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Volatile Organic Compound Release During Litter Decomposition in the Arctic

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ABSTRACT

Litter decomposition is a source of gaseous products, including volatile organic compounds (VOCs) to the atmosphere. The quantity and the chemical composition of the VOC blends released from litter vary between plant species and depend on environmental factors and litter microbial communities. Here, we assessed VOC release from decomposing litter in a 3-year incubation conducted in a climate manipulation experiment close to the Zackenberg Research Station in the High Arctic Greenland. Litter from two circumpolar species, the evergreen shrub, *Cassiope tetragona*, and the deciduous shrub, *Salix arctica*, were incubated for 11, 22 and 35 months in litterbags in tundra heath ecosystems dominated by the two species. The litterbags were subjected to climate change treatments that applied warming, shading, or manipulation of the growing season length (i.e., prolonging or shortening the growing season by moving snow). The decomposing litter of *S. arctica* and *C. tetragona* emitted common major VOC constituents, acetic acid, methanol, acetaldehyde, acetone, and ethanol, but the species differed in terms of litter chemical composition, VOC emission rates and blend compositions, and microbial DNA numbers. In the course of litter decomposition, VOC emission rates overall decreased over time as the chemical composition of the litter material and its prokaryotic and fungal numbers also changed. The effects of the climate change treatments were minor and complex, compared to the large between-species and temporal differences. The local environment, that is, the variation between microsites, also had a larger effect than the treatments. Overall, VOC emissions from litter decomposition in Arctic ecosystems are controlled by vegetation changes determining the amount and chemical composition of the litter material as well as the local microenvironment.

1 | Introduction

Litter decomposition plays a vital role in the element cycles of Arctic tundra ecosystems. During the decomposition of leaf litter, leaf tissue is gradually broken down, organic molecules and nutrients are released to the soil, and transformed into new compounds (Prescott and Vesterdal 2021). Gaseous products, including CO_2 and volatile organic compounds (VOCs), are emitted to the atmosphere from decomposing litter both biotically and abiotically (Gray et al. 2010). Despite its importance, our understanding of the chemical composition and emission rates of VOCs during litter decomposition remains limited (Isidorov and Zaitsev 2022), which constrains our ability to assess their contribution to ecosystem VOC fluxes. Given the rapid warming of the Arctic, which may influence both decomposition rates and litter inputs due to advancing shrubification (Mekonnen

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et al. 2021), quantification of litter VOCs is becoming increasingly important.

Plants are the main sources of biogenic VOCs (Laothawornkitkul et al. 2009), while soils have been shown to both release and take up VOCs (Gray et al. 2014; Jiao et al. 2023; Trowbridge et al. 2020). Leaf litter also releases VOCs in a plant species-specific manner (Gray et al. 2010; Isidorov and Jdanova 2002; Leff and Fierer 2008; Svendsen et al. 2018; Viros et al. 2020). However, most studies on litter VOCs have characterized litter-emitted VOC blends only at a single time point. Our understanding of how VOC emissions evolve in the course of decomposition as well as how they are affected by climatic factors is limited.

The quantity and blend of VOCs emitted from decomposing litter are determined by a complex interplay of litter chemical properties and microbial activity (Gray et al. 2010). There are two primary VOC sources in litter: (1) compounds synthesized by the plant, released from decaying storage compartments or leaf tissues, and (2) compounds produced by microbial communities as part of their metabolic processes, such as aerobic heterotrophic carbon metabolism, fermentation, amino acid degradation, terpenoid biosynthesis, or sulphur reduction (Insam and Seewald 2010; Peñuelas et al. 2014). These processes produce compounds like pyruvate, glyceraldehyde-3-phosphate, lactate, and acetate, which can then be further converted to volatile forms (Peñuelas et al. 2014). Methanol is both a typical microbial VOC and a compound released from the pectin and/or lignin in plant cell walls (Fall and Benson 1996), making it a universal VOC released from leaf litter (Gray et al. 2010; Viros et al. 2021). Other primarily plant-derived litter VOCs include different terpenoids, emitted from litter of plant species that store these compounds, such as evergreen trees or shrubs (Leff and Fierer 2008; Svendsen et al. 2018; Viros et al. 2020). Arctic plant litter also exhibits distinct VOC blends, with litter of the evergreen *Cassiope tetragona* emitting stored terpenoids and litter of the deciduous *Salix* spp. emitting non-terpenoid VOCs (Svendsen et al. 2018).

Decomposition rates in these high latitude ecosystems are particularly slow due to low temperatures and moisture-limitation, yet they vary significantly between different plant growth forms, with herbaceous and deciduous species generally decomposing faster than evergreen shrubs and mosses (Cornelissen et al. 2007; Hobbie et al. 2000). Hence, changes in vegetation composition, such as the increasing dominance of deciduous or evergreen shrubs, affect both the quantity and the quality of litter inputs, thereby influencing overall decomposition processes and associated VOC emissions (Elmendorf et al. 2012; Myers-Smith et al. 2011; Vowles and Björk 2019).

The litter VOC emission rates and blends are likely highly responsive to the ongoing environmental changes, which are taking place in the Arctic. Synthesis articles on litter decomposition in high latitude soils have identified climate, especially temperature, as the most important factor controlling decomposition rates (Cornelissen et al. 2007; Hobbie et al. 2000). The Arctic temperature is rising more rapidly than elsewhere on the planet due to Arctic amplification. During the recent decades, the annual mean air temperature increase has been almost four times faster than that for the global average (Rantanen et al. 2022).

Along with temperature, changes in cloud cover and precipitation also affect high latitude ecosystems and their biogeochemical cycling (ACIA 2005; Bintanja and Selten 2014; McCrystall et al. 2021). Soil moisture is a critical factor mediating effects of temperature on decomposition and soil respiration (Carey et al. 2016). Reduced soil moisture due to lower precipitation or less melt water from glacial and springtime snow melt sources can restrict microbial activity and decomposition rates. Furthermore, increasing temperature leads to enhanced evapotranspiration, causing drying of litter, which may reduce litter decomposition rates in moisture-limited Arctic environments (Christiansen et al. 2017). Changes in cloudiness would also affect the received solar radiation, including ultraviolet radiation, which can be important factors contributing to photodegradation of litter in arid, open canopy ecosystems, like grasslands and tundra (Austin and Vivanco 2006). An earlier snowmelt or later snowfall could thus lead to a longer period of photodegradation, given that the radiation levels are high enough to cause changes in the shoulder seasons.

