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Impact of insect herbivory on plant stress volatile emissions from trees: A synthesis of quantitative measurements and recommendations for future research

C. Faiola [a,b,*], D. Taipale [c,d]

[a] Department of Ecology and Evolutionary Biology, University of California Irvine, Irvine, CA, 92697, USA
[b] Department of Chemistry, University of California Irvine, Irvine, CA, 92697, USA
[c] Institute for Atmospheric and Earth System Research / Physics, Faculty of Science, University of Helsinki, P.O. Box 64, 00014, Helsinki, Finland
[d] Hyytiälä Forestry Field Station, Hyytiäläntie 124, 35500, Korkeakoski, Finland

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ABSTRACT

Plants, and particularly trees, are the largest source of atmospheric volatile organic compounds globally. Insect herbivory alters plant volatile emission rates and the types of compounds that are emitted. These stress volatiles are a major contribution to total plant volatile emissions during active herbivore feeding, with important implications for atmospheric chemistry processes. However, emission models do not currently have a quantitative description of plant volatile emission rates during and after insect herbivore feeding. This review provides a brief background on plant volatile organic compounds, the urgency of including biotic stress emissions in models, and a summary of plant volatile emission models and steps they have taken to incorporate stress emissions into their framework. The review ends with a synthesis of volatile emissions from trees during insect herbivory. This synthesis highlights key gaps in studied systems and measurement approaches. We provide a summary of recommendations for future work to address these gaps, improve comparability between studies, and generate the data-sets we need to develop a descriptive model of these plant stress volatile emissions.

1. Background

Volatile organic compounds (VOCs) are molecules with a carbon-based backbone that readily evaporate under ambient temperature and pressure conditions. Their molecular structures are primarily composed of carbon and hydrogen atoms, but they can additionally contain heteroatoms, most commonly oxygen, nitrogen, or, more rarely, sulfur (Dudareva et al., 2013) and halogens (Keng et al., 2013; Lovelock, 1975). VOCs emitted by vegetation exceed those emitted by humans by over an order of magnitude on a global scale (Guenther et al., 2012), and play an important role in ecological and atmospheric processes. Plant stress substantially alters both the emission rate and spectrum of emitted VOCs (Holopainen, 2004; Holopainen et al., 2018; Holopainen and Gershenzon, 2010; Niinemets, 2010a, 2010b; Niinemets et al., 2013, 2010). One cause of biotic plant stress is insect herbivory, which increases emissions of biogenic VOCs from vegetation during feeding - hereafter referred to as insect herbivory biogenic VOCs, or IH-BVOCs. There have been thorough reviews summarizing the published research on IH-BVOCs and their ecological implications (Dicke, 2009; Dicke et al., 2003; Loreto et al., 2014). However, a quantitative synthesis of this research that focuses on dominant plant VOC emission sources (e.g. trees) is missing, which would set the stage for integrating IH-BVOCs into emissions models. The primary objective of this paper is to synthesize IH-BVOC emission measurements from trees, highlight gaps in the existing literature, and provide recommendations for future IH-BVOC experiments. We first provide an introduction to biogenic VOC (BVOC) emissions and emission models, and briefly summarize approaches that have been used to integrate stress BVOC emissions into the models. We then present a synthesis of the existing IH-BVOC emission measurements and make recommendations for future measurements that are needed before IH-BVOCs can be comprehensively integrated into models.

More than 1,700 different VOCs have been identified in plant emissions (Dudareva et al., 2006). These BVOCs serve many ecological functions summarized by Holopainen (2004). They are important for ecological processes such as plant-plant communication (Arimura et al.,

* Corresponding author. Department of Ecology and Evolutionary Biology, University of California Irvine, Irvine, CA, 92697, USA.
E-mail address: cfaiola@uci.edu (C. Faiola).

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2009; Baldwin et al., 2006), plant-pollinator communication (Schiestl and Johnson, 2013), plant-insect communication (Blande, 2017; Moreira et al., 2018a, 2018b), and tritrophic signalling (Dicke, 2008). BVOCs provide defenses such as deterring herbivory through toxicity (Mangione et al., 2004), increasing fluidity of cell membranes for thermotolerance (Peñuelas and Llusià, 2002; Singsaas et al., 1997; Siwko et al., 2007), and protecting leaf tissue from atmospheric oxidants within and around plant leaves (Loreto et al., 2004, 2001). BVOCs are highly reactive compounds with atmospheric lifetimes ranging from seconds to days depending on the VOC structure and oxidant levels (Atkinson and Arey, 2003). The highly reactive nature of the compounds also means BVOCs play an important role in atmospheric chemistry and physics including new particle formation (Donahue et al., 2013; Kulmala et al., 2014; Riccobono et al., 2014; Schobesberger et al., 2013), growth of existing atmospheric particles via gas-to-particle condensation (Ehn et al., 2014; Riipinen et al., 2012), ozone generation (Calfapietra et al., 2013), and determination of the oxidative capacity of the atmosphere (Mogensen et al., 2015, 2011). The production and growth of atmospheric particles from BVOCs, called secondary organic aerosol (SOA), can increase the number of cloud condensation nuclei and influence cloud formation processes (Makkonen et al., 2009; Merikanto et al., 2009; Pierce et al., 2012; Spracklen et al., 2008). Furthermore, atmospheric aerosols scatter incoming radiation, which can increase productivity of terrestrial ecosystems (Cohan et al., 2002; Ezhova et al., 2018; Kanniah et al., 2012; Matsui et al., 2008; Rap et al., 2018). Thus, there are important biosphere-atmosphere interactions related to the atmospheric processing of BVOC emissions that play a crucial role in maintaining ecosystem health and function.

Biotic plant stresses account for more than half of the damage caused to trees globally (FAO, 2012; Karel and Man, 2017; Michel et al., 2018). These biotic stressors include most significantly insect herbivory, but also fungal disease or other pathogens. Biotically caused damage from these stressors has been globally increasing during recent decades (FAO, 2012; Hunter et al., 2014; Kautz et al., 2017; Michel et al., 2018), and their extent, frequency and intensity are predicted to increase further in the future (Bale et al., 2002; Cannon, 1998; FAO, 2012; Harrington et al., 2007; Kurz et al., 2008). The reasons for the predicted increase are complex and depend on many environmental factors such as temperature, humidity, precipitation, and drought, but also on e.g. plant nutritional quality and host resistance. Generally, herbivores are favoured by warm and dry conditions (Speight and Wainhouse, 1989), though extreme heat waves might affect populations negatively; higher temperatures during the growing season can cause an acceleration in larval development by shortening the egg and larval periods, which increases the survival rate by decreasing the duration of a life stage where insects are most susceptible to predators (Rouault et al., 2006). Higher summer temperatures can also cause earlier onset and prolonged time period for reproduction and accelerate the development of bark beetles (Baier et al., 2007; Wermelinger and Seifert, 1998) and aphids (Cannon, 1998; Harrington et al., 2007). Whether increased winter time temperatures will favour insect development or not depends on the individual species (Battisti, 2004), but normally, warmer winters enhance egg survival rate (Bale et al., 2002; Leather et al., 1996). Finally, rising frequencies of drought are expected to promote bark beetle attacks (Bakke, 1983; Faccoli, 2009; Ogris and Jurc, 2010).

Currently, no BVOC emissions model quantitatively predicts biotic stress BVOC emissions. This synthesis focuses on one category of biotic stress emissions, insect herbivore stress emissions, because the impacts of insect herbivory on plant stress emissions have been the most widely studied and published by the research community of all the biotic stressors and because it is the predominant cause of tree damage worldwide (Canadian Council of Forest Ministers, 2019; Kautz et al., 2017; Michel et al., 2018). The recommendations presented in this review would also be relevant for guiding future plant stress measurements from other biotic stressors.

2. The urgency of including biotic plant stress emissions into models

Biotic plant stressors are very common worldwide and stand level severity can vary from mild to complete defoliation and ultimately result in plant death. For example, several thousands of square kilometres of forests have previously been entirely denuded by herbivores (McManus et al., 1989; Nikula, 1993; Tenow, 1975). During the past three decades, ~16.6 million ha forest/year have on average been moderately to severely defoliated by insects in Canada (Canadian Council of Forest Ministers, 2019). In the US, insects have yearly defoliated 2-5.2 million ha of forested land during the past five years (Karel and Man, 2017). The mean defoliation (i.e the percentage of needle/leaf loss in the crown compared to a reference tree with full foliage) of European forests has in recent years been slightly larger than 20%, and about one quarter of the evaluated trees in European forests are usually reported to have a defoliation rate of >25% (Michel et al., 2018). Systematic monitoring of tropical rainforest and savannas have not been conducted, but ~25 year old estimates suggest that ~40% and ~35% of net foliar production is consumed by herbivores in the two different ecosystems, respectively (Randerson et al., 1996). Defoliators are not the only cause of damage. Wood-boring insects are responsible for a significant fraction of forest damage also. For example, bark beetles have affected ~3 million ha/yr of forest in Canada during the past three decades and they thereby account for about 18% of the total disturbance by insects in the country (Canadian Council of Forest Ministers, 2019). In the US, more than 5 million ha were affected by bark beetles during 1997-2010 (Bentz and Klepzig, 2014), while wood-boring insects in general were responsible for almost 4% of all total damage symptoms observed in the EU during 2017 (Michel et al., 2018). Thus, insect herbivory is a large source of plant stress and vegetation damage around the globe, and it is a source of stress that is continuously growing (Bale et al., 2002; Cannon, 1998; FAO, 2012; Harrington et al., 2007; Hunter et al., 2014; Kautz et al., 2017; Kurz et al., 2008; Michel et al., 2018).

