

REVIEW

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Basal emission rates of isoprene and monoterpenes from major tree species in Japan: interspecies and intraspecies variabilities

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Abstract

Uncontrolled terpenoid emissions from forest trees in Japan may have contributed to high O₃ concentrations observed in urban and suburban areas. To estimate ozone formation via a series of reactions between NO_x and terpenoids using atmospheric chemistry models, it is important to produce terpenoid emission inventories by collecting all reported emission data for the major tree species in Japan and examining their reliability. In this review, we first describe three different plant terpenoid emission types, i.e., isoprene-emitting type, monoterpene-emitting type with storage tissues and organs, and monoterpene-emitting type without storage tissues and organs. Second, we describe various methods for measuring plant terpenoid emissions, including a recently developed simplified method, and explain their reliability. We emphasized that applicable measurement methods depend on the terpenoid emission types. Data obtained using static chamber methods should not be considered because they have the highest uncertainty resulting from normal chamber materials that are not specific to terpenoid measurements and lack humidity control. Finally, we show the absolute values of the collected emission rates and describe their variability. The deciduous oak species, *Quercus serrata* and *Quercus mongolica* var. *crispula*, and bamboo species, *Phyllostachys pubescens* and *Phyllostachys bambusoides*, are strong isoprene emitters. Among the monoterpene emitters, four evergreen broadleaf trees, including three *Quercus* species, had the highest basal emission rate (BER). The monoterpene storage type conifers *Larix kaempferi* and *Pinus densiflora* have relatively lower BERs. Emission data are not available for *Castanopsis cuspidata*, and seasonal changes in emission rates have not been reported for several major tree species in the top 20 rankings. Within species, the reported emission rates of some tree species differed by threefold. These differences may be attributed to the reliability of the measurement and analytical systems, tree age, leaf morphology, environmental conditions, and genetic diversity. We emphasize the need for reliable measurements to achieve a more precise terpenoid emission inventory for major tree species in Japan.

Keywords Tower flux measurement, Flow-through chamber, Static chamber, Temperature, Light intensity, *Quercus*, Bamboo

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1 Introduction

Higher plants produce terpenoids, including isoprene and monoterpenes, as secondary metabolites. They are major biogenic volatile organic compounds (BVOCs), and their total annual emissions are estimated to be 600–800 Tg C (Arneth et al. 2008). This value is higher than the estimated annual emissions of anthropogenic volatile organic compounds (AVOCs) (98–158 TgC) (Boucher et al. 2013). Given their high reactivity in the atmosphere (Atkinson and Arey 2003), terpenoids play a significant role in the production of photochemical oxidants, including ozone (O_3), and secondary organic aerosols (SOA). Tropospheric O_3 negatively affects humans, animals, and plants (Tani and Mochizuki 2021; Masui et al. 2023). The scattering and absorption of sunlight by SOA can influence global radiation, and cloud condensation nuclei derived from SOA may also affect climate. Nevertheless, accurately quantifying the extent of their contribution remains challenging, with significant uncertainties persisting (Shrivastava et al. 2017).

In the urban areas of Japan, the O_3 concentration remains high despite the reduction in NO_x and AVOC emissions under the national air pollution control law. It has been suspected that the uncontrolled BVOC emissions might contribute to the O_3 formation (Churkina et al. 2017; Gu et al. 2021). Thus far, BVOC emission models have been developed (Evans et al. 1985; Tingey et al. 1991; Guenther et al. 1993, 2006; Niinemets and Reichstein 2002, 2003) to explain VOC emission processes in plants. G93 model (Guenther et al. 1993) and Model of Emissions of Gases and Aerosols from Nature (MEGAN) (Guenther et al. 2006) are widely used to describe leaf-level and large-scale VOC emissions, respectively. The G93 model describes temperature-dependent monoterpene and temperature- and light-dependent isoprene emissions. MEGAN employs these functions as a basic theory but includes the effects of cumulative temperature and other environmental stresses. MEGAN can produce a BVOC emission map and provide data for atmospheric chemical reaction models to estimate O_3 formation.

There are considerable uncertainties in the BVOC emission estimates owing to uncertainties in the data input to G93 and MEGAN. The basic inputs are (1) biomass distribution (the fraction map of land cover by vegetation and the map of leaf area index [LAI]), (2) emission rates (leaf area-based emission rate in G93 and ground area-based emission rate in MEGAN), and (3) environmental factors, including light intensity, temperature, and environmental stresses. Among these inputs, (1) and (2) are the major factors affecting BVOC emission estimates (Guenther et al. 2006, 2012).

As the terpenoid emission rates are affected by temperature and light intensity, they are standardized

to a photosynthetic photon flux density (PPFD) of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a leaf temperature of 30°C (i.e., BER). The BERs data for different tree groups or tree species are used as inputs for MEGAN and other emission models. The values are not constant throughout the year for both evergreen and deciduous trees and usually the highest in summer, lower in spring and autumn, and the lowest in winter. However, exceptions have been reported for some tree species (Tani et al. 2002; Matsunaga et al. 2013; Okumura et al. 2013) in Japan and the seasonality of terpenoid emission rates may differ for different tree types. In addition, the reported BERs were obtained using different measurement methods, indicating that their degree of reliability is dependent on the advantages and disadvantages of the methods.

Several studies have reported the influence of input data uncertainty on BVOC emission estimates (Kim et al. 2014; Wang et al. 2018; Batista et al. 2019). For example, the global estimates of BVOC emission with MEGAN can differ by -9% and $+75\%$ for isoprene and α -pinene, respectively, when using updated basal emission rates (BERs) instead of the default MEGAN's BERs (Henrot et al. 2017). In China, using different vegetation land cover data as inputs to MEGAN can result in a 52% difference in O_3 concentrations (Ma et al. 2023).

In Japan, Kannari et al. (2007) developed a nationwide annual BVOC emission inventory for Japan, namely the East Asian Air Pollutant Emissions Grid Database (EAGRID2000-Japan), based on a procedure similar to that of the BVOC emission model called the Biogenic Emissions Inventory System (BEIS) (Pierce and Waldruff 1991). Although the emission inventory was made at a fine resolution (1-km spatial and 1-h temporal resolutions), the land cover data of vegetation as inputs were categorized into only two large general groups of trees (broadleaf and coniferous trees) and six crops (rice, wheat, beans, forage/manure crops, industrial crops, and others). Thus, these data are still too coarse to properly represent vegetation characteristics specific to Japan. Further improvements in emission inventories have been made in various studies. Inoue et al. (2010) improved the EAGRID2000-Japan and estimated the nationwide BVOC emission as 3312 Gg yr^{-1} based on the G93 algorithm by incorporating species-specific BERs of the major vegetation (10 species) in the Kinki region of Japan derived from Bao et al. (2008). However, there exists high uncertainty in the deduced emission value because some of the BERs (e.g., rice paddy) provided by Bao et al. (2008) are suggested to be overestimated (Tani et al. 2023). A recent study of nationwide BVOC emissions (Chatani et al. 2015) demonstrated a lower emission value of 2378 Gg yr^{-1} (isoprene 35%, monoterpenes 20%, sesquiterpenes 10%, and other VOCs 35%) via MEGAN

using species-specific BERs obtained from the latest literature. Chatani et al. (2018) also used updated data of vegetation land cover and species-specific BERs (16 species) for MEGAN and obtained a slight improvement in the model's performance of air quality simulation for predicting O_3 concentrations. They used some of available BERs data including overestimated ones (Chatani et al. 2015, 2018).

To produce a reliable inventory of tree terpenoid emissions, it is important to collect as much BERs from the literature as possible and examine the reliability of the reported individual terpenoid emission rates obtained using a wide variety of methods. In this review, we first describe different types of plant terpenoid emissions because the reliability of the measurement methods depends on the emission type. Second, we describe various methods, including one recently developed, for measuring plant terpenoid emissions and explain degrees of their reliability. Finally, we show the variabilities of the collected emission rates, which are affected by tree origin and age, growing conditions, and measurement methods, and emphasize the need for future measurements to achieve a better terpenoid inventory of major tree species. Crops in Japan might be terpenoid sources, and therefore, terpenoid emission data from crops are also collected from the literature and shown in this review.