Here, our aim was to characterize and quantify VOC emission rates in the course of decomposition of litter from two dominant tundra shrub species. The species were the deciduous willow, *Salix arctica*, and the evergreen Arctic bell heather, *C. tetragona*. Litter VOC emissions were measured during a 3-year-long decomposition period in a field experiment with climate change treatments mimicking changes in temperature (warming treatment), cloud cover (shading treatment) and length of the snow-free growing season (snow addition treatment, i.e., short growing season and snow removal treatment, i.e., long growing season). We expected that VOC emission rates would decrease over time as VOC release from storage reserves and labile substrates available for decomposition would be depleted. We also expected this decrease to be faster for *S. arctica*, which doesn't have dedicated terpene storage compartments, as compared to terpene-storing *C. tetragona*. We hypothesized that warming treatment would accelerate litter decomposition, thus altering correspondingly the VOC emissions, unless warming significantly reduced litter moisture in this treatment. We expected the shading treatment mimicking increased cloud cover to reduce litter decay. This could lead to higher VOC emissions from the larger remaining stored VOC reserves and lower emissions of VOCs from the microbial communities developing in the decomposing litter. Snow addition in the shortened growing season treatment was expected to add additional moisture to the litter layer, besides reducing the length of the most active decomposition period, whilst the snow removal treatment was expected to change litter conditions in an opposite way. In addition to VOC measurements, we also analyzed changes in the chemical composition of the leaf material as well as prokaryotic and fungal counts to assess how their changes link to the VOC emissions at different time points during decomposition.

2 | Materials and Methods

2.1 | Field Site

Field incubation of litter was carried out near the Zackenberg Research Station in Northeast Greenland (74°30′ N, 20°30′ W) from 2012 to 2015. Litter decomposition was assessed in 1 m^2

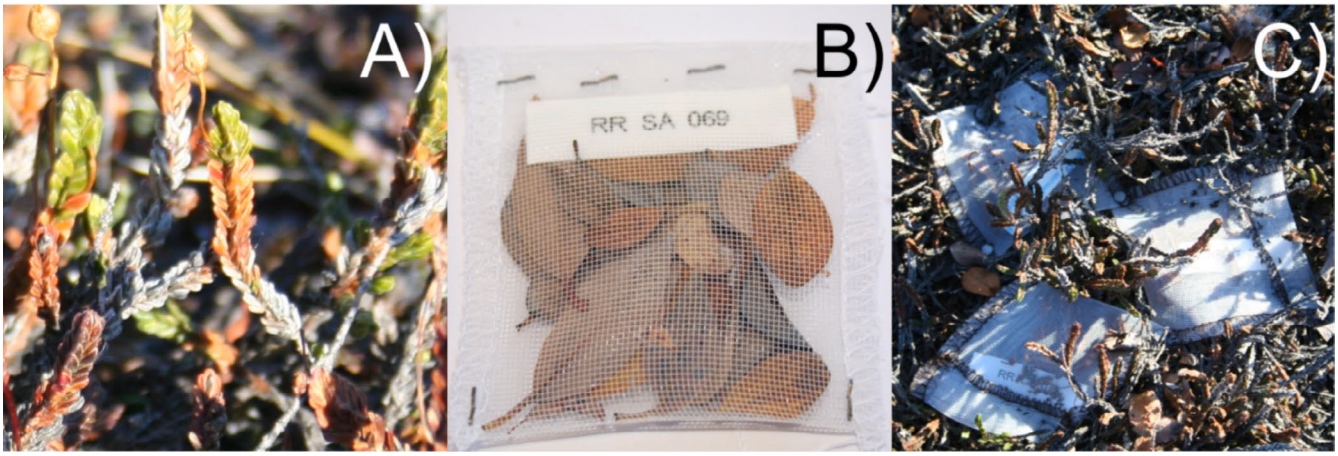


FIGURE 1 | (A) *Cassiope tetragona* shoots showing the green photosynthetic top, the brown senescing part used in this study, and the lowest grey part. (B) A litter bag with *Salix arctica* litter. (C) Three *C. tetragona* litter bags anchored in the litter layer of the *Cassiope* heath.

experimental plots subjected to climate change treatments. The treatments included warming (W), shading (S), long growing season (LG), and short growing season (SG), in addition to unmanipulated control plots (C). These treatments were distributed in five blocks in two ecosystem types, *Salix* heath and *Cassiope* heath, yielding a total of 50 plots.

The climate change treatments had been initiated in 2004 and applied since then. The experiment has been described earlier by Ellebjerg et al. (2008) and Rousk et al. (2018). Briefly, open-top plastic tents were used to increase the air temperature by approx. 1°C in the warming treatment. Shading was applied using sackcloth tents to mimick an increased cloud cover and increased growth of taller shrubs with larger canopies shading the ground. The sackcloth tents decreased the incoming photosynthetically active radiation (PAR) by 50%–60% and reduced temperature by 1.5°C–2.0°C in air and at 2–5 cm depth in soil. The growing season length was altered in the spring either by adding snow to delay the start of the growing season in the SG treatment or by removing snow to advance the start of the growing season in the LG treatment. In practice, the snow manipulation was performed by shoveling snow from LG plots to SG plots while avoiding any disturbance to the vegetation below the snowpack.

2.2 | Incubation of Litterbags

We assessed decomposition of plant material with the litterbag approach, using fresh litter collected outside the experimental plots in the Zackenberg Valley in September 2012. Leaf litter from the deciduous *Salix arctica* Pall. was incubated in the *Salix* heath, and the litter of the evergreen *Cassiope tetragona* (L.) D. Don was incubated in the *Cassiope* heath. For *C. tetragona*, litter was composed of the brown parts of the living branches taken from between the photosynthetic green parts and the grey parts of branches. These brown parts were cut into 1 cm-long pieces (Figure 1A). *S. arctica* litter was whole, senescent, leaves that detached from the stems with a light touch (Figure 1B).

Litterbags (6 × 6 cm) were sewn using white 0.68 mm mesh polyester, which gave a 67% open surface area allowing the litter material to be in contact with water and micro-arthropods (Blok et al. 2016). We filled the litterbags with fresh litter corresponding to 0.7 g d.w. for *C. tetragona* litter and 1.1 g d.w. for *S. arctica* leaf litter, sealed the bags with non-corroding staples, and pinned them to the soil surface in the litter layer with non-corroding steel nails (Figure 1C).

The incubation of litterbags started on September 3, 2012 and two bags were harvested from each plot on August 16–20, 2013, July 12, 2014 and August 20, 2015, yielding 11, 22 and 35 months of incubation time, respectively. Ten litterbags for each species were not incubated, but kept for reference of the initial litter. A total of 320 litterbags were handled (2 sites × 5 blocks × treatments × 2 replicate litterbags × 3 harvests + the initial bags for each species). After harvesting, the litterbags were air-dried before transport to Copenhagen, where they were stored individually in zip lock bags at −20°C until analyses.

During the incubation period, temperature in the litter layer was monitored using Ibuttons (Maxim Integrated, San Jose, USA) placed in litterbags. One single Ibutton was placed in one plot of each treatment in the *Cassiope* heath.

2.3 | Measurement of Litter VOC Emissions

In 2016, VOC emissions from the litter were measured under controlled conditions. The litterbags were taken from the freezer, placed in desiccators with the bottom filled with wet tissue paper to maintain high relative humidity, and the zip lock bags were opened to allow the litter to remoisten at 4°C for 7 days.

VOC emission rates were determined at 22°C in 200 mL glass jars. The two litterbag replicates harvested from the same plot on the same date were pooled and measured together in a single glass jar.

