

Review Article

Biological and Chemical Diversity of Biogenic Volatile Organic Emissions into the Atmosphere

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Received 13 March 2013; Accepted 20 May 2013

Academic Editors: P. Massoli, K. Schaefer, and E. Tagaris

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Biogenic volatile organic compounds (BVOC) emitted by terrestrial ecosystems into the atmosphere play an important role in determining atmospheric constituents including the oxidants and aerosols that control air quality and climate. Accurate quantitative estimates of BVOC emissions are needed to understand the processes controlling the earth system and to develop effective air quality and climate management strategies. The large uncertainties associated with BVOC emission estimates must be reduced, but this is challenging due to the large number of compounds and biological sources. The information on the immense biological and chemical diversity of BVOC is reviewed with a focus on observations that have been incorporated into the MEGAN2.1 BVOC emission model. Strategies for improving current BVOC emission modeling approaches by better representations of this diversity are presented. The current gaps in the available data for parameterizing emission models and the priorities for future measurements are discussed.

1. Introduction

Terrestrial ecosystems produce and emit many biogenic volatile organic compounds (BVOCs) into the air where they influence the chemistry and composition of the atmosphere including aerosols and oxidants [1–3]. These BVOCs are produced by a variety of sources in terrestrial ecosystems (e.g., flowers, stems, trunks, roots, leaf litter, soil microbes, insects, and animals), but most of the global total emission is from foliage [4–6]. The increasing awareness of the importance of these emissions for earth system modeling has resulted in numerical models of regional air quality and global climate that now routinely include BVOC emissions that are estimated as a function of landcover and environmental driving variables. This is a considerable challenge due to both the hundreds of different BVOC chemical species emitted into the atmosphere [7, 8] and the vast differences in the capacity of various plant species to produce and emit terpenoids and other BVOCs [9, 10]. Furthermore, an individual compound can be emitted by different ecosystem sources that are controlled by a variety of processes. Some compounds are stored in plant tissues that are isolated from the atmosphere and are emitted only if these tissues are damaged, while other compounds are stored in structures

that are open to the atmosphere and are continuously being emitted [11]. There are additional compounds that are not stored in tissues but instead are released immediately after production which may happen only in response to stress or specific environmental conditions [12].

Quantitative attempts to account for these BVOC emissions in models must consider all of the processes that control emission variability. Among the greatest of these challenges is characterizing the enormous diversity in BVOC emission types in ecosystems across the world. This paper provides an overview of our current understanding of the chemical and biological diversity of BVOC emissions into the atmosphere. Section 2 describes a compilation of observations in the scientific literature that have been used to quantify BVOC emissions in a widely used numerical model, the Model of Emissions of Gases and Aerosols from Nature (MEGAN) [5], and considers the suitability of these observations for characterizing regional to global BVOC emissions. The known chemical diversity of BVOC emissions is summarized in Section 3, and an approach for improving the representation of this diversity in numerical models is described. BVOC biological diversity is discussed in Section 4, and a framework for better representation of BVOC emission diversity types is presented. Section 5 presents the major conclusions of this

summary of our current understanding of the chemical and biological diversity of BVOC emissions.

2. BVOC Emission Observations and Models

Quantitative estimation of global BVOC emissions into the atmosphere began with Went's [13] seminal work that extrapolated measurements of a single group of compounds, monoterpenes, from a single plant species, *Artemisia tridentata*, to the entire earth. Rasmussen [9] recognized the great diversity in BVOC emission capacities of different plants species and introduced an approach for classifying the biosphere into different vegetation groups in order to quantify regional emissions. He noted that at least some vegetation types had "fingerprints" that could be used to represent the emission behavior of those plant species. He combined estimates of USA areas of different forest types (e.g., Loblolly-shortleaf pine forest, oak-gum-cypress forest) with observations of their representative emission rates in order to quantify total BVOC emissions on a USA national and on a global scale. Zimmerman [14] extended this approach using more comprehensive land cover data including broad natural vegetation types (e.g., shrub and brush rangeland, deciduous forest, and mixed forest), agricultural lands (e.g., crops, pasture, and orchards), and a category for residential areas. This approach was limited by the large differences in the emission rates of plant species in landscapes that, for example, are classified as deciduous forest or mixed forest because of the highly variable emission rates of these broad categories of vegetation. Zimmerman made additional progress towards accounting for this by collapsing USA forests into four types: high isoprene (e.g., oak) deciduous forest, low isoprene (e.g., sycamore) deciduous forest, no isoprene deciduous (e.g., maple), and coniferous forest (e.g., loblolly pine). Lamb and colleagues [15] refined this approach using higher resolution (county scale) landcover data that included land area planted with the major crop species. This approach was extended to the global scale [16, 17] by assigning emission factors to ecosystem types in global gridded databases. This was straightforward for categories dominated by a few species (e.g., paddy rice and mangrove) but not for most categories (e.g., farm/city-cool, temperate mixed, and dry evergreen) which did not represent a uniform BVOC emission type. For regions with detailed plant species data, the Biogenic Emission Inventory System 2 (BEIS2) [1] was developed to apply BVOC emission factors for individual tree genera and crop types. However, these data were only available for forests in some regions, and BEIS2 used broad categories for grassland and shrubland ecosystem types.

The MEGAN version 2.1 (MEGAN2.1) [5] BVOC emission model assigns emission factors and parameters to 19 BVOC chemical compound classes for each of the 15 plant functional types (PFTs) used for the Community Land Model (CLM4) [18]. MEGAN2.1 can be run embedded in CLM4 and can also run offline using observations or variables from other models. BVOC emission rate measurements from about 300 studies were synthesized to estimate the emission factors used for MEGAN2.1 including data representative of the major

global vegetation types. Measurements representing temperate landscapes are compiled in Table 1 [19–186]. Studies in tropical and boreal landscapes are summarized in Tables 2 [187–229] and 3 [230–268], respectively. Measurements characterizing BVOC emissions from agricultural crops are compiled in Table 4 [70, 269–282]. Terpenoid (e.g., isoprene, MBO, and monoterpene) emission factors were estimated for each of the 15 PFTs. For most of the other compounds, one or a few (e.g., one for woody PFTs and one for herbaceous PFTs) emission factors were used for all PFTs. Terpenoid emission factors are represented with a greater diversity in MEGAN2.1 both because of the greater actual diversity and because more observations have been reported.

Until recently, most BVOC emission measurements were conducted using enclosure techniques, but whole canopy flux measurements using micrometeorological approaches are now becoming more common [215]. Characterizing BVOC emissions with enclosure measurements is challenging due to difficulties in accessing all parts of a mature forest canopy and because of the presence of storage structures which can be disturbed resulting in emissions at rates much higher than for undisturbed conditions [283]. These issues resulted in BVOC emission factors reported by earlier studies that greatly underestimate isoprene emissions, because isoprene emission rates are lower for the shaded leaves in the more easily accessed portion of a forest canopy, and overestimate monoterpene emissions because of disturbances to terpenoid storage structures [284]. The above-canopy flux measurements integrate over the entire canopy and landscape without disturbing emission rates [86]. Capabilities for quantifying biogenic VOC fluxes have steadily improved over the past decades including recent analytical advances such as the time-of-flight proton-transfer reaction mass spectrometer (PTR-TOF-MS) that enables whole canopy measurement of a wide range of BVOC fluxes [285]. Aircraft VOC flux systems have footprints of several km and can characterize fluxes over entire domains of hundreds of km and so are suitable for evaluating fluxes estimated by regional models [286]. Tower-based VOC flux systems typically have a footprint of hundreds of meters and are well suited for quantifying diurnal, seasonal, and interannual variations. Biogenic VOC fluxes have been measured at more than 45 tower locations (Tables 1 to 4 and summarized in [287, 288]), but most of these studies were for a short period (a few weeks or less) of time. The availability of more than 500 above-canopy flux towers constructed for water, carbon, and energy flux studies provides an opportunity to add biogenic VOC measurements without the cost of basic site development [289]. Measurements at a large number of sites can be accomplished with low-cost and low-power relaxed eddy accumulation measurements systems [238].

Figure 1 shows that there were relatively few BVOC emission rate observations reported in the 1960s and 1970s, and all but one of these studies were in temperate regions. Interest in the role of BVOC emissions in regional ozone pollution in the 1970s [9] stimulated publications on this topic by the early 1980s including some investigations of tropical, boreal, and agricultural ecosystems. This interest peaked in the mid-1980s and then declined as some researchers

TABLE 1: Compilation of studies used to estimate temperate vegetation BVOC emission factors for the MEGAN2.1 model [5]. Emission measurement approaches include enclosure (E), canopy micrometeorological (C), and landscape inverse modeling (L) techniques. Compounds include isoprene (Iso), monoterpenes (MT), sesquiterpenes (SQT), and other (Other). PFTs include broadleaf deciduous shrub (BDS), broadleaf evergreen shrub (BES), broadleaf deciduous tree (BDT), C3 grass (C3G), and needleleaf evergreen tree (NET).

