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Shifts in soil C stabilization mechanisms are linked to reindeer-induced changes in plant communities and associated fungi in subarctic tundra

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ABSTRACT

Arctic tundra ecosystems store a significant proportion of the global soil organic carbon (C). However, warming-induced shrub encroachment and reindeer (*Rangifer tarandus* L.) grazing regimes promoting graminoid vegetation may strongly influence tundra soil C stability. Here, we studied how reindeer grazing intensity and experimental warming affect soil C stabilization in a tundra ecosystem. We hypothesized that under light grazing, persistent complexes formed by fungal necromass (FNM) and condensed tannins (CT) from shrub roots stabilize the soil C, whereas, under heavy grazing, the soil C stabilization is affected by glomalin-related soil proteins (GRSP) produced by arbuscular mycorrhizal fungi of graminoids. In addition, we expect warming to mediate grazing effects, diminishing the potential for C stabilization.

Our results show no effect of grazing on stable C concentration, however, under light grazing the labile C concentration was higher. We found higher concentrations of chitin and tannins under light grazing, indicative of soil C stabilization potential through FNM-CT complexes. By contrast, we found more root ergosterol under heavy grazing, suggesting a high abundance of endophytes, usually melanized, and a slightly higher GRSP concentration. Warming did not cause changes in stable C concentration but was associated with changes in the soil chemical quality, pointing to a decrease of lignin, polypeptides, and polysaccharides.

We conclude that different soil C stabilization mechanisms operate under light and heavy grazing pressures and that these mechanisms are closely linked to changes in the vegetation and the fungi typically associated with them.

1. Introduction

Arctic tundra stores half of the global soil C (Tarnocai et al., 2009), most of which is in the soil organic C (SOC). In subarctic tundra, grazing by reindeer (*Rangifer tarandus* L.) is a major determinant for tundra vegetation dynamics and soil processes, although the direction and the intensity of this effect varies among sites depending on both habitat type and reindeer grazing patterns (Bernes et al., 2015; Schmitz et al., 2014; Stark et al., 2023a; Sundqvist et al., 2019). Under relatively low reindeer grazing intensities, subarctic tundra vegetation is dominated by evergreen and deciduous shrubs such as *Vaccinium* L. species, *Empetrum nigrum* L. ssp. *hermaphroditum*, and *Betula nana* L. In cases where tundra ecosystems experience regularly occurring intensive grazing pulses during the growing season, reindeer grazing may transform the predominant dwarf shrub-dominated tundra into a graminoid and herb-dominated tundra (Olofsson et al., 2004). This vegetation shift exerts several consequences for the soil environment, such as a warmer microclimate during the growing season (Olofsson et al., 2004; Ylänne et al., 2018), higher nitrogen (N) concentrations (Stark and Väisänen, 2014) and different fungal (Ahonen et al., 2021) and microfaunal community compositions (Stark et al., 2023b).

The ongoing climate warming is expected to change Arctic ecosystem functioning considerably through accelerated soil organic matter decomposition rates via increased microbial respiration (e.g., García-Palacios et al., 2021) and shifts in vegetation composition (Wang et al., 2017). The consequences of climate warming on soil C stocks and vegetation are thought to relate closely with an increasing abundance of evergreen and deciduous shrubs that establish mycorrhizal symbioses with ericoid and ectomycorrhizal fungi, respectively (Deslippe et al., 2012; Parker et al., 2021; Read and Perez-Moreno, 2003; Smith and Read, 1997; Vowles and Björk, 2019). Yet, the consequences could also be mediated by arbuscular mycorrhizal fungi that form symbioses with

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graminoid plants. A common feature of the three abovementioned mycorrhizal types (ericoid mycorrhiza, ectomycorrhiza, and arbuscular mycorrhiza) is that they enhance the plant's access to soil nutrients by extramatrical mycelia, which can turn over or accumulate, resulting in a build-up of fungal mycelia both alive (fungal biomass) and dead (fungal necromass, FNM) (Ekblad et al., 2013; Smith and Read, 1997). However, these three mycorrhizal types are also known to have contrasting ecologies and interact differently with the surrounding soil organic matter.

SOC persistence has been traditionally thought to be driven by inputs of aboveground plant litter containing lignin, however, recent studies have shown that persistent molecule structure alone does not control SOC stability (Lehmann and Kleber, 2015; Schmidt et al., 2011). Instead, belowground C inputs from roots and microorganisms are now identified as key factors in SOC accumulation (Clemmensen et al., 2013; Fernandez and Kennedy, 2018; Fernandez and Koide, 2012), and particularly, FNM has been found to be one of the main C-containing constituents of SOC (Liang et al., 2019; Schweigert et al., 2015). However, the compounds related to soil C stabilization differ among the mycorrhizal types. In arbuscular mycorrhiza, "glomalin", a glycoprotein that enhances soil aggregate formation, has been suggested to contribute to persistent (=stable) soil C pools (Rillig, 2004; Rillig et al., 2002), whereas, in ericoid and ectomycorrhizal types, the formation of soil persistent C is linked to complexes formed between FNM and root-derived secondary compounds, tannins (Adamczyk et al., 2019). In addition, Arctic plant roots are frequently colonized by dark septate endophytes (DSE), a group of fungi that may contribute to SOC build-up via their melanized mycelia (Kohn and Stasovski, 1990; Olsson et al., 2004; Siletti et al., 2017; Väre et al., 1992). DSE are associated with a vast number of plant species and seem to be more abundant in graminoids (monocots) than in shrubs (dicots) (Weishampel and Bedford, 2006).

