

# Terpenoids in Plant Signaling: Chemical Ecology

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doi: 10.1002/9780470048672.wecb652

Terpenoids constitute the largest class of secondary metabolites in the plant kingdom. Because of their immense structural diversity and the resulting diversity in physicochemical properties, these molecules are particularly important for plant communication with other organisms. In this article, we will describe the ecological significance of terpenoids for plants, how terpenoid formation is regulated, and the tools we have to improve our understanding of the role of terpenoids in plant ecology and to create crop plants with improved resistance.

As plants are sessile, they cannot run away to avoid confrontation. Instead, they have evolved many different defense strategies, which include morphological (e.g., thorns, spines, and thick cuticle) and chemical defenses (e.g., repellents, toxic proteins, and toxic metabolites). Here, we will focus on the chemical defense of plants mediated by chemical compounds and one class of metabolites in particular: the terpenoids. They are of great importance to plants because of their multitude of functions in signaling and defense. Virtually all plant species have been shown to contain terpenoids and/or to release them from leaves, flowers, fruits, and roots into the environment to defend themselves—directly or indirectly—against herbivores and pathogens or to provide a reproductive advantage by attracting pollinators or seed dispersing animals.

Terpenoids, which are also known as isoprenoids, constitute the most abundant and structurally diverse group of plant secondary metabolites, consisting of more than 40,000 different chemical structures. The isoprenoid biosynthetic pathway generates both primary and secondary metabolites that are of great importance to plant growth and survival. Among the primary metabolites produced by this pathway are phytohormones, such as gibberellic acid (GA), abscisic acid (ABA), and cytokinins; the carotenoids, such as chlorophylls and plastoquinones involved in photosynthesis; the ubiquinones required for respiration; and the sterols that influence membrane structure (Fig. 1). Monoterpenoids (C10), sesquiterpenoids (C15),

diterpenoids (C20), and triterpenoids (C30) are considered to be secondary metabolites (Fig. 1). Many secondary metabolite terpenoids are of commercial interest because of their flavor, fragrance, or medicinal properties. Here, we will discuss the role of terpenoids in plant signaling.

## Biological Background

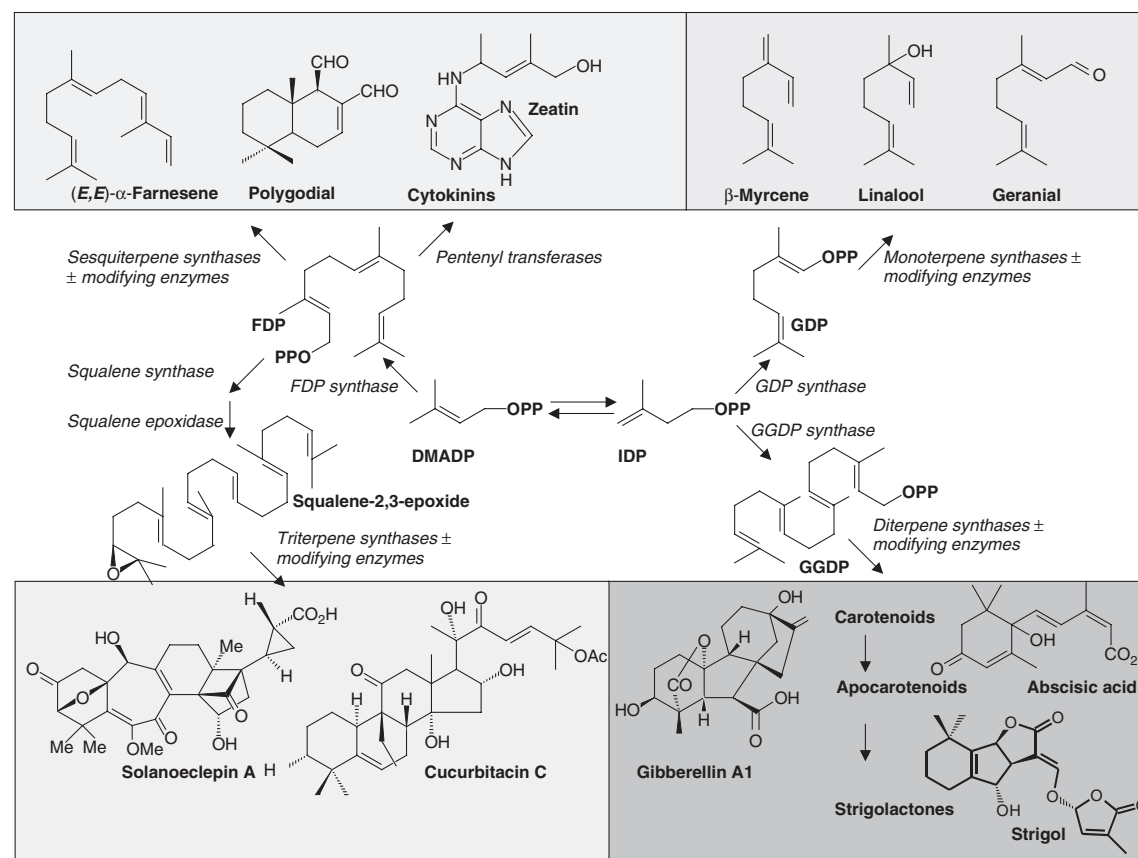
### Induction of biosynthetic pathways, mechanisms, and functions

