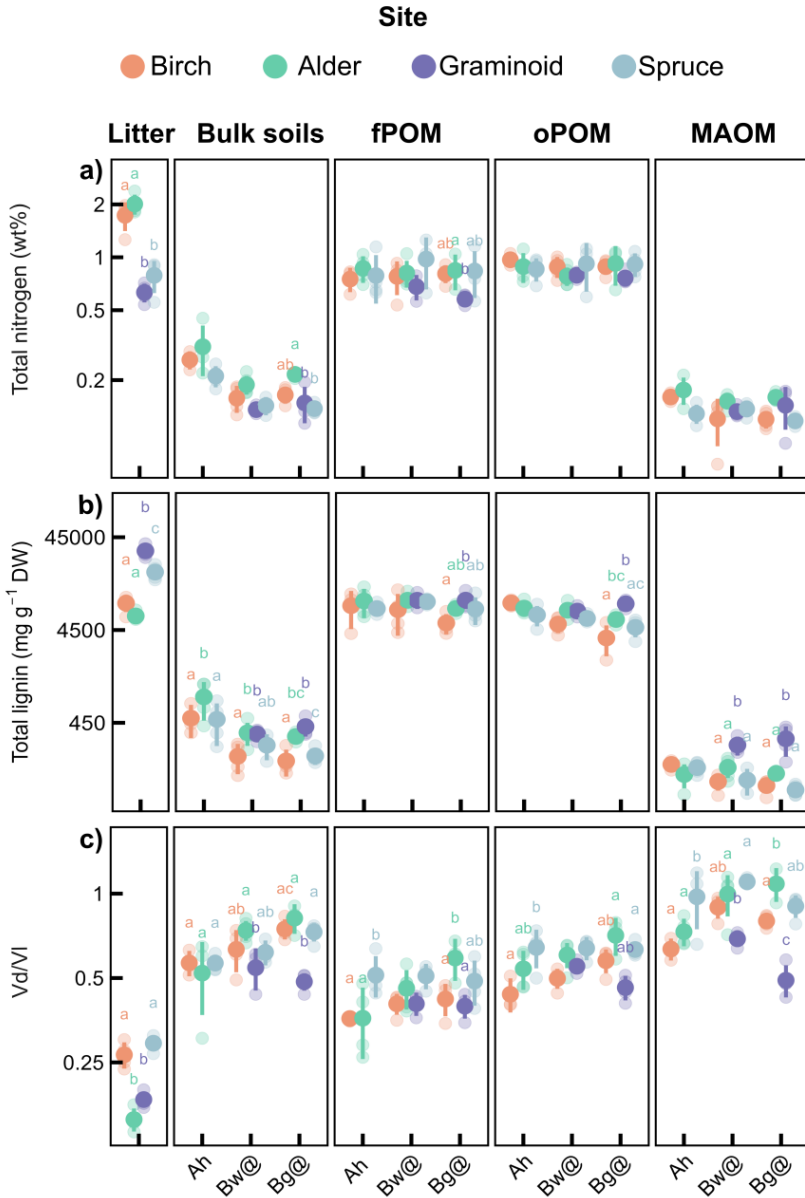


Figure 8: Comparison of aboveground litter properties with properties of bulk soils and soil organic matter fractions (fPOM (free particulate organic matter), oPOM (occluded particulate organic matter) and MAOM (mineral associated organic matter)). The different panel rows show a) total nitrogen, b) total lignin and c) vanillic acid to vanillin ratio as lignin degradation proxy. A higher ratio indicates higher lignin degradation. Data is displayed as mean (circle) with standard deviation (error bars) on a logarithmic scale. Transparent circles visualize the underlying data. Letters indicate statistical differences between plant types ($p < 0.05$). Figure adapted from Paper I.

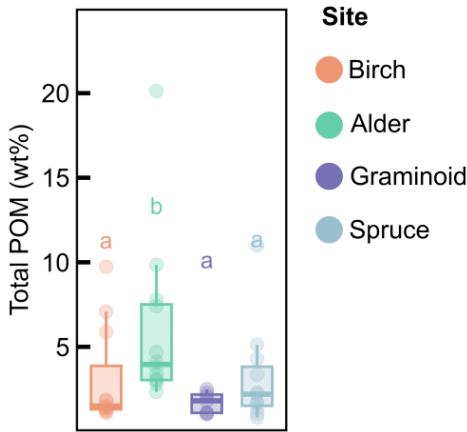


Figure 9: Total particulate organic matter (POM) in soils below different plant horizons of all mineral horizons. Boxplots represent median value as thick line, 25th and 75th percentiles as the box and hinges as 1.5 x interquartile range. In all plots transparent circles represent the underlying data points. Letters indicate statistical differences between plant types ($p < 0.05$).

3.2. Root exudate composition is plant-specific

Parts of the photosynthesized carbon are directly allocated belowground and released as root exudates. Root exudates provide labile carbon to microorganisms and thereby can accelerate microbial SOM decomposition, which in turn enhances soil carbon losses as CO₂ (rhizosphere priming effect). Whether plants exhibit different priming responses due to differences in root exudation is unclear as Arctic plant root exudate composition and release rates are largely unknown. In Paper II, root exudate composition and release rates of naturally grown tussock-forming graminoids, birch and alder shrubs were characterized with LC-MS.