Sites with clear grazing-induced vegetation transitions in subarctic tundra provide an invaluable tool for investigating mechanisms for SOC stabilization and its sensitivity to climate warming. Here, we studied the effect of reindeer grazing and warming on the SOC persistence mechanisms in a subarctic-alpine tundra heath in northern Norway, where a seasonal pasture rotation fence built in the 1960s separates a lightly grazed (LG) tundra from a heavily grazed (HG) tundra. In 2014, fifty years after the establishment of the pasture rotation fence, the vegetation in the lightly grazed area was dominated by evergreen and deciduous shrubs (Ylänne et al., 2020). In contrast, the heavily grazed area was mainly dominated by graminoids with some evergreen shrubs (Ylänne et al., 2020). At both grazing intensities, a randomized block design study with eight blocks was established in 2010. Within each block, two treatments were assigned: control (C) and warming with open-top chambers (W) – a method commonly used in the Arctic and other environments with low-growing vegetation to experimentally manipulate the soil and air temperatures (Hollister et al., 2023).

A combination of biochemical and microbiological methods (i.e., soil C concentrations and total N, C:N, CT, chitin and ergosterol analyses for FNM and fungal biomass, GRSP analysis, and SOC quality with Fourier transform infrared spectroscopy, FTIR) were used to gain a comprehensive understanding of the soil microbiological and biochemical drivers of SOC persistence in the O horizon under contrasting grazing pressures and warming. We hypothesized that I) in the dwarf shrub-rich, lightly grazed tundra, the C stabilization potential resulting from FNM and CT should be higher than in the graminoid-rich, heavily grazed tundra; II) in the graminoid-rich, heavily grazed tundra, C stabilization is driven by GRSP concentration and DSE; III) warming decreases the stable SOC concentration under both grazing regimes.

2. Materials and methods

2.1. Study site and sampling

The study area, Raisduoddar, is located on a mesic subarctic, alpine tundra heath on the north slope of the fell Gahpperus in north Norway (69°39′ N, 27°30′ E, at 600–630 m a.s.l.). The predominant vegetation is the Arctic *Empetrum-Dicranum*-Lichen type, and the soil is classified as Inceptisol. The average soil organic layer depth at the site is 4.25 cm (Ylänne et al., 2018). Reindeer herding is a traditional livelihood in the area dating back several centuries. During the 1960s, a pasture rotation fence was built dividing the tundra heath into lightly and heavily grazed tundras (Fig. 1). The lightly grazed (LG) tundra is only briefly used by reindeer for passage twice a year during spring and autumn when reindeer pass through the area and is dominated by evergreen and deciduous dwarf shrubs (*Empetrum nigrum* L. ssp. *hermaphroditum*, *Betula nana* L., *Vaccinium vitis-idaea* L.). The heavily grazed (HG) tundra is subjected to more intensive reindeer use during reindeer autumn migrations. Reindeer stay in the area as large herds for approximately two weeks in early August, because the pasture rotation fence keeps the reindeer in the area until reindeer herders allow them to move into winter ranges (Olofsson et al., 2001; Stark and Väisänen, 2014). In 2014, there were around 13,000 reindeer in the reindeer herding district of Čohkolat in Raisduoddar (Ylänne et al., 2018). The regular grazing pulses repeating annually since the 1960s have shifted the vegetation from dwarf shrub dominance towards the dominance of grasses and sedges with sporadic patches of *E. nigrum* L. ssp. *hermaphroditum* (e.g., Ylänne et al., 2020). The vegetation change is paralleled by a warmer soil microclimate and higher N availability. In 2010–2012, the average soil temperatures at 3 cm depth in June–August were 7.6 ± 0.3 °C and 9.3 ± 0.3 °C under light and heavy grazing intensities, respectively (Stark et al., 2015). The increase in N concentrations in the heavily grazed area is particularly strong during the reindeer migration (Stark and Väisänen 2014).

In 2010, a randomized block design study with eight blocks was established. Within each block, two treatments were assigned: control (C) and warming with open-top chambers (W) and repeated on both sides of the pasture rotation fence receiving either light or heavy grazing. The hexagonal chambers with a height of 0.4 m, basal diameter of 1.04 m, and an area of 0.935 m^2 were built using a 1.5 mm thick polycarbonate, and constructed directly after snowmelt in late spring and removed before reindeer arrival in early fall (Väisänen et al., 2013). On average, In Raisduoddar, the open-top chambers increased surface temperatures by 0.9 °C and 1.8 °C on LG and HG, respectively, with no effect on soil temperature (Väisänen et al., 2014). Soil samples were collected in 2014 in each plot by combining three to four soil cores (diameter 29 mm) from the organic horizon (mean depth for LG: 4.5 cm; mean depth for HG: 4.3 cm). After removing the roots, litter, and mineral soil layers, the cores were homogenized in the field with a 2 mm sieve and pooled together. The roots were washed and dried. The soil was dried (at 60 °C for 70 h) and milled into a fine powder. Vegetation abundances were analyzed with a modified point intercept method as described in Ylänne et al. (2020)). The number of hits was normalized to hits per 100 pins, and species abundances were pooled into growth forms (evergreen shrubs, deciduous shrubs, graminoids, and forbs). The vegetation in the lightly grazed area was dominated by evergreen and deciduous shrubs (57% and 32% of total vascular plants, respectively) (Ylänne et al., 2020). In contrast, the heavily grazed area was mainly dominated by graminoids (61% of total vascular plants) with some evergreen shrubs (20% of total vascular plants) (Ylänne et al., 2020). The average soil pH under LG was 5.1 and under HG 5.3 (analyzed in 3:5 (v/v) soil:water suspensions, Model 220 pH conductivity meter; Denver Instrument, Bohemia, NY, USA).

