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Environmental impacts on biogenic emissions of volatile organic compounds (VOCs)

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Environmental impacts on biogenic emissions of volatile organic compounds (VOCs)

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by

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Abstract: Environmental impacts on biogenic emissions of volatile organic compounds (VOCs)

This review summarizes the current knowledge about functions, drivers and impacts of biogenic VOCs. A particular focus is put on influencing factors other than direct temperature and radiation, which are known to be positively correlated with emissions and which are conventionally used for modelling the release of VOCs. Reactive air pollutants, drought stress and interaction with insects and diseases have been identified as major additional driving forces. However, none of these are currently considered in regional emission inventories. Nevertheless, first attempts have been made to implement drought stress as a linear relation to relative available soil water, disregarding differences in species and plant types as well as shifting compound composition. In addition, it is investigated how the existing uncertainty in determining biogenic emissions is influencing the estimation of air quality and regional climate. However, literature information on this is rudimentary and inconclusive.

Kurzbeschreibung: Einflussfaktoren auf biogene Emissionen volatiler organischer Kohlenwasserstoffe (VOC)

Die vorliegende Literaturstudie fasst den Stand des Wissens über die Funktionen, Triebkräfte, und Auswirkungen von biogenen VOCs zusammen. Insbesondere wird untersucht, welche Einflüsse zusätzlich zu Temperatur und Strahlung – welche seit langem bekannt sind und in Modellen abgebildet werden können – als bedeutsam angesehen werden. Dies sind vor allem ein direktes Einwirken von Luftschadstoffen und Trockenheit, sowie indirekte Faktoren wie das Auftreten von Insekten. Von allen diesen Einflüssen wird erwartet, dass sie sich im Rahmen des Klimawandels und der Luftreinhaltepolitik ändern. Allerdings wird keine dieser Triebkräfte in regionalen Emissionsabschätzungen berücksichtigt. Existierende Ansätze, die Wirkung des Trockenstresses in Modellen abzubilden vernachlässigen artspezifische Unterschiede und Veränderungen in der Zusammensetzung der Emissionen. Zusätzlich wird untersucht, inwiefern sich die existierenden Unsicherheiten bei der Bestimmung biogener Emissionen auf die Abschätzung der Luftqualität und des regionalen Klimas auswirken. Entsprechende Informationen aus der Literatur sind jedoch kaum verfügbar.

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List of abbreviations

AVOCs	Anthropogenic Volatile Organic Compounds
ATP	adenosine triphosphate, a molecule used to provide chemical energy for physiological processes
BVOCs	Biogenic Volatile Organic Compounds
CTM	Chemistry Transport Model
DGVM	Dynamic Global Vegetation Model
DMADP	Dimethylallyldi(or pyro)phosphat (important compound for terpenoid synthesis)
DMNT	Dimethyl-Nonatriene
GLVs	Green Leaf Volatiles, include LOX products and esters, particularly released when plants suffer tissue damage
LOX products	Compounds originating from the lipoxygenase pathway, i.e. aldehydes (hexanal, hexenal, nonenal, nonadienal) and alcohols (hexanol, hexenol, nonenol, nonadienol)
MBO	2-methyl-3-buten-2-ol, a partially oxidized form of isoprene produced by the MEP pathway
MEP pathway	Methyl-Erythritol-Phosphat pathway. Compounds produced are precursors for isoprene
MeSA	Methyl Salicylate
NADP	Nicotinamide adenine dinucleotide phosphate, a cofactor used in anabolic reactions
NOx	Generic term for the nitrogen oxides that are most relevant for air pollution, namely nitric oxide (NO) and nitrogen dioxide (NO_2).
OVOCs	Oxygenated Volatile Organic Compounds such as LOX products
PFT	Plant Functional Type
RCP	Representative Concentration Pathway
ROS	Reactive Oxygen Species
SOA	Secondary Organic Aerosols
VOCs	Volatile Organic Compounds

Summary

The aim of this report is to summarize the state of the art about emission of biogenic volatile organic compounds (BVOCs), their importance for the environment, and the impacts that control them. Focus is on reactions of living plants in terrestrial ecosystems. BVOCs are known to contribute to air chemistry processes that determine the formation of ozone and particles (aerosols) and thus influence air quality as well as the climate system. The mechanistic description of BVOC emission is needed in order to improve air chemistry and climate modelling but processes are heavily simplified regarding controlling influences and compound diversification. Therefore the issue of uncertainty needs to be addressed raising the question if simplifications are still suitable for providing highly resolved emission amounts as needed for climate change scenario analysis with regional and global models.

The environmental importance of BVOCs can be distinguished into three topics: Their impact on aerosol formation, the reactions with nitrous oxide and radicals which influence the concentration of ozone, and the biological functions such as protection and signaling. Regarding aerosol, the presence of highly reactive compounds such as isoprene is only slightly favoring aerosol yield or even tends to have a decreasing effect, while aerosol formation is enhanced in the presence of other compounds such as mono- or sesquiterpenes. In contrast, the importance of isoprene for ozone formation is higher than that of other terpenoids. Besides the reactivity of the compound and the availability of nitrous oxides as reaction partner, recent investigations show that positive feedbacks exist between biogenic and anthropogenic VOCs for aerosol as well as ozone formation. This cannot easily be represented by models yet. Regarding biological functions, various protective effects of terpenoids have been readily described. They can stabilize membranes and detoxify oxidative substances thus increasing the resistance of the photosynthetic apparatus against aggressive substances such as ozone. However, production costs are high so that a positive net-effect on carbon balance could not always be shown. Without doubt, BVOCs play an important role for signal transfer between leaves, individual plants, as well as between plants and insects. They repel herbivores and parasites but attract the enemies of these organisms, thus contributing to numerous interactions within the ecosystem.

Impacts on BVOC emissions are numerous with direct and indirect influences on temperature and radiation being the most important as well as the ones that are best described. Two model approaches have been developed that differ in their relation to photosynthesis. CO_2 air concentration and drought are known to also impact BVOC emission directly and indirectly (by affecting the production of precursor compounds as well as the leaf area), but much less is known about the nature of this relationship. For representing the impact of these two influences, (almost) only very simplified empirical relations are available. These suffice to represent specific case studies but are prone to large errors when applied generally. In particular considering drought impacts is cumbersome since mild stress is not affecting or even increasing emissions, while prolonged and intensive stress leads to substantial emission reductions. This (in relation to CO_2) fast response pattern is difficult to establish in dependence on spatially varying soil- and vegetation.

There are hardly any modelling approaches for considering other potentially important impacts (nutrients, air quality, and disturbances) although it seems a ubiquitous feature of BVOCs to be sensitive to any kind of stress. Emissions are increased when ozone degrades membranes on subcellular levels as well as in response to damages that are due to hailstorm or insect attacks of any kind. It should be noted that stress induced emissions mostly consist of non-terpenoids. Thus, accounting for stress responses not only changes the quantity but also the quality, resp. the mixture of the emission events. Considering stress-related responses is a major challenge for

the future, in particular since stress events are supposed to increase in intensity as well as frequency under climate change conditions. Therefore, a realistic representation of non-terpenoids without considering this response type seems to be impossible.

The emission of terpenoids, in particular isoprene, is simulated by regional and global emission models, which are prone with high uncertainties. These result from lumping species-specific plant properties into inflexible vegetation types, the interaction between direct and indirect impacts such as leaf biomass change and shift of vegetation types, and the simplified representation of dynamically changing environmental conditions such as CO_2 and drought. In particular the representation of drought requires knowledge of soil conditions that is often not sufficiently available. Depending on whether indirect effects are considered and how CO_2 and drought impacts have been implemented, scenarios of how BVOC emissions develop in future vary widely not only in amount but also in direction.

Zusammenfassung

Das Ziel dieser Arbeit ist es, den Stand des Wissens über die Emission von natürlichen Kohlenwasserstoffen zusammen zu tragen, und ihre Bedeutung für die Umwelt sowie die sie beeinflussenden Faktoren zu beschreiben. Dabei liegt der Focus auf den Reaktionen von lebenden Pflanzen in terrestrischen Ökosystemen. Von diesen sogenannten biogenen volatilen organischen Komponenten (BVOCs) ist bekannt, dass sie an luftchemischen Prozessen beteiligt sind, die die Ozon- und Partikelbildung wesentlich bestimmen, und damit die Luftqualität und das Klimasystem beeinflussen. Bei ihrer Berücksichtigung im Rahmen von Luftchemie- und Klimamodellierung werden stark vereinfachte Annahmen hinsichtlich Emissionsmenge und Zusammensetzung gemacht. Es ist also die Frage, wie groß die Unsicherheiten sind, die sich aus diesen Vereinfachungen ergeben, und wie stark sie sich auf Szenarioanalysen auswirken.

Die Bedeutung der BVOCs kann in drei Bereiche gegliedert werden: Ihre Wirkung auf die Partikelbildung, die Reaktionen mit Stickstoffoxiden und Radikalen, die die Ozonkonzentration beeinflussen, und die Schutz- und Signalfunktionen, die sie für die Pflanzenwelt ausüben. Grundsätzlich wird die Partikelbildung durch hoch reaktive Komponenten wie das Isopren nur wenig gefördert oder sogar gedämpft, während die Emission weniger reaktiver Substanzen wie Mono- und Sesquiterpene sie eher fördern. Umgekehrt, steigt die Bedeutung der BVOC für die Ozonbildung mit der Reaktivität – ist also für Isopren höher als für die meisten anderen Terpenoide. Neuere Untersuchungen zeigen, dass neben der Reaktivität der Komponente und ihrem Mengenverhältnis zu den Stickstoffoxiden in der Luft auch Wechselwirkungen zwischen anthropogenen und biogenen Kohlenwasserstoffen sowohl auf die Partikel als auch auf die Ozonbildung verstärkend wirken. Diese Wechselwirkungen können bisher nur unvollständig in Modellen berücksichtigt werden. Bei den biologischen Funktionen sind verschiedene Schutzeffekte von Terpenoiden beschrieben worden. Sie können eine Stabilisierung von Membranen bewirken und haben antioxidative Wirkungen, die vor allem die Empfindlichkeit des Photosynthese-Apparates gegenüber aggressiven Substanzen wie Ozon vermindern. Allerdings sind die Kosten der Produktion von BVOCs oft hoch, so dass eine positive Netto-Wirkung auf die Kohlenstoffbilanz nicht immer eindeutig nachgewiesen werden kann. Unbestritten ist die Bedeutung von BVOCs bei der Signalübermittlung zwischen Pflanzenteilen, Einzelpflanzen sowie zwischen Pflanzen und Insekten. BVOC Emissionen wirken abwehrend auf Parasiten und Herbivoren, locken aber Feinde dieser Organismen an. Sie tragen daher maßgeblich zum Zusammenwirken von Ökosystemen bei.

Von den Umweltbedingungen, die die Emission von BVOCs bestimmen, können sowohl kurzfristige als auch langfristige Wirkungen von Temperatur und Strahlung relativ gut beschrieben werden. Dafür werden zwei unterschiedliche Modellansätze verwendet, die sich in der Art ihrer Verknüpfung mit der Photosynthese unterscheiden. Über den Einfluss des CO_2 Gehaltes der Luft und von Trockenheit, die beide sowohl direkte als auch indirekte Wirkungen (über die Produktion von Vorläufersubstanzen und die Variation der Blattfläche) auf die Emission haben, ist weniger bekannt. Für die direkten Wirkungen dieser beiden Einflüsse werden bisher (fast) nur stark vereinfachte empirische Funktionen eingesetzt, mit denen sich zwar Anpassungen an spezifische Fallstudien erreichen lassen, eine allgemeine Anwendung aber mit hohen Fehlern behaftet ist. Insbesondere die Berücksichtigung von Folgen einer verminderten Wasserverfügbarkeit stellt eine Herausforderung dar, da Trockenheit die Emissionen bei mildem Stress nicht vermindert sondern eventuell sogar erhöht, während längere und intensive Trockenheit zu gravierenden Emissionsreduktionen führt. Es ist daher notwendig, den (relativ zu CO_2) schnellen Wechsel in Abhängigkeit von räumlich stark variierenden Boden- und Vegetationsbedingungen darzustellen.

Für die Abbildung weiterer Umweltbedingungen (Nährstoffe, Luftqualität, Störungen) sind bisher kaum Modellansätze beschrieben, obwohl kein Zweifel daran besteht, dass verschiedenste Stresseinflüsse BVOC Emissionen provozieren oder erhöhen können. Dies betrifft sowohl die zersetzende Wirkung von Ozon auf subzellularer Ebene wie auch die Verletzungen die durch Wind, Hagel, kauende oder stechende Insekten hervorgerufen werden. Allerdings ist zu berücksichtigen, dass hierdurch vor allem Nicht-Terpenoide induziert werden und dadurch also nicht nur die Intensität sondern auch die Mischung der Emissionen verändert wird. Die Abbildung solcher induzierter Emissionen wird als eine Hauptherausforderung gesehen, insbesondere unter dem Aspekt einer durch globale Veränderungen möglicherweise zunehmenden Störungsintensität und –frequenz. Ohne eine Berücksichtigung dieses Einflusses erscheint allerdings eine realistische Abbildung der Emission von Nicht-Terpenoiden unmöglich.

Die Emission von Terpenoiden, insbesondere Isopren, wird in regionalen und globalen Simulationen abgeschätzt, die allerdings mit großen Unsicherheiten behaftet sind. Diese resultieren vor allem aus der Zusammenfassung von Arten in grob klassifizierte Vegetationstypen, der Wechselwirkung mit indirekten Einflüssen wie der Veränderung von Blattbiomasse oder einem Wechsel der Vegetationsart, und aus der vereinfachten Abbildung von sich dynamisch verändernden Umweltbedingungen, insbesondere CO_2 und Trockenheit. Gerade die Abbildung der Trockenheit erfordert die Berücksichtigung von Bodeneigenschaften, die häufig nur unzureichend bekannt sind und zudem horizontal stark variieren. Je nachdem ob und wie indirekte Entwicklungen berücksichtigt werden und wie stark der CO_2 und Trockenheitseinfluss gewertet wird, unterscheiden sich Szenario-analysen über die zukünftigen Entwicklungen der BVOC Emission nicht nur in der Menge sondern auch im Vorzeichen.

1 Background

Besides reactive nitrogen oxides, VOCs are important precursors for the formation of tropospheric ozone and secondary aerosols. Excessively high ozone concentrations are representing a considerable threat to human health, causing yield losses in agriculture and forestry, and reduce carbon sequestration as well as other ecosystem services. Secondary aerosols or fine particles are also causing pulmonary diseases and are important cloud condensation nuclei.

In order to reduce health risks and environmental decline, precursors of air pollutants should be diminished. Since these are produced and transported across national boundaries, international agreements are necessary, such as the Convention on Long-Range Transboundary Air Pollution forged under the umbrella of the UN Economic Commission for Europe (UN ECE) in 1979. Every such commitment is bound to be founded on scientific evidence as comprehensive as possible.

A considerable share of VOCs originates from biogenic emissions (BVOCs), even in densely populated regions such as Central Europe. In addition, the reactivity (or ozone forming potential) of many BVOCs is much higher than the usual blend of anthropogenic VOCs (AVOCs). Therefore, in order to evaluate the most efficient air pollution reduction strategies, it is important to know the quantity and composition of BVOC emissions.

BVOC emissions have been studied since the late 1980's and relationships between some main compounds and environmental conditions have been quantified for many plant species. However, a growing body of evidence indicates that other drivers than temperature and radiation exist that cannot be neglected. These drivers as well as the compound variability need to be quantified in order to be used as input for coupled air chemistry transport models (CTMs) which can then calculate air quality from emissions and meteorology data.

2 Objectives

This literature review aims to summarize the state of the art regarding function, emission, and impact of biogenic VOCs. Special interest is put on environmental conditions that affect BVOC emissions and composition but are not or not sufficiently considered in conventional air chemistry transport models. These models are important tools to estimate air quality development under scenarios of climate change or air pollution control. Therefore, it is highly important to incorporate any mechanism that is sensitive to one or both kinds of scenarios and that has the potential to significantly alter air pollutant concentrations. Scenario calculations are needed to develop efficient air pollution mitigation strategies on national and international level.

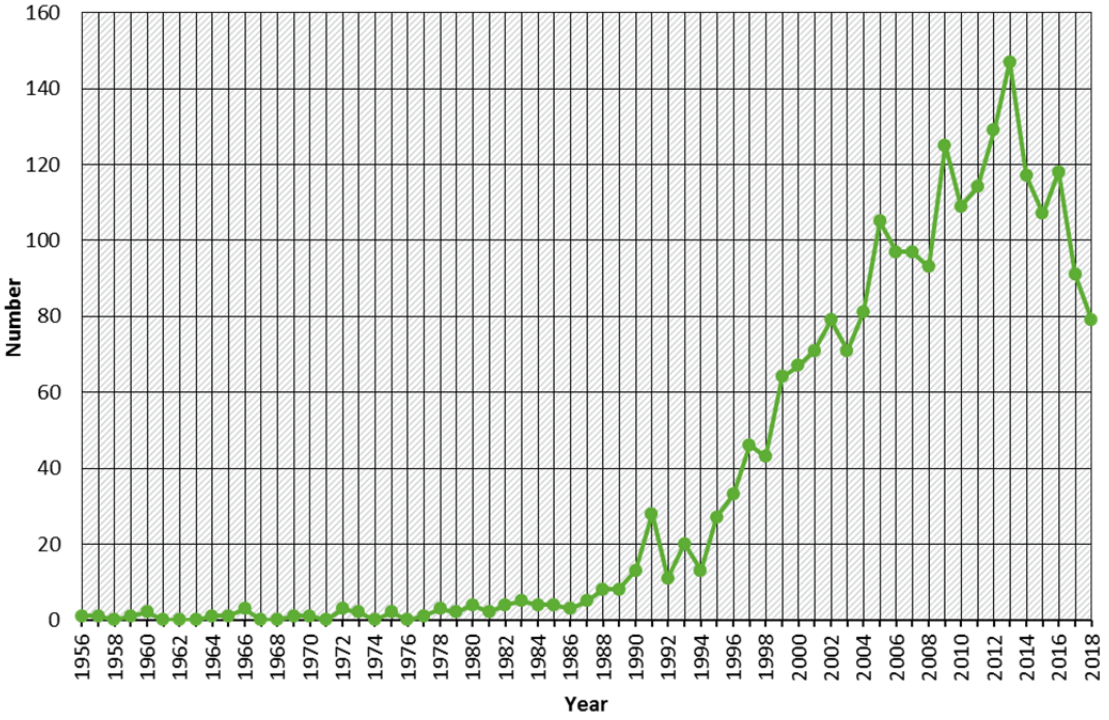
Furthermore, this study should help to interpret measurement results that are not easily explained by current knowledge. For example, ozone concentration may be different in years of similar temperature development, indicating that temperature may not be the major driver under all circumstances. Results will be provided to working groups of the Long-Range Transboundary Air Pollution Convention.