The results show that exudation rates of total organic carbon and most organic acids, amino acids and carbohydrates were not significantly different among the studied plant types when normalized by FRSA (Figure 10), and also not when normalized by total root surface area, root dry-weight or plant individual. Despite these similarities in total carbon and primary metabolite exudation, the non-targeted screening of root exudates revealed that between 80 and 94% (positive and negative screening mode) of the root exudate metabolome was not similar between the plant types and that graminoids exhibited the highest metabolic diversity. We therefore conclude that different nutrient acquisition strategies led to differences in overall root exudate metabolome, but did not affect total organic carbon and primary metabolite exudation for the plants studied here. Consequently, laboratory additions of primary metabolites at varying concentrations or compositions are insufficient to evaluate the effects of changing vegetation distribution on soils. Besides primary metabolites, root exudates contain a large variety of other low molecular weight compounds, like secondary metabolites (Jones et al., 2009). Secondary metabolites can be more plant-specific as they are involved in the attraction of surrounding microorganisms (Koprivova and

Kopriva, 2022; Yu et al., 2021) and plant defense mechanisms (Upadhyay et al., 2025). It can be speculated that the high metabolic diversity in graminoid exudates is a mechanism for a non-symbiotic plant to cope with nutrient limitation by attracting beneficial microorganisms (Hao et al., 2022; Zhong et al., 2020). Such plant-specific changes in microbial activity or community composition could indirectly affect SOM decomposition (Broeckling et al., 2008; Steinauer et al., 2016; Wu et al., 2024; Zhou et al., 2022). However, priming studies are largely limited to primary metabolites and effects of other compounds on rhizosphere priming need more exploration. In addition, root exudation composition could vary with season and growth stage, but this has not been investigated yet for Arctic plants.

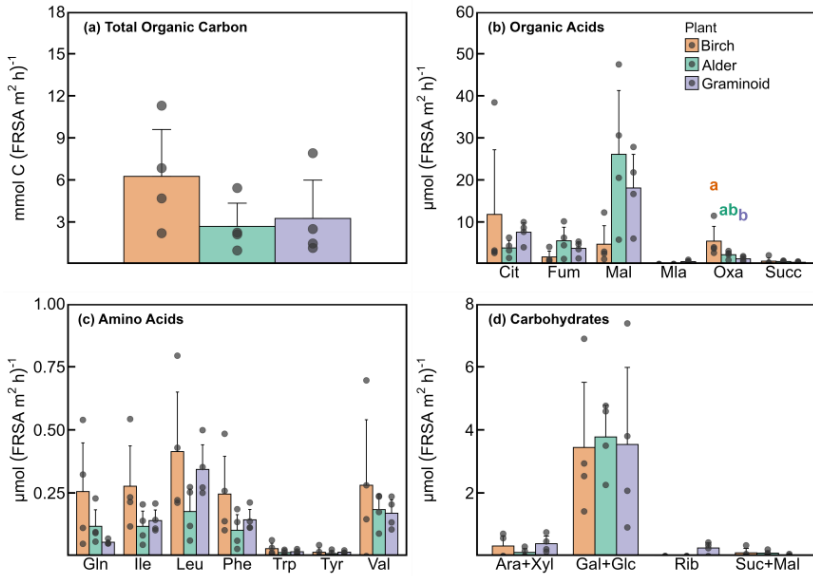


Figure 10: Root exudation rates from tussock-forming graminoids, birch and alder shrubs normalized by fine root surface area (FRSA, roots with a diameter of ≤ 2 mm). Average rates and standard deviations of total organic carbon (a), organic acids (b), amino acids (c) and carbohydrates (d) are shown. Letters indicate significant differences ($p < 0.05$) between plant types. Compounds are abbreviated as follows: Citric acid (Cit), fumaric acid (Fum), malic acid (Mal), malonic acid (Mla), oxalic acid (Oxa), succinic acid (Succ), glutamine (Gln), iso-leucine (Ile), leucine (Leu) phenylalanine (Phe), tryptophan (Trp), tyrosine (Tyr), valine (Val), arabinose and xylose (Ara + Xyl), galactose and glucose (Gal + Glc), ribose (Rib) and sucrose and maltose (Suc + Mal). Figure adapted from Paper II.

3.3. Rhizosphere priming studies could be improved by adjusting substrate additions to observational root exudation rates

The current knowledge on rhizosphere priming largely rests on soil incubation studies that simulate root exudation by adding primary metabolites in varying concentrations to soils. However, how well substrate concentrations applied to Arctic soils simulate root exudation of naturally grown Arctic plants has not been examined yet. In Paper II, in-situ exudation rates of different Arctic plants were compared to substrate additions of previous studies adjusted to 1.2% of SOC (Wild et al., 2014), 100% of microbial carbon (Chen et al., 2019) and 6.2% of soil nitrogen (Wild et al., 2014).

