Where, When, and Why Do Plant Volatiles Mediate Ecological Signaling? The Answer Is Blowing in the Wind

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Keywords

plant volatiles, plant interactions, ecological signaling, spatial distributions, temporal dynamics, environmental chemistry and physics, research gaps

Abstract

Plant volatiles comprise thousands of molecules from multiple metabolic pathways, distinguished by sufficient vapor pressure to evaporate into the headspace under normal environmental conditions. Many are implicated as ecological signals, but what is the evidence—and how do they work? Volatiles diffuse, are carried by wind, and may be taken up by other organisms or degrade with exposure to atmospheric ozone, radicals, and UV light; visual signals such as color are not subject to these complications (but require a line of sight). Distantly related plants—and nonplants—produce many of the same volatiles, yet specific compounds and blends may be distinct. Here, I present a quantitative review of the literature on plant volatiles as ecological signals, illustrating a field that has focused on developing ideas as much as reporting primary data. I discuss advantages and constraints, review recent advances, and propose considerations for primary studies to elucidate particular functions of plant volatiles.

Contents

1. INTRODUCTION

Atmospheric measurements of fluxes and mixing ratios have become possible in the last decades. Such measurements have shown that at a global scale, volatile organic compounds in the atmosphere are due primarily to vegetation (89, 102). Land plants return about one-fifth of their fixed carbon to the atmosphere daily in the form of volatiles (10). Recent evidence indicates that plant volatile emission is an active process, which is controlled by transport of compounds across cell membranes and cuticles, and is affected by stomatal opening and closing as well as by tissue damage (1, 96, 142, 158). The most abundantly emitted plant volatile, the hemiterpene isoprene, is largely responsible for the blue haze over forested mountains and hills due to particulate formation in the atmosphere (136). The many thousands of other volatile chemicals produced by plants are individually less abundant, although methanol and acetic acid, released during cell wall modification, may come close (37). Most plant volatile compounds are likely more important as mediators of ecological interactions and stress responses than as modifiers of atmospheric chemistry (although in bulk, they contribute significantly to atmospheric properties) (65, 84, 129). Their diverse structures emerge from several pathways closely related to general metabolism, such as the biosynthesis of fatty acids, photosynthetic pigments, and amino acids (10, 112). An overview of plant volatiles is provided in **Table 1** and its footnote.

While plant volatiles were once thought to be waste products of metabolism, their role as ecological signals is now well accepted (131). Yet there are still critical gaps in our understanding. It is challenging to measure the production of plant volatiles under realistic conditions and to characterize their distributions in complex environments. In many cases, behavioral and

Volatile organic compound:
a carbon-containing molecule with a sufficiently high vapor pressure at standard atmospheric pressure (101.3 kPa) to evaporate under normal conditions on Earth

Table 1 Major biosynthetic classes of plant volatiles, their characteristics, and reported functions (updated from Reference 132)

Class[a]	Compounds	Biosynthesis	Reported functions	Volatility (BP, 760 mm Hg)[b]	Known structures
Fatty acid derivatives	Jasmonates	From 16:3 and 18:3 fatty acids dioxygenated at C13 by 13-LOX (155)	Floral scent (35) and volatile forms of plant hormones (14, 82, 86, 116)	Methyl jasmonate, 303°C; (Z)-jasmone, 291°C	Four stereo-isomers
	Green leaf volatiles (C6 and esters)	From cleavage of 13-LOX products by HPL to yield hexanal (from 18:2 fatty acids) or (Z)-3-hexenal (from 18:3 fatty acids), which may be converted to alcohols by ADH and further esterified (100)	Typical damaged leaf or cut grass scent (61), also emitted from other organs (38); antimicrobial or antifungal (36, 137); may stimulate animal consumption as flavor components (57); part of direct (147) and indirect antiherbivore defense (137); may prime or elicit defense within (49) and between plants (11, 109, 140)	(Z)-3-hexenal, 122.7°C; (Z)-3-hexenol, 156.5°C; (Z)-3-hexenyl acetate, 191°C	Tens: four aldehydes [hexanal, (Z)-3-hexenal, (E)-2-hexenal, (E)-3-hexenal], thus four alcohols, each potentially with esters, including acetates, propionates, butyrates, isobutyrates, valerates, isovalerates, benzoates, and salicylates
	Nine-carbon volatile aldehydes, alcohols, and esters	From 9-LOX products of 18:2 and 18:3 fatty acids, HPL, and ADH; some HPLs cleave only 9- or 13-hydroperoxides, whereas others cleave both; products from 18:2 have one double bond and those from 18:3 have two (33)	Fruit odor and flavor components (147); antifungal (100); possibly involved in almond seed development (103)	(E,E)-3,6-nonadienal, 202°C; (E,E)-3,6-nonadienol, 215°C; (E,E)-3,6-nonadienyl acetate, 247°C	Tens: five aldehydes and thus five alcohols, which can be esterified; acetate esters most frequently reported
Terpenoids	Canonical terpene hydrocarbons: hemiterpenes (C5), monoterpenes (C10), sesquiterpenes (C15), and some diterpenes (C20) (161)	From five-carbon precursors IPP and DMAPP via one of two pathways in plants, the MEP pathway in plastids or the MVA pathway in the cytosol; generally, hemiterpenes and monoterpenes are synthesized in plastids and sesquiterpenes in the cytosol; some sesquiterpenes may be synthesized in mitochondria from cytosolic substrate (81, 123); production is usually light dependent (94)	Odors from green tissue, flowers, fruits, and roots; many reported to be allelopathic (104) or antimicrobial or antifungal (29, 88), to function as direct (19) or indirect (34) antiherbivore defenses, to attract pollinators (124), and to be involved in defense elicitation and priming (7); most react with atmospheric ozone (23) and could be involved in plant oxidative stress responses (150)	Isoprene, 34°C; (Z)-(β)-ocimene, 175°C; (S)-(-)-limonene, 177°C; (E)-(β)-farnesene, 273°C; (-)-(β)-caryophyllene, 263°C; kaurene, 347°C	Hemiterpenes: only isoprene; perhaps 1,000 mono- and 5,000 sesquiterpenes (52, 133); most are mono- or polycyclic
	Norsesquiterpenes and norditerpenes (often referred to as homoterpenes) and apocarotenoids (C8–C18)	Norditerpenes and norsesquiterpenes are derived from diterpenes (C20) in plastids or sesquiterpenes (C15) in the cytosol by oxidation, possibly catalyzed by Cyp450 (16, 24a, 38, 68); apocarotenoids are cleaved from carotenoids in plastids by CCO; some mono- and sesquiterpenoids arise as apocarotenoids (9, 153)	(E,E)-TMTT and (E)-DMNT are commonly reported to mediate indirect defense of leaves (38); apocarotenoids are flavor and odor components of fruits, flowers, and green tissue, are reported as both attractants and repellents of pollinators and predators, and are associated with fruit ripening (18, 24); some are antifungal (97)	(E)-DMNT, 196°C; (E,E)-TMTT, 293°C; β-ionone, 282°C	Only (E)-DMNT and (E,E)-TMTT are widely reported from plants, although a handful of other homoterpenes are reported from insects (157)

(Continued)

Table 1   (Continued)

Class[a]	Compounds	Biosynthesis	Reported functions	Volatility (BP, 760 mm Hg)[b]	Known structures
	Oxidized terpenoids and derivatives	Derived from terpenes by oxidation (e.g., by Cyp450); products may be further oxidized, esterified, or reduced; some TPSs synthesize oxidized terpenoids by incorporating CO_2 (38)	Odor components of fruits, flowers, green tissue, and roots (39) with ecological roles similar to those for terpene hydrocarbons, but more often directly toxic (88); precursors of aerosols (15)	Prenol, 142°C; linalool, 199°C; (E,E)-farnesol, 283°C	Similar to those for terpene hydrocarbons
Shikimate pathway	Acids, aldehydes, and alcohols derived from L-phenylalanine, indole (tryptophan precursor), and other derivatives of shikimate products	L-phenylalanine is converted to *trans*-cinnamic acid, with a C3 side chain, by PAL and then to other phenylpropanoids by steps of monolignol biosynthesis; the side chain may be enzymatically shortened to produce benzenoids or other derivatives having a C2 side chain; indole is a direct precursor of tryptophan (38)	Common in floral scents (151) and source of capsaicinoids (pungence in pepper); methyl salicylate is a common herbivore-induced leaf volatile that attracts some predators and parasitoids (6, 146)	Methyl salicylate, 222°C; indole, 253°C	Approximately 20% of known plant volatiles (118)
Other amino acid derivatives	Acids, aldehydes, alcohols, esters, nitrogen- and sulfur-containing volatiles from nonaromatic amino acids, ethylene (from methionine) (38, 98), and nitrous oxide (from arginine)	Amino acids are deaminated or transaminated to α-keto acids, which are carboxylated and may be reduced, oxidated, or esterified; may also be precursors for acyl CoA molecules used in esterification by alcohol acyltransferases (38)	Amino acid–derived esters are found in flowers and fruits (98); branched-chain amino acid (Leu, Ile, Val) derivatives are common in fruit (38); putrid sulfur-containing compounds, likely from methioinine (98), may act as direct defenses (13); ethylene and nitrous oxide are endogenous signals	Ethylene, −104°C; 2-methylbutanal, 94°C; 3-(methylthio)propyl acetate, 201°C	Unclear

[a]In addition to these classes, methanol and acetic acid are produced abundantly from cell wall *O*-acetyl and methyl esterification processes during leaf development (37), and other volatiles are produced from precursors of fatty acids and carbohydrates.

[b]Data from the Royal Society of Chemistry and ChemSpider (**http://www.chemspider.com/**).

Abbreviations: ADH, alcohol dehydrogenase; BP, boiling point; CCO, carotenoid cleavage oxidase; Cyp450, cytochrome P450; DMAPP, dimethylallyl pyrophosphate; DMNT, 4,8-dimethyl-1,3,7-nonatriene; HPL, hydroperoxide lyase; IPP, isopentyl pyrophosphate; LOX, lipoxygenase; MEP, 2-C-methyl-derythritol 4-phosphate; MVA, mevalonic acid; TMTT, 4,8,12-trimethyltrideca-1,3,7,11-tetraene.

phenomenological evidence demonstrates responses to plant volatiles for which the mechanism of action remains unknown. We know how animals and insects are able to smell, but plants have neither noses nor antennae, and their sense of smell is not generally understood. This review focuses on the following main questions: What is the evidence that plant volatiles mediate ecological signaling? What interactions do they mediate, and what are their particular characteristics as signals?

