Modelling Impacts of Lateral N Flows And Seasonal Warming on an Arctic Footslope Ecosystem N Budget and N₂O Emissions Based on Species-Level Responses

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Abstract

Future Arctic tundra primary productivity and vegetation community composition will partly be determined by nitrogen (N) availability in a warmer climate. N mineralization rates are predicted to increase in winter and summer, but because N demand and –mobility varies across seasons, the fate of mineralized N remains uncertain. N mineralized in winter is released in a “pulse” upon snowmelt and soil thaw, with the potential for lateral redistribution in the landscape. In summer, the release is into an active rhizosphere with high local biological N demand. In this study, we investigated the ecosystem sensitivity to increased lateral N input and near-surface warming, respectively and in combination, with a numerical ecosystem model (CoupModel) parameterized to simulate ecosystem biogeochemistry for a tundra heath ecosystem in West Greenland. Both model and measurements indicated that plants were poor utilizers of increased early-season lateral N input, indicating that higher winter N mineralization rates may have limited influence on plant growth and carbon (C) sequestration for a hillslope ecosystem. The model further suggested that, although deciduous shrubs were the plant type with overall most lateral N gain, evergreen shrubs had a comparative advantage utilizing early-season N. In contrast, near-surface summer warming increased plant biomass and N uptake, moving N from soil to plant N pools, and offered an advantage to deciduous plants. Neither simulated high lateral N fluxes nor near-surface soil warming suggests that mesic tundra heaths will be important sources of N₂O under warmer conditions. Our work highlights how winter and summer warming may play different roles in tundra ecosystem N and C budgets depending on plant community composition.

Introduction

Lateral nitrogen (N) redistribution and uptake in Arctic ecosystems have been documented in mesic tundra heath (Rasmussen et al. 2021), and tussock tundra (Giblin et al. 1991; Yano et al. 2010). It moves with meltwater flux or precipitation on the frozen surface found in seasonally and permanently frozen soils, at shallow depths in the early season and deeper in the soil in the later growing season (Treat et al. 2016). N loss from one part of the ecosystem may thereby result in an N input further downslope. Thus, as Arctic ecosystems are often N limited (Sistla et al. 2012; Wild et al. 2013), N leaching from adjacent areas could be important for the nutrient status and carbon (C) sink strength of downslope ecosystems (e.g. Lopez-Blanco et al. 2020).

Winter N mineralization causes an often observed “pulse” of nitrate (NO₃⁻), which is released to the soil solution upon the first spring thaw (Schimel et al. 2004; Buckeridge et al. 2010, 2013; Semenchuk et al. 2015; Rasmussen et al. 2020; 2021) and may enter the lateral flux of water moving in and on the soil around snowmelt (Slater et al. 2007; Westergaard-Nielsen et al. 2020). Later in the growing season, precipitation events can cause osmotic release of small organic compounds and movement of water and N in solution around the landscape (e.g. Rastetter et al. 2004; Rasmussen et al. 2020).

The availability of N regulates the ecosystem in various ways. Vegetation community composition (Bobbink et al. 2010) and plant productivity (Liu et al. 2018) responds to and feeds back into the soil N pool and microbial turnover rates (Sista et al. 2012), which together regulate the C uptake and release of the tundra ecosystem (Lüers et al. 2014). The most well-known pathway for production of the powerful greenhouse gas N₂O depends on NO₃⁻ as substrate and may thus in part be regulated by N availability (Voigt et al. 2020).

Soils take up most of lateral N input in the early and the late growing season, whereas plants seem to be poor competitors for the N source (Rasmussen et al. 2021), possibly due to low plant demand in the early season (Bilbrough et al. 2000) and poor root penetration to the depths in which water and N is moving in the later season (Pedersen et al. 2020; Zhu et al. 2016). Under ambient conditions, a peak in N₂O emissions was not observed to follow a “pulse” of nitrate (NO₃⁻) in a mesic tundra heath (Rasmussen et al. 2021). The dominating pathways for early season thaw release of NO₃⁻ may therefore be immobilization and downslope leaching. With soil N bound in organic compounds and adsorbed on to mineral surfaces as the by far largest N pool in Arctic ecosystems (Shaver et al. 1992), the lateral N input may not be an important N source for the soil. However, with differences in N access among plant functional types in the early and the late growing season (Larsen et al. 2012), the season-specific N sources can be critical for both plant growth and changes in plant community composition.

In a future warmer Arctic, N mineralization rates are expected to increase in winter (Rustad et al. 2001; Weintraub and Schimel 2003) and in summer (Zhang et al. 2015; Salmon et al. 2018; Salazar et al. 2020). More N mineralized during winter could increase the size of the spring thaw pulse (Schimel et al. 2004; Semenchuk et al. 2015), which would increase the amount of lateral N being redistributed in the landscape upon thaw. Increase in summer N mineralization rates could increase N availability locally, releasing more bioavailable N into soil solution throughout the growing season. Higher lateral N input or increased local N mineralization rates could increase vegetation N uptake and, by alleviating plant N limitation, could increase the tundra C sink strength (Weintraub & Schimel 2005a; Lopez-Blanco et al. 2020).