Biotic stressors can induce the emissions of compounds, increasing total VOC emission rates, with substantial implications for atmospheric chemistry processes. Any process that alters VOC emissions to the atmosphere will influence the atmospheric concentration, the boundary layer oxidation capacity and ultimately the concentration and size of SOA, which are capable of modifying climatically important cloud properties (Charlson et al., 1992; Kerminen et al., 2005; Twomey, 1991, 1977). Biotic stress can alter the emission profile of emitted terpenoids leading to increases in OH and O_3 reactivity up to two orders of magnitude (Faiola et al., 2015). Some induced emissions have a high potential to form and grow atmospheric secondary organic aerosol particles (such as methyl salicylate, monoterpenes, and sesquiterpenes) (Joutsensaari et al., 2015; Mentel et al., 2013; Yli-Pirilä et al., 2016). In contrast, biotic stress can also decrease the sesquiterpene-to-monoterpene ratio or increase acyclic terpene compounds, which reduce SOA formation potential of the plant emission profile (Faiola et al., 2019, 2018). The rate of emission of isoprene – a VOC that has been linked to the suppression of new particle formation and growth (Kiendler-Scharr et al., 2012, 2009; Lee et al., 2016; McFiggans et al., 2019) - is often simultaneously strongly reduced (Brilli et al., 2009; Copolovici et al., 2017), though not always (Schaub et al., 2010; Ye et al., 2018). The widespread and growing presence of IH-BVOCs, combined with their impact on atmospheric chemistry, makes it imperative for the community to integrate them into emissions models, but we are missing key information about their emission rates that precludes comprehensive integration of IH-BVOCs into existing models.

3. Introduction to biogenic emissions models

There are a variety of emissions models designed with different approaches to predict the emission of major BVOCs. Though many of these

models were developed from some process-based understanding of the underlying mechanisms controlling the production and emission of VOCs, all emission models remain largely empirical (Grote et al., 2013; Monson et al., 2012). Grote and Niinemets (2008), Monson et al. (2012), and Grote et al. (2013) present extensive reviews of the history of emission models from different perspectives. Here we only briefly mention the most commonly used models with a summary of their approach. In the electron transport rate (ETR)-model (Arneth et al., 2007; Niinemets et al., 2002a, 2002b, 1999) the rate of emission is limited by the supply of substrate for isoprenoid synthesis and synthase activity, which depends on the photosynthetic electron transport rate. The ETR-model has been extended to account for non-specific storage of monoterpenes in leaves (Niinemets and Reichstein, 2002), consider the electron availability for isoprene emission relative to the needs of CO_2 assimilation (Morfopoulos et al., 2013), and include an explicit link between the electron transport and enzyme activity (Grote et al., 2014). Several other emission models, that are also tied to photosynthesis, have simultaneously emerged, e.g. the seasonal isoprenoid synthase model-biochemical isoprenoid biosynthesis model SIM-BIM model (Grote et al., 2009, 2006; Lehning et al., 2001; Zimmer et al., 2000), but also others (Bäck et al., 2005; Martin et al., 2000). In these models, the rate of emission is controlled by the rate of synthesis of Calvin cycle intermediates.

The Model of Emissions of Gases and Aerosols (MEGAN) is the most extensively used biogenic emissions model in canopy, earth system, and chemical transport models. MEGAN is a simple mechanistic model that considers the major environmental variables driving emission rates - primarily light, temperature, atmospheric carbon dioxide, leaf age, soil moisture, and leaf area index. It was developed from simple algorithms relating terpene emissions to light and temperature (Guenther et al., 1993, 1991). The algorithms described monoterpene emissions with an exponential temperature dependence, and isoprene emissions with both a light and temperature dependence that reached a saturation point for the former and a maximum emission before rapidly decreasing for the latter. These simple relationships could explain most of the observed diurnal variability in emissions measurements. The algorithms are also consistent with a process-based understanding of light and temperature controls on emission rates, production rates, and how those relate to plant storage of volatiles (Grote and Niinemets, 2008; Laothawornkitkul et al., 2009). For example, emission rates of compounds that reside in specialized storage structures (i.e. many monoterpenes and sesquiterpenes) are de-coupled from production rates, and exhibit an exponential temperature-dependence that is a function of increased saturation vapor pressure at higher temperatures. In contrast, emission rates of non-stored compounds (i.e. isoprene, some monoterpenes, and all VOCs emitted from plants without specialized storage structures) are tightly coupled with production rate. Production is a function of photosynthesis rates and enzyme activity. Photosynthesis increases with light up to a saturation point (700-900 μmol m^{-2} s^{-1} for isoprene), and enzyme activity increases exponentially with temperature up to a denaturation point (~40 °C) after which it decreases. The algorithms were used to develop a global emissions model where the foliar flux of volatile organic compounds was estimated from the foliar density, an ecosystem-specific emission factor, and a non-dimensional activity adjustment factor that accounted for the influence of light and temperature (Guenther, 1997; Guenther et al., 1995). The foliar density was assigned based on climatic variables and satellite-derived global vegetation indices. The model also includes a canopy radiative transfer model to account for light attenuation within the canopy. Importantly, this model estimates a canopy-scale emission factor as opposed to a leaf-level scale like most other emissions models. Comparisons with aircraft and flux tower measurements demonstrated that the model was able to estimate emissions within a factor of two if constrained with representative field measurements (Guenther et al., 1999).

The development of the canopy-scale emissions model continued for many years after its first introduction. The model was improved with a focus on isoprene emissions in Guenther et al. (2006) and officially given the name, MEGAN. One major improvement over the previous version included the addition of thousands more measurements, particularly in the tropics which had been under-represented in the previous versions. This was a significant limitation in the previous versions given that the tropics account for the majority of global isoprene emissions. Further improvements were made in MEGANv2.02 to update the parameterization of monoterpene and sesquiterpene emissions in Sakulyanontvittaya et al. (2008). Emissions were estimated for 138 different compounds from four different plant functional types: broadleaf trees, needleleaf trees, shrubs and bushes, and crops and grasses. The most recent version, MEGANv2.1, simulates the emissions of 150 individual compounds for fifteen different plant functional types (Guenther et al., 2012). One important addition to MEGANv2.1 is the inclusion of fifteen "stress compounds" and a monoterpene (ocimene) and sesquiterpene (farnesene) that are particularly stress-sensitive. However, variability and uncertainty in plant stress emission studies have presented obstacles to simulating these stress emissions quantitatively. The treatment of plant stress compounds remains a significant limitation for using MEGAN in climate change simulations where various stressors, such as drought and increased herbivore outbreaks, have the potential to significantly alter the types of compounds emitted and their emission rates. This is discussed further in the next section.

4. Stress emissions in models

The production and emission of VOCs are influenced by many environmental factors. All emissions models described in the last section account for instantaneous light, leaf or ambient temperature and CO_2 concentration. Several of the models also include ontogeny and temperature and light acclimation (e.g. MEGAN and SIM-BIM). The underlying process-based idea of the ETR model makes it able to reproduce the emission of VOCs during episodes of drought, while Grote et al. (2014, 2010, 2009) and Guenther et al. (2006, 2012) include explicit functions for the effect of limited water on the emission of VOCs. To our knowledge, no VOC emission model accounts for the abiotic stress effects of oxidative air pollution, flooding, soil infertility, ultraviolet radiation, frost, or mechanical wounding. Similarly, no emission model accounts for biotic stress effects due to herbivores and pathogens.

Stress emissions are included as a general compound class in MEGANv2.1, but estimates of their emissions are based on a limited number of studies showing induction of VOC emissions due to various types of stressors including mechanical wounding, herbivores, ozone, temperature and water availability. MEGAN calculates the stress emissions in a highly simplified manner due to a lack of observations that are appropriate for integrating into an emissions model. First, MEGAN assumes the stress emission factor is the same for all fifteen plant functional types. Second, it defines the light dependent fraction to be 0.8 - a value lower than that used for isoprene and higher than most monoterpenes. Finally, the light and temperature dependence is modulated using the same parameters as monoterpenes - a weighted average of the light-dependent and light-independent fractions using the same exponential temperature dependence for the light independent fraction and the same empirical coefficients for the light dependent fraction. This is a reasonable first estimate given the large gaps in observations, but there is no clear evidence that the stress emissions would be modulated by temperature and light in the same way as constitutive emissions. In fact, the limited evidence available suggests that biotic stress emissions are not modulated by light and temperature in the same way as constitutive emissions (Kari et al., 2019; Staudt and Lhoutellier, 2007). It is likely that herbivore activity will play a major role in controlling emission rate fluctuations and emission intensity. This has been shown to be true for green leaf volatile (GLV) emissions, in particular, where emission rates rapidly fluctuate with herbivore feeding activity (Maja et al., 2014).

