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Published in:
Environmental and Experimental Botany

DOI:
10.1016/j.envexpbot.2021.104387

Publication date:
2021

Document version
Publisher's PDF, also known as Version of record

Document license:
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Citation for published version (APA):
Volatile organic compound emission in tundra shrubs – Dependence on species characteristics and the near-surface environment

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A R T I C L E   I N F O

Keywords: Salix myrsinoides Betula nana Cassiope tetragona Rhododendron laponicum Leaf temperature VOC Tundra Photosynthesis MEGAN

A B S T R A C T

Temperature is one of the key abiotic factors during the life of plants, especially in the Arctic region which is currently experiencing rapid climate change. We evaluated plant traits and environmental variables determining leaf temperature in tundra shrubs and volatile organic compound (VOC) emissions with field measurements on deciduous tundra shrubs, Salix myrsinoides and Betula nana, and evergreen Cassiope tetragona and Rhododendron laponicum. Higher leaf-to-air temperature difference was observed in evergreen, compared to deciduous shrubs. Evergreen shrubs also showed continuously increasing photosynthesis with increasing temperature, suggesting high thermal tolerance. For the deciduous species, the optimum temperature for net photosynthesis was between our measurement temperatures of 24 ºC and 38 ºC. Air temperature and vapor pressure deficit were the most important variables influencing leaf temperature and VOC emissions in all the studied plants, along with stomatal density and specific leaf area in the deciduous shrubs. Using climate data and emission factors from our measurements, we modelled total seasonal tundra shrub VOC emissions of 0.3–2.3 g m–2 over the main growing season. Our results showed higher-than-expected temperature optima for photosynthesis and VOC emission and demonstrated the relative importance of plant traits and local environments in determining leaf temperature and VOC emissions in a subarctic tundra.

1. Introduction

Temperature is one of the most important factors affecting the distribution and activity of plants (Berry and Bjorkman, 1980). Temperature is especially important for the plants growing in the Arctic, the region of the world with the average air temperature in July at 10 ºC or lower, and an area which experiences the most rapid increase in temperature with climate change (Post et al., 2019). Helliker and Richter (2008) found that plants from subtropical to boreal biomes maintain their leaf temperature at constant 21 ºC during maximal carbon assimilation, which means that leaf temperature of arctic tundra plants can be much higher than the surrounding air temperature to maximize carbon uptake (Körner, 2003b; Lindwall et al., 2016). Nevertheless, we have poor understanding of quantified relationships between leaf temperature and ecophysiological processes in tundra shrubs. Volatile organic compounds (VOCs) are a large group of reactive hydrocarbons that can impact atmospheric chemistry (Glasius and Goldstein, 2016). While some VOCs are produced anthropogenically, the majority are biogenic and released by living organisms, mainly plants (Kesselmeier and Staudt, 1999). Isoprene, C5H8, is the most emitted biogenic VOC (Guenther et al., 2012) and a building block for monoterpenes, C10H16, oxygenated monoterpenes, C16H32On, and sesquiterpenes, C15H24, collectively known as terpenoids or isoprenoids.

VOCs are important for coping with biotic and abiotic stresses and play an important role in communication with other plants and other organisms(Laathawornkitkul et al., 2009; Penuelas and Staudt, 2010; Pollastri et al., 2014).

Inside plant leaves, VOCs fluctuate between liquid and gaseous phase according to their Henry’s law constant (kH) which is considerably high (kH ~ 7500 Pa m3 mol–1 for isoprene at 25 ºC; Niinemets et al., 2004). Compounds de-novo synthesized in the leaf mesophyll, like isoprene and certain terpenoids, are usually directly linked to photosynthetic activity (Loreto and Sharkey, 1990; Delwiche and Sharkey, 1993; Loreto et al., 1996; Laathawornkitkul et al., 2009). However, some other terpenoids...
can be stored in specific leaf structures, like ducts or glandular trichomes (Laathawornkitkul et al., 2009; Schollett et al., 2015). The strong temperature dependency of VOC emission is a direct result of faster enzymatic reactions and compound diffusion from stored pools. The coupled responses of photosynthesis and VOC emission to leaf temperature have been documented for lower latitude herbs (Monson et al., 1992) and evergreen trees (Filella et al., 2007), but we do not know how tundra shrubs respond.

Tundra shrubs possess a set of physiological adaptations to their harsh living environment (Körner, 2003c). Their photosynthetic apparatus is highly specialized to the overall low growth temperature (Körner, 2003a). However, experimental studies suggest strong temperature responses of VOC emissions at branch and ecosystem levels (Kramshøj et al., 2016; Lindwall et al., 2016), directly coupled to plant ecophysiology. Tang et al. (2016) also suggested stronger temperature sensitivity for VOC emissions from tundra vegetation than currently implemented in models. According to the classic review by Berry and Björkman (1980), we would expect tundra plants to have lower than the global average optimum temperature for photosynthesis, but we lack empirical data e.g. in the form of temperature response curves to estimate optimum temperatures of photosynthesis and VOC emissions.

Studies investigating the influence of climate change on VOC emission from tundra plants have found that the warmer climate generally leads to higher VOC emission (Adams et al., 2001; Faubert et al., 2010; Bjorkman (1980), we would expect tundra plants to have lower than the global average optimum temperature for photosynthesis, but we lack empirical data e.g. in the form of temperature response curves to estimate optimum temperatures of photosynthesis and VOC emissions.

In this study, we assessed factors determining leaf temperature and evaluated the importance of plant traits and near-surface environmental variables driving VOC emission in two evergreen and two deciduous tundra shrubs. We also compared temperature response curves for photosynthesis, transpiration and VOC emission. Finally, the obtained temperature, the leaf surface temperatures of each leaf in the measured twig was 9.7 ± 0.1°C and over 30 years (1986–2015) taken at the Abisko Scientific Research Station (ANS, 2020). The growing season usually starts after snowmelt in June and ends with senescence in late August or early September. The vegetation of the area mainly consists of deciduous and evergreen shrubs, graminoids and mosses with some herbs and herbivores (Tiiva et al., 2008). The bedrock is covered by highly organic soil with a pH of 6.9 (Rinnan et al., 2008).

The plant species in this study consisted of the most common species in the area, the deciduous dwarf shrubs Salix myrtilloides L., and Betula nana L. and the evergreen dwarf shrubs Cassiope tetragona (L.) D. Don, and Rhododendron lapponicum (L.) Wahlenb. (Fig. 1a–d). We did not distinguish between the sexes in Salix.