3 Literature Basis

The study is mostly based on literature published in international peer-reviewed journals that has been collected from data repositories of publishers (ScienceDirect (Elsevier), SpringerLink, Wiley Online Library) and other organizations (Scopus, Clarivate Analytics (formerly Thomson Reuter), Mendeley, ResearchGate). Additional data sources are book chapters and theses since they occasionally include complementary data sources not (yet) published or conclusions from literature summaries that are valuable for this analysis. The literature research has been done with a special emphasize on temperate regions, i.e. Central Europe, The United States of America and (to a lesser extent) East Asia (i.e. China). Occasionally, additional areas such as the Amazon and the Mediterranean region have been included since some mechanisms have been demonstrated particularly in hotter environments but are - or may be under future conditions - relevant for temperate regions too.

Overall 2224 peer-reviewed papers and 44 other publications related to BVOC emission and chemistry, published between 1957 and 2018 (see Figure 1), were evaluated for this report. These papers were derived from almost 300 journals, the first three contributing 325 (15 %, 'Atmosphere Environment', 224 (10 %, from 'Atmospheric Chemistry and Physics') and 176 (8 %, 'Journal of Geophysical Research') publications. From these, 751 publications were directly used for the review.

Figure 1: Number of publications with BVOC relation, considered in this review



In addition to the reference list given in the end of this report, all cited literature is provided in an EndNote compatible (RIS formatted) literature data base which also includes abstracts, DOI numbers and web-URLs.

4 Experimental Basis

Keyword: BVOC measurements

Measurements of BVOC emissions go back until 1957 (Sanadze 1957) but have usually been conducted by indirect techniques and are analyzed off-line with labor-intensive methods. These resulted in disjoint results and were generally restricted to only a few compounds. Since the end of the millennium, new instruments became available that allowed near-continuous measurements of several compounds combined with on-line spectroscopy analysis (De Gouw *et al.* 1999; Fall *et al.* 1999). An overview about the methodology of biogenic emission measurements is given in Ortega and Helmig (2008) and Materic *et al.* (2015).

The majority of measurements available today are from chamber measurements that cover soil samples, small plants or parts of trees, i.e. branches. They may be carried out in the field where conditions are fully or partly ambient (e.g. Amin *et al.* 2013; Bourtsoukidis *et al.* 2014a; Bourtsoukidis *et al.* 2014c; Eller *et al.* 2016; Genard-Zielinski *et al.* 2015; Helmig *et al.* 2013; Kajos *et al.* 2013; Kivimäenpää *et al.* 2013; Valolahti *et al.* 2015) but are more frequent in controlled environments such as a greenhouse or laboratory. Such measurements are particular useful for estimating emissions under standard temperature and radiation conditions (emission factors) that can be used as input for models. Thus, determining these emission factors comprises the majority of emission measurements today.

Controlled experimental studies also serve to observe emission responses under various environmental gradients and stressors such as drought (e.g. Bamberger *et al.* 2017; Dani *et al.* 2014b; Loreto *et al.* 2001a; Lüpke *et al.* 2017b), heat (e.g. Behnke *et al.* 2007; Copolovici *et al.* 2015; Kleist *et al.* 2012; Velikova *et al.* 2006), light quality (e.g. Arena *et al.* 2016; Kegge *et al.* 2013; Laffineur *et al.* 2013; Pallozzi *et al.* 2013b), herbivory (e.g. Copolovici *et al.* 2011; Faiola *et al.* 2015; Litvak and Monson 1998; Prieme *et al.* 2000), nutrition (e.g. Harley *et al.* 1994; Hu *et al.* 2018; Litvak *et al.* 1996; Muzika *et al.* 1989), CO_2 concentration (e.g. Constable *et al.* 1999b; Kreuzwieser *et al.* 2006; Monson *et al.* 1991; Rosenstiel *et al.* 2003; Staudt *et al.* 2001), UV radiation (e.g. Guidolotti *et al.* 2016; Pallozzi *et al.* 2013a; Tiiva *et al.* 2007a), wounding (e.g. Brilli *et al.* 2011; Kanagendran *et al.* 2018b; Portillo-Estrada *et al.* 2017; Rinnan *et al.* 2013), salt stress (e.g Loreto and Delfine 2000; Teuber *et al.* 2008), or ozone air exposure (e.g. Cojocariu *et al.* 2005; Fares *et al.* 2010; Llusia *et al.* 2002; Loreto *et al.* 2004; Pellegrini *et al.* 2012; Tani *et al.* 2017).

Emission determination in open environments is less frequent and long-term measurements that provide seasonal or even inter-annual information are exceptionally rare. An overview of ecosystem-scale isoprene flux data until 2010/2011 has been provided by Unger *et al.* (2013), which is reproduced in Table 1. A compilation of measurements in tropical sites for the same period is available from Alves *et al.* (2016). Further studies on grasslands that concentrate on methanol emissions are listed in Wohlfahrt *et al.* (2015), which cover sites in Switzerland, Austria and Sweden (Brunner *et al.* 2007; Holst *et al.* 2010; Hörtnagl *et al.* 2011). Field campaigns determining BVOC emissions from more recent publications are listed in Table 2.

In addition, remote sensing methodology based on aircrafts (e.g. Davis *et al.* 1994; Greenberg *et al.* 2014; Gu *et al.* 2017; Wiedinmyer *et al.* 2005; Yu *et al.* 2017) or satellites is increasingly applied. The latter usually serves to determine the concentration of formaldehyde, which is indicative for BVOC emissions (e.g. Abbot *et al.* 2003; Barkley *et al.* 2009; Barkley *et al.* 2013; Foster *et al.* 2014; Han *et al.* 2013; Marais *et al.* 2012; Palmer *et al.* 2006; Stavrakou *et al.* 2018). Very recently, a new satellite-based methodology has been put forward that aims to directly

estimate BVOC emission activity from light use efficiency that can be derived from photochemical reflectance (Filella *et al.* 2018).

Overall, BVOC emission fluxes have been measured at a range of ecosystem types and regions. A focus has been put on measurements in tropical forests since these are the main contributors for isoprene emissions globally. Despite the efforts at a well-equipped site in Finland, boreal forests are less well investigated although they are assumed to dominate the world's budget of monoterpene emissions. However, a closer look also reveals knowledge gaps that occur due to differences between ecosystems of the same type. For example forests of the same type generally don't have the same species composition so that the response of African rainforests might be different from those in South America or Malaysia. The same is valid for temperate ecosystems that include many high-isoprene emitters in the US (many observations) but hardly any species of this emitter type in Central Europe (few observations).

Another major deficit is the generally short period of observation, concentrating in one or two years. Since BVOC emissions very much depend on the previous weather conditions as well as the general plant health and development state, the extrapolation from a short campaign up to the full seasonal cycle throughout the years is very questionable. Recognizing the scarcity of long-term emission data from the field, Rinne *et al.* (2016) concluded that a 'reliable network of observations' that is equipped with continuous free-air measurement techniques is urgently needed.

TextBox: Location of BVOC Measurements

Interdisciplinary BVOC measurement campaigns have been conducted mainly in areas where high isoprene and monoterpene emissions had been expected that are likely to influence global air chemistry. These are in particular boreal forests (Finland, Canada), tropical areas (Brazil, China) and the southeast United States. In addition, selected ecosystems have been investigated in order to determine the potential impacts of expected climate and land-use changes. These are in particular the Mediterranean area (Italy, France) and plantation forests (Belgium, China, and USA). In Germany, integrated measurements were established for the main forest ecosystems with dominating species pine (Hartheimer Wald, 1998-1999), spruce (Waldstein, 2001-2002), and mixed beech (Research Centre Jülich, ECHO 2002-2003). Smaller campaigns were carried out for agricultural sites (POPCORN, 1994; CARBOZALF, 2014-2016). In addition, measurements were conducted in few urban areas (Stadtwald Frankfurt, 1995; BAERLIN campaign, 2014; Essen, 2012 (Wagner and Kuttler 2014)) and at other particular places (Taunus (Bourtsoukidis *et al.* 2014c); Ozone fumigation site Kranzberger Forst (Cojocariu *et al.* 2005)).

Table 1: Description of field campaigns determining above-canopy isoprene fluxes, collected throughout 1995–2010 across a wide range of ecosystem types, regions and seasons

Site	Ecosystem	Period	Location	Reference
Belgium	Temperate mixed	08/2009 06–08/2010–2011	50° N, 6° E	(Laffineur *et al.* 2011) (Laffineur *et al.* 2012)
Brazil, Manaus	Tropical rainforest	07/2001, 09/2004	2.35° S, 60°W, 2.6° S, 60°W	(Kuhn *et al.* 2007) (Karl *et al.* 2007)
Brazil, Santarem	Tropical rainforest	07/2000 04/2001	2.9° S, 55°W	(Rinne *et al.* 2002) (Müller *et al.* 2008)
Canada	Boreal coniferous	07/1994 09/1994	54° N, 105°W	(Pattey *et al.* 1999)
China	Plantation (rubber)	02–03/2002 07/2002	21° N, 101° E	(Baker *et al.* 2005)
Congo	Tropical rainforest Savanna	03/1996 11/1996 11/1996	2° N, 16° E 2° N, 16° E 4° N, 18° E	(Greenberg *et al.* 1999)
Costa Rica	Tropical lowland Tropical rainforest	10/1999 03–04/2003	10° N, 84°W	(Geron *et al.* 2002) (Karl *et al.* 2004)
Finland	Boreal coniferous	08/2001 10–10/2010-11	61° N, 24° E	(Spirig *et al.* 2004) (Hakola *et al.* 2012)
Germany	Agriculture (maize)	08/1994	53° N, 11° E	(Koppmann *et al.* 1998; Wedel *et al.* 1998)
Germany	Urban forest	08/1995	50° N, 8.4° E	(Steinbrecher *et al.* 2000)
Germany	Temperate deciduous	07/2002-2003	50° N, 6° E	(Spirig *et al.* 2005)
Germany	Temperate coniferous	04/1998 08/1999	48° N, 7.4° E	(Komenda and Koppmann 2002)
Germany	Temperate coniferous	07/2001–2002	50° N, 11° E	(Graus *et al.* 2006; Plewka *et al.* 2006)
Italy	Mediterranean shrubland	06/2007	41° N, 12° E	(Davison *et al.* 2009)
Malaysia, Borneo	Tropical rainforest	11/2003 04-07/2008	3° N, 102° E 4.6° N, 118° E	(Saito *et al.* 2008) (Langford *et al.* 2010)
Mongolia	Mountainous grassland	06–08/2002, 09/2002	44° N, 116° E	(Bai *et al.* 2006)
South Africa	Savanna	02/2001	25° S, 31° E	(Harley *et al.* 2003)
Sweden	Plantation (willow)	07/2001	58° N, 12° E	(Olofsson *et al.* 2005)
US, California	Mediterranean coniferous	06/1999	39° N, 120°W	(Schade and Goldstein 2001)

Site	Ecosystem	Period	Location	Reference
US, Massachusetts	Temperate deciduous	06–08/1995 06–08/2007	45° N, 72°W	(Goldstein *et al.* 1998) (McKinney *et al.* 2011)
US, Michigan	Temperate deciduous	08/1998 06–08/2000–2002	46° N, 85°W	(Westberg *et al.* 2001) (Pressley *et al.* 2005)
US, Wisconsin	Temperate deciduous	07/1993	46° N, 90°W	(Isebrands *et al.* 1999)

Reproduced from Unger *et al.* (2013), with additions for the sites in Finland, Germany, Italy, Malaysia and California (US).

Table 2: Description of campaign results of above-canopy BVOC flux measurements published since 2013

Site	Ecosystem	Period	Compounds	Location	Reference
Australia	Grassland	02-05/2012 01-02/2013	isoprene monoterpenes	44° S, 151° E	(Emmerson *et al.* 2016)
Australia	Eucalypt forest	02/2011 04-05/2012	isoprene monoterpenes	36° S, 148° E	(Emmerson *et al.* 2016)
Belgium	Plantation (poplar)	06–10/2012 01–12/2015	isoprene, OVOCs*	51° N, 3.5°E	(Zenone *et al.* 2016) (Brilli *et al.* 2014) (Portillo-Estrada *et al.* 2018)
Belgium	Agriculture (maize)	05-10/2012	monoterpenes alkenes OVOCs*	50° N, 4.4°E	(Bachy *et al.* 2016)
Brazil (Manaus)	Tropical rainforest	09–01/2010–11	isoprene monoterpenes sesquiterpenes	2.35° S, 60°W	(Alves *et al.* 2016)
China	Plantation (pine)	05–01/2013–2016	isoprene monoterpenes	26° N, 115° E	(Bai *et al.* 2017)
China	Plantation (bamboo)	07–01/2012–2013	isoprene monoterpenes	30° N, 119° E	(Bai *et al.* 2016)
China	Temperate mixed	07–09/2010–11	isoprene monoterpenes	42° N, 129° E	(Bai *et al.* 2015)
Czech Republic	Mountainous coniferous	07/2014	isoprene monoterpenes OVOCs*	49° N, 18° E	(Juráň *et al.* 2017)
England	Temperate deciduous	06-08/2005	isoprene monoterpenes OVOCs*	51° N, 0.9° E	(Langford *et al.* 2017)
Estonia	Hemi-boreal mixed	09-10/2012	Monoterpenes sesquiterpenes OVOCs*	58° N, 27° E	(Bourtsoukidis *et al.* 2014a)

Site	Ecosystem	Period	Compounds	Location	Reference
Finland	Boreal coniferous	04–06/2013 05–11/2015-16	isoprene monoterpenes sesquiterpenes OVOCs*	62° N, 24° E	(Schallhart *et al.* 2018) (Hellén *et al.* 2018a) (Rantala *et al.* 2014)
France	Mediterranean deciduous	06/2014	isoprene monoterpenes OVOCs*	43° N, 5.4° E	(Zannoni *et al.* 2016)
Germany	Urban greens	06–08/2014	monoterpenes, OVOCs*	53° N, 14°E	(Bonn *et al.* 2016)
Germany	Agricultural (maize)	06–08/2015**	monoterpene, OVOCs*	53° N, 14°E	(Wiß *et al.* 2017)
Italy	Mediterranean mixed	09/2011	isoprene monoterpenes OVOCs*	42° N, 12° E	(Fares *et al.* 2013) (Langford *et al.* 2017)
Italy	Mediterranean deciduous	06-07/2012	isoprene monoterpenes OVOCs*	45° N, 11° E	(Schallhart *et al.* 2016) (Acton *et al.* 2016)
Sweden	Subarctic heath	06–08/2012**	isoprene monoterpenes sesquiterpenes OVOCs*	28° N, 18° E	(Tang *et al.* 2018)
US, California	Temperate coniferous	06-07/2009	isoprene monoterpenes OVOCs*	39° N, 121°W	(Park *et al.* 2014)
US, Carolina	Plantation (pine)	06–08/1995 06–08/2007	monoterpenes OVOCs*	36° N, 79°W	(Geron *et al.* 2016b)
US, Colorado	Mountainous coniferous	07/2014	isoprene alkenes	39° N, 105°W	(Rhew *et al.* 2017)
US, Missouri	Temperate deciduous	05–10/2011 05–10/2012	isoprene monoterpenes methanol	38° N, 92°W	(Potosnak *et al.* 2014) (Seco *et al.* 2015)

* OVOCs = oxygenated VOCs including alcohols, ketones, aldehydes, etc.

** use of a large chamber measurement technique that enclosed representative parts of the ecosystem.

5 Biogenic Emissions

Keyword: BVOC emissions

Biogenic compounds are emitted from most living beings and are also released during senescence processes. Therefore BVOCs that potentially affect air chemistry are emitted from any ecosystem including marine ones (Fischer *et al.* 2012; Greenberg and Zimmerman 1984; Loreto *et al.* 2014; Millet *et al.* 2008; Monson and Holland 2001; Rinnan *et al.* 2014; Shaw *et al.* 2010). However, the focus in this review is on terrestrial processes which are more directly influencing the environmental quality at places where humans are living. Quantifying terrestrial emissions and their impacts is also particularly challenging due to the heterogeneity of ecosystems (Arneth *et al.* 2010a; Arneth *et al.* 2011; Guenther 2013; Monson 2002) and because they are subject to intensive human management.

5.1 Environmental Importance and Quantification of BVOCs

Keyword: Environmental impact

As their name implies, VOCs are bound to develop their impact in or by transport through the air. The direct impacts are threefold:

a) Particles are formed by aggregation with other organic or inorganic substances (so called secondary organic compounds, SOA) (Fuentes *et al.* 2000; Goldstein *et al.* 2009; Hayden 1998; Riipinen *et al.* 2012). These particles directly affect the radiation regime and can influence precipitation patterns by forming cloud condensation nuclei (Carslaw *et al.* 2010; Satheesh and Moorthy 2005; Scott *et al.* 2014). Fine particles may also cause pulmonary diseases or affect ecosystems by deposition (Burkhardt and Pariyar 2016; Tuet *et al.* 2017).

b) Many BVOCs are highly reactive and are thus important components of air chemical processes. This includes their interaction with nitrous oxides that contribute to ozone formation, but also affects the lifetime of greenhouse gases such as methane (Derwent *et al.* 1995; Fehsenfeld *et al.* 1992; Laothawornkitkul *et al.* 2009; Monson and Holland 2001; Pike and Young 2009; Shallcross and Monks 2000).

c) Finally, BVOCs have to have impacts on plant development and survival which comprises protection from abiotic stressors and modulate interactions between plant organs, different plants, and between plants and other organisms (Gershenzon and Dudareva 2007; Holopainen and Gershenzon 2010; Lerdau and Gray 2003; Loreto *et al.* 2014; Loreto and Fineschi 2015; Meena *et al.* 2017; Schnitzler *et al.* 2010; Sharkey *et al.* 2008; Theis and Lerdau 2003).