Location	Approach	Compounds	PFTs	Reference
MI, USA	C	Iso	BDT	[19]
NC, USA	C	MT	NET	[20]
N T, Australia	L	Iso	BDS, BES	[21]
CO, USA	E	MT, SQT, and Other	BDT	[4]
Inner Mongolia, China	E	Iso, MT	C3G	[22]
CA, USA	C	MBO	NET	[23]
Various, USA	C	MBO, Other	NET	[24]
Austria	C	Other	C3G	[25]
NY, USA	E	MT	BES	[26]
Portugal	L	Iso, MT	BET	[27]
Various, Canada	L	Iso	BDT, NET	[28]
Potted plants	E	MT, SQT, and Other	BDS, BDT, BES, BET, and NET	[29]
FL, USA	E	Iso	BET	[30]
Potted plants	E	Other	NET	[31]
WI, USA	E	Iso	BDT	[32]
UK	E, C	Iso, MT	BES	[33]
Hangzhou, China	E	Iso, MT	BDT, BET, and NET	[34]
Italy	E, C	Iso, MT	BES, BET	[35]
Spain	E, C	MT, SQT	BET	[11]
CA, USA	E	Iso, MT	BDT, BET, and NET	[36]
Italy	C	Iso, MT, and Other	BDS, BES	[37]
Potted plants	E	MT	BES	[38]
CO, USA	C	Other	NET	[39]
Germany	E	MT	BDT	[40]
Mexico	E	Iso, MT	BDT, NET	[41]
MA, USA	L	Iso, Other	BDT	[42]
Potted plants	E	Iso, MT	BDS, BDT, BES, BET, C3G, and NET	[43]
CA	C	MT, SQT, and Other	BET	[44]
Potted plants	E	Other	BDT, BET, and NET	[45]
ON, Canada	C	Iso, MT	BDT	[46–48]
IL, USA	E	Other	C3G	[49]
Zhejiang, China	L	Iso, MT	BDT, NET	[50]
NC, USA	E, C	Iso	BDT	[51]
Various, USA	E	Iso, MT	BDT, BET	[52–54]
CO, USA	L	MBO	NET	[55]
MA, USA	C	Other	BDT	[56]
MA, USA	C	Iso	BDT	[57]
Various, USA	L	Iso, MT	BDT, NET	[58]
CO, USA	E	MT, Other	C3G	[6]
Potted plants	E	Iso, MT	BDT, BET	[59, 60]
NC, USA	C	Iso	BDT	[61]
Various, USA	E, L	Iso, MT	BDS, BDT, BES, and NET	[62–64]
TX, USA	E, C, and L	Iso, MT	BDS, BDT, and BES	[65]
Various, USA	E	Iso, MT	BDT	[66, 67]
CA, USA	E	MBO	NET	[68]
South Africa	E, C	Iso, MT	BDS, BDT, and BES	[69]
Potted plants	E	Other	BDT, C3G, and NET	[70]

TABLE 1: Continued.

Location	Approach	Compounds	PFTs	Reference
Greece	E, L	Iso, MT	NET	[71]
Potted plants	E	MT	BET	[72]
Potted plants	E	Other	NET	[73]
Various, USA	E	MT, SQT	BDT, BES, BET, and NET	[74]
Various, USA	E	MT, SQT	NET	[75, 76]
ID, USA	L	MT	NET	[77]
CA, USA	C	MT	NET	[78]
Germany	E	MT, SQT	NET	[79]
Shenzhen, China	E	Iso, MT	BDS, BDT, BES, BET, C3G, and NET	[80]
WI, USA	E, C, and L	Iso, MT	BDT, C3G, and NET	[81]
Russia	E	Iso, MT, and Other	NDT, NET	[82]
Various, USA	E, C	Other	BDT, NET	[83, 84]
AZ, USA	E, L	Iso, MT, and Other	BES	[85]
CO, USA	C	Iso, MT, Other, and MBO	NET	[86]
MI, USA	C	Iso, MT, and Other	BDT, NET	[87]
CA, USA	C	MT, SQT, and Other	BDT	[88]
CA, USA	E	Iso, MT	BDS, BDT, BES, BET, C3G, and NET	[89]
Italy	E	Iso, MT, and Other	BET	[90, 91]
France	E	Iso, MT	BDT, BET	[92]
Potted plants	E	Other	BDT	[93]
FL, USA	E	MT	NET	[94]
Republic of Korea	E	MT	NET	[95]
MI, USA	C	SQT	BDT	[96]
CO, USA	E, L	MT, SQT, and Other	NET	[97]
MI, USA	E	Iso, MT, SQT, and Other	BDT, NET	[98]
Republic of Korea	L	Iso, MT, and Other	BDT, NET	[99]
VIC, Australia	E	Other	C3G	[100]
Various, China	E	Iso, MT	BDS, BDT, BES, BET, C3G, and NET	[101]
Potted plants	E	Other	BDT, C3G	[102]
Potted plants	E	Other	BDT	[103]
Switzerland	E	Other	BET, BDT	[104]
Various, USA	E, C	Iso, MT	BDT, NET	[105]
WA, USA	E, C	Iso	BDT	[106]
OR, USA	E	MT	NET	[107]
Potted plants	E	MT	NET	[108]
Shenyang, China	E	Iso, MT	NET	[109]
Republic of Korea	E	Iso	BDT, BET	[110]
Potted plants	E	Iso	BDT	[111]
Spain	E	MT	BET	[112]
FL, USA	C	Iso, MT	NET	[113]
Potted plants	E	Iso	BDT	[114]
Various, USA	E	Other	BDS, BDT, and NET	[115, 116]
MI, USA	E	MT	C3G	[117]
PA, USA	L	Iso	BDT	[118]
NM, USA	E	Iso, MT, and Other	BDT, BET, NET	[119]
Various, USA	C	Other	BDS, BDT, and BES	[120]
US, Japan, and Australia	E	SQT	BDS, BDT, BES, and BET	[121]
Japan	E	Iso, Other	NET	[122, 123]
MA, USA	C	Iso, MT, and Other	BDT	[124]
Potted plants	E	Iso	BDT	[125]
CO, USA	E	Iso	BDT	[126]

TABLE 1: Continued.

Location	Approach	Compounds	PFTs	Reference
France	E	Iso	BDT	[127]
Estonia	E	Iso	BDT	[128, 129]
Portugal	E	Iso, MT	BET	[130]
Japan	E	Iso	BET	[131]
Spain	E	MT, SQT	BES, BET, and NET	[132]
MI, USA	E	Iso, MT, and SQT	BDT, NET	[133]
Various, USA	E	Iso, MT, and SQT	BDT, BET, and NET	[134]
Zambia, Botswana	E	Iso, MT	BDS, BDT, BES, and BET	[135]
Italy, France, Spain	E	Iso, MT	BDS, BDT, BES, BET, and NET	[136, 137]
NV, USA	E	Iso, MT, and SQT	BDS, BDT, BES, BET, and NET	[138]
Potted plants	E	Iso	BET	[139]
Spain	E	Iso, MT	BET	[140]
Potted plants	E	Iso	BDT	[141]
AL, USA	E	Iso	BDT	[142, 143]
Portugal	E	MT	NET	[144]
Belgium	E	Iso, MT, and Other	BDT, NET	[145, 146]
WA, USA	E	MT	NET	[147]
MI, USA	C	Iso	BDT	[148]
Austria	L	Other	C3G	[149]
Italy	E	Iso, MT	BDT, BET	[150]
Various, USA	E	Iso	BDT, BET, and NET	[151]
Various, USA	E, L	Iso, MT	BDT, BET, C3G, and NET	[152]
CA, USA	E	Other	C3G	[153]
CO, USA	L	MT	BDT, NET	[154, 155]
Potted plants	E	Iso, MT	BDT	[156]
Potted plants	E	Other	NET	[157]
Potted plants	E	Other	BDT, NET, and C3G	[158]
CA, USA	C	MBO, Other	NET	[159]
Potted plants	E	MT, Other	BET	[160]
NC, USA	E	Iso	BDT	[161]
Various, USA	E	Iso	BDT	[162]
Nepal	L	Iso, MT	NET, BDT, and C3G	[163]
Georgia, USSR	E, L	Iso, MT	BDT, NET	[164]
Belgium	E	MT, Other	BDT	[165]
Various, USA	L	Other	BDT, NET	[166]
Germany	C	Iso, MT, and Other	BDT	[167]
Potted plants	E	MT	BET	[168]
Germany	C	Iso, MT	BDT, NET	[169]
Japan	E	Iso	BDT, BET	[170]
Japan	C	MT	NET	[171]
Potted plants	E	Iso	BET	[172]
Potted plants	E	MT	NET	[173]
Greenhouse	E	Iso, MT	BET, BDT	[174]
Inner Mongolia, China	E	Iso, MT	C3G	[175]
Various, USA	L	Iso, MT	BDT, NET	[176]
France	E	Iso, MT	BDT, BET	[177]
Potted plants	E	MT	BES	[13]
MI, USA	C	Iso	BDT	[178]
TX, USA	L	Iso, MT	NET, BDT	[179]
Various, USA	L	Iso, MT	BDT, C3G	[180]
WA, Australia	E	Iso, MT, and Other	BET	[181]

TABLE I: Continued.

