

Review

Research on the Emission of Biogenic Volatile Organic Compounds from Terrestrial Vegetation

Dingyi Pei ^{1,2} , Anzhi Wang ¹, Lidu Shen ¹ and Jiabing Wu ^{1,*} 
¹ Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China; peidingyi21@mails.ucas.ac.cn (D.P.); waz@iae.ac.cn (A.W.); shenlidu@iae.ac.cn (L.S.)

² University of Chinese Academy of Sciences, Beijing 100049, China

* Correspondence: wujb@iae.ac.cn

Abstract

Biogenic volatile organic compounds (BVOCs) are low-boiling-point compounds commonly synthesized by secondary metabolic pathways in plants. As key precursors of ozone (O₃) and secondary organic aerosols (SOA), BVOCs play a critical role in ecosystem-atmosphere interactions. However, their emission from both marine and terrestrial ecosystems, as well as their association with climate and the environment, remain poorly characterized. In light of recent advances in BVOC research, including the establishment of emission inventories, identification of driving factors, and evaluation of ecological and environmental impacts, this study reviews the latest advancements in the field. The findings underscore that the carbon losses via BVOC emission should not be overlooked when estimating the terrestrial carbon balance. Additionally, more work needs to be conducted to quantify the emission factors of specific tree species and to establish links between BVOC emission and climate or environment change. This study contributes to a deeper understanding of vegetation ecology and its environmental functions.

Keywords: forest; biogenic volatile organic compounds (BVOCs); carbon balance; emission inventory



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1. Introduction

Volatile organic compounds (VOCs) refer to organic compounds that easily volatilize under normal temperature and pressure, typically with boiling points ranging from 50 to 260 °C and melting points below room temperature [1]. These compounds are significant not only for their direct effects on human health but also because they participate in photochemical reactions in the atmosphere, contributing to the formation of secondary air pollutants.

The sources of VOCs in the global atmosphere can be categorized into anthropogenic and natural sources, of which approximately 10–35% comes from human activities, mainly including industrial emissions, transportation, and solvent usage [2–4]; the remaining approximately 65–90% comes from natural sources, mainly from soil, ocean, and plant emissions [5]. Naturally emitted VOCs are usually referred to as biogenic volatile organic compounds (BVOCs). Among the emission sources, forests are the main contributors, accounting for more than 70% of the biological source emissions.

BVOCs primarily consist of isoprene, monoterpenes, sesquiterpenes, carbonyl compounds, a series of alcohols, oxides, and esters, etc. [6,7]. They can be broadly categorized

as active or inactive based on their atmospheric reactivity and ecological functions. The inactive BVOCs have low reactivity in the atmosphere and tend to persist longer, including isoprene, acetone, methanol, and so on. The active BVOCs react quickly with atmospheric oxidants (e.g., ozone, OH radicals, NO_x) and influence air quality and climate, including monoterpenes, sesquiterpenes, ethylene (C_2H_4), and so on [8–10]. BVOCs are secondary metabolites involved in various plant physiological processes including growth, development, reproduction, and defense [11]. They are produced and released by plants through various biological and environmental processes, and the major metabolic pathways include the Methylerythritol Phosphate (MEP) pathway, which produces isoprene and monoterpenes, the Mevalonic Acid (MVA) pathway, which produces sesquiterpenes and triterpenes, the Lipoxygenase (LOX) pathway, which produces hexenal and hexanol, the Shikimate pathway, which produces aromatic compounds like eugenol and isoeugenol [12,13]. Beyond their physiological roles, BVOCs also function as communication mediators within plant communities and between plants and insects [14]. Numerous studies have demonstrated that BVOCs are important precursors to the production of O_3 and secondary organic aerosols (SOA) [15,16], playing a crucial role in influencing atmospheric environmental quality [17,18]. Moreover, BVOC emissions play a central role in global carbon cycle. Global annual BVOC emissions exceed 1.0 billion tons of carbon [6,19]. From the perspective of ecosystem carbon balance, the carbon loss via BVOC emission is also an important component of the global carbon cycle.

As early as the 1960s, researchers first observed the phenomenon of BVOC emission from forests [20]. However, due to a lack of understanding of its significance in the field of ecology and environment, there were relatively few studies conducted during that time. From the 1960s to the 1980s, researchers utilized closed chamber techniques to measure BVOC emissions from plants, primarily focusing on Pinaceae plants [21]. Since the 1990s, substantial advancements have been made in the field of BVOC research, driven by the development and refinement of BVOC emission models and breakthroughs in observation technology. These advancements have collectively led to a new era of BVOC research. The emission model has transitioned from a single-leaf isoprene emission model to a comprehensive global BVOC emission model [22]. The study of vegetation VOC emissions has evolved into a systematic endeavor. This research encompasses investigations into emission sources, the application of observation technology, responses to land-use or global change, emission inventory estimates, the functions of these emissions in forest ecosystems, and their influence on O_3 concentration [23,24]. Such work allows for a deeper understanding of vegetation VOC emissions and their broader environmental implications. However, previous studies demonstrate limitations, as they typically focused on specific aspects of BVOC emissions, neglecting a comprehensive perspective, while traditional reviews generally overlooked the implications of BVOC emissions on the ecosystem carbon balance [25].

2. Monitoring Methods

2.1. Off-Line Method

Currently, the mainstream monitoring methods for BVOCs are mainly offline analysis, using tools such as syringes, gas bags, sampling bottles, or adsorption tubes to collect samples. These samples need to be transported to the laboratory and analyzed using gas chromatography and mass spectrometry techniques. Although this method has a relatively simple operation process and can achieve automated analysis through mature technical procedures, it has several limitations. First, the sampling process tends to significantly interfere with the target gas. Second, the low sampling frequency fails to meet the demands

of long-term continuous monitoring, thereby hindering the precise calculation of the BVOC emission inventories [26].

