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Nitrogen immobilization could link extreme winter warming events to Arctic browning

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ABSTRACT

Arctic extreme winter warming events (WW events) have increased in frequency with climate change. WW events have been linked to damaged tundra vegetation (“Arctic browning”), but the mechanisms that link episodic winter thaw to plant damage in summer are not fully understood. We suggest that one mechanism is microbial N immobilization during the WW event, which leads to a smaller release of winter-mineralized N in spring and therefore more N limitation for vegetation in summer.

We tested this hypothesis in a Western Greenlandic Low arctic tundra, where we experimentally simulated a 6 day field-scale extreme WW event and 1) used stable isotopes to trace the movement of N as a consequence of the WW event, 2) measured the effect of a WW event on spring N release in top soils in the laboratory, and 3) measured the carry-over effect on summer aboveground vegetation C/N ratio in tundra subject to a WW event.

Our results show that soil mineral N released by a WW event followed by soil thaw is taken up by microbes and stored in the soil, whereas vascular plants acquired almost none, and significant amounts were lost to leaching and gaseous emissions. As soils thawed in spring, we saw weak but not significant evidence (P = 0.067) for a larger N release over the first month of spring thaw in Control soils compared to WW event soils, although not significantly. A weak signal (P = 0.07) linked WW event treatment to higher summer C/N ratios in evergreen shrubs, whereas deciduous shrubs were not affected.

We conclude that our results did not show significant evidence for WW events causing Arctic browning via N immobilization and summer N limitation, but that we had indications (P < 0.1) which merits further testing of the theory in various tundra types and with repeated WW events. Evergreen shrubs could be especially sensitive to winter N immobilization, with implications for future vegetation community composition and tundra C storage.

1. Introduction

Arctic ecosystems experience rapid changes in climate, not least during the winter months (IPCC, 2019). Arctic winters have especially seen an increase in the frequency of extreme weather events, with both extraordinarily large or low amounts of snow (Vikhamar-Schuler et al., 2016; Westergaard-Nielsen et al., 2018), as well as warm periods during the non-growing season (Vikhamar-Schuler et al., 2016; Hansen-Bauer et al., 2019).

Extreme winter warming events (WW events) are defined as periods of 5–10 days during winter where the air temperature increases to above freezing, causing snow melt and thawing of the upper part of the soil (Bokhorst et al., 2011; Phoenix and Bjerke 2016; Hansen-Bauer et al., 2019). This is sometimes accompanied by rain, which can result in “rain-on-snow” events (Vikhamar-Schuler et al., 2016).

Although many areas of the Arctic have shown a greening trend due to a climate change-related increase in plant biomass (Berner et al., 2020; Mekonnen et al., 2021b), WW events may contribute to a decline...
in the greening trend (Xu et al., 2013; Frost et al., 2021). WW events may even cause browning of Arctic tundra landscapes (damaged or dead vegetation), which has been observed in recent decades (Phoenix and Bjerke 2016; Myers-Smith et al., 2020; Frost et al., 2021).

Damaged and brown vegetation, decrease in shoot and root growth and bare patches of ground are all aspects of browning, which cause reduced carbon (C) uptake in vegetation and less storage of soil organic C (Bokhorst et al., 2011; Bjerke et al., 2014; Myers-Smith et al., 2015; Treharne et al., 2019). The special sensitivity of evergreen shrubs to browning (Bjerke et al., 2014) is important as evergreen shrubs have been found expanding in tundra heath ecosystems as a result of increasing temperatures (Hein et al., 2021; Scharn et al., 2022a, 2022b).

Several mechanisms link WW events to vegetation browning. Proposed causes of browning include frost damage to leaves (Bokhorst et al., 2011; Parmentier et al., 2018) combined with premature budburst (Phoenix and Treharne 2022 and references herein), but the importance of each mechanism is yet uncertain (Phoenix and Treharne 2022). To better model the future plant-soil-C dynamics of the tundra, understanding the processes that mechanistically link the WW events to browning is crucial (Phoenix and Treharne 2022). A potential mechanism, which has not yet been explored, is plant nitrogen (N) limitation caused by microbial N immobilization during such WW events.