Six glass jars were connected to the Proton Transfer Reaction Time-of-Flight Mass Spectrometer (PTR-TOF-MS) setup at a time, allowing sequential measurement of five litterbag jars and a blank jar, which consisted of two empty litterbags without litter. The sampling system was controlled using

Teflon solenoid valves (Parker Hannifin, Cleveland, USA) connected to a datalogger (Campbell Sci, Logan, USA). During the 10-min-long measurements, the inflow rate of zero air to the jars was 300 mL min^{-1} and the PTR-TOF-MS instrument (PTR-TOF 8000, Ionicon Analytik, Innsbruck, Austria) drew 150 mL min^{-1} for VOC analysis, and the remaining 150 mL min^{-1} was let out as excess air. All tubing was PFA (Swagelok, Solon, USA). The airflows were monitored with flow meters (Alicat Scientific, Tucson, USA and Key Instruments, Trevose, USA). The PTR-TOF-MS was calibrated against a gas standard mixture (ca. 1 ppmV, Table S1) purchased from Ionicon Analytik (Innsbruck, Austria) and diluted to different concentrations using a Gas Calibration Unit (GCU-b, Ionicon Analytik, Innsbruck, Austria). For details in the PTR-TOF-MS operation, see Kramshøj et al. (2018).

After the VOC measurements, the litter was subsequently freeze-dried, weighed, and ground to powder for further analyses.

2.4 | PTR-TOF-MS Data Processing

The PTR-TOF-MS spectra were processed with the software PTRwid. The PTRwid first identifies mass peaks by comparing all detected mass peaks to reveal the true peak shape, and next evaluates the mass peaks with several existing peak lists. Secondly, it automatically employs mass scale calibration, using an ion mass library, and finally converts count rates to mixing ratios (Holzinger 2015). These tentative mixing ratios were used for all other masses, while compounds in the calibration gas were quantified as in Kramshøj et al. (2018). Acetic acid was considered as the sum of m/z 43.018 and 61.028, methanol as the sum of m/z 33.034 and 51.043, acetaldehyde as the sum of m/z 45.033 and 63.042, total monoterpenes as the sum of m/z 81.070 and 137.134, and the total sesquiterpenes as the sum of m/z 149.133 and 205.196 (Kim et al. 2009; Yáñez-Serrano et al. 2021). For these product ions, Pearson's correlation coefficients, $r > 0.9$.

As the steady state concentration was reached during the last couple of minutes of the measurement period, the period between 8 and 9 min was averaged for calculation of the emission rate per hour. The concentrations in the blank jars were subtracted from the corresponding sample concentrations.

2.5 | Analyses of Litter Chemical Composition

Total carbon and nitrogen contents were analyzed in powdered litter with a Euro EA elemental analyzer (EuroVector, Pavia, Italy).

Untargeted analysis of the litter chemical composition was done using a near-infrared reflectance (NIR) spectrometer (Antaris II FT-NIR Analyzer, Thermo Scientific, Waltham, MA, USA). We recorded the reflectance spectra for a spectral range of 800–2500 nm at 2 nm intervals in three replicate measurements per sample. Each spectrum was an average of 32 scans.

2.6 | DNA Extraction and Microbial Quantification

DNA was extracted from 20 mg dry ground plant litter samples using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). DNA extracts were stored at −20°C prior to qPCR analyses.

Prokaryotic 16S rRNA and fungal ITS2 gene copy numbers were quantified using qPCR (CFX Connect, Bio-Rad, Richmond, VA, USA). qPCR analysis was conducted as described in Bang-Andreasen et al. (2020). For 16S rRNA, a dilution series of genomic DNA from *Escherichia coli* K-12 (with seven copies of 16S rRNA genes) was used as a standard (Blattner et al. 1997). The master mix consisted of 2 μL bovine serum albumin (BSA; 20 mg/mL; BIORON, Ludwigshafen, Germany), 10 μL SsoFast EvaGreen Supermix (Bio-Rad, Richmond, VA, USA), 0.8 μL of primer 341f (5′-CCTAYGGGRBGCASCAG-3′), 0.8 μL of primer 806r (5′-GGACTACNNGGGTATCTAAT-3′; Hansen et al. 2012), 1 μL of 10× diluted template and 5.4 μL of sterile DEPC-treated water. PCR conditions for 16S rRNA gene amplification were 98°C for 15 min, followed by 35 cycles of 98°C for 30 s, 56°C for 30 s and 72°C for 30 s (with fluorescence measurements) and ending with 72°C for 7 min and production of melt curves. ITS gene copies were quantified as described for the 16S rRNA above with minor modifications: Vector cloned ITS2 DNA regions from *Aureobasidium pullulans* were included as standards, primers used were gITS7 (5′-GTGARTCATCGARTCTTTG-3′; Ihrmark et al. 2012) and ITS4 (5′-TCCTCCGCTTATTGATATGC-3′; White et al. 1990), annealing temperature was 60°C and 40 amplification cycles were used.

2.7 | Statistical Analyses

Statistical analyses were performed within the R statistical framework, version 4.5.0 (R Core Team 2025) and SIMCA 17 (Sartorius Stedim Data Analytics). VOC data were log-transformed prior to statistical analyses to better meet assumptions of normality and homogeneity of error variances. To assess the changes in the emissions of the most abundant VOCs and the terpenes in the course of litter decomposition, we used linear mixed models with the desired VOCs as the response variables and incubation time and species as fixed factors and block as a random factor. We used the "lmer" function from the *lme4* package.

To assess for treatment effects, we excluded the initial litter samples that had not been subjected to the climate treatments to maintain symmetrical data structure of equal sample numbers in each group. Then we conducted a linear mixed model analysis with incubation time and treatment as fixed factors and block as a random factor separately for the two species, which differed considerably from each other. Significant treatment effects were followed by Dunnett's post hoc test to compare the control to other treatments using the *emmeans* package. Further, we analyzed how VOC composition blends differed between incubation times, species, and treatments using principal component analysis (PCA) on the log-transformed and unit variance-scaled VOC data consisting of all detected masses as variables. The PCA was done with SIMCA 17.

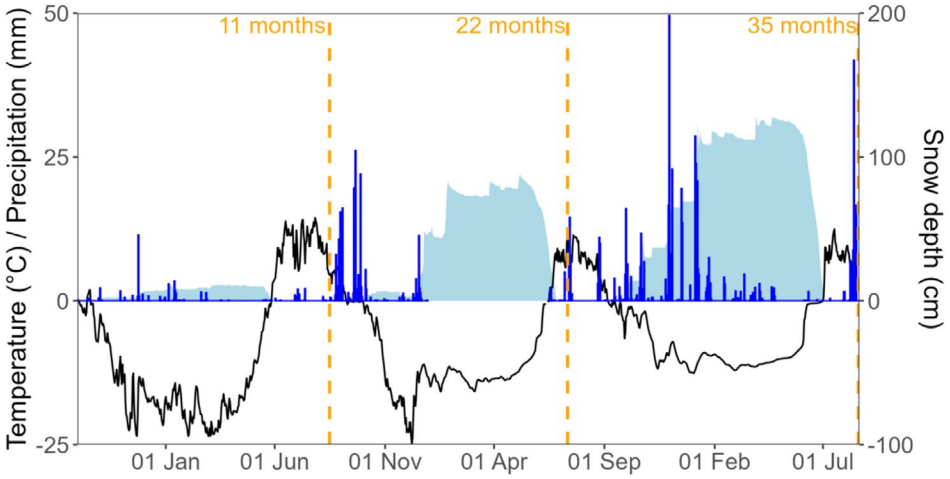


FIGURE 2 | Climate data during the litter incubation period in Zackenberg, northeast Greenland. Daily mean temperature at ground surface (black line), precipitation (dark blue bars), and snow depth (light blue bars) in the period September 1, 2012–September 20, 2015. Time points for litter bag sampling are shown as orange vertical dashed lines. The precipitation data are missing for the period January 1–June 13, 2014.