At the level of individual plants, static chamber sampling and dynamic headspace sampling are two commonly used sampling methods. Both approaches employ specialized plant chambers to concentrate and measure BVOC emissions. Among them, the static chamber sampling method uses bags or chambers to cover the branches and leaves of the selected tree species, measuring the gas concentration inside the chamber before and after sealing, and then calculating the emission rate based on the change in concentration over time [27,28]. Compared with this, the dynamic headspace sampling method maintains air circulation during sampling, avoiding the drastic fluctuations in environmental temperature and humidity in the static sealed chamber, and reducing its potential impact on the experimental results.

In the field of detection technology, gas chromatography–mass spectrometry (GC-MS) technology is the most widely used [29]. This technology uses gas chromatography to efficiently separate compounds, and then combines a mass spectrometer to conduct qualitative and quantitative analysis of target compounds, with extremely high selectivity and resolution, especially suitable for the identification of components in complex mixed samples. By adding internal standards (such as deuterated toluene) and using the selective ion monitoring (SIM) mode [30], the quantitative accuracy and detection sensitivity of low-concentration BVOCs can be significantly improved. In addition, flame ionization detection (GC-FID) is an economical and practical alternative, and has certain applications in the quantitative analysis of BVOCs in hydrocarbon compounds [30]. However, both GC-MS and GC-FID [31] require pre-concentration and time-integrated sampling of the samples, resulting in a long detection cycle and inability to achieve real-time dynamic monitoring. The dynamic branch sealing system is a semi-offline detection method, obtaining real emission data from the plant through the sampling chamber, combined with adsorption enrichment and GC-MS analysis, which can effectively control environmental factors, but may cause certain interference to the plant's physiological state. In recent years, portable membrane extraction-GC systems (MESI-Portable GC) have been used for the in situ monitoring of plant emissions [32], and although they exhibit certain on-site adaptability, these systems face challenges such as discontinuous sampling and limited sensitivity.

2.2. On-Line Method

In the 1990s, researchers began to use Relaxed Eddy Accumulation (REA) technology to monitor BVOC emissions, aiming to obtain a large range of BVOC emission flux and reduce measurement errors associated with the closed chamber method [33]. While this method can estimate canopy scale flux to some extent, its inability to measure in real time and continuously significantly impacts the accuracy of BVOC inventory estimation.

Proton transfer reaction mass spectrometry (PTR-MS) is currently the most widely used and technically mature online monitoring method. It utilizes the proton transfer reaction between H_3O^+ ions and BVOC molecules to generate positively charged product ions, which are then detected by a mass spectrometer [29,30]. It has a detection sensitivity at the pptv level and a time resolution of seconds, enabling real-time tracking of BVOC changes on a rapid time scale. The new generation of proton transfer reaction time-of-flight mass spectrometry (PTR-TOF-MS), by combining a proton transfer ion source with time-of-flight mass spectrometry technology, can qualitatively and quantitatively detect trace volatile organic compounds at the ppbv or even pptv level within seconds. It features rapid response, high sensitivity, and low detection limits [34]. Researchers have successfully used PTR-TOF-MS for online monitoring of BVOC emissions from plant branches [34]. However, due to the cost of the equipment, online monitoring of volatile organic compounds in the

surrounding air is not yet widespread, and its main application area is in urban atmospheric environment monitoring.

It is worth noting that PTR-MS has limitations in identifying isomers or compounds with the same mass-to-charge ratio (m/z), and often requires correction in combination with GC-MS [35]. To overcome this problem, the combined technology of fast GC and PTR-TOF-MS emerged [36]. This system can rapidly separate and analyze complex BVOC mixtures within a few minutes and improve the structural identification ability to a certain extent, although its sensitivity is still slightly lower than that of traditional GC-MS. Additionally, Selected Ion Flow Tube-MS (SIFT-MS) [37] achieves absolute quantification through the reaction of ions with known reaction rates to the target molecules, and is suitable for detecting humid gases such as plant leaf transpiration gases. Proton-Transfer Ion Trap-MS (PIT-MS) [38] enhances the structural analysis ability through the collision-induced dissociation (CID) technique [39] and can be used to distinguish isomers with similar structures, demonstrating good development potential.

Furthermore, micro-VOC sensors based on infrared spectroscopy have gained increasing attention in recent years due to their non-destructive nature, rapid response capabilities, and miniaturized design [40]. These sensors utilize the absorption characteristics of VOC molecules in specific infrared bands for qualitative and quantitative identification, and are widely applied in VOC emissions monitoring in urban and industrial settings, such as traffic exhaust and industrial waste gas [40]. Although currently mainly used for rapid detection of anthropogenic pollution, their compact structure and simple operation also provide the possibility for on-site rapid screening and long-term automated deployment of BVOC in ecosystems in the future.

2.3. Model Simulation

Model simulation methods are the core tools for constructing large-scale (regional, national, and even global) emission inventories. Since the 1990s, various models have been developed successively. For instance, the Biogenic Emissions Inventory System (BEIS) was initially applied to simulate mid-scale vegetation emissions and was later upgraded to BEIS3 [41]. Meanwhile, the Model of Emissions of Gases and Aerosols from Nature (MEGAN) has become one of the most widely used models for assessing BVOC emissions globally [26]. The MEGAN model uses a multi-level approach to extrapolate the leaf-scale observations of isoprene emissions to global-scale emission simulations. Firstly, at the leaf scale, the basic emission factors are obtained based on leaf chamber experiments, and temperature and light response functions are constructed. Secondly, at the canopy scale, a hierarchical model is used to simulate the vertical distribution of light and temperature, combined with factors such as leaf area index (LAI), leaf age structure, and soil moisture, to calculate the comprehensive emission factors and correct the losses in the canopy process. Finally, at the global scale, the model uses MODIS vegetation types (seven types of PFT) and NCEP meteorological data to calculate the emissions of various vegetation types at a 1 km spatial resolution, thereby estimating the global isoprene emissions and verifying them through satellite HCHO inversion data and ground flux observations. Additionally, climate system models like the Community Climate System Model (CCSM) have attempted to incorporate the BVOC emission mechanisms from plants to enhance their response capabilities to global-scale emission dynamics [42]. Most of these models are based on empirical relationships constructed using variables such as temperature, light, and leaf area density [43–45], while some models have attempted to introduce plant physiological processes and photosynthesis mechanisms to strengthen the physical basis of predictions [46,47].