These impacts are discussed in more detail in the following sections, with the 'impact' relating not only to effectivity but also to quantity. It is therefore interesting to know the amount and composition of BVOCs that are globally released from terrestrial sources. In total, BVOC emissions are estimated to be approximately 1 Pg (10^{15}g, 1000 Tg, 1 Gt) yr^{-1} and are thus about one magnitude (10-fold) larger than anthropogenic non-methane VOC (AVOC) emissions (Piccot *et al.* 1992).

Table 3: Global emission estimates for isoprene and monoterpenes in Tg yr^{-1}

Isoprene emission	Monoterpene emissions	Simulation period	Reference
175**		not specified	(Went 1960b)
438**		not specified	(Rasmussen and Went 1965)
285		present (not specified)	(Turner *et al.* 1991)
568	144	1990	(Guenther *et al.* 1995)
597		1986-1989	(Wang *et al.* 1998a)
530		9/1990–8/1991	(Wang and Shallcross 2000)
561	117	present (not specified)	(Adams *et al.* 2001)
559		not specified	(Potter *et al.* 2001)
549		1990s	(Sanderson *et al.* 2003)
507	33	1990	(Levis *et al.* 2003)
454	72	1971–1990	(Naik *et al.* 2004)
601	103	2000	(Tao and Jain 2005)
566		9/1996–8/1997	(Shim *et al.* 2005)
594	99	Pre-industrial	(Valdes *et al.* 2005)
402	131	1990–1999	(Lathiere *et al.* 2005)
438	117	2000	(Liao *et al.* 2006)
522		1990–2000	(Wiedinmyer *et al.* 2006)
503		2003	(Guenther *et al.* 2006)
541	121	Pre-industrial	(Kaplan *et al.* 2006)
460	117	1983–1995	(Lathiere *et al.* 2006)
412	32	1981–2000	(Arneth *et al.* 2007b; Schurgers *et al.* 2009)
410		1995-2006	(Müller *et al.* 2008)
350-678		2003	(Pfister *et al.* 2008)
401	137***	present (not specified)	(Young *et al.* 2009)
523-560		1981-2002	(Arneth *et al.* 2011)
529-578	157-167	2006	(Guenther *et al.* 2012)
460		2000-2009	(Pacifico *et al.* 2012)
429		2000	(Wu *et al.* 2012)
467		2000	(Squire *et al.* 2014)
532	84	1980-2010	(Sindelarova *et al.* 2014)
465/444	108/98	2000-2009	(Messina *et al.* 2016)

Isoprene emission	Monoterpene emissions	Simulation period	Reference
385	29	1971-2000	(Hantson *et al.* 2017)
417	76	2000-2012	(Henrot *et al.* 2017)
363	77	2010	(Harper and Unger 2018)

* reproduced from Arneth (Arneth *et al.* 2008a) and Guenther (Guenther *et al.* 2012), complemented with further studies

** unspecified or not differentiated by compounds, representing total BVOC emissions

*** includes other BVOCs

Isoprene (2-methyl-1,3-butadiene, C_5H_8) is arguably the most abundant BVOC and contributes between **360 and 750 Tg yr^{-1}** to the total amount (see Table 3, excluding early calculations). The second largest homogeneous group of BVOC compounds is that of monoterpenes (various C_{10}-chains, for example α- and β- pinene, limonene, myrcene and sabinene), which emissions are estimated to be between **30 and 150 Tg yr^{-1}** (see Table 3). The large differences of estimates depend on various assumptions about land coverage and climate sensitivity and might have been even larger if the uncertainty in emission parameterization would be included (Arneth *et al.* 2008a). Other BVOCs have been differentiated into reactive BVOCs (e.g. alcohols, aldehydes, acetone, ethane, propene) and less reactive other BVOCs (mostly other terpenoids such as sesquiterpenes) with net release estimates between **150 and 260 Tg yr^{-1}** for each group (Guenther *et al.* 1995; Guenther *et al.* 2012). However, net terrestrial emission for methanol alone has been independently estimated to be up to 150 Tg yr^{-1} (Jacob *et al.* 2002; Wohlfahrt *et al.* 2015), indicating large uncertainties in the group of reactive BVOCs others than isoprene and monoterpenes.

5.1.1 Small Particle Formation and Impact on Regional Climate

Keyword: Aerosol formation

Small particles from various sources such as volcanic eruptions, desert dust, sea salt, pollen, and industrial combustion that are dispersed in the air are called aerosols. They can have natural or anthropogenic origins and be directly emitted from its sources or formed in the air by aggregation of gases, liquids and ions. The latter group is called secondary aerosols; if carbon is involved they are called secondary organic aerosols (SOA).

SOA from biogenic origin are thought to be about 10-fold more abundant than those of anthropogenic origin (Farina *et al.* 2010). Their environmental impacts were first detected when certain weather conditions produced a blue haze over forest areas emitting BVOCs (Went 1960a). Since then, aerosols have been known to function as seeds for cloud formation, and boundary conditions as well as processes have been investigated with aerosol chambers and field measurements. A number of reviews are documenting these developments (Barth *et al.* 2004; Barthelmie and Pryor 2000; Carlton *et al.* 2009; Fowler *et al.* 2009; Kroll and Seinfeld 2008; Lee *et al.* 2016; Mang *et al.* 2009; Riipinen *et al.* 2012; Shrivastava *et al.* 2017), showing for example that several oxidation steps have to be considered, seeds need to be differentiated by their composition and reactivity, and that the interaction of BVOCs can be synergistic or antagonistic (Hoffmann *et al.* 1997; Ng *et al.* 2006; Orlando *et al.* 2010). In addition, the number and properties of other compounds, such as sulfuric acid, play important roles for particle formation from BVOCs (Hu *et al.* 2017; Spittler *et al.* 2006). Nevertheless, evidence suggests that it is also possible that the formation of aerosols can origin solely from BVOCs (Kirkby *et al.* 2016). The research led to model developments (Archibald *et al.* 2010; Bonn *et al.* 2009; Bonn *et al.* 2008; Cheng *et al.* 2010; Jokinen *et al.* 2015; Taraborrelli *et al.* 2012; van Donkelaar *et al.*

2007) which have recently been evaluated to an overall satisfactory degree under a range of conditions (Feiner *et al.* 2016; Fisher *et al.* 2016). However, other simulations still yield considerable deviations from measurements pointing towards remaining uncertainties particular in the field of deposition and radical regeneration (Kelly *et al.* 2018).

Case studies have tried to specify the role of different BVOCs in aerosol formation. For the Eastern US, isoprene is suggested to be responsible for more than half of the share with aromatic compounds, sesquiterpenes and monoterpenes following with shares between 10 and 14 % (Helmig *et al.* 2006; Worton *et al.* 2013). Variability in spatial distribution was related to forest abundance and species distribution: While over a forest where isoprene emitters were highly abundant, isoprene oxidation dominated SOA formation (Link *et al.* 2015), aerosols over coniferous forests were formed by a larger degree from monoterpenes, while the biological contribution of SOA formation over agricultural areas seem to be of minor significance (Barthelmie and Pryor 2000). High isoprene concentrations, however, might also decrease SOA formation over the Amazon (Kanawade *et al.* 2011). In Europe, SOA formation seems to be dominated by monoterpenes and sesquiterpenes (Aksoyoglu *et al.* 2012), which originates from the larger share of coniferous forests (Kurpius and Goldstein 2003). However, in the Mediterranean area with less monoterpene emitters, monoterpene emissions were predicted to contribute only about 25% to SOA production over forested areas (Andreani-aksoyoglu *et al.* 2004). In addition, carbonyls may be as important as terpenoids for aerosol formation over specific areas such as boreal coniferous forests (Hellen *et al.* 2004), where VOC oxidation products have been found to play a key role for spatial and temporal distribution of nucleation events (Laaksonen *et al.* 2008). Globally, other BVOCs should also be considered. Green leaf volatiles (GLVs), a heterogeneous group of compounds that includes alcohols, aldehydes and esters, have shown contrasting experimental results regarding SOA production similar to isoprene (Mentel *et al.* 2013) and have been estimated to form about 1-5 TgC yr^{-1} of SOA (Hamilton *et al.* 2009) which is - depending on the literature source to compare with - approximately one tenth of the total global biogenic production (Claeys *et al.* 2004; Kanakidou *et al.* 2005).

The effective SOA yield determined from field studies were sometimes puzzling since the experimentally determined yield (= amount SOA per contributing compound) directly from isoprene oxidation products is less than 3 % (Kroll *et al.* 2005; Rollins *et al.* 2009). The small yield is likely related to the radical scavenging properties of isoprene which reduces OH radical concentrations to a level that prevents SOA formation (Kiendler-Scharr *et al.* 2009; Kleindienst *et al.* 2007). Furthermore, SOA formation potential of isoprene is supposed to decrease with NO_X air concentrations (Kroll *et al.* 2006) although this might not hold under very high NO_X conditions (Couvidat and Seigneur 2011). However, if secondary reactions are considered that form or regenerate radicals, SOA yields can be very high also when isoprene is abundant. Such a process has first been suggested involving CO and NO_X (Lelieveld *et al.* 2008). Also, the isoprene reaction with NO_3 increases the concentration of nitrate radicals and thus may result in high SOA yields (Rollins *et al.* 2009). Another, potentially very important recycling process of OH radicals is involving epoxide formation. This process has been estimated to be responsible for up to 100 Tg aerosol carbon yr^{-1} (Paulot *et al.* 2009; Taraborrelli *et al.* 2012). Overall, isoprene seems to be able to act in both ways: suppress aerosol formation but can also form SOA in relatively clean air if temperatures are not too high (Clark *et al.* 2016), see Figure 2. SOA yield from mono- and sesquiterpenes tends to increase in polluted air masses (Fry *et al.* 2009; Ng *et al.* 2007; Zhang *et al.* 2018), which seems to be related to the differences of volatility and O/C ratio in the mixture of AVOCs and BVOCs (Emanuelsson *et al.* 2013). In contrast, NO_X levels are supposed to decrease SOA yield but have more effect on particle numbers than mass (Wildt *et al.* 2014). The synergistic interaction of biogenic and anthropogenic influences has been shown for the United

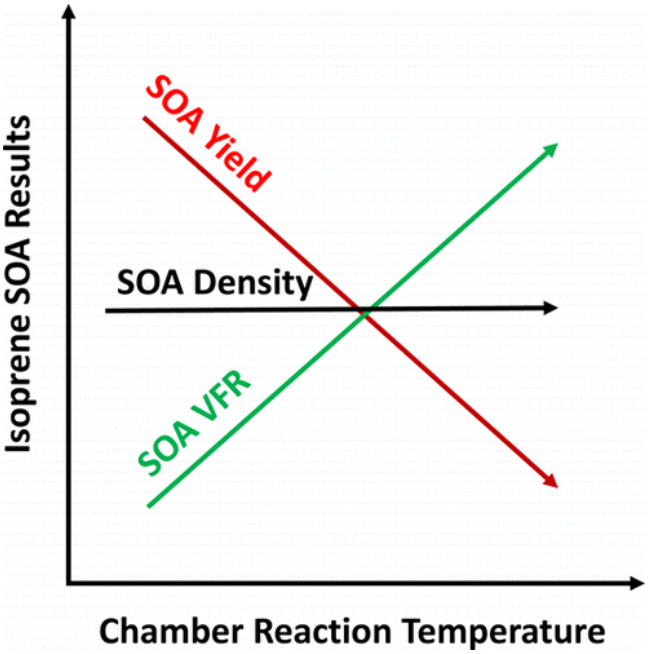
States (Hogrefe *et al.* 2011), as well as Hong Kong (Hu *et al.* 2008). In the latter case 21 % contribution of BVOCs to SOA formation has been estimated for days under local emission influences but 49% and 10fold higher SOA loads are simulated if rural input is considered.

Scenarios that include climate change up until the end of the century indicate a 5-6fold SOA increase, dominantly due to increased BVOC emissions with isoprene having a large but not dominant contribution (Tsigaridis and Kanakidou 2007). Somewhat smaller estimates (plus 36 %) are obtained from another study where BVOCs contributed app. 75 % (Heald *et al.* 2008). In a specific investigation of boreal forest emissions, a BVOC emission increase of 50 % has been estimated due to climate change which yielded a SOA increase of 19 % (Mentel *et al.* 2009).

TextBox: BVOC Contribution to Secondary Particle Formation

In contrast to early assumptions, BVOCs are assumed to contribute considerably to aerosol formation and particle growth, often being more important than anthropogenic precursors. However, despite some progress in chemical understanding the complexity of possible reactions still precludes general predictions. Overall, isoprene seems to suppress aerosol formation in polluted air while increasing SOA yields in relatively clean air masses such as over forests in the eastern United States. Over tropical forests, however, the depletion of radicals seems to prevent or at least reduce aerosol production based on isoprene. Mono- and sesquiterpenes are increasing aerosol yields – a process that does not show any apparent decreasing effect of NO_3. Interestingly, a synergistic effect seem to exist between biogenic and anthropogenic VOC emissions that leads to enhanced SOA formation in areas with intensive urban-rural air mass exchanges.

Figure 2: SOA yield from isoprene and particle size in dependence of temperature



As temperature increases, SOA yield is shown to generally decrease, particle density is shown to be stable (or increase slightly), and formed SOA is shown to be less volatile (this is expressed in 'Volume Fraction Remaining', VFR, which describes the fraction of aerosol mass left after heating particles under standardized conditions).
Source: Reproduced from Clark *et al.* (2016)

5.1.2 Photochemistry and Ozone Forming Potential

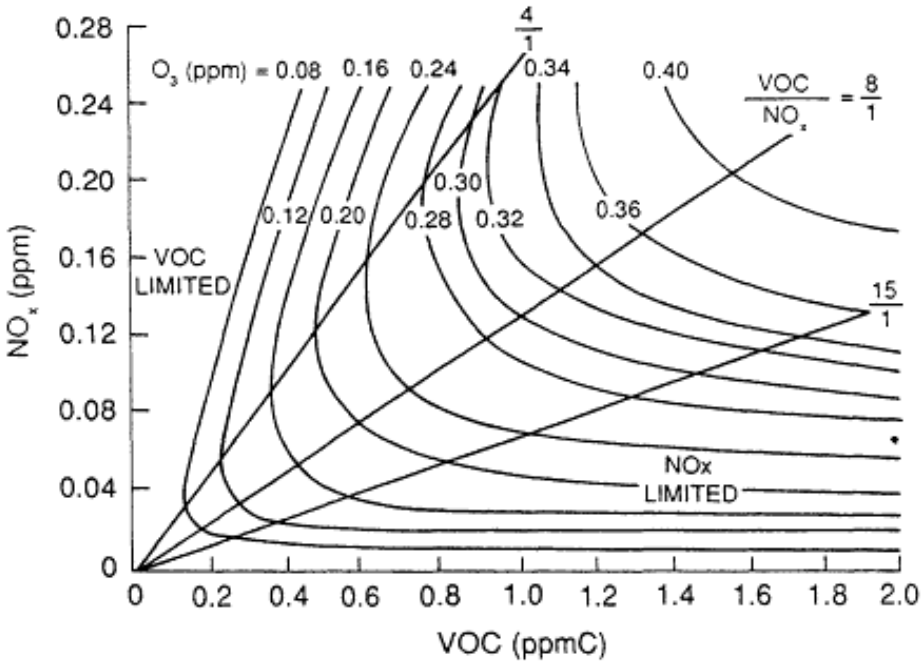
Keyword: Ozone formation

In the early 80's it has been assumed that BVOC emissions are insignificant for ozone formation (Altshuller 1983) and only play a minor role in cities (Lurmann *et al.* 1983) although the general relation between VOCs and nitrous oxides had already been known (see Figure 3) (Dodge 1977). Significant importance of BVOCs has first been indicated by modelling when only a few years later realistic emission inventories were available (Chameides *et al.* 1988; Trainer *et al.* 1987). Nevertheless, air chemistry simulations over Europe still indicated only a minor contribution of BVOCs to ozone concentrations (Simpson 1992; Simpson 1995).

Solid evidence for the contribution of BVOCs to ozone formation were delivered with airborne measurements in the US, Tennessee (Williams *et al.* 1997). The importance of BVOCs relative to other VOCs as has been demonstrated in this study is presented in Figure 4. Dependent on the precursors, however, reaction time interval of ozone formation is very different (Butler *et al.* 2011) with isoprene being one of the most effective compounds (Aschmann *et al.* 2002; Calogirou *et al.* 1999; Carter 1994; Derwent *et al.* 1996). In order to cover chemical reactions with a multitude of partners, air chemistry models processes and parameterizations have been continuously improved (Atkinson 2000; Carter 1996; Gao *et al.* 1993; Gill and Hites 2002; Paulson and Seinfeld 1992; Pierce *et al.* 1998; Saunders *et al.* 2003; Zimmermann and Poppe 1996). Nevertheless, many publications show that models were far from perfect (Aumont *et al.* 2005; Berndt 2012; Fiore *et al.* 2005; Steiner *et al.* 2008; von Kuhlmann *et al.* 2004) or that compounds are missing (Choi *et al.* 2010; Dlugi *et al.* 2010). However, also the initialization of boundary conditions such as emission inventories contribute to the uncertainty and need to be improved (Chatani *et al.* 2015; Huang *et al.* 2015a). The importance of BVOCs along with suggestions to improve the estimates of their contributions have been presented and discussed in a number of reviews (Atkinson and Arey 2003; Calogirou *et al.* 1999; Fuentes *et al.* 2000; Monks *et al.* 2015; Monson and Holland 2001; Pike and Young 2009; Seinfeld 1988; Shallcross and Monks 2000; Sillman 1999; Sillman and He 2002; Zimmer 1997).

