



Field-deployable branch enclosure system for biogenic volatile organic compounds emitted from conifers

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- 15 Abstract. Biogenic volatile organic compounds (BVOCs), emitted primarily from terrestrial plants, significantly
- 16 influence atmospheric chemistry and climate change. Conifers are major sources of BVOCs in temperate regions.
- 17 However, their unique physiology, particularly the storage of terpenes within their tissues, makes accurate
- 18 measurements of BVOC emissions challenging owing to contact-induced release. We developed a portable
- 19 dynamic branch enclosure system specifically optimized for BVOC measurement in conifers, which enables
- 20 measurements of multiple trees in a single day. The system uses filtered ambient air as a purge gas to reduce
- 21 logistical challenges and features a foldable bag design to minimize excessive BVOC release induced by physical
- 22 contact. It provides BVOC- and ozone-free air, maintains stable internal temperature and humidity conditions
- 23 closely approximating those of natural environments, and ensures repeatable measurements of BVOC emissions.
- 24 Field testing with Japanese cedar (Cryptomeria japonica) revealed significant individual variations in BVOC
- 25 emission rates and compositions. These findings demonstrate the system's reliability and applicability for assessing
- 26 BVOC emissions under field conditions, offering a practical solution for advancing our understanding of BVOC
- 27 dynamics in diverse ecosystems.

28 1. Introduction

- 29 Biogenic volatile organic compounds (BVOCs), emitted primarily from terrestrial plants, play a significant role in
- 30 atmospheric chemistry. Through atmospheric degradation processes, BVOCs contribute to the formation of
- 31 tropospheric ozone and secondary organic aerosols (Chatani et al., 2015; Ghirardo et al., 2016; Laothawornkitkul
- 32 et al., 2009), which significantly affect air quality. These atmospheric constituents can alter radiative forcing and
- 33 precipitation patterns, influencing the global climate (Randall et al., 2013; Rotstayn et al., 2009).
- 34 Among terrestrial plant species, conifers are major BVOC emitters in temperate regions, and their emissions have
- 35 important implications for regional air quality and climate (Peñuelas & Staudt, 2010). They release a diverse array
- 36 of BVOCs, notably monoterpenes (MTs), sesquiterpenes (SQTs), and diterpenes (DTs) (Chatani et al., 2018;
- 37 Guenther et al., 1993; Matsunaga et al., 2011). Monoterpenes (C10 compounds) are highly volatile and major
- 38 BVOCs in temperate and boreal regions (Guenther et al., 1993). Sesquiterpenes (C₁₅) have a notable role in
- 39 atmospheric processes, particularly in particle formation, as their oxidation produces ultra-low volatility organic