When upper soil layers thaw in spring, the pool of mineral N accumulated during winter is partly released into the soil (Buckeridge and Grogan 2010; Rasmussen et al., 2020) (Fig. 1A). This pool can either be immobilized by microbes and stored in the soil as organic N, released as gas in the form of N₂ or N₂O (Rasmussen et al., 2022c), adsorbed, or leached downhill to lower lying ecosystems (Rasmussen et al., 2022a; Mekonnen et al., 2021a; Rasmussen et al., 2022c). Only little N is assimilated by plants (about 2% according to Rasmussen et al., 2022a). However, evergreen shrubs may be better at utilizing early season N to support their early-season photosynthesis (Rasmussen et al., 2022a, 2022b). During extreme WW events, the ecosystem experiences climatic conditions that resemble a “false spring”, followed by re-freezing when temperatures drop back to winter conditions (Fig. 1B). This ‘false spring’ can lead to spring-like N dynamics, which result in N immobilization or ecosystem N loss. Hereby, the bioavailable N pulse will be reduced when the real spring occurs and growing season begins. Although plants do not rely only on the spring N pulse, evergreen shrubs do appear to specialize in assimilating N in the early growing season and could therefore be affected by this decrease in N availability (Rasmussen et al., 2022a).

This study tests the hypothesis that WW events can shift plant-available N release from spring to winter and induce winter N immobilization in the soil, leading to a loss of plant N resources for the following growing season. We do this by 1) quantifying the fate of mineral N released during an experimental WW event in the field; 2) determining whether the spring pulse of mineral N is reduced in soils that have experienced a WW event, and 3) testing the growing season plant-N status following a WW event. As part of the experimental WW event in a Greenlandic tundra heath, we warmed the upper soil layer in situ, introduced stable isotope 15N tracers and followed the fate of 15N the following growing season.

2. Materials and methods

2.1. Study site

The Blæsedalen study site is located on Disko island, Western Greenland (69.28°N, 53.48°W). The area is dominated by basaltic bedrock, which has been glacially carved so that U-valleys are lined by tabletop mountains rising to 800–900 m (Humlum et al., 1976). The climate is Arctic Maritime with a mean annual air temperature of −3 ± 1.8 °C (1991–2017) and annual precipitation of 418 ± 131 mm y⁻¹ from the same period, with about 40–50% snow share (Hansen et al., 2006). The area has experienced an increase in mean annual air temperatures of 0.16 °C y⁻¹ in the same period (Zhang et al., 2019), and an increase in the frequency of extreme winters (e.g., extreme snow amounts) and summer conditions (e.g., drought) (Westergaard-Nielsen et al., 2018). The most dominating ecosystem type in this valley is mesic tundra heath established on a sandy loam soil, which (as described in Rasmussen

![Stable winter N dynamics](image1.png)

**Fig. 1.** Illustration of the hypothesized link between extreme winter warming (WW) events and reduced N availability for tundra vegetation in summer. A: During a stable winter, net N mineralization occurs and a mineral N pool builds up (light blue on the figure), which is then released into soil solution and is biologically available for plants and microbes when snowmelt and soil thaw happens in spring. B: During a winter with a WW event (illustrated by yellow triangle), the build-up of mineral N in the soil is interrupted by a “false spring”, as the snow melts and the topsoil thaws when vegetation is not competitive at assimilating N, and the mineral N pool is therefore immobilized by microbes or drains away, hence the mineral N returns to the organic N pool. After the WW event, the build-up of a mineral N pool resumes, but because of the early release, the spring N pulse is smaller, which could amplify tundra vegetation N limitation.
et al., 2022a) in the top 10 cm contains approx. 12,000 g C m$^{-2}$ and 640 g N m$^{-2}$ and had NO$_3^-$ content in soil solution varying between 19.5 μg L$^{-1}$ in the early growing season and 0.5 μg L$^{-1}$ in the peak growing season of 2018–2019 (NH$_4^+$ 3.7–19 μg L$^{-1}$ with a similar seasonal pattern). Here, the dominating vegetation is evergreen and deciduous dwarf shrubs such as Betula nana L., Empetrum nigrum ssp. hermaphroditum Hagerup, Cassiope tetragona (L.) D. Don, Salix glauca L., Vaccinium uliginosum L., interlain by mosses such as Tomentypnum nitens (Hedw.) Loeske, Raconitrium laruginosum (Hedw.) Brid., Sphagnum spp. and lichens (D’Imperio et al., 2017).