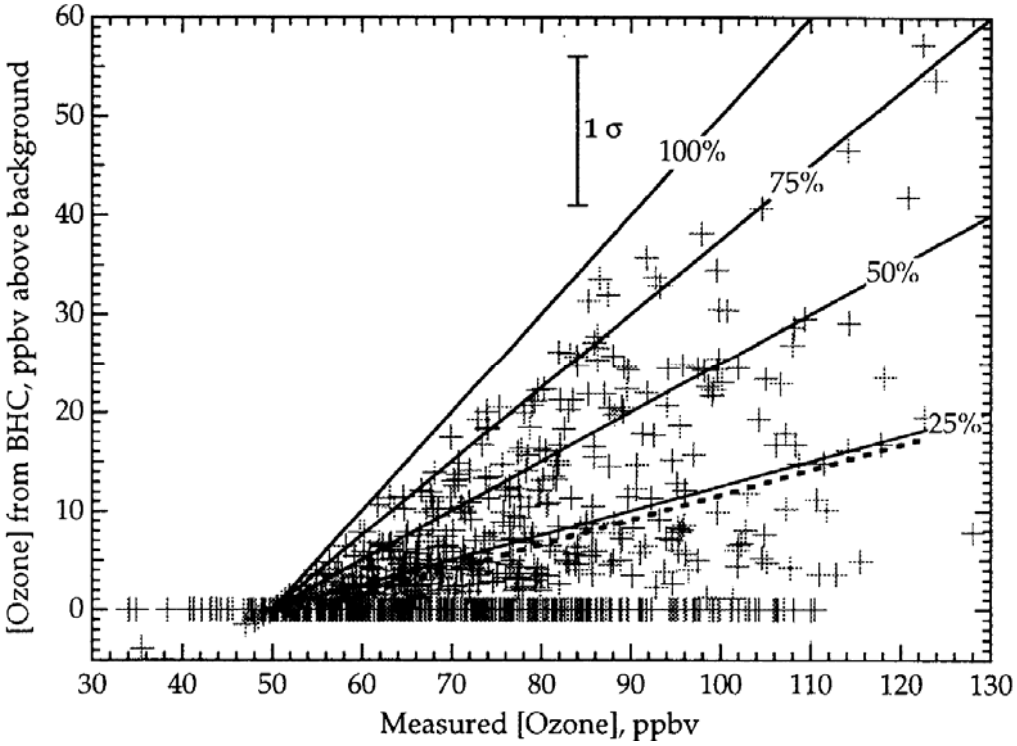
Ozone formation has been investigated particularly at sites either related to high BVOC emitters (forests) or at places that are susceptible to ozone damage (urban areas). Isoprene was indeed responsible for ozone concentration over highly isoprene emitting rainforest sites (Jacob and Wofsy 1988). Here, even considerable anthropogenic emissions from the oil industry have only a minor effect on ozone formation (Donoso *et al.* 1996). Also a plot in Italy showed isoprene contribution to ozone formation to be 50-75% (Duane *et al.* 2002), which is similar to the 60 % that have been measured as maximum for a forested rural area in Greece (Tsigaridis and Kanakidou 2002). Over coniferous and other Mediterranean evergreen forests, emissions are dominated by monoterpenes, which however, form only minor portions of ozone (Johansson and Janson 1993; Thunis and Cuvelier 2000) or even decrease ozone concentrations (Kurpius and Goldstein 2003). Instead, sesquiterpenes had the greatest impact on ozone chemistry and ozone forming potential over a boreal forest in Finland (Hellén *et al.* 2018b). Together, terpenes and isoprene contributed 50-100 % to net ozone daytime production above a Eucalypt forest in Portugal (Poisson *et al.* 2001). Urban areas are more complex to judge since there is usually a high background of VOCs from anthropogenic sources. For a site in the temperate city of Berlin, BVOC contribution to ozone formation has been estimated to be small (Thijsse *et al.* 1999) and even decrease ozone in the direct vicinity of coniferous urban forests (Bonn *et al.* 2016). At Barcelona, however, ozone formation was predominantly driven by local BVOC emissions, with GLVs and isoprene being equally important (Filella and Peñuelas 2006). The high importance of isoprene had also been derived from measurements within Bejing, where it was responsible for up to 23% of all observed ozone (Pang *et al.* 2009; Xie *et al.* 2008).

Figure 3: **Typical ozone isopleths. The NO_X -limited region is typical of locations downwind of urban and suburban areas, whereas the VOC-limited region is typical of highly polluted urban areas.**



Source: Reproduced from Dodge (1977)

Figure 4: **Estimated ozone from BVOCs (BHC-O3) is plotted against measured ozone. The solid lines correspond to 100%, 75%, and 25% BHC-O3 contribution. The dashed line is the linear least-squares fit and the error bar is the uncertainty of this estimate.**



Source: Reproduced from Williams *et al.* (1997)

The relatively short list of measurement-based estimates of the role of vegetation emissions for ozone concentrations in urban areas is complemented with a rather large number of modelling studies. These studies are based on inventories of anthropogenic and biogenic emissions and are driven by local climate. Sensitivity studies for the urban plume in London, where photochemistry is strongly VOC limited, showed a potentially large effect of BVOCs on ozone formation (Lee *et al.* 2006; MacKenzie *et al.* 1991). More specifically, calculations for Paris, France, yielded a BVOC contribution of about 18-30 % (Solmon *et al.* 2004). Similar numbers were simulated for the region of Berlin, although BVOC contribution for urban ozone concentration could increase up to 60 % for specific days during a heat wave (Churkina *et al.* 2017). Also for Osaka, Japan, a substantial contribution of BVOCs to ozone concentration of about 10 ppb was shown (Nishimura *et al.* 2015), the same amount as determined for metropolitan regions in China, where ozone concentrations could be increased by 34 ppb during warm summer days (Mo *et al.* 2018; Situ *et al.* 2013). This means that up to half of the ozone concentration can be attributed to BVOC emissions at these sites (Kim *et al.* 2008; Ran *et al.* 2011).

Regional simulations enable the aggregation of influences that affect site level measurements but cannot be distinguished or quantified at this level, such as spatial distribution and transport of emissions. For example an increase of 37 ppb ozone in Seoul, South Korea, has been attributed to isoprene emission partly originating from nearby forests (Kim *et al.* 2013; Kwang-Yeon 2013). At this site, NO_X limited (VOC saturated) air was accumulating ozone during air mass transport and led to high pollutant concentrations quite far away of the city (Jeon *et al.* 2014). In a simulation for Marseille, France, ozone concentration was increased by up to 37 % by means of a suburban isoprene emitting oak forest (Cortinovis *et al.* 2005). Similar, about half of the BVOCs that increased ozone concentration by about 40ppb in Paris, France, originated from outside the area (Derognat *et al.* 2003). These case studies demonstrate that the impact of suburban forests is important and ozone formation depends not only on the kind of vegetation but also on location and wind direction. Overall, regional simulation studies indicate that anthropogenic emissions are still the most important for ozone formation in Germany (Vogel *et al.* 1995), Europe (Derwent *et al.* 1996; Simpson 1995), the US (Li *et al.* 2007; Wiedinmyer *et al.* 2001) as well as in Southeast Asia (Qu *et al.* 2013; Shao *et al.* 2000), but that the spatial variability is large (Han *et al.* 2005). Since the chemical reactions are complex, the input of NO_X and BVOC emissions from highly resolved inventories is crucial for simulations targeting ozone formation (Vieno *et al.* 2010; Xiao *et al.* 2010).

In addition to spatial distribution, the effect of BVOCs can be expected to vary with climate conditions related to radiation, temperature, and wind - and thus with time. Simulations for regions in Spain and the US indicated that BVOC emissions are responsible for morning peaks of ozone concentrations (Andronopoulos *et al.* 2000; Reissell and Arey 2001). Such morning peaks have been explained by concentration processes of isoprene during the night when OH radical concentration as well as air mass mixing is at a low level (Millet *et al.* 2016; Venkanna *et al.* 2016). In areas where traffic emissions and BVOC meet, afternoon peaks of ozone commonly occur for example in the Mediterranean area (Toll and Baldasano 2000), in the area of Santiago de Chile (Rappenglück *et al.* 2000), in Mexico City (Jaimes-Palomera *et al.* 2016) or in the Po valley, Italy (Steinbacher *et al.* 2005). These peaks are generally explained by the peak of BVOC emissions shortly after midday, considering a time-delay for chemical reactions and possible synergistic interactions with anthropogenic emissions that often also peak in the afternoon due to increased traffic (Han *et al.* 2005; Lee and Wang 2006; Lee *et al.* 2006; Li *et al.* 2007; Ryu *et al.* 2013). The important influence of temperature has also been shown at the seasonal and inter-

annual scale. For example BVOCs played only a minor role for Canadian ozone concentrations throughout the year (Plummer *et al.* 1996) but during particular warm summer episodes, the contribution increased to 13 % (Biesenthal *et al.* 1997). Similar, the impact of BVOCs on the summer ozone maxima in Europe is relatively small but increases 2-6-fold in Mediterranean regions, particularly when the summers are hot (Curci *et al.* 2009). Also in northern countries, hot years such as 2003 can increase the contribution of BVOCs to ozone up to a level of approximately 20 % (Solberg *et al.* 2008).

Globally, BVOC emissions dominate tropospheric chemistry (Poisson *et al.* 2000). However, the picture is complex; also involving indirect negative effects of isoprene. Some of these have been assumed to even decrease ozone yield in the presence of isoprene under specific conditions (Ran *et al.* 2011; Roelofs and Lelieveld 2000) although more recent modelling approaches indicate that the overall dependence of surface ozone on isoprene emission is always positive (Mao *et al.* 2013). This might be the reason for some discrepancies in global projections where BVOCs are sometimes supposed to play the major role for ozone formation in the southern hemisphere while being driven by AVOCs in the North (Lelieveld and Dentener 2000; Wang *et al.* 1998b). Other studies see the larger effect on ozone formation in the northern hemisphere (Wang and Shallcross 2000). Part of the explanation may also be that in the southern hemisphere more reactive isoprene is released in great quantities from the tropical rainforests but in the North, higher emissions of NO_X are increasing the efficiency of less reactive or less abundant BVOCs due to more effective radical recycling (Fuchs *et al.* 2013; Lelieveld *et al.* 2008). In addition, also the interaction between biogenic and anthropogenic emissions is important for the efficiency of ozone formation (Chen and Brune 2012; Shallcross and Monks 2000; Vlachogiannis *et al.* 2000), showing a synergistic behavior that increases ozone formation in particular when AVOC emission is dominating (Li *et al.* 2018).

Model simulations have been used for providing decision support, in particular regarding emission reduction strategies that aim to decrease ozone damages to human health and agricultural yields. Therefore, sensitivity of ozone concentrations to NO_X and AVOC reductions has been explored e.g. for cities in the Mediterranean area, for Beijing or Sao Paulo (Im and Kanakidou 2012; Orlando *et al.* 2010; Shao *et al.* 2009). Another major line of research explores the development of ozone concentration under climate change and/or land use changes. Thereby considering that BVOC emissions are generally assumed to increase due to their temperature sensitivity, leaf area increases and changes in species composition (see chapter 5.3). For the US, for example, higher NO_X and AVOC emissions as well as emissions from wildfires are calculated to increase ozone concentrations and the duration of high ozone episodes by 2050. This is despite overall BVOC emission is projected to decrease due to land use changes which overcompensate higher emission rates per unit ground area (Chen *et al.* 2009; Weaver *et al.* 2009). In these simulations it is considered that BVOCs are more effective forming ozone than AVOCs (Bell and Ellis 2004). For Europe, ozone has been projected to increase mainly due to increasing BVOC emissions which are estimated to have a larger effect than temperature increases alone: 2-10 ppb until 2040 (Forkel and Knoche 2007), -2-16 ppb until 2050 (Varotsos *et al.* 2013), and 6-14 % up until 2095 (Doherty *et al.* 2013). The change would need a reduction of NO_X larger than 20 % in order to be completely compensated (Doherty *et al.* 2013). If it would be considered that a realistic fraction of crop- and grassland would be converted into woody bioenergy production sites, isoprene emissions could increase by 45 % causing ozone peak values to rise by another 6% (Beltman *et al.* 2013). Global scenarios did not yield consistent results due to the multitude of assumptions, impacts and feedbacks that are differently treated. The average estimate of global ozone concentration change is an increase of about 10-20 ppbv by 2090 but can vary between -9 and +55 ppbv (Avise *et al.* 2012; Sanderson *et al.* 2003; Squire *et al.* 2014; Wiedinmyer *et al.* 2006).

TextBox: BVOC Contribution to Ozone Formation

The impact of BVOC to ozone formation depends on various factors, including temperature and radiation, the concentration and reactivity of other (anthropogenic VOCs), and the availability of NOx. In particular the relation between highly reactive BVOCs, i.e. isoprene, and NOx plays a major role for ozone formation although sesquiterpenes and GLVs are occasionally also important. Some evidence exist that anthropogenic and biogenic VOCs react synergetic. In general, higher isoprene emissions increase ozone production, particularly in pollution-influenced regions. Based on empirical and modelling studies the contribution of isoprene on ozone concentration in the vicinity of urban areas can rise to more than 50 % at warm sites or during heat waves.

5.1.3 Biological Functions

Keyword: Biological functions

While it is certainly true that some BVOCs are emitted simply because of their physicochemical properties in solubility and volatility (Niinemets *et al.* 2004), it is also evolutionary very unlikely that costly production of a wide array of compounds does not serve a biological function (Pichersky *et al.* 2006). Early explanations for BVOC emissions concentrated on isoprene and hypothesized a role in carbon dioxide assimilation (references in Sanadze 1991b). This theory could not be supported and the positive relationship between isoprene production and oxygen concentration led to the assumption that isoprene was a by-product of photorespiration (Rasmussen and Jones 1973). However, detailed physiological studies in the late 1980s disproved this putative function (Hewitt *et al.* 1990). Following investigations that demonstrated a protective impact of BVOCs for isoprene (Loreto *et al.* 2001b; Loreto and Velikova 2001; Velikova *et al.* 2004; Velikova *et al.* 2012), several theories about how this protection is achieved have been brought forward. One possibility is that BVOC formation presents a "safety valve" to get rid of excess energy and/or carbon accumulating during dysfunctional photosynthesis under high light and temperature conditions. Other explanations focus on chemical reactions that protect from dangerous reactive oxygen species (ROS) (antioxidant hypothesis) (Niyogi 2000; Peñuelas and Llusia 2004), or assume stabilizing membrane properties by means of the isoprene molecule (thermal protection hypothesis).

Based on a failure to increase thermotolerance by exogenously given isoprene (Logan and Monson 1999) the emergency valve theory indicating that the enhanced consumption of energy and carbon rather than the final product eases heat stress has been brought forward (Logan *et al.* 2000) but has also been criticized to be to ineffective (Sharkey and Yeh 2001). Variants of the theory state that the main effect may be dissipation of excess energy (Sanadze 2004) or a mean to prevent overflow of intermediate compounds related to assimilation (Rosenstiel *et al.* 2004). An antioxidative effect of isoprene has been suggested when it became apparent that isoprene formation can be located close to the photosynthetic apparatus (Affek and Yakir 2002; Peñuelas and Llusia 2002; Zeidler *et al.* 1997). Indeed, scavenging of ROS by isoprene has been shown first under specifically controlled conditions (Sauer *et al.* 1999) and later in various plants (Behnke *et al.* 2007; Pollastri *et al.* 2014; Velikova *et al.* 2005a; Vickers *et al.* 2009b). Particular indicative for the antioxidative role of isoprene before emission was that direct emission of oxidation products could be detected (Jardine *et al.* 2012). Another prominent hypothesis to explain protective effects of BVOCs is that they are deposited within cell membranes and stabilize their functionality (Loreto *et al.* 1998; Sharkey and Singsaas 1995; Sharkey *et al.* 2008;

Velikova 2008). It has been shown that isoprene (Loreto and Velikova 2001; Sharkey *et al.* 2001; Sharkey and Singsaas 1995; Singsaas *et al.* 1997; Siwko *et al.* 2007; Velikova *et al.* 2015; Velikova *et al.* 2011) and in exceptional cases also monoterpenes (Copolovici *et al.* 2005; Llorens *et al.* 2009; Nogues *et al.* 2014) support membrane stability but the physiological concentrations of the compounds have been questioned to be sufficient, suggesting indirect effects on stabilizing proteins instead (Harvey *et al.* 2015; Velikova *et al.* 2014; Velikova *et al.* 2015).

Another function of volatile compounds that has been known for a long time is the role that BVOCs play in signaling among and between organisms (Ameye *et al.* 2018; Gershenzon and Dudareva 2007; Heil and Karban 2009; Kessler and Morrell 2010; Muhlemann *et al.* 2014; Theis and Lerdau 2003; Turlings and Erb 2018). Terpenoids are involved in attracting pollinators (Dobson 1987; Dobson and Bergström 2000) as well as deter herbivores (Armbruster *et al.* 1997) or to attract predatory insect that feed on parasites and herbivores (Dicke and van Loon 2000; Weissbecker *et al.* 2000). In addition, BVOC signaling has been shown to serve the coordination of plant responses within and between plants of the same species (Baldwin *et al.* 2002) and can affect responses in other plant species too. The latter has first been described as "talking trees" (Baldwin and Schultz 1983; Rhoades 1983) and has been corroborated by findings of defense induction by volatile compounds (Karban *et al.* 2000).

It can be concluded that several direct protection mechanisms exist that indicate an important role for BVOCs before emitted into the air. The protection from oxidative stress, often occurring during high radiation episodes (sun flecks) and an accompanying increase of leaf temperature, seems to be the most important. Since oxidative stress also occurs due to direct oxidant exposure (such as ozone) the mechanism may be important under a range of environmental conditions (Fini *et al.* 2017). Overall, emission seems to assist C3 plants (not C4!) to run efficient photosynthesis and to overcome transient and mild stresses, especially during periods of active plant growth in warm seasons (Loreto and Fineschi 2015). It should be noted, however, that protective functions have almost exclusively been detected for terpenoids, with isoprene being the single most investigated compound. In contrast, signaling functions have been demonstrated for a huge array of purposes and for various BVOCs, originating from different biosynthetic pathways (Fineschi and Loreto 2012; Loreto and Schnitzler 2010).

5.2 Drivers of BVOC emissions

Keyword: Emission determinants

There are various ways to differentiate between emission drivers. For example, many carbon compounds that are released from the biosphere are due to fire (Pandey and Sahu 2014), which is however not further considered here. Often, BVOC emissions are distinguished into induced and constitutive trying to find environmental drivers that act fundamentally different on these two groups. For example, assuming oxidative and mechanical stress to trigger the first, and continuously developing boundary conditions to drive the second (Ali *et al.* 2011; Brilli *et al.* 2009; Copolovici *et al.* 2017; Jiang *et al.* 2016; Joo *et al.* 2011; Litvak and Monson 1998). The distinction between the two is, however, not a sharp one since already 'normal' temperature and radiation conditions can be seen as inducing the build-up of emission potentials over time. Therefore, the following chapters are focusing on the environmental impacts one by one and indicate their role as inductors of emission if relevant as has been proposed by Holopainen *et al.* (2018). This doesn't exclude that interactions between the different drivers occur. For example, the immediate impact of drought is a reduction in canopy evaporation that at the same time increases leaf temperature because evaporative cooling is missing. These interactions are occasionally mentioned if it is deemed necessary, but a complete coverage is beyond the scope of this report.