40 compounds that act as efficient nucleators (Dada et al., 2023). Diterpenes (C20) have even lower volatility but high 41 reactivity, which may make them particularly important for particle formation, although these properties also pose 42 challenges for their observation. 43 The profiles of BVOC emissions from plants are determined by a complex interplay of factors, including 44 environmental conditions such as temperature and drought (Birami et al., 2021), genetic factors, and biotic stresses 45 such as plant-microbe interactions (Saunier et al., 2020). Moreover, some plant species alter their emission profiles 46 in response to BVOCs emitted by neighbouring plants (Arimura et al., 2012). However, how these factors influence 47 the composition and rates of BVOC emission remains insufficiently understood (Tani et al., 2024). Quantifying 48 emission characteristics at the level of individual plants is crucial for understanding how emissions change in 49 response to varying environmental conditions. This understanding is essential for predicting future changes in 50 BVOC-aerosol-climate feedbacks. 51 One challenge hindering individual-level BVOC measurements under natural conditions is the logistical difficulty 52 associated with conventional sampling methods. Since conifers store terpenes within their needles (Saito et al., 53 2022), physical contact can trigger a burst release of these compounds, making it difficult to accurately measure 54 their emission rates. The cuvette method, which clamps an individual leaf, is generally unsuitable for conifers for 55 this reason. The dynamic branch enclosure method (Ortega et al., 2008; Ortega & Helmig, 2008) reduces direct 56 leaf contact but still contacts the stem during device installation, which is particularly important consideration for 57 conifers such as cedars that store terpenes in both leaves and stems. Several studies using dynamic branch 58 enclosure methods on coniferous trees allowed a stabilization period after device installation of approximately 24 59 h (Helin et al., 2020; Helmig et al., 2013; Hiura et al., 2021; Matsunaga et al., 2011, 2012, 2013), 48 h (Bouvier-60 Brown et al., 2009), or 1-2 weeks (Praplan et al., 2020) to mitigate the effects of excessive emissions associated 61 with physical contact during device installation. During the stabilization period, it is essential to either maintain 62 continuous gas flow (Helin et al., 2020; Helmig et al., 2013; Hiura et al., 2021; Matsunaga et al., 2011, 2012, 2013) 63 or avoid fully sealing an enclosure (Praplan et al., 2020) to sustain normal physiological conditions and prevent 64 condensation before measurements are taken. However, when gas cylinders are used as the purge gas source in 65 locations without a power supply, numerous cylinders must be transported to the site to maintain continuous gas 66 flow throughout the measurement period, posing significant logistical challenges for field measurements (Hiura et 67 al., 2021; Matsunaga et al., 2011, 2012, 2013). Instead of gas cylinders, pumps can be used to supply purge air by 68 drawing in external air. However, to our knowledge, no studies have clearly shown whether a pump-based system 69 can be entirely powered by a portable battery, which is essential in remote areas without a power supply. These 70 difficulties highlight the need for simplified, field-deployable techniques for BVOC measurement. 71 Here, we developed a simplified dynamic branch enclosure system for measuring BVOC emissions from conifers, 72 which enables measurements of multiple trees in a single day. Our system addresses the limitations of conventional 73 methods by using filtered ambient air as the enclosure purge gas and minimizing purge air consumption with a 74 foldable bag design. The introduction of a foldable bag eliminates the need for purge gas during equipment setup. 75 It enables a single person to measure BVOCs from up to five trees per day using the dynamic branch enclosure 76 method. We describe the design and evaluation of our enclosure system and demonstrate its applicability through 77 measurements of BVOC emissions from Japanese cedar (Cryptomeria japonica), one of the dominant conifer 78 species in Japanese forests.

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2. Methodology

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2.1 Branch enclosure system

2.1.1 System design and components

The branch enclosure system is designed to deliver VOC- and ozone-free air while ensuring stable internal conditions for BVOC measurements (Fig. 1a). It uses a diaphragm pump (FD-15, IBS, Osaka, Japan) and an activated carbon cartridge (CHC-50, Advantec, Tokyo, Japan) to purify the purge air. The chamber consists of an open-ended fluorinated ethylene propylene (FEP) bag (25 cm width × 60 cm long, GL Sciences Inc., Tokyo, Japan) to enclose the branch under observation. To ensure circulation and homogenization of air inside the bag, purified air is introduced through 6 mm PTFE tubing formed into 2 rings, each containing 12 holes (approximately 1.5 mm in diameter) for the air to exit from. The 2 rings also provide structural integrity to avoid contact with the branch. The PTFE rings are supported by a tripod equipped with a flexible arm to minimize stress on the branch (Fig. 1b). A mass flow controller (D-6361-DR/FAS, Bronkhorst Japan, Tokyo, Japan) maintains a constant purge air flow rate of 5 L/min. Power for the mass flow controller and the diaphragm pump is supplied by a portable battery (JE-1000D, 30.4Ah/35.2V DC, Jackery, Tokyo, Japan). The temperature inside the bag and the nearby photosynthetically active radiation (PAR) are monitored by a PTFE-coated thermocouple (GL Sciences Inc., Tokyo, Japan) and a PAR sensor (MIJ-14PAR Type 2/K2, Environmental Measurement Japan, Fukuoka, Japan), respectively, using a data logger (Thermic model 2400A, ETOdenki, Tokyo, Japan). All purge lines were made with 6 mm PTFE tubing. The enclosure bag and PAR sensor were secured at an appropriate height on a tripod. A parasol was used to reduce solar radiation and prevent leaf temperature increases during purging and sampling.





