Chapter 2
BVOC-Mediated Plant-Herbivore Interactions

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Abstract Plants release unique blends of biogenic volatile organic compounds (BVOCs) into the atmosphere, part of a silent language used to communicate with other organisms in their community. Within this high traffic chemical environment, plants and insects, among other organisms, are receiving, processing, modifying, and responding to information conveyed through varying suites of molecules. Because plants and insects are part of an integrative complex of food web relationships, one common topic of conversation is defence. Plants maintain a baseline level of BVOC emissions as a bottom-up constitutive defence, emitting compounds that act as repellents or deterrents to feeding and/or egg deposition by herbivores. Due to the autonomy of their attackers, plants can also employ an indirect top-down defence strategy, releasing induced volatiles in response to feeding that attract the natural enemies of their herbivore attackers, such as predators and parasitoids. Both bottom-up and top-down BVOC-mediated strategies have important consequences for herbivore preference, performance, and survival with even broader ecological and evolutionary consequences for tritrophic interactions. In this chapter we discuss how constitutive BVOCs mediate aspects of plant defence within a hierarchical spatiotemporal framework. Next we bring to light some of the most recent research on oviposition- and herbivore-induced BVOC synthesis and subsequent effects on the recruitment of natural enemies. We follow up by discussing the ecological effects of induced BVOCs in the context of multiple herbivores, expression from various plant organs, time-lags associated with BVOC induction, and heterogeneity within the infochemical environment. The critical feature of insect learning is described and we highlight some of the major evolutionary implications of BVOC-mediated plant defence syndromes that rely on the unique timing of events at the biochemical, atmospheric, organismal, and community scales.

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Ü. Niinemets and R.K. Monson (eds.), *Biology, Controls and Models of Tree Volatile Organic Compound Emissions*, Tree Physiology 5, DOI 10.1007/978-94-007-6606-8_2,

2.1 Introduction

Organisms are in continuous communication with each other to facilitate survival, defence, cooperation, and social connections. The study of the ability of organisms to interpret and communicate information is known as biosemiotics (von Uexküll 1926) and extends far beyond the signals that human are most adept at perceiving. We are constantly in the midst of countless mutualistic, antagonistic, and uninformative dialogs that are carried out in a chemical language that developed long before humans walked the Earth. The terrestrial fossil record provides evidence of volatile chemical signalling at the beginnings of the evolutionary arms race between species via structures such as plant essential oil glands (Fahn 2002; Krings et al. 2002) and olfactory appendages (Strausfeld and Hildebrand 1999; Labandeira 2002). The ability of plants to *communicate* with plants and other organisms via volatile organic compounds (BVOCs) is fascinating, and influences important evolutionary and ecological processes that we are only beginning to understand.

Definitions

Allelopathy: Biogenic phenomenon where secondary chemicals produced by one organism affect the development, growth, survival, and reproduction of other organisms.
Constitutive defence: A plant defence strategy that is always expressed in the plant.
Direct plant defence: Plant traits that negatively influence the physiology or behavior of herbivores.
Indirect plant defence: Plant traits that enhance the efficacy of the natural enemies of herbivores, such as herbivore-induced BVOCs.
Induced response: Change in a plant following stress or damage.
Induced resistance: An induced response that reduces herbivore survival, reproduction, or preference for the plant of interest, but may not necessarily benefit the plant.
Induced defence: A response that decreases the negative *fitness* consequences of attacks on plants, but may not necessarily affect herbivores.
Infochemical: A chemical that conveys information between two organisms or individuals resulting in a physiological or behavioral response in the receiver that is adaptive to one or both parties.
Tritrophic interactions: Relationship between a plant, an herbivore, and the natural enemies of the herbivore, mediated by plant chemistry and/or BVOCs.

Plants emit more than 30,000 different BVOCs including terpenoids, green leaf volatiles, phenylpropanoids, benzenoids, and methyl esters of plant hormones (i.e., methyl jasmonate and methyl salicylate). These BVOCs mediate plant-plant, plant-insect, and multitrophic interactions and play critical roles in plant defence (Yuan et al. 2009; Fineschi et al. 2013). Effective defence is critical for plant survival and reproduction as plants are subject to constant attack from pathogens, fungi, insects, mammalian herbivores, and other biotic agents. To combat herbivory by