The integration of remote sensing data and ground observation data has further enhanced the spatial accuracy and ecological representativeness of regional-scale BVOC estimations. Diem and Comrie [48] used Landsat TM data to refine the land cover of the Tucson area in the United States into 17 categories and coupled it with the BEIS2 model, finding that the BVOC emission intensity of urban green spaces was much higher than that of shrublands in arid areas. Nichol and Wong [49] integrated multi-source satellite image data such as Landsat, ASTER, and SPOT with the MEGAN model, and through the fine classification of vegetation types, effectively improved the applicability of isoprene emission estimation in tropical regions. Oderbolz et al. [50] used an empirical formula model, combined with WRF meteorological data and CAMx air quality simulation, and then combined with land cover data and vegetation inventory, systematically analyzed the distribution and seasonal variation patterns of BVOC emissions in different climate zones in Europe. At the same time, the inversion method based on satellite HCHO column concentration also provides an indirect constraint means for BVOC emission estimation. Morfopoulos et al. [51] distinguished the contributions of biogenic and combustion sources using OMI data, and although there was a source location error of 200–300 km, it demonstrated an outstanding ability in identifying emission spikes during extreme climate events. Kefauver et al. [3] developed a BVOC emission estimation system based on the vertical column assessment of satellite-based formaldehyde. This system not only takes into account environmental variables such as temperature, light, and leaf area density, but also incorporates plant physiological processes and photosynthetic mechanisms. It estimates the formaldehyde slant column concentration through differential absorption spectroscopy (DOAS) technology, achieving the quantification of biogenic emissions.

Although these methods have their own advantages, uncertainties still prevail, including errors in temperature and radiation correction parameters, LAI inversion deviations, and systematic errors caused by the cross-regional migration of emission factors [52]. Additionally, the differences in spatial scales between different vegetation inventories and land cover data can significantly affect the model output results [53], leading to large fluctuations in the estimated emissions. Based on this, current research is gradually moving towards the development of multi-source data integration, the establishment of region-specific emission factors, and the integration of remote sensing, models, and ground flux observations, aiming to improve the accuracy of BVOC emission estimation while providing more powerful support for climate model input and environmental management decisions.

3. Emission Characteristics

3.1. BVOC Emission Source and Components

The composition of BVOCs is complex, containing about 30,000 compounds [6], including isoprene, terpene, alkanes, olefins, alcohols, esters, and more, of which isoprene and terpene are the two main compounds, while volatile terpenes mainly include monoterpenes, sesquiterpenes, and diterpenes [54], which are mainly stored in different organs of plants: roots, stems, leaves, fruits, seeds, as well as flowers. Different plant species and even different plant organs of the same plant species can release different VOC components [55,56]. Research indicates that most of the tree species emit isoprene, while conifer species are the major source of monoterpene emission [57]. For example, studies [58,59] found 60 different BVOCs in three common European conifer species—Austrian pine, Scotch pine, and spruce, most of which belong to monoterpenes and sesquiterpenes. Coniferous species such as *Abies*, *Picea*, and *Pinus* typically emit distinct profiles of monoterpenes [60]. Broadleaf species, including poplars, willows, oak, and magnolias [61], primarily release isoprene. Some deciduous species, such as *Acer*, *Magnolia*, and *Eucalyptus*, are also known to emit monoterpenes [62]. The composition of BVOCs released by fruit trees varies significantly.

For example, lemons and broad-skinned citrus fruits mainly emit methanol, followed by acetone and acetaldehyde, whereas orange trees predominantly release oxygenated monoterpenes, monoterpenes, and sesquiterpenes [63]. The leaves of apple trees mainly emit methanol, acetic acid, green leaf volatiles (GLVs), and acetone, while their fruits mainly emit acetaldehyde and acetic acid [17]. Some components are shown in Table 1.

Table 1. BVOC components.

BVOC Class	Representative Compounds	Sources	Reactivity (Lifetime)
Isoprene (C ₅ H ₈)	Isoprene (C ₅ H ₈)	Broadleaf deciduous trees (e.g., oak, poplar)	Very high (~1.3 h) [8,59]
Monoterpenes (C ₁₀ H ₁₆)	α -Pinene, β -Pinene, Limonene, Myrcene, Sabinene, 3-Carene, Camphene, Terpinolene	Coniferous trees (e.g., pine, spruce)	Moderate to high (~1–10 h) [14,59]
Sesquiterpenes (C ₁₅ H ₂₄)	β -Caryophyllene, α -Humulene, Germacrene D, Longifolene, Farnesene, Bisabolene, Nerolidol	Tropical trees, grasses, and some shrubs	Extremely high (minutes to <1 h) [9]
Oxygenated Terpenoids	Linalool, 1,8-Cineole, Terpineol, Borneol, Geraniol, Verbenone	Flowering species, stress-induced emissions	Variable (hours to days) [10]
Green Leaf Volatiles (GLVs)	(Z)-3-Hexenal, (E)-2-Hexenal, (Z)-3-Hexen-1-ol, Hexanal, Hexenyl acetate	Leaf damage	High (minutes to a few hours) [64]
Aromatic Compounds	Benzaldehyde, Methyl salicylate, Styrene, p-Cymene, Eugenol, Cresol [65]	Floral emissions, understory vegetation	Variable [65]
Small Oxygenated VOCs	Methanol, Ethanol, Acetone, Acetaldehyde, Formaldehyde, Acetic acid	leaf development	Low (days) [66,67]

3.2. Emission Inventory

The global emissions of BVOC are estimated by various models to range approximately from 175 to 1145 Tg C per year [20,42,44,68–77], of which plant-derived isoprene and monoterpene emissions are estimated to be 299.1–800 Tg C and 24–184 Tg C [8,42,44,68–71,76–86] per year, respectively.