2. Weather station

A weather station was set up in the center of the measurement area of ca. 1200 m² in late May 2018. It consisted of a wind speed anemometer (R3–50; 327 cm above ground; GILL, Lymington, UK), two shielded relative humidity and temperature sensors (CS215; 20 cm and 200 cm above ground; Campbell Scientific, Lincoln, NE, USA), an incoming photosynthetic photon flux density (PPFD) sensor (LI-190; 115 cm above ground; LI-COR, Lincoln, NE, USA), and PT-100 temperature probes (W-EYK, Heraeus, Kleinothen, Germany) at different soil depths (3, 10, 15 and 20 cm) connected to a Campbell CR1000 data logger.

Air temperature, PPFD and VPD during the measurement period are presented in Fig. 1. Mean annual temperature in 2018 was 0.2 °C (ANS, 2020). Mean air temperature for the period between June 8 and September 2 measured at the site in 2018 was 11.7 ± 0.05 °C (Fig. 1e). Air temperature for the same period averaged over 100 years (1914–2013) taken at the Abisko Scientific Research Station (ANS, 2020), ca. 1 km away, was 9.9 ± 0.12 °C and over 30 years (1986–2015) was 9.7 ± 0.16 °C. Therefore, when taken a whole, 2018 was an ordinary year in Abisko in terms of air temperature, but with a very warm summer.

2.3. Leaf temperature and photosynthesis measurements

In order to understand the importance of leaf temperature on physiology of tundra shrubs, two types of gas exchange measurements were performed, 1) measurements at prevailing leaf temperature at varying environmental conditions across the growing season and 2) temperature response curves. At each sampling date, three plant individuals from each species were measured. For each measurement, new plant individuals were randomly selected from the heath area of approx. 100 m × 100 m. In each measurement, a twig containing 5–25 leaves from an unshaded, uppermost branch of the shrub was measured. The gas exchange measurements were conducted using a portable photosynthesis system, a LI-6400 XT (LI-COR, Inc, Lincoln, Nebraska, U.S.A) with a red/blue light leaf chamber (6400–02 B), which was used as a branch cuvette, rather than a leaf cuvette, due to the small size of the leaves.

Prior to the gas exchange measurements at prevailing leaf temperature, the leaf surface temperatures of each leaf in the measured twig were determined from the adaxial side using an Optris Laser Sight infrared thermometer (OPTRIS GmbH; Berlin, Germany) and averaged across all the leaves on the twig. The LI-6400 XT was used in situ on living twigs of tundra shrubs to measure plant physiological variables such as net photosynthesis (Aₙ) and stomatal conductance (Gₛ). Twigs
were carefully inserted to the leaf chamber to avoid physical stress, clamped around the stem and the flowrate through the chamber was maintained at 400 μmol s⁻¹ (~595 mL min⁻¹). Photosynthetic photon flux density (PPFD) in the leaf chamber was set to 1000 μmol m⁻² s⁻¹, relative humidity (RH) was targeted to 60 % and the reference CO₂ concentration in the leaf chamber was set to 400 μmol mol⁻¹ using the LI-6400 XT’s mixer system. In order to correct the data for the leaf area and mass, the twigs were harvested after the finished measurements.

To produce temperature response curves, we measured gas exchange with the LI-6400 XT over five leaf temperature steps targeting 10°C, 17°C, 24°C, 31°C, and 38°C, while the same twig was clamped inside the leaf chamber. This temperature range was chosen to reflect on the natural range of peak growing season temperatures the tundra plants experience. To increase the temperature range beyond that provided by the Peltier system of LI-6400 XT, which can alter temperature by 6°C, we used ice packs or hand warmers (The Heat Company; A - 5541 Altenmarkt, Austria) around the chamber. We measured temperature response curves for three replicates/species.

2.4. Sampling of VOC emissions

A charcoal filter (Supelco Inc., Bellefonte, Pennsylvania, USA) was installed on the air intake of the LI-6400 XT to filter the air entering the leaf chamber for hydrocarbons (Ortega et al., 2008). VOCs were then sampled in parallel to photosynthesis measurements using a trace gas kit (8100–664) as a flow divider attached to the outlet of the LI-6400 XT leaf chamber (Ekberg et al., 2009). Air was pulled from this flow divider with a pocket pump (TOUCH; SKC Ltd, Blandford Forum, UK) at 200 mL min⁻¹ through a stainless steel cartridge (Markes International, Llantrisant, UK) containing Tenax TA and Carbograph 1TD adsorbents, which capture compounds with 5 or more C atoms. After sampling, the cartridges were sealed with Teflon-coated brass caps and stored at 4°C until analysis. The VOC sampling and logging of the physiological parameters were started simultaneously following a period of 20 min after twig insertion to avoid stress-induced VOC emissions (Ninemets et al., 2011). Since the biological activity is expected to be lower at lower temperatures, sampling time for Betula, Salix and Rhododendron was 30 min at leaf temperatures between 10°C and 17°C, and 20 min at higher leaf temperatures. Sampling time for Cassiope was 30 min at all temperatures, as it is known to have low levels of photosynthetic activity (Saddeley et al., 1994). Sampled air volume varied accordingly, between 4 and 6 L. Blank measurements with an empty leaf chamber were made to determine the compounds originating from the sampling system. They were done every day under the same conditions the plants were exposed to and once at each step of the temperature response curve.

2.5. VOC analysis

The adsorbent cartridges were transported to Copenhagen and analyzed using gas chromatography-mass spectrometry (7890A Series GC coupled with a 5975C inert MSD/DS Performance Turbo EI System, Agilent) after thermal desorption (TD100-xr, Markes International Ltd, Llantrisant, UK). Helium was used as the carrier gas and the temperature of the oven was held at 40°C for 1 min, followed by raising it to 210°C at 5°C min⁻¹, and finally to 250°C at a rate of 20°C min⁻¹. Individual compounds were separated by a HP-5 capillary column (50 m length, 0.2 mm diameter, 0.33 μm film thickness).

The chromatograms were analyzed using the software PARADiSe (v3.87, Johnsen et al., 2017). The VOCs were identified according to 28 authentic standards (Table S1) and, for the compounds with no standards available, using the mass spectra in the NIST 14 library (National Institute of Standards and Technology, Gaithersburg, MD, USA). Compounds for which the NIST 14 library Match Factor was <800 were excluded. The sample concentrations were calculated based on the standards. The VOCs were classified into non-oxygenated monoterpenes (MTs), oxygenated monoterpenes (OMTs), sesquiterpenes (SQTs), and non-isoprenoid VOCs. Compounds for which no standard was available were quantified using α-pinene for MTs, 1,8-cineole for OMTs, trans-caryophyllene for SQTs and toluene for non-isoprenoid VOCs.