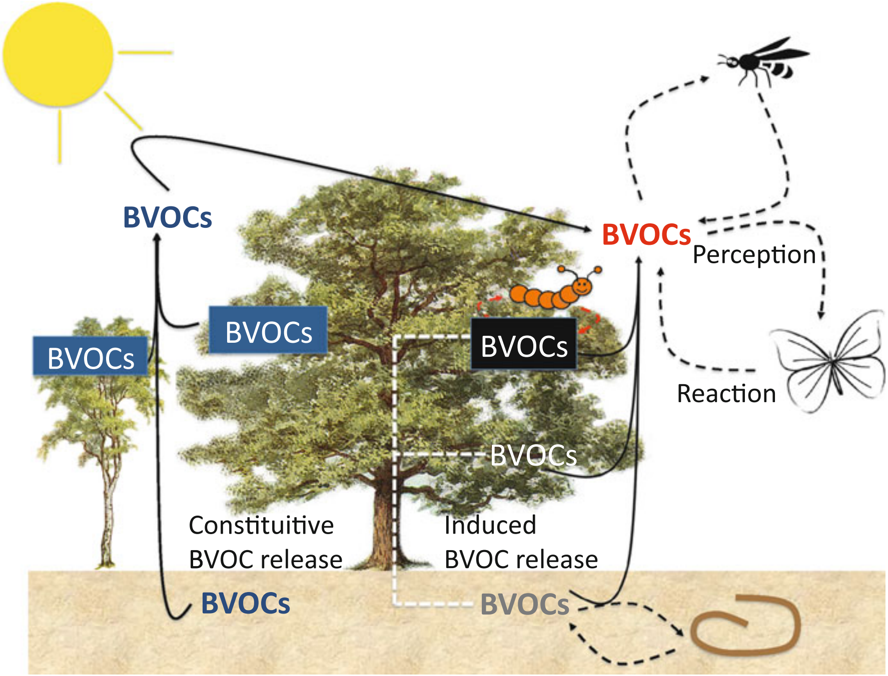

Fig. 2.1 Scheme highlighting the role of biogenic volatile organic compounds (BVOCs) in mediating interactions between trees and herbivores. Plants constitutively synthesize and release BVOCs from leaves, stems, and roots, as demonstrated on the *left hand side* of the figure. Constitutive BVOC emissions from different organs within a tree and trees within a forest (*blue*) are transported to the atmosphere (*black lines*) where they are mixed by turbulence. Different mixtures and concentrations of BVOCs are present in different plant parts, as indicated by coloration. Constitutive BVOC emissions are also mixed with BVOCs whose synthesis and/or emission was induced by herbivores, as demonstrated on the *right-hand side* of the figure, resulting in the total BVOC signal in *red*. Herbivores perceive and respond to BVOC concentrations within the plant (*red dashed lines*), and their feeding activities may induce plants to produce and release a different combination of BVOCs locally, or in other parts of the plant as demonstrated by the *dashed white lines*. Other organisms perceive and respond to BVOCs in their environment (or *Umwelt* following von Uexküll 1926), as represented by *dashed black lines*. The multitrophic interactions that are mediated by BVOCs, including herbivore activity and parasitoid oviposition behavior, are central components of forest population, community and ecosystem ecology

heterotrophic organisms that span multiple taxa and developmental stages, plants employ a diverse arsenal of chemical defence mechanisms that include BVOCs. Thus, BVOCs are an integral part of a comprehensive bottom-up and top-down plant defence strategy because they enable plants to resist herbivory within and beyond the leaf, stem, and root (Fig. 2.1).

This chapter focuses on the role BVOCs play in interactions between plants and insects. We place particular emphasis on spatial and temporal aspects of both constitutive and insect-induced BVOC dynamics to highlight the role played by BVOCs in tritrophic ecological interactions. We also discuss above- and belowground factors that control BVOC emissions, and the influence of the resulting emissions on tritrophic interactions associated with both roots and leaves. Our focus here is on biotic interactions in natural unpolluted environments, and we refer the reader to the chapter of Holopainen et al. (2013) in this book for a discussion of the modification of biotic interactions in polluted atmospheres and under global change. We further refer the reader to Peñuelas and Llusià (2003), Loreto and Schnitzler (2010), and Possell and Loreto (2013) and Calfapietra et al. (2013) in this book about the role of abiotic stresses, including climate change, in altering BVOCs, and subsequent consequences for ecological signalling. We conclude with a brief overview of the evolutionary implications of BVOCs in the context of insect learning in complex environments.

2.2 Constitutive BVOCs

Constitutive BVOCs serve as constant barriers to herbivore attack by deterring colonization through their antixenotic function and inhibiting growth, reproduction, development, and/or survival through their antibiotic function (Paiva 2000; Walling 2000). We refer to these characteristics as ‘bottom-up’ defences as they directly impact herbivore performance. In a natural setting, both the rate at which volatiles are released and their spatial and temporal persistence in the environment determine their relevance in ecological signalling. However, complex feedbacks exist between the phylogenetic constraints on biosynthesis, environmental controls on emissions, and compound-specific physico-chemical responses to the environment. As a result, the spatial and temporal heterogeneity of BVOC emission rates is often pronounced, with important implications for multispecies interactions. We discuss consequences of BVOC emissions at the leaf level and then describe controls on and consequences of BOC emissions at the organ, whole plant, and community scale.

2.2.1 Role of Constitutive BVOCs in Defence and Host Selection

Trees maintain a baseline level of volatile metabolites that are released from the leaf upon production, or some time after production from storage sites (e.g., resin canals) (Paré and Tumlinson 1999). Within the last decade, an emphasis has been placed on understanding the role of constitutive vegetative BVOCs in deterring herbivory. Unfortunately we still lack a mechanistic understanding of how BVOCs released from plants *directly* repel herbivores and/or inhibit feeding. One possibility is that constitutive emissions are directly toxic to impending attackers, potentially affecting physiological and neurological processes by influencing gene expression and/or interfering with the macronutrient digestion. However, studies have yet to demonstrate how relatively low-emission rates, typically on the scale of nano- or micrograms per hour per gram of leaf tissue, elicit toxic physiological effects (Unsicker et al. 2009).

Herbivores must discriminate between true ecological signals that might increase their fitness, and background noise resulting from a highly variable infochemical environment. Most phytophagous insects are specialist feeders that utilise a limited number of species as resources, and chemical cues are critical in selecting suitable hosts. It is not in the best interest of a plant to attract herbivores; however, specialists are capable of exploiting the characteristic volatiles emitted by their hosts to gain information on quality, susceptibility, and natural enemy status. Reddy and Guerrero (2004) give two examples of how insects exploit BVOCs with different pheromone-mediated implications for plant resistance. Some insects can use constitutive BVOCs for their own defence. For instance, green leaf volatiles (GLVs) released from non-host tree species serve as repellents in host selection and inhibit the pheromone response of several bark beetles. Other insects can use constitutive BVOCs to their advantage in finding mates. When male *Ips* and *Dendroctonus* spp. are exposed to the volatile myrcene, they modify the compound, which results in the production of oxygenated pheromones in their hindgut. However, predators and parasitoids attacking adults and eggs have learned to eavesdrop on these pheromone signals to locate prey more effectively (Stowe et al. 1995). As a consequence, constitutive BVOC signals that are attractive to specialists can be intercepted and used by the herbivore's natural enemies as a type of *indirect* defence. Thus, constitutive and induced defence strategies should be assessed in an integrative fashion to fully appreciate the ecological role played by BVOCs.