Location	Approach	Compounds	PFTs	Reference
Beijing, China	E	Iso, MT	BDT	[182]
Potted plants	E	Other	NET	[183]
Japan	L	MT	NET	[184]
Potted plants	E	MT	NET	[185, 186]
Various, USA	E	Iso, MT, and Other	BDS, BDT, BES, BET, C3G, and NET	[14]

concluded that BVOC emissions did not have an important role in regional air quality [290]. An improved understanding of the magnitude of BVOC emissions and the relatively high sensitivity of ozone to BVOC emissions demonstrated that this was not the case [291, 292] and led to a resurgence in BVOC emissions research in boreal, tropical, and agricultural ecosystems in the 1990s. Interest in tropical landscapes was driven by the recognition that the tropics are responsible for 80% of global emissions [17]. There was initially little interest in BVOC from agricultural ecosystems because of the generally low terpenoid emissions from these plant species, but the discovery of substantial amounts of oxygenated VOC emissions from crops [102, 115] led to more studies. The annual publication rate decreased in the mid-2000s, but there has been a recent increase in the number of publications. This has likely been driven by the recognition of the important role of BVOC in secondary organic aerosol production [3, 293].

Figure 2 shows that temperate, tropical, and boreal ecosystems each cover 25 to 35% of the global vegetation-covered land surface with croplands covering the remaining 15%. This figure also shows that although the estimated global BVOC emission is dominated by tropical ecosystems, most studies have focused on temperate ecosystems. Needleleaf trees, broadleaf trees, shrubs, grass and crops each cover 10 to 30% of the global vegetation-covered land area but broadleaf trees are estimated to contribute nearly 80% of the emissions (Figure 3). Investigations of BVOC emission have generally focused on the important emission sources although broadleaf trees are somewhat understudied. Figure 2 shows that isoprene contributes about half of total emissions and was also investigated in about half of these studies. In contrast, other VOC are 36% of the estimated emissions and were examined in only ~20% of the studies. Recent studies provide some balance with relatively more investigations in the tropics and measurements of other VOC (Figure 1).

3. BVOC Chemical Diversity

Terrestrial ecosystems produce thousands of chemical species that can be emitted into the atmosphere [294] but only a few of these compounds are emitted at the rates required to have a significant impact on atmospheric composition [5]. Most of these chemicals are organic compounds including some that contain oxygen, nitrogen, sulfur, or halogens. Biogenic emission models often reflect this dominance by including only a few major compounds, such as isoprene and α -pinene, and omitting the rest or including them as a generic undefined “other” category. More recently, the

MEGAN2.1 biogenic emission model [5] was developed to estimate emissions of 147 compounds that were thought to be significant or potentially significant. This section describes BVOC chemical diversity and potential improvements over the MEGAN2.1 scheme.

3.1. Terpenoid Compounds. Terpenoid compounds have long been considered the dominant global BVOC [9]. This incredibly diverse group includes thousands of chemical species that can be classified as hemiterpenoids (C₅), monoterpenoids (C₁₀), sesquiterpenoids (C₁₅), homoterpenes (C₁₁ and C₁₆), diterpenoids (C₂₀), and larger compounds with such low volatility that it is unlikely that they are emitted into the atmosphere in a gaseous form. Terpenoids include oxygenated terpenes such as the hemiterpenoid methylbutenol (MBO), the monoterpene linalool, and the sesquiterpenoid cedrol. These oxygenated terpenoids are a small portion of the global total terpenoid emission but may be important in some regions. About half of the 147 BVOC species included in MEGAN2.1 are terpenoid compounds including some that are major contributors to global BVOC emissions (e.g., isoprene, α -pinene) and others that are minor components.

Investigations of BVOC began centuries ago with interest in commercial applications for monoterpenes in the flavor and fragrance industries. These activities led to the development of diverse analytical techniques and a considerable body of the literature describing terpenoid production and distribution in the oleoresins stored within plant tissues. Very little of this information has been incorporated into BVOC emission models because the production of monoterpenes by plants and their release into the atmosphere are not always well correlated, and only a small fraction of the hundreds of monoterpene compounds identified in essential oils have been observed as significant atmospheric BVOC emissions. Some monoterpenoids are oxygenated compounds including some multifunctional oxygenates and acetylated compounds that may make a disproportionate contribution to secondary aerosol production. Early studies indicated that a few monoterpenes (α -pinene, β -pinene, limonene, sabinene, 3-carene, and myrcene) dominated the total monoterpene flux into the atmosphere [284]. However, these studies typically did not attempt to measure all compounds, and some monoterpenes may have been reported more frequently simply because these were the only compounds targeted. It was initially thought that all monoterpenes emanated from storage pools and were controlled only by leaf temperature. The discovery of high emission rates of light-dependent monoterpene emissions, produced from recently synthesized carbon in a manner similar to isoprene,

TABLE 2: Compilation of studies used to estimate tropical vegetation BVOC emission factors for the MEGAN2.1 model [5]. Emission measurement approaches include enclosure (E), canopy micrometeorological (C), and landscape inverse modeling (L) techniques. Compounds include isoprene (Iso), monoterpenes (MT), and other (Other). PFTs include broadleaf deciduous tree (BDT), broadleaf evergreen tree (BET), and warm C4 grass (C4G).

Location	Scale	Compounds	PFTs	Reference
Yunnan, China	C	Iso, MT	BDT	[187]
Malaysia	E, L	Iso, MT	BDT, BET	[188]
AM, Brazil	L	Iso, MT	BDT, BET	[189]
Venezuela	L	Iso	C4G	[190]
Costa Rica	E, C	Iso, MT, and Other	BDT, BET	[191]
AM, Brazil	C	Iso, MT	BDT, BET	[192]
CAR	L	Iso	BDT, C4G	[193]
Botswana	C	MT	BDT	[194]
Various, Brazil	L	Iso, MT	BDT, BET	[195]
Guyana	L	Iso	BDT, BET	[196]
South Africa	E	Iso, MT	BDT, BET	[197]
Various, Brazil	E	Iso, MT	BDT, BET	[198]
Peru	L	Iso, MT	BDT, BET	[199]
Venezuela	L	Iso, MT, and Other	C4G	[200]
Costa Rica	C	Iso, MT, and Other	BDT, BET	[201]
AM, Brazil	C	Iso, MT, and Other	BDT, BET	[202]
AM, Brazil	C	Iso, MT, and Other	BDT, BET	[203]
Panama	E	Iso	BDT, BET	[204]
AM, Brazil	L	Iso, MT	BDT, BET	[205]
RO, Brazil	E, C	Iso, MT, and Other	BDT, BET	[206]
Cameroon, CAR, and Congo	E	Iso, MT	BDT, BET	[207]
Yunnan, China	E	Iso, MT	BDT, BET	[101]
RO, Brazil	E	Iso, MT	BDT	[208]
AM, Brazil	E	Iso, MT	BDT, BET	[209]
AM, Brazil	C	Iso, MT	BDT, BET	[210]
Sabah, Malaysia	C	Iso, MT, and Other	BDT, BET	[211, 212]
Potted plants	E	Iso, MT	BDT, BET	[213]
Sabah, Malaysia	C	Iso, MT, and Other	BET	[214, 215]
PA, Brazil	C	Iso, MT	BDT, BET	[216]
Potted plants	E	Iso	BDT, BET	[217]
India	E	Iso	BDT, BET	[218]
Panama	E, L	Iso	BDT, BET	[151]
AM, Brazil	L	Iso	BDT, BET	[219]
PA, Brazil	C	Iso, MT	BDT, BET	[220]
Malaysia	E, L	Iso, Other	BDT, BET	[221]
Venezuela	L	Iso	C4G	[222]
Benin	E, L	Iso, MT	BDT, BET	[223]
Congo	C	Iso	BDT, BET	[224]
India	E	Iso	BDT, BET	[10]
AM, Brazil	E, L	Other	BDT, BET	[225]
India	E	Iso	BDT, BET	[226]
Surinam	L	Iso, MT, and Other	BDT, BET	[227, 228]
Nigeria, AM, Brazil	L	Iso, MT	BDT, BET	[229]

from European [90] and African [194] savannas, tropical forests [202], and boreal needleleaf trees [237] led to the introduction of multiple emission processes for an individual chemical species in BVOC emission models.

Organic chemists investigating monoterpenes in the late 1800s identified the hemiterpene, isoprene (2-methyl-1,3-butadiene), as the biochemical precursor of monoterpenes, but isoprene was thought to exist only within plant tissues

TABLE 3: Compilation of studies used to estimate boreal vegetation BVOC emission factors for the MEGAN2.1 model [5]. Emission measurement approaches include enclosure (E), canopy micrometeorological (C), and landscape inverse modeling (L) techniques. Compounds include isoprene (Iso), monoterpenes (MT), sesquiterpenes (SQT), and other (Other). PFTs include broadleaf deciduous shrub (BDS), broadleaf deciduous tree (BDT), arctic C3 grass (AC3), needleleaf deciduous tree (NDT), and needleleaf evergreen tree (NET).