Values for subsample measurements of litter chemistry and microbial quantification were aggregated to a mean value per field replicate. Then we used linear mixed models to assess effects of incubation time, species, and treatments on C and N concentrations, as well as 16S and ITS gene copy numbers using the same methods as for VOC data. The NIR spectra were preprocessed with multiplicative scatter correction (MSC) to remove noise due to scatter effects from different particle sizes. The MSC-corrected and centered data were subjected to a PCA to assess how the samples differed from each other based on the litter chemical composition. Covariance between the emissions of major VOC constituents (Y variables) and litter chemical and microbial variables (X variables) was assessed with a partial least squares (PLS) regression analysis using SIMCA 17.

3 | Results

3.1 | Environmental Conditions During Litter Incubation

During the first 11 months of litter incubation, accumulated precipitation amounted to 48 mm. In the incubation periods from then to 22 months and from 22 to 35 months the precipitation was 216 and 519 mm, respectively. However, the 11–22 month period precipitation amount is underestimated due to a data gap for the period January 1–June 13, 2014. Most of the precipitation in Zackenberg falls as snow, and the maximum snow depth was indeed only 11.5 cm in the first incubation period, 88 cm in the second and 128 cm in the last incubation period (Figure 2). The insulation effect of the snowpack affected the temperature at ground surface; the minimum temperature was −23.5°C and −24.8°C in the first two incubation periods and only −12.6°C in the last incubation period (Figure 2).

Temperature in the litter layer was higher during the summer up to the 11-month litter bag sampling compared to the two following summers (Table S2). During this first summer, temperature in the warming treatment was on average 3.8°C higher than in the control treatment (Table S2).

3.2 | VOC Emission Composition in *C. tetragona* and *S. arctica* Litter

The main components in the VOC emissions from the litter of *C. tetragona* and *S. arctica* were acetic acid, methanol, acetaldehyde, and acetone (Figure 3). The emission profiles also contained a large number of other compounds, including terpenoids, emitted in lower quantities. The complete lists of all detected masses are presented as Tables S3 and S4.

In the initial litter, acetic acid emissions contributed 37% and 35% for *C. tetragona* and *S. arctica*, respectively (Figure 3). For *C. tetragona*, acetic acid contributed 76%–80% averaged across the treatments after incubation for 11 and 22 months, decreasing to 31% after 35 months. For *S. arctica*, the contribution by acetic acid remained largely similar, while the contribution by methanol increased from the initial 3% to 32% after 11 months and to 50% after 22 months. Acetaldehyde comprised at most 10% and 20% of the emissions of *S. arctica* and *C. tetragona*, respectively. Acetone and ethanol comprised at most 5%–6% of the emissions.

3.3 | Emission Rates of the Major VOCs During Decomposition

VOC emission rates from the litter changed over time ($p < 0.001$, mixed model). The changes over time in the emissions of the major VOC constituents (acetic acid, methanol, acetaldehyde, ethanol, and acetone) and terpenes differed between *C. tetragona* and *S. arctica* (Figure 4A–F; time × species interaction, $p < 0.001$).

For *S. arctica* litter, the emission of all the five major VOC constituents decreased from 11 to 22 months of incubation, and stayed similar (acetic acid, acetaldehyde, ethanol) or increased (methanol and acetone) from 22 to 35 months of incubation (Figure 4A–E). For *C. tetragona*, the emission rates of the major VOCs were similar at 11 and 22 months of incubation except for methanol, which decreased, and ethanol, which increased from 11 to 22 months. The five major VOCs

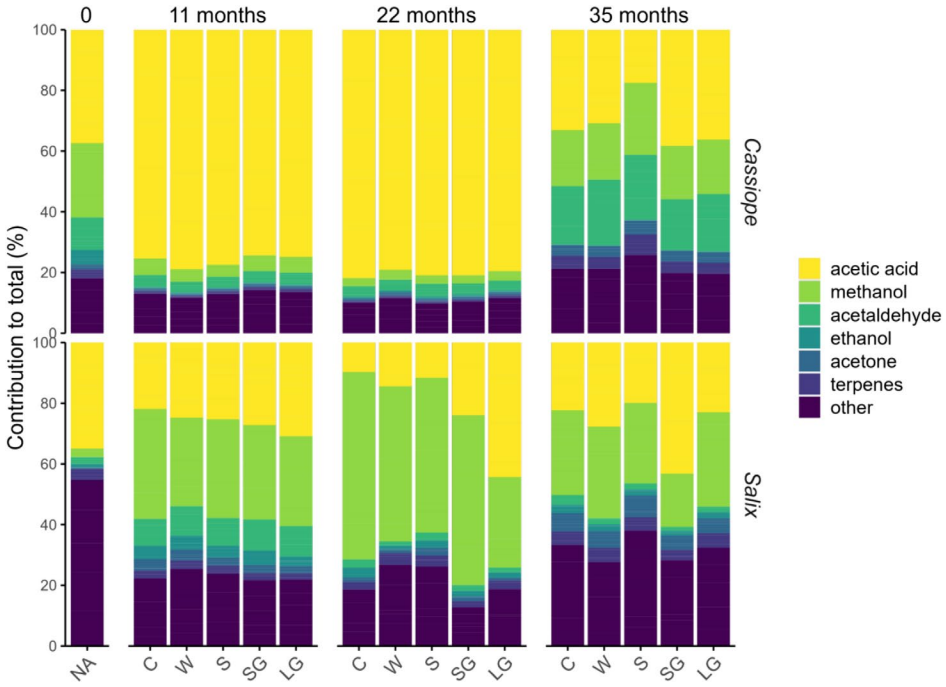


FIGURE 3 | Proportion contributions of the most emitted VOCs to the total net emissions from litter of *C. tetragona* and *S. arctica*. Data are shown for the initial litter (0) and litter incubated for 11, 22, or 35 months in the litter layer of a field experiment in a High Arctic tundra heath. The field treatments were C, control; W, warming; S, shading; SG, short growing season; and LG, long growing season. NA, not applicable, initial litter. The shown compounds comprise the following protonated m/z: Acetic acid (43.018, 61.028), methanol (33.034, 51.043), acetaldehyde (45.033, 63.042), ethanol (47.049), acetone (59.049), and terpenes including monoterpenes and sesquiterpenes (81.070, 137.134, 149.133, 205.196).

