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Strong toluene and p-cymene emission from waterlogged hotspots of a temperate mixed-forest soil

Hojin Lee[1], Tim Stippich[1], Jan Petersen[1], David Meine[1], Julian Brzozon[2], Markus Sulzer[3], Lea Dedden[4], Andreas Christen[3], Teja Kattenborn[5], Christiane Werner[1], Jürgen Kreuzwieser[1]

[1]Ecosystem Physiology, University of Freiburg, Georges-Köhler-Allee 53, 79110 Freiburg, Germany
[2]Soil Ecology, University of Freiburg, Bertoldstr. 17, 79098 Freiburg, Germany
[3]Environmental Meteorology, University of Freiburg, Werthmannstraße 10, 79085 Freiburg, Germany
[4]Hydrology, University of Freiburg, Friedrichstr. 39, 79098 Freiburg, Germany
[5]Sensor-based Geoinformatics, University of Freiburg, Tennenbacherstr. 4, 79106 Freiburg, Germany

Correspondence to: Jürgen Kreuzwieser (juergen.kreuzwieser@ctp.uni-freiburg.de)

Abstract. Ecosystem processes taking place at hotspots, i.e., at areas of small spatial extent, but at high intensity, might potentially affect the whole system. Due to their great importance for atmospheric chemistry, we studied the exchange of volatile organic compounds (VOCs) from the forest floor of the ECOSENSE forest, a temperate mixed forest, at selected waterlogged sites. These sites were mainly located along skid trails, hence, characterized by soil compaction and strongly reduced drainage of rainwater. In addition, we monitored VOC exchange from undisturbed, well-drained forest floor during summer and the transition from summer to autumn/winter when strong changes in soil moisture occurred. We complemented these field measurements by experiments under controlled conditions in the laboratory, in which soil cores collected from well-drained and waterlogged sites in the forest were exposed to anoxia. Anoxic conditions enormously stimulated emissions of aromatic compounds, particularly of toluene and the aromatic monoterpene p-cymene 50-fold and 20-fold, respectively. Moreover, anoxia also strongly enhanced the emission of the monoterpenes camphene, limonene, δ-3-carene and α-pinene. In the field, the forest floor changed from a sink of toluene and p-cymene to a strong source of these compounds in response to waterlogging. We observed enormously increased toluene and p-cymene emissions from the waterlogged forest floor along skid trails, amounting to over 5000 ng m^{-2} h^{-1} and 3000 ng m^{-2} h^{-1}, respectively. Considering that the share of skid trails of managed forests can be considerable, we further investigated a potential impact of these hotspots of toluene emission at the ecosystem scale. Indeed, ambient atmospheric mixing ratios of toluene in the ECOSENSE forest peaked in autumn when soil moisture levels were increased. The work therefore suggests that the soil of temperate forests might be a yet underestimated source of toluene and p-cymene for the atmosphere. Still, elevated ambient toluene levels co-occurred with litterfall and senescence of European beech leaves which might be an additional source of atmospheric toluene. At periods with high ambient toluene mixing ratios, the well-drained forest floor acted as a significant sink of toluene. Our results underline the importance of the forest floor's spatial heterogeneity to act as a concurrent sink (main area) and a source (from waterlogged hotspots) of aromatic VOCs.

1 Introduction

Forests play a crucial role in the global carbon cycle, exchanging not only the greenhouse gases carbon dioxide (CO_2) and methane (CH_4) with the atmosphere but also a large array of volatile organic compounds (VOCs) (Guenther et al., 1995; Holopainen et al., 2017). VOCs are highly reactive trace gases, that are assigned to a wide variety of chemical classes and can have thousands of different structures. Quantitatively most important compounds belong to the groups of terpenes, aromatics as well as alkanes, alkenes, alcohols, carboxylic acids and carbonyls (Kesselmeier and Staudt, 1999). Depending on their reactivity, they contribute to ozone (O_3) and secondary organic aerosol (SOA) formation, hence influencing air quality (Atkinson et al., 1992; Atkinson, 2000). As SOA may result in the formation of cloud condensation nuclei (CCN), VOCs are indirectly involved in cloud formation (Ehn et al., 2014) and, therefore, influence ecosystem albedo and ecosystem energy balance (Kourtchev et al., 2016). In addition, VOCs affect the oxidative capacity of the atmosphere, thereby influencing the lifetime of greenhouse gases such as CH_4 (Atkinson, 2000; Bonn et al., 2014; Wigley et al., 2024).

Both, anthropogenic and biogenic sources contribute to the global budget of VOCs in the atmosphere with biogenic sources exceeding anthropogenic sources by a factor of 7 (Guenther et al., 1995). Among biogenic sources, plants, particularly trees and shrubs are of outstanding importance, making up to ca. 90% to total biogenic VOCs (Guenther et al., 1995). Noteworthy, terpenes contribute to ca. 80% to biogenic VOC emission (Sindelarova et al., 2022). Since they are of great importance for atmospheric chemistry, many studies aimed at identifying and quantifying biogenic sources of terpenes. In contrast, the significance of other compounds, including aromatic VOCs, is far less well researched. Misztal et al. (2015) underline the quantitative significance of volatile biogenic aromatics, but there is still a large gap of knowledge on potential sources and sinks of this group of compounds (Misztal et al., 2015; Wu et al., 2023). Moreover, since green plant parts are the main source of VOCs from plants, numerous studies focused on control of VOC emission from leaves of trees, whereas the role of other important ecosystem components like the forest floor remains relatively understudied, particularly for temperate forests (Isidorov and Zaitsev, 2022; Sindelarova et al., 2022).

Forest floors can act as both sources and sinks of VOCs, depending on environmental conditions such as temperature, microbial activity, soil moisture content, ambient VOC concentrations and tree species abundance (Peñuelas et al., 2014; Rinnan and Albers, 2020; Jiao et al., 2023b; Kreuzwieser et al., 2025). The interaction of these abiotic and biotic factors determines VOC exchange patterns, which accordingly vary in composition and quantity over days and season in different forest ecosystems (Hakola et al., 2003; Asensio et al., 2007b; Aaltonen et al., 2011; Mäki et al., 2019b; Kreuzwieser et al., 2025). Soil moisture is one of the key drivers of VOC exchange between forest floor and the atmosphere, as it regulates microbial community composition and activity and the physicochemical properties of the soil matrix, hence modulating VOC exchange in a certain range (Ma et al., 2015; Misztal et al., 2018; Crocker et al., 2025).

