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Title: Impact of severe drought on biogenic volatile organic compounds emissions from Sphagnum mosses in boreal peatlands

Year: 2024

Version: Published version

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Please cite the original version:

Elisa Männistö, Henni Yläne, Nicola Kokkonen, Aino Korrensalo, Anna M. Laine, Pasi Yli-Pirilä, Markku Keinänen, Eeva-Stiina Tuittila, Impact of severe drought on biogenic volatile organic compounds emissions from Sphagnum mosses in boreal peatlands, Science of The Total Environment, Volume 951, 2024, 175738, <https://doi.org/10.1016/j.scitotenv.2024.175738>

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Impact of severe drought on biogenic volatile organic compounds emissions from *Sphagnum* mosses in boreal peatlands

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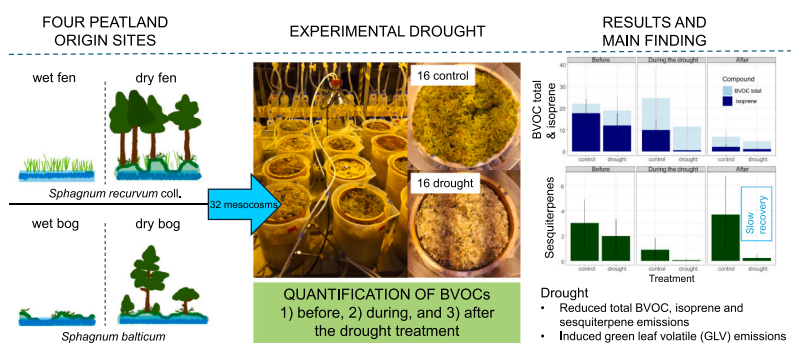
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HIGHLIGHTS

- First time direct quantification of severe drought impact on *Sphagnum* BVOC release.
- Drought reduced total BVOC, isoprene and sesquiterpene emissions from *Sphagnum*.
- Total BVOC and isoprene emissions recovered from the drought.
- Sesquiterpene emission remained low after six weeks since the ending of the drought.
- Seasonal drought may negate the effect of warming on boreal peatland BVOC release.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Zhaozhong Feng

Keywords:

Bog
Fen
Isoprene
Mire
Sesquiterpene
Water table

ABSTRACT

Climate change and the associated increased frequency of extreme weather events are likely to alter the emissions of biogenic volatile organic compounds (BVOCs) from boreal peatlands. Hydrologically sensitive *Sphagnum* mosses are keystone species in boreal peatland ecosystems that are known to emit various BVOCs. However, it is not known how their emissions respond to seasonal droughts. In this study, we quantified the effect of severe drought, and subsequent recovery, on the BVOC emissions from *Sphagnum* mosses using mesocosms originating from wet open and naturally drier treed boreal fens and bogs. Here we report the emissions of 30 detected BVOCs, of which isoprene was the most abundant with an average flux rate of $5.6 \mu\text{g m}^{-2} \text{h}^{-1}$ (range 0–31.9 $\mu\text{g m}^{-2} \text{h}^{-1}$). The experimental 43-day ecohydrological drought reduced total BVOC and isoprene emissions. In addition, in mesocosms originating from bogs, sesquiterpene emissions decreased with the drought, while the emissions of green leaf volatiles were induced. Sesquiterpene emissions remained low even six weeks after rewetting, indicating a long and limited recovery from the drought. Our results further imply that long-term exposure to deep water tables does not decrease sensitivity of *Sphagnum* to an extreme drought; we did not detect differences in the emission rates or drought responses between *Sphagnum* originating from wet open and naturally drier treed habitats. Yet, the differences between fen and bog originating *Sphagnum* indicate local

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<https://doi.org/10.1016/j.scitotenv.2024.175738>

Received 9 April 2024; Received in revised form 17 August 2024; Accepted 21 August 2024

Available online 23 August 2024

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variability in the BVOC quality changes following drought, potentially altering the climate feedback of boreal peatland BVOC emissions.

1. Introduction

Boreal peatlands are key ecosystems in controlling the climate as they store an estimated 1/3 of global soil carbon (C), serve as a sink for carbon dioxide (CO₂) and are a major natural source of methane (CH₄) (Strack, 2008; Zhang et al., 2023). These ecosystems also release a diversity of biogenic volatile organic compounds (BVOCs), which are reactive hydrocarbons common to terrestrial vegetation (Guenther et al., 1995; Laothawornkitkul et al., 2009). When released into the atmosphere, BVOCs are oxidised resulting in various impacts to atmospheric chemistry. They can have a warming impact on climate by prolonging the lifetime of methane by competing for OH radicals (Kaplan et al., 2006) and take part in the formation of tropospheric ozone (Atkinson, 2000). However, BVOCs can also mitigate climate warming through their negative radiative forcing effects (Paasonen et al., 2013) as they contribute to the formation of secondary organic aerosols (SOA) (Hoffmann et al., 1997; Virtanen et al., 2010; Kulmala et al., 2014). As a result, BVOCs may have a net climate cooling effect, as suggested in boreal forests (e.g., Cleveland and Yavitt, 1998; Aaltonen et al., 2013; Mäki et al., 2017; Hellén et al., 2018 and the references therein). Additionally, forest BVOC emissions are known to respond to environmental changes, and for example, severe droughts have been reported to reduce BVOC emissions (Rennenberg et al., 2006; Lappalainen et al., 2009; Haberstroh et al., 2022). The BVOC emissions from boreal peatland ecosystems composition, climate impact and response to environmental changes remain less studied than forest emissions, despite that peatlands cover up to one quarter of the boreal zone.

Peatland BVOC emissions have been shown to be dominated by isoprene (2-methyl-1,3-butadiene; C₅H₈) (e.g., Janson and De Serves, 1998; Haapanala et al., 2006; Männistö et al., 2023), and include smaller proportions of numerous monoterpenes (C₁₀), sesquiterpenes (C₁₅), and other BVOCs (Janson and De Serves, 1998; Janson et al., 1999; Rinnan et al., 2005; Hellén et al., 2006; Faubert et al., 2010a, 2010b; Holst et al., 2010; Lindwall et al., 2016; Seco et al., 2020; Hellén et al., 2020; Männistö et al., 2023). The quality and quantity of BVOC emissions depend on environmental factors, such as temperature and light (e.g., Guenther et al., 1993; Kesselmeier and Staudt, 1999; Peñuelas and Llusià, 2001; Tarvainen et al., 2005; Duhl et al., 2008; Ma et al., 2024), as well as on the vegetation type (Isebrands et al., 1999; Rinnan et al., 2005; Männistö et al., 2023; Wang et al., 2023). While some BVOCs, e.g., isoprene, sesquiterpenes, and green leaf volatiles (GLV) are strongly connected to vascular vegetation (Männistö et al., 2023), equally high emission rates are also reported from a variety of mosses (Hellén et al., 2006; Edtbauer et al., 2021; Männistö et al., 2023) with species-specific differences in their BVOC emission rates and composition (Hanson et al., 1999; Ekberg et al., 2011; Ryde et al., 2022). Also, *Sphagnum* mosses, a fundamental part of boreal peatland ecosystems, are a significant source of BVOCs (Janson and De Serves, 1998; Tiiva et al., 2009; Faubert et al., 2010b; Ekberg et al., 2011; Ryde et al., 2022; Männistö et al., 2023), but it is not well known how their emissions respond to environmental factors and stressors.