I begin by quantifying trends in the literature and discussing gaps in the evidence. Toward filling these gaps, I highlight examples in which multiple approaches provide more conclusive answers to open questions. In particular, these examples comprise studies incorporating laboratory analyses to measure plant volatiles, their production by emitters, and appropriate markers of perception and response in receivers; functional analyses in ecologically relevant, complex, and realistic environments; and modeling studies to connect observations with physical properties, information, and signaling theory (129, 159, 164).
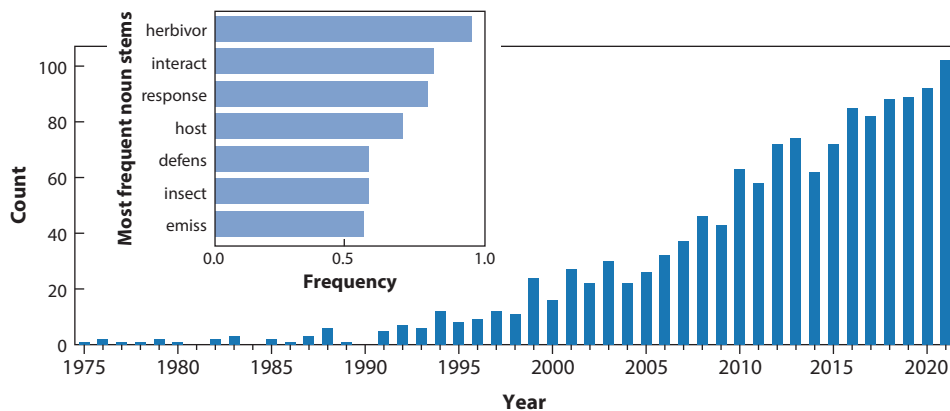
Publication over time of scientific literature on plant volatiles as ecological signals, from a database of 1,634 entries. The inset shows the relative frequency of the most frequent noun stems after the search terms "plant," "volatile," "signal," and "ecology," their derivatives, and irrelevant words were removed [stopwords, words incorrectly filtered as nouns or verbs, spelling inconsistencies (behavior = behaviour), and word fragments; see Section 6]. The year 2022 is not shown due to incomplete data at the time the database was generated (see Section 7).

2. WHAT IS THE EVIDENCE THAT PLANT VOLATILES MEDIATE ECOLOGICAL SIGNALING?

There are many reviews on plant volatile signaling but few systematic attempts to quantify trends and gaps in the literature, which has grown exponentially since the first publications in the 1970s–1980s (**Figure 1**), generally mirroring the trends in biology (46). Here, a broad literature search was conducted across six databases using variants of terms ("plant volatile" signal ecology) (for details, see Section 7). After removing off-target results, the resulting set of literature contained 1,634 entries published between 1975 and 2022 (where specified) (**Figure 1**; Section 6).

The most-studied interactions and mechanisms are indicated by the most prevalent noun stems found in entry titles (**Figure 1**), which demonstrate a focus on plant–herbivore interactions. By far the most common verb stem was "mediat" (with a relative frequency of 1.0), followed by "attract" (0.59), indicating that behavioral evidence is most often reported. The terms "bind" (0.24) and "induc" (0.28) were also within the top ten most frequent verb stems, indicating that literature on insect olfaction (odorant-binding proteins), on the one hand, and herbivore-induced plant responses, on the other, also represent relatively large shares of the mechanistic evidence (see Section 6).

The results were furthermore ranked for their approximate relevance using an active learning platform (ASreview with default settings) (145), and the top most relevant 25% of entries were examined in detail (409 total, provided publication dates from 1994 to 2022). Of these, 387 unique entries could be coded to retrieve the class(es) of volatile compounds, type(s) of interaction(s), and experimental environment(s) (if specified) on which they reported (for details, see Section 7). All source code and data are provided, including the literature search output files, scripts, and curated set of 1,634 entries, and coding output (see Section 6).

The 387 coded studies comprised 182 primary data publications, 177 qualitative review articles, six reviews or syntheses systematically quantifying data from primary literature, two opinion articles (labeled as opinion articles by the authors or by placement in the opinion section of a journal),

14 theses [monographs (six) or paper based (eight; papers resulting from these theses were also retained in the database)], and six modeling papers. The modeling papers did not report primary data, but half (three) used data from primary literature to parameterize simulations. Some of the 182 entries reporting primary data also included simulations (e.g., using information theory) (164).

These results indicate that scientific literature on plant volatiles as ecological signals comprises approximately as many qualitative review articles as reports of primary data. They hint at the importance of plant volatiles produced by nonplant interaction partners, which include many ubiquitous chemicals known from plants (**Figure 2a,b**). The literature as a whole is dominated by the study of plant–herbivore, tritrophic, and plant-plant interactions but includes a smaller number of reports on other types of interactions, including interactions between insect herbivores mediated by plant volatiles (**Figure 2c**). Most primary evidence comes from refined environments (**Figure 2d**), even though the most prevalent mechanistic evidence is behavioral, and behavioral studies are more plausible when conducted under realistic conditions.

2.1. Plant Volatile Signaling in Ecology May Be More Often Discussed than Directly Studied

The results indicate that scientific literature on plant volatile signaling in ecology comprises nearly as many qualitative review or opinion articles as sources of primary data, data-based simulations, or quantitative analyses of any kind. It is not uncommon (64/387 entries) to test and discuss ecological functions of plant volatiles without either specifying volatile compounds and compound classes or measuring plant volatiles and without reference to known compounds or classes identified from studies in relevant systems.

Fewer than half of coded entries (182/387) were publications reporting primary data, and five of the 182 were reviews or addenda that reported primary data but with incomplete methods. Next most abundant were qualitative review articles (177/387). Most of these (150/177) discussed functions and mechanisms related to specific plant volatile compounds or biosynthetic classes of volatiles, whereas 27 discussed plant volatiles as (potential) ecological signals without ever specifying chemical compounds or classes (publication dates from 1999 to 2021). This was also the case for 25 of the 182 primary studies (published 1997–2022), which used plants as a volatile production source and usually (24/25 publications) employed experiments that isolated aerial contact of plants with receivers (e.g., emitting plants in cages, wind tunnels, olfactometers) or transferred volatiles in sampled headspaces or extracts but did not measure plant volatiles. In one primary article, the potential of volatiles as signals in indirect defense was discussed without using plants as volatile sources at all, instead investigating how the feeding of experimentally parasitized versus nonparasitized herbivores affected seed production (69). Thus, in 14% of relevant articles reporting primary data, plant volatiles were not measured.

2.2. Plant Volatiles Produced by Nonplant Interactors

Given the proximity of plant volatiles to pathways of general metabolism, most of which are shared with other eukaryotes and some also with prokaryotes, it is perhaps not surprising that plant volatiles may be found in the odors and emissions from nonplant species. Literature on plant volatiles as ecological signals occasionally also reported on the same volatiles, or structurally related compounds, produced by interacting organisms, especially herbivores and microbes. Most publications that reported on specific compounds, or compound classes, discussed multiple classes of volatile compounds produced by plants and their interaction partners: Single publications discussed up to 11 of the identified producer-class pairs (**Figure 2a**). Note that volatiles attributed to plants in **Figure 2a** from the reviewed literature cannot be assumed to be produced by plant cells

except where demonstrated biochemically: Sampled plants and plant parts were not sterile, and sometimes herbivores or other interactors used to elicit plant volatiles were also present during sample collection (which is realistic).

Indeed, some insect species, and many plant-associated microbes, produce some of the most ubiquitous plant volatiles: simple compounds such as ethylene and methanol, as well as more complex structures such as the terpenoids linalool and (E)-β-farnesene (124) (**Figure 2b**). A fitting
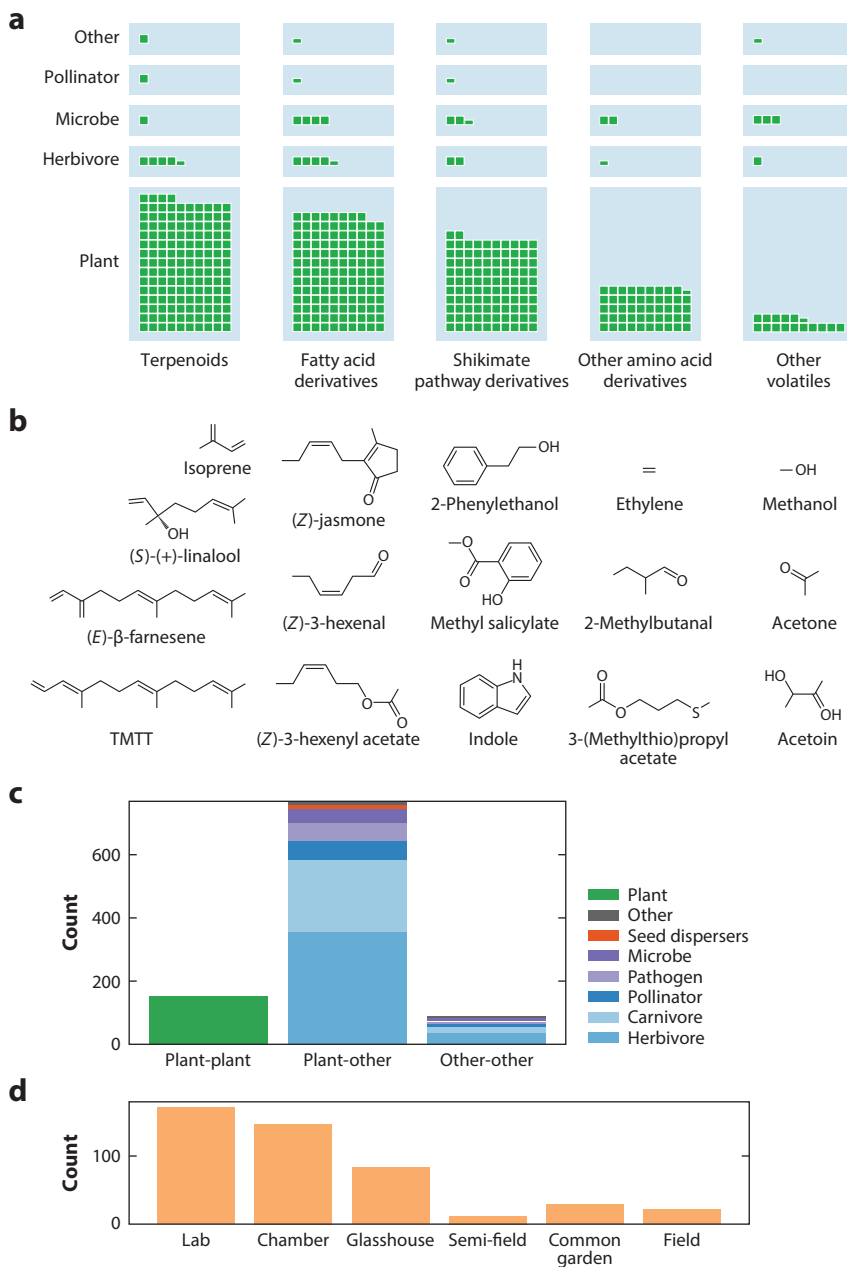
Figure 2 (*Figure appears on preceding page*)

Results from 387 coded references representing the top 25% of publications (ranked as most relevant) on plant volatile signaling in ecology reviewed for this article. (*a*) Reported production of plant volatiles attributed to plants and other groups of interacting organisms. Each full square represents two reports from a class and a group, with a maximum of 288 reports for plant terpenoids. A report refers to a class-producer pair mentioned in one publication; a publication may report multiple categories. Classes correspond to the descriptions in **Table 1**; oximes and glucosinolate derivatives are included in the row Other amino acid derivatives. For primary literature, only classes reported in results were included, and unknowns were not considered. Classes were attributed to producers as reported in publications, regardless of whether biosynthesis was investigated; thus, it is possible, for example, that some reports of plant production are actually due to production by plant-associated microbes. (*b*) Example structures for each biosynthetic group. (*c*) Reports of plant volatiles mediating interactions within or between plants (e.g., priming of defense responses), of plants with other organisms (e.g., indirect defense against herbivores), and between organisms that are not plants (e.g., mating herbivores, parasitoid-hyperparasitoid interactions). Plant-plant interactions include between- and within-plant signaling via volatiles but not nonvolatile hormones; priming of neighboring plants by herbivore-induced volatiles from focal plants was counted as plant-plant and plant-other, with other coded as herbivore. Tritrophic interactions were attributed as plant-other (herbivore and carnivore). (*d*) Counts of studies reported in 182 primary, 14 thesis, and four quantitative review publications, from more refined (lab) to more realistic (field) environments (one publication may report multiple studies). Lab refers to laboratory analyses, bioassays, and measurements conducted explicitly in laboratories. Chamber refers to growth or experimental chambers, including wind tunnels, exposure chambers, olfactometers, and rigid enclosures used for plant volatile measurement. Glasshouse refers to studies conducted in glasshouses and greenhouses. Semi-field refers to potted plants placed under field conditions or plants placed outdoors in nets or tents. Common garden refers to experimental plantations. Field refers to plants already growing outdoors under natural conditions and not planted or placed by the experimenters (usually naturally occurring populations).

example, linalool is commonly emitted from flowers, but also from plant leaves, as two enantiomers, the (*R*)- and (*S*)- forms, which may be produced individually or in a blend and which have distinct odors and biological activities (120). Thus, the functions of linalool are manifold in plants and likely to depend strongly on contexts such as plant ontogeny and ecological setting (63, 120) (see Section 3). Both enantiomers of linalool are produced across kingdoms, from bacteria to fungi to animals—in particular insects, in which linalool is thought to function as a pheromone and possibly as an antimicrobial compound (63, 163).