2.2.2 Spatiotemporal Patterns

2.2.2.1 Leaf-Level Responses

BVOC emissions exhibit significant variations across space and time at the scales of leaves, organs, whole plants, and ecosystems. At the leaf level, rates of constitutive BVOC production and emission are sensitive to a number of abiotic factors, including light and temperature as discussed by Niinemets et al. (2004) and other chapters in this volume. These factors can interact with ontogenetic changes in emissions and result in variable emission rates from leaves close in proximity. For instance, constitutive monoterpene (C_{10}) emissions can be detected from young hybrid poplar leaves (*Populus deltoides* x *Populus nigra*). However, mature leaves on the same tree were found to emit only isoprene (C_5) and at a rate of about five times greater than monoterpenes released from young leaves (Brilli et al. 2009), suggesting that the amount of carbon invested towards isoprenoid biosynthesis changes with leaf ontogeny. Differences in BVOC quality and quantity between leaves have important consequences for herbivore host selection, and these differences can result from the presence of specialized structures and/or the vascular connections within the tree. Even subtle spatial variation can be critical for specialists that have learned to associate proximate volatile signals with host quality. For example, BVOC emissions tend to be significantly higher in sunlit leaves when compared to shaded leaves on the same plant and/or branch, due largely to an increase in light and temperature and higher rates of physiological activity (Harley et al. 1996). While this increase in emissions may have consequences for herbivore preference, it is also possible that BVOCs serve multiple ecological functions simultaneously (e.g., protecting leaves from photodamage at high temperature and light conditions) (Peñuelas and Llusià 2002) with evolutionary implications via multiple selection pressures. Furthermore, some plant BVOCs with low vapour pressures tend to condense on leaf surface as a function of leaf temperature and position in the canopy and may serve as defence agents against herbivores and pathogens (Holopainen and Gershenzon 2010), but it is unknown if this mode of BVOC function represents an effective defence.

2.2.2.2 BVOC Variation Between Vegetation and Flowers

The suite of volatiles released by healthy trees can also vary spatially within a plant among organs including leaves, stems, flowers, and roots (Fineschi and Loreto 2012; Mumm and Hilker 2006; Takabayashi et al. 1994). The survival of a plant is determined by investment in reproduction (e.g., flowers, nectar) and growth (e.g., vegetative biomass). Thus, allocation of resources to defence may come at the expense of investment in reproductive tissues and affect mutualistic relationships, pollination events, and fitness (Mothershead and Marquis 2000). For instance, floral and vegetative BVOC emissions are differentially attractive and repellent to species that specifically feed on those organs, yet BVOCs from both plant parts are likely to be mixed in the atmosphere before their perception by an insect. Thus, chemical information from other plant organs may confound perception and host identification, particularly in response to damage (see *Induced Responses*). Because both herbivores and pollinators are selective agents on floral chemistry and emissions, it is critical to understand the degree to which defensive vegetative BVOC production alters nectar and pollen quality and thereby affects fitness. Furthermore, compound type and emission rate can vary substantially between organs as a function of the predictability of attack on various plant parts (see optimal defence theory, Rhoades (1979); Zangerl and Rutledge (1996)) and ecophysiological constraints (e.g., tissue-specific biosynthesis or allocation, Niinemets et al. 2004). While many BVOCs appear to be exclusively produced in either flowers or leaves, compounds can also be passively transported into the nectar and/or pollen and subsequently released into the atmosphere. Future studies should focus on plant allocation and tissue type to fully understand the dynamics of plant-pollinator-herbivore-interactions (Kessler and Halitschke 2009).

2.2.2.3 Belowground BVOC-Mediated Interactions

While most studies focus on BVOC-mediated interactions between aboveground plant parts and herbivores, plants must also defend themselves against soil-dwelling herbivores including rodents, insects, and nematodes, all of which play key roles in terrestrial ecosystem community structure. Due to the limited mobility of soil organisms and the low transport rates of root compounds, interactions in the soil occur over significantly smaller spatial scales than aboveground interactions (van der Putten et al. 2001). Despite the difference in characteristic spatial scales of influence, the role of BVOCs might be more important for belowground communities where visual cues are lacking and with soil-dwelling herbivores often exhibiting poor eyesight (Rasmann et al. 2005; van Dam and Heil 2011). A number of compound classes emitted from aboveground organs have been shown to mediate plant-herbivore interactions belowground, but in different compositions (Wenke et al. 2010). Nonetheless, BVOCs can directly or indirectly influence belowground communities, support symbioses, combat competitive plant species, and defend against pathogenic fungi, bacteria, and herbivores (Nardi et al. 2000).

Herbivore host choice for oviposition is critical for the next successful generation of soil dwelling herbivores. Adults of the large pine weevil (*Hylobius abietis*) are attracted to suitable hosts in a dose-dependent manner, depending on BVOC concentrations released from conifer roots (Nordlander et al. 1986). BVOC composition is also important; larvae of the forest cockchafer (*Melolontha hippocastani*) exhibited a noted preference for monoterpenes released from carrots over the fatty acid derivatives emitted from oak roots (Weissteiner and Schütz 2006). Despite being separated in space, roots, shoots, leaves, and flowers are connected and so are their resources, metabolic activities, and defences. Belowground organisms can induce defence responses aboveground and vice versa, the cost: benefit ratio of these induced responses and their consequences are discussed in more detail in the Sect. 2.3: *Induced BVOCs*.

2.2.2.4 BVOC Variability Between Plants

At the whole-plant level, BVOC emission rates are dependent on a number of environmental and biotic factors, including developmental stage as well as plant species, genotype, and age (see Dicke 1999; Paré and Tumlinson 1999). Constitutive plant defences are expressed differentially with ontogeny, and while BVOC emissions have been shown to decrease in mature cultivated herbs (Cole 1980), information about their ontogenetic patterns in mature trees and seedlings remains largely unknown (Boege et al. 2011). Studies focused on ontogenetic changes in tree BVOC emissions, foliar chemistry, and predator/parasitoid foraging dynamics may offer mechanistic insight into tritrophic patterns observed in the field. In addition to age, specific chemotypes and plant varieties have differential growth and resistance properties (Staudt et al. 2001). For example, mango (*Mangifera indica*) tree cultivars that are the most susceptible to mango gall flies (*Procontarinia* spp.)

emit significantly higher levels of α-pinene and β-pinene throughout the growing season; these volatiles are highly attractive to this pest (Augustyn et al. 2010). At the plant population level, BVOCs emitted by particular genotypes of seedlings of *Pinus pinaster* in plantations have been found to be susceptible to a generalist phloem-feeding pine weevil (*Hylobius abietis*). Blanch et al. (2012) showed that under high nutrient availability, susceptible trees exhibited higher terpene emission rates, including α-pinene, an attractant for *H. abietis* (Moreira et al. 2008), which could explain the pattern of weevil damage observed in the field (Zas et al. 2008). Thus, BVOC emission rates must be investigated in the context of plant genetics, development, *and* the environment to better-understand herbivore-natural enemy development, behavior, and natural ecological patterns.