Unlike vascular plants, *Sphagnum* mosses do not have vascular system to regulate their water content but rely on external capillary water to keep their living cells turgid and physiologically active (Hájek, 2013; Weston et al., 2018). Therefore, *Sphagnum* mosses are specialized to wet habitats and are susceptible to extreme fluctuations in moisture conditions, e.g., with drying decreasing their photosynthesis and severe drought stopping it completely (Titus and Wagner, 1984; Gerdol et al., 1996; Schipperges and Rydin, 1998; Winnicka et al., 2018; Kokkonen et al., 2024). They are strongly associated with peatlands where they form dense carpets; bogs and poor fens in the boreal region usually have

nearly continuous *Sphagnum* cover. Fens are peatlands that have a connection to surrounding mineral soil (i.e. minerotrophic) making them generally more nutrient-rich, whereas nutrient-poor bogs are solely dependent on rainwater for moisture (i.e. ombrotrophic). *Sphagnum* mosses are so-called “ecosystem engineers” in peatlands where they modify their environment (Van Breemen, 1995), especially by maintaining high water level (Van Breemen, 1995; Laing et al., 2014; Bengtsson et al., 2016; Laine et al., 2021). Species specialized to either dry hummocks or very wet conditions avoid desiccation by retaining water within their dense structure or via their submerged location, respectively. In contrast, the *Sphagna* growing in intermediate lawns are often exposed to fluctuations in the moisture conditions and can thus develop desiccation tolerance (Hájek and Vicherová, 2014). As different *Sphagnum* species have adapted to different moisture conditions and nutrient availability (Andrus, 1986; Väliiranta et al., 2007) also their BVOC emission response to water table fluctuations may also differ between species (Ekberg et al., 2011) and habitats. BVOC emission from *Sphagna* growing in naturally dry habitats could be less responsive to drought than emissions from *Sphagna* growing in open wet habitats because of adaptation to drier conditions, and subsequently, have a better capacity to tolerate and recover from moisture limitation. Yet, to our knowledge, the impact of habitat on the *Sphagnum* BVOC responses to drought has not been studied.

The ongoing climate warming is predicted to increase precipitation and evapotranspiration as well as prolong the growing season in boreal regions, while also increasing the frequency of extreme climatic events such as heatwaves and seasonal droughts (Donat et al., 2016; IPCC, 2023). These combined factors are projected to have a long-term drying effect on peatlands (Gorham, 1991; Roulet et al., 1992; Gong et al., 2012; Helbig et al., 2020). This drying can drive significant changes in their vegetation composition (Kokkonen et al., 2019) and thus alter the whole ecosystem dynamics. Lowering the water table has been shown to trigger species turnover of both vascular plants and *Sphagnum* mosses in nutrient-rich fens, whereas nutrient-poor bogs are more resilient to long-term drying (Kokkonen et al., 2019). Additionally, heatwaves and seasonal droughts such as the ones in Europe in summers 2018 and 2021 (Rinne et al., 2020; FMI, 2021) can also have direct short-term impacts on the functioning of peatland plants and especially *Sphagnum* mosses. Previously, water level drawdown in peatlands has decreased isoprene emission from a boreal bog (Tiiva et al., 2009), as well as emissions of monoterpenes, sesquiterpenes and other BVOCs (Faubert et al., 2010b; Faubert et al., 2011). Lowering the water table can also change the emission mixture of peatlands by increasing emissions of individual compounds (Faubert et al., 2010b; Männistö et al., 2023). These drought responses could revert once the stress is relieved, and lead to higher BVOC emissions than before the stress (Sharkey and Loreto, 1993; Brilli et al., 2007; Niinemets, 2010; Peñuelas and Staudt, 2010). However, studies on the effect of drought stress on peatland BVOC emissions are scarce and concentrate only on ombrotrophic bogs (Tiiva et al., 2009; Faubert et al., 2010b; Faubert et al., 2011). There are not yet any studies directly quantifying the impact of severe seasonal drought on BVOC emissions from *Sphagnum* mosses.

This study aims to experimentally quantify the effects of severe seasonal drought and recovery after drought on BVOC emissions from *Sphagnum* mosses originating from two habitat types with naturally differing moisture within a boreal fen and a bog. We expect the experimental drought to decrease total BVOC emissions from *Sphagnum* and alter their emission composition. The response is expected to be higher in mosses originating from wetter habitats and in fens. Mosses from bogs and naturally dry habitats are expected to be more resistant to drought stresses and recover faster.

2. Materials and methods

2.1. Study areas and collection of mesocosms

For this experiment, *Sphagnum* moss surface cores (“mesocosms”) were collected from Lakkasuo located in Southern Finland (61° 47' N; 24° 18' E) and transported to a controlled greenhouse environment. Lakkasuo is a ca. 130 ha boreal peatland complex, which contains a large range of peatland habitat types owing to variation in ecohydrology. Fertility and pH levels range from minerotrophic fen to more acidic ombrotrophic bog areas and water tables (WTs) range from the surface in wet open habitats to ca. -30 cm in naturally drier treed habitats.

Eight mesocosms were collected from each of four different sites (wet fen, dry fen, wet bog, dry bog) resulting in 32 mesocosms in total. Each mesocosm had at least 90 % cover of the targeted *Sphagnum* species and the species were selected to represent intermediate lawn habitats that are expected to be most responsive to drought (Hájek and Vicherová, 2014). From the fen sites, the moss species that we collected was *Sphagnum recurvum* coll., while *Sphagnum balticum* was taken from the bogs. The mesocosms were collected into PVC cylinders (15 cm diameter, 10 cm deep) lined with Teflon tape and care was taken to preserve the natural structure and density of the mosses.

The mesocosms were collected in the beginning of the growing season on 7th – 9th May 2018 and stored at 6 °C in dark conditions for 14 weeks until they were placed in a greenhouse at the Joensuu campus of University of Eastern Finland. As the summer of 2018 was exceptionally hot (Rinne et al., 2020), mesocosms were in cool storage over the hottest period and the experiment was started on August 14th. Storing the mesocosms in dark and cool conditions after collecting them from the field in the spring extended their winter dormancy and delayed the beginning of their growing season until they were placed in the greenhouse.

2.2. Experimental design

The *Sphagnum* mesocosms were exposed to an experimental ecohydrological drought in a controlled greenhouse environment to quantify the effect of seasonal drought period on BVOC emissions from the mosses. All the vascular plants were removed from the mesocosms prior to placing them in the greenhouse. For the experiment, the mesocosms were placed into hydrologically controlled cylinders constructed following the design in Nijp et al. (2014). WT in the mesocosms was first set to the depth of 15 cm and adjusted to 10 cm three weeks later. Mesocosms were allowed to acclimatise to the greenhouse conditions for seven weeks before the drought treatment was started on 1st October.

