

Disentangling the Effects of Goose Disturbance and Warming on Aboveground and Belowground Processes

Insights from the Thawing High Arctic Tundra of Svalbard

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Independent Master's Thesis project • 60 credits Swedish University of Agricultural Sciences, SLU Faculty of Forest Sciences/Department of Forest Ecology and Management Master program in Forest Ecology and Sustainable Management/ SLU 2024:11 • ISSN 1654-1898 Umeå 2024 Disentangling the Effects of Goose Disturbance and Warming on Aboveground and Belowground Processes: Insights from the Thawing High Arctic Tundra of Svalbard

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Abstract

The High Arctic tundra is experiencing disproportionate warming compared to the global trend. This warming allows for carbon emissions to be released from organic soil at a higher rate: nevertheless, the warming conditions pose a higher risk in terms of permafrost thaw. Permafrost is any soil that remains frozen for a period of two or more years, trapping carbon and other nutrients in an inaccessible environment. Hence, permafrost acts as a carbon sink. When the permafrost region warms, it allows for this resource to become available for decomposition and release into the atmosphere. This study has been designed to further understand permafrost thaw in the High Arctic under conditions of grubbing disturbance, vegetation community composition shifts, and warming climates. Above-ground and below-ground interactions were investigated through a field study and compared to a 4-month incubation experiment measuring CO₂ and CH₄ fluxes in organic layer soil The field study found that wet moss tundra created a habitat with high plant productivity and high moisture content. Furthermore, areas with higher grubbing had a thinner organic layer depth, increasing the soil temperature and reducing the moisture level. Nutrient availability was highly dependent on the vegetation, but organic N was the most abundant form of N no matter the site. Through the incubation, it was discovered that CO₂ was emitted at much higher levels than CH4. The permafrost inoculated with 10% organic soil had much higher levels of CH4 than organic soils. Furthermore, CH₄ emissions changed based on the vegetation, with dry moss tundra emitting higher levels. Overall, this field of study still needs continued research, yet this study has helped to add to the search for an understanding of this environment in changing conditions.

Keywords: Carbon Emissions, Goose Grubbing, High Arctic Tundra, Moisture Gradient, Moss Tundra, Nitrogen limitation, Organic Soils, Permafrost Thaw

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Abbreviations

С	Carbon
SOC	Soil Organic Carbon
Ν	Nitrogen
CO_2	Carbon Dioxide
CH ₄	Methane
UiB	University of Bergen
DOC	Dissolved Organic Carbon
C:N	Carbon Nitrogen Ratio
TN	Total Nitrogen
NO ₃	Nitrate
NH ₄	Ammonium
PO ₄	Phosphate ion
OL	Organic Layer
ANOVA	Analysis of Variance

1. Introduction

1.1 A Changing Arctic

In alpine and arctic regions, any soil that remains at or under 0°C for a period of two years or longer is considered permafrost (Lawrence and Slater, 2005). Permafrost is a mixture of frozen mineral soil, ice, and partially decomposed plant material. This is covered by a layer of soil termed the active layer, which thaws every summer, then refreezes during the cold season (Faucherre et al., 2018). The permafrost region is disproportionately vital to the global carbon (C) cycle as it has double the amount of organic C as all atmospheric C (Schuur et al., 2015). Furthermore, high latitude permafrost regions hold approximately 50 % of all global soil organic carbon (SOC), yet the region only accounts for 16 % of global soil environments (Tarnocai et al., 2009). A large portion of this SOC is unavailable to the active C cycle as it is trapped in frozen permafrost region has ~ 1300 Pg of C with only ~500 Pg located in active layer soil (Hugelius et al., 2014).

The mean annual temperature in most arctic regions has risen by 2 - 4 °C in the last few decades, and this increase is further pronounced during the spring and fall seasons (IPCC, 2021). The influx of warming temperature is permitting permafrost thaw over a large geographic scale, resulting in an extensive deepening of the active layer (Schuur et al., 2015; Schaefer et al., 2014). Microbial communities from the active layer then have access to invade this thawed permafrost soil; therefore, C stored in this previously unavailable, frozen soil layer will be exposed to microbial decomposition (Biskaborn et al., 2019; Plaza et al., 2019; Howard et al., 2020). Recent predictions suggest that permafrost could decline by 30 % - 80 % during the 21st century (IPCC, 2013).

1.2 Soil N Cycling and C Emissions

The active layer contains almost all belowground biological processes, making it essential to arctic C and nutrient dynamics (Sazonova et al., 2004). Furthermore, High Arctic ecosystems are largely controlled through nutrient processing, as the availability of nutrients, such as nitrogen (N), is strongly limited (Chapin, 1987; Mauclet et al., 2022). This creates an ecological system in which C and N cycles

are tightly combined (Thornton et al., 2007). CO_2 is released into the atmosphere through soil respiration in the presence of oxygen (Westermann et al., 2010). With warming, higher soil temperatures stimulate microbial organic matter decomposition and the release of CO_2 into the atmosphere (Howard et al., 2020). CH_4 is produced in anaerobic conditions by methanogens breaking down organic C in deeper soil, typically below the water table (Howard et al., 2020). CH_4 emissions from the active layer are much lower than CO_2 emissions, however CH_4 has a much higher warming potential (approximately 28 times higher than CO_2) due to its larger radiative forcing per unit mass (IPCC, 2021). Soil temperature and soil moisture are thought to be the key drivers of C fluxes from the active layer and thawing permafrost in the High Arctic (Schädel et al., 2016).

1.3 Goose Grubbing

Warming climate conditions can have a profound effect on the active layer and permafrost biogeochemical processes when paired with co-occurring environmental disturbances. Goose grubbing from the pink-footed goose, Anser brachyrhynchus, is a prevalent disturbance on a landscape scale due to extensive herbivory damage on the High Arctic environment of the Svalbard archipelago (Fox et al., 2006). Grubbing is a foraging behavior where geese dig below the moss and organic soil surfaces in order to extract below-ground plant biomass (Fox and Bergersen, 2005). The intensity of this grubbing has a significant effect on High Arctic ecosystem functioning (Pedersen et al., 2013). A. brachyrhynchus populations have exponentially increased in Svalbard, doubling between the 1980s and early 2000s as a result of conservation efforts, global warming, and an increase in agricultural practices at their wintering grounds (Fox et al., 2005; van der Wal et al., 2007). In a 5-year period in the 2000s, the population increased by over 30,000 individuals, resulting in a 400 % increase of grubbing in Svalbard (Pedersen et al., 2013). This considerable increase in the geese population has the potential to amplify the already significant effect of grubbing in the High Arctic ecosystem, and continue as the temperature conditions increase (Fox et al., 2005; van der Wal et al., 2007).

Moss is one of the most dominant plant groups in the High Arctic tundra, and grubbing can strongly reduce the moss layer, significantly modifying soil temperature and introducing shifts in soil hydrological regimes (van der Wal et al., 2001; Schuur et al., 2008; Gornall et al., 2009). Grubbing occurs within smaller patches, instead of a widely dispersed scale, as the flocks will intensely graze and grub at one site, then move to another (Petit Bon et al., 2023b). This causes high disturbance to the organic layer and loss of above-ground vegetation across the landscape (Pedersen et al., 2013). Vegetation recovery from grubbing depends on vegetation type with wetlands having higher resilience; nevertheless, wet vegetation tends to showcase higher levels of grubbing (Speed et al., 2010; Speed et al., 2009).

1.4 Contrasting Vegetation Types

The effect of warming climate conditions and goose grubbing on the biogeochemical processes within the active layer and thawing permafrost, such as C emissions and nutrient dynamics, can vastly diverge between plant communities with contrasting abiotic and biotic properties. Soil moisture and temperature, solar radiation, and topography in the Arctic tundra can rapidly change within short distances inducing a high variability in soil nutrient availability, C dynamics and plant community composition (Dobbert et al., 2021; Kemppinen et al., 2021). The Arctic tundra is typically composed of a mosaic of vegetation types due to the observed soil and surface microclimates (Björk et al 2007; Longton 1984; Kemppinen and Niittynen, 2022). Thus, there is a great need to integrate the response of divergent plant communities when investigating soil nutrient dynamics and C fluxes from the active layer and thawing permafrost.

1.5 Research Questions and Hypotheses

The effects of goose grubbing as well as the effect of warming on soil biotic and abiotic properties have been studied through many experiments in the Arctic; however, they are rarely studied together while biogeochemical processes in permafrost remain largely unknown (Gornall et al., 2009; Henry et al., 2012; Hugelius et al., 2014; Schuur et al., 2008). In this thesis, I aim to explore the interactive effect of goose grubbing, warming, and vegetation type on N dynamics as well as CO_2 and CH_4 emissions from organic soils and permafrost soils through a complete above- and belowground approach. Furthermore, I investigate the effect of the microbial community from top organic soil layers invading thawed permafrost. This thesis combines above- and belowground field data of goose grubbing and plant communities from the High Arctic tundra in the Svalbard archipelago with CO_2 and CH_4 gas measurements from a 4-month laboratory incubation of organic soils, permafrost soils and permafrost soils inoculated with 10 % organic soils.

I hypothesize:

- (1) Grubbing would reduce the abundance of all plant functional groups with moss being the most affected. I anticipate the strongest effects will be seen for the wet moss tundra.
- (2) Vegetation type and grubbing will induce a change in plant nutrient contents and plant N uptake; however, this shift will be highly dependent on plant functional group.
- (3) Moss layer depths will determine soil microclimates, which in turn will influence soil nutrient availability and carbon stock.

- (4) Total C emissions will be higher in organic soil than in permafrost soil, and these emissions will be more closely tied with the aboveground vegetation type.
- (5) CO_2 emissions will constitute a much larger flux than CH_4 emissions.
- (6) Warming will increase emissions for both C and CH₄, yet CH₄ will respond the most.

2. Materials and Methods

2.1 Study Site

The field site for this study was established in Adventdalen $(78,17^{\circ} \text{ N}, 16,03^{\circ} \text{ E})$ in the archipelago of Svalbard (Figure 1). Adventdalen is a valley in the center part of Svalbard and is considered a periglacial landscape (Rouyet et al., 2019). This area has a dry Arctic climate with an average annual precipitation of 204 mm and mean annual temperature of - 4,0 °C, as recorded from 1989 to 2018 at the Svalbard airport (Petit Bon et al., 2023b).