Recently, Grote et al. (2019) proposed a modeling framework for predicting *de novo* stress VOC emissions resulting from both abiotic and

biotic stressors. The new framework is represented with a revised Fraser-Suzuki function, which describes an initial exponential increase followed by a slow decay. Parameters are included to define the time delay and broadness of the stress emission peak. Parameters were defined based on 13 publications with 5 using an ozone stress (abiotic), 7 representing herbivory stress (biotic), and 1 considering both. The model places all plant volatiles into nine categories based on their biosynthetic pathway: methyl salicylate, monoterpenes, isoprene, DMNT, sesquiterpenes, green leaf volatiles, acetaldehyde, acetone, and methanol. Six of the nine compound categories are modeled with a bimodal pattern whereby a second term was introduced to describe both a "fast" and "slow" emission response. This model focuses on *de novo* stress emissions and does not include increased emissions released from storage after wounding. In some cases, particularly bark-boring herbivory, it is likely that released compounds could be the dominant source of stress emission (Blande et al., 2009; Faiola et al., 2018; Kari et al., 2019). Other limitations include a linear response to stress severity that might not hold at high levels of stress, and no explicit dependence of stress emissions on temperature. It is very likely that temperature would still influence stress emission rates because temperature affects compound saturation vapor pressure and diffusion rates. Thus, a complete model of stress emissions would require both stress intensity and temperature controls on stress VOC emission rates. The model was used to predict emissions for a few case studies and reproduces measured values reasonably well. However, the authors highlight there are few data-sets that contain both the chemical breadth and time resolution required to fully evaluate the model. Additionally, no model accounts for the variables that would drive the severity and duration of the stress exposure, differentiate between various sources of stress (e.g. ozone, temperature, different herbivore types, combinations of stressors, etc.) which cause different responses, or include feedbacks between plant stress volatiles and the stress intensity (i.e. some plant stress volatiles directly repel prospective herbivores).

5. Summary of herbivore stress volatiles

The different compounds and compound classes that we will discuss are shown in Fig. 1. The major IH-BVOCs are split into three general classes: terpenoids, plant hormones, and green leaf volatiles. The terpenoid class includes monoterpenes (MT, C_{10}), sesquiterpenes (SQT, C_{15}) and terpene derivatives like DMNT. In the plant hormone class of compounds, we will focus on methyl salicylate because it is the hormone that is most commonly reported from wounded plants. Green leaf volatiles include C_6-oxygenated VOCs that are produced following damage to plant tissues, and include aldehydes, alcohols, and acetates. Fig. 1 provides some examples of representative terpenoids and GLVs but it does not comprise an exhaustive list of all terpenoids and GLVs that have been reported in insect herbivore stress studies. Isoprene, which accounts for the largest biogenic VOC emission globally (Guenther et al., 2012), is not included in our synthesis due to a lack of quantitative studies on the influence of insect herbivory on isoprene emission rates from trees. Generally, insect herbivory produces a short-term elevation in isoprene emissions after wounding (Loreto et al., 2006) followed by a longer-term decrease as carbon substrate is depleted (Brilli et al., 2009). Isoprene emissions decrease more substantially at higher levels of defoliation damage, even while GLV and monoterpene emissions increase (Copolovici et al., 2017).

Despite the overwhelming evidence that IH-BVOC emissions are substantial, it has been prohibitively challenging to represent herbivore stress emissions quantitatively in emissions models. This is, in part, due to the wide variation in observations. Plant emission responses to herbivore stress treatments can vary by plant species, genotypes, individuals, herbivore species, and extent of herbivore damage. For example, Table 1 provides a qualitative summary of the overall impact of insect herbivory on the emissions of different BVOC compound classes separated by herbivore type. This qualitative summary includes more breadth in plant types than just trees to provide a more comprehensive summary. In this paper, we define three general types of insect herbivory, or "bug functional types" (Arneth and Niinemets, 2010): external defoliator (leaf and needle chewing), bark borer, and aphid (sucking-piercing herbivory). We acknowledge the existence of internal defoliators, but the impact of internal defoliation on plant stress emissions has not been studied extensively or quantitatively enough to be included in this synthesis. We propose that plant stress responses to insect herbivory will (in part) be driven by the mechanism of herbivory, which is why we have categorized the bug functional types in this way. Classifying them by herbivore type could also synergize well with future model development describing climate change impacts on insect biogeographical distributions and outbreak frequency, intensity, and extent.

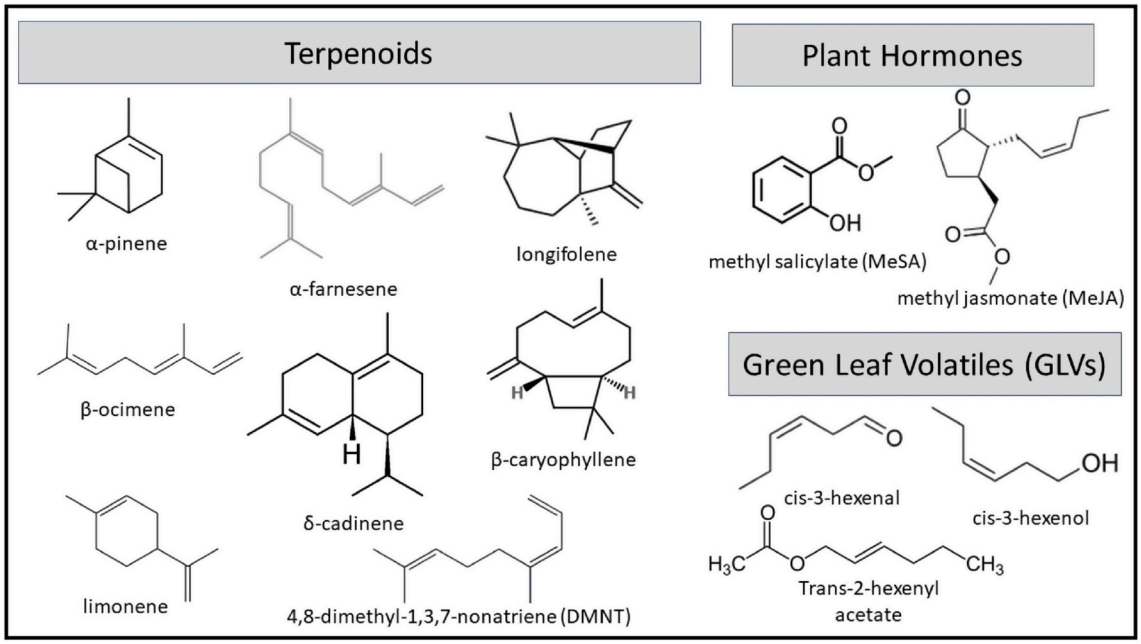

Fig. 1. IH-BVOC compound classes and example compounds.

Table 1
Summary of herbivore impacts on IH-BVOC emissions separated by herbivore type and compound type. +, -, and Ø symbols correspond to an increase, decrease, or non-significant effect on IH-BVOC emissions. A "?" indicates we could not locate any published material with quantitative results for that particular herbivore/IH-BVOC impact.

Herbivore Type	GLV	MT	SQT	MeSA	MeJA	DMNT	Refs
Bark borer	Ø	+ Ø	+ - Ø	+ Ø	Ø	Ø	Amin et al. (2012), 2013; Blande et al. (2009); Faiola et al. (2018); Ghimire et al. (2016); Heijari et al. (2011); Joutsensaari et al. (2015); Kari et al. (2019); Kovalchuk et al. (2015); Maja et al. (2014); Miller et al. (2005); Turlings et al. (1998)
External defoliator	+ Ø	+ Ø	+ -	+ Ø	+	+	Achotegui-Castells et al. (2013); Arimura et al. (2004); Blande et al. (2010), 2007; Brilli et al. (2009); Copolovici et al. (2017), 2011; Engelberth et al. (2004); Ghimire et al. (2013); Ghirardo et al. (2012); Joutsensaari et al. (2015); Li et al. (2012); Litvak and Monson (1998); Maja et al. (2014); Mäntylä et al. (2008); Mccormick et al. (2014); Prieme et al. (2000); Schaub et al. (2010); Staudt and Lhoutellier (2007); Turlings et al. (1998); Vuorinen et al. (2007); Yli-Pirilä et al. (2016)
Piercing-sucking	+ Ø	+	+ Ø	+ Ø	?	+ Ø	Birkett et al. (2003); Blande et al. (2010); Du et al. (1998); Gosset et al. (2009); Harmel et al. (2007); Joó et al. (2011), 2010; Li et al. (2014); Moreira et al. (2018a); Nissinen et al. (2005); Pareja et al. (2007); Paris et al. (2010); Pettersson et al. (2008); Sasso et al. (2007); Scutareanu et al. (2003); Staudt et al. (2010); Turlings et al. (1998); Zhu and Park (2005)

5.1. Synthesis of measurements

To synthesize quantitative measurements of IH-BVOCs, we included only papers that contained quantitative data that were normalized to either biomass or surface area. To focus on broad-scale impacts for the quantitative synthesis, we excluded data from agricultural crops and focused on tree species only. This is because crops contribute an order of magnitude less BVOC emissions globally than forests (Guenther et al., 2012). The final number of studies that fit this criteria are shown in Table 2 separated by herbivore type, tree type (conifer vs broadleaf), and measurement location. Note that some studies presented data from multiple types of plant/herbivore systems, and consequently one publication could have been counted as multiple "studies" for the purposes of constructing this table. The references are provided as a footnote below the table. A detailed description of the data used from each paper and any unit conversions that were applied to the data to make them comparable with one another is provided in the supplementary information. Briefly, all emission rates were converted to units of $\mu g\ m^{-2}\ h^{-1}$ and temperature-normalized to 30 °C (if enough information was provided to do the temperature correction). We are focusing on monoterpenes, sesquiterpenes, green leaf volatiles, and methyl salicylate so we did not normalize emissions to light – most papers did not contain enough information to do so and the majority of these compounds have not exhibited a large light-dependent emission rate. However, we also acknowledge this is a potential source of variability between studies and more research should be conducted to better understand the light-dependence of these emissions from different plant species.