Half of the mesocosms from each of the four sites were subjected to a drought treatment, where the WT was lowered by 20 cm (to 30 cm below the moss surface). The water table drop was based on field observations during the severe drought period in Northern Europe and peatlands in the summer 2018 (Rinne et al., 2020) when the WT in Lakkasuo fen and bog dropped ca. 23 cm and 33 cm, respectively, below pre-drought levels (unpublished data). The WT in the other half of the mesocosms was kept unchanged at 10 cm below the moss surface as a control. During the experimental drought, the treated mesocosms did not receive simulated precipitation, while the control mesocosms were watered by manually misting them once a week with 320 mL of deionized water with pH adjusted to 5.6 (based on the 30-year average monthly rainfall during the growing season at weather station of Hyytiälä Forest Station located ca. 6 km north from Lakkasuo (FMI, 2021)). The drought was ended after 43 days on 14th November by applying a simulated rain event and returning the WT in the drought-treated mesocosms back to the pre-drought level (10 cm below the surface). The experimental drought period exceeded the longest rainless period in the area since 1986 (36 days) by seven days, which is based on historical climate records at the Hyytiälä Forest Station (FMI, 2021; table S1). Because we wanted to quantify the effect of severe drought

event, the duration of the experimental drought was reasonable considering both the historical records and increased extremes in precipitation due to climate change in the future (Donat et al., 2016). During the six-week recovery period, the WT of all mesocosms was maintained at 10 cm below the surface and weekly surface misting was applied until the experiment ended on 21st December.

The water supplied to the mesocosms was adjusted to match the water chemistry of samples taken from the peatland sites (Kokkonen et al., 2024). Water for the fen-originating mesocosms was made using a mix of tap water and deionized water in 1:9 dilution with the pH adjusted to 5.2. For bog-originating mesocosms, we used deionized water with the pH adjusted to 3.9. Additionally, temperature and light conditions were controlled in the greenhouse throughout the experiment and monitored continuously using DHT22 sensors. To extend the daylength as autumn progressed, high-pressure sodium lamps were initially used between 06:00–08:00 and 17:00–20:00, then between 06:00–20:00 from 1st November onwards. Daytime temperature was targeted to maintain between 18 and 25 °C and nighttime temperatures between 10 and 15 °C. However, the maximum daily photosynthetically active radiation (PAR) and average daily ambient temperature in the greenhouse declined over the duration of the experiment as it extended into the fall. To test the stability of the conditions during the experiment, we applied linear mixed effects models to test differences in PAR as well as in temperature and relative humidity (RH) in the BVOC measurement chamber between the campaigns, treatments, and sites. Temperature and PAR were significantly higher in the beginning of the experiment (mean T with standard error (SE): 20.5 ± 0.19 °C and mean PAR with SE: 175 ± 7.18 during the first campaign) than later during the drought and recovery periods (mean T with SE: 18.6 ± 0.16 °C and 18.7 ± 0.22 °C, and mean PAR with SE: 147 ± 1.71 and 144 ± 0.90 during the second and the third campaigns, respectively). However, there were no differences in these factors between the treatments or sites.

2.3. BVOC measurements

BVOC (C₅–C₁₆) emissions were measured as campaigns three times during the experiment: once before the drought was initiated, a second time at the end of the drought, and a third time at the end of the recovery period. In the second and the third campaigns each mesocosm was measured once resulting in 32 measurements per campaign, whereas in the first campaign we were only able to measure half of the mesocosm replicates resulting in 16 measurements because of the limited amount of sample tubes in use at the time. The first measurement campaign (24th–29th September) was conducted after six weeks of acclimation in the greenhouse. During the first campaign, all the mesocosms had the same WT, which simulated normal conditions in the peatland. The second measurement campaign (5th–13th November) was conducted after five weeks of the drought treatment, and the third measurement campaign (11th–19th December) was done four weeks after WT of drought-treated mesocosms had been returned to 10 cm.

BVOC emissions from *Sphagnum* mesocosms were measured with dynamic chamber method (Tiiva et al., 2009; Faubert et al., 2010b; Mäki et al., 2017). For measurements, a glass chamber was placed on round mesocosms (diameter 15 cm; chamber height 26.8 cm, and measured volume 3.6 L) (fig. S2). Ingoing and outgoing air of the chamber was sampled for 90 min by pumping the air through Tenax TA-Carbopack B adsorbent tubes at a flow rate of 0.15 L min⁻¹ resulting in two samples per measurement. To keep the chamber over pressurized and prevent ingress air, filtered ambient air was pumped continuously into the chamber at a flow rate of 2 L min⁻¹. This air was filtered through an active carbon trap and a MnO₂-coated copper net to remove volatile organic compounds (VOCs) and ozone. The chamber air volume was flushed with filtered air for 15 min before each sampling to stabilise the system. Temperature and RH inside the chamber were measured using a standard temperature and moisture data logger (Art.no 36–4208, Model ST-171).

In addition to samples collected from moss mesocosms, we conducted two measurements in the third campaign from empty mesocosms with no mosses as controls for the potential BVOC release from the experimental design. One measurement was done from an empty mesocosm with water adjusted to fen conditions and the other measurement from an empty mesocosm provided with water adjusted to bog conditions. In total, we collected 32 samples in the first measurement campaign, 64 samples in the second campaign, and 64 plus the four empty mesocosm samples in the third campaign.

2.4. Analyses of BVOC samples and flux calculations

After sample collection, the sample tubes were kept at 5 °C until they were analysed in University of Eastern Finland (Kuopio) using an Automatic Thermal Desorption system (Perkin-Elmer ATD400, USA) that was connected to a gas chromatograph (Hewlett-Packard GC 6890, Germany) with a HP-5MS (60 m, 0.25 mm, 0.25 µm) column and a mass selective detector (Hewlett-Packard MSD 5973, USA). All the samples were analysed as described for samples of 8/2018 and 10/2018 campaigns by Männistö et al. (2023). Four standards in methanol solution were used for calibration by injecting them into sample tubes. The amounts injected were 2 µL of terpenoid, green leaf volatiles (GLV) and HC48 indoor air standards, and 3 µL of isoprene standard. Methanol was flushed away from the Tenax TA and Carboxen B adsorbent tubes using nitrogen (N₂) at a flow rate of 100 mL min⁻¹ for 1 min. Empty sample tubes were analysed together with the real samples each time for quality control of the analyses.

Flux rates (E , µg m⁻² h⁻¹) of each compound were calculated for the area of the mesocosm (m²) and time (h) using Eq. (1).

$$E = (C_{out} - C_{in}) \times F_{chamber} / 60 / 1000 / A \quad (1)$$

where C_{in} is the concentration of ingoing air sample (µg m⁻³) and C_{out} is the concentration of the outgoing air sample (µg m⁻³), $F_{chamber}$ (m³ min⁻¹) is the flow rate of air pumped into the chamber, and A (m²) is the moss surface area of the mesocosm.