2.3. Plant Volatiles Are Reported as Ecological Signals Most Often in the Context of Tritrophic and Plant-Plant Interactions

Most reported interactions were among plants, herbivores, and carnivores (including parasitoids, entomopathogenic nematodes, and omnivores functioning as carnivores), followed by plant-plant interactions. There were far fewer reports on plant-microbe, plant-pathogen, and plant-pollinator interactions and on plant volatiles participating in direct interactions between organisms that are not plants (mostly mating herbivores; **Figure 1***c*). Studies of plant-pollinator interactions mediated by floral volatiles may not be well represented in this literature review if they focus on pollination and floral visitation specifically rather than on plant volatiles as ecological signals more generally. When pure substances were used, these were attributed to the source in which they were found and the interaction they were meant to test; for example, a blend of volatiles composed on the basis of measurements of flowers used to test the attraction of pollinators was counted as plant-other interactions (pollinator). The use of jasmonate and herbivore elicitors to induce responses to herbivore attack was attributed to plant-other interactions (herbivore). The other-other category included signaling between insects using plant volatiles, for example, to enhance mate location, the interference of plant volatiles in mate location, or the increased susceptibility of

Pheromone:
a chemical mediator of intraspecific interactions, resulting in a change in physiology or behavior in the recipient

insects to pathogens in association with plant volatiles, in addition to the use of plant volatiles by hyperparasitoids to find parasitoids (115) (see Sections 3 and 4). Tests of abiotic conditions were occasionally identified in the database entries but not coded, as these represent plant acclimation to the abiotic environment rather than interactions with other biota.

For interaction types and for study environments (**Figure 2*d***), each entry was coded as providing multiple reports as appropriate: For example, a reference reporting on both field studies and lab analyses would count once toward the laboratory and once toward the field.

2.4. Studies Are Most Frequently Conducted in Refined Environments

Most entries reported results from laboratory trials and analyses, with a minority reporting on field experiments. Overall, there was a pattern of decreasing reports along a gradient from more refined, controlled environments (most reports) to more realistic environments (fewest reports) (**Figure 2*d***). Environments were scored only for entries reporting quantitative data: primary research articles, quantitative reviews specifying source environments, and theses. Individual entries included results from as few as one to as many as four different environments. Most entries reporting quantitative data coupled laboratory analyses profiling volatile composition and biological activity—in the form of plant gene expression, for example, or insect electrophysiology—with the study of interactions under environments ranging from growth and experimental chambers (most often) to natural field conditions (least often).

In the following two sections, individual aspects are discussed in more detail, with examples that may help guide new empirical studies to fill gaps quantified above.

3. ECOLOGICAL INTERACTIONS MEDIATED BY PLANT VOLATILES

Plant volatiles are reported to function as pheromones and allelochemicals (90) in a variety of interactions. In the following examples, I highlight studies of interactions in realistic experimental environments, especially when these were paired with laboratory analyses of signaling and response chemistry.

3.1. Interactions Within and Between Plants

Most literature on plant volatile–mediated interactions within and between plants concerns the priming or induction of defense responses by herbivore-induced plant volatiles, perhaps functioning as alarm pheromones within species or as kairomones within and between species (8, 84). The phenomenon initially termed talking trees was first indicated in field studies in the 1980s, where caterpillars were observed to grow more slowly on leaves from trees with herbivore-damaged neighbors (122). Potted plants sharing experimental enclosures were used to attribute this phenomenon to aerial factors (12). Since then, more and more studies have shown that plants exposed to herbivore-induced volatiles from neighbors (7, 12, 83, 122, 140), pure substances (49, 66), and damaged leaves on the same plant (67), without a direct vascular connection (48), experience reduced herbivore damage (83, 122) and rapid changes to defense-related specialized chemistry, such as phenolic compounds (12) or a glycoside of the green leaf volatile (*Z*)-3-hexenol (140), increased production of extrafloral nectar (66, 67) or production of herbivore-induced volatiles in the absence of herbivory (76), more rapid induction of proteinase inhibitors (2, 86), herbivore-induced volatiles or defensive hormones (44) following herbivory, greater abundance of defense-related gene transcripts (48, 49), and epigenetic changes to the regulation of defense-related genes (2, 7, 108). Priming specifically refers to the preparation of plants for more rapid defense induction upon elicitation (99), likely via epigenetic changes (2, 108), as opposed to immediate induction of a response.

Both priming and induction of defense by plant volatiles are now established phenomena that, taken together, have been observed more often than not in studies of more than 30 plant species across at least 14 families, with no strong evidence of publication bias (reviewed in 84, 129). Effects are generally initially transient but induce a memory (8, 84). Although a growing number of studies are conducted in natural settings (66, 67, 83, 86, 111), it is still the case here, as in other subdomains of research on plant volatile signaling, that most studies use more refined environments (129) and that the studies conducted in realistic environments may not include measurements of plant volatiles (83, 111).

More recently, several studies have indicated that volatiles emitted from undamaged plants can influence tritrophic interactions by affecting neighbor plant volatile emission, mostly in agricultural systems (31, 107, 152). This finding is promising for intercropping systems (see next section) but less relevant for understanding the evolution of plant volatile signaling. A recent study from Kalske and colleagues (80) indicates that insect herbivory selects for volatile-mediated communication among genotypes of the tall goldenrod (*Solidago altissima*) under field conditions, as measured by reduction in insect damage following neighbor volatile exposure, and that *S. altissima* from populations not subject to herbivore pressure communicate preferentially with neighbors of the same genotype.

3.2. Interactions Between Plants and Organisms from Other Kingdoms

In 1980, Price and colleagues (117) proposed that plants manipulate interactions between insect herbivores and higher trophic levels and that these tritrophic interactions determine outcomes of plant-insect interactions and plant fitness. Laboratory studies of experimentally infested plants have since compiled catalogs of herbivore-induced plant volatiles that can attract captive parasitoids and thus are seen as candidate synomones (providing advantages to both plant emitters and foraging carnivorous receivers). Although few, the number of field studies demonstrating volatile-mediated tritrophic interactions in natural and ecologically relevant settings is growing (e.g., 4, 56, 78, 85, 127, 130; reviewed in 64, 128, 143). Schuman and colleagues (130) demonstrated for the first time that green leaf volatiles benefit the fitness of a wild plant (measured as flower and seed capsule production) specifically by attracting predators and reducing herbivore load. This may still be the only demonstration that volatile-mediated tritrophic interactions increase plant fitness, although these interactions appear to be widespread.

The growing evidence that plant volatiles mediate attraction of (mostly insect) predators and parasitoids and entomopathogenic nematodes (121, 144) in natural and field environments is promising for their application in more sustainable ecosystem management. Push-pull mixed cropping systems, which can control pests while increasing yield and reducing input, are thought to function in part by co-opting volatile emissions from different plant species in spatially structured fields comprising a focal crop, a repellent intercrop, and an attractive trap crop (113). So far, measurements of pest control and yield greatly outpace measurements of chemistry and receiver responses in these systems (91). A better mechanistic and functional understanding of volatile-mediated tritrophic interactions in complex natural environments could support efforts toward sustainable intensification using push-pull and related approaches (113, 143).

The study of plant volatiles in plant-insect interactions is supported by advances in insect neuroethology. These include behavioral bioassays in realistic environments, electrical neurophysiology, and the use of chemical tracers of calcium signaling and genetic engineering of marker proteins, which allow demonstration of perception mechanisms for specific volatiles and volatile blends by insects (58). The mechanisms of olfaction in insects share some superficial commonalities with mechanisms in vertebrates but are distinct (59). Data on the molecular perception of odors via odorant-binding proteins and odorant receptors in the insect olfactory system, and on

integration of odor information in the antennal lobe, close the loop in demonstrations of volatile-mediated insect-plant interactions. As an example, Allmann and colleagues (5) demonstrated reduced oviposition by *Manduca* spp. moths in response to herbivore-induced green leaf volatile blends compared with mechanical damage-induced blends, differing in the relative abundance of (*Z*)- versus (*E*)-structures, on naturally growing *Datura wrightii* plants. They furthermore measured *Manduca sexta* larvae–induced versus mechanically induced volatile blends from *D. wrightii* in the field and demonstrated the ability of gravid female *M. sexta* moths to differently integrate olfactory information from damage- versus larvae-induced blends in laboratory electrophysiological studies. From this, they could demonstrate that ovipositing moths can distinguish blends induced by herbivore feeding from those induced by mechanical damage and use these blends to avoid oviposition on herbivore-damaged plants in nature.

Such tools, which rest in part on a mechanistic understanding of volatile perception, are largely missing in plants and most of their noninsect interaction partners, although bioassay approaches are well established for plant-microbe and especially plant-pathogen interactions (e.g., 92). Effects of plant volatiles on microbes and pathogens have been demonstrated in more controlled environments, in direct interactions with both plants and insect herbivores; however, we are far from a systematic understanding of how plant volatiles influence two-way, three-way, and higher interactions among plants, microbes, and other organisms (40, 51, 135). Research on plant-plant interactions mediated by volatiles, as well as investigations of plant growth promotion by microbial volatiles (134), has provided increasingly specific response markers for bioassays but has not revealed the mechanisms of olfaction in plants—with the exception of plant ethylene hormone perception, for which the receptor proteins and signaling cascades have been characterized by studies of mutant and transgenic plants (reviewed in 129). Many plant-growth-promoting bacteria produce ethylene precursors, which may be the best-understood mechanism underlying volatile-mediated plant-microbe interactions (45). Similarly, studies of volatile-mediated interactions with bacteria and fungi rely primarily on bioassays and response markers. A recent review by Howard and colleagues (73) discusses the study of plant volatiles and their role in mediating plant-microbiome interactions in the context of plants interacting with each other and provides recommendations based on lessons learned from the study of volatile-mediated plant-plant interactions. The article highlights the problems of pseudoreplication and refined environments and the pitfalls of proceeding in the absence of a mechanistic understanding of volatile perception.