Concentrations of the VOCs in the blank samples were subtracted from the plant VOC samples. In addition, VOCs with high concentrations in the blanks were omitted as they were assessed to originate from the LI-6400 XT system.

The VOC emission rate was calculated according to Eq. 1 (Ortega and Helmig, 2008)

\[
\text{Emission rate} = \frac{(C_{\text{Out}} - C_{\text{In}})F}{\text{Dry weight}}
\]

where Cout and Cin are the concentrations of VOCs in the outlet and inlet air and F is the flow rate into the leaf chamber. The concentration in the filtered inlet air was presupposed to be zero (Ortega et al., 2008; Ninemets et al., 2011).

2.6. Determination of specific leaf area and leaf dry mass content

Directly after VOC sampling and photosynthesis measurements, the measured twig was harvested, the leaves were separated from the stem, and the leaf area was scanned and calculated using ImageJ (v. 1.52a; Wayne Rasband, National Institutes of Health, Bethesda, USA). For
Cassiope with square-based parallelepiped twigs (Fig. 1c), we kept the leaves on the twig, scanned from one side and doubled the projected area to obtain an estimate of the leaf area (Campioli et al., 2009). The fresh leaves were weighed, oven dried at 70 °C for 48 h, and weighed to determine dry mass. The specific leaf area (SLA, leaf area per dry weight) and leaf dry mass content (LDMC, dry weight divided by fresh weight) were calculated.

2.7. Plant height, soil moisture, chlorophyll fluorescence, and leaf surface structures

Plant height was measured using a ruler from the soil surface to the top of the measured twig. A portable chlorophyll fluorometer, PAM-2100 (Heinz Walz GmbH, Effeltrich, Germany) was used to determine the light-adapted fluorescence and the quantum yield under ambient conditions of two leaves from the same plant, but from a twig adjacent to the one used for gas exchange measurements and VOC sampling. Electron transport rate (ETR) for each plant was calculated according to Genty et al. (1989) from the average of the two quantum yield measurements. Soil moisture was determined 10 cm from each measured plant using a Theta Probe ML3 (Delta T-Devices, Cambridge, UK) after the gas exchange measurements and VOC sampling.

After the gas exchange measurements, the twig was harvested, and we took four leaves per plant from an adjacent twig to obtain replicas of the leaf surface structures. These leaves were put on a microscope slide in a drop of superglue (Loctite, Westlake, Ohio, USA), pressed for 1 min, and were then carefully removed to leave a print of the leaf surface in the glue (Valkama et al., 2003). Of these four leaves, two represented the abaxial and the other two the adaxial side of a leaf in Salix and Betula. Rhododendron leaves were separated into current year (2018) and previous year (2017) leaves, and only the adaxial side was used for surface structure analysis as the concave leaves prevented making abaxial leaf prints. Leaf structures of Cassiope are in within-leaf cavities (Schollert et al., 2015), and therefore this species was omitted from leaf surface structures analysis.

We counted stomatal density in Salix, stomatal density and glandular trichome density in Betula and glandular trichome density in Rhododendron. Stomatal densities were counted for areas of 0.6 mm² and averaged between four measurements on two replicas of each side of the leaf. Glandular trichome densities were counted and averaged similarly to stomata, but the inspected areas were 3.14 mm².

2.8. Statistical analyses

We used one-way ANOVA to test whether species and the evergreen vs. deciduous groups differed from each other in leaf-to-air temperature difference.

For each plant species and compound separately, partial least squares (PLS) regression analysis was used to assess the covariance between the emission rates of the two most emitted VOCs (dependent variables, Y) and explanatory plant trait and environmental variables (independent variables, X) using SIMCA 16.0.1 (Umetrics, version 13.0.3.0, Umeå, Sweden). We opted to explain the emission of the most dominant compounds instead of VOC groups, because compounds within a group are likely differently controlled. For example, we could not obtain significant models for Betula and Rhododendron using groups. The X variables included photosynthesis, stomatal conductance, SLA, LDMC, density of stomata and glandular trichomes (where applicable), intercellular CO₂ concentration, transpiration, water use efficiency, ETR, twig height, leaf temperature as output from LI-6400 XT, VPD based on leaf temperature (obtained from the LI-6400 XT that uses calculations of Buck (1981)), soil moisture, ambient PPFD, air temperature and relative humidity at 2 m height and soil temperature at 10 cm. Variables with a VIP (Variable Influence on Projection) < 0.5 were excluded from the models. The extracted PLS models had one component and were tested using analysis of variance of the cross-validated residuals (CV-ANOVA, Eriksson et al., 2008).

One-component PLS models were also calculated to assess the covariance between the leaf temperature (Y) and the explanatory plant trait and environmental variables (X). The X variables were stomatal conductance, transpiration, density of stomata and glandular trichomes (where applicable), SLA, LDMC, twig height, VPD based on leaf temperature, PPFD from the weather station, air temperature at 2 m height, relative humidity at 2 m, wind speed, friction velocity as a proxy for turbulence (u*), soil moisture and soil temperature (at 10 cm depth).

2.9. Modelling of seasonal VOC emissions

An excel-based site version of MEGAN v3.1, mostly based on Guenther et al. (2012), was used to estimate seasonal emissions of VOCs for the four studied dwarf shrubs using the continuous weather data (at hourly resolution) and the species-specific emission factor (EF, μg m⁻² leaf area h⁻¹) derived from the measurement data as inputs. To model emissions from each single species, the model assumes a continuous canopy of one species at a time.

MEGAN accounts for radiation transfer within canopy environment and leaf-level energy balance. Radiation is partitioned into direct and diffuse light for both visible (PAR) and near infrared (NIR) ranges (equations used from Spitters et al., 1986a; and 1986b, Lizaso et al., 2005; Jacobides et al., 2007). In the canopy layer, reflection and scattering coefficients for PAR and NIR are specified as properties of plant functional type. The canopy in the model is divided into 5 layers, based on Gaussian distribution of leaf area from the top of canopy. For each canopy layer, the received 4 components of radiation change when going deeper into the canopy and the extinction coefficients are calculated based on Spitters et al. (1986b). After radiation partitioning, the canopy energy balance is solved to derive leaf temperature for both sunlit and shaded leaves based on Leuning (1989) and Goudriaan and Van Laar (1994). In the model, a spherical leaf angle distribution is assumed for canopy.