Table 2 demonstrates that most quantitative bark borer IH-BVOC studies have been conducted on conifers rather than broadleaf trees. Very few IH-BVOC studies have been conducted on piercing-sucking insects' effect on tree VOC emissions, and the studies that have been conducted were on broadleaf trees only. The majority of IH-BVOC studies have investigated defoliator emissions from broadleaf trees (12 studies) with a handful of defoliator studies conducted on conifers (four studies). This table highlights there is a research gap in the following systems: bark borer/broadleaf, defoliator/conifer, and piercing-sucking insects/all tree types. Most piercing-sucking IH-BVOC studies have been focused on smaller herbaceous plants and/or crops. Table 2 also shows the number of studies conducted in different measurement locations for each herbivore type. We defined three categories for the measurement location: laboratory, field site with the plants rooted in the ground, or potted plants located in a greenhouse or research garden. Generally, true field measurements are lacking - particularly for bark borer and piercing-sucking insects. This is concerning because there does appear to be drastic differences between field measurements and other

Table 2
Summary of quantitative IH-BVOC studies on trees separated by tree type and measurement location for the three different herbivore classes.

Number of quantitative studies based on the type and measurement location					
Herbivore Type	Tree type	Measurement Location			
	Conifer	Broadleaf	Laboratory	Field	Potted Greenhouse or Field/Garden
Bark Borer	6	1	3	1	3
Defoliator	4	12	6	6	4
Piercing-Sucking	0	2	1	0	1

References used to construct this table: Achotegui-Castells et al. (2013); Blande et al. (2010), 2009, 2007; Brilli et al. (2009); Copolovici et al. (2011), 2011; Faiola et al. (2018); Ghimire et al. (2016), 2013; Ghirardo et al. (2012); Heijari et al. (2011); Joutsensaari et al. (2015); Kari et al. (2019); Kovalchuk et al. (2015); Li et al. (2012); Litvak and Monson (1998); Maja et al. (2014); Mäntylä et al. (2008); Mccormick et al. (2014); Schaub et al. (2010); Yli-Pirilä et al. (2016).

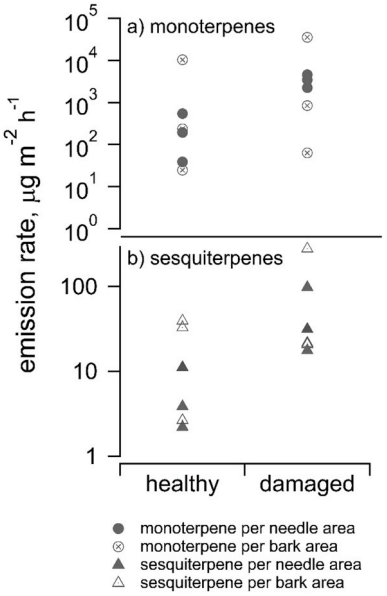

Fig. 2. Summary of IH-BVOC emissions for a) MT and b) SQT compounds from the bark borer/conifer system. Papers included in this analysis are Blande et al. (2010); Ghimire et al. (2016); Heijari et al. (2011); Kovalchuk et al. (2015); Joutsensaari et al. (2015); Faiola et al. (2018).

measurement locations. We will come back to this concept later in the paper.

First, we could not perform a synthesis of the bark borer/broadleaf system because there was only one study with quantitative data. A synthesis of quantitative results for the bark borer/conifer system is shown in Fig. 2. Error bars are not shown to improve clarity of the plot, but readers are directed to the original papers for the variability in the measurements. The variability of the measurements from individual papers is much smaller than the overall variability between studies, which is being highlighted in this figure. Three studies normalized the emission rate to leaf surface area or biomass and three studies normalized the emission rate data to bark surface area or mass. Two studies (Blande et al., 2009; Joutsensaari et al., 2015) reported Norway Spruce emissions normalized to biomass of tissue in the branch enclosure. All data were converted to units normalized to surface area as described in the supplemental information.

Healthy and insect-stressed emissions are shown for monoterpenes (a) and sesquiterpenes (b). Healthy plant emission rates between studies varied by an order of magnitude or more. Healthy conifer monoterpene emissions normalized to needle surface area ranged from 39-550 μg m^{-2} h^{-1}. Healthy conifer monoterpene emissions normalized to bark surface area ranged from 25-10,400 μg m^{-2} h^{-1}. Similarly, healthy conifer sesquiterpene emissions normalized to needle surface area ranged from 2-11 μg m^{-2} h^{-1}. Healthy conifer sesquiterpene emissions normalized to bark surface area ranged from 3-40 μg m^{-2} h^{-1}. Healthy monoterpene emissions exhibited a wider range than the healthy sesquiterpene emissions in the studies normalized to needle surface area.

Stressed conifer monoterpene emissions normalized to needle surface area were more consistent with one another than the healthy emissions, ranging from 2,200-4,600 μg m^{-2} h^{-1}. Stressed conifer monoterpene emissions normalized to bark surface area ranged from 63-35,600 μg m^{-2} h^{-1}. Stressed conifer sesquiterpene emissions normalized to needle surface area ranged from 18-98 μg m^{-2} h^{-1}. Stressed conifer sesquiterpene emissions normalized to bark surface area ranged from 21-279 μg m^{-2} h^{-1}. In this case, two of the studies reported nearly identical sesquiterpene emissions at 20.8 μg m^{-2} h^{-1} (Ghimire et al., 2016) and 21.6 μg m^{-2} h^{-1} (Kovalchuk et al., 2015), while the third study reported 279 μg m^{-2} h^{-1} (Heijari et al., 2011). Heijari et al. (2011) also reported substantially higher healthy monoterpene emissions than the other two studies at 10,400 μg m^{-2} h^{-1} versus 236 μg m^{-2} h^{-1} (Ghimire et al., 2016) and 25 μg m^{-2} h^{-1} (Kovalchuk et al., 2015). The studies normalized to bark surface area generally exhibited a broader range than those reported from studies normalized to needle surface area. This broad range was driven in large part by the Heijari et al. (2011) results, which investigated the exact same tree type (Scots pine) and herbivore type (*Hylobius abietis*) as Kovalchuk et al. (2015). This demonstrates all the variability cannot be explained by differences in the plant/herbivore system being studied. This comparison generally calls into question the reproducibility of normalization procedures, and highlights the need for a more standardized protocol to improve measurement comparability.

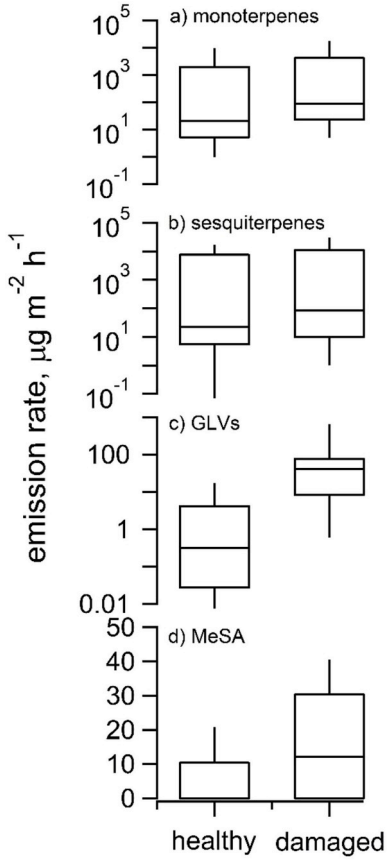

Fig. 3. IH-BVOC emissions from defoliator/broadleaf system. Papers included in this analysis are Blande et al. (2010), 2017; Maja et al. (2014); Brilli et al. (2009); Copolovici et al. (2011), 2017; Ghirardo et al. (2012); Li et al. (2012); Mäntylä et al. (2008); Mccormick et al., 2014; Schaub et al. (2010); Yli-Pirilä et al. (2016).