2 Terpenoid emission characteristics of plants

Plants synthesize terpenoids via secondary metabolism and release them into the atmosphere. The major compounds emitted by plants are volatile terpenoids, including isoprene (C_5H_8) and monoterpenes ($C_{10}H_{16}$). Some plants also emit sesquiterpenes ($C_{15}H_{24}$) and diterpenes ($C_{20}H_{32}$) which are semi-volatile. These compounds are generally highly reactive and thus are highlighted by their high O_3 -forming capacity in the atmosphere. Notably, not all plants produce or emit these compounds. Here, we briefly summarize these terpenoids and the commonly observed terpenoid-emitting plant species.

Isoprene (2-methyl-1,3-butadiene) is one of the most remarkable compounds among the terpenoids emitted by plants, with a molecular weight of 68.12 and a boiling point of 34.07 °C. Typical isoprene-emitting species are deciduous broadleaf trees such as *Quercus serrata*, *Quercus crispula*, *Populus* spp., and bamboo (Stewart et al. 2003; Tani and Kawawata 2008; Tani and Mochizuki 2021). The global annual emission is estimated to be $500 \pm 100 \times 10^{12}$ g C yr⁻¹ (Arneth et al. 2008). The isoprene precursor dimethylallyl diphosphate (DMAPP) is converted to isoprene by isoprene synthase, which is embedded in the thylakoid membrane of the plastid (Sasaki et al. 2005). The rate of isoprene emission typically increases with increasing

temperature and light intensity, reaching a light saturation point of 200–1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ depending on plant growth conditions (Fig. 1). Additionally, the optimum temperature for isoprene synthase activity is approximately 40 °C (Guenther et al. 1993).

Monoterpene is the general term of $C_{10}H_{16}$ terpenoid compounds and sometimes includes oxygenated compounds such as monoterpene alcohols (e.g., linalool, $C_{10}H_{18}O$) and monoterpene ketones (e.g., camphor, $C_{10}H_{16}O$). Monoterpenes are the main components that make a plant “fragrant.” The typical isomer of monoterpenes emitted from plants is α -pinene, β -pinene, camphene, and limonene. The composition of monoterpene isomers varies among plant species. Monoterpenes are synthesized in the plastids of leaves and flowers. Geranyl diphosphate (GPP), a monoterpene precursor in plants, is synthesized from DMAPP and isopentenyl pyrophosphate (Dudareva et al. 2005; Dong et al. 2016). GPP is converted into monoterpenes by the synthases corresponding to each monoterpene (Degenhardt et al. 2009). Plants that emit monoterpenes can be classified into storage and non-storage types. The storage type plants include most of the conifers such as *Cryptomeria japonica*, *Chamaecyparis obtusa*, *Pinus densiflora*, *Larix kaempferi*, and *Picea jezoensis* var. *hondoensis*. The non-storage type plants are evergreen broadleaf trees such as *Quercus ilex*, *Quercus phillyraeoides*, and *Castanopsis sieboldii* var. *sieboldii*. Monoterpene emissions from storage type plants typically follow a temperature-dependent evaporation process from the organs in which monoterpenes are stored (e.g., resin canals and oil glands) (Fig. 1) (Gershenzon et al. 2000). In contrast, monoterpene emission in the non-storage type plants depends on temperature and light intensity, showing a pattern similar to that of isoprene emission from isoprene-emitting plants. Notably, some plants do not usually produce monoterpenes, but metabolic pathways may be activated to produce them when stimulated by external stresses, such as feeding damage by insects or mechanical damage.

During biosynthesis, farnesyl pyrophosphate and geranylgeranyl pyrophosphate are converted to sesquiterpenes and diterpenes, respectively (Davis and Croteau 2000). Their emission rates are generally influenced by abiotic factors such as temperature and light, as well as biotic factors such as diurnal cycle, seasonality, and plant developmental stage (Duhl et al. 2008). Currently, the emissions of sesquiterpenes and diterpenes from plants are less well understood than those of isoprene and monoterpenes because of difficulties in the sampling processes associated with the higher boiling point and stronger adhesion of these semi-volatile compounds (Helmig et al. 2004; Duhl et al. 2008).

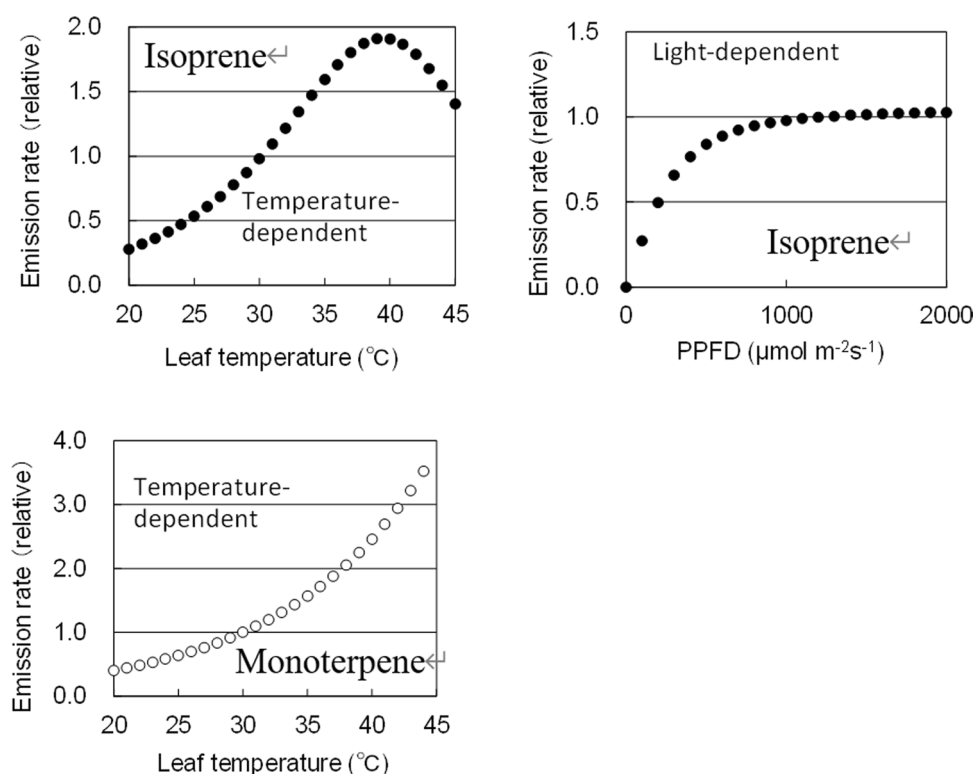


Fig. 1 Isoprene and monoterpene emission rates in response to environmental factors. Isoprene and monoterpene emission rates from non-storage type plants are shown as relative to those at a temperature of 30 °C and a photosynthetically photon flux density (PPFD) of 1,000 $\mu\text{mol m}^{-2}\text{s}^{-1}$. Monoterpene emission rate from monoterpene storage type plants, which depends on temperature only in most cases, is shown as relative to that at 30 °C. The figure was drawn using values calculated using so-called G93 algorithm (Guenther et al. 1993)

3 Measurement methods for plant terpenoid emissions

The methods used to measure the terpenoid emission rates of trees are listed in Table 1. These methods can be broadly classified into two types: tower flux and chamber methods. Tower flux method includes eddy covariance (EC), relaxed eddy accumulation (REA), and gradient flux (GF) methods. The chamber method is classified into flow-through and static chamber methods.

Tower flux method can provide large-scale observations of regional terpenoid emission characteristics. This method is advantageous as it does not require physical contact with plant leaves and branches, and can thus avoid mechanical stimuli that may induce the emission of certain species of monoterpenes, including linalool (Tani et al. 2023). The chamber method is used for the emission measurement of potted trees, branches, and single leaves, and is easy to install on site. In this section, we describe the characteristics, advantages, disadvantages, and reliabilities of these methods, because they may cause variability in the terpenoid emission rates of identical tree species.

3.1 EC method

To conduct an EC measurement on a flux tower, the real-time terpenoid concentration must be measured above the forest canopy, coupled with the three-dimensional wind direction and velocity. High-time-resolution measurement instruments are required to measure the concentrations. Proton transfer reaction mass spectrometry (PTR-MS) was used in many cases to obtain a concentration signal at approximately 10 Hz (Müller et al. 2010; Mäki et al. 2019; Sarkar et al. 2020). Frequent calibrations must be conducted onsite using standard gases. However, PTR-MS cannot precisely discriminate the isomers of monoterpenes and produces fragment ions originating from them and other VOCs that may interfere with accurate concentration determination (Tani et al. 2003, 2004). In an atmosphere dominated by isoprene, m/z 69 is the ion mainly produced from isoprene, facilitating more accurate concentration determinations. Through the application of data processing techniques such as axis rotation, this method can be extended to encompass slopes and complex terrain.