The model simulates emissions of 19 VOC groups based on a multiplication of EF with environmental response functions (Guenther et al., 1991, 2012). The EFs of 19 MEGAN compound groups for each plant species were extracted from the measurements, which had the measured leaf temperature within the range of 29–31 °C and standardized to uniform conditions (PPFD of 1000 μmol m⁻² s⁻¹ and temperature of 30 °C). In total, the numbers of samples used for parameterizing EFs were 5, 3, 4, and 5 for Salix, Betula, Cassiope, and Rhododendron, respectively. The measurements used for parameterizing EFs were excluded from model evaluation. The commonly-used EF values in MEGAN used for shrubs are also listed for comparison (Table 1). Furthermore, the hourly measured air temperature (at 20 cm and 2 m), PPFD, relative humidity and soil moisture from the weather station were used to drive the model. As all VOC samples were taken near the weather station, the same weather inputs were used for simulating the ecosystem emissions from these 4 species.

Since there were no in situ measurements of leaf area index (LAI), a LAI value of 0.95 was used for Cassiope based on Campioli et al. (2009). For the other species, the LAI values were taken from the nearest grid of MODIS product (MCD15A2H Version 6, with LAI value for every 8 days). The MODIS LAI ranged from 0.9 to 1.7 m²/m² from early June to the end of August. The model has been parameterized with the measured canopy height, canopy depth and leaf size based on the measurements. The detailed observation data used for the modelling part has been listed in Table S2.

3. Results

3.1. Leaf temperature

According to our measurements in the field, the leaf temperature mean was not substantially different between the four plant species
Table 1

Emission factors\(^\dagger\) (standardized emission rate ± SD, μg m\(^{-2}\) leaf area h\(^{-1}\)) used in MEGAN based on the leaf-level measurements with leaf temperature in the range of 29-31\(^\circ\)C.

<table>
<thead>
<tr>
<th>Compound groups</th>
<th>Salix (n = 5)</th>
<th>Betula (n = 3)</th>
<th>Cassiope (n = 4)</th>
<th>Rhododendron (n = 5)</th>
<th>ME-GAN(*)</th>
</tr>
</thead>
<tbody>
<tr>
<td>isoprene</td>
<td>2534.1 ± 1505.2</td>
<td>9.2 ± 15.9</td>
<td>23.1 ± 46.2</td>
<td>25.5 ± 31.7</td>
<td>1471.4</td>
</tr>
<tr>
<td>MBO</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>0.6</td>
</tr>
<tr>
<td>MT1: pinenes (α and β)</td>
<td>12.4 ± 8.9</td>
<td>6.0 ± 6.8</td>
<td>100.0 ± 67.7</td>
<td>4.3 ± 3.2</td>
<td>112.8</td>
</tr>
<tr>
<td>MT2: acyclic 3 bonds; myrcene; ocimes</td>
<td>10.4 ± 5.0</td>
<td>0.04 ± 0.07</td>
<td>21.2 ± 13.1</td>
<td>1.8 ± 1.7</td>
<td>54.0</td>
</tr>
<tr>
<td>MT3: carene; camphene; others</td>
<td>2.1 ± 3.0</td>
<td>206.0 ± 281.0</td>
<td>1544.0 ± 1442.0</td>
<td>N/A</td>
<td>44.1</td>
</tr>
<tr>
<td>MT4: limonene; terpinenes; others</td>
<td>50.7 ± 67.4</td>
<td>1.5 ± 1.4</td>
<td>6321 ± 4446</td>
<td>0.8 ± 0.8</td>
<td>78.5</td>
</tr>
<tr>
<td>C10 aromatic: cymenes; cymenenes</td>
<td>5.5 ± 3.1</td>
<td>1.3 ± 1.1</td>
<td>32.7 ± 19.8</td>
<td>N/A</td>
<td>77.3</td>
</tr>
<tr>
<td>C8-C13 Oxygenated (e.g. camphor)</td>
<td>N/A</td>
<td>55 ± 55</td>
<td>194 ± 135</td>
<td>9.0 ± 15.0</td>
<td>43.8</td>
</tr>
<tr>
<td>highly reactive SQT (e.g. caryophyllene)</td>
<td>421.1 ± 264.2</td>
<td>28.4 ± 22.5</td>
<td>37.0 ± 29.3</td>
<td>2825.0 ± 1450.0</td>
<td>7.4</td>
</tr>
<tr>
<td>less reactive SQT (e.g. copane)</td>
<td>3.5 ± 3.9</td>
<td>30.0 ± 31.6</td>
<td>99.7 ± 53.8</td>
<td>8.9 ± 9.9</td>
<td>29.4</td>
</tr>
<tr>
<td>methanol</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>150.0</td>
</tr>
<tr>
<td>acetone</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>37.6</td>
</tr>
<tr>
<td>acetaldehyde and ethanol</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>29.16</td>
</tr>
<tr>
<td>organic acids: formic, acetic, pyruvic</td>
<td>0.04 ± 0.07</td>
<td>0.02 ± 0.04</td>
<td>65.20 ± 87.10</td>
<td>0.01 ± 0.01</td>
<td>28.0</td>
</tr>
<tr>
<td>C2 to C4 HC (e.g.; ethene; ethane)</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>102.5</td>
</tr>
<tr>
<td>oxidation products: aldehydes</td>
<td>168.2 ± 166.2</td>
<td>N/A</td>
<td>43.1 ± 44.1</td>
<td>92.2 ± 140.0</td>
<td>4.7</td>
</tr>
<tr>
<td>Stress compounds (e.g.; linalool)</td>
<td>746.0 ± 299.0</td>
<td>418.0 ± 64.0</td>
<td>364.0 ± 226.0</td>
<td>465.0 ± 731.0</td>
<td>5.6</td>
</tr>
<tr>
<td>other VOCs (e.g., indole, pentane)</td>
<td>9.1 ± 6.8</td>
<td>3.6 ± 5.8</td>
<td>304.3 ± 190.2</td>
<td>188.1 ± 155.3</td>
<td>22.9</td>
</tr>
<tr>
<td>carbon monoxide</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>0.3</td>
</tr>
</tbody>
</table>

\(^\dagger\) Emission rate standardized to the temperature of 30 \(^\circ\)C and PPFD of 1000 μmol m\(^{-2}\) s\(^{-1}\) based on Guenther et al. (1993).