In contrast, extreme environmental conditions, particularly if lasting over extended time, have the potential to completely change, both quality and quantity of VOC exchange. Long lasting drought, for example, caused unexpected emission of acetone, sulphur- and nitrogen containing volatiles, but inhibited uptake of isoprene and monoterpenes by the forest floor of a tropical ecosystem (Pugliese et al., 2023), most likely due to altered microbial use of soil carbon (Honeker et al., 2023). Opposite to drought, excess abundance of water also dramatically changes soil physicochemical properties and microbial communities (Frey et al., 2011). Waterlogging reduces the diffusion of oxygen from the atmosphere into the soil by a factor of 10,000. In addition, soil and microbial respiration quickly consume the remaining oxygen, thereby causing anoxic conditions. Under anoxia, facultative and obligate anaerobic microorganisms maintain the respiration chain by using electron acceptors other than oxygen (Fitter and Hay, 2002). As a consequence, anoxia leads to reduced redox potential and to a succession of microbial anaerobic processes, thereby causing increased levels of NO_2^-, N_2O, N_2, (by denitrification, redox potential: +220 to +300 mV) Mn^{2+} (redox potential +220 to +280 mV), Fe^{2+} (redox potential: +150 to +180 mV), H_2S (redox potential: -120 to -180 mV), and eventually CH_4 (by methanogenesis, redox potential: below -200 to -280 mV) (Ponnamperuma, 1984; Fitter and Hay, 2002). It is unknown, if a reduced redox potential also affects microbial biosynthesis and emission of VOCs in forest soil. Nevertheless, hints for possible impacts on VOC exchange are provided from research on natural wetlands and other oxygen limited (hypoxic or anoxic) environments. For example, boreal peatlands such as fens show elevated emissions of isoprene, sesquiterpenes, and aliphatic hydrocarbons (Hellén et al., 2006a; Hellén et al., 2020). In subarctic fens and thaw ponds and lakes, there was a notable emission of oxygenated VOCs, including methanol, acetaldehyde, and acetone, as well as certain hydrocarbons (Seco et al., 2020; Wang et al., 2023). Significant emissions of aromatic hydrocarbons such as toluene and xylene were observed in permafrost thaw zones and water saturated hollows in peatlands, where organic matter decomposition occurs under conditions of limited oxygen availability (i.e., under hypoxia: reduced oxygen availability or anoxia: absence of oxygen) (Faubert et al., 2010; Rinnan et al., 2005; Jiao et al., 2023a). Wu et al. (2023) report on strong acetone and toluene emission from waterlogged agricultural soil after addition of straw.

In temperate forests, such extreme conditions of prolonged periods of waterlogging usually only occur at spatially small scales, i.e., at hotspots where particular microbial activities are strongly enhanced compared to the average soil conditions (Kuzyakov and Blagodatskaya, 2015). Oxygen deficiency due to waterlogging is very likely after heavy rain events at locations with clay rich soil or at patches where the soil is compacted. In managed forests, severe soil compaction is often given along skid trails, parallel unpaved access lines within the productive forest area of 3-4 m width at distances of 20-40 m (Werder et al., 2025). They are used by heavy forestry machinery for timber harvest or other management practices (Cambi et al., 2015). It is estimated that in Germany skid trails make up 10-20% of the forest area (Ebeling and Gaertig, 2016). Globally even larger areas of managed forests might be affected, depending on management intensity, terrain, and logging methods (see Vantellingen and Thomas, 2021a, and citation therein). The soil below skid trails is usually heavily compacted, rainwater infiltrates slowly or not at all (Labelle and Jaeger, 2011) and the soil becomes permanently waterlogged, i.e., oxygen limited (Mercier et al., 2019). We suspect that despite their relatively small area, strongly enhanced emission of VOCs from such

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hotspots and similarly disturbed patches (like log landing sites; Vantellingen and Thomas, 2021b) might exert significant impacts on the entire forest ecosystem. This assumption is supported by studies demonstrating strongly enhanced methane emission along skid trails which seem to be related to changes in microbial activity and communities (Frey et al., 2011). Whereas non-trafficked, i.e., undisturbed forest floor of a mixed temperate forest, was a strong sink of methane, skid trails showed emissions of the trace gas (Vantellingen and Thomas, 2021a). An upscaling approach indicated that methane uptake of the whole ecosystem was reduced by 45% because of methane emissions from skid trails, hence, demonstrating strong effects of these hotspots at the ecosystem scale. If such effects of anoxic hotspots of VOC biosynthesis and emission exist in mixed temperate forests, and if they exert similar impact on the whole forest ecosystem is completely unknown.

Therefore, the present study aims to test the hypothesis that (i) the water saturation level affects VOC exchange from the forest floor in a mixed temperate forest ecosystem. We assume that in contrast to most undisturbed and well drained areas of the forest floor, enhanced emission of aromatic hydrocarbons occurs at waterlogged hotspots similar to oxygen limited environments such as boreal peatlands and fens. We further aim to clarify the hypothesis (ii) that oxygen limitation is responsible for altered VOC emissions. For this purpose, we conducted VOC exchange measurements under controlled conditions in the laboratory, where soil cores collected in the field were exposed to normoxia and anoxia for several weeks. We further hypothesize (iii) that enhanced VOC emission from waterlogged hotspots in the forest affects the VOC budget at the ecosystem scale. Therefore, we determined the mixing ratios of VOCs in forest air and related them to VOC exchange rates by the forest floor over several months in the field.

2 Methods

2.1 Study site

The field study was conducted in the ECOSENSE forest (48°16'N, 7°52'W, 480 m asl) located in the western area of the Black Forest near the city of Ettenheim (Werner et al., 2024). Details on field site characteristics are described elsewhere (Kreuzwieser et al., 2025; Tesch et al., 2025). Briefly, it is a mixed forest mainly consisting of 55 to 110 years old European beech (*Fagus sylvatica*) (tree height ca. 30 m) and 55 years old Douglas fir (*Pseudotsuga menziesii*) (tree height ca. 36 m). According to IUSS Working Group WRB (2022), the soil is a Dystric Stagnic Cambisol (loamic) derived from carbonate-free quaternary loess over strongly weathered mesozoic sediments. Redoximorphic features occur below 40 cm depth. The thin forest floor consists mainly of (OL) litter with a patchy thin OF-layer, pH (in KCl) throughout the profile is between 3.5 and 4 (further details see Kreuzwieser et al. 2025). Long-term mean air temperature (reference period 1991-2020) at a meteorological station nearby (Lahr, DWD ID: 2812, 155 m asl) is 10.8°C and annual precipitation 792 mm (DWD, 2023). The measurements of VOC exchange between soil and the atmosphere lasted from summer (July 2024) until late autumn (December 2024), covering the months of highest leaf vitality and abundance (Leaf Area Index, LAI 6-7 m^2 m^{-2}) over the period of leaf senescence (yellowish leaves, still full LAI) and after shedding of European beech leaves (LAI around 1 m^2 m^{-2}) (see also sequence of photographs) (Fig. 1).

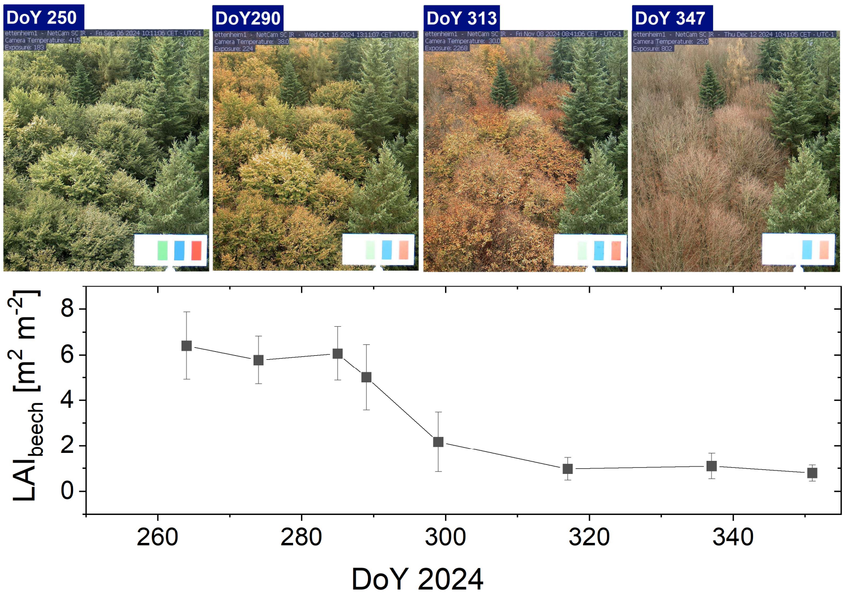

Figure 1 Seasonal phenotypic changes (a) and LAI development (b) in the ECOSENSE forest. Photographs were taken with a PhenoCam positioned on top of a 46 m eddy covariance tower at the field site. LAI was derived from Digital Hemispherical photographs acquired regularly at different subplots of the mixed forest Lotz et al., 2025). Data shown only represent LAI values of selected beech plots. DoY, day of year 2024, Photographs publicly available at https://phenocam.nau.edu/data/archive/ettenheim1.

