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Shifts within the carbon cycle in response to the absence of keystone herbivore *Ovibos moschatus* in a high arctic mire



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Master thesis, 30 credits, in *Physical Geography and Ecosystem Analysis*

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Abstract

Tundra ecosystems are generally recognized as globally important carbon sinks, yet the knowledge on threats to such ecosystems is narrow. Climate change is predicted to reduce the number of muskox (*Ovibos moschatus*) in the arctic, it is therefore essential to understand the effect herbivores induce on the arctic ecosystem. The muskox is known as a keystone species in the arctic tundra. Such keystone herbivores can induce strong top-down control, resulting in a transformed landscape when not present. Little is known about how herbivores impact the terrestrial carbon cycle, especially in arctic mires. Within this study, I evaluate whether the absence of grazing and trampling by the large herbivore muskox influences vegetation density and composition, subsequently altering the exchange of greenhouse gases between the atmosphere and tundra. During July 2016, CO₂ and CH₄ fluxes were measured in experimental muskox enclosure and control plots at Zackenberg, north-east Greenland. Vegetation and core samples were analysed for variances in composition and density. Furthermore, environmental parameters including soil temperature, water table depth, active layer and photosynthetic active radiation were measured. A significant change in the composition of vascular plants occurred and lower number of tillers of *Eriophorum scheuchzeri* and *Dupontia psilosantha* were recorded in enclosure plots. This change in vegetation resulted in no significant difference between net ecosystem exchange, gross primary production and ecosystem respiration with no below-ground root biomass variance. However, significantly lower CH₄ fluxes were recorded within the enclosure plots. I speculate that the difference between treatments is an ongoing divergence from a vascular plant community towards a less diverse moss dominated layer. As time goes on more structural differences below ground are predicted to occur. While it is uncertain if herbivory in the arctic will increase or decrease, this experiment indicates potentially significant effects on the vegetation composition and its subsequent impact on fluxes of the greenhouse gas CH₄.

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List of abbreviations

NEE – Net Ecosystem Exchange

GPP – Gross Primary Production

R_{eco} – Ecosystem Respiration

WtD – Water Table Depth

PAR – Photosynthetic Active Radiation

C – Control treatment

Sn – Snow treatment

Ex – Exclosure Treatment

CO₂ – Carbon Dioxide

CH₄ – Methane

O₂ – Oxygen

1.0 Introduction

The arctic environment has undergone rapid change throughout the late Pleistocene and Holocene (Larsen et al., 2014). In 2014, the Intergovernmental Panel on Climate Change (IPCC) predicted with *medium confidence* that the transformed phenological responses observed in arctic terrestrial ecosystems can be attributed to the observed warming trend (Larsen et al., 2014). The IPCC showed that a significant greening of the pan arctic area had occurred during 1982 to 2012 and is expected to increase primary production within the arctic region (Xu et al., 2013). It is *likely* that the vegetation changes will result in an overall positive feedback on the climate (Larsen et al., 2014). However, predictions made by the IPCC models have not yet include herbivory within these regions; therefore, it remains important to investigate such affects.

The arctic covers about 16% of the global land surface, but it is estimated to hold approximately 50% of the Earth's below-ground stores of organic carbon (Post et al., 1982; Tarnocai et al. 2009). Mires are highly productive and sequester large amounts of carbon due to the slow decomposition rates experienced under anoxic conditions (Tarnocai et al., 2009). It has been demonstrated that herbivory influences whether arctic mires act as a net sink or source of carbon (Sjögersten et al., 2011; Falk et al., 2014; Falk et al., 2015) and that certain species of herbivores, such as the muskox (*Ovibos moschatus*) might act as keystone species to ecosystem productivity (Sjögersten et al., 2011; Falk et al., 2014; Falk et al., 2015).

Kerby and Post (2013) investigated this rapid change in the arctic. Their study discovered multiple ecological changes within the arctic and included phenological mismatches to structural change in the composition of biotic communities (Kirby and Post, 2013). One such structural change highlighted, was the ability of herbivores to alter tundra ecosystems (Post and Pedersen, 2008; Olofsson et al., 2009; Kirby and Post, 2013; Falk et al., 2015). As half of the Earth's land surface is influenced by large herbivores (Olf et al., 2002), it is important to consider the influence herbivores hold on global ecosystems. Large herbivores not only graze vegetation but also trample upon it, thus altering the competitive interactions between different plant species (Barrio et al., 2016).

Falk et al (2015) found that muskox grazing and presumably trampling in mires influences the vegetation density and composition, which results in less primary production and a weaker carbon sink. However, when investigating the carbon cycle previous studies have primarily focused upon environmental driving processes. Often studies excluded the physical processes such as herbivore trampling that may be contributing towards shifts within the carbon cycle. Therefore, within this study I aim to investigate whether the shifts in vegetation density and composition of plant species within exclosure plots discovered by Falk et al (2014), has continued to deviate from control plots. I therefore hypothesise that:

- H₁: The exclusion of large herbivores will lead to a decrease in plant density with lower total number of tillers.

Falk et al. (2015) results indicated that the arctic landscape shifts from vascular plants to a moss cover when large herbivores are absent. The lack of vascular plants will result in less below ground biomass therefore; I aim to investigate whether this shift contributes to a lower density of below ground biomass. Due to its dense nature, the root biomass may act as a physical barrier inhibiting or slowing the flux of greenhouse gases. This physical process may work in collaboration with biological processes and alter the rate of CH₄ flux and contribute to the concentration of dissolved CH₄ in pore water. Therefore, my second hypothesis states that:

- H₂: The exclusion of muskox trampling will result in a lower root biomass density thus leading too lower CH₄ fluxes.

The combination of the two hypotheses within this study aims to strengthen the results discovered by Falk et al. (2015). This study differs from Falk et al. (2015), by examining the development of the vegetation community and investigating whether the observed progression has contributed to below ground biomass.

2.0 Background

2.1 Components of the carbon cycle

Amongst the global environment, freshwater wetlands hold one of the highest gross primary production (GPP) rates reported in terrestrial ecosystem (Keddy, 2000). Emergent and comparably productive plants such as *Eriophorum*, *Dupontia* and *Carex* often dominate the vegetation of many arctic wetland ecosystems (Jensen et al., 2016).

The indication of whether an ecosystem acts as a sink or source of carbon can be estimated by measuring the net ecosystem exchange (NEE), which represents the balance of carbon fixed via photosynthesis, i.e., GPP, and carbon loss through ecosystem respiration (R_{eco}) and is represented in equation 1. The carbon dioxide (CO_2) returned to the atmosphere via R_{eco} is the sum of both plant (autotrophic) and biota (heterotrophic) respiration. The major component of heterotrophic respiration originates from below ground organisms decomposing organic matter, such as litter fall, root turnover, root exudation, dead organism and faecal matter (Kirschbaum et al., 2001). A negative value indicates a net uptake of carbon while, a positive value indicates a release to the atmosphere (Luysaert et al., 2007). Two common methods to estimate NEE are by the closed-chamber analysis or eddy-covariance approach (Schlesinger and Bernhardt, 2013).

$$NEE = GPP - R_{eco} \quad (1)$$

There are two likely explanations as to why such high productivity occurs in wetlands. First, wetlands hold high rates of GPP, which directly lead to high NEE if R_{eco} is low (Rocha and Goulden, 2008). Often in wetland ecosystems, R_{eco} is low due to the anoxic conditions created from the high water table depth (WtD) and low temperatures (Gibbs and Greenway, 2003; Schlesinger and Bernhardt, 2013). These low temperatures and WtD limit the O_2 reaching the peat layer (Marion and Black, 1987), thus slows the decomposition of organic material. Therefore many arctic wetlands often show a net accumulation of carbon, consequently acting as sinks to atmospheric CO_2 (Oechel et al., 2000).

2.2 Methane production in wetlands

2.2.1 Production

In order to understand the productivity in wetlands, it is necessary to understand the final product of the process, methane (CH₄). CH₄ is a product in the complex process of anaerobic degradation of carbon and is produced by microbes from the domain *archaea* (Zehnder and Stumm, 1988). This process is only used when all other higher favoured electron acceptors have been exhausted (Schlesinger and Bernhardt, 2013). In anaerobic environments, methanogens derive energy through electron transfer received from an external electron donor (Zehnder and Stumm, 1988). Whether an electron acceptor will be reduced, depends upon the competition between electron acceptors (Migonigal et al., 2004). The order in which the electron acceptors are favoured is: NO₃⁻ reduction, Mn(IV) reduction, Fe(III) reduction, SO₄²⁻ reduction, and finally methanogenesis HCO₃³⁻ reduction. Therefore, methanogenesis is the least thermodynamically favourable pathway due to the lack of oxidants (Migonigal et al., 2004; Schlesinger and Bernhardt, 2013).

CH₄ is mainly produced by two different pathways: CO₂ reduction and acetate splitting (table 1). The energy obtained from acetoclastic methanogenesis yields much lower total energy than anaerobic metabolic pathways and is performed by just two genera of methanogens: *Methanosarcina* and *Methanosaeta* (Cicerone et al., 1992). Methanogens split acetate to produce CH₄ and CO₂ (table 1), but when acetate is unavailable a much larger group of methanogens use hydrogen fermentation together with CO₂ reduction to reduce organic matter.