Location	Scale	Compounds	PFTs	Reference
Finland	E	MT	NET	[230]
Jilin, China	C	Iso, MT	BDT, NET	[231]
Sweden	E	Iso	AC3	[232, 233]
Sweden	E	Iso	AC3	[234]
Potted plant	E	Iso, MT, and Other	NET	[235]
SK, Canada	C	Iso	BDT	[236]
Finland	C	MT	BDT, NDT, and NET	[237]
Finland	C	Iso, Other	AC3	[238]
Finland	E	MT, SQT	BDS, BDT	[239]
Finland	E, L	Iso, MT, and SQT	BDT	[240, 241]
Finland	E	MT, SQT	NET	[242]
Potted plants	E	Iso	AC3	[243]
Finland	E	Iso, MT, and Other	AC3	[244]
Sweden	C	Iso, MT, and Other	AC3	[245]
Norway	L	MT	NET	[246]
WI, USA	E, C, L	Iso, MT	NDT	[81]
Various, Russia	E	Iso, MT, and Other	BDT, NDT, and NET	[82]
Sweden	L	MT	NET	[247]
Sweden	E	Iso	AC3, NET	[248]
Sweden	E	Iso, MT, and Other	AC3, NET	[249]
ON, Canada	L	Iso	BDT, NET	[250]
Potted plants	E	Iso, MT	NET	[251]
ON, Canada	E	Iso, MT	AC3	[252]
Jilin, China	E	Iso, MT	AC3, BDS, BDT, NDT, and NET	[101]
Potted plants	E	MT, SQT	NET	[253]
SK, Canada	C	Iso	BET	[254]
Sweden	E, L	MT	NET	[255]
AL, USA	C	Iso, MT, and Other	AC3, BDS	[256]
Finland	E, C	MT	NET	[257]
Finland	C	MT	NET	[258]
Finland	E, C	Iso, MT	BDT, NET	[259]
Finland	C	Iso, MT, and Other	NET	[260]
Finland	E	Iso, MT, and SQT	NDT	[261]
Finland	L	Iso, MT	BDT, NET	[262]
Finland	E	MT, SQT	NET	[263]
Sweden	E	Iso	AC3	[264, 265]
Finland	E	MT, SQT, and Other	BDS, BDT	[266]
Sweden	E	MT, SQT, and Other	BDS, BDT	[267]
Various, Canada	C	Iso	AC3, BDS, BDT, and NET	[268]

[151]. The discovery of substantial isoprene emissions from plants into the atmosphere was discovered more than 50 years ago and was initially controversial [152]. Isoprene later became recognized as the dominant global BVOC emission into the atmosphere [17]. Isoprene contributes about half of the total global BVOC flux, and so it is not surprising that it has been investigated more extensively than any other atmospheric BVOC.

Sesquiterpenes (SQTs) are a major component of essential oils stored by some plants, especially broadleaf trees, and can also be directly emitted without being stored [295]. SQTs are emitted from numerous plant species including conifer and broadleaf trees, shrubs, and agricultural crops [296]. While some sesquiterpenes, such as longifolene, have atmospheric oxidation lifetimes on the order of hours, similar to that of the dominant monoterpenes such as α -pinene, some of the

TABLE 4: Compilation of studies used to estimate cropland BVOC emission factors for the MEGAN2.1 model [5]. Emission measurement approaches include enclosure (E), canopy micrometeorological (C), and landscape inverse modeling (L) techniques. Compounds include isoprene (Iso), monoterpenes (MT), sesquiterpenes (SQT), and other (Other).

Location	Scale	Compounds	Crop	Reference
Potted plants	E	MT, SQT, and Other	Potato	[269]
CA, USA	E	Iso, MT, and Other	Various	[270, 271]
CA, USA	E	Iso, MT, and Other	Various	[272]
UK	E	Iso, MT, and Other	Miscanthus, willow coppice	[273]
Potted plants	E	SQT, Other	Tobacco	[274]
Potted plants	E	Iso, MT, SQT, and Other	Switchgrass	[275]
Potted plants	E	SQT	Corn	[276]
Potted plants	E	Other	Sorghum	[70]
Potted plants	E	Iso	Arundo donax	[277]
Spain, Italy	E	Other	Corn, pea, barley, and oat	[93]
VIC, Australia	E	Other	Clover	[100]
Potted plants	E	Iso, MT, SQT, and Other	Wheat, rye, rape, and grape	[102]
Potted plants	E	Iso	Velvet bean, kudzu	[278]
Potted plants	E	Other	Soybean, tomato, bean, and Corn	[115]
Potted plants	E	SQT	Corn	[279]
Potted plants	E	SQT, Other	Sunflower	[280]
Italy	E	Other	Fescue	[281]
CO, USA	C	Other	Alfalfa	[282]
Various, USA	E	Iso, MT, Other	Various	[14]

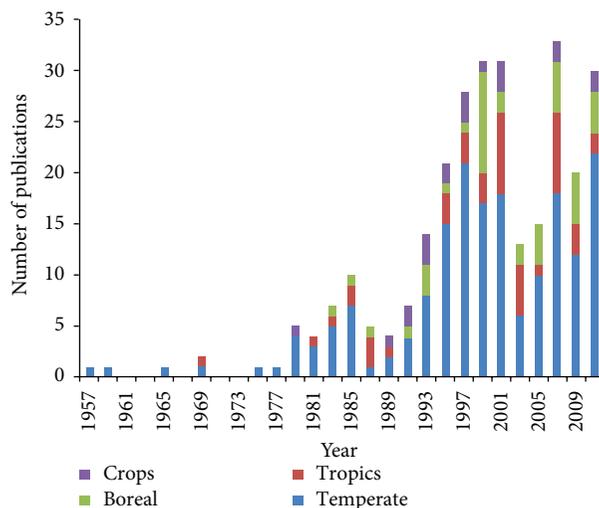


FIGURE 1: Illustration of the number of publications during two-year periods that were used to develop the BVOC emission factors for the MEGAN2.1 model [5].

most dominant sesquiterpenes emitted into the atmosphere (β -caryophyllene and farnesene) are much more reactive and have typical lifetimes of minutes [297]. The low volatility, and in some cases high reactivity, of sesquiterpenes makes them considerably more difficult to detect and quantify. As a result, few studies considered sesquiterpene emission measurements since they were generally thought to be a minor contribution in comparison to monoterpenes. Efforts to quantify sesquiterpene emissions increased in the past decade with the growing interest in atmospheric secondary organic aerosol [76]. Although sesquiterpenes are only a minor

fraction of total BVOCs, they are recognized as important for the atmosphere due to their relatively high SOA yields [298].

Large emissions of an oxygenated hemiterpene, 2-methyl-3-buten-2-ol (referred to here as MBO) were observed from pine trees in the early 1990s although emissions of MBO from insects and flowers had been observed previously [55]. MBO is emitted at high rates from some pine species, such as *Pinus ponderosa*, and low rates from other pines, including most Eurasian pines [299]. The global MBO emission is less than 1% of the global total BVOC, but MBO is the dominant emission in ecosystems dominated by high