2.2 Field measurements

2.2.1 Seasonal VOC measurements

We conducted VOC exchange measurements at 1) undisturbed and 2) disturbed locations. In the undisturbed areas of the ECOSENSE forest, we assessed VOC exchange at a total of 26 pre-selected plots. Measurements took place every 2-3 weeks from July 2024 to December 2024. For disturbed locations, we selected (i) waterlogged (soil moisture 95±11%) patches, (ii) very wet (soil moisture 59±10%) patches near the waterlogged ones and (iii) well-drained (soil moisture 33±3%) areas to study the effects of water saturation levels on VOC exchange. Waterlogged patches were mainly found along skid trails where soil compaction inhibited drainage. Measurements at disturbed plots were conducted on December 6, 8, 12, 17 and 20, 2024.

For all VOC exchange measurements in the ECOSENSE forest, we applied a dynamic chamber method (Kreuzwieser et al., 2025). Briefly, per undisturbed plot (26 plots; plot size ca. 1.5 x 1.5 m) one self-constructed Plexiglass chamber (40 x 25 x 10 cm, length, width, height) was randomly placed on the forest floor. Per disturbed plot (waterlogged/anoxic, intermediate/hypoxic, well-drained/normoxic control) six of these chambers were installed. For all measurements, the chambers were shaded by aluminum foil to avoid heating and condensation within chambers but not affecting the air flow into and out of the chambers. Via an exit opening at one front side of the chamber, air was sucked at a controlled flow rate of 200 mL min^{-1} (Pocket Pump TOUCH, SKC, Dorset, UK) over air sampling tubes filled with Carbotrap (20-40 mesh, 45mg) and Tenax TA (60-80 mesh, 35mg) as VOC adsorbers. Sampling immediately started when the chamber was placed on the soil and occurred for two hours resulting in 24 L of chamber air sucked over the adsorbents. To avoid pressure changes in the chambers, three inlet openings (diameter 4 mm) on top of the chamber, opposite to the exit opening, allowed ambient air to enter the chamber. Chamber air was mixed by internal fans. During each soil chamber measurement, ambient air below the closed canopy of the forest at 120 cm height above soil surface and in close vicinity to the soil chambers was sampled as well for 2 h at the same flow rate (200 mL min^{-1}). Amounts of VOCs of these background controls were subtracted from soil chamber VOC contents to calculate soil VOC exchange according to the following equation:

$$Exchange\ rate\ (\mu g\ m^{-2}\ h^{-1}] = \frac{\mathrm{VOC}_{exit}(\mu\mathrm{g}) - \mathrm{VOC}_{ambient\ air}(\mu g)}{\mathrm{A}\ (m^2) \times \mathrm{Duration(h)}}$$

where $\mathrm{VOC}_{\mathrm{exit}}$ and $\mathrm{VOC}_{\mathrm{ambient\ air}}$ are the amounts (µg) of the respective VOC on air sampling tubes, which were placed at the chamber outlet and in the forest (background control). A reflects the soil surface area covered by the chamber (m^2) and duration, the sampling duration (h) . Moreover, $\mathrm{VOC}_{\mathrm{ambient\ air}}$ was used to determine ambient mixing ratios of forest air. After sampling, air sampling tubes were transported to the laboratory and stored at 4°C until analysis, which usually occurred within some days after sampling.

2.2.2 Environmental parameters

In parallel with field VOC measurements, soil temperature and soil moisture were recorded with permanently installed SMT100 sensors (Truebner GmbH, Neustadt, Germany) every 15 minutes. The seven sensors used for this work were installed in 12 cm depth and distributed in vicinity to the plots where VOC exchange was determined. In addition, air temperature in 2 m height within the forest (HygroVUE5, Campbell Scientific Inc., Logan, USA) (1 min resolution) and precipitation at a resolution of 0.1 mm (tipping bucket 52202, Young, Traverse City, USA) in 47 m height on top of our eddy covariance tower (Tesch et al., 2025) were monitored. Soil redox potential was measured in situ using Pt redox electrodes according to Mansfeldt (2003) (Ecotech, Germany), with an Ag/AgCl (KCl) reference electrode. The potential difference was read out using a portable voltmeter (GMH 3530, Greisinger Electronic GmbH, Germany). LAI was monitored using digital hemispherical photography (DHP) conducted at 15 locations across the ECOSENSE forest, arranged in a regular grid with 50 m spacing, and repeated at 2–4-week intervals to capture seasonal canopy dynamics (details see Lotz et al. 2025). DHP images were processed using the R package hemispheR (Chianucci and Macek, 2023), applying gap-fraction inversion at a zenith angle of 20°. Parameter settings were optimized through comparison with litter-trap-derived LAI, resulting in close agreement between optical and direct estimates (R^2 up to 0.97).

2.3 Experiments under controlled conditions in the laboratory

2.3.1 Collection of soil cores

Soil cores were collected in close vicinity of the plots where the effect of waterlogging was studied. We collected six from waterlogged plots and six from the well-drained control plots on February 14, 2025. These samples were directly measured for VOC emissions under controlled conditions. In addition, soil cores from well-drained control plots were sampled on March 5, 2025. These samples were used for anoxic treatment, to elucidate if oxygen deficiency leads to formation of aromatic VOCs in the soil. For soil core collection, a stainless-steel soil core sampler (Pürckhauer type) (inner diameter 1.5 cm, height 50 cm) was carefully driven 12-16 cm into the forest soil without destroying the soil layers. The soil cores were immediately (within minutes) transferred into glass tubes (length 19.5 cm, ID 3.0 cm) and then transferred to the laboratory, where they were weighed, and directly used for experiments. Glass tubes containing soil cores from waterlogged sites and soil cores dedicated for anoxic treatment, were immediately filled with demineralized water to minimize oxygen diffusion into the soil. Remaining headspace ranged between 35 to 65 mL. Glass tubes were closed with glass lids equipped with an air inlet and an outlet on top (see Supplemental Fig. S1) Both openings were closed by screw caps with Teflon septa until beginning of experiments.

2.3.2 VOC exchange under controlled conditions

Depending on the experiment to be performed (normoxia or anoxia), the gas inlet of the glass tube was either connected to VOC-free synthetic air (80% N_2, 20% O_2, Messer, Germany) or VOC-free nitrogen (N_2 5.0, Messer, Germany), which were channelled at a rate of 220 mL min^{-1} (mass flow controller GFCS-014433, Aalborg Instruments & Controls, Inc., USA) through the glass tube (Supplemental Fig. S1). The inlet gas was directed by a PFA tubing to the bottom of the glass tube and it bubbled along the soil to facilitate gas exchange with the soil. At the outlet on top of the glass tubes, an air sampling tube (see section 2.2.1) was installed and gas from the glass tube sucked at a defined rate of 180 mL min^{-1} over the VOC adsorbent (Pocket Pump TOUCH, SKC, Dorset, UK) for 90 min. The excess gas entering the system (~40 mL min^{-1}) was drained via a T-piece over a 1 m long 1/8” PFA tubing connected to the outlet to avoid overpressure in the glass tube. During the measurements, soil temperature was kept constant at 23°C. After running the VOC emission measurements, the soil was dried in a drying oven at 60°C and the dry weight used for flux calculations. For this purpose, the equation (section 2.2.1) was adjusted: $VOC_{\text{ambient air}}$ was deleted as neither synthetic air nor nitrogen contained any VOC if channelled through empty blank chambers. Soil surface area (A) was replaced by the dry weight of the soil core analysed. Hence, the resulting VOC flux was expressed as ng g^{-1} dry weight h^{-1}.

