Chapter 21
Ecological Roles of Vegetative Terpene Volatiles

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With their enormous number and large structural diversity, terpenes dominate most plant volatile blends. Terpenes were shown to mediate the interactions between plants and many organisms including arthropods, nematodes, and other plants. Often, these interactions are based on volatile mono- and sesquiterpenes which are released from the plant after damage by herbivores. The terpenes attract herbivore enemies that attack the herbivore and thereby may reduce the damage to the plant. This interaction was termed 'indirect defense' and will often benefit the plant, but other organisms like parasitic plants or insects and can utilize the volatile signals to their advantage. Despite the relatively low number of volatile terpene-mediated interactions identified today, many more are likely to be discovered with the advance of volatile collection methods and molecular techniques.

21.1 Introduction

Terpenes form the largest group of volatile compounds among the natural products of plants. Many of the 30,000 terpenes, especially monoterpenes, sesquiterpenes, and irregular terpenes of low molecular weight have high vapor pressures (Connolly and Hill 1991). High vapor pressure results in the emission of these compounds from the plant into the environment. Although terpene volatilization from flowers has been known for many years (Knudsen et al. 2006), these compounds are also emitted from the vegetative tissues of plants. A detailed analysis of emission patterns in plants revealed that most tissues produce specific blends of terpenes (Connolly and Hill 1991; for the model plants *Arabidopsis* and maize, see Chen et al. 2004; Köllner et al. 2004; Tholl et al. 2005). Some of these are emitted from specialized terpene storage organs, for example the glandular trichomes of mints and the resin ducts in conifers, but many volatiles are not emitted from anatomically-specialized storage sites. Less than two decades ago, it was demonstrated that volatiles emitted from

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plants after herbivore damage can attract enemies of the herbivore (Dicke et al. 1990; Turlings et al. 1990). Under favorable environmental conditions, this attraction of herbivore enemies can limit herbivore damage to the plant. This review will focus on volatile terpene signals from vegetative plant tissues and their roles in plant defense against herbivores.

21.2 Terpenes as Volatile Plant Signals

Unlike fatty acid-derived signals and aromatic volatiles (see contributions by Tumlinson and Engelberth this volume and Qualley and Dudareva this volume), terpenes are commonly emitted in complex blends with a large structural diversity between the compounds. Responsible for most of this terpene diversity are multi-product terpene synthases, the key enzymes of terpene biosynthesis (see Bohlmann this volume; Gershenzon and Kreis 1999). Terpene synthases can produce blends of up to 50 different compounds from one substrate and form mixtures with defined relative ratios of products (Steele et al. 1998). In communication with other organisms, these mixtures might provide a more specific signal than signals consisting of single terpenes.

While low concentrations of volatile terpenes are produced in almost every plant tissue, the highest terpene concentrations from vegetative tissues are released in response to environmental cues. Terpene emission is increased in response to damage and contact with elicitors of herbivores (Mattiacci et al. 1995; Alborn et al. 1997; Halitschke et al. 2001; Spiteller and Boland 2003; Tumlinson and Lait 2005), and abiotic factors like wounding (Howe 2004; Schmelz et al. 2001; Mithöfer et al. 2005), UV-radiation (Johnson et al. 1999), O_3 and CO_2 concentration (Vuorinen et al. 2004a, b; Jasoni et al. 2004; Beauchamp et al. 2005), nutritional status of the plant (Schmelz et al. 2003), as well as temperature and light (Guenther et al. 1993; Takabayashi et al. 1994; Gouinguene and Turlings 2002). In contrast to many compounds of the lipoxygenase pathway, terpenes are usually released after de novo synthesis (Paré and Tumlinson 1997) involving gene transcription (Schnee et al. 2002, 2006; Gomez et al. 2005), and within a time window starting one to two hours after elicitation (Turlings et al. 1998).

Despite the enormous number of terpenes emitted by plants, relatively few terpenes have been clearly identified as signals between organisms to date. In this chapter, we will present some of these interactions involving volatile terpenes and discuss the problems associated with the study of terpene-mediated interactions.

