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Nitrogen uptake patterns by snow addition in a sub-Arctic dry heath tundra ecosystem



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Abstract

The Arctic heath tundra ecosystem is undergoing rapid transformations driven by climate change, which particularly affects snow accumulation and the length of the growing season. In this study, I examined the influence of snow depth on parameters such as water content, soil temperature, microbial activity, and nutrient availability and investigated their implications for plant water availability and nitrogen cycling processes. Through snow fence experiments and ¹⁵N isotope labelling and simulations of carbon fluxes with the CoupModel, I found that a longer growing season positively impacted plant productivity, carbon accumulation, and nutrient assimilation. Both evergreen and deciduous plants benefited from an extended growing season, but when the growing season was shortened, evergreen species exhibited greater resilience, while deciduous species were more susceptible to detrimental effects on growth and photosynthesis. Non-growing season alterations in snow cover could have intricate consequences on annual photosynthesis and greenhouse gas emissions, as increased snow depth favored microbial activity in winter and resulted in higher carbon dioxide emissions. These emissions counteracted the carbon sequestration advantages of the growing season, underscoring the importance of considering both the duration of the growing season and snow dynamics in conservation and management strategies.

Keywords: Arctic ecosystem, snow accumulation, growing season length, nutrient availability, carbon sequestration, greenhouse gas emissions, climate change impacts, CoupModel.

Resumen

El ecosistema de tundra ártica experimenta cambios rápidos debido al cambio climático, especialmente en la acumulación de nieve y la duración de la temporada de crecimiento. Este estudio investigó los impactos de la profundidad de nieve en parámetros clave, como el contenido de agua, la temperatura del suelo, la actividad microbiana y la disponibilidad de nutrientes, y sus efectos subsiguientes en la disponibilidad de agua para las plantas y los procesos de ciclado de nitrógeno. A través de experimentos con vallas de nieve y etiquetado con el isotopo ¹⁵N y simulaciones de flujos de carbono con el modelo CoupModel, se determinó que una temporada de crecimiento más larga influyó positivamente en la productividad de las plantas, la acumulación de carbono y la asimilación de nutrientes. Una temporada de crecimiento extendida benefició tanto a las plantas perennes como a las caducifolias. Sin embargo, en caso de una temporada de crecimiento más corta, las plantas perennes demostraron una mayor resistencia, mientras que las plantas caducifolias fueron más susceptibles a los efectos adversos en su crecimiento y fotosíntesis. Las alteraciones en la cobertura de nieve durante la temporada no productiva podrían tener efectos complejos en la fotosíntesis anual y las emisiones de gases de efecto invernadero, ya que el aumento de la profundidad de nieve favorecía la actividad microbiana en invierno y resultaba en niveles más altos de dióxido de carbono. Estas emisiones contrarrestaban los beneficios de la captura de carbono de la temporada de crecimiento, lo que resalta la necesidad de considerar tanto la duración de la temporada de crecimiento como la dinámica de la nieve en las estrategias de conservación y manejo.

Palabras clave: ecosistema ártico, acumulación de nieve, duración de la temporada de crecimiento, disponibilidad de nutrientes, captura de carbono, emisiones de gases de efecto invernadero, impactos del cambio climático, CoupModel.

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1. Introduction

The Arctic tundra is a cold, high-latitude ecosystem characterized by long cold winter periods and short growing seasons (Harmsen & Grogan, 2013). Although the snow-free period allows vegetation to develop in the tundra biome (Bowden, et al., 2020), low nutrient availability due to harsh environmental conditions affects plant growth and primary productivity, particularly the availability of nitrogen (N) (Peterson, 2014), which is essential for plant growth (Ohyama, 2010), development, and reproduction. The forms of N available to plants tend to decrease as latitude increases, (Du, et al., 2020; Liu, et al., 2016) since low temperatures slow down the biological processes of soil mineralization and decomposition (Conant, et al., 2011; Onwuka & Mang, 2018), causing more N to accumulate in organic matter than is used by plants. However, rapid warming due to climate change in the Arctic (Vincent, 2020) could stimulate soil N mineralization and plant growth (Lee, et al., 2021; Phoenix & Treharne, 2022), depending on the time when warming occurs (summer or winter) and how it affects the biotic and abiotic conditions of the local environment (Liang, et al., 2020).

The changing climate has significantly impacted the snow cover in the Northern Hemisphere due to the alteration of annual snowfall patterns (Bintanja & Andry, 2017) and changes in the timing of snowmelt and freeze-up. The presence or absence of snow cover can strongly influence the soil's temperature and moisture (Vavrus, 2007; Wipf & Rixen, 2010), as well as the frequency of freeze-thaw and the duration of the growing season. These factors, in turn, can impact critical ecosystem processes, such as carbon and N cycling (Wang, et al., 2020). Consequently, winter snow cover has become one of the most significant climate-changing features under current global change scenarios (IPCC, 2021).

The accumulation of snow plays a critical role in determining the availability of nutrients in the soil through the continuous decomposition of organic matter (Schimel, et al., 2004). Furthermore, it influences the onset of the growing season, as a thick layer of snow can cause a delayed thaw, postponing plant growth (Hallinger, et al., 2010). In dry heath tundra ecosystems, where soil conditions are characterized by coldness and dryness (Bowden, et al., 2020), the impact of increased snow cover accumulation becomes even more significant (Rixen, et al., 2022). These extreme environmental stresses limit the activity of microorganisms (Salazar, et al., 2020). However, greater

snow accumulation can alleviate these limitations by providing insulation and moisture to the soil, potentially facilitating microbial processes and nutrient availability (Schimel, et al., 2004).

Arctic soils are crucial for the growth and survival of vegetation in the region (Bilbrough, et al., 2018). Two processes that increase nutrient availability in these soils are warming-accelerated decomposition (Ofiti, et al., 2021; Tao, et al., 2020; Semenchuk, et al., 2019) and N release due to permafrost thaw (Pedersen, et al., 2020; Schuur, et al., 2022; Plaza, et al., 2019). The former process increases N availability in the upper soil layers (Geml, et al., 2021), which is essential for Arctic vegetation (Bilbrough, et al., 2018), as arctic plant mainly allocates its root biomass in the topsoil (D'Imperio, et al., 2018). On the other hand, permafrost contains N available to plants (Pedersen, et al., 2022). Since the frost layers of permafrost begin to thaw, the N that remains trapped in the soil becomes available for microbial turnover and plant uptake (Albano, et al., 2021). How arctic species use the newly available N depends on various factors, such as the distribution of N within the soil profile (Pedersen, et al., 2020; D'Imperio, et al., 2018), release timing, (Rasmussen, et al., 2022; Hansen & Elberling, 2023), and competition with other species and microorganisms (Albano, et al., 2021). For instance, plants' rooting depth, density, and mycorrhizal associations may determine their ability to acquire N at different depths within the soil profile (Michelsen, et al., 1998). Moreover, pools of N may become essential to plants (Hewitt, et al., 2018). The utilization of N released during autumn relies on the ability of arctic plants to continue absorbing N from the most productive period of growth and relocating or storing these vital elements for future utilization in the subsequent growing season (Pedersen, et al., 2020; Rixen, et al., 2022).

The impacts of snow accumulation, N uptake patterns, soil-plant interactions, and below-ground processes in the Arctic are poorly studied (Arndal, et al., 2018; Pedersen, et al., 2020; Li, et al., 2016), leading to many uncertainties. Nevertheless, the availability of soil nutrients plays a pivotal role in the impact of climate change on the productivity of Arctic plants (Larsen , et al., 2012). The Arctic ecosystem stands to benefit from heightened N availability, leading to increased plant productivity and shifts in species composition (Hobbie, et al., 2009). These alterations have the potential to impact the equilibrium of carbon and energy within ecosystems and contribute to

significant climate feedbacks on a broader scale (Wang, et al., 2020). Consequently, it is of utmost importance to gain a comprehensive understanding of how diverse plant species respond to changes in the availability of N below the surface. This knowledge is vital for accurately predicting the potential transformations in Arctic vegetation patterns caused by the effects of climate change.

2. Theoretical background

The Arctic tundra is a complex ecosystem susceptible to changes in Nitrogen (N) availability, plants, microbes, and weather, which are all interrelated (Harmsen & Grogan, 2013). The region is experiencing significant increases in air temperatures, particularly during the winter, leading to increased in precipitation that can be in the form of snowfall (IPCC, 2021). The thicker snow cover can insulate the soil and enhance N mineralization, but a spring onset delay can hinder early-growing plant species (Schimel, et al., 2004). Meanwhile, the low temperatures, short growing season, and permafrost in the Arctic tundra limit N availability (Sistla, et al., 2012), which is essential for plant growth and primary production (Nordin, et al., 2004). However, winter snowfall and subsequent snowmelt can enhance N mineralization rates, increasing N availability in the growing season and stimulating plant growth and photosynthesis (Kreyling, 2019).

Microbes play a crucial role in the cycling of N, and the insulating snow cover during winter can provide a favorable environment for microbial metabolism, resulting in higher rates of organic matter decomposition and N mineralization (Schimel, et al., 2004). Changes in winter precipitation patterns and snow cover duration can significantly impact the plant-microbe interactions and ecosystem processes in the Arctic tundra (DeMarco, et al., 2011), making accurate projections of future terrestrial carbon and N dynamics relevant.

Plants uptake N from the soil in different forms, such as ammonium, nitrate, and organic N (e.g., free amino acids) (Zhu, et al., 2019). Plant species in the Arctic differ in their preferences for N forms (Yang, et al., 2022), which may depend on the plant's physiology, habitat, and availability of N sources.

N-fixing bacteria have a crucial role in adding N to Arctic ecosystems (Hobara, et al., 2018; Steward, et al., 2018), converting N_2 gas from the atmosphere into a biologically

available form, such as ammonia or nitrate, through the process of N fixation (Rousk, 2022), increasing the amount of N available for plant growth and primary production in these ecosystems (Nordin, et al., 2004). N-fixing bacteria also play an important role in facilitating plant community composition and diversity (Hobara, et al., 2018). Many arctic plant species are dependent on N-fixing bacteria to obtain the necessary N for growth and survival (Ramm, et al., 2022). Atmospheric N deposition is another source of N (Ackerman, et al., 2018), but its input is low in high-latitude ecosystems (Liang, et al., 2020).

