

Nitrogen Transport in a Tundra Landscape: The Effects of Early and Late Growing Season Lateral N Inputs on Arctic Soil and Plant N Pools and N₂O Fluxes

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Abstract

Understanding N budgets of tundra ecosystems is crucial for projecting future changes in plant community composition, greenhouse gas balances and soil N stocks. Winter warming can lead to higher tundra winter nitrogen (N) mineralization rates, while summer warming may increase both growing season N mineralization and plant N demand. The undulating tundra landscape is inter-connected through water and solute movement on top of and within near-surface soil, but the importance of lateral N fluxes for tundra N budgets is not well known. We studied the quantity and fate of lateral N fluxes in the snowmelt period with a shallow thaw layer, and the late growing season with a deeper thaw layer. We used ^{15}N to trace inorganic lateral N movement in a Low-arctic mesic tundra heath slope in West Greenland and to quantify the fate of N in the receiving area. We found that half of the early-season lateral N input was retained by the receiving ecosystem, whereas half was transported downslope. Plants appear as poor utilizers of early-season N, indicating that higher winter N mineralization may influence plant growth and carbon (C) sequestration less than expected. Still, evergreen plants were better at utilizing early-season N, highlighting how changes in N availability may impact plant community composition. In contrast, later growing season lateral N input was deeper and offered an advantage to deeper-rooted deciduous plants. The measurements suggest that N input driven by future warming at the study site will have no significant impact on the overall N_2O emissions. Our work underlines how tundra ecosystem N allocation, C budgets and plant community composition vary in their response to lateral N inputs, which may help us understand future responses in a warmer Arctic.

Introduction

Arctic ecosystems are often limited by the availability of nutrients (Marion and Miller, 1982; Sistla et al. 2012; Wild et al. 2013) - especially nitrogen (N) and phosphorous (P). While most N turnover occurs during summer, winter N mineralization may provide an important N source upon thaw in spring, where a pulse of water-soluble nitrate (NO_3^-) in soil solution has been observed in studies of Arctic ecosystems (Schimel et al. 2004; Buckeridge et al. 2013; Rasmussen et al. 2020), resulting in plant N uptake (Semenchuk et al. 2015).

A growing body of research has focused on Arctic soil N turnover at plot scales, i.e. in one dimension (e.g. Schimel et al. 2004; Sistla and Schimel 2013; Semenchuck et al. 2015; Rasmussen et al. 2020). However, because the shallow thaw layer in spring, where the spring pulse of N in solution occurs, can be infiltrated by meltwater from snow melt (Slater et al. 2007), the spring N pulse can be transported and utilized biologically downslope (Giblin et al. 1991; Yano et al. 2010).

Such coupling of landscape hydrology and N cycling may lead to N-loss in one part of the landscape, but N-input to other parts, and may be relevant especially at the beginning of the snow-free season, when plant demand for N is limited and the internal turnover is relatively slow (e.g. Bilbrough et al. 2000). The redistribution of N across the landscape can be important for understanding the spatial variability of N cycles in the Arctic landscapes. The availability of N impacts vegetation community composition and

plant growth (Bobbink et al. 2010; Liu et al. 2018), N competition with microbes (Sistla et al. 2012) as well as ecosystem N losses of N_2O and N_2 (Voigt et al. 2020). Because Arctic ecosystems have only little external N input (Rousk et al. 2017), a naturally occurring, unaccounted for, N input to downslope “receiving” ecosystems after thaw, would therefore be an important yet not quantified N source into lower-lying Arctic ecosystems that should be taken into account in the future. With future Arctic winter warming (IPCC 2019), and corresponding increase in winter N mineralization (Rustad et al. 2001; Weintraub and Schimel 2003; Salmon et al. 2018), summer belowground N cycling (Zhang et al. 2015), and changes in soil moisture content, microbial community structure and litter quality (e.g. Rinnan et al. 2008; Rousk et al. 2018; Rasmussen et al. 2020; Salazar et al. 2020), the importance of N redistribution in the landscape could increase. If the lateral N input is an important source for downslope ecosystems, this additional N could alleviate plant N limitation, thus increase tundra C uptake (Weintraub & Schimel 2005), however, it could also be substrate for increased N_2O emissions (Voight et al. 2017a,b). In N limited ecosystems, however, N might not move very far before being re-incorporated into the ecosystem, making laterally transported N a negligible source for downslope vegetation or soil (Rastetter et al. 2004). With highest root density and most microbial biomass concentrated in the upper layers of the soil (Ouhlele et al. 2016; Xu et al. 2013), the retention of lateral N could be highest in this horizon. With differences in rooting depth and N access between different plant species (Pedersen et al. 2020), future increased lateral N transport in the later season could offer comparative advantages to some species. The importance of lateral N inputs following early spring thaw and throughout the growing season for plant growth, soil N stocks or $\text{N}_2\text{O}/\text{N}_2$ fluxes is thus necessary to quantify in order to understand present and future downslope ecosystem N dynamics, but is yet unclear.

The aim of this study is to investigate the importance of lateral N flows from upslope to the downslope, receiving ecosystems, and to quantify which parts of the receiving ecosystems that benefit the most from lateral N input. We do this by conducting a field experiment along a naturally vegetated arctic hillslope, where we use a ^{15}N tracer experiment to quantify N pathways and address the following questions: Does NO_3^- -N released upon thaw move downslope through the ecosystem, or is it retained, making lateral transport a negligible N source – and how does this depend on the season (i.e. thaw depth)? If retained, will plants benefit from the lateral NO_3^- -N input in the receiving area? Will the early season mineral N pulse and transport fuel a pulse of N_2O emissions?

We hypothesize that 1) a major part of laterally transported NO_3^- is utilized by the downslope ecosystem, and the amount of N transported further downslope depends on seasonal variations in lateral water flow related to snowmelt and plant demand/uptake along flow paths, 2) more laterally transported NO_3^- is retained in the early season, when the input is in near-surface layers with greater root density and microbial biomass compared to the later season when it is released further down in the soil profile, 3) the input of lateral N is small compared to internal N turnover in the system, but is an important source for plants in the early season, and 4) the lateral N input in the early season with shallow thaw layer fuels an early-season pulse of N_2O production and gaseous N loss from the ecosystem.

Methods

Study site

Disko Island is located off the coast of Western Greenland. The southern part of the island consists of Early Tertiary basaltic plateau mountains cut through by ancient glaciers forming U-shaped valleys such as the study site valley Blæsedalen (69°18'40.9"N; 53°30'40.9"W).

The climate in Blæsedalen is Arctic Maritime with mean annual air temperatures of $-3 \pm 1.8^\circ\text{C}$ (1991–2017) and an increase of $0.16^\circ\text{C y}^{-1}$ in the same period (Zhang et al. 2019). The average precipitation (1991–2017) was $418 \pm 131 \text{ mm y}^{-1}$, with about 40 % falling as snow (Hansen et al. 2006; Zhang et al. 2019).

The area is affected by permafrost with active layer depths largely related to drainage conditions. On the well-drained tundra slopes, maximum active layer depths reach 2–3 m, whereas the water-saturated fen areas have maximum thaw depths of 40–80 cm (D'Imperio et al. 2017). On the eastern slope with aspect towards the west, a snow accumulation area supplies meltwater from a semi-permanent snow fan throughout most of the summer. The slope is made up of colluvial stones to boulders, intersected by alluvial and nival deposits and with a soil depth of 40–90 cm.