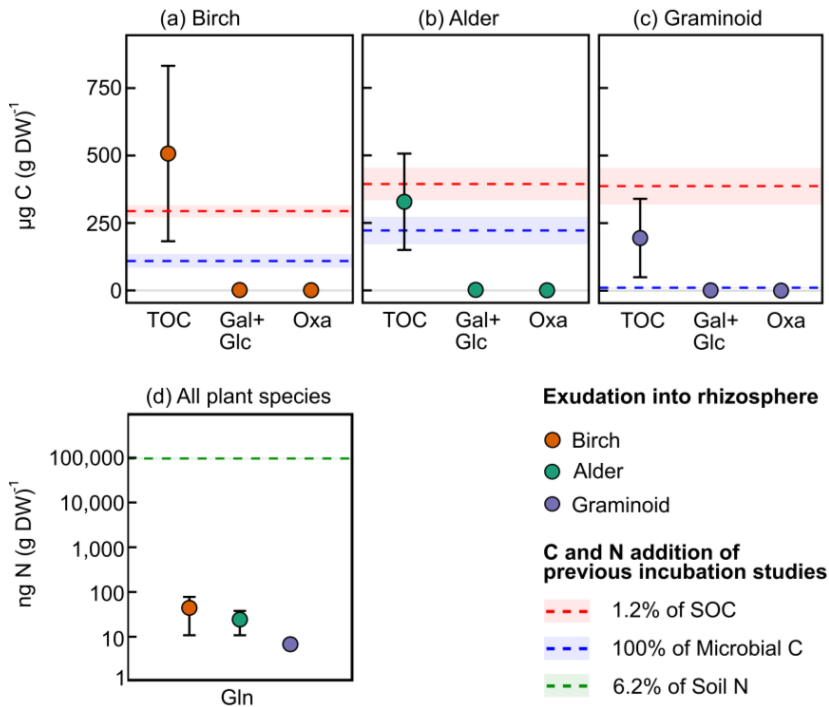


Figure 11: Comparison of carbon (C) and nitrogen (N) exudation into the rhizosphere within 24 h with previously applied substrate concentrations. Root exudation of (a) birch shrubs, (b) alder shrubs and (c) tussock-forming graminoids are shown as average and standard deviation for total organic carbon (TOC), galactose + glucose-C (Gal + Glc), oxalic-C (Oxa) exudation and glutamine-N (Gln). Dashed lines show average \pm standard deviation of previously applied concentrations. For the comparison with previous N additions a logarithmic scale was used. Figure adapted from Paper II.

The comparison showed that previous approaches approximate well total organic carbon exudation from plant roots, but not compound-specific exudation of primary metabolites, which accounted for less than 10% of the

total exuded organic carbon of plant roots. Accordingly, substrate additions as e.g. glucose, oxalic acid or glutamine equivalent to 1.2% of SOC, 100% of microbial carbon or 6.2% of soil nitrogen corresponded to root exudation of several growing seasons, particularly in the case of amino acids (Figure 11). This demonstrates that in previous experiments microorganisms were likely oversaturated with specifically labile substrates. Consequently, it can be questioned whether the current understanding on Arctic rhizosphere priming is biased by the use of highly concentrated substrates. Following up on this finding, we tested in Paper III the concentration dependence of abiotic and biotic effects of organic acids on soil carbon and nutrient cycling. To that end, organic acid concentrations were adapted to previously applied concentrations of 1% of average SOC and a realistically lower concentration which corresponds to 7 days of root exudation into the birch rhizosphere (0.054 % of average SOC, based on Paper II). 1) Abiotic effects were determined in sterilized bulk soils and MAOM fractions, and 2) the interactions between abiotic and biotic effects were determined in sterilized and inoculated bulk soils. Due to the complexity of these effects the results are discussed in three separate sections (1, 2a, 2b).

1) Abiotic effects of organic acids on soil minerals

The results from the sterile incubation show that only highly concentrated acids can significantly decrease the soil pH and release dissolved organic carbon (DOC_{SOM}) and phosphate from the MAOM fractions (Figure 12), while realistically low concentrated acids had no impact on soil pH and phosphate and decreased the extractability of DOC_{SOM} . Acids exhibited similar but more variable effects in sterile bulk soils. For instance, DOC_{SOM} and dissolved organic nitrogen (DON) concentrations increased only in four replicates and decreased in the remaining three (one replicate was excluded due to invalid measurements). Effects of both organic acid concentrations on dissolved nitrogen were inconsistent between MAOM fractions and bulk soils, however, in sterile bulk soils effects of DON at both concentrations resembled DOC_{SOM} patterns. Therefore, changes in dissolved nitrogen in the MAOM fraction were considered to play a minor role in natural settings and only acid effects on dissolved nitrogen in bulk soils are further considered. Unlike DON, ammonium and nitrate were not released by both acid concentrations in sterile bulk soils.