Table 1: Chemical reactions and associated free energy yield for the methane-producing pathways of acetate splitting and CO₂ reduction. (Adapted from Schlesinger and Bernhardt, 2013).

Name	Reaction	-ΔG° (KJ mol ⁻¹)	Organisms
Acetate Splitting	$CH_3COOH \rightarrow CH_4 + CO_2$	28	<i>M. barkeri</i> , <i>M. mazei</i> , <i>M. söhngenii</i>
CO ₂ Reduction	$CO_2 + 4H_2 \rightarrow CH_4 + H_2O$	17.4	Most CH ₄ Bacteria

2.2.3 CH₄ oxidation

CH₄ is oxidized by prokaryotic methanotrophs in parts of the soil where oxygen is present (Christensen, 2010). Methanotrophs have been found to out-compete nitrifiers for oxygen when CH₄ is abundant, as more energy is released from oxidation of CH₄. Therefore, the majority of CH₄ produced within the peat layer is reduced to CO₂ before it is released from the sediments. However, when CH₄ concentration at depth exceeds the hydrostatic pressure of the WtD CH₄ gas bubbles can escape to the surface in a process known as ebullition (Christensen, 2010). CH₄ bypassing the water-atmosphere boundary layer escapes methanotrophs oxidation, resulting small almost pure CH₄ bubbles.

2.2.4 Pathways and controls of CH₄ emissions

As a result of the low solubility of CH₄ in water (23-40mg l⁻¹), combined with the large difference in the concentration within the soil pore space CH₄ can escape through the sediment into the atmosphere either by diffusion, ebullition or plant-mediated transport through vascular plants (Joabsson et al., 1999). The three different pathways represent different emission rates, and therefore increase variability in CH₄ emissions (Schlesinger and Bernhardt, 2013). Diffusion is found to contribute the least to the flux of CH₄ emission due to difficulty passing the water-atmosphere boundary (Joabsson et al., 1999; Schlesinger and Bernhardt, 2013).

Ebullition occurs when the partial pressure of the CH₄ gas in the water surpasses the hydrostatic pressure in the soil (Comas and Wright, 2012; Schlesinger and Bernhardt, 2013). This pressure increase only takes place when the production of CH₄ and CO₂ is higher than the diffusion potential of the gas (Joabsson et al., 1999; Lai, 2009). The ebullition process bypasses the oxic zone without exposure to oxidation due to the low solubility of CH₄ and rapid transfer from the anaerobic zone to the atmosphere (Lai, 2009). Outside of the growing season, when production is limited by low temperature and photosynthetic active radiation (PAR), plant-mediated transport becomes the highest contributing factor to the magnitude of the CH₄ flux.

Some wetland plant species have developed phenological responses to soil anoxia in a process known as plant-mediated transport. This strategy involves developing air-filled channels within their tissues, named aerenchyma (Greenup et al., 2000; Schlesinger and Bernhardt, 2013). The aerenchyma tissue allows plants to survive for long periods of time inundated under water by

facilitating the transport of oxygen to the water-logged roots (Greenup et al., 2000). However, at the same time, aerenchyma tissue acts as a conduit, facilitating the uninhibited transport of CH₄ to the atmosphere. During the growing season it is believed to be responsible for the majority of CH₄ flux to the atmosphere from wetland ecosystems (Christensen, 2010).

2.3 Controls of CH₄ productivity

Numerous studies have discovered relationships between multiple influences which contribute to the controlling factors of wetland CH₄ emissions. Environmental controls included soil temperature, WtD and active layer plus environmental controls such as vegetation composition, substrate quality and herbivory (Christensen et al., 2000; Ström et al., 2003; Lai et al., 2014; Falk et al., 2015). While a combination various factors contribute strongly to the magnitude of CH₄ flux, it is well documented that specific controls of CH₄ flux alter between sites (Christensen, 2014).

2.3.1 Soil temperature and snow melt

Soil temperature is commonly reported as the main controlling factor for the seasonal variation in CH₄ emissions (Long et al., 2010). However, snow and time of snow melt are a strong control at the beginning of the season. The initiation of greenhouse gas exchange at is strongly controlled by timing of the snow melt (Mastepanov et al., 2013), which triggers a strong energy flux into the soil resulting in a temperature increase. Following snow melt, the soil temperature in upper layers can reach positive values with two days (Tagesson et al., 2012), which then directly affects the metabolisms of micro-organisms. This energy flux increases the microbial activity, therefore increasing the rate of production in both methanogens and methanotrophs (Christensen et al., 2003, Mastepanov et al., 2013). The rate at which CH₄ emissions increase with temperature has been described as linear, logarithmic, polynomial or exponential (Whalen and Reeburgh, 1992).

Tagesson et al. (2012), discovered that when the relationship between soil temperature and CH₄ flux deviates away from the exponential one, that other environmental factors are of higher influence. Examples of such factors influencing the production of CH₄ include: optimal metabolic activity of the methanotrophs, sizes of the peat zones where production or oxidation takes place i.e. an increased active layer, substrate availability and resistance along the

transport pathways. As the relationship is not usually linear, it suggests that the relationship between soil temperature and CH₄ emissions cannot be explained only by temperature alone (Whalen and Reeburgh, 1992).

2.3.2 Water table depth

Anaerobic conditions are a prerequisite for the production of CH₄; therefore, the WtD is crucial in controlling the magnitude of the CH₄ flux (Schlesinger and Bernhardt, 2013). The position of the WtD ensures that conditions are kept anaerobic by inundating the oxic soil horizon, thus reducing the possibility for CH₄ oxidation (Lai et al, 2009). In saturated wetland soils, oxygen does not diffuse deeper than a few millimetres below the surface (Schlesinger and Bernhardt, 2013) which results in an accumulation of reduced compounds and trace gases such as N₂O, H₂S and CH₄.

The WtD regulates the size of the oxic and anoxic zone by either rising or dropping as the growing season progresses (Bubier and Moore, 1994). The magnitude of the flux can then become dependent upon size of which zone dominates, thus leading to higher or lower substrate availability dependent upon the WtD (Bubier and Moore, 1994, Schlesinger and Bernhardt, 2013). An additional factor which influences the magnitude of flux is the active layer. The main source of CH₄ originates from the top layer of the soil, therefore when the active layer approaches its maximum the CH₄ flux is affected least (Whalen, 2005).

Grünfeld and Brix (1999) observed that the WtD significantly affected methanogenesis, while Whalen and Reeburgh (1992) found that the CH₄ flux and WtD did not correlate well. The importance of WtD, temperature and depth of active layer indicates that the combination of multiple factors are important, signifying that singular factors alone do not control the flux of CH₄.

2.3.3 Vegetation

Wetland vegetation occupies a special niche between the terrestrial to aquatic continuum. Holding similar light and nutrient requirements as plants in upland systems, wetland vegetation has adapted to the constraints of rooting in waterlogged soils with low O₂ concentration (Bailey-Serres and Voeselek, 2008). Wetland plants have developed a range of morphological

and physiological traits that allow them to continue living in saturated sediments (Gibbs and Greenway, 2003). Greenway and Gibbs (2003) have shown that some wetland plants use anaerobic fermentation in their roots during periods of low or no oxygen, while others have developed aerenchyma to facilitate gas exchange between the atmosphere and the sediments adjacent to their roots (Greenup et al., 2000).

Current research on vegetation composition and presence of vascular plants has shown that vegetation is critical factor in controlling CH₄ fluxes from wetlands (Joabsson et al., 1999; Ström et al., 2012; Falk et al., 2014). Therefore, the proportion, density and composition of vegetation are an important factor for controlling the magnitude of CH₄ flux. Vegetation offers a physical transportation pathway and also affects the substrate availability and quality (Joabsson et al., 1999; Ström et al., 2003; Ström et al., 2005; Ström and Christensen, 2007; Ström et al., 2012).

In addition to providing mechanical support and nutrient/water uptake, roots can perform specialized functions. These functions include the ability to synthesise, accumulate and secrete various compounds (Walker et al., 2003). The compounds secreted into the soils, are often named root exudates. Exudates include a variety of labile compounds such as organic acids, amino acids and carbohydrates (Ström et al., 2012). These compounds account for a small proportion of the dissolved organic matter, but are highly bioavailable and play an important role in carbon cycling. In wetlands, acetic acid is of particular interest as it is an important substrate used by methanogens. Ström et al. (2003) showed that the wetland sedge *Eriophorum spp.* have higher acetate formation rates in the root vicinity than other common wetland species such as *Carex spp.* and *Dupontia spp.*

2.4 Herbivore interaction

Herbivores are central to the functioning of tundra ecosystems (Barrio et al., 2016); impacting multiple aspects of the arctic environment (Olofsson et al., 2004; Sjögersten et al., 2012; Falk et al., 2015).