Negative net fluxes indicating BVOC uptake were excluded from the data analyses by assuming these fluxes to be 0 (32 % of all observations). We do not report the negative net fluxes here, because our sampling method is not designed to measure uptake. Quantified compounds were classified into eight functional groups based on their chemistry following the approach described in Guenther et al. (2012): hemiterpenes (isoprene), monoterpenoids, sesquiterpenes, alkanes, oxygenated alkanes, organic halides, benzenoids and green leaf volatiles (GLV). For isoprene, we further calculated isoprene emission potential by standardising isoprene release for both temperature and light ($T = 30$ °C and PPFD = 1000 µmol m⁻² s⁻¹) using the algorithm by Guenther et al. (1993) to make results comparable with previous literature.

2.5. Statistical analyses

We tested the impact of campaign, peatland type (fen, bog), habitat type (wet open, dry treed), and drought treatment, as well as the campaign-dependent and treatment-within-campaign -dependent impact of peatland type and habitat type (Table S3) on total BVOC emission and standardised isoprene emission using linear mixed-effects models (package *nlme* version 3.1–160; Pinheiro et al., 2014). We accounted for the repeated measures by setting mesocosm as a random variable in the model and used logarithmically transformed BVOC emission data as input data following the logarithmic conversion by Anderson et al. (2006).

The qualitative inspection of the eight BVOC groups and the individual compounds was conducted using multivariate generalized linear models (package *mvabund*, version 4.2.1; Wang et al., 2012) using the same model design as in the linear mixed effect models and similarly logarithmically transformed BVOC emission data. Compounds detected

only once or twice in all collected samples (altogether 10 compounds) were excluded. The models were fitted with negative binomial distribution using 999 bootstrap iterations and reported with log-likelihood ratio statistics. The multivariate analyses were followed by univariate tests, for which we report the p -values unadjusted. For groups and compounds showing a significant campaign \times treatment interaction, the impact of treatment (T) on each campaign (C) occasion was tested with Tukey's pairwise comparison in a separate mixed-effects model.

To visualise the variation in the composition of BVOC groups, we ran a principal component analysis (PCA) on the log-transformed data using the R package *vegan* (version 2.6–4). All statistical analyses were done using R version 4.2.2. and data were visualised with package *ggplot2* (version 3.4.0).

3. Results

3.1. Quantity of BVOC emissions

In total, 30 compounds were identified, 10 of which were detected only once or twice (Table 1). The majority of the total BVOC emissions consisted of isoprene, which was the only detected hemiterpene and had ten times higher flux rates than other BVOC groups (range: 0–31.9 µg m⁻² h⁻¹; mean 5.6 µg m⁻² h⁻¹) (Table 1). The emission potential of isoprene ($T = 30$ °C and PPFD = 1000 µmol m⁻² s⁻¹) ranged from 0 to 293.1 µg m⁻² h⁻¹ with a mean of 46.3 µg m⁻² h⁻¹, being similar in both the peatland and the habitat types (Table S3).

Similarly to the standardised isoprene emissions, peatland type and habitat had no significant impact on the total BVOC release (Table S3). This was also seen in the principal component analysis during the first campaign before drought, where mesocosms from different origins grouped among each other (Fig. 1b). However, multivariate analysis of BVOC groups revealed a clear effect of peatland type on the BVOC composition (Table 2) driven by high sesquiterpene emissions in the bog-originating mesocosms which were close-to-absent in the fen originating mesocosms (Table 3). Also, GLV emission depended on the peatland type, and were driven by few observations from bog-originating mesocosms (Table 3). Habitat type had no impact on the detected BVOC emissions (Table 2).

3.2. Immediate responses of BVOC emissions to the experimental water table drop

Overall, the total BVOC emissions were lowered by the drought-treatment (Fig. S4). In addition to quantity, the drought treatment altered the quality of peatland BVOC emissions as seen from both the principal component analysis (Fig. 1) and the multivariate analysis (C \times T effect in Table 2). The drought impact was driven by the most abundant BVOC groups: isoprene and sesquiterpenes, whose emissions were significantly reduced by the drought (Fig. 2, Table 3). The experimental drought decreased mean isoprene emission by 95 % and mean sesquiterpene emissions by 97 %. Due to the scarcity of sesquiterpene emissions from the fen-originating mesocosms, the drought effect on sesquiterpene emissions was seen only as a significant interaction of peatland type, campaign and treatment (Table 3, Fig. 2). One alkane compound, n-decane, was not detected at all during the drought, while before and after drought it was found from both bog and fen originating mesocosms (compound-specific univariate results in Table S6).

Drought-induced GLV emissions from the bog species *S. balticum*, as two GLV compounds, 1-hexanol and 1-octen-3-ol, were detected from mesocosms originating from both bog sites during the 2. campaign but not otherwise (Figs. 1 and S4, Tables 1 and 3). 1-hexanol was found once from a mesocosm originating from the wet bog, while 1-octen-3-ol was found from two mesocosms originating from the dry bog.

Six weeks after the drought, sesquiterpene emissions were still on average 91 % lower in the drought treatment than in the control treatment (Fig. 2). For both isoprene and total BVOC emissions, the impact of

Table 1

Mean emission rate ($\mu\text{g m}^{-2} \text{h}^{-1}$) and standard error (SE) of the biogenic volatile organic compounds detected from control mesocosms ('control') and mesocosms exposed to drought ('drought') before the drought treatment ('Before'), in the end of the 43 days drought treatment ('During the drought'), and six weeks after water table was raised back to normal ('After'). GLV denotes green leaf volatiles.