Terpenoids are derived from the cytosolic mevalonate pathway or from the plastidial 2-C-methyl-D-erythritol-4-phosphate (MEP) pathway. Both pathways lead to the formation of the C5 units isopentenyl diphosphate and its allylic isomer dimethylallyl diphosphate, which are the basic terpenoid biosynthesis building blocks (Fig. 1). Although increasing evidence suggests that exchange of intermediates occurs between these compartments, the cytoplasmic mevalonate pathway is generally considered to supply the precursors for the production of sesquiterpenes and triterpenes (including sterols) and to provide precursors for protein prenylation and for ubiquinone and heme-A production in mitochondria. In the plastids, the MEP pathway supplies the precursors for the production of isoprene,

## Advanced Article

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**Figure 1** Schematic overview of the biosynthesis of the monoterpenoids, sesquiterpenoids, diterpenoids, and triterpenoids. Representatives of these classes with biological relevance are shown. Enzymatic steps are indicated in italics *DMADP*, dimethylallyl diphosphate; *GDP*, geranyl diphosphate; *GGDP*, geranylgeranyl diphosphate; *FDP*, farnesyl diphosphate; *IDP*, isopentenyl diphosphate.

monoterpenes, diterpenes (e.g., GAs), and tetraterpenes (e.g., carotenoids).

After the formation of the acyclic precursors geranyl diphosphate, farnesyl diphosphate, and geranylgeranyl diphosphate, terpenoid scaffolds are generated through the action of terpene synthases (TPSs). Primary terpene skeletons formed by TPSs can be modified even more by the action of various other enzyme classes, such as the cytochrome P450 hydroxylases, dehydrogenases (alcohol and aldehyde oxidoreductases), reductases, glycosyl transferases, and methyl transferases (**Fig. 1**).

### Localization of terpenoid biosynthesis

Terpenoids are implicated in several ecological and physiological functions and are often emitted from specific tissues at particular times related to their function. Many monoterpene and sesquiterpene synthase genes have been isolated and characterized from terpene-accumulating cells and tissues, such as leaf glandular trichomes, specific floral tissues, and fruits of agriculturally important plants. For plants that contain glandular trichomes, monoterpene production is considered to be localized exclusively in these organs. Resin ducts or oil glands can accumulate large amounts of terpenoids.

In floral tissues, volatile terpenes are often emitted at particular times to attract pollinators or to repel herbivores or microbial pathogens. Biosynthesis of the monoterpenes  $\beta$ -ocimene and myrcene in snapdragon flowers, for example, is correlated with expression patterns of the corresponding genes in the flower petals that showed a (weak) diurnal oscillation under the control of a circadian clock (1). This finding indicates that these terpenes function as attractants for pollinating insects. In *Arabidopsis*, monoterpene and sesquiterpene synthases are not expressed in flower petals, but they are limited to the stigma, anthers, nectaries, and sepals (2), which suggest the importance of terpenoids for the defense of floral tissues against herbivores or microbial pathogens next to attraction of pollinators. Some terpene synthase genes exhibit expression in flowers as well as in fruits, whereas other genes are specifically expressed at particular stages of fruit development or ripening.