2.4 GC-MS analysis of VOCs

VOCs accumulated on air sampling tubes (sections 2.2.1 and 2.3.2) were analysed by Gas Chromatography – Mass Spectrometry (GC-MS) (GC 7820A; mass-selective detector 5975C, Agilent Technologies Böblingen, Germany) (Kreuzwieser et al., 2025). Initially, adsorbed VOCs were desorbed at 240°C in a thermodesorption unit and trapped at -70°C in a cold injection system (TDU-CIS4, Gerstel, Germany). The CIS was then heated to 240°C, hence, releasing the VOCs onto the separation column (DB-5UI, 60 m × 0.25 mm ID, 0.25 µm film thickness, Agilent Technologies Böblingen, Germany). Helium at a constant flow of 1ml min^{-1} was used as carrier gas. The oven program started at 40°C and was stepwise increased to 270°C which was held for 17 min (details see Lee et al., 2025). The mass spectrometer was run with an ionization energy of 70 MeV at a temperature of 230°C in the ionization source and 150°C at the quadrupole. Mass spectra from 40 m/z to 300 m/z were recorded. Mass spectral data were analyzed with the MassHunter Software (Agilent Technologies Böblingen, Germany). For peak identification, we used the NIST mass spectral library and the fragmentation patterns and retention times of the authentic standards, toluene, ethylbenzene, styrene, and the terpenes p-cymene, α-pinene, camphene, sabinene, limonene and δ-3-carene. For quantification of these VOCs, we ran calibration curves by diluting the pure liquid standards (Merck, Germany) in either hexane (α-pinene, camphene, sabinene, limonene, δ-3-carene) or methanol (toluene). Aliquots of 1 µL were pipetted into thermal desorption tubes and injected into the GC via the TDU-CIS system like the samples. Dependent on dilution and VOC, injected masses ranged from 1 to 455 ng. Slopes of linear regressions per VOC were used to calculate the masses of VOCs on the air sampling tubes.

2.5 Statistics

Data was processed in MS-Excel (Microsoft Excel 2016, Santa Rosa, CA, USA). Statistical analysis and figure design were made with OriginPro (Version 2025, OriginLab Corporation, Northampton, MA, USA). Because data was not normally distributed, the Mann-Whitney U test was applied to test for differences between two groups of different treatments (e.g., emission differences from normoxic vs anoxic treatment). If more than two groups were compared, the Kruskal-Wallis test was employed, followed by Dunn's posthoc-tests. For both Mann-Whitney U test and Kruskal-Wallis tests, a p-value <0.05 was considered statistically significant.

To investigate the relationships between the variables, a Pearson correlation analysis was performed. The Pearson correlation coefficient quantifies the strength and the direction of a linear relationship. Correlation coefficients range from -1 to +1, with values closer to one indicating a strong correlation, and values around 0 suggesting no correlation. Statistical significance was determined at $p<0.01$. Results of this analysis are shown in a correlation matrix.

3 Results

3.1 Strong toluene and p-cymene emissions from waterlogged soil in the ECOSENSE forest

To test the hypothesis that VOC exchange is related to water saturation level, we determined VOC fluxes at well-drained control plots (redox potential ranging from +367 to +599 mV), and at patches characterized by high soil moisture (59±10%; redox potential +142 to -76 mV) and waterlogging (soil moisture 95±11%, redox potential -11 to -96 mV) (located along skid trails) during December 2024 (Fig. 2). As hypothesized, VOC exchange, particularly of monoaromatic compounds, was strongly influenced by water saturation levels. Whereas toluene was taken up by the well-drained forest floor (flux rate -49±52 ng m^{-2} h^{-1}), there was a switch from uptake to emission at plots with high soil moisture (25±79 ng m^{-2} h^{-1}). Notably, extremely high toluene emissions (2400±1570 ng m^{-2} h^{-1}) were detected from waterlogged forest floor. Besides toluene also some other aromatic compounds showed enhanced emissions from the waterlogged compared to the well-drained forest floor. Among these compounds, emission of the aromatic monoterpene p-cymene was highest with rates of 1170±912 ng m^{-2} h^{-1} under waterlogging conditions. This reflects an increase by a factor of 50 compared to emission from well-drained forest floor (24±53 ng m^{-2} h^{-1}). Similarly, emissions of ethylbenzene and styrene increased significantly due to waterlogging, but emission rates were ca. one order of magnitude lower compared to toluene and p-cymene. Interestingly, also the emission of the monoterpene camphene significantly increased due to waterlogging, whereas sabinene emission tended to increase, but the effect was not significant. In contrast, the fluxes of other aromatics (benzaldehyde, acetophenone) and monoterpenes (α-pinene) abundant in forest air did not depend on waterlogging (data not shown).

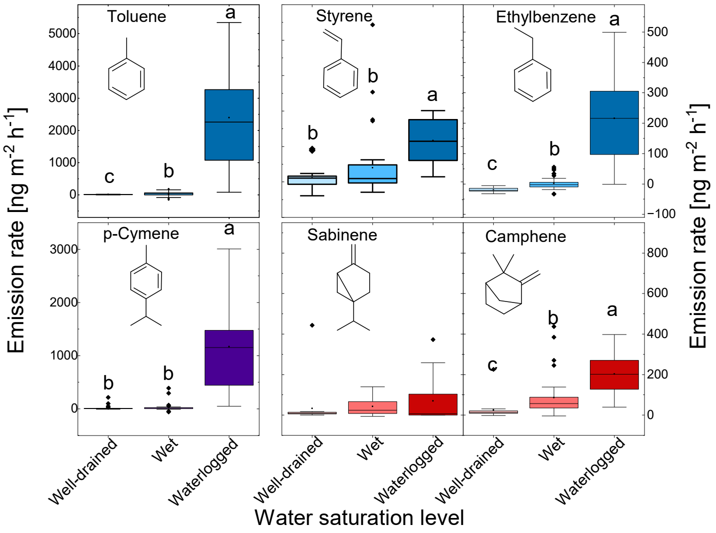

Figure 2 Effect of water saturation on the exchange of aromatic volatiles and major terpenes in the ECOSENSE forest. Chamber measurements were conducted in the ECOSENSE forest in December 2024 at disturbed plots characterized by different water

saturation levels (well-drained, wet, waterlogged). Redox potentials amounted to 438±77, 4±62, and -65±23 mV, respectively. Data of n=16 (waterlogged) to n=38 (wet) chamber measurements per level are shown. Since data was not normal distributed, the Kruskal-Wallis test followed by Dunn's posthoc test was applied. Different letters indicate statistically significant differences at p<0.05 between water saturation levels.