In 2014, a study site was established on the slope, covering an area of 35×50 m. The slope site represents a vegetation gradient from top to bottom, with gradually different environmental conditions (Table 1). The growing season is longest at the footslope (> 10 weeks) and shorter upslope as a snow drift melts back. Some years, the snow drift persist the entire summer, some years it is gone by mid-July. This affects the vegetation types along the slope; with upslope dominated by *Salix herbacea* and downslope featuring dwarf shrubs (e.g. *Salix arctica*, *Betula nana*, *Cassiope tetragona* and *Empetrum nigrum*). The shrubs are interlaid with mesic tundra mosses such as *Tomentypnum nitens*, *Racomitrium lanuginosum* and *Sphagnum sp.* The active layer development is delayed upslope with later snowmelt, causing generally lower temperatures and higher soil moisture upslope in the early thaw season. In the peak and later parts of the growing season, snow meltwater drains downslope through deeper active layers, restricted by underlying frozen ground. The resulting conditions are generally warmer and drier upslope compared to downslope (Table 1). Water table depth at the footslope moves downward with the thawing of the active layer and fluctuates over the growing season from ~ 50–100 cm depending on evaporation and precipitation.

N deposition is low ($\sim 1 \text{ kg N ha}^{-1} \text{ y}^{-1}$), and N fixation supplies between 1 and 2 $\text{kg N ha}^{-1} \text{ y}^{-1}$ to the ecosystem with little variation (< 10 %) between years (Hobara et al. 2006; Rousk et al. 2017).

Table 1

General relationship between position on the slope and different environmental parameters.

Environmental parameter	Top	Bottom
Growing season length	Shorter	Longer
Soil moisture level	Drier	Wetter
Soil temperature, growing season	Warmer	Cooler
Dominating plant species	<i>Salix Herbaceae</i>	<i>Salix arctica</i> , <i>Betula nana</i> , <i>Cassiope tetragona</i> , <i>Empetrum nigrum</i>
N mineralization rate	Lower	Higher

Experimental design

At the foot of the slope site, five plots were established in June 2018 for monitoring of the physical and chemical ambient conditions (figure 1). The plots were positioned on a line perpendicular to the slope on mesic tundra heath with 2-5 m apart and had similar vegetation community (figure 1A). The plots thus represent the same position on the slope based on the vegetation composition. The study site receives meltwater from the above-lying snow drift area and is henceforth referred to as the Reception area. Water from the study site drains further into a lower-lying fen area 100 m further away.

In July 2018, plots (Fig. 1B) were equipped with sensors for hourly measurements of volumetric soil moisture and temperature at 2, 10 and 20 cm depth, in one plot also at 40 and 60 cm depth (Tinytag, Gemini Datalogger, UK; Decagon Devices, METER Group, USA).

Soil water suction cups (Prenart Equipment Aps, DK) were installed in all plots at 10–20 and 20–30 cm depth and water extracted twice a week during the growing seasons 2018 and 2019. Water was analyzed for Total Organic Carbon (TOC) (Shimadzu TOC analyzer; Kyoto, Japan), NH_4^+ -N, NO_3^- -N and Total Dissolved Nitrogen (TDN) (FIAstar 5000; Höganäs, Sweden). Soil moisture may affect the volume, from which water is extracted, but the method is regarded a reasonable measure of soil water solute concentration in natural ecosystems (Singh et al. 2018). In immediate vicinity of the plots, a HOBO-20 pressure transducer (Onset Computer Corporation, MA, USA) measured water table depth during the thaw season.

Soil cores from 0–30 cm taken near the plots were split 0–10, 10–20 and 20–30 cm and analyzed for grain size distribution, total C and N content (Flash 2000, Thermo Scientific, Bremen, Germany), root biomass, root C and N, gravimetric water content (GWC%), and microbial C and N using chloroform-fumigation direct-extraction (Brookes et al. 1985). Aboveground vegetation was sampled in a 10×20 cm area in each plot; leaves and stems were ground and analyzed for total C and N.

Vertical soil hydraulic conductivity was measured near monitoring plots at depths 1–7, 12–18, 23–29, 35–41 and 51–57 cm using HYPROP/KSAT rings (Meter Group, CA, USA) carefully excavated for

complete, undisturbed samples. Similarly, horizontal soil hydraulic conductivity was measured at 1–9, 12–20, 23–31, 35–43 and 51–59 cm depth.. Samples were analyzed using the falling head method (e.g. Angulo-Jaramillo et al. 2016).

In all plots, the surface exchange of CO₂ and N₂O was measured weekly from late June to late August using static chambers (Ambus et al. 1993). Chambers with fans to ensure air mixing and temperature loggers were placed on pre-installed frames in the plots for three hours, and every 45 minutes, an air sample was withdrawn and sent for analysis for content of trace gases (Agilent 7890A, CA, USA). On 30th June and 4th August 2018, six top soil samples (4 cm depth, 5.5 cm diam.) were taken adjacent to the plots, wrapped in plastic foil and bags, and frozen during transport. The N₂O and N₂ emissions were determined at *in-situ* water content at the Austrian Research Centre for Forests in Vienna using the gas-flow-core method, where gas exchange is measured in the headspace atmosphere, where N₂ has been replaced prior to the accumulation phase with He/O₂, such as described in Butterbach-Bahl et al. (2002).

¹⁵N tracer experiment.

In order to test the fate of NO₃⁻ moving laterally, ten plots were established downstream of the Reception area plots (a view of one from above in figure 1C). 3rd of July, when active layer had reached a depth of 30 cm, and 3rd of August with an active layer depth of 90 cm, a ¹⁵NO₃⁻ solution was applied on to the top of the frozen surface in a line perpendicular to the slope above the tracer experiment plots so that the solution would move downslope and into the plot with the lateral water input on the frozen surface (cross-sectional view (A) and conceptual view from above (B) in figure 2). The solution consisted of KNO₃-N (99% ¹⁵N) dissolved in 1.1 L H₂O (0.085 g N L⁻¹), corresponding to 0.15 g N m⁻². A 110 mL solution was injected through a thin hollow rod at the top of the frozen surface for each 10 cm in a line of 125 cm perpendicular to the slope for each of the five replicates (figure 2B). Due to the low concentrations, the added N is not considered to have any fertilization effect, but is used only as a highly enriched tracer. To investigate the fate of the added ¹⁵N, soil samples 0-30 cm were taken and vegetation was harvested in an area of 10×20 cm on day 1, 3, 7 and 25 after injection, and the following year on the day with thaw depth corresponding to the thaw depth at injection (figure 2). The horizontal distance between injection and upper limit of sampling areas was 5-10 cm.

The following procedure was adopted and the following samples were obtained inside the plot and analyzed for % C, % N and ¹⁵N recovery using elemental analysis (Flash 2000, Thermo Scientific, Bremen, Germany) coupled to an isotope ratio mass spectrometer (Thermo Delta V Advantage IRMS, Thermo Scientific, Bremen, Germany). Soil samples were split in depths 0–10, 10–20 and 20–30 cm. As many roots as were feasible were manually removed from the samples, which were subsequently homogenized and analyzed for grain size distribution, gravimetric water content, bulk C and N and δ¹⁵N of the bulk soil N. Soil bulk density was measured on a subset of samples. Furthermore, subsamples were obtained and analyzed for microbial C, N and ¹⁵N recovery by comparing water extractable N and C with replicates subject to chloroform fumigation (Brookes et al. 1985) for 24 h prior to extraction. Root dry weight was

quantified, and the roots were crushed and analyzed for total C, N and $\delta^{15}\text{N}$. In an area of 10×20 cm (Fig. 2), all aboveground biomass was harvested and separated based on plant species before air drying. Leaf and stem was separated, and each fraction was crushed and analyzed for % C, % N and $\delta^{15}\text{N}$.