2.2. Soil stable and labile C and total N

Chemically stable SOC was assessed with acid hydrolysis fractionation (Kallenbach et al., 2016). Briefly, 12 mL of 6 M HCl was added to 250 mg of soil. Samples were vortexed for 30 s and incubated at 105 °C for 18 h. After cooling down, the samples were washed four times with H_2O to remove the acid and dried at 60 °C. Total C contents and total N

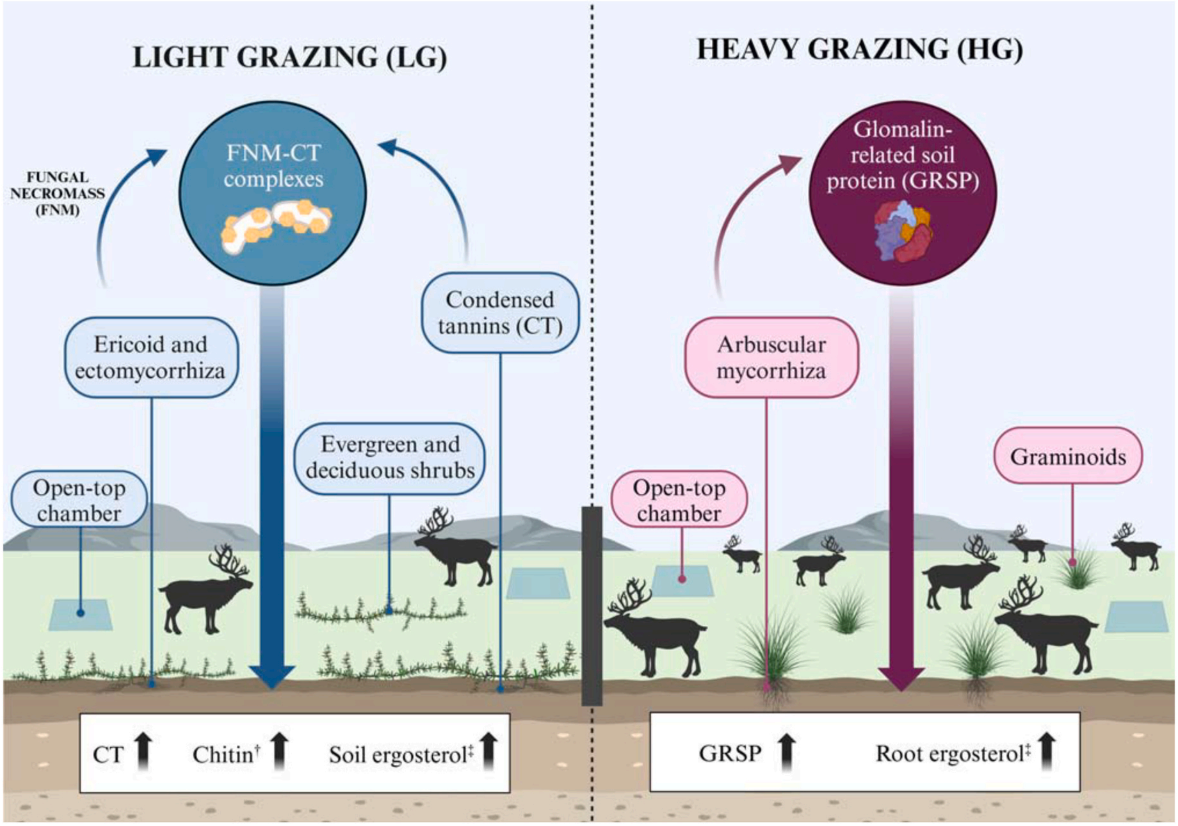

Fig. 1. Schematic presentation of the studied SOC stabilization mechanisms under light (LG) and heavy grazing (HG) pressures and warming. A pasture rotation fence separates the pasture into light and heavy grazing areas. Under LG, the vegetation mostly consists of evergreen and deciduous shrubs, that have ericoid and ectomycorrhizal symbionts and produce secondary metabolites called condensed tannins (CT). The tannins form recalcitrant complexes with fungal necromass (FNM) and contribute to soil persistent C. Under HG, where the vegetation has been transformed into a graminoid-dominated one due to the heavy grazing, arbuscular mycorrhizal fungi participate in the soil C dynamics by producing glomalin-related soil proteins (GRSP). Under both grazing regimes, open-top chambers were built after snow melt in the spring and removed before reindeer arrival in the fall. The quantified soil parameters are presented in the white boxes at the bottom of the image and listed under the grazing intensity where they are expected to be higher. The soil chitin † is indicative of FNM, and soil/root ergosterol ‡ of fungal biomass. Figure created with BioRender.com.

were determined with an elemental CN analyzer (LECO, Michigan, USA). Chemically stable and labile C fractions were then determined based on the differences in C remaining in the non-acid hydrolyzable residues and the initial C content of the sample.

2.3. Condensed tannins (CT)

The concentration of CT was measured with the acid-butanol assay as described by Hagerman (2002). Briefly, 200 mg of organic soil was extracted twice with 4 mL of 7:3 (v:v) acetone:H_2O. The samples were shaken on a planar shaker (200 rpm) for an hour, supernatants from both extractions were pooled together and evaporated to 500 μL under N_2 at 40 °C on a heat block. To 70 μl of the sample, 600 μL of 5:95 HCl: butanol was added, and the samples were incubated at 95 °C for an hour. After cooling down, the absorbance was measured at 555 nm (BMG LABTECH CLARIOstar® microplate reader). Different CT concentrations (0.001–0.1% (w/v) dissolved in H_2O) extracted from fine pine roots were used as standards (Adamczyk et al., 2011).