In 1995, Guenther et al. [68] proposed the G95 model and estimated the annual global BVOC emission to be 1145 Tg C. In 2014, Katerina et al. [70] used MEGANv2.1 along with the Modern Era Retrospective Analysis for Research and Applications (MERRA) meteorological fields to create a global emission data set of BVOC on a monthly basis for the time period of 1980–2010. The model estimated a mean annual total BVOC emission of 760 Tg C yr^{−1}, consisting of isoprene (70%), and monoterpenes (11%). The mean annual BVOC emissions were also estimated for different regions, including East and South Asia (73 Tg C yr^{−1}), North America (34.5 Tg C yr^{−1}), South America (163 Tg C yr^{−1}), and Africa (150 Tg C yr^{−1}). In 2021, Katerina et al. [44] updated the European isoprene emission potential data based on high-resolution land cover maps, tree species composition, and emission factors, which resulted in the annual total isoprene in Europe reduced by 35% from 10.03 Tg C to 6.55 Tg C, and global annual BVOC emissions were estimated at 424 to 591 Tg C, with isoprene emissions at 299.1 to 440.5 Tg C. The annual emissions of BVOCs in China were estimated to range from 10 to 58.89 Tg C, with isoprene ranging from 6.13 to 37.45 Tg C and monoterpene emissions ranging from 1.03 to 6.68 Tg C [87–94].

It is important to note that considerable uncertainty persists in the global estimation of BVOC emissions, with existing estimates varying considerably across research reports and exhibiting discrepancies as large as an order of magnitude.

4. The Factors Affecting BVOC Emission

4.1. Intrinsic Factors

4.1.1. Tree Species

Diverse species of trees exhibit distinct BVOC emission patterns. For instance, broad-leaved tree species predominantly emit isoprene, while coniferous tree species generally emit monoterpenes. Bao et al. [95] conducted a meta-analysis of VOC emissions from different plants and found that the emission of isoprene, monoterpene, and sesquiterpene, the three major types of BVOCs, were more common in deciduous plants than in evergreen plants. Gerhard [96] reported that in western Germany, rubber trees were the primary emitters of isoprene, while coniferous forests in central Germany were found to predominantly emit monoterpenes. Conversely, some broad-leaved trees in southern China, such as *Cinnamomum camphora*, *Albizia julibrissin*, and *Acacia macrophylla*, were observed to mainly emit monoterpenes. Furthermore, research has indicated that the emission of isoprene is generally higher than that of monoterpenes. For instance, tropical *Ficus* plants typically emit approximately 100 $\mu\text{g C}/(\text{g}\cdot\text{h})$ of isoprene, while few plants release such a high concentration of monoterpenes under similar conditions [97]. Isoprene is synthesized from dimethylallyl diphosphate under the catalysis of isoprene synthase via the methylerythritol 4-phosphate pathway in chloroplasts. Broad-leaved trees generally contain more chloroplasts with a larger leaf area than coniferous trees, which is favorable for isoprene synthesis and emission. Monoterpenes, on the other hand, are produced from geranyl diphosphate under monoterpene synthase and are typically stored in palisade tissue, spongy tissue, oil glands, and vascular bundles. Needle-leaved trees often contain specific storage tissues and organs, which facilitates the storage and emission of monoterpenes [98].

4.1.2. Gene

The genetic control of BVOC emissions is a fascinating area of research. The variability in monoterpene components within conifer populations, such as the diverse concentration of monoterpenes in the Scottish pine population, highlights the influence of genetic variation on BVOC emissions within and between populations. Understanding the genetic basis of BVOC emissions is crucial for comprehending the ecological and evolutionary implications of these emissions. However, monoterpenes in *Pinus* can also be induced by environmental factors such as herbivory, adding to the source of variability of natural populations [99]. Chen et al. [100] conducted a proteomic analysis of *Chamaecyparis formosensis* and *C. obtusa* var. *formosana*, and found that *C. obtusa* var. *formosana* saplings exhibited fewer differentially expressed proteins, both in terms of the number of protein species and the magnitude of fold changes, in response to the growth conditions. These proteins were mainly involved in photosynthesis (ATP synthase subunit β , ferredoxin-NADP reductase, leaf isozyme, cytochrome *f*, and thioredoxin-like protein CDSP32), carbon metabolism (RuBisCO large subunit-binding protein subunit α), amino acid (glutamate-glyoxylate aminotransferase and glycine cleavage system T protein), and protein processing (5-methyltetrahydropteroyltriglutamate-homocysteine methyltransferase 2 and S-adenosylmethionine synthase 2), signal transduction, and stress responses. They may serve as key regulatory factors influencing the BVOC emissions of these two species under different environmental conditions. Gene expression and regulation ensure that proteins are synthesized at specific times, in specific locations, and at appropriate levels to perform

their biological functions. This research provides valuable insights into the genetic and molecular mechanisms underlying BVOC emissions and their ecological significance.

Under temperature stress, the expression of the isoprene synthase gene (*ispS*) in *Ficus septica* is highly synchronized with isoprene emission [101]. Low temperature inhibits its transcription and protein abundance, and it quickly recovers after re-warming, indicating that *ispS* is a key rate-limiting factor for temperature-regulated isoprene emission. In defense responses, plants can rapidly activate BVOC synthesis genes through signaling pathways. For example, methyl jasmonate (MeJA) in *Selaginella martensii* induces the up-regulation of the MTPSL22 gene, promoting the release of linalool, and this process mainly relies on 12-oxo-phytodienoic acid (OPDA) rather than the classical jasmonic acid (JA) signaling pathway [102], reflecting the differences in signal regulation among different groups. Additionally, plants also optimize the timing of BVOC synthesis through seasonal regulation. Some tree species increase the expression of terpene synthesis genes before the onset of photosynthesis, thereby achieving the pre-accumulation of defense substances [103]. Cross-species studies have found that although seed plants and non-seed plants have conserved expression of terpene synthase families, they activate BVOC synthesis through different signaling pathways, which fully demonstrates the commonalities and diversity of plant regulatory mechanisms.