2.2.2.5 Community-Level Variability

Observed spatial variations in foliar BVOC emissions range over several orders of magnitude at the community level due to changes in species composition and foliar density (Guenther 1997). Spatial patterns in both the magnitude and composition of BVOCs that herbivores and their natural enemies perceive are critical for their behavior, and therefore, for their reproduction and survival. However, the identification of specific cues signalling host availability and quality may be influenced by the background of chemicals present in the habitat from other species, requiring adaptive and integrative abilities to extract useful search information from the milieu of chemicals present in the environment (Hilker and McNeil 2008). Drastic community shifts, via invasive species or changes in climate, can influence plant-herbivore interactions by altering the proportion of species that produce varying types and quantities of BVOCs. Depending on the ability of the insect to learn (see Sect. 2.4, *Insect Perception and Learning*) and the time required to make new host-BVOC associations, changing habitats can modify the probability of a particular plant-herbivore interaction occurring, the intensity of the interaction, and coevolutionary processes (Agrawal and Fishbein 2006).

2.2.2.6 Variation in Time: Diurnal Cycles of BVOC Release

The effects of time on BVOC emissions extend beyond ontogeny. BVOC emissions are a product of day length (light), corresponding changes in temperature and water status, as well as seasonality. Many BVOCs released constitutively from trees exhibit diurnal cycles, increasing rapidly in the morning with temperature and solar radiation, peaking in the middle of the day, and decreasing during the afternoon and evening (Pio et al. 2005; Grabmer et al. 2006). High emissions make plants more “apparent” to insects, and may determine the employment of other defensive strategies used by plants to protect against herbivory (Feeny 1976; Rhoades and Cates 1976). However, “apparency” due to high daytime emissions and their role in increasing plant vulnerability to herbivores is dependent upon the peak foraging time of the insect attacker as well as the searching behaviors of their natural enemies. Furthermore, because vegetative and reproductive tissues exhibit diurnal variability in emissions, plasticity in volatile production from both types of plant organs can be critical, as the specificity with which insects choose to visit flowers on fruiting trees may be the result of the quantitative relationship between the attractant and repellent components in the blend contributed from leaves (Euler and Baldwin 1996).

2.2.2.7 Variation in Time: Seasonal Trends

Seasonal trends in BVOC emissions have been observed in a number of forest types, including mixed hardwood (Karl 2003), boreal coniferous (Hakola et al. 2003), and Mediterranean (Owen et al. 2001; Pio et al. 2005). Similar to emission rates observed over a shorter time scale, the seasonal release of BVOCs is a function of changes in light, temperature, and compound-specific physico-chemical controls (see Niinemets et al. 2004 and Grote et al. 2013 for detailed discussion of controls on seasonal changes in emissions). For example, within a mixed hardwood forest, Karl (2003) found, among other patterns, a spring peak for methanol and attributed it to rapid leaf expansion. While the large amount of methanol released from vegetation has long been assumed to be a metabolic waste product, studies have shown that herbivory can also elicit its release, suggesting the potential role of methanol in mediating plant-insect relationships (Peñuelas et al. 2005). Furthermore, application of methanol to plants in quantities mimicking herbivore-elicited release affects bottom-up controls by decreasing plant foliar defences (e.g., trypsin proteinase inhibitors) and enhancing the performance of the herbivore (von Dahl et al. 2006). Thus, seasonally-driven BVOC-specific spikes may not only impact plant-insect signalling, but also force within-plant feedbacks that negatively impact defence capabilities resulting in higher herbivore pressure at key developmental times of the year.

2.3 Induced BVOCs

Plants are the primary food source for millions of insect species, each using unique strategies to obtain nutrients from both above- and belowground tissues. In contrast to constitutive ‘hard-wired’ plant traits that confer resistance to insect pests regardless of insect infestation risk, herbivore-challenged plants can exhibit phenotypic plasticity and can mount active defence responses that are induced by insect behavior. Trees are thought to have evolved induced defences to save on allocation costs when pressure from herbivores is low (Heil 2002). When expressed following herbivory, induced responses can serve as *direct* defences, affecting the herbivore through immediate toxicity (i.e., a ‘bottom-up’ defence) or as an *indirect* (‘top-down’) defence, affecting the herbivore via recruiting its natural enemies (Dicke and Vet 1999). Both induced direct and indirect defences can alter herbivore behavior and development. BVOCs released immediately after herbivory consist of preformed volatiles, some resulting from the bursting of storage structures, and depend on the mode of damage such as wounding, egg deposition, and herbivore feeding (Walling 2000). Other BVOCs released with feeding are synthesized *de novo* and exhibit delayed emissions on time scales of minutes, hours, days, and potentially seasons. These emissions can also be expressed both locally and systemically (Paré and Tumlinson 1999). Plant BVOCs are not only mediators of aboveground plant-insect interactions, but also affect herbivore dynamics in the soil. In fact, damage by below- and/or aboveground herbivores has been found to affect pollinators and higher trophic levels, particularly the natural enemies of herbivores in both root and shoot food webs (see van Dam and Heil (2011) and references therein). Here we briefly expand upon these topics, with particular focus on herbivory and oviposition-induced BVOCs and the consequences of the spatiotemporal dynamics of emissions on above- and belowground defence.

2.3.1 Herbivore and Oviposition-Induced BVOCs: Induction Depends on Mode of Damage, Elicitors, and Signal Transduction

The synthesis of novel BVOCs in response to herbivory is not part of a general syndrome in response to stresses (i.e., drought, ozone, temperature, etc.), but is a *specific* response to herbivory with a well-documented defensive role in trophic interactions (Staudt and Lhoutellier 2007). Some of the earliest studies of induced host volatiles were performed on trees, (e.g., *Populus* spp. (Baldwin and Schultz 1983)). With the ability to release hundreds of BVOCs, how do trees release such specific chemical signals in response to herbivore attack? The quality and quantity of herbivore-induced BVOCs are dependent on a variety of factors, including the plant species, plant age, the tissue type being attacked, as well as the herbivore species, feeding mode, and its developmental stage (De Moraes et al. 1998). The mode, frequency, and severity of physical damage by herbivores and herbivore-specific chemical elicitors initiate highly regulated modifications in the plant's transcriptional and metabolic processes by activating signalling pathways (Kessler and Halitschke 2007). While these pathways are well known in herbaceous species, there exists a gap in our knowledge regarding signals and pathways that induce resistance in many tree systems. In light of a few recent studies, many assume similar signal cross-talk and activation in trees as observed in herbaceous plants (Eyles et al. 2010).