In contrast to the above-ground organs of plants, roots represent an unexplored area of terpene biosynthesis and function. To date, just a small number of terpene synthases have been identified in plant roots. In *Arabidopsis*, the terpene synthase genes that encode 1,8-cineole synthase and (*Z*)- $\gamma$ -bisabolene synthase are expressed differentially in the stele of younger root growth zones and in the cortex and epidermis of older roots (reviewed in Reference 3). Little is known about the biological functions

of volatile terpenes in roots at different developmental stages and in the interactions with root herbivores, microorganisms, and parasites. Terpene biosynthesis can be induced in roots under stress conditions, as shown in maize roots in response to attack by herbivores (4).

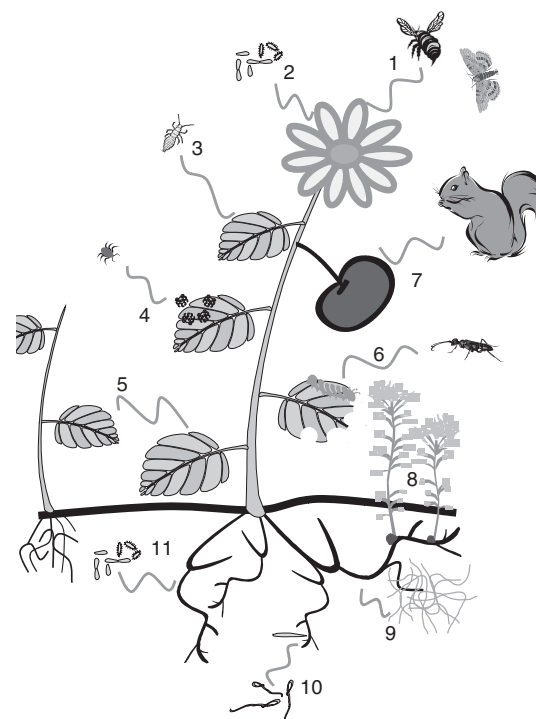
## Terpenoids and Plant Signaling

Terpenoids are one of the major classes of compounds used by plants to communicate with their environment. This communication includes attraction of beneficial organisms (and unwanted attraction of herbivorous organisms!) as well as defense against harmful organisms. With regard to the latter, plants employ direct as well as indirect defense mechanisms, against herbivores or fungal and bacterial pathogens. Direct defense includes physical structures, such as thorns and trichomes, and the accumulation of toxic metabolites or proteins to deter or even kill attackers. In many plant species, diterpenes and sesquiterpenes act as phytoalexins, which are low-molecular-weight compounds that are produced as part of the plant defense system against microorganisms. Compounds such as the bitter triterpenoid cucurbitacins and the pungent sesquiterpenoid polygodial have been shown to be involved in direct defense against insects (Fig. 2).

Indirect defense implies that plants defend themselves against herbivores by enhancing the effectiveness of the natural enemies of these herbivores. These defense mechanisms can be constitutive like the formation of domatia, which serve as homes for ants and mites, or the production of foliar nectaries and nutritional structures that can be used by natural enemies of the herbivores. In addition, indirect defense mechanisms in plants can be induced. One of the most intriguing examples of this function is the emission of herbivore-induced plant volatiles, which attract the carnivorous natural enemies of herbivores. These herbivore-induced plant volatiles predominantly consist of terpenoids that mediate many interactions in a plant–insect community, both above and below ground (4, 5). The volatiles that plants produce in response to herbivore damage can affect various other interactions of the plant with community members (5, 6). Moreover, herbivore-induced plant volatiles can affect herbivore–plant and carnivore–herbivore interactions on neighboring plants through their effect on the neighbor's phenotype (5, 7).

