Biology, Controls and Models of Tree Volatile Organic Compound Emissions

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Preface

Ülo Niinemets and Russell K. Monson

Discoveries that plants are in part responsible for the blue haze commonly observed in the atmosphere above many forests (Went 1960; Rasmussen and Went 1965) and for the tropospheric ozone pollution in many forested urban and suburban areas (Rasmussen 1972; Chameides et al. 1988) have compelled researchers to ask what are the plants emitting, how much is being emitted and how do these emissions impact our environment? These very important questions are at the heart of a highly interdisciplinary research field: biogenic volatile organic compounds (BVOC) in the biosphere–atmosphere component of the Earth system.

Fritz Went, a plant physiologist famous for discoveries on plant growth regulators, was also intrigued by the potential for plants to form atmospheric hazes above forests. He hypothesized that the organic compounds emitted from plants, many of which he could detect with his own sense of smell, contributed to this haze. In 1960, he made measurements on the mass of leaf oils in shrubs from the Western United States and estimated global terpene emissions to be 175 Tg C year^{-1} (1 Tg = 10^{12} g) (Went 1960). Since that seminal study, estimates of global BVOC emissions (excluding methane) have been refined through coupled vegetation–atmosphere models and better maps of global vegetation. Currently, the worldwide emissions are estimated to be around 1 Pg C year^{-1} (1 Pg = 10^{15} g) (Guenther et al. 2012). Much of the past research on plant volatile emissions has been, and continues to be, on the simple C5 volatile hydrocarbon, isoprene, which is emitted from leaves in a light- and temperature-dependent manner and is coupled to the metabolic processes of photosynthesis (Sanadze 1956; Rasmussen and Went 1965; Rasmussen 1970). Since its initial discovery, the research on biogenic isoprene has

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focused on understanding its source strength and distribution among different plant taxa, resulting in the construction of first list of isoprene-emitting plants (Rasmussen 1978) and first biogenic emission inventory system (BEIS, Pierce and Waldruff 1991), followed by more biologically oriented emission algorithms and inventories (e.g., Guenther et al. 1991, 1994, 2006, 2012; Arneth et al. 2007; Monson et al. 2012). By now, it is widely acknowledged that multiple plant BVOC emissions play a major role in atmospheric dynamics within the Earth system with highly reactive compounds reacting in the gas phase to affect atmospheric chemistry, including influences on less reactive compounds that affect the atmosphere's global warming potential, e.g., methane (Fuentes et al. 2000). Furthermore, condensation of photo-oxidation products of BVOCs leads to the formation of secondary organic aerosols, which also generate cloud condensation nuclei and have profound implications for the Earth's solar radiation budget and climate (Kulmala et al. 2004; Huff Hartz et al. 2005; Hallquist et al. 2009; Arneth et al. 2010). Trees have been traditionally thought to contribute the most to BVOC emissions due to the presence of multiple tree species with high emission rates (e.g., the oaks and poplars) and large aerial coverage, which gives forests a unique global role in regulating atmospheric chemistry. Apart from strong constitutive emitters, emissions induced by abiotic and biotic stresses have also been identified in many important forest species previously considered "non-emitters" (Holopainen and Gershenzon 2010; Loreto and Schnitzler 2010; Niinemets 2010), implying that there are strong biological controls on the emissions of BVOCs that we still do not understand and that continue to cause large uncertainties in our models and inventories.

From a biological perspective, the key question has been why do plants emit these volatiles? What are the costs and benefits for the plant, and why do some plant species emit these compounds constitutively and in others the emissions must be induced? The role of isoprene emissions was unknown until the mid-1990s when it was discovered that isoprene enhances plant thermotolerance (Sharkey and Singsaas 1995) and increases the resistance of plant metabolism to atmospheric oxidants (Loreto et al. 2001), followed by the development of a hypothesis of general enhancement of cellular oxidative stress tolerance (Vickers et al. 2009a). Lately, breakthroughs in the genetic engineering of plants have allowed us to test these hypotheses with unprecedented specificity in the processes affected (Behnke et al. 2007, 2010; Vickers et al. 2009b; Velikova et al. 2011). Rapid developments in the availability of genomic information have also recently allowed researchers to gain insight into evolutionary patterns and past influences by natural selection on the isoprene emission capacity (Monson et al. 2013; Sharkey et al. 2013). Furthermore, the role of multiple plant BVOCs in abiotic and biotic stress signalling within and among plants, and among plants and insects has drawn strong attention from a broader complement of the ecological research community (Owen and Peñuelas 2005; Dicke et al. 2009; Dicke and Baldwin 2010; Holopainen and Gershenzon 2010).