A number of elicitors initiating signal cascades involved in BVOC synthesis have been isolated and characterized from insect saliva, regurgitants, and oviposition fluids, and include enzymes, fatty acid-amino acid conjugates, and bruchins (Paré et al. 2005). Once in contact with plant cells, these elicitors activate signal transduction pathways (e.g., the octadecanoid (C_{18}-fatty acids) pathway) that ultimately lead to gene expression and the synthesis of particular defence-related BVOCs (for more detail on signal cascades see Kessler and Baldwin (2002)). Numerous studies in trees have shown that in the absence of wounding, pathways can also be induced through the application of herbivore oral secretions, elicitors themselves, or phytohormones such as jasmonic acid (JA), ethylene, and salicylic acid (SA) (Dicke et al. 1999; Eyles et al. 2010; Van Poecke et al. 2001). The early steps in the herbivore elicitation process remain to be elucidated as well as the mechanisms responsible for plant recognition of these herbivore-specific compounds. Nonetheless, the result of these signal cascades is an herbivore-induced BVOC blend comprised of tens to hundreds of compounds. While a number of these compounds are species-specific and actively produced in response to herbivory, many BVOCs also "leak out" or are released simply due to mechanical damage. These compounds, known as green leaf volatiles (GLVs), consist of saturated and unsaturated C_6 alcohols, aldehydes, and esters produced by the oxidative breakdown of membrane lipids (Paré and Tumlinson 1999). Within this complex blend of GLVs and novel compounds synthesized *de novo*, however, only a subset of compounds play a biological role in mediating higher trophic level interactions with herbivores and natural enemies (see Dicke (2009) and references therein).

Individual signal cascades, as described above, have the ability to serve a variety of functions. The involvement of several signal cascades in response to specific forms of herbivory may help explain the specificity of BVOC profiles (Kessler and Baldwin 2002). As such, plants must be able to not only identify the source of damage, but also prioritize and tailor the signalling pathway that will mount the most effective defence strategy (Reymond and Farmer 1998). A rich body of literature exists regarding induced plant responses to attack by *chewing* insects and the subsequent interactions between the two organisms (e.g., Karban and Baldwin 1997). There are also many studies that demonstrate the specific and differential chemical response of plants to chewing insect species (e.g., De Moraes et al. 1998). However, plants are constituents of complex communities, and as such, are rarely attacked by a single herbivore. Multiple biotic stressors can significantly alter herbivore-induced BVOC emissions as concurrent feeding may induce cross-resistance (Kessler and Halitschke 2007) or competing plant defence pathways, both of which have important implications for defence and evolution (Rodriguez-Saona et al. 2005). While far less is known about the induction of BVOCs by herbivores of feeding guilds that cause less tissue damage (i.e., miners, galls, and piercing-sucking insects), a study by Delphia et al. (2007) demonstrated that simultaneous herbivory by insects with different feeding habits significantly alters BVOC emission and defence strategies. However, ways in which plants simultaneously integrate responses to multiple herbivores and the ecological and evolutionary consequences for plant-insect interactions after attack, remains largely unknown.

Herbivores not only induce changes in plant leaf BVOCs through feeding, but also through egg deposition. Hilker and Meiners (2002) describe the mechanism involved in oviposition-induced BVOCs in Scots pine (*Pinus sylvestris*) and field elm (*Ulmus minor*). In both systems, the adult female wounds the surface of the leaf and needle just before oviposition. The eggs are then laid into the wounded tissue along with oviduct secretions that surround the eggs securing them to the plant. Only when the secretions, containing an elicitor, make it past the cuticular barrier do leaves release parasitoid attractant BVOCs (Hilker and Meiners 2006). To date, only a few oviposition-associated elicitors have been identified, including bruchins (Doss 2005) and benzyl cyanide (Fatouros et al. 2008). The application of jasmonic acid can also elicit the release of BVOCs that attract the egg parasitoids associated with each species, suggesting the involvement of the octadecanoid pathway in driving oviposition-induced responses (Hilker and Meiners 2002; Meiners and Hilker 2000). Similar to herbivory, insect egg deposition induces plant responses that are specific to both the plant and herbivore species attacking it, yet whether this specificity is due to species-specific elicitors or a dosage-dependent response remains unknown for most systems (Hilker and Meiners 2010). While the induced BVOCs produced via feeding and oviposition differ in composition, both BVOC blends may be perceived by the herbivore and parasitoid with either negative or positive consequences. For example, herbivore-induced BVOCs have been shown to deter female herbivores from oviposition in an attempt to avoid competition (Kessler and Baldwin 2001; De Moraes et al. 2001). Future work aimed at understanding the interaction of herbivore- and oviposition-induced signalling pathways, the BVOCs emitted, and consequences for herbivores and their natural enemies will offer insights into the evolutionary importance of these compounds.

What is a parasitoid anyway?!?

Parasitoids spend only part of their lifecycle associated with a host. They feed exclusively in or on the body of another arthropod, eventually killing it. Only a single host is required for the parasitoid to complete its lifecycle.

Predators kill their prey, usually more than one species, but do not need a host to complete any part of their lifecycle.

Parasites spend their entire life associated intimately with its host, usually at the host's expense, but without causing death.