The ratio of the occurrence of stable isotopes $^{14}\text{N}/^{15}\text{N}$ compared to the reference $^{14}\text{N}/^{15}\text{N}$ ratio in Air- N_2 is expressed as the $\delta^{15}\text{N}$ value. The $\delta^{15}\text{N}$ value of all sample materials was calculated as:

$$\delta^{15}\text{N}(\text{‰}) = \frac{^{15}\text{N}_{\text{sample}}/^{14}\text{N}_{\text{sample}}}{^{15}\text{N}_{\text{reference}}/^{14}\text{N}_{\text{reference}}} \times 1000 \quad (1)$$

In order to achieve the recovery, the measured $\delta^{15}\text{N}$ relative to the amount of N g^{-1} in the background samples was converted to atom percentage of ^{15}N and subtracted from the measured amount in the experiment samples, and all pools were scaled to plot size using dry soil bulk density and the known size of the sampling areas. The scaled amount of ^{15}N was subtracted from the known added ^{15}N to obtain recovery in each pool, respectively, and the total recovery in percentage of added ^{15}N .

Results

Measured C and N pools

Figure 3 shows the N pools and budget of the measured variables in the Reception area in 2018. The largest pool was total soil N (including humus), followed, orders of magnitude below, by microbial N. Smaller yet were the pools of root, stem and leaf N, and two orders of magnitude smaller again were the average pools of dissolved N in soil solution over the summer season 2018. N_2O fluxes varied from -1.6×10^{-4} to 2.4×10^{-4} g N with a mean of 8.0×10^{-7} . The measured ratio of $\text{N}_2/\text{N}_2\text{O}$ was 56, and the estimated average N_2 loss was 4.5×10^{-6} g $\text{N m}^{-2} \text{d}^{-1}$.

Pool sizes varied slightly over the season. Pools of C and N at each specific sampling date, and divided into depth intervals, are specified in table S1-4 as well as C/N ratios of leaf and stem of the aboveground vegetation.

Soil physics and chemistry 2018 and 2019

The year 2019 had an early snowmelt (50 % of the Reception area plots were snow free on 15th of May), which resulted in higher summer soil temperatures and lower soil moisture levels in 2019 than on the same day of the year in 2018. The summer 2018 had a late snowmelt (50 % snow free 13th of June 2018). Soil moisture varied from almost 0 % vol. when the soil was frozen in winter to 50 % vol. after snowmelt, with growing season averages in the top 30 cm of 35 vol. %, whereas soil temperatures varied

from $-7.4\text{ }^{\circ}\text{C}$ in winter to 13°C in the upper 15 cm in mid-summer. Figure S1 shows the soil moisture levels and soil temperatures to 60 cm in the Reception area throughout this period. Soil saturated vertical hydraulic conductivity was $127 \pm 50\text{ cm d}^{-1}$. Horizontal hydraulic conductivity was smaller with an average of $18 \pm 4\text{ cm d}^{-1}$.

Soil water NO_3^- -N and NH_4^+ -N concentrations varied over the summer seasons 2018 and 2019, with maximum concentrations immediately after soil thaw and minimum concentrations in the peak growing season (figure 4). The average of five replicate NO_3^- -N concentrations spanned from $3.5\text{--}5.1\text{ }\mu\text{g L}^{-1}$ (10-20 cm) and $5.7\text{--}14.2\text{ }\mu\text{g L}^{-1}$ (20-30 cm) in 2018, whereas NH_4^+ -N varied more and spanned from $2.0\text{--}21.3\text{ }\mu\text{g L}^{-1}$ (10-20 cm) and $0.1\text{--}7.0\text{ }\mu\text{g L}^{-1}$ (20-30 cm) over the 2018 season. In 2019, soil water collection began as soon as liquid water was present in 10-20 cm depth and therefore has more focus on the early growing season and less detail in the peak season. NO_3^- -N concentrations in 2019 varied from below detection to $45\text{ }\mu\text{g L}^{-1}$ (10-20 cm) and below detection to $48\text{ }\mu\text{g L}^{-1}$ (20-30 cm). NH_4^+ -N varied from below detection to $28\text{ }\mu\text{g L}^{-1}$ (10-20 cm) and below detection to $29\text{ }\mu\text{g L}^{-1}$ (20-30 cm).

TDN concentrations reached a maximum of $210\text{ }\mu\text{g L}^{-1}$ in 10–20 cm depth during late June of 2019. A similar, but smaller, peak was observed at further depth (Fig. 4). 2019 had a higher content of TOC in 10–20 and 20–30 cm with concentrations of $5\text{--}7\text{ mg L}^{-1}$ than 2018, where concentrations varied between $1\text{--}3\text{ mg L}^{-1}$.

In situ N_2O fluxes, incubated N_2 emissions

N_2O fluxes in situ varied from (as the absolute minimum) small uptakes of $-0.24\text{ mg N d}^{-1}\text{ m}^{-2}$ to (absolute maximum) small emissions of $0.24\text{ mg N d}^{-1}\text{ m}^{-2}$, with an average of $0.01\text{ mg N d}^{-1}\text{ m}^{-2}$ as net balance (Fig. 5). The numbers reported here were used for Fig. 3, but are broken down into seasonally specific fluxes here.

Fluxes were generally stable over the season, varying around net $0\text{ mg N d}^{-1}\text{ m}^{-2}$.

The topsoil (0–4 cm) samples had on average very small N_2O fluxes, an order of magnitude smaller than the in situ measurements (Table 2). N_2 emissions were much higher, with the largest $\text{N}_2/\text{N}_2\text{O}$ ratio in the early season. Scaled to the whole growing season (here calculated as 15th of June–31st of August, the total gaseous N loss from the soil was $0.51 \pm 0.21\text{ g N m}^{-2}$.

Table 2

N₂O and N₂ fluxes from top soil samples 0–4 cm incubated at 10 °C at ambient soil water content.

Position on slope	Sampling date	Ambient soil moisture (vol %)	Net N ₂ flux (mg m ⁻² h ⁻¹)	Net N ₂ O flux (µg m ⁻² h ⁻¹)	N ₂ /N ₂ O ratio ± SE
Reception area	30-06-2018	58.8 ± 4.8	0.654 ± 0.429	0.003 ± 0.001	168 ± 74
Reception area	04-08-2018	55.4 ± 6.8	0.106 ± 0.041	0.002 ± 0.001	57 ± 31

¹⁵N recovery

In total 50 % of the added ¹⁵N in July (30 cm) was recovered in soil and vegetation (figure 6A), whereas 50 % leached through the profile and downslope. On day 1 after injection, microbes and bulk soil (excluding microbes) had recovered 9.4 % and 28.2 %, respectively, while less than 1% was recovered in roots and stem. On day 3, 7 and 25, bulk soil and microbial ¹⁵N recovery were still high, but a minor but significant fraction of the added N was also recovered in vegetation: Leaf dominated with 2.4 % recovery on day 25, where roots and stem ¹⁵N recovery amounted to 0.6 % and 0.4 %, respectively. One year after addition, roots still held just below 1 % of added N, whereas leaf and stem held 0.6 % and 0.4 %, respectively. 18.7 % was still present in the soil.

At sites with addition in 90 cm depth in August (Fig. 6B), a maximum of 35 % of added ¹⁵N was recovered on day 7 after addition. Bulk soil and microbes were the dominating retainers of added ¹⁵N, with 3.3 % and 18 % recovery on day 1, respectively. Day 3 and 7 the bulk soil recovered 10 and 30 %, respectively. Roots recovered less than 1 % of added ¹⁵N, but was the largest receiver of added N in the actual vegetation. A year after addition, only 6.4 % was present, of which 5 % was in the soil.