Table 1 Measurement methods for terpene emission rates and their characteristics

Measurement method	Measurement object	Measurement technique	Key points and constraints	Conversion to emission inventory data
Eddy covariance (EC)	Plant canopy	Measurement instruments with high time resolution (~10 Hz) are required to measure the concentration. The method can be applied to slope and complex terrain	A proton transfer reaction mass spectrometry (PTR-MS) is used to obtain the concentration signal. Isomers of monoterpenes and fragments originating from monoterpenes and other VOCs may interfere with the accuracy of the determined concentration	Emission data on land area basis are obtained. They can be used as inventory data without unit conversion
Relaxed eddy accumulation (REA)	Plant canopy	Real-time sampling is required depending on vertical wind direction	The method cannot be applied to slope and complex terrain. Axis rotation is not efficient if horizontal wind direction is not constant	Emission data on land area basis are obtained. They can be used as inventory data without unit conversion
Gradient flux (GF)	Plant canopy	Terpenoid concentrations are measured at two heights above the forest canopy. Flux is calculated from the concentration gradient and eddy diffusion coefficient	This method is valid only under neutral and unstable atmospheric conditions	Emission data on land area basis are obtained. They can be used as inventory data without unit conversion
Bag enclosure (BE)	A branch with several leaves	A branch is enclosed with a transparent bag made from fluorine-based resin. The lid of the bag is tightened, and clean air is sent to the sealed bag	Water vapor should be removed in the air preparation process. Touching stimulus may cause unexpected VOC emissions	Coefficient (leaf area index [LAI] or specific leaf weight [SLW]) to convert the rate on leaf area or dry weight basis to that on land area basis is required
Leaf cuvette (LC)	A part of a leaf	LC method requires commercial portable photosynthetic measurement systems or man-made cuvette. Stomatal conductance and net assimilation rate can be obtained simultaneously. As the commercial systems can control light intensity and leaf temperature, basal emission rate can be directly measured	Replicate measurements are required to obtain representative basal emission rate. Mechanical stimulus may induce temporary terpenoid emissions from monoterpane storage type trees	LAI is required
Flow-through plant chamber (FPC)	Individual plant	FPC requires commercial environmentally controlled chambers or man-made flow-through chambers	Flow rate must be adjusted to avoid water condensation inside. Terpenoid adsorption on the inner surface of the chamber may not be negligible if the chamber is not made using proper materials. As a young sapling is used in most cases, scaling up of the emission rate to that of an adult tree should be carefully performed	Coefficient (SLW or LAI) to convert the rate on leaf area or dry weight basis to that on land area basis is required

Table 1 (continued)

Measurement method	Measurement object	Measurement technique	Key points and constraints	Conversion to emission inventory data
Static chamber (SC)	A whole plant or a part of a plant	The SC method uses commercial or man-made closed chambers	Water vapor originating from plant transpiration is condensed on the inner surface without removing water vapor in the chamber. This results in the loss of water-soluble VOCs. As most of the chambers are not made using special materials, adsorption and desorption of terpenoids may occur on the surface. As a young sapling is used in most cases, scaling-up of the emission rate to that of an adult tree should be carefully performed	Coefficient (SLW or LAI) to convert the rate on leaf area or dry weight basis to that on land area basis is required
Leaf-tip vial (LV)	Excised leaf tip (~ 1 × 2 cm)	A leaf tip in a vial is incubated at constant temperature and light intensity for a certain period (30–60 min), followed by the sampling of the gas inside. The LV method is suitable for fast screening of isoprene emission capacity as simultaneous measurements can be conducted for multiple vials	Excising leaf tip may induce terpenoid emission from monoterpene storage organs. A cross check of this method with more reliable methods such as the LC method is required	Coefficient (SLW or LAI) to convert the rate on leaf area or dry weight basis to that on land area basis is required

3.2 REA method

Similar to the EC method, the REA method measures the regional flux on a tower, but it does not require real-time or high-time-resolution concentration measurements. The upward and downward air is separately sampled into adsorbent tubes or evacuated canisters according to the vertical wind direction (Mochizuki et al. 2014; Sarkar et al. 2020). Because real-time sampling according to the vertical wind direction is required, this method may not be applicable to slopes and complex terrains unless the horizontal wind direction is almost constant, which is not realistic in the field.

3.3 GF method

The GF method is a basic method for determining the fluxes of trace gases, including terpenoids. Terpenoid concentrations are measured at two heights above the forest canopy, and the flux is calculated from the concentration gradient and eddy diffusion coefficient (Tani et al. 2002; Schween et al. 1997). The eddy diffusion coefficient can be determined using the vertical profile of wind velocity or heat balance above forests. This method is only valid under neutral and unstable atmospheric conditions.

3.4 Bag enclosure method

The bag enclosure (BE) method is a flow-through chamber method (Guenther et al. 1993; Owen and Hewitt 2000; Okumura et al. 2008b). A branch with several leaves is enclosed in a transparent bag made of fluorine-based resin. The lid of the bag is tightened, and clean air is sent to the sealed bag at a flow rate of 5–10 L min⁻¹ depending on the total leaf area. Clean air is produced using activated charcoal or a heated platinum catalyst. It is better to remove water vapor during the air preparation process to avoid water condensation on the inner surface of the bag caused by the water vapor increment by plant transpiration. This prevents VOC dissolution into condensed water. Physical contact with branches and leaves can trigger VOC emissions. Therefore, it is important to allow the branch to rest for a designated period ranging from several hours to a day to mitigate such emissions. Because the emission rate is determined based on leaf area or dry weight, a coefficient is necessary to convert this rate to that on a land area. This coefficient represents LAI or the specific leaf weight.

3.5 Leaf cuvette method

The leaf cuvette (LC) method is a flow-through chamber method that uses commercial portable photosynthetic measurement systems (Pétron et al. 2001; Tani and Kawawata 2008) or hand-made cuvettes (Monson and Fall 1989; Lehning et al. 1999). A portion of the air

outflowing from the leaf cuvette is collected into adsorbent tubes. Some of the latest systems already have an embedded sampling port (e.g., LI-6800, Li-Cor Inc., Lincoln, NE, USA), whereas modifications are needed for older systems (e.g., LI-6400, Li-Cor Inc.). As these systems can control environmental factors, such as light intensity and leaf temperature, and measure stomatal conductance and net assimilation rate, it is possible to investigate the effects of environmental factors on terpenoid emission rates and address the relationships between plant physiological parameters and emission rates. It is easy to directly obtain BER, defined as the emission rate normalized to 30 °C leaf temperature and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (Guenther et al. 1993), by controlling the measurement conditions. However, chamber wall, gasket surfaces, and O-rings may potentially cause adsorption/desorption problems for VOC studies (Niinemets et al. 2011).

Obtaining representative BERs of sunlit and sun shaded leaves necessitates conducting replicate measurements of individual trees. As the measured leaf is held down by a gasket to seal the cuvette, this mechanical stimulus may induce temporary terpenoid emissions from monoterpenes storage type trees. LAI is required to convert the emission rate from a leaf area basis to a land area basis.

3.6 Flow-through plant chamber method

The flow-through plant chamber (FPC) method uses commercial environmentally controlled chambers or man-made flow-through chambers (Kim et al. 2001; Tani et al. 2023) for the entire plant. In this method, water condensation can be avoided by controlling humidity. However, with an increase in the number of plant leaves higher rates of air inflow into the chamber are required to avoid water condensation. If the chamber is not made of special materials to avoid VOC adsorption, terpenoid adsorption on its inner surface may not be negligible, particularly for oxygenated monoterpenes and less-volatile terpenoids. In this case, desorption of previously adsorbed terpenoids from the chamber may also occur, resulting in an increased uncertainty in the obtained emission rates. As potted plants are used in many cases, the emission rate on a plant basis needs to be converted to that on a leaf area basis or dry weight basis, and thereafter, the value is recalculated on a land area basis. When young saplings are used for measurement, the emission rate should be carefully scaled up to one of the adult trees because the emission rate may be different for trees of different ages (Kim et al. 2005).