We could not present a synthesis of IH-BVOC emissions for the conifer/defoliator system due to limited overlap of compound classes that were reported. No more than two studies could be compared for any given category of monoterpene, sesquiterpene, green leaf volatile, or methyl salicylate emissions. A synthesis of results for the broadleaf/defoliator system is shown in Fig. 3. There were enough studies in this case to produce box and whisker plots. Average healthy monoterpene emissions were 20 μg m^{-2} h^{-1} with a 25th and 75th quartile range from 5-2000 μg m^{-2} h^{-1}. Average stressed monoterpene emissions were 88 μg m^{-2} h^{-1} with a 25th and 75th quartile range from 23-4200 μg m^{-2} h^{-1}. Average healthy sesquiterpene emissions were 22 μg m^{-2} h^{-1} with a 25th and 75th quartile range from 5-7600 μg m^{-2} h^{-1}. Average stressed sesquiterpene emission were 83 μg m^{-2} h^{-1} with a 25th and 75th quartile range from 10-11,000 μg m^{-2} h^{-1}. Average healthy green leaf volatile emissions were 0.3 μg m^{-2} h^{-1} with a 25th and 75th quartile range from 0.03-4 μg m^{-2} h^{-1}. Average stressed green leaf volatile emissions were 42 μg m^{-2} h^{-1} with a 25th and 75th quartile range from 8-78 μg m^{-2} h^{-1}. Only

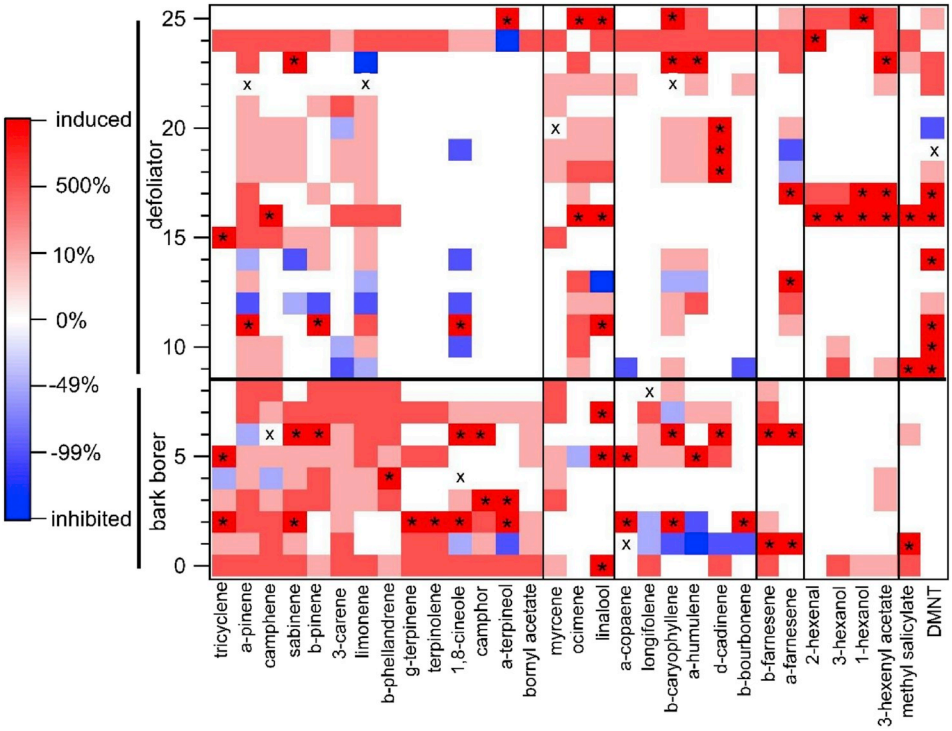

Fig. 4. Percent change in chemically-speciated emissions from the literature. Numbers on the y-axis reference the publication. 0: Blande et al. (2009), 1-4: Ghimire et al. (2016), 5: Heijari et al. (2011), 6: Kovalchuk et al. (2015), 7: Joutsensaari et al. (2015), 8: Faiola et al. (2018), 9-11: Blande et al. (2010), 12-14: Blande et al. (2007), 15: Achotegui-Castells et al. (2013), 16: Copolovici et al. (2017), 17: Copolovici et al. (2011), 18-20: Li et al. (2012), 21: Litvak and Monson (1998), 22: Mäntylä et al. (2008), 23: Schaub et al. (2010), 24: Joutsensaari et al. (2015), 25: Yli-Pirilä et al. (2016).

one study reported significant methyl salicylate (MeSA) emissions from healthy broadleaved trees. Average stressed MeSA emissions were 12 μg m^{-2} h^{-1} with a 25th and 75th quartile range of 0-30 μg m^{-2} h^{-1}.

The clearest IH-BVOC effect in the broadleaf/defoliator system is an increase in green leaf volatiles and MeSA emissions. In most individual studies, the monoterpene and sesquiterpene emissions also increased after defoliator herbivory, but the range in reported values was very large. The 25th – 75th quartile range for healthy monoterpene emissions spans over two orders of magnitude and the healthy sesquiterpene emissions range spans over three orders of magnitude. Some of this variability could be attributed to different plant types. In this category, four of the studies measured emissions from birch species (silver birch and mountain birch). The healthy monoterpene emissions from those four studies were 0, 5, 36, and 109 μg m^{-2} h^{-1}. Two of the studies measured emissions from alders (black alder and common alder) with a healthy monoterpene emission range from 1-16 μg m^{-2} h^{-1}. One of the studies measured emissions from oak with healthy monoterpene emissions of 32 μg m^{-2} h^{-1}. Five of the studies measured emissions from poplar/aspens with a healthy monoterpene emission range of 1.5-11,500 μg m^{-2} h^{-1}. The wide range of values in Fig. 3 is thus being primarily driven by the huge variability in values reported from aspen/poplars. In fact, ten of the twelve studies included in this analysis reported healthy monoterpene emissions less than 50 μg m^{-2} h^{-1}.

The percent change in chemically speciated emission rates from each of the bark borer and defoliator papers (all tree types) is summarized in Fig. 4. The x-axis lists the different compounds. We presented the compounds that were included in most papers from either bark borer or defoliator studies. Some of the green leaf volatiles and methyl salicylate were not reported from most studies but were still included in this synthesis because they are frequently noted in the plant stress literature. The compounds are separated by compound structure type with thin vertical bars. From left to right the compound structures are as follows: cyclic monoterpenoids, acyclic monoterpenoids, cyclic sesquiterpenes, acyclic sesquiterpenes, green leaf volatiles, and "other" compounds where "other" includes the plant hormone, methyl salicylate, and the homoterpene DMNT. The y-axis denotes the literature reference with the key included in the caption. Note some references are listed multiple times because the paper presented multiple tree types, multiple herbivore types, and/or reported measurements from multiple locations that were separated for this analysis. This is why the number of lines on the y-axis do not necessarily correspond with the number of studies presented in Table 2. The color-scale denotes the relative change in emission rate from healthy to stressed. Deep red indicates the compound was induced, or only detected after insect herbivory. These are further emphasized in the figure with an asterisk. Medium red indicates a change of 500% or more. Light red indicates a change between 10-499%. Light blue indicates the compound emission decreased up to 49% and medium blue indicates the compound emission decreased up to 99%. Dark blue indicates the compound was inhibited after herbivory stress (or a 100% decrease). Spaces marked with an, "x", indicate a change of less than 10% (increase or decrease), and a completely white space indicates there was no value reported for that compound.

The first thing to notice about Fig. 4 is the vast amount of white space. This could indicate 1) most studies are not providing a comprehensive report of all compounds detected in the emissions and/or 2) each study is identifying different types of compounds. We believe it is due to a combination of these effects. Some studies are reporting less than a handful of compounds, which is not representative of the complex emission profile from most tree species. Comparability between studies would be improved if a comprehensive list of all peak retention times measured above detection limit were reported in the supplemental information whether they were identified or not. This would provide information about how many peaks were omitted from the final report. In addition, to enable synthesis of data-sets, we recommend that the mass spectra of each peak observed above detection limited be included in a supplemental data file so peak identifications can be cross-referenced between papers. Ideally, researchers would also run a standard alkane ladder with associated retention times to provide further validation of peak identification using known retention indices. This would improve comparability, because it is also possible that some of the same compounds are being reported with different names because single component standards are not available for all these compounds and thus, we must rely on NIST database matches and retention indices. Consequently, including retention times for each peak in the supplemental

information with the raw peak area would allow researchers to use retention indices to determine if they are detecting the same compounds, but identifying them differently. It would also provide the research community with some idea about the percent contribution to total emission rates that could be attributed to unidentified compounds.

The second thing to notice about Fig. 4 is that most compounds exhibited an increase in emission rate, not a decrease. One notable exception is 1,8-cineole (also sometimes referred to by the common name, "eucalyptol"). 1,8-cineole emissions decreased after defoliator herbivory in most studies. However, 1,8-cineole emissions were found to increase, or even be induced, in most bark borer studies. Bark borer stress studies reported more types of cyclic monoterpene emissions, were more likely to show inducible monoterpene emissions, and in general exhibited a higher increase in monoterpene emissions than defoliator studies. Bark borer stress induced linalool emissions in the only studies to report linalool. Bark borer stress also was more likely to reduce cyclic sesquiterpene emissions than defoliator stress. Acyclic sesquiterpene emissions increased or were induced by both herbivore types, with just a couple of defoliator studies reporting a decrease in α-farnesene. Green leaf volatile emissions were most notable after defoliator stress. Bark borer stress does not appear to have a significant effect on most green leaf volatile emissions, but three studies reported an increase in hexenyl acetate after bark borer herbivory. Methyl salicylate was not reported or not detected in most studies. However, the studies that did detect methyl salicylate all observed an increase or induction of methyl salicylate emissions. It is also worth noting that different sample collection approaches and analytical systems can vary in recovery, and ultimately detection, of different plant volatile compounds, so this could contribute to some variation in reports as well. This is particularly true for acyclic terpenes, such as linalool and β-myrcene, and sesquiterpenes which are prone to decomposition and instrument line losses, respectively, as demonstrated in Faiola et al. (2012). This variation is likely not attributable to the specific herbivore type because most bark borer herbivore studies (6 out of 7) were looking at the same pine weevil, *Hylobius abietis*. Rather, it could be due to measurement location. No study performed in the lab observed MeSA emissions. MeSA was observed only in studies conducted in the field or a research garden. Although, it should also be noted that MeSA was not reported in all field or research garden studies, either. Alternatively, some of this variability could be due to inconsistencies in which compounds different research groups are mining in their GC-MS data. DMNT was not reported in any bark borer studies. However, defoliators consistently induced or increased DMNT emissions with just one exception.