	Before		During the drought		After	
	Control	Drought	Control	Drought	Control	Drought
Hemiterpenes						
isoprene	17.557 (3.278)	11.874 (2.893)	9.815 (2.279)	0.546 (0.225)	2.088 (0.609)	1.084 (0.280)
Monoterpenoids						
alpha-pinene	0.319 (0.159)	0.077 (0.043)	0.555 (0.253)	0.445 (0.139)	0.392 (0.144)	0.630 (0.164)
camphene	0.697 (0.427)	0.153 (0.101)				
sabinene		0.151 (0.151)		0.046 (0.046)	0.039 (0.039)	
beta-pinene	0.077 (0.051)	0.873 (0.659)	0.106 (0.058)	0.895 (0.564)	0.087 (0.050)	0.132 (0.042)
beta-myrcene ^a		0.074 (0.059)				
3-carene	0.077 (0.044)	0.068 (0.068)	0.055 (0.038)	0.016 (0.016)		
limonene	0.204 (0.156)	1.286 (1.072)	0.236 (0.135)	0.929 (0.438)	0.342 (0.153)	0.854 (0.643)
sum of monoterpenoids	1.375 (0.638)	2.682 (1.955)	0.952 (0.438)	2.332 (1.049)	0.860 (0.297)	1.616 (0.674)
Sesquiterpenes						
beta-elemene ^a		0.030 (0.030)				
beta-caryophyllene ^a		0.054 (0.054)				
aromadendrene ^a			0.075 (0.075)			
alpha-humulene	1.504 (0.786)	0.900 (0.544)	0.365 (0.245)	0.028 (0.028)	1.839 (0.938)	0.157 (0.074)
sum of sesquiterpenes	1.504 (0.786)	0.983 (0.531)	0.439 (0.249)	0.028 (0.028)	1.839 (0.938)	0.157 (0.074)
Alkanes						
hexane	1.067 (0.382)	1.337 (0.807)	0.489 (0.189)	0.451 (0.207)	0.482 (0.235)	0.519 (0.192)
iso-octane			0.114 (0.062)			
n-decane	0.018 (0.018)	0.033 (0.033)				0.099 (0.046)
n-heptane				0.034 (0.034)	0.351 (0.161)	0.404 (0.169)
n-undecane ^a						0.011 (0.011)
pentadecane ^a			0.027 (0.027)			
sum of alkanes	1.085 (0.380)	1.370 (0.806)	0.630 (0.236)	0.485 (0.227)	0.834 (0.266)	1.034 (0.299)
Oxygenated alkanes						
n-butanol	0.032 (0.021)	0.023 (0.023)	0.109 (0.073)	0.067 (0.047)	0.720 (0.685)	0.151 (0.151)
decanal	0.285 (0.185)	1.849 (0.913)	0.039 (0.039)	0.121 (0.094)	0.033 (0.033)	
sum of oxygenated alkanes	0.317 (0.191)	1.872 (0.906)	0.149 (0.079)	0.189 (0.108)	0.753 (0.684)	0.151 (0.151)
Organic halides						
dichloromethane ^a			0.301 (0.301)	1.487 (1.487)		
chloroform	0.005 (0.005)		8.276 (4.139)	4.125 (2.241)	0.030 (0.030)	
1-chlorooctane ^a					0.106 (0.106)	
sum of organic halides	0.005 (0.005)		8.576 (4.110)	5.612 (3.378)	0.136 (0.108)	
Benzenoids						
ethylbenzene	0.006 (0.006)		0.043 (0.025)	0.007 (0.007)	0.058 (0.024)	0.115 (0.035)
styrene			0.020 (0.020)	0.041 (0.041)	0.019 (0.019)	0.015 (0.015)
o-xylene			3.540 (2.235)	1.861 (1.252)	0.081 (0.040)	0.201 (0.060)
1,2,4-trimethylbenzene			0.030 (0.021)	0.014 (0.014)	0.019 (0.013)	0.084 (0.031)
m- & p-xylene	0.008 (0.007)	0.005 (0.005)	0.096 (0.058)	0.089 (0.069)	0.108 (0.050)	0.186 (0.080)
sum of benzenoids	0.013 (0.013)	0.005 (0.005)	3.730 (2.311)	2.013 (1.266)	0.286 (0.125)	0.601 (0.209)
GLV						
1-hexanol ^a				0.029 (0.029)		
1-octen-3-ol ^a				0.142 (0.098)		
sum of GLV				0.171 (0.099)		

^a Detected only once or twice

drought treatment was no longer evident (Fig. 2; Fig. S4).

3.3. Trends in BVOC emissions during the experiment

Generally, BVOC emissions decreased during the experiment. This linear trend aligned with a change in abiotic conditions, as also temperature and PAR were higher during the first campaign. The emissions of total BVOCs, isoprene, sesquiterpene, and oxygenated alkanes were highest during the first campaign (Figs. S4, 2, S5). Unlike other BVOCs, benzenoid emissions increased during the experiment from the beginning towards the end of the experiment; the emissions were significantly lower during the first campaign than in the third campaign (Tables 1 and 3, Fig. S5). Additionally, organic halide emissions were highest during the 2. campaign but not related to the treatment (Tables 1 and 3, Fig. S5).

4. Discussion

4.1. BVOC emission as impacted by drought

Our results supported the hypothesis that severe ecohydrological drought decreases the total BVOC emissions from *Sphagnum* mosses and alters their emission composition. This study, was motivated by our earlier finding (Männistö et al., 2023) of a sudden drop in boreal peatland BVOC emission between July and August 2018 during an exceptional drought (Rinne et al., 2020). Here, we similarly found that a 20 cm drop in water table for 43 days decreased total BVOC emissions and the emissions of the most abundant BVOC groups, isoprene and sesquiterpenes from *Sphagnum* mesocosms. This adds evidence that drought-induced reduction of BVOC emission is not limited to the response of vascular plants (Tiiva et al., 2009; Faubert et al., 2010b; Faubert et al., 2011). While studies on individual vascular plant species and trees have shown that drought may induce an increase in BVOC emission rates after severe water stress has ended (Sharkey and Loreto, 1993; Pegoraro et al., 2004; Brilli et al., 2007; Penuelas et al., 2009),