3.7 Static chamber method

The static chamber (SC) method uses commercial or hand-made closed chambers for the entire plant and part

of a plant (Kim et al. 2005; Bao et al. 2008; Brennan et al. 2022). Without removing water vapor from the chamber, water vapor originating from plant transpiration condenses on the inner surface of the chamber, resulting in the loss of water-soluble VOCs. Even if heat exchangers are used to remove water vapor, VOCs dissolve into liquid water condensed on the cooled fin. In some commercially available closed chambers, environmental factors, such as light intensity, air temperature, and humidity, can be controlled (Bao et al. 2008). As most of the chambers are not made of special materials to avoid VOC adsorption, attention should be paid to the adsorption and desorption of terpenoids. As young plants are used in many cases, the scaling up of the emission rate follows the same manner as described in the FPC method. The unit conversion follows that of the FPC method. The SC method has the highest uncertainty, and therefore, it is not preferred for determining terpenoid emission rates.

3.8 Leaf-tip vial method

The leaf-tip vial (LV) method uses an excised leaf tip ($\sim 1 \times 2$ cm) to determine the terpenoid emission rate (Chang et al. 2022b). The leaf tip is placed horizontally in a laid-down vial (10 mL volume) and incubated at a constant temperature and light intensity for a certain period (30–60 min), followed by the sampling of the gas inside. The LV method is particularly suitable for fast screening of isoprene emission capacity because measurements can be conducted almost simultaneously for multiple vials (5–10 vials). To validate the LV method for a target plant, it must be cross-checked with more reliable methods such as the LC method. If a good correlation, such as a linear regression, is observed for the terpenoid emission rates determined by the LV and LC methods, the LV method is judged to be applicable. Mechanical wounding by cutting a leaf tip may induce monoterpene emissions from monoterpene storage organs; therefore, the LV method is not suitable for monoterpene-storage plants. Currently, this method is applicable to the measurements of isoprene emission from palm trees (Chang et al. 2022b) and monoterpene emissions from *Q. phillyraeoides* (Chang et al. 2024).

4 Terpenoid emission data of trees and crops grown in Japan

Data on BERs were collected from published literature and our original experiments (unpublished). The target tree species were selected from the top 20 dominant tree species in Japan, based on a survey by the Japanese Forestry Agency (Table 2). Terpenoid emission data of major crop species are also added. The BERs are defined as the emission rate normalized to 30 °C leaf temperature and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD for both isoprene emitters and

non-storage types of monoterpene emitters and to 30 °C leaf temperature without any specific light conditions for the storage type monoterpene emitters (Guenther et al. 1993).

4.1 Deciduous broadleaf trees

4.1.1 Monoterpene emitters

Many wild *Acer* species occur in Japan, and many of them are known to be monoterpene emitters. *Acer* species are categorized as a group in the dominant tree ranking in Japan and ranked 11th. Mochizuki et al. (2020a) reported monoterpene BERs of *Acer* and Fagaceae tree species grown in Japan. Six *Acer* tree species (*A. palmatum*, *A. japonicum*, *A. sieboldianum*, *A. shirasawanum*, *A. rufinerve*, and *A. micranthum*) were identified as monoterpene emitters (Table S1). Seasonal variation in the monoterpene emission rate of *A. palmatum*, a non-storage type monoterpene emitter, was measured using the LC method (Mochizuki et al. 2020b; Figure S1), which showed that it increased from April, peaked in August, and decreased in winter. The dominant component was α -pinene followed by sabinene and β -pinene. In other studies, *A. platanoides*, *A. campestre*, and *A. buergerianum* have also been shown as monoterpene emitters (Acton et al. 2016; Baraldi et al. 2019; Chang et al. 2021a; Table S1). Although the seasonal trend of monoterpene emissions from *A. palmatum* may offer insights applicable to other *Acer* species, it is advisable to gather additional data on various *Acer* species. Currently, seasonal variation data on monoterpene BERs are limited to *A. palmatum*.

In contrast, monoterpene emissions were not detected in other 14 *Acer* species (*A. amoenum*, *A. tenuifolium*, *A. crataegifolium*, *A. pictum*, *A. cissifolium*, *A. argutum*, *A. distylum*, *A. nipponicum*, *A. miyabei*, *A. maximowiczianum*, *A. tataricum*, *A. pycnanthum*, *A. diabolicum*, and *A. carpinifolium*) and two *Fagus* species (*F. crenata* and *F. japonica*) (Table S1), even in summer. However, *A. pictum* (19th rank in the dominant tree species) occurring in China (Klinger et al. 2002) and Korea (Chang et al. 2021a) has been reported to emit monoterpenes, indicating a discrepancy in terpenoid emission trends between Japan and other Asian countries.

Castanea crenata, 14th rank in the dominant tree species, was reported as a monoterpene (e.g., α -pinene, sabinene, and β -pinene) emitter with a BER of 1.1 $\text{nmol m}^{-2} \text{s}^{-1}$ obtained using the LC method (Mochizuki et al. 2020a). However, the peak and seasonal variations in the monoterpene BERs of *C. crenata* have not been reported.

Betula trees in Japan are reported to be monoterpene emitters (Yang et al. 2021; Masui et al. 2022). For example, *B. platyphylla* var. *japonica* has a monoterpene BER

Table 2 Top 20 ranking dominant tree species in Japanese forest and their terpenoid emissions characteristics

Tree species	Rank	Total area (10 ³ ha)	Data availability of basal emission rate					
			Isoprene in summer		Monoterpene in summer			Seasonality
			Value	Unit	Type**	Value	Unit	
<i>Cryptomeria japonica</i>	1	4369.6	0		S	<0.1–5.2	μg g ⁻¹ h ⁻¹	0.03–0.17 ●
<i>Chamaecyparis obtusa</i>	2	2730.4	0		S	0.1–1.0	μg g ⁻¹ h ⁻¹	0.08–0.12 ●
<i>Quercus serrata</i>	3	1596.0	20.5–42.9	nmol m ⁻² s ⁻¹		0		●
			6.4–114.9	μg g ⁻¹ h ⁻¹				
<i>Abies sachalinensis</i>	4	1330.4	0			NA		NA
Other broad-leaved trees	5	1131.2	*			*		*
<i>Pinus densiflora</i>	6	1092.8	0		S	0.6–2.5	nmol m ⁻² s ⁻¹	<0.01–0.19 ●
					S	1.5–1.9	μg g ⁻¹ h ⁻¹	0.12–0.14
<i>Fagus crenata</i>	7	1051.2	[Non-emitter of terpenoids]					
<i>Quercus mongolica</i> var. <i>crispula</i>	8	972.0	26.3–29.5	nmol m ⁻² s ⁻¹		0		●
<i>Larix kaempferi</i>	9	876.0	0		S	1.2–1.7	nmol m ⁻² s ⁻¹	0.09–0.20 ●
<i>Betula ermanii</i>	10	640.0	0			NA		NA
<i>Acer</i> spp.	11	313.6	0			*		*
<i>Tilia japonica</i>	12	277.6	0		S	1.0	μg g ⁻¹ h ⁻¹	0.10 NA
<i>Castanopsis cuspidata</i> var. <i>sieboldii</i>	13	273.6	0		NS	15.0	nmol m ⁻² s ⁻¹	NA
<i>Castanea crenata</i>	14	239.2	0			1.1	nmol m ⁻² s ⁻¹	NA
<i>Alnus</i> spp.	15	227.2	0			*		NA
<i>Carpinus</i> spp.	16	200.8	*			*		*
<i>Quercus glauca</i>	17	192.0	0		NS	8.0	nmol m ⁻² s ⁻¹	NA
<i>Castanopsis cuspidata</i>	18	184.8	NA			NA		NA
<i>Acer pictum</i>	19	182.4	<0.1	μg g ⁻¹ h ⁻¹	NS	0–3.3	μg g ⁻¹ h ⁻¹	NA
<i>Phyllostachys pubescens</i>	20	181.6	12.8–22.8	nmol m ⁻² s ⁻¹		0		●
<i>Phyllostachys bambusoides</i>	24	115.2	17.6	nmol m ⁻² s ⁻¹		0		●

This table is arranged based on a dataset of "Forestry Agency Forest Ecosystem Diversity Basic Survey, Phase 3 (2009–2013 at 13,357 survey sites)." The survey sites were divided into a 4-km square grid, and the intersection of the squares with 0.1 ha area was surveyed for the dominant tree species. The dominant tree species has score of "1" (one dominant tree species: 11,719 sites) or "0.5" (two dominant tree species: 1,631 sites)

The total area of trees was calculated by multiplying the accumulated score of each tree species by 16 km², assuming that a 4 km square around a survey site has the same tree composition

The BER of isoprene type and monoterpene non-storage type is a normalized rate under the standard condition of 1,000 μmol m⁻² s⁻¹ PPFD and 30 °C leaf temperature. The BER of monoterpene storage type is a normalized rate under the standard condition of 30 °C leaf temperature. For monoterpene storage type, temperature dependence coefficient β was experimentally determined in most cases

●: Seasonality data are available, NA: not available, 0: no emission. *The availability of emission data depends on the tree species. **S: monoterpene storage type, NS: monoterpene non-storage type

The detailed information including references, measurement techniques, and tree age for each data is provided in supporting information S1–S3 and Table 3

of 2.8 nmol m⁻² s⁻¹ in July (β = 0.09; Masui unpublished) as determined by the BE method. *B. ermanii* is the 10th ranked dominant tree species in Japan; however, data on whether it is a monoterpene emitter are unavailable. However, the impact of BVOC emissions on O₃ formation in urban areas seems to be negligible because *Betula* spp., including *B. ermanii*, are found only in the northern and alpine regions. *Tilia japonica* is ranked 12th in the dominant tree species and is found to be a monoterpene emitter with a BER of 0.97 μg g⁻¹ h⁻¹ (Jing et al.