3.3. Interactions Between Organisms That Are Not Plants

A few of the studies coded in this systematic review focused on the effects of plant volatiles on interactions between other organisms. Most of these investigated the influence of plant volatiles on interactions between herbivores, especially in mating or aggregation mediated via herbivore pheromones, which may be either enhanced or disrupted by plant volatiles (e.g., 17, 26, 28, 62, 93, 95, 139, 154, 156). It may be generally expected that host plant volatiles enhance sex pheromone activity (125), for example, by indicating that a food source for larvae (and perhaps for adults) is close to a mating site, and this has been demonstrated in longhorn beetles (Coleoptera: Cerambycidae); however, the opposite effect has also been demonstrated, depending on the specific combination of beetle species and host plant, ranging from conifers to oaks (28). A study by Hatano and colleagues (62) demonstrated that the herbivore-induced volatile (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) suppressed the electrophysiological response of *Spodoptera littoralis* moths to the sex pheromone (*Z*)-9-(*E*)-11-tetradecenyl acetate and to the structurally related, attractive host plant volatile (*Z*)-3-hexenyl acetate. There is evolutionary pressure on herbivores to separate their response circuits to sex pheromones and host plant cues, and there is evidence

for conserved perception of these cues and signals (53). However, the structural similarity of many fatty acid–derived host plant volatiles and insect sex pheromones may impose constraints.

In extreme cases, insect pheromones are identical to herbivore-induced host plant volatiles. For example, most aphid species produce the sesquiterpene (E)-β-farnesene, a common plant volatile, as an alarm pheromone (148). Bruce and colleagues (20) reported the generation of a transgenic wheat genotype that constitutively produced (E)-β-farnesene as a means of aphid control. While the transgenic plants were less attractive to aphids and more attractive to their enemies in laboratory bioassays, in the field, there was no difference in aphid infestation between the transgenic plants and controls. This fascinating study provides evidence that even when the host plant volatile and insect pheromones are identical, insects can learn to differentiate. Herbivore induction may function in part to prevent volatile signals from being ignored as background noise (see next section). The study by Bruce and colleagues (20) advertises the importance of conducting behavioral bioassays under realistic conditions: There is a translation gap between behaviors and outcomes observed under refined conditions and those observed in the complex real world (129).

4. WHAT ARE THE CHARACTERISTICS OF ECOLOGICAL SIGNALING MEDIATED BY PLANT VOLATILES?

Finally, I discuss aspects of signal content, distribution, persistence and transience, and spatiotemporal patterns in ecological signaling, considering the physical distribution of plant volatiles due to diffusion and wind (**Figure 3**) and the modification of plant volatiles in the environment.

4.1. Information Content

Plant volatiles directly affect the health and survival of interaction partners, for example, by stimulating herbivore feeding (57), increasing the susceptibility of herbivores to entomopathogens (51, 72), or acting as antimicrobials (100, 119). However, the idea that volatiles also function in information transfer has long been discussed in the literature on plant volatiles as ecological signals (87, 149). In a 2009 quantitative review, Allison & Hare (3) argued that in order for plants to manipulate tritrophic interactions for their defense, it is likely that enemies of herbivores (e.g., predators, parasitoids, entomopathogens) must often learn to respond to plant volatiles, and that there is not sufficient empirical evidence of how such learning occurs in nature. They identified 293 studies of responses by the enemies of herbivores to herbivore-induced plant volatiles, of which 74 tested naive responses; of these, 41 studies observed attraction and 33 observed no response (3). In laboratory studies of tritrophic interactions, parasitoids are commonly exposed beforehand by having a parasitization experience in the presence of herbivore-induced volatiles (e.g., 81). In contrast, studies conducted under field conditions generally do not control for a history of exposure to volatiles and instead simply observe response patterns. Both Allmann & Baldwin (4) and Schuman and colleagues (130) measured aspects of predator learning in field or common garden studies. This was done either by tracking the response of predators to herbivore-induced versus mechanical wounding–induced volatile blends over time in a natural population, as plants received damage from herbivores (4), or by exposing natural predator populations to herbivore bait in the presence of an experimentally provided herbivore-induced volatile blend, during a time in the season when plants were largely undamaged, and then measuring the response of predators to newly applied bait in the presence or absence of the blend (130).

Other studies have approached the issue from a different perspective, asking whether we can determine the information content of plant volatiles that could be available for associative learning. A study by Wilson and colleagues (160) investigated the production of volatiles from *D. wrightii* in response to variation in herbivory and abiotic factors and found that most volatiles
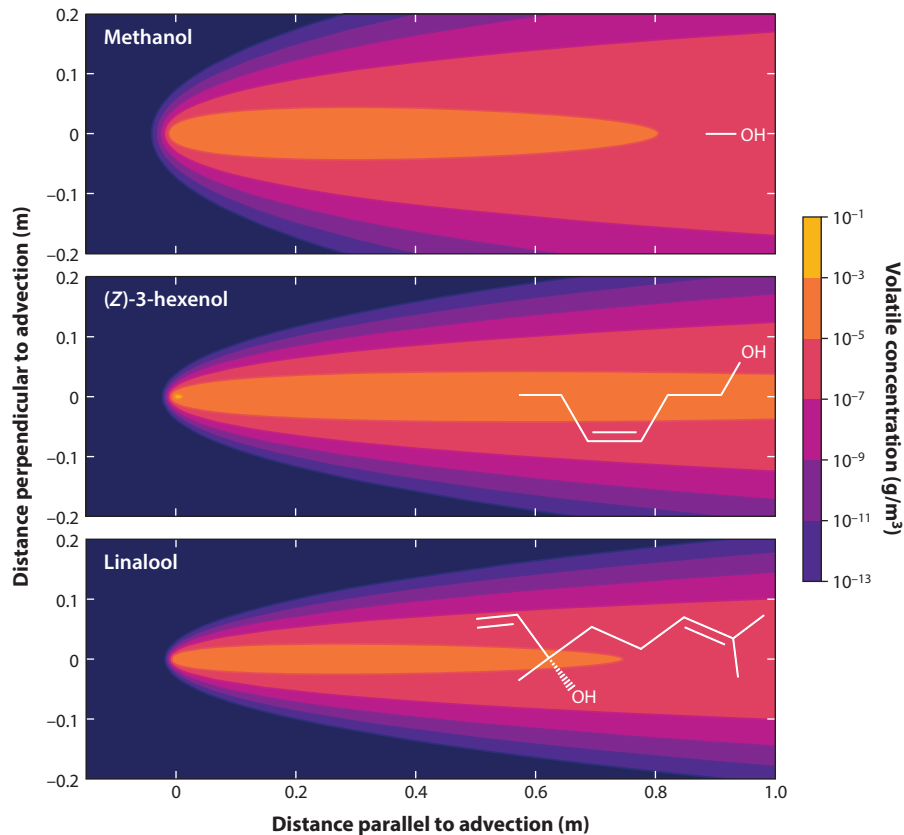
Figure 3

Diffusion of plant volatiles with similar emission rates but different molecular masses and structures. Emission is modeled as a series of rapid puffs emitted at a constant rate over 3 min, from a small initial source of approximately 1 cm^2, for an imaginary leaf weighing 1 g (fresh mass) over a flat plane under windstill conditions close to ground level (0.01 m s^{-1}). On this timescale, we assume that there is not yet any measurable accumulation, uptake by other organisms, or degradation by UV light or ozone within the depicted plume, and we ignore any influence of vegetation structure. Plausible emission rates of 1.67 ng s^{-1} for methanol released from pectin demethylation (*top*), 1.53 ng s^{-1} for the green leaf volatile (Z)-3-hexenol (*middle*), and 0.56 ng s^{-1} for the monoterpene linalool (racemic, *bottom*) were calculated as middle values from References 60 and 86. Gradients indicate relative mass concentrations with distance from the emitting plant.

did not covary, or covaried little, with either set of factors, whereas a few compounds covaried specifically with herbivory or with abiotic factors. Recently, Zu and colleagues (164) tested whether the observed patterns of shared versus distinct plant volatiles, and their association with insect host plant use among species in a diverse tropical forest, could be modeled based on the calculated entropy of their (potential) information content. They designed a simple model that assumed that plant species benefit over evolutionary time by minimizing the information about their identity encoded in their emitted volatiles, whereas herbivores benefit by maximizing the information about host plant identity retrieved from plant volatiles. This simple model of an information arms race accurately predicted the number of volatile compounds needed to identify plant species in a matrix of species ⊗ volatiles, as measured from undamaged leaves of host plants in a tropical forest. This approach leaves open many questions, including how this information

is encoded and decoded (although herbivore perception is increasingly understood) and what patterns might be expected if plants also seek to maximize information provided to beneficial interactors such as predators and parasitoids of herbivores while minimizing information for herbivores (165). In a study of 52 *Quercus* species, Pearse and colleagues (110) could differentiate species based on volatiles from wounded leaves but not those from unwounded leaves. The approach used by Zu and colleagues does not utilize any of the mechanistic insights about insect volatile perception and plant and insect physiology that have supported advances in other subfields of plant volatile research, as discussed above. However, it is a promising demonstration that information theory can help explain patterns of observed plant volatile production in plant–herbivore interactions.

4.2. Sources of Variation in the Production of Plant Volatiles

The production and abundance of plant volatiles vary in space and time, resulting in complex patterns and landscapes of scent. However, many components of this variation are mechanistically understood and predictable, as discussed in the following sections.

4.2.1. Diurnal, circadian, and ontogenetic patterns.
Plants actively coordinate their volatile production with the daily activity patterns of their interaction partners and availability of substrate from photosynthesis. Volatiles also serve different functions at different life stages: In flowering plants with insect pollinators, indirect defense of photosynthetic tissue is more important during vegetative growth, whereas the attraction of pollinators gains priority with flowering, and seed dispersers with fruit set. These topics have been reviewed in depth elsewhere (132) and are discussed here in light of recent advances.

Volatile production may occur from seconds to hours after induction and last from seconds to days; the composition of induced plant volatile blends thus varies over time (132). Most plant volatiles show diurnal patterns of production. In the case of terpenoids, this is associated with plant photosynthetic activity, which is thought to provide ~75% of carbon for isoprene biosynthesis, for example; however, isoprene emission in fact shows a strong circadian rhythm under constant conditions and thus does not depend only on light (reviewed in 132). In contrast to most cases reviewed in this article, the role of the circadian clock in controlling temporal patterns of plant volatile production was first reported for flowers (reviewed in 132) and only more recently for leaves. This may be inspired by observations of the strikingly predictable timing of floral opening and other floral displays, which famously underlie Linnaeus's flower clock and also include more recently discovered patterns of floral movement mediating pollinator access (162).

Joo and colleagues (78) recently investigated the importance of circadian and diurnal regulation of herbivory-induced leaf volatiles in tritrophic interactions. They found that *Nicotiana attenuata* plants elicited at dawn emitted green leaf volatile blends with a greater proportion of esters than a dusk-elicited blend, and the morning blend was more attractive to day-active insect predators of herbivores in field experiments. The same study found that terpenoid production was required to attract predators to plants in a common garden when plants were damaged at dusk; this indicated that the combination of rapidly emitted green leaf volatiles and more slowly emitted terpenoids ensures plants' capacity for indirect defense, regardless of when herbivores feed (78). Using a combination of experiments under free-running conditions and transgenic plants silenced in circadian clock genes, Joo and colleagues (79) found that the green leaf volatile biosynthetic gene hydroperoxide lyase (*HPL*) (**Table 1**) was under circadian control. Shifting plants' internal clocks compromised their indirect defense responses as measured by predation of herbivores from plants in a common garden experiment, even though much of the induced volatile blend (i.e., all of the terpenoids) displayed diurnal, not circadian, patterns of production (77).