Protons and ligands from organic acids can release carbon and nutrients from mineral surfaces by weakening electrostatic bonds and cation bridges or by direct ligand exchange (Bölscher et al., 2025). At high acid concentrations, protons and ligands occupy sorption sites and increase competition for them, thereby enhancing the release of carbon and nutrients (Bölscher et al., 2025). In contrast, low concentrated acid additions likely did not saturate

sorption sites and thus organic acids were effectively immobilized by sorption to minerals, without triggering significant mobilization of DOC_{SOM} , DON and phosphate (Oburger et al., 2009; Oburger et al., 2011; Yang et al., 2019). Accordingly, a significantly higher proportion of the added organic acids could be recovered by an extraction with 0.5 M K_2SO_4 (considered as labile bound and dissolved carbon) in high-acid than in low-acid treatments (Figure 13). The decrease in DOC_{SOM} and phosphate observed among treatments might be attributed to an increase in the surface area and hence sorption capacity of goethite (Gao et al., 2017). This effect likely also occurred when carbon and phosphate were released, although the magnitude was likely lower than the release from mineral surfaces.

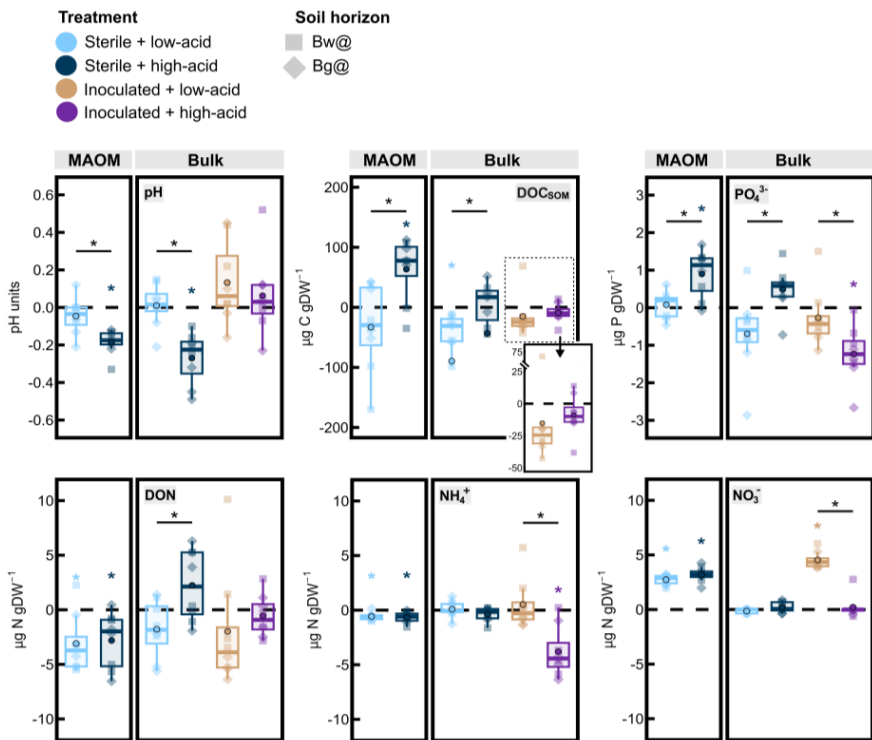


Figure 12: Absolute differences between control and acid treatments in soil pH, soil organic matter derived dissolved organic carbon (DOC_{SOM}), dissolved organic nitrogen (DON), ammonium (NH_4^+), nitrate (NO_3^-) and phosphate (PO_4^{3-}). Boxplots represent median value as thick line, 25th and 75th percentiles as the box and hinges as 1.5 x inter-quartile range. Underlying data points are presented behind the boxplot. Colored asterisks indicate significant differences between treatments and the control, while black lines with asterisks indicate significant differences between the low- and high-acid treatment ($p < 0.05$). Figure adapted from Paper III.

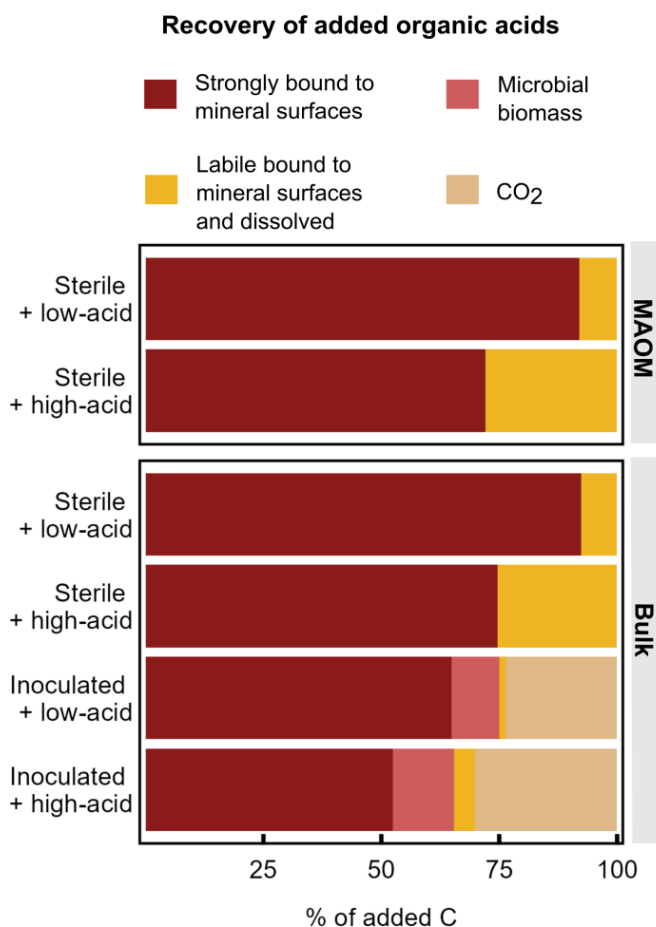


Figure 13: Median recovery of the added organic acids for different treatments as percentage of added carbon (C). Results were scaled to 100% for visualization. Figure from Paper III.