Although summer and winter warming may increase N availability, the effects of bioavailable N for the ecosystem may be quite different at different seasons and the potential N transport. Rasmussen et al. (2021) showed that only half of available N input was retained in a downslope ecosystem during early thaw, mainly due to plant phenology and fast runoff in the snowmelt season. In contrast, an increased N release linked to warmer summer temperatures and increased mineralization, will be available in soil solution during drier conditions and while the N demand is higher from plants and microbes (e.g. Schimel et al. 2004; Semenchuk et al. 2015; Rasmussen et al. 2020; Salazar et al. 2020). While increased lateral N input following increased winter N mineralization and summer warming, respectively, may have individual and cumulative effects on ecosystem N dynamics, the relative importance of the two for plant growth, soil N stocks or N₂O fluxes is thus as yet unclear.

The sensitivity of the Arctic C cycle to warmer conditions has been modelled at plot scale (Sistla et al. 2014), landscape scale (Hollesen et al. 2011; Zhang et al. 2019) and pan-Arctic (e.g. Lopez-Blanco et al. 2018), but the terrestrial arctic N cycle in a warmer climate is simulated mainly as a control on C uptake (e.g. Wright and Rocha 2018; Meyerholt et al. 2020) with little thought to the effects of topographic N redistribution (although see Rastetter et al. 2004; Westergaard-Nielsen et al. 2020). In this study, we quantify and simulate the importance of lateral N input to a downslope, receiving ecosystem, compared to ambient internal N cycling and near-surface warming. Based on a published experimental dataset (Rasmussen et al. 2021), we calibrate a process-oriented numerical ecosystem model (CoupModel) using abiotic and biotic measurements of ambient conditions at the site and simulate N dynamics of ambient and increased lateral N input.

The CoupModel has successfully been used to simulate heat and water flow, as well as ecosystem C pools and fluxes in the Arctic (Hollesen et al. 2011; Rasmussen et al. 2018; Zhang et al. 2019). In this study, based on the model setup in Zhang et al. (2019), we expand the model structure to include the ecosystem N cycle. In order to estimate the importance of lateral N input now and in the future, we apply the calibrated model to scenarios with warmer surface conditions and increased lateral N supply individually and in combination. We address one major question: How can an increase in lateral N transport affect the downslope ecosystem N budget and vegetation with or without additional climate warming?

We hypothesize that 1) the uptake of lateral N is small compared to internal N turnover in the system, but important in the early season, 2) increase in lateral N input from winter mineralization will increase leaching of NO₃⁻, decrease C/N ratios of the downslope vegetation and increase N₂O emissions. Summer near-surface warming, however, will 3) stimulate plant growth and N demand, decreasing soil mineral N and N leaching.

Materials And Methods

Study site description

The studied Low Arctic tundra heath is located in a north-south directed valley off the coast of Western Greenland (69°18'40.9"N; 53°30'40.9"W) and described in detail in Rasmussen et al. (2021). During 1991–2018, mean annual air temperature was $-3 \pm 1.8^{\circ}\text{C}$ and mean total precipitation $418 \pm 131 \text{ mm y}^{-1}$ with 42 % falling as snow (Hansen et al. 2006; Zhang et al. 2019). Permafrost underlies most of the area, and on a west-facing slope, a snow fan supplies meltwater downslope during most of the summer. The area has a small external N input of $\sim 1 \text{ kg N deposition ha}^{-1} \text{ y}^{-1}$ and $1\text{--}2 \text{ kg N fixation ha}^{-1} \text{ y}^{-1}$ (Hobara et al. 2006; Rousk et al. 2017).

At the footslope, vegetation is dominated by evergreen and deciduous dwarf shrubs including *Betula nana*, *Empetrum nigrum*, *Cassiope tetragona*, *Salix glauca*, *Vaccinium uliginosum*, interlain by mosses such as *Tomentypnum nitens*, *Racomitrium lanuginosum*, *Sphagnum sp.* and lichen. In 2018, a study site was established on this footslope where water drains in the shallow thaw layer during snowmelt and deeper in the later parts of the growing season (Rasmussen et al. 2021). The study site soil temperature, soil moisture, soil water chemistry, plant C:N, and surface gas exchange of N₂O was monitored closely throughout 2018 and 2019 (Fig. 1; Rasmussen et al. 2021).

Further, soil was analyzed for grain size distribution, vertical and horizontal hydraulic conductivity to 60 cm depth, C and N content in bulk soil, microbes and roots 0–30 cm, and N₂ and N₂O development was measured in soil cores sampled in the early and late growing season (Rasmussen et al. 2021). Aboveground vegetation was analyzed for C and N in stem and leaf, split into different plant types (Rasmussen et al. 2021).

Model description and setup

CoupModel is a process-based, numerical ecosystem model that simulates a one dimensional soil-plant-atmosphere system, where biological and abiotic processes are fully coupled via water, heat and mass transfer (Jansson and Karlberg 2011; Jansson 2012).