Decomposing biomass releases organic N, which can be taken up by plants and microbes (Nordin, et al., 2004) or by the mineralization process would release ammonia (Ohyama, 2010). Compounds such as nitrate, nitrite, ammonia, and ammonium can be taken up from soils by plants and become accessible to microbes (Salazar, et al., 2020). Nitrifying bacteria in the soil convert ammonia into nitrite and then into nitrate, a more mobile form of N (Salazar, et al., 2020). This process is called nitrification.

In addition, N can be transported laterally through the soil depending on the terrain's topography. The transport of N downslope in the Arctic landscape occurs during the spring pulse of N in solution (Semenchuk, et al., 2015), which infiltrates the shallow thaw layer due to meltwater from snow melt. The redistribution of N across the landscape affects the spatial variability of N cycles in the Arctic ecosystems (Pedersen, et al., 2022). While the lateral movement of N can increase plant Carbon (C) uptake, it can also contribute to increased N₂O emissions (Rasmussen, et al., 2022). Strong N limitation in Arctic plants makes them efficient at capturing and retaining available N. However, deep-soil N moving downslope may bypass shallow-rooted plants, leading to N loss from the ecosystem (Pedersen, et al., 2022). Plant N uptake is also determined by species-specific characteristics, including rooting depth (D'Imperio, et al., 2018; Pedersen, et al., 2022; Rasmussen, et al., 2022).

Plant type is another important factor influencing N uptake by plants in the Arctic tundra. Evergreen and deciduous plants have different N uptake and allocation strategies (Rasmussen, et al., 2022), which can influence their competitive interactions and community dynamics (Semenchuk, et al., 2019). Evergreen plants tend to have lower N uptake rates but higher N use efficiency than deciduous plants (Vowles & Björk, 2018) because evergreen plants have a longer growing season and can allocate

more resources to N assimilation and storage. Deciduous plants, on the other hand, tend to have higher N uptake rates but lower N use efficiency, as they allocate more resources to rapid growth and biomass production (Hobbie, et al., 2009).

Root distribution is another key factor influencing N uptake by plants in the Arctic tundra (D'Imperio, et al., 2018). The shallow permafrost layer in this ecosystem restricts root growth to the upper soil layer, where N availability is limited (Semenchuk, et al., 2015). As a result, plants have evolved different strategies to explore and exploit this nutrient-poor soil layer (Pedersen, et al., 2020). For instance, some plant species have developed shallow, spreading root systems that can efficiently capture nutrients from the upper soil layer (Addis & Bret-Harte, 2019). In contrast, others have deeper taproot systems that can access deeper soil layers with higher nutrient availability (Dobbert, et al., 2021).

N uptake by plants in the Arctic tundra is a complex process influenced by several factors, including mycorrhizal fungi, N deposition, plant types, and root distribution. Understanding these mechanisms is crucial for predicting the response of Arctic ecosystems to global change and developing effective management strategies to mitigate the impacts of environmental stressors on this fragile ecosystem.

3. Aim and hypothesis.

This study aims to understand the relationship between vegetation and the microbial community in terms of N acquisition patterns in a dry Arctic tundra ecosystem, answering the following questions:

- (i) What are the present patterns of N acquisition in dry heath ecosystems?
- (ii) How do snow additions affect these N uptake patterns?
- (iii) How do these N uptake patterns affect vegetation growth and the carbon cycle?

We hypothesize that due to the thickness of the snow cover, the soil temperature would be warmer by insulation, which stimulates microbial activity during winter and results in greater N availability which may result in the utilization of some plants (depending on their physiology), showing higher concentrations of N in their leaves. However, it is likely that if the snow cover gets higher and higher, growing seasons will start later, limiting the growth of early growing season plants and, thus, their capability of taking up N via deeper roots.

4. Methods

4.1.Study site and experimental setup

The study was conducted at the Snow fence site (dry ecosystem) in the Blæsedalen valley (69°14'N - 53°32'W) (Figure 1a) near the Quequertarsuaq Arctic Station on Disko Island in western Greenland. The site has six plots $(3 \text{ m} \times 3 \text{ m})$ installed in 2012 (Figure 1b).

According to data from the Greenland Ecosystem Monitoring (GEM) database, the average air temperature of the location spanning from 1993 to 2022 was -2.45 °C. February is the coldest month with an average temperature of -13.24°C followed by March with an average temperature of -12.84°C, while July and August are the warmest months with an average temperature of 8.29 °C and 7.41 °C respectively. The area receives around 60% of its annual precipitation through rainfall (Hansen, et al., 2006). The mean annual precipitation, including rain and snowfall, is approximately 400 mm (Hollesen, et al., 2015).



Figure 1.Study site an experimental setup in the arctic tundra ecosystem in Greenland. **a)** Blæsedalen map, Disko Island constructed by Andreas Westergard-Nielsen,2014 and **b)** Snow fence site - dry heath ecosystem in the Blæsedalen valley. Photo: Kimberly Montañez

The terrain at the Blæsedalen Valley comprises a blend of sand, gravel, and rocks deposited by glaciers. The location is on a dry sub-Arctic tundra that rests on a sediment of till, mainly consisting of basaltic rock deposited by glaciers less than 10,000 years ago. This unique geological formation has allowed the ecosystem on the dry tundra to establish a shallow organic layer since its deposition (Svennevig, 2019). Various land features, including terraces, a moraine, slopes, and a depressed area, encompass the study site.

At the study site, we identified five distinct species belonging to the functional types of evergreen and deciduous (Figure 2). Evergreen species accounted for 31.5% of the vegetation cover and exhibited shallower root systems. On the other hand, deciduous species were the most abundant, comprising 63.5% of the vegetation cover, and possessed deeper roots. Additionally, a small portion, approximately 5% of the total cover, consisted of grasses, with the presence of the species Graminoids carex sp.



Figure 2. Plant species located in the experimental site, Arctic tundra, divided by functional type Deciduous (Vaccinium uliginosum, salix glauca, Betula nana) and Evergreen (Empetrum nigrum and white arctic bell-heather).

Betula nana emerged as the dominant species among the deciduous species, contributing to 70% of the surface cover and displaying maximum rooting depths ranging from 3 to 30 cm (D'Imperio, et al., 2018). The maximum rooting depths of this species ranged from 1.3 to 10 cm (D'Imperio, et al., 2018). Within the evergreen functional type, *Empetrum nigrum*, commonly known as "*crowberry*," stood out as the most abundant species, with a surface cover of 66%.

4.2.Experimental setup

The experiment aimed to investigate potential differences in N uptake across three treatments in the tundra biome. The study, known as the Snow Fence experiment, involved the installation of a fence measuring 14.7 m in length and 1.5 m in height within each of the six main plots (Figure 1b).

Snow fences protect the leeward side from snow accumulation and wind during winter. Each side of the fence featured a plot under ambient conditions without any modifications, known as the Control Treatment (C). On the other side of the fence, where snow accumulates, was the Snow Treatment plot (S), where snow accumulation could reach up to approximately 1.5 m at its peak. Additionally, a tail formed due to snow accumulation, where the maximum snow accumulation was about 0.75 cm (half that of the Snow Treatment zone) was situated in the Melting Treatment (M).



Figure 3. Experimental set-up. **a**) Schematic representation of the location of the plots, the letter **C** indicates the Control treatment, the letter **S** indicates the Snow treatment, and the letter **M** indicates the Melt treatment. **b**)Aerial photograph of a main plot. Unlike figure (a), figure (b) shows the actual location of the Control treatment sub-plots, which were located between 4 and 5 meters east and west. (south-west and south-east) **c**) Top view of a sub-plot (40 cm x 40 cm). Photos: Kimberly Montañez.

In August 2022 (9th and 10th), during the growing season, we established eighteen subplots (40 cm \times 40 cm) (Figure 3a) within three of the main plots (Plot 2, Plot 4, and Plot 6 (Figure 1b)). In every single main plot, two sub-plots were positioned 4 to 5 meters apart in the Control Treatment area (C) (Figure 3b), while two others were placed in the Snow Treatment zone (S) (Figure 3a). Additionally, two sub-plots were situated 1 to 2 meters apart in the Melting Control area (M) (Figure 3a). All plots were located within an area of homogeneous vegetation, with a distance greater than 15 m between them.

4.3.Isotopic labeling

To simulate the release of nitrogen (N) within each sub-plot, a specific quantity of stable isotope ¹⁵N was injected into the soil at a depth of 30 cm. The isotopically labeled N was introduced in the form of ¹⁵N-enriched ammonium chloride in solution (¹⁵N-NH4Cl, \geq = 99%(CP)). A total of 0.1 g of ¹⁵N was added to each plot by injecting 100 ml of solution with a syringe through a narrow hollow tube inserted into the soil (Figure 4a) at the given depth through four injection points (25 ml each) (Figure 4b) an amount large enough to ensure detectable levels of 15N, but small enough to prevent fertilization (Pedersen, et al., 2020).



Figure 4. ¹⁵N solution (¹⁵N-NH4Cl, >= 99%(CP)) addition in each sub-plot **a**) The four red dots indicate the points where 25 ml of the solution was injected. The larger pink dots represent schematically (not on a real scale) the distribution of the solution around the injection point. **b**) Photo of the injection process in one of the subplots in the field. Photo: Kimberly Montañez.

4.4.Sampling

From August 10th to August 20th, soil samples were collected from the uppermost layer of soil (5cm to 10 cm) from every single sub-plot at various intervals (one day, three days, seven days, and eight days) following the injection of the isotope (Figure 5). After

the seven and eight labeled days, soil samples were also collected at 15cm to 20 cm depth, to examine the total and dissolved N and C content. To establish a baseline for comparison, soil samples were also collected from every single sub-plots at the same depths before the isotope injection.

To assess the recovery of the isotopic label in plant material, vegetation was harvested from a 5×5 cm area both before injection and on days 1, 3, 7, 8, and 25 after injection. Plant species sorted above-ground biomass (leaves and stems).