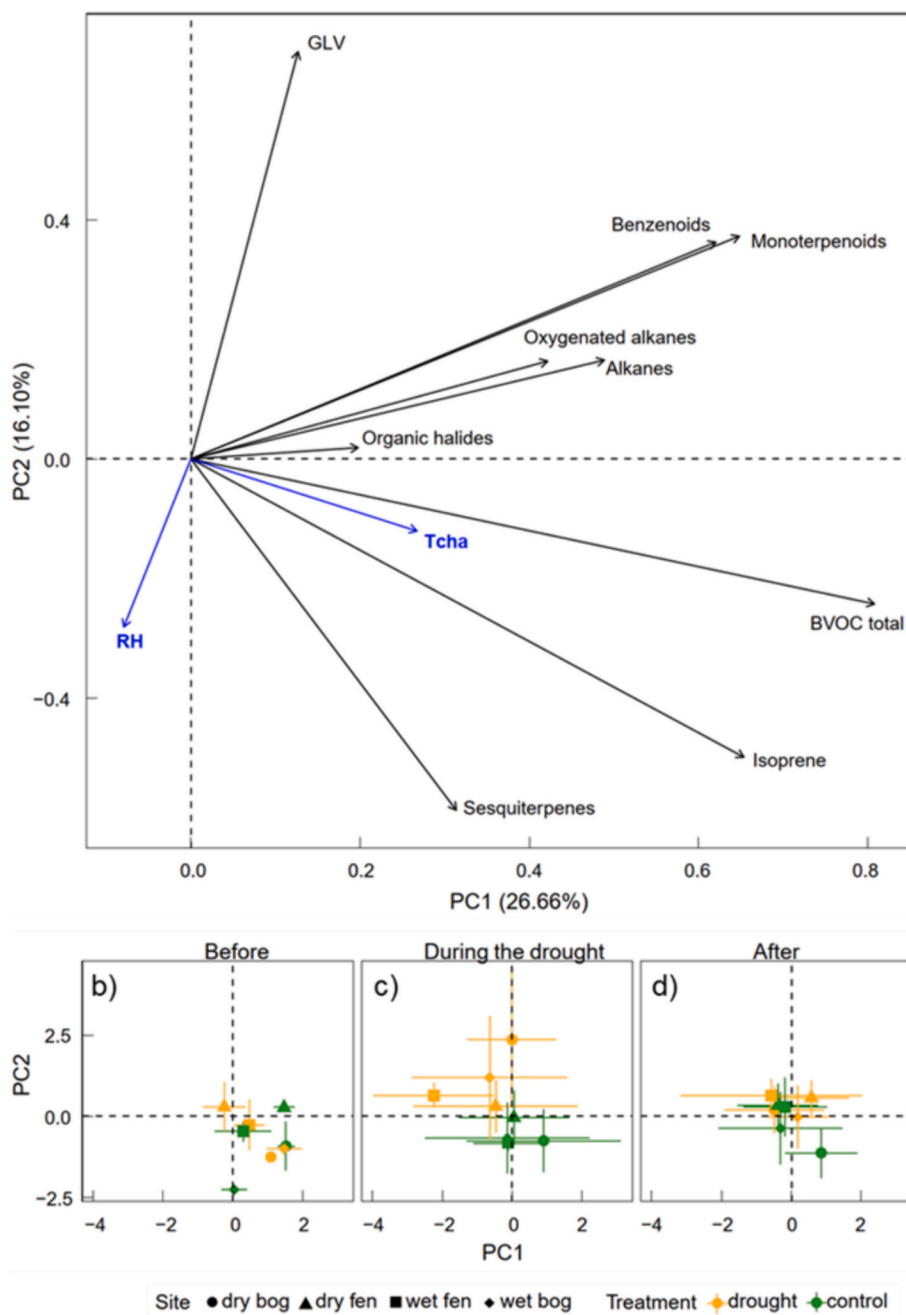


Fig. 1. a) Principal components analysis of biogenic volatile organic compound (BVOC) group emissions (black vectors) and b–d) the treatment differences on each campaign. The principal component analysis (PC) is based on the log-transformed emissions of the eight BVOC groups. GLV denotes green leaf volatiles. In frame a, blue vectors represent increase in temperature in the chamber (Tcha), and relative humidity (RH). Frames b–d show mean \pm standard deviation separately for the two treatments (control and drought) and the mesocosm sites (naturally drier treed bog = dry bog, naturally drier fen = dry fen, open bog = wet bog, open fen = wet fen) in the different measurement campaigns (“Before”, “During the drought”, and “After”).

however we found no such compensative emissions in this study six weeks after the drought treatment had ended. In contrast, the emissions of sesquiterpenes, the second most abundant BVOC group remained lower in the mesocosms that had been subjected to experimental drought.

The experimental drought reduced isoprene emission by over 90 %, aligning with the decrease in total BVOC emission. Previously, Tiiva et al. (2009) showed that water table drawdown decreased isoprene emission by only 25 % from boreal ombrotrophic microcosms. The difference in the response rate may relate to a difference in species; while Tiiva et al. (2009) lowered the water table by 20 cm similarly to us, they measured microcosms collected from wet depressions and dominated by

Sphagnum majus. This was unlike our study that targeted intermediate lawn microhabitats with *S. recurvum* and *S. balticum*. The strong response of the intermediate lawn species studied here does support that lawn Sphagna have a higher desiccation tolerance compared to hollow species (Hájek and Vicharová, 2014). However, the lowered isoprene emissions could also partly be driven by microbial responses, as aerobic conditions increase following a lowered WT, potentially increasing isoprene uptake by microbes (Cleveland and Yavitt, 1998).

In addition to isoprene, drought treatment reduced sesquiterpene emissions from the *Sphagnum* mesocosms. These emissions remained low weeks after the drought treatment had ended, indicating that the Sphagna had a limited or restricted capacity to recover from the drought

Table 2
Multivariate generalized linear model results of the effects of campaign (C), treatment (T), peatland type (P), habitat type (H), peatland type (P; fen, bog), habitat type (H; open wet, treed dry) and their interactions on the overall composition of biogenic volatile organic compound (BVOC) emissions. The test was conducted for eight detected BVOC groups (see group-specific univariate statistics in Table 3) and for 20 detected compounds (compound-specific univariate results in Table S6).

	Campaign (C)		Treatment (T)		Peatland type (P)		Habitat type (H)		C × T		C × P		C × H		C × T × P		C × T × H	
	Dev _{2,77}	p	Dev _{1,76}	p	Dev _{1,75}	p	Dev _{1,74}	p	Dev _{2,72}	p	Dev _{2,70}	p	Dev _{2,68}	p	Dev _{3,65}	p	Dev _{3,62}	p
BVOC groups	24.39	0.001	16.99	0.006	26.23	0.001	3.74	0.788	20.98	0.076	12.78	0.422	9.70	0.726	28.66	0.145	22.29	0.514
Individual compounds	Dev _{2,61}	p	Dev _{1,60}	p	Dev _{1,59}	p	Dev _{1,58}	p	Dev _{2,56}	p	Dev _{2,54}	p	Dev _{2,52}	p	Dev _{3,49}	p	Dev _{3,52}	p
	36.23	0.004	24.39	0.067	23.65	0.131	13.49	0.722	25.36	0.105	27.76	0.077	18.13	0.308	29.05	0.543	28.53	0.671

Statistically significant results are shown in bold text.

Table 3
Univariate test results of the effects of campaign (C), treatment (T), peatland type (P; fen, bog), habitat type (H; open wet, treed dry) and their interactions on the abundance of the eight biogenic volatile organic compound (BVOC) groups. Statistically significant results are shown in bold text. GLV denotes green leaf volatiles.

	Campaign (C)		Treatment (T)		Peatland type (P)		Habitat type (H)		C × T		C × P		C × H		C × T × P		C × T × H	
	Dev _{2,77}	p	Dev _{1,76}	p	Dev _{1,75}	p	Dev _{1,74}	p	Dev _{2,72}	p	Dev _{2,70}	p	Dev _{2,68}	p	Dev _{3,65}	p	Dev _{3,62}	p
Isoprene	2.950	0.013	5.833	0.001	0.002	0.936	1.348	0.108	5.477	0.012	0.196	0.851	1.507	0.359	0.177	0.967	2.988	0.372
Monoterpenoids	0.335	0.566	0.799	0.136	0.531	0.227	0.843	0.163	0.168	0.823	0.468	0.660	0.690	0.570	1.476	0.562	1.967	0.549
Sesquiterpenes	2.261	0.040	1.539	0.100	19.575	0.001	0.042	0.876	7.106	0.092	6.719	0.018	0.896	0.670	12.394	0.006	6.845	0.263
Alkanes	2.266	0.037	0.067	0.702	0.311	0.366	0.013	0.872	0.507	0.603	0.800	0.518	0.094	0.939	0.756	0.810	1.684	0.638
Oxygenated alkanes	3.124	0.025	0.061	0.763	0.072	0.775	0.008	0.926	2.026	0.411	0.068	0.971	3.426	0.227	9.966	0.094	2.212	0.653
Organic halides	4.581	0.038	3.986	0.054	0.297	0.609	0.013	0.892	5.663	0.075	2.138	0.429	1.051	0.618	0.245	0.725	1.216	0.356
Benzenoids	3.095	0.015	0.045	0.765	0.081	0.703	1.265	0.148	0.028	0.978	2.395	0.267	2.034	0.374	3.647	0.452	5.382	0.236
GLV	5.779	0.060	4.664	0.020	5.358	0.023	0.210	0.675	0.001	0.569	0.001	0.615	0.000	0.613	0.000	0.584	0.000	0.640