BVOC emissions are best described if long- and short-term impacts of environmental influences at the site of emission production are described (Peñuelas and Llusia 2001). These are not only different for different plant compartments (e.g. differences within a plant may be triggered by different nutrient concentrations in leaves of different crown parts) but also within the same compartment at different locations (e.g. radiation is usually higher at the top of the plant than at the bottom, resulting in higher emission rates from overstory plants and upper canopy fractions) (Genard-Zielinski *et al.* 2015; Harley *et al.* 1996; 1997; Sharkey *et al.* 1991).

It should be noted that all emission responses are based on species-specific genetically determined properties (Fineschi *et al.* 2013). For example, the ability to produce significant amounts of isoprene may or may not be shared by members of the same plant family or genus, but emitting species have been found among bryophytes, ferns, conifers and in approximately one-third of the 122 angiosperm families examined (Harley *et al.* 1999; Sharkey and Yeh 2001). The ability to form particular isoprenoids has seemingly developed and lost repeatedly in different genera (Dani *et al.* 2014a). Also, the ability to communicate within and between plants and insects seems to be very specific depending on the evolutionary history of the species (Dicke and Baldwin 2010). Thus, all responses described here depend on the sensitivity of the particular plants and cannot be transferred universally even within the same family.

Focusing on environmental impacts, it is assumed that intrinsic plant developments do not change the species-specific sensitivity regarding the ability to emit BVOCs. This might not totally be true since different isoprene emission rates have been detected in young and older eucalypt plantations despite a similar nutrition (Funk *et al.* 2006). Furthermore, monoterpene emissions might be limited by storage size under certain conditions and photosynthetic capacity as well as storage capacity of leaves depend on properties that change with age (Gray *et al.* 2003; Lin *et al.* 2001; Schurgers *et al.* 2009). However, reports of such impacts are scarce and differentiating environmental conditions that change due to growth-related structural developments (leaf area distribution, nutrient distribution, etc.) from real age effects is virtually impossible. Intrinsic (age related) changes that are disregarded as major driving forces should not be mixed up with seasonal and phenological changes in potential emission rates. These are either delayed responses of previously experienced environmental conditions (e.g. enzymatic synthesis and degradation due to stimuli) or depend on physiological (e.g. photosynthesis apparatus) and anatomical (e.g. hardening of growing tissue) properties that are part of the seasonal development (Monson 2013).

Finally, it should be clearly stated that all responses are referred to the leaf scale. For the tree or canopy scale, it is generally assumed that all leaves of a specific species experiencing the same environmental conditions are emitting in the same way. This is not contradicting observations of more BVOCs emitted from sun than from shade leaves under the same light and temperature conditions since these leaves have a different environmental history as well as different nutrient concentrations, storage capacities, and precursor supply rates (i.e. different photosynthetic capacities) (Esposito *et al.* 2016; Lin *et al.* 2001; Niinemets *et al.* 2010). However, it clearly indicates that environmental within-canopy differences need to be considered for upscaling (Fall and Wildermuth 1998; Šimpraga *et al.* 2013).

5.2.1 Temperature and Radiation

Keyword: Temperature impact

Temperature and radiation are the most important drivers for photosynthesis and thus for the provision of energy as well as BVOC precursor compounds (Sanadze 1991a). Thus, all de-novo emissions somehow depend on these two influences in combination. We distinguish these from

emissions that are released from specific storage structures mainly by passive diffusion which has a direct dependency on temperature but not on radiation (Tingey *et al.* 1991). Apart from direct impacts, integrated temperature (and radiation) over longer periods affect storage refilling and enzyme activity and thus have an indirect impact on emission as well (Arneth *et al.* 2011; Guenther 1997; Peñuelas and Llusia 2001).

5.2.1.1 Emissions from De-novo Production

Keyword: Directly emitted BVOCs

Emissions that are not persistently occurring in the dark are supposed to be synthesized directly before emissions, requiring energy and precursor compounds that are provided by photosynthesis. Therefore, the shape of the light response function is a saturation curve, similar to that of photosynthesis (although at a higher saturation level), which has been demonstrated in particular for the most important BVOC, isoprene (Monson and Fall 1989; Monson *et al.* 1991; Sharkey *et al.* 1991). A similar behavior has been shown for several other compounds, including 2-methyl-3-buten-2-ol (MBO) (Harley *et al.* 1998; Rosenstiel *et al.* 2002), sesquiterpenes (Geron and Arnts 2010; Staudt and Lhoutellier 2011) and various GLVs (Kesselmeier *et al.* 1998; Kesselmeier *et al.* 1997; Kirstine *et al.* 1998). Some BVOCs, in particular monoterpenes can be emitted directly as well as indirectly from storages (see also next chapter). For example for summer emissions from boreal Scots pine trees, the fraction of de-novo emission was estimated to be between 30 and 58 % (Ghirardo *et al.* 2010; Lüpke *et al.* 2017a; Taipale *et al.* 2011). The dependency of other BVOC compounds, in particularly highly oxygenated ones (OVOCs), to radiation intensity is blurred because they are at least partly soluble and thus can be stored temporarily in the cytosol or rely on pathways with relatively slow kinetics so that emission reaches well into the dark periods (Graus *et al.* 2004; Monson 2013).

Overall, light and temperature influences can be differentiated into two aspects. First they are modifiers of emission responses while kinetic properties of the contributing enzymes and stresses of various kinds are determining the pattern of emission. The shape or peak of a response curve is therefore generally fixed but the expression might vary. For example emission shifts from a given maximum at light saturation down to negligible in the dark (Fall and Wildermuth 1998). Secondly, it is not unlikely that high radiation and temperature can also function as a stress, inducing the production of BVOCs that directly and indirectly protect the plant tissue from oxidative damage. This has been demonstrated particularly for heat stress (Copolovici *et al.* 2015; Copolovici *et al.* 2012; Kleist *et al.* 2012), with not only increasing emission rates of constitutive emissions but also new emission blends favoring GLV were induced (Joo *et al.* 2011; Kask *et al.* 2016; Kleist *et al.* 2012; Pazouki *et al.* 2016). It should be noted, however, that a separate radiation stress also seem to exist (van Meeningen *et al.* 2017) and that in many publications high light and high temperatures (imitating sun- or lightflecks) are co-occurring so that emission induction cannot easily attributed to either heat or radiation stress (Behnke *et al.* 2010; Loreto *et al.* 2006).

A specific induction effect of light, however, might be related particularly to the ultraviolet (UV) spectrum of radiation. Investigating the effect of UV-A, isoprene and methanol emission has been shown to increase (Pallozzi *et al.* 2013b) or at least not to decrease while photosynthesis was negatively affected (Fraser *et al.* 2015; Guidolotti *et al.* 2016). However, exposition to UV-B did little to terpenoid production under ambient conditions but modified the responses to heat stress (Blande *et al.* 2009; Maja *et al.* 2016).

While generally light is investigated in the form it occurs in the field, few studies indicate that emission intensity is not only affected by light quantity but also quality. Higher blue light fractions seem to decrease isoprene and monoterpene emissions in oaks and poplar (Arena *et al.*

2016; Pallozzi *et al.* 2013b), while emission response of GLVs are suppressed under higher red light fractions in *Arabidopsis* (Kegge *et al.* 2013). This phenomenon might be related to herbivore behavior, signaling either high defense capability or trying not to attract enemies in specific places. Overall, the effect of light quality on BVOC emissions is certainly underexplored. Considering that changes in the aerosol load of the atmosphere due to modified anthropogenic or increased biogenic emission loads might result in a changed radiation spectrum, further investigations of these relationships are certainly needed.

5.2.1.2 Emissions from Storage Pools

Keyword: Emissions from storages

Emissions from storages are driven by the concentration difference between ambient air (generally assumed to tend towards zero) and concentration within the plant tissue (e.g. resin ducts), and depend on diffusion resistance as well as temperature (Hietz *et al.* 2005). Stomatal conductance plays a minor role (Tingey *et al.* 1991). Storages can be specific for a compound or a group of compounds such as resin ducts or can be unspecific such as the cytosol (Loreto *et al.* 2000). In contrast to de-novo synthesis, emission from pools can be considered independent from photosynthetic production for short-term periods. Since the pool size is generally assumed to be much larger than emission rates from storages, dynamics only depend on a physical-derived exponential relation to temperature (Vanhatalo *et al.* 2018).

It should be noted that the basal assumption about emissions from storages are not always met in reality. For example, storages need to be filled which takes time or is not possible under severe stress periods and thus may result in supply limitations (Haberstroh *et al.* 2018; Llusia *et al.* 2010; Schurgers *et al.* 2009). In addition, resistances are not always constant but may change due to mechanical damage, as e.g. triggered by parasite colonization (Clancy *et al.* 2016; Räisänen *et al.* 2009). In case of resin, resistances may even be decreased to zero when resin is exuded from woody tissue, which may in fact be responsible for more than 10 % of monoterpene emissions in Ponderosa pine forests (Eller *et al.* 2013). None of these modifiers, however, has been considered in upscaling BVOC emission from storages yet.

5.2.1.3 Seasonality of Emission Responses

Keyword: Seasonality impact

Given the same immediate environmental conditions (temperature, radiation, nutrient supply, degree of physical or chemical stress), a unit of foliage can emit different kinds and amounts of BVOCs (Demarcke *et al.* 2010; Genard-Zielinski *et al.* 2018; Goldstein *et al.* 1998; Karl *et al.* 2003; Nogues *et al.* 2014; Schade *et al.* 2000). For emissions originating from de-novo production, establishment of the precursor provision chain and the specific activity of compound synthesis determine standard emission rates (Vanhatalo *et al.* 2018). The first impact is generally relevant only in the period of flushing when new tissue develops, while the second is hardly reaching a steady state but is subjected to continuous synthesis and degradation processes (Lehning *et al.* 1999; Monson *et al.* 1994). The emission capacity thus particularly depends on the climate conditions of the previous days. The length of this period may differ by the relevant compound and has been estimated to range between 3 and 10 days (Geron *et al.* 2000; Gray *et al.* 2003; Petron *et al.* 2001). Under temperate conditions in a Norway spruce forest, terpene emissions that were dominantly from de-novo synthesis varied from 0.05 to 332.5 µg gdw^{-1} h^{-1} with a peak in August (Wang *et al.* 2017). In contrast, emission capacity dynamics in tropical forests seem much less intense and are driven by leaf aging and flushing, probably triggered by dry and wet season (Alves *et al.* 2018; Barkley *et al.* 2009; Kuhn *et al.* 2004; Trostdorf *et al.* 2004).

Another reason of seasonality that has long been neglected is also related to tissue development but independent of precursor production or enzyme activity: Monoterpene and sesquiterpene emission rates from buds are up to 500 times and OVOCs up to 20 times higher than of mature needles in Scots pine (Aalto *et al.* 2014; Duhl *et al.* 2008) or in the flowering phase of grass (Fukui and Doskey 1998), maize plants (Wiß *et al.* 2017) and rapeseed (Müller *et al.* 2002). Similarly, young leaves of various species have been shown to emit much higher rates of methanol and acetone than their mature counterparts (Bracho-Nunez *et al.* 2011; Brilli *et al.* 2016; McKinney *et al.* 2011; Schade and Goldstein 2006), possibly supporting the dilatation of cells or providing protection for premature tissues. On the other hand, specific BVOCs are increased particularly in senescent tissue such as methanol and some other OVOCs in maize leaves (Mozaffar *et al.* 2018).

As mentioned in the previous chapter, also emissions from storages perform a certain degree of seasonal cycles, connected to periods of supply limitations in foliage during early development stages (Schurgers *et al.* 2009). It follows that compounds emitted from de-novo synthesis and those emitted from storages have different seasonal patterns, independent on their sensitivity to immediate climate conditions (Geron and Arnts 2010; Holzke *et al.* 2006; Nogués *et al.* 2015; Schurgers *et al.* 2009; Vanhatalo *et al.* 2018).

5.2.2 CO_2 Concentration

Keyword: CO2 impact

The impact of CO_2 on BVOC emission is one of the earliest investigated but the mechanisms of action are far less well explained than those of temperature and radiation. As has been pointed out by several reviews, the dominating effect is a decrease of emission with increasing CO_2 concentration (Baraldi *et al.* 2004; Holopainen 2013; Monson *et al.* 2009). This result is based on the clear majority of investigations on isoprene that are mainly done on strongly emitting poplar and oak species (see Table 4). The shape of the response has been described as an exponential decline by various authors as is exemplarily shown in Figure 5. Nevertheless, the exceptions are remarkable since they indicate that species with different sensitivities exist (Li *et al.* 2009) and that acclimation responses are possible if plants are developing in a high CO_2 environment (Tognetti *et al.* 1998). Other experiments indicate that the response might describe an optimum curve because very low CO_2 concentrations are again negatively affecting emission since precursor supply from alternative sources is slow (Affek and Yakir 2003). It is also noted that this response pattern depends on boundary conditions, as a decreasing CO_2 effect has been observed at increasing temperatures (Loreto and Sharkey 1990). The effect is also apparent for sesquiterpenes although only one investigation on this compound is available (Huang *et al.* 2018) but much less obvious for (de-novo synthesized) monoterpenes and OVOCs where equal numbers of increasing and decreasing or neutral observations have been found.

Several explanations have been brought forward to explain the responses, focusing on the feedback from carbon metabolism. First, it was hypothesized that high carbon availability leads to an exhaustion of energy which is then not available for BVOC synthesis (Sharkey *et al.* 1986) whereas Sanadze (1991a) and Monson (2009) proposed competing carboxylation schemes that result in a reduction of essential isoprene precursors with increasing CO_2. Similarly, photorespiration under low carbon availability has been proposed as competition process for precursors (Dani *et al.* 2014b). Experimental evidence led to a combination of these theories, suggesting that DMADP pool size is the decisive carbon compound that is regulated by energetic metabolites (Rasulov *et al.* 2009; Rasulov *et al.* 2016). This has been supported by the finding that DMADP pool is indeed smaller under elevated CO_2 (Sun *et al.* 2012b) and that it is faster refilled under high temperatures when CO_2 inhibition is lost (Niinemets and Sun 2015).

It should be noted that all of these explanations focus on de-novo production, while the effect on storages is difficult to assess since a higher supply rate is only effective in limiting conditions (see chapter 5.2.1.2) or over longer time periods. Currently, a general trait cannot be depicted since investigations about increasing (in pine) (Sallas *et al.* 2001) as well as decreasing (in spruce) (Sallas *et al.* 2003) terpenoid concentrations under elevated CO_2 have been found.

Table 4: BVOC emission response to increasing CO_2 concentrations

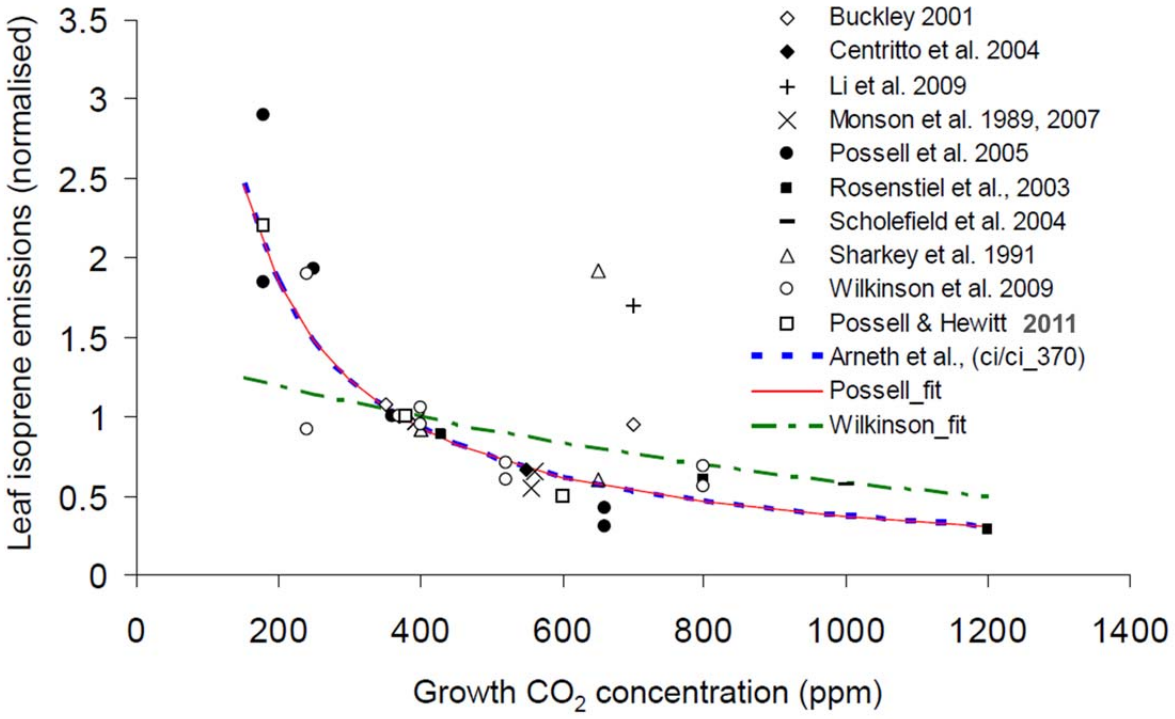
Emission type	Emission response	Plant species/ type	Reference
isoprene	decrease	*Acacia*	(Possell and Hewitt 2011)
isoprene	decrease	*Arundo, Mucuna*	(Possell *et al.* 2005)
isoprene	decrease	*Liquidambar*	(Monson *et al.* 2007)
isoprene	decrease	*Phragmites*	(Scholefield *et al.* 2004)
isoprene	decrease	*Platanus*	(Velikova *et al.* 2009)
isoprene	decrease	*Populus*	(Monson and Fall 1989)
isoprene	decrease	*Populus*	(Monson *et al.* 1991)
isoprene	decrease	*Populus*	(Sharkey *et al.* 1991)
isoprene	decrease	*Populus*	(Rosenstiel *et al.* 2003)
isoprene	decrease	*Populus*	(Centritto *et al.* 2004)
isoprene	decrease	*Populus*	(Pegoraro *et al.* 2004a)
isoprene	decrease	*Populus*	(Monson *et al.* 2007)
isoprene	decrease	*Populus*	(Pegoraro *et al.* 2007)
isoprene	decrease	*Populus*	(Wilkinson *et al.* 2009)
isoprene	decrease	*Populus*	(Eller *et al.* 2012)
isoprene	decrease	*Quercus (d)**	(Jones and Rasmussen 1975)
isoprene	decrease	*Quercus (d)**	(Tingey *et al.* 1981)
isoprene	decrease	*Quercus (d)**	(Loreto and Sharkey 1993)
isoprene	decrease	*Quercus (d)**	(Rapparini *et al.* 2004)
isoprene	decrease	*Quercus (d)**	(Possell *et al.* 2004)
isoprene	decrease	*Quercus (d)**	(Monson *et al.* 2007)
isoprene	decrease	*Tropical rainforest*	(Pegoraro *et al.* 2005)
isoprene	decrease / increase	*Populus*	(Loreto and Sharkey 1990)
isoprene	increase	*Ginkgo*	(Li *et al.* 2009)
isoprene	increase	*Populus*	(Sun *et al.* 2013)
isoprene	increase	*Quercus (d)**	(Sharkey *et al.* 1991)