2.4. Fungal necromass (FNM)

Chitin is the main component of fungal cell walls, and although it is also found in the exoskeleton of micro-arthropods, their contribution to soil chitin content is negligible (Joergensen, 2018) because of their lower chitin content (Finke, 2007) and biomass (Bar-On et al., 2018) compared to fungi. Additionally, because the contribution of living microbial biomass to the total amino sugar (including chitin) content of the soil is inconsequential (Glaser et al., 2004), chitin is a valid marker of FNM. The concentration of chitin was studied as in Adamczyk et al. (2020). Briefly, 250 mg of organic soil was weighed in a glass tube with 10 mL of 0.2 M NaOH. The sample was shaken for a total of 6 h and fresh NaOH interchanged every 2 h. Final incubation with 0.2 M NaOH was done overnight at 105 °C. After cooling down, acid hydrolysis was done with 6 M HCl, resulting in the release of chitin monomers, glucosamine. The supernatant was evaporated, and the sample dissolved in 0.5 mL of H_2O. With 100 μL of the sample, 100 μL of 10 μM homocysteic acid (internal standard), 50 μL of 0.5 M borate buffer (pH 9.3), and 250 μL of 7.5 mM fluorenylmethyloxycarbonyl chloride (FMOC-Cl) was added, mixed, and incubated at RT for 10 min after which 1 mL of n-heptane was added, and the samples were mixed again. After centrifugation, the lower phase was filtered through a 0.2 μm filter (Phenex™ PTFE 4 mm syringe filters) into a high-performance liquid chromatography (HPLC) vial, and the amount of chitin determined with an HPLC with a fluorescence detector (Arc HPLC, Waters) with excitation of 260 nm and emission of 330 nm at a flow rate of 0.7 mL min^{-1} using an ODS Hypersil column (Hewlett Packard, 5 μm, 250 × 4 mm). Different concentrations (12.5–200 μM) of glucosamine (D-(+)-glucosamine hydrochloride, 99% pure, Sigma), a monomer of chitin, were used as standards.

2.5. Fungal biomass

The concentration of ergosterol, a marker of fungal biomass, was determined as described before by Frostegård and Bååth (1996) from soil and root samples. Briefly, 250 mg of the sample was weighed in a glass tube with 0.5 mL of cyclohexane and 2 mL of 10% (w/v) KOH in methanol. The samples were vortexed and sonicated for 15 min, after which they were incubated at 70 °C for an hour. After cooling down, 0.5 mL of H_2O and 1 mL of cyclohexane was added and the samples vortexed and centrifuged at 2500 g for 5 min. The upper cyclohexane phase was transferred into a new glass tube and another 1 mL of cyclohexane added to the first tube. The sample was then vortexed, centrifuged and the upper cyclohexane phase combined with the previous one. The cyclohexane was evaporated under N_2 at 40 °C, and the ergosterol residue dissolved in 250 μL of methanol. The solute was filtered through a 0.2 μm filter (Phenex™ PTFE 4 mm syringe filters) into an HPLC vial. For HPLC-UV (Arc HPLC, Waters), the conditions were: flow rate 1 mL min^{-1}, 10 μL sample injection, isocratic elution with 100% methanol, and UV detection at 282 nm. We used an HPLC reversed-phase column Innoval C18 (Agela Technologies, 5 μm, 150 × 4.6 mm). Different ergosterol concentrations (0.05–0.5 μg mL^{-1}, ergosterol dissolved in methanol) were used as standards.

2.6. Glomalin-related soil protein (GRSP)

The soil GRSP fraction was extracted and quantified as described by Cissé et al. (2023). Briefly, 250 mg of soil was autoclaved in 2 mL of 20 mM citrate solution (pH 7) for 30 min at 121 °C. After cooling, the supernatant was separated by centrifuging (first 10 min at 3500 g, then 5 min at 15,000 g for an aliquot of the supernatant). Bradford assay was used to determine the protein content of the extract: 250 μL of Bradford reagent (ITW Reagents) was added to 20 μL of the sample, and the mixture homogenized. Absorbances were measured at 595 nm with a microplate reader (BMG LABTECH CLARIOstar®) and different bovine serum albumin concentrations (0.05–1.0 mg^{-1} mL) dissolved in 20 mM sodium citrate buffer) were used as standard.

2.7. SOC chemical quality

To assess the overall chemical quality of the organic soil, we used Fourier transform infrared spectroscopy with attenuated total reflectance (FTIR-ATR; Shimadzu IRPrestige-21 FTIR spectrophotometer, Kioto, Japan; Specac Quest diamond ATR accessory, Orpington, UK). Spectra were acquired by averaging 20 scans per sample at a resolution of 4 cm^{-1} over the range of 4000–400 cm^{-1} with atmospheric corrections (CO_2, H_2O, and smoothing at level 7) as in Adamczyk et al. (2016). We focused on the absorbance values 1265 cm^{-1} indicative of lignin backbone, 1653 and 1550 cm^{-1} both indicative of lignin-like compounds, 1450 and 1371 cm^{-1} both indicative of phenolic compounds, and 1080–1030 cm^{-1} indicative of polysaccharides.

2.8. Statistical analyses

All statistical analyses were done using RStudio statistical software (v. 4.2.1; R Core Team 2023). To meet the assumptions of a linear mixed model, the data was tested for outliers, homoscedasticity, and normality of the residuals. Where the assumptions of homoscedasticity or normality were not met, we used square-root transformation. First, we tested the single and interactive effects of warming and grazing on total, stable and labile C, total N, C:N, CT, chitin, soil and root ergosterol, and GRSP concentrations using a linear mixed model with grazing and warming as fixed factors and block nested to treatment as a random factor with nlme (Pinheiro and Bates 2000; Pinheiro et al., 2023). Second, we explored the relationship between the variables mentioned above and the relative abundance of shrubs (i.e., deciduous, and evergreen shrubs) and non-shrubs (i.e., forbs and graminoids), using a combination of linear correlation analysis (Pearson's correlation coefficients) and principal component analysis (PCA). For these, we used the packages psych (Revelle 2023) and corrplot (Wei and Simko 2021) with unstandardized variables (stable and labile C, total N, C:N, CT, chitin, soil and root ergosterol and GRSP concentrations, pH, shrubs (evergreen and deciduous shrubs, hits 100 $pins^{-1}$), and non-shrubs (forbs and graminoids, hits 100 $pins^{-1}$)) and the packages missMDA (Josse and Husson, 2016), FactoMineR (Lê et al., 2008) and ggbiplot (Vu 2011) with standardized variables (stable and labile C, total N, C:N, CT, chitin, soil and root ergosterol, and GRSP concentrations, and pH).