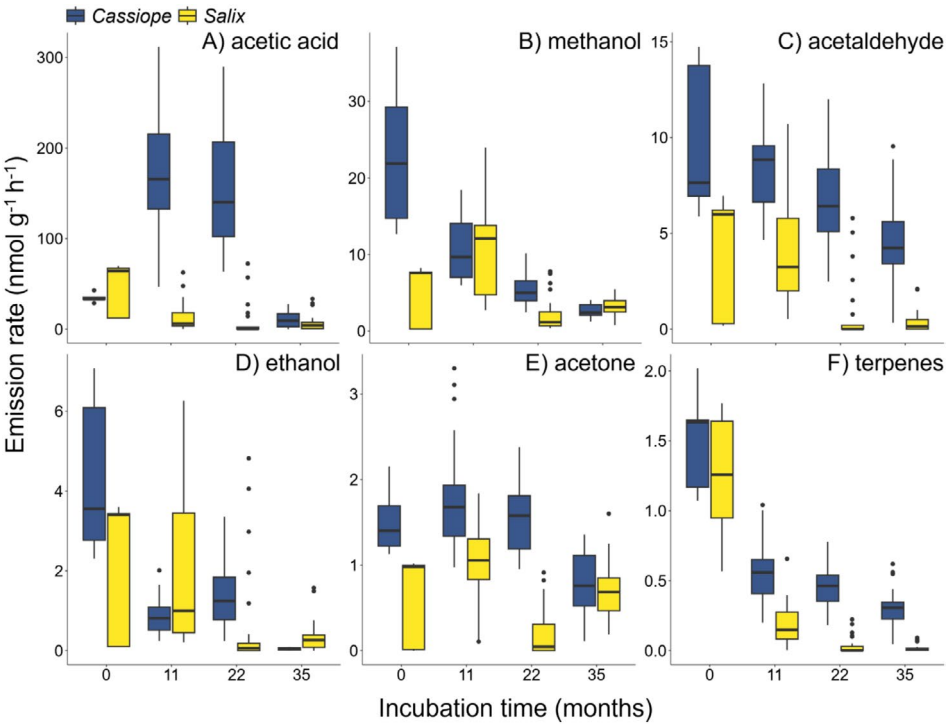


FIGURE 4 | VOC emission rates for *C. tetragona* and *S. arctica* litter in the course of litter decomposition in a High Arctic tundra heath. Emission rates are shown for acetic acid (A; sum of 43.018, 61.028), methanol (B; sum of 33.034, 51.043), acetaldehyde (C; sum of 45.033, 63.042), ethanol (D; 47.049), acetone (E; 59.049), and terpenes including monoterpenes and sesquiterpenes (F; sum of 81.070, 137.134, 149.133, 205.196) in the beginning of litter bag incubation, and after 11, 22, and 35 months of incubation. Box plots show the median, the 25th and 75th percentiles (boxes), the 10th and 90th percentiles (error bars), and outlying values. The emissions of these compounds were not significantly affected by the climate change treatments and hence pooled across the treatments ($n = 25$). For all shown compounds, the effect of incubation time, species, and incubation time × species were significant at $p < 0.001$, except for the main effect of species on ethanol emission, which was significant at $p < 0.05$, mixed model. Note different *y*-axis scales.

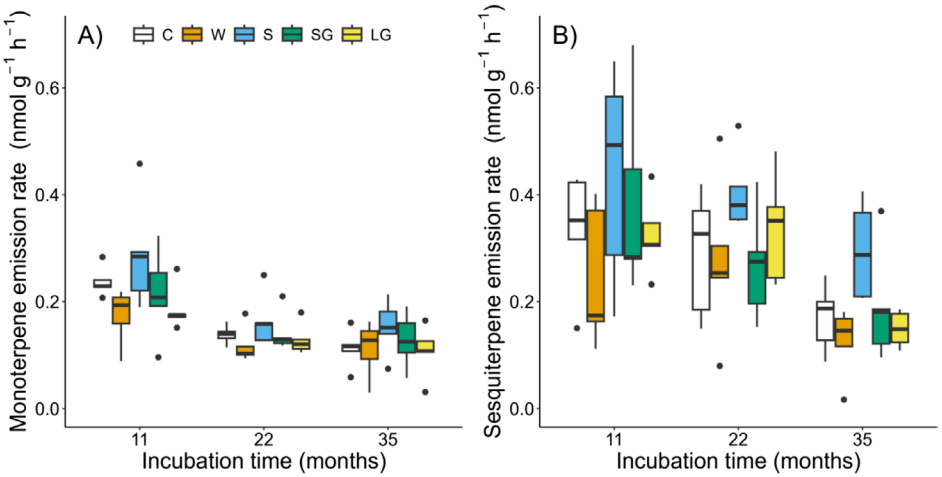


FIGURE 5 | Monoterpene (A; sum of 137.134, 81.070) and sesquiterpene (B; sum of 149.133, 205.196) emission rates from *C. tetragona* litter in climate treatments in the course of litter decomposition in a High Arctic tundra heath. The field treatments were C, control; W, warming; S, shading; SG, short growing season; LG, long growing season. Box plots show the median, the 25th and 75th percentiles (boxes), the 10th and 90th percentiles (error bars), and outlying values ($n = 5$).

all significantly decreased from 22 to 35 months of incubation in *C. tetragona*.

Terpene emissions were similar from the initial litter and decreased over time. After 11 months of incubation, terpene emissions from the *S. arctica* litter were less than half of those from *C. tetragona* litter (Figure 4F).

3.4 | Treatment Effects on Litter VOC Emissions

The emission rates of the five major VOCs were unaffected by the climate change treatments. However, the emissions of mono- and sesquiterpenes were significantly affected by treatments in *C. tetragona* (Figure 5A,B, $p < 0.01$ for the main effect of treatment), but not in *S. arctica*. Shading treatment had consistently higher sesquiterpene emissions ($p = 0.008$, Dunnett's test) and a tendency for higher monoterpene emissions as compared to the control ($p = 0.057$), with the largest difference after 35 months of incubation (Figure 5). Other treatments did not significantly differ from the control.

3.5 | Variation in VOC Blends

The VOC composition blends (unit variance-scaled values for all individual masses) yielded a clear separation of the incubation times along the first principal component (PC1), which explained 58% of the variance in the data (Figure 6). The initial litter samples had overall high values on PC1, then the 11-month samples, and the 22- and 35-month samples. Overall, the diversity of VOCs emitted decreased as the litter decomposition advanced most masses had high loading values on PC1 (Table S5). The second PC (explained variance 9.4%) separated the two species from each other, *S. arctica* with higher and *C. tetragona* with lower values on this axis. The local microclimate, that is, differences between blocks in the field experiment, had a larger impact on the VOC blends than the treatments (Figure 6).

3.6 | Litter Mass Loss and Chemical Composition

Litter mass loss could not be directly measured in our study as this measurement conflicted with the VOC measurements. Instead, we report here litter mass losses estimated in an identical litterbag experiment conducted with litter from the same species in the same field experiment parallel to our experiment after 11 and 22 months of incubation (Blok et al. 2018). Litter mass decreased more for *C. tetragona* than for *S. arctica* over time, but treatment effects were similar in both species (Table S6, $p < 0.001$, Time × Species). After 11 months, both shading and warming treatments had reduced mass loss, while after 22 months, the LG treatment had increased the mass loss as compared to the control ($p < 0.01$, Dunnett).