2020); however, it also occurs in the northern and alpine regions.

4.1.2 Isoprene emitters

Data on isoprene BERs of *Quercus* species are available in the literature (Bao et al. 2008; Okumura et al. 2008c; Tani and Kawawata 2008; Lim et al. 2011; Kim and Lee 2012; Chang et al. 2021a) and are summarized in Table 3. Some studies have reported seasonal variations in isoprene emission rates of *Q. mongolica* var. *crispula* (Kim

Table 3 Basal emission rates (BERs) of isoprene reported for deciduous *Quercus* trees

Tree species	Age	Method	Season	BER	Citation
<i>Quercus mongolica</i> var. <i>crispula</i>	(Adult tree)	BE	Jun. Jul. Aug. Sep. Oct.	4.70 29.50 26.30 nmol m ⁻² s ⁻¹ 10.90 2.90	Matsunaga et al. (2012)
	3 years	LC	May–Jul.	27.30 nmol m ⁻² s ⁻¹	Tani and Kawawata (2008)
	3–5 years	SC	–	26.0 ug g ⁻¹ h ⁻¹	Bao et al. (2008)
	3 years	LC	May–Jul.	27.80 nmol m ⁻² s ⁻¹	Tani and Kawawata (2008)
<i>Quercus serrata</i>	40 years	LC (sunlit leaf) LC(sunshade leaf)	Jun.	42.90 20.50 nmol m ⁻² s ⁻¹	Okumura et al. (2008c)
	3 years	FPC	–	6.39 ug g ⁻¹ h ⁻¹	Chang et al. (2021a)
	3–5 years	SC	–	224.2 ug g ⁻¹ h ⁻¹	Bao et al. (2008)
	(10m height)	FPC	Spring Summer Fall	64.0 ug g ⁻¹ h ⁻¹ 79.5 ug g ⁻¹ h ⁻¹ 60.1 ug g ⁻¹ h ⁻¹	Kim and Lee (2012)
<i>Quercus aliena</i>	21–50 years	BE	Spring Summer Fall	147.90 ug g ⁻¹ h ⁻¹ 114.92 ug g ⁻¹ h ⁻¹ 114.92 ug g ⁻¹ h ⁻¹	Lim et al. (2011)
	3 years	LC	May–Oct.	18.30 nmol m ⁻² s ⁻¹	Tani and Kawawata (2008)
	(middle age)	BE	Jul.–Sep.	2.46 ug g ⁻¹ h ⁻¹	Jing et al. (2020)
	21–50 years	BE	May–Jun.	72.31	Lim et al. (2011)
<i>Quercus dentata</i>		BE	Aug.	89.31	
		BE	Oct.	11.14 ug g ⁻¹ h ⁻¹	
	21–30 years	BE BE	May–Aug.	88.40 74.80	
	3 years	LC	May–Oct.	30.00 nmol m ⁻² s ⁻¹	Tani and Kawawata (2008)
<i>Quercus acutissima</i>	(10m height)	BE	Spring Summer Fall	1.35 ug g ⁻¹ h ⁻¹ 1.71 ug g ⁻¹ h ⁻¹ 0.88	Kim and Lee (2012)
	3 years	LC	May–Oct.	0.00 nmol m ⁻² s ⁻¹	Tani and Kawawata (2008)
	3 years	FPC	Aug.–Sep.	0.02 ug g ⁻¹ h ⁻¹	Chang et al. (2021a)
	3–5 years	SC	–	0.18 ug g ⁻¹ h ⁻¹	Bao et al. (2008)
<i>Quercus variabilis</i>	41–50 years	BE	Jun.–Jul. Sep. Oct	0.04 ug g ⁻¹ h ⁻¹ 0.07 ug g ⁻¹ h ⁻¹ 0.05	Lim et al. (2011)
	3 years	LC	May–Oct.	0.00 nmol m ⁻² s ⁻¹	Tani and Kawawata (2008)
	3 years	FPC	–	0.00 ug g ⁻¹ h ⁻¹	Chang et al. (2021a)
	15–20 years	BE	Spring Summer Fall Winter	2.14 5.63 2.19 ug g ⁻¹ h ⁻¹ 0.00	Chen et al. 2020
<i>Quercus mongolica</i>	11–50 years	BE	May–Jun.	72.99 ug g ⁻¹ h ⁻¹	Lim et al. (2011)
		BE	Aug.	65.85 ug g ⁻¹ h ⁻¹	
	21–30 years 41–50 years	BE	Oct.	8.00 ug g ⁻¹ h ⁻¹	
		BE	May–Aug.	78.20 62.33	Kim and Lee (2012)
	(10 m height)	BE	Spring Summer Fall	13.6 ug g ⁻¹ h ⁻¹ 15.2 ug g ⁻¹ h ⁻¹ 12.0 ug g ⁻¹ h ⁻¹	

The BER of isoprene type and monoterpene non-storage type is a normalized rate under the standard condition of 1000 μmol m⁻² s⁻¹ PPFD and 30 °C leaf temperature

NA not available, LC leaf cuvette method, BE branch enclosure method, FPC flow-through plant chamber method, SC static chamber method

Q. mongolica is not endemic to Japan, but its BER is shown here for comparison purpose

and Lee 2012; Matsunaga et al. 2012) and *Q. serrata* (Lim et al. 2011; Kim and Lee 2012). In *Q. mongolica* var. *crispula*, isoprene emission is the highest in summer and lower in spring and fall (Table 3). This trend has also been observed in other *Quercus* species such as *Q. aliena* (Lim et al. 2011) and *Q. mongolica* in South Korea (Lim et al. 2011; Kim and Lee 2012). The isoprene BER of *Q. serrata* is highly variable even for the same tree age ($6.39 \mu\text{g g}^{-1} \text{h}^{-1}$; Chang et al. 2021a) to $224.2 \mu\text{g g}^{-1} \text{h}^{-1}$ (Bao et al. 2008), and the average value is higher than that of *Q. mongolica* var. *crispula*. The isoprene BER on a land area basis was determined using the REA method to be $13.3 \text{ nmol m}^{-2} \text{s}^{-1}$ for a needle-broad mixed forest including *P. densiflora*, *Q. serrata*, and *Q. mongolica* var. *crispula* (Mochizuki et al. 2020c). The isoprene was estimated to be emitted from *Q. serrata* (2.2% based on total basal area) and *Q. mongolica* var. *crispula* (1.0%).

F. crenata, 7th in the dominant tree species, was reported as a non-emitter of isoprene and monoterpenes (Mochizuki et al. 2020a). We obtained the same results using the LV and LC methods (unpublished). An exception was reported by Bao et al. (2008), who employed the SC method using a commercial chamber and obtained an isoprene BER of $0.79 \mu\text{g g}^{-1} \text{h}^{-1}$.

4.2 Evergreen broadleaf trees

Some evergreen *Quercus* and *Castanopsis* trees emit monoterpenes (Okumura et al. 2008b; Mochizuki et al. 2020a; Table S2). They are non-storage type monoterpene emitters, and their emissions depend on light intensity and leaf temperature. Particularly, *C. cuspidata* var. *sieboldii* (13th rank) and *Q. glauca* (17th rank) have high monoterpene BERs of 15.0 and $8.0 \text{ nmol m}^{-2} \text{s}^{-1}$, respectively (Mochizuki et al. 2020a). Data for the 18th ranked *C. cuspidata*, a species related to *C. cuspidata* var. *sieboldii*, are not available.