21.2.1 Tritrophic Interactions of Plants with Herbivores and Natural Herbivore Enemies

Almost two decades ago, researchers in the Netherlands and the United States first observed that herbivore damage to certain plants induces the emission of volatile organic compounds that attract natural enemies of the herbivores (Dicke et al. 1990; Turlings et al. 1990). This phenomenon has been reported in more than 15 different plant species after feeding by an assortment of arthropod herbivores and was termed ‚indirect defense' (Dicke 1999; Dicke and van Loon 2000; Kessler and Baldwin 2002; Meiners and Hilker 2000). The herbivore enemies that respond to volatiles from herbivore-damaged plants include various carnivorous arthropods, both predators and parasitoids. Attraction of herbivore enemies has been shown to benefit the plant by reducing subsequent herbivory and increasing reproductive fitness (Hoballah and Turlings 1999; van Loon et al. 2000; Kessler and Baldwin 2001), although such advantages are not realized in all cases (Coleman et al. 1999).

The attraction of the predatory mite *Phytoseiulus persimilis* to lima bean plants infested with the spider mite *Tetranychus urticae* has been studied in detail (Dicke et al. 1990). Olfactory assays testing the attraction of single compounds from the complex volatile blend demonstrated that the predatory mite was not only attracted to the aromatic compound methyl salicylate (De Boer et al. 2004; De Boer and Dicke 2004; see also chapter of Qualley and Dudareva this volume), but also the sesquiterpene alcohol nerolidol. Transgenic *Arabidopsis* overexpressing a nerolidol synthase from strawberry were used as volatile source in olfactometer experiments with *P. persimilis*. Nerolidol-emitting transgenic plants were more attractive to the predator than undamaged wild type plants (Kappers et al. 2005). In addition to an innate attraction to compounds of the plant volatile bouquet, the predatory mites also have the ability to associate odors with host presence (De Boer and Dicke 2006). The homoterpene (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene, a irregular C_{16} terpene olefin, is released from lima bean in response to feeding by *T. urticae* but not by the non-host organism *Spodoptera exigua* (Fig. 21.1A). After a series of experiences with the presence and absence of the prey, the predatory mite utilized the homoterpene as an indicator for the presence of prey (De Boer et al. 2004). The ability for associative learning may guide the predatory mites to locate their prey under natural conditions in a complex environment (De Boer and Dicke 2006). Not only does this help the predator to identify plants infested with prey, but also allows it to adapt when the prey switch between different host species during the season (Drukker et al. 2000).

Maize plants damaged by larvae of lepidopteran herbivores like *Spodoptera littoralis* emit a complex blend of volatiles dominated by mono- and sesquiterpenes (Turlings et al. 1991). These volatiles attract females of the parasitic wasp *Cotesia marginiventris* which use the lepidopteran larvae as hosts (Turlings et al. 1990). The parasitation might benefit the maize plants under permitting circumstances since the parasitized larvae feed less and will not procreate (Hoballah et al. 2004; Degenhardt et al. 2003). Since the herbivore-induced volatiles of maize consist of a complex blend of compounds, it is difficult to demonstrate which of the compounds are attractive to the parasitic wasp. The major sesquiterpenes of herbivore-induced maize are produced by the terpene synthase TPS10 which is strongly expressed after herbivory by lepidopterans. TPS10 forms (*E*)-β-farnesene, (*E*)-α-bergamotene, and other herbivory-induced sesquiterpene hydrocarbons from the substrate farnesyl diphosphate (Fig. 21.1B; Schnee et al. 2006). Overexpression of TPS10 in

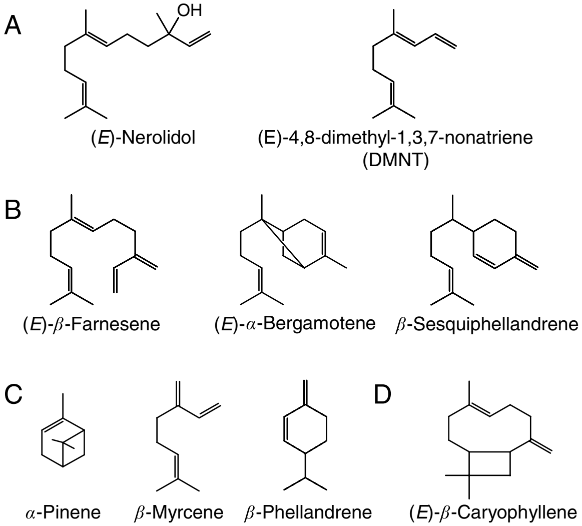

Fig. 21.1 Structures of volatile plant terpenes involved in interactions with other organisms. (**A**) (*E*)-nerolidol and (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) are used by the predatory mite *P. persimilis* to locate spider mites. (**B**) (*E*)-β-farnesene, (*E*)-α-bergamotene and (*E*)-β-sesquiphellandrene attract parasitic wasps to maize damaged by lepidopteran larvae. (**C**) α-pinene, β-myrcene and β-phellandrene attract dodder (*C. pentagona*) to its host plant. (**D**) (*E*)-β-Caryophyllene guides entomophatogenic nematodes to maize roots damaged by *D. v. virgifera*