3.2 Enhanced toluene and p-cymene emissions also under controlled conditions

For more detailed studies, we collected soil cores in the ECOSENSE forest, transferred them into glass tubes and performed VOC measurements under controlled conditions in the laboratory. Comparing VOC emissions from soil cores under normoxic and anoxic conditions in vitro (Fig. 3), showed similar results than in situ between well-drained and waterlogged forest floor (Fig. 2). Toluene emissions under anoxic conditions exceeded emissions under normoxia by ca. 5000%, i.e., they were 50-times higher. Ethylbenzene and p-cymene emissions increased 100- and 30-times under anoxia, respectively. Also, camphene emission was ca. 20-times enhanced, like the increase observed in situ. Compared to the field measurements, we did not detect styrene and sabinene emission in the present in vitro assays.

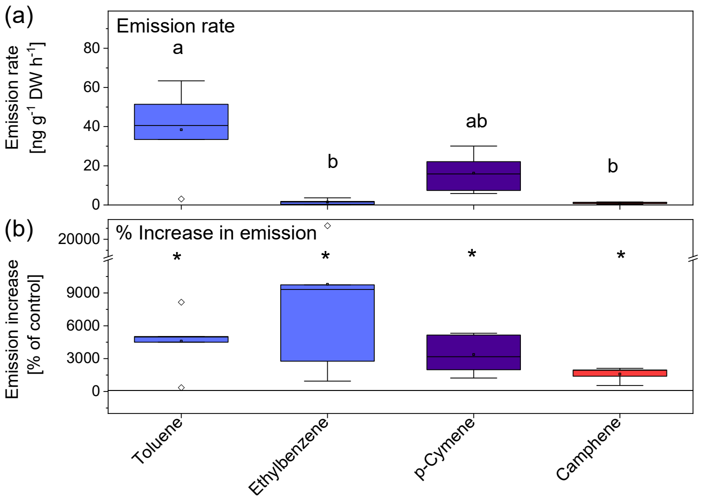

Figure 3 Emission of main aromatics and terpenes under anoxic conditions (a) and percent increase of emission under anoxia compared to normoxic conditions (b). Five soil cores from waterlogged plots and five soil cores from well-drained control plots were collected in the ECOSENSE forest and transferred to the lab. (a) Emission of volatiles was immediately determined. Different letters indicate statistically significant differences at p<0.05 as calculated by Kruskal-Wallis test followed by Dunn's posthoc tests. (b) Percentages of increase of emissions between waterlogged soil compared to well-drained soil was calculated by setting emission rates of controls 100%. Asterisks indicate significant differences between waterlogged and well-drained soil as calculated by Mann-Whitney test at p<0.05.

To test if enhanced emission of toluene really depends on the occurrence of anoxic conditions, we applied another in vitro approach. We used soil cores collected in the field from well-drained forest floor and incubated half of them under anoxia for up to six weeks. In consistence with the previous approaches, we observed strongly enhanced emission of toluene (46-fold), p-cymene (14-fold) and ethylbenzene (3-fold) after six weeks of treatment (Fig. 4). Although α-pinene also showed a trend to higher emissions under anoxia compared to normoxia, the increase was not statistically significant. However, in contrast to the previous measurements (Figs. 2 and 3), we observed significantly enhanced emission of the monoterpenes camphene, limonene and δ-3-carene. Interestingly, the temporal patterns of increased emissions were similar for ethylbenzene, p-cymene, δ-3-carene and limonene (highest median of emissions after four weeks of treatment), and for toluene, α-pinene and camphene (highest median of emissions after six weeks of treatment).

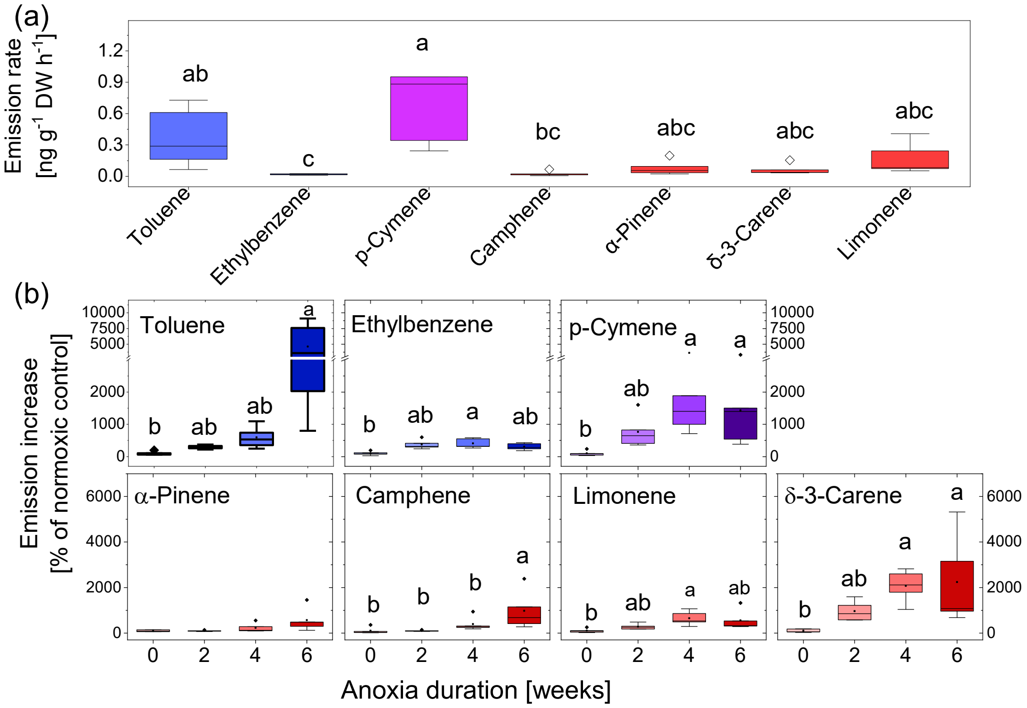

Figure 4 Emission of main aromatics and terpenes after six weeks of anoxia under controlled conditions (a) and increase of emission compared to normoxic conditions (b). Volatile aromatics (blue), the aromatic monoterpene p-cymene (violet) and major terpenes (red). Thirty soil cores from well-drained plots were collected in the ECOSENSE forest and transferred to the laboratory. Fifteen soil cores were kept under normoxic conditions serving as controls and 15 were fumigated with nitrogen and covered with water to induce anoxia. Every second week, five samples each were used for VOC emission measurements. Data shown represent emissions rates after six weeks of anoxia (a) and the increase as percentages of exchange rates from anoxic compared to normoxic conditions,

which were set 100%. Different letters indicate significant differences between emission rates of different compounds (a) or treatments (b) as calculated by Kruskal-Wallis test followed by Dunn's posthoc tests at p<0.05, DW, soil dry weight.

To obtain hints on common production pathways of the emitted compounds, we performed linear correlation analysis (Fig. 5). Surprisingly, strongest positive linear correlations were observed between toluene and the monoterpenes α-pinene and camphene. Similar strong positive correlations existed between α-pinene and camphene, between α-pinene and limonene and between δ-3-carene and limonene. In contrast, only weak, non-significant correlations were observed between toluene and the other aromatic compounds, hence, suggesting production of these compounds from different pathways. Emission of the monoaromatic p-cymene correlated significantly with camphene and δ-3-carene emissions.

