

Interactions of insect pheromones and plant semiochemicals

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Plant semiochemicals are known to produce a wide range of behavioral responses in insects. Some insects sequester or acquire host plant compounds and use them as sex pheromones or sex pheromone precursors. Other insects produce or release sex pheromones in response to specific host plant cues, and chemicals from host plants often synergistically enhance the response of an insect to sex pheromones. Plant volatiles can also have inhibitory or repellent effects that interrupt insect responses to pheromones and attract predators and parasitoids to the attacking species after herbivory injury. Here, we review different interactions between plant semiochemicals and insect pheromones, paying attention to those that can result in the development of more efficient and reliable programs for pest control.

Interactions between insect pheromones and semiochemicals (molecules that carry signals from one organism to another) from the host plant have been known for nearly as long as pheromones (substances secreted by an individual that induce a specific reaction in another individual of the same species) have been recognized as a key communication system within species. Such interactions are manifested as effects of the host plant on insect physiology and behavior, reflecting different types of insect strategies to optimize feeding, mating and reproduction [1]. Some insects acquire host plant chemicals to use them as sex pheromones or sex pheromone precursors. Other host plant volatiles can induce the production or release of

pheromones in certain insects and often synergize or enhance insect responses to sex pheromones. Host compounds can also have an inhibitory or repellent effect, interrupting the response of insects to their own pheromone. In other cases, host-derived compounds resulting from herbivorous attack can attract predators to the attacking insect and therefore serve as a defense mechanism for the plant. Here, we discuss various interactions between host semiochemicals and insect pheromones, and their ecological implications in terms of insect behavior, feeding and reproduction.

Plant stimulation of pheromone production

Host plants play a key role in the production and use of sex pheromones by herbivorous insects through larval or adult sequestration of chemically active compounds and pheromone precursors [2]. One of the best examples of sequestration of plant chemicals by larvae and their subsequent use by adult males in sex attraction or courtship interactions is shown in *Utetheisa ornatrix* (Arctiidae), whose courtship pheromone derives from pyrrolizidine alkaloids (PAs) ingested at the larval stage from the host plant *Crotalaria spectabilis* (Figure 1) [3]. *U. ornatrix* larvae sequester PAs (e.g. monocrotaline) and retain the alkaloids through metamorphosis into the adult stage to provide egg protection for the next generation. Females receive PAs from males during copulation and transmit the alkaloids together with their own load to the eggs [4]. PA sequestering species are found in the

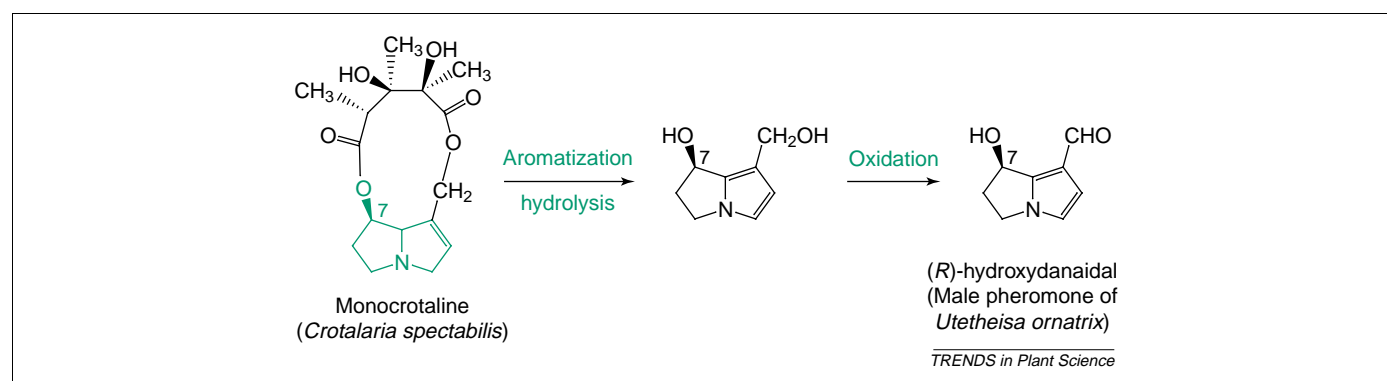


Figure 1. Example of acquisition of pheromone compounds from host plant precursors. Male *Utetheisa ornatrix* (Lepidoptera: Arctiidae) produces (R)-hydroxydanaidal from dietary pyrrolizidine alkaloids (e.g. monocrotaline) obtained by larvae from the host plant *Crotalaria spectabilis* [84].