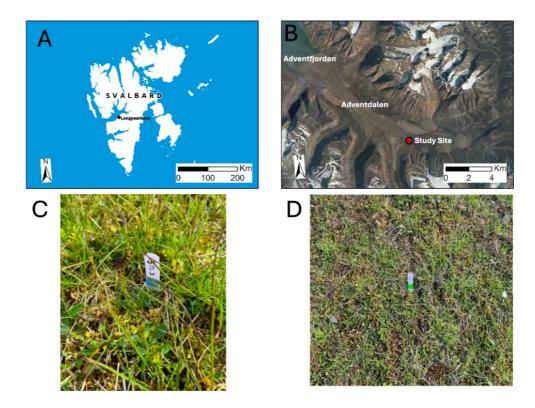


Figure 1 Map of Site location with (A) Svalbard map with location of the town, (B) map of Adventdalen with the location of the study site marked, (C) low grubbing, wet moss tundra plot, and (D) low grubbing dry moss tundra plot

The vegetation in this area is distinguished by a mosaic of different plant communities over short distances due to differences in topography, permafrost pattern, and soil microclimate conditions (Tømmervik et al., 2014). Five sampling sites were selected in a dry moss tundra and in a wet moss tundra (in total 10 sites) (Figure 1). In this area, wet sites tend to have a higher abundance of bryophytes, such as *Tomentypnum nitens* or *Aulacomnium turgidum* and graminoids while the drier sites have less bryophytes and more ferns and forbs (Tømmervik et al., 2014). Two sampling plots were established within each site, one with high grubbing intensity (Figure 2) and one with low grubbing intensity (Figure 1(C) and (D)). Both the low grubbing and associated high grubbing plot had the same plant community in order to reduce any confounding variables within the soil properties or plant chemistry. In each vegetation site, the low and high grubbing plots were established within a distance of 100 m.



Figure 2 Site 1 in the dry moss tundra (left) and Site 5 in the wet moss tundra (right) showing high grubbing where the effects of geese on the moss layer can be clearly seen, Adventdalen, Svalbard, July 2022

2.2 Background Field Measurements

2.2.1 Organic layer and permafrost thaw front depth

The organic layer depth was recorded from the profile of soil cores taken at two or three locations in each plot. The organic layer is defined here as fragmented dead plant materials and decaying organic matter. The permafrost thaw depth was measured through a graduated pointed metal rod. The rod was inserted into the active layer of rhizosphere soil until it reached the permafrost front thaw. Each plot had three to four measurements due to the variability of thaw depth. All background field measurements were performed by Hélène Barthelemy with the University of Bergen (UiB).

2.2.2 Soil microclimates

Soil temperature and moisture were recorded for each plot utilizing the Delta-T Devices HH2 Moisture Meter to measure volumetric soil moisture content (6 cm \times 3 cm sample size) and the Xylem Analytics Ebro TFX 410 soil thermometer (120 mm probe). Five measurements were taken in each plot in order to take into account for natural variation in soil microclimates.

2.2.3 Plant community composition and moss layer depth

The vegetation composition was measured using a point frequency recording system in a subplot of 35 cm \times 35 cm positioned in the middle of each plot (Figure 3). A point frame of seven pins (diameter 2,5 mm) was used at seven evenly spaced intervals resulting in a grid of 49 points per plot. All living vascular and non-vascular plants were identified at the species level and the number of hits on each pin was recorded. Plant litter was not identified at the species level. The absence of vegetation was also noted. Moss layer depth was recorded by establishing three transects (50 cm long and 20 cm apart) in each plot and measuring the extent of green living moss layer every 10 cm. In heavy grubbed plots, the extent of the grubbed dead moss layer was also measured.



Figure 3 Vegetation subplot frame with established grid for point frequency, July 2022

2.2.4 Plant chemical analysis

Green and healthy leaves of *Bistorta vivipara, Equisetum arvense, Sa lix polaris, Dupontia fisheri,* and *Tomentypnum nitens* were collected in each plot (Figure 4). These species represented the most common plant species of the main functional groups – in both vegetations – forb, fern, dwarf shrub, grass, and moss in the same order as the species. Once collected, all plant samples were immediately stored in a freezer and then dried at 60 °C for 48 h. These samples were then ground into a fine powder and shipped to Terrestrial Ecology lab, at the University of Copenhagen for chemical analysis of the ¹⁵N, N and C:N ratio. This was accomplished by Prof. Anders Michelsen using a Isoprime Isotope Ratio Mass Spectrometer coupled to a C:N Elemental Analyser.



Figure 4 Mosaic of analysed plant species, (A) Bistorta vivipara, (B) Equisetum arvense, (C) Tomentypnum nitens, (D) Dupontia fisheri, and (E) Salix polaris. Photos were taken by svalbardflora.net (2024)

2.3 Soil Sampling and Processing

2.3.1 Organic Layer Collection

Organic layer was collected in each plot through 15 cm \times 15 cm soil blocks on September 15th - 21st, 2022 (Figure 5). Each block was dug at least 5 cm deep using completely sterile equipment. Once collected, the soil blocks were placed in sterile plastic bags then transported using cooling elements. All samples were placed in a fridge (5 °C) for two weeks, then moved into a freezer at UiB until further processing.



Figure 5 Organic layer collection from the field site in September 2022

2.3.2 Permafrost Core Collection

Permafrost cores were collected using a Stihl BT 131 gas powered drill at three locations within each vegetation type on October 11th and 12th, 2022 (in total six permafrost cores, 10 cm diameter each). Permafrost soils contain a low abundance of microorganisms compared to the active layer. Contamination problems could occur during the drilling of the permafrost cores in the field or during post-drilling handling; therefore, the outer layer (5 mm) of each permafrost core was removed and the remaining inner parts of the cores were stored in new sterile bags. Only the top 15 cm part of the cores (15 cm below the thaw front) were prepared for the incubation (Figure 6). Organic layer sampling as well as all permafrost core collection was performed by Hélène Barthelemy. The permafrost cores were kept frozen at all times. The post-drilling processing was also performed by Hélène Barthelemy.



Figure 6 Retrieved permafrost cores from wet and dry moss tundra sites (left and right respectively) in a sterile, frozen environment at UiB

2.3.3 Soil processing

The organic soil samples were transferred on June 9th, 2023, into sterile climate chambers and slowly thawed at 2 °C. The top vegetation layer was first removed from each sample. This included the thick moss layer, leaves, and other plant materials. Then, the remaining soil was sieved (8 mm). All roots measuring larger than 1 cm were removed, with wet moss tundra having a higher level of roots to remove. Soil samples within the same sampling plot were combined, homogenized, and stored in sterile plastic bags at 2 °C.

Organic soils and frozen permafrost cores were transported to the Vegetation Ecology lab at SLU. Permafrost cores were thawed in a sterile climate chamber at 2 °C two days before the start of the incubations. After thawing, permafrost cores from the same vegetation were combined into one large sample to represent a composite permafrost sample for the dry moss tundra vegetation and a composite permafrost sample for the wet moss tundra vegetation respectively.

2.4 Soil Incubation Design and Measurements

2.4.1 Experimental set up

The set up of the incubation was designed to test the effects of grubbing intensity, warming climate conditions, and soil hydrological shifts upon C fluxes, organic matter decomposition, and N mineralization in organic soils. Furthermore, I tested the effect of inoculating permafrost soils with microorganisms from the organic layer on permafrost geochemical properties and C fluxes. Therefore, I performed three experiments (Figure 7):

Experiment 1 set out to test the effects of grubbing intensity, climate conditions, and soil hydrological shifts on organic soil alone. Jars were filled with 30 g of the homogenized organic soils.

Experiment 2 set out to test the effects of inoculating 10 % of organic soil on permafrost soils. Jars were filled with 4 g of rhizosphere soil and 36 g of permafrost soil (total 40 g).

Experiment 3 set out to test the effect of temperature on thawed permafrost alone. Jars were filled with 40 g of permafrost soil.

Each designated soil quantity was placed within a pre-weighed 250 ml glass jar for each lab sample from the corresponding sieved sample. Jars were sealed with parafilm with holes created using a sterile needle. I created two scenarios (Figure 7): half of the samples were incubated in a climate chamber set at 4 °C which correspond to the average summer temperature at the field site (ambient scenario) and the other half of the samples were incubated in a climate chamber set at 10 °C (predicted warming scenario). All samples remained in the climate chambers for 4 months starting in July 2023 to represent the 4-month period without snow at the study site.

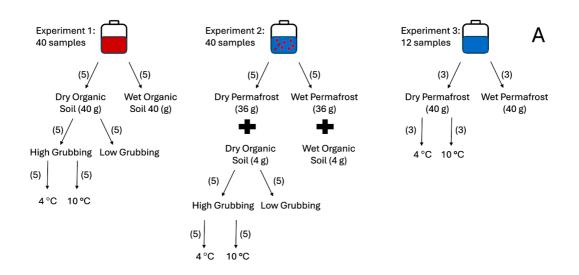




Figure 7 (A) Schematic representation of the incubation design. The three experiments yielded a total of 92 jars, with 40 organic soils (20 in the ambient chamber and 20 in the warming chamber), 40 permafrost soils inoculated with organic soils (20 in the ambient chamber and 20 in the warming chamber) and 12 permafrost soils (6 in the ambient chamber and 6 in the warming chamber) (B) Incubation Chamber for 4 °C (left) and 10 °C (right) with all jars for the three experiments labelled with Lab ID

2.4.2 CO₂ and CH₄ measurements

The first measurement of CO_2 and CH_4 gas was taken two days after the jars entered the climate chambers, giving time for the soils to be acclimated to their new climatic conditions. The following CO_2 and CH_4 gas measurements were then completed once every month until the end of the overall experiment. One week prior to the gas measurements for CO_2 and CH_4 , the lab samples were adjusted for moisture variation utilizing a sterile pipette with Milli-Q water (Millipak® Express 40 Filter Water Purification System). The difference in weight for a specific sample from one month to the next was added back to the sample as Milli-Q water to three significant figures in order to account for total mass.