The small plant N recovery was split between species falling within the three functional plant type groups: Evergreen shrubs, deciduous shrubs and mosses + lichen (pooled because of their shared role as N-fixers). In the early thaw season, the evergreen shrubs gained most lateral ¹⁵N input during the first days and generally benefitted the most from lateral N (Fig. 6C). However, from day 7, deciduous shrubs and moss-lichen had incorporated similar amounts of the lateral N into their tissue. After one year, the evergreens still held on to more than half of the early season lateral N input.

In the later growing season with a 90 cm active layer (Fig. 6D), deciduous plants dominated the (small) lateral N uptake during the first day, and although the evergreen shrubs and the mosses and lichen did retain some of the lateral N, in the long term, deciduous shrubs were the main benefactors of the late season lateral N input.

The full dataset of N recovery is shown in table S5.

Discussion

To what extent is lateral N flow retained or transported away– and does the vegetation benefit from the N?

Ambient soil water chemistry

The low content of inorganic N in soil solution at the study site compared to e.g. temperate heathlands (Andresen, 2008) is in line with the general understanding of N-limited tundra heath ecosystems (Fig. 4). The levels are comparable to previously reported inorganic N values at other sites in the Blæsedalen (Rasmussen et al. 2020) and with measurements made in soils from High arctic Greenland during peak growing season (Lopez-Blanco et al. 2020). The variations in soil water N concentrations over the growing season agree with observations of early season inorganic N release in response to thawing soil, making N from winter mineralization biologically available (Buckeridge et al. 2010; Larsen et al. 2012; Semenchuk et al. 2015). The peak in inorganic N is subsequently followed by a peak in TDN, but no peak in N₂O emissions, which suggests incorporation of inorganic N into microbial biomass and not direct denitrification.

TOC was significantly higher in 2019 than in 2018, which is likely due to the warmer summer and earlier snowmelt of 2019 with consequently higher mineralization rates and possible more root exudates as result of deeper snow (Rasmussen et al. 2020).

N₂O emissions and gaseous N loss

No peak in N₂O emissions was observed at times with lateral N input in the early thaw and late growing season, i.e. following peaks in mineral soil solution N, and where the soil took up much lateral N. This is contrary to e.g. Buckeridge et al. (2009) and expectations in hypothesis 4, and the results suggest that other limitations inhibited N₂O production, or, in line with the results, that a strong microbial sink immobilized N.

However, the N₂/N₂O ratios offer an alternative explanation for the results obtained here. The larger ratio in the early season compared to the late season suggest a more complete denitrification or less nitrification-sourced N₂O emissions in the early thaw period (Butterbach-Bahl et al. 2013). The fact that soil water content was higher in the early thaw season with snowmelt water moving through the shallow thaw layer, supports the explanation that more lateral N input and mineral N released in situ may have ended as N₂ in the early season, resulting in little effect on N₂O fluxes of early season lateral N input.

N₂O emissions from topsoil cores sampled and incubated were an order of magnitude smaller than in situ measurements. This may be caused by the shallow nature of the cores (4 cm), which do not capture the integrated top- and subsoil activity that is picked up in *in situ* measurements. Hence, N₂/N₂O ratios can therefore only be applied to the top 0–4 cm depth.

Shallow active layer: Half of released N is retained, mostly within the soil

A 50 % ^{15}N recovery of NO_3^- -N added laterally in the early season shows that some N, when moving on top of the frozen surface in a shallow active layer, is taken up immediately by the downslope ecosystem, supporting our hypothesis 1, which stated that a significant proportion of lateral N input would be utilized directly by the downslope ecosystem. Most of the N is retained as microbial biomass and soil organic compounds. This is aligned with several other N cycling studies based on stable isotopes within soil profiles (Sørensen et al. 2008; Larsen et al. 2012; Zhu et al. 2016). Lateral N input in the early season thus follows a pattern similar to N from deposition or mineralized within the plot - fast microbial uptake and incorporation into organic matter, followed by mineralization of a fraction and movement into plant biomass. In contrast to expectations in hypothesis 3, only a few percentage of early-season added N was, however, accumulated in plant biomass after 25 days, which can be explained by a limited active root biomass (Oulehle et al. 2016), but may also imply that microbes are better than plants at utilizing nitrate at this time of the year (Pedersen et al. 2020). Additionally, simple physics of root acquisition may decrease recovery when water moves through the root zone at a flow rate of 54 cm d^{-1} during snowmelt than if water was pooling for longer (Yano et al. 2010). Combined, microbial competition and hydrology of the Arctic tundra may explain the small plant recovery of lateral N-input. A year after lateral input, however, N is still retained in soil and vegetation, suggesting that lateral N input is a natural part of the ecosystem N budget.

Half of released N is transported further downslope

With 50 % of laterally transported N recovered in the early growing season, 50 % was lost from the system. Low levels of measured N_2O and N_2 fluxes (Fig. 3) suggest that most of the 50 % “lost N” is drained out of the profile, thus offers potential for biological uptake further downslope. This is consistent with Giblin et al. (1991) and Yano et al. (2010), who concluded that mineralization rates within an Arctic permafrost-affected lowland were too low to explain soil water plant-available N concentrations, and that nutrients therefore must be transported into the lowlands from surrounding areas. It is in contrast to the Rastetter et al. (2004) model calculations, which estimated that an N atom moved only on average 26 cm y^{-1} across an Arctic tussock tundra slope. Early season lateral N flow is therefore likely a naturally occurring input, which explains phenomena such as the higher nutrient content found in a High arctic tundra surrounded by cation and nutrient-rich rock and sediment compared to a Low arctic tundra surrounded by more silicate rock and poor soils (Lopez-Blanco et al. 2020), or the lack of seasonal patterns in soil water inorganic N content found in a tundra fen with through-flow of drainage water (Rasmussen et al. 2020).

Deep active layer means less retained N and more lateral N leaching

Later in the growing season with an active layer of 90 cm, the amount of $^{15}\text{NO}_3^-$ recovered within the soil profile was smaller than in the early season, such as expected in hypothesis 2. Based on a 35 % recovery, soil microbes and soil bulk N were again the largest N recipients, whereas plants recovered even less than following July addition in 30 cm depth. This can be explained by physical separation of lateral N movement and the root zone, which was also seen by Treat et al. (2016). Few roots penetrate to 80–90 cm in the permafrost-affected tundra (Zhu et al. 2016), and assimilation of N from these depths is limited (Pedersen et al. 2020). As such, 35 % recovery of deep N input emphasizes the adaptation of tundra heath to N limitation, with few deep roots able to move N into shallow layer biological pools.

Evergreens access early season N, deciduous access deeper N

The evergreen plant type benefitted the most from early season N input in 30 cm depth. In the late season, deeper N input benefitted deciduous types more than evergreens, especially in the long term (Year 1). Many evergreen species are able to take up early thaw season N, whereas deciduous plant types will rather utilize N made available during later spring and summer (Larsen et al. 2012), which is in line with our results. Although plant N recovery was only 2 % of lateral N input, this could give evergreen shrubs a competitive advantage in the early season. Rooting depth was suggested as a plant functional type-specific trait important for understanding depth-specific (tracer) N uptake (Oulehle et al. 2016; Zhu et al. 2016; Pedersen et al. 2020). Deciduous plant types such as *Salix arctica* was comparatively efficient at accessing N released in the mid-active layer (45 cm depth) (Pedersen et al. 2020), and that pattern is repeated in our results with most of plant-retained lateral late season N input was retained by deciduous shrubs a year after input.

However, the fact that less than 1 % of lateral N input was recovered by plants in the later growing season suggests that the ability to utilize early season N is more important than later in the growing season.