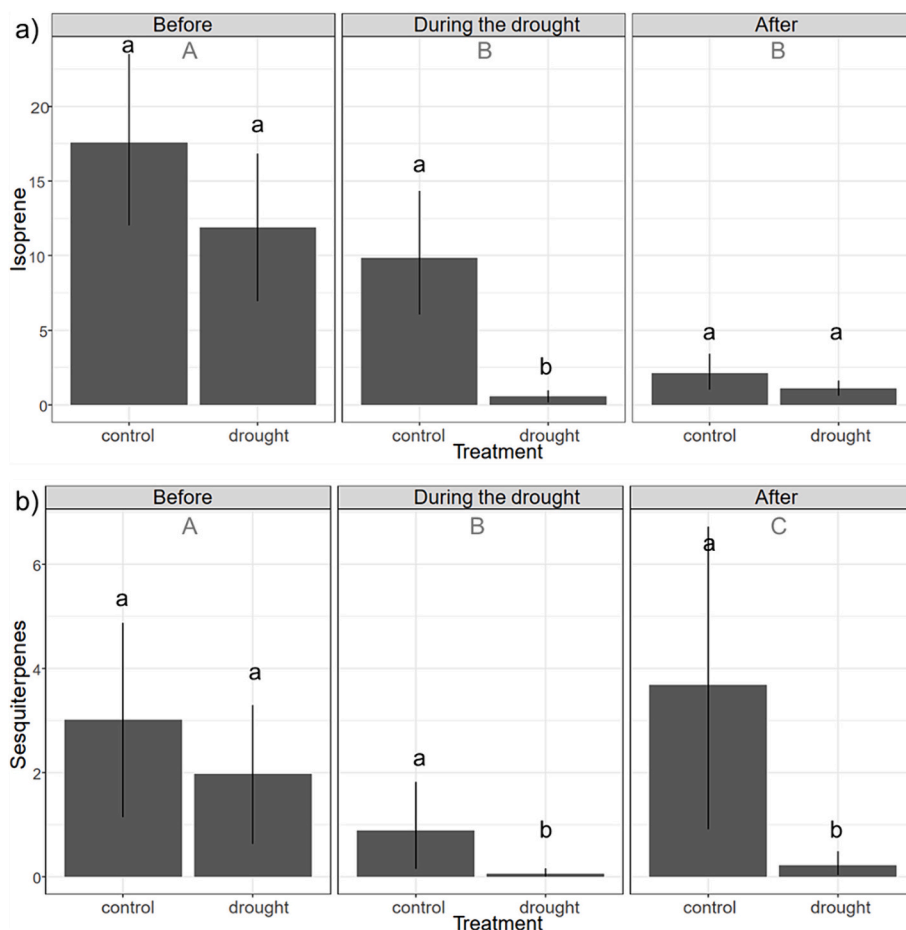


Fig. 2. Observed mean emissions and 95 % confidence interval of a) isoprene and b) sesquiterpenes ($\mu\text{g m}^{-2} \text{h}^{-1}$) from the *Sphagnum* mesocosms with normal water table (-10 cm, “control”) and with lowered water table (-30 cm, “drought”) in three different measurement campaigns conducted before the drought treatment (“Before”), after 43 days drought treatment (“During the drought”), and six weeks after the recovery of the water table (“After”). Isoprene emissions are pooled across peatland types and habitats, whereas sesquiterpene emissions are shown only for mesocosms originating from bogs, as emissions from fen originating mesocosms were detected only twice in the last campaign (“After”). Sesquiterpene emissions from the dry and wet habitats are pooled together. Letters *a* and *b* denote significant differences between the treatments within the campaigns, and grey capital letters A, B, and C denote the significant differences between the campaigns. Note the difference in y-scale between the figures. Because there were no significant changes due to the drought in the other compound groups, we chose to only show changes in isoprene and sesquiterpenes in this figure. Similar figures for all the other compound groups are presented in fig. S4 in the Supplementary material.

stress. Water level drawdown has been found to generally reduce sesquiterpene emissions, as well as monoterpene and other VOC emissions from ombrotrophic peatland mesocosms (Faubert et al., 2010b; Faubert et al., 2011), but this is the first study to quantify emission rates directly from *Sphagnum* mosses after drought as well as during it.

Isoprene biosynthesis in plants uses carbon directly from Calvin cycle of photosynthesis but can also utilise carbon from other sources when needed (Brilli et al., 2007; Sharkey et al., 2008). Therefore, emissions of isoprene and other terpenoids, such as sesquiterpenes, that are synthesised via a common precursor with isoprene (Kesselmeier and Staudt, 1999) can first be resistant to mild drought stress (Loreto and Schnitzler, 2010) until they decrease under severe drought that can completely stop photosynthesis (Loreto and Schnitzler, 2010). As *Sphagnum* mosses rely on external water to stay physiologically active, severe drought inhibits their functioning and quickly decreases their photosynthesis (Gerdol et al., 1996; Schipperges and Rydin, 1998; Kokkonen et al., 2024), reducing thus likely also the isoprene and terpenoid emissions. Additionally, drought stress can cause severe desiccation damage to *Sphagnum* tissues including damage of cell membranes and leakage of cell compounds, which may explain slow recovery of *Sphagnum* from drought (Gerdol et al., 1996) and further affect their BVOC biosynthesis. Moreover, *Sphagnum* serves as a habitat for a diversity of microbes, some of which may take part in carbon cycling of *Sphagnum*, but the signalling

pathways between *Sphagnum* and its microbiome are not yet known (Weston et al., 2018). Because many BVOCs are used in both intra- and interspecific communication of plants and other organisms (Peñuelas and Staudt, 2010; Sharifi et al., 2018; Vicheroová et al., 2020), it is possible that some BVOC emission responses to drought found in this study are related to microbial processes and to signalling between *Sphagnum* and microbes.

Furthermore, we found two GLV compounds that are commonly related to stress reaction of green leaves (Ameje et al., 2018), 1-hexanol and 1-octen-3-ol, from *S. balticum* mesocosms. These were found only during the drought treatment, indicating stress. Although the majority of GLV emissions in boreal peatlands are from vascular plants (Männistö et al., 2023), both 1-hexanol and 1-octen-3-ol emissions have also been found earlier from *Sphagnum* mosses (Ryde et al., 2022; Männistö et al., 2023), as well as from the forest moss *Pleurozium schreberi* and lichens (Kesselmeier and Staudt, 1999). While 1-octen-3-ol is known to have anti-fungal properties (Insam and Seewald, 2010), 1-hexanol has been linked to drought stress also previously (Asensio et al., 2007). Generally, drought increases oxidative stress in plants (Kaur and Asthir, 2017), which induces lipid peroxidation in both vascular plants (Yamauchi et al., 2015) and mosses (Dhindsa and Matowe, 1981; Zhao et al., 2019) by enzymes that also take part in the GLV biosynthesis pathway, and thus lead to GLV production (Ameje et al., 2018; Matsui and Engelberth,

2022).

The majority of other compound emissions - monoterpenoids, alkanes, oxygenated alkanes, organic halides or benzenoids - were not affected by the drought. While Männistö et al. (2023) reported organic halide emissions to be absent during a seasonal drought period in a boreal peatland sample plots with *Sphagnum*, this was not found in the current study.