 CO_2 and CH_4 fluxes were measured by two individuals in order to keep a stabile schedule. The first person was in charge of capping the lab sample jars. The samples, in trays of six, were removed from their respective climate chambers in Styrofoam cooler boxes filled with ice then brought to the lab. One at a time, the jars were taken out and placed on ice. The parafilm was discarded and the jar was capped with a sterile, airtight silicone lid and placed back in the appropriate climate chamber. The next jar would receive the same treatment. This continued for each of the 92 jars.

A second person was in charge of taking the CO_2 and CH_4 gas measurements exactly one hour after capping occurred. For the measurement, an air sample was taken through the airtight silicone lid and transferred to an evacuated vial. The silicone lid was then removed and a new piece of parafilm was placed on the jar. New holes were then drilled in the parafilm with a separate needle.

Due to the large number of samples, the data collection was separated into two days of measurements. Experiment 1 with its associated 40 jars was completed on the first day. Experiment 2 and 3 with jars #41 through #92 was completed on the following day. This order of sampling was done every month following the same schedule.

2.4.3 Pre and post incubation soil analysis

Fresh Soil

The analysis of fresh soil included soil moisture, gravimetric moisture, loss on ignition (LOI), and soil pH. Gravimetric soil moisture and LOI were collected using a Nabertherm Muffle Furnace set to 105 °C overnight, then 660 °C for a 6 h period. The pH was measured through 10 g of fresh soil dried for 48 h then combined with 50 ml of deionized water, and measured using a Mettler Toledo Seven Compact pH/Ion Meter

Bulk soil

Dried (60 °C, 48 h) and ground soil samples (field samples) were submitted to Anders Michelsen at the Stable Isotope Facility of the Department of Biology at the University of Copenhagen, for nitrogen (N), ¹⁵N, and carbon:nitrogen ratio (C:N) analysis. Researchers will utilize ¹⁵N (an easily identifiable isotope) as it is easier visualizing the movement of N in the ecosystem through this isotope (Clemmensen et al., 2008; Ravn et al., 2017). Soil samples were analyzed on a Elemantar Isoprime Isotope Ratio Mass Spectrometer coupled to a C:N Elemental Analyser.

Soil Extraction

Bulk dissolved organic C (DOC), total nitrogen (TN), as well as phosphate ion (PO₄), nitrate (NO₃), and ammonium (NH₄) analyses on pre-incubation samples were conducted by the SLU Stable Isotope Laboratory. Measurements were completed on field ID fresh soil (20 samples: the 2 vegetations with 5 for each associated grubbing intensity). For each sample, 5 g of fresh soil was combined with 50 ml of MilliQ water and filtered through a 0,45 μ m filter. The resulting solution was processed through a Shimadzu TOC-L + TNM-L, ASI-L for DOC and TN. PO₄, NO₃, and NH₄ levels were determined by processing the solution through an Auto Analyzer 3 Spectrophotometer from Omniprocess at wavelength 880nm for PO₄, wavelength 660nm for NH₄, and wavelength 550nm for NO₃.

2.5 Statistics

All statistical analyses were performed using the statistical R packages (version 2023.12.1, R Core Team, 2023). I performed linear mixed-effect models to investigate the effects of vegetation type, grubbing intensity, and temperature treatment (fixed variables) on soil geochemical properties, plant communities and CO_2 and CH_4 gas fluxes with the sampling sites as the random effect. These models took into account the pseudo-replication of the plots through the five sampling sites per vegetation type. The modelling was performed with the function lme within the R package nlme (Pinheiro et al., 2023). I applied an ANOVA to the fitted models using the anova function to retrieve *F*-statistics and corresponding *P* values. Following the detection of significant effects, post hoc tests were performed with the R package emmeans (Lenth, 2024). Significance levels were set at $\alpha = 0.05$. All data was log transformed and checked the assumptions of the model.

3. Results

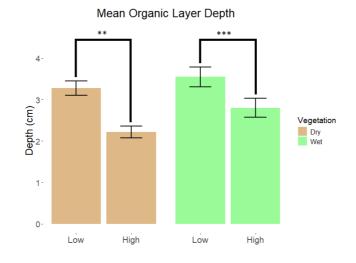
3.1 Ecosystem Properties

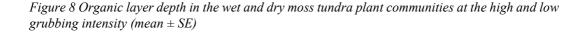
3.1.1 Soil abiotic properties

The results of this experiment found that the organic layer was deeper in the wet moss tundra (Table 1, Figure 8). This vegetation also had a higher soil moisture content, higher moisture microclimates, and lower soil temperatures than what was observed in the dry moss tundra (Table 1, Figure 9). By contrast, the dry moss tundra had a higher active layer thickness (lower permafrost front thaw). High grubbing intensity increased soil temperature and moisture microclimates (Figure 9), but reduced organic layer depths (Table 1).

Table 1 Effect of vegetation type and grubbing intensity on active layer depth, organic layer (OL) depth, and soil microclimates (temperature and moisture). F values are expressed (linear mixed effect ANOVA) and the level of significance is indicated (*<0.05, **<0.01, ***<0.001). Degrees of Freedom are noted in the first row

v	Active Layer	OL Depth	Temperature	Moisture
Degrees of Freedom	1,59	1,76	1,92	1,92
Vegetation	7,959**	5,880*	10,948**	22,441***
Grubbing	1,190	21,425***	9,473**	11,284**
Vegetation:Grubbing	1,541	0,633	2,448	2,535





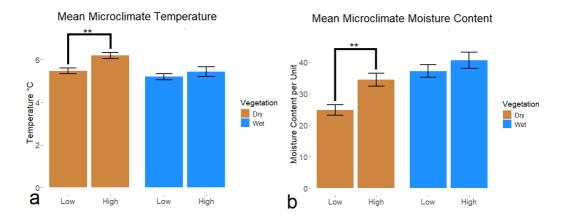
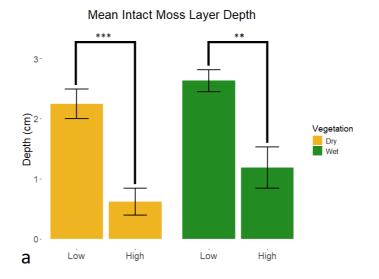


Figure 9 Mean soil temperature (a) and moisture content (b) in the wet and dry moss tundra plant communities at the high and low grubbing intensity as recorded through microclimates (mean \pm SE)

3.1.2 Vegetation composition

The overall plant abundance varies depending on vegetation type, grubbing intensity, and plant functional group. The wet moss tundra had a higher plant abundance ($F_{1,108} = 12,157, P = 0,001$), and moss largely dominated in both habitats ($F_{6,108} = 107,238, P < 0,001$). At the functional group level, graminoids $(F_{1,12} = 45,901, P < 0,001)$ and forbs $(F_{1,12} = 8,918, P = 0,011)$ had higher abundances in the wet moss tundra compared to drier habitat. Graminoids increased threefold in the wet moss tundra $(75,9 \pm 11,348)$ compared to the dry site $(24,9 \pm 4,729)$ while forb presence doubled $(9,0 \pm 1,333$ to $19,2 \pm 3,999)$ between sites. High grubbing intensity decreased moss abundance by approximately 85 % in both vegetations ($F_{1,52} = 99,075, P < 0,001$). High grubbing intensity also decreased deciduous shrubs in the dry moss tundra ($F_{1,12} = 31,746, P$ < 0,001) and graminoids in the wet moss tundra ($F_{1,12} = 16,309, P = 0,002$). There was a higher percentage of grubbed mosses at the dry moss tundra remaining on the plots ($F_{1,52} = 24,745, P < 0,001$). Therefore, total moss layer thickness (Figure 10b) was significantly higher when compared to intact moss layer depth (Figure 10a) at the high grubbing intensity ($F_{1,52} = 36,535, P < 0,001$).



Mean Total Moss Layer Depth Combined Intact and Grubbed Moss

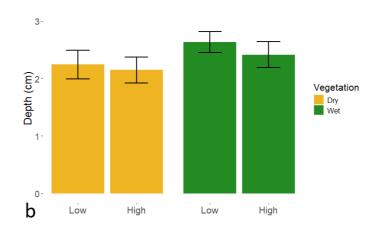


Figure 10 (a) Intact moss layer after grubbing is taken into account (mean \pm SE), (b) Combination of intact and grubbed moss to create a total moss representation for the field site (mean \pm SE)

3.2 Plant Chemistry

Nitrogen content in the collected plant samples ranged between 0,541% and 3,417%. This N content was higher in dry moss tundra (Figure 12, Table 2a) and highly dependent on species, with *B. vivpara* (3,058 \pm 0,050%) and *S. polaris* (2,376 \pm 0,069%) having the highest levels (Table 2b). The N content of *E. arvense* and *D. fisheri* increased by approximately 10% and 20% in the dry moss tundra compared to what was observed in wet moss tundra. Additionally, high grubbing intensity increased overall plant N content (Figure 11, Table 2a). On the species level, grubbing tended to have a positive effect on nitrogen with both *B. vivpara* (3,235 \pm 0,035%) and *S. polaris* (2,608 \pm 0,066%) having increased levels at high grubbing sites (Table 2b).

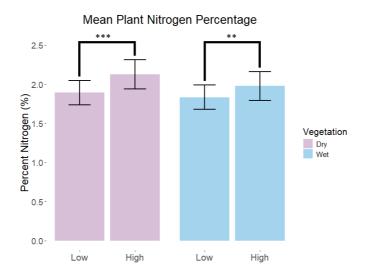


Figure 11 Nitrogen content (%) in the wet and dry moss tundra plant communities at the high and low grubbing intensity (mean \pm SE)

¹⁵N was highly dependent on species with *E. arvense* (4,718 ± 0,228 ‰) having the highest level and *S. polaris* (-4,044 ± 0,277 ‰) having the lowest (Table 2). It was found that across all species ¹⁵N levels ranged from -7,150 to 6,789 ‰. This was higher in wet moss tundra for *D. fisheri* (0,656 ± 0,301) and *E. arvense* (5,486 ± 0,252 ‰) while *B. vivipara* (-2,289 ± 0,348 ‰) had higher levels in the dry moss tundra. Furthermore, *B. vivipara* (-2,193 ± 0,316 ‰) and *S. polaris* (-3,562 ± 0,201 ‰) had higher levels at high grubbing intensity. ¹⁵N increased in wet moss tundra at both grubbing intensities for *E. arvense* ($F_{1,12}$ = 6,662, *P* = 0,024), nevertheless, grubbing did not affect overall plant ¹⁵N appearance. The ratio between carbon and nitrogen (C:N) was highly dependent on the plant species ranging between 12,20 and 69,31 (Table 2a). C:N was higher at wet moss tundra for *D. fisheri* (27,600 ± 0,611) and *E. arvense* (17,974 ± 0,279). *B. vivpara* (17,369 ± 0,468) and *S. polaris* (19,831 ± 0,535) had higher levels of C:N at low grubbing sites (Table 2).