Lepidoptera (many butterflies and moths), Coleoptera (some leaf beetles), Orthoptera (certain grasshoppers) and Homoptera (certain aphids), and are used as strong feeding deterrents against invertebrate predators such as spiders, ants, coccinellids and lacewings [2]. In addition, PAs are strongly hepatotoxic and pneumotoxic to vertebrates and genotoxic to insects [5]. PAs are stored and maintained in the form of the non-toxic oxides and, upon feeding, they are reduced in the gut and adsorbed as tertiary alkaloids. They can be detoxified by N-oxidation with a soluble NADPH-dependent flavin monooxygenase present in the hemolymph of PA-sequestering insects and used them as chemical defense [6] or can be bioactivated by microsomal liver cytochrome P450-dependent monooxygenases into unstable pyrrolic intermediates that are highly reactive alkylating agents [7]. In the case of the arctiid *Tyria jacobaeae*, PAs are oxidized in the hemolymph by senecionine N-oxygenase (SNO), a flavin-dependent monooxygenase (FMO) with high substrate specificity for PAs. Peptide microsequences obtained from purified *T. jacobaeae* SNO were used to clone the corresponding cDNA [8]. *T. jacobaeae* SNO possesses an N-terminal signal peptide characteristic of extracellular proteins and belongs to a large family of FMO-like sequences of mostly unknown function. The gene for *T. jacobaeae* SNO, highly specific for toxic PAs, was probably recruited from a pre-existing insect specific FMO gene family of unknown function [8].

Adult males can also obtain PAs from plants and use them as pheromone precursors. This happens in some arctiids, most Dancinae and Ithomiinae butterflies. *Cysseps fulvicollis* (Arctiidae) males produce hydroxydarnaldal from PAs of dead and damaged plants, and release it as a sex attractant [9]. The butterflies are attracted to PAs and ingest them with nectar or, most frequently, from dead parts or withered twigs of the plants [5]. These butterflies advertise their unpalatability to potential predators by conspicuous warning coloration. Conversion of plant PAs into the pheromone has been suggested to occur in *U. ornatrix* through aromatization of the dihydropyrrole ring of monocrotaline, followed by ester hydrolysis and oxidation [3] (Figure 1). It should be realized that the chiral *R* configuration of both the alkaloid precursor and the pheromone is maintained. This mechanism was confirmed by feeding labeled PA heliotrine to larvae of *Cretonotos transiens* [10] and in *Estigmene acrea* [11].

The acquisition of chemicals from plants and their use in a sexual context is also known for certain species of orchid bees and tephritid fruit flies. Male bees collect a mixture of terpenoids from orchids and use them as an aggregation pheromone to induce the formation of leks (sites where males compete for females) or as a sex pheromone that also attracts opportunistic males [12].

Host plant stimulation of pheromone biosynthesis by Lepidoptera has been reported in *Helicoverpa* spp. [13] Volatile organic chemicals (VOCs) from corn silk or tomatoes triggered sex pheromone production in female abdominal glands so that moths removed from the host do not exhibit reproductive activity, including production of sex pheromones.

Many species of beetles feed and mate on host plants as a result of attraction to sex pheromone. In the earliest

studies, the association between feeding and sex attraction suggested the acquisition of plant compounds and their use as pheromone or pheromone precursors by the insect. Thus, exposure to myrcene in the volatile headspace increased the amounts of ipsenol and ipsdienol in hindgut tissues of male *Ips paraconfusus* [14] and other *Dendroctonus* spp. [15] Application of ^2H -labeled myrcene and (–)- and (+)- α -pinene resulted in production of ^2H -ipsenol and ^2H ipsdienol and *cis*- and *trans*-verbenol [16] in hindguts of *I. paraconfusus*, providing convincing evidence of pheromone biosynthetic relationships in scolytids. The bioorganic reactions whereby monoterpenes are metabolized to oxygenated compounds are likely to involve P450 enzymes [17].