Predicting ecosystem response to increased lateral N inputs in a warmer future

Future increases in winter air temperatures may increase soil temperatures, thus winter N mineralization and the corresponding N release in spring (Rustad et al. 2001; Weintraub and Schimel 2003). Warmer winter air temperature can also result in more precipitation and thicker snowpack, which, in addition to also increasing soil temperatures (e.g. Rasmussen et al. 2018), will increase the amount of lateral water moving along slopes (Westergaard-Nielsen et al. 2020).

The downslope ecosystem may be affected by increasing winter and summer temperatures directly, but also by increasing the lateral N input. The effects of increased lateral N may affect the ecosystem in various ways, which, based on our detailed observations of an ambient system and literature regarding warmer tundra, will be discussed in the following.

Plant functional type: competition may be altered by higher lateral N input

In a future warmer climate, where lateral N input may be larger, functional plant type specific advantages in accessing the N are exacerbated. More lateral N input in the early season may thus disproportionately benefit evergreen species, whereas deeper-rooted species may have advantages of less competition at depth (Xu et al. 2013), of reaching lateral N moving at deeper depths and accessing newly available mineral N from the thawing permafrost (Pedersen et al. 2020; Salmon et al. 2018). The difference in N access at depth may be one of the mechanisms behind vegetation community changes observed in the last decades (Myers-Smith et al. 2019) and in warming experiments (Hollesen et al. 2015) and model projections (van der Kolk et al. 2016). Deeper rooted species in a warmer climate may thus benefit from higher lateral N input in the late season.

N₂O emissions and gaseous N loss

Increase in easily available N in the early thaw season can increase field observed N₂O emissions in a tundra ecosystem (Buckeridge, 2009), as can summer warming (Salazar et al. 2020). However, warming may also lead to a decrease in soil moisture (Andresen et al. 2020), which can create more aerobic conditions and inhibit an N₂O pulse following early season mineral N release (Altschuler et al. 2019), or, if slumping or thermokarst formation occurs due to warming, waterlog the soil and suppress N₂O emissions (Voigt et al. 2017a).

Higher winter mineralization rates may thus in fact not result in increased N₂O emissions, but predicting the consequences of warming on N₂O fluxes depend on predictions of microbial immobilization rates and soil moisture changes. This is challenging in permafrost environments, where thermokarst phenomena and patterned ground features result in heterogeneous flow patterns (Grosse et al. 2013), and projections of future soil moisture conditions in the active layer thus also span widely (Andresen et al. 2020). A key question remains therefore: which parts of the tundra will further dry out as a result of warming, and which parts will become moister and facilitate increasing N₂O production.

Loss of ecosystem N as N₂ may also decrease with near-surface warming, which, although N loss was small under ambient conditions, contributes to increasing ecosystem N content and alleviate biological N limitation.

C and N interactions in future scenarios

N availability is projected to be a strong limitation on future increases in plant C sequestration as result of climate warming (Meyerholt et al. 2020). Arctic 'greening', which has been observed with warming (e.g. Jia et al. 2009; Vickers et al. 2016; Edwards and Treitz 2017) may increase CO₂ uptake and counter future increases in greenhouse gas emissions from Arctic areas (IPCC 2019; Natali et al. 2012). However, biomass growth in a warmer climate depends on future availability of N (Rinnan et al. 2009; Rasmussen et al. 2020), which is thus critical for predicting vegetation response to warmer air temperatures. Lopez-Blanco et al. (2020) showed that higher nutrient availability, which they attributed to lateral input from adjacent slopes, meant that a High arctic tundra was a stronger C sink than a Low arctic tundra, in spite of vegetation being of larger stature in the latter. Foliar C/N ratios were lower and the primary productivity

was higher at the High arctic site with richer soil in spite of a considerably cooler climate. If mineralization rates increase such as indicated in a warmer climate (Schimel et al. 2004), the bioavailable N could relieve plant N limitation and increase tundra C uptake. However, whether the soil is as strong a sink in a warmer climate as indicated for ambient conditions in this study will be a determining factor for how tundra plant N and C uptake could develop in the future.

Conclusions

Our combined results indicate that lateral N transport *does* occur in the early and the late growing season despite N limitation of the ecosystem. Lateral N flow is thus a component of N budgets of lowlands, and with the soil benefitting most from the retained N, this is the pool which can be impacted by lateral N input. With soil N being also the by far the largest pool, the relatively small amount of lateral N input may, however, not have a large influence on the pool size.

Microbes are the best competitors for early season lateral N, and will likely benefit the most from enhanced lateral N input as a result of winter warming and higher N mineralization rates. This could mean that while vegetation benefited only little from lateral N input directly, it may benefit gradually during the growing season, as microbial turnover frees some of the immobilized N.

The evergreen plant type was the best at utilizing N released in the early season, while deciduous plants retained relatively more in the late season. This implies that future studies of spatial N connectivity need temporal resolutions small enough to capture the dynamic nature of the snowmelt and later growing season. In a future warmer climate with more N mineralization in the active layer and release from thawing permafrost, the deciduous shrubs and deep-rooted species could gain competitive advantages, impacting the vegetation community composition.

While lateral N fluxes are a part of the vegetation and soil N budgets, lateral N fluxes across the landscape in the snowmelt season did not fuel N₂O emissions, indicating that the early season mesic tundra heath is not a notable present source of the powerful greenhouse gas. Whether this will continue, however, depends on accurate prediction of surface layer soil moisture and future mineralization rates.

Our conclusions have implications for the Arctic C sink strength, because they suggest that lateral N input is more readily retained in the soil compared to plant tissue. Plant N limitation will increase with warmer temperatures, however, with warmer temperatures, N mineralization will also increase. Whether plant N demand is met is a key question to determine the C balance of the Arctic tundra in the future, and whether the soil continues to immobilize and adsorb also increased lateral N input or reaches a “saturation” point in competition with plants is part of that equation. Studies with experimental or simulated increase in lateral N inputs and direct effects of surface warming are needed for assessing the future implications of that issue for a wider arctic region.

Declarations

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Conflicts of interest

The authors have no conflicts of interest to declare that are relevant to the content of this article

Availability of data and material

Data is available in Supporting information and further upon reasonable request from the authors