The litter C content was significantly higher in *C. tetragona* than in *S. arctica*, and it decreased over time in both species, but the decrease was larger in *S. arctica* (Table S6, $p < 0.001$ for species, time and their interaction). The C content was significantly higher in the LG treatment compared to the control ($p = 0.026$, Dunnett).

The litter N content increased during incubation in both species, and the increase was greater in *S. arctica* than *C. tetragona* ($p < 0.001$ for species × time interaction). In *C. tetragona*, the treatment effects were not significant, but in *S. arctica*, the litter in LG treatment tended to have higher N content than control ($p = 0.09$, Dunnett). These changes in the C and N contents led to a decrease in the C:N ratio during the incubation period (Table S6; $p < 0.001$). This decrease was larger in *S. arctica* than *C. tetragona* ($p < 0.001$ for species × time interaction). There were no significant treatment effects.

The chemical composition of the litter, as fingerprinted by NIR spectroscopy and summarized by PCA, differed significantly for the two species, incubation times, and the species differed in changes over time (Figure S1; $p < 0.001$ for the main effects and interactions). The first PC described changes over the incubation period with the initial samples with highest values

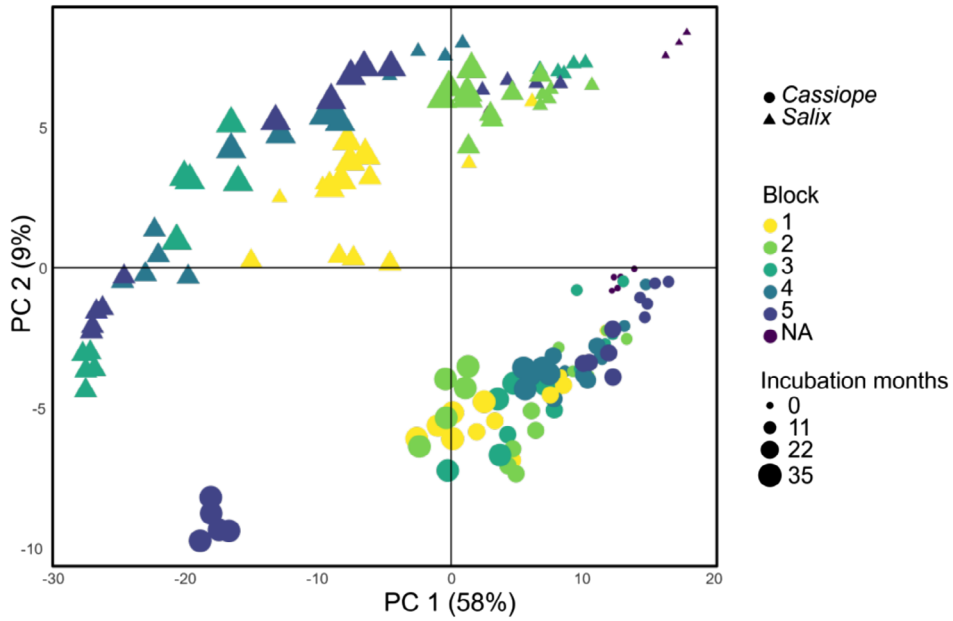


FIGURE 6 | Clustering of litter samples based on their VOC blends analyzed by principal component analysis. The score plot shows the samples for *C. tetragona* and *S. arctica* in the beginning of incubation and after 11, 22 and 35 months of incubation. The symbols are sized by number of incubation months and colored by the block of the field experiment (blocks 1–5; NA, not applicable, initial litter). The corresponding loadings are shown in Table S5.

along this axis, then the 11 month incubation period, followed by partly overlapping 22- and 35-month incubation periods. The second PC separated *C. tetragona* from *S. arctica*.

Treatment effects were similar in the two species and showed changes during the incubation period (PC1, $p = 0.093$ for Time × treatment interaction). Analysis of the incubation periods separately showed that the treatment effects developed over time from no significant effects after 11 month incubation period to significant effects after 22- and 35- month incubations ($p = 0.046$ and $p = 0.01$, respectively). After 35 months, the litter quality in the LG treatment differed from that in the control (Dunnett's *t*-test, data not shown).

3.7 | Prokaryotic and Fungal DNA Copy Numbers

The general temporal trend was an increase in the 16S gene copy numbers (representing prokaryotes) and a decline in the ITS gene copy numbers (fungi) during the incubation period (Figure S2; $p < 0.001$ for the effect of time). The ITS copy numbers were lower in *S. arctica* than *C. tetragona* ($p < 0.001$) and were not significantly affected by the treatments ($p > 0.1$ for the main effect of treatment and all interactions).

The 16S gene copy numbers tended to be differently affected by the climate change treatments in the two species ($p = 0.089$ for the treatment × species interaction). In *C. tetragona*, the LG treatment had higher 16S gene copy numbers than the control (Figure S2, $p = 0.066$, Dunnett). In *S. arctica*, the effects of treatments were not statistically significant.

3.8 | Covariance Between VOC Emissions and Litter Chemical and Microbial Variables

Litter chemical and microbial variables explained about 46.5% of the variance in the emission data of the dominant VOC constituents when analyzed across the two species and all incubation periods by PLS regression (Figure 7). Emissions of acetone and acetaldehyde were most linked to the litter C:N ratio and fungi (ITS copy numbers). Emissions of ethanol and methanol were intercorrelated and pulled towards the first PC of the NIR spectroscopy data and were negatively correlated with litter N content and bacteria (16S gene copy numbers). Acetic acid and terpene emissions covaried with the second PC of the NIR spectroscopy data and litter C content.

4 | Discussion

Decomposing litter of two circumpolar species, the deciduous willow, *S. arctica*, and the evergreen Arctic bell heather, *C. tetragona*, differed in terms of litter chemical composition, VOC emissions, and microbial DNA numbers. Changes in the litter during the 3-year decomposition period in the High Arctic also showed species-specific characteristics. We observed that during the litter decomposition, VOC emission rates overall decreased over time as the chemical composition of the litter material and its prokaryotic and fungal biomass also changed. All litter samples originated from similar conditions but were exposed to different climate treatments during decomposition. The effects of these treatments were minor and complex compared to the large between-species and temporal differences.