### 2.2. Experimental design

On this mesic tundra heath, we established four replicate blocks, each containing four 100 × 100 cm plots. Two plots in each block were equipped with custom-made heating probes, which when connected to an electrical power source warmed up and heated the surrounding soil (winter warming plots, WW). Other eight plots were un-heated controls (Ctrl) (Fig. 2).

In April (late winter) 2022, we simulated an extreme winter warming event by connecting the heating probes in the WW plots to generators via a power regulator (Stairville DDS-405 LC DMX 4 Channel Dimmer, Thomann, SE). During heating and subsequent thawing, we increased the soil temperature in each WW plot to reach a target soil temperature of 0.5–2.5 °C at 5 cm depth throughout 6 full days and nights (134 h) (Fig. 3).

In addition to soil temperature at 5 cm, we also measured continuous soil temperatures at 10, 20, 40 and 70 cm (OxyBases, PreSens Precision Sensing GmbH, Regensburg, DE) as well as surface temperatures using Tinytag Plus 2 - TGP-4017 (Gemini Data Loggers, UK) in a subset of both Ctrl and WW plots. For overview image and photos of warming plots at the beginning and end of the 6 days of warming, see Figs. S1–2.

### 2.3. The fate of mineral N during WW events

About 24 h after the start of the WW event, when the soil contained liquid water, a solution of distilled water containing ($^{15}$NH$_4$)$_2$SO$_4$ (99% $^{15}$N purity, Cambridge Isotope Laboratories, Andover, MA, USA) corresponding to 0.66 g N m$^{-2}$ was injected through a syringe to the topsoil (0–6 cm depth) of a sub-area of 20.4 cm$^2$. The total amount of solution injected to each sub-area was 13.8 ml containing 1342 μg ($^{15}$NH$_4$)$_2$SO$_4$, which was injected homogeneously in a grid pattern with 1.5 cm spacing.

After 6 d (the complete duration of the WW event), aboveground plant material and soil (a 3-cm diameter core down to 6 cm) was sampled within the sub-area and used to quantify the movement of $^{15}$NH$_4^+$ during the WW event according to the following procedure:

After manually removing roots immediately after sampling, the soil was analyzed for gravimetric water content, bulk C and N content, and δ$^{15}$N of the bulk soil N (GSL elemental analyzer coupled to a 20–22 isotope ratio mass spectrometer, Sercon Ltd., Crewe, UK). On a subset (n = 3) of samples, we measured soil bulk density.

Roots were washed, dried, crushed, and root dry weight was quantified, followed by analysis of total C, N and δ$^{15}$N content of the roots.

Furthermore, microbial C, N and $^{15}$N recovery was measured using the chloroform fumigation-extraction technique also immediately after
sampling (Brookes et al., 1985). Shortly, water-extractable N and C concentrations were analyzed in subreplicates with and without chloroform fumigation for 24 h (elemental analysis coupled to mass spectrometry (Eurovector, Pavia, Italy and Elementar, Cheadle Hulme, UK, respectively)). Demineralized water was chosen for extraction as opposed to KHSO$_4$ (Brookes et al., 1985) in order to be comparable to extractions previously done in the same area (e.g. Ravn et al., 2017; Kolstad et al., 2021; Xu et al., 2022a, b; Rasmussen et al., 2022a).

In aboveground vegetation sampled at the termination of the WW experiment (day 6), leaf and stem fractions were species-specifically crushed and analyzed for % C, % N and $\delta^{15}$N (GSL elemental analyzer coupled to isotope ratio mass spectrometer, Sercon Ltd., Crewe, UK).