Arabidopsis thaliana resulted in plants emitting high quantities of TPS10 sesquiterpene products identical to those released by maize. Using these transgenic *Arabidopsis* plants as odor sources in olfactometer assays showed that females of the parasitoid *C. marginiventris* learn to exploit the TPS10 sesquiterpenes to locate their lepidopteran hosts after prior exposure to these volatiles in association with hosts (Schnee et al. 2006). This gene-based dissection of the herbivore-induced volatile blend demonstrates that a single gene such as *tps10* can be sufficient to mediate the indirect defense of maize against herbivore attack. Furthermore, associative learning can also adapt parasitoids to alterations of the herbivore-induced volatile blend by plant species, age and tissue of the plant, and abiotic conditions (Takabayashi et al. 1994; De Moraes et al. 1999; Schmelz et al. 2003; Van den Boom et al. 2004). However, females of *C. marginiventris* are also attracted to the full blend of maize volatiles without prior association, indicating that the blend contains additional attractive compounds that elicit an innate response (Hoballah and Turlings 2005). Bioassay-guided fractionation of the maize volatiles has not yet identified such compounds (D'Alessandro and Turlings 2005, 2006). The combination of both innate and learned responses might allow this generalist parasitic wasp to locate a wide range of hosts on different plant species in a natural, complex environment (Turlings and Wäckers 2004; Degenhardt et al. 2003). Interestingly, the emission of volatiles in response to herbivore damage is not only beneficial for the maize plant since larvae of lepidopteran *Spodoptera frugiperda* use these volatiles as a cue to find their food plants (Carroll et al. 2006). Further studies are required to determine whether the benefit of the volatile signal outweighs its disadvantages under specific environmental conditions.

The function of terpenes as defense signals under field conditions was studied on a wild tobacco species, *Nicotiana attenuata*. The release of terpenes was mimicked by application of a lanolin paste that emitted physiological concentrations of the monoterpene linalool and the sesquiterpene (*E*)-α-bergamotene (Kessler and Baldwin 2001). The emission of exogenous linalool decreased lepidopteran oviposition rates on *N. attenuata* plants while the release of (*E*)-α-bergamotene increased egg predation rates by a generalist predator. These observations provided conclusive evidence that indirect, terpene-based plant defenses can reduce the herbivore load of a plant in a natural environment (Kessler and Baldwin 2001).

Terpene-mediated interactions were not only observed in response to damage of the leaves but also in response to root-feeding herbivores. Larvae of the beetle *Diabrotica virgifera virgifera* (Western corn rootworm) are an important pest of maize. In response to feeding by the larvae, maize roots release a signal that strongly attracts the entomopathogenic nematode *Heterorhabditis megidis* (Boff et al. 2001; van Tol et al. 2001). The signal released by the maize roots was identified as (*E*)-β-caryophyllene, a sesquiterpene olefin (Fig. 21.1D; Rasmann et al. 2005). Most North American maize lines do not release (*E*)-β-caryophyllene, whereas European lines and the wild maize ancestor, teosinte, do so in response to *D. v. virgifera* attack. Field experiments showed a five-fold higher nematode infection rate of *D. v. virgifera* larvae on a maize variety that produces the signal than on a variety that does not. Spiking the soil near the latter variety with authentic (*E*)-β-caryophyllene decreased the emergence of adult *D. v. virgifera* to less than half (Rasmann et al. 2005).

Not only feeding, but also oviposition of the herbivore can induce terpene emission in plants. The pine sawfly (*Diprion pini*) lays its eggs on pine twigs and wounds the surface of the needles in the process. The volatiles emitted in response to oviposition attract a wasp that parasitizes saw fly eggs (Hilker et al. 2002). The signal attracting the wasp is the sesquiterpene (*E*)-β-farnesene which is only recognized in combination with other, constitutively released pine volatiles (Mumm et al. 2003; Mumm and Hilker 2005).