4.1.3. Tree Age

Tree age also impacts the emission of BVOCs from trees. Lim [104] studied the emission of isoprene from five oak species in East Asia and found that the emission rate of isoprene from trees aged 21 to 30 years was significantly higher than that of trees aged 41 to 50 years. Karlsson [105] found that younger plants had several times higher emissions of non-isoprenoids (other VOCs) than the corresponding 1-year-old trees. However, some studies indicated that the emissions from old forests were higher than those from young trees. For example, Kim et al. [106] found that the emission rate of BVOCs from mature *Cryptomeria* and red pine was higher than that from saplings. Hakola et al. [107] found that none of the younger trees (33–40 years) in Hyytiälä, Southern Finland, emitted isoprene, while one 50-year-old tree was a strong isoprene emitter. On average, older trees (>80 years) emitted about ten times more isoprene and monoterpenes than younger ones (<80 years), but no clear difference was observed in sesquiterpene emissions. The impact of tree age on BVOC emissions varies depending on different regions, tree species, and types of emissions.

4.1.4. Growth Rhythms

The emission of BVOCs varies at different growth stages, particularly for isoprene, monoterpenes, methanol, acetaldehyde, and sesquiterpenes. Baggesen et al. [108] observed that monoterpene emissions significantly differed between the green-up and flowering stages, with higher emissions during flowering ($1.5\text{--}3\text{ mmol m}^{-2}\text{ h}^{-1}$). Acetaldehyde and sesquiterpene emissions were also significantly higher during flowering compared to green-up and seed dispersal, while isoprene had significantly lower emissions during flowering compared to green-up and seed dispersal. Methanol fluxes showed a significant difference between flowering and seed dispersal, with lower emissions during seed dispersal. Dani et al. [109] demonstrated that flowers of certain plant species increased monoterpene emissions during flowering and aging, suggesting that this increase protects against seed predators. Leaf age composition in enclosed branches of evergreen conifers is a common aspect of phenology. Previous studies have reported that different levels or types of BVOCs are emitted depending on the leaf's growth stage. Greenberg et al. [110] reported that the composition of monoterpenes in the leaf oil of *Pinus ponderosa* changed with leaf age. The emission rates of isoprene from mature leaves were 90–130% higher than those from young

leaves and senescent leaves. Monoterpenes are mainly synthesized during the bud stage, when the leaf is 1–30 days old. The highest and lowest emission rates of monoterpenes are during the bud stage and in mature leaves, respectively [111]. Minna [112] indicated that monoterpene concentrations were low at the germination stage of Norwegian needles, but increased rapidly at the needles' maturation stage.

4.2. External Factors

4.2.1. Temperature

Temperature is one of the key factors affecting the emission of BVOCs, and the emission curves of isoprene and monoterpene are influenced by temperature. Within a certain range, the emission rate of BVOCs increases with rising temperature. However, when the temperature reaches a certain level, the emission rate of BVOCs will decrease, mainly due to the activity of photosynthesis. Yu et al. [113] reported that BVOC emissions will increase with global warming, with non-oxygen-containing monoterpenes, oxygen-containing monoterpenes, and sesquiterpenes in *P. sylvestris* seedlings projected to increase by 9 to 64 times with a 1.0 °C temperature rise. In European poplar saplings, a 1.0 °C increase significantly boosted the emission of total monoterpenes and GLV [114]. Temperature also directly causes seasonal and diurnal variations in BVOC emissions. Emissions of isoprene, monoterpenes, and other volatile organic compounds are typically higher in summer when temperature, light intensity, and plant biomass are at their peak [93]. In deciduous broad-leaved forests and coniferous forests, isoprene concentration is highest in summer, while in subtropical evergreen broad-leaved forests, isoprene concentration is higher not only in summer, but also in spring and autumn [115]. Seasonal changes in BVOC emissions are generally smaller in tropical ecosystems than in temperate ecosystems [116].

4.2.2. Illumination

The rate at which plants release isoprene is affected by photosynthetically active radiation (PAR). In dark environments or under low light intensity, the release rate of isoprene in plants is low, and it increases with rising light radiation intensity [117]. Leaf temperature and light can regulate isoprene production by affecting its precursor, γ -dimethylallyl pyrophosphate, and isoprene synthase [6]. Bai et al. [118] monitored the emission flux of volatile organic compounds from subtropical pine plantations in China and observed a strong diurnal change in the emission of isoprene and monoterpene, with lower emissions in the morning and evening and the highest emissions around noon. The peak emission of BVOC usually occurred several hours after the peak of PAR at noon. It was suggested that isoprene and monoterpenes were more closely related to photosynthetically active radiation than temperature or water vapor. The extent of the effects of light intensity on the isoprene emission rate reflected the dependence of isoprene biosynthesis on primary substrate products generated through photosynthesis, such as glucose [100,119]. The experiments conducted by Wang and others also yielded the same conclusion [111].

4.2.3. Water Conditions

The sensitivity of BVOCs released by different plants to changes in humidity varies. Some plants are greatly impacted by changes in humidity, while others are not sensitive to ambient humidity fluctuations. For instance, some coniferous tree species such as *Pinus ponderosa* and *Picea* spp. [10,14,26] have their emissions mainly driven by temperature and light, and are not sensitive to short-term changes in air relative humidity or soil drought. For most tree species, the release rate of BVOCs is proportional to changes in environmental humidity, but for a few tree species, the release rate is inversely proportional to changes in environmental humidity [6]. Li et al. [120] found that drought stress inhibited isoprene emission in *Pinus massoniana*, with the emission rate decreasing by approximately 50%.