Northern terrestrial ecosystems yield low annual primary productivity; most systems are dominated by plant-herbivore interactions and are a central biological disturbance (Horset et

al., 2014). Herbivores affect the structure and composition of plant communities through direct consumption of plant material, thus, altering the competitive interactions between different species (Olofsson et al., 2004; Barrio et al., 2016). Competitive interactions between species are often the result of the intermediate disturbance hypothesis (IDH). The IDH suggests that species diversity is highest when disturbances (e.g. herbivory) are neither too high nor too low. The mechanisms controlling the IDH can be viewed as a complex of different coexistence-promoting mechanisms (Roxburgh et al., 2004).

Indirectly, herbivores can influence nutrient cycles by altering plant and soil chemistry via the mineralization of nutrients in faecal matter (Van der Wal et al., 2004). Herbivory influences vegetation structure, species composition and productivity; through these processes herbivores can alter the balance of the carbon cycle (Van der Wal et al., 2007; Falk et al., 2014; Falk et al., 2015).

Falk et al. (2015) recently discovered significant differences following the exclusion of muskoxen over three years. The results showed a significant decrease in the total number of vascular plants in un-grazed plots, while the moss-layer and litter level had increased substantially. This resulted in a significant decrease in net ecosystem uptake of CO₂ and a decrease in CH₄ emission in un-grazed plots. While Van der Wal et al., (2001) discovered that the exclusion of barnacle geese and reindeer grazing over a period of seven years reduced soil temperature by 0.9°C. This increase was caused by an increase in the thickness of the moss layer usually grazed upon by the herbivores.

3.0 Methods

3.1 Site description

The study took place in the lowland mire, *Rylekæret*, located in the high arctic Zackenberg valley, North East Greenland (74°30'N 20°30'W) (figure. 1). The average temperature in July is 6.8°C with an annual precipitation of 229mm, mostly falling as snow outside of the growing season (Jensen et al., 2016). Despite the low annual precipitation, the Rylekæret mire is often water saturated between late June to early August (Bay, 1997). The area is dominated by sedges such as *Carex stans*, *Dupontia psilosantha* and *Eriophorum scheuchzeri* with an underlying dense layer of mosses covering the shallow peat layer, which ranges between 7-18cm deep (Ström et al., 2015).

The study area is located within the continuous permafrost zone and holds a maximum active layer depth of 73cm (Jensen et al., 2016). The *Rylekæret* mire ecosystem is highly affected by a small population of muskoxen (*Ovibos moschatus*) (Kristensen et al., 2011; Falk et al., 2014), sustaining a population of 219 individuals within a 47km² census area (Jensen et al., 2016). During the early growing season, small herds of muskoxen usually graze in the *Vestelven* and *Vestkæret* region (figure 1) before crossing the Zackenberg river to forage on graminoids in the *Rylekæret* mire (Kristensen et al., 2011). During this time the density of muskox population increases.

3.2 Experimental design

Data was collected within a muskox enclosure set-up established in August 2010 (Ström et al., 2014). The experiment consisted of four replicate blocks, each containing three 10 × 10m treatments. First, an un-treated control area (C), second an enclosure (Ex) consisting of one-meter-high surrounding fence that prevents the muskoxen from grazing and trampling. Finally, a snow control (Sn) area, established to evaluate the potential effect of the experimental fence. This treatment was established to see whether the fence itself, directly affected the snow depth and residence time. Previous studies established that this treatment has no effect on the snow, carbon fluxes and vegetation composition.

Within each treatment area (C, Ex & Sn), plots with pre-installed aluminium frames, permanently inserted into the peat and were used to preform closed chamber gas analyses of CO₂ and CH₄ (Christensen et al., 2000; Ström and Christensen, 2007). To establish the relationship between gas fluxes and the concentrations of CH₄ in pore water, pore water samples were taken at three different depths and were analysed using gas chromatography to determine the concentration of dissolved CH₄ in the soil water.

To estimate the soil and plant density and the composition of the vascular plants, core samples (10 x 10cm) were removed from C and Ex plots. The number of tillers per sample was counted including the mean height. Following this, core samples were divided into four subsections (grass, moss, large roots and fine roots) to obtain the density of the different layers. Finally, environmental parameters including surface photosynthetic active radiation and water table depth were measured directly following each chamber measurement.

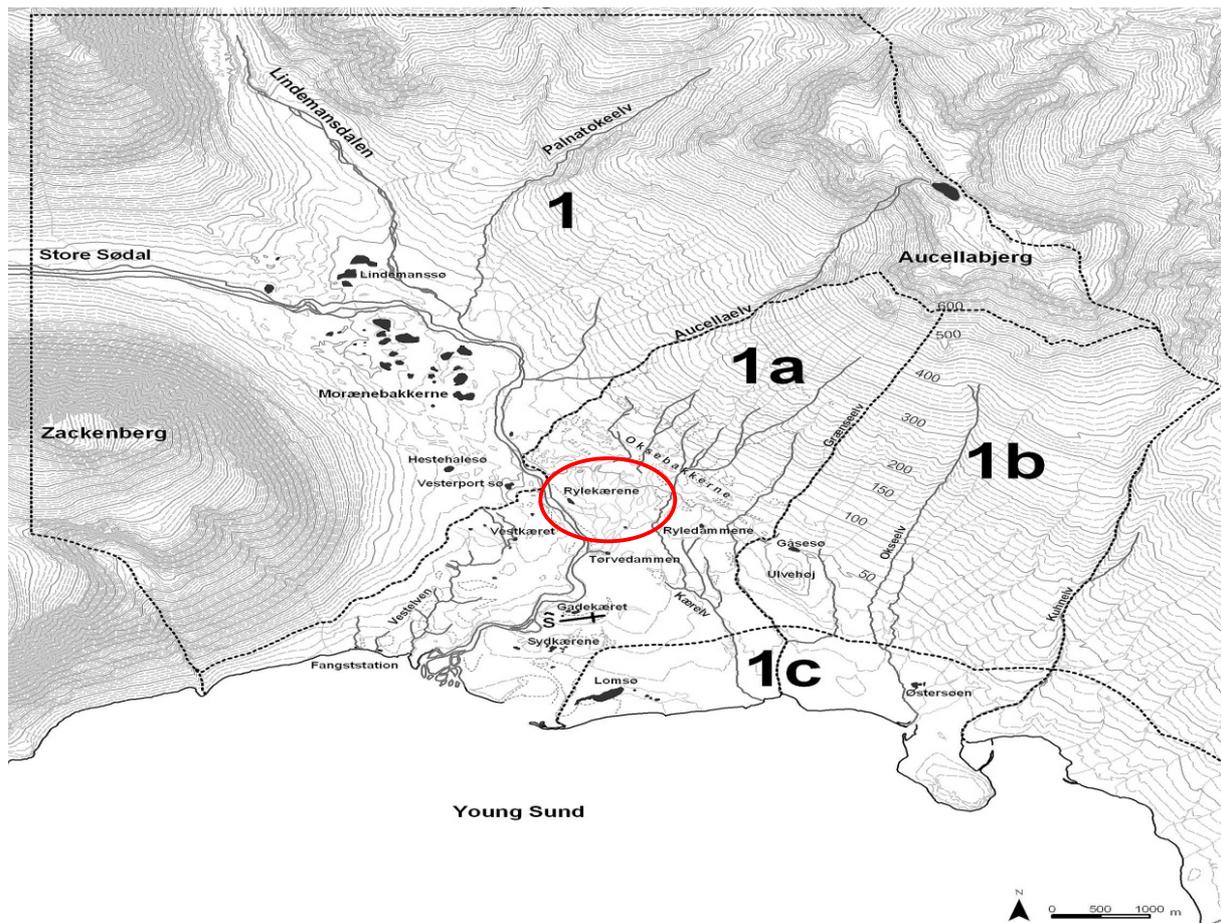


Figure 1: The Zackenberg valley research zone 1 and subdivisions. The Rylekæret mire located within zone 1a and highlighted by the black circle (*printed with permission from zackenberg.dk*).

3.3 Flux measurements

Flux measurements of CO₂ and CH₄ from within the C, Sn and Ex treatments were, as mentioned above, obtained using the closed chamber technique. Both gas concentrations (CO₂ and CH₄) were instantaneously measured via a portable Fourier transform infrared (FTIR) spectrometer (Gasmeter Dx 40-30, Gasmeter Technologies Oy, Finland).

Measurements were performed by placing a transparent 41L *Plexiglas* chamber on the pre-installed 30 x 30cm aluminium frames (figure 2). The base of the chamber was equipped with a rubber lip to ensure an airtight seal. Each measurement lasted between three and seven minutes, or until a stable slope was observed on the Calcmeter Lite software (Calcmeter Lite V1000.04, Gasmeter Technologies Oy, Finland). The system logged gas concentrations at five second intervals. CO₂ measurements in light conditions were used to obtain GPP, while dark CO₂ measurements were used for R_{eco} and the difference between the two for the NEE (equation 1). Dark measurements were conducted by covering the *Plexiglas* chamber by a non-transparent cover.

Between measurements the *Pexiglas* chamber was flushed until gas concentrations returned to atmospheric levels. The release of gas from the ecosystem to the atmosphere was denoted by positive values and uptake by negative measured in mg CO₂/CH₄ m⁻² h⁻¹.