3. Results

3.1. Soil stable and labile C, total N, and C:N

We found more labile C ($p < 0.05$) and a higher C:N ($p < 0.01$) under LG compared to the HG treatments (Fig. 2a–c; Table 1). LG tended to have a higher concentration of total C ($p < 0.1$) compared to the HG treatments (Fig. 2a; Table 1). Warming and the interaction of warming and grazing had no significant effects on the C fractions, total N, or C:N (Fig. 2a–c; Table 1).

3.2. CT, chitin, ergosterol, and GRSP

We found more CT ($p < 0.05$) and chitin ($p < 0.01$) under LG soil compared to the HG treatments (Fig. 3a and b; Table 1). In addition, we found more root ergosterol ($p < 0.01$) and a tendency of more GRSP under HG ($p < 0.19$) compared to LG treatments (Fig. 3d and e; Table 1) but found no difference in soil ergosterol concentration (Fig. 3c–Table 1). Warming had no significant effect on CT, the fungal markers chitin and ergosterol in soil and roots, or GRSP (Fig. 3a–e; Table 1).

3.3. The relationships among soil variables

Across all sites and treatments, we found strong positive correlations between the soil C fractions and CT, chitin, and soil ergosterol concentrations (Fig. 4; Table S1), whereas the GRSP concentration was negatively correlated with both soil ergosterol and pH (Fig. 4; Table S1). We also found that the abundance of shrubs (deciduous and evergreen shrubs) had a strong positive correlation with soil C:N and CT, whereas the abundance of non-shrubs (forbs and graminoids) had a strong negative correlation with the previously mentioned (Fig. 4; Table S1). In addition, PCA1 and PCA2 explained 63.3% of the total variance, and most samples were separated according to the grazing intensity (Fig. S1). Labile C, chitin, CT, and soil ergosterol concentrations were aligned with LG samples and were positively correlated with PCA1, whereas root ergosterol and GRSP were aligned with HG samples (Fig. S1).

3.4. SOC chemical quality

FTIR analysis of the soil samples showed that warming tended to decrease the amount of polypeptides (absorption bands at 1653 and 1550 cm^{-1}), lignin-like compounds (absorption bands at 1650–1600 cm^{-1}), phenolic compounds (absorption bands at 1450 and 1371 cm^{-1}), as well as compounds associated with the lignin backbone (absorption band at 1265 cm^{-1}) (Fig. 5; Table S2). Also, polysaccharides (absorption bands at 1080–1030 cm^{-1}) tended to decrease with warming and were generally more abundant under heavy than light grazing (Fig. 5, Table S2). Overall, the effect of the warming treatment on the SOC chemical quality was more pronounced under HG than under LG (Fig. 5).

4. Discussion

4.1. Soil C stabilization in the lightly grazed tundra

Earlier studies from the same experiment showed no difference in C stocks between LG and HG, although plant community structure has changed significantly (Ylänne et al., 2018). Here, we searched for a

