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Emissions of biogenic volatile organic compounds from arctic shrub litter are coupled with changes in the bacterial community composition

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ABSTRACT

Emissions of biogenic volatile organic compounds (BVOCs) from natural ecosystems impact atmospheric chemistry as well as biological interactions and even soil biogeochemical processes. Plant litter emits substantial amounts of BVOCs. These emissions may contribute to total ecosystem emissions especially in the Arctic where the living plant biomass is low and the amount of litter is expected to increase as the deciduous shrubs expand in response to a warmer climate. Here, we incubated in the laboratory litter from the evergreen *Cassiope tetragona* and deciduous *Salix* spp. from a high arctic and a low arctic location. The 8-week-long incubation was conducted with temperature increasing from 5 °C to 26 °C, mimicking the transition from winter to summer. BVOC emissions from the decomposing litter were sampled weekly in adsorbent cartridges and analyzed using gas chromatography–mass spectrometry, and the bacterial community composition was investigated by sequencing of PCR amplified 16S rRNA gene fragments. Our results showed that litter from *C. tetragona*, which is a terpenoid storing species, had higher BVOC emission rates (mainly terpenoids) than the *Salix* litter, which does not have specialized BVOC storing compartments. The *C. tetragona* litter emissions were higher in the high arctic than the low arctic samples. The emission rates from the *C. tetragona* litter increased during the incubation period, whereas emission rates from the *Salix* litter decreased, suggesting that the emissions originated from different sources and/or processes. The bacterial community composition in the *Salix* litter, but not in the *C. tetragona* litter, changed in parallel with the changes in the BVOC emissions during the incubation period. Therefore, we suggest that bacteria may be more important for the BVOC emissions from decomposing *Salix* litter than *C. tetragona* litter.

1. Introduction

Emissions of biogenic volatile organic compounds (BVOCs) from natural ecosystems have significant impact on chemical and physical properties of the atmosphere and therefore also affect the climate (Atkinson and Arey, 1998; Shindell et al., 2009; IPCC, 2013; Ehn et al., 2014; Scott et al., 2014). Most attention has been given to emissions from plants and whole ecosystems and far less to the litter and soil. This is despite the fact that a wide range of BVOCs can be emitted in substantial amounts from both litter and soil (Leff and Fierer, 2008; Gray et al., 2010; Aaltonen et al., 2011; Mäki et al., 2017). In particular, aboveground litter BVOC emissions can be significant, especially during spring and autumn when monoterpenes can emitted in high amounts from pine litter (Hellén et al., 2006; Aaltonen et al., 2011; Peñuelas et al., 2014; Mäki et al., 2017). Other BVOCs emitted in substantial amounts from leaf litter are methanol, acetone and acetaldehyde (Gray et al., 2010). Even though we know that aboveground litter BVOC emissions might be important, we lack understanding of different mechanisms controlling the litter emissions, such as the effect of temperature, litter types and the microbiome of the litter.

Emissions of BVOCs may influence the climate by changing the atmospheric concentrations of important greenhouse gasses. For instance, in the presence of atmospheric nitrogen oxides, the breakdown of BVOCs can lead to the formation of NO_2, which, in turn, can be

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photodissociated to form tropospheric ozone (Atkinson and Arey, 1998; Peñuelas and Staudt, 2010). Furthermore, if BVOCs react with hydroxyl radicals it will decrease the oxidation capacity of the atmosphere and thereby prolong the lifetime of methane (Laothawornkitkul et al., 2009; Peñuelas and Staudt, 2010). The atmospheric breakdown of BVOCs may also increase the formation of secondary organic aerosols and cloud condensation nuclei, which can lead to increased cloud cover and radiative reflection (Shindell et al., 2009; IPCC, 2013; Scott et al., 2014).

Emissions of BVOCs do not only influence processes in the atmosphere but also several belowground biogeochemical processes related to the decomposition of organic matter. For instance, by acting as substrate for microorganisms, monoterpenes have been suggested to increase microbial N (nitrogen) immobilization and thereby decrease the net N mineralization rate (White, 1994; Paavolainen et al., 1998; Smolander et al., 2006). Monoterpenes have also been suggested to decrease the rate of nitrification (White, 1986, 1988, 1991; Ward et al., 1997; Paavolainen et al., 1998), and this may e.g. be a consequense of ammonia monooxygenase inhibition (White, 1988, 1994) or decreased net N mineralization (White, 1994; Paavolainen et al., 1998). Furthermore, it has been proposed that different BVOCs can promote or restrain bacterial and fungal growth (Effmert et al., 2012; Peñuelas et al., 2014) and function as signaling molecules between belowground organisms (Wheatley, 2002; Bending et al., 2006; Schmidt et al., 2015; Tyc et al., 2017). Many BVOCs are also released without having any known specific function, for instance isopropanol, isoprene and different ketones may be emitted as intermediate products of microbial metabolism (Korpi et al., 2009; Insam and Seewald, 2010). In particular, a wide range of BVOCs are emitted under anaerobic conditions as products of fermentation processes (Insam and Seewald, 2010; Seewald et al., 2010; Faubert et al., 2011).