### Terpenoids in direct defense

Direct-defense compounds can be either constitutively present in (specific parts of) the plant or be produced after induction by pathogens or herbivores. The latter compound will be less costly for the plant. For example, elicitor-induced accumulation of the antimicrobial sesquiterpenoid capsidiol correlated with the induction of 5-*epi*-aristolochene synthase, which is a branch-point sesquiterpene cyclase involved in the synthesis of sesquiterpene phytoalexins (8). In rice (*Oryza sativa* L.), 14 diterpenoid phytoalexins have been identified. All these compounds are accumulated in rice leaves after inoculation with the pathogenic blast fungus *Magneportha grisea* and exhibit antimicrobial properties (9). Another example is polygodial, which

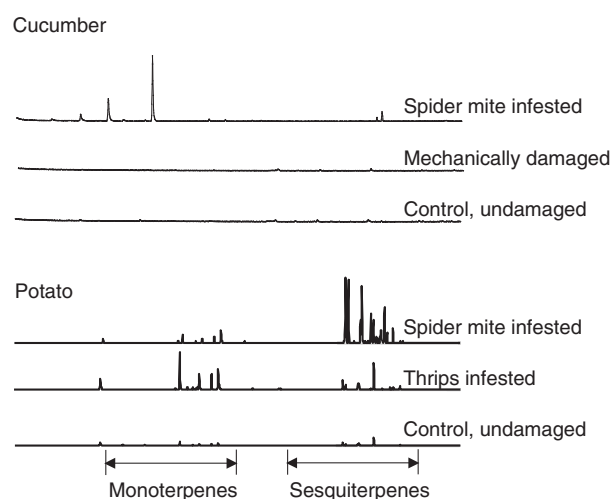


**Figure 2** An overview of terpenoid-mediated interactions between plants with the surrounding environment. Floral scent to attract pollinators (1, e.g.,  $\beta$ -myrcene); Protection of reproductive organs from fungal or bacterial infection (2, e.g., thujopsene); Direct defense: repellency of herbivorous insects by volatile terpenoids (3, e.g., zingiberene); Attraction of predators and parasitic wasps on insect or spider mite herbivory (4, e.g., 4,8-dimethyl-1,3(E),7-nonatriene); Priming or elucidation of defense in neighboring plants (5, e.g.,  $\beta$ -ocimene); Defense compounds in leaves against insect herbivores, fungi and bacteria (6, e.g., polygodial); Fruit aroma to stimulate consumption and thereby seed dispersal (7, e.g.,  $\beta$ -ionone); Germination of parasitic plant seeds (8, e.g., strigol); Stimulation of growth and attachment of symbiotic mycorrhizal fungi (9, e.g. 5-deoxystrigol); Attraction of entomopathogenic nematodes after root feeding of beetle larvae (10,  $\beta$ -caryophyllene); Direct defense to protect against insect herbivores, fungal infection, or bacterial infection (11, rhisitin).

has generated considerable interest because of its potent insect antifeedant activity. In cotton (*Gossypium spp.*), gossypol and related sesquiterpene aldehydes, which are all derived from (+)- $\delta$ -cadinene, provide both constitutive and inducible protection against pests and diseases.

### Terpenoids in indirect defense

In many recent studies, the role of terpenoids in indirect defense has been studied. A broad range of plant species such as *Arabidopsis*, corn, lima bean, cucumber, tomato, tobacco, apple, and poplar serves as models for studies on the genetic, biochemical, physiological, and ecological aspects of these tritrophic interactions between plants, herbivores, and natural enemies (e.g., Reference 10). Plants have been shown to respond with quantitatively and qualitatively different volatile blends to different herbivore species, and predators can exploit this behavior to respond specifically to their prey (Fig. 3)



**Figure 3** Induction of terpenoids in cucumber and potato leaves after herbivory by spider mites (*Tetranychus urticae*) or thrips (*Franklinella occidentalis*) (Kappers IF, Bouwmeester HJ, Dicke M, Unpublished results).