4.2.2. Induction of volatiles by environmental factors.

Plant volatiles may be emitted constitutively or induced by different abiotic and biotic environmental factors, including changes in light (75) and temperature, ozone, drought, herbivory (22), pathogen attack (137), mechanical damage, and other sources of oxidative stress (71). The production of plant volatiles may be triggered by damage; for example, green leaf volatiles form rapidly upon wounding (101, 106), but induced plant volatiles, including green leaf volatiles, may also be released systemically from intact plant tissue (reviewed in 143). Induced volatile blends may be specific to particular plant species (e.g., 110); genotypes (e.g., 63); and stress events, including particular herbivores (reviewed in 27), numbers of herbivores (e.g., 138), and stages of herbivore development (54). Consistent with the results of this literature review, herbivore-induced plant volatiles are among the best-studied induced phenomena in the field of plant–herbivore interactions and have served as highly specific phenotypic readouts in studies of herbivore elicitors (74).

Induction proceeds through the perception of an environmental trigger by plant cells—in most cases, with the exception of pathogen attack, the receptor proteins have not been identified—triggering a signal transduction cascade in which an increasing number of molecular players are known (43, 143). Specific oxylipin hormones, as well as salicylate, ethylene, and abscisic acid, affect plant volatile production, and many damage- and herbivore-induced plant volatiles can be induced by jasmonate application (22, 132). More recently, it has been proposed that both constitutive and induced plant volatiles also act as regulators of plant hormone signaling, homeostasis, and stress responses both within and between plants (32, 42). The intricate phenomena related to plant volatile induction, which appear to occur both universally and with the potential for great specificity in higher plants, are taken as strong evidence that plant volatiles function both in stress response and in information transfer (42, 132, 149).

4.3. Spatial Distributions, Signal Persistence, and Transience

The persistence and transience of plant volatiles are influenced by patterns of biosynthesis and release, as well as by the longevity of compounds in the environment (70, 143). This is affected by their uptake and metabolism by other organisms (141), and by breakdown into degradation products or agglomeration into particulates due to, for example, oxidation by ozone, attack by radicals, or photo-oxidation (15, 114). The lifetime of plant volatiles in the atmosphere is expected to range from under 10 min to over 1 day, depending on levels of atmospheric pollution, the specific structure of the volatile, and its susceptibility to degradation. Generally, green leaf volatiles and shikimate pathway derivatives are more stable than terpenoids (see **Figure 2b**; **Table 1**), and nitrate radicals degrade plant volatiles more rapidly than ozone and hydroxy radicals do (70). The degradation of volatiles in the atmosphere can change blend composition when some volatiles are more prone to degradation than others. The local persistence or transience of the signal is determined by its diffusion away from the emitting plant and advection; compounds with lower volatility (higher boiling points) are likely to be retained closer to the boundary layer between the emission source and the headspace and are also more likely to adsorb to surfaces (15), and diffusion patterns differ depending on media (for a discussion of soil versus air, see 144). For an excellent introduction to signal persistence (in the context of insect pheromones), readers are referred to Reference 47.

Diffusion is predictably governed by physical constants and determined by molecular mass and shape, but in air, changeable wind speed, convection patterns, and direction distort the spherical diffusion pattern and generate plumes from a constantly emitting source or packets of volatiles from transient emissions. Turbulence caused by vegetation radiative transfer and roughness generates more complex patterns of eddy covariance, which are the subject of micrometeorological modeling and can also be assessed by proton transfer reaction mass spectrometry (PTR-MS) (105).

Plant volatiles are hydrophobic, which contributes to their high vapor pressure and also prevents them from being absorbed in water droplets in the environment (until they are sufficiently oxidized or form particulates). However, volatiles adhere to hydrophobic surfaces such as cuticles, where they may be reemitted from a new source such as a neighboring plant or taken up and metabolized (25, 141).

Figure 3 depicts the diffusion of three plant volatiles with very different structures and molecular masses that may be released at roughly similar rates according to the literature: methanol, (Z)-3-hexenol, and linalool [shown as (S)-(+)-linalool]. Emission is modeled as a series of rapid puffs emitted at a constant rate over 3 min, from a small initial source of approximately 1 cm^2, produced from an imaginary leaf weighing 1 g (fresh mass) over a flat plane under windstill conditions close to ground level. (Windspeed on Earth is never zero; we assume a windspeed of 0.01 m s^{-1}.) On this timescale, accumulation, uptake by other organisms, or degradation is minimal. Diffusion constants were calculated using diffusion volume increments or volumes for different atoms and molecular structures from Reference 50; diffusion equations are built from Reference 30 (see chapter 2, especially sections 2.7 and 2.8). Plausible emission rates of 1.67 ng s^{-1} for methanol released from pectin demethylation, 1.53 ng s^{-1} for the green leaf volatile (Z)-3-hexenol, and 0.56 ng s^{-1} for the monoterpene linalool are taken as middle values from the following sources: for methanol, 0.52–25.5 µg g^{-1} dry leaf mass h^{-1}, corresponding roughly to 0.1–12 µg g^{-1} fresh leaf mass h^{-1}, assuming a water content of 50% to 80%, from different growth stages of six plant species (60); for (Z)-3-hexenol, 3.11 ± 2.68 versus 8.30 ± 5.36 ng mg^{-1} fresh mass h^{-1}; and for linalool (stereoisomer not determined), 1.25 ± 0.92 versus 3.54 ± 2.28 ng mg^{-1} fresh mass h^{-1}, for undamaged versus clipped sagebrush (*Artemisia tridentata*) (86). For the source code, readers are referred to Section 6.

The gradients in **Figure 3** indicate relative mass concentrations with distance from the emitting leaf. At its center, the concentration ranges from 10 ng to 1 µg of compound per liter of air, and for (Z)-3-hexenol, the concentration at the source may approach 100 µg L^{-1}. Linalool displays the steepest concentration gradient from the center of its plume, followed by methanol and then (Z)-3-hexenol; whereas methanol displays the broadest plume perpendicular to advection, followed by (Z)-3-hexenol and then linalool. If we imagine all three plumes emitted by the same source, a neighboring leaf or plant would have greatest exposure to (Z)-3-hexenol, followed by methanol and then linalool if it is downwind; if it is perpendicular to the wind direction, it may be exposed most to methanol, followed by (Z)-3-hexenol and then linalool.

Effective distances of volatile-mediated plant-plant interactions have been estimated for only a handful of species and range from 0.6 m for the bush *A. tridentata* to 5–10 m for the trees *Alnus glutinosa* and *Fagus crenata* (55). This range corresponds well to the simulated range of the plume center from a 1-g leaf parallel to advection, which would increase with greater emitting biomass. The estimated distances of activity are comparable to the diameter of individual plant canopies (shrubs or trees), consistent with the hypothesis that volatile-mediated plant-plant communication evolved primarily for plant-internal signaling (84).

Estimated activity distances for insect receivers are better documented. In this case as well, numbers come primarily from empirical studies but are estimated to reach up to hundreds of meters or even kilometers (41). Simple models of odor range have been helpful perhaps for considering the impact of more and less diverse, or dense, plant patches on insect host orientation, and for placing the use of plant volatiles as orientation cues by insects in the context of other cues (visual, acoustic, and geomagnetic; 126). Meteorological and micrometeorological phenomena and environmental structure strongly limit the utility of simple diffusion models in accounting for activity ranges of volatiles in real environments, and reasonable predictions must also incorporate the great differences (orders of magnitude) in the sensitivity of olfactory systems for different components

(21, 59). With these caveats, the model presented here indicates that a foraging insect moving along a mixed plume of our candidate components in **Figure 3** may first sense (*Z*)-3-hexenol before sensing methanol and linalool.

Generally, green leaf volatiles are thought to be active over longer ranges and terpenoids over shorter ranges, which fits both to their diffusion behavior in air (but not soil; 144) and to their expected atmospheric lifetime; however, more rapidly degraded terpenoid volatiles may be better indicators of the current status of a plant or its flowers, even at greater distances (depending on advection). Perhaps the differences in the atmospheric lifetimes of terpenoids (shorter) and green leaf volatiles (longer) are also drivers of their herbivory-induced emission patterns from leaves, allowing time for a rapid burst of green leaf volatiles upon damage to be detected, whereas more transient terpenoids must be continually produced.

5. CONCLUSION

There is a growing body of literature on plant volatiles as ecological signals, comprising similar numbers of review articles as sources of primary data. It seems that the field, at this stage, is focused on developing ideas. This may be related to large gaps in our mechanistic knowledge of how plant volatiles function as signals, especially in plant-plant interactions, and how these functions play out in complex natural environments with many emitters and potential receivers, pollutants, and wind. In light of the very large effects that neighbor volatile production can have on plant survival and defense, even in the absence of defense induction or priming (127, 131), evidence that plants may adjust their volatile profiles in response to the scent of their neighbors is intriguing. Further investigation of such phenomena, and their decay with distance, in naturally evolved systems may shed new light on our understanding of how plant volatiles mediate interactions among plants and of their cascading effects to other trophic levels.

6. SOURCE CODE AND DATA

The following code and data files are available for this article:

Supplemental Material >

- literature search results (RIS files)
- code for curation of search results and generation of curated list (Python notebook)
- curated title list from search results (text file)
- code to analyze nouns and verbs (**Figure 1** from curated titles, Python notebook)
- image to mask the word clouds in the form of trees (PNG file)
- coded literature search results and initial exploration (Excel file)
- code to generate most of **Figure 2** (the input for **Figure 2*a,c,d*** from the coded literature search results, Python notebook)
- isomeric SMILEs to generate structures in **Figure 2*b*** (text file)
- code to generate the diffusion simulations in **Figure 3** (Python notebook)

7. SUPPLEMENTARY METHODS

The literature search was conducted across six databases on May 8, 2022, using the set of terms ("plant volatile" signal ecology) [for Science.gov, Base (**https://www.base-search.net/**), ScienceDirect, and Google Scholar] or ("plant volatile*" AND signal* AND ecol*) (for Web of Science and Scopus), according to the query syntax of the individual database. The complete list of results was obtained for all databases, except for Google Scholar, for which only the first 400 results, sorted by an undisclosed relevance rating, were obtained, as access to the full search results is not provided.

The total number of results, 2,427, contained only 532 duplicates, which were excluded based on titles. Thus, despite the advertised broad coverage of the individual databases, a substantial amount of literature may be accessible only by considering the union of their results. After removing off-target results (those from Cancer.gov; entries that were neither articles, theses, reports, books, nor book sections; and entries without authors), the resulting set of literature contained 1,634 entries published between 1975 and 2022 (where specified) (**Figure 1**; Section 6).

The results were further ranked for their approximate relevance using an active learning platform (ASreview with default settings) (145), and the top most relevant 25% of entries were examined in detail (409 total, provided publication dates from 1994 to 2022). Of these, one reported on relevant ecological interactions but without mentioning plant volatiles, one was a supplementary file, 11 were not found (no full text or abstract), and nine were duplicates that had not been caught by title-based deduplication, leaving 387 entries that were coded further to retrieve class(es) of volatile compounds, type(s) of interaction(s), and experimental environment(s) (if specified) on which they reported. For 10 of the 387 coded studies, no full text could be retrieved, and so not all of these fields were evaluated. All source code and data are provided, including the literature search output files, scripts, curated set of 1,634 entries, and coding output (see Section 6).