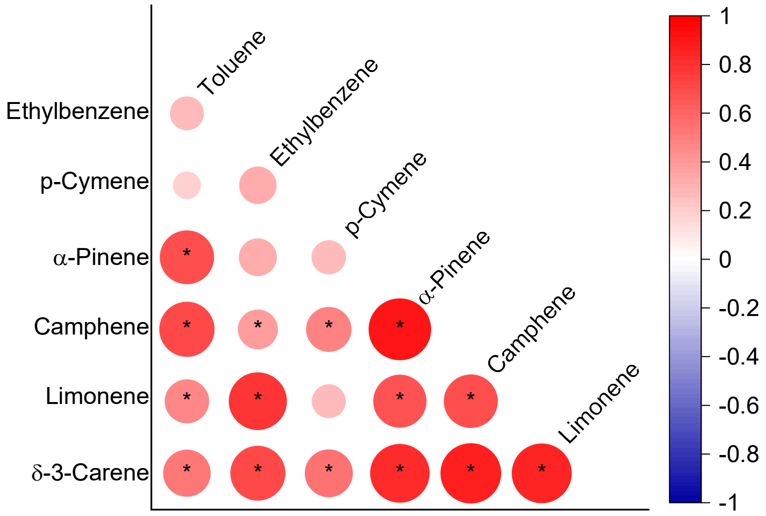

Figure 5 Pearson correlation analysis between the emission of different VOCs to identify if common synthetic pathways exist. Size and colour of circles present direction and strength of correlation (see also scale, right). Asterisks indicate statistically significant correlations (p<0.01). Colour scale reflects Pearson's correlation coefficients.

3.3 Seasonal variation in ambient toluene and p-cymene mixing ratios and soil-atmosphere exchange

The present experiments under controlled conditions and at selected waterlogged field sites clearly indicated that soil water saturation levels have a strong impact on the emission of toluene, p-cymene and some other aromatic volatiles and terpenes. To test if waterlogged hotspots have visible impacts at the ecosystem scale, we monitored ambient mixing ratios of toluene and p-cymene under the closed canopy of the ECOSENSE forest at 1.2 m height and determined their exchange rates between soil and the atmosphere during the transition from summer to autumn and winter (Fig. 6).

During this period, volumetric soil moisture levels showed a broad range with lowest levels of ca. 10-20% in August (DoY 200-230) to highest levels of 30-40% by the end of December (Fig. 6). Decreases in soil moisture levels between July and August were a consequence of warm temperatures and low precipitation. Rain events caused slightly increased soil moisture levels in September and beginning of October (DoY 250-280). Some heavier rain events led to the high soil moisture in November and December. The mean daily air temperatures were around 19.5°C in July 2024. August was the warmest month, with a mean daily temperature of 23.8°C (Fig. 6). The highest air temperature of 30.1°C was recorded on August 12. Thereafter, air temperatures steadily decreased to ca. 0°C by end of December. Soil temperatures were tightly correlated to air temperatures (Fig. 7) with a certain time delay. Accordingly, highest soil temperatures of around 20°C were recorded in August, lowest soil temperatures of ca. 3-4°C in December. The ambient mixing ratios of toluene followed a distinct seasonal pattern whereas p-cymene mixing ratios remained relatively constant over the season. Toluene showed low ambient mixing ratios of ca. 50-100 ppt during summer/early autumn before they strongly increased up to 800 ppt, followed by mixing ratios around 300-400 ppt during the rest of the season. The VOC exchange rates between forest floor and the atmosphere differed considerably between these compounds. Toluene exchange rates were mostly slightly negative during summer. However, when ambient mixing ratios of toluene increased in autumn, toluene was strongly taken up by the forest floor. Toluene uptake by the forest floor was also observed in December after complete shedding of European beech leaves. For p-cymene no clear exchange pattern became visible.

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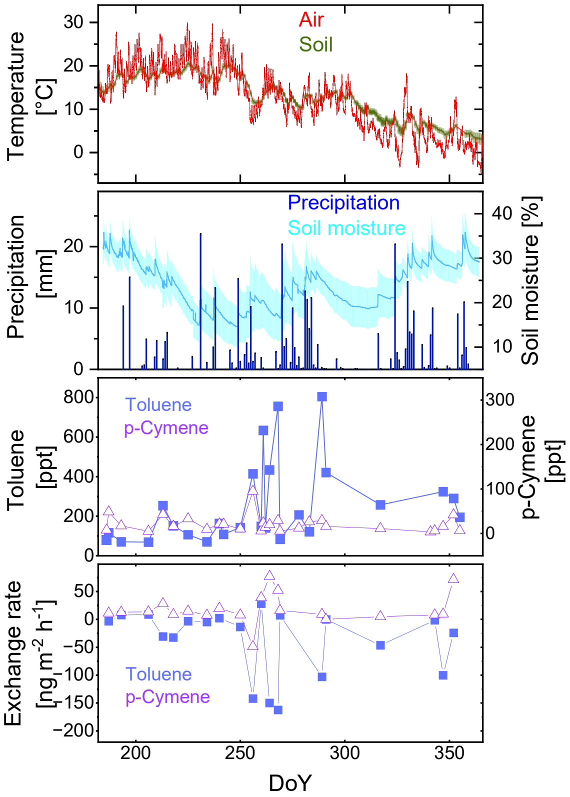

Figure 6 Air temperature (at 2m height in-canopy) and soil temperature (at 12 cm depth) (a), precipitation (at top of 46 m tower) and volumetric soil moisture (b), ambient (in canopy) toluene and p-cymene mixing ratios (c), and toluene and p-cymene exchange between forest floor and the atmosphere (d) at the ECOSENSE forest during the experimental period from July-December 2024. DoY, day of year 2024.

To understand which factors might control the exchange of toluene and p-cymene in the field, we performed correlation analysis considering LAI, soil moisture, soil and air temperature, day of year (DoY) and ambient VOC mixing ratios (Fig. 7). This analysis suggested a dependence of toluene exchange on ambient mixing ratios of toluene (see also Supplemental Fig. S2). The higher the mixing ratios the stronger the compound was consumed by the forest floor. Interestingly toluene mixing ratios positively correlated with precipitation 7 d before VOC measurement (Pr_{-7d}) but not with precipitation on the day of measurement (Pr). However, a correlation between soil moisture and ambient mixing ratios of toluene was not observed. The weak and not significant correlation was even negative and not positive as assumed. As mentioned above and expected, air temperature and soil temperature tightly positively correlated. Both, air and soil temperature and LAI negatively correlated with day of year, and LAI positively correlated with both temperatures (high LAI in summer when temperatures are high).

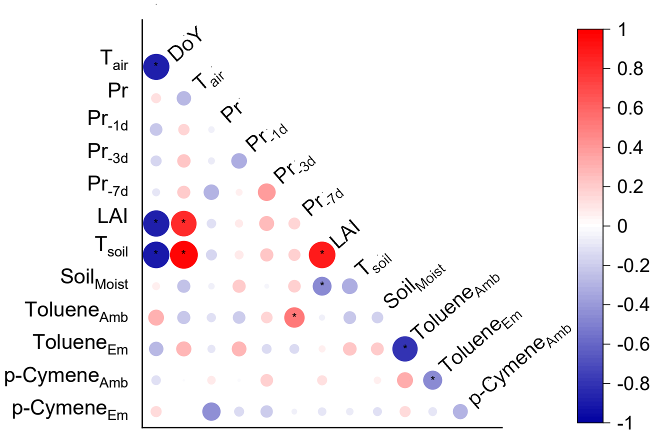

Figure 7 Pearson correlation analysis between the abiotic parameters and ambient mixing ratios and exchange rates of toluene and p-cymene at the ECOSENSE forest. Size and colour of circles present direction and strength of correlation (see also scale, right). Asterisks indicate statistically significant correlations ($p<0.05$). DoY, day of year 2024, Pr, precipitation, T_{air}, daily average air temperature, T_{soil}, soil temperature, $soil_{moist}$, volumetric soil moisture, Amb, ambient (in-canopy) mixing ratio, Em, emission rate. Precipitation data of the day of VOC measurement (Pr), as well as 1 day (Pr_{-1d}), 3 days (Pr_{-3d}) and 7 days (Pr_{-7d}) before VOC measurements were used for correlation analysis. Colour scale reflects Pearson's correlation coefficients.