Figure 5. Soil sampling process. A schematic representation of the soil sampling process in a plot is shown. Red bars indicate the injection points and brown bars represent soil samples taken at two different depths (5 to 10 cm and 15 to 20 cm). The numbers shown on the brown bars correspond to the number of days that the sample was collected after the isotope injection. Illustration: Kimberly Montañez.

4.5.Samples treatment and laboratory analyses

Multiple soil samples were collected and analyzed to characterize the ecosystem for microbial N uptake, ¹⁵N recovery, and soil nutrients. Ninety soil samples were collected and all were divided into sub-samples for further analysis (Figure 6). Gravimetric soil water content (GWC) was calculated by drying 5 or 10 grams of soil at 60°C for 48 hours, and then the GWC was calculated based on each sample's totally fresh and dry weight. The total N and C soil content was determined using an isotope ratio mass spectrometer (IRMS) after finely grinding the soil samples and folding 10 mg of the samples into tin capsules.

The chloroform fumigation extraction method (Brookes, et al., 1985) was used to determine the N and C content of the microbial biomass and ¹⁵N enrichment. The

dissolved N and C were extracted from fresh soil samples using demineralized water and filtered through GFF microfiber filters. Another set of soil subsamples was fumigated with chloroform for 24 hours to release microbial N and C from the soil and then extracted. In total, 90 samples were extracted, and 90 were fumigated and then extracted. The fumigated and non-fumigated soil extracts are analyzed after a freezedrying process in an IRMS.



Figure 6. Soil sample treatment procedure for every plot in the experimental side. Each soil sample was cleaned sorting out rocks and roots by hand and then divided in four sub-samples for each treatment, Gravimetric Water Content (GWC), Total Nitrogen + Carbon (Total N+C), Extraction and Fumigation.

To determine the isotopic ratio ¹⁵N:¹⁴N and the total concentrations of N and C, aboveground biomass was dried, finely ground, and 5 mg of the sample was folded into tin capsules for IRMS analysis. The above-ground biomass was separated into leaves and stems, and they were sorted by species and functional type (Figure 7). Approximately 300 samples were processed. Roots were also sorted by hand, rinsed, dried, and weighed at 50°C for 24 hours. The roots' isotopic composition and N and C content were analyzed using the same IRMS method. In total, 90 root samples were processed.



Figure 7. Above-ground biomass (Stems and plants) treatment procedure for every of the sampled plants. The plants were divided according with their specie and then the stems and leaves were grinded and process through the Isotopic Radio Mass Spectrometer machine (IRMS).

Field measurements in the experiment were conducted by designated personnel throughout the study period. Carbon fluxes were measured using chamber-based techniques. Water content was assessed using Water Level Loggers, while soil temperature was monitored using Digital temperature sensors. Snow depth measurements were obtained using a ranging pole, and the depth of the active layer was determined using a metal rod.

4.6.Statistical analysis, modeling, and data sets

The statistical analysis was conducted on the ¹⁵N-recovery data from soil and plants collected in the field. The first step involved assessing the normality of the data using the Shapiro test. This test was used to determine if the data follows a normal distribution. It is important to perform this test before conducting an ANOVA (analysis of variance) test because ANOVA assumes that the data is normally distributed. By checking for normality, we ensure that the assumptions of ANOVA are met and that the test results are valid.

Once the normal distribution of the data was confirmed, one-way and two-way ANOVA tests were conducted for the soil samples. One-way ANOVA evaluated the differences in means among multiple groups, in this case, the treatment, depth, and day after labeling. Two-way ANOVA examined the interaction between two independent variables, such as the interaction of ¹⁵N-recovery with treatment, depth, and the day after labeling (the day after injection). These tests helped to determine if there were

significant differences between the groups being compared and provided insights into the effects of different factors on the ¹⁵N-recovery data.

Similar analyses were performed for the plant samples, considering the treatment, plant type, and day after injection. Additionally, separate analyses were conducted for deciduous and evergreen, regarding the treatment and day after injection as variables.

To further investigate significant differences identified through the ANOVA tests, a post hoc Tukey test was employed. This test helped to determine which specific groups have means that differ significantly from one another. The Tukey method compares pairs of sample means using the absolute differences between them, then compared to the Tukey criterion. The Tukey criterion is derived from the studentized range distribution and is multiplied by the square root of the ratio of the mean square error and the sample size of a particular group. The Tukey test was used when the null hypothesis of the ANOVA test was rejected, indicating the presence of statistically significant differences between the group means.

The coefficient of determination (R^2) and the root mean square error (RMSE) were used to validate the model. A higher R^2 value indicates a better fit of the model to the data. RMSE, on the other hand, quantified the average difference between the simulated values of the model and the observed values. A lower RMSE indicates a better fit of the model, with smaller errors between predicted and observed values.

By utilizing R^2 and RMSE, the validity and quality of the statistical model used for the analysis can be assessed, providing insights into the accuracy and reliability of the results obtained.

4.7.Model setup

To simulate carbon fluxes, we used the one-dimensional process-oriented model CoupModel which simulates the processes of water and heat for soil-plant-atmosphere Systems (Jansson & Karlberg, 2013). The CoupModel can simulate processes that are associated with the impacts of snow accumulation on carbon (C) and nitrogen (N) uptake as well as many other relevant drivers, like climate, soil types, and plant species. For instance, the model can estimate the amount of carbon that plants take up in a given ecosystem based on factors such as temperature, precipitation, and the availability of nutrients in the soil. It can also estimate the amount of N taken up by different plant species based on their physiological characteristics and the availability of N in the soil.

In the simulation, we included soil temperature, snow depth, soil moisture, chamber fluxes, and above- and below-ground biomass datasets to validate the model (Zhang, et al., 2019). We did two simulations, one corresponding to the control plot (the ambient conditions of ecosystems), and the other, was a manipulation by adding snow to see how snow accumulation influences mineralization and nutrient uptake.

The model was based on a multilayer soil profile structure, on which two types of plants corresponding deciduous and evergreen, were simulated. We spin up the model with a long time series of meteorological data from 1956 to 2019. The measurement of the snow fences started in 2012.

The configuration of the model for the treatment plots was carried out considering the temperature and water content of the soil measured with sensors in the plots at different depths and flux measurements with automatic chambers, in addition to measurements of snow level and CN content in the soil and biomass (Table 1). The soil texture and details of the study area were based on soil cores from a nearby site (Zhang, et al., 2019).

Table 1. CoupModel inputs considering the plant types deciduous and evergreen. The data for every functional type is: Max plant height (m) provides the maximum height, in meters, that the plant can reach when fully grown. Lowest rooting depth (m) specifies the minimum depth, in meters, at which the plant's roots can extend into the soil. Max surface cover (%) indicates the maximum percentage of ground surface area that the plant can cover when fully grown. Initial C/N Leaf represents the initial carbon-to-nitrogen ratio in the plant's leaves. The initial C/N Stem represents the initial carbon-to-nit o in the plant's stems. Initial Leaf C (g m-2) denotes the initial carbon content in grams per square meter of the plant's stems.

Plant type	Max plant height (m)	Lowest rooting depth (m)	Max surface cover (%)	Initial <u>^C</u> N Leaf	Initial <u>^C</u> Stem	Initial Leaf C (g m ⁻²)	Initial Stem C (g m ⁻²)
Deciduous	0.15	-0.2	60	40	50	30	30
Evergreen	0.1	-0.05	40	30	50	30	30

To simulate the treatment plots (snow and control), the model was switched on the modules of the nitrogen and carbon, plant type, and snowpack. The nitrogen and carbon modules were used to represent the main N and C components in the soil-plant system,

in this case, the simulation was made considering a dynamic interaction between the abiotic and biotic components (Jansson & Karlberg, 2013).



Figure 8. Conceptual diagram of the CoupModel framework customized for the tundra dry heath ecosystem at Disko, Greenland. Red arrows refer to heat fluxes, black arrows to C or N fluxes, and blue arrows to water fluxes. The (1),(2),(3) and (4)numbers refer to the main equations used in the model (A-table 5). Diagram modified from (Zhang, et al., 2018).

The snowpack module was used to simulate the impact of snowfall on water and heat processes. In CoupModel, snow was simulated considering its accumulation, melting, heat conduction, and energy exchange between the interfaces of soil-snow-climate (Jansson & Karlberg, 2013). Thanks to the plant type module, a separation was made between evaporation from the soil and transpiration from the canopy. In this case, the "Explicit big leaves" option was used, which allows the simulation of different plant species, in our case, evergreen and deciduous, which will compete for radiation, water, and nutrients. The conceptual diagram of the configured model is presented in Figure 8.

5. Results

5.1.General ecosystem data

The results from five years of data (2013-2017) at the experimental site provide insights into the characteristics of the study area in which the experiment was conducted (Figure 9). The control treatment represents the environmental conditions characterized by an average snow depth of 0.44 meters (Figure 9a). In contrast, the snow treatment emulates snow accumulation conditions, with an average snow depth of 1.03 meters (Figure 9a).

These contrasting snow depths in the control and snow treatments provide a basis for examining the impacts of snow accumulation on various ecosystem parameters.

The average water content in the control treatment was 20.3% (Figure 9b), while the snow treatment showed a slightly higher value of 21.4% (Figure 9b). This indicates a modest increase in water content due to snow accumulation, which could affect plant water availability in the ecosystem.

Accumulated snow significantly influenced soil temperature, resulting in a notable difference compared to the control treatment. The control treatment had an average of 6.4°C (Figure 9c), whereas the snow treatment exhibited a slightly higher average of 8.17°C (Figure 9c). The elevated soil temperature in the snow treatment can affect nutrient availability and microbial activity, potentially affecting various ecosystem processes.



Figure 9. Study site characteristics for Control Treatment (Control) and Snow Accumulation Treatment (Snow). (a) snow depth (p<0.001), (b) water content, (c) soil surface temperature 5cm depth (p<0.05), (d) photosynthesis (p<0.001), (e) ecosystem respiration (p<0.001), (f) flux carbon. (*) significantly different. The limits of the box indicate the range of the middle 50% of the data, with a center line marking the median value. Lines extend from each box to capture the range of the remaining data, with circles placed beyond the edges of the line to indicate outliers.