Code availability

Not applicable

Authors' contribution

Not applicable

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Figures

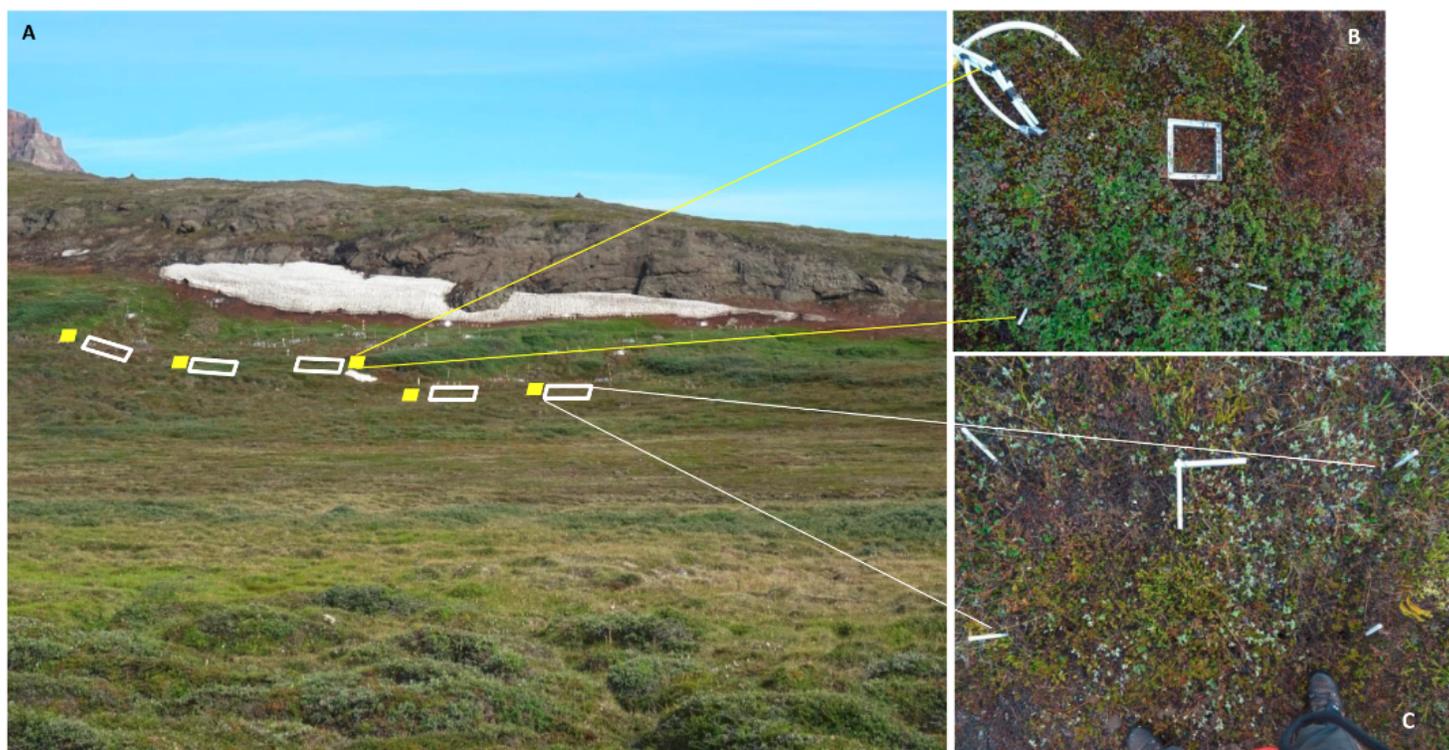


Figure 1

Overview of the experimental design. A: Positioning of the monitoring plots (yellow, filled squares) and tracer addition plots (white, open rectangles) on the snow accumulation hillslope. B: View of a monitoring

plot from above, where soil moisture, soil temperature, soil water chemistry and trace gas exchange was monitored. C: View of a tracer injection plot from above, where ^{15}N tracer was used to follow lateral N input in the ecosystem. See also a conceptual representation in figure 2B. Plots are not exact to scale, and only five tracer plots are shown, whereas ten was in fact established in the same vegetation zone of the slope. Photos: Laura H. Rasmussen.

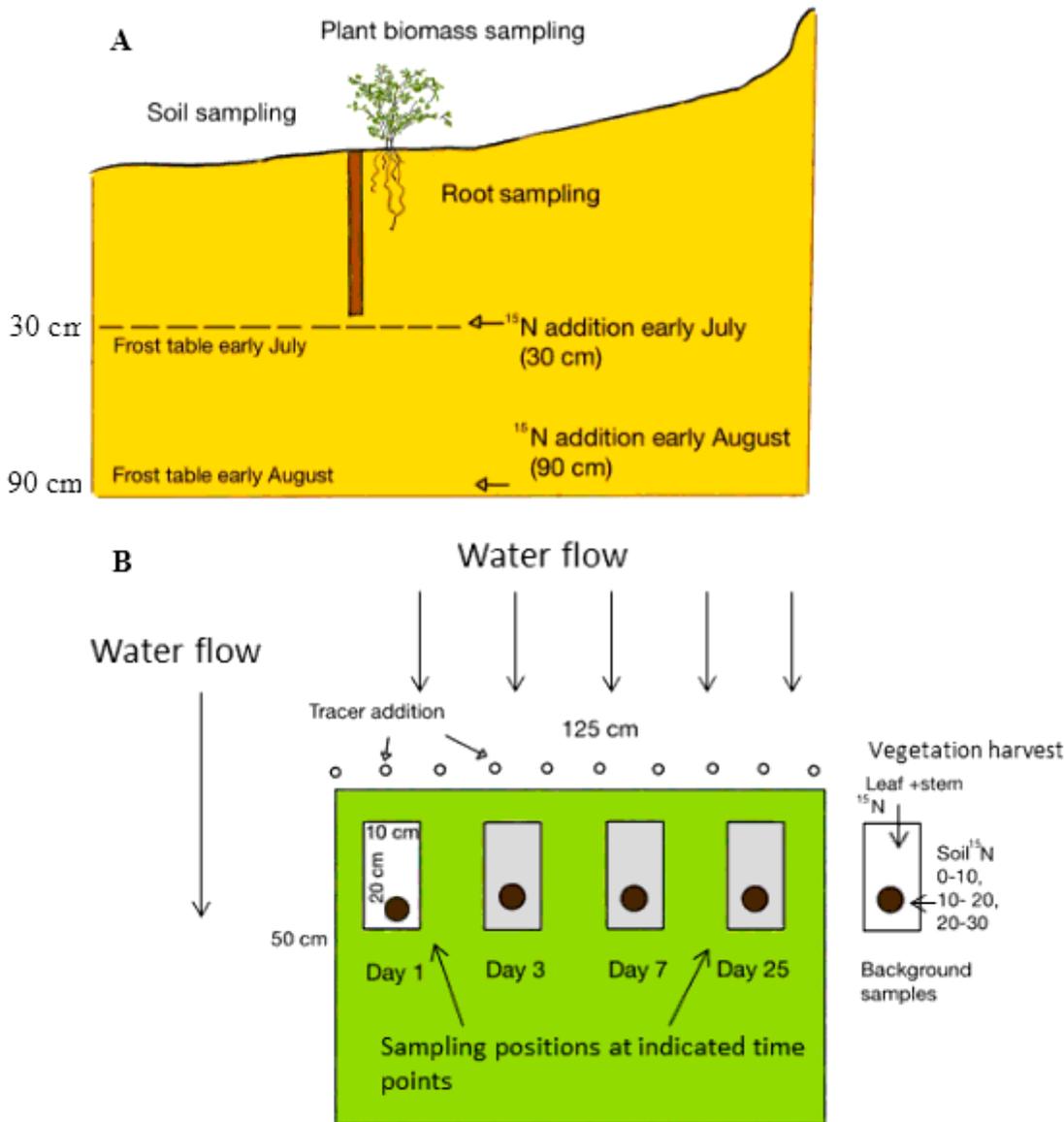


Figure 2

Illustration of tracer experiment in a cross-section of the tracer plot (A) and a view of the plots from above (B, compare to photo in figure 1C). Sampling was done at day 1, 3, 7 and 25 after tracer injection in defined areas of 10x20 cm within the plot on a line perpendicular to the water flow and the slope direction (B). The tracer experiment was conducted in early July with appr. 30 cm active layer, and in early August with appr 90 cm active layer (A).