(reviewed in Reference 11). Within a plant species, the quality of the volatile blend may be affected by the developmental stage of the herbivore, and the volatiles produced by plants upon insect egg deposition may differ from the one induced by feeding (11). Typical volatiles released from a multitude of species after herbivory are the so-called green leaf volatiles such as C6-alcohols, -aldehydes, and -esters, which are derivatives of the shikimate pathway such as methyl salicylate, and terpenoids such as (*E*)- $\beta$ -ocimene, linalool, (*E*)- $\beta$ -caryophyllene, (*E,E*)- $\beta$ -farnesene, and the homoterpenes 4,8-dimethyl-1,3(*E*),7-nonatriene and 4,8,12-trimethyl-1,3(*E*),7(*E*),11-tetradeca-tetraene. The terpenoids are by far the most important contributors to the induced volatile blend. To date, little information exists about how natural enemies respond to individual components found in induced odor blends, even though it is known whether they can distinguish between complex odor mixtures. Also, it is still unclear whether natural enemies use only a few compounds present in an odor blend for prey identification, or whether they use information from all odor compounds. For a multitude of tritrophic systems, it was shown that predatory mites and parasitoid wasps were attracted by terpenoid components from induced volatile blends, for instance (*E*)- $\beta$ -ocimene, linalool, (*E*)- $\beta$ -caryophyllene, (*E,E*)- $\beta$ -farnesene, 4,8-dimethyl-1,3(*E*),7-nonatriene, and 4,8,12-trimethyl-1,3(*E*),7(*E*),11-tetradecatetraene (4, 6, 12).

### Terpenoids in aboveground plant–plant communication

Volatiles released from herbivore-infested plants mediate plant–plant interactions and may induce the expression of defense genes and emission of volatiles in healthy leaves on the same plant or of neighboring unattacked plants, thus increasing their attractiveness to natural enemies and decreasing their susceptibility to the damaging herbivores (Fig. 2) (reviewed in Reference 13). This phenomenon is called priming, and it prepares neighboring plants to respond more rapidly and intensively against subsequent attack by herbivorous insects (13),

for example by increasing extra-floral nectar secretion to attract predatory arthropods (14).

Several reports showed that herbivore- and elicitor-induced plant volatiles, in particular green leaf volatiles and terpenoids, influence gene expression and result in priming of defense responses of neighboring conspecific and nonconspecific plants that were not attacked. Terpenoids emitted from herbivore-infested *Nicotiana attenuate* affected the expression of numerous genes of neighboring conspecifics (15). One example is (*E*)- $\beta$ -ocimene that can act as plant–plant signal by upregulating signaling pathways of jasmonic acid and ethylene in neighboring plants (16).

### Terpenoids in rhizosphere communication

In the rhizosphere, plants use terpenoids for communication with other organisms. The fact that only a few such relationships have been demonstrated probably more reflects the difficulty of studying chemical signaling in the soil than the actual contribution of rhizosphere signaling to plant functioning. Surprisingly, among those rhizosphere-signaling relationships that have been uncovered, several constitute the attraction of pathogenic organisms by highly specific signaling molecules. Examples are the hatching of cyst nematodes, which is triggered by triterpenoids (e.g., soybean cyst nematodes by glycoeclepin and potato cyst nematodes by solanoelepin) (Figs. 1 and 2). From an evolutionary point of view, one must conclude that these molecules must have another, as yet unknown, positive function for plants or otherwise they would have been selected against. This function is illustrated by the example of strigolactones, which are apocarotenoid-signaling molecules that are secreted by the roots of many plant species. In the 1960s, these compounds were identified as the germination stimulants that trigger germination of the seeds of the root parasite Orobanchaceae (*Striga* spp. and *Orobanche* spp) (17). These obligate parasites can only survive if they grow on the roots of a host plant from which they take water, assimilates, and nutrients. Several *Striga* and *Orobanche* species can be a nuisance in agriculture, where they can destroy complete harvests. To prevent the tiny seeds from germinating at too large distance from a host root, parasitic plants have evolved a requirement for so-called germination stimulants, collectively called the strigolactones, which are compounds that are produced by the roots of their hosts (Figs. 1 and 2).

The reason for the existence of the strigolactones remained unknown until 2005 when it was discovered that they are an important host-finding factor for arbuscular mycorrhizal (AM) fungi (18). In the arbuscular mycorrhizal symbiosis, plants obtain water and mineral nutrients from their fungal partners, which allow them to survive under various stressful conditions. AM fungi are obligate symbionts that have facilitated the adaptation of primitive plant species to life on land and colonize the roots of most land plant species. Apparently, mycorrhizal symbiosis required the production of strigolactones throughout the plant kingdom and then, indirectly, allowed for the later evolution of the host detection mechanism of parasitic plants using the same compounds (17).