4.3 Deciduous coniferous trees

In Japan, deciduous coniferous tree species are limited to *L. kaempferi* and some exotic trees such as *Ginkgo biloba* and *Metasequoia glyptostroboides*. Among these tree species, *L. kaempferi* is 9th in the dominant tree species and has been reported to be a monoterpene emitter (Ieda et al. 2006; Mochizuki et al. 2014). The monoterpene emission from *L. kaempferi* depends on the leaf temperature, and the most dominant compound is α -pinene followed by sabinene, β -pinene, myrcene, and camphene (Mochizuki et al. 2014). Using the REA method, Mochizuki et al. (2014) obtained an almost constant value ($\sim 1 \text{ nmol m}^{-2} \text{s}^{-1}$) of averaged BER standardized to 30°C for an *L. kaempferi* plantation from the bud break period to fall (Figure S2, Table S3).

4.4 Evergreen coniferous trees

In most cases, monoterpene emissions from coniferous trees depend on leaf temperature. Data on the monoterpene BERs of the dominant evergreen coniferous trees, *C. japonica* (1st), *Chamaecyparis obtusa* (2nd), and *P. densiflora* (6th) are shown in Table S3 described individually in the following subsections.

4.4.1 Pinus densiflora

The monoterpene flux of a forest of *P. densiflora* (with 95% dominance) was measured by Tani et al. (2002) using the GF method (Table S4). Major components of the monoterpene emissions from *P. densiflora* were α - and β -pinene, limonene, and β -phellandrene. The monoterpene basal flux was calculated using a fixed β -value of 0.19. It increased from May ($1.32 \text{ nmol m}^{-2} \text{s}^{-1}$) to June ($3.76 \text{ nmol m}^{-2} \text{s}^{-1}$), decreased below $1.0 \text{ nmol m}^{-2} \text{s}^{-1}$ in summer, and increased again to $5.28 \text{ nmol m}^{-2} \text{s}^{-1}$ in October and November. The monoterpene basal flux of the same tree species (with 84.5% dominance) in another forest measured using the REA method in August was reported to be $2.50 \text{ nmol m}^{-2} \text{s}^{-1}$ (Mochizuki et al. 2020c), which is not largely different from that reported by Tani et al. (2002).

4.4.2 Cryptomeria japonica

C. japonica has three natural populations, including Japan Sea, Pacific Ocean, and southwestern. Matsunaga et al. (2013) reported that seasonal variations in the monoterpene BER of *C. japonica* measured using the BE method differed at different sites (Figure S3). For example, *C. japonica* individuals in Tanashi (around 50 years old), a Pacific Ocean side population, had a monoterpene BER of $0.3 \mu\text{g g}^{-1} \text{h}^{-1}$ through a whole year except for summer in which it was $< 0.1 \mu\text{g g}^{-1} \text{h}^{-1}$. In contrast, a decreased emission rate in summer was not observed for the southwestern population of Shiiba. Okumura et al. (2013) employed the BE method for the Japan Sea side population and found the highest monoterpene BER in fall without suppression in summer (Figure S3, Table S5).

Hiura et al. (2021) obtained the monoterpene BERs of *C. japonica* collected from 12 different planting sites in three populations. In this study, three saplings of *C. japonica* were transplanted from each planting site to a nursery in the Miyagi Prefecture (38.78°N , 140.73°E). Three years later, BVOCs emitted from the saplings were collected using the BE method. The BER was largely different among the planting sites and even in identical populations (Figure S4). This study and the above-mentioned studies suggest that differences in the reported monoterpene BERs may be due to intraspecies variations.

All data collected by Okumura et al. (2013) are plotted against the leaf temperature (Figure S5). A clear temperature dependence of monoterpene BER on leaf temperature ($\beta=0.09$, $\text{BER}=0.65 \mu\text{g g}^{-1} \text{h}^{-1}$, $\text{RMSE}=0.93 \mu\text{g g}^{-1} \text{h}^{-1}$; $\beta=0.10$, $\text{BER}=0.74 \mu\text{g g}^{-1} \text{h}^{-1}$, $\text{RMSE}=0.88 \mu\text{g g}^{-1} \text{h}^{-1}$) was observed, suggesting that it can be approximately estimated using leaf temperature without considering seasonal variations and populations.

4.4.3 *Chamaecyparis obtusa*

Matsunaga et al. (2013) employed the BE method and observed relatively constant values of the monoterpene BER of *C. obtusa* from spring to summer but a higher value in winter. There were no differences in the monoterpene BERs between the Tanashi and Shiiba sites from spring to fall (Figure S6). However, Okumura et al. (2008a) found high variability in monoterpene BERs among trees at the same growing site (Figure S6, Table S6). By plotting all data (Figure S7) collected by Okumura et al. (2008a), clear temperature dependence of the monoterpene emissions of a *C. obtusa* individual (Tree B) was observed throughout the year (Figure S7; $\beta=0.09$, $\text{BER}=0.15 \mu\text{g g}^{-1} \text{h}^{-1}$, $\text{RMSE}=0.46 \mu\text{g g}^{-1} \text{h}^{-1}$; $\beta=0.10$, $\text{BER}=0.17 \mu\text{g g}^{-1} \text{h}^{-1}$, $\text{RMSE}=0.48 \mu\text{g g}^{-1} \text{h}^{-1}$). However, the correlation between temperature and monoterpene emission rate was poor in “Tree A” (Figure S7; $\beta=0.09$, $\text{BER}=0.63 \mu\text{g g}^{-1} \text{h}^{-1}$, $\text{RMSE}=1.35 \mu\text{g g}^{-1} \text{h}^{-1}$; $\beta=0.10$, $\text{BER}=0.72 \mu\text{g g}^{-1} \text{h}^{-1}$, $\text{RMSE}=1.31 \mu\text{g g}^{-1} \text{h}^{-1}$). It may be plausible to use the median or arithmetic mean of the BERs; however, a relatively high error should be considered because of the high variation in the monoterpene BERs among the individual trees.

4.5 Bamboo

In Japan, bamboo forests accounted for 0.6% of the total forest area in 2012 (Forest Agency, 2018), and this area has been increasing (Suzuki 2015). Most native or naturalized bamboo species in Japan belong to the Arundinarieae family. Only Kyushu Island and the Okinawa Islands have large populations of Bambuseae species. Among the species of Arundinarieae, *Phyllostachys pubescens*, *Phyllostachys bambusoides*, and *Phyllostachys nigra* var. *henonis* are dominant bamboo species in Japan, which are ranked as 20th, 24th, and 58th among the dominant tree species, respectively.

Chang et al. (2021b) demonstrated that the isoprene BER of *P. pubescens* had a maximum of $22.8 \pm 7.0 \text{ nmol m}^{-2} \text{s}^{-1}$ in August. It then quickly decreased to approximately one-tenth of its initial value in autumn and completely seized by January. The emission increased back to a rate of $2.2 \pm 0.2 \text{ nmol m}^{-2} \text{s}^{-1}$ in May. Additionally, Chang et al. (2022a) measured

isoprene BER of below-canopy culms in a pure *P. pubescens* forest using the LC method and determined the BER to be $12.8 \pm 5.7 \text{ nmol m}^{-2} \text{s}^{-1}$ in August, with a strong correlation with specific leaf weight. Observation data of tower flux measurements for *P. pubescens* vegetation are currently absent in Japan, but in China, Bai et al. (2016) employed the REA method above a *P. pubescens* forest and revealed a regional-scale isoprene BER of $0.42 \text{ mg m}^{-2} \text{h}^{-1}$ ($1.71 \text{ nmol m}^{-2} \text{s}^{-1}$) in autumn (November 2012).

For *P. bambusoides*, Chang et al. (2021b) determined the isoprene BER to be $17.6 \pm 1.3 \text{ nmol m}^{-2} \text{s}^{-1}$ in August. For *P. nigra* var. *henonis*, Chang et al. (2021b) obtained the isoprene BER of $5.0 \pm 3.9 \text{ nmol m}^{-2} \text{s}^{-1}$ in August.

4.6 Understory vegetation

In addition to canopy trees, understory vegetation, such as herbaceous species and shrubs, should be considered when estimating BVOC fluxes in forest ecosystems. Usually, the light intensity in the understory layer and forest floor is lower than that in the upper layer, which may cause decreased BVOC emission rates. However, even in such environments, BVOC emissions from the understory vegetation may not be negligible in some specific cases. Isoprene flux ($>0.5 \text{ nmol m}^{-2} \text{s}^{-1}$) above a *L. kaempferi* plantation in summer originated from an understory fern species *Dryopteris crassirhizoma* (Mochizuki et al. 2014).