A total of 175 light measurements and 175 dark measurements were recorded for CO₂ and CH₄ across the July sample period. Measurements were completed at varied times of day to obtain different weather growing conditions. The values for the individual plots were averaged across the five replicates to obtain an average flux. Following this average, the plots were sorted into treatments to obtain treatment affect.



Figure 2: The 41l *Plexiglas* chamber sitting on top of the 30 x 30cm aluminum base. Inside is a small fan and to the right are the inlet and outlet lines which deliver the gas sample to the Gasetm DX 40-30 FTIR spectrometer (image: Joel White).

3.4 Pore water CH_4

Pore water was sampled from the main root zone across three different depths to obtain a mean pore water value. Soil probes were prepared with a 3mm diameter stainless steel tube connected to a three-way-stopcock valve. The three different depths were pressed through a rubber float to prevent the probe from changing depth. The probes were permanently installed within the Ex and C plots for block 3 (C n = 2, Ex n = 2), block 4 (C n = 2, Ex n = 2), and block 5 (C n = 1, Ex n = 1).

Starting from the deepest depth, a 10ml syringe was used to remove 2ml of spoiled water which was discarded and the syringe was flushed with distilled water to ensure no cross contamination. Using the same syringe, a 5 ml sample was removed and injected using a 21G needle to a 10ml crimp self-sealing vial. Samples were frozen for transport between the site and the laboratory at Lund University where the gas chromatography (GC) analysis were made. Samples were taken at the beginning and end of the measurement period.

The GC samples were analysed on a Shimadzu GC-2014 gas chromatograph (GC-2014, Shimadzu Corporation, Tokyo, Japan) using a Flame Ionization Detector, for analysis of CH₄. Standard gas sample (5 ppm) analyses were repeated 20 times to obtain correct calibration. The ppm of the sample was calculated via equation 2.

$$\text{Concentration (ppm)} = \frac{A \cdot C}{B} \quad (2)$$

Where A is the area of sample peak, B represents the peak area of standard gas and C the known ppm of the standard gas. Once the concentration of the samples was obtained the ideal gas law (equation 3) was used to convert ppm into mg CH₄/L of pore water.

$$PV = nRT \rightarrow n = \frac{P \cdot V}{R \cdot T} \quad (3)$$

Where P is atmospheric pressure (1 atm), V equals the volume of the head space (0.010L), R is the universal gas constant (0.08206 L atm. / mol. K) and T is the temperature in Kelvin, assuming 20°C (the general temperature of the laboratory).

3.5 Core samples

Core samples were removed from both C and Ex treatments in block 3, 4 and 5. Using a large serrated knife, cores were first cut to 15cm² plots to ensure no compression occurred when extracting samples from the peat layer. Once removed, cores were reduced to 10cm² and drained until field capacity of the peat sample was reached. In the lab, the cores were measured, weighed and separated into the desired functional zones: vegetation, moss, large roots and fine roots (figure 3) for plant and soil density analysis.

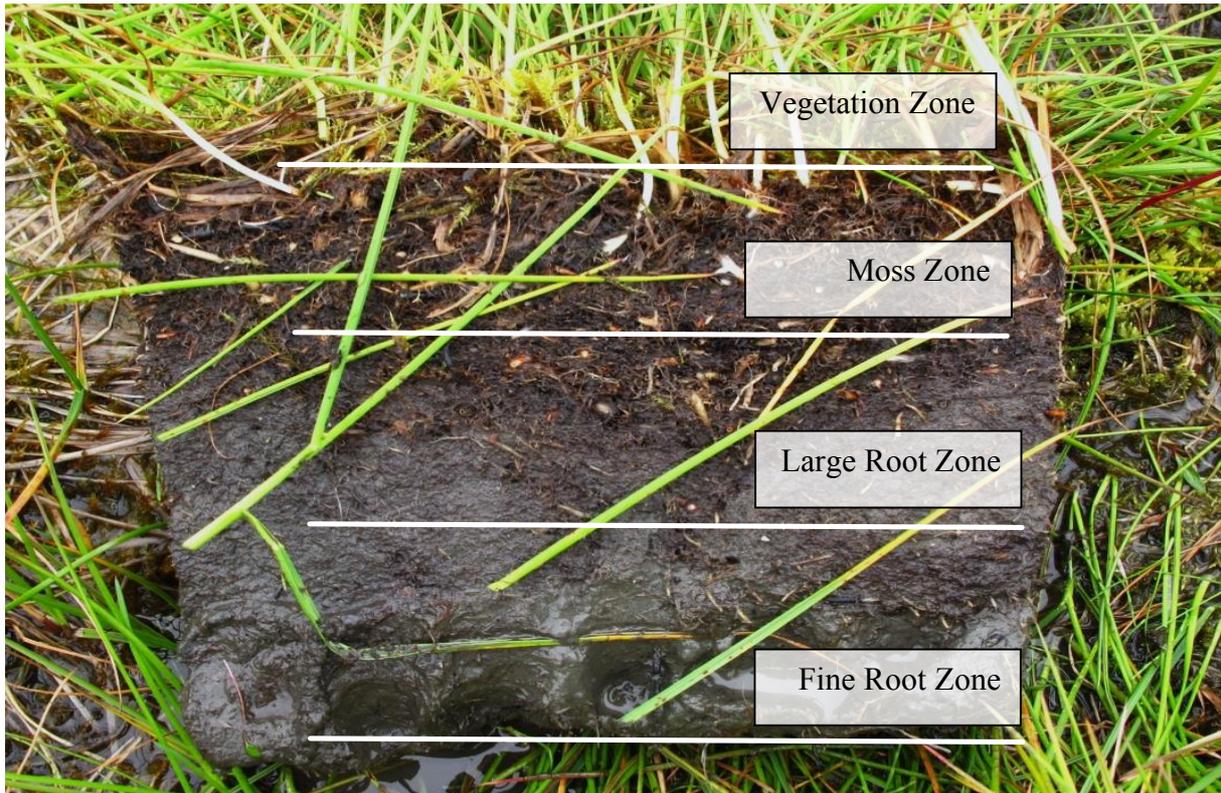


Figure 3: Example of a pre-cut core sample. Identifiable layers include the Grass, Moss, Large Root and Fine Root zones with the final silt layer at the bottom (image: Joel White).

3.5.1 Plant density

To estimate the density and composition of vascular plants, the number of tillers per core sample (10cm^2) of the dominant plant species were counted. Each individual tiller was removed from the core sample in whole and divided into species *Carex*, *Equisetum*, *Dupontia*, *Eriophorum*, *Salix* and unidentified mosses. The wet and dry weights were determined by weighing pre and post drying. Samples were dried at $85\text{ }^\circ\text{C}$ for 24 hours in a heating Oven (Binder BD-400, Binder Inc. NY, USA) to obtain the dry weight of biomass. In each of the vascular plant fractions the mean tiller height was measured and the number of individual tillers was counted.

3.5.2 Combined soil and biomass density

To estimate the density of the moss, large root and fine root zone the core sample was first measured to determine dimensions for volume. Once the volume was calculated the individual zones were carefully separated by hand and weighed. After the lengths and

weights were recorded the samples were again dried in a heating oven at 85°C for 24 hours. To determine the density of the individual zones the bulk density was calculated using equation (equation 4).

$$BD = \frac{M_{\text{solids}}}{V_{\text{soil}}} \quad (4)$$

Where BD is the dry bulk density, M_{solids} is the weight of the dry soil and V_{soil} is the total soil volume. The total soil volume is the combined volume of solids and pores which may contain air V_{air} or water V_{water} (Cresswell and Hamilton, 2002; McKenzie et al., 2004).

3.6 Data treatment

All plots for CO_2 and CH_4 fluxes ($\text{mg m}^{-2}\text{h}^{-1}$) were calculated using the change in gas concentration as a function of time using linear fitting. Methods included correction for ambient air temperature and pressure according to techniques established by Crill et al. (1988). Due to the high correlation ($R^2 = 0.98$, $p = <0.001$) between the light and dark CH_4 fluxes for individual plots, the mean of the two measurements was used for the CH_4 flux.

Prior to data analysis, the fluxes (CO_2 and CH_4), plant and soil density and number of tillers were tested for normal distribution using the Shapiro Wilk test of normality. Outliers were identified using boxplots and removed afterwards. All data which was not normally distributed was transformed using a log10 function to obtain normal distribution. Statistical analysis of the treatment effect included one-way ANOVA followed by a post-hoc test (Tukey HSD) to determine significant differences between treatments.

To identify the variables that best explain the main plot drivers of fluxes, a bivariate correlation (Pearson 2-tailed test for significance) analysis was performed on the mean of additional parameters measured during the July sample period (PAR, soil temperature and WtD).

All statistical analysis was performed in Lund during November and December 2016. All statistics were performed using SPSS 20.0.0.1 for PC. The statistics were regarded as significant if values were below $p = 0.05$.