2a) Combined abiotic and biotic effects of organic acids on soil carbon cycling

Overall, priming effects of both acid treatments were negative in inoculated soils, as microorganisms preferred the added acids over SOM. However, in soils with highly concentrated acids, priming effects were highly variable within the first seven days after acid additions as in some replicates relative SOM respiration increased and exceeded control values (Figure 14). This variability was likely related to the variable DOC_{SOM} release, observed in sterile bulk soils with highly concentrated acids, since the exact replicates with enhanced SOM respiration coincided with those where DOC_{SOM} (and also DON) were mobilized. This suggests, that abiotically released DOC_{SOM}

was microbially respired, as supported by a negative correlation between the treatment induced differences in DOC_{SOM} and $\text{CO}_{2\text{SOM}}$. In contrast, in sterilized bulk soils with addition of low concentrated acids, DOC_{SOM} availability was not enhanced and most organic acids were immobilized on mineral surfaces (Figure 13). Consequently, in the corresponding inoculated treatments, the majority of the acids were quickly consumed and SOM respiration returned three days after substrate addition towards control levels (Figure 14). These results suggest, whether organic acids mobilize carbon and nutrients from soil minerals, can vary between soils as it depends on the sorption site capacity and the applied acid concentration.

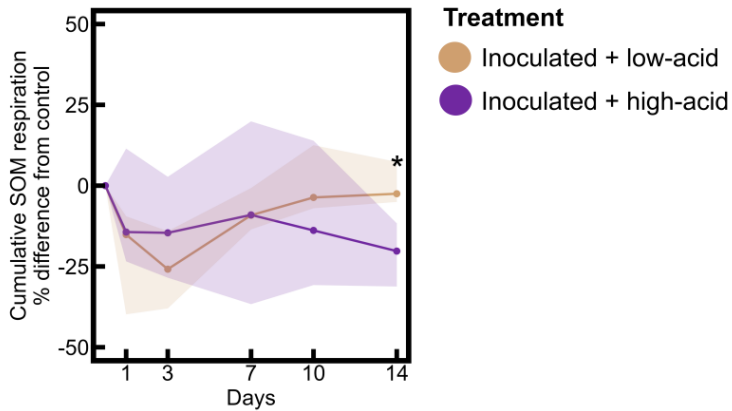


Figure 14: Cumulative (from day 0 onwards) soil organic matter (SOM) derived respiration as percentage from control. Dots indicate median value at the sampling days 1, 3, 7, 10 and 14 after substrate addition. Ribbons indicate interquartile range. Asterisks show significant differences between low-acid and high-acid acid treatments ($p < 0.05$). Data is only presented for the inoculated bulk soil treatments. Figure adapted from Paper III.

However, despite the temporary mineralization of abiotically released DOC_{SOM} in the inoculated soils with highly concentrated acids, both acid additions contributed substantially to carbon stabilization rather than to destabilization of mineral-associated carbon at the end of the experiment. At both concentrations, a greater proportion of organic acid-derived carbon was strongly associated with minerals and microbial biomass than was lost through respiration (Figure 13). In inoculated high-acid treatments the stabilization of organic acids exceeded losses by combined respiration of SOM and organic acids by 13% (Figure 15). When it was additionally considered that both organic acids concentrations lowered SOM-derived carbon in the labile DOC pool and in respiration compared to the control, low concentrated acids stabilized amounts of carbon corresponding to half of the carbon which was lost as CO_2 . Highly concentrated acids even stabilized 28% more

carbon than was lost as CO_2 (Figure 15). The decrease in DOC_{SOM} in the low-acid treatments was most likely driven by abiotic sorption as the decrease in DOC_{SOM} in inoculated soils was of similar magnitude as in corresponding sterile treatments. As discussed above, decrease in DOC_{SOM} in high-acid treatments, was in the beginning lost as $\text{CO}_{2\text{SOM}}$. This effect was however neutralized after 14 days as $\text{CO}_{2\text{SOM}}$ release was lower from soils with highly concentrated acids than from control soils by the end of the incubation (Figure 14). These results reveal that organic acids rather support MAOM formation than destabilization.