Tritrophic interactions, for which so much evidence exists aboveground, are gradually being uncovered in the rhizosphere

(Fig. 2): Rasman et al. (4) reported the first and fascinating example of an insect-induced rhizosphere plant signal, (*E*)- $\beta$ -caryophyllene, which is attractive to an entomopathogenic nematode. Maize roots release this sesquiterpene in response to feeding by *Diabrotica virgifera* larvae, which is a maize pest that is currently invading Europe. Most North American maize lines do not release (*E*)- $\beta$ -caryophyllene, whereas European lines and the wild maize ancestor, teosinte, readily do so in response to *Diabrotica* attack. This phenomenon was consistent with striking differences in the attraction of nematodes, which are the natural enemy of *Diabrotica*, toward the larvae when feeding on representative maize lines in the laboratory. Field experiments showed a 5-fold greater nematode infection rate of *Diabrotica* larvae on a maize variety that produces the signal than on a variety that does not. North American maize lines must have lost the (*E*)- $\beta$ -caryophyllene signal during the breeding process. Development of new varieties that release the attractant in adequate amounts should help enhance the efficacy of nematodes as biological control agents against root pests like *Diabrotica* (4).

## Regulation of Terpenoid Formation

### Biotic and abiotic factors affecting terpenoid formation

The production of secondary metabolites by plants has been shown by many authors to be influenced by environmental conditions. Therefore, it can be expected that this finding holds for terpenoids involved in signaling. Knowledge of these effects may be important for improvement of biological control, resistance against attackers, or attraction of beneficial organisms (e.g., by applying the most optimal conditions for efficient signaling molecule production). The factors that have been shown to affect secondary metabolite production such as light, temperature, and water availability have also been investigated for their effect on herbivore-induced volatile biosynthesis. High light intensity and water stress are generally reported to increase induced volatile production and/or predator attraction for example in lima bean, kidney bean, maize, and cotton (reviewed in Reference 19). Fertilization had a strong positive effect on emission of induced volatiles in maize, even when results were corrected for plant biomass (19). Hence, climatic conditions and nutrient availability can be important factors in determining the intensity and variability in the release of induced plant volatiles.

In rhizosphere signaling, environmental conditions affect the production of signaling molecules. A particularly clear case is the production of strigolactones, which are the host-presence signaling molecules for AM fungi (see above). AM fungi help plants to absorb nitrogen and phosphate and hence improve plant growth in areas of the world where the concentration or availability of particularly phosphate in the soil is limited (17). Interestingly, root exudates of red clover, tomato, and rice grown under phosphate limitation produce much more strigolactones. It can be argued that in this way, plants improve the chance to attract AM fungi as quickly as possible. After

colonization by AM fungi, plants seem to produce less strigolactones, which would be consistent with improved phosphate availability.

### Genetic variation

Variability in induced plant volatiles complicates the reliance of natural enemies on these cues. One way of dealing with variability is through associative learning, which may allow parasitoids to learn which cues are most likely to lead them to suitable hosts at a particular time in a particular area. Moreover, recent studies suggest that plant volatile blends alone carry specific information on the herbivores by which they are attacked. For example, predatory mites can distinguish between the blends of apple trees infested by two herbivores species (20). Du et al. (21) showed that different aphid species elicit different volatile blends in bean plants and that the aphid parasitoid, *Aphidius ervi*, can use these differences to distinguish plants infested by its host, *Aphis pisum* from those infested by a nonhost, *Aphis fabae*.