To calculate the recovery of tracer $^{15}$N in each fraction, we followed a similar method as in e.g. Rasmussen et al. (2022a). The $\delta^{15}$N value of all sample materials was calculated as:

$$\delta^{15}N(\%) = \frac{^{15}N_{sample}}{^{15}N_{reference}} \times 1000$$  

(1)

where the $^{15}N_{reference}$ refers to the $\delta^{15}N$ value of air-N$_2$. In order to achieve the recovery, the measured $^{15}N$/g DW material was converted to atom fraction, expressed as percentage (AT%) of $^{15}$N, adjusted for on-site measured natural abundance of $^{15}$N, and all pools were scaled to plot size (10 cm depth) with dry soil bulk density and the known size of the sampling areas (20.4 cm$^2$). The scaled amount of $^{15}$N was subtracted from the (scaled) known amount of added $^{15}$N to obtain recovery (%) in each pool, respectively, and the total recovery in percentage of added $^{15}$N. Table S1 details N pools and natural abundance used in the calculations.

The difference between $^{15}$N tracer recovery in the plant functional types moss, deciduous shrubs and evergreen shrubs were tested with a one-way ANOVA with functional type as factor.

2.4. Spring N pulse at thaw

In all Ctrl and WW plots, frozen topsoil cores from 0 to 10 cm depth (diameter 5 cm) were sampled 1–2 days after the WW event finished, by hammering a metal corer into the frozen soil (Fig. 2). The cores were transported frozen to the laboratory, where they were kept at $-18$ °C until a ‘spring’ experiment started. The week before the spring thaw initiated, 410 cm$^3$ glass jars covered with gas- but not water permeable film and moved to $-6$ °C to acclimatize to winter soil temperatures in Blæsedalen (Hansen et al., 2006).

We simulated spring thaw by moving the incubated samples to 1 °C in a closed incubator for 2 days, then 5 °C for 28 days, hereby simulating the first month of spring thaw conditions. During this period, we measured net N$_2$O fluxes and soil water mineral N concentration using the following approach:

Right after spring start initiated by moving cores from $-6$ °C to 1 °C (0 h) and after 24 h, 48 h, 72 h, 6 d, 10 d, 18 d and 31 d, each core was moved into a cooling box at 5 °C and connected to a LGR N20IA2-915 gas analyzer (Los Gatos Research, CA, USA) via a closed loop system, in which headspace air N$_2$O concentrations were measured over at least 20 min, and fluxes were calculated using the HMR package (Pedersen et al., 2010) in R 4.2.2.

At the same sampling intervals, soil water was extracted from the cores using microrhizons (0.5 mm diameter, 1.5 cm long) (Rhizosphere Research Products B. V., Wageningen, Netherlands), which were inserted horizontally into the cores in pre-drilled holes in the frozen core before spring thaw was initiated. Upon thaw, the soil collapsed and therefore enclosed the suction cup, so that 0.2–0.5 ml of water per sampling could be extracted using a syringe. Right after thaw start (0 h), liquid water could not be extracted from the cores. A total amount of 4 ml was extracted per core during the experiment, accounting for $\sim 5$ % of the total soil water content. The soil water was stored frozen until analysis of NO$_3^-$, SO$_4^{2-}$ and PO$_4^{3-}$ content using Ion Chromatography (ThermoFisher Scientific, MA, USA). After end of the spring thaw experiment, remaining cores were analyzed for soil moisture content, total N and total C (Flash 2000, Thermo Scientific, Bremen, Germany).

The difference in NO$_3^-$, SO$_4^{2-}$ and PO$_4^{3-}$ release upon spring thaw (content at 24 h) between Ctrl and WW event plots was tested with a t-test and the Cohen’s D effect size was calculated (Cohen, 1988; Rasmussen et al., 2022a). The overall difference over the thaw period was tested with a mixed model with plot as random effect, WW treatment as fixed effect and time step as repeated effect. The change in N$_2$O flux with time was tested using a paired samples t-test for each time step.