However, many studies of the endocrine regulation of pheromone production in scolytids foreshadowed the observation that pheromone compounds are often synthesized from short-chain metabolic building blocks rather than from host precursors. Strong evidence for *de novo* synthesis of isoprenoids by scolytids came from *in vivo* studies in which ipsenol, ipsdienol and amitinol in *I. paraconfusus* and ipsdienol and amitinol in *Ips pini* appeared to be labeled from ^{14}C -acetate [18,19] or ^{14}C -mevalonolactone [19]. As an alternative biosynthetic route to an aggregation pheromone component of *Dendroctonus frontalis*, a fatty-acid-like elongation of leucine or catabolism of leucine to acetyl-CoA followed by isoprenoid synthesis via 3-hydroxy-3-methylglutaryl-CoA (HMG-CoA) has been proposed [20].

Juvenile hormone III (JHIII) appears to play a central role as a regulator for pheromone production in Scolytidae. For instance, the HMG-CoA reductase (HMG-R) inhibitor compactin and the JH analog methoprene were used to offer indirect evidence that JH regulates *de novo* pheromone biosynthesis in male *Ips duplicatus* [21]. In ^{14}C -acetate- and ^{14}C -mevalonolactone-based experiments, *I. pini* was found to release JHIII in its corpora allata, and increasing topical JHIII dose resulted in an increase of radiolabeled acetate into ipsdienol [19]. This unequivocally demonstrated that JHIII regulates *de novo* pheromone production (Figure 2). However, incorporation of radiolabeled mevalonolactone into ipsdienol by this insect was unaffected by increasing JHIII dose, suggesting that JH primarily influences enzymes before mevalonate in this pathway [i.e. HMG-CoA synthase (HMG-S) and HMG-R] [22]. However, it is not clear whether JHIII alone is sufficient to upregulate *de novo* pheromone biosynthesis in all *Ips* spp. Comparative studies of *I. paraconfusus* and *I. pini* indicated: (a) that JHIII induces 150 times more of the main pheromone component (ipsdienol) in *I. pini* than of the main pheromone component (ipsenol) in *I. paraconfusus*; (b) that JHIII stimulates HMG-R activity in male *I. pini* but not in male *I. paraconfusus*; and (c) that JHIII induces similar increases in the transcript for HMG-R in both species [22]. It appears that, in *I. paraconfusus*, JHIII can act in concert with a second feeding-associated hormonal factor to activate HMG-R fully and that this factor does not appear to be necessary in *I. pini*. The difference of regulation of the *de novo* pheromone biosynthesis in these two closely related species of Scolytidae is surprising and represents a