\(*\) MEGAN original values for shrub plant functional type; MTs: monoterpenes; N/A. means no data available from the measurements. MBO: Methylbutenol; HC: hydrocarbon.

Fig. 2. Regression coefficients from PLS regression models on leaf temperature in Salix (a), Betula (b), Cassiope (c) and Rhododendron (d). Error bars show ± 2 standard deviations of the regression coefficients. Significant variables are marked with grey bars. Significance of the model (CV-ANOVA) is shown p < 0.001 ***. p < 0.05 *.
Soil temperature (Fig. 2c). Leaf temperature in Salix correlated negatively with stomatal density. Leaf temperature in Betula correlated positively with VPD, soil and air temperature and transpiration rate (Fig. 2a). Leaf temperature in Salix correlated negatively with stomatal density. Leaf temperature in Betula correlated positively with VPD, soil and air temperature, PPDF, soil moisture, and transpiration. It correlated negatively with the SLA (Fig. 2b). Leaf temperature in Cassiope showed a positive correlation to air temperature and VPD but negative correlations with air humidity, soil moisture, and soil temperature (Fig. 2c). Leaf temperature in Rhododendron was positively correlated with air temperature and negatively with wind speed, but the model was not significant (Fig. 2d; p = 0.34, CV-ANOVA).

3.2. VOC emissions

3.2.1. Salix myrsinites

VOC emission from Salix was on average 21.7 μg g⁻¹ dw h⁻¹ (Fig. 3a). Isoprene was the most emitted VOC (contributing 64% of the total by mass), whilst non-isoprenoid VOCs, sesquiterpenes and monoterpenes constituted 24%, 7%, and 5%, respectively (Fig. 3b).

Emission rates for all compounds across the measurement period are presented in the supplementary Table S4. On June 30, when air temperature was below 10 °C and leaf temperature approx. 13 °C, isoprene emission was low, around 0.04 μg g⁻¹ dw h⁻¹ (Table S4). Isoprene emission was much higher on July 17, at 23.4 μg g⁻¹ dw h⁻¹ and peaked on July 22 at 28.3 μg g⁻¹ dw h⁻¹, when leaf temperature was around 24 °C. Finally, the isoprene emission was again low, ca. 3.7 μg g⁻¹ dw h⁻¹ on August 15 measurement with leaf temperatures of 14 °C. Other VOC groups emitted by Salix followed a similar pattern (Table S4).

3.2.2. Betula nana

Averaged over the measurement period, Betula had a total VOC emission rate of 9.8 μg g⁻¹ dw h⁻¹ (Fig. 3a). Of all VOC groups, non-isoprenoid VOCs were the most abundant (77% by mass), followed by non-oxygenated monoterpenes (21%), with other groups contributing by 2% (Fig. 3b). The single most emitted VOC was 2-hexenal with 2.4 μg g⁻¹ dw h⁻¹, followed by the monoterpenes-3-carene with 1.9 μg g⁻¹ dw h⁻¹ (See Table S5 for individual compounds).

On June 30, when the air temperature was below 10 °C and leaf temperature at 14 °C, the emission of non-isoprenoid VOCs was low, 3 μg g⁻¹ dw h⁻¹, but the emission of non-oxygenated monoterpenes was, compared to the rest of field season, relatively high with 4.6 μg g⁻¹ dw h⁻¹ (Table S5). With the higher air (16 °C) and leaf temperature (23 °C) on July 10, non-isoprenoid VOC emission reached a high of 18.5 μg g⁻¹ dw h⁻¹, while the MT emission was at its lowest, 0.006 μg g⁻¹ dw h⁻¹. Later measurements on July 20 and 24 were characterized by lower leaf temperature and VOC emissions. On August 18, when the air and leaf temperatures were 16 °C and 18 °C, respectively, the non-isoprenoid VOC emission reached a low of 1.1 μg g⁻¹ dw h⁻¹, while the MT emission reached a peak of approximately 4.9 μg g⁻¹ dw h⁻¹.

3.2.3. Cassiope tetragona

Cassiope had a total VOC emission rate of 52.1 μg g⁻¹ dw h⁻¹ averaged over the measurement period (Fig. 3a). Non-oxygenated monoterpenes accounted for almost 85% of the total VOCs (Fig. 3b) by mass. α-terpinene at 39.3 μg g⁻¹ dw h⁻¹ was the dominant compound and responsible for 82.5% of the total VOC emission (Supplementary Table S6). MT emission was highest on July 2, at 121.9 μg g⁻¹ dw h⁻¹, when both air (21 °C) and leaf temperatures (28 °C) were highest as well (Table S6). On July 10, MT emission was 35.7 μg g⁻¹ dw h⁻¹, even though the air and leaf temperatures remained similar as in the previous measurement (18 °C and 26 °C, respectively). In the two last measurements, on July 20 and 24, MT emissions were low (7.0 and 12.0 μg g⁻¹ dw h⁻¹).

3.2.4. Rhododendron lapponicum

The total VOC emission from Rhododendron averaged over the measurement period was 38.9 μg g⁻¹ dw h⁻¹ (Fig. 3a). Sesquiterpenes dominated the VOC blend of this species (92% by mass) followed by non-isoprenoid VOCs (8%; Fig. 3b). The most emitted sesquiterpene, responsible for over half of the total VOC emission, was β-elemene at 21.7 μg g⁻¹ dw h⁻¹, followed by α-selinene and α-humulene (Supplementary Table S7). Rhododendron emissions were only measured in July, through which sesquiterpene emission, together with leaf and air temperature, remained high (mean ± SE of 35.7 ± 7.1 μg g⁻¹ dw h⁻¹, Table S7).

3.3. Covariance between explanatory variables and VOC emission

We used PLS regression to test if plant traits and environmental factors (X variables) can explain the variation in the emissions of the most emitted individual VOCs (Y-variables) of the investigated plants species. Data on all the plant traits are shown in the Supplementary Table S8.

The dominating compounds we analyzed with the PLS regression were isoprene in Salix, 3-carene and 2-hexenal in Betula and α-terpinene in Cassiope (Fig. 4).

The PLS regression model for Salix showed significant positive correlation between isoprene emission and soil, leaf and air temperatures, ETR and VPD (Fig. 4a). Isoprene emission also positively correlated with transpiration, but due to large variation in transpiration, this was not statistically significant. Isoprene emission correlated negatively with stomatal density of adaxial side of the leaves.