In contrast, the emissions of monoterpenes and sesquiterpenes were enhanced, reaching 2.9-fold and 2.0-fold those under non-stressed conditions, respectively. Yang et al. [121] showed that mild drought stimulated isoprene, monoterpene, sesquiterpene, and total BVOC emissions, while moderate and severe drought inhibited emissions. The research conducted by Duan et al. [98] also found that low relative air humidity (RH) or drought would increase the emission rate of monoterpenes.

5. Ecological and Environmental Impacts of BVOCs

BVOCs released by plants have extremely strong chemical reactivity in the atmospheric environment and are key precursor substances for the formation of ground-level O₃ and SOA [122–124]. Relevant studies have shown that there are approximately 30,000 species of BVOCs emitted in nature in a species-specific manner [125], and these compounds, due to differences in chemical structure and reactivity, have lifetimes ranging from several minutes to several hours in the atmosphere [123,126]. Once they enter the atmosphere, they quickly react with various oxidants such as hydroxyl radicals ($\cdot\text{OH}$), O₃, and nitrate radicals (NO₃), thereby triggering complex photochemical and non-photochemical chain reactions [127–129].

Under light conditions, BVOCs first react with $\cdot\text{OH}$ to form alkyl radicals (R $\cdot$). This intermediate product then rapidly combines with oxygen to form organic peroxide radicals (RO₂ $\cdot$). If nitrogen oxides (NO_x) are present in the environment, RO₂ $\cdot$ will react with NO to form NO₂, and NO₂, under ultraviolet light irradiation, photolyzes to produce oxygen atoms (O), which, when combined with oxygen, generate ozone. This typical photochemical process makes BVOCs an important contributor to the formation of near-surface ozone [122]. During the night or under low light conditions, BVOCs react with NO₃. Although this process does not directly generate ozone through photolysis, it can indirectly affect the nocturnal ozone concentration by influencing the cycling process of NO_x [122]. In addition, NO_x also directly affects BVOC emissions by regulating the plant metabolic pathways. Relevant studies have shown that when the concentration of NO₂ increases, it will induce the expression of enzyme genes related to terpene compound synthesis in plants, thereby promoting the release of monoterpenes and sesquiterpenes and other substances—this is a defense mechanism that plants activate in response to oxidative stress [74,130]. However, it should be noted that if plants are exposed to high concentrations of NO_x for a long time, it may lead to impaired metabolic functions or decreased enzyme activity, ultimately inhibiting BVOC emissions and even changing their composition [130].

In addition to participating in the aforementioned free radical reactions, terpenoid compounds containing carbon-carbon double bonds (such as α -pinene, β -pinene, and isoprene, etc.) can also directly undergo addition reactions with ozone. These reactions will generate unstable primary ozonolysis products (POZs), which rapidly decompose into carbonyl products and Criegee intermediates (CIs). The latter further react to form oxidative products such as organic acids, aldehydes, and peroxides. These reactions not only consume BVOCs but also release heat and trigger a series of secondary reactions that promote ozone formation [123].

Numerous studies have clearly demonstrated the significant role of BVOCs in the formation of near-surface ozone [131,132]. For instance, Calfapietra et al. [18] and Fitzky et al. [16] pointed out that with global warming, the sensitivity of urban tree species' BVOC emissions to changes in ozone concentration will significantly increase, and the role of plants in the ozone formation process will become increasingly crucial. Wu et al. [94] demonstrated that, during China's summer, plant BVOC emissions can lead to an increase in ozone concentration to rise by up to 47 ppb·m^{−3}. Through field monitoring,

Matsuno [133] discovered that ozone concentration is significantly positively correlated with BVOC (especially monoterpenes) content, and this correlation can even be used to predict the emission levels of BVOCs. By using satellite observation, Wang et al. [87] also found that in areas with high vegetation coverage, ozone concentration is significantly positively correlated with the emissions of BVOCs such as isoprene, suggesting that when making urban greening policies, we must fully consider the potential environmental impact of BVOC emissions.

Meanwhile, BVOCs are also important precursors for the formation of SOA. The low-volatility products generated by their oxidation degradation (such as organic acids, alcohols, nitrate esters, organic sulfates, etc.) are highly prone to undergoing condensation or reacting with aerosol particles, thereby generating secondary organic aerosols [122,124]. A large number of experimental studies have shown that the molecular structure and emission composition of BVOCs directly affect the nucleation rate and particle size growth process of SOA. For example, the plant system dominated by monoterpenes (such as the Homok community) has a stronger particle generation potential compared to the plant system dominated by sesquiterpenes (such as loquat pine, cypress pine, etc.) [134]. Tunved et al. [135] confirmed through long-term field observations that the emission of monoterpene BVOCs can increase the number of condensation nuclei by 1000 to 2000 per cubic centimeter in the forest air, which has a profound impact on regional climate processes. In addition, BVOCs containing abundant oxygen groups (such as 3-hexenol, methyl salicylate, etc.) are more likely to promote the formation of new particles during photolysis, further enhancing the formation capability of SOA [136].

6. Discussion and Prospect

The VOC emissions from plants play a crucial role in shaping atmospheric environmental quality. Additionally, it plays a significant role in the carbon budget pathway within the terrestrial ecosystems' carbon balance. Therefore, studying the emission inventory of VOCs, as well as their ecological and environmental impacts, is of critical importance. This paper presents the cutting-edge observation technologies for BVOC emissions and provides a comprehensive review of research advancements in this field. Based on this systematic review, we emphasize the following key priority areas as crucial directions for future research:

(1) *The BVOC emission inventory has yet to be clarified*

Figure 1 illustrates the substantial variation in estimated annual global emissions of BVOCs reported by different studies, ranging from 175 Tg to 1145 Tg C [20,42,44,68–77]. It is evident that before around 1995, the total reported BVOC emissions exhibited a consistent annual increase, aligning with the findings that global warming and rising CO₂ concentrations enhance BVOC emission rates. However, after 1995, there is a clear downward trend in the reported values. The possible reasons for this change mainly include the following aspects: Firstly, the emergence of new observation technologies enables people to measure and understand the emission factors of trees more precisely, thereby obtaining assessment results that are closer to the true values. Secondly, the introduction and application of new models enhance the accuracy and reliability of emission estimation. Notably, in the previous studies, Guenther and MEGAN models were widely used, and their estimated values were generally higher than those of other models. Thirdly, human-induced land use changes have played a significant role in the observed decline in global isoprene emissions during the 21st century. This decline is attributed to the direct impacts of deforestation, agricultural expansion, and urbanization on vegetation cover. Finally, the change in the composition of natural vegetation, especially the reduction in the proportion of certain species with

strong release capacity of monoterpene, is an important natural factor contributing to the declining trend of monoterpene emissions.