2.5. Growing season plant N status

A vegetation survey was done on all plots in the summer of 2019 using the point intercept method (Jonasson, 1989). In early August 2022, following the winter warming event, we sampled aboveground plant material in all WW and Ctrl plots, picking randomly in the entire
plot, but avoiding the tracer experiment sub-area (Fig. 2). The species-specific plant material was air-dried. Leaf and stem material was separately crushed and analyzed for % C, % N and δ¹⁵N (GSL elemental analyzer and isotope ratio mass spectrometer, Sercon Ltd., Crewe, UK). The difference between C/N ratios in WW and Ctrl plots was tested using a paired sample t-test and the Cohen’s D effect size was calculated (Cohen, 1988).

3. Results

3.1. Soil temperature and soil moisture during WW event

Ambient temperatures were between −6.6 °C (soil surface) and −4.6 °C (70 cm depth) during the field WW experiment (Fig. 4A). The in situ WW experiment caused a temperature increase of about 4 °C (from −2 to 2 °C) at 5 cm in the soil surrounding the heating probes, where our ¹⁵N-experiment was conducted (Fig. 3). Soil temperatures measured at the surface approx. 20 cm from the heating sources increased by ~5.5 °C during the WW event (from −6 to 0.5 °C); at 10, 20 and 40 cm depth by ~2 °C (from −5 to −3 °C), and at 70 cm −1.5 °C (from −4.6 to −3 °C) at the final day of the WW event (Fig. 4B). Heating probes did as such not yield a completely homogeneous warming in the entire WW plots, but did affect the soil in most of the plots.

3.2. Fate of the WW-released N

At the end of the in-situ WW experiment (hour 134/day 6), most of the mineral ¹⁵N–NH₄ tracer was found in the non-microbial bulk soil (34 % ± 7) and to a lesser extent in the living microbial N pool (2.5 % ± 0.5) (Fig. 5 and Table S1). Moss contained 0.9 % ± 0.5 of the ¹⁵N–NH₄, whereas aboveground vascular biomass contained almost none (0.1 % for both aboveground evergreen and deciduous shrubs, respectively, and 0.2% in roots) of the tracer ¹⁵N.

Of the ¹⁵N fraction assimilated by vegetation, most (0.9 %) was taken up by mosses, which contained 92.4 ± 48 μg ¹⁵N g⁻¹ DW plant material. This was significantly (P < 0.05) more compared to deciduous shrubs and evergreen shrubs, which contained, respectively, 11.5 ± 2.1 and 10.15 ± 1.5 μg ¹⁵N g⁻¹ DW plant material (0.1% of all tracer).

![Fig. 4. Average soil temperatures during April 2022 in the Ctrl plots with ambient conditions(A) (n = 8–14 for each depth) and plots subject to a late-winter extreme WW event (B) (n = 4–8 for each depth). Vertical lines denote the beginning and end of the simulated extreme WW event. Note the difference in scales of the y-axes. Loggers were distributed over the plots and never in close contact with heating probes, so they represent a measure of heat distribution in the 1 × 1 m plots.](image-url)
3.3. N-release during the spring thaw experiment

On the first day of thaw, the topsoil released mineral N so that after 24 h Ctrl soils contained on average 5.3 ± 0.7 mg NO$_3$N L$^{-1}$ (median 3.92) (Fig. 6A and Table S2). The concentration subsequently decreased over time so that after 48 h soil solution contained 2.3 ± 0.2 mg NO$_3$N L$^{-1}$, after 72 h 1.7 ± 0.1 mg NO$_3$N L$^{-1}$, and then varied between 1.5 and 1.8 mg NO$_3$N L$^{-1}$ on day 6, 10, 18 and 31 days after spring onset (see Fig. 6A).

The topsoils from WW plots (exposed to a WW event before frozen core sampling) also released mineral N during the first day of thaw (Fig. 6B and Table S2). After 24 h soil solution contained on average 3 ± 1.4 mg NO$_3$N L$^{-1}$. The concentration subsequently decreased to 2.5 ± 0.1 mg NO$_3$N L$^{-1}$ after 48 h, 2.3 ± 0.7 mg NO$_3$N L$^{-1}$ after 72 h and then stabilized on day 6, 10, 18 and 31 around 1.7–1.9 NO$_3$N L$^{-1}$. The pulse (24 h) concentrations of the WW and Ctrl soil cores were not different (P = 0.167), but there was weak evidence for an overall higher release over the month in the Ctrl cores (P = 0.067) with a Cohen’s D effect size of −0.37 in plots subjected to a WW event.