Photosynthesis, measured as gross primary productivity (GPP), displayed an average rate of 4.8 g m⁻²d⁻¹ in the control treatment Figure 9d). In the snow treatment, the

average photosynthesis rate was slightly lower at 4.14 g m⁻²d⁻¹ Figure 9d). This reduction in photosynthetic activity suggests that increased snow depth may limit plant productivity and their capacity to assimilate C through photosynthesis.

The averaged ecosystem respiration rates in the control treatment was 4.18 g m⁻²d⁻¹ Figure 9e), while in the snow treatment, it was slightly lower at 4.06 g m⁻²d⁻¹ Figure 9e). The relatively small differences in respiration rates between the two treatments indicate comparable C release rates from the ecosystem, despite increased snow accumulation.

The slight decrease in photosynthesis rates in the snow treatment suggests that plants may face limitations due to higher snow depth, potentially reducing their capacity to assimilate C. However, the comparable ecosystem respiration rates between the control and snow treatments indicate that C release from the ecosystem remained relatively consistent.

Net Ecosystem Exchange (NEE), representing the net C balance in the ecosystem, considering both photosynthesis and respiration, revealed an average NEE of -0.123 g m⁻²d⁻¹ Figure 9f) in the control treatment, indicating a net C uptake. In contrast, the snow treatment exhibited an average NEE of -1.06 g m⁻²d⁻¹ Figure 9f), suggesting a slight net C release.

5.2.¹⁵N Recovery

5.2.1. Soil recovery at 10 cm and 20 cm depth

The recovery of ¹⁵N added to the soil provides insights into its fate and distribution within different treatments (Figure 10). Approximately 35% of the initially added ¹⁵N was recovered in the soil, suggesting potential losses through leached or runoff.

On the first day after labeling, the recovery of ¹⁵N in the 10 cm soil depth showed distinct patterns among the treatments. The snowpack treatment (Snow) exhibited the highest average recovery of 14%, significantly higher than the control treatment (Control) and the snow melting treatment (Melting), which had average recoveries of 6% and 5%, respectively (Figure 10).

As labeling time progressed (3, 4, 7, and 8 days), the ¹⁵N recovery in the 10 cm soil depth increased gradually in all three treatments. However, the difference in recovery

between the Snow treatment and the Control and Melting treatments became less pronounced. By the end of the 8-day labeling period, the Snow treatment showed the highest recovery at 10 cm depth with 27.8%, followed by the Control treatment at 25.5% and the Melting treatment at 17.5% (Figure 10).

At a greater depth of 20 cm, similar patterns were observed on days 7 and 8 after labeling, albeit with lower recovery percentages overall. Notably, the Melting treatment on day 8 exhibited a recovery of approximately 21% at the 20 cm depth, while the recovery at the 10 cm depth was around 17.5% (Figure 10).

These findings indicate that the recovery of ¹⁵N in the soil varied with treatment and depth, with the Snow treatment generally showing higher recoveries than the Control and Melting treatments. The distribution and fate of ¹⁵N within different soil layers and treatments highlight the importance of snowpack and melting dynamics in nutrient movement and availability in the ecosystem.



Figure 10. ¹⁵N Soil Recovery at Two Depths in Different Treatments. The figure illustrates the recovery of 15N in the soil at two depths, namely 10 cm and 20 cm (hashes), across three different treatments: control (teal color), snow (tomato color), and melting (blue color). Each treatment consisted of six replicates, and data were collected over multiple days. The error bars represent the standard deviation. It is important to note that the soil recovery measurements include the contribution from soil microbes.

The recovery of ¹⁵N in the soil is primarily influenced by the number of days after labeling, while treatment, depth, and their interactions do not have a significant impact on soil ¹⁵N recovery (A-table 1)(A-table 2).

The p-value for the Treatment factor (T) is 0.548 (A-table 1), indicating no statistically significant difference in soil ¹⁵N recovery among the treatment groups, suggesting that the different treatments applied did not result in different variations in ¹⁵N recovery.

Similarly, the Depth factor (D) shows a p-value of 0.426 (A-table 1), indicating no significant difference in soil ¹⁵N recovery between the two depths tested (10 cm and 20 cm). This implies that the depth at which the measurements were taken does not substantially affect the recovery of ¹⁵N in the soil.

In contrast, the Days after Injection (DAI) factor significantly affects soil ¹⁵N recovery, with a p-value of 0.000268 (A-table 1). This result suggests that the recovery of ¹⁵N in the soil significantly varies depending on the number of days after the labeling. The longer the time elapsed since the labeling, the more pronounced the recovery of ¹⁵N in the soil.

Considering the interactions between factors, the $T \times D$ (Treatment & depth) interaction yields a p-value of 0.590 (A-table 1), indicating no significant interaction effect between treatment and depth on soil ¹⁵N recovery. This implies that the combined influence of treatment and depth does not significantly affect the recovery of ¹⁵N in the soil.

Likewise, the T × DAI (Treatment & Days after Injection) and D × DAI (Depth & Days after Injection) interactions have p-values of 0.994 and 0.133, respectively (A-table 1), suggesting that there are no significant interaction effects between treatment or depth with days after injection on soil ¹⁵N recovery. This indicates the interaction between treatment or depth with the duration since the labeling does not significantly influence the recovery of ¹⁵N in the soil.

5.2.2. Plants (Stems and leaves)

The plants (stems and leaves) showed an average recovery of approximately 8% of the ¹⁵N added to the soil (Figure 11a). The recovery patterns in the three experimental treatments closely resemble those observed in the soil. Notably, on the third day after labeling, the snow accumulation treatment (Snow) demonstrated higher recovery than the other two treatments. This suggests that the snow cover positively influences N uptake and assimilation by the aboveground biomass. However, starting from day four, the recovery in all treatments showed a gradual increase. By day eight, the snow

treatment displayed the highest N recovery, with an average of 3.3%, followed by the snow melting treatment (Melting), with an average of 3%. On day 25 after labeling, the treatment under ambient conditions (Control) exhibited the highest recovery, averaging 2.3%; This indicates that as time progresses, the plants in all treatments become more efficient in utilizing N from the soil.

Regarding the recovery of aboveground biomass by plant functional type (Figure 11b), deciduous plants demonstrated faster recovery on the third day across all treatments (Control, Snow, and Melting), particularly in the snow treatment, indicating higher initial N uptake than evergreen plants. However, starting from day seven after labeling,



Figure 11. ¹⁵N Plant Recovery in Different Treatments. (a) Recovery of ¹⁵N in the plants (stems and leaves) and (b) Deciduous and evergreen (bar with hashes) across three different treatments: control (teal color), snow (tomato color), and melting (blue color). Control treatment consisted of 13 replicates, snow treatment consisted in 13 replicates, melting treatment consisted in 17 replicates and data were collected over multiple days. The error bars represent the standard deviation. It is important to note that the days after labelling without data mean no enrichment.

evergreen plants (represented by the bars with hashes) displayed an increase in recovery across all treatments: Control, Snow, and Melting, with average recoveries rising from 1.3% to 1.8%, 0.4% to 1.5%, and 0.3% to 1.3%, respectively.

In contrast, deciduous plants remained relatively constant or experienced a slight decrease in recovery from day seven after labeling onwards. This implies that deciduous plants may have already acquired sufficient N by day seven or that other factors may have influenced their N uptake.

An analysis of variance (ANOVA) test was conducted to examine the effects of different factors on ¹⁵N recovery in plants, specifically focusing on the recovery of deciduous and evergreen plant functional types (A-table 1).

For the overall analysis of ¹⁵N-recovery in plants, the Treatment (T) factor showed a p-value of 0.412, indicating no significant difference in ¹⁵N-recovery among the treatment groups. Similarly, the Plant Functional Type (PFT) factor had a p-value of 0.1061, suggesting no significant variation in ¹⁵N recovery between deciduous and evergreen plants. However, the Days after Injection (DAI) factor displayed a highly significant p-value of 0.00000225, indicating that the number of days after injection significantly influences ¹⁵N recovery in plants. Additionally, the interactions between the Treatment and PFT factors (T × PFT) showed a p-value of 0.0103, suggesting a significant interaction effect on ¹⁵N-recovery. The interactions between Treatment and DAI (T × DAI) and PFT and DAI (PFT × DAI) also displayed significant p-values of 0.0144 and 0.0087, respectively, indicating that the combined effects of Treatment and DAI, as well as PFT and DAI, have a significant impact on ¹⁵N-recovery.

Furthermore, when focusing specifically on deciduous plants, the Treatment factor exhibited a highly significant p-value of 0.00143 (A-table 1), indicating that different treatments significantly affect ¹⁵N-recovery in deciduous plants. The DAI factor also showed a highly significant p-value of 0.000303, suggesting that the number of days after injection significantly influences ¹⁵N recovery in deciduous plants. The interaction between Treatment and DAI (T × DAI) had a p-value of 0.0285, indicating a significant combined effect on ¹⁵N-recovery.

In the case of evergreen plants, the Treatment factor yielded a non-significant p-value of 0.446 (A-table 1), suggesting that the treatments do not significantly impact ¹⁵N-recovery in evergreen plants. However, the DAI factor exhibited a highly significant p-value of 0.0000088, indicating that the number of days after injection significantly influences ¹⁵N recovery in evergreen plants. The interaction between Treatment and DAI (T × DAI) also showed a significant p-value of 0.0169, indicating a combined effect on ¹⁵N-recovery in evergreen plants.

5.3.Biomass

5.3.1. Above ground biomass

The results indicate notable differences in total biomass and biomass distribution between the treatments (Figure 12). The control treatment showed a total biomass of 90.084 g cm⁻², with a higher proportion contributed by deciduous plants (49.015 g cm⁻²) compared to evergreen plants (41.068 g m⁻²). The melting treatment showed a slightly higher total biomass of 97.059 g cm⁻², with a similar pattern of greater deciduous biomass (65.558 g cm⁻²) than evergreen biomass (31.500 g cm⁻²). In contrast, the snow treatment displayed the highest total biomass of 102.397 g cm⁻², with a higher distribution in evergreen (66.508 g cm⁻²) than deciduous (35.889 g cm⁻²).