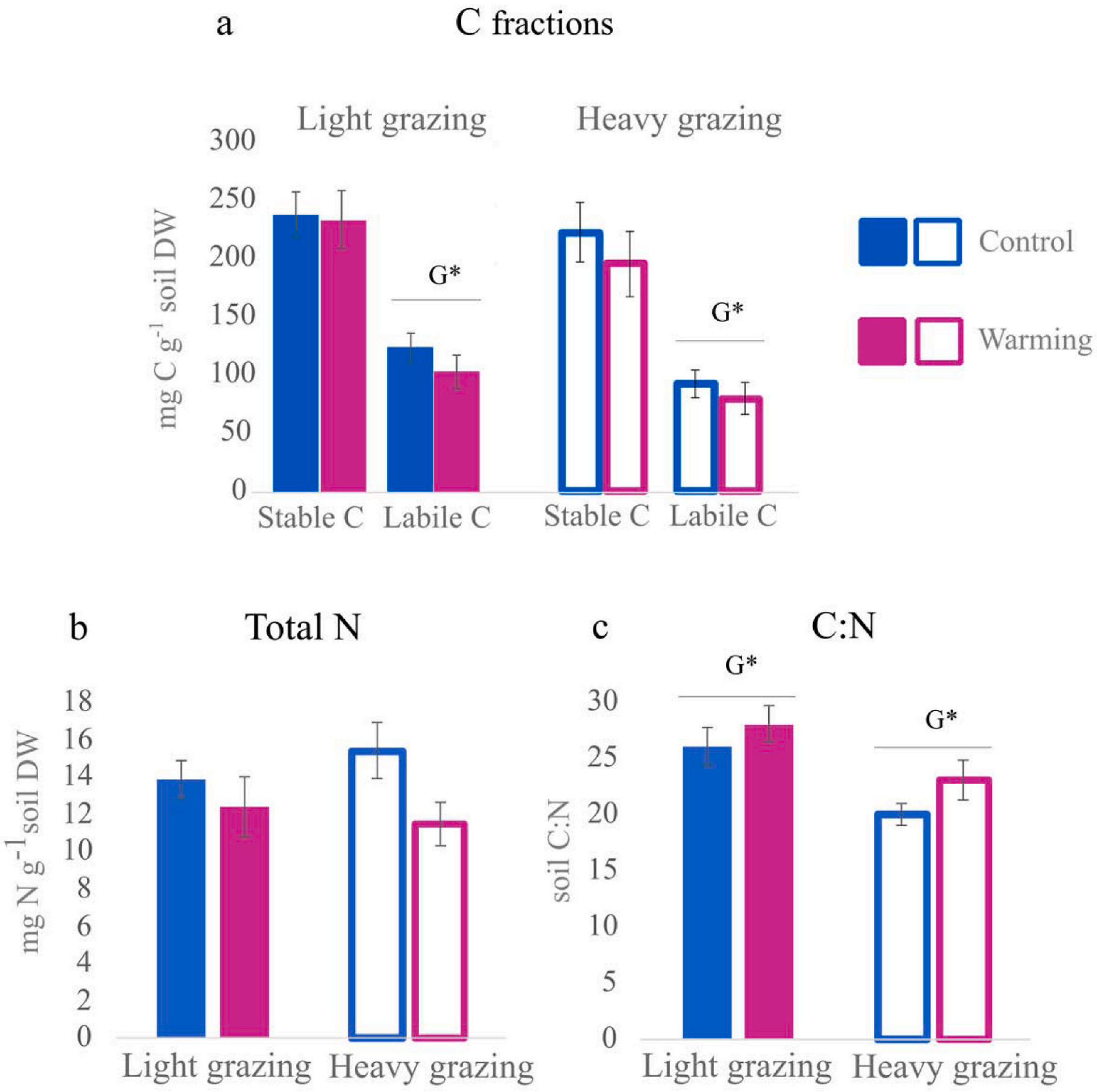

Fig. 2. Soil C fractions, total N (mg g^{-1} soil DW)**, and C:N under light and heavy grazing pressures and warming.** Filled and open bars represent samples collected from blocks under light and heavy grazing intensities, respectively. Blue and pink colors represent samples collected from blocks without warming (control) and warming, respectively. DW = dry weight. Statistically significant ($p < 0.05$) grazing effects are marked with G*. Error bars represent the standard error of the mean (SEM).

Table 1

Treatment effects (*F*-values with significance levels) on the soil total, stable and labile C, total N (mg g^{-1} soil DW), C:N, CT, chitin, soil and root ergosterol, and GRSP concentrations (mg g^{-1} soil DW). DW = dry weight, GRSP = glomalin-related soil protein, $^{‡}p < 0.1$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

	Warming	Grazing	Warming × Grazing
	F	*F*	*F*
Total C	0.97	**3.03**‡	0.05
Stable C	0.53	1.73	0.27
Labile C	1.90	**5.65***	0.10
Total N	1.25	0.04	1.07
C:N	2.59	**12.77****	0.22
CT	0.05	**6.02***	0.27
Chitin	0.72	**9.31****	0.09
Soil ergosterol	2.30	2.72	0.55
Root ergosterol	0.09	**12.97****	1.44
GRSP	0.27	1.77	0.85

mechanistic explanation for this phenomenon and aimed to elucidate the drivers of soil C stabilization under the two different grazing intensities and warming. In line with our first hypothesis, we found higher concentrations of FNM (chitin) and CT under the dwarf shrub-rich, lightly grazed tundra. The higher CT concentration under LG than HG reflects the vegetation difference, as graminoid plant species, dominant under HG, do not produce CT (Hättenschwiler and Vitousek, 2000). Here, we found that the proportion of soil ergosterol to chitin was relatively low (on average, the amount of soil ergosterol was 4.6 ± 0.3% of the amount of chitin), indicating that the majority of fungal mass in the soil is FNM (Ekblad et al., 1998). In combination, the strong correlation, and the high values of FNM and CT in the LG tundra are indicative of a soil C stabilization mechanism involving FNM-CT complexes (Adamczyk et al., 2019). Ahonen et al. (2021) found that ericoid mycorrhizal fungi, living in symbiosis with shrubs, were more abundant under light grazing (LG) at the same study site, which increases the potential for the formation of FNM-CT complexes. The dominant fungal orders under LG in Raisduoddar were Helotiales and Chaetothyriales