CoupModel has successfully been used to simulate energy and water movement in the Arctic (Hollesen et al. 2011; Rasmussen et al. 2018) and arctic tundra C dynamics (Zhang et al. 2019). Nitrogen turnover, plant-soil interaction and drainage were built in to the predecessor of the CoupModel (Johnsson et al. 1987), and have been applied to simulate grassland (Korsaeth et al. 2003) and forest ecosystems (Christiansen et al. 2006). A trace gas model was later built into the CoupModel and used successfully for agricultural and forest applications as well (Norman et al. 2008; He et al. 2016).

In this study, the model structure was based on a 25-layer soil profile, above which three plant types corresponding to evergreen dwarf shrubs, deciduous dwarf shrubs and moss were simulated. Based on the measurements of soil grain size distribution in the 0–60 cm soil, soil water and temperature, pools of C and N in the 0–30 cm soil and in plant compartments, soil texture and the initial conditions of soil water, temperature, C and N contents of aboveground biomass and root biomass were specified (Table 1). Soil texture for deeper layers (below 60 cm) was based on soil cores from a nearby site (e.g. Zhang et al. 2019). Table S1 shows the model profile with corresponding depths of data collection. Layer-specific initial conditions of soil C and N (Table S2), soil properties related to water retention and hydraulic conductivity (Table S3), C and N contents in aboveground plant compartments (Table S4.1 and S4.2), and soil Total N and C pools and water chemical composition over the summers of 2018 and 2019 (Table S5.1 and S5.2) are also given in the supplementary information.

Table 1
Measured variables specified in the soil profile setup of CoupModel.

Depth	Dominating vegetation type (%)	Hydraulic conductivity vertically + horizontally (m s^{-1})	Soil water chemical composition ($\mu\text{g L}^{-1}$)	Soil Total N (g g dw^{-1})	Soil Total C (g g dw^{-1})	N in root biomass (g g dw^{-1})	C in root biomass (g g dw^{-1})	N in aboveground vegetation (g g dw^{-1})	C in aboveground vegetation (g g dw^{-1})	N ₂ O flux ($\text{g N m}^{-2} \text{h}^{-1}$)
Surface	x							x	X	x
10 cm		x	x	x	x	x	x			
20 cm		x	x	x	x	x	x			
30 cm		x		x	x	x	x			
40 cm		x								
50 cm										
60 cm		x								

Specific traits of the three plant types, (1) deciduous shrubs, e.g. *Betula nana*, *Salix arctica*, (2) evergreen shrubs, e.g. *Empetrum nigrum*, *Cassiope tetragona*, and (3) moss, e.g. *Racomitrium lanuginosum*, *Aulacomnium turgidum*, *sphagnum sp.*, observed in the plots, were specified in the initial conditions of vegetation setup according to the measured traits, C/N ratio, biomass [g m^{-2}] and surface coverage [%] of each plant type (Table 2).

Table 2
Specified traits for each plant type (deciduous, evergreen and moss) defined in the setup.

Plant type	Max plant height (m)	Specific Leaf area ($\text{m}^2 \text{kg}^{-1}$)	Maximum rooting depth (m)	Initial Surface cover (%)	Max surface cover (%)	Initial C/N Leaf	Initial C/N Stem	Initial N Leaf (g m^{-2})	Initial N Stem (g m^{-2})	Initial Leaf C (g m^{-2})	Initial Stem C (g m^{-2})
Deciduous	0.15	30	-0.35	20	60	20	50	2	3	40	80
Evergreen	0.1	30	-0.25	30	60	20	75	0.7	0.8	50	65
Moss	0.05	30	-0.02	10	40	30	30	3.5	0.1	50	30

The following modules in the CoupModel have been switched on to simulate processes that regulate ecosystem abiotic and biological processes and soil gas dynamics (Jansson and Karlberg 2011): soil heat and water transport, snow pack, soil evaporation, plant transpiration, plant growth, soil mineral and organic processes. The details of equations and parameters that regulate all these processes are provided in Table S6. The following description mainly covers the details about how the CoupModel simulates plant growth, soil mineral and organic processes (Jansson and Karlberg 2011).

The plant simulation scheme was set to “Dynamic” so that seasonal development of leaf area index, canopy height, root depth and length were estimated based on plant biomass and allometry. Multiple plants were enabled to grow in the same stand accounting for competition within the plant community. Plant transpiration and soil evaporation were simulated separately using the “explicit big leaf” option, which calculated transpiration using the Penman-Monteith equation. The leaf assimilation of CO₂ used the light-use efficiency approach, accounting for responses of temperature, water and C:N ratio of leaf. Plant respiration consisted of both maintenance and growth respiration using the “Q₁₀” type temperature response function. Litter turnover was simulated as steps in which above-ground plant litter moves from first a surface litter pool with no microbial activity into the litter pool, and then to the humus pool. Plant N uptake was simulated based on the demand created by potential growth. Root uptake of N was calculated depending on the N demand, root depth and ratio of nitrate to ammonium. If the actual mineral N uptake was less than the plant demand, organic N uptake (amino acids) can optionally be added to the root uptake by letting plants take up a portion of the litter N pool relative in size to the difference in plant demand and actual mineral N uptake, but with a maximum organic N uptake amount.