Little is known about the genetic variability in such herbivore-induced plant signals and about how the emissions in cultivated plants compare with those of their wild relatives. For conventional plant breeding for improved biological control through enhanced volatile production and hence predator attraction to be successful, genetic variation in the ability to produce herbivore-induced predator-attracting volatiles is a prerequisite. The little information available on the extent of the variability comes mostly from studies on cultivated plants. Although rice plants infested with the brown planthopper, *Nilaparvata lugens*, were more attractive than uninfested plants, Rapusas et al. (22) showed that constitutively produced rice volatiles in 6 out of 15 uninfested rice cultivars also attractive to the predator *Cyrtorhinus lividipennis* when compared with clean air. In gerbera, several cultivars differed in composition and amount of volatiles produced in response to spider mite feeding (23). Y-tube olfactometer experiments revealed differences between the gerbera cultivars in the odor-preference of predatory mites. The composition of the volatile blend seemed to be more important for this difference than the total amount of volatiles produced, and particularly the terpenoids (*E*)- $\beta$ -ocimene and linalool were mentioned by the authors as possibly important candidates in determining the difference in attractiveness between cultivars. Between maize cultivars and between different *Zea* species, large differences were found in the composition of the volatile blend induced by the application of the oral secretion of *Spodoptera littoralis* to mechanically damaged leaves (24).

Several problems have been associated with the comparison of genotypes for their production of induced volatiles when other differences between the genotypes can not be controlled (23). For example, differences may exist in direct defense between genotypes that cause differences in developmental rate of herbivores that may lead to differences in volatile formation. To circumvent this problem, in addition to spider mite infestation, we used jasmonic acid treatment in a comparison between seven cucumber genotypes. Earlier research had shown that jasmonic acid treatment mimics the effect of spider mite infestation in several plant species. Different cucumber genotypes

produced different volatile blends on jasmonic acid treatment or spider mite infestation that are reflected in differences in the attractiveness of these genotypes to predatory mites (Kappers, Bouwmeester, Dicke, unpublished results).

## Role of Terpenoids in Other Aspects

### Terpenoids in plant reproduction

To attract pollinators and seed-dispersing animals and to ensure reproductive and evolutionary success, many flowering species release blends of volatile compounds from their flowers and fruits in addition to visual and tactile cues (Fig. 2). The biogenetic pathways of fruit and flower volatiles can be derived from enzymatically controlled lipid, terpene, amino acid, carbohydrate, and phenyl propane metabolism. Floral scent bouquets may contain from 1 to 100 different volatiles, but most species emit between 20 and 60 different compounds (25). The total amount of emitted floral volatiles varies from the low picogram range to more than 30  $\mu\text{g}/\text{hour}$  (25). Although flowers could be identical in their color or shape, no two floral scents are exactly the same because a large diversity of volatile compounds and their relative abundance and interactions within the scent bouquet. In addition to attracting insects to flowers and guiding them to food resources within the flower, floral volatiles are essential in allowing insects to discriminate among plant species and even among individual flowers of a single species (1).

To date, little information exists about how insects respond to individual components found in floral scents, even though it is known that they can distinguish between complex floral scent mixtures. It is still unclear whether insect pollinators use only a few compounds present in a scent for floral identification or whether they use information from all scent compounds. Recently, it was shown that honeybees can use all floral volatiles to discriminate subtle differences in the scent of four snapdragon cultivars that emit the same volatile compounds but at different levels (26).

Floral volatiles could play many roles instead of or in addition to pollinator attraction. For example, many terpenes, including  $\beta$ -myrcene, (*E*)- $\beta$ -ocimene, linalool, and (*E*)- $\beta$ -caryophyllene, react readily with ozone and other reactive oxygen species (27). Thus, floral volatiles could function to protect the reproductive organs from oxidative damage. A variety of monoterpenes and sesquiterpenes is reported to have antimicrobial activity (28). Hence, floral terpenes could help defend floral organs, like the moist stigma, from bacterial or fungal infection.

## Practical Applications and Future Prospects

### Practical applications

The great significance of terpenoids in mediating the interactions of plants with other organisms has prompted many researchers to explore the possibilities to use this knowledge to improve resistance of plants against attacking organisms.

Now that many induced volatile blends have been identified, artificial mixtures could be composed that are effective in attracting natural enemies and could be used in crops. Alternatively, crops could be sprayed with jasmonic acid to induce volatile production that should lead to the increased presence of natural enemies. Occasionally, an example exists in which this approach has been unsuccessful (29), and several authors have expressed the feeling that this approach should fail in the long term, as the presence of the volatile cue and a prey are uncoupled.