A final point to note about Fig. 4: there is no clear single group of compound emissions that are affected by insect herbivory more than others. We point this out because reviews on this topic have stated that insect herbivores induce emissions of acyclic terpenoids in particular; the acyclic terpenoids are specifically called out as though they are affected more exclusively than other compounds. However, we do not see any basis for that conclusion in this data compilation. Yes, acyclic monoterpenoid and sesquiterpene emissions often increase following bark borer and defoliator herbivory, but no more so than many of the cyclic monoterpenoids and sesquiterpenes. Perhaps this conclusion was originally derived from papers reporting IH-BVOCs from herbaceous plants, which were not included in the quantitative synthesis. What we can say from this synthesis is that this conclusion is not supported for IH-BVOC emissions from broadleaf and conifer trees.

A summary of the averaged reported values converted to the same units used for basal emission rates in the MEGAN model are provided in Table 3. The current values used in MEGAN for the three most similar emission types are also shown for comparison. There is poor agreement between the current baseline MEGAN emissions and the average values reported from these papers for the unstressed emissions for all compound classes. For unstressed monoterpene emissions, the reported values are higher than that used for the same plant functional type in MEGAN. The unstressed sesquiterpene emissions are an order of magnitude lower for needleleaf evergreen boreal measurements than they are for the corresponding baseline MEGAN emission type, and the stressed SQT emissions are closer to the MEGAN baseline value. In contrast, the unstressed SQT emissions are two orders of magnitude higher for broadleaf deciduous measurements than they are for the corresponding baseline MEGAN emission type. The reported unstressed GLV emissions are lower than the baseline MEGAN values. This lack of agreement between the unstressed reported emissions and the MEGAN baseline emissions is perhaps unsurprising since MEGAN is based on a synthesis of many more papers than those included in this work. However, this table highlights the complexity of trying to define a new "stressed emission type" in MEGAN. The stressed values are sometimes similar to the MEGAN baseline values (but not always), and it is entirely possible that some of the measurements used to define the MEGAN

Table 3
Summary of average monoterpene (MT), sesquiterpene (SQT) and green leaf volatile (GLV) emission rates from healthy and damaged plants. "sd" denotes the standard deviation of the measurements. The final two rows are from MEGAN emission types that correspond to similar plant functional types as those included in the measurements. Emissions are normalized to a leaf area index of 5 to correspond with MEGAN default emission factors.

Plant Functional Type / Herbivore Type (if applicable)	healthy						damaged					
	MT	sd	SQT	sd	GLV	sd	MT	sd	SQT	sd	GLV	sd
Needleleaf Evergreen Boreal / bark borer	4500	980	27	4	8	2	17219	1180	245	49	97	19
Needleleaf Evergreen Boreal / external defoliator							40811	8162	417	83	46	9
Broadleaf Deciduous Temperate & Boreal / external defoliator	7700	1500	18000	3600	120	20	21000	4200	31000	6200	590	120
MEGAN ET2: Needleleaf Evergreen Boreal	1450	N/A	240	N/A	42*	N/A						
MEGAN ET7 & ET8: Broadleaf Deciduous Temperature & Boreal	990	N/A	180	N/A	42*	N/A						

*The GLV emissions from MEGAN include only 6-carbon oxygenated VOCs that were included in the "other compounds" category in MEGAN. These values are from MEGANv2.1.

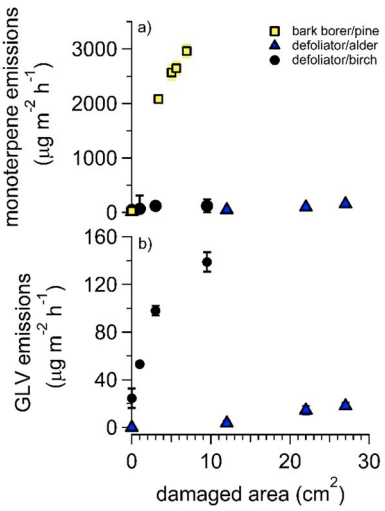

Fig. 5. Emission rates as a function of degree of herbivore damage for (a) monoterpenes and (b) green leaf volatiles (GLV). Bark borer/pine data from Kari et al. (2019). Defoliator/alder data from Copolovici et al. (2011). Defoliator/birch data from Yli-Pirilä et al. (2016) (supplementary information). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

emission types could have inadvertently included stressed emissions as well.

5.2. Degree of damage

IH-BVOC emission rate is positively related to the extent of damage for most IH-BVOC compounds (Niinemets et al., 2013). Fig. 5 shows a synthesis of literature data on the relationship between emission rate and extent of herbivore damage. Undamaged monoterpene emissions from all three studies were between 10-50 μg m^{-2} h^{-1}. The relationship between monoterpene emissions and extent of leaf damage for the defoliator/alder (Copolovici et al., 2011) system was linear between 0-27 cm^2 of damage (linear fit: y=5x, r^2=0.93). In contrast, the relationship between monoterpene emissions and extent of leaf/bark damage for the defoliator/birch (Yli-Pirilä et al., 2016) and bark borer/pine (Kari et al., 2019) systems was more logarithmic. This is particularly evident in the defoliator/birch system where monoterpene emissions reached a threshold of 122 μg m^{-2} h^{-1} after 3 cm^2 of damage. Monoterpenes from the bark borer/pine system jumped from 28 μg m^{-2} h^{-1} for undamaged plants to 2080 μg m^{-2} h^{-1} at 3.4 cm^2 bark damage and 2570 μg m^{-2} h^{-1} at 5.0 cm^2 bark damage, and while no threshold value was reached for the range of damage observed, the decreasing rate of increase with additional damage suggests a logarithmic relationship. Notably, IH-BVOC monoterpene emission rates increased much more with damaged bark area from bark borers than from damaged birch and alder leaf area from defoliators. A potential mechanism for this is that bark borer damage exposes large terpene resin pools with much higher emission capacity than the small amount of monoterpenes that are non-specifically stored in leaf tissues or the *de novo* monoterpene emission increases, which would be limited by synthesis rates. GLV emissions were not observed following bark borer herbivory from pines, but statistically significant increases were observed following defoliation of birch and alder. Similar to monoterpene stress emissions, the relationship between birch GLV emissions and damaged leaf area exhibited a potential threshold while the relationship between alder GLV emissions and damaged leaf area exhibited a linear relationship (linear fit: y=0.7x-1.6, r^2=0.94). Defoliation of common oak exhibited a similar "threshold effect" for monoterpene emissions, while GLV emissions showed an exponential increase (Copolovici et al., 2017). This data was not included in Fig. 5 because it was reported as % damage rather than damaged area, and consequently the data-sets could not be directly compared. The emissions of VOCs are most frequently reported in the literature as a function of either amount of larvae or time since onset of infestation. This information serves various purposes, but it is not sufficient for model implementation. Instead it is vital that the emissions are provided as a function of damaged leaf area - either in units of surface area or as a % damage - preferably as both. It is clear that the relationship between IH-BVOC emission rate and damaged area is important and can vary between different herbivore/plant systems and even between different compound classes of IH-BVOCs. This presents a challenge for model integration and characterizing this relationship is therefore of high priority in future research.

6. Other considerations

The IH-BVOC synthesis presented in this paper was focused on the short-term emission response located at the site of damage. It should be noted that there are other important considerations to achieve a comprehensive integration of IH-BVOCs into emission models. We will briefly discuss those considerations here, but there are not enough observations at this point to conduct a quantitative synthesis and make a recommendation for integrating these processes/issues into an existing emission model framework. The topics we consider include 1) systemic vs. localized response to herbivory, 2) short-term vs. long term emission effects, 3) influence of multiple stressors, and 4) other biotic stressors.

Insect herbivory not only affects plants at the site of physical damage, but it can induce changes at a systemic level - including effects on health and emissions from intact leaves on the infested plant, but also from neighbouring, undamaged plants. The systemic effect from insect herbivory can be substantial. For example, defoliation of oaks reduced photosynthesis both by directly damaging leaf tissue and indirectly by reducing photosynthesis from neighbouring, undamaged leaves. When the effect was integrated across the canopy, the indirect effect reduced photosynthesis considerably more than the direct effect (45.5% vs 8.5%; Visakorpi et al., 2018). Insect herbivory can increase systemic emissions of monoterpenes, sesquiterpenes, and GLV, where the effect varies for different plant species (Arimura et al., 2004; Blande et al., 2009; Ghimire et al., 2017, 2016; Heijari et al., 2011). For example, Scots pine and Norway spruce both have a significant systemic response during pine weevil herbivory. Intact Norway spruce shoots located on an insect-stressed plant demonstrated a 1-fold and 55-fold increase in monoterpene and sesquiterpene emissions, respectively (Blande et al., 2009), and Scots pine intact shoots demonstrated a 2.8-fold and 2.9-fold increase in monoterpene and sesquiterpene emissions, respectively (Heijari et al., 2011). In contrast, silver birch has shown no evidence of systemic induction of monoterpene or sesquiterpene emissions after pine weevil herbivory (Maja et al., 2014).