For simulating soil decomposition, two C pools (litter and humus) were considered and produced CO₂, at a fast and slow rate, respectively. Their decomposition rates were controlled by first order kinetics, temperature and moisture response functions. Microbes were generally simulated implicitly in the soil as opposed to the explicit option, but for nitrification and denitrification rates, the microbe-based option was used. With implicit microbes, there was no pool of microbial N, but they were accounted for in the litter pool of N. The mineralization or immobilization by microbes depended on the respective C/N ratios of the decomposing litter pool. Nitrification rates, understood as transformation of N from the NH₄⁺ pool to the NO₃⁻ pool, can be adapted to the ecosystem by adapting the response functions of denitrification to temperature, soil moisture and substrate availability. The simulation of denitrification from NO₃⁻ to gaseous N₂O and N₂ depended on the response functions of denitrification to temperature, soil moisture and substrate availability.

Meteorological drivers

The hourly air temperature, global radiation, longwave radiation, wind speed, relative humidity and precipitation for 2013–2019 were obtained from a nearby weather station (~ 200 m) used as drivers of the simulation. Model spin-up drivers used the meteorological data from 1950–2013 according to Zhang et al. (2019). Table S7 shows the climate parameters used for driving the model setup and the measurement periods and frequencies of data collection.

Calibration and validation

After identifying parameters governing microbial turnover rates and plant organic N uptake, a Monte-Carlo sampling of calibration parameters with 10,000 iterations was done for a multi-criteria based calibration. Based on measured soil temperatures and soil moisture in 10 cm from 2013–2019 with coefficient of determination ($R^2 > 0.9$ for soil temperature and $R^2 > 0.7$ for soil moisture) and Mean Error (ME < 0.5°C and < 5 % vol.) as constraints, an ensemble of 25 runs was accepted as the posterior runs that best represent the studied ecosystem abiotic and biological process. The model performance of the accepted ensemble was further evaluated against the measured pools of root C and N, leaf C and N, stem C and N (scaled to g m⁻²), N₂O fluxes and soil solution mineral and total dissolved N over time. A list of parameters used for calibration is available in Table S8. Table S9 shows the performance statistics of the selected ensemble after calibration, and Figures S1-4 shows how the model has captured the temporal variations in soil moisture (10, 20, 40 and 60 cm), soil temperature (10, 20, 40 and 60 cm), above- and belowground C and N pools for three species and the soil water chemical composition.

Based on the accepted ensemble of 25 runs as the control runs, we constructed sensitivity experiments testing the impact of lateral water and N input, and the effect of near-surface warming, respectively.

Lateral water input experiments

The control run was made by simulating lateral water input at depth increment 25–35 cm without any N input. Based on this, an ambient scenario was simulated for the years 2012–2019, where the lateral input water had a concentration of NO₃⁻ and NH₄⁺ representative of measured concentrations in that depth in the summers 2018 and 2019 (0.03 mg L⁻¹, Rasmussen et al. 2021).

Additionally, two sensitivity simulations were made for the years 2012–2019, where the NO₃⁻ and NH₄⁺ concentrations were 10 × ambient levels and 100 × ambient levels (0.3 and 3 mg L⁻¹), testing the ecosystem resilience to increased (winter) mineralization and thus N release; the latter considered extreme levels and was rather a test of the model stability than of actual realistic input amounts.

In order to test the effect of near-surface warming compared to increased lateral N input, we made four parallel sensitivity simulations with 0, 0.03, 0.3 and 3 mg N L⁻¹ in lateral input water, but with surface temperatures increased by 2°C. In total, this yielded one control run and eight sensitivity simulations (Table 3):

Table 3
Overview over experimental simulations with lateral water input in depth 25–35 cm.

Surface temperature	0 mg L ⁻¹	0.03 mg L ⁻¹	0.3 mg L ⁻¹	3 mg L ⁻¹
Ambient T	(Control)	(Ambient N)	(High N)	(Very high N)
Near-surface warming (+ 2°C)	(Warming)	(Warming +Ambient N)	(Warming + High N)	(Warming +Very High N)

The input followed the thawing of the soil so that no input was made in a frozen soil.

Partitioning of the lateral N input was calculated by comparing the control run to the experimental runs. The N input, Acc_{Ninput} is defined as:

$$Acc_{Ninput} = N_{Fix} + N_{dep} + N_{lateral}$$

1

where N_{Fix} is the amount of N fixated by vegetation [g N m⁻²], N_{dep} is the amount of N deposited on leaves [g N m⁻²] and $N_{lateral}$ is the amount of lateral N input on the frozen surface [g N m⁻²].

As such, internal fluxes of N, such as litter N input to the soil, is not counted as an input to the ecosystem.

Similarly, the total N output, $Acc_{Noutput}$, is defined as:

$$Acc_{Noutput} = N_{Emission} + N_{Leaching}$$

2

where $N_{Emission}$ is the amount of N lost as gaseous N from the system [g N m⁻²] and $N_{Leaching}$ is the amount of N lost as (horizontal) drainage out of the profile.

Internal fluxes of N, such as plant N uptake from the soil, is thus not counted as an output from the ecosystem.