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

LITERATURE CITED

1. Adebesin F, Widhalm JR, Boachon B, Lefèvre F, Pierman B, et al. 2017. Emission of volatile organic compounds from petunia flowers is facilitated by an ABC transporter. *Science* 356(6345):1386–88
2. Ali M, Sugimoto K, Ramadan A, Arimura G-i. 2013. Memory of plant communications for priming anti-herbivore responses. *Sci. Rep.* 3:1872
3. Allison J, Hare J. 2009. Learned and naïve natural enemy responses and the interpretation of volatile organic compounds as cues or signals. *New Phytol.* 184(4):768–82
4. Allmann S, Baldwin IT. 2010. Insects betray themselves in nature to predators by rapid isomerization of green leaf volatiles. *Science* 329(5995):1075–78
5. Allmann S, Späthe A, Bisch-Knaden S, Kallenbach M, Reinecke A, et al. 2013. Feeding-induced rearrangement of green leaf volatiles reduces moth oviposition. *eLife* 2:e00421
6. Ament K, Kant MR, Sabelis MW, Haring MA, Schuurink RC. 2004. Jasmonic acid is a key regulator of spider mite–induced volatile terpenoid and methyl salicylate emission in tomato. *Plant Physiol.* 135:2025–37
7. Arimura G, Ozawa R, Shimoda T, Nishioka T, Boland W, Takabayashi J. 2000. Herbivory-induced volatiles elicit defence genes in lima bean leaves. *Nature* 406(6795):512–15

8. Arimura G, Pearse I. 2017. From the lab bench to the forest: ecology and defense mechanisms of volatile-mediated "talking trees." *Adv. Bot. Res.* 82:3–17

9. Auldridge ME, McCarty DR, Klee HJ. 2006. Plant carotenoid cleavage oxygenases and their apocarotenoid products. *Curr. Opin. Plant Biol.* 9(3):315–21

10. Baldwin IT. 2010. Plant volatiles. *Curr. Biol.* 20(9):R392–97

11. Baldwin IT, Halitschke R, Paschold A, Von Dahl CC, Preston CA. 2006. Volatile signaling in plant-plant interactions: "talking trees" in the genomics era. *Science* 311:812–15

12. Baldwin IT, Schultz JC. 1983. Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. *Science* 221:277–79

13. Berkov A, Meurer-Grimes B, Purzycki KL. 2000. Do Lecythidaceae specialists (Coleoptera, Cerambycidae) shun fetid tree species? *Biotropica* 32(3):440–51

14. Birkett M, Campbell C, Chamberlain K, Guerrieri E, Hick A, et al. 2000. New roles for *cis*-jasmone as an insect semiochemical and in plant defense. *PNAS* 97(16):9329–34

15. Blande JD, Holopainen JK, Niinemets U. 2014. Plant volatiles in polluted atmospheres: stress responses and signal degradation. *Plant Cell Environ.* 37(8):1892–904

16. Boland W, Gäbler A. 1989. Biosynthesis of homoterpenes in higher plants. *Helv. Chim. Acta* 72:247–53

17. Borrero-Echeverry F, Bengtsson M, Nakamuta K, Witzgall P. 2018. Plant odor and sex pheromone are integral elements of specific mate recognition in an insect herbivore. *Evolution* 72(10):2225–33

18. Bouvier F, Isner JC, Dogbo O, Camara B. 2005. Oxidative tailoring of carotenoids: a prospect towards novel functions in plants. *Trends Plant Sci.* 10(4):187–94

19. Brattsten L. 1983. Cytochrome P-450 involvement in the interactions between plant terpenes and insect herbivores. In *Plant Resistance to Insects*, ed. P Hedin, pp. 173–95. Washington, DC: Am. Chem. Soc.

20. Bruce TJA, Aradottir GI, Smart LE, Martin JL, Caulfield JC, et al. 2015. The first crop plant genetically engineered to release an insect pheromone for defence. *Sci. Rep.* 5:11183

21. Bruce TJA, Wadhams L, Woodcock C. 2005. Insect host location: a volatile situation. *Trends Plant Sci.* 10(6):269–74

22. Bruinsma M, Dicke M. 2008. Herbivore-induced indirect defense: from induction mechanisms to community ecology. In *Induced Plant Resistance to Herbivory*, ed. A Schaller, pp. 31–60. Dordrecht, Neth.: Springer

23. Calogirou A, Larsen B, Kotzias D. 1999. Gas-phase terpene oxidation products: a review. *Atmos. Environ.* 33(9):1423–39

24. Camara B, Bouvier F. 2004. Oxidative remodeling of plastid carotenoids. *Arch. Biochem. Biophys.* 430(1):16–21

24a. Chappell J, Coates RM. 2010. Sesquiterpenes. In *Comprehensive Natural Products II: Chemistry and Biology*, Vol. 1, ed. H-W Liu, L Mander, pp. 609–41. Amsterdam: Elsevier

25. Choh Y, Shimoda T, Ozawa R, Dicke M, Takabayashi J. 2004. Exposure of lima bean leaves to volatiles from herbivore-induced conspecific plants results in emission of carnivore attractants: active or passive process? *J. Chem. Ecol.* 30(7):1305–17

26. Clavijo McCormick A, Heyer J, Sims JW, Mescher MC, De Moraes CM. 2017. Exploring the effects of plant odors, from tree species of differing host quality, on the response of *Lymantria dispar* males to female sex pheromones. *J. Chem. Ecol.* 43(3):243–53

27. Clavijo McCormick A, Unsicker SB, Gershenzon J. 2012. The specificity of herbivore-induced plant volatiles in attracting herbivore enemies. *Trends Plant Sci.* 17(5):303–10

28. Collignon RM, Swift IP, Zou Y, McElfresh JS, Hanks LM, Millar JG. 2016. The influence of host plant volatiles on the attraction of longhorn beetles to pheromones. *J. Chem. Ecol.* 42(3):215–29

29. Cowan MM. 1999. Plant products as antimicrobial agents. *Clin. Microbiol. Rev.* 12(4):564–82

30. Cushman-Roisin B. 2012. *ENGS 43: Environmental transport and fate*. Lectures, Dartmouth Coll. **https://cushman.host.dartmouth.edu/courses/engs43.html**

31. Dahlin I, Rubene D, Glinwood R, Ninkovic V. 2018. Pest suppression in cultivar mixtures is influenced by neighbor-specific plant-plant communication. *Ecol. Appl.* 28(8):2187–96

32. Dani KGS, Loreto F. 2022. Plant volatiles as regulators of hormone homeostasis. *New Phytol.* 234(3):804–12

33. De Domenico S, Tsesmetzis N, Di Sansebastiano GP, Hughes RK, Casey R, et al. 2007. Subcellular localisation of *Medicago truncatula* 9/13-hydroperoxide lyase reveals a new localisation pattern and activation mechanism for CYP74C enzymes. *BMC Plant Biol.* 7:58

34. Degenhardt J, Gershenzon J, Baldwin IT, Kessler A. 2003. Attracting friends to feast on foes: engineering terpene emission to make crop plants more attractive to herbivore enemies. *Curr. Opin. Biotechnol.* 14(2):169–76

35. Demole E, Lederer E, Mercier D. 1962. Isolement et détermination de la structure du jasmonate de méthyle, constituant odorant caractbristique de l'essence de jasmin. *Helv. Chim. Acta* 45(79–80):675–85

36. Deng W, Hamilton-Kemp TR, Nielsen MT, Andersen RA, Collins GB, Hildebrand DF. 1993. Effects of six-carbon aldehydes and alcohols on bacterial proliferation. *J. Agric. Food Chem.* 41:506–10

37. Dewhirst RAO, Afseth CA, Castanha C, Mortimer JCO, Jardine KJ. 2020. Cell wall *O*-acetyl and methyl esterification patterns of leaves reflected in atmospheric emission signatures of acetic acid and methanol. *PLOS ONE* 15(5):e0227591

38. Dudareva N, Negre F, Nagegowda DA, Orlova I. 2006. Plant volatiles: recent advances and future perspectives. *Crit. Rev. Plant Sci.* 25(5):417–40

39. Dudareva N, Pichersky E, Gershenzon J. 2004. Biochemistry of plant volatiles. *Plant Physiol.* 135:1893–902

40. Eberl F, Uhe C, Unsicker SB. 2019. Friend or foe? The role of leaf-inhabiting fungal pathogens and endophytes in tree-insect interactions. *Fungal Interact.* 38:104–12

41. Eigenbrode S, Birch A, Lindzey S, Meadow R, Snyder W. 2016. A mechanistic framework to improve understanding and applications of push-pull systems in pest management. *J. Appl. Ecol.* 53:202–12

42. Erb M. 2018. Volatiles as inducers and suppressors of plant defense and immunity—origins, specificity, perception and signaling. *Curr. Opin. Plant Biol.* 44:117–21

43. Erb M, Meldau S, Howe GA. 2012. Role of phytohormones in insect-specific plant reactions. *Trends Plant Sci.* 17(5):250–59

44. Erb M, Veyrat N, Robert CA, Xu H, Frey M, et al. 2015. Indole is an essential herbivore-induced volatile priming signal in maize. *Nat. Commun.* 6(1):6273

45. Farag MA, Zhang H, Ryu CM. 2013. Dynamic chemical communication between plants and bacteria through airborne signals: induced resistance by bacterial volatiles. *J. Chem. Ecol.* 39(7):1007–18

46. Fire M, Guestrin C. 2019. Over-optimization of academic publishing metrics: observing Goodhart's law in action. *GigaScience* 8(6):giz053

47. Francke W, Schulz S. 1999. Pheromones. In *Comprehensive Natural Products Chemistry*, Vol. 8: *Miscellaneous Natural Products Including Marine Natural Products, Pheromones, Plant Hormones, and Aspects of Ecology*, ed. D Barton, O Meth-Cohn, pp. 197–261. Amsterdam: Elsevier

48. Frost CJ, Appel M, Carlson JE, De Moraes CM, Mescher MC, Schultz JC. 2007. Within-plant signalling via volatiles overcomes vascular constraints on systemic signalling and primes responses against herbivores. *Ecol. Lett.* 10(6):490–98

49. Frost CJ, Mescher MC, Dervinis C, Davis JM, Carlson JE, De Moraes CM. 2008. Priming defense genes and metabolites in hybrid poplar by the green leaf volatile *cis*-3-hexenyl acetate. *New Phytol.* 180(3):722–34

50. Fuller EN, Schettler PD, Giddings JC. 1966. New method for prediction of binary gas-phase diffusion coefficients. *Ind. Eng. Chem.* 58(5):18–27

51. Gasmi L, Martinez-Solis M, Frattini A, Ye M, Carmen Collado M, et al. 2019. Can herbivore-induced volatiles protect plants by increasing the herbivores' susceptibility to natural pathogens? *Appl. Environ. Microbiol.* 85(1):e01468–518

52. Gershenzon J, Croteau R. 1991. Terpenoids. In *Herbivores: Their Interactions with Secondary Plant Metabolites*, ed. GA Rosenthal, MR Berenbaum, pp. 165–219. San Diego, CA: Academic. 2nd ed.