Figure 12. Total aboveground biomass (stem + leaf) distribution for evergreen and deciduous plants in three different treatments: Control (teal), Melting (blue), and Snow (tomato). The figure illustrates the variations in biomass distribution between the treatments and provides insights into the response of evergreen and deciduous plants to different snow depths in the heath Arctic tundra. Control treatment consisted of 13 replicates, melting treatment consisted of 17 replicates, and data were collected over multiple days. The error bars represent the standard deviation.

5.3.2. Below ground biomass

In the 0-5cm depth interval, the fine root biomass was 215.8 g cm⁻² in the environmental conditions treatment (Control) and increased to 228.8 g cm⁻² in the snow accumulation treatment (Snow) (Figure 13). However, the coarse root biomass in the same depth interval decreased from 240.9 g cm⁻² in the environmental conditions treatment (Control) to 42.0 g cm⁻² in the snow accumulation treatment (Snow) (A-table 4). Consequently, the total root biomass decreased from 456.7 g cm⁻² in the environmental conditions treatment (Snow) (Figure 13).

In the 5-10 cm depth interval, the fine root biomass decreased from 130.2 g cm⁻² in the environmental conditions treatment (Control) to 104.3 g cm⁻² in the snow accumulation

treatment (Snow) (Figure 13). However, no measurements of coarse root biomass were recorded in this depth interval for both treatments (A-table 4).

Similarly, in the 10-15cm depth interval, the fine root biomass increased from 32.1 g cm⁻² in the environmental conditions treatment (Control) to 45.7 g cm⁻² in the snow accumulation treatment (Snow) (Figure 13). No measurements of coarse root biomass were obtained for this depth interval in both treatments (A-table 4).



Figure 13. Below ground biomass. (a) Total root biomass and (b) fine root biomass under two different treatments, snow (tomato) and Control (teal), measured at different depth intervals. The error bars represent the SE. The number of samples are shown in A-table 4.

5.4. Model

5.4.1. Snow depth – validation

For the ambient conditions treatment (C), the simulated snow depth is represented by a solid line, while a dotted line depicts the measured snow depth (Figure 14-a). The goodness of fit between the simulated and measured values is indicated by the coefficient of determination (\mathbb{R}^2), which measures the proportion of the variation in the measured data that the simulated data can explain. In this case, the \mathbb{R}^2 value is 0.896, indicating a strong correlation between the simulated and measured snow depth.

The root mean square error (RMSE) is also provided to estimate the average deviation between the simulated and measured values. In this instance, the RMSE value is 0.241, indicating a relatively small error between the simulated and measured snow depth in the control treatment. Similarly, for the snow accumulation treatment (S), the simulated and measured snow depth are represented by a solid and dotted line, respectively (Figure 14-b).



Figure 14. Snow depth validation results from environmental conditions (C) and snow accumulation (S) plots. Measured values are represented as solid lines teal for C and red for S. Simulated values are represented as dotted lines teal for C and red for S.

The R^2 value for this treatment is 0.803, indicating a good correlation between the simulated and measured snow depth. The RMSE value of 0.3687 suggests a slightly higher average deviation between the simulated and measured values than the control treatment.



5.4.2. Carbon fluxes of total plants

Figure 15. Carbon-Related parameters in the control and snow accumulation treatments (2013-2017) monthly results over five years, highlighting the differences in simulated (a) Gross Primary Productivity (GPP) and carbon allocation between the control treatment and the snow accumulation treatment in (b) total plants, (c) evergreen, and (d) deciduous.

Simulated Gross Primary Productivity (GPP) is higher in the control treatment than the snow accumulation treatment (Figure 15a), suggesting that the control treatment, with its lower snow depth, promotes greater photosynthetic activity and plant C uptake. The total C content in plants is higher in the control treatment than in the snow accumulation treatment (Figure 15b, c, & d); this suggests that the control treatment provides more favorable conditions for C accumulation in plant biomass.

5.4.3. Carbon total roots



Figure 16. Simulated (CoupModel) comparison of carbon total root content between the ambient condition's treatment (control – teal color) and the snow addition treatment (snow – tomato color).

Comparison of C Root Content in the Control and Snow Accumulation Treatments in the study site (2013-2017). The simulated data span five years, providing insights into the dynamics of C root content in the study site. Notably, there is higher C root content in the control treatment than the snow accumulation treatment, highlighting the impact of snow depth on below-ground C allocation (Figure 16).

5.4.4. Soil temperature – validation

There is a good agreement between the simulated and measured soil temperature in the control treatment (Figure 17a), as indicated by the coefficient of determination (R^2) value of 0.782 and the root mean square error (RMSE) value of 3.202. The simulated values closely match the measured values, suggesting that the simulation accurately represents the soil temperature dynamics in the control treatment.



Figure 17. Soil temperature validation results from (a) environmental conditions (C) and (b) snow accumulation (S) treatments. Measured values are represented as solid lines in teal for C and red for S. Simulated values are expressed as dotted lines in teal for C and red for S.

Similarly, the graph demonstrates a strong correlation between the simulated and measured soil temperature in the snow accumulation treatment (Figure 17b), with an R^2 value of 0.813 and an RMSE value of 3.457. The simulation captures the variations in soil temperature reasonably well, reflecting the influence of the higher snow depth in this treatment.

5.4.5. Water content – validation

There is a moderate agreement between the simulated and measured water content in the control treatment (Figure 18a), as indicated by the coefficient of determination (R^2) value of 0.324 and the root mean square error (RMSE) value of 8.575. Although there is some correlation between the simulated and measured values, there is notable variability and deviation, as reflected by the relatively low R^2 value and the relatively high RMSE value.

Similarly, the graph depicts a moderate correlation between the simulated and measured water content in the snow accumulation treatment (Figure 18b), with an R^2 value of 0.570 and an RMSE value of 16.015. The simulation captures some of the variations in water content, but there is still significant variability and discrepancy between the simulated and measured values.



Figure 18. Water content validation results from (a) environmental conditions (C) and (b) snow accumulation (S) treatments. Measured values are represented as solid lines in teal for C and red for S. Simulated values are expressed as dotted lines in teal for C and red for S.

5.4.6. Photosynthesis – validation

There is a moderate agreement between the simulated and measured photosynthesis in the control treatment (Figure 19a), as denoted by the coefficient of determination (\mathbb{R}^2) value of 0.550 and the root mean square error (RMSE) value of 4.833. The simulation and measurement data show a reasonably correlated trend, although there is some variability and deviation, as indicated by the \mathbb{R}^2 and RMSE values.

Likewise, the graph presents a moderate correlation between the simulated and measured photosynthesis in the snow accumulation treatment (Figure 19b), with an R^2 value of 0.459 and an RMSE value of 4.326. The simulation captures some of the variations in photosynthesis, but there is still noticeable variability and a degree of discrepancy between the simulated and measured values.



Figure 19. Photosynthesis validation results from (a) environmental conditions (C) and (b) snow accumulation (S) treatments. Measured values are represented as solid lines in teal for C and red for S. Simulated values are represented as dotted lines in teal for C and red for S.



5.4.7. Ecosystem respiration – validation

Figure 20. Ecosystem respiration validation results from (a) environmental conditions (C) and (b) snow accumulation (S) treatments. Measured values are represented as solid lines in teal for C and red for S. Simulated values are represented as dotted lines in teal for C and red for S.

There is a moderate agreement between the simulated and measured ecosystem respiration in the control treatment (Figure 20a), as evidenced by the coefficient of determination (R^2) value of 0.377 and the root mean square error (RMSE) value of 3.349. The simulation and measurement data exhibit a partially correlated trend, although there is a noticeable degree of variability and deviation, as indicated by the R^2 and RMSE values.

In contrast, the graph indicates a relatively weak correlation between the simulated and measured ecosystem respiration in the snow accumulation treatment (Figure 20b), with an R^2 value of 0.149 and an RMSE value of 3.357. The simulation captures only a limited portion of the variations in ecosystem respiration, and there is substantial variability and divergence between the simulated and measured values.



5.4.8. Carbon flux – validation

Figure 21. Carbon flux validation results from (a) environmental conditions (C) and (b) snow accumulation (S) treatments. Measured values are represented as solid lines in teal for C and red for S. Simulated values are represented as dotted lines in teal for C and red for S.

There is a moderate level of agreement between the simulated and measured C flux in the control treatment (Figure 20a), as indicated by the coefficient of determination (R^2) value of 0.334 and the root mean square error (RMSE) value of 4.580. The simulation and measurement data exhibit a partially correlated trend, although there is noticeable variability and deviation from the measured values, as suggested by the R^2 and RMSE values.

In contrast, a relatively stronger correlation between the simulated and measured C flux in the snow accumulation treatment was shown (Figure 20b), with an R^2 value of 0.398 and an RMSE value of 2.711. The simulation aligns better with the measured values, capturing a more significant proportion of the variations in C flux. However, there is still some variability and divergence between the simulated and measured values.

6. Discussion

The results of this study demonstrate the influence of snow accumulation on water, C and N dynamics in the Arctic dry heath tundra ecosystem. The snow treatment's increased depth led to slightly higher water content, indicating potential implications for plant water availability (Figure 9 a & b). The higher soil temperature observed in the snow treatment (Figure 9c) can influence nutrient availability and microbial activity, affecting ecosystem processes.

Although the chloroform fumigation extraction method (Brookes, et al., 1985) was conducted as part of this project to investigate microorganism behavior, the findings could not be included in this report due to the lengthy analysis process. However, we can draw insights from other studies to understand the potential interactions at our study site.