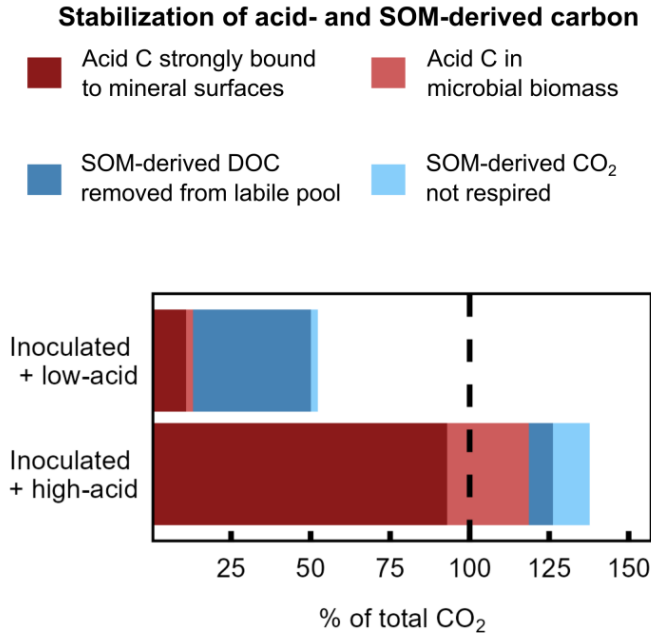


Figure 15: Median of carbon (C) that was additionally stabilized after addition of organic acids compared to the control, expressed as fraction of total carbon lost as carbon dioxide (CO_2 , from soil organic matter (SOM) and added acids). Visualization shows stacked medians and not the median of total stabilized carbon. Figure from Paper III.

2b) Combined abiotic and biotic effects of organic acids on soil nutrient cycling

Similar to the mineralization of DOC_{SOM} , it could be expected that abiotically released DON is microbially transformed and thereby enhances inorganic nitrogen availability in the corresponding inoculated treatments. However, ammonium and phosphate concentration were significantly lowered in inoculated high-acid treatments compared to the control and low-acid treatments. There was further a decline in nitrate towards the detection limit in

the high-acid as well as in the control treatment. It can be suspected, that the high availability of labile carbon increased microbial nutrient demand above biotic production and abiotic release rates. The increased demand likely originated from the microbial need to maintain a constant elemental composition, after enhanced carbon incorporation (Mooshammer et al., 2014). The plausibility of this hypothesis was supported by the close correspondence between the potential stoichiometric demand and the observed decreases in ammonium and phosphate from the control (Table 1, Figure 12). In contrast, low concentrated acids increased nitrate in inoculated soils and concentrations exceeded even the initial concentrations at the beginning of the experiment by 37%. This indicates that in the inoculated low-acid treatments, organic acid addition did not substantially increase the microbial nutrient demand (Table 1), but promoted nitrification. These findings further underline, the concentration dependence of observed effects.

Summarized, all results of Paper III demonstrated that the abiotic and biotic effects of organic acids are concentration-dependent. This highlights the necessity to consider natural plant root exudation in experiments to avoid biases in the understanding of plant-soil mechanisms. Different from the common conception that organic acids support the breakdown of SOM, the results suggest that organic acids increase soil carbon stocks through (1) rapid adsorption of organic acids to mineral surfaces and incorporation into microbial biomass, (2) binding of surrounding SOM to mineral surfaces, and (3) further through promoting plant CO₂ uptake by increasing nitrate availability (DeMarco et al., 2014; Mekonnen et al., 2018). However, organic acids alone do not simulate the complexity of the root exudate metabolome and effects might depend on the provision of other carbon sources. Therefore, results need to be verified with the use of real root exudates.

Table 1: Comparison of the potential microbial carbon (C) uptake and resulting stoichiometric nitrogen (N) and phosphate (P) demand. Table adapted from Paper III.

	Inoculated bulk soil + low-acid			Inoculated bulk soil + high-acid		
	Median	25 th	75 th	Median	25 th	75 th
Respiration of acid-C ($\mu\text{g C g DW}^{-1}$)	3.2	1.9	6.9	71.0	68.2	94.2
Pot. microbial C uptake ($\mu\text{g C g DW}^{-1}$)	1.4	0.8	2.9	30.4	29.2	40.4
Pot. N demand ($\mu\text{g N g DW}^{-1}$)	0.2	0.1	0.5	5.1	4.9	6.7
Pot. P demand ($\mu\text{g P g DW}^{-1}$)	0.1	0.0	0.2	1.9	1.8	2.5

3.4. Carbon allocation differs between plant types and soil depths

In Paper II, shrubs and graminoids did not vary in total carbon exudation despite different nutrient acquisition strategies. However, this paper could not resolve whether plants differ in the proportions of how much photosynthesized carbon is invested into root exudation, or at what depths they are released. In paper IV, a $^{13}\text{CO}_2$ pulse-chase experiment was conducted with subsequent incubation of the labeled and root-picked soils to understand how much of photosynthesized carbon is allocated into different soil depths and how turnover of photosynthates varies. Soil surface respiration, including autotrophic and heterotrophic respiration, of the photosynthesized carbon was determined from in-situ gas measurements. By the incubation of the root-picked soils from different soil depths, heterotrophic respiration was isolated from autotrophic respiration. In this study spruce trees, birch and alder shrubs were included, but labeling of tussock-forming graminoids could not be established.