4.0 Results

4.1 Vegetation analysis

The vegetation analysis shows that different treatments resulted in different species communities. Despite small spatial distance between plots, the vegetation analysis displayed high variability in the number of tillers within plots, and between treatments. The results show that the largest variation occurred within the C plots for the plant species *Eriophorum scheuchzeri*, yielding a total difference of 1200 tillers between the maximum and minimum values recorded (table 2). The most abundant vascular plant species was *Dupontia psilosantha*, followed closely by *Eriophorum scheuchzeri* (table 2). On average, *Dupontia psilosantha* and *Eriophorum scheuchzeri* dominated, accounting for 90% of the total number of plant tillers in the C plots and 77% in Ex.

The results indicate that the mean species density of *Dupontia psilosantha* was reduced by 60% between C to Ex treatments. While *Eriophorum scheuchzeri* decreased by 64% between C and Ex treatments.

The vegetation analysis indicated that the choice of the treatment had a clear and significant (independent samples t-test) effect on the total density of all vascular plants as well as on species level. A lower density was discovered in the Ex, compared with the C treatment $t(8)$, $p = 0.002$. The density of individuals was significantly higher for *Dupontia psilosantha* within C ($M=32$, $SD=4.77$) as opposed to Ex ($M=12$, $SD=3.84$); $t(8) = 6.929$, $p = 0.001$. The same results were also observed in *Eriophorum scheuchzeri* between the C ($M=21$, $SD=9.7$) and Ex ($M=8$, $SD=5.94$) treatments, $t(8) = 2.63$, $p=0.030$.

No significant differences were observed between the remaining fractions of the plant species (table 2). However, an interesting observation was the presence of the arctic willow (*Salix arctica*), which was only recorded in the C plots, and was not present in any of the Ex treatments.

Table 2: The mean, maximum and minimum, standard deviation (SD), standard error (SE±) and p-value (p) number of tillers of the dominant vascular plant species sampled (m²) from C and Ex areas (C n = 5, EX n = 5). Samples were identified and divided into vascular plants: *Carex stans*, *Dupontia psilosantha*, *Eriophorum scheuchzeri*, *Equisetum spp.* and *Salix arctica* with total number of tillers. Significant differences (independent T-Test) between C and EX are displayed in bold formatting.

	<i>Carex stans</i>		<i>Salix arctica</i>		<i>Dupontia psilosantha</i>		<i>Eriophorum scheuchzeri</i>		<i>Equisetum spp</i>	
	Control	Exclosure	Control	Exclosure	Control	Exclosure	Control	Exclosure	Control	Exclosure
Mean	140	280	100	0	3140	1250	2100	760	300	300
Max	400	600	300	0	3800	1700	3200	1400	1100	1000
Min	0	0	0	0	2600	700	900	200	0	0
SD	167	294	141	0	477	384	972	594	479	412
SE (±)	74	131	63	0	213	172	434	265	214	184
p	(C vs. Ex)	0.153	(C vs. Ex)	0.383	(C vs. Ex)	0.001	(C vs. Ex)	0.030	(C vs. Ex)	1.00

4.2 Exclosure experiment

4.2.1 CO₂ flux

Similar to the results of the vegetation analysis, the CO₂ flux measurements indicated high variability spatially between plots (figure 4). The results show that the exclosure experiment yielded no significant difference between C, Sn and Ex treatments for GPP, NEE and R_{eco} (table 3).

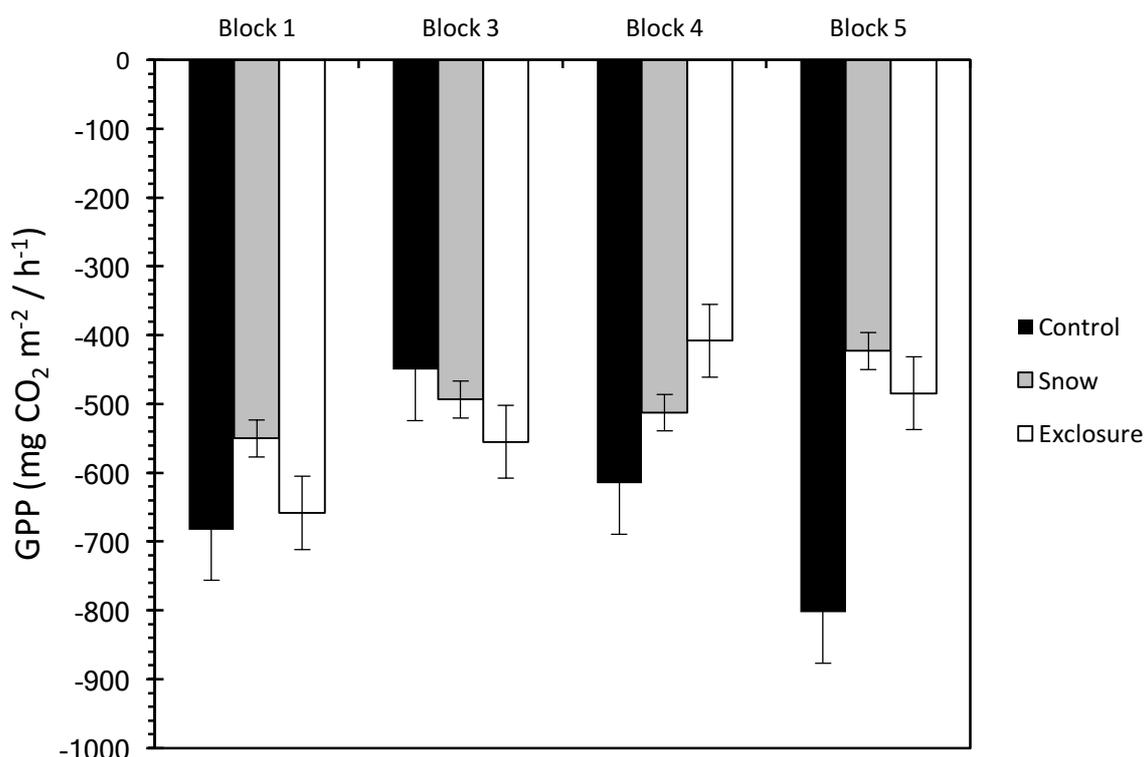


Figure 4: Mean GPP (mg CO₂ m⁻² h⁻¹ ± SE) per block, for July 2016 in C (n = 15), Sn (n = 8) and Ex treatments (n = 12). Data is based upon plots from block 1, 3, 4 and 5.

Overall, plots within the C treatment yielded the highest average NEE at -284 mg CO₂ m⁻² h⁻¹, followed by the Ex and Sn plots respectively. The highest mean GPP flux was recorded in the C treatments, with a mean value of -594 mg CO₂ m⁻² h⁻¹, 18% higher than the Sn plots and 15% higher than Ex. In R_{eco}, the largest flux was recorded in C treatments at 310 CO₂ m⁻² h⁻¹. Only small percentage differences occurred between treatments for the R_{eco} with 12% and 13% reduction in Sn and Ex treatments compared to the C.

However, these differences between groups were not statistically significant as determined by the one-way ANOVA in NEE ($F_{(2, 31)} = 1.524$, $p = 0.234$), GPP ($F_{(2, 32)} = 1.457$, $p = 0.248$) or R_{eco} ($F_{(2,33)} = 1.420$, $p = 0.257$).

Table 3: The mean (SE±), maximum and minimum net ecosystem exchange (NEE), photosynthesis (GPP) and respiration (R_{eco}) ($\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), water table depth (WtD) (cm below the peat surface) in July of 2016 for C, Sn and Ex (C n = 15, Sn n = 8 and Ex n = 12). Significant differences (p) were tested (One-Way ANOVA) between C and Sn and C and EX with significant differences discovered between WtD treatments.

		NEE	GPP	R_{eco}	WtD
Control	Mean (SE)	-284 (± 34)	-594 (± 40)	310 (± 22)	-1.4 (± 0.52)
	Max	-504	-822	464	3.6
	Min	-69	-324	181	-7.1
Snow	Mean (SE)	-222 (± 23)	-494(± 19)	272 (± 21)	2.6 (± 0.71)
	Max	-314	-564	350	5.5
	Min	-133	-416	169	7.1
	p (C vs S)	0.361	0.184	0.426	0.996
Exclosure	Mean (SE)	-241 (± 26)	-511 (± 32)	269 (± 14)	-3.1 (± 0.62)
	Max	-446	-730	359	3.4
	Min	-110	-349	200	- 6.8
	p (C vs Ex)	0.299	0.221	0.294	0.001

4.2.2 CH₄ flux

On average, the results showed clear differences between the C and Ex treatments. It was discovered that the largest recorded mean CH₄ flux occurred within the C treatment at 11.9 mg CH₄ m⁻²h⁻¹ while the smallest flux was located within the Sn treatment at 0.3mg CH₄ m⁻²h⁻¹ (table 5). The largest mean July flux was observed in the C (M=4.48, SE=±0.80), followed by Sn (M=4.36, SE=±1.82) and finally Ex treatments (M=1.27, SE = ±0.45). The measurement results show that on average, fluxes within C plots were 72% larger than Ex and 71% smaller than Sn treatment fluxes (figure 5).