Litter emissions associated with microbial decomposition of organic matter are quantitatively more important than abiotic emissions (Leff and Fierer, 2008; Gray et al., 2010; Gray and Fierer, 2012; Wu and Wang, 2015). Here, BVOCs can be released from microorganisms, from extracellular biochemical processes in the organic matter or directly from the substrate (Korpi et al., 2009). The quantity and composition of the emissions depend both on the type of litter and on the composition of the decomposer community (Insam and Seewald, 2010; Peñuelas et al., 2014). Additionally, a range of different parameters in the environment such as temperature, pH, oxygen level, the availability of nutrients and soil moisture can change both the consumption and the emissions of BVOCs (Insam and Seewald, 2010). In particular, temperature is highly important since it changes the volatility of BVOCs and the transport resistance along the diffusion path out of the litter (Kesselmeier and Staudt, 1999). Furthermore, temperature may also change the emissions by altering the activity and community composition of the decomposing microorganisms (Kirschbaum, 1995; Deslippe et al., 2012; Rinnan et al., 2014).

Global warming is proceeding strongly in the Arctic with the predicted temperature increase of 2.2–2.4 times the global average (IPCC, 2013). In addition to the direct temperature effect on litter BVOC emissions, global warming will also increase plant biomass and alter the composition of vegetation. Especially the biomass of deciduous shrubs and leaf litter is expected to increase in the Arctic (Walker et al., 2006; Elmendorf et al., 2012a, 2012b). Furthermore, changes in plant species composition are likely to change litter emissions since different plant litter types emit different BVOC emission profiles (Leff and Fierer, 2008; Gray et al., 2010; Gray and Fierer, 2012).

The aim of this work was to assess how BVOC emissions from arctic leaf litter change during spring as temperature increases and microbial community potentially changes. We measured emissions of BVOCs (size range: 5C-25C) from aboveground litter of common arctic species during an eight-week-long laboratory incubation, where temperature was stepwise raised, mimicking typical spring soil surface temperatures in the Arctic. Litter of three species grown under different climatic conditions was used in order to assess differences between plant litter types. We used litter from *Salix glauca* collected from a low arctic location, *Salix arctica* collected from a high arctic location and *Cassiope tetragona* which was collected from both a low and a high arctic location. *C. tetragona* is an evergreen dwarf shrub that is characterized by having glandular trichomes on the leaf surface (Schollert et al., 2015) which are specialized storage structures for BVOCs (Laothawornkitkul et al., 2009; Loreto and Schnitzler, 2010). The *Salix* species are deciduous shrubs and trees with high isoprene emission capacity and no specialized BVOC storage structures (Fineschi et al., 2013). Changes in the bacterial community during the course of the experiment were assessed in parallel with the BVOC measurements. We hypothesized 1) that litter with BVOC storage structures would have higher emission rates than litter without the known storage structures, 2) that the release of BVOCs from litter would decrease over time due to a faster decomposition of the more labile litter constituents at the beginning of the decomposition and due to a depletion of BVOCs inside the plant tissue as the litter decomposes, 3) that BVOC emissions would be higher from high arctic *C. tetragona* litter than from low arctic *C. tetragona* litter because the density of terpenoid storing trichomes have been found to be higher on plants grown under colder conditions and 4) that the BVOC emission profiles would change in the course of incubation parallel with microbial community changes.

2. Materials and methods

2.1. Plant litter collection

Leaf litter of *Salix glauca* L. coll and *C. tetragona* (L.) D. Don was collected at Low Arctic Disko Island (69°14′N, 53°32′W) with an annual accumulated precipitation of 436 mm (1991–2004; Hansen et al., 2006) and mean annual temperature of −1.7 °C (1992–2013). Litter of *Salix arctica* P. Pallas and *C. tetragona* was collected in High Arctic Zackenberg Valley (74°30′N, 20°30′W) with mean annual temperature of −9.1 °C and mean annual accumulated precipitation of approximately 205 mm (2003–2013; Mylius et al., 2014). The litter was a composite of samples collected from tens of individual plants growing on an area of appr. 100 × 100 m in each location. Litter from Zackenberg was collected in August with a mean temperature of 5.4 °C and litter from Disko Island was collected in September with a mean temperature of 3.5 °C. *Salix* leaf litter was collected by taking senescent leaves that were still loosely attached to the stem or collected from the ground within 7 days of litter fall. *C. tetragona* litter was collected by taking the brown parts of the braches between the green and grey parts. Litter samples were stored at 5 °C during transport to Denmark (9 days for Zackenberg samples and 12 days for Disko Island samples), where they were stored at −18 °C.

2.2. Experimental set-up for laboratory incubation

The litter samples were prepared at −10 °C. *Salix* litter was cut into pieces of 0.5 cm × 0.5 cm and the needle-like *C. tetragona* litter into 0.5 cm long pieces. This procedure was done to enhance homogeneity of material for DNA extractions, but it may also have led to higher BVOC emissions and decomposition rates. Approximately 1.3 g dry weight of *Salix* litter and 2.7 g dry weight of *C. tetragona* litter from each location were used per 210 ml glass jar. This corresponded to 2.5 g fresh weight for *Salix* and 3.3 g fresh weight for *C. tetragona*. Litter for each location and species was weighed into six glass jars, giving six replicates per species and location. In addition, six empty 210 ml glass jars were used as experimental blanks. The whole experimental setup thus consisted of 30 glass jars.

Prior to the experiment, all litter samples were pre-conditioned to equal water holding capacity by placing the 210-ml glass jars into larger glass containers containing deionized water and a relative humidity in headspace of 95%. The glass jars were open, while the larger containers were covered with Parafilm and stored in dark at 5 °C. Parafilm allows