As this 19-week experiment continued in the greenhouse beyond the end of the natural growing season, both photosynthesis and respiration rates of the *Sphagnum* mesocosms slowly decreased during the course of the experiment (Kokkonen et al., 2024). This overall decline of the conditions and activity of the mosses could relate to the trends in BVOC emissions found during the experiment such as the low total emission found in the end of the experiment from the drought and control mesocosms alike.

This was the first study to experimentally explore the effect of drought and subsequent recovery on peatland BVOC emissions between *Sphagnum* mosses from the two main types of boreal peatlands, minerotrophic fens and ombrotrophic bogs. Previous studies on peatland BVOC emission response to drought have been primarily carried out in bogs (Tiiva et al., 2009; Faubert et al., 2010b; Faubert et al., 2011). We hypothesised that fen *Sphagnum* would be more sensitive to seasonal drought than bog *Sphagnum* but did not find support for this. The only difference in drought response between the mosses originating from different peatland types, was that drought treatment reduced sesquiterpene emissions from the bog-originating but not the fen-originating mesocosms. This, however, could be explained by the overall low sesquiterpene emission rates from the mesocosms originating from the fens. There was also no evidence that *Sphagnum* living in wet habitats are more sensitive to seasonal drought compared to the same species adjusted to naturally drier habitats: there were no differences in the drought response of any BVOC emissions between mesocosms originating from wet open and drier treed habitats. However, our study covered only one *Sphagnum* species from each peatland type and thus further measurements with more species are needed for a more comprehensive understanding.

4.2. Diversity of emissions

Although vascular plants have been shown to be the main isoprene emitters in boreal peatlands (Tiiva et al., 2009; Männistö et al., 2023), we found that isoprene also dominated the BVOC emissions from *Sphagnum* mosses accounting up to 80 %, 40 % and 30 % of the total emission in the control mesocosms during the three measurement campaigns, respectively. The mean isoprene flux rate ($5.6 \mu\text{g m}^{-2} \text{h}^{-1}$) was within the same order of magnitude as reported previously from *Sphagnum* mosses (Tiiva et al., 2009; Männistö et al., 2023). While the standardised mean isoprene emission rate of $46.3 \mu\text{g m}^{-2} \text{h}^{-1}$ ($T = 30^\circ\text{C}$ and $\text{PPFD} = 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) was lower than found earlier (Hanson et al., 1999; Ekberg et al., 2011), the highest standardised emission potential of our study ($293.1 \mu\text{g m}^{-2} \text{h}^{-1}$) was in the same range with previous studies (Hanson et al., 1999; Hellén et al., 2006; Ekberg et al., 2011).

The next most emitted compound groups were monoterpenoids, sesquiterpenes and alkanes, which had similar flux rates as those reported earlier from *Sphagnum* mosses (Faubert et al., 2010b; Männistö et al., 2023). Additionally, organic halides and benzenoids had relatively high emission rates during the second measurement campaign in the end of the drought treatment, but this was seen in both the wet control mesocosms, and the drought treated mesocosms. Short-chained BVOCs ($<C_5$) that include some highly volatile compounds were not measured in this study, but they could potentially have substantial emission rates as has been shown for a peatland ecosystem (Seco et al., 2020).

Similar to Männistö et al. (2023), we found higher sesquiterpene emissions from the bog-originating mesocosms compared to the fen-

originating ones. In contrast to the field study of Männistö et al. (2023) that also included vascular plants, we did not find other BVOC groups to differ between mosses originating from different peatland types. Still, the difference found in sesquiterpene emissions originating from fens and bogs, implies a significant impact of peatland type on *Sphagnum* BVOC emissions.

We found no difference in emissions between wet open and drier treed habitats. This is supported by Ekberg et al. (2011) who found that isoprene emission capacities from *S. balticum* growing naturally at different water table positions in a subarctic peatland had no consistent differences along the moisture gradient.

5. Conclusions and implications of the study

In this first experimental study on the effect of periodic drought on fen and bog *Sphagnum* emissions, we showed that a severe drought period can change both the quality and quantity of BVOC emissions from *Sphagnum* mosses. These extreme drought events that disrupt the carbon cycling of boreal peatlands and alter their feedback to climate (Rinne et al., 2020) are predicted to occur more frequently in the future (IPCC, 2023). However, the current understanding on the interactions of peatland ecosystems and climate is mainly based on the CO_2 and CH_4 dynamics, while BVOC dynamics as well as the factors controlling them are far less studied. Yet, the significant emissions of different BVOCs and their versatile contribution to atmospheric chemistry can have further impact on the climate feedback of boreal peatlands. This calls for a stronger understanding on the controls of BVOC emissions in order to increase the performance of global climate models.

While a rising temperature can increase isoprene emissions (e.g., Guenther et al., 1993; Männistö et al., 2023), our results imply that severe drought periods decrease the emissions, which can partly overrule the direct effect of temperature. As isoprene can reduce the yield of low-volatility products of monoterpene oxidation that would otherwise form SOA (McFiggans et al., 2019), the drought-induced decrease in isoprene emissions can have a direct impact on atmospheric chemistry and thus on the climate feedback of boreal peatland ecosystems. Seasonal droughts may further change the BVOC emission composition meaning the peatland-atmosphere feedback driven by BVOCs is likely to be strongly controlled by extreme events such as droughts. Our study also indicates that *Sphagnum* mosses from minerotrophic fen and ombrotrophic bog ecosystems may respond differently to severe drought periods, but further studies in multiple sites and with more *Sphagnum* species are needed to better understand the controls of boreal peatland BVOC emissions under pressure.

Role of the funding source

This study was supported by Research Council of Finland through project and infrastructure funding (grant numbers 330840, 337064, 345527, 358650, and 338980) and through the ACCC Flagship. Additionally, EM was kindly supported by Finnish Cultural Foundation (grant number 00180750). Research Council of Finland provided financial support for the experimental set-up in the field and in the greenhouse. The financial support provided by Research Council of Finland through ACCC Flagship and Finnish Cultural Foundation allowed EM to collect, analyse and interpret the data as well as write and submit the report. The financial support provided by Research Council of Finland for AK (grant number 338980) allowed her to work on the experiment and co-author the report.

CRediT authorship contribution statement

Elisa Männistö: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Henni Ylännö:** Writing – review & editing, Visualization, Formal analysis. **Nicola Kokkonen:** Writing – review & editing,

Investigation. **Aino Korrensalo:** Writing – review & editing. **Anna M. Laine:** Writing – review & editing. **Pasi Yli-Pirilä:** Writing – review & editing, Resources, Methodology. **Markku Keinänen:** Writing – review & editing, Resources, Methodology. **Eeva-Stiina Tuittila:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

Acknowledgements

We thank Risto Ikonen, Jarmo Pennala, Maini Mononen, Jinnan Gong, and Joni-Matti Kusmin for help with building and maintaining the experimental set-up. We are also grateful to Jelmer Nijp for his expert advice when planning the experiment, and to Professor Annele Virtanen for her valuable insights regarding BVOC measurements and dynamics.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.175738>.

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