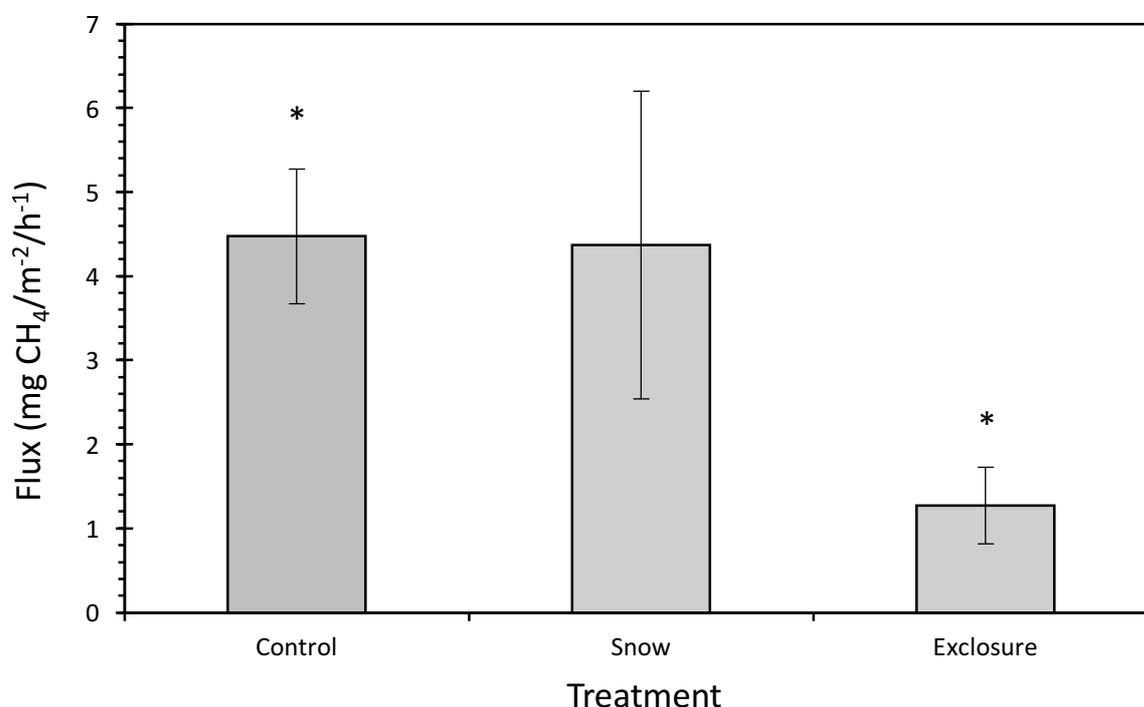


Figure 5: Mean CH₄ flux (mg CH₄ m⁻² h⁻¹ ± SE), for July 2016 in C (n = 15), Sn (n = 8) and Ex treatments (n = 12). Data is based upon plots from block 1, 3, 4 and 5. Significant differences (one-way ANOVA) between C and Ex are indicated with asterisk above the bars, p = 0.001

On average, measurements indicated clear significant difference (p = 0.001) between fluxes within C and Ex treatments (figure 5, table 5). Significant differences between treatments were determined via a one-way ANOVA of variance. The C plots were significantly higher ($F_{(2, 29)} = 8.617$, p = 0.001) than Ex but not significantly greater than Sn plots ($F_{(2, 29)} = 8.617$, p = 0.321), while no significant difference occurred between the Sn and Ex ($F_{(2, 29)} = 8.617$, p = 0.80). A Tukey post-hoc test was used to determine which flux measurements were statistically different within the groups.

4.3 Soil water CH₄

The soil water CH₄ concentration indicated that no treatment effect. It was discovered that the largest CH₄ concentration within the soil water was recorded in the C treatment at 4.21 mg CH₄/L⁻¹, while the smallest concentration was measured within the Ex treatment at 0.29 mg CH₄/L⁻¹ (table 4). The mean value for the C treatments were 4.48 mg CH₄/L⁻¹ (SE= ± 0.80), while the Ex treatments were marginally smaller at 1.93 mg CH₄/L⁻¹ (SE = ± 0.46). The measurement results show that, on average, differences within C plots were 25% larger than Ex plots. An independent-samples t-test was used to test whether significant differences occurred between treatments. It was discovered that no significant difference occurred between the treatments $t(8) = 0.862$, $p = 0.414$.

4.4 Drivers of ecosystem CH₄ production

A Pearson correlation test was run to determine the main drivers of all CH₄ flux between treatments. Parameters tested were GPP, R_{eco}, WtD and PAR. The analysis showed significant relationships between GPP R_{eco} and PAR (table 4). The analysis indicated a positive correlation between the CH₄ to GPP flux, CH₄ to R_{eco} flux, and a negative relation existed between the flux of CH₄ and PAR

Table 4: The correlation matrix displaying the Pearson correlation, significance and number of sample (N) between main environmental drivers. *Correlation is significant at the 0.05 level, ** Correlation is significant at the 0.001 level

		Flux CH ₄	PAR	WtD	GPP	R _{eco}
Flux CH ₄	Pearson Correlation	1	-.204*	.112	-.343**	.501**
	Sig. (2-tailed)		.014	.143	.000	.000
PAR	Pearson Correlation	-.204*	1	.052	-.275**	.020
	Sig. (2-tailed)	.014		.540	.001	.809
WtD	Pearson Correlation	.112	.052	1	-.086	.003
	Sig. (2-tailed)	.143	.540		.260	.969
GPP	Pearson Correlation	-.343**	-.275**	-.086	1	-.609**
	Sig. (2-tailed)	.000	.001	.260		.000
R _{eco}	Pearson Correlation	.501**	.020	.003	-.609**	1
	Sig. (2-tailed)	.000	.809	.969	.000	

Table 5: The mean maximum and minimum CH₄ Flux (mg CH₄ m⁻² h⁻¹ ± SE) (C n = 15, Sn n= 8, Ex n = 12) and soil water CH₄ concentrations (mg/L⁻¹ SE±) (n = 10) and the p-value (P) for the statistical comparison between control (C), snow (Sn) and exclosure (Ex) (One-Way ANOVA) and between C and Ex (independent-samples t-test) Sn soil water CH₄ was not measured.

		Flux CH ₄	Soil Water CH ₄
Control	Mean (±SE)	4.48 (± 0.80)	2.57 (±0.58)
	Max	11.91	4.77
	Min	2.29	0.88
Snow	Mean (±SE)	4.36 (± 1.82)	-
	Max	9.14	-
	Min	0.32	-
	p (C vs Sn)	0.321	-
Exclosure	Mean (±SE)	1.27 (± 0.45)	1.93 (±0.46)
	Max	4.81	3.11
	Min	0.046	0.26
	p (C vs Ex)	0.001	0.414

4.5 Combined Soil and Biomass density

The total density of the combined dried soil and biomass was not significantly different between C and Ex treatments ($F_{(1,9)} = 1.147$ $p=0.315$). C plots averaged 0.02, 0.07, 0.20 and 0.52 (g/cm^{-3}) for grass, moss, large roots and fine roots zones (figure 6). While the Ex treatment held 0.09, 0.08, 0.23 and 0.48 (g/cm^{-3}) for the same respective core zones (figure 6).

Individual zones were tested by using one-way ANOVA to determine if any significant variances occurred between the densities of the different zones. Although large difference in soil density appear to occur between individual zones, the fine roots zone ($F_{(1,9)} = 0.381$, $p = 0.554$), large roots ($F_{(1,9)} = 0.196$, $p = .670$), moss layer ($F_{(1,9)} = 0.38$, $p = 0.850$) and grass layer ($F_{(1,9)} = 2.354$, $p = 0.163$) held no statistical significant difference in density between layers (figure 6).

The largest spatial variation between the C and Ex layers occurred within the C plots, with a $0.81 \text{ g}/\text{cm}^{-3}$ differences between the maximum and minimum samples. While the largest within Ex plots was 0.38, resulting in a 53% lower variation in this treatment than in C.