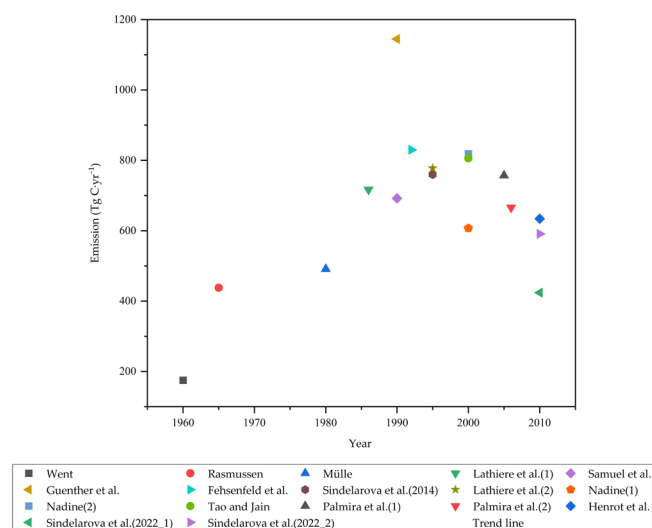


Figure 1. Summary of global annual BVOC emission inventory [20,42,44,68–77].

Additionally, extensive literature exists on the annual emissions of the two primary BVOC components, isoprene and monoterpene, with reported ranges of 299.1–800 Tg C and 24–184 Tg C [8,42,44,68–71,76,77,79,81,83,84,86,137], respectively (refer to Figure 2). In terms of reported values for isoprene, which accounts for the absolute majority of BVOC emissions, we also observe similar dynamic changes as with the total emissions. Hence, the BVOC emission inventory and the reasons behind its changing trend are worth further exploration.

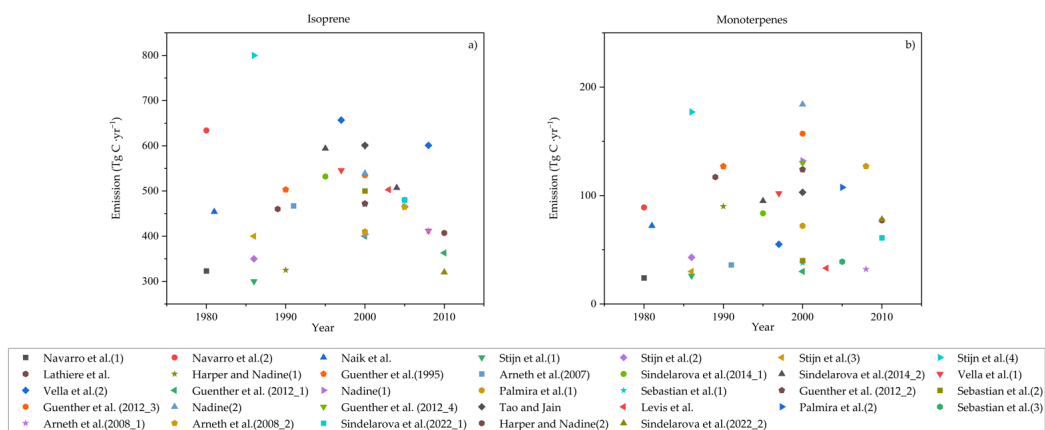


Figure 2. Global annual emission inventory of isoprene (a) and monoterpenes (b) [8,42,44,68–71,76,77,79,81,83,84,86,137].

Climate change poses a challenge to the scientific evaluation of BVOC emissions. Factors such as warming, drought, increasing carbon dioxide concentrations, and ozone levels all exert influence on the release of BVOCs. For example, rising temperatures can lead to exponential increases in emission rates for most BVOCs, supported by most studies indicating that medium- to long-term warming will result in elevated BVOC emissions [11,113]. Furthermore, the increase in temperature may also disrupt the balance between heat and drought (heat–drought balance), intensify evapotranspiration, lead to soil moisture loss, thereby enhancing the drought stress effect, and further influence the emission pattern of BVOC. The effects of drought stress on plant BVOC emissions remain

subject to debate [138], though most researchers believe that BVOC emissions could be depressed under prolonged drought conditions [139]. Elevated CO₂ concentrations tend to enhance BVOC emissions [140,141], although some studies have shown that CO₂ inhibits terpenoid emissions [142]. Similarly, moderately elevated ozone concentrations can increase terpenoid emissions from conifers [143] but inhibit the emission of isoprene [142]. The impact of ozone also depends on other global change components, such as drought, which induces lower stomatal conductance in plants, thereby reducing ozone absorption and diminishing ozone-induced GLV emissions [144].

What is even more complex is that plants may also respond to high concentrations of BVOCs in the environment through self-regulation mechanisms. For instance, in an environment with high concentrations of isoprene, plants may inhibit their own emissions through negative feedback mechanisms, such as reducing the expression of isoprene synthase or reallocating carbon resource priorities to limit further BVOC synthesis [145]. Thus, the interaction between climate change factors and BVOCs not only stems from the direct impact of environmental stress, but also involves the complex regulatory network within plants. This multi-factor interwoven feedback system undoubtedly increases the difficulty of predicting future BVOC emission patterns and poses higher requirements for related scientific assessments.