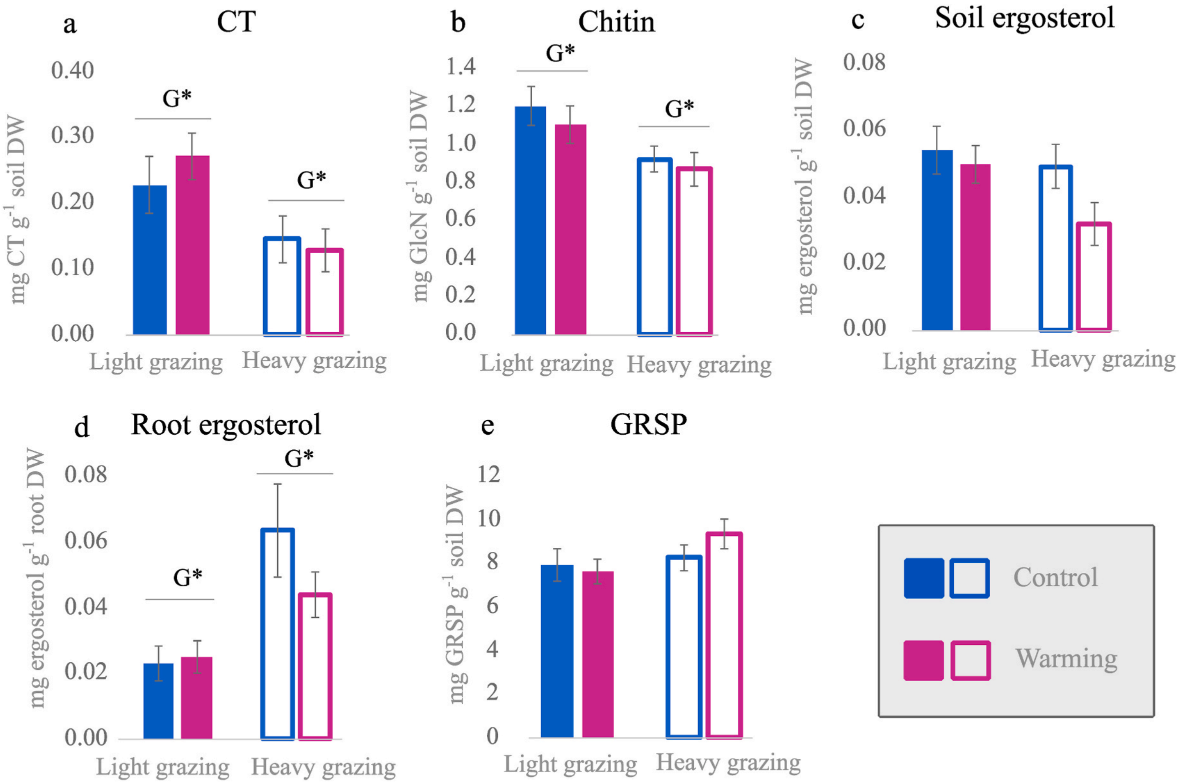

Fig. 3. CT, chitin, soil and root ergosterol, and GRSP concentrations (mg g^{-1} soil/root DW) **under light and heavy grazing pressures and warming.** Filled and open bars represent samples collected from blocks under light and heavy grazing, respectively. Blue and pink colors represent samples collected from blocks without warming (control) and warming, respectively. DW = dry weight. Statistically significant ($p < 0.05$) grazing effects are marked with G*. Error bars represent the standard error of the mean (SEM).

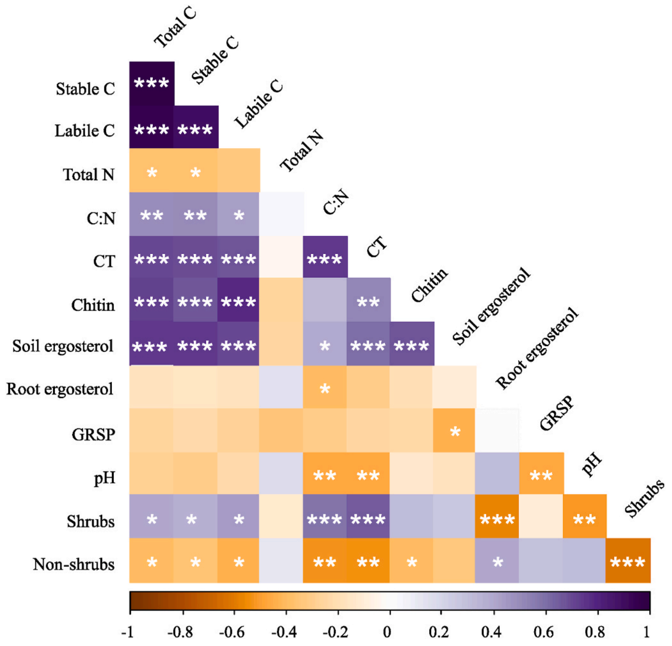

Fig. 4. Pearson's correlation coefficients and significance levels. Data are presented across all sites and treatments for C concentrations and total N (mg g^{-1} soil DW), C:N, CT, chitin, soil and root ergosterol, GRSP concentrations (mg g^{-1} soil DW), pH, shrubs (deciduous and evergreen shrubs, hits 100 $pins^{-1}$) and non-shrubs (forbs and graminoids, hits 100 $pins^{-1}$). DW = dry weight, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

(Ahonen et al., 2021). The order Helotiales includes many well-known ericoid mycorrhizal fungi (Fehrer et al., 2019), and dominance by ericoid mycorrhizal fungi has been shown to result in an increasing accumulation of FNM in a heath-dominated tundra (Clemmensen et al., 2013). The ecology of Chaetothyriales varies, but a common denominator across the order is that their mycelia are melanized (Quan et al., 2020), which might also contribute to soil persistent C (Fernandez and Koide, 2014).

4.2. *Soil C stabilization in the heavily grazed tundra*

In line with our second hypothesis, we found a trend of increased concentration of GRSP under HG, although this was not significant. Whereas previous studies have emphasized the role of arbuscular mycorrhizal fungi-derived GRSP in soil C accumulation, Wu et al. (2024) have proposed a broader conceptual framework to explain the role of arbuscular mycorrhizal fungi in soil C dynamics. This framework highlights the complex role of arbuscular mycorrhizal fungi in soil organic matter generation, reprocessing, reorganization, and stabilization. With relation to our study, the framework by Wu et al. (2023) suggests that arbuscular mycorrhizal fungi contribute to persistent soil C through not only GRSP but rather by producing a plethora of organic compounds (fungal exudates and/or fungal biomass and necromass) with varying degrees of decomposability. Part of the necromass is processed by soil microorganisms, and the high incidence of saprotrophic fungi found under HG in a previous study from the same site (Ahonen et al., 2021) could explain why we found less FNM (chitin) in the HG soil compared to the LG soil (Ahonen et al., 2021; Steinberg and Rillig, 2003). Moreover, we found more root ergosterol under HG, potentially indicative of frequent colonization of plant roots by dark septate endophytes (Newsham, 2011), since graminoids are more often colonized by DSE than shrubs (Weishampel and Bedford, 2006). Dark septate endophytes