4 Discussion

The present work was conducted to clarify if waterlogging related oxygen limitation in the soil of a temperate forest changes VOC flux patterns compared to well-drained normoxic forest floor and if such hotspots of altered VOC fluxes have the potential to influence the VOC budget at the ecosystem scale. We conducted the study in the ECOSENSE forest, a temperate mixed European beech and Douglas fir ecosystem, where seasonal measurements of terpenoid exchange have been performed previously (Kreuzwieser et al., 2025). Experiments with collected soil cores under controlled conditions in the laboratory complemented the field measurements.

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4.1 Enormous toluene and p-cymene emission from anoxic soil

Both, the ECOSENSE forest floor and the soil cores collected in the forest and studied under controlled conditions, exhibited tremendous stimulation of VOC exchange if the soil was exposed to waterlogging (field) or anoxic conditions (laboratory), hence, supporting our hypothesis (i). Anoxia exerted strongest effects on the emission of several monoaromatic compounds but also caused enhanced release of some monoterpenes. At the waterlogged plots of our field site, we observed unexpected high emissions of toluene and p-cymene with rates up to 5000 ng m^{-2} h^{-1} and 3000 ng m^{-2} h^{-1}, respectively. To the best of our knowledge this is the first report on dramatically induced toluene and p-cymene emissions from the forest floor of a mixed temperate forest. So far only studies from wetland/peatland, thawing permafrost soils and waterlogged agricultural soil with added straw demonstrated significant toluene and, in some cases, p-cymene release. For example, Jiao et al. (2023a) report on toluene and p-cymene emission from permafrost influenced soil, indicating similar toluene emission rates (Palsa soil: ca. 5000 ng m^{-2} h^{-1}) but lower p-cymene emissions (<10 ng m^{-2} h^{-1}) compared to our field study. Li et al. (2020) examined the effect of thawing on soil cores collected from Arctic permafrost peatland soil and observed a strong release of toluene at rates (20-60 ng g^{-1} dry weight h^{-1}) exactly in the range of our field collected soil cores analyzed under controlled, anoxic conditions (ca. 40 ng g^{-1} dry weight h^{-1}, Fig. 1). Similar to our work in a temperate forest, Wu et al. (2023) demonstrate strong toluene release if straw was added to a flooded agricultural soil. Due to the temporal patterns observed, they conclude on microbial production taking place under anoxic conditions in the soil. Toluene emission from thawing permafrost soil was also shown in a laboratory study on collected soil cores but in contrast to our findings, emission rates decreased with lower drainage of the soil (Kramshøj et al., 2019).

4.2 Anoxic soil as a potential source of atmospheric toluene

Toluene is the most abundant monoaromatic compound in the atmosphere of urban areas, but is also found in terrestrial ecosystems, including tropical, Mediterranean, boreal and temperate forests (Jüttner, 1986; 1988; Kesselmeier et al., 2000; Kajos et al., 2015; Ji et al., 2017; Asensio et al., 2007a, b; Vestenius et al., 2021). In contrast, ambient mixing ratios of p-cymene are lower and often not reported. For atmospheric chemistry, toluene is of great interest because its photochemical oxidation produces tropospheric ozone and secondary organic aerosols (SOA) (Ng et al., 2007; Faiola et al., 2014; Zhang et al., 2015; Ji et al., 2017), both of which negatively affect air quality. Most important sources of atmospheric toluene arise from the use of fossil fuels (Skorokhod et al., 2017). However, toluene can also be of biogenic origin. Among biogenic sources, plants play the most important role as first identified by Heiden et al. (1999) and thereafter confirmed in numerous studies on a great variety of plant species (White et al., 2009; Graus et al., 2013; Misztal et al., 2015; Fasbender et al., 2018). Besides, biomass burning (Tawfiq et al., 2015) and many microbial processes mainly under anaerobic conditions contribute to global toluene emission (Kang et al., 2025). For example, microbial contribution to toluene formation has been demonstrated in marine environments (Middelburg et al., 2009; Srain and Pantoja-Guttierrez, 2022; Wohl et al., 2023), freshwater environments (Jüttner and Henatsch, 1986; Jüttner, 1991; Fischer-Romero et al., 1996), sewage sludge (Mrowiec et al., 2005), tree root associated fungi (Bäck et al., 2010), leaf litter decomposition (Isidorov and Jdanova, 2002; Fedele et al., 2007; Gray et al., 2010; Isidorov and Zaitsev, 2022; Rocco et al., 2025), and as mentioned above, in waterlogged agricultural soils (Wu et al., 2022), permafrost and wetland soils (Kramshøj et al., 2019; Li et al., 2020; Jiao et al., 2023a). The present work suggests that the soil of temperate forests might be another important, yet underestimated source of toluene and p-cymene for atmospheric abundance. In contrast to p-cymene, seasonal patterns of ambient mixing ratios of toluene were observed. Toluene mixing ratios were relatively low (most of the time below 100 ppt) during the drier warmer months July-August and increased (up to 800 ppt) when soil moisture at the field site increased and waterlogged patches could be observed in later autumn. Similar atmospheric toluene mixing ratios (0.1-1.4 ppb) and patterns in the air of a temperate forest have been described earlier (Jüttner, 1988). Even more pronounced differences in toluene mixing ratios (factor of 4) between summer (55 pptv) and winter (229 pptv) were observed in a boreal coniferous forest at the Hyytiälä research station in Central Finland (Hakola et al., 2003) and similar patterns at the same station were confirmed later (Hakola et al., 2012). Although in a Mediterranean holm oak forest (Seco et al., 2011) summer and winter maximum toluene mixing ratios were similar (1.34 vs. 1.9 ppbv, respectively), in winter much more peaks with high mixing ratios (~6-times > 1ppbv vs. 1-time >1 ppbv) were observed with maxima occurring at days with low radiation and high relative humidity. Interestingly, at some (but not at all) field sites in Amazonia, higher toluene mixing ratios were observed during the wet season compared to the dry season (Paralovo et al., 2016).

Therefore, the present results together with literature data provide circumstantial evidence that ambient toluene mixing ratios might be related to enhanced toluene emission from the forest floor, which is not the case for p-cymene. At a first glance, this assumption seems to be in contradiction to the seasonal VOC exchange between forest floor and the atmosphere, indicating strong uptake of toluene from the soil, when ambient mixing ratios are high (Figs. 5, 6; Supplemental Figure S2), suggesting microbial consumption of toluene in the soil as also seen by Jiao et al. (2023b). However, soil conditions in forest ecosystems are characterized by extreme heterogeneity. While observing toluene uptake from undisturbed, well-drained soil, tremendous emissions of toluene and p-cymene were identified at waterlogged patches (Fig. 1). Such small areas represent hotspots according to the definition of Kuzyakov and Blagodatskaya (2015). We assume in agreement with our hypothesis (iii), that the strong toluene release from these hotspots might overcompensate toluene uptake at other areas of the forest. Such waterlogged patches occurred mainly along skid trails, which are characterized by reduced soil pore volume in the topsoil and strongly enhanced soil compaction (Cambi et al., 2015). We assume that despite the relatively small area of skid trails in a managed forest, the emission from such hotspots and similar disturbed patches (like log landing sites; Vantellingen and Thomas, 2021b) might significantly impact the entire forest ecosystem as already demonstrated for the exchange of methane (Vantellingen and Thomas, 2021a, b). Further work is urgently needed to obtain estimates of the contribution of skid trails to the whole forest. Still, other potential sources of atmospheric toluene might be leaf litter (Gray et al., 2010; Isidorov and Zaitsev, 2022; Rocco et al., 2025) or senescing European beech leaves. This is because the time of highest atmospheric toluene abundance coincided with leaf senescence, when leaves were yellowing but still not shed as seen from available LAI data. Future work should also consider this potential source of toluene. It should also be mentioned that the observed seasonal pattern of toluene mixing ratios might be influenced by long-distance transport of toluene from anthropogenic sources, mixture with air from the free (above-canopy) atmosphere by turbulence, and by possible adsorption/desorption processes within the forest.