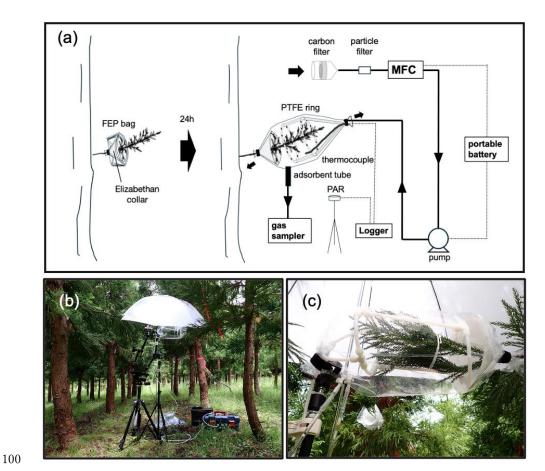


Figure 1: (a) Schematic of Branch enclosure and associated apparatus, (b) enclosure setup, and (c) close-up of the enclosure. MFC, mass flow controller; Logger, data logger; PAR, photosynthetically active radiation sensor.

2.1.2 System operation and sampling protocol

The sampling procedure is as follows:

- Pre-attachment: One day before sampling, an open-ended FEP bag and a funnel-shaped support, referred to
 as an 'Elizabethan collar', are attached to a branch (Fig. 1a). The collar is used to minimize contact between
 the bag and the branch. The trunk end of the FEP bag is secured around the branch with hook-and-loop tape.
 The bag is folded back so that it remains off the collar.
- 2. Enclosure deployment: On the sampling day, the PTFE ring is inserted over the branch, the branch is enclosed by unfolding the FEP bag, and the distal end of the bag is secured around the branch with hook-and-loop tape.

 After the branch is enclosed, the inside of the bag is purged with the purified air for at least 1 h before BVOC collection. The bag is secured to maintain a slight positive pressure inside, ensuring that purge air is discharged from both ends.
- 115 3. BVOC collection: Air in the bag is drawn through an adsorbent tube (6 mm OD × 90-mm-long glass tube;

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Supelco, Bellefonte, PA, USA) at 200 mL/min for 10 min by a portable sampler (GSP-300FT-2, Gastec, Kanagawa, Japan). Two types of sorbent tubes are used: one for MTs, packed in series with Tenax TA (20/35 mesh, approximately 100 mg; Supelco) and Carbopack B adsorbents (20/40 mesh, approximately 50 mg; Supelco), and another for SQTs and DTs, packed with HayeSep Q adsorbent (60/80 mesh, Hayes Separations Inc., Bandera, TX, USA). After sampling, compounds collected on the HayeSep Q adsorbent tubes are immediately extracted with approximately 2 mL of hexane (special grade; Fuji Film Wako, Osaka, Japan). The solvent is transferred into 2 mL glass vials, stored in a cooler box (approximately 0 °C) for 1 day, and then frozen (approximately below –30 °C) until analysis. The MT sorbent tubes are also stored in a cooler box and then frozen until analysis.

2.2 Measurements

2.2.1 Monoterpenes

The MT adsorbent tubes were analysed by a custom-built thermal desorption unit coupled to a gas chromatograph (GC) equipped with a mass selective detector (MSD) and a flame ionization detector (FID) (Agilent 6890/5973, Agilent Technologies, Santa Clara, CA, USA). The adsorbent tubes were purged at 40 °C with nitrogen at 40 mL/min for 1 min, then heated to 250 °C. The desorbed analytes were transferred in helium at 10 mL/min to a focusing trap packed with 2 mg Tenax TA and 2 mg Carboxen 1000 (Supelco) maintained at −130 °C. The trap was then heated to 180 °C, and desorbed analytes were injected onto an HP-5 column (60 m, 0.32 mm I.D., 1 μm film thickness; Agilent) in the GC oven. The GC oven temperature was held at 35 °C for 2 min, increased to 160 °C at 4 °C/min, then to 300 °C at 45 °C/min, and held at 300 °C for 10 min. Analytes eluting from the column were split between the MSD and FID. Methyl salicylate was also analyzed using this method. MSD analysis was performed in SIM/SCAN mode. Peaks were identified by comparing retention times with those of standards (Table S1) prepared in methanol. MTs were quantified using the FID, based on calibration curves constructed from the peak areas of standards introduced at various concentrations.