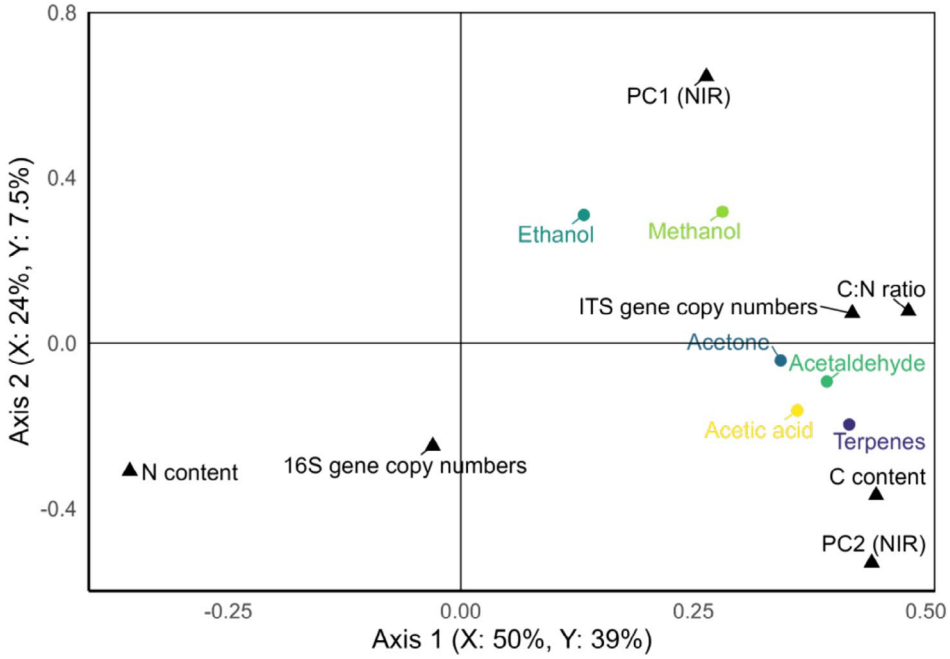


FIGURE 7 | Partial least squares regression analysis on covariance between VOC emissions and litter chemical and microbiological variables. The major VOC constituents in litter emissions (*Y*-variables) are shown as colored round symbols and the variables describing litter characteristics (*X* variables: C content, N content, C:N ratio, 16S gene copy numbers, ITS gene copy numbers, and the first two principal components from the principal component analysis of the NIR spectra) as black triangles. The analysis was conducted across species and incubation times. The variances explained are shown in parentheses.

Litter VOC emissions constitute an abiotically emitted fraction (Gray et al. 2010), biological production of different compounds, and release from decaying storage reserves. Consumption of VOCs by microbial communities, an especially efficient process at the litter-soil interphase (Gray et al. 2015; Ramirez et al. 2010), further adds complexity to understanding the net VOC emissions.

4.1 | Litter VOC Emissions Have Common and Species-Specific Constituents

Despite different bacterial and fungal counts (qPCR data) and chemical compositions of the litter material (NIR fingerprints and C/N measurements), litter VOC emissions were dominated by common compounds. The main VOC profile constituents in both *C. tetragona* and *S. arctica* litter were oxygenated VOCs—acetic acid, methanol, acetaldehyde, acetone, and ethanol. This is consistent with other studies that have used a PTR-MS instrument to measure litter VOCs (Gray et al. 2010; Greenberg et al. 2012; Viros et al. 2021). In our data, acetic acid (m/z 43 + m/z 61) constituted a large part of the emissions throughout the litter incubation period in both species. For *C. tetragona* around 80% of the total mass comprised acetic acid after 11–22 months of incubation. For *S. arctica* litter, acetic acid made up about one third of the emitted masses. Acetic acid was also the main initial constituent of senescent *Pinus halepensis* needles, but its dominance decreased over time (Viros et al. 2021). Acetic acid is a central microbial metabolite produced microbially both under aerobic and anaerobic conditions (Vidra and Németh 2018) and stimulated, for example, in soil VOC emissions under drought stress (Honeker et al. 2023). In our data, acetic acid emissions covaried with litter C content and the litter chemical composition as fingerprinted by NIR spectroscopy.

The high proportion of acetic acid is in contrast with the findings by Gray et al. (2010) and Gray and Fierer (2012), who reported that methanol constituted between 55% and 99% (on molar basis) of the total VOC emissions from litter of different tree species. In our study, the proportional contribution of methanol was 4% to 25% for *C. tetragona* litter, and 3% to 50% for *S. arctica* litter. The differences between studies may be related to different sample handling procedures: Gray et al. (2010) and Gray and Fierer (2012) oven-dried the litter samples prior to VOC measurements. Methanol is released from living plant leaves upon pectin demethylation when cell walls expand and from decomposing leaves both microbially as well as abiotically (Galbally and Kirstine 2002; Warneke et al. 1999). Methanol, ethanol, acetaldehyde and acetone have also been observed to dominate the VOC emissions from Arctic permafrost soils (Kramshøj et al. 2018; Li et al. 2020). In our dataset, emissions of methanol and ethanol covaried with litter chemical composition (NIR spectroscopy), but emissions of acetaldehyde and acetone were closest correlated to litter C:N ratio and fungal abundance (ITS gene copy numbers).

In species that have specialized storage compartments, like *Pinus* spp. or *Eucalyptus* spp., litter monoterpene emissions are also relevant (Gray et al. 2010; Viros et al. 2020, 2021). In the current study, monoterpene and sesquiterpene emissions from litter were low, even for the litter of *C. tetragona* known to be a mono- and sesquiterpene emitting plant (Schollert et al. 2014; Simin et al. 2021). An earlier study on *C. tetragona* litter VOC emissions that used a GC–MS technique, which did not allow

quantification of the low molecular weight oxygenated compounds that were the most abundant in the present work, suggested that terpenoids actually dominated *C. tetragona* litter VOCs (Svendsen et al. 2018). *C. tetragona* leaf surfaces are covered with trichomes (Schollert et al. 2015), which can function as storage compartments for monoterpenes and sesquiterpenes (Li and Sharkey 2013) releasing these compounds upon rupture. The GC–MS study of Svendsen et al. (2018) also assessed *S. arctica* litter VOC emissions, and they found that *S. arctica* litter had lower terpene emissions than *C. tetragona*, which is in agreement with the present study. Our study also demonstrates that despite the similar dominant compounds (low molecular weight oxygenated compounds), the volatile blends in the two litter types we studied were clearly distinct based on the PCA based on the individual VOCs scaled to similar magnitudes.

4.2 | Temporal Changes in Litter VOC Emissions During Decomposition

We observed a decrease in litter VOC emission rates over the 35-month-long incubation period, both for the dominant oxygenated VOCs as well as for the terpenes. This decrease was overall more consistent for *C. tetragona* than *S. arctica*. The initially lower emissions from *S. arctica* decreased clearly from 11 to 22 months of decomposition but remained then largely similar at 22 and 35 months. This species-dependent difference was also illustrated by the PCA on the VOC blends: For *C. tetragona*, the change in the blends advanced chronologically on PC1, while for *S. arctica* the 22 and 35 month samples had similar VOC blends. The trends in the changes of litter chemical composition as analyzed by NIR spectroscopy were similar.

Other studies have assessed shorter term temporal changes during decomposition. In the GC–MS study of Svendsen et al. (2018) on VOC emissions from *S. arctica* litter and *C. tetragona* litter over an 8-week period, VOC emissions from *Salix* litter decreased, and emissions from *C. tetragona* litter increased. Gray et al. (2010) measured initial VOC emissions from decomposing litter of 12 different species over a 20-day incubation period and found that half the species showed increasing VOC emissions, and the other half had overall decreasing emissions. Over a longer time period, 125 days, litter VOC emissions from these same species in general decreased (Gray and Fierer 2012). Decreasing emissions in the longer term (up to 15 months) after a short-term increase in terpenoid emissions observed at 3 months were also documented for *P. halepensis* litter (Viros et al. 2021). Taken together, these earlier studies and our long-term field incubation provide evidence for decaying litter VOC emissions as decomposition progresses. However, the period during which VOC emissions from litter remain significant differs in different biomes, being longest in cold ecosystems like the Arctic tundra.