The published literature on herbivory stress emission almost exclusively includes short term measurements. The emission is most commonly measured for a couple of days to one week when herbivores are feeding, and continued for a few extra days after removal of the herbivores. Rarely is the emission measured during a time span that is comparable to a full feeding period in nature (~4-8 weeks). Such measurements are, however, crucial since the emission response to herbivory is not necessarily the same during short-term and long-term exposure. The impact of insect herbivory is generally to increase BVOC emission rates (per unit leaf area, Fig. 5) during feeding, but the leaf area is simultaneously decreased. This has an impact on the immediate emission, but also on the long-term plant biomass. It can take several growing seasons for evergreen species to recover the lost needles (Cedervind and Långström, 2003; Kurkela et al., 2005; Langström et al., 2001), and deciduous species produce significantly less leaves/needles in the years that follow defoliation (Piper et al., 2015; Tenow and Bylund, 2000). Tree mortality is furthermore enhanced, while tree growth is reduced, for multiple years following a season with defoliation and/or attacks by wood-boring insects (Cedervind and Långström, 2003;

Hoogesteger and Karlsson, 1992; Kulman, 1971; Langström et al., 2001; Naidoo and Lechowicz, 2001). Hence, long-term effects of insect herbivory could result in a reduction in forest emissions if tree mortality is extensive (Geddes et al., 2016). It is therefore vital that also long-term impacts are considered in emissions models.

Vegetation is usually impacted by multiple stresses in nature. Unfortunately, there are very few studies on how the emissions of IH-BVOCs from trees are modified by these interacting stresses, and often the results are not consistent with each other. For example, considering the interacting effect of elevated temperature and herbivory, Kivimäenpää et al. (2016) found both mono- and sesquiterpenes, from pine-sawfly infested Scots pine, to increase (2-4 fold) in response to slightly elevated temperatures (~1 °C) in an open-field experiment. Ghimire et al. (2017) conducted a similar experiment (same measurement set-up, tree and herbivore species), but showed the opposite effect; that a very modest temperature increase (<1 °C) reduced the emission of non-oxygenated monoterpenes (by 77%). Usually warming alone enhances BVOC emissions until a certain threshold, which is plant specific. Kleist et al. (2012) showed that temperatures above this threshold decreased *de novo* emissions of European beech, Palestine oak, Scots pine and Norway spruce, infested by unidentified aphids. This reduction was larger than the observed increase in monoterpenes released from damaged resin ducts in pine and spruce.

Elevated temperature is not the only interacting abiotic stressor of interest; tropospheric ozone pollution can also influence plant emissions. Elevated ozone usually stimulates the emissions of IH-BVOCs (Heiden et al., 1999; Kivimäenpää et al., 2016; Loreto et al., 2004), though the response is not always significant (Blande et al., 2007). Blande et al. (2007) discovered that the emission of IH-BVOCs from aspen infested by common leaf weevil was further enhanced when exposed to moderately elevated ozone levels (1.3 × ambient concentrations), but ozone was not observed to have this effect in the case of autumnal moth feeding on aspen. In contrast, Kivimäenpää et al. (2016) found that an enhanced level of ozone (1.5 × ambient concentrations) increased the emission rate of monoterpenes, but only in the absence of herbivory. Finally, Ghimire et al. (2017) showed that the systemic emission of non-oxygenated monoterpenes increased 8.6-fold in response to enhanced ozone levels (1.5 × ambient concentrations) and herbivory stress, in comparison to herbivory alone. The three-way interaction of herbivory, thermal and ozone stress has been investigated. Ghimire et al. (2017) demonstrated that such a combination of stressors enhanced the emission of sesquiterpenes greatly (16-fold) from pine, while Kivimäenpää et al. (2016) observed that mild herbivory enhanced the effects of warming, but repressed the effects of ozone on the emissions of IH-BVOCs in the spring that followed a summer with herbivory.

Increasing anthropogenic nitrogen deposition has created concerns about ecosystems reaching so-called, "critical loads" of soil nitrogen content, which could interact with herbivory to alter emissions. However, the impact of higher soil nitrogen levels on plant emissions is unclear. Some studies have demonstrated that BVOC emissions increase with higher soil nitrogen levels (Ghimire et al., 2017; Kivimäenpää et al., 2016; Lerdau et al., 1995), but the opposite response has also been observed (Blanch et al., 2007). Kivimäenpää et al. (2016) showed that the emissions were further enhanced when exposed to both higher temperatures and soil nitrogen levels (120 kg N ha^{-1} a^{-1}) than when the plants were only exposed to elevated temperature or soil nitrogen alone. In the same study, herbivory also enhanced the emissions further when the plant had higher levels of soil nitrogen available. Ghimire et al. (2017) showed that higher nitrogen levels enhanced the systemic emissions of total non-oxygenated monoterpenes (4.4-fold) post-feeding. Finally, Kivimäenpää et al. (2016) observed that the emission of myrcene was strongly enhanced during herbivory combined with enhanced levels of both ozone and soil nitrogen.

On its own, mild drought stress usually enhances emission of IH-BVOCs while severe drought decreases the emissions (Copolovici et al., 2014; Ebel et al., 1995; Mu et al., 2018; Peñuelas and Staudt, 2010), though the emission of individual monoterpenes from the same plant can respond to the stress differently (Bonn et al., 2019 and references therein). The effect can be enhanced when combined with herbivory stress. Alder, under stress by the feeding of green alder sawfly and drought, was shown to emit monoterpenes, GLV and methyl salicylate at a higher rate (and more quickly) than alder experiencing only herbivory stress (Copolovici et al., 2014). Ultimately, the literature on emission responses due to multiple simultaneous stresses is highly sparse for replicated conditions and it sometimes shows opposite effects for combinations of same stresses. Generally, herbivory emission response is further enhanced when the plant is also under the influence of abiotic stresses, though it is not always so. When multiple stresses are co-occuring their effects are sometimes additive, sometimes subtractive, or the effect of one single stress dominates the plant emission response (Holopainen and Gershenzon, 2010; Vapaavuori et al., 2009). It is clear that more measurements are needed to tease out the influence of multiple stressors.

Biotic stresses do not exclusively consist of insect herbivory. Other biotic stressors that can induce an emission response of VOCs in trees are for example insect oviposition (Hilker and Meiners, 2006; Mumm et al., 2003), gallmakers (Borges, 2018; Jiang et al., 2018) and pathogens (Copolovici et al., 2014; Jiang et al., 2016; Toome et al., 2010; Vuorinen et al., 2007). Insect herbivory is globally estimated to account for a wider spread (7 times larger area) and more severe damage than pathogens (Porta et al., 2008; van Lierop et al., 2015), though it is quite possible that the damage by pathogens is underestimated when conducted via aerial surveys (Hall et al., 2016; MacLean and MacKinnon, 1996; van Lierop et al., 2015). Non-aerial surveys in European forests show that insects are responsible for ~2.5 times more damage symptoms than fungi (Michel et al., 2018), while the risk of insect infestation in the USA has been estimated to be 3.6 times higher than by pathogens (Krist et al., 2007). Though fungal infections might account for less damage than insect herbivory, they are still ubiquitous in nature, and especially important to account for when the conditions are humid. Unfortunately, there are very limited studies investigating the influence of pathogens on VOC emissions from trees in nature. Most work has been done on vegetable- or fruit-carrying plants (see Jansen et al., 2011 and references therein), however, it is unclear if these emission responses can be applied to the types of pathogens and trees present in forested environments. The emission responses, including magnitude and VOC blend, from pathogen infected trees is different from herbivory stressed trees (e.g Copolovici et al., 2017, 2014; Vuorinen et al., 2007). For example, Toome et al. (2010) did not find the sum of monoterpenes to significantly increase from willow infected by leaf rust. This is opposite to what is usually observed from herbivory stressed plants (Figs. 2-5). Vuorinen et al. (2007), on the other hand, found that the emissions of monoterpenes and sesquiterpenes were within the same range for silver birch infected by either autumnal moth larvae or leaf spot, and that these emissions were more dependent on the specific clone used. However, leaf spot infected birch did not emit any methyl salicylate (above the limit of detection) and the pathogen only induced a slight response in the emission of DMNT. This was in stark contrast to the emission from herbivory infected birch in Vuorinen et al. (2007). Copolovici et al. (2014) and (2017), which measured mildew and gypsy moth infected oak, respectively, reported induced emissions in methyl salicylate and DMNT in case of feeding by gypsy moth, but only methyl salicylate, and not DMNT, was emitted by mildew infected oak. Finally, Jiang et al. (2016) found that rust infected poplar emits both DMNT and methyl salicylate. The evidence suggests other biotic stressors could be very important sources of plant volatile emissions, but more studies are needed to better understand their role.