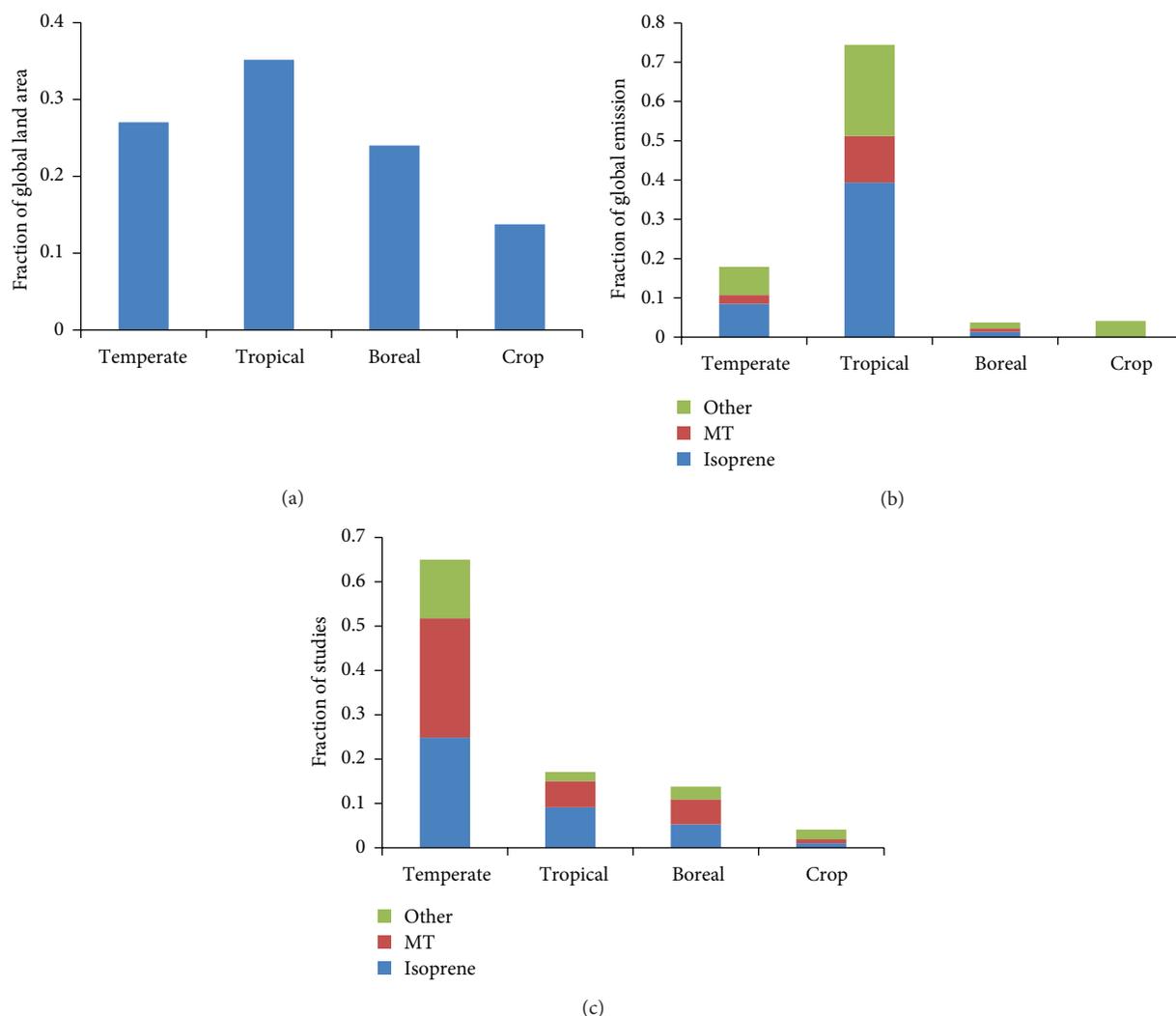


FIGURE 2: Comparison of the global fraction of vegetation-covered land area, global BVOC emissions estimated by [5], and the number of BVOC emission diversity studies (Tables 1–3) for major biomes types (temperate, tropical, boreal, and crop) and compound categories (isoprene, monoterpene, and other).

MBO emitting pines including large areas of western USA forests. Recent studies suggest that MBO may be emitted from most isoprene emitting vegetation at a rate that is ~1% of the isoprene emission rate [300]. This low level emission over a large part of global terrestrial ecosystems could be of the same magnitude as the localized emission from high MBO emitters.

The production of some terpenoid compounds is elevated in response to stress and is often observed as a light dependent, de-novo emission [301]. These include monoterpenes (e.g., ocimene), oxygenated monoterpenes (e.g., linalool), sesquiterpenes (e.g., farnesene), the homoterpenes dimethylnonatriene (DMNT), and trimethyl-tridecatetraene (TMTT). Emissions of these compounds are not always present, but when they are observed they can exceed typical monoterpene or sesquiterpene emission rates. The large variability and limited knowledge of factors controlling stress-induced BVOC emissions result in high uncertainties

associated with emissions of these compounds, but they may be a substantial component of total BVOC emissions into the atmosphere, and a better understanding is needed.

3.2. Methanol and Acetone. Methanol and acetone are among the most abundant VOCs in the global atmosphere. High concentrations of atmospheric methanol and acetone observed by investigators in the 1960s were attributed primarily to the atmospheric oxidation of VOC with minor contributions from bacteria, biomass burning, and anthropogenic sources [302]. In the early 1990s, high rates of methanol emissions were observed from vegetation foliage, especially young expanding leaves [115]. Lower rates of acetone emissions were observed from conifer buds [116]. A few years later, decaying leaf litter was found to be a smaller but significant abiotic source of methanol and acetone [303].

Jacob et al. [304] estimated that terrestrial ecosystems (biotic and abiotic) dominate global methanol emissions with

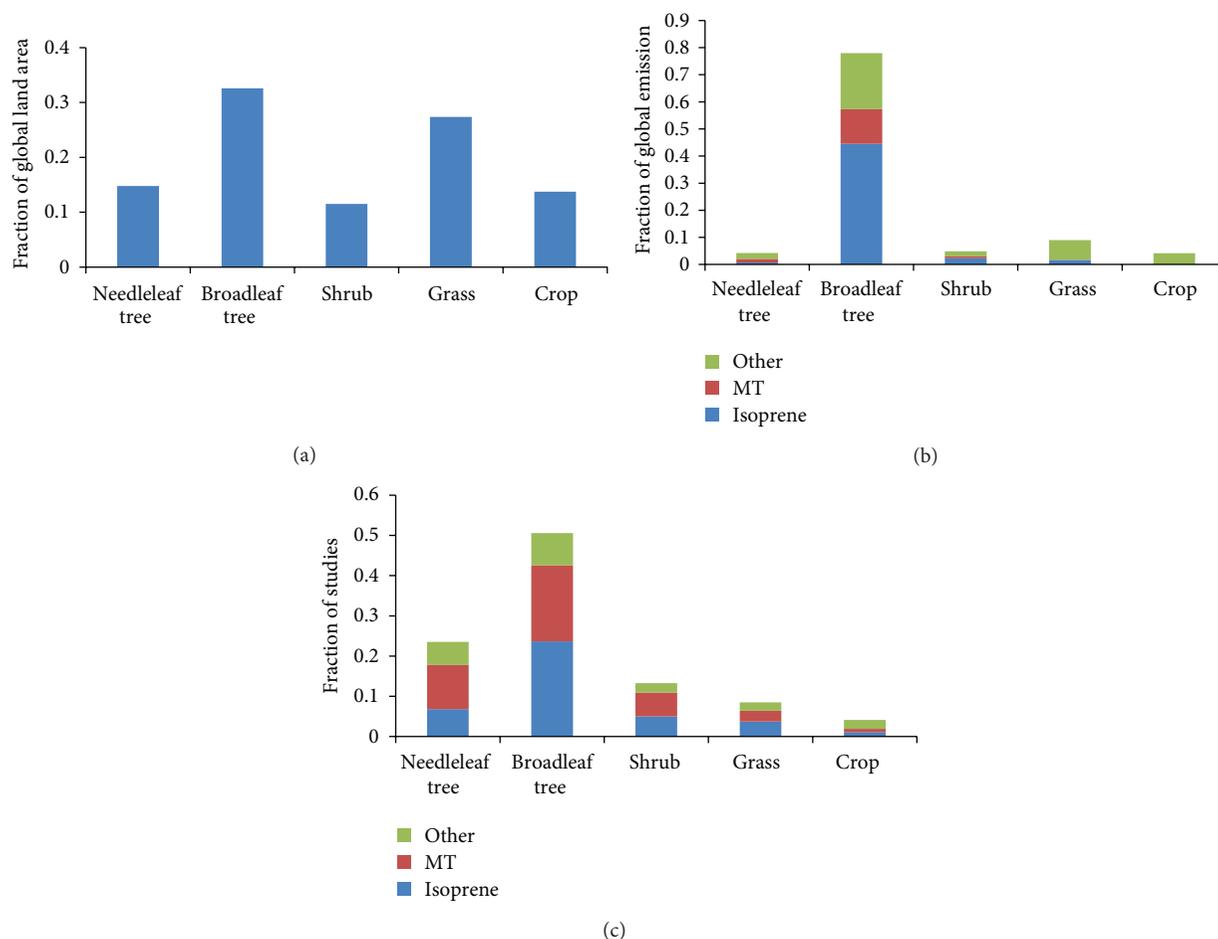


FIGURE 3: Comparison of the global fraction of vegetation-covered land area, global BVOC emissions estimated by [5], and the number of BVOC emission diversity studies (Tables 1–3) for major plant functional types (needleleaf tree, broadleaf tree, shrub, grass, and crop) and compound categories (isoprene, monoterpene, and other).

78% of the global annual production with the remainder being from atmospheric oxidation of VOC (15%), biomass burning (5%), and urban (2%) sources. Millet et al. [305] used additional in situ observations and concluded that oceans were responsible for 35% of the global methanol emission and assigned a contribution of 42% to terrestrial ecosystems. Stavrou et al. [306] used both satellite and aircraft observations to constrain global methanol distributions and report annual emissions of 187 Tg per year with a contribution of 53% from vegetation. They also identified missing sources in arid and semiarid regions of Central Asia and Western USA.

An analysis of the global acetone budget by Jacob et al. [307] indicated contributions to total emissions from terrestrial ecosystems (37%), atmospheric oxidation of VOC (29%), ocean (28%), biomass burning (5%), and anthropogenic emissions (1%). A more recent analysis concluded that terrestrial ecosystems were responsible for only 22% and oceans contributed 55% [308].