Emission type	Emission response	Plant species/ type	Reference
isoprene	increase	*Quercus (d)**	(Tognetti *et al.* 1998)
isoprene	neutral	*Populus*	(Sun *et al.* 2012b)
isoprene	neutral	*Quercus (d)**	(Buckley 2001)
monoterpenes	decrease	*Betula*	(Vuorinen *et al.* 2005)
monoterpenes	decrease	Heathland	(Tiiva *et al.* 2017)
monoterpenes	decrease	*Larix*	(Mochizuki *et al.* 2017)
monoterpenes	decrease	*Picea*	(Huang *et al.* 2018)
monoterpenes	decrease	*Populus*	(Eller *et al.* 2012)
monoterpenes	decrease	*Quercus (e)**	(Loreto *et al.* 2001a)
monoterpenes	decrease	*Quercus (e)**	(Rapparini *et al.* 2004)
monoterpenes	increase	*Brassica*	(Himanen *et al.* 2009)
monoterpenes	increase	*Populus*	(Staudt *et al.* 2001)
monoterpenes	increase**	*Pinus*	(Sallas *et al.* 2001)
monoterpenes	neutral	*Ginkgo*	(Li *et al.* 2009)
monoterpenes	neutral	*Pinus*	(Räisänen *et al.* 2008)
monoterpenes	neutral	*Pinus, Pseudotsuga*	(Constable *et al.* 1999a; Constable *et al.* 1999b)
monoterpenes	neutral	*Quercus (e)**	(Loreto *et al.* 1996)
OVOCs	decrease	*Betula*	(Vuorinen *et al.* 2005)
OVOCs	neutral	*Carpinus*	(Kreuzwieser *et al.* 2006)
OVOCs	neutral	*Quercus (d)**	(Kreuzwieser *et al.* 2006)
OVOCs (methanol)	increase	*Populus*	(Eller *et al.* 2012)
sesquiterpenes	decrease	*Picea*	(Huang *et al.* 2018)

* oak species are differentiated into deciduous (d) and evergreen (e) species

** only plant tissue concentrations were investigated

Figure 5: Leaf-level response of isoprene emissions to varying CO_2 growth environment



Symbols represent observations from a number of studies and plant species, and are normalized to be unity at growth CO_2 concentration of 370 ppm. The lines represent three different algorithms that are currently being applied to represent the observed response in global models: (i) the empirical function proposed by Possell *et al.* (2005); (ii) a function representing the ratio of change in leaf-internal CO_2 concentration; (iii) a "Hill"-type function proposed by Wilkinson *et al.* (2009). The Figure is adapted from Young *et al.* (2009), and updated with latest published observations.
Source: Reproduced from Arneth *et al.* (2011)

5.2.3 Drought

Keyword: Drought impact

Plants take up water from the soil in order to provide turgor pressure that enables the uptake of CO_2 through stomata. If water supply is insufficient for this task, plants are supposed to suffer on drought. The first response to this stress is stomata closure which is easily revertible and aims to establish equilibrium between water uptake and loss, while further water depletion leads to wilting and tissue damages such as leaf and root senescence as well as embolism (Bartlett *et al.* 2016; Sperry *et al.* 2002). Such direct responses to drought result in numerous physical and biochemical changes that also affect the emission of BVOCs which is elaborated in this chapter. Long-term water deficits may also lead to acclimation responses such as producing less leaves, more roots or less susceptible hydraulic systems (Chaves *et al.* 2003). Together with shifts in species abundance towards more drought tolerant vegetation communities these are, however, considered indirect and thus not discussed here.

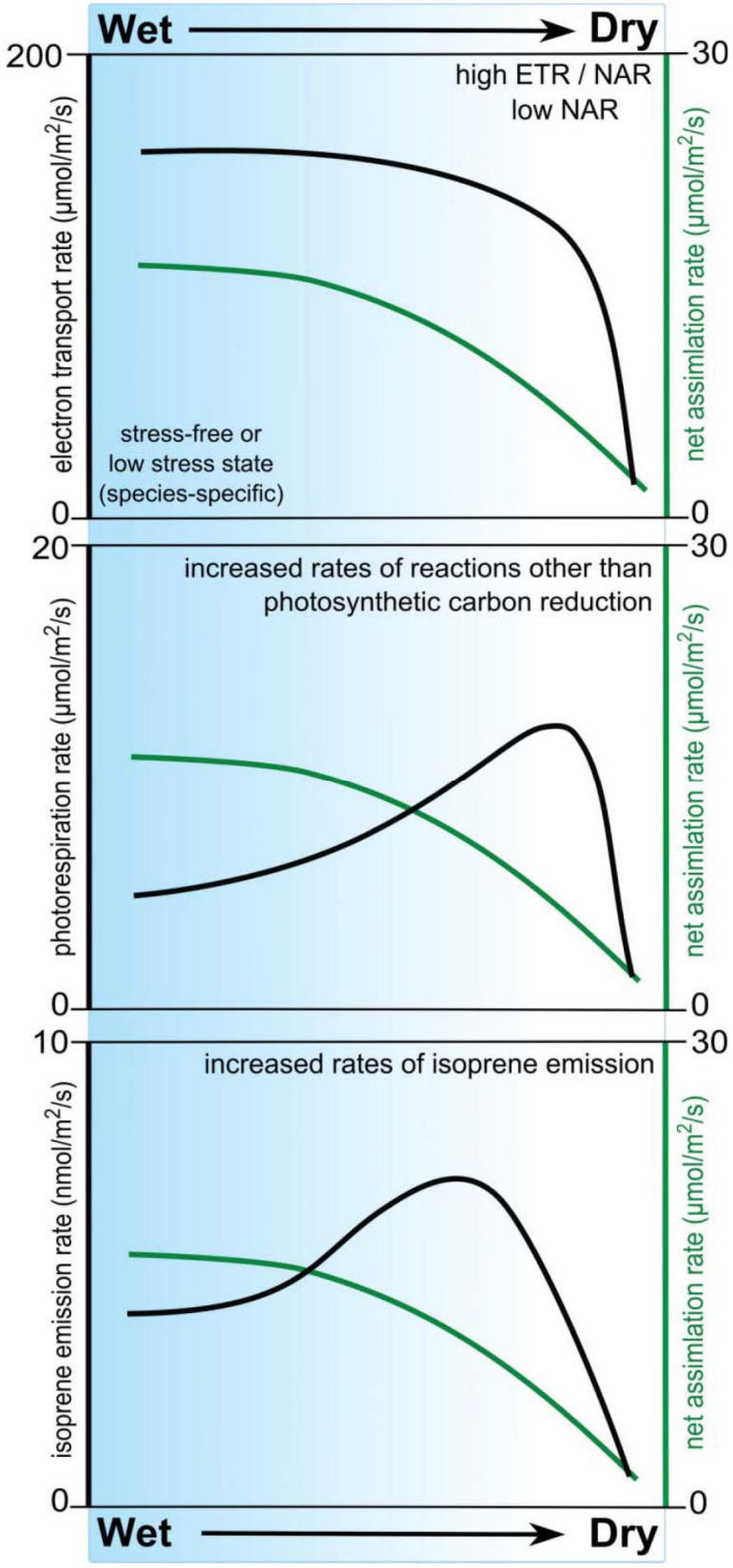
Stomatal closure leads to a higher internal gas pressure which causes soluble BVOC compounds such as methanol to be temporarily stored in the cytosol and released when stomata open, leading e.g. to emission bursts in the morning or after drought release (Niinemets *et al.* 2018; Niinemets and Reichstein 2003; Saunier *et al.* 2017). In contrast, isoprenoid emission doesn't directly depend on stomata conductance, indicating that it accumulates within the leaf up to a level that enables exchange through the cuticle or remaining stomata conductance (Harley

2013). Different from accumulating internally produced gases, CO_2 within the plant is depleted due to limited supply. As evaluated in chapter 5.2.2, this effect is generally favoring isoprenoid production. In fact, an increasing isoprene emission that is attributed to a higher internal CO_2 has been reported in various investigations (Dani *et al.* 2014b; Pegoraro *et al.* 2004a; Potosnak 2002). However, a competing theory has be developed that residual reducing power unused by carbon assimilation drives increased isoprene emission under various abiotic stresses (Niinemets *et al.* 1999) which is supported by a number of experimental results (Dani *et al.* 2014b; Morfopoulos *et al.* 2014; Possell *et al.* 2004; Zheng *et al.* 2017). The theory explains different emission responses with increasing drought stress as is illustrated in Figure 6.

It is difficult to distinguish the biochemical impacts from another BVOC enhancing effect: Due to the reduced transpiration, evaporative cooling of the leaves is less effective or is not available anymore at all. Thus, leaf temperature is rising and increases isoprene emission as depicted in chapter 5.2.1 (Arab *et al.* 2016; Monson *et al.* 2007). Nevertheless, decreased internal CO_2 concentration and increased temperature might still not be sufficient to explain the wide-spread phenomenon of increased isoprenoid emissions due to mild and moderate drought stress (Llusia *et al.* 2008; Llusia *et al.* 2016; Monson *et al.* 2007; Ormeno *et al.* 2007b; Pegoraro *et al.* 2007; Staudt *et al.* 2008; Tattini *et al.* 2015; Yuan *et al.* 2016). In addition, higher tissue temperatures during drought periods may also induce BVOC production in order to protect membranes and increase antioxidative defense capacity (Velikova 2008; Vickers *et al.* 2009a) (see also chapter 5.1.3). This is supported by increases in ROS (Marino *et al.* 2017; Ryan *et al.* 2013) as well as emission of methyl salicylate, often found in response to stress conditions (Bourtsoukidis *et al.* 2014b). Although seldom investigated, GLV also seem to be emitted in response to acute drought stress which is strongly indicative for induced emissions (Šimpraga *et al.* 2011; Wenda-Piesik 2011).

Although emission in some arid ecosystems seem not to be affected by drought (Guenther *et al.* 1999), the majority of investigations indicate a decline of BVOC emission under severe drought stress (Asensio *et al.* 2007a; Brilli *et al.* 2007; Brüggemann and Schnitzler 2002; Fang *et al.* 1996; Funk *et al.* 2005; Geron *et al.* 2016a; Llusia and Peñuelas 1998; Llusia *et al.* 2016; Lusebrink *et al.* 2011; Nogues *et al.* 2018; Plaza *et al.* 2005; Pressley *et al.* 2006; Seco *et al.* 2015; Staudt *et al.* 2008; Tani *et al.* 2011). This decline has been described as linearly related to soil water potential (Wu *et al.* 2015). It is uncoupled from photosynthesis and considerable less expressed as the response of assimilation (Centritto *et al.* 2011; Fortunati *et al.* 2008; Genard-Zielinski *et al.* 2014). Although most investigations focus on isoprene and monoterpenes, the decline can be observed on other emissions from de-novo production too (Haberstroh *et al.* 2018; Niinemets *et al.* 2018; Saunier *et al.* 2017). There are slight indications that sesquiterpenes are more sensible to decreasing water availability than other isoprenoids but the uncertainty is high due to the scarcity of measurements (Ormeno *et al.* 2007b). BVOC emissions from pools are generally less affected but longer stress periods are likely to decrease these emissions too (see chapter 5.2.1.2). Indeed, observations in a deciduous mixed forest have indicated a slow decline of methanol emissions throughout the drought period (Seco *et al.* 2015) and terpenoid emission development measured at a Mediterranean shrub (Gum rockrose) indicated a depletion of the leaf storage (Haberstroh *et al.* 2018). This implies that if the blend of emissions originates from de-novo production as well as from storages, the emission composition changes during the drought event as has been documented for the Mediterranean shrub rosemary (Rosmarinus officinalis L.) (Nogués *et al.* 2015), eucalypts (Brilli *et al.* 2013), as well as for Scots pine seedlings (Lüpke *et al.* 2017a).

Figure 6: **A notional view of the relationship between net assimilation rates (green line in all images) and electron transport rate, photorespiration rate and isoprene emission rate (top to bottom) as eucalypts are exposed to diminishing water supply.**



Reproduced from Dani *et al.* (2015)

While the responses of isoprenoid emissions seem to have the same general response pattern, species-specific sensitivities are large. For example the decline of isoprene emission started earlier in Pedunculate oak than in Holm oak trees (Brüggemann and Schnitzler 2002) and Red oak species showed to be more sensitive than White oak species in experiments providing the same boundary conditions (Geron *et al.* 2016a). Other literature references indicated that some species such as orange trees are very insensitive, reducing mono- and sesquiterpene emissions only by 6 % for under severe drought (Hansen and Seufert 1999) while in others such as Aleppo pine and rubber trees emission declines to levels just above the detection limit (Baker *et al.* 2005; Seco *et al.* 2017).

BVOC emissions also recover faster and more complete from severe water limitations than photosynthesis (Fang *et al.* 1996; Pegoraro *et al.* 2004b; Peñuelas *et al.* 2009). In some cases, emission increased considerable beyond the pre-stressed level (Saunier *et al.* 2017; Sharkey and Loreto 1993; Staudt *et al.* 2008). Interestingly, the intensity of emission also determines the degree of photosynthesis recovery, indicating a protective function so that damages were less severe and repair was faster (Lüpke *et al.* 2017a; Vanzo *et al.* 2015). If the drought event led to tissue damages, the process of senescence, degradation and repair is likely related to particular BVOC emissions. These processes are known to release OVOCs in substantial amounts e.g. in senescing grass crops (Karl *et al.* 2005), poplar (Brilli *et al.* 2016; Sun *et al.* 2012a), birch (Holopainen *et al.* 2010), and maize (Mozaffar *et al.* 2018) while costly terpenoids are assumed to be reduced.

For the ecosystem exchange it may also be important that not only emissions from soil (that are generally of minor importance) but also its sink strength is altered during drought events. For example it has been found that sink capacity of the soil decreased with decreasing water content (Pegoraro *et al.* 2006). However, results are not consistent and may depend strongly on soil properties as also increased exchange rates have been observed for which autotrophic metabolism in roots might be responsible (Asensio *et al.* 2007b; Geron *et al.* 2016a).

5.2.4 Nutrient Supply

Keyword: Nutrient impact

Soil nutrient impact on BVOC fluxes has received relatively little attention (Ormeño and Fernandez 2012; Peñuelas and Staudt 2010), despite a number of physiological relations that seem to indicate a significant relevance of this influence: Nitrogen concentrations in plant tissue should affect terpenoid emissions due to their effect on electron transport rate and leaf photosynthesis which provide chemical energy and carbon substrate availability (Lerdau *et al.* 1995). Phosphorus is expected to influence terpenoid production since terpenoid precursors contain high-energy phosphate bonds and phosphorus is a key component of ATP and NADP which are required for terpenoid synthesis (Niinemets *et al.* 2002). But not only de-novo emissions but also emissions from storages are related to nutrient availability. For example resin acid concentrations have been found to increase in fertilized Scots pine trees (Björkman *et al.* 1991; Kivimäenpää *et al.* 2016).

Most studies focused on isoprene emissions under fertilization treatments, indicating that there is a positive dependence between nutrients and terpenoid concentration within the plants (Fernández-Martínez *et al.* 2018; Litvak *et al.* 1996; Powell and Raffa 1999) as well as between nutrient concentrations and BVOC emissions (Materic *et al.* 2016; Ormeno *et al.* 2007a). This has mostly been demonstrated for nitrogen (Gouinguené and Turlings 2002; Lerdau *et al.* 1997; Ormeno *et al.* 2009; Possell *et al.* 2004). However, a considerable number of invariant and even

negative relationships have also been found (Blanch *et al.* 2007; Kainulainen *et al.* 2000; Llusia *et al.* 2014; Mihaliak and Lincoln 1985; Sampedro *et al.* 2010).

These seemingly contradictory results might be related to responses being triggered on different time scales. For example, nutrient availability at one point in time might initialize the building of storage structures that are difficult to fill once they are finished. Therefore, phenology and long-term allocation processes need to be considered, linking leaf morpho-anatomy with cell biochemistry and physiology (Lerdau *et al.* 1997; Lerdau *et al.* 1995; Ormeño and Fernandez 2012). Another explanation might result from a shift in the blend of emissions that has not been explored until recently since methodological difficulties prevent the continuous observation of many compounds at the same time over a prolonged period. For example, a nitrogen-induced shift has been found from terpenoids towards GLV and LOX products in birch trees (Carriero *et al.* 2016).

The effect of nutrients on BVOC emissions is largely indirect, acts on different time scales and competes with various other processes that might require or release nutrients. Thus, considering interactions with other environmental factors (abiotic and biotic) is particularly important. Only few studies have explicitly addressed interactions with drought (Blanch *et al.* 2007) or light (Lamontagne *et al.* 2000; Litvak *et al.* 1996) yet. When growth periods or even successional developments should be evaluated, even competition among plants needs to be considered because it strongly affects nutrient uptake and allocation processes (Kegge and Pierik 2010; Peñuelas and Llusia 1999).

5.2.5 Air Pollution

Keyword: Air pollution impact

Air pollution is per-definition a detrimental influence on plants with effects on various levels reaching from reducing radiation due to aerosols and particle deposition (Prajapati 2012) to the disruption of membranes due to oxygenated stress (Sharma *et al.* 2012). These influences and damages reduce the photosynthetic capacity (Dizengremel 2001) and deteriorate stomatal regulation (Onandia *et al.* 2011). On the longer term, air pollution-triggered damages reduce yield, enhance foliage senescence and may finally lead to premature death (Leisner and Ainsworth 2012). Since BVOC emissions are related to photosynthesis and leaf area, the effect on constitutive emissions is closely correlated to these damages (Tiwari *et al.* 2016).