3-carene emitted by Betula correlated positively with SLA and the intercellular CO₂ concentration and negatively with leaf, soil and air temperatures (Fig. 4b). 2-hexenal emission from Betula showed positive
Fig. 4. Regression coefficients from PLS regression model of isoprene emission in *Salix* (a), 3-carene emission in *Betula* (b), 2-hexenal emission in *Betula* (c) and γ-terpinene emission in *Cassiope* (d). Error bars show ±2 standard deviations of the regression coefficients. Significant variables are marked with grey bars. Significance of the model (CV-ANOVA) is shown $p < 0.001^{***}$, $p < 0.05^*$. 

Fig. 5. Temperature response curves of net photosynthesis ($A_n$), emission rate (Er) of the main VOC group and the transpiration rate (Tr) for the investigated plant species. The symbols show three (two for *Salix*) independent measurements and the solid line shows the fitted average.
correlation with ETR, VPD and leaf temperature. It correlated negatively with intercellular CO\textsubscript{2} concentration and SLA (Fig. 4c).

\(\Gamma\)-terpinene emission from Cassiope was positively correlated with leaf and ambient air temperature, as well as ambient PPFD and negatively correlated with transpiration, stomatal conductance, soil temperature and relative humidity of the ambient air (Fig. 4d).

No PLS models converged for the emissions of the dominant VOCs from Rhododendron.

3.4. Temperature response curves

In Salix, net photosynthesis (\(A_n\)) increased from 10 °C, plateaued around 24 °C and decreased at the higher temperatures (Fig. 5a). Isoprene emission increased exponentially within our temperature range of 10–38 °C (Fig. 5b).

In Betula, \(A_n\) increased until our measurement temperature of 31 °C and was lower at our highest temperature (Fig. 5d). The emission of the dominant VOC group, non-isoprenoid VOCs, varied considerably for the three independent replicates with no clear temperature dependency (Fig. 5e).

Cassiope showed a nearly linear response of \(A_n\) to temperature increase until our highest measurement temperature of 38 °C (Fig. 5g). Monoterpenes emission increased steadily until 31 °C and then sharply for the two replicates measured at 38 °C (Fig. 5h).

In Rhododendron, net photosynthesis increased until around our measurement temperature of 31 °C with no clear decrease at our highest temperature (Fig. 5j). The emission of sesquiterpenes increased exponentially with temperature (Fig. 5k).

The transpiration rate increased exponentially with leaf temperature in Salix and Cassiope (Fig. 5c, i), potentially causing water stress for plants. In Betula and Rhododendron (Fig. 5f, l), the transpiration rates at higher leaf temperatures differed between individual samples, and the fitted average reached a plateau, potentially indicating stomatal closure to reduce water loss through transpiration.

The percentage of carbon emitted as VOCs relative to the amount fixed in photosynthesis varied between species and temperature (Supplementary Table S9). In Betula and Salix, under 1% of carbon fixed was emitted as VOCs, except for the last temperature step in Salix with

![Fig. 6. The measured and modelled VOC emissions (\(\mu g \text{ m}^{-2} \text{ ground area h}^{-1}\)) for S. myrsinites (a), B. nana (b), C. tetragona (c), and R. lapponicum (d). The emissions were measured at the conditions of PPFD at 1000 \(\mu mol \text{ m}^{-2} \text{ s}^{-1}\) and leaf temperature comparable to ambient, and the modelled emissions were recalculated to the same PPFD level using the light response function in MEGAN. The 13 out of the 19 MEGAN VOC groups (see Table 1) with values are shown. MT1: \(\alpha\) and \(\beta\)-pinenes; MT2: Acyclic 3 bonds; myrcene; ocimenes; MT3: carene, camphene, and others; MT4: sabinene, limonene, terpinenes, and others. HighR and LessR refer to highly reactive and less reactive, respectively.](image-url)
3.5 ± 2.6 % C loss as VOCs. In *Cassiope* and *Rhododendron*, there was large variation between the replicates and a tendency of the percentages increasing with temperature. Photosynthetically fixed carbon emitted as VOCs in *Cassiope* was between -1.3 ± 1.7 % and 15.9 ± 4.5 % and between 0.8 ± 2.2 and 3.7 ± 2.5 % in *Rhododendron*.

With increasing leaf temperature, WUE decreased in deciduous shrubs, increased in *Rhododendron* and had no distinct pattern in *Cassiope* (Table S9). Stomatal conductance ($g_s$) decreased throughout the temperature response curves in all species, except in *Cassiope* where it stayed around 0.05 mol H$_2$O m$^{-2}$ s$^{-1}$ (Table S9). Supplementary Table S9 also contains information about photosynthesis and transpiration of the measured plants throughout temperature response curves.

3.5. Modelled VOC emissions

The studied species varied considerably in EFs for different compound groups. For some groups, the measured EFs were much higher than the original EFs used for shrubs in MEGAN (Table 1), for example, for isoprene from *Salix*, MT3 and MT4 from *Cassiope*, highly reactive SQT from *Salix* and *Rhododendron*, oxidation products from *Salix* and other VOCs from *Rhododendron* and *Cassiope*. Also, the EFs for the stress-related compounds were much higher than the original EFs in MEGAN.

The VOC emissions measured at ambient leaf temperature were matched to the modelled ones at corresponding time points and averaged over the same day for each species (Fig. 6). The wide spread of emission magnitudes of different compounds was generally captured by the model for *Salix* and *Rhododendron* (Fig. 6a,d). For *Betula*, the model largely underestimated the measured emissions for some groups, e.g., organic acids (less than 0.01 % of the observed), MT2 (13.2 % of the observed) and stress-related compounds (0.07 % of the observed) (Fig. 6b). For the compounds with high emission rates, the model overestimated the MT3 and MT4 (158.5 % and 71.0 % of the observed, respectively) emissions from *Cassiope* (Fig. 6c), but underestimated the isoprene emissions (32.2 % of the observed) and high reactive SQT (17.8 % of the observed) emissions from *Salix* and *Rhododendron*, respectively.

After evaluating the modelled output at the time of the measurements, the seasonal variability in VOC emissions was also quantified (Fig. 7). Using 20 cm air temperature instead of the 2 m air temperature were 44 %, 33 %, 31 %, and 48 % for *Salix*, *Betula*, *Cassiope* and *Rhododendron*, respectively. When summing up the modelled emissions for the period June 8 to September 2 using 2 m air temperatures, the total VOC emissions for *Salix*, *Betula*, *Cassiope* and *Rhododendron* were 0.9, 0.3, 2.3 and 0.7 g m$^{-2}$, respectively. By applying air temperature at 20 cm height instead, the modelled seasonal emissions increased by 21.4 %, 15.2 %, 14.1 % and 23.0 % for *Salix*, *Betula*, *Cassiope* and *Rhododendron*, respectively.