4.7 Crops

4.7.1 Rice

The rice cultivation area in Japan is 1,404,000 ha (The Portal Site of Official Statistics of Japan, 2021), which lies between the 3rd and 4th dominant tree-growing areas (Table 2). Several studies have been conducted to qualitatively and quantitatively assess terpenoid emissions from rice paddies. Winer et al. (1992) employed the BE method in a rice paddy in California and found no emission of isoprene or monoterpenes from rice cultivar “M202.” Redeker et al. (2003) employed the SC method for rice cultivar “Cocodrie” in a rice paddy and detected no emission of monoterpenes, but detected a trace quantity of isoprene. The isoprene emission rate converted on a land area basis was very low ($3.7 \mu\text{g m}^{-2} \text{h}^{-1} \approx 0.015 \text{ nmol m}^{-2} \text{s}^{-1}$). Tani et al. (1999) used the FPC method for four cultivars grown in pots and reported that a trace quantity of linalool was emitted from a rice cultivar “Mutsuhomare,” but not from the other three cultivars. Recently, Tani et al. (2023) observed linalool emission from three Japanese rice cultivars using the BE method. They attributed this emission to touching stimuli by hand while enclosing the aboveground parts of the rice in the enclosure bag. Thereafter, Tani et al.

(2023) employed the REA method to measure the terpenoid flux above a rice paddy and reported a low quantity of α -pinene emission. The obtained flux of α -pinene was $0.006 \text{ nmol m}^{-2} \text{ s}^{-1}$ on a land area basis, with a 95% confidence interval of $0.004 \text{ nmol m}^{-2} \text{ s}^{-1}$.

By contrast, Bao et al. (2008) employed the SC method using a commercial chamber for Japonica rice (cultivar information was not provided). They found emissions of five species of monoterpene (α -pinene, limonene, myrcene, p-cymene, and β -pinene). Tani et al. (2023) converted this emission rate on dry weight basis to that on land area basis and reported that it corresponded to $600 \mu\text{g m}^{-2} \text{ h}^{-1}$ ($1.2 \text{ nmol m}^{-2} \text{ s}^{-1}$).

Except for Bao (2008), the other four studies reported very small or negligible terpenoid emissions from rice plants. As the REA method can avoid mechanical stimuli and is more reliable compared to other methods that might induce monoterpene emissions by mechanical stimuli, the terpenoid emission rate seems to be very low.

4.7.2 Other crops

Wheat is the 2nd most dominant crop in Japan, with a cultivation area of 220,000 ha (The Portal Site of Official Statistics of Japan, 2021), lying between the 15th and 16th most dominant tree areas (Table 2). Some studies conducted abroad provided the BERs of isoprene and monoterpenes at $0\text{--}0.16$ and $0\text{--}0.006 \mu\text{g g}^{-1} \text{ h}^{-1}$, respectively (Evans et al. 1982; Winer et al. 1992; König et al. 1995; Morrison et al. 2016; Gonzaga Gomez et al. 2019). Soybean is the 3rd most dominant crop in Japan, with a cultivation area of 146,200 ha (The Portal Site of Official Statistics of Japan 2021), lying between 21st and 22nd dominant tree areas (Table 2). Isoprene and monoterpene emissions from soybean are negligible (Li and Sharkey 2013). Buckwheat is the 4th most dominant crop, but its cultivation area (65,500 ha) is lower than that of the 40th tree species and no report on its isoprene or monoterpene emission is available.

Potatoes (70,900 ha), cabbage (34,300 ha), sweet potatoes (32,400 ha), and radish (29,200 ha) are widely cultivated (The Portal Site of Official Statistics of Japan 2021). Cabbage is reported to emit monoterpenes at a rate of $<1 \mu\text{g g}^{-1} \text{ h}^{-1}$ (Vuorinen et al. 2004). Reports on terpenoid emissions from the other three crops are not available.

4.8 Others

Chrysanthemum is the most widely cultivated cut flower (425,800 ha) followed by lily (65,900 ha). However, there are no reports on terpenoid emissions from their leaves. Pasture plants are grown in rural areas (717,600 ha). Oxygenated alcohols have been reported to be emitted from pasture plants, but the emissions of isoprene and

monoterpenes are negligible (Kirstine et al. 1998). During harvesting, high quantities of green alcohols and aldehydes are emitted, but isoprene and monoterpenes are not present (Karl et al. 2001). Green alcohols and aldehydes are considerably less reactive in the atmosphere and do not contribute significantly to O_3 formation. Monoterpenes were reported to be emitted from some fruit trees including peach ($1.2 \mu\text{g g}^{-1} \text{ h}^{-1}$) and orange ($2.5 \mu\text{g g}^{-1} \text{ h}^{-1}$) (Gentner et al. 2014). During the flowering stage, the emission rate increased. The cultivation area of any fruit tree species in Japan is $<40,000$ ha.

5 Discussion

5.1 Interspecific variation in terpenoid emission rate

Figure 2 shows the BERs of isoprene and total monoterpenes from major plant species in Japan. The BERs on a leaf area basis vary widely among plant species. When comparing data across species, it is observed that the isoprene emission rate is higher than that of total monoterpenes. Two each of deciduous *Quercus* and bamboo species are strong isoprene emitters (Fig. 2, upper panel). Among the monoterpene emitters, four evergreen broad-leaf trees, including three *Quercus* species, have the highest BERs. The monoterpene storage type conifers *L. kaempferi* and *P. densiflora* have relatively low BERs ($0.7\text{--}2.5 \text{ nmol m}^{-2} \text{ s}^{-1}$) that were expressed on the ground area basis (i.e., tower flux data). These values are similar to the monoterpene fluxes of other coniferous trees grown in Europe and the USA (Tani and Mochizuki 2021).

Emission data on a dry weight basis are summarized for various major species and are shown in the lower panel of Fig. 2. Emission data hidden by dark gray bars were collected using the least reliable SC method and are not discussed here. Although most of the data were sourced from reports distinct from those providing leaf area-based emission rates, a consistent trend was observed. Specifically, deciduous *Quercus* species and evergreen *Quercus* species exhibited higher emission rates of isoprene and monoterpenes, respectively.

5.2 Terpenoid emission rates within tree species

The leaf area-based BERs of total monoterpenes from *Q. phillyraeoides* exhibited up to a 3.1-fold difference between reports (upper panel of Fig. 2). Similarly, the difference in the isoprene BER of *P. pubescens* is 1.8-fold between the two reports (Chang et al. 2021b, 2022a). In contrast, the BERs of *Quercus mongolica* var. *crispula* and *Quercus serrata* remained consistent at $27.3\text{--}27.9$ and $27.8\text{--}31.7 \text{ nmol m}^{-2} \text{ s}^{-1}$, respectively. These substantial variations in terpenoid emission rates might be caused by factors such as the reliability of measurement and analytical systems, tree age, leaf morphology, environmental conditions, and genetic diversity within the