3.3. Acetaldehyde, Formaldehyde, Ethanol, and Organic Acids. Kesselmeier [309] described both the atmospheric importance of short-chained oxygenated VOCs (e.g., acetaldehyde,

formaldehyde, acetic acid, and formic acid) and the challenge of quantifying their atmospheric budgets. This includes the following challenges: (1) there are both natural and anthropogenic sources of these compounds, (2) there are primary and secondary (atmospheric oxidation) sources, (3) these compounds are difficult to measure, and (4) vegetation is both a source and a sink of these compounds. The strong bidirectional exchange exhibited by these compounds requires that both emission and deposition need to be considered. Accurate simulation of land-atmosphere fluxes of these compounds requires estimates of their atmospheric concentrations and the compensation point for each compound.

Alcoholic fermentation in the leaves and roots of plants produces ethanol which is converted to acetaldehyde in a pathway leading to acetate consumption [83]. Millet et al. [310] identified the major sources of atmospheric acetaldehyde as oxidation of VOC (60%), ocean (27%), and terrestrial ecosystems (11%). Biomass burning and anthropogenic emissions contribute the remaining 2%. The introduction of the PTRMS technique has provided an increasing number of measurements of acetaldehyde emissions from vegetation,

including whole canopy flux measurements, while there remain relatively few data for ethanol [310].

Substantial emissions of formaldehyde, and lesser amounts of formic and acetic acid, have been reported from studies using enclosure measurements to investigate various tree species [103, 309]. While emissions can be considerable, there is also the potential for a strong uptake of these compounds. These enclosure measurements suggest that the net flux of these compounds is a small emission into the atmosphere. Recent studies using above-canopy measurements have provided evidence that formaldehyde and formic acid emissions could be much larger. An analysis of satellite data suggests that formic acid emissions are two to three times higher than estimated from known sources [311] and that 90% of formic acid has a biogenic origin which includes direct emission and production from terpenoids. The first whole canopy fluxes of formaldehyde measured by eddy covariance have recently been reported [39]. The above-canopy flux, a net emission, was much higher than predicted from enclosure measurements which may be because the flux included both primary emissions and within canopy production. Measurements to better constrain formic acid and formaldehyde fluxes are needed.

3.4. Stress Compounds. Environmental and biotic stresses are important factors controlling BVOC emissions [128]. This includes BVOCs that are emitted at relatively low levels with unstressed conditions and then are elevated under stressed conditions (e.g., α -pinene) and compounds that are typically observed only when plants are stressed (e.g., methyl salicylate). BVOCs associated with pathogen or herbivore-induced stress include ethene, methanol, terpenoids, benzenoids, and green leaf volatiles [73, 128, 312–315]. The biochemical pathways and the defensive roles of these compounds have been the subject of many investigations [316], but there have been few attempts to quantify these emissions and they have not been integrated into regional BVOC emission models. The current limited understanding of the processes controlling stress-induced emissions makes any numerical approach for estimating stress BVOC emissions highly uncertain. Observations that provide an initial assessment of stress-induced emissions provide a first step towards assessing their contribution to total BVOC emissions and the need for accounting for these processes in BVOC emission models.

Ethene is an important phytohormone, and its emission rate from plants has been used as an indicator of stress [317]. Sawada and Totsuka [158] estimated an annual global flux of 18 to 45 Tg of ethene with 74% released from natural sources. This was the first global emission estimate of a nonterpenoid BVOC and was based on an extrapolation of enclosure measurements that indicated widespread ethene production by plants in most landscapes. Canopy scale fluxes measured above a temperate deciduous forest confirmed that substantial amounts of ethene were released into the atmosphere from this landscape [56]. The canopy scale fluxes are in reasonable agreement with the earlier enclosure measurements.

The green leaf volatiles are a major category of BVOC that is associated with plant response to herbivory and other

stresses [12]. These compounds are produced in plants from linoleic and linolenic acid which are unsaturated fatty acids. The most prominent of these with respect to emissions into the atmosphere are cis-3-hexenal, trans-2-hexenal, hexanal, 1-hexanol, and cis-3-hexenol [287]. The compound methyl jasmonate is also produced from this pathway and has an important role in plant signaling [318].

3.5. Leaf Surface Compounds. Leaf surfaces are covered by a waxy material that serves as a barrier for keeping water in and pathogens out [319]. Long-chain hydrocarbons, acids, alcohols, and esters are the dominant components of these leaf waxes, but there are a variety of other constituents [320]. While these high molecular weight compounds have low volatility, a small fraction can volatilize into the gas phase, and this may be significant, especially with the high leaf temperatures ($>40^{\circ}\text{C}$) that occur in hot deserts. A study by Matsunaga et al. [120] concluded that some compounds, including homosalate and 2-ethylhexyl salicylate, were emitted at significant rates from a wide variety of plants. These are sunscreen compounds that protect plant tissues from UV solar radiation [120]. The estimated contribution to total emissions from most ecosystems was small, but a large contribution was estimated for desert regions dominated by mesquite (*Prosopis* spp.) which is an important component of large areas in the southwestern USA.

Another source of VOC emissions from vegetation is the oxidation of organics on the surface of leaves and other structures. Fruekilde et al. [45] fumigated leaves with ozone and reported elevated emissions of 6-methyl-5-hepten-2-one, acetone, geranyl acetone, and 4-oxopentanal and suggested that ozonolysis at vegetation surfaces could explain the widespread occurrence of these compounds in ambient air. Karl et al. [321] noted that elevated oxygenated VOC emission from foliage exposed to ozone could also be due to increased production of these compounds in leaves in response to stress or to gas phase oxidation (secondary compounds). They conducted experiments to isolate the mechanisms responsible for oxygenated VOC production and concluded that a substantial amount of oxygenated VOC was primary emissions, originating from reaction of ozone inside of the plant or on plant surfaces, although there were also some secondary products from gas phase reactions.

3.6. Organic Halides. Organic halides including methyl bromide, methyl chloride, and methyl iodide are produced by vegetation and emitted into the atmosphere. Emissions are controlled by environmental conditions including soil moisture and temperature [322]. Even though methyl halide fluxes are small compared to terpenoid emissions, they are an important source of halogens in the stratosphere where they play a role in stratospheric ozone depletion [153]. Quantifying fluxes of methyl halides is challenging because terrestrial ecosystems are both a source and a sink of these compounds [166, 323]. Stable isotopes are now being used to individually quantify gross emission and uptake rates to improve understanding of the processes driving net fluxes [322, 324].

3.7. Organic Sulfur Compounds. Biogenic organic sulfur emissions from marine and terrestrial ecosystems are an important source of atmospheric sulfur compounds in clean environments [325]. Soil microbes and plants are both sources of compounds that include methyl mercaptan, dimethyl sulfide, and dimethyl disulfide. A more recent study [326] estimated that terrestrial ecosystems contribute about 15% of the global dimethyl sulfide flux with the remainder coming from oceans. Higher weight organic sulfur compounds such as diallyl disulfide, methyl propenyl disulfide, and propenylpropyldisulfide can be emitted in substantial amounts from a few plant species [149].

3.8. Alkanes (including Oxygenated Alkanes). Zimmerman [14] reported that a variety of alkanes were a substantial fraction of the biogenic VOCs emitted from vegetation. This was based on gas chromatograph retention times, rather than identification by mass spectrometry, and later studies have found only very low level of emissions of alkanes including ethane [100], propane [249], pentane [82], hexane [136], heptane [157], C6 to C10 saturated aldehydes [327], alcohols [281], ketones [282], pyruvic acid [85], and methane [328]. The potentially large source of methane [328] has been controversial as following studies found either much lower or no methane emission from living plants [329]. Terrestrial ecosystems are, however, a major source of methane emission from soil microbes and termites [328].

3.9. Benzenoid Compounds. The extensive BVOCs emission surveys of Zimmerman [14] also indicated that benzenoid compounds were a substantial fraction of total BVOC emissions. As was the case for alkanes, later studies found much lower benzenoid emissions. However, it is widely recognized that there are many benzenoid compounds (e.g., benzaldehyde, anisole, and benzyl alcohol) emitted as floral scents [330]. These floral benzenoid emissions are thought to make a small contribution to annual regional BVOC emissions [4] but can be a major emission at specific locations [214]. At least some of these compounds (e.g., toluene and methyl salicylate) are associated with plant stress and have been observed at elevated rates from stressed plants [73, 88].

3.10. Other Alkenes (including Oxygenated Alkenes). The terpenoids are not the only alkenes emitted into the atmosphere from terrestrial ecosystems. Propene and butene emissions have been observed in enclosures and confirmed by above-canopy flux measurements [56]. Other longer-chain alkenes have only been observed using enclosure techniques. This includes 1-dodecene and 1-tetradecene [270]. Oxygenated alkenes such as 1,3-octenol [281], neryl acetone [75], terpinyl acetate [183], and nonenal [74] have also been observed but are thought to be minor in comparison to terpenoid emissions.