For each experimental run, the total lateral N gained by the system was calculated as the difference in in- and output of N in 2018 subtracted the control run difference of N in- and output in 2018:

$$Ngainbyecosystem_{ambient} = (Acc_{input} - Acc_{output})_{ambient} - (Acc_{input} - Acc_{output})_{control}$$

3

The difference for each possible N pathway was then calculated as the difference between experimental and control runs, and the difference was related to the total amount of lateral N gained by the system (here the plant pool):

$$\%lateralN_{plant_{ambient}} = \frac{PlantNUptake_{ambient} - PlantNUptake_{Control}}{Ngainbyecosystem_{ambient}} * 100$$

4

By calculating the amount of N in the different pools this way, the fluxes may also include N from other sources than lateral input water, since e.g. plant N uptake also comes from internal cycling of N and not only external N input. Thus, numbers above 100 % or negative numbers indicate a shift in the balance of fluxes indirectly impacted by the lateral N input, which is the only difference between the control and experimental runs.

Results

Modelled N partitioning with lateral water and N input

Using ambient conditions, we were able to simulate the general level and degree of variability of soil water inorganic N (Fig. 2). In 2019, Total dissolved Nitrogen (TDN) was simulated generally a bit higher than observed, but with similar variability, and Total dissolved Organic Carbon (TOC) was simulated too low in 2019 compared to observations.

The pools of N and C in leaf, root and stem in 2018 for the three plant types were simulated at the right level compared to observations in the start and mid-season (Figures S3 and S4). Simulated N₂O fluxes at ambient conditions were on average $0.05 \pm 3.5 \times 10^{-5}$ µg N m⁻² d⁻¹,

which was within the variability of observed fluxes (Rasmussen et al. 2021). Based on the mean of the model ensemble runs, the model experimental run with 2°C warming decreased the summer soil moisture at 0–5 cm by 2–8 %. In 25–35 cm depth, the decrease in soil moisture was 5–15 % (Figure S5).

Simulated external ecosystem N input and -output

Using ambient N concentrations, the lateral N input added in the CoupModel mixed with internal N pools. Results shown are from the simulation of the year 2018, six summers after beginning of the simulation. Throughout the following Figs. 3–6 illustrating results, the four different scenarios are represented with consistent colors: grey/black for ambient conditions, yellow-brown for High N input (0.3 mg L^{-1}), red for surface warming (2 °C) and blue for High N input in combination with surface warming ($0.3 + 2 \text{ °C}$).

With higher N concentration in the lateral input water, more N was retained in the ecosystem (Figure 3A, 3C). Outputs for all simulated years and scenarios are shown in Tables S10.0-S10.6 and all fluxes are listed in Table S11.

Near-surface warming caused similar increased N gain (Figure 3A, 3C). The additional external N input in the near-surface warming scenario was driven by increase in N fixation and leaf N deposition rates (Figure 4, Table S11).

N output did not vary significantly with different lateral N input or warming (Fig. 3B).

With an overall higher N input, the total ecosystem N accumulation in 2018 was 0.3 g N m^{-2} with near-surface warming or increased N input, and 0.4 g N m^{-2} with near-surface warming and extremely high N input in combination (Fig. 4, Table S10.0), which makes up about 1-1.5 % of the total plant N pool and negligible parts of the soil N pool (Rasmussen et al. 2021).

Partitioning and internal ecosystem N dynamics

N mineralization rates increased with warming, but decreased in high lateral N input scenarios (Fig. 4). However, the modelled soil mineral N pool did not increase significantly, while plant N uptake rates almost tripled with near-surface warming (Fig. 4, Table S11). Increase in lateral N input combined with near-surface warming did not increase N uptake further.

Larger plant biomass gave more litter N input in the warming scenarios, where rates of litter fall N doubled. Nevertheless, the soil organic N pool decreased over time with near-surface warming (Fig. 4, Table S12). The experimental runs thus linked lateral N input to a small increase in the overall soil N pool, while a warmer surface temperature was linked to increased plant uptake at the partial expense of the soil N pool (Fig. 5D).

Simulated N_2O emissions were less than $1 \text{ } \mu\text{g N m}^{-2} \text{ d}^{-1}$ at ambient conditions, which did not change with increased lateral N input (Figure 4). With warming, N_2O emissions decreased, and lateral N input combined with warming had no significant effect on N_2O emissions. Simulated N_2 emission followed N_2O emission patterns closely. These results were aligned with the fact that neither nitrification nor denitrification rates were significantly affected by simulated variations in lateral N input (Figure 5A-B).

Changes in C dynamics

In the CoupModel simulation, the near-surface warming-induced increase in N availability and -uptake was accompanied by around 210 g more plant C m^{-2} (310 g C m^{-2} additional photosynthesis subtracted 100 g C m^{-2} more accumulated plant respiration). The larger biomass with near-surface warming was facilitated by increased gross primary production (GPP), which made the Net Ecosystem Exchange (NEE) solidly negative six years after beginning of near-surface warming simulation (Figure 6C). GPP or NEE was not affected by high lateral N input as an isolated factor. Larger biomass meant, apart from more N fixation and N deposition on to leaves, that further primary production was effectively N limited (Figure 5C).