Table 2 (a) Effect of the vegetation type, grubbing intensity, and species on nitrogen, carbonnitrogen, and ¹⁵N, (b) Effect of vegetation type and grubbing intensity on some selected individual species. F values are expressed (linear mixed effect ANOVA) and the level of significance is indicated (*<0.05, **<0.01, ***<0.001). Degrees of Freedom are 1,74 for the total dataset and 1,12 for each species

a.	Ν	C:N	15 N
Vegetation Type	14,365***	11,165	9,061
Grubbing	45,998***	10,768	14,702
Species	868,966***	848,302	329,798***
Vegetation:Grubbing	2,753	1,267	0,338
Vegetation:Species	3,521*	2,264	8,410***
Grubbing:Species	11,726***	1,265	3,844
Vegetation:Grubbing:Species	0,290	0,241	3,461

b.	Ν	C:N	¹⁵ N			
Bistorta vivipara (forb)						
Vegetation	0,577	0,034	14,281**			
Grubbing	36,714***	33,4951***	18,523**			
Equisetum arvense (fern)						
Vegetation	11,091**	13,677**	51,760***			
Grubbing	1,148	1,991	2,708			
Salix polaris (dwarf shrub)						
Vegetation	0,233	0,016	2,982			
Grubbing	24,900***	28,143***	7,146*			

3.3 CO₂ and CH₄ Fluxes

3.3.1 Total CO₂ and CH₄ emissions

Throughout the 4-month incubation period, CO_2 (1201,18 ± 68,614 ppm) had a much larger emission scale than CH_4 (4,150 ± 0,26 ppm), with over 99 % of all gas emitted as CO_2 . Nonetheless, when broken down into individual soil types, the highest mean CO_2 was emitted through organic soil (1345,09 ± 112,25 ppm) while the CH_4 organic soil emissions (1,900 ± 0,016 ppm) were the lowest of its divergent soil types (Figure 12). The organic soil (20 %) and permafrost alone samples (18 %) emitted around the same percentage out of the total sum of CH_4 emissions measured, even though there were only 12 permafrost samples in contrast to the 40 organic soil (5,885 ± 0,487 ppm) and permafrost alone (5,864 ± 0,930 ppm) did not have a divergent emission rate.

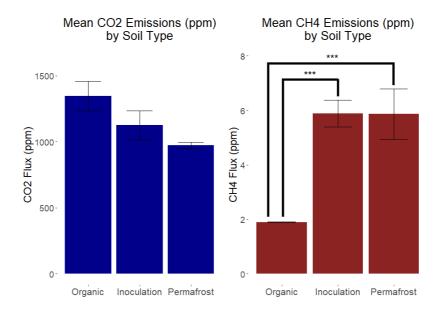


Figure 12 CO₂ and CH₄ emissions (ppm) in organic soils, permafrost soils inoculated by 10 % organic soils (Inoculation), and permafrost soils alone (mean \pm SE)

3.3.2 CO₂ and CH₄ Emissions over time

Emissions for both gases shifted between increasing and decreasing throughout the five measurement periods ($F_{4,455}$ = 11,96, P < 0,001 for CO₂; $F_{4,455}$ =7,889, P < 0,001 for CH₄ Figures 13 – 16). When analyzed by measurement period, CO₂ emissions were highest at Time 0 and steadily declined during the following months with the exception of a sudden increase in emission by 8 % for Time 3. CH₄ emissions experienced a similar increase between Time 2 and Time 3 with a 22 % increase; nevertheless, CH₄ emissions had no clear pattern throughout the incubation. Unlike CO₂, CH₄ did not have its highest emission period in Time 0, but rather in Time 1. Furthermore, there was a 112 % increase between Time 0 (253,610 ppm) and Time 1 (538,430 ppm).

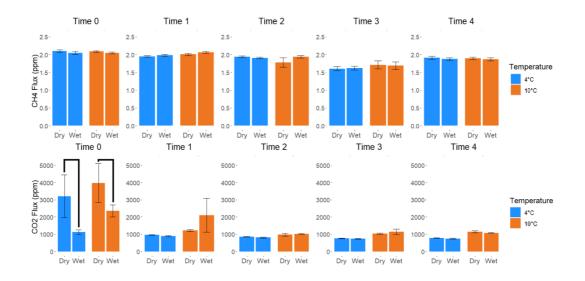


Figure 13 Experiment 1: CH_4 and CO_2 emissions (ppm) from organic soils in function of the vegetation type (dry and wet moss tundra) and the temperature treatment (4 °C: ambient scenario and 10 °C: warming scenario) over the 4 month incubation

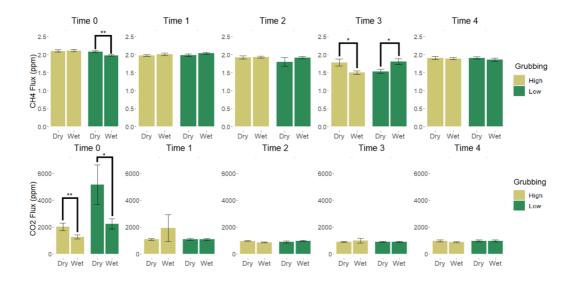


Figure 14 Experiment 1: CH_4 and CO_2 emissions (ppm) from organic soils in function of the vegetation type (dry and wet moss tundra) and grubbing (High: High grubbing intensity and Low: Low grubbing intensity) over the 4 month incubation

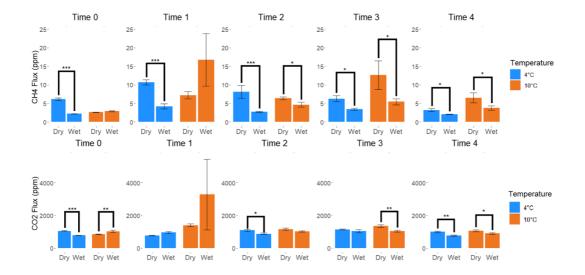


Figure 15 Experiment 2: CH_4 and CO_2 emissions (ppm) from permafrost soils inoculated with organic soils in function of the vegetation type (dry and wet moss tundra) and the temperature treatment (4 °C: ambient scenario and 10 °C: warming scenario) over the 4 month incubation

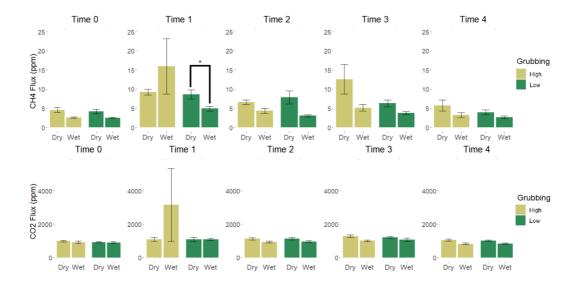


Figure 16 Experiment 2: CH_4 and CO_2 emissions (ppm) from permafrost soils inoculated with organic soils in function of the vegetation type (dry and wet moss tundra) and grubbing (High: High grubbing intensity and Low: Low grubbing intensity) over the 4 month incubation

3.3.3 Effects of vegetation, grubbing and temperature

Vegetation

Overall CO₂ (1251,635 ± 85,458 ppm) and CH₄ (4,915 ± 0,369 ppm) emissions were higher in the dry moss tundra ($F_{1,75} = 7,327$, P = 0,007 for CO₂; $F_{1,75} = 20,271$, P = 0,001 for CH₄). In organic soils, CO₂ emissions were only higher in the dry moss tundra at Time 0 (Table 5). In inoculated permafrost soils, CO₂ emissions were higher in the dry moss tundra from the second month until the end of the incubation period (Table 4, Figure 12). CH₄ emissions were higher in dry moss tundra during the entire incubation period with the exception of the CH₄ measurements at the second month (Table 3 and 5, Figure 7).

Grubbing

 CO_2 emissions from organic soils (1264,790 ± 99,384 ppm) were higher at low grubbing intensity (Table 4, Figure 14). CH_4 emissions were only higher in high grubbing conditions at Time 0 (Table 3 and 5, Figure 14). CO_2 emissions were higher in high grubbing plots in the final measurement (Table 4 and 6, Figure 14). In permafrost inoculated with organic soil, CH_4 emissions were only higher for grubbing conditions at Time 1 and 3 (Table 3 and 5, Figure 16).

Temperature Treatment

The warming scenario (10 °C) increased total emissions for both CO₂ (1392,674 ± 121,816 ppm) and CH₄ (4,749 ± 0,480 ppm) gases ($F_{1,458} = 41,814$, P < 0,001 for CO₂; $F_{1,458} = 4,077$, P = 0,044 for CH₄). In organic soil, CO₂ emissions were higher at the 10 °C climate in all months. In contrast, the warming treatment also

increased CO₂ emissions in permafrost inoculated with organic soils, but only in the first and last month (Table 4 and 6, Figure 13). CH₄ emissions from organic soils were less affected by temperature than CO₂ as only Time 1 had high CH₄ emissions at 10°C (Table 3 - 4, Figure 13). Permafrost soils inoculated with organic soils responded more to warming with higher CH₄ emissions observed at Time 0, 3, and 4 (Table 3 and 5, Figure 16).

Table 3 Effect of vegetation type, grubbing intensity, and temperature on CH_4 emissions from organic soils (experiment 1) and from permafrost inoculated with 10 % of organic soils (experiment 2). F values are expressed (linear mixed effect ANOVA) and the level of significance is indicated (*<0.05, **<0.01, ***<0.001). Degrees of Freedom values are 1,28.