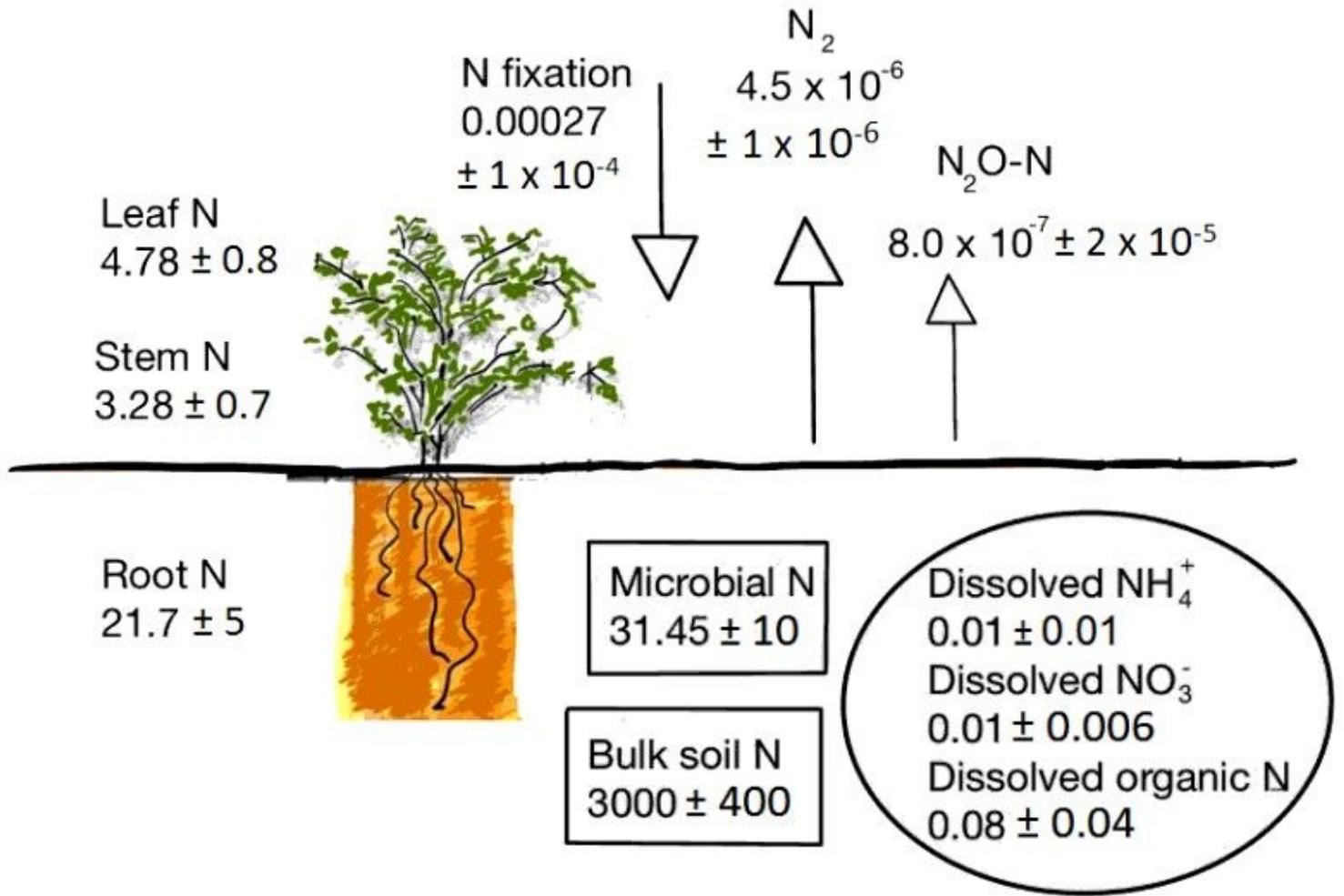


Figure 3

N pools and atmosphere-soil fluxes as measured at the Reception area site in 2018 ($n = 5$ plots). Pool units are $g\ m^{-2}$ to a depth of 100 cm. Root N is estimated based on root C with C/N ratio of 28 such as observed by e.g. Sullivan et al (2007). Flux units are $g\ m^{-2}\ d^{-1}$. N-fixation is estimated from literature and scaled down from $kg\ h^{-1}\ y^{-1}$ (Hobara et al. 2006; Rousk et al. 2017).

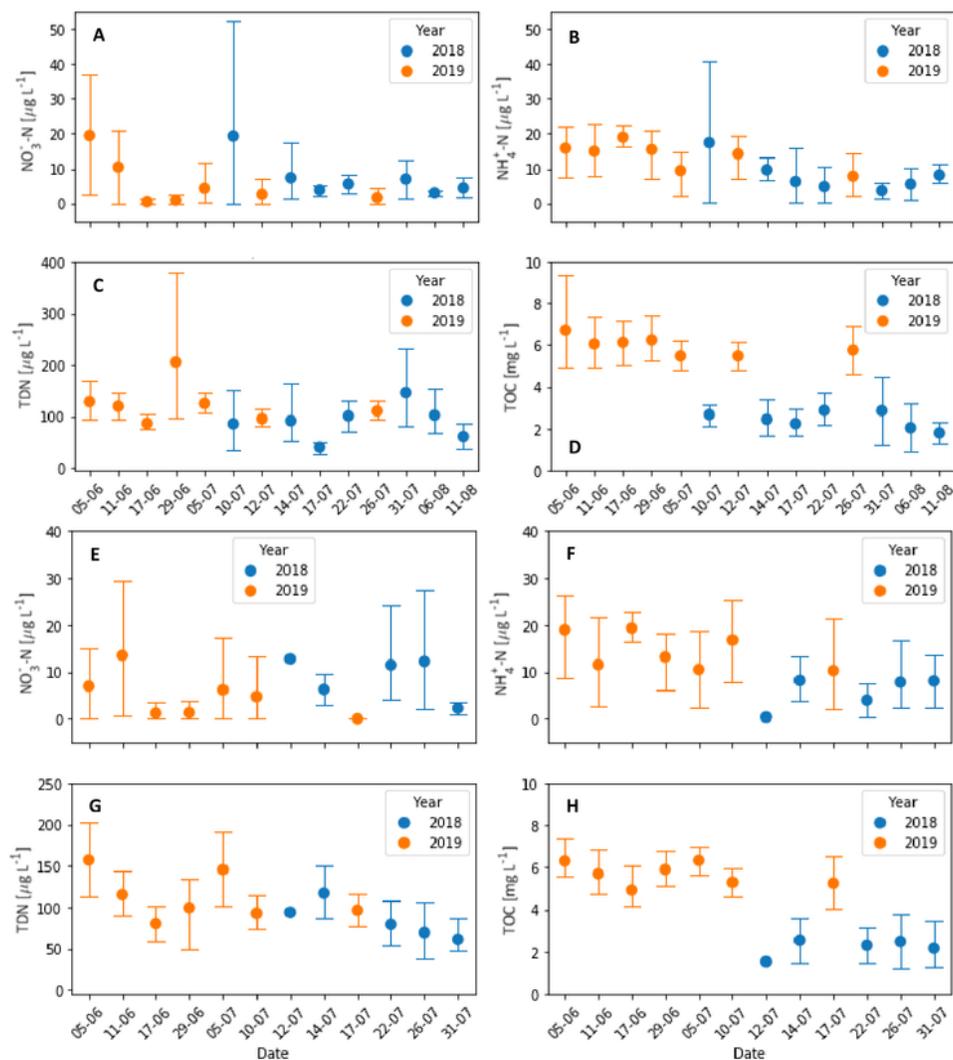


Figure 4

Soil water chemical composition over the two snow-melt and growing season 2018 and 2019 for 10-20 cm (A-D) and 20-30 cm (E-H). N=5.