2.3.2 *Induced Volatiles Serve as Direct Plant Defences*

Immediately following release, herbivore- and/or oviposition-induced BVOCs carry a vast array of information through the environment with the potential to directly influence the behavior of different members of the ecological community. Some herbivore-induced volatiles have been shown to function as a plant defence by deterring herbivore feeding and oviposition (Kessler and Baldwin 2001; Laothawornkitkul et al. 2008; De Moraes et al. 2001). For instance, when foraging, starved adult willow leaf bugs (*Plagiodera versicolora*) orient towards odors elicited from willow leaves infested by conspecifics as opposed to intact leaves, perhaps due to increased quality or lower concentrations of secondary compounds (Yoneya et al. 2009). Deception is another way in which plants use herbivore-induced BVOCs to their advantage, such as in the case of the sesquiterpene, (*E*)-β-farnesene, which is also an aphid alarm pheromone that signals aphids to stop feeding and disperse (Bernasconi et al. 1998). Even oviposition-induced BVOCs can affect the egg laying choice of other female herbivores. To avoid inter- and intraspecific competition and a site attractive to egg parasitoids, laboratory choice tests showed adult *Xanthogaleruca luteola* to prefer BVOCs from field elm (*Ulmus minor*) leaves without eggs over those with eggs and/or feeding damage (Hilker and Meiners 2002). In addition to directly resisting the attacking herbivore, induced BVOCs can also influence herbivores on neighboring plants by priming non-infested plants to chemically respond faster to future insect attacks. One study showed that rates of herbivory were lower in black alder (*Alnus glutinosa*) trees growing close to damaged conspecifics (Dolch and Tscharntke 2000). This is similar to observations made by Rhoades (1983), who reported that undamaged Sitka willow trees (*Salix sitchensis*) in close proximity to herbivore-infested conspecifics mounted a more aggressive chemical defence in response to fall webworm larvae (*Hyphantria cunea*) than distant controls. If induced BVOCs can directly influence the chemical defences within neighboring trees, it is not surprising that they can also elicit defence responses in undamaged parts of the same tree. For instance, gypsy moth (*Lymantria dispar*) feeding on branches previously exposed to herbivore-induced BVOCs from nearby damaged branches was reduced by 70% compared with controls (Frost et al. 2007). In addition, extrafloral nectaries have been shown to increase in output when undamaged leaves are exposed to herbivore-induced BVOCs emitted from damaged leaves on the same plant, resulting in increased visits from predators (Heil and Silva Bueno 2007). Despite evidence from experimental observations, we lack an understanding of *how* the signals that induce priming are received by plants, which compounds are biologically active within an herbivore-induced mixture, and the signalling cascades responsible for indirect BVOC-mediated plant defence.

2.3.3 Induced Volatiles Serve as Indirect Plant Defences

The attraction of the natural enemies of herbivores by damage-induced volatiles is a well-established phenomenon in many plant species, and probably the first defence strategy that comes to mind when discussing induced BVOCs. For over 40 years (Green and Ryan 1972), a vast array of herbivore-induced plant BVOCs has been shown to effectively recruit insects of the third trophic level that prey upon or parasitize larval herbivores, as well as eggs. By doing so, BVOCs reduce the preference and/or performance of herbivores, serving as an indirect defence and an important mediator of tritrophic interactions (Karban and Baldwin 1997). Nonetheless, because most palatable herbivores are cryptically coloured and well hidden on the undersides of leaves, the probability of parasitoids effectively finding their hosts using visual cues and random searches is relatively low. However, the suite of compounds released following herbivore-damage is quite sophisticated and unique, differing in total abundance and composition following attack by different herbivores (e.g., De Moraes et al. 1998). The species-specific plumes present within the local environment contain critical host-location information for parasitoids, which have developed the ability to learn chemical cues associated with the presence and quality of their specific host (see Sect. 2.4, *Insect Perception and Learning*). For instance, some parasitoids are capable of differentiating between parasitized and unparasitized larval hosts in flight due to the different odor blends induced by each caterpillar (Fatouros et al. 2005). While herbivore-induced volatile blends can be quite complex, a number of individual BVOCs involved in attraction of parasitoids have been identified (e.g., Halitschke et al. 2008; Ibrahim et al. 2005). However, it is highly unlikely that a parasitoid will be exposed to only one BVOC in nature, and the context within a BVOC blend is perceived may be important. In fact, the eulophid egg parasitoid (*Chrysonotomyia ruforum*), while attracted to the herbivore-induced release of (*E*)-β-farnesene, requires the presence of background non-induced pine odor to locate its sawfly host (*Diprion pini*) (Mumm and Hilker 2005). While individual herbivore-induced BVOCs may be involved in parasitoid host location, it is often critical that they are perceived in the context of other BVOCs so as to distinguish variation in quality and quantity.

Although most available information on BVOC-mediated tritrophic interactions comes from studies in agricultural or herbaceous species, a number of studies has also demonstrated the attraction of the natural enemies to herbivore-induced BVOCs elicited by pests attacking trees, particularly in fruit trees [e.g., apple (*Malus domestica*), mango (*Mangifera indica*), and grapefruit (*Citrus paradisi*)], conifers [e.g., Scots pine (*Pinus sylvestris*) and loblolly pine (*Pinus taeda*)], as well as some deciduous species [e.g., elm (*Ulmus minor*) and black poplar (*Populus nigra*)] (see Dicke (1999) and Mumm and Dicke (2010)). For instance, fruit fly parasitoids (*Diachasmimorpha longicaudata*: Braconidae) significantly preferred BVOCs from infested mangoes (with higher BVOC concentrations) and their extracts (particularly 2-phenylethyl acetate) over healthy and mechanically damaged fruits, suggesting that parasitoids use induced BVOCs to locate hosts in this system (Carrasco et al. 2005). In conifers, a dosage-dependent synergistic effect among pine terpenoids and bark beetle pheromones can attract predators and parasitoids to their hosts. For instance, the attraction of the predatory beetle *Thanasimus dubius* was positively correlated with the concentration of α-pinene when mixed with the pheromones of its scolytid prey (Mumm and Hilker 2006). Parasitized herbivores have also been shown to induce different BVOC blends compared to unparasitized herbivores, affecting parasitoid choice (Fatouros et al. 2005). However, mutualistic interactions with herbivores (e.g., aphids and ants) can also alter induced BVOCs with potential consequences for parasitoid host location (Paris et al. 2011). There is also evidence that oviposition-induced plant BVOCs successfully recruit egg parasitoids, such as in the case of *Pinus sylvestris* and egg deposition by *Diprion pini* (Meiners and Hilker 2000). In the deciduous species *Ulmus minor*, terpenoid hydrocarbons induced by oviposition of the elm leaf beetle (*Xanthogaleruca luteola*) are exploited by the egg parasitoid *Oomyzus gallerucae*. Despite the work in these systems, more studies are needed to fill gaps in our knowledge pertaining to the importance of induced indirect defences employed by trees, particularly in determining community structure and outbreak dynamics.