53. Gonzalez F, Borrero-Echeverry F, Jósvai JK, Strandh M, Unelius CR, et al. 2020. Odorant receptor phylogeny confirms conserved channels for sex pheromone and host plant signals in tortricid moths. *Ecol. Evol.* 10(14):7334–48

54. Gouinguené S, Alborn H, Turlings TC. 2003. Induction of volatile emissions in maize by different larval instars of *Spodoptera littoralis*. *J. Chem. Ecol.* 29(1):145–62

55. Hagiwara T, Ishihara MI, Takabayashi J, Hiura T, Shiojiri K. 2021. Effective distance of volatile cues for plant–plant communication in beech. *Ecol. Evol.* 11(18):12445–52

56. Halitschke R, Stenberg JA, Kessler D, Kessler A, Baldwin IT. 2008. Shared signals – "alarm calls" from plants increase apparency to herbivores and their enemies in nature. *Ecol. Lett.* 11(1):24–34

57. Halitschke R, Ziegler J, Keinänen M, Baldwin IT. 2004. Silencing of hydroperoxide lyase and allene oxide synthase reveals substrate and defense signaling crosstalk in *Nicotiana attenuata*. *Plant J.* 40(1):35–46

58. Hansson B, Wicher D. 2016. Chemical ecology in insects. In *Chemosensory Transduction*, ed. F Zufall, SD Munger, pp. 29–45. Amsterdam: Elsevier

59. Hansson BS, Stensmyr MC. 2011. Evolution of insect olfaction. *Neuron* 72(5):698–711

60. Harley P, Greenberg J, Niinemets Ã, Guenther A. 2007. Environmental controls over methanol emission from leaves. *Biogeosciences* 4(6):1083–99

61. Hatanaka A, Kajiwara T, Sekiya J. 1987. Biosynthetic pathway for C_6-aldehydes formation from linolenic acid in green leaves. *Chem. Phys. Lipids* 44:341–61

62. Hatano E, Saveer AM, Borrero-Echeverry F, Strauch M, Zakir A, et al. 2015. A herbivore-induced plant volatile interferes with host plant and mate location in moths through suppression of olfactory signalling pathways. *BMC Biol.* 13(1):75

63. He J, Luck K, Köllner TG, Murdock MH, Ray R, et al. 2019. An unbiased approach elucidates variation in (*S*)-(+)-linalool, a context-specific mediator of a tri-trophic interaction in wild tobacco. *PNAS* 116(29):14651–60

64. Heil M. 2008. Indirect defence via tritrophic interactions. *New Phytol.* 178(1):41–61

65. Heil M. 2014. Herbivore-induced plant volatiles: targets, perception and unanswered questions. *New Phytol.* 204(2):297–306

66. Heil M, Kost C. 2006. Priming of indirect defences. *Ecol. Lett.* 9(7):813–17

67. Heil M, Silva Bueno JC. 2007. Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. *PNAS* 104(13):5467–72

68. Herde M, Gärtner K, Köllner TG, Fode B, Boland W, et al. 2008. Identification and regulation of TPS04/GES, an *Arabidopsis* geranyllinalool synthase catalyzing the first step in the formation of the insect-induced volatile C_{16}-homoterpene TMTT. *Plant Cell* 20(4):1152–68

69. Hoballah M, Turlings T. 2001. Experimental evidence that plants under caterpillar attack may benefit from attracting parasitoids. *Evol. Ecol. Res.* 3(5):553–65

70. Holopainen J, Blande J. 2013. Where do herbivore-induced plant volatiles go? *Front. Plant Sci.* 4:185

71. Holopainen JK, Gershenzon J. 2010. Multiple stress factors and the emission of plant VOCs. *Trends Plant Sci.* 15(3):176–84

72. Hountondji F, Sabelis M, Hanna R, Janssen A. 2005. Herbivore-induced plant volatiles trigger sporulation in entomopathogenic fungi: the case of *Neozygites tanajoae* infecting the cassava green mite. *J. Chem. Ecol.* 31(5):1003–21

73. Howard MM, Bass E, Chautá A, Mutyambai D, Kessler A. 2022. Integrating plant-to-plant communication and rhizosphere microbial dynamics: ecological and evolutionary implications and a call for experimental rigor. *ISME J.* 16(1):5–9

74. Howe G, Jander G. 2008. Plant immunity to insect herbivores. *Annu. Rev. Plant Biol.* 59:41–66

75. Jardine K, Barron-Gafford G, Norman J, Abrell L, Monson R, et al. 2012. Green leaf volatiles and oxygenated metabolite emission bursts from mesquite branches following light-dark transitions. *Photosynth. Res.* 113(1–3):321–33

76. Jing T, Qian X, Du W, Gao T, Li D, et al. 2021. Herbivore-induced volatiles influence moth preference by increasing the β-Ocimene emission of neighbouring tea plants. *Plant Cell Environ.* 44(11):3667–80

77. Joo Y, Goldberg JK, Chrétien LT, Kim SG, Baldwin IT, Schuman MC. 2019. The circadian clock contributes to diurnal patterns of plant indirect defense in nature. *J. Integr. Plant Biol.* 61(8):924–28

78. Joo Y, Schuman MC, Goldberg JK, Kim SG, Yon F, et al. 2018. Herbivore-induced volatile blends with both "fast" and "slow" components provide robust indirect defence in nature. *Funct. Ecol.* 32:136–49

79. Joo Y, Schuman MC, Goldberg JK, Wissgott A, Kim S-G, Baldwin IT. 2019. Herbivory elicits changes in green leaf volatile production via jasmonate signaling and the circadian clock. *Plant Cell Environ.* 42(3):972–82

80. Kalske A, Shiojiri K, Uesugi A, Sakata Y, Morrell K, Kessler A. 2019. Insect herbivory selects for volatile-mediated plant-plant communication. *Curr. Biol.* 29(18):3128–33.e3

81. Kappers IF, Aharoni A, van Herpen TWJM, Luckerhoff LLP, Dicke M, Bouwmeester HJ. 2005. Genetic engineering of terpenoid metabolism attracts bodyguards to *Arabidopsis*. *Science* 309:2070–72

82. Karban R, Baldwin IT, Baxter KJ, Laue G, Felton GW. 2000. Communication between plants: induced resistance in wild tobacco plants following clipping of neighboring sagebrush. *Oecologia* 125:66–71

83. Karban R, Shiojiri K, Ishizaki S. 2010. An air transfer experiment confirms the role of volatile cues in communication between plants. *Am. Nat.* 176(3):381–84

84. Karban R, Yang LH, Edwards KF. 2014. Volatile communication between plants that affects herbivory: a meta-analysis. *Ecol. Lett.* 17(1):44–52

85. Kessler A, Baldwin IT. 2001. Defensive function of herbivore-induced plant volatile emissions in nature. *Science* 291(5511):2141–44

86. Kessler A, Halitschke R, Diezel C, Baldwin IT. 2006. Priming of plant defense responses in nature by airborne signaling between *Artemisia tridentata* and *Nicotiana attenuata*. *Oecologia* 148(2):280–92

87. Kessler A, Heil M. 2011. The multiple faces of indirect defences and their agents of natural selection. *Funct. Ecol.* 25(2):348–57

88. Khosla C, Keasling JD. 2003. Metabolic engineering for drug discovery and development. *Nat. Rev. Drug Discov.* 2:1019–25

89. Koppmann R, ed. 2007. *Volatile Organic Compounds in the Atmosphere*. Oxford, UK: Blackwell Publ.

90. Kost C. 2008. Chemical communication. In *Encyclopedia of Ecology*, ed. SE Jørgensen, BD Fath, pp. 557–75. Oxford, UK: Academic

91. Lang J, Chidawanyika F, Khan ZR, Schuman MC. 2022. Ecological chemistry of pest control in push-pull intercropping systems: what we know, and where to go? *Chimia* 76(11):906

92. Lazazzara V, Avesani S, Robatscher P, Oberhuber M, Pertot I, et al. 2022. Biogenic volatile organic compounds in the grapevine response to pathogens, beneficial microorganisms, resistance inducers, and abiotic factors. *J. Exp. Bot.* 73(2):529–54

93. Lee SC, Lee JW, Lee DH, Huh MJ, Nam I, et al. 2022. Identification of sex pheromone components of Korean *Dioryctria abietella* (Lepidoptera: Pyralidae) population and synergism of pheromone and pine cone volatile blends. *J. Econ. Entomol.* 115(1):178–86

94. Lerdau M, Gray D. 2003. Ecology and evolution of light-dependent and light-independent phytogenic volatile organic carbon. *New Phytol.* 157(2):199–211

95. Li Y, Zhao P, Yin C-Y, Liu X-X, Zhang Q-W. 2010. Attraction of *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) by several plant volatiles and aggregation pheromone. *Acta Entomol. Sin.* 53(7):734–40

96. Lin PA, Chen Y, Chaverra-Rodriguez D, Heu CC, Zainuddin NB, et al. 2021. Silencing the alarm: An insect salivary enzyme closes plant stomata and inhibits volatile release. *New Phytol.* 230(2):793–803

97. Maffei M. 2010. Sites of synthesis, biochemistry and functional role of plant volatiles. *S. Afr. J. Bot.* 76(4):612–31

98. Maoz I, Lewinsohn E, Gonda I. 2022. Amino acids metabolism as a source for aroma volatiles biosynthesis. *Curr. Opin. Plant Biol.* 67:102221

99. Martinez-Medina A, Flors V, Heil M, Mauch-Mani B, Pieterse CM, et al. 2016. Recognizing plant defense priming. *Trends Plant Sci.* 21(10):818–22

100. Matsui K. 2006. Green leaf volatiles: hydroperoxide lyase pathway of oxylipin metabolism. *Curr. Opin. Plant Biol.* 9:274–80

101. Matsui K, Sugimoto K, Mano J, Ozawa R, Takabayashi J. 2012. Differential metabolism of green leaf volatiles in injured and intact parts of a wounded leaf meet distinct ecophysiological requirements. *PLOS ONE* 7(4):e36433

102. Misztal P, Hewitt C, Wildt J, Blande J, Eller A, et al. 2015. Atmospheric benzenoid emissions from plants rival those from fossil fuels. *Sci. Rep.* 5(1):12064

103. Mita G, Quarta A, Fasano P, De Paolis A, Di Sansebastiano GP, et al. 2005. Molecular cloning and characterization of an almond 9-hydroperoxide lyase, a new CYP74 targeted to lipid bodies. *J. Exp. Bot.* 56(419):2321–33

104. Mizutani J. 1999. Selected allelochemicals. *Crit. Rev. Plant Sci.* 18(5):653–71

105. Monteith JL, Unsworth MH. 2013. Micrometeorology. In *Principles of Environmental Physics: Plant, Animals, and the Atmosphere*, ed. JL Monteith, MH Unsworth, pp. 289–320. Oxford, UK: Elsevier

106. Nakashima A, von Reuss SH, Tasaka H, Nomura M, Mochizuki S, et al. 2013. Traumatin- and dinortraumatin-containing galactolipids in *Arabidopsis*: their formation in tissue-disrupted leaves as counterparts of green leaf volatiles. *J. Biol. Chem.* 288(36):26078–88

107. Ninkovic V, Dahlin I, Vucetic A, Petrovic-Obradovic O, Glinwood R, Webster B. 2013. Volatile exchange between undamaged plants – a new mechanism affecting insect orientation in intercropping. *PLOS ONE* 8(7):e69431

108. Onosato H, Fujimoto G, Higami T, Sakamoto T, Yamada A, et al. 2022. Sustained defense response via volatile signaling and its epigenetic transcriptional regulation. *Plant Physiol.* 189(2):922–33

109. Paschold A, Halitschke R, Baldwin IT. 2006. Using "mute" plants to translate volatile signals. *Plant J.* 45:275–91

110. Pearse IS, Gee WS, Beck JJ. 2013. Headspace volatiles from 52 oak species advertise induction, species identity, and evolution, but not defense. *J. Chem. Ecol.* 39(1):90–100