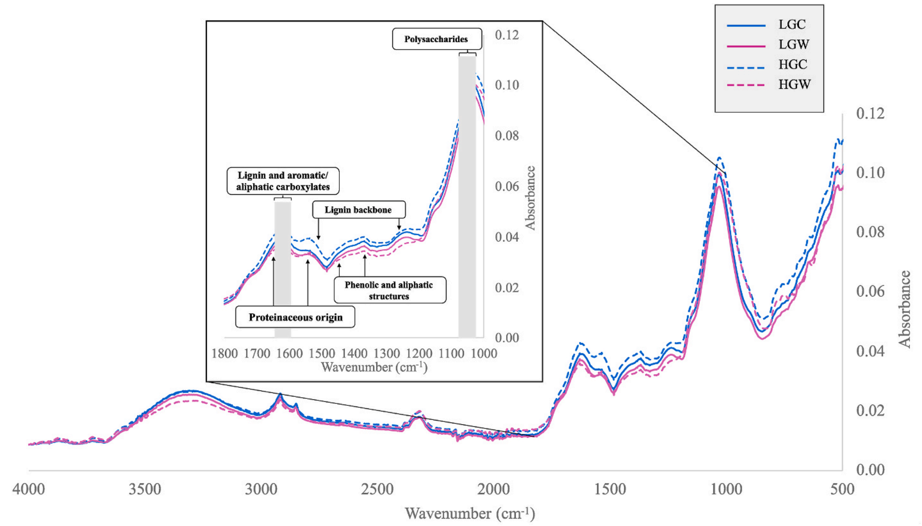

Fig. 5. FTIR spectra of organic soil samples under light and heavy grazing pressures and warming. Solid and dashed lines represent light and heavy grazing intensities, respectively. Blue and pink colors represent no warming (control) and warming, respectively. The whole spectra acquired from the range 4000–400 cm^{-1} are depicted at the bottom; on top are the spectra from the range 1800–1000 cm^{-1}. LG = light grazing, HG = heavy grazing; C = no warming, W = warming.

are a heterogenous group of fungi that are characterized by "dark" i.e., melanized mycelia (Jumpponen and Trappe, 1998). Melanin consists of phenolic or indolic monomers that make the melanin structurally resistant to decomposition (Fernandez and Kennedy, 2018), and high initial melanin concentration of fungal mycelium is negatively correlated with the decomposition rate (Fernandez and Koide, 2014). Therefore, the ubiquity of melanized fungi under HG could likely result in an increased potential for soil C stabilization.

A shift in the mechanism of C stabilization could at least partially explain why studies have not found differences in C stock in response to reindeer grazing either in our study area, Raisduoddar (Ylänne et al., 2018, 2020) or other sites (Köster et al., 2013, 2015; Stark et al., 2019; Windirsch et al., 2023) despite drastic differences in the aboveground vegetation. We found no evidence of heavy grazing (HG) affecting soil stable C, but there was a trend of reduced total C under HG. The lower C concentration or organic matter content under HG than in LG areas may reflect the trampling impact that mixes organic soil with mineral soil particles (Tuomi et al., 2021). At the same time, an increased amount of minerals in the organic layer under HG may increase soil stabilization via the interaction of organic C with minerals (Xiao et al., 2023). Further studies of the consequences of plant community changes into graminoid-dominated environments due to HG should also consider the effect on the C storage in deeper soil layers. Studies in the Arctic tundra suggest that graminoids have more roots deeper in the soil profile compared to shrubs (Blume-Werry et al., 2019; Hewitt et al., 2019; Wang et al., 2016), although meta-analysis did not prove it at biome scale (Blume-Werry et al., 2023).

4.3. *The possible effect of warming on soil C stabilization*

In general, long-term warming (over 10 years and warming larger than 2 °C) changes the fungal community composition in the soil (Baldrian et al., 2022). Fungal biomass, on the other hand, is usually decreased after 3–5 years of warming, but after that, the effect becomes less prominent (Baldrian et al., 2022). We did not see significant changes in the concentrations of soil ergosterol or chitin under warming. Long-term warming has been shown to accelerate the turnover of labile C (Stuble et al., 2019) and increase the rate of soil respiration and litter decomposition (Hobbie, 1996). In our study, the open-top chambers were in place for five years, but only approximately from the beginning of June to the beginning of August each year, which might not have been enough to induce significant changes in the soil chemistry or ergosterol and chitin concentrations. However, our analysis of the SOC chemical quality studied with FTIR showed that polymeric compounds (lignin-like, polypeptides, and polysaccharides) were the highest under HGC but the lowest under HGW and similarly, within the LG treatments, these compounds were more abundant under LGC compared to LGW. This would suggest that changes in soil chemical quality were associated with additional warming and not grazing intensity alone but contrary to our third hypothesis, with no significant changes in the stable C concentration.

Although we did not find significant grazing-dependent responses to warming, our results indicate potential differences in the resilience of the two grazing regimes. We found a higher labile C concentration under LG, which - in the long-term - might render LG soils more vulnerable to soil C loss under the changing climate. However, as labile C is also a prerequisite for persistent C (e.g., Cotrufo et al., 2013; Gunina et al., 2014; Knicker, 2011), there might be a higher C stabilization potential associated with LG. Moreover, the pronounced warming effect we found under HG may suggest that high grazing intensity combined with warming might make soil chemistry more vulnerable in the long term. As adding a second stressor may cause a combined effect that is not equal to the sum of the effects of the stressors (Pirotta et al., 2022), the interrelation of warming and grazing deserves more studies.

5. Conclusions

Grazing intensity has led to significant changes in plant communities and associated fungi, with graminoids dominating under HG and shrubs under LG. We showed that although the soil stable C concentrations were not significantly affected by grazing intensity or warming, there was a significant difference in the chitin, CT, and root ergosterol concentrations between the two grazing regimes. Thus, we conclude that soil C stabilization is driven by different mechanisms under light and heavy grazing pressures: under LG, the soil C stabilization potential is linked to increased FNM-CT complexing, whereas under HG the potential is linked to arbuscular mycorrhizal fungi and their multiple functions in soil C dynamics and potentially more melanized endophytes in roots of graminoids. While previous studies have also reported no grazing effect on the soil C stocks, our study further provides a mechanistic understanding of the soil C stabilization potential in the tundra. Although FNM, CT, and stable C were not directly affected by warming, it caused a change in the SOC chemical quality. This suggests that not only grazing patterns, but also warmer temperatures may alter soil C dynamics with potentially far-reaching consequences. Our findings add to the existing knowledge of soil persistent C and further highlight the importance of a holistic understanding of Arctic tundra soil ecosystems.

CRediT authorship contribution statement

Anne Tyvijärvi: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Sari Stark:** Writing – review & editing. **Henni Ylänne:** Writing – review & editing. **Carles Castaño:** Writing – review & editing. **Bartosz Adamczyk:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, 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

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2024.109441.

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Further reading

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