However, the impact of air pollution, in particular that of compounds that exert oxidative stress such as ozone, on BVOC emissions is not a one-way street but is characterized by a complex net of interaction. Two aspects have to be considered: First, BVOCs are supposed to play an important role in defense and damage repair, particularly related to impacts of oxidative stress (Fineschi and Loreto 2012; Holopainen 2004; Iriti and Faoro 2009; Loreto and Fares 2007; Tiwari *et al.* 2016; Velikova 2008; Vickers *et al.* 2009a). Second, BVOCs can be emitted in increased amounts and with different composition if exposed to certain stimuli (Calfapietra *et al.* 2013; Iriti and Faoro 2009; Pinto *et al.* 2010; Spinelli *et al.* 2011). In the following, an overview is presented of case studies that evaluate if air pollution can induce a stimulus that is able to trigger the production and emission of BVOCs, without going into details regarding the function of emissions, i.e. the mechanisms of defense and repair. The presented list is only considering ozone effects since the vast majority of investigations concentrate on this pollutant, but the few studies that are available on the topic indicate a similar response to NO_2 and SO_2 exposure (Mayer *et al.* 2018; Wannaz *et al.* 2003).

Table 5: BVOC emission response to increasing ozone concentrations

Emission type	Emission response	Plant species/ type	Reference
terpenes	increase	Broadleaved (Birch)	(Carriero *et al.* 2016)
terpenes	increase	Broadleaved (Croton)	(Bison *et al.* 2018)
terpenes	increase	Broadleaved (Croton)	(Cardoso-Gustavson *et al.* 2014)
terpenes	increase	Broadleaved (Ginkgo)	(Li *et al.* 2009)
terpenes	increase	Broadleaved (Holm oak)	(Loreto *et al.* 2004)
terpenes	increase	Broadleaved (Holm oak)	(Vitale *et al.* 2008)
terpenes	increase	Broadleaved (Holm oak, Olive)	(Llusia *et al.* 2002)
terpenes	increase	Conifers (Pine)	(Heiden *et al.* 1999)
terpenes	increase	Conifers (Pine)	(Kivimäenpää *et al.* 2016)
terpenes	increase	Conifers (Pine)	(Kivimäenpää *et al.* 2013)
terpenes	increase	Conifers (Spruce)	(Bourtsoukidis *et al.* 2012)
terpenes	increase	Gras (Phragmites)	(Velikova *et al.* 2005a)
terpenes	increase	Herbaceous (Tobacco)	(Kanagendran *et al.* 2018b)
terpenes	increase	Peatland	(Rinnan *et al.* 2005)
terpenes	neutral	Broadleaved (Birch)	(Vuorinen *et al.* 2005)
terpenes	neutral	Conifers (Pine)	(Peñuelas *et al.* 1999)
terpenes	neutral	Conifers (Spruce)	(Lindskog and Potter 1995)
terpenes	neutral	Conifers (Larch)	(Lindskog and Potter 1995)
terpenes	decrease	Herbaceous (*Ornithopus, Trifolium)*	(Llusia *et al.* 2014)
terpenes	decrease	Herbaceous (Rapeseed)	(Himanen *et al.* 2009)
OVOCs, MeSA	increase	Broadleaved (Croton)	(Cardoso-Gustavson *et al.* 2014)
OVOCs, MeSA	increase	Herbaceous (Bean)	(Li *et al.* 2017)
OVOCs, MeSA	decrease	Broadleaved (Birch)	(Hartikainen *et al.* 2012)
OVOCs, DMNT	increase	Broadleaved (Birch)	(Carriero *et al.* 2016)
OVOCs	increase	Broadleaved (Beech)	(Cojocariu *et al.* 2005)
OVOCs	increase	Broadleaved (Poplar)	(Fares *et al.* 2010)
OVOCs	increase	Herbaceous (Tobacco)	(Jud *et al.* 2016)
OVOCs	increase	Herbaceous (Tobacco)	(Kanagendran *et al.* 2018b)
OVOCs	increase	Peatland	(Rinnan *et al.* 2005)
isoprene	increase	Broadleaved (Downy oak)	(Velikova *et al.* 2005b)
isoprene	increase	Broadleaved (Ginkgo)	(Li *et al.* 2009)

Emission type	Emission response	Plant species/ type	Reference
isoprene	increase	Broadleaved (Poplar)	(Fares *et al.* 2006)
isoprene	increase	Broadleaved (Eucalypt)	(Kanagendran *et al.* 2018b)
isoprene	increase	Herbaceous (Tobacco)	(Kanagendran *et al.* 2018a)}
isoprene	neutral	Broadleaved (Poplar)	(Blande *et al.* 2007)
isoprene	neutral	Broadleaved (Poplar)	(Hartikainen *et al.* 2009)
isoprene	neutral	Peatland	(Tiiva *et al.* 2007b)
isoprene	decrease	Broadleaved (Oaks)	(Tani *et al.* 2017)
isoprene	decrease	Broadleaved (Poplar)	(Calfapietra *et al.* 2007)
isoprene	decrease	Broadleaved (Poplar)	(Calfapietra *et al.* 2008)
isoprene	decrease	Broadleaved (Poplar)	(Fares *et al.* 2010)
isoprene	decrease	Broadleaved (Poplar)	(Yuan *et al.* 2016)
??	increase	Conifers (Pine)	(Xu *et al.* 2012)
??	increase	Herbaceous (Tomato)	(Peñuelas *et al.* 1999)

Despite the difficulties in comparing responses that originate from a wide array of ozone concentrations and experimental boundary conditions, it is obvious from the overview in table 5 that ozone induced emissions are widespread but differ with respect to compound and species. While in few studies no emission change has been found, terpene and OVOC emission mostly increased in response to ozone exposure. Only in two herbaceous species in case of terpenes (Himanen *et al.* 2009; Llusia *et al.* 2014) and one study on birch with respect to OVOCs (Hartikainen *et al.* 2012) decreases were recorded. In particular conifers seem to enhance their de-novo production and emission of monoterpenes. In contrast, isoprene was decreased or showed no response in the majority of investigations. Still strong indication exist that isoprene emissions can principally also be enhanced (Fares *et al.* 2006; Kanagendran *et al.* 2018b; Li *et al.* 2009; Velikova *et al.* 2005b).

Different responses can be explained by different environmental conditions, species and clone sensitivities (Calfapietra *et al.* 2008; Pellegrini *et al.* 2012; Peñuelas *et al.* 1999), as well as experimental setups. For example very high ozone exposure might easily overburden any defense capacity destroying the basis for BVOC production while intermediate ozone concentrations stimulate emissions (Pinelli and Tricoli 2008), particularly if applied over longer periods (Heiden *et al.* 1999). In the latter cases, BVOCs can play important roles in the defense system and need to be upregulated on the genetic level such as isoprene and many terpenes (Fares *et al.* 2006; Velikova *et al.* 2005b) (see also chapter 5.1.3). In contrast, the release of various OVOCs can be very fast, leading to so-called emission bursts that may not be long-lasting but serve as stress signal to other plants and to initiate a cascade of defense reactions (Beauchamp *et al.* 2005; Heiden *et al.* 2003; Li *et al.* 2017; Vainonen and Kangasjärvi 2014). Defensive compounds might not necessarily be de-novo synthesized but can be released from specialized storage structures, called secretory cavities or oil glands (Jud *et al.* 2016). Other OVOCs are indicators for membrane damage and might occur particularly after prolonged

periods of ozone exposure (Vitale *et al.* 2008) or during sensitive periods such as leaf flushing (Fares *et al.* 2010).

Overall, ozone exposure is likely to increase the emission of BVOCs although it might be more effective at intermediate than at very high levels. The magnitude of the response depends on the sensitivity of the exposed tissue, magnifying effects in spring in relation to late summer. On the short-term, the overall emission blend will tend to increase OVOC emission relative to terpenoids although this may shift over time (Farré-Armengol *et al.* 2016).

5.2.6 Pathogen Induced Emissions and Wounding

Keyword: Wounding impact

In addition to induction by light, temperature and oxidative air pollutants, BVOCs may also be induced mechanically by biting, sucking, cutting or wounding by abrasion due to wind movement (Haase *et al.* 2011) or freeze/thaw cycles (Fall *et al.* 2001). Although the drivers can be physical, biological or anthropogenic, the signal and thus the responses of plants are often similar. The emission compounds may be de-novo produced or released from storages when the diffusive resistance is decreased by wounding of any kind. Both can have direct repellent properties, serve as signals that induce defensive compounds in other leaves or plants, or mediate interactions with organisms from higher trophic levels (i.e., parasitoids or carnivores) (Arimura *et al.* 2005; Gatehouse 2002). Indeed, BVOC releases are assumed to be one of the fastest exploited weapons, with respect to minimizing the yield losses and providing tolerance to various stresses. Many of the volatile terpenes are nonspecific toxins active against a wide range of organisms (bacteria, fungi, plants and animals) (Meena *et al.* 2017). This doesn't exclude the emission of specific BVOC blends particularly in cases where wounding is connected to the induction of chemical compounds such as the release of saliva from herbivores or while fungi infest plant tissue (Heil 2014; Jansen *et al.* 2011; McCormick *et al.* 2012).

The production and release of BVOCs in response to wounding generally occurs within very short time periods after the induction event independent of the kind of induction. However, at least fungal influences seem to increase their inductive strength with time leading to an increasing effect on production. In general, insects seem to induce the lowest effect on BVOC production, with piercing/sucking impacts being considerable less effective than chewing insects (Ameye *et al.* 2018). In a case study on poplar, an emission cascade was rapidly elicited after wounding, resulting in sequential emissions of key stress volatiles methanol, acetaldehyde, and volatiles of the LOX pathway. The maximum emission rates were reached after one to three minutes after the start of the treatment (Portillo-Estrada *et al.* 2015).

The emission compounds are numerous but OVOCs, and more specifically GLVs, constitute a general element in most of these blends, in particular aldehydes, alcohols and acetates (Blande *et al.* 2014). In most observed cases, wounding, herbivory or fungal infection doesn't change the relative composition of GLVs, with the exception of aldehydes that increase particularly after fungal infection (Ameye *et al.* 2018). The emission is generally proportional to the extent of wounding (Mithöfer *et al.* 2005; Niinemets *et al.* 2013; Portillo-Estrada *et al.* 2015) and occurs in attached or detached leaves, and even increases when detached leaves dry out, indicating that a considerable part of these emission fraction are released from the litter layer (Fall *et al.* 1999). However, large and rapid bursts of acetaldehyde have been reported not only at the cutting site but also on parts of the leaf distant from the cut (Loreto *et al.* 2006).

Other BVOCs are induced too. For example homoterpenes such as dimethyl-nonatriene (DMNT) have often been found in response to herbivore attack (Copolovici *et al.* 2014; Ibrahim *et al.* 2008; Kigathi *et al.* 2009; Oluwafemi *et al.* 2012; Tholl *et al.* 2011; Vuorinen *et al.* 2004) and

together with methyl salicylate (MeSA) are assumed to particularly contribute to so-called 'tri-trophic interactions' (Mooney *et al.* 2012). By sending a signal which attracts predators of parasites that feed on the plant, an indirect defense mechanism can be established (Copolovici *et al.* 2011; Holopainen *et al.* 2010; Kigathi *et al.* 2009). Since wounding is often related to membrane damage, also isoprene and terpene production may be upregulated in species that provide the necessary genetic preconditions (Achotegui-Castells *et al.* 2013; Brilli *et al.* 2011; Faiola *et al.* 2015; Kanagendran *et al.* 2018b; Litvak *et al.* 1999; Piesik *et al.* 2010; Prieme *et al.* 2000; Semiz *et al.* 2017; Visakorpi *et al.* 2018) but may also been downregulated in favor of GLVs (Brilli *et al.* 2009; Copolovici *et al.* 2017). The upregulation of terpenoids have been found to increase emissions by a factor of approximately 10 to 20 in response to needle damages of feeding insects (Ghimire *et al.* 2017) as well as to bark beetle infestations (Amin *et al.* 2012; Amin *et al.* 2013).

It should be noted that wounding includes cutting which is a widespread management activity in grasslands and forests. Grasslands and pastures release high amount of GLVs, in particular alcohols into the air (Davison *et al.* 2008; Karl *et al.* 2001; Warneke *et al.* 2002). Due to the large abundance of this ecosystem and management activity, it has been estimated that the large transient fluxes, when integrated over time, could be of the same order of magnitude as constitutive emissions from undisturbed pasture. This would virtually double emission estimates from these ecosystems (Kirstine *et al.* 1998). Forest harvests and thinning are by definition much less frequent. Nevertheless, a thinning of half the trees in a Scots pine forests has triggered a monoterpene release from wounded tissue that was 40 times the constitutive emission rate (Schade and Goldstein 2003). Similar increases of monoterpenes have been observed after hailstorms (Kaser *et al.* 2013), which didn't effect MBO releases, indicating that these emissions originate from damaged storages.

TextBox: The Most Important Drivers for Intensity and Composition of BVOC Emissions

It should be noted that emission potentials, the ability for VOC storage, and the composition of de-novo produced and constitutive BVOCs are determined on the genetic level. Various environmental conditions are responsible for the expression of this species-specific potential, from which temperature and radiation are the most important factors, both for short- and longer term impacts. Water availability affects BVOC emission directly and indirectly and may act in different directions dependent on stress severity. While minor stress tends to increase emissions, BVOCs decline under intensive drought. CO_2 and nutrient availability do also change BVOC emission intensity but the exact mechanism is not known indicating considerable uncertainties in the estimation of future BVOC responses. Induced emission by biotic or abiotic disturbances can overtop constitutive emissions by more than one order of magnitude and has important functions for plant defense and repair.

5.3 Expected BVOC Emissions under Global Change

Keyword: Global change impact

Models are required to assess the impacts of future climate- and land-use changes on BVOC emissions as well as their feedback responses to air chemistry and climate (Arneth *et al.* 2010b; Peñuelas and Llusia 2001). To this end, few approaches have been established that are still further developed (Grote and Niinemets 2008; Langford *et al.* 2017). When coupled to dynamic

vegetation models, it becomes apparent that not only direct impacts on the emission per unit leaf area have to be considered, but also indirect impacts that are related to the changes in vegetation properties (Arneth *et al.* 2011; Harrison *et al.* 2013; Niinemets and Monson 2013; Sharkey and Monson 2014). Therefore, management decisions that influence species abundance and vegetation distribution are expected to have strong influences on BVOC emissions (Pike and Young 2009).

5.3.1 Model Approaches for Scenario Analysis

Keyword: BVOC emission modelling

A number of model estimates for global BVOC emissions have already been presented in Table 3. The similarity of results at least with respect to isoprene has been attributed to the application of the same model approach and similar parameters for potential emissions of widely lumped ecosystems (Arneth *et al.* 2008a). Indeed, only few model approaches have been applied starting with a simple integrated formulation (Tingey 1979), which has been elaborated particularly by Guenther et al. who differentiated between light and temperature dependency and de-novo and storage emissions (Guenther 1999; Guenther *et al.* 1995; Guenther *et al.* 1993). A different approach using the dependence of emission from photosynthesis (or more specifically electron transport) has been developed by Niinemets with elaborations from other authors (Grote *et al.* 2014; Morfopoulos *et al.* 2013; Niinemets *et al.* 1999). Other approaches have been developed focusing on the precursor supply for BVOC production (Bäck *et al.* 2005; Martin *et al.* 2000) and enzyme kinetic properties (Grote *et al.* 2006; Zimmer *et al.* 2000), which are however not adapted in regional models. Besides temperature and radiation, seasonality has been accounted for by either modifying emission potentials by empirically-derived sinus-shaped curves, considering an influence on emission parameters by temperature and radiation conditions averaged over the preceding couple of days, or by calculating enzyme capacity considering temperature-related formation and degradation processes (Grote *et al.* 2010; Grote *et al.* 2013; Monson *et al.* 2012). In addition, the age effect has been considered in modelling vegetation types that are dominated by evergreen plants, by differentiating the canopy in different leaf age classes and designating specific reduction factors to each (Guenther *et al.* 2006).

Regional inventory models have been developed with the Model of Emissions of Gases and Aerosols from Nature, MEGAN, being the most prominent one (Guenther *et al.* 2006; Heald *et al.* 2008; Jiang *et al.* 2018). Another very similar approach which is also based on the Guenther algorithm is the Biogenic Emission Inventory System (BEIS) (Apel *et al.* 2002; Goldstein *et al.* 1998; Lamb *et al.* 1993; Pierce and Waldruff 1991). Both of these models have been run as stand-alone versions as well as coupled to atmospheric model systems. The Guenther approach has also been directly implemented in regional chemistry transport models (CTMs) to feed BVOC into the atmosphere, as well as into dynamic vegetation models in order to produce emission inventories or to investigate the relationship between BVOC emission and other plant processes. Prominent examples for the first type of models are EMEP MSC-W (Simpson 1992; Simpson *et al.* 2012; Vieno *et al.* 2010) and LOTOS-EUROS (Schaap *et al.* 2009). Vegetation models that have been used with the Guenther approach comprising e.g. CANVEG (Baldocchi *et al.* 1999), IBIS (Naik *et al.* 2004), ORCHIDEE (Lathiere *et al.* 2006), and GOTILWA (Keenan *et al.* 2011; Keenan *et al.* 2009). The Niinemets approach has been used to add the BVOC functionality to the dynamic global vegetation models (DGVMs) Lund Potsdam Jena General Ecosystem Simulator (LPJ-GUESS) (Arneth *et al.* 2007b), the Joint UK Land Environmental Simulator (JULES), and the Hadley Global Environment Model (HadGEM) (Pacifico *et al.* 2011). In some models such as the Yale Interactive terrestrial Biosphere (YIB) model (Unger *et al.* 2013; Yue and Unger 2015; Yue *et al.* 2015), both emission approaches have been implemented for uncertainty analysis. Similar

to the models using the Guenther approach, JULES, HadGEM and YIB have also been used as land surface models that are online-coupled with atmosphere models to evaluate climate and air chemistry impacts of BVOCs (Harper and Unger 2018; Oliver *et al.* 2018). Since all models within one of these two groups use the same emission functions, parameterization and approaches to scale from the leaf to the canopy are the major source of diverse results (Simpson *et al.* 1995).