Plant functional type specific responses

Figure 7 shows the primary productivity limitation caused by N limitation in the three functional plant types (1 = maximum possible productivity). Aboveground, while being overall the most N limited of the three functional plant type, the evergreen plant type took up most N to reduce its N limitation in the early season and benefitted the most from additional N input in 30 cm in the high lateral N input scenarios compared to deciduous plants and moss (Fig. 7).

The C/N ratio of evergreen plant leaves similarly decreased following higher lateral N input (Figure S6). However, warmer near-surface temperatures had the opposite effect on the evergreen plant, which resulted in an increase in C/N ratio of the leaves over time (Figure S7).

Belowground N

Model simulations suggested increased belowground N accumulation in 2018 in the deciduous plant type as a response to lateral N input increase, however, only during ambient conditions. Warming appears to increase belowground N stored from the year 2018 in all plant types, but especially for the deciduous plant functional type (Table 4).

Table 4
Simulated belowground N accumulation in 2018 with different lateral N input concentrations under ambient (2018) and warmer surface conditions.

Belowground N accumulated during 2018 [g N m ⁻²]				
Plant functional type	Lateral input concentration mg N L ⁻¹			
Deciduous	0	0.03	0.3	3
Ambient surface temperature	0.4605	0.4631	0.569	1.8283
Warming	3.186	3.1863	3.183	3.1861
Evergreen				
Ambient surface temperature	0.4631	0.4641	0.4611	0.5683
Warming	0.7692	0.7695	0.7689	0.7705
Moss				
Ambient surface temperature	0.569	0.567	0.5683	0.4631
Warming	0.9493	0.95	0.949	0.9494

Discussion

Simulation of ambient soil water chemistry

Observed low levels of inorganic N pools were modelled well (Fig. 2) and are in line with an N limited tundra ecosystem (Rasmussen et al. 2021). Dissolved Organic N and C levels were modelled less accurately in 2019. Specifically, 2019 had significantly higher TOC concentrations compared to 2018, which could be caused by a warmer summer and earlier snowmelt in 2019, which can result in increasing rates of root exudation and higher mineralization rates (Rasmussen et al. 2020). These higher observed TOC levels were not possible to capture in the CoupModel simulations and remain therefore a puzzle, which suggests that e.g. root exudates are not well validated in the model.

Modelling high lateral N inputs and near-surface warming

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 be accompanied with more precipitation and thicker snowpack (ACIA 2004), 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). In simulations presented here, we modify N concentration in the soil water flux, but not the amount of water. Consequently, we simulate increasing air temperature only, assuming unchanged precipitation. The simplification of a complicated system is made in order to isolate the N concentration in inflow soil water, as compared to summer air warming.

N fluxes: The soil wins additional lateral N– but the amounts are small compared to internal cycling

The ecosystem downslope was resilient to increased N concentrations in lateral input water. The absolute amounts of N reallocation were insignificant compared to pool sizes and internal fluxes. The resilience is reasonable considering that lateral N inputs were small compared to internal N fluxes of the ecosystem (Fig. 4, Table S10.0), which agrees with hypothesis 1.

Model simulations indicate that the soil retained most of the laterally transported N, and that N uptake in plants did not increase significantly. This agrees with field observations at the site, where plants retained a maximum of 2 % of the lateral N input in the early thaw season, whereas soil, including microbes, retained > 40 % (Rasmussen et al. 2021). At this point in the growing season, lateral N input may

thus lead to immobilization. The fact that mineralization rates actually decreased with more lateral N input (Fig. 4) may be due to lateral N input substituting otherwise mineralized N (e.g. Wild et al. 2019), or other limitations to N mineralization rates (Salazar et al. 2020).

Increase in easily available N in the early thaw season can increase field observed N₂O emissions in a tundra ecosystem (Buckeridge 2009). However, in the present study, neither N₂O emissions nor denitrification increased significantly in the simulations of the year 2018 with increased lateral N, suggesting other limitations on the processes governing N₂O emissions and that higher winter mineralization rates will not in fact result in increased N₂O emissions. As climate and snow conditions were used as drivers directly in the simulation, they may have imposed other limitations than N availability on microbes involved in processes related to N₂O production (Zhou et al. 2016). This, and the insignificant change in mineral N leaching refutes hypothesis 2, where we expected increasing mineral N leaching and N₂O emissions with increased lateral N input.

N Pools: Warming matters more than lateral N input concentration, but not for N₂O emissions