	Time 0	Time 1	Time 2	Time 3	Time 4
Vegetation	2,901	2,290	0,980	0,000	0,668
Grubbing	7,310*	0,377	1,016	0,196	0,090
Temperature	0,023	6,013*	0,971	0,912	0,045
Vegetation:Grubbing	4,380*	0,134	0,765	13,352**	0,234
Vegetation:Temp	0,006	0,187	1,671	0,057	0,005
Grubbing:Temp	1,013	0,689	0,995	0,012	1,164
Vegetation:Grubbing:Temp	3,098	0,071	1,377	3,152	0,378

CH₄ – Experiment 1: Organic soils

CH₄ - Experiment 2: Permafrost soils inoculated with 10 % organic soils

	Time 0	Time 1	Time 2	Time 3	Time 4
Vegetation	144,408***	4,847*	27,710***	11,299**	9,060**
Grubbing	1,761	5,328*	0,843	4,720*	1,763
Temperature	54,139***	2,840	2,409	5,459*	14,349**
Vegetation:Grubbing	0,707	2,244	1,711	0,384	0,134
Vegetation:Temp	202,248***	22,428***	4,682*	0,017	0,013
Grubbing:Temp	0,294	15,124**	2,515	3,454	4,041
Vegetation:Grubbing:Temp	0,301	4,758*	2,041	0,254	0,503

Table 4 Effect of vegetation type, grubbing intensity, and temperature on CO_2 emissions from organic soils (experiment 1) and from permafrost inoculated with 10% of organic soils (experiment 2). F values are expressed (linear mixed effect ANOVA) and the level of significance is indicated (*<0.05, **<0.01, ***<0.001). Degrees of Freedom values are 1,28.

	Time 0	Time 1	Time 2	Time 3	Time 4
Vegetation	16,253***	0,112	0,045	0,043	3,866
Grubbing	18,680***	0,142	0,016	0,035	4,738*
Temperature	16,917***	8,005**	6,838*	50,022***	249,056***
Vegetation:Grubbing	0,642	0,142	3,684	0,065	4,862*
Vegetation:Temp	0,824	0,799	1,232	0,942	0,115
Grubbing:Temp	0,080	0,807	0,656	1,552	0,231
Vegetation:Grubbing:Temp	0 1,731	0,924	0,665	0,667	0,075

CO₂ – Experiment 1: Organic soils

CO₂- Experiment 2: Permafrost soils inoculated with 10 % organic soils

	Time 0	Time 1	Time 2	Time 3	Time 4
Vegetation	2,573	0,812	9,680**	12,914**	17,537***
Grubbing	1,293	0,479	0,067	0,008	0,000
Temperature	0,586	10,477**	3,838	2,729	4,374*
Vegetation:Grubbing	0,495	0,358	0,041	1,203	0,352
Vegetation:Temp	39,072***	0,166	0,932	1,433	0,662
Grubbing:Temp	0,769	1,260	3,792	3,558	0,232
Vegetation:Grubbing:Temp	0,517	1,401	0,414	0,322	0,409

Table 5 Effect of vegetation type, grubbing intensity, and temperature on CH_4 emissions from organic soils (experiment 1) and from permafrost inoculated with 10 % of organic soils (experiment 2) depicted through each measurement period's mean value and associated standard error.

	Dry High Grubbing		Low Grubbing		Wet High Grubbing		Low Grubbing	
	A	Т	А	Т	A	Т	A	Т
Time	2,094 ±	2,108 ±	2,098 ±	2,068 ±	2,152 ±	2,072 ±	1,942 ±	2,014 ±
0	0,053	0,042	0,052	0,021	0,033	0,049	0,031	0,025
Time	1,938 ±	2,010 ±	1,960 ±	2,004 ±	1,950 ±	2,066 ±	2,010 ± 0,049	2,060 ±
1	0,036	0,028	0,029	0,062	0,030	0,059		0,025
Time	1,924 ±	1,916 ±	1,952 ±	1,642 ±	1,922 ±	1,938 ±	1,890 ±	1,942 ±
2	0,050	0,076	0,010	0,248	0,032	0,056	0,035	0,050
Time	1,664 ±	1,894 ±	1,540 ±	1,528 ±	1,536 ±	1,466 ±	1,698 ±	1,912 ±
3	0,114	0,153	0,020	0,125	0,051	0,086	0,085	0,131
Time	1,898 ±	1,906 ±	1,924 ±	1,890 ±	1,854 ±	1,918 ±	1,894 ±	1,822 ±
4	0,066	0,073	0,066	0,021	0,028	0,054	0,068	0,066

CH₄ Experiment 1: Organic soil

CH₄ Experiment 2: Permafrost soils inoculated with 10 % organic soils

	Dry High Grubbing		Low Grubbing		Wet High Grubbing		Low Grubbing	
	A	Т	А	Т	А	Т	A	Т
Time 0	6,368 ± 0,443	2,732 ± 0,086	5,888 ± 0,513	2,51 ± 0,061	2,162 ± 0,080	2,964 ± 0,192	2,212 ± 0,071	2,782 ± 0,167
Time	9,916 ±	8,492 ±	11,422 ±	5,898 ±	3,406 ±	28,534 ±	4,978 ±	4,886 ±
1	0,702	1,421	1,156	1,140	0,690	12,505	1,112	0,758
Time	6,924 ±	6,228 ±	9,252 ±	6,512 ±	2,582 ±	6,052 ±	2,84 ±	3,252 ±
2	1,117	0,452	3,383	0,727	0,252	0,706	0,244	0,616
Time	6,252 ±	18,904 ±	6,266 ±	6,300 ±	3,462 ±	6,784 ±	3,422 ± 0,463	4,070 ±
3	0,985	6,787	1,358	1,433	0,261	1,261		0,677
Time	2,87 ±	8,594 ±	3,53 ±	4,406 ±	2,032 ± 0,060	4,396 ±	2,144 ±	3,160 ±
4	0,092	2,228	0,758	1,119		1,014	0,151	0,657

Table 6 Effect of vegetation type, grubbing intensity, and temperature on CH_4 emissions from organic soils (experiment 1) and from permafrost inoculated with 10 % of organic soils (experiment 2) depicted through each measurement period's mean value and associated standard error.

	Dry High Grubbing A	Т	Low Grubbing A	Т	Wet High Grubbing A	Т	Low Grubbing A	т
Time	1356,8 ±	2659,6 ±	5054,2 ±	5286,2 ±	910,2 ±	1606 ±	1342,8 ±	3108,6 ±
0	154,200	362,417	2252,691	2174,692	76,015	208,606	237,247	461,321
Time	958,6 ±	1210 ±	949,2 ±	1223,8 ±	831,8 ±	3006 ±	955,8 ±	1203 ±
1	46,899	73,159	33,227	96,528	32,948	1977,776	52,008	74,502
Time	858,4 ±	1038,8 ±	849,2 ±	917,6 ±	758 ±	952 ±	861 ±	1078,4 ±
2	38,907	47,179	37,739	166,595	23,994	37,409	43,205	39,921
Time	750,4 ±	1037,8 ±	769,4 ±	1016,6 ±	703,6 ±	1253,4 ±	765 ±	1020,2 ±
3	22,502	64,465	28,215	50,070	21,381	298,894	44,559	37,887
Time	789,2 ±	1131,4 ±	772,4 ±	1157 ±	713 ±	1020,6 ±	789 ±	1138,6 ±
4	42,437	54,991	28,331	85,968	12,625	24,782	34,756	43,415

CO₂ Experiment 1: Organic soil

CO₂ Experiment 2: Permafrost soils inoculated with 10 % organic soils

	Dry High Grubbing		Low Grubbing		Wet High Grubbing		Low Grubbing	
	A	Т	А	Т	A	Т	А	Т
Time	1078,6 ±	883,4 ±	1010,2 ±	818,2 ±	761,4 ±	1069,4 ±	794,8 ±	985,2 ±
0	49,490	35,298	25,340	17,628	22,884	102,670	20,575	82,193
Time	777,2 ±	1389,4 ±	758,8 ±	1402,4 ±	878 ±	5430 ±	1038,2 ±	1126,4 ±
1	20,991	104,394	25,755	153,125	57,679	4336,812	87,338	86,757
Time	1010,4 ±	1231,6 ±	1178,6 ±	1079 ±	822,6 ±	1041,2 ±	917,8 ±	993,8 ±
2	74,534	83,423	109,066	102,852	50,085	62,861	88,452	62,454
Time	1134,4 ±	1435,4 ±	1147,8 ±	1253,8 ±	917 ±	1082,6 ±	1147,6 ±	992 ±
3	16,818	126,109	59,502	97,350	31,354	99,625	182,076	43,696
Time	1006 ±	1088,8 ±	975,4 ±	1035,6 ±	777,6 ±	867,4 ±	754,8 ±	923,2 ±
4	77,390	105,941	43,969	61,071	53,664	99,240	44,893	24,983

3.4 Soil Geochemistry

3.4.1 Soil properties

As expected, wet moss tundra soils had higher soil gravimetric moisture content compared to dry moss tundra soils ($F_{1,40} = 13,630 P < 0,001$). Furthermore, grubbing decreased soil gravimetric moisture content for both vegetations ($F_{1,40} = 20,418, P < 0,001$). LOI ranged from 6,122 % to 54,047 % and it was higher in organic soils (34,135 ± 1,310 %) compared to permafrost alone soils (9,078 ± 3,046 %) ($F_{1,40} = 87,011, P < 0,001$). Vegetation did not have any main effect on organic soil; however, permafrost soil was almost doubled in dry moss tundra (11,836 ± 0,585 %) compared to wet moss tundra (6,319 ± 0,183 %). All organic soil LOIs were decreased by high grubbing ($F_{1,40} = 24,580, P < 0,001$). In both soils, pH ranged from 5,550 to 5,760. Organic soils for wet moss tundra (6,125 ± 0,075) had higher pH values than dry moss tundra (6,045 ± 0,073) ($F_{1,40} = 5,454, P = 0,008$) and grubbing decreased pH for all organic soils ($F_{1,40} = 3,275, P = 0,048$). Moss tundra type did not affect pH for permafrost soils.