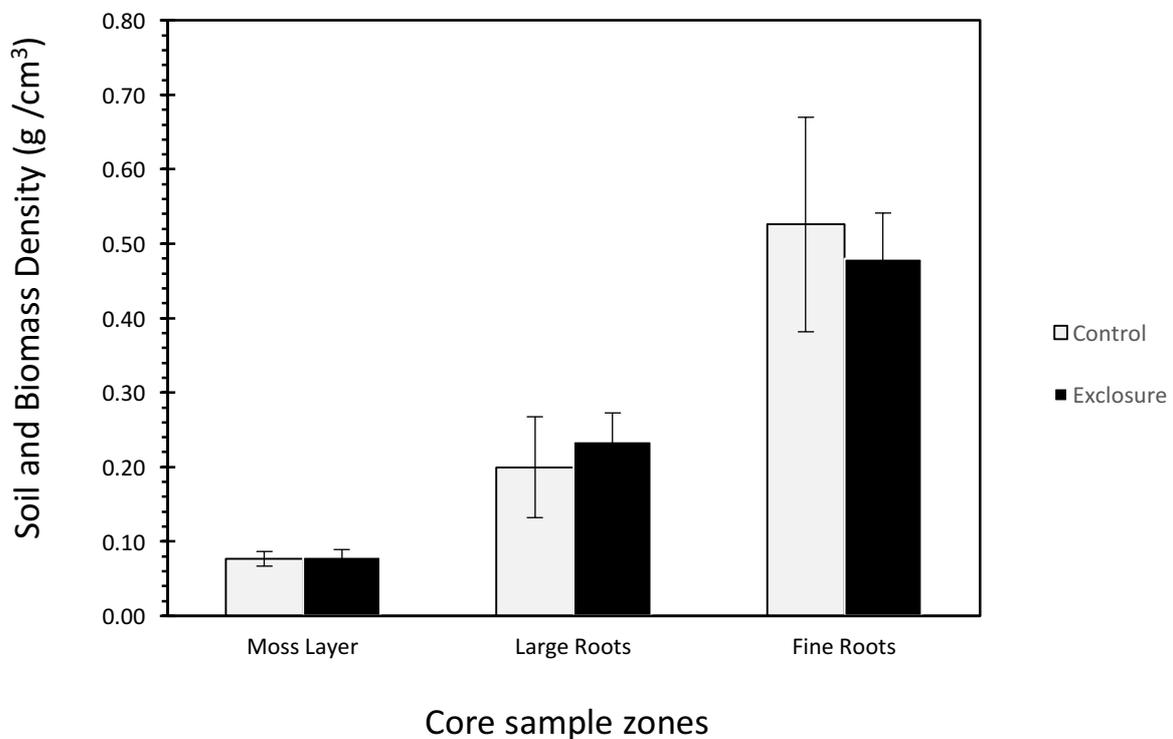


Figure 6: Soil and biomass density ($\text{g}/\text{cm}^3 \pm \text{SE}$) of samples harvested (0.10 m^2) in July 2016 within C ($n=5$) and Ex ($n=5$) treatments. Samples were separated into functional zones of the soil horizon dominated by: Moss, large roots and fine roots. No significant differences between zones and treatments were discovered (One-Way ANOVA).

The thickness of the individual zone's moss, large roots and fine roots, did not differ significantly between the C and Ex treatments. The thickest zone recorded was the fine roots within the Ex treatments ($M = 11.2$, $\text{SE} = 0.64$), while the smallest was the moss zone in C plots ($M = 6$, $\text{SE} = 0.51$) (figure 7). The largest variation occurs between the mean the moss layer and fine roots. The fine roots on average are 44% larger in C and 41% in Ex than the moss layer. A one-way ANOVA of variance returned no significant difference in thickness between zones of the C and Ex moss layer ($F_{(1,9)} = 0.25$, $p = 0.878$), large roots ($F_{(1,9)} = 0.008$, $p = 0.931$) and fine root zone ($F_{(1,9)} = 1.001$, $p = 0.346$).

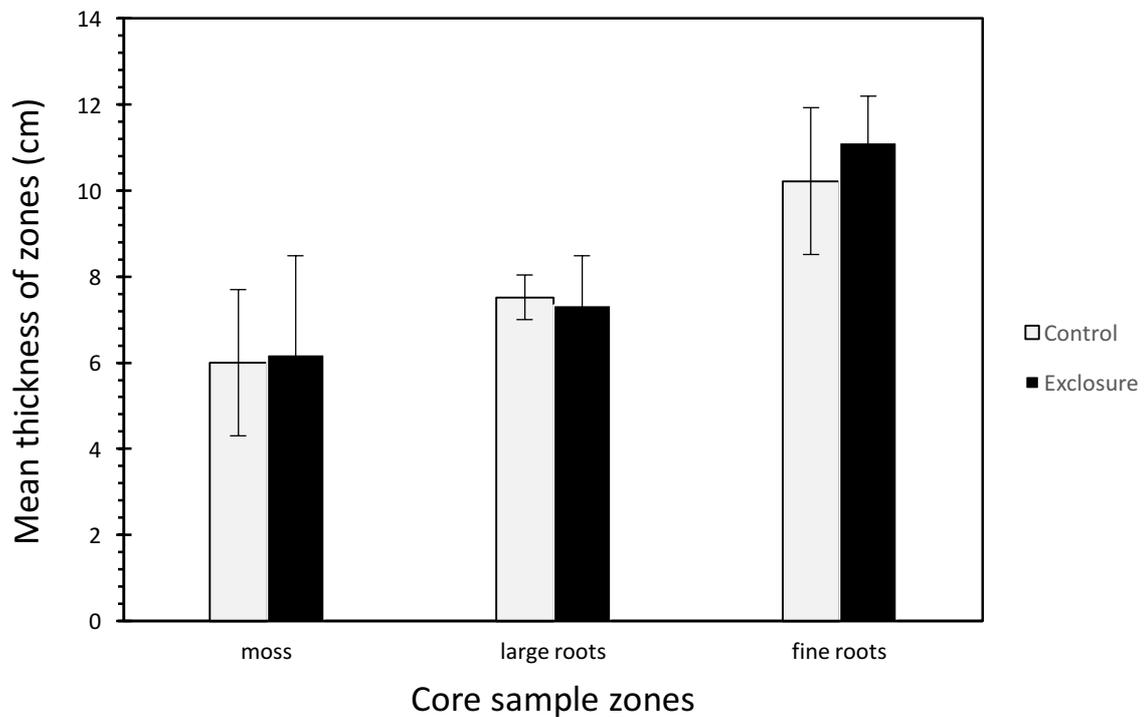


Figure 7: Mean thickness of zones ($\text{cm} \pm \text{SE}$) of samples (0.10 m^2) collected in July 2016 within C ($n = 5$) and Ex ($n = 5$) treatments. Samples were separated into functional zones of the soil horizon dominated by: Moss, large roots and fine roots. There were no significant differences between zones and treatments (One-Way ANOVA).

5.0 Discussion

This experiment shows that muskox grazing and trampling influence CH₄ emissions from arctic peat-lands. The results suggest that the exclusion of large herbivores leads to a decrease in plant density with a lower total number of tillers; however, the results cannot confirm that trampling by large herbivores results in lower root-mass density, and consequently, lower CH₄ fluxes.

5.1 Vegetation analysis

The vegetation analysis clearly displays significant differences between the total number of tillers in C and Ex treatments (table 2). This means, that on average, the total number of tillers was found to be significantly lower in the Ex treatment compared to the C. The density of individual species was also significantly lower between treatments; indicating that the total number of tillers for each individual species of *Eriophorum scheuchzeri* and *Dupontia psilosantha* is significantly lower in Ex plots, than in C. As *Eriophorum scheuchzeri* and *Dupontia psilosantha* dominate the composition of the *Rylekæret* mire, it can be concluded that the presence of the keystone herbivore, *Ovibos moschatus*, heavily influences the surrounding ecosystem with respect to the density of vegetation species.

After the commencement of the muskox enclosure experiment, Falk et al. (2015) discovered no significant differences in the total number of tillers and density of individuals after one year. However, at the conclusion of the third year, Falk et al. (2015) discovered that not only were the number of tillers significantly lower in Ex plots, but also that the density of individuals for *Eriophorum scheuchzeri* were significantly different between treatments. This study observed similar results, except that in addition to *Eriophorum scheuchzeri* being significantly lower in Ex plots, that *Dupontia psilosantha* is also significantly lower. The addition of *Dupontia psilosantha* being significantly lower in Ex plots, indicates a shift in the vegetation community, as now two species are significantly lower (table 2) than the previous one species discovered by Falk et al. (2015). Of interest, is the presence of *Salix arctica*, currently only discovered within a small number of C plots (table 2).

The presence of a dwarf shrub such as the *Salix arctica* within the C plots could indicate an alteration in growing conditions in the Ex plots. Falk et al. (2015) speculated that, increased competition in response to the higher amount of litter in Ex plots and a more developed moss-layer, may force physiological adaptations in graminoids. Such adaptations could include a higher allocation of carbon invested in tiller length. If this the case, the height of the tillers and the developed moss layer could be shading of the *Salix arctica* resulting in higher competition and less likelihood of establishment within Ex plots. However, in this experiment, it is difficult to conclude that such a shift is occurring, as shrub expansion, following herbivore exclusion, occurs within a time period of approximately 5 years (Olofsson et al., 2004; Post and Pedersen, 2008). The combination of results from Falk et al., (2015) and my measurements span over six years, suggesting that we may expect to see a shift in the vegetation community in the near future.

5.2 CO₂ flux

The results confirm that no significant variation in the magnitude of CO₂ flux occurred between treatments with respect to NEE, GPP and R_{eco} (table 3). This indicates that, even though significantly fewer total numbers of tillers occurred in Ex treatments, that this factor alone, does not affect the productivity of the ecosystem. We can speculate that the remaining amount of photosynthetic material (such as the moss layer) may be compensating for the remaining difference in photosynthetic activity. This ‘fill-in’ effect could ensure that no difference in NEE, GPP and R_{eco} was detectable between treatments.

Falk et al. (2015), recorded large inter-annual variation between fluxes of CO₂ for the same site. However, after three years of herbivore exclusion, the flux of NEE, GPP, R_{eco} and WtD measurements were all significantly different between C and Ex treatments, in contrast to the first measurement year conducted (2011). By contrast, within my study, the same parameters were measured (GPP, R_{eco}, NEE and WtD) and yielded no difference between treatments, except for the WtD (table 3). This lack of difference between NEE, GPP and R_{eco} in my results compared to Falk et al., (2015) could be explained by two factors.