7. Conclusions

Plant stress emissions are substantial, and IH-BVOC emissions in

particular will likely increase in many regions around the world as climate changes. These highly reactive emissions will influence atmospheric oxidant concentrations (and thus atmospheric reactivity) and aerosol processes, which are important for accurate climate predictions. We have provided a quantitative synthesis of the IH-BVOC emissions measurements presented in the scientific literature for trees that dominate global VOC emission rates, and have identified a number of important measurement gaps that we summarize in bulleted form below. These gaps preclude a quantitative treatment of IH-BVOC emissions (and biotic stress emissions more broadly) in models. Thus, filling these gaps should be the focus of future research to improve predictions of plant VOC emissions and chemistry in a changing climate.

- **More field measurements**

True field observations of IH-BVOC emissions are rare, but the limited evidence available indicates that plant VOC emissions (both undamaged and herbivore-damaged) differ greatly between locations like laboratory, research garden, and forest. It is true that field measurements are logistically more challenging. For example, it is difficult to predict when and where an insect outbreak will occur, and field observation campaigns take time to plan and prepare so there are legitimate barriers to conducting a comprehensive, well-planned measurement campaign. Furthermore, it can be difficult to find a control "undamaged" tree in the same vicinity where a large outbreak is occurring and it is problematic to use undamaged trees from a different geographical locations where light, temperature, soil moisture, etc. could also vary and influence plant VOC emissions. Despite these logistical challenges, it is clear from this synthesis that more field observations are critical for developing mathematical descriptions of IH-BVOC emissions that adequately represent real emissions in a forest environment.

- **Standard measurement reporting practices, including temperature normalization, surface area normalization, and critically, extent of damage**

A lot of the reported variability between IH-BVOC emissions could be related to differences in the extent of herbivore damage during each of the observation periods. IH-BVOC emission rates are very sensitive to the extent of damage and we recommend that both the absolute surface area of damage and the percent area of damage are reported in all future publications. It is likely that some (if not most) of the variability observed in IH-BVOC emissions between different individuals of the same tree species with the same insect herbivore is related to differences in extent of damage. This will be an important driving variable in any IH-BVOC emission model that needs to be well characterized for different compounds and at different levels of damage. These are particularly important targets for future research because 1) different types of compounds will exhibit a different dependence on extent of damage and 2) it is unclear currently if IH-BVOC compounds that are positively related to extent of damage will exhibit some sort of "threshold effect" and what level of damage is required before the IH-BVOC emissions plateau. Temperature and light conditions should be reported for all field and lab measurements in order to normalize between studies and improve comparability. Information about the developmental stage of the measured leaves/needles is also needed, as the leaves'/needles' potential to emit BVOCs changes throughout its lifetime (e.g. Aalto et al., 2014; Duhl et al., 2008; Guenther et al., 1991; Hakola et al., 2001). In practise such information could be given as "days after budburst" or "second year needles were measured".

- **More comprehensive reporting of all compounds observed**

Some of the reported variability between IH-BVOC emissions is likely related to which compounds' emission rates are reported. Some papers only present emission rates for a handful of compounds, which likely represent a fraction of the total number of compounds emitted. We recommend providing the raw GC chromatogram and mass spectra data for each peak in the supplementary information with identified peaks labeled and a list of peaks with retention times. This will improve comparability between studies, or could at least better explain discrepancies in total monoterpene, sesquiterpene, or green leaf volatile emissions. Additionally, more focus should be placed on reporting the behaviour of the emission of isoprene during and after biotic stress. This is particularly important since isoprene, the world's mostly emitted BVOC (Guenther et al., 2012), might suppress the formation and growth of atmospheric aerosol particles (McFiggans et al., 2019) and hence dampen the climatic cooling effects of clouds. Currently there is a lack of quantitative studies on the influence of insect herbivory on isoprene emission rates.

- **Quantitative measurements of IH-BVOC emissions from a broader spectrum of plant functional types (PFTs) and different PFT/"bug functional type" (BFT) combinations**

Some combinations of plant functional types and bug functional types have been studied more frequently than others. For example, bark borer/needleleaf and external defoliator/broadleaf have more measurements than bark borer/broadleaf and external defoliator/needleleaf. Meanwhile, piercing-sucking insects are generally underrepresented in the quantitative IH-BVOC emission literature and emissions following internal defoliation have not been reported. Widespread outbreaks of internal leaf defoliators, such as the aspen leaf miner, are occurring regularly across Alaska (Doak and Wagner, 2015). In European forests, leaf miners account for slightly more damage than bark borers (Michel et al., 2018), but still no quantitative data currently exists on IH-BVOC emissions resulting from internal leaf defoliation on large tree species. This is a missing combination of plant/herbivore in the IH-BVOC emission literature that could be a significant source of plant VOC emissions in certain areas. Most measurements of biotic stress are conducted on boreal forest plant species. The taiga biome is one zone that is expected to experience increased frequency and severity of insect outbreaks, but it is far from the only area that is affected. For example, the tropics is the biome that is estimated to emit by far the largest amounts of BVOCs (Guenther et al., 2012), and though biotic stresses are ubiquitous in the tropics, there exists no quantitative publications on biotic stresses of tropical forest species. A broader survey of IH-BVOC emissions from trees and shrubs that dominate BVOC emissions in different regions should be assessed.

- **Quantitative measurements of systemic emissions following herbivory including the temporal dynamics of those emissions**

A comprehensive IH-BVOC emission model will need to include emissions from the site of damage as well as systemic-induced emissions. These two sources of emissions will likely have very different temporal dynamics and a different relationship with driving environmental variables, like light and temperature. Systemic stress emissions are, by definition, *de novo* emissions. Consequently, they will depend on substrate availability and enzyme activity, and thus would likely be light and temperature dependent. There are a few studies investigating systemic IH-BVOC emissions following insect herbivory, but there are no continuous measurements isolating systemic emissions from the site of damage to provide insight on temporal dynamics and environmental controls.

- **Report time after onset of outbreak for field measurements**

IH-BVOC emission rates exhibit clear temporal dynamics that will be relevant for model integration. Reporting how long the herbivory has occurred will help interpret observations and provide valuable

information for understanding the temporal dynamics of IH-BVOC emissions.

- **Longer-term measurements**

There is a lack of information about how long biotic stress emissions last during active herbivory and after the herbivore activity has ceased. For example, are there multi-season historical effects? Future field work should prioritize multiple seasons of sampling in herbivore-affected areas. Future lab work should investigate how long IH-BVOC emissions last after herbivores are removed. The emission rate, as a function of the extent of damage, should also be measured during an entire natural feeding period. Until now this has only been measured during a few days, and hence it is unclear if this relationship can be extrapolated to the full length of the feeding season.

- **Controlled measurements of environmental controls on IH-BVOC emissions**

The instantaneous influence of light and temperature on IH-BVOC emission rates needs to be described. These are the current driving variables in plant VOC emission models, and it is highly probable there will still be a temperature (and sometimes light) dependence for certain types of IH-BVOC emissions.

- **More measurements of how the emission of IH-BVOCs is modified by interacting/multiple stresses**

Plant stress does not occur in isolation in the natural environment. Plants are often exposed to insect herbivory concurrently with drought, elevated tropospheric ozone, thermal stress, increased nitrogen deposition, or a combination of these. There have been some studies on this topic, but rarely are the same combinations of stressors used, and when they are, the results are often inconsistent with one another. It is critical to target field measurements of multiple interacting stressors because repeated exposure to different combinations of stress could alter the subsequent stress response. Long-term monitoring programs would likely be the most comprehensive approach to characterize plant stress responses to multiple stressors.

A number of these recommendations will be greatly aided by rapid instrumentation developments occurring in the field. On-line, rapid VOC measurements can be acquired using proton transfer reaction mass spectrometry (PTR-MS) to characterize emission rates from individual plants (Brilli et al., 2011; Maja et al., 2014) and fluxes at the canopy scale (Karl et al., 2008; Müller et al., 2010). Improvements to the detector, inlet, and ionization chamber have led to progressively better detection of VOCs, including the PTR3 (Breitenlechner et al., 2017) and the VOCUS (Krechmer et al., 2018). PTR-MS is particularly useful for capturing rapid temporal dynamics of emission rates from different compound classes. One limitation is that it does not separate structural isomers. For example, it does not separate different monoterpenes from one another or different sesquiterpenes from one another. Obtaining molecular-level detection and quantitation is important to understand implications for atmospheric chemistry because different structural isomers can have reactivities that vary by over an order of magnitude (Atkinson and Arey, 2003, 1998). For this reason, we highly recommend that all PTR measurements are supplemented with gas chromatography, which is primarily available for off-line analysis approaches at the moment. This includes commonly used methods such as thermo-desorption GC-MS (TD-GC-MS). Development and commercialization of rapid on-line GC-MS instrumentation is in progress. This instrument will likely provide the plant VOC emission community with a valuable tool to address all of the recommendations we have listed above, particularly those that target faster time resolution such as, “Quantitative measurements of systemic emissions following herbivory including the temporal dynamics of those emissions” and “Controlled measurements of environmental controls on IH-BVOC emissions.”

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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