3.4.2 Bulk soil C and N

Soil N and C % did not differ between the two vegetation types (Figure 17). Soil N had an average of 0,616 % while soil C was 14,693 %. N ranged from 0,216 % to 1,067% and C ranged from 2,981 % to 26,706 %. For the factors studied, grubbing decreased N and C content in organic soils by approximately 18 % and 26 % respectively from their low grubbing quantities. In permafrost soils, the dry moss tundra had approximately 36 % higher nitrogen and 72 % higher carbon than the wet moss tundra (Figure 17). Furthermore, C:N in permafrost was approximately 26 % higher in the dry moss tundra (17,248 \pm 0,407) than in the wet moss tundra (13,625 \pm 0,102). C:N did not differ between vegetation type in organic soil, yet it ranged from 20,440 to 29,060 with a mean of 24,96 in comparison to the 13,440 to 17,790 range in permafrost with a mean of 15,440.

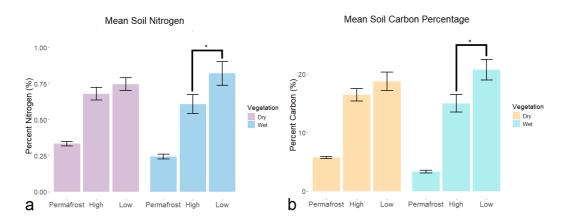


Figure 17 Nitrogen (a) and C (b) content (%) in organic soils in the wet and dry moss tundra vegetation at the high and low grubbing intensity and in permafrost soils in the wet and dry moss tundra vegetation (mean \pm SE)

3.4.3 Soil extractable nutrient availability

Soil total extractable N (TEN) was higher in the wet moss tundra compared to the dry moss tundra, and this was true for both organic (1892,000 ± 217,503 µg/L) and permafrost soils (4000,000 ± 305,505 µg/L) ($F_{1,40} = 16,403, P < 0,001$). Organic soils in the wet moss tundra had an average of double the TEN compared to dry moss tundra. Nevertheless, grubbing did not affect TEN. Permafrost had more than double the TEN than in organic soil ($F_{1,40} = 35.859, P < 0,001$).

Higher levels of NO₃ ($F_{1,40} = 11,284$, P = 0,002) and NH₄($F_{1,40} = 6,989$, P = 0,012) were observed in the wet moss tundra. NO₃ ranged between 6,340 and 50,340 µg/L with a mean of 14,830 µg/L while NH₄ ranged between 3,290 and 1500,50 µg/L with a mean of 432,030 µg/L. NH₄ was affected by grubbing intensity, and had higher values with grubbing ($F_{1,40} = 6,989$, P = 0,012). Organic N ranged between 491,100 and 4262,100 µg/L due to the presence of a few high outliers; nevertheless, the mean was only 941,600 µg/L for the 40 samples. While organic N was unaffected by grubbing, it was influenced by vegetation type. Wet moss tundra (1246,178 ± 246,617 µg/L) had more organic N than dry moss tundra (637,1025 ± 28,859 µg/L). PO₄ ranged from 2,610 to 9,160 µg/L and was higher in low grubbing ($5,023 \pm 0,406 \mu g/L$) than high grubbing ($3,799 \pm 0,279 \mu g/L$) conditions ($F_{1,40} = 6,421$, P = 0,016).

Dissolved organic carbon (DOC) was highest in permafrost soils (263,000 \pm 26,800 mg/L), with double the amount in the organic soils (132,00 \pm 14,700 mg/L) ($F_{1,20} = 18,598$, P < 0,001). DOC ranged between 7,190 and 395,000 mg/L.

4. Discussion

The study sites of this thesis were located in the High-Arctic tundra of Svalbard, typically composed of mosaic plant communities due to the ecosystem's rapid change in topography and soil microclimates over short distances (Petit Bon et al., 2023b; Tømmervik et al., 2014). A deep understanding of both aboveground and belowground abiotic and biotic properties is vital in order to comprehend the processes directing C emissions from soils in this environment. Additionally, biotic disturbances, such as *Anser brachyrhynchus* grubbing, can change the abiotic interactions dramatically, leading to divergent soil respiration and plant community composition (Pedersen et al., 2013; Petit Bon et al., 2021). Therefore, this study has set out to combine observational field data with a controlled laboratory experiment to better understand the effect of different soil properties and plant communities on overall ecosystem processing, specifically C and N cycling.

4.1 Contrasting Plant Communities

At the field site, the two vegetation types were defined by their moisture content in the topsoil layers: a dry moss tundra habitat and a wet moss tundra. Both soil gravimetric moisture content and field moisture microclimates confirmed that the wet moss tundra plant communities had higher moisture content than the drier habitat. In past literature, high abundance of bryophytes has been found to be directly related to higher soil moisture levels (Tømmervik et al., 2014; Petit Bon et al., 2023a). However, in this study, moss abundance did not differ between the dry and wet moss tundra. It is likely that other biotic and abiotic properties also played an important role in determining soil moisture in both habitats, such as soil texture, topography and plant root network. Therefore, I was unable to find a divergence based on moisture content alone.

Mosses were the most abundant functional group in both vegetation types, which is consistent with past observations of High Arctic ecosystems (Longton, 1984; Gornall et al., 2009; Tømmervik et al., 2014). In terms of all species, wet vegetation had a higher abundance of vascular plants. Higher soil moisture has been identified to lead to higher plant productivity according to previous research (Campbell et al., 2021). Moisture content in Arctic soils is an important factor to plant productivity, and water stress has been seen to potentially limit plant productivity as well as CO₂ uptake, creating a habitat without the abiotic conditions to use available resources during peak growing season (Zona et al., 2023). Furthermore, higher moisture increases water availability, transportation of nutrients to plant roots, regulation of soil temperature, and it provides favourable conditions for microbial activities which can increase pathways for nutrient availability (Kemppinen et al., 2021; Berdanier and Klein, 2011). This can, therefore, explain why the wet moss tundra habitat had a higher plant abundance.

In our site, graminoids and forbs were more abundant in the wet moss tundra compared to the drier vegetation. Graminoid growth is dependent upon the moisture content within the upper 10 cm of the soil profile, causing the functional group to dominate in wet soils as shown in this study's threefold abundance in wet moss tundra (van der Kolk et al., 2016). However, the co-dominance of forbs is divergent from previous work, with forbs being typically found at higher abundance at drier sites (Tømmervik et al., 2014). In combination with slower decomposition rates caused by moisture saturation and lower soil temperature, the higher productivity contributes to a thicker organic layer at wet moss tundra vegetation. The organic layer is composed of dead plant material and decaying organic matter which tend to accumulate under unfavourable conditions.

Active layer thickness (ALT) can shift based on a variety of factors, such as organic layer thickness, topography, and soil drainage on a local scale (Schaefer et al., 2014; Sazonova et al., 2004; Nelson et al., 1998); nevertheless, the regional climate highly impacts ALT due to the ability to thaw at higher temperatures and period of spring snowmelt (Schuur et al., 2015; Nelson et al., 1997). It was found that the site dry moss tundra had a larger ALT with a smaller organic layer depth. This is consistent with findings in the Siberian Arctic, where areas with a lower moisture content were found to have larger ALT (Sazonova et al., 2004). However, studies in Alaska have found ALT near bodies of water as well as high moisture environments to be thicker (Nelson et al., 1997; Nelson et al., 1998). This shows a high variability depending on other abiotic factors, such as topography and soil type, as ALT is not consistent across the arctic, nor local areas (Westerman et al., 2010; Schuh et al., 2017). Both studies in Alaska showed variability in these factors when recording the depth of the ALT (Nelson et al., 1997; Nelson et al., 1998); nevertheless, neither had data relating to the organic layer depth. Hence, for studies with organic layer depth, even areas where higher moisture had a thicker ATL, the organic later was still smaller (Shiklomanov et al., 2010). This suggests that the relationship between the organic layer and ALT could be more important than the relationship between ALT and moisture content. Organic layer thickness has been found to indirectly correlate with ALT in the Arctic tundra (Zhou et al., 2013; Schaefer et al., 2014; Shiklomanov et al., 2010). So, less plant biomass and a thinner organic layer can explain the increase in active layer in the dry vegetation.

I hypothesized that vegetation type would induce changes in plant nutrient contents. This proved correct for N as the levels were higher in dry moss tundra. This is supported by previous High Arctic tundra studies where N levels were 13 % higher in mesic than wet habitats (Petit bon et al., 2023a). In comparison, Alaskan low arctic N mineralization rates have been shown to increase with higher moisture content (Binkley et al., 1994). Another study divided leaf N levels

into plant functional groups and found a scale of N abundance: forbs, graminoids, deciduous shrubs, then evergreen shrubs from highest to lowest (Thomas et al., 2019). This correlated with the overlapping functional groups, as *B. vivipara* (a forb) had the highest N level by a wide margin, followed by *S. polaris* (a dwarf shrub). Furthermore, previous studies have suggested that the species differentiation in compound for N uptake could be a form of competition to allow coexistence in the harsh High Arctic tundra, and that the dominant species can be determined by the available N source (McKane et al., 2002). This correlates with the differentiation of each species and their N content.

As hypothesized, the effect of vegetation on ¹⁵N also changed dramatically between functional groups. This is consistent with previous studies on ¹⁵N, as species uptake different forms of N either in the soil or the atmosphere, creating a wide range of ¹⁵N between groups (Nadelhoffer et al., 1996). Mosses mainly obtain N through N₂ fixation through the atmosphere (Rousk et al., 2017), while other plant functional groups uptake N through organic or inorganic forms, leaving behind divergent ¹⁵N signatures: NH₄ and NO₃ (through denitrification) increase ¹⁵N while organic N decreases ¹⁵N (Nadelhoffer et al., 1996). Furthermore, the relationship between the species and mycorrhiza will differentiate ¹⁵N, as non-mycorrhizal species will have higher ¹⁵N while mycorrhizal relationships allow for isotope fractionation when ¹⁵N is transferred to the plant (Craine et al., 2009).