First, I speculate that the variance in results between Falk et al., (2015) and my study is explained by different weather conditions. My study period (July, 2016) was dry in

comparison to other measurement periods, with a low WtD which may have resulted in decreased productivity. However, the WtD is significantly different between the treatments and yielded no difference between the flux of NEE, GPP and R_{eco} . Falk et al. (2015) reported similar results during the 2013 sample period, which was a dry year, with little precipitation. The second factor influencing this difference may be the timing and amount of herbivore grazing pressure. During July 2016, it was observed that the muskox herds were not grazing in the *Rylekæret* mire. So it could be assumed that the effects of trampling and grazing were the result of the previous year (2015). This may help explain why the differences in magnitudes of NEE, GPP and R_{eco} between my results and Falk et al. (2015).

Multiple studies have concluded that the magnitude of NEE decreases with higher grazing pressure (Sjögersten et al., 2011; Cahoon et al., 2012). Therefore, if the muskoxen were present at the time of measurements, we could expect higher grazing pressure on our C and Sn treatments resulting in less photosynthetic material and a more compressed moss layer. With less photosynthetic material present, the flux of GPP would be reduced, therefore altering the balance between fluxes. If this were the case, we could speculate that a significant difference between the magnitudes of fluxes may have occurred amongst treatments.

5.3 CH₄ flux

There is a strong relationship between the species vegetation density and the flux of CH₄ (Ström and Christensen, 2007; Falk et al., 2015). When present in higher concentrations, the sedge species *Eriophorum scheuchzeri* has been proven to increase the magnitude of CH₄ fluxes (Ström and Christensen, 2007). This higher flux is associated with how species-specific root exudation patterns affect the availability of acetate, the precursor to CH₄ formation (Ström et al., 2003). Following CH₄ production, the aerenchyma acts as a ventilation system transporting CH₄ from the root tips in saturated soil to the atmosphere (Greenup et al., 2000). Therefore, the CH₄ is provided with an easier pathway to diffuse across the water-atmosphere barrier. Thus, it is reasonable to conclude that the significantly higher number of *Eriophorum scheuchzeri* present in the C plots, is a main contributor to the sizable difference in fluxes between treatments.

Another plausible reason for difference in fluxes between treatments is the process of CH₄ oxidation. Previous studies have observed a more highly developed moss layer following

herbivore exclusion (Van der Wal and Brooker, 2004; Van der Wal, 2007; Falk et al., 2015). This taller, developed moss layer affects the CH₄ flux by altering the WtD and plant phenology. The higher moss layer results in a lower WtD, this process exposes the anoxic peat layer to the atmosphere, resulting in the oxidation of CH₄ to CO₂. This theory is supported by the significantly lower WtD observed in the Ex treatment (table 3). Alternatively, due to the deeper moss layer, the existing plant species need to invest more carbon in tiller length to reach the photic zone (Bazzaz and Grace, 1997). Subsequently, the need for resource allocation to longer tillers appears to reduce the number of tillers produced, resulting in fewer root rhizomes. The plant may therefore allocate carbon to taller tillers instead of additional tiller tips (Bazzaz and Grace, 1997). This reallocation of carbon away from the roots reduces the amount of root exudation which supplies the methanogen's organic acids necessary for the production of CH₄ (Ström et al., 2003).

5.4 Soil water CH₄

The concentration of soil water CH₄ was measured in an attempt to see whether the supply of from the soil altered between treatments. The results show that no significant difference occurred between treatments. This indicates that, even though the flux of CH₄ between treatments was different, the supply from the peat layer was the same.

A close relationship exists between the concentration of the soil water CH₄ and vegetation type. A field experiment conducted by Ström et al. (2003) illustrated how particular species-specific root exudation patterns affect the availability of organic acids, dissolved organic carbon and acetate, all base elements used in the production of CH₄. The authors found significantly higher acetate formation rates in the root vicinity of *Eriophorum scheuchzeri*, in comparison to the other species studied (Ström et al., 2003). As my vegetation analysis revealed, significantly higher number of *Eriophorum scheuchzeri* occur within C plots. We can, therefore, assume a higher concentration of soil water CH₄ may occur within the C plots. However, in contrast to the finding from Ström et al. (2012) no significant difference in soil water CH₄ existed between treatments (table 5). Thus we can speculate that the concentration of CH₄ is at a 'holding capacity' for the soil water, and is replaced at a higher rate than can be vented.

5.5 Drivers of ecosystem CH₄ flux

The results show a significant correlation between GPP, R_{eco} and PAR with R_{eco} the most significant factor determining the flux of CH₄ ($R^2 = 0.25$). The results obtained are not broadly consistent with the major trends which usually conclude that GPP or peat temperature are the largest drivers of CH₄ flux (Ström and Christensen, 2007; Ström et al., 2014; Lai, Roulet and Moore, 2014). However, within this study, the significant correlation between Reco, GPP and WtD indicate a slightly different conclusion. The magnitude of CH₄ flux is dependent upon the amount of available substrate for methanogens to re-mineralise organic carbon (Schlesinger and Bernhardt, 2013). The carbon that is usually sourced in the form of low molecular weight compounds becomes available in the peat layer following respiration, (Ström et al., 2003). Therefore, with a large R_{eco}, more substrates will be available for methanogens. The dry conditions observed will also increase the R_{eco} since aerobic decomposition rates increase with low water availability (Schlesinger and Bernhardt, 2013).

In addition to R_{eco}, high plant productivity (GPP) was significantly correlated with the WtD (table 4). Several studies have found that GPP is significantly correlated CH₄ emissions (Ström and Christensen, 2007; Ström et al., 2014; Lai et al., 2014). Using stable isotope techniques Chanton et al. (1995) revealed that, a significant amount of emitted CH₄ is sourced from recently fixed carbon. This effect is commonly attributed to higher supply of substrate to methanogenic CH₄ production. WtD largely controls the anoxic zone and therefore, in the absence of water, leads to less methanotrophic CH₄ oxidation with a shallower WtD.

5.6 Combined soil and biomass density

The results show no significant variation in the density of soil and biomass and thickness of the zones. This indicates that the observations in the field of a thick dense root mass observed in the C plots were not significantly different in comparison to Ex plots. It was hypothesised that the presence of the muskox's weight, from grazing in the fen, would compact the soils and root mass.

In contrast to my results, Van Klink et al. (2015), discovered that the effects of soil compaction via use of an artificial rammer were most pronounced under waterlogged conditions. Their results exhibited increased density, soil moisture content and decreased air-filled porosity. The most likely explanation of our different results may be clarified again by

the lack of observed muskox grazing during the measurement period. During the experiment conducted by Van Klink et al. (2015), measurements were made four months after the effect of trampling. During our measurement period we are unable to specify when the last trampling event may have occurred. Therefore the ‘bounce back’ effect of the compaction within the ecosystem cannot be captured, suggesting the results are non-conclusive.

One main limitation of the soil density results could be linked to the experimental design. Measurements were made to capture the below ground biomass as a final result. The technique used, captures the combination of both soil and biomass. Therefore to gain a better understanding of this, it would be better to remove the soil content completely. This would result in the specific root biomass, which could be compared between the two treatments and yield a more accurate result.

6.0 Summary and Conclusion

This study shows that the prevention of muskox grazing and trampling within arctic wetland ecosystems can rapidly alter the composition and structure of wetland vegetation, and in turn affect the magnitude of CH₄ fluxes. Based on the work of Falk et al. (2015), I hypothesised that the exclusion of large herbivores would lead to a change in plant composition with a lower total number of tillers, subsequently altering the carbon cycle. This hypothesis was supported with regards to the composition and total number of tillers; however, the predicted change in NEE, GPP and R_{eco} was not found. One explanation for the limited difference between NEE, GPP and R_{eco} was the lack of observed grazing during the measurement period. As no muskox were present during measurements, the direct effect of grazing was difficult to detect. I speculated that as the amount of vascular plants decreased, the space available for photosynthetic activity was taken up by moss. Therefore, negating any measurable difference between treatments. The exclusion of muskox did, however reduce the magnitude of the CH₄ flux. Presumably, this decrease in CH₄ flux was a result of less plant-mediated transport from a lower number of tillers in the Ex treatment.

My second hypothesis, based upon observations made in the field, stated that the exclusion of trampling will result in a higher root-mass density. The results showed no significant difference in root mass density from trampling. I speculated that the lack of difference between the root mass density was, again, due to the absence of observed grazing during the measurement period. Without any trampling present, it was difficult to conclude whether the observed difference in root mass was from trampling or other means, such as vegetation composition.

A limiting factor in developing estimates for the effects of herbivory on carbon cycling is quantifying the area and intensity of herbivore pressure. Estimating the total number of herbivores present in a given area, their grazing intensity combined with long-term experiments, may help address such questions in the future. Future research will help improve the understanding of herbivory and associated processes that affect the carbon cycle within the arctic; thus, resulting in a more robust foundation for future predictions in ecosystem models and management of grazing herbivores.

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7.0 References

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