2.2.2 Sesquiterpenes and diterpenes

Following solvent extraction and concentration (Matsunaga et al., 2012), SQTs and DTs were measured by GC-MSD/FID (Agilent 6890/5973). An internal standard (approximately 10 ng of cyclopentadecane dissolved in hexane at a concentration of around 10 ng/µL; Tokyo Chemical Industry Co., Ltd., Tokyo, Japan) was added to the hexane extract, which was then concentrated to approximately 30 µL by using nitrogen blowdown at 60 mL/min. A 1µL aliquot of the concentrated extract was manually injected into the GC. The GC oven temperature was programmed to hold at 60 °C for 2 min, ramp to 120 °C at 30 °C/min, increased to 150 °C at 2 °C/min, and finally ramped to 320 °C at 5 °C/min, holding at 320 °C for 10 min. The separated compounds were split between MSD and FID, with MSD operated in SIM/SCAN mode; quantification was performed using the SIM mode signals. Peaks were identified by comparing retention times with those of standards (Table S1). SQTs and DTs were quantified by using calibration curves based on the peak areas of standards introduced at various concentrations.

2.3 Calculation of basal emission rate





The basal emission rate $(E_S, \text{ ng (gdw)}^{-1} \text{ h}^{-1})$, representing emission rate at a standard temperature of 30 °C (T_S) , was calculated by following the G93 algorithm (Guenther et al., 1993, 2012), as:

$$E = \frac{F_{\text{in}} \times (M - M_{\text{blank}}) \times 60}{F_{\text{samp}} \times W_{\text{dry}} \times t_{\text{samp}}}$$
(1)

$$E_{\rm S} = \frac{E}{\exp[\beta(T - T_{\rm S})]} \tag{2}$$

where E is the rate of BVOC emission, F_{in} is the airflow rate inside the enclosure (L/min), F_{samp} is the sampling flow rate (L/min), M is the mass of the measured BVOCs (ng), M_{blank} is the mass of the BVOCs in the blank (ng), W_{dry} is the dry weight (g dw), estimated from Shirota (2000), t_{samp} is the sampling time (min), T_s is the standard temperature (30 °C), and T is the temperature inside the enclosure. The species-specific coefficient β quantifies the sensitivity of BVOC emissions to temperature changes. The values of β used for Japanese cedar were 0.17 for MTs, 0.20 for SQTs, and 0.21 for DTs (Matsunaga et al., 2011, 2012, 2013).

3. Method evaluation

3.1 Performance of activated carbon cartridge

We evaluated the efficiency of the activated carbon cartridge at removing BVOCs and ozone. Cedar branches collected from trees growing in the premises of the National Institute for Environmental Studies were chopped into pieces enclosed in a FEP bag. BVOC emission rates were measured with and without the activated carbon cartridge (n = 4–6). Ozone removal efficiency was similarly evaluated by measuring ambient ozone with and without the cartridge using a UV absorption ozone monitor (1006-AHJ, Dasibi, Glendale, CA, USA). Ozone was measured for 10 min a day over 2 days.

Total BVOC concentration was significantly lower with the cartridge than without (P = 0.0117, Welch's two-sample t-test; Table 1). Ozone concentrations in the air passing through the activated carbon cartridge were significantly lower than ambient (Table 1). This confirms that the activated carbon cartridge effectively removes ozone, consistent with findings from a previous study (Namdari et al., 2021). These findings confirm that our system is capable of supplying ozone- and BVOC-free air to the enclosure.

Table 1. Ozone mixing ratio and total concentration of the measured BVOCs with and without the activated carbon cartridge. Both new and used activated carbon cartridges were tested. The used cartridge had been employed for approximately 8 hours in field experiments. Results obtained with the used cartridges are shown in parentheses. The limit of detection (LOD) was 1 ppb for ozone and 0.77 ng L⁻¹ for total BVOCs. The LOD for total BVOCs was calculated by taking the root sum of squares (RSS) of the individual compound LODs (Table S1) and dividing by the 2 L sampling volume.