Sulphate concentrations followed a pattern similar to the NO$_3$ concentrations (Fig. 6C and Table S2). An initial pulse of 23.0 mg SO$_4$N L$^{-1}$ at 24 h after thaw start decreased to 13 mg SO$_4$N L$^{-1}$, then stabilized between 9 and 11 mg SO$_4$N L$^{-1}$ for the rest of the first month of thaw. In the WW plots, there was weak evidence (P = 0.08) to suggest a smaller short term SO$_4$ release, with mean SO$_4$ content at 24 h of 7.19 mg L$^{-1}$. The SO$_4$ concentrations then varied only slightly throughout the rest of the month between 6 and 8.5 mg SO$_4$N L$^{-1}$ on average (Fig. 6D), and the total SO$_4$ release over the month of thaw was significantly smaller in the WW cores (P = 0.01). The Cohen’s D effect size of WW events on the SO$_4$ content after 24 h was −0.8, whereas the effect on the overall release over the month was −0.55.

Phosphate concentrations varied from below detection limit to 5 mg L$^{-1}$ over the course of the first month but did not show a pulse or a stabilization pattern in the Ctrl or the WW plots (Fig. 6E and F and Table S2).

3.4. N$_2$O emissions during the spring thaw experiment

The topsoil cores emitted small amounts of N$_2$O immediately when exposed to spring thaw conditions (Fig. 7), with the largest variability between replicates during the first 24 h in the Ctrl cores and with an overall small, but significant increase over the first month (P < 0.001 in a paired samples t-test). WW cores had average N$_2$O fluxes similar to the Ctrl cores, with a similar small increase in average emissions (P < 0.001).

Generally, variability was larger with occasionally larger N$_2$O fluxes in the Ctrl topsoils that had experienced a stable, uninterrupted winter, compared to the topsoils which had experienced a WW event. (see Table S3).

3.5. Carry-over effect to the growing season

The vegetation cover in the Ctrl and WW plots was similar and consisted of 39.5 ± 0.6 % evergreen shrubs (cover percentage), 12.2 ± 0.9 % deciduous shrubs, 12.3 ± 2.2 % mosses, 9.4 ± 2.8 % lichens, and <1% graminoids and herbs. The summer after the WW event, the C/N ratio of deciduous shrub leaves in WW plots (19.1 ± 1.1, mean ± standard error) was similar to the C/N of deciduous shrubs from Ctrl plots (19.9 ± 0.5, Fig. 8 and Table S4). Contrastingly, a weak signal (P = 0.07) indicated that the C/N ratio of evergreen shrubs in WW plots could be higher (48.4 ± 3) compared to Ctrl plots (43.2 ± 2). This difference was due to a lower N content in WW plots compared to in Ctrl (1.06 ± 0.08 % and 1.18 ± 0.07 %, respectively) and had a Cohen’s D effect size of 0.65.
4. Discussion

WW events share the physical characteristics of spring (snowmelt and upper soil thaw), and the ecosystem N movement during this short “false spring” in the mid- or late winter could influence the real spring and summer N availability, as argued below.

Our results suggest that during soil thaw, mineral N along with P and S is released into the soil solution. Most of the N released during the WW event is incorporated into the soil within the duration of the WW event, either through microbial immobilization and subsequent turnover into organic soil N, or adsorbed inorganically to soil colloids during the WW event. Living microbes had actively taken up the WW-released N at the end of the WW event, without any significant uptake by vascular plants. About 60% of the $^{15}$NH$_4$–N tracer was unaccounted for in the field experiment, and we suggest this may have been leached from the plots as NO$_3$ or dissolved organic N (Yano et al., 2010; Rasmussen et al., 2022a) or lost as N-gas (we only measured N$_2$O in this study). The N$_2$O emission following spring thaw was in the same order of magnitude as in other Arctic soils (e.g. Kolstad et al., 2021), and was more variable in Ctrl soil. Microbes in soil anaerobic microsites with high potential for N$_2$O release through denitrification (Butterbach-Bahl et al., 2013) may have used the mineral N released during the WW event. The amount of N lost by this pathway in the present study was, however, insignificant compared to the fluxes between soil, vegetation and microbes. If N$_2$ was the end product of the denitrification process (Rasmussen et al., 2022c), denitrification could still be an important pathway of N loss.