The results show that a significantly lower fraction (8 to 17-fold) of photosynthesized carbon was recovered in the soil surface efflux below alder shrubs and spruce trees than below birch shrubs (Figure 16a). Depth-specific heterotrophic respiration from soil incubations showed that during the first 10 days of incubation $^{13}\text{CO}_2$ release was higher from O horizons than from mineral B horizons. In addition, significantly less photosynthesized carbon was respired from O horizons below alder shrubs compared with birch shrubs (Figure 16b). Differences in $^{13}\text{CO}_2$ release can be caused by differences in e.g. carbon allocation, exudate adsorption, microbial abundance and microbial carbon use efficiencies. However, the data points towards that the lower recovery of photosynthesized carbon in the soil surface efflux and soil incubations from alder shrubs is related to lower belowground carbon allocation. This is because for all plant types the $\delta^{13}\text{C}$ values of the root-free incubation experiment were consistently exceeded by the $\delta^{13}\text{C}$ values of the in-situ sampled pore gas CO_2 (Figure 17). This indicates that differences in $^{13}\text{CO}_2$ release from the soil surface were primarily derived from autotrophic respiration. In addition, turnover rates of $^{13}\text{CO}_2$ during the 47-day soil incubation were similar among the different plant types. Differences in turnover time would be expected if $^{13}\text{CO}_2$ release is related to soil processes. Whether carbon allocation of alder shrubs is lower in O horizons due to lower root exudation or lower root biomass could not be examined in this study. Nevertheless, $^{13}\text{CO}_2$ release in soil incubations is likely derived from root exudates since litter production is negligible on the time scale of this experiment.

Lower belowground than aboveground carbon allocation of Arctic alder shrubs could be related to their distinct nutrient acquisition strategy and has been suggested by another in-situ pulse-chase labeling study which found lower ^{13}C enrichment in bulk soils below Arctic alder shrubs (Street et al.,

2018). Alder shrubs fix atmospheric nitrogen symbiotically and are likely less depended on nitrogen release by SOM decomposition. Therefore, it could be beneficial to invest more carbon in aboveground biomass than into root biomass and root exudation. This aligns with Paper I where larger biomass production of alder shrubs possibly increased POM in soils. In contrast, higher recovery of photosynthesized carbon in root respiration below birch shrubs suggests greater belowground investments to develop dense root networks and maintain ectomycorrhizal associations that optimize soil nutrient acquisition (Bergmann et al., 2020; Chen et al., 2016).

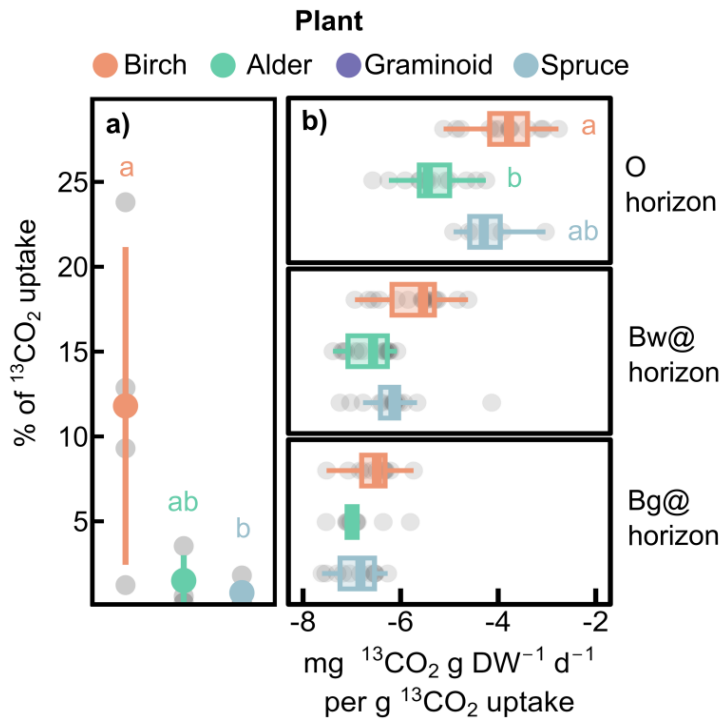


Figure 16: Recovery of photosynthesized $^{13}\text{CO}_2$ in the soil surface efflux and in the incubation. a) The relative amount of $^{13}\text{CO}_2$ tracer taken up during the $^{13}\text{CO}_2$ pulse event that was recovered in the surface effluxes during the chase period as average (circle) and standard deviation (error bars), b) amount of released $^{13}\text{CO}_2$ relative to the amount of $^{13}\text{CO}_2$ tracer taken up from organic (O) and mineral soil horizons (Bw@ and Bg@) during the first 10 days of soil incubation across all timepoints after the $^{13}\text{CO}_2$ pulse on log10-scale. Boxplots represent median value as thick line, 25th and 75th percentiles as the box and hinges as 1.5x interquartile range. In all plots grey circles represent all data points. Letters indicate statistical differences between plant types ($p < 0.05$). Figure adapted from Paper IV.