4. Discussion

4.1. Factors affecting leaf temperature and VOC emission in tundra shrubs

The main aim of our study was to assess the control of leaf temperature in four tundra shrub species and to study effects of plant traits, leaf temperature and other environmental factors on VOC emission from four common arctic shrubs. Despite high natural variation, we identified some plant traits linked to leaf temperature and VOC emission in the studied deciduous, but not in the evergreen shrub species.

The most important plant traits that correlated with leaf temperature in the studied deciduous shrubs were morphological leaf traits, LDMC and SLA, as well as stomata-related variables stomatal density, stomatal conductance and transpiration. SLA (ratio between leaf area and dry mass), differed largely between thicker and thinner leaves, which is important for determining the efficiency of heat retained inside the leaves (Leigh et al., 2012; Rosbakh et al., 2015). We observed that leaves with higher SLA were cooler, while plants with lower SLA had higher leaf temperatures. The findings of Schollert et al. (2015, 2017) suggest that the palisade parenchyma, epidermis and overall leaf thickness of the dwarf birch leaves might increase under a warmer climate. However, a trend of larger and thinner leaves at elevated temperatures has been observed for silver birch, *Betula pendula*, and other woody species at lower latitudes (Luomala et al., 2005; Hartikainen et al., 2009; Rasulov et al., 2015).

Leaf temperature naturally correlated with air (and soil) temperature, which is intercorrelated with PPFD. Solar radiation, here expressed as PPFD, effectively heats up the surface of leaves in low, dense tundra plant communities (Lindwall et al., 2015; Körner, 2019).

Fig. 7. The growing season VOC emissions (mg m$^{-2}$ ground area h$^{-1}$) modelled using air temperature at 2 m height (left-side axis). The modelled difference ratio (in percentage, %) between using 20 cm and 2 m air temperature inputs is plotted on the right-side axis.
Notwithstanding the structure of our setup, we observed that VPD was positively related to leaf temperature in all studied plant species. VPD has earlier been shown to be important for photosynthesis through increased stomatal closure at higher VPD (Lin et al., 2012). Increased air temperature was recently coupled to high VPD and increased terpenoid emission in an evergreen tree species (Duan et al., 2019). Furthermore, high air temperature and water deficit have been observed in earlier studies to strongly stimulate VOC emission of tundra plants (Kramshoj et al., 2016; Lindwall et al., 2016; Tang et al., 2018).

Our results showed that plant traits contributed to the measured VOC emission variations. We observed a positive correlation of ETR with isoprene emission in Salix. This correlation has been described before (Guenther et al., 1991; Monson et al., 1992; Sharkey and Monson, 2017) and reinforces the findings of Niinemets et al. (2004) that the ETR can be used for estimating isoprene emission. Isoprene emission provides protection against short-term periods of high leaf temperature (Singsaas and Sharkey, 1998; Singsaas et al., 1999) and is thought not to be limited by stomata (Monson and Fall, 1989). Our negative correlation between stomatal density of Salix leaves and isoprene emission is likely related to strong direct temperature response rather than an actual negative correlation.

The positive correlation between ETR and 2-hexenal emission in Betula suggests that, like isoprene, this compound is likely synthesized de-novo. The Betula leaves emitting most VOCs such as 2-hexenal were the ones with low SLA values (smaller and thicker leaves) and low intercellular CO2 concentration. Contrary, the plants emitting most 3-carene were the ones with larger, thinner leaves and high intercellular CO2 concentration. We suggest this is due to the natural physiological variation of this species. B. pendula and B. pubescens have been documented to exhibit large within-species variation in VOC emissions (Hakola et al., 2001; Maja et al., 2015).

We also observed a negative correlation between stomatal conductance/transpiration and γ-terpinene emission in Cassiope. We suggest that this relationship is due to leaf temperature, which was negatively correlated with stomatal conductance.

The lack of correlation between VOC emission in R. lapponicum and the studied variables could be due to unquantified plant traits (for example number of flowers, leaf anatomy or N and P content in leaves) determining the relationship in this species or due to the technical challenges of sesquiterpene measurements (Duhl et al., 2008) leading to high variation in emission rates.

4.2. Temperature response of photosynthesis and VOC emission

We observed that the subarctic S. myrsinites photosynthesis increased with temperature until our measurement temperature of 24 °C and remained at a similar level still at our next measurement temperature of 31 °C, which suggests a higher Topt than the values derived for Salix polaris from the High Arctic (15 °C, Muraoaka et al., 2002), for Salix myrsinifolia from a Finnish boreal forest (~20 °C, Kaipiainen and Pelkonen, 2007), and even for Salix viminalis from southwest Sweden (20 °C, Genciala and Lindroth, 1995). According to the work of Körner (2003a, d), the photosynthetic apparatus of alpine plants is optimized for their growth temperature. The higher Topt values in the low-statured tundra shrubs are likely related to the elevated leaf temperatures the plants experience.

Monson et al. (1992) determined that Topt for isoprene synthase activity for the velvet bean, Mucuna pruriens L. is usually 5–10 °C higher than Topt for photosynthesis. In our two samples, isoprene emission in S. myrsinites indeed increased to higher temperatures than photosynthesis. Thus, the temperature sensitivity for isoprene emission in tundra vegetation seems stronger than that for photosynthesis. Warming by 3.4 °C increases photosynthesis in boreal tree species when soil moisture is high (Reich et al., 2018). However, a large discrepancy has been earlier reported in response to warming between ecosystem-level isoprene emission and CO2 exchange: A field experiment conducted on a Greenlandic tundra heath dominated by Salix glauca showed that warming by approx. 3 °C caused a 240 % increase in isoprene emission (Kramshoj et al., 2016), while the same treatment significantly decreased gross primary production (Dahl et al., 2017), through enhanced soil respiration at higher temperatures.

We observed that the Topt of B. nana An was between 24 °C and 38 °C, which matches the findings of (Chapin and Shaver, 1996) for the same species, and is similar to the optimum of B. pendula (Wittmann and Pfanz, 2007). B. nana is known for high non-isoprenoid emission rates (Rinnan et al., 2011; Scholliert et al., 2015; Vedel-Petersen et al., 2015; Li et al., 2019). However, the temperature responses of the emissions did not show a consistent pattern between the samples, probably as this is a complex group of compounds with different molecular structures or it can reflect the individual differences between plants.