111. Pearse IS, Porensky LM, Yang LH, Stanton ML, Karban R, et al. 2012. Complex consequences of herbivory and interplant cues in three annual plants. *PLOS ONE* 7(5):e38105

112. Pichersky E, Noel JP, Dudareva N. 2006. Biosynthesis of plant volatiles: nature's diversity and ingenuity. *Science* 311(5762):808–11

113. Pickett JA, Khan ZR. 2016. Plant volatile-mediated signalling and its application in agriculture: successes and challenges. *New Phytol.* 212(4):856–70

114. Pinto D, Blande J, Souza S, Nerg AM, Holopainen J. 2010. Plant volatile organic compounds (VOCs) in ozone (O_3) polluted atmospheres: the ecological effects. *J. Chem. Ecol.* 36(1):22–34

115. Poelman EH, Bruinsma M, Zhu F, Weldegergis BT, Boursault AE, et al. 2012. Hyperparasitoids use herbivore-induced plant volatiles to locate their parasitoid host. *PLOS Biol.* 10(11):e1001435

116. Preston CA, Laue G, Baldwin IT. 2001. Methyl jasmonate is blowing in the wind, but can it act as a plant-plant airborne signal? *Biochem. Syst. Ecol.* 29:1007–23

117. Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weis AE. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annu. Rev. Ecol. Syst.* 11:41–65

118. Qualley A, Dudareva N. 2008. Aromatic volatiles and their involvement in plant defense. In *Induced Plant Resistance to Herbivory*, ed. A Schaller, pp. 409–32. Dordrecht, Neth.: Springer

119. Radulović N, Denić M, Stojanović-Radić Z. 2010. Antimicrobial phenolic abietane diterpene from *Lycopus europaeus* L. (Lamiaceae). *Bioorg. Med. Chem. Lett.* 20(17):4988–91

120. Raguso RA. 2016. More lessons from linalool: insights gained from a ubiquitous floral volatile. *Curr. Opin. Plant Biol.* 32:31–36

121. Rasmann S, Köllner TG, Degenhardt J, Hiltpold I, Toepfer S, et al. 2005. Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature* 434(7034):732–37

122. Rhoades DF. 1983. Responses of alder and willow to attack by tent caterpillars and webworms: evidence for pheromonal sensitivity of willows. In *Plant Resistance to Insects*, ed. P Hedin, pp. 55–68. Washington, DC: Am. Chem. Soc.

123. Rodríguez-Concepción M. 2006. Early steps in isoprenoid biosynthesis: multilevel regulation of the supply of common precursors in plant cells. *Phytochem. Rev.* 5(1):1–15

124. Schiestl FP. 2010. The evolution of floral scent and insect chemical communication. *Ecol. Lett.* 13(5):643–56

125. Schmidt-Büsser D, von Arx M, Guerin P. 2009. Host plant volatiles serve to increase the response of male European grape berry moths, *Eupoecilia ambiguella*, to their sex pheromone. *J. Comp. Physiol. A* 195(9):853–64

126. Schowalter TD. 2022. Resource acquisition. In *Insect Ecology*, ed. TD Schowalter, pp. 93–162. Cambridge, MA: Academic. 5th ed.

127. Schuman MC, Allmann S, Baldwin IT. 2015. Plant defense phenotypes determine the consequences of volatile emission for individuals and neighbors. *eLife* 4(2008):e04490

128. Schuman MC, Baldwin IT. 2012. Asking the ecosystem if herbivory-inducible plant volatiles (HIPVs) have defensive functions. In *The Ecology of Plant Secondary Metabolites*, ed. GR Iason, M Dicke, SE Hartley, pp. 287–307. Cambridge, UK: Cambridge Univ. Press

129. Schuman MC, Baldwin IT. 2018. Field studies reveal functions of chemical mediators in plant interactions. *Chem. Soc. Rev.* 47(14):5338–53

130. Schuman MC, Barthel K, Baldwin IT. 2012. Herbivory-induced volatiles function as defenses increasing fitness of the native plant *Nicotiana attenuata* in nature. *eLife* 1(1):e00007

131. Schuman MC, Palmer-Young EC, Schmidt A, Gershenzon J, Baldwin IT. 2014. Ectopic terpene synthase expression enhances sesquiterpene emission in *Nicotiana attenuata* without altering defense or development of transgenic plants or neighbors. *Plant Physiol.* 166(2):779–97

132. Schuman MC, Valim HA, Joo Y. 2016. Temporal dynamics of plant volatiles: mechanistic bases and functional consequences. In *Deciphering Chemical Language of Plant Communication*, ed. JD Blande, R Glinwood, pp. 3–34. Cham, Switz.: Springer

133. Seigler D. 1998. *Plant Secondary Metabolism*. Boston: Springer

134. Selvaraj G. 2015. Flying whispers of inter-kingdom conversation: a complementary perspective of plant and bacterial volatile signals. *Adv. Bot. Res.* 75:285–310

135. Sharifi R, Ryu CM. 2021. Social networking in crop plants: wired and wireless cross-plant communications. *Plant Cell Environ.* 44(4):1095–110

136. Sharkey TD, Wiberley AE, Donohue AR. 2008. Isoprene emission from plants: why and how. *Ann. Bot.* 101(1):5–18

137. Shiojiri K, Kishimoto K, Ozawa R, Kugimiya S, Urashimo S, Arimura G. 2006. Changing green leaf volatile biosynthesis in plants: an approach for improving plant resistance against both herbivores and pathogens. *PNAS* 103(45):16672–76

138. Shiojiri K, Ozawa R, Kugimiya S, Uefune M, van Wijk M, et al. 2010. Herbivore-specific, density-dependent induction of plant volatiles: honest or "cry wolf" signals? *PLOS ONE* 5(8):e12161

139. Song J, Lee G, Jung J, Moon JK, Kim SG. 2022. Effect of soybean volatiles on the behavior of the bean bug, *Riptortus pedestris*. *J. Chem. Ecol.* 48(2):207–18

140. Sugimoto K, Matsui K, Iijima Y, Akakabe Y, Muramoto S, et al. 2014. Intake and transformation to a glycoside of (Z)-3-hexenol from infested neighbors reveals a mode of plant odor reception and defense. *PNAS* 111(19):7144–49

141. Sugimoto K, Matsui K, Takabayashi J. 2016. Uptake and conversion of volatile compounds in plant-plant communication. In *Deciphering Chemical Language of Plant Communication*, ed. JD Blande, R Glinwood, pp. 305–16. Signal. Commun. Plants. Cham, Switz.: Springer

142. Tissier A, Morgan JA, Dudareva N. 2017. Plant volatiles: going "in" but not "out" of trichome cavities. *Trends Plant Sci.* 22(11):930–38

143. Turlings TC, Erb M. 2018. Tritrophic interactions mediated by herbivore-induced plant volatiles: mechanisms, ecological relevance, and application potential. *Annu. Rev. Entomol.* 63:433–52

144. Turlings TC, Hiltpold I, Rasmann S. 2012. The importance of root-produced volatiles as foraging cues for entomopathogenic nematodes. *Plant Soil* 358(1):51–60

145. van de Schoot R, de Bruin J, Schram R, Zahedi P, de Boer J, et al. 2021. An open source machine learning framework for efficient and transparent systematic reviews. *Nat. Mach. Intell.* 3(2):125–33

146. Van Poecke RM, Posthumus MA, Dicke M. 2001. Herbivore-induced volatile production by *Arabidopsis thaliana* leads to attraction of the parasitoid *Cotesia rubecula*: chemical, behavioral, and gene-expression analysis. *J. Chem. Ecol.* 27(10):1911–28

147. Vancanneyt G, Sanz C, Farmaki T, Paneque M, Ortego F, et al. 2001. Hydroperoxide lyase depletion in transgenic potato plants leads to an increase in aphid performance. *PNAS* 98(14):8139–44

148. Vandermoten S, Mescher MC, Francis F, Haubruge E, Verheggen FJ. 2012. Aphid alarm pheromone: an overview of current knowledge on biosynthesis and functions. *Insect Biochem. Mol. Biol.* 42(3):155–63

149. Vet LEM, Dicke M. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 37:141–72

150. Vickers CE, Gershenzon J, Lerdau MT, Loreto F. 2009. A unified mechanism of action for volatile isoprenoids in plant abiotic stress. *Nat. Chem. Biol.* 5(5):283–91

151. Vogt T. 2010. Phenylpropanoid biosynthesis. *Mol. Plant* 3(1):2–20

152. Vucetic A, Dahlin I, Petrovic-Obradovic O, Glinwood R, Webster B, Ninkovic V. 2014. Volatile interaction between undamaged plants affects tritrophic interactions through changed plant volatile emission. *Plant Signal. Behav.* 9:e29517

153. Walter MH, Floss DS, Strack D. 2010. Apocarotenoids: hormones, mycorrhizal metabolites and aroma volatiles. *Planta* 232:1–17

154. Wang F, Deng J, Schal C, Lou Y, Zhou G, et al. 2016. Non-host plant volatiles disrupt sex pheromone communication in a specialist herbivore. *Sci. Rep.* 6(1):32666

155. Wasternack C. 2007. Jasmonates: an update on biosynthesis, signal transduction and action in plant stress response, growth and development. *Ann. Bot.* 100(4):681–97

156. Weber DC, Blackburn MB, Jaronski ST. 2022. Biological and behavioral control of potato insect pests. In *Insect Pests of Potato: Global Perspectives on Biology and Management*, ed. A Alyokhin, SI Rondon, Y Gao, pp. 231–76. London: Academic. 2nd ed.

157. Wegener R, Schulz S. 2002. Identification and synthesis of homoterpenoids emitted from elm leaves after elicitation by beetle eggs. *Tetrahedron* 58:315–19

158. Widhalm JR, Jaini R, Morgan JA, Dudareva N. 2015. Rethinking how volatiles are released from plant cells. *Trends Plant Sci.* 20:545–50

159. Wilson JK, Kessler A, Woods HA. 2015. Noisy communication via airborne infochemicals. *BioScience* 65(7):667–77

160. Wilson JK, Woods HA, Kessler A. 2018. High levels of abiotic noise in volatile organic compounds released by a desert perennial: implications for the evolution and ecology of airborne chemical communication. *Oecologia* 188(2):367–79

161. Yáñez-Serrano A, Fasbender L, Kreuzwieser J, Dubbert D, Haberstroh S, et al. 2018. Volatile diterpene emission by two Mediterranean *Cistaceae* shrubs. *Sci. Rep.* 8(1):6855

162. Yon F, Joo Y, Llorca LC, Rothe E, Baldwin IT, et al. 2016. Silencing *Nicotiana attenuata* LHY and ZTL alters circadian rhythms in flowers. *New Phytol.* 209:1058–66

163. Zhang C, Chen X, Lee RTC, T R, Maurer-Stroh S, Rühl M. 2021. Bioinformatics-aided identification, characterization and applications of mushroom linalool synthases. *Commun. Biol.* 4(1):223

164. Zu P, Boege K, Del-Val E, Schuman MC, Stevenson PC, et al. 2020. Information arms race explains plant-herbivore chemical communication in ecological communities. *Science* 368(6497):1377–81

165. Zu P-J, García-García R, Schuman MC, Saavedra S, Melián CJ. 2022. Plant–insect chemical communication in ecological communities: an information theory perspective. *J. Syst. Evol.* **https://doi.org/10.1111/jse.12841**