If the volatile cue and the presence of a prey are not uncoupled (i.e., attractive volatiles are only or mainly produced on herbivory), then an adequate response of the crop to herbivory is most important. We have reviewed several studies in which the effect of environmental conditions on volatile production and herbivore attraction has been demonstrated, and researchers should take these results into account when designing their experiments. However, for a practical application such as the optimization of biological control, these factors may be important. It would be of interest to observe whether environmental conditions that stimulate induced volatile formation actually improve biological control in a field situation. Another as yet completely ignored factor in the optimization of biological control is the selection for genotypes with improved (faster, stronger) response. Our results on cucumber and the results of other plant species demonstrate that genetic variation for this response is available. Additional research could demonstrate the effectiveness and the best and easiest way to exploit this variation in breeding.

### Metabolic engineering

Several research groups have made significant progress with the metabolic engineering of particularly monoterpene and sesquiterpene biosynthesis in a range of plant species (reviewed in Reference 30). These studies have shown that a high production rate of terpenes, including modified products, can be obtained using metabolic engineering. The importance of terpenoids in the interaction of plants with other organisms implies that their modification by plant metabolic engineering will have major effects on their response to the environment. *Petunia* plants that express the *Clarkia breweri* linalool synthase showed a delayed and less severe natural infection by mildew than the nontransformed plants under standard greenhouse conditions. Fruit of tomato plants transformed with the same gene were much more resistant to postharvest pathogens than the nontransgenic controls (30). Some effects of transgenic, volatile producing plants on insects have been reported. Transgenic tobacco plants transformed with three lemon monoterpene synthases were visited much less by herbivorous insects (e.g., whiteflies) but more by fruit flies than wild-type tobacco plants in the same greenhouse compartment (30). In

choice assays, Arabidopsis plants transformed with the strawberry linalool/nerolidol synthase, which emit greater linalool levels than the control plants, significantly repelled the aphid *Myzus persicae* (reviewed in Reference 30). Recently, these observations were extended with even more convincing results: Transgenic chrysanthemum (*Chrysanthemum x grandiflorum*) producing linalool repelled western flower thrips (*Frankliniella occidentalis*) (reviewed in Reference 30). Increased levels of the diterpenoid cembratrienols in trichome exudates of the transgenic tobacco plants resulted in greater resistance to aphids, which also occurred in field tests (reviewed in Reference 30). In studies on tritrophic interactions, transgenic plants become an important tool. Arabidopsis plants transformed with the strawberry linalool/nerolidol synthase with mitochondrial targeting signal emitted (3S)-*E*-nerolidol and (*E*)-DMNT and were attractive to carnivorous predatory mites (*Phytoseiulus persimilis*), which are the natural enemies of spider mites (reviewed in Reference 30). Transgenic Arabidopsis plants engineered for the production of sesquiterpenes, which is normally emitted by maize, attracted females of the parasitoid *Cotesia marginiventris* that located their lepidopteran hosts (the parasitoids were first exposed to the volatiles in association with their hosts) (reviewed in Reference 30). The sesquiterpene (*E*)- $\beta$ -farnesene acts as alarm pheromone for many species of aphids, which causes dispersion in response to attack by predators or parasitoids. Overexpression of an (*E*)- $\beta$ -farnesene synthase cloned from *Mentha x piperita*, in *Arabidopsis thaliana*, yielded plants that had high emission of pure (*E*)- $\beta$ -farnesene (31). These plants elicited potent effects on behavior of the aphid *Myzus persicae* (alarm and repellent responses) and its parasitoid *Diaeretiella rapae* (an arrestant response).

It is conceivable that changes in the (induced) volatile production in commercial crops could lead to the development of biological control packages in which biological control agents trained specifically for the modified crop are included. It will be exciting to see whether these approaches can lead to plants with altered (improved) predator behavior and to crops with improved biological control.

## Acknowledgments

This work was supported in part by the Technology Foundation (STW) of the Netherlands Organisation for Scientific Research (NWO) to I.F.K. (WPB 5479) and the Netherlands Organisation for Scientific Research (NWO) to M.D. and H.J.B. (Vici-grants).

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