A 2°C warmer summer surface temperature is commonly obtained in experimental near-surface warming experiments (Salazar et al. 2020). This, in light of measured and predicted Arctic warming, modest temperature increase, seemed nevertheless to have larger impact on N pools than large increases in lateral N input. Plant N uptake increased almost 300 % with near-surface warming at the expense of the soil N pool, which was much larger, but experienced a 1.3 % decrease, which is in absolute numbers almost equivalent to the plant N content increase. Plant biomass also increased, but combining with high lateral N input did not further increase plant N uptake. This suggests that near-surface warming is more important for plant N uptake rates than the amount of lateral N input in spring, likely because summer N release happens gradually and during the growing season, when plants are not limited by temperature or phenology. Soil N depletion under warmer surface conditions has been observed experimentally (e.g. Stark et al. 2018) and has been attributed to a faster mineralization of organic N (Natali et al. 2012). Soil N content limited a warming-induced simulated increase in Siberian Low Arctic tundra vegetation biomass (Yu et al. 2009), which with plenty of soil N and surface warming gained appr. 350 g C m⁻², while N limitation decreased this biomass gain to 200 g C m⁻² at the same site. The CoupModel results support this interpretation of field and model data by showing an increase in mineralization rates and a similar biomass increase as a result of near-surface warming. External N inputs (N fixation and N leaf deposition) increased 200 % with warming, which is likely linked to biomass increase and creates a positive feedback loop for external N inputs. More plant biomass provided more plant N litter, increasing the internal N cycling and stimulating plant growth – but breakdown of litter N was more slow than plant N uptake, making the soil N balance overall negative with near-surface warming.

The model showed that warming increased belowground N with 57 % (Fig. 4), which is in line with the results of Salazar et al. (2020). They also found an increase in mineralization rates, but not plant-available mineral N concentration, which they suggested was due to assimilation and immobilization within the ecosystem. This may explain why no increase in mineral N leaching was noted with higher surface temperature, even though the plant litter N input, N fixation and leaf N deposition rates were higher.

While extreme increases in lateral N inputs increased root N by about half the effect of warming (Table 4), this effect disappeared combined with warming, indicating that increased mineralization rates and assimilation of internal N under warming overprinted any effects of higher external N input.

In contrast to the studies in Salazar et al. (2020), summer warming with increased mineralization rates did not seem to increase emissions of N₂O and N₂ from the mesic tundra heath studied here. Warming in fact decreased N₂O and N₂ emissions, although the decrease did not bring N₂O fluxes below the lower end of variability of measured *in situ* fluxes in Rasmussen et al. (2021). The lack of an expected increase in N₂O and N₂ emissions (hypothesis 2) may be due to lower soil moisture in the warming scenarios, creating more aerobic conditions (Figure S5, S8).

Predicting future N₂O fluxes will depend on predictions of soil moisture changes in a warmer climate. As permafrost environments often display undulating geomorphology with thermokarst and patterned ground features, meltwater and precipitation flow patterns are often heterogeneous, giving a heterogeneous soil moisture landscape (Grosse et al. 2013). Predictions of future soil moisture conditions in the active layer thus also span widely (Andresen et al. 2020). Our results suggest that a drier surface soil will reduce N₂O emissions, even with warmer temperatures and increased lateral N input. Accurately predicting which parts of the tundra that will be drier as a consequence of warming, and which parts that will be wetter is thus key for accurate estimates of future N₂O tundra fluxes.

While N₂ is not a potent greenhouse gas, loss of N₂ is an ecosystem N loss such as also leaching losses or herbivory. Warmer (and drier) surface conditions lead to a decrease in N₂ emissions, which suggests that warming-induced N₂ emission decreased could retain more N in

the ecosystem, counteracting a soil N loss caused by warming such as seen here.

Plant functional type: competition may be altered by higher lateral N input, but is overruled by near-surface warming

In this study, the model implies that the evergreen plant type benefitted the most from early season N input in 30 cm depth. In the late season, the deciduous plant type was more efficient at acquiring lateral N and was the overall better competitor for lateral N as measured in the root N gain. This pattern is the same as observed at the modelled site in Rasmussen et al. (2021), where evergreen shrubs took up most lateral N input in the early season, whereas deciduous shrubs retained relatively more in the later season. Many evergreen species are able to take up early thaw season N where deciduous plant types will rather utilize N made available during later spring and summer (Larsen et al. 2012). 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). Evergreen maximum rooting depth was smaller than the deciduous plant type and did not increase with high lateral N input (Table S13). The deciduous plant type, on the other hand, increased rooting depth slightly and also accumulated more root N in response to increased lateral N input. This suggests that the phenological ability to utilize early season N is overall less efficient than deeper roots for acquiring lateral N input, giving deciduous shrubs a competitive advantage.

Warmer surface temperatures caused the effect of increased lateral N input to disappear, and were a comparative disadvantage for the evergreen plant type. 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 deciduous plant type roots were deeper and grew longer under warmer temperatures than evergreen roots (Table S13), making it easier for deciduous plants to access newly mineralized N. The adverse effects of warming may thus be a result of increased competition for N. The effect of near-surface warming dominated the effect of increased lateral N input, suggesting that summer warming is a more important control on plant community composition than winter warming. With possible release of mineral N from thawing permafrost in a warmer Arctic (Salmon et al. 2018; Christiansen et al. 2010), the advantage of deeper rooted deciduous shrubs may increase.