Wet moss tundra had higher levels of inorganic N in extracted soil in the form of NO₃ and NH₄.; however, N levels were small as supported by the fact that N is a limited resource in the Arctic tundra (Chapin, 1987). N mineralization in the Arctic is significantly smaller than lower latitude ecosystems, with tropical soils having the potential for more than 200 times greater N mineralization than the Arctic (Nadelhoffer et al., 1991). NO₃ was smaller than NH₄ in the study. This is consistent with previous field studies of Arctic tundra N predominance (Nadelhoffer et al., 1991), as one chemical process to form NO₃ is nitrification starting from NH₄ (Paul and Clark, 1989). Hence, NH₄ is more dominant in the Arctic tundra where low soil temperatures may limit chemical processes during unfavourable conditions. Furthermore, NO₃ is much more easily leached by water content in the organic soil due to its negative charge, allowing for N loss in the local habitat (Nadelhoffer et al., 1991). Overall, organic N is the main form of N, with a mean value double the NH₄ and 63 times the NO₃.

The C:N ratio was higher for organic soil than permafrost soil, suggesting an increase in fungi dominance in the organic soil (Cleveland and Liptzin, 2007). As the permafrost soil was frozen until after removal from the field site, this would suggest that permafrost has a limited mycorrhiza community due to the inaccessibility of the soil before thawing. Fungi have a higher C:N ratio because they need more C for each N, therefore, immobilizing less N (Cleveland and Liptzin, 2007). This fits well with a N limited environment and has already been seen in High Arctic tundra ecosystems (Chapin, 1987). C and N cycling is highly dependent on soil properties, such as microclimates and plant interactions (Thornton et al., 2007). C:N dynamics are vital to understanding the Arctic tundra

with warming temperatures because systems with higher C availability then increase the demand for N uptake in plants, which can further amplify the N limitation of the High Arctic tundra (Thornton et al., 2007)

DOC content did not vary depending on the vegetation, but instead the soil type. This is consistent with previous studies that show permafrost DOC to be higher than the active layer DOC; additionally, the permafrost DOC has higher biological decay potential due to the release of C from long term storage (Panneer Selvam et al., 2017). TEN was also higher in permafrost soils and can be explained through the long-term storage without microbial access. TEN doubled in organic wet moss tundra compared to dry moss tundra. This contrasts with previous studies where higher moisture limited N mineralization (Nadelhoffer et al., 1991); nevertheless, only 10 % of the total N mineralization in this environment is absorbed by plants, with the remainder kept by the microbial community, or leached (Nadelhoffer et al., 1992). Hence, it is more important to observe that form of N, instead of the high TEN levels.

4.2 Goose Grubbing

Anser brachyrhynchus arrives in Svalbard in the spring for mating with limited body fat due to the long migration; therefore, in order for the females to produce offspring, they must consume 25 % of their body weight from grubbing in a short period of time (Fox et al., 2006; Fox and Bergersen, 2005; Owen, 1980). This study found a large decrease in the organic layer depth as the geese remove this top soil layer in order to reach their belowground food source. The geese must also remove the moss layer to reach their food source; therefore, grubbed patches have a significant reduction in moss layer (Gornall et al., 2009).

The moss and organic layers combine to create an insulation effect for the organic soil, explaining why the higher grubbing sites had warmer microclimates. Essentially, the two layers create an insulation layer on the soil correlating directly to the thickness of the layers (Schuur et al., 2008). Any potential changes in soil temperature must have a large enough quantitative increase in energy to raise the temperature above the threshold of this insulation layer (Gornall et al., 2009). In context of soil microclimates, sites with less intact moss present a diminished insulating layer; therefore, less energy is needed to raise the temperature in these locations. This insulation effect can explain why high grubbing intensity decreased gravimetric soil moisture in both vegetation types. Geese removed sections of the organic and moss layers, decreasing the organic layer depth and allowing for the patches of bare soil or patches with unconnected moss to be exposed to the atmosphere. Hence, soil evaporation will occur and the moisture per unit of soil will decrease. This does not mean that the two vegetations will have the same moisture, as is apparent by the divergent moisture content, but that moisture is decreased in these patches.

Furthermore, it was found that within grubbed sites, a higher percentage of grubbing occurred in dry vegetation. Previous reports in the Arctic have produced

slightly divergent results based on which moisture habitat geese prefer to grubwet (Anderson et al., 2012; Speed et al., 2009) or dry (Pedersen et al., 2013). Anderson et al. (2012), predicted wet vegetation to have higher grubbing preference due to the higher abundance of plant matter. Pedersen et al. (2013) found that grubbing has increased in dry vegetation in relation to snow cover melting earlier in the spring season. Nevertheless (Anderson et al., 2012) found that even if geese are selecting to grub in dry conditions, it was found that they still prefer wet conditions and geese will grub wet habitats at a higher frequency even if dry habitats are available. One reason that higher grubbing was recorded in the dry habitat at the end of July (about 2 months after spring grubbing) based on percentage of moss removed, could be that dry habitats have a lower resilience to grubbing (Speed et al., 2010). This slow recovery rate in dry habitats, in particular, is common across High Arctic ecosystems (Pedersen et al., 2013).

Despite the observed strong reduction in the moss layer, mosses were still abundant after grubbing in both high and low intensity conditions. In the post grubbing habitat, plant functional groups can shift due to changed abiotic conditions (Petit Bon et al., 2023b; Bjorkman et al., 2020). It was found that graminoids, forbs, deciduous shrubs, and moss were all reduced by grubbing. Vascular plants are more responsive in C and N content from disturbances than soil or mosses; therefore, grubbing could create shifts in plant chemistry with a higher sensitivity in dry habitats (Petit Bon et al., 2021; Pedersen et al., 2013). This was partly in line with our observation with *B. vivpara* and *S. polaris* having increased N levels with high grubbing conditions.

Nevertheless, grubbing is a single factor affecting the functional group dominance. When discussing the effect of grubbing as a disturbance towards Arctic ecosystem functioning, temperature can have an opposing effect. A warmer climate promotes some of these same species being decreased by grubbing: graminoids and deciduous shrubs (Bjorkman et al., 2020; Martin et al., 2017). However, these two effects could also work together. This study found that deciduous shrubs were decreased in the dry moss tundra with high grubbing. Bjorkman et al. (2020) found this the functional group to decrease in colder, dry tundra. Hence, deciduous shrubs could increase in warmer, wetter climates while being removed from dry, colder climates.

Previous models have suggested that current losses in plant and soil N through herbivore disturbances will be stabilized over longer periods of time through the appearance of new dominant species and competitive N uptake (Walker et al., 2003). However, this does not account for the exponential increase in *A. brachyrhynchus* populations, and the associated increase in grubbing intensity (Pedersen et al., 2013; Fox et al., 2005; Fox et al., 2006; van der Wal et al., 2007). Across previous studies, there is still no consistent observation towards the consequences of herbivory, such as goose grubbing, on the nutrient content in plants in the High Arctic tundra. Herbivores do cause a shift in nutrient uptake in plants (Barthelemy et al., 2018), yet there is not a reliable change for all Arctic habitats with some herbivory increasing and others decreasing nutrient content (Barthelemy et al., 2017; Barthelemy et al., 2018; Fox and Bergersen, 2006; Gornall et al., 2009).

Large herbivores have been shown to increase the soil and plant nutrient availability through grazing (Barthelemy et al., 2017); however, this study did not show the same effect for grubbing based on the lack of effect on TEN, organic N, and NO₃. Only NH₄ had increased levels with grubbing. Locations with grubbing or grazing from larger herbivores such as reindeer, will have N uptake through urine and faeces (Barthelemy et al., 2018). Faeces are quite rich in nutrients, especially N from consumed plant matter, allowing for recycling of nutrients after removal (Hobbs, 1996). Nevertheless, the availability of nutrients from faeces can take years before plants can uptake it (Barthelemy et al., 2018) Urine on the other hand quickly returns across all functional groups (Barthelemy et al., 2018). In the study, N content across all functional groups increased after grubbing, and it tended to have a positive effect on the species level. This could be explained partially through urine.

Another, more prevalent, explanation could be the effects of herbivores on ¹⁵N. High herbivory intensity can increase ¹⁵N levels within Arctic tundra plants due to reduction of mycorrhiza in plant roots and increase of easily accessible N compounds (Barthelemy et al., 2017; Barthelemy et al., 2018). The two species with increased plant N content, also had increased ¹⁵N levels at high grubbing, showcasing that they were able to adapt to the grubbed conditions. *B. vivipara* and *S. polaris* have been documented to have ectomycorrhiza symbiosis in some Arctic tundra habitats (Clemmensen et al., 2008; Ryberg et al., 2011). One job for mycorrhizae in Arctic tundra is to access N at a deeper soil profile, as 90 % of tundra plant roots are located in the soil at the top 30 cm (Hewitt et al., 2018; Jackson et al., 1996). It is possible that the two species decreased symbiosis with their ectomycorrhiza due to the high N content. Essentially, mycorrhizal relationships are expensive for the plant and in abundance, there is no need to waste energy on the potential deep nutrient uptake (Hewitt et al., 2018).

4.3 Laboratory Soil Incubation: CO₂ and CH₄ Emissions

I incubated organic soils, permafrost soils and permafrost soils inoculated with 10% organic soils for 4-months under two climatic conditions, 4 °C and 10 °C with monthly C flux measurements. The inoculation treatment was a combination of 36 g permafrost and 4 g organic soil (10 % inoculation) in order to showcase the effect of permafrost thaw mixing with the microbial community of the active layer. I hypothesized that the total C emissions would be higher in organic soil in recognizable patterns for vegetation type, CO_2 emissions would be found at a higher magnitude than CH_4 , and warming conditions would increase both gas emissions with CH_4 being more sensitive to the shift in temperature.

Carbon emissions in this study were significantly higher in organic soil for CO_2 while CH_4 organic emissions were the smallest of its soil types. This can be explained by the movement of C throughout Arctic soil profiles. Organic soil is found within the active layer and is where the majority of organic decomposition and soil respiration occurs (Schuur et al., 2008). This is likely why organic soil in my study emitted more CO_2 . Nevertheless, CH_4 is released through the consumption of organic matter by methanogens in anoxic conditions (Le Mer and Roger, 2001); therefore, thawed permafrost provides a better environment for this production compared to aerobic conditions of the organic soil. This can clearly be seen by the total emissions. The percentage of CH_4 emissions from organic and permafrost soils were almost the same, yet organic soil had over 3 times as many samples (40 compared to 12 samples). Hence, it can be concluded that permafrost is a much better environment for CH_4 emissions than organic soil.