3.11. Representing BVOC Chemical Diversity in Numerical Models. The first detailed biogenic VOC emission inventory [9] included estimates of just two compounds: isoprene and α -pinene. Several decades later, the USA EPA released the first widely available biogenic emission inventory approach,

called BEIS [331]. In addition to emission of isoprene and α -pinene, BEIS included lumped categories for “other monoterpenes” and an “unidentified” category. While this made the emission inventory more comprehensive, the “unidentified” category had limited use in atmospheric chemistry models because BVOCs have such varied atmospheric impacts (e.g., a wide range in aerosol yields and ozone production potential). In addition, some highly reactive BVOC may control the local atmospheric oxidizing capacity, while other less reactive compounds are transported long distances to remote areas or to the stratosphere where they can impact the chemistry of these pristine regions. An initial attempt to account for this was made [17] by using two “other” BVOC categories that included “other reactive VOC,” such as 232-MBO and “other VOC” which included less reactive compounds such as methanol and acetone. Emissions of 39 individual BVOCs were later estimated [287] in addition to three other categories: other terpenoids, other reactive NMVOCs, and other NMVOCs. The 39 identified compounds contributed about 94% of the total emission. MEGAN2.1 [5] eliminated the use of any “unidentified” categories and estimated emissions of 149 known compounds.

Most atmospheric chemistry schemes include at most only a few BVOCs and may lump these together with other compounds which limits the advantages of a detailed emissions chemical speciation. The increased number of compounds is a disadvantage if there is a significant increase in the computational resources associated with emissions parameterization, processing inputs, and emission calculations. MEGAN2.1 [5] uses a balanced approach that includes individual representations of 13 major BVOCs along with 5 additional categories for which an emission was calculated, and then the total was speciated into individual BVOC. This approach required the calculation of the emission activity of 18 BVOC types. The emission behavior of a compound, for example, the light dependent response, was treated the same for all vegetation types. This is reasonable for some compounds, such as isoprene, but not for others, such as α -pinene, which have different emission behavior in a tropical forest than in a temperate needleleaf forest [202]. This approach can be improved by using a smaller number of compound types but allowing a different emission behavior for different vegetation types. The 18 BVOC categories used for MEGAN2.1 [5] could be reduced to about half that number. For example, a nine BVOC category scheme could include hemiterpenes, light-dependent monoterpenes, light-independent monoterpenes, sesquiterpenes, methanol, acetone, bidirectional compounds, stress compounds, and other compounds. Each of these nine BVOC emission categories could have a different speciation profile for each vegetation type to simulate differences such as the contributions of individual monoterpenes to the total monoterpene flux from different landscapes.

4. BVOC Biological Diversity

Just as the scent of various flowers can be quite distinct, the total BVOC emission rates of various plants can differ. Some plants have total BVOC emission rates that are less than $0.01 \mu\text{g}$ per gram (dry weight) per hour ($\mu\text{g g}^{-1} \text{h}^{-1}$), while

others have rates that exceed $100 \mu\text{g g}^{-1} \text{h}^{-1}$. In addition to the three orders of magnitude variability in total emission, chemical composition can vary greatly with some plants dominated by isoprene, while emissions of other plants are dominated by other compounds such as α -pinene, MBO, or methanol. The BVOC emission rates of different terrestrial ecosystems vary by more than three orders of magnitude because the landscape average emission is determined both by the variability associated with plant-specific BVOC emission rates and the variability in vegetation cover fraction. In order to investigate BVOC emission variations associated with biological diversity, it is useful to define an emission factor for a set of standard conditions such as leaf age, growth environment, light, temperature, CO_2 concentration, soil moisture, and others [5, 129]. While there are clear taxonomic patterns associated with BVOC emissions, with plants of the same species or genus tending to be more similar, there are also many exceptions [332, 333]. This is not unexpected since the taxonomic schemes used to classify plants are not based on their BVOC emissions characteristics. In addition, some BVOC emissions variability is expected within plant species. For example, pine trees emit a variety of monoterpenes that are used for chemical defense against many different pests [334]. If all individuals of a pine species emit the same mix of monoterpenes, then a herbivore that manages to overcome this particular chemical mixture could devastate that pine species. If there are pine populations with different monoterpene emission types, then at least some pine tree individuals will survive.

Welter et al. [177] investigated BVOC emissions of an isoprene emitting oak species (*Quercus canariensis*), a monoterpene emitting oak species (*Q. suber*), and a species that is a hybrid of those two oak species (*Q. afares*). They found that *Q. afares* individuals were monoterpene emitters but at relatively low rates and with high variability. Geron et al. [54] examined isoprene emissions from *Populus* hybrids and found that their emission factors were a factor of two higher than their parents and that the second generation crosses had even higher emission factors. Bäck et al. [230] measured terpenoid emissions of individual Scots Pine (*Pinus sylvestris*) trees in a forest stand in Finland. They found that emissions of some trees were dominated by α -pinene, while others emitted primarily D3-carene, and still others emitted similar amounts of both. These studies demonstrate that there can be substantial within-species variation in terpenoid emissions for at least some plant species. Geron et al. [54] also considered whether there were significant interspecies differences in the isoprene emission factors of isoprene-emitting temperate broadleaf tree species and concluded that there was no clear evidence of this. Variability within and between species was similar suggesting that all temperate broadleaf trees could be divided into just two categories with respect to their isoprene emission: low emitters ($<1 \mu\text{g g}^{-1} \text{h}^{-1}$) and high emitters (about $90 \mu\text{g g}^{-1} \text{h}^{-1}$). Isoprene emission factors for high emitting temperate needleleaf trees were much lower than broadleaf trees indicating a need to assign different isoprene emission factors to different PFTs.

Numerical land surface models typically classify terrestrial ecosystems as either a landcover type [335] or a mixture of PFTs [336]. A savanna is an example of an ecosystem that is a mixture of grass and tree PFTs. Models based on a landcover classification have parameterizations that are intended to represent the weighted average for all of the vegetation species found in the biome. Plant functional types represent groups of vegetation species that are similar for at least some physiological and ecological traits. While it is possible for biome schemes to have very detailed classes, those used in global land surface models are simple approaches that provide a limited ability to represent BVOC emission diversity. A scheme with just five vegetation types (e.g., broadleaf forests, needleleaf forests, shrublands, grasslands, and croplands) was able to account for a significant part of BVOC emission diversity [337]. A small to moderate number (5 to 25) of global PFTs provide a reasonable approach for estimating global isoprene emissions at coarse resolution but cannot represent the considerable within-biome emission diversity which results in large errors in local to regional isoprene emission estimates [5].

The MEGAN2.1 [5] approach for simulating BVOC emission diversity is based on the Community Land Model version 4 PFT scheme [338]. The CLM4 approach is typical of the PFT schemes used for the land surface component of global earth system models and includes 6 temperate, 5 boreal/arctic, 3 tropical, and 1 crop PFTs. Table 5 outlines a framework to improve BVOC emission model estimates by expanding the 15 CLM PFTs to 39 PFTs that can better represent the biological BVOC diversity in earth system models. This approach includes a representative “type” species for each of the PFTs listed in Table 5. The first step towards implementing this approach is to conduct an extensive and systematic quantification of the BVOC emission rates of each of these species. This can be accomplished with enclosure measurements [129] or above-canopy flux measurements above monospecific stands [194]. Additional PFTs can be added when it can be demonstrated that their emission characteristics are substantially different from those on this list.

The three needleleaf tree PFTs included in CLM4 are temperate evergreen, boreal evergreen, and boreal deciduous. Figure 3 shows that needleleaf trees cover about 15% of the global vegetation covered land area but are estimated to contribute less than 5% of the total BVOC. Figure 3 also shows that nearly 25% of BVOC studies have targeted needleleaf trees indicating that they are relatively well studied. The studies summarized in Table 4 show that all three PFTs include a monoterpene emitting type. Both temperate and boreal evergreen species also include high isoprene [251] and high MBO [68] emitters, and there is some indication that there should be a low emission category for at least the temperate evergreen trees [284]. It should be noted that the available data for characterizing emissions is limited, and the results of different studies are often conflicting. For example, a literature review [284] indicated that the *Pseudotsuga menziesii* (Douglas fir) monoterpene emission factor is a factor of 8 higher than that of *Tsuga heterophylla* (western hemlock). In contrast, another study [147] found that the

TABLE 5: Plant functional type (PFT) scheme for representing BVOC emission biological diversity. The 15 CLM4 PFTs are subdivided into BVOC emission types (BVOC-PFT). The measured emission characteristics of the indicated representative species can be used to assign BVOC emission factors.