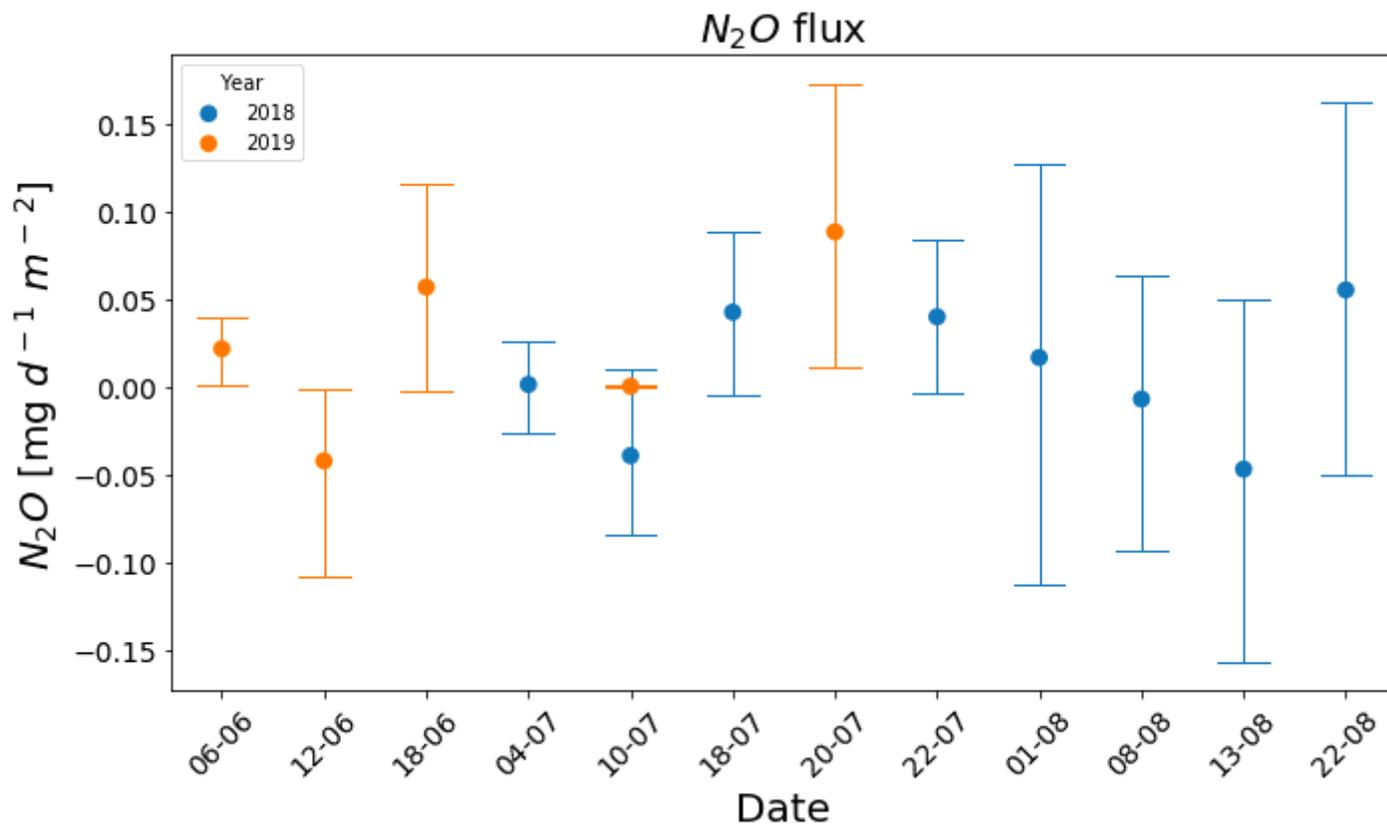


Figure 5

N₂O fluxes measured at the soil surface over the early and later growing seasons 2018 and 2019. Error bars represent one standard error of the mean. N=5.

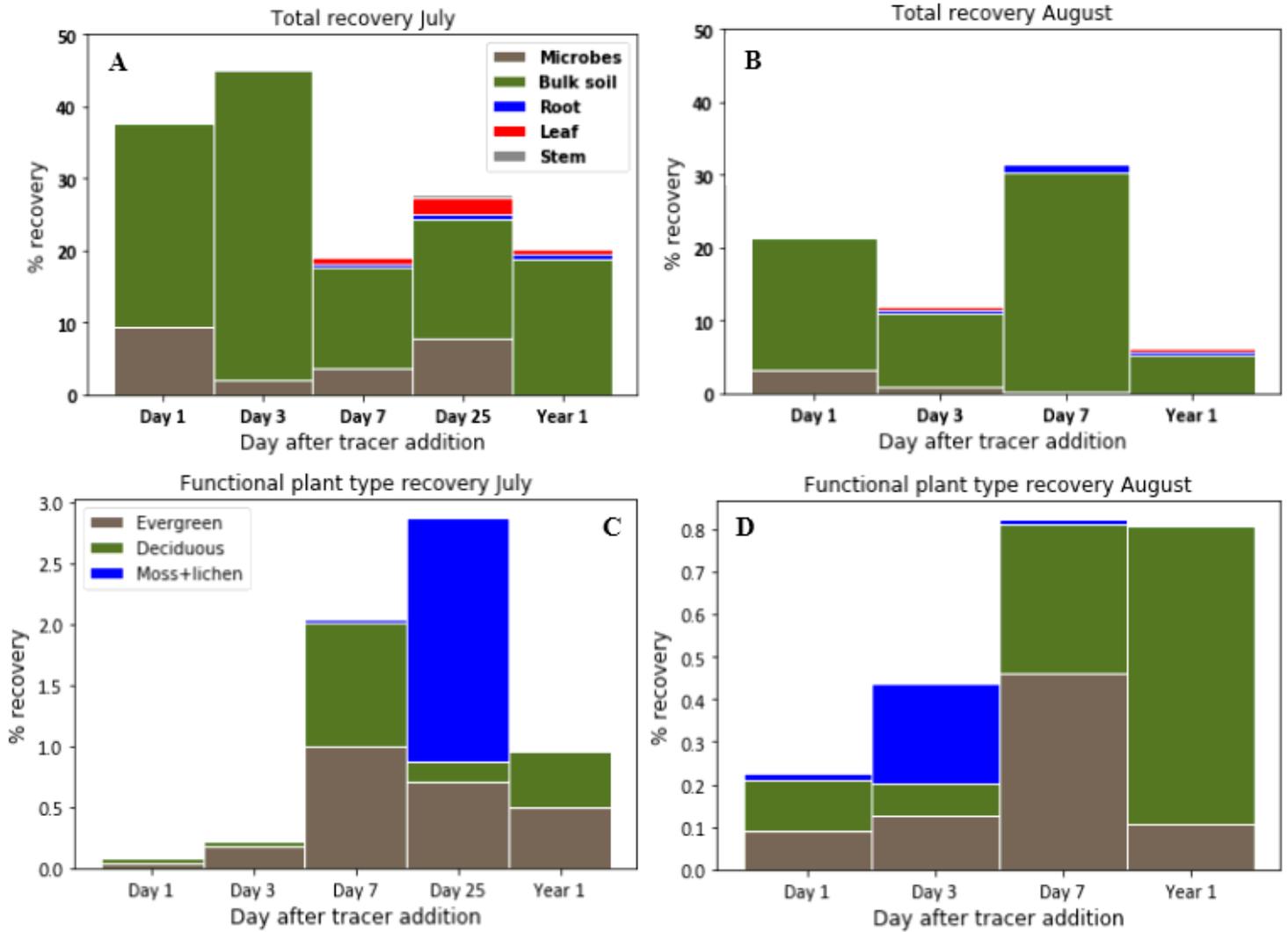


Figure 6

Total recovery of ^{15}N in different ecosystem pools after addition in (A) the early season (30 cm active layer) and (B) later in the season (90 cm active layer). Specific plant N recovery for the three functional plant types (leaf+stem) in (C): the early season (30 cm active layer) and (D) later in the season (90 cm active layer). $N=5$. Bulk soil is exclusive microbes.

Supplementary Files

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