In the past, three comprehensive treatises have been published on trace gas emission from vegetation (Sharkey et al. 1991; Hewitt 1999; Gasche et al. 2003). Only the book by Sharkey et al. (1991) deals exclusively with biological controls on BVOC, while the book by Hewitt (1999) focuses on quantification of emissions, and the book by Gasche et al. (2003) only briefly considers biological controls. Since the publication of these books, there has been rapid progress in understanding the controls over isoprene emissions, including the discovery of isoprene synthase (Silver and Fall 1991), its sequence in several organisms (e.g., Miller et al. 2001; Vickers et al. 2010; Sharkey et al. 2013) and establishment of the reaction mechanism (Köksal et al. 2010). Furthermore, there has been a significant increase in our knowledge of multiple terpene synthase structures and regulation (Bohlmann et al. 1998; Fischbach et al. 2001; Degenhardt et al. 2009; Chen et al. 2011; Keeling et al. 2011; Köksal et al. 2011). Due to the development of sensors and detection technology that was in its infancy at the time of the appearance of the book edited by Hewitt (1999), a large volume of literature has emerged on BVOC flux quantifications (Karl et al. 2002, 2007; Müller et al. 2010). Finally, since the publication of the three past books, the field of BVOC emissions has matured greatly in our understanding of BVOC emission models and their connection to underlying metabolic processes (Monson et al. 2012).

This book intends to cover all biological scales of organization from molecular to globe and to make a major leap in summarizing and synthesizing the existing information accumulated since the publication of the past comprehensive summaries of BVOC emissions. The book consists of 17 primary chapters followed by a synthesis. The chapters focus on four major topics: evolutionary diversification and perspectives for genetic engineering of volatile organic compound emissions (chapters 1–4), controls over emissions (chapters 5–7), emissions under stress (chapters 8–11), and emission models (chapters 12–17).

Chapters 1–4 cover tree BVOC emission diversity and evolutionary aspects as driven by abiotic (chapter of Fineschi et al.) and biotic (chapter of Trowbridge and Stoy) stresses, and molecular diversity (chapters of Rajabi Memari et al. and Rosenkranz and Schnitzler), specifically asking how and why the capacity for constitutive volatile production has evolved, what are the key biochemical pathways and factors that determine the blend of emitted volatiles. Here also the diversity in elicited emissions (chapter of Trowbridge and Stoy) and ways of genetic modification to alter emissions (chapter of Rosenkranz and Schnitzler) are analysed.

Chapters 5–7 provide an overview of the cellular and leaf-level mechanisms controlling BVOC emissions. The group of these chapters starts with short-term molecular pathway and leaf-level metabolic controls (chapters of Li and Sharkey, and Monson), then covers longer-term controls by carbon availability and gene expression level acclimation responses to environmental variability (chapter of Monson) and finishes with stomatal and physico-chemical controls driven by variations in compound volatility (chapter of Harley).

Chapters 8–11 review the effects of abiotic and biotic stresses on volatile emissions. Consideration of this topic starts with a chapter analysing the modification of tree abiotic stress tolerance by the capacity for volatile emissions, emphasizing tolerance to heat, drought, salinity and resulting oxidative stress (chapter of Possell and Loreto). Then responses of emissions to flooding (chapter of Kreutzwieser and Rennenberg) and air pollution and elevated [CO_2] (chapter of Calfapietra et al.)

are reviewed. This topic is concluded with a chapter investigating the multitrophic interactions between trees, herbivores and herbivore enemies in future polluted atmospheres that significantly alter the role of volatile compounds as important ecological signals that organize food webs and host parasite relations (chapter of Holopainen et al.).

The chapters 12–17 put the information summarized in previous chapters into the quantitative framework of predictive emission models. This topic starts with a review of leaf-level emission algorithms (chapter of Grote et al.), then covers canopy and landscape (chapters of Niinemets et al. and Guenther) and biome level models (chapter of Ashworth et al.), emphasizing the philosophy of model parameterization and validation. Finally, global feedbacks to climate and atmospheric composition due to tree BVOC emissions are analysed (chapter of Kulmala et al.).

The book concludes with a synthesis section that puts the contents of the book into global biosphere–atmosphere science context and provides a perspective for future developments in the field. In addition to summarizing the state-of-the-art information of tree volatile emissions, the book, in particular, explores the ways that rich archives of molecular, physiological and ecological evidence can be best included in quantitative emission models. The content and focus of the chapters are intended for use by graduate students, researchers and policy professionals interested in the recent developments in the field. As in many interdisciplinary, complex and rich science fields, the challenge in BVOC research is to get to an intellectual place beyond the fragmented, and increasingly more detailed, knowledge provided in the primary literature to one of synthetic understanding, utility for framing further hypotheses and application to devising observation and regulation policies that improve the global human condition. We hope that this book can serve as a springboard for those interested in starting a career in BVOC research, those continuing to pursue research at the frontier of this fascinating field and those interested in applying the research to the better management of our Earth system.

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