4.3 Metabolic origin of toluene and other volatiles emitted by waterlogged soil

The strong emission of toluene, p-cymene and other monoaromatic compounds from waterlogged soil at the ECOSENSE forest was surprising as comparable emissions of such compounds from temperate forests have not been described before. In good agreement with our hypothesis (ii), our experiments under controlled conditions show that normoxic, well aerated soil emits VOCs at very low levels (Figs. 2, 3). This finding provides evidence that emission of toluene and p-cymene is not due to release of trace gases abundant in soil pores or adsorbed at soil particles as demonstrated for toluene and p-cymene release from thawing permafrost soil (Kramshøj et al., 2019; Li et al., 2020). In our approach, changing conditions from normoxia to anoxia strongly induced emission of toluene and p-cymene together with some monoterpenes. Whereas monoterpene emission might be explained by release from decay of terpene storing Douglas fir needles (Lee et al., 2025), enhanced toluene enhanced emission can only be explained by de novo formation in the soil. De novo biosynthesis of toluene is also suggested by Wu et al. (2023) observing strongly enhanced toluene release from a flooded agricultural soil. There are two known pathways possibly contributing to formation of toluene in the present study. Notably, both pathways require anoxic conditions and soil, which is rich in organic matter. Both requirements are fulfilled at the waterlogged patches of the ECOSENSE forest. A well understood microbial pathway of toluene biosynthesis depends on the abundance of phenylacetate in the soil, which can be formed by conversion of the amino acid phenylalanine (Zargar et al., 2016; Beller et al., 2018; Srain and Pantoja-Gutiérrez, 2022). The reaction releasing toluene is catalysed by the enzyme phenylacetate decarboxylase (Beller et al., 2018; Zargar et al., 2016). If the phenylacetate pathway is indeed responsible for toluene emission from the soil in the present study remains unclear, but the presence of enzymes of phenylacetate catabolism in bacterial isolates from soils provide strong hints for its contribution (Pickup et al., 1983; Kang et al., 2025). Interestingly, the key enzyme of this pathway, phenylacetate carboxylase, also reacts with some analogues of its substrate phenylacetate. As a result, other monoaromatic volatiles than toluene can be formed by phenylacetate carboxylase, such as ethylbenzene, which was emitted by the anoxic forest soil in the present work.

Phenylalanine and other similar precursors of phenylacetate and analogues might be produced during protein degradation of organic matter in the soil, for example, leaf or root litter. However, because the degradation of proteins is rather inhibited but not stimulated by anoxic conditions (Greenwood, 1961; Noll et al., 2019), we assume that other processes are involved. One alternative source of phenylacetate precursors might be related to the anoxic degradation of lignin. This idea is supported by a recent study elucidating the high rate of soil organic matter (SOM) mineralization and surprisingly strong CO_2 release from soil under oxygen limited conditions (Merino et al., 2021b). The authors demonstrated that anoxic conditions favour the abiotic Fenton reaction, which together with peroxidases yields hydroxyl radicals (Merino et al., 2021a). As a strong reactive oxygen species, the hydroxyl radical reacts with lignin-like compounds of SOM, thereby contributing to CO_2 formation and lignin mineralization (Merino et al., 2021a, b; Dong et al., 2023; Merino et al., 2025). Several monoaromatic compounds serving as phenylacetate and, hence, toluene precursors might arise from such lignolytic processes (Janusz et al., 2017).

The second pathway of toluene formation arises from an acid-catalyzed dealkylation of the monoaromatic monoterpene p-cymene, a reaction yielding toluene (Richards and Sandau, 2018). The abundance of the possible toluene precursor, p-cymene, was demonstrated recently in the Douglas fir influenced soil of the ECOSENSE forest, with highest contents (around 10 µg g^{-1} soil dry weight) in the organic soil layers and sharply decreasing contents in the mineral soil layers (Lee et al., 2025). Therefore, it cannot be excluded that conversion of p-cymene contributes to toluene formation in the ECOSENSE forest. To undoubtedly identify the responsible mechanism of toluene formation, i.e., p-cymene transformation or phenylacetate decarboxylase pathway, experiments with ^{13}C-labelled lignin, protein and/or p-cymene are required.

Interestingly, there seems to be a connection between toluene and p-cymene formation, as also the latter showed dramatically increased emissions from anoxic soil in the present work. As highlighted by Richards and Sandau (2018), many different terpenes such as α-pinene and terpinolene possess the para-alkylation basic structure. This structure can be dehydrogenated to directly yield p-cymene (Hylemon and Harder, 1999). This reaction is thought to be particularly important under anoxia (Harder and Probian, 1995) and several studies have shown its potential to convert monoterpenes into p-cymene (Maxwell et al., 1971; Harder and Probian, 1995; Miyazawa et al., 1996; Hylemon and Harder, 1999; Harder and Foss, 2010). (). Notably, Lee et al. (2025) observed many of these terpenes with contents around 300 µg g^{-1} in the organic soil layer of the Douglas fir influenced area of the ECOSENSE forest. Most important terpenes were α-pinene, β-pinene and limonene (Lee et al., 2025), which potentially could function as precursors of p-cymene formation by the same transformation process.

5 Conclusions

Taken together, the present study shows that waterlogging over extended time within a mixed temperate forest strongly enhances the emission of the monoaromatic compounds toluene and p-cymene, two VOCs significant for atmospheric chemistry, mainly for SOA formation. Such anoxic sites mainly occur at disturbed areas in the managed forest, mainly along skid trails or at sites of tree landing during timber harvest (Vantellingen and Thomas, 2021b). The study further indicates that despite the relatively small area of disturbed sites within a managed forest, toluene emission from anoxic hotspots has the potential to impact the whole ecosystem's toluene budget, i.e., increasing atmospheric toluene mixing ratios. The metabolic origin of toluene emitted by the anoxic forest floor must be elucidated in further work using stable carbon isotopes. Toluene might be derived from phenylacetate synthesized from the amino acid phenylalanine, or from p-cymene, which can be a product of monoterpene transformation processes, depending on the abundance of monoterpenes in leaf and/or root litter. The present work provides evidence that the forest floor has to be considered a significant source of atmospheric toluene.

Data availability

Data are available upon request.

Author contributions

HL: formal analysis, investigation, writing – review & editing, JP, TS, MS, DM, JB, LD: formal analysis, investigation. AC, CW, TK: writing – review & editing, resources, supervision. Julian Brzozon: writing – review & editing, formal analysis, investigation. JK: writing – original draft, methodology, supervision, conceptualization, funding acquisition.

Competing interests

The authors declare that they have no conflict of interest.

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