A spring N pulse, i.e. increase in soil water inorganic N content in the days following soil thaw, has been observed in field experiments in the Scandinavian Subarctic (Grogan and Jonasson, 2003), Canadian Arctic (Buckeridge and Grogan, 2010), Alaska (Stetla and Schimel, 2013), High Arctic Svalbard (Semenchuk et al., 2015) and Low Arctic Greenland (Rasmussen et al., 2022a), with a concomitant increase in soil N.

Fig. 6. Soil solution content of NO$_3$, SO$_4$ and PO$_4$ over the first month of spring thaw for Ctrl top soils (A,C,E) and WW topsoils, which have experienced an extreme winter warming event (B,D,F). N = 16 for each time point. Boxplots show the median (line) and 25% and 75% distribution (box), with 95% as the bar end. Individual points outside the bars are single measurements falling outside the 95% distribution but kept in the analyses. Indications of significance are: *p < 0.1 (weak signal), **p < 0.05 (good signal).
availability and plant N uptake. As opposed to the N assimilation during spring thaw (ibid), tundra vascular vegetation in our study assimilated almost none (0.2%) of the WW-released mineral N into their above-ground biomass. Although field studies are sparse and results are ambiguous, vascular plants tend to compete poorly for N during wintertime (Grogan and Jonasson, 2003; Weih, 2000; Edwards and Jeffries 2010). Because of this apparent winter disadvantage, tundra shrubs may not be able to assimilate the newly available N released by a WW event. Most deciduous and evergreen tundra shrubs, however, form associations with ericoid mycorrhizae or ectomycorrhizae (Iversen et al., 2015 and references herein), which are efficient in N uptake. The 0.2% of $^{15}$N tracer found in root biomass in our study could illustrate this belowground uptake potential (Edwards and Jeffries 2010).

Our spring thaw experiment results further showed a weak signal ($P = 0.067$) with, however, a medium effect size ($-0.37$) indicating that the WW event release of mineral N has the potential to decrease the size of the following spring N pulse, although the difference was not significant. With a sample size of 8 WW and Ctrl plots, respectively, in a heterogeneous environment like the tundra soil, an indication with $P < 0.1$ and medium effect size does, however, warrant further testing of the WW effect on spring mineral N release (Halsey et al., 2015). Bokhorst et al., 2011 contrastingly concluded that nutrient availability in their Subarctic tundra heath (major anions and cations measured during the growing season using ion exchange membranes) was unaltered in plots which had experienced field scale WW events; however, their treatments involved infra-red heating lamps to simulate the WW event, so the effects on the soil-nutrient-plant-interaction could be different from ours.

A smaller spring N pulse following a WW event, as compared to a spring after stable winter conditions, would have consequences for plant available N at the beginning of the growing season. Arctic plant functional types differ in their ability to assimilate mineral N early in the growing season, and the importance of the spring N pulse could therefore also differ between plant functional types (Bilbrough et al., 2000; Weih 2000; Larsen et al., 2012). We have previously showed that evergreen shrubs were most efficient in taking up early season N in a West Greenlandic mesic tundra heath (Rasmussen et al., 2022a, 2022b).
In the present study, evergreen shrubs were also the plant functional type, which showed a weak signal ($P = 0.07$) with medium effect size (0.65) of increased summer C/N ratio in response to a WW event. The higher efficiency at taking up early season N could cause more reliance on the ecological niche of early season N acquisition, making evergreen shrubs more sensitive to WW event N dynamics. Supporting that theory, Riley et al. (2021) concluded that evergreen shrub cover decreased more than deciduous shrub cover if non-growing season N uptake was excluded in their process-based mechanistic model, suggesting that evergreen shrubs are more dependent on winter-early spring N uptake than deciduous shrubs. As a consequence, in a highly N-limited tundra environment, loss of the early season N source could reduce evergreen shrub growth in areas that experience increased frequency in WW events.