2.3.4 Spatiotemporal Aspects of Induced Indirect Defence

Similar to constitutive BVOCs, herbivore-induced BVOCs not only vary over space and time, but their associated costs to plant fitness vary as well. Most factors influencing constitutive emissions have similar effects on herbivore-induced volatile defences as discussed in previous sections here and in other chapters in this volume. Thus, rather than reiterating these points, we place the spatial and temporal variability of herbivore-induced BVOCs in an ecological framework by discussing ecological interactions influenced by the location of induction in a plant and the timing and patterns associated with the response.

2.3.4.1 Local vs. Systemic Induced Responses

Induced BVOCs that serve a resistant or defensive role for plants can be expressed locally at the wounding site or systemically via mobile signals and phloem transport (Turlings and Tumlinson 1992; Heil and Ton 2008). The ability to respond systemically to herbivory enables a plant to have a larger BVOC response, potentially serving as long range cues capable of recruiting natural enemies that forage over spatial scales of metres to kilometres (Puente et al. 2008). Furthermore, these systemic signals can give parasitoids an initial estimate of patch quality (e.g., number of hosts in a habitat) to aid in determining whether or not to pursue hosts in a given area. However, once parasitoids orient themselves within the general vicinity of their host, the specific blend associated with the herbivore at the damage site itself becomes more important, and constitutes a reliable indicator of host location (Cortesero et al. 1997). BVOC communication between branches or leaves of the same individual could enable faster responses, particularly when signalling via phloem and xylem is thwarted by limited vascular connections or distance, for example in larger trees (Dicke 2009). For instance, Frost et al. (2008) demonstrated that both mechanically-injured and gypsy moth-damaged leaves of hybrid poplar (*Populus deltoides x P. nigra*) primed defence responses in undamaged leaves of the same plant. This “second route” for signal transduction within plants can provide a relatively large benefit to the emitting plant in lieu of synthesis costs. Herbivore-infested plants also mediate plant-plant interactions in unattacked neighboring plants, thus increasing their attractiveness to natural enemies and decreasing their susceptibility to herbivory (Baldwin et al. 2006). While within-plant BVOC signalling has gained much interest, interspecific volatile signalling between plants has remained a topic of debate (Agrawal 2000; Baldwin and Schultz 1983; Bruin and Dicke 2001; Dudareva et al. 2006; Farmer and Ryan 1990).

2.3.4.2 Spatially Separated but Connected: Above- and Belowground Induced Responses

Herbivores can attack spatially-disparate plant organs, such as roots and leaves simultaneously, leading to variation in herbivore-induced BVOCs and consequences for above- and belowground defences. Due to vascular connections, aboveground herbivory can change the quantity and composition of root BVOCs and *vice versa*. While the majority of studies focus on BVOC-mediated tritrophic interactions above-ground, these relationships occur belowground as well and have important effects on aboveground communities (Van der Putten et al. 2001). To our knowledge, no studies to date have described the integration of above and belowground BVOC-mediated tritrophic interactions in trees. While such interactions are likely to exist, they will likely occur at different temporal time scales due to longer generation times and contributing phenological factors. Recent studies focused on herbaceous plants have shown that the vegetative portions of plants experiencing belowground herbivory emit lower total BVOC emissions and produce different BVOC profiles compared to plants solely attacked by an aboveground herbivore (Rasmann and Turlings 2007). Thus, the presence of soil herbivory in this case appears to lower the potential for defence, particularly when the belowground herbivore causes increased damage as a function of development and size (Soler et al. 2007). Another study demonstrated the effects of belowground herbivory on aboveground indirect defence by showing that black mustard (*Brassica nigra*) plants experiencing root herbivory emit high levels of sulfur-containing BVOCs, highly toxic for insects, and low levels of (*E*)-β-farnesene, an attractant for parasitoids (Soler et al. 2007). In addition to soil herbivores, mutualistic mycorrhizal associations can also effect aboveground signalling, as in the case with parasitoids of aphids attracted to mycorrhizal plants in the absence of their aphid hosts (Guerrieri et al. 2004). Because of signal cross-talk, the timing of attack by above- and belowground herbivores can be crucial when examining the extent to which communities are affected. Clearly, more studies investigating BVOC responses to simultaneous attacks by above- and belowground herbivores in forest species are needed.

2.3.4.3 Induced BVOCs Exhibit Diurnal Patterns

The release of herbivore-induced BVOCs occurs both locally and systemically in space and also varies over time. For example, hybrid poplar leaves (*Populus trichocarpa* × *P. deltoides*) attacked by forest tent caterpillars (*Malacosoma disstria*) released similar characteristic blends of volatiles, including mono-, sesqui-, and homoterpene compounds, that peaked during the light period (Arimura et al. 2004). This diurnal pattern could be critical depending on parasitoid and predator foraging patterns and the biologically-active compounds present. In *Nicotiana tabacum*, several herbivore-induced BVOCs are exclusively released at night and repel female moths (*Heliothis virescens*) searching for oviposition sites (De Moraes et al. 2001). Because most parasitoids search during the day, these nighttime emissions may not be relevant as top-down defences, but the impact of daytime indirect forcings and nighttime bottom-up effects may have significant multiplicative consequences for herbivore densities. Currently, we lack studies describing exclusive and additive diurnal ecological relationships mediated by herbivore-induced emissions in tree systems.