21.2.2 Interference of Plant Volatile Terpenes with Insect Pheromones

Many species of aphids release a sesquiterpene alarm pheromone, (*E*)-β-farnesene, which lowers the risk of predation of other aphids in the vicinity, either by causing them to move away (Hardie et al. 1999), or by increasing their proportion of winged progeny (Kunert et al. 2005). To determine if plant-produced (*E*)-β-farnesene can mimic these effects, transgenic *Arabidopsis* plants overexpressing a (*E*)-β-farnesene synthase from *Mentha x piperita* were generated by Beale et al. (2006).

These transgenic plants emitted high levels of (*E*)-β-farnesene and elicited potent alarm and repellent responses in the aphid *Myzus persicae*, and an arrestant response in the aphid parasitoid *Diaeretiella rapae* (Beale et al. 2006). In addition, (*E*)-β-farnesene attracts further predators and parasitoids which are natural enemies of aphids (Molck et al. 1999; Du et al. 1998; Al Abassi et al. 2000; Foster et al. 2005). Thereby, the emission of (*E*)-β-farnesene after aphid-infestation provides the plant with both direct and indirect defenses. The monoterpene alcohol linalool, albeit no alarm pheromone, also repelled *M. persicae* in experiments with transgenic *Arabidopsis* plants overexpressing a terpene synthase from strawberry (Aharoni et al. 2003).

21.2.3 Terpene-Mediated Interactions Between Plants

Volatile-emitting plants can prime the defense metabolism in adjacent plants. The process involves increased transcription of defense-related genes and allows the plant to respond faster and more vigorously to herbivore attack (Baldwin et al. 2006; Turlings and Ton 2006). Most of these interactions were shown to be based on volatiles derived from the lipoxygenase pathway, the so called 'green leaf volatiles' (Bate and Rothstein 1998; Arimura et al. 2001; Farag and Pare 2002; Engelberth et al. 2004; Farag et al. 2005; Ruther and Kleier 2005). Little is known about the role of terpenes in priming and plant–plant interaction. Only one study in lima bean (*Phaseolus lunatus*) suggests a role of terpenes in this interaction. When these plants were attacked by the spider mite *T. urticae*, the neighboring plants became less susceptible to spider mites and more attractive to predatory mites like *P. persimilis* (Bruin et al. 1992). Lima bean infested by spider mite released a volatile blend dominated by (*E*)-β-ocimene and (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), a monoterpene and C_{11} homoterpene, respectively. In neighboring plants, each of these compounds induced the transcript level of pathogen-related proteins and phenylalanine ammonia lyase (Arimura et al. 2000). The volatiles also increased the transcript concentrations of two enzymes involved in terpene biosynthesis: lipoxygenase catalyses an early step in jasmonate biosynthesis, an important regulator of terpene biosynthesis, and farnesyl diphosphate synthase, which is an enzyme of terpene biosynthesis. Interestingly, the transcript levels of these genes were induced more quickly after exposure of lima bean to DMNT and a related homoterpene, (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (Arimura et al. 2000). In other plant species, these terpenes were not effective in priming. In maize, for example, no effects were observed after exposure of the plant to exogenous DMNT (Ruther and Fürstenau 2005).

Volatile terpenes also play an important role in host finding by parasitic plants. Seedlings of dodder (*Cuscuta pentagona*) display a host finding behavior that is guided by volatiles of the host plant. (Runyon et al. 2006). The seedling is able to distinguish between the volatiles of tomato (*Solanum lycopersicum*), impatiens (*Impatiens wallerana*) and wheat (*Triticum aestivum*) as well as several synthetic mono- and sesquiterpenes (Fig. 21.1C). This indicates a finely tuned recognition of host plants by the composition of their terpenes emissions (Runyon et al. 2006).

21.3 Perspectives

In the last decades, advances in sensitive, reliable methods for volatile collection and identification have provided us with better insight into terpene-mediated interactions among plants and their enemies. Given the large numbers of terpenes emitted and the large families of terpene synthase genes present in plants, the discovery of many more such interactions is most likely. The advances in molecular biology facilitate the research on genes of terpene biosynthesis and the regulation of terpene emission in response to outside cues. The characterization of terpene biosynthesis genes also provides tools to engineer transgenic plants with specifically altered volatile emission. In the future, such plants will continue to be helpful to unravel the complex ecological functions of terpene emission.

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