Microbes are sensitive to changes in environmental conditions, including temperature and nutrient availability (DeMarco, et al., 2011), and their activity can directly influence N cycling processes (Nordin, et al., 2004). In terms of cooperation, certain microbial communities establish mutualistic relationships with plants. For instance, mycorrhizal fungi form symbiotic associations with plant roots, providing benefits such as increased nutrient uptake, including N (Hobbie, et al., 2009). These fungi extend the root system's reach, enhancing the plant's ability to acquire nutrients from the soil. This cooperative interaction between microbes and plants can be significant in nutrientlimited Arctic environments where N availability is a limiting factor for plant growth (Rousk, 2022).

On the other hand, in N-limited conditions, microbial communities can outcompete plants for available N (Sullivan, et al., 2020), potentially impacting plant growth and nutrient acquisition (Schmidt, et al., 2002). The competition for N between microbes

and plants becomes particularly relevant when N availability is low (Pedersen, et al., 2020), such as in Arctic heath tundra ecosystems.

In the context of the three treatments (Control, Melting and Snow), microbes' interactions with plants and their competition or cooperation for N can vary. The differences in snow depth and resulting soil conditions can influence microbial community composition, activity, and N cycling processes (Salazar, et al., 2020). Increased snow depth in the Snow treatment may create a microenvironment more conducive to microbial growth and activity, potentially affecting plant N availability (Mörsdorf, et al., 2019). The Melting treatment, with its intermediate snow depth, represents a transitional stage where the effects of snow accumulation and subsequent melting can influence microbial communities and their interactions with plants.

The slight decrease in photosynthesis rates in the snow treatment (Figure 9d) suggests that the plants may be experiencing limitations due to increased snow depth (Mörsdorf, et al., 2019), potentially reducing their C assimilation capacity. However, the comparable ecosystem respiration rates between the Control and Snow treatments indicate that C release remained relatively consistent (Figure 9e).

The slight difference in C fluxes between the Control and Snow treatments suggests that the overall C balance of the ecosystem was not significantly affected by the increased snow accumulation treatments (Figure 9f). Other factors, such as temperature, nutrient availability, and plant responses to snow accumulation, may interact and modulate the C dynamics in this ecosystem.

6.1. Nutrient distribution in the soil

The ¹⁵N soil recovery results provide valuable insights into the fate and distribution of N within the different treatments and soil depths in the arctic heath tundra experiment (Figure 10). The Melting treatment was included by the desire to explore the variations in the snow depth. At the study site, the snow depth for the Melting treatment is approximately 0.75 m (medium snow depth), which falls between the control treatment with around 0.4 m (normal or minimal snow depth) and the snow treatment with about 1.5 m (maximum snow depth). By incorporating the Melting treatment, we aimed to investigate the potential impact of meltwater on nutrient uptake and distribution patterns. This allowed us to examine how variations in snow depth and the subsequent melting process may influence these factors of interest.

Based on previous studies (Semenchuk, et al., 2015; Mörsdorf, et al., 2019; Wang, et al., 2020), we expected that the ¹⁵N recovery would be smaller in the Control treatment than the Melting treatment and higher in the Snow treatment due to the varying snow depths. However, the results revealed unexpected findings. The ¹⁵N recovery in the Control treatment was higher than in the Melting treatment (Figure 10). This discrepancy can likely be attributed to the flow of snowmelt water through the Snow treatment side, which dilutes the system in the Melting treatment (Young, et al., 2022). Interestingly, despite the initial hypothesis, the additional snow from the Snow treatment seems to be running off (Schneider, et al., 2019) rather than significantly penetrating the soil in the Melting treatment.

The active layer depth during the measurements ranged from 25 to 40 cm, indicating the possibility that snowmelt running through the frozen soil could carry away the labeled ¹⁵N (Rasmussen, et al., 2022). This could explain the lower recovery ¹⁵N in the Melting treatment compared to the Control treatment. It is worth noting that the recovery of ¹⁵N depends on the time elapsed since labeling (A-table 1-soil), as it takes time for ¹⁵N to move through the soil and reach the topsoil, either through root uptake or water transport.

Root distribution is crucial in redistributing ¹⁵N within the soil (Iversen, et al., 2015). Deeper roots primarily transport water from deeper layers to the topsoil (Pedersen, et al., 2020). In contrast, the topsoil contains a higher concentration of fine roots (Figure 13b), which can also influence the distribution of ¹⁵N. The presence of fine roots in the Snow treatment, likely facilitated by warmer soil conditions during winter (D'Imperio, et al., 2018), may contribute to an earlier increase in ¹⁵N at the topsoil. This suggests that the Snow treatment experiences a more rapid response to the deeper ¹⁵N than the Control treatment (Figure 13), which exhibited a delayed response after the third day of labeling (Figure 10).

Overall, the distribution and recovery of ¹⁵N in the soil are influenced by a combination of factors, including treatment conditions, snow dynamics, soil properties, and root distribution (Iversen, et al., 2015; D'Imperio, et al., 2018; Salazar, et al., 2020; Pedersen, et al., 2020). The unexpected results observed in the Melting treatment highlight the complexity of nutrient movement and availability in the ecosystem.

6.2.¹⁵N uptake by plants

Plants in the Snow treatment exhibit higher N uptake than the Control and Melting treatments, with uptake gradually increasing over time (Figure 11). Notably, it takes more time for above-ground plant responses to show in the Snow treatment, indicating a delayed uptake due to N transportation to the topsoil (Figure 11). The presence of dense, fine roots in the Snow treatment (Figure 13b) suggests that tapping roots aid in redistributing nutrients through the fine roots, facilitating uptake (D'Imperio, et al., 2018).

Deciduous plants exhibit an earlier response to N addition than evergreen plants, particularly in the Snow treatment where root density is higher (Figure 11-b). This can be attributed to their longer root length, enabling access to deeper soil layers where the labeled N was applied (Pedersen, et al., 2020). Deciduous plants' initial rapid N recovery aligns with their active growth and leaf expansion during this stage (Addis & Bret-Harte, 2019). While deciduous plants require more time to initiate N uptake due to dormancy and leaf development (Chapin & Shaver, 1996), they demonstrate a faster recovery in this experiment due to their deeper root system (Figure 23a).

Conversely, evergreen plants steadily increase N recovery over time in all treatments (Figure 11b). This indicates a conservative strategy in N acquisition, sustaining a steady uptake instead of an initial rapid response. This approach allows evergreen plants to utilize available N resources efficiently and continuously, enabling their survival in nutrient-limited Arctic heath tundra environments (Blok, et al., 2015).

The contrasting root depths between deciduous and evergreen plants significantly influence their N uptake behavior (D'Imperio, et al., 2018). Deeper root systems in deciduous plants enhance access to a larger soil volume and deeper nutrient reservoirs (Larsen , et al., 2012), facilitating efficient uptake of labeled N. In contrast, evergreen plants optimize nutrient uptake within the shallower active layer and leverage their leaves to initiate N uptake as soon as the snow melts (Mörsdorf, et al., 2019).

The Control treatment, with a longer growing season, allows plants to uptake and utilize nutrients over an extended period (Bilbrough, et al., 2018). This gradual and sustained nutrient uptake facilitates N accumulation in deciduous and evergreen plants within the Control treatment (Blok, et al., 2016). Higher N recovery on day 25 after labeling in

the control treatment reflects the extended time for plants to access and assimilate labeled N (Figure 11).

6.3.Total biomass distribution

6.3.1. Plants (leaves + stems)

The Control treatment, representing natural environmental conditions, exhibited a higher contribution of biomass from deciduous plants (Figure 12), which can be attributed to their deeper roots and enhanced access to soil nutrient resources (Brookes, et al., 1985). In contrast, the Melting treatment, characterized by moderate snow depth, showed decreased total biomass in deciduous and evergreen (Figure 12). This decline can be attributed to the shallower snow depth, reducing water availability and nutrient retention, affecting plant growth (Blok, et al., 2015).

Interestingly, the Snow treatment, experiencing the highest snow accumulation, displayed an overall increase in total biomass compared to the Control treatment (Figure 12). This balanced biomass distribution between deciduous and evergreen plants suggests a positive influence of snow accumulation on both plant types (Hallinger, et al., 2010). The deeper snow depth in this treatment likely provided insulation against extreme temperatures (DeMarco, et al., 2011).

Regarding seasonality, evergreen plants exhibited earlier responses in the presence of snow, whether in winter or spring (Blok, et al., 2015). This resulted in higher biomass in the Snow treatment (Figure 12). In the Melting treatment, evergreen plants may have experienced N release or leaching, possibly due to the cooling effect of melting water draining into the area (Moriana-Armendariz, et al., 2022). This cooling effect likely created a cooler soil environment than the Control treatment, offering more benefits to evergreen plants than deciduous plants (Mamet, et al., 2018; Dobbert, et al., 2021). It can be inferred that the Melting treatment, which involves the transition from cool to warm soil over time, influenced the growing season dynamics (Graham, et al., 2017).

The higher biomass contribution from deciduous plants in the Control treatment can be attributed to the longer growing season compared to the Snow and Melting treatments (Li, et al., 2016). With its lower snow depth, the Control treatment allows for an extended active growth and nutrient uptake period. In contrast, due to the higher snow depths, the shorter growing season in the Snow and Melting treatments limit the

duration for plant growth and nutrient acquisition (Larsen, et al., 2012). This difference in growing season length likely contributes to the observed higher biomass of deciduous plants in the Control treatment (Figure 12), where they have more time to accumulate biomass and utilize available resources (Rixen, et al., 2022).

6.3.2. Root biomass

Root biomass distribution is primarily dense in the topsoil layers (Iversen, et al., 2015). The increased fine root biomass observed in the 0-5cm depth interval (Figure 13b) in response to snow accumulation indicates plants' strategic allocation of resources towards exploiting the nutrient-rich soil layers beneath the deeper snow cover (D'Imperio, et al., 2018). This adaptive response allows plants to optimize nutrient uptake and enhance their below-ground performance (Larsen, et al., 2012).

On the other hand, the substantial reduction in coarse root biomass suggests a shift in resource allocation towards the proliferation of finer roots (Iversen, et al., 2015). Finer roots have been shown to possess higher nutrient-absorbing capacity, making them more efficient in nutrient uptake from the surrounding soil (Hobara, et al., 2018). This reallocation of resources towards finer roots in the presence of snow accumulation indicates plants' ability to adapt and optimize nutrient acquisition under challenging environmental conditions (Pedersen, et al., 2020).