Cassiope, together with other evergreen tundra shrubs, is known to have a low rate of photosynthesis compared to deciduous shrubs (Chapin and Shaver, 1985) with a clear temperature limitation to shoot growth (Havström et al., 1999; Campbell et al., 2013). In our temperature response curves, An of Cassiope increased with temperature until our last step, at 38 °C, suggesting good heat tolerance. Emission of mono-terpenes, the most abundant VOC group, increased steadily with temperature and then drastically above 30 °C.

R. lapponicum showed increasing An towards our highest measurement temperatures, which suggests that it is also a very heat tolerant species. The Topt for R. lapponicum An may indeed be higher than the average surrounding air temperature, and even higher than the leaf Topt for An of more southern species (25 °C for Rhododendron hyperythrum from Taiwan and Rhododendron catawbiense from eastern USA, 20 °C for Rhododendron rassatum from China; Ranney et al., 1995). The overall low rate of carbon assimilation compared to Salix and Betula may be due to that tundra Rhododendron spp. have high autotrophic respiration rates (plant metabolism) which creates a major electron sink (Huang et al., 2015). The emission rate of sesquiterpenes, which dominate the total VOC blend of Rhododendron, continued to rise through our temperature increment range. Sesquiterpene emissions are known to increase drastically at higher temperatures (Duhl et al., 2008).

The percentage of photosynthetically fixed carbon emitted as VOCs generally increased at higher temperatures. The changes in the loss of fixed carbon as VOC with leaf temperature are important when assessing the ecosystem carbon budget (Kesselmeier et al., 2002).

4.3. Modelled tundra ecosystem VOC emissions

The used VOC measurement technique only quantified VOCs with minimum five carbon atoms, and therefore six out of the 19 MEGAN groups could not be compared in this study (Table 1). For the 13 groups that were quantified, the studied four dwarf shrubs differed greatly from each other and also from the default MEGAN values, which demonstrates the diversity of emission profiles at species level. As VOC emissions vary between species, it is ultimately necessary to consider species composition and their contribution to emissions at community or regional levels (Valolahti et al., 2015). The sample size used for parametrizing EFs was small and there was high within-species variation, which means that the modelled magnitudes for different compound groups may change when including more samples.

The modelled total VOC emissions for the growing season 2018 are in the range 0.3–2.3 g m⁻². These modelled seasonal totals are higher than the annual totals of isoprene and monoterpene emissions in the same region, obtained previously using a different ecosystem model (LPJ-GUESS, Tang et al., 2016). However, other issues could explain the discrepancy: 1) Stress-related compounds seem abundant for all the studied species but this compound group was not considered in the previous modelling study; 2) The summer 2018 was warm, some days with an air temperature at 2 m of 30 °C (Fig. 1e), and temperature differences between years of course contribute to modelled differences in different years. We cannot elucidate whether part of the stress
compounds were emitted in response to this particularly hot summer. It should also be noted that, as it was not possible to derive significant temperature response curves for all compound groups used in MEGAN, the modelled seasonal values in this study were based on the standard G93 temperature response curve (Guenther et al., 1993), which may underestimate emissions as compared to using a temperature response curve derived from arctic species (Tang et al., 2016; Seco et al., 2020).

The modelled summer season emissions increased by 14–23 % when replacing the model input of 2 m air temperature with temperature measured close to the shrub canopy, at 20 cm height from the ground. The differences can be even larger if we also include the effect of wind speed contribution on leaf boundary layer conductance. At the canopy height (often 20 cm or less), the wind speed is typically lower than at 2 m height, indicating less efficient vertical mixing and decoupling between air temperature and leaf temperature. The conventional way of using 2 m air temperature for modelling inputs may cause large uncertainties in simulating ecosystem processes in this region.

4.4. Limitations and future directions

To our knowledge, this is the first study to assess the importance of leaf temperature on gas exchange and VOC emission from tundra shrubs on the branch scale. As such, it carried some limitations with it, mainly in the limited number of replicates, studied plant species and locations covered. A higher number of independent, replicate measurements would allow for more robust PLS models and more detailed analysis within a single plant species.

It would be relevant also to compare further plant species, including other growth forms important in the tundra, such as graminoids and bryophytes. Tundra ecosystems span an enormous area of our planet with plants that are adjusted to the local environmental conditions, and still the field studies focus on a few hotspot study locations, including our study site Abisko (Metcalfe et al., 2018). As this can bias our understanding, other studies across the Arctic would be appreciated.

5. Conclusions

We showed that air temperature and VPD were the most important environmental factors driving leaf temperature and VOC emission from the studied sub-arctic tundra, while plant traits affecting leaf temperature and VOC emissions of arctic tundra shrubs were species-specific. With the ongoing climate change, we expect increasing temperatures and alterations in cloudiness and soil water availability, which are likely to have a profound effect on both leaf temperature and VOC emission from tundra shrubs. Leaf temperature of these low-statured plants tends to be decoupled from the air temperature at 2 m height, which is commonly used as model input, leading to underestimation of VOC emission rates. Indeed, our study illustrated a higher-than-expected $T_{opt}$ for both photosynthesis and VOC emissions for the studied tundra species showing that they are well acclimated to a near-surface temperature that often exceeds the commonly used air temperature taken at a standard height. This suggests strong responses with climatic warming.

Author contributions

T.S. performed field measurements, analyzed data, prepared graphs and wrote the original manuscript with contributions from all authors; J.T. performed modeling and prepared graphs; T.H. provided instrumentation and set up the weather station; R.R. designed the experiment and coordinated and supervised the research; All authors discussed the results and edited the manuscript.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgements

This work was supported by the European Research Council (ERC) under the European Union’s Horizon 2020 research and innovation programme (grant agreement No 771012) and the Danish National Research Foundation (Center for Permafrost, CENPERM DNRF100). Jing Tang was financially supported by European Union’s Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No. 707187 and FORMAS grant (No. 2016-01580). We thank Abisko Scientific Research Station for being able to use their excellent facilities. We appreciate Prof. Alex Guenther’s instructions on the MEGAN model setup. We would also like to thank Marios Vazakas for the help in fieldwork preparation, Trine Mariager and Nanna Schroder Baggesen for assistance in data collection, and Tatjana Simin for language revision.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.envexpbot.2021.10387

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