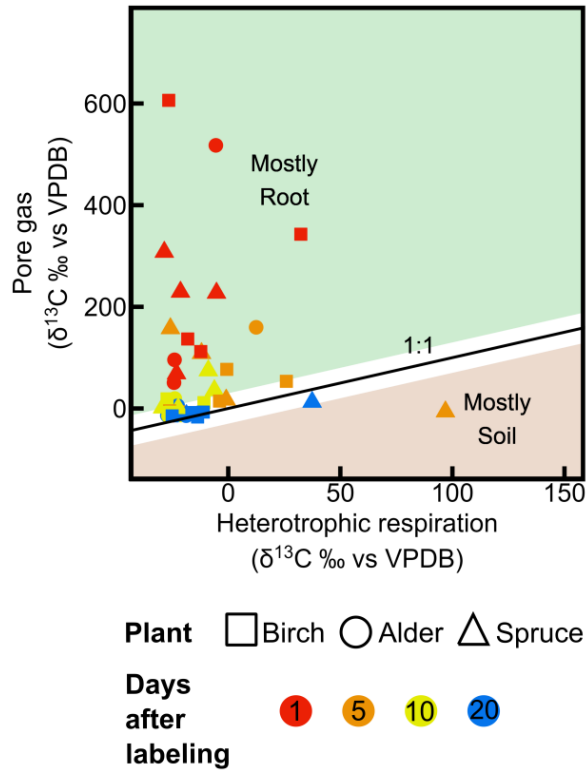


Figure 17: Comparison of $\delta^{13}\text{C}$ (vs VPDB) between gas samples from pore space gas at 25 cm and initial respiration of incubations from Bw@ horizons. Figure adapted from paper IV.

Carbon exudation of Paper II was similar among shrubs and graminoids when normalized per root surface area, root dry-weight or plant individual, despite their distinct nutrient acquisition strategies. Although the two studies differ in methodology and spatial resolution, the findings may suggest that root exudation into different soil depths depends on rooting density and may also vary seasonally or across growth stages. Uncovering these differences will improve model prediction assessing carbon losses via priming during ongoing shrub expansion (Keuper et al., 2020). Especially, more insights into depth-specific root exudation can improve model accuracy as Arctic mineral soils are particularly susceptible to priming (Wild et al., 2014). Thus, although exudation into mineral horizons was lower than into organic horizons, this could still induce higher CO_2 losses.

4. Conclusions

The main objective of this PhD thesis was to 1) advance the understanding of whether and how four plant types common to the tundra and forest-tundra interface (i.e., spruce trees, tussock-forming graminoids, birch and alder shrubs), exhibit different effects on soil carbon cycling, and 2) provide new observational data to improve laboratory experiments. The results of this thesis demonstrate...

- ... that plant shifts, particularly between alder shrubs and tussock-forming graminoids, can affect SOM properties and stability through differences in litter composition. Besides litter composition, biomass production and soil physical conditions may influence SOM cycling. **(Paper I)**
- ...that the overall root exudate metabolome is different between tussock-forming graminoids, birch and alder shrubs and therefore these plant types might have different effects on SOM decomposition. These differences are not reflected in total carbon and primary metabolite exudation and thus vegetation shifts cannot be simulated in laboratory experiments by adding varying amounts of primary metabolites to soils. **(Paper II)**
- ...that simulated exudation in previous studies corresponds to root exudation over several growing seasons. Since abiotic and biotic effects of organic acids on soil carbon and nutrient cycling were proven to be concentration-dependent, laboratory experiments need adaptation with observational data from living plants to better assess how plant root exudates alter soil carbon cycling. Different from previous suggestions, organic acids promote carbon stabilization over destabilization at high and low concentrations. **(Paper II and III)**
- ...that carbon allocation is plant- and depth-specific. Alder shrubs allocate less carbon into O horizons and more aboveground than birch shrubs. **(Paper IV)**

In summary, this thesis shows that vegetation shifts can affect soil carbon cycling through litter deposition and root exudation and that not all changes will result in a loss of soil carbon.

5. Outlook

While this thesis shows that vegetation shifts can affect soil carbon cycling, more research is required to fully understand the overall effects on the carbon balance and how they might vary in space, with plant growth stage, season and further rise in temperature. This is particularly important since root exudation is modulated by environmental conditions. The next step in this direction is to unravel the variability of root exudation over different plant growth stages and seasons and to determine whether this variability drives changes in soil carbon cycling. In this respect, more elaboration on the role of secondary metabolites in SOM decomposition and persistence time of mineral-stabilized exudates is needed. This can be achieved by working with root exudates of living plants instead of artificial root exudate mixtures and by integrating biogeochemical, microbial, and metabolic analyses. However, due to the large complexity of the root exudate metabolome, future research requires field experiments which could include the comparison of in-situ breakdown of isotopically labeled plant litter or common SOM polymers (e.g. protein) in root-free and root-containing soils of different plant types. To further improve model predictions on plant-mediated carbon losses and to disentangle the effects of plant litter and root exudates a plant-specific assessment of litter production and root distribution is inevitable.

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