Our results are based on one site in West Greenland, with a sample size limited by logistics of doing winter field work in the Arctic, which can cause sampling bias compared to the true population (Halsey et al., 2015). More studies with ideally larger sample sizes and more data and tundra types (e.g. tussock tundra, wet meadow) are needed to further test how important N immobilization during WW events is as a mechanism linking WW events to vegetation performance during the subsequent growing season. With evergreen shrubs reported to be especially sensitive to browning (Bjerke et al., 2014), however, the WW event N immobilization followed by summer N limitation hypothesis is worth testing further.

Mosses and lichen were important vegetation types in our sites and their summer C/N response to N-immobilization during WW events also warrants study. Because their N fixation capability lends them an alternative N source (Rousk et al., 2017), we did, however, not test their C/N status, assuming that they would not be as sensitive as vascular plants to our hypothesized soil N immobilization during the WW event and subsequent smaller spring N pulse. The results further suggested that mosses were better than vascular plants at obtaining WW-released N during the WW event.

WW events that cause snow melt followed by re-freezing occur in different tundra types in the Arctic, but also in alpine ecosystems such as the Tibetan plateau (Zhu et al., 2022) and the Alps (Colucci et al., 2017). A threat to common evergreen shrub types could therefore stretch beyond the Arctic, and the short-term impact on C storage could be considerable (see e.g. Treharne et al., 2019, 2020; Parmentier et al., 2018). In contrast, lichen seem to be resilient to WW events (Bjerke et al., 2011), and in a future with more frequent WW events (Vikhamar-Schuler et al., 2016; Hansen-Bauer et al., 2019), we could see a shift in vegetation community composition with reduced evergreen shrub cover.

Our results highlight the implications of wintertime changes on summer ecosystem interactions. Changes in snow depth has been shown to alter nutrient status of Arctic soils and plants (Buckeridge et al., 2010; Semenchuk et al., 2015). Also, tundra vegetation winter N uptake rates could have consequences for ecosystem C storage, because N limitation is an important control on photosynthesis and shrub growth (Weintraub and Schimel 2005). Riley et al. (2021) found that excluding winter N uptake caused a 23 % decrease in the spring NPP in an Arctic polygonal tundra ecosystem. The ability of tundra plants to acquire N during winter is, however, very sparsely studied experimentally (but see Larsen et al., 2012; Riley et al., 2021). More studies of tundra plant winter N uptake and sensitivity to WW events are therefore needed in order to better understand tundra winter N dynamics now and in the future.

5. Conclusions

Our results suggest that extreme winter warming events, which implies soil thaw followed by re-freezing during winter, release mineral N into soil solution at a time when vascular plants are less competitive for accessing it than microbes. Rather, the mineral N is stored in the soil or immobilized in microbes and enter the soil organic N pool. Because of this untimely winter mineral N release, our results indicated ($P = 0.067$) that the mineral N pulse at spring thaw can be reduced, which can increase N limitation in evergreen shrubs ($P = 0.07$), as they are adapted to utilizing the early season N pulse.

Our results did not show significant evidence for WW events causing Arctic browning via N immobilization and summer N limitation, but we had indications in favor of the theory ($P < 0.1$) which merit further testing in various tundra types and with repeated WW events. The importance of this mechanism should be studied further due to the limitations of any single study, as should tundra winter N fluxes, because vegetation damage could mean less C storage in Arctic tundra plants.

CRediT authorship contribution statement

Laura Helene Rasmussen: Writing – review and editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Birgitte Kortegaard Danielsen: Validation, Resources, Methodology, Investigation, Conceptualization.

Bo Elberling: Writing – review and editing, Validation, Supervision, Resources, Methodology, Data curation, Conceptualization.

Per Ambus: Writing – review and editing, Resources, Methodology, Data curation, Conceptualization.

Mats P. Björkman: Writing – review and editing, Funding acquisition, Conceptualization.

Riikka Rinnan: Writing – review and editing, Validation, Supervision, Methodology, Conceptualization.

Louise C. Andresen: Writing – review and editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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