	Ozone (ppb)		Total BVOCs (ng L ⁻¹)	
No cartridge		21 ± 1		2400 ± 1800
Activated carbon cartridge		<lod (<lod)<="" th=""><th></th><th><lod (<lod)<="" th=""></lod></th></lod>		<lod (<lod)<="" th=""></lod>





3.2 Environmental control

We evaluated the effect of purge gas source on environmental conditions inside the bag enclosure, using purge gas from ambient air (as described in section 2.1.2) and from gas cylinders (compressed air, Tomoe Shokai Co., Ltd., Tokyo, Japan) as used in previous studies (Hiura et al., 2021; Matsunaga et al., 2011). The experiments were conducted at Tsukuba University Mountain Science Centre. During the experiments, the temperature and relative humidity inside the bag were measured every minute with a hygrometer (2119A, ETO denki, Tokyo, Japan) and a PTFE-coated thermocouple (GL Sciences Inc., Tokyo, Japan). Those outside the bag were obtained from a meteorological station at Tateno, Tsukuba, operated by the Japan Meteorological Agency.

The humidity within the enclosure more closely reflected the external humidity when purge air was supplied via the air delivery system than from a cylinder (Table 2). Thus, our system is likely to reduce desiccation stress in branches during measurement, which can affect BVOC emission rates (Byron et al., 2022; Haberstroh et al., 2018). The temperature within the enclosure remained consistent with the external temperature, regardless of whether purge air was supplied via the air delivery system or from a cylinder (Table 2). In some cases, Praplan et al. (2020) found that prolonged direct sunlight causes an enclosure to heat up, resulting in a maximum temperature difference of 27.5°C. In this study, it is assumed that the use of a sunshade prevented direct sunlight, thereby mitigating the temperature increase.

Table 2. Temperature and relative humidity inside and outside the bag enclosure when air supply was drawn from cylinder and ambient air

	Air source			
	Cylinder			
	Inside enclosure	Outside enclosure	Inside enclosure	Outside enclosure
Humidity (%)	40 ± 1	70 ± 3	59 ± 2	63 ± 0.9
Temperature (°C)	30.4 ± 0.6	$5 29.0 \pm 0.4$	30.0 ± 1	27.7 ± 0.4

3.3 Measurement repeatability

We evaluated the repeatability of BVOC emission rate measurements using a 1-m-long branch collected from a 10-year-old cedar tree at the Tsukuba University Mountain Science Centre. After trimming its base, we cut the branch under water to maintain its vascular integrity. Following the procedure described in section 2.1.2, air in the enclosure bag was collected in adsorbent tubes (9 tubes for MTs, 5 tubes each for SQTs and DTs). Blank samples were also taken from the empty enclosure.

The relative standard deviations (RSDs) of MTs ranged from 4.1% to 19%, with an average of 10%. That of SQT was 5.6% (Fig. 2). That of individual-level BVOCs in the field was 139% (data not shown).





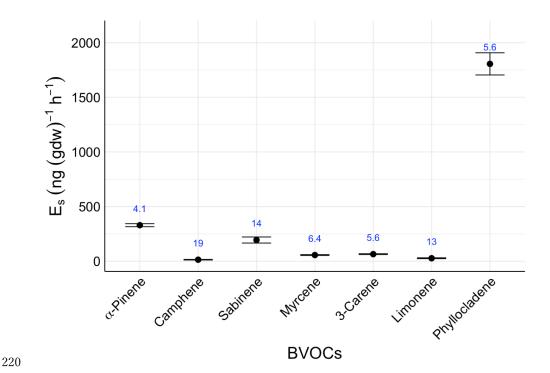


Figure 2: Basal emission rates of terpenes (E_S) and relative standard deviations (%, n = 5, blue)

These findings suggest that RSDs of the new measurement method are sufficiently low compared with the variability in individual-level BVOC emission rates, confirming the method's reproducibility in assessing individual emission rates. The RSDs are comparable to those reported in previous studies with other tree species (Li et al., 2019). Although some terpenes were below detection limits, at least one terpene was detected in each

category.