Interestingly, the lack of measurable root biomass in the 5-10cm and 10-15cm depth intervals (Figure 13) suggests that snow accumulation may impede root growth and penetration at greater depths (Alvarez-Uria & Körner, 2007). The limited availability of soil resources caused by snow cover can restrict root development in these deeper soil layers (DeMarco, et al., 2011). This phenomenon underscores the importance of the topsoil layers as the primary site for nutrient uptake and resource utilization in the context of snow accumulation (Mörsdorf, et al., 2019).

6.4.Model results

6.4.1. Influence of growing season in N uptake by plants

The results of our study provide valuable insights into the effects of snow accumulation on various aspects of the heath arctic tundra ecosystem. By utilizing the CoupModel, which incorporates biological and abiotic processes (Jansson & Karlberg, 2013), we were able to gain a deeper understanding of the complex interactions between snow depth, plant biomass, N uptake, C content, and root characteristics.

N uptake patterns in the simulation revealed that the Control treatment, characterized by a lower snow depth, experienced an earlier start to the growing season than the Snow treatment (Figure 22b). This early start benefited evergreen plants in the control treatment (Figure 22a), as their leaves remained on the plant throughout the winter season (Blok, et al., 2016). Evergreen leaves are well-adapted to withstand cold temperatures and maintain their photosynthetic capacity (Mamet, et al., 2018). With continuous green foliage, evergreen plants can efficiently capture sunlight and carry out photosynthesis, allowing for early N uptake (Bilbrough, et al., 2018). This advantage enables them to maximize C uptake and nutrient assimilation during the growing season (Weijers, et al., 2018), contributing to their year-round growth and sustained productivity.

On the other hand, deciduous plants in the Control treatment exhibited a slight delay in N uptake (Figure 22a), beginning a few days after the snow-free season. Deciduous leaves undergo a process called abscission (Pop, et al., 2000), where they are shed from the plant. Before shedding, deciduous leaves undergo senescence, involving the breakdown of chlorophyll and reabsorption of nutrients (Chapin & Shaver, 1996). As a result, the leaves change color and eventually fall. During winter, deciduous plants enter a period of dormancy, conserving energy and resources until favorable conditions return (Dobbert, et al., 2021).

The regrowth phase in deciduous plants begins in spring as temperatures warm and days lengthen (Blok, et al., 2016). This initiates budburst, the development of new buds that will eventually open and produce new leaves (Liang, et al., 2020). These fresh leaves are vital for photosynthesis and provide the plant with the energy needed for growth and development in the upcoming growing season. Deciduous leaves have a finite lifespan (Chapin & Shaver, 1996), actively photosynthesizing during the growing season but ultimately preparing for leaf senescence and shedding as autumn approaches, followed by another winter dormancy period.



Figure 22. Nitrogen Uptake and Snow Depth in Control and Snow Accumulation Treatments in the study site. (a) The graph shows the N uptake in the deciduous and evergreen plant types under ambient conditions (Control - teal color) and snow accumulation (Snow - tomato color) treatments. The solid lines represent the N uptake by deciduous plants, while the dotted lines indicate the N uptake by evergreen plants. (b) The graph also displays the snow depth for the Control and Snow treatments, with the blue light line representing the beginning of the snow-free zone in the Control treatment and the orange light line indicating the start of the snow-free zone in the Snow treatment. The x-axis represents the days of the year (DOY) from day 120 to day 300 of 2013.

The delayed N uptake observed in deciduous and evergreen plants in the Snow treatment, characterized by a higher snow depth, suggests that winters with greater snow accumulation result in a shorter growing season (Figure 22b). The shorter growing season restricts the time available for plants to carry out essential processes, potentially affecting their overall growth and development. A shorter growing season can significantly impact deciduous plants more than evergreen plants (Gamm, et al., 2018). Deciduous plants may experience reduced photosynthesis, limited nutrient uptake, and impaired storage reserves, potentially affecting their growth and survival (Gamm, et al., 2018). In contrast, evergreen plants can maintain continuous photosynthesis, efficient resource utilization, and consistent growth and vigor (Dobbert, et al., 2021), allowing them to adapt better to environments with a shorter growing season (Vowles & Björk, 2018). This finding highlights the sensitivity of deciduous

and evergreen plants to the duration of the growing season (Wipf & Rixen, 2010; Gamm, et al., 2018; Pedersen, et al., 2020; Dobbert, et al., 2021; Rasmussen, et al., 2022) and emphasizes the potential consequences of shorter growing seasons on plant productivity and ecological dynamics.

6.4.2. Total carbon content

Regarding total C content, our findings revealed that the Control treatment exhibited higher gross primary productivity (GPP) than the Snow treatment, indicating greater photosynthetic activity and overall vegetation growth (Goulden, et al., 1996; Starr & Oberbauer, 2003) in contrast to the results of Bosiö, et al., 2014. The total C content in deciduous plants was also higher in the Control treatment than the Snow treatment (Welker, et al., 2005). The lower snow depth in the Control treatment allowed for a longer growing season, enabling deciduous plants to allocate more resources to C storage (Rasmussen, et al., 2022). Similarly, evergreen plants in the Control treatment demonstrated higher total C content than in the Snow treatment. The extended period of photosynthesis and improved nutrient availability in the Control treatment likely contributed to the increased C accumulation in evergreen plants (Blok, et al., 2016).



Figure 23. Root Depth Variation in Response to Ambient Conditions and Snow Accumulation Treatment in the study site. (a) Simulated root depth data for deciduous plants under the control treatment (solid teal line) and the snow treatment (red dotted line). (b) Simulated root depth data for evergreen plants under the control treatment (solid teal line) and the snow accumulation treatment (red dotted line). The x-axis represents the years from 2013 to 2017.

For root characteristics, we observed that the Control treatment had higher root biomass than the Snow treatment (Figure 13). This suggests that the length of the growing season plays a crucial role in driving root growth (Pedersen, et al., 2020), as roots rely on photosynthesis to allocate C resources. The longer growing season in the Control treatment likely allows earlier root development. Additionally, the Control treatment exhibited longer root lengths for deciduous and evergreen plants than the Snow treatment (Figure 23) (D'Imperio, et al., 2018). This can be attributed to the favorable growing conditions, including nutrient availability and water accessibility, in the Control treatment.

Furthermore, our study involved validating the C cycle in the CoupModel. We observed a mismatch between simulated and measured soil temperatures (Figure 17), which could be attributed to variations in soil water content. The control treatment performed better in simulating water content (Figure 18) than the snow treatment, as the model did not account for lateral flow in the latter. This discrepancy in water dynamics may have influenced the accuracy of simulated soil temperatures. Regarding C fluxes (Figure 21), differences were observed between the modeled and measured values, potentially due to the measurements' timing and environmental conditions' variations. For instance, the spike in C fluxes observed in 2014 (Figure 21) could respond to a particularly warm period during the day.

7. Conclusions

The results of this study highlight the influence of snow accumulation on several important parameters in the Arctic heath tundra ecosystem. Increased snow depth in the Snow treatment affects water content, soil temperature, microbial activity, and nutrient availability, which in turn can impact plant water availability and N cycling processes. The distribution of nutrients in the soil is influenced by snow dynamics, root distribution, and other factors, with unexpected findings in the Melting treatment indicating the complexity of nutrient movement.

Both field data and model simulations highlight the crucial role of the length of the growing season in shaping plant responses and ecosystem dynamics. The findings underscore the significance of this factor in understanding the impacts of climate change on Arctic ecosystems and the need for its consideration in conservation and management strategies.

Field observations consistently demonstrate that a longer growing season positively affects plant productivity and C accumulation. A sufficient time window for photosynthetic activity allows plants to maximize their nutrient uptake, increasing biomass and C content. This relationship is evident in both deciduous and evergreen plants, albeit with some variations in their specific responses.

The model results further confirm the importance of the growing season length and its influence on plant growth and development. Simulations show that a longer growing season leads to higher GPP and total C content, indicating enhanced C sequestration potential. The extended duration of favorable conditions allows for prolonged photosynthetic activity, promoting plant nutrient assimilation and storage reserves. In contrast, a shorter growing season restricts nutrient uptake and can hinder plant growth and productivity, particularly affecting deciduous species.

In addition to the importance of the growing season length, it is crucial to acknowledge that the Arctic ecosystem only partially benefits from increased C uptake due to climate change. Climate extremes during the non-growing season, such as alterations in snow accumulation, can have complex and potentially adverse effects on annual photosynthesis and greenhouse gas emissions.

Moreover, alterations in snow cover can also influence the release of greenhouse gas emissions. Increased snow can create an anaerobic environment, favoring microbial activity that produces higher methane and carbon dioxide emissions. These emissions counteract the C sequestration benefits of the growing season, potentially exacerbating climate change in a feedback loop.

These findings have critical implications for understanding and predicting the impacts of climate change on Arctic ecosystems. As the region experiences changes in temperature and precipitation patterns, alterations in snow accumulation and subsequent effects on the growing season length are expected. Such shifts can have cascading effects on plant communities, nutrient cycling, and C dynamics, ultimately impacting the overall functioning and resilience of the ecosystem.

Considering the importance of the growing season length, it is essential to incorporate this factor into conservation and management strategies. Protecting and restoring habitats that provide optimal conditions for plant growth and maintaining a longer growing season can help preserve biodiversity, sustain ecosystem services, and mitigate climate change impacts. Additionally, efforts to reduce greenhouse gas emissions and limit the rate of global warming can help safeguard the length and stability of growing seasons in Arctic ecosystems.

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APPENDICES

Appendix A. Statistical analysis

a. ANOVA test

A-table 1. ANOVA test - ¹⁵N soil and plants recovery. results of an analysis of variance (ANOVA) test conducted to assess the recovery of 15N (nitrogen-15) in both soil and plants. The ANOVA test is used to determine if there are significant differences among groups or treatments.