The emergence of online monitoring technology has facilitated the assessment of BVOC emission factors and mechanisms. The PTR-TOF-MS, an effective tool for measuring a wide range of BVOCs, enables real-time concentration measurements and the calculation of dynamic BVOC emission rates. Its high temporal resolution allows for a more profound understanding of BVOC emission dynamics. Furthermore, the PTR-TOF-MS's ability to simultaneously detect a broad range of mass-to-charge ratios and distinguish isobaric compounds based on isotopic patterns allows for the qualitative and quantitative analysis of a wider variety of BVOC species [146], while minimizing interference from other compounds. The proton reaction theory enables accurate mass identification, and when the instrumental settings and operating conditions of the TOF-MS remain stable over time—such as during continuous measurements within the same day—recalibration is not required for each run, thereby reducing experimental time when high-precision quantification is not essential.

The development and application of new mechanisms and robust models have significantly improved the accuracy of BVOC emission inventory estimations. For example, the MEGAN model, commonly used to simulate global BVOC emissions, continues to be enhanced through the incorporation of new parameters and quantitative algorithms, which are integrated into large-scale computer models [8,26,44,69,70,78,147,148]. Despite these advancements, the complexity of BVOC emission mechanisms and processes still leads to notable discrepancies between simulated and observed values, introducing uncertainty into regional and global emission estimates. Additionally, the selection of assessment models further contributes to this uncertainty. Regardless of improvements in physical frameworks or theoretical foundations, accurately determining vegetation-based emission factors and scientifically interpreting the relationship between plant emission intensity and climatic and environmental drivers remains critical. Therefore, further research is necessary to deepen our understanding of BVOC emission processes and their driving mechanisms across different vegetation types and under various climate change scenarios.

(2) *The climatic and environmental impacts of BVOCs needs to be further explored*

Biogenic volatile organic compounds play an important role in global environmental chemistry and climate. While their local atmospheric chemical effects are becoming increasingly apparent, further investigation is required to fully elucidate their potential climate impact. Once released into the atmosphere, BVOCs exhibit high chemical reactivity with other atmospheric gases and are readily oxidized by atmospheric oxidants such as ozone,

OH, and nitrate (NO_3^-) radicals. This oxidation results in the condensation of some oxidation products on existing aerosol particles, forming small aerosol particles [149]. Given the strong size dependence of aerosol scattering coefficients, this process is anticipated to increase the proportion of diffuse solar radiation. The resultant increase in diffuse radiation, in turn, promotes plant photosynthesis by providing more light to the shaded areas of forest canopies.

In boreal forest environments, the secondary organic aerosols formed by BVOCs often dominate the aerosol particle number concentration, significantly impacting aerosol light scattering [135,150]. These aerosol particles contribute to cooling the climate by scattering solar radiation and serving as cloud condensation nuclei. Furthermore, increased temperatures have been linked to elevated BVOC emissions, resulting in higher concentrations of biogenic secondary organic aerosols and cloud condensation nuclei, creating a negative climate feedback mechanism [151]. Nevertheless, further exploration is needed to determine how its impact can be quantitatively evaluated through coupling with climate models.

(3) *The role of BVOCs in the carbon cycle of terrestrial ecosystems needs to be further investigated*

Traditionally, studies examining the interactions between terrestrial ecosystems and the global climate system have focused predominantly on CO_2 as the central mediator of biosphere-atmosphere carbon exchange [152]. Nowadays, BVOCs have garnered increasing attention due to their notable role in mediating carbon fluxes between the terrestrial ecosystem and the atmosphere.

It is estimated that approximately 1% of the annual carbon assimilated by terrestrial ecosystems is re-emitted to the atmosphere in the form of BVOCs [71]. This fraction, though seemingly small, constitutes a non-negligible component of the net ecosystem carbon balance (NECB), considering that it flows one-way from terrestrial ecosystems to the atmosphere [153]. Vegetation-derived BVOCs, such as isoprene and monoterpenes, are synthesized using carbon fixed during photosynthesis [154]. Once released, this carbon re-enters the atmosphere, effectively bypassing respiratory pathways. On a global scale, emissions of BVOC carbon are estimated to reach 1150 teragrams per year, highlighting their substantial contribution to atmospheric carbon cycling [155]. However, discrepancies in species-specific emission factors—sometimes varying by orders of magnitude across studies—limit the accuracy of global assessments. The omission of BVOC fluxes from carbon budget analyses risks underestimating carbon losses and mischaracterizing regional and global sink strengths [144,156]. This gap is particularly relevant in reconciling top-down estimates from atmospheric CO_2 inversion models with bottom-up flux measurements obtained from ground-based monitoring networks. As BVOCs constitute a significant portion of what are termed minor carbon flows (MCFs)—relatively small but cumulatively important carbon exchanges such as those from wildfires, land-use changes, and non- CO_2 gaseous emissions—their inclusion is essential to improving the accuracy of global carbon accounting [157].

In light of the above-mentioned three topics, the development of a comprehensive, species-specific BVOC emission inventory—one that integrates both environmental and physiological drivers—represents a critical step toward enhancing our understanding of the significance of BVOC emissions. For example, current BVOC inventories primarily focus on isoprene and monoterpenes, relegating many other BVOCs to minor roles. Consequently, available emission data for numerous other BVOCs are rare or roughly estimated. Furthermore, the few considerations of BVOC release from agricultural crops or grasslands, and hence underestimate the release from such areas, disregarding their significant contribution. However, field investigations have demonstrated that certain crops, like sunflowers, emit substantial amounts of monoterpenes [158].

Therefore, in order to accurately assess annual VOC releases from vegetation, a comprehensive understanding of emission characteristics for all species and their regulation is crucial. While models provide valuable assistance, field measurements, coupled with concurrent physiological assessments such as CO₂ exchange and transpiration, are indispensable. Such efforts will help bridge existing data gaps and enable more precise predictions of biosphere-atmosphere interactions under changing environmental conditions.

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