2.3.4.4 Induced BVOCs: Immediate vs. Delayed Responses

A limitation of inducible volatile defences is the time-lag between damage, induction, signalling, and the actual plant response (Dicke 2009). Upon feeding or oviposition, the plant can emit BVOCs within seconds to minutes. Most of these emissions, are not under control of the plant, but rather released as a consequence of exposure to the atmosphere (Maffei et al. 2007). Compounds synthesized in response to metabolic changes and involved in indirect plant defence are usually expressed within hours or days following damage (Kunert et al. 2002). Thus, parasitoids and predators must perceive and respond to these compounds within a critical window of time before the benefits of effective host-location are missed. Abiotic conditions and emissions from other organisms in the environment can also influence herbivore-induced cues with important implications for top-down controls over time, the scope of which is beyond this chapter. Rapid herbivore-induced BVOCs active in plant resistance may stabilise insect densities; however, delayed induced resistance, via foliar chemistry, potentially contributes to population cycles (e.g., Roden and Mattson 2008). Some studies demonstrate that needles of previously defoliated trees exhibit higher suitability for subsequent defoliator generations (Lyytikäinen 1992; Clancy et al. 2004), while others have demonstrated induced resistance after defoliation (Hódar et al. 2004; Šmits and Larsson 1999). The susceptibility or resistance of previously defoliated trees depends on a number of variables (i.e., tree age, intensity of defoliation, herbivore species, etc.), yet the influence of BVOCs emitted during and after defoliation on higher trophic level interactions has not been studied.

2.4 Insect Perception, Learning, and Evolutionary Considerations

Insects must perceive and process enormous amounts of sensory information, including chemical information, to locate their hosts within dynamic heterogeneous environments (Vet 2001). BVOC infochemicals are sensed by olfactory sensory neurons, primarily within antennae but also located within chemosensory sensilla on other parts of the insect's body, to aid in perceiving chemical signals in the atmosphere. The ability to perceive BVOCs plays a key role in host location for both herbivores and their natural enemies (Meiners et al. 2003), and many insects are capable of identifying compounds present in the atmosphere at levels much lower than some of our most sensitive analytical instruments.

The ability of an insect to perceive and respond to stimuli is not fixed, and can change upon association with favorable or unfavorable stimuli. For example, female parasitic wasps have a well-developed learning capacity to associate herbivore-induced plant BVOCs with the presence of suitable hosts (de Boer and Dicke 2006). The ability of insects to exploit information from BVOCs can be both innate (Gandolfi et al. 2003a; Steidle and van Loon 2003; Wang et al. 2003) and learned (Dicke 1999; Wäckers and Lewis 1999). We briefly highlight studies that focus on parasitoid learned behavior to emphasize the important role of behavioral ecology in BVOC-mediated multitrophic interactions.

Regardless of the strict categorical descriptions, learning a given task in nature likely involves a combination of stimulus-stimulus and stimulus-response associations, allowing a parasitoid to take advantage of a variety of cues, including unrewarding experiences, which might aid in future decisions and actions (Vet et al. 2003). Learning behavior tends to be more prevalent in generalist parasitoids (Geervliet et al. 1998) than in specialists (Mumm et al. 2005), suggesting that specialist parasitoid species are more 'hardwired' when it comes to responding to plant BVOCs expressed in response to their specific host. While this genetic component may be beneficial in relatively stable environments, changes in climate and/or community composition could confound host-associated signals with important consequences for parasitoid adaptations and herbivore dynamics. Furthermore, not all generalist species have the capability to learn (Tamò et al. 2006), which complicates our ability to generalize parasitoid behavior in response to dynamic chemical cues.

The ability of parasitoids to remember learned behavior also varies with time and stimulus. Recollection of unrewarded activities often fade within a few hours to days (Peri et al. 2006), but learning responses to odors of advantageous activities tend to be more persistent (Takasu and Lewis 2003), and can even occur at preimaginal stages before the adult stage (Gandolfi et al. 2003b). The coordination of plant BVOC emissions with the window of parasitoid 'memory' is thus critical for eliciting parasitoid response. Importantly, learning behavior has been found to positively impact fitness (Dukas and Jun 2000) and contributes to coexistence between parasitoids and their insect hosts (Hastings and Godfray 1999), which emphasizes that learning plays an important role in not only chemical ecology, but also in insect evolution and plant-insect coevolution.

BVOCs impact evolutionary pressures on herbivores and parasitoids through their role in determining fitness. Biogenic BVOCs are involved in a range of ecological functions (Fig. 2.1), and as a consequence, their role in plant evolution is dynamic (Yuan et al. 2009). Adaptive explanations have been offered to address the diversity of BVOCs found among and within plant families (Lerdau and Gray 2003; Wink 2003). It has also been argued that natural selection also exploits the volatility of the compounds themselves and thereby the context in which they are perceived by herbivores and their natural enemies (Peñuelas and Llusià 2004). The precise ecological functions and evolutionary consequences of every BVOC are not yet known (Niinemets et al. 2004), so their full contribution to plant-insect evolution has yet to be characterized. However, the importance of BVOCs to plant, herbivore, and parasitoid fitness highlights their role in the evolution of each taxonomic group, and their role in ecological signalling suggests that they play a substantial role in coevolution among taxonomic groups.

2.5 Conclusions

BVOCs influence plant-insect interactions across multiple levels of ecological organization and play active roles in bottom-up and top-down defences against herbivory. Important ecological consequences stem from feedbacks that exist between constitutive and herbivore-induced BVOC emissions, herbivore and parasitoid behavior, and the environment. Researchers are only beginning to uncover the role BVOCs play in mediating tritrophic interactions and influencing coevolutionary processes that exist between plants and insects. An improved understanding of the impacts of global change on plant and insect ecology and evolution will help us understand the full consequences of BVOC-mediated plant-insect interactions in forested ecosystems, including the role of insects in recently observed forest die-off (Raffa et al. 2008; Rhoades 1983). Models of surface-atmosphere exchange have long had the capability to include BVOC dynamics (Guenther et al. 1995), and their mechanistic representation of BVOC emissions is continuously being improved (Monson et al. 2012). We suggest that including plant-insect interactions into models of BVOC emissions will improve our understanding of the impacts of these interactions on ecosystems, and to the entire Earth system.

Acknowledgments The authors acknowledge Russell K. Monson and Deane Bowers for enlightening conversations and sharing their enthusiasm for plant-insect interactions. PCS also acknowledges funding from the National Science Foundation (‘*Scaling ecosystem function: Novel Approaches from MaxEnt and Multiresolution*’, Division of Biological Infrastructure #1021095) and the State of Montana.

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