CLM4 PFT description	BVOC-PFT	Representative species
Needleleaf evergreen temperate tree	NETT-IM	<i>Picea engelmannii</i> (Engelmann spruce)
Needleleaf evergreen temperate tree	NETT-MT	<i>Abies grandis</i> (grand fir)
Needleleaf evergreen temperate tree	NETT-MBO	<i>Pinus ponderosa</i> (ponderosa pine)
Needleleaf evergreen temperate tree	NETT-Low	<i>Thuja plicata</i> (western redcedar)
Needleleaf evergreen boreal tree	NEBT-MBO	<i>Pinus contorta</i> (lodgepole pine)
Needleleaf evergreen boreal tree	NEBT-Iso	<i>Picea mariana</i> (black spruce)
Needleleaf evergreen boreal tree	NEBT-MT	<i>Pinus sylvestris</i> (Scots pine)
Needleleaf deciduous boreal tree	NDBT-MT	<i>Larix sibirica</i> (Siberian larch)
Broadleaf evergreen temperate tree	BETE-Iso	<i>Quercus virginiana</i> (southern live oak)
Broadleaf evergreen temperate tree	BETE-IM	<i>Eucalyptus globulus</i> (blue gum)
Broadleaf evergreen temperate tree	BETE-MT	<i>Quercus ilex</i> (holm oak)
Broadleaf evergreen temperate tree	BETE-Low	<i>Lithocarpus densiflorus</i> (tanoak)
Broadleaf evergreen tropical tree	BETR-Iso	<i>Mangifera indica</i> (mango)
Broadleaf evergreen tropical tree	BETR-MT	Tropical evergreen MT emitters
Broadleaf evergreen tropical tree	BETR-Low	<i>Panda oleosa</i>
Broadleaf deciduous tropical tree	BDTR-Iso	<i>Hymenaea courbaril</i> (jatobá)
Broadleaf deciduous tropical tree	BDTR-MT	<i>Apeiba tibourbou</i>
Broadleaf deciduous tropical tree	BDTR-Low	<i>Combretum molle</i> (velvet bushwillow)
Broadleaf deciduous temperate tree	BDTE-Iso	<i>Quercus rubra</i> (red oak)
Broadleaf deciduous temperate tree	BDTE-IM	<i>Liquidambar styraciflua</i> (sweetgum)
Broadleaf deciduous temperate tree	BDTE-MT	<i>Acer saccharum</i> (sugar maple)
Broadleaf deciduous temperate tree	BDTE-Low	<i>Sassafras albidum</i> (sassafras)
Broadleaf deciduous boreal tree	BDBT-Iso	<i>Populus tremuloides</i> (aspen)
Broadleaf deciduous boreal tree	BDBT- Low	<i>Betula pendula</i> (silver birch)
Broadleaf evergreen temperate shrub	BETS-MT	<i>Larrea tridentata</i> (creosote bush)
Broadleaf evergreen temperate shrub	BETS-Iso	<i>Karwinskia humboldtiana</i> (coyotillo)
Broadleaf evergreen temperate shrub	BETS-Low	<i>Atriplex canescens</i> (four-wing saltbush)
Broadleaf deciduous temperate shrub	BDTS-MT	<i>Ambrosia dumosa</i> (white bursage)
Broadleaf deciduous temperate shrub	BDTS-Iso	<i>Psoralethamnus fremontii</i> (Fremont's dalea)
Broadleaf deciduous temperate shrub	BDTS-Low	<i>Baccharis texana</i> (prairie false willow)
Broadleaf deciduous boreal shrub	BDBS-Iso	<i>Salix arctica</i> (arctic willow)
Broadleaf deciduous boreal shrub	BDBS-Low	<i>Alnus crispa</i> (mountain alder)
C3 grass	C3G-Iso	<i>Carex appendiculata</i> (sedge)
C3 grass	C3G-Low	<i>Koeleria cristata</i> (June Grass)
C4 Grass	C4G-low	<i>Bouteloua curtipendula</i> (sideoats grama)
Arctic C3 grass	AC3G-Iso	<i>Eriophorum angustifolium</i> (cottongrass)
Arctic C3 grass	AC3G-Low	<i>Festuca rubra</i> (red fescue)
Crop	CRP-MT	<i>Helianthus annuus</i> (sunflower)
Crop	CRP-Iso	<i>Mucuna pruriens</i> (velvet bean)
Crop	CRP-Low	<i>Triticum aestivum</i> (wheat)

western hemlock monoterpene emission factor is more than twice as high as the value for Douglas fir.

The CLM4 PFTs for broadleaf trees include tropical evergreen, tropical deciduous, temperate evergreen, temperate deciduous, and boreal deciduous trees. These broadleaf trees cover about a third of the vegetation-covered earth surface and are estimated to account for almost 80% of the global total

BVOC emission (Figure 3). About half of the BVOC emission diversity studies in Tables 1 to 3 have focused on broadleaf trees resulting in a relatively good characterization of temperate and boreal species, but tropical broadleaf tree emissions have not received enough attention (Figure 2). Each of the five CLM4 broadleaf tree PFTs (Table 5) include a high isoprene emitting type. Some also include a high MT emission type

[241, 339], a high isoprene and high monoterpene emission type [181], and a low emission type [284].

The CLM4 scheme includes just three shrub PFTs: broadleaf deciduous temperate, broadleaf evergreen temperate and broadleaf deciduous boreal. The two temperate shrub PFTs include high monoterpene, high isoprene, and low emitter categories [65, 138, 340, 341]. The boreal shrub PFT includes both high isoprene and low emitters [256].

The three CLM4 grass PFTs are C3 grass, C4 grass, and arctic C3 grass. All three PFTs are dominated by a low terpenoid emitting category, but the temperate and arctic C3 PFTs also include some isoprene emitting species [22, 49, 100, 233, 342]. The crop PFT is dominated by low terpenoid emitters, but there are some examples of high isoprene and high monoterpene emitters [275, 278, 280, 343].

5. Conclusions

This review summarizes the current understanding of BVOC chemical and biological diversity. There are hundreds of BVOCs emitted into the atmosphere, but a relatively few compounds (e.g., isoprene, methanol, α -pinene, acetone, and ethene) dominate the total flux. All BVOCs can influence atmospheric composition, if they are emitted at sufficient rates, but some BVOCs have a relatively high impact due to their reaction rates, products, ozone production potentials, organic aerosol yields, and other properties. As a result, there is a strong need to quantify the chemical diversity of BVOC emissions. On the other hand, a detailed numerical description of BVOC chemical speciation increases computational requirements and the personnel needed to process input variables. In addition, the large uncertainties associated with BVOC emission estimates do not justify an overly detailed parameterization of these compounds. An approach for accurately representing BVOC chemical diversity in emission models requires a balance between providing the appropriate level of details while also minimizing the complexity.

Global land surface models simulate regional variations in ecosystem-atmosphere carbon exchange by assigning values of the photosynthetic parameter $V_{c\max}$ to each PFT. This parameter describes the maximum rate of carboxylation by the photosynthetic enzyme Rubisco. The values of $V_{c\max}$ assigned to the 15 PFTs used by CLM4 vary from $52 \mu\text{mol m}^{-2} \text{s}^{-1}$ for grasses to $72 \mu\text{mol m}^{-2} \text{s}^{-1}$ for broadleaf evergreen trees and shrubs [18]. In contrast, the isoprene emission factor, which describes the isoprene emission rate at a set of standard conditions, ranges from $1 \mu\text{g m}^{-2} \text{h}^{-1}$ for boreal deciduous needleleaf trees to $11000 \mu\text{mol m}^{-2} \text{s}^{-1}$ for broadleaf deciduous boreal trees [5]. This comparison illustrates that there is a much greater range in the ability of plants to emit isoprene than there is for photosynthesis. Assigning BVOC emission factors to 15 PFTs is a good initial step towards characterizing BVOC biological diversity, but it is insufficient. A scheme with about 39 PFTs is proposed to improve regional to global BVOC emission estimates.

Reducing uncertainties in BVOC emission estimates will require additional observations. Measurements are especially needed for specific vegetation types (e.g., tropical broadleaf

forest and crops) and some nonterpenoid compounds (e.g., ethene, propene, ethanol, ocimene, and hexenal). Leaf-level enclosure measurements are needed to improve representations of the processes controlling emission variations. Tower- and aircraft-based above-canopy flux measurements are also needed to quantify BVOC diversity on landscape to regional scales.

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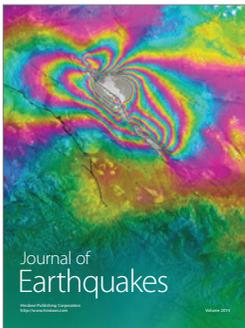
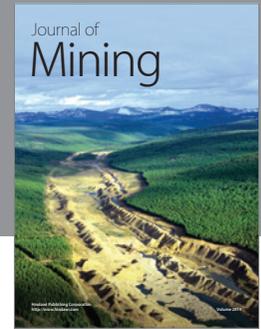
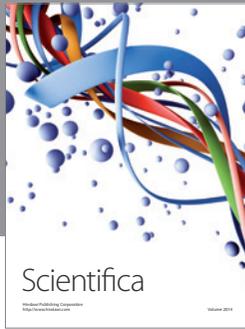
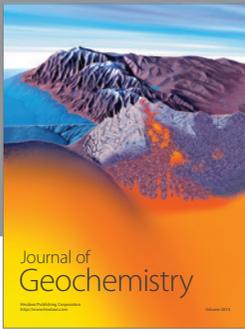
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