3.4 System stabilization time

We conducted an indoor experiment to evaluate the time required for the excessive release of BVOCs due to contact during the attachment of the enclosure system to subside. A cut cedar branch placed in a thermostatic chamber was used. Measurements were taken with a TDU-GC-MS system, as in section 2.2.1, but equipped with a dual trapping system for online preconcentration and refocusing of BVOCs. Air was drawn from the enclosure at 45 mL/min into the TDU for 12 min and analysed by GC-MS. Measurements were taken every 45 min over 3 days. Throughout the experiment, the chamber was maintained at a constant 25 °C. As the temperature remained constant, no temperature correction was applied in the calculation of the basal emission rate.

We also investigated effects of extending the pre-attached FEP bag on basal emission rates during the measurement day. Using the same materials as before, we tied a FEP bag to a cedar branch, folded it, and left it for approximately





24 h. The bag was then extended to cover the branch again. Samples were taken every 45 min, 20 times in total, while the bag was purged with air, and we compared basal emission rates before and after the bag was extended. Installation of an enclosure (i, Fig. 3) initially triggered an excessive release of BVOCs. Emission decreased to approximately 5% of its peak value within 24 h of installation.

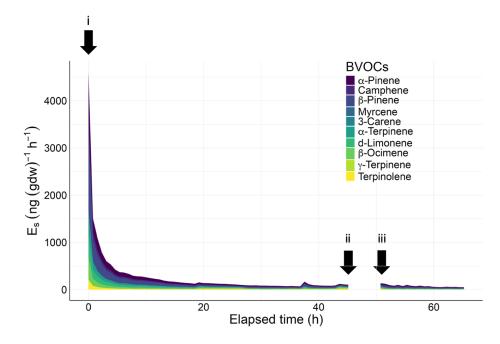


Figure 3. BVOC emission rates from a tree branch over time under different enclosure conditions. A branch was covered with a bag (0 h, i), and continuous measurements were taken until 45 h. The bag was folded back (ii), and this state was maintained until 52 h (iii). The bag was unfolded over again to cover the branch, and measurements were resumed until 72 h.

These results indicate that allowing 24 h after enclosure installation mitigates potential overestimation of BVOC emission rates due to the installation. Previous studies allowed 24 h or more (Helin et al., 2020; Helmig et al., 2013; Hiura et al., 2021; Matsunaga et al., 2011). Our results suggest that 24 h is enough.

The results also reveal that the emission rate 1 h after bag unfolding (Fig. 3, iii) was virtually unchanged from the pre-unfolding level (ii), so the potential effect of excessive emissions during the bag-unfolding process was sufficiently accounted for. Notably, Mochizuki et al. (2011) showed that the excessive emission of MTs induced by vibration stimulus in Japanese cedar subsided within approximately 20 min. We anticipate that the effects of minor vibrations during bag unfolding will subside within 1 h.

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264 4. Field deployment 265 The enclosure system was tested on Japanese cedar trees grown in a common garden setup at the Kawatabi Field 266 Centre, Tohoku University, using cedar trees grown from cuttings of natural populations collected across Japan 267 (Tsumura, 2022). Geographical differentiation in several functional traits of Japanese cedar has been revealed 268 through common garden experiments (Hiura, 2022). We used cuttings derived from three populations: 9 269 individuals from Ajigasawa (40.67° N, 140.20° E, 297m a.s.l.), 9 from Azoji (34.48° N, 131.96° E, 1060m a.s.l.), 270 and 6 from Yakushima (30.33° N, 130.46° E, 1267m a.s.l.). Details of each population are provided in Kimura et 271 al., (2014). The mean annual temperature at Kawatabi is 10.5 °C and the mean annual precipitation is 1697 mm. 272 We selected one branch per tree, approximately 1.3 m above the ground and facing south, and sampled during 273 daytime from 29 May to 9 June 2023. 274 275 Measurements at the Kawatabi Field Centre detected 16 compounds, principally α-pinene, sabinene, β-farnesene, 276 and ent-kaurene (Fig. 4).