During decomposition of litter, the litter undergoes transformations. We used NIR spectroscopy to fingerprint the chemical composition of litter material and observed that—although *S. arctica* and *C. tetragona* differed from each other—similar temporal changes in the chemical composition were the main difference observed on PC1 for both species. Also, the changes in total bacterial and fungal counts were overall similar in the two species: Bacterial 16S gene copy numbers increased, while fungal ITS gene copy numbers decreased during the incubation. Svendsen et al. (2018) found that changes in the VOC emission blends in *Salix* spp. litter correlated with parallel changes in the bacterial community analyzed by amplicon sequencing. We were not able to directly determine mass loss in our samples, but another litter bag study conducted at the same time on the same field site with the same species showed that the accumulated mass loss was higher in *S. arctica* litter during the first 11 months, but similar or higher in *C. tetragona* litter after 22 months (Table S6; Blok et al. 2018).

4.3 | Effects of Climatic Factors on Litter VOC Emissions May Develop in Long Term

We expected that higher temperatures in the warming treatment would accelerate litter decomposition and alter VOC emissions, unless water limitation would interact with this treatment. Litter dry-out appears to have played an important role in the first 11 months of incubation as the warming treatment reduced litter mass loss by 30%–40%. During this first incubation period, total precipitation was only 48 mm, which is only one fifth of the mean annual precipitation (2008–2018 average of 253 mm) (López-Blanco et al. 2020). The litter VOC emissions were not significantly affected by warming, probably as effects of dryness reducing decomposition-related emissions and elevated temperature stimulating emissions cancelled out each other.

Overall, the emissions of the dominant low molecular weight compounds were unaffected by the climate treatments, while some effects were manifested in terpene emissions of *C. tetragona* (in *S. arctica* terpene emissions were very low after incubation). Effects of the shading treatment developed over time and were strongest after 35 months of decomposition, when the emission rates of monoterpenes and sesquiterpenes were twice as high from the shading treatment compared to the control. The higher terpene emission from litter material in this treatment is in agreement with our hypothesis and suggests that litter decay and VOC release from terpene storage compartments was slowed down by reduced solar radiation. Besides by reducing surface temperatures (Kramshøj et al. 2016), although not evident in our study site (Table S2), shading treatment would slow down abiotic photodegradation of litter. Photodegradation is important in open canopy ecosystems with sparse vegetation, like semi-arid grasslands (Austin and Vivanco 2006) and potentially tundra, although its contribution to litter decomposition has yet to be quantified in the Arctic.

We expected that manipulating growing season length—by snow removal/addition during the early spring—would influence litter via soil moisture changes, since snowmelt is a key water source in dry Arctic ecosystems (Zona et al. 2022). In the long growing season treatment where snow had been removed from the plots allowing an earlier start of the growing season, the bacterial gene copy numbers were increased compared to other treatments, especially in *C. tetragona* litter; C content was higher and our NIR analysis showed that the litter chemical composition was different, but VOC emissions were unaffected. Earlier snow melt increases vegetation greenness, primary productivity and ecosystem respiration in tundra ecosystems in early to mid-growing seasons (Lindwall et al. 2016; Zona et al. 2022). Other

studies have evaluated effects of deeper snow cover that can increase wintertime temperature in the litter layer. Effects of this deeper, insulating snow layer on decomposition are minimal relative to effects of variation in environmental factors during the growing season (Parker et al. 2018).

The minor effects of the climate change treatments in our field experiment may be partly hidden by the large natural variation in the parent litter material and the microscale variation between the experimental plots. In fact, the significant block effects, that is, effects caused by variation between microsites in which the experimental plots were located, were larger than the effects of the experimental treatments. Soil temperature and soil moisture, major controlling factors behind litter mass loss rates and likely the dynamics of VOC emissions (Blok et al. 2016; Parker et al. 2018), show large variation in tundra landscape and are linked to local topography and snow (Aalto et al. 2022).

In this study, the litter material we used originated from vegetation outside the climate change experiment, that is, the parent material was initially similar and unaffected by climate change treatments. A study that assessed litter decomposition rates observed that such treatment effects on decomposability of litter were minimal compared to the effects of climate controlling the actual decomposition processes and the differences between plant growth forms (Cornelissen et al. 2007). Little is known about the effects of climate change on VOC, for example, terpenoid, concentrations in the leaf tissue of tundra plants, although there is some evidence for increasing terpenoid concentrations under warming, and decreasing concentrations under light limitation in forest tree foliage (Holopainen et al. 2018).

4.4 | Importance of Litter VOC Emissions in Arctic Ecosystems

Plant VOC emissions dominate ecosystem VOC emissions in the Arctic through the early to peak growing season, and are characterized by different compound contributions along phenological changes from leaf expansion through flowering to defoliation (Baggesen et al. 2021; Rinnan 2024). Litter is a minimal contributor to the ecosystem VOC emissions during this period, but has increasing importance in late growing season and autumn, when the vegetation VOC emissions cease and the ecosystem as a whole may turn into a VOC sink (Baggesen et al. 2022).

Early studies into VOC emissions from decaying plant material (Warneke et al. 1999) have likely overestimated the atmospheric impacts as their measurements aimed to estimate maximal pools of VOCs that could be released from litter while it was exposed to high temperatures. In fact, the effects of litter VOCs might not manifest via atmospheric chemistry; in contrast, they can have implications on ecosystem carbon cycling. Litter-derived VOCs can be readily degraded by adjacent soil microbial communities (Albers et al. 2018; Ramirez et al. 2010). The carbon emitted as VOCs during litter decomposition contributes to different soil carbon pools, including microbial biomass carbon (McBride et al. 2020). Litter VOC emission rates also correlate with CO_2 respiration rates (Leff and Fierer 2008; Ramirez et al. 2010), and they can also affect microbial diversity and community composition in the adjacent soil (McBride et al. 2020).

To conclude, VOC emissions from two circumpolar species, the deciduous *Salix* and the evergreen *C. tetragona*, have common low-molecular weight VOC components, but also inherent differences. The VOC emissions from the two species show strong variations in both quantity and chemical composition when litter decomposes and changes in its chemical composition, and the decomposition and related VOC emissions are affected by microsite-specific environmental controls, like moisture and temperature. Our study suggests that the ongoing vegetation changes occurring as the Arctic climate changes are thus likely to drive major changes in litter VOC emissions.

Author Contributions

Riikka Rinnan: conceptualization, investigation, funding acquisition, writing – original draft, visualization, formal analysis, supervision, resources, project administration. **Mira Skardhamar:** investigation, formal analysis, writing – review and editing. **Magnus Kramshøj:** writing – review and editing, investigation. **Tao Li:** data curation, writing – review and editing, formal analysis, validation. **Sarah H. Svendsen:** conceptualization, investigation, writing – review and editing. **Toke Bang-Andreasen:** writing – review and editing, investigation. **Lars H. Hansen:** writing – review and editing, resources. **Thomas Holst:** investigation, writing – review and editing, methodology, resources.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in the Electronic Research Data Archive at the University of Copenhagen at https://doi.org/10.17894/ucph.4420e7cd-136b-48af-a635-b733236ce258.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** gcb470006-sup-0001-Supinfo.docx.