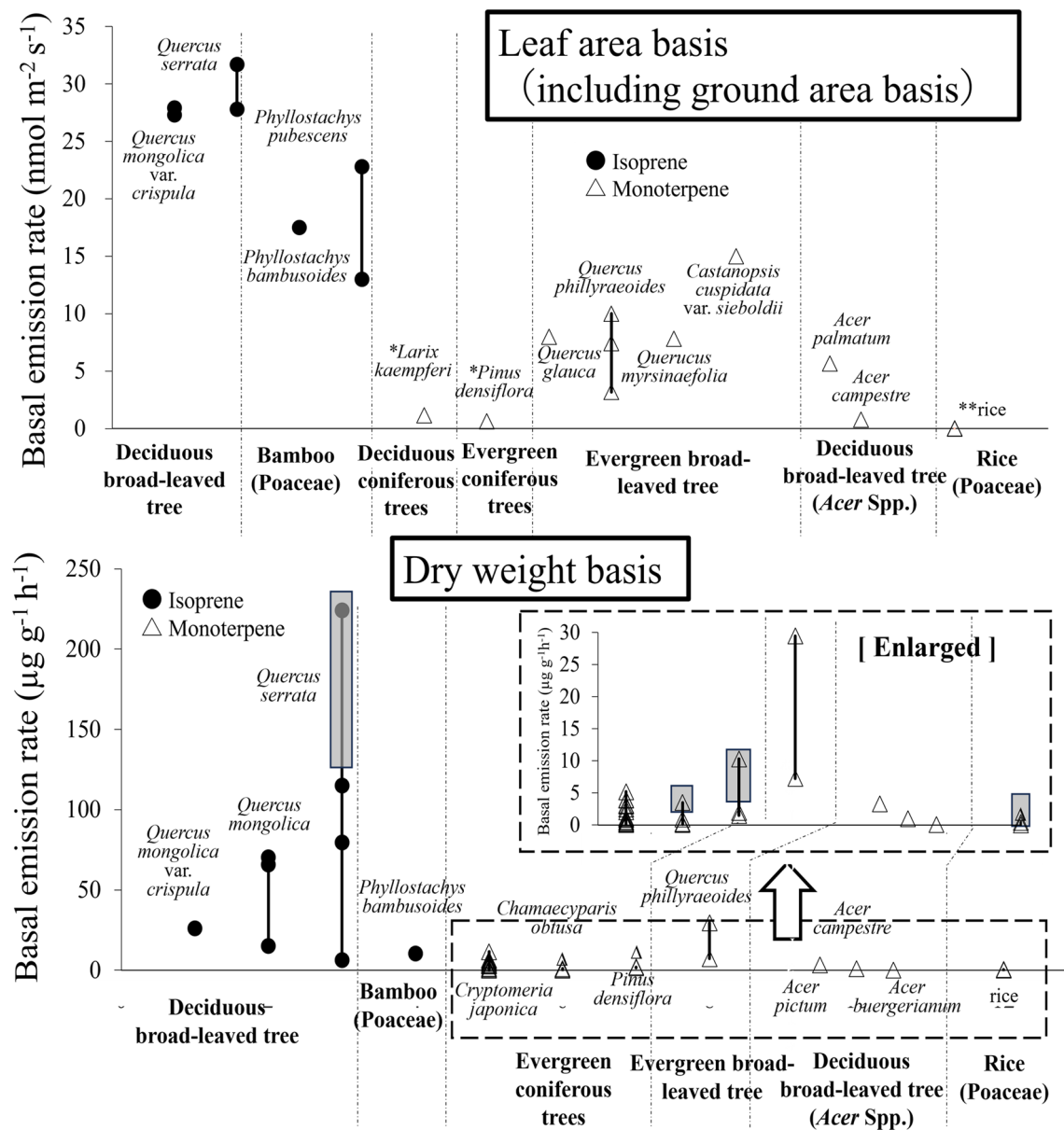


Fig. 2 Basal emission rates (BERs) of isoprene and total monoterpenes from major plant species in Japan. Upper and lower panels show BERs on leaf area basis and dry weight basis, respectively. Dots show the BERs collected in summer season in individual reports. *Expressed on a ground area basis, **one of three data is expressed on ground area basis. Data hidden by dark bars were removed because they were collected using a less reliable measurement method (static chamber method). The detailed information including references, measurement techniques, and tree age for each data is provided in supporting information S1-S3 and Table 3

species. Leaf morphology, particularly leaf thickness, is linked to cell volume or the number of cells existing per unit leaf area, which can significantly influence terpenoid production, as it occurs within chloroplasts. For instance, this phenomenon is evident in isoprene emission from *P. pubescens* (Chang et al. 2022a). Moreover, various environmental conditions affect terpenoid emissions from plants. For example, monoterpene emissions

from sunlit leaves of *Quercus ilex* were an order of magnitude higher than those from shaded leaves (Staudt et al. 2003). Furthermore, the light and temperature conditions experienced by plants during the preceding several to 14 days have been reported to regulate isoprene emission potentially through enhanced enzyme activity and/or increased precursor content (Hanson and Sharkey 2001; Pétron et al. 2001). Genetic diversity may contribute to

intraspecies differences in terpenoid emission rates (Funk et al. 2005). The monoterpene emission rate of *Q. phillyraeoides* was significantly different among 56 individuals, with six non-emitter variants identified among the tree group (Chang et al. 2024).

On a leaf dry weight basis, the BER within species varied more than threefold in some plant species, including *Q. serrata*, *C. japonica*, and *Q. phillyraeoides* (lower panel of Fig. 2). Leaf morphology need not be considered for the emission rate expressed on a leaf dry weight basis because leaf weight reflects leaf thickness. Therefore, the variabilities in terpenoid emission rates within species may be influenced by the reliability of measurement and analytical systems, tree age, environmental conditions, and genetic diversity within the species.

5.3 Inventory data required for evaluating the formation of urban O₃ and SOA in Japan

Gathering information on the BERs of the top 20 ranked trees is essential to generate a BVOC inventory in Japan as they cover approximately 70% of the forest area. For the remaining 30%, limited data are available. The BVOC inventory will be used to estimate O₃ and SOA formations in urban areas to evaluate air quality in current and future climates. For this purpose, trees occurring in the alpine and northern areas, including *Abies sachalinensis*, *Betula ermanii*, *Tilia japonica*, and *Alnus* spp., which are in the top 20 rankings, are not important. Among the other tree species within the top 20, the BER was not available for *Castanopsis cuspidata*. The seasonality of the BER is unavailable for *Castanopsis cuspidata* var. *sieboldii*, *C. crenata*, *Quercus glauca*, and *C. cuspidata*. Therefore, collecting such data is a priority.

In this review, we describe the high variability in the isoprene and monoterpene emission rates among tree species. Higher isoprene emission rates were observed in two deciduous *Quercus* species and two bamboo species, and higher monoterpene emission rates were observed in several evergreen broadleaf tree species. Among them, the bamboo species *P. pubescens* is spreading to suburban areas, including undeveloped woodlands near populated areas known as Satoyama (Takano et al. 2017). The expansion of invasive bamboo forests can result in an increase in isoprene emission in suburban areas, which might deteriorate air quality around the area.

Large variations in terpenoid emissions have been documented even within the same species. Several factors contribute to these discrepancies. To obtain representative values of BERs of individual tree species, emission data must be collected using reliable measurement methods and under representative environmental conditions. In addition, the average emission rates must be determined using multiple reliable data points.

6 Conclusions

Available data of BERs of isoprene and monoterpenes for major tree species in Japan were collected from literature and its datasets were listed in tables. Reliability and validity of the terpenoid measurement methods were evaluated based on their advantages and disadvantages, and the least reliable data were removed from the datasets in discussion section. By examining the remaining data, we found the high variability in the isoprene and monoterpene emission rates among tree species. Higher isoprene emission rates were observed in two deciduous *Quercus* species and two bamboo species, and higher monoterpene emission rates were observed in several evergreen broadleaf tree species. We also found large variations in terpenoid emissions within the same species. Several factors may contribute to these discrepancies, including the reliability of measurement and analytical systems, tree age, leaf morphology, environmental conditions, and genetic diversity within the species. To obtain representative values of BERs of individual tree species, emission data must be collected using reliable measurement methods and under representative environmental conditions. The BERs need to be determined using multiple reliable data points.

Abbreviations

BVOCs	Biogenic volatile organic compounds
AVOCs	Anthropogenic volatile organic compounds
O ₃	Ozone
SOA	Secondary organic aerosols
MEGAN	Model of Emissions of Gases and Aerosols from Nature
PPFD	Photosynthetic photon flux density
BER	Basal emission rate
LAI	Leaf area index
SLW	Specific leaf weight
EAGRID2000-Japan	East Asian Air Pollutant Emissions Grid Database
DMAPP	Dimethylallyl diphosphate
GPP	Geranyl diphosphate
EC	Eddy covariance
REA	Relaxed eddy accumulation
GF	Gradient flux
PTR-MS	Proton transfer reaction mass spectrometry
BE	Bag enclosure
LC	Leaf cuvette
FPC	Flow-through plant chamber
SC	Static chamber
LV	Leaf-tip vial

Supplementary Information

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Additional file 1.

Additional file 2.

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Author contributions

Conceptualization was performed by A.T.; validation by A.T.; data collection by N.M., T.-W.C., and M.O.; data curation by A.T.; writing—original draft preparation—by A.T., T.-W.C., N.M., and Y.K.; writing—review and editing—by A.T.; visualization by N.M., T.-W.C., and A.T.; supervision by A.T.; project administration by A.T.; funding acquisition by A.T. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets supporting the conclusions of this article are included within the article and its additional files.

Declarations

Competing interests

The authors declare that they have no competing interest.

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