Not only temperature and radiation effects are treated similar, at least within a group of models using the same mechanism, but also CO_2 and drought response functions are considered similarly. In order to account for the CO_2 effect, both the Guenther and the Niinemets model have been complemented with negative exponential functions that have been empirically determined (Arneth *et al.* 2007a; Arneth *et al.* 2007b; Goldstein *et al.* 1998; Heald *et al.* 2009; Wilkinson *et al.* 2009). For the consideration of drought effects, a simple linear function has been used that decreases emission between wilting point and a threshold water capacity (Grote *et al.* 2009; Guenther *et al.* 2006). There is currently no relationship implemented in emission models that account for induced emissions in response to air pollution, insect gradations, or mechanical disturbances although this issue has been recognized as important (Arneth and Niinemets 2010). However, experimentally determined relations between stress induced and constitutive emissions have been used to quantify the impact of spruce aphids in the field (Bergström *et al.* 2014).

Another reason for the relatively small differences in global simulations, at least regarding isoprene, is that over the course of one or few years, changes in environmental boundary conditions, i.e. air quality related issues (CO_2, nitrogen deposition, ozone concentration) and land cover properties (vegetation type, species composition, leaf area) can be assumed as fairly constant. Nevertheless, these effects that are here referred to as 'indirect global change impacts' can be very large. The ability to capture the influence of boundary conditions on emission changes depends on:

1. The method of scaling from the leaf to the canopy which needs to be able to differentiate between different canopy structures (Bryan *et al.* 2015) and has been shown to be potentially responsible for large differences in emission (Keenan *et al.* 2011; Langford *et al.* 2017).
2. The variation of foliage amount and distribution in time (Gulden *et al.* 2007; Huang *et al.* 2014; Messina *et al.* 2016), particularly in dependence on plant growth influencing factors (i.e. water, CO_2 and nutrient availability, air pollution and herbivore impacts).
3. The consideration of changing species abundances within one vegetation type which is particularly important if transition phases should be covered (Grote *et al.* 2011; Wang *et al.* 2018).
4. The consideration of shifted distribution of vegetation types (except changes in vegetation properties are based on traits and not on species). For example the impact of different abundance of various vegetation types (mainly expansion of tropical forests) in an early double CO_2 scenario has increased isoprene emissions by 25 % (Turner *et al.* 1991).

These issues are also major topics in research on plant development under climate change and are therefore particularly addressed in DGVMs. Improvements may be expected also for CTMs since land-use models are developed in a similar fashion to DGVMs or DGVMs are coupled to CTMs. Nevertheless, global integrated simulations still adhere to the concept of plant functional types (PFTs) where transient changes are difficult to realize and the underlying assumption of static species composition is questionable for different regions as well as future conditions.

TextBox: State of the Art of Modelling BVOCs

There is some confidence about the representation of short- and long-term impacts on BVOC emissions. Two model approaches have been implemented in vegetation models of different complexity and also have been coupled to various CTMs. For the challenging consideration of CO_2 and drought impacts simple solution have been found and implemented that are able to reproduce some observations. However, these implementations rely on uncertain boundary conditions (soil properties, species-specific water use strategies) and still seem too simple to respond adequately under dynamic environmental conditions. Induced emissions from abiotic as well as biotic disturbances have been recognized as extremely important as they can increase short- and medium term emission by at least one order of magnitude. They are also of a different blend than emissions in undisturbed conditions. For these processes a general model relationship with the environment has not been found yet.

5.3.2 Direct Effects of Climate Change on BVOC Emission

Keyword: Direct scenario impact

Due to the exponential relationship between BVOC emission and temperature, it can be assumed that this will be a dominant impact on constitutive emissions under climate change. For example simulated BVOC emission for Europe varied between warm and cool years between 1985 and 1991 by a factor of 1.5 (Simpson *et al.* 1995). Also, equilibrium simulations for the year 2100 that assumed no change in vegetation pattern and neglected direct CO_2 and drought impacts, yielded a total BVOC emission increase of approximately 70 % (Liao *et al.* 2006; Pacifico *et al.* 2012). However, another study quantified the global emission increase in an expected climate in the year 2095 as only 17 % (Squire *et al.* 2014). This expresses an uncertainty related to different models and model settings but also depends on different assumptions regarding temperature increases and temperature distribution. For example it has been shown that climate scenarios for the next 100 years based on different representative concentration pathways (RCPs) resulted in emission increases of 7, 33 and 83 % for RCP 2.6, 4.5, and 8.5, respectively (Bauwens *et al.* 2018). Since temperature is expected to develop differently in different regions, also emission increases vary with location. For example, simulated isoprene and terpene emission increases for the year 2052 vary for the United States by 20-92 % (Zhang *et al.* 2008), thereby compensating expected decreases of anthropogenic VOC emissions from several states (Woo *et al.* 2008). Since climate warming is expected to be much stronger towards the poles, temperature driven increase of BVOC emission will also be stronger in the northern hemisphere (Lathiere *et al.* 2005), which is also the reason why a higher share of monoterpenes, mainly emitted from temperate and boreal forests, is expected in a future climate (Liao *et al.* 2006). This is corroborated by results from warming experiments of arctic heathlands that showed a 280 % increase in response to 4 °C temperature increase (Lindwall *et al.* 2016). It should be noted, however, that temperature responses are simulated based on empirical emission potentials measured at plants that are adapted to their environments today. A high sensitivity to temperature changes in such plants thus might be related to their physiological system that might adapt to warmer conditions (within the same species). For example sensitivity to warming might decrease due to smaller protective requirements or simply due to less effective surface warming resulting from higher transpiration (Lindwall *et al.* 2016).

The inhibition of emission due to increasing CO_2 concentration is mostly only considered for isoprene de-novo production. Global and regional inventory calculations often (but not always) include this effect since the end of the last decade. According to the functional relationship

presented in chapter 5.2.2, the effect is a decrease between 25 and 60 % with a doubling of CO_2, which means that the effect by 2100 mainly depends on the climate change scenario. Correspondingly, incorporating this effect resulted in global isoprene emissions in the year 2100 that were less than half the amount that would have been expected otherwise (Pacifico *et al.* 2012; Young *et al.* 2009). In several studies, the CO_2 effect has been estimated to more than compensate the positive temperature impact and lead to a net isoprene emissions decrease of about 5 % in 2050 (Tai *et al.* 2013) and 24 % in 2100 (Squire *et al.* 2014). Since monoterpenes are emitted from de-novo as well as from storage sources, and the response of de-novo production of monoterpenes to CO_2 is far less clear, few investigations apply the CO_2 reduction impact on monoterpenes as well as to isoprene. In these cases, the decreasing effect on overall emission is even stronger, and the difference between regions where either isoprene or monoterpene emitting species dominate is less obvious (Yue *et al.* 2015).

Incorporating the drought impact using a linear approach as described in the previous chapter predicts a 50% reduction of isoprene emissions on a global scale, most significantly in specific regions of Africa, South America and Australia (Sindelarova *et al.* 2014). For well parameterized regions such as the United States, the drought impact contributed significantly to explain variations in isoprene emissions (Tawfik *et al.* 2012). Similarly in southern France, it has been estimated that emissions were not only decreased by 50% but also the number of days with high emission peaks were widely reduced (Lavoir *et al.* 2011). However, the scheme has been criticized to overestimate emission responses for central African rainforests (Marais *et al.* 2012) and other tropical regions (Zheng *et al.* 2015) as well as for semi-arid and arid conditions (Bauwens *et al.* 2016). It has also been shown to be very sensitive to uncertain soil parameterization and inventory data (Huang *et al.* 2015b; Stavrakou *et al.* 2014). In a new implementation that relates isoprene production to the drought impact on photosynthesis, a BVOC emission reduction due to drought of 17 % on a global annual average seems to be somewhat more realistic (Jiang *et al.* 2018). The approach, however, still relies on a parameterization that is based on roughly stratified vegetation types and soil properties that are difficult to determine on a larger scale.

According to the state of knowledge, induced emissions have hardly been simulated on a regional or global scale. However, the emissions of sesquiterpenes and MeSA have been quantified for European forests, based on experimentally determined relations between emission degrees of infestation by aphids (Bergström *et al.* 2014). Using estimates of current infestation levels and coupling the emission inventory data to a common CTM, the authors estimated stress induced emissions to be responsible for 50-70 % of biogenic SOA production. Coming from a very different angle of research, a module that is suitable for coupling with a dynamic vegetation model has been developed (Landry *et al.* 2016). This module describes insect gradations and their impacts on bio-geochemical and bio-geophysical fluxes. Thus it would already be possible to account for impacts of insect developments on vegetation properties in an integrated manner, paving the way for a fully coupled model that also considers direct impacts of insect damages on BVOC fluxes.

5.3.3 Effects of Vegetation Property Changes

Keyword: Indirect scenario impact

The impact on BVOC emissions due to changes in boundary conditions such as interannual changes in leaf area, vegetation structure, species abundance and vegetation type distribution are generally supposed to be in the same order of magnitude than direct impacts. These vegetation changes are either driven by climate that has a species-specific influence on physiology and growth or by anthropogenic influences such as planting and harvesting. For

example **higher CO_2 concentrations** are supposed to favor photosynthesis, growth and thus leaf area index, leading to higher emissions simply because of a larger amount of emitting tissue (Naik *et al.* 2004). This effect together with temperature increase was found to increase isoprene emissions until the end of the century by 15 % (RCP2.6), 52 % (RCP4.5) and 141 % (RCP8.5) (Bauwens *et al.* 2018). However, this effect is highly uncertain. Despite similar performance under current conditions, net ecosystem production and biomass sequestration for decades ahead can be very different in dynamic vegetation models (Cramer *et al.* 2001; Friedlingstein *et al.* 2014). The reason being that short- and long-term effects of elevated CO_2 on plant physiology and growth vary under different temperature and water regimes, among functional groups, and photosynthetic pathways (Gutschick 2007; Wang *et al.* 2012). Depending on the assumptions about how the vegetation responds, BVOC emissions might increase, compensating the assumed direct effect of CO_2 on emission, or decrease even more (see Figure 7).

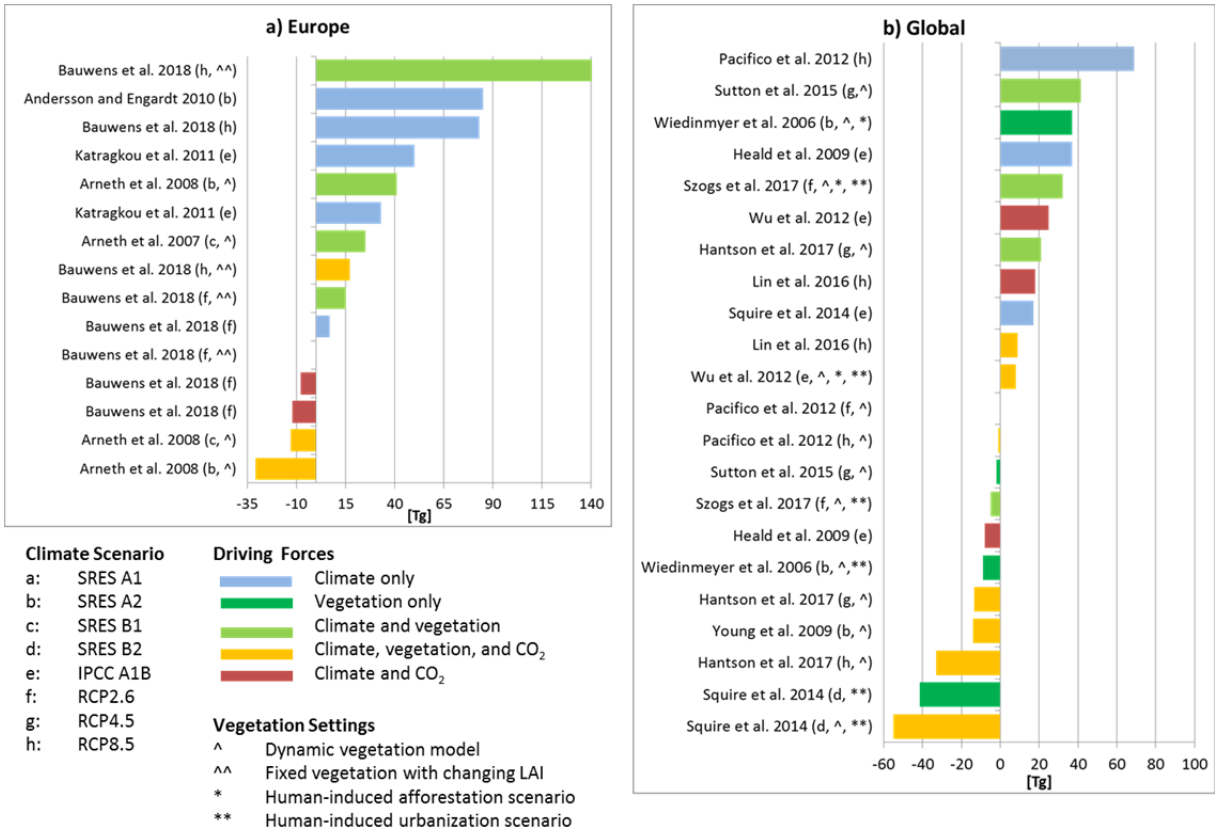
Different species responses to CO_2 and climate changes affects not only biomass and leaf area but shifts species competition strength and thus **species composition** over time, even if the vegetation cover type remains the same. The impact on BVOCs has been demonstrated by investigating developments over the past decades, for example plant succession in southern France has been estimated to cause an increase of total emission by a factor of 4.4 (Schaab *et al.* 2000). In contrast, the recent decrease of oak abundance within an oak/maple temperate deciduous forests in the northeastern United States has resulted in in declining isoprene emission rates (Drewniak *et al.* 2014). Being in line with the notion that terpenoids providing some advantage under a higher temperature regime (see chapter 5.1.3), global changes in natural vegetation composition have been speculated to be responsible for a decreasing trend for monoterpene emissions over the 20th century (Hantson *et al.* 2017).

Following a shift in species composition supported by large scale declines and disturbances, eventually **vegetation types** will also shift, with shrubland and forests increasing their abundance in the subarctic regions (Schollert *et al.* 2014), savannas replacing Mediterranean ecosystems, and tropical forests increasing or decreasing depending on the assumptions on precipitation development. For example isoprene emissions under a future vegetation type distribution were about 25 % higher than current emissions but the dominating reason was not a direct effect but the expansion of tropical humid forests which had the highest annual emission rates (Turner *et al.* 1991). Climate-driven vegetation changes over the period 2000–2100 lead to general increases in isoprene emissions, globally by 15% in 2050 and 36% (Wu *et al.* 2012). Since all of these ecosystems have specific species compositions containing BVOC emitters or non-emitters to different amounts, emission at a whole varies considerably depending on vegetation type distribution (Wang *et al.* 2018).

Also the effect of **management-induced land cover changes** such as deforestation or increased bioenergy plantations has been investigated and found to be a key factor for global air quality in the 21st century (Tai *et al.* 2013; Wiedinmyer *et al.* 2006). Deforestation is a widespread phenomenon in the tropics and is estimated to have led to large decreases of isoprene in the past (Steiner *et al.* 2002) which is expected to proceed in the Amazon although at a smaller pace due to declining coverage as well as leaf area per unit ground (Ganzeveld *et al.* 2010; Lathiere *et al.* 2005; Pacifico *et al.* 2012). If replaced with agriculture and grasslands, isoprene emission until 2100 should decrease by 29 % and methanol emission increase by 22 % (Lathiere *et al.* 2006). Similar impacts of deforestation are also expected for the United States (Chen *et al.* 2009) and for China (Yue *et al.* 2015), albeit not to the same degree. Overall, land use change might develop to be the single most important impact on isoprene production, possibly causing a global decline of approximately 190 TgC yr^{-1} by 2100 (Squire *et al.* 2014).

The impact of land cover conversion, however, depends on the plant species that replaces the previous vegetation. With this respect, a particular interest has been dedicated to a conversion of agricultural areas and grasslands into bioenergy plantations. Since many biofuel plants, in particular fast growing trees such as poplars, willows and eucalypts, are intensively emitting isoprene, it has been speculated that this conversion might have detrimental effects on air pollution and human health. Indeed it has been calculated that turning only 5 % of the crop- and grassland in Europe into poplar plantations would increase isoprene emissions in Europe by about 45 % (Ashworth *et al.* 2015; Beltman *et al.* 2013). Similarly, isoprene also increased over Southeast Asia under scenarios of rainforest conversion into oil palm plantations (Ashworth *et al.* 2012; Pyle *et al.* 2011). In contrast, a widespread adoption of biofuel crops such as Miscanthus would decrease terpenoid emissions (Miresmailli *et al.* 2013).

Figure 7: **Comparison of literature results for European (a) and global (b) changes in projected isoprene emissions. The different colors indicate the driving parameters considered in the various simulations. The periods are end-of-century for all studies.**



Source: Reproduced from Bauwens *et al.* (2018); cited references: (Andersson and Engardt 2010; Arneth *et al.* 2007b; Arneth *et al.* 2008b; Bauwens *et al.* 2018; Hantson *et al.* 2017; Heald *et al.* 2009; Katragkou *et al.* 2011; Lin *et al.* 2016; Pacifico *et al.* 2012; Squire *et al.* 2014; Sutton *et al.* 2015; Szogs *et al.* 2017; Wiedinmyer *et al.* 2006; Wu *et al.* 2012; Young *et al.* 2009)

TextBox: Expected BVOC Emissions under Climate Change

The direct temperature dependence on BVOC production is expected to considerably increase emission in the foreseeable future on a ground level basis. This increase, however, will partly be compensated by increasing CO_2 levels and more frequent drought events. On a regional and global scale, total BVOC are likely to strongly increase in the boreal and subarctic regions due to changes of vegetation properties as well as range shifts of vegetation types. In the Mediterranean region as well as the tropics, forest decline is expected to decrease emissions, in particularly isoprene while OVOCs might increase. However, developments in tropical and temperate regions will largely depend on anthropogenic land-use change, i.e. deforestation and plantation establishment. Where woody plantations and oil palm fields are established, isoprene is expected to be more abundant while the increased abundance of bioenergy crops will decrease terpenoid emissions. A major uncertainty is the interaction between BVOC emissions and disturbances, in particular insect attacks. Prolonged or more frequent gradations could potentially increase emission loads and air quality during summer periods.

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