Soil									
p-value									
	Treatment (T)	Depth (D)	Days after injection (DAI)	T x D	T x DAI	D x DAI			
¹⁵ N-Recovery	0.548	0.426	0.000268	0.590	0.994	0.133			
Plants									
			p-value						
	Treatment (T)	Plant functional type (PFT)	Days after injection (DAI)	T x PFT	T x DAI	PFT x DAI			
¹⁵ N-Recovery	0.412	0.1061	0.00000225	0.0103	0.0144	0.0087			
Decid	uous								
			p-value						
	Treatme	ent (T)	Days after injec	tion (DAI)	Тx	DAI			
¹⁵ N-Recovery	0.001	43	0.000303		0.0285				
Evergreen									
			p-value						
	Treatment (T) Days after injection (DAI) T x DAI								
¹⁵ N-Recovery	0.44	16	0.00000	88	0.0	169			

b. Tukey test – Treatments

A-table 2. Tukey test - Different soil treatments. outcomes of the Tukey test, which was employed to compare the recovery of 15N (nitrogen-15) across different treatments: Snow, Control, and Melting. The Tukey test is a statistical method used for pairwise comparisons to determine if there are significant differences between specific treatment groups.

Soil - Treatment								
Group1	Group2	Mean-diff	P-value	Upper	reject			
С	М	0.131	0.6184	-0.2218	False			
С	S	-0.0153	0.9	-0.3682	False			
М	S	-0.1464	0.5561	-0.4992	False			

c. Tukey test - soil depths

A-table 3. Tukey test - Different depths. Comparisons which was conducted to assess the recovery of 15N (nitrogen-15) across two different soil depths: Group 1 = 5-10 cm (10 cm) and Group 2 = 15-20 cm (20 cm).

Soil - Depth					
Group1	Group2	Mean-diff	P-value	Upper	reject
10 cm	20 cm	3.0446	0.4065	-4.4164	False

Appendix B. ¹⁵N – recovery



A-figure 1. ¹⁵N recovery Deciduous across three different treatments: control (teal color), snow (tomato color), and melting (blue color). Control treatment consisted of 13 replicates, snow treatment consisted of 13 replicates, melting treatment consisted of 17 replicates, and data were collected over multiple days. The error bars represent the standard deviation. It is important to note that the days after labeling without data mean no enrichment.



A-figure 2. ¹⁵N recovery Evergreen across three different treatments: control (teal color), snow (tomato color), and melting (blue color). Control treatment consisted of 13 replicates, snow treatment consisted of 13 replicates, melting treatment consisted of 17 replicates, and data were collected over multiple days. The error bars represent the standard deviation. It is important to note that the days after labeling without data mean no enrichment.

Appendix C. Biomass

a. Root biomass

A-table 4. Below ground biomass

Depth	Treatment	Fine root biomass	n	SE	Coarse root	n	SE	Total root	n	SE
(cm)		g _{dw} m ⁻²			biomass g _{dw} m ⁻²			biomass g _{dw} m ⁻²		
0-5	С	215.8	11	40.4	240.9	8	-	456.7	19	112.5
0-5	S	228.8	8	70.5	42	3	-	270.8	11	82.7
5-10	С	130.2	12	28.2	-	-	-	130.2	12	28.2
5-10	S	104.3	12	34.8	-	-	-	104.3	12	34.8
10-15	С	32.1	10	6.8	-	-	-	32.1	10	6.8
10-15	S	45.7	7	10.4	-	-	-	45.7	7	10.4

Appendix D. Model equations

A-table 5. Main equations used in the model. Taking from Zhang, et al., 2018. More detailed description can be found in Jansson & Karlberg, 2013. Equation (1) Snow dynamics, Equation (2) Plant growt, equation (3) Soil organic matter, equation (4) Abiotic responses

(1) Snow dynamics

Densification as a function of ice and liquid water content

$$\rho_{old} = \rho_{s\min} + s_{dl} \frac{S_{wl}}{S_{wl\max}} + s_{dw} S_{res}$$

 $ho_{\it old}$: Density of old snow [Kg m^{-3}]

 $\rho_{\rm smin}$: Density of new snow [Kg m^{-3}]

 S_{dl} : Liquid water coefficient [$Kg \ m^{-3}$]

 $S_{wl\,{
m max}}$: Retention capacity of liquid water in the snow pack [m]

 $S_{\scriptscriptstyle wl}$: Fraction of liquid water in the snow [*m*]

 $S_{{}^{dw}: \; {\rm Mass\; coefficient}\, [m^{-1}]}$

 $S_{\it res}$: Water equivalent of snow [m]

Upper limit of aerodynamic resistance in extremely stable conditions

$$r_{aa,snow} = (\frac{1}{r_{aa,snow}} + r_{a,\max,snow}^{-1})^{-1}$$

 $r_{a,\max,snow}$: Minimum turbulent exchange coefficient (inverse of the maximum allowed aerodynamic resistance) over bare soils $[s^{-1}]$

Aerodynamic resistance at neutral conditions

$$r_{aa,snow} = \frac{1}{k^2 u} \ln \left(\frac{z_{ref} - d}{z_{OM,snow}} \right) \ln \left(\frac{z_{ref} - d}{z_{OH,snow}} \right) f(\mathbf{R}_{ib})$$

- ${\it u}$: wind speed at the reference height $[m\,s^{-1}]$
- k : Von Karmns constant
- $d_{: \text{Displace height } [m]}$

 z_{ref} : Reference height [m]

 R_{ib} : Bulk Richardson number

 $Z_{OM,snow}$: Roughness length for momentum above snow [m]

Z_{OH,snow}: Roughness length for heat flux above snow [m]

Snow albedo

$$a_{snow} = a_{\min} + a_1 e^{a_2 S_{age} + a_3 \sum T_a}$$

 a_1, a_2, a_3 : Parameters used to calculate albedo of snow.

 a_{\min} : Lowest albedo in the albedo function to accounts for snow age and positive sum of air temperature since latest new snow.

(2) Plan growth

Light use efficiency approach

$$C_{Atm \to a} = f(T_1) f(CN, p_{fixedN}) f(E_{ta} / E_{tp}) \mathbf{R}_{s, pl}$$

 $C_{Atm \rightarrow a}$: Carbon assimilation [$g \ m^{-2} d^{-1}$]

 p_{fixedN} : N supply capacity for photosynthesis

 $\mathbf{R}_{\mathrm{s,pl}}$: Radiation absorbed by canopy [J $m^{-2}d^{-1}$]

 $E_{_{ta}}$: Actual transpiration [mm]

 E_{vp} : Potential transpiration [mm]

Leaf temperature response

$$0$$

$$(T_{1} - p_{mm}) / (p_{o1} - p_{mm}) \qquad p_{mm} \le T_{1} \le p_{o1}$$

$$f(T_{1}) = 1 \qquad p_{mm} \le T_{1} \le p_{o1}$$

$$1 - (T_{1} - p_{o2}) / (p_{mx} - p_{o2}) \qquad p_{mm} \le T_{1} \le p_{o1}$$

$$0$$

 P_{mn} : Minimum mean air temperature for photosynthesis [°C]

 P_{o1} : Limit mean air temperature for optimum photosynthesis [°C]

 P_{o2} : High limit mean air temperature for optimum photosynthesis [°C]

 $P_{_{\it mx}}$: Maximum mean air temperature for photosynthesis [°C]

Litter fall from leaves

 $C_{Leaf \rightarrow LitterSurface} = f(\mathbf{l}_{Lc})\mathbf{C}_{Leaf}$

 l_{Lcl} : Rate coefficient for the litter fall from leaves before the first threshold temperature sum is reached.

Maintenance respiration of leaves/roots

$$C_{respleaf} = k_{mrespleaf} f(\mathbf{T}_{a}) \mathbf{C}_{Leaf} + k_{gresp} \mathbf{C}_{a \to leaf}$$

 $k_{mresproot}$. Maintenance respiration coefficient for roots [d^{-1}]

 $k_{\it mresleaf}$. Maintenance respiration coefficient for leaves [d^{-1}]

The temperature response function for plant respiration

$$f(\mathbf{T}) = t_{Q10}^{(\mathbf{T} - t_{Q10bas})/10}$$

 t_{Q10} : Respiration response to a 10 °C soil temperature change on the microbial activity, mineralization, immobilization, nitrification and denitrification.

(3) Soil organic matter

The decomposition of soil organic matter

$$C_{Decompl} = k_l f(T) f(\theta) C_{Litter}$$

 k_{l} :Rate coefficient for the decay of litter [d^{-1}]

$$C_{Decompl} = k_h f(T) f(\theta) C_{Humus}$$

 k_h : Rate coefficient for the decay of humus [d^{-1}]

(4) Abiotic responses

Soil moisture response function

$$f(\theta) = p_{\theta satact} \times \max(0, \min(1, 1-[CO_2]/CO_2Threshold)) \quad \theta = \theta_s$$

$$f(\theta) = \min\left(\left(\frac{\theta_s - \theta}{p_{\theta Up}}\right)^{p_{\theta p}} (1 - p_{\theta satact}) + p_{\theta satact} \left(\frac{\theta - \theta_{wilt}}{p_{\theta Low}}\right)^{p_{\theta p}}\right) \times \max(0, \min(1, 1-[CO_2]/CO_2Threshold)) \quad \theta_{wilt} < \theta < \theta_s$$

$$f(\theta) = 0 \qquad \theta < \theta_{wit}$$

 $P_{\theta Low}$: Water content interval in the soil moisture response function for microbial activity, mineralisation-immobilisation, nitrification and denitrification.

Soil temperature response function (Ratkowsky function)

$$f(\theta) = 1 \qquad T > t_{\max}$$

$$f(T) = \left(\frac{T - t_{\min}}{t_{\max} - t_{\min}}\right)^2 \quad t_{\min} < T < t_{\max}$$

$$f(\theta) = 0 \qquad T < t_{\min}$$

 t_{\min} : Minimum temperature in the temperature response for microbial activity, mineralisation-immobilisation,

 t_{max} : Mitrification and denitrification Maximum temperature in the temperature response for microbial activity, mineralisation-immobilisation, nitrification and denitrification

Appendix – References

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