 CO_2 emissions in this experiment were much higher than CH_4 because an aerobic decomposition of organic matter results in a much lower emission level than aerobic conditions (Schuur et al., 2008). Nevertheless, even if CH_4 emissions are less abundant, CH_4 has a higher global warming potential than CO_2 (IPCC, 2014; Schädel et al., 2016). Therefore, it can be said that permafrost thawing has a higher potential of warming by allowing this stored carbon to enter the carbon cycle, as well as providing a potential source of CH_4 production. If large amount of CH_4 is emitted into the atmosphere, it could create a feedback loop of continued warming as CH_4 holds more heat than CO_2 , and would, therefore, create a warming effect to further thaw permafrost (Hugelius et al., 2014; Schaefer et al., 2014; Schuur et al., 2008).

Warming temperature conditions induced higher C emissions for both gases, as hypothesized. This is supported through the International Panel on Climate Change (IPCC) reports, as well as research experiments throughout the High Arctic (IPCC, 2013; IPCC, 2014; IPCC, 2021; Faucherre et al., 2018; Hugelius et al., 2014). However, in this study, temperature had a more predominant effect on CO₂ emissions for organic soil, and on CH₄ emissions for inoculated soils. The effect of temperature on organic soil was largely independent from the other factors. Furthermore, CH₄ emissions in organic soil were unresponsive over time to the factors other than temperature. Nevertheless, the effect of temperature was not consistent through the measurement periods. The increase in CO₂ emissions with higher temperature can be explained by the increase in kinetic energy allowing for increased metabolic activity, resulting in a higher breakdown of organic C by microbial communities (Le Mer and Roger, 2001; Tarnocai et al., 2009; Schädel et al., 2016). The increase in microbial decomposition will release higher quantities of CO₂ as the byproduct of soil respiration (Le Mer and Roger, 2001). While not addressed in this thesis, warming conditions can induce shifts in the microbial community composition, in order to favour bacteria and fungi species that are better at organic matter decomposition and less easily accessible organic matter (Yang et al., 2021). Therefore, it is important to fully understand the processes driving CO₂ emissions in a warming climate in order to predict how the Arctic ecosystem will respond to the predicted change in climate.

Higher CH₄ emissions observed in permafrost inoculated with 10 % organic soils could be explained by CH₄ production, which is more prevalent in warmer temperatures as the methanogenic microbes (archaea communities) are more active at higher temperatures (Howard et al., 2020). Methanogens can convert organic substrates into the byproduct of CH4 across a wide range of temperatures (Nozhevnikova et al., 1997); nevertheless, methanogenic microbe metabolism increases directly with temperature, allowing for a higher consumption of organic matter (Blake et al., 2015). The permafrost inoculation with 10 % organic soil in this experiment creates an environment with a higher potential number of methanogenic microbes as well as new substrates that can decompose and be converted into CH_4 . The high CH_4 emission at the first measurement for the higher temperature can be explained by the increased temperature and substate availability creating a more suitable environment for methanogenesis. The incubation jars were in the climate chambers for 48 h before the first measurement, granting plenty of time for the microbial community in the organic soil to access the thawed carbon in the permafrost (Howard et al., 2020).

The main treatment effect on permafrost was not temperature, but vegetation type. Dry moss tundra vegetation had higher CH_4 emissions in every measurement other than at the second month, and higher CO_2 emissions from the second month until the end of the incubation at 4 months. This late appearance of vegetation significance in permafrost CO_2 emissions could potentially be explained by more labile organic matter in the wet soil that would have been more easily available; however, once used, the organic matter, which is harder to break down, would allow for higher emissions as the incubation progressed. Wet vegetation had higher plant abundance and organic matter, which could potentially explain this. Currently, studies looking at permafrost processes in different vegetation types are rare, suggesting that our data contributes to addressing this significant knowledge gap.

Grubbing had an initial effect on organic soil in both gases, but in opposite directions. CO₂ had higher emissions at low grubbing conditions which could be explained through the presence of organic matter from the higher proportion of remaining plant abundance as CO₂ respiration increases with SOC in favourable conditions (Tarnocai et al., 2009). High herbivore grubbing can directly reduce the level of C uptake in the habitat (van der Wal et al., 2007), and so low grubbing and high plant productivity would increase CO₂ emissions. This disappeared after one month of C respiration, suggesting that the additional SOC in this condition was heavily used throughout that month, creating a more even SOC level between grubbing conditions by the second measurement. CH₄ had higher emissions with high grubbing which could potentially be from the warmer microclimate conditions creating a better suited environment for methanogens (Howard et al., 2020; Blake et al., 2015). Permafrost soil inoculated with 10 % organic soil had higher CH₄ emissions with high grubbing intensity in two unconnected measurements. This was unexpected, and there is a large probability that this is background noise as the measurements are separated by 2 months. If there was a factor in the above- and belowground interaction, it would appear consistently or with a pattern compared to this random result.

Petit Bon et al. (2023b) ran a field experiment in the same location as this study (Adventdalen) to see how geese grubbing and reindeer grazing affected C fluxes in the organic soil. He created two study systems: one for 15 years with no geese grubbing, and one for 21 years without reindeer grazing. In the short term, the removal of geese increased CO_2 emissions four-fold (Petit Bon et al., 2023b). This is a similar result to this study's increased CO_2 in the first measurement period. Nevertheless, the long-term rate of CO_2 emissions observed by Petit Bon et al., (2023b) did not continue to increase rapidly, and instead got smaller throughout time. This could help explain why grubbing was not significant in each measurement in this study, because if a long-term field experiment with renewed plant abundance failed to increase each year, it is unlikely an incubation study with limited SOC could continue to show the effect for 4-months once SOC starts to be used.

4.4 Conclusion and Future Directions

In this thesis, I examined the effects of plant composition and grubbing on abovebelowground relationships. This included an in-depth investigation of field data in the High Arctic tundra from two contrasting plant communities at Svalbard and a montly measurement of C fluxes in a laboratory 4-month incubation of organic soil, permafrost soil, and permafrost inoculated with 10 % organic soils. I found that wet vegetation supported higher plant productivity and a thicker organic layer decreased that ALT. Vegetation type had a direct effect on nutrient availability in plants and soil for forms of inorganic N, yet this was dependent plant functional groups. However, the main finding is confirming that Arctic tundra habitats are N limited with a large organic N level, and small inorganic N levels. Furthermore, goose grubbing has an effect on below-ground factors due to the above-ground effect on moss depth, organic layer, and plant removal. This, therefore, changes the soil temperature, moisture, N content, and mycorrhizal interactions.

These background interactions then come together to affect C emissions. CO_2 emissions were over 99 % of the total emissions; nevertheless, soil type, vegetation type, and warming conditions shifted the level of emissions observed. Warming conditions resulted in higher CO_2 and CH_4 emissions, with a prevalent effect for CO_2 in organic soil and CH_4 in permafrost soil. Additionally, dry vegetation had higher CH_4 emissions in 4 measurement periods, and higher CO_2 emissions after the second period. The inoculation of permafrost soil with 10 % organic soil led to novel findings for vegetation type and temperature.

The important and novel findings of this thesis call for further investigations. There are certain factors that would benefit from changes to the experimental methods, such as an increase in sample size for permafrost soil. Organic soil had 40 samples and permafrost soil with 10 % organic soil had 40 samples, yet permafrost soil only had 12 samples. These 12 samples consisted of two pseudoreplicates repeated for a total of 6 replicates for each vegetation as all permafrost cores of the same vegetation were combined into a singular sample. If it was possible to have a higher quantity of permafrost cores, and corresponding samples, this could produce much better results on the release of CH₄ in a changing environment. Furthermore, it would be interesting to have shorter measurement intervals, as significant changes occurred within the two-day period of incubation prior to the first measurement. If I could run the experiment with measurements twice a month, a clearer timeline could be established for changes due to temperature and interaction effects.

The findings of this thesis are important to understand High Arctic ecosystems response to two important ongoing threats, the overexploitation of the tundra by the *A. brachyrhynchus* population and warming with dramatic increase in temperature in two contrasting plant communities. This work highlights the importance of investigating C emissions from organic and permafrost soils and their impact on a global climate. Permafrost thawing is occurring at an unprecedent rate across the Arctic (IPCC, 2013) with a disproportionate impact to the global carbon cycle. Therefore, it is vital to research all possible factors contributing to it. In this thesis, I selected three important factors: herbivory disturbance, warming, and contrasting soil types with their complete above-belowground interactions. The future rate of permafrost thawing, and release of carbon remains largely unknown, promoting the need for continued research into understanding the implications and components of permafrost thaw in High Arctic ecosystems.

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Popular science summary

High Arctic locations are exhibiting an increase in temperatures. This warming environment is allowing for the deep soil to thaw, even though it has been frozen for thousands of years. This can be dangerous because the deep soil can contribute more to warming through the release and breaking down of carbon. The soil is thawing at divergent rates throughout the Arctic depending on factors such as vegetation, moisture levels, thickness of the moss covering it, and disturbance from herbivores such as reindeer and geese. My study set out to look at a combination of these factors to see how the environment changed, and how the level of carbon being released changed in Adventdalen. This was accomplished by taking measurements at the location, collecting soil, and then placing the soil in an incubation chamber, which is similar to a fridge in which the temperature can be adjusted. One chamber was set to a normal summer temperature for Adventdalen, and another was set to a warmer temperature predicted to occur in the future from previous studies. I was able to figure out that areas in Adventdalen with higher moisture in the soil support a higher level of plant life and these plants provide a better nutrient availability in the soil. Nevertheless, the nutrients depend on the type of plant, but they were present in small amounts. This environment is heavily limited by nutrients, as it is cold, and it can be hard for nutrients to form. I was able to find that geese create a large shift in nutrients as they dig for food, removing plants and the moss covering the soil. This can warm the soil and reduce moisture levels as the sun can evaporate it. Through the climate chambers, I found that the soil emitted carbon at a much higher rate in the shallow soil, but that a different form of carbon, called methane, was released more from the deeper soil being thawed. The warmer environment released more carbon for both shallow and deep soil. Finally, the soil released more methane if it had less moisture.

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