C and N interactions in warmer scenarios

Future C sequestration will likely be regulated and limited by N availability in a warmer climate (Meyerholt et al. 2020). Shrubification and 'greening' of the Arctic have been observed alongside warming (Tape et al. 2006; Jia et al. 2009; Vickers et al. 2016; Edwards and Treitz 2017), and the phenomenon could increase tundra CO₂ uptake and function as a negative feedback to Arctic warming (Natali et al. 2012). However, N limitation could inhibit future biomass increase (Rinnan et al. 2009; Rasmussen et al. 2020), and knowing the ecosystem response to different N sources is thus crucial for predicting plant response to higher temperatures. Our results suggest that lateral N input is more readily retained in the soil than in plants, so that warming-induced increase in winter mineralization rates would not benefit vegetation much in the short term. Plant N demand increased in a scenario with warmer temperatures, however, in that scenario N mineralization also increased by almost half, and much (although not all) of the higher plant N demand was in fact met. This allowed for increase in above- and belowground biomass similar to seen in Yu et al. (2009), which effectively stored C from the atmosphere (Fig. 6, C). Warmer summers thus seem to increase ecosystem C stocks of the Arctic tundra, while the N release effect of warmer winters does not.

Conclusion

We tested how much lateral flows of N across the Arctic tundra could control future vegetation type and C balance, soil N stocks and N₂O fluxes, and compared it to the effects of direct summer warming. Our results indicate that microbes are the best competitors for early season lateral N and will benefit the most with larger lateral N input as a result of winter warming and higher N mineralization rates, whereas plants were not competitive in terms of utilizing the extra N available so early in the season. Warmer summers increased internal ecosystem N cycling and plants assimilated almost 300 % more N and increased aboveground biomass and C sink strength at the expense of the soil N pool, which decreased slightly. Near-surface warming during summer is thus more efficient at increasing plant N uptake than winter warming, and the seasonality of future warming is therefore important for ecosystem N response and biomass increase.

While increased lateral N fluxes alone and in combination with near-surface warming affect vegetation and soil N stocks, N₂O emissions did not increase in the tundra heath, indicating that mesic tundra heath is not a notable future source of the powerful greenhouse gas. This will, however, depend on accurate prediction of surface layer soil moisture.

Deciduous shrubs had overall competitive advantage over evergreens and mosses in a warmer summer and winter climate, however, the evergreen plant type was the best at utilizing N released in the early season. This study thus suggests that warming could induce a deciduous shrubification trend for mesic tundra based on the N availability, although the degree of seasonal warming and the possible release of mineral N from thawing permafrost are complicating factors important to quantify.

These conclusions have major implications for tundra C sink strength, but future field and model studies will need to clarify to which degree they are scalable in the heterogeneous landscape of the Arctic.

Declarations

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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

The CoupModel is freely available for download at www.coupmodel.com

Authors' contribution

Not applicable

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Figures

Figure 1

Cross-section of one plot (of 5 replicates) in the footslope reception area. Soil and vegetation sampling and environmental variable monitoring have been denoted.

Figure 2

Soil water chemical composition over the early to later growing season 2018 and 2019 as measured in Rasmussen et al. (2021) (points) and modelled (lines with shading). Lines denote the simulated compound concentration for an ambient scenario, whereas the shading denotes the confidence intervals 5 % and 95 %. All points are averages of five replicates.

Figure 3

Model sensitivity results: (A): total external N input to the ecosystem and (B): total N output from the ecosystem. The total ecosystem N gain (C) as compared to ambient conditions. Fluxes denoted by 'a' are significantly different from same plot fluxes denoted by 'b' and vice versa.

Figure 4

Overview of the simulated ecosystem pools and fluxes for the year 2018 (six years after beginning of simulation) at Ambient conditions, and the change in pool size or rate with High N (0.3 mg L^{-1}) in the lateral input water at 30 cm depth, with near-surface 2°C Warming and with a combination of High N and near-surface Warming. Pools are shown as boxes (g N m^{-2}) while fluxes are shown as arrows between boxes ($\text{g N m}^{-2} \text{ d}^{-1}$). Arrow style indicates the unit of the flux and box outline thickness indicates the relative size of the pool, but is not directly proportional to pool size.

Figure 5

Model sensitivity simulations on (A) rates of nitrification and (B) denitrification [$\mu\text{g N m}^{-2} \text{ d}^{-1}$], (C) the degree of plant N satisfaction (plant N demand- plant N uptake,) and (D) the soil N balance from 2011-2018 [g N] for Ambient scenario, (0.3) a scenario with lateral N input with a concentration of $0.3 \mu\text{g N L}^{-1}$ in the input water, (2°C) a near-surface warming scenario with ambient N input and ($0.3+2^\circ\text{C}$) the combination of near-surface warming and high N input. Error bars represent one standard deviation. -

Figure 6

Model sensitivity simulations on (A) Gross primary Production, (B) Ecosystem Respiration and (C) Net Ecosystem Exchange [$\text{g C m}^{-2} \text{ d}^{-1}$] for Ambient scenario, (0.3) a scenario with lateral N input with a concentration of $0.3 \mu\text{g N L}^{-1}$ in the input water, (2°C) a near-surface warming scenario with ambient N input and ($0.3+2^\circ\text{C}$) the combination of near-surface warming and high N input. Error bars represent one standard deviation.

Figure 7

N limitation impact on primary production in the early season for three different simulated plant functional types. 1 = no limitation, 0 = no activity due to total N lack. Ambient scenario lateral N input concentration = 0.03 mg L^{-1} . High N lateral N input concentration = 0.3 mg L^{-1} .

Supplementary Files

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