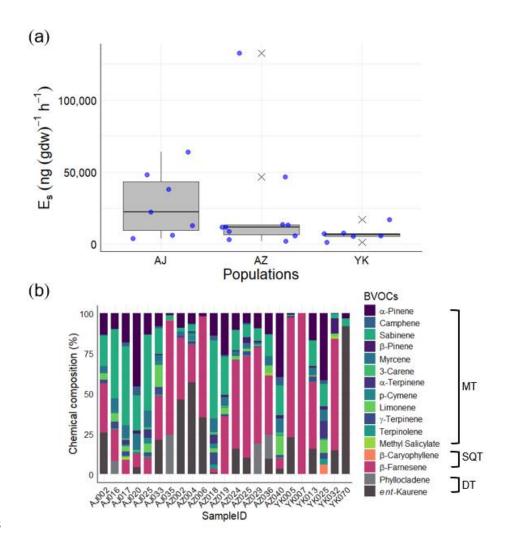


Figure 4 Field experiment results showing BVOC emissions from Japanese cedar (*Cryptomeria japonica*). (a) Total BVOC emission rates from different populations (Yakushima [YK], Azouji [AZ], Ajigasawa [AJ]). (b) Chemical composition of BVOCs measured from individual trees from three populations. This data is consistent with our previous data, although the detection limit has been revised.

Total emission rates did not significantly differ among populations (P = 0.417; F = 0.913; ANOVA). There was considerable individual variation in emission compositions (Fig. 4b). For example, in some trees (AJ016, AJ017, AJ020, AJ025, AJ033, AZ018, AZ019, AZ040, YK025) MTs accounted for more than 50% of the emission composition. In other trees (AJ002, AJ035, AZ002, AZ004, AZ006, AZ024, AZ025, AZ029, AZ036, YK005, YK007, YK013, YK032, YK070) SQTs and DTs accounted for more than 50% of the emission composition. Among all trees, β-farnesene was the most dominant SQT detected. Concentrations of β-farnesene varied





significantly. Among trees emitted β -farnesene (all individuals with the exception of YK025, YK070), β -farnesene accounted for 2.6~100% of total emissions. β -Farnesene is a crucial volatile organic compound, exerting significant influence on interactions between plants, aphids, and predator insects (Wang et al., 2024). β -Farnesene emission can be triggered by parasitism (Kivimäenpää et al., 2020). This compound is also suggested to be involved in responses to abiotic stresses, and it may help prevent leaf necrosis caused by local ozone reduction (Palmer-Young et al., 2015). Therefore, we can infer that trees with high β -farnesene emission rates may be experiencing some form of stress. BVOC emissions are broadly influenced by various biotic and abiotic factors (Holopainen & Gershenzon, 2010; Loreto & Schnitzler, 2010). Therefore, the variations in overall emission characteristics observed here may be attributed to environmental differences in the field and responses to biotic stress. However, the main objective of this study was the development of methods, and the sample size is not large enough to draw any conclusions about factor determining BVOC emissions. Further sampling will be necessary to clarify these factors, while detailed analyses of the relationships with phyllosphere microbial communities are being conducted elsewhere (Ishizaki et al., in submission).

5. Conclusion

We successfully developed a portable, field-deployable system for measuring BVOC emissions from conifers. By using scrubbed ambient air as a purge gas and implementing a foldable bag design, the system addresses the logistical and methodological challenges associated with conventional techniques. The system maintained stable environmental conditions, provided BVOC- and ozone-free air, and ensured high measurement repeatability, making it suitable for field applications.

Field testing revealed significant variability in BVOC emissions both among individual trees and across geographical origins. These findings highlight the complex interplay of multiple factors in determining BVOC emission characteristics. This variability emphasizes the critical need for individual-level assessments to enhance

313 our understanding of BVOC dynamics in diverse ecosystems.

By providing a practical and reliable tool for BVOC measurement under natural conditions, the system can advance our understanding of the ecological roles and atmospheric effects of BVOCs, supporting studies of their spatiotemporal patterns and climatic interactions.

Data availability

Data are available at 10.5281/zenodo.14965367, or upon request by contacting the corresponding authors.

Author contributions

- 323 SJA and TS developed and maintained the instruments. YS and YT designed and managed the common gardens.
- 324 YO collected and analysed the samples. TIK provided assistance with data analysis. TS and TH supervised the
- research. YO analysed the data and wrote the manuscript with contributions from all coauthors.





- 326 Competing interests
- 327 The authors declare that they have no conflict of interest.
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