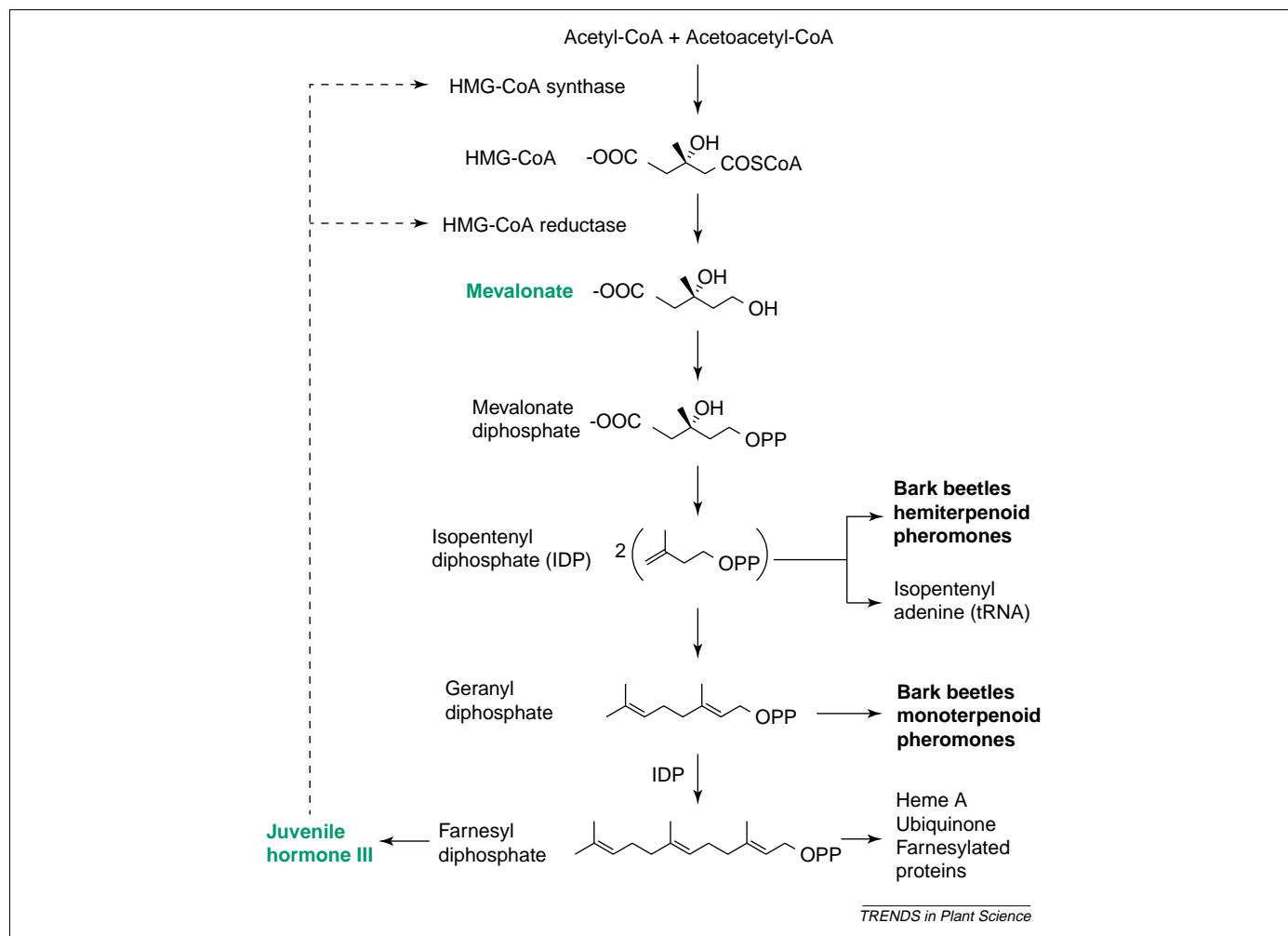


Figure 2. Isoprenoid biosynthetic pathway leading through mevalonate to hemiterpenoid (C_5) and monoterpene (C_{10}) pheromones in Scolytidae. The biosynthesis is regulated by juvenile hormone III [85]. Abbreviation: HMG-CoA, 3-hydroxy-3-methylglutaryl-CoA. Adapted from Ref. [22].

cautious note about the possibility of extrapolating pheromone regulation studies from one bark beetle to another [22].

Recently, northern blot experiments have shown that JHIII regulates HMG-R gene expression in a dose- and time-dependent manner in male *I. paraconfusus*, *I. pini* and *Dendroctonus jeffreyi* [23]. The expression of the gene encoding HMG-S in *D. jeffreyi* has also been demonstrated but the modest maximum expression levels (up to fourfold above non-induced level) for HMG-S obtained after JHIII treatment is consistent with the minor role played by HMG-S in regulating the mevalonate pathway [24]. However, our current understanding of the effects of JHIII and feeding on HMG-R and HMG-S is limited to the mRNA level and the HMG-R activity level, and we know little about the mechanism by which JHIII increases HMG-R transcription and mRNA stability, or the influence of JHIII on HMG-R protein localization, abundance and stability. Moreover, most of the progress in our knowledge of pheromone production in Scolytidae is based on only few species (*I. paraconfusus*, *I. pini* and *D. jeffreyi*), in comparison with nearly 6000 known species of Scolytidae. New biochemical and genomics approaches will be essential for a more complete understanding of how scolytids produce their pheromone components, thus

targeting key points for the control of these economically important insects. In this context, a comprehensive sequence tag database has been produced from a cDNA library of midguts from JHIII treated male *I. pini* [22].

Plant stimulation of pheromone release

Stimulation of pheromone release by plant volatiles occurs in many species of Coleoptera and Lepidoptera. In the Coleoptera, some beetle species, including the boll weevil *Anthonomus grandis* [25], are thought to release the pheromone after feeding on the host plant, but this has only been definitely proved in a few cases. However, it has been adequately documented that the oil palm *Elaeis guineensis*, a host of the African palm weevil *Rynchophorus phoenicis* (Curculionidae), produces a mixture of volatile esters from which ethyl acetate induces males to release the pheromone (E)-6-methyl-2-hepten-4-ol (rhyncophorol) [26]. This compound is not active in the field unless mixed with ethyl acetate or other host volatiles such as hexanal, iso-amyl acetate or isopentanol. In view of these results, traps baited with rhyncophorol, sugarcane and ethyl acetate have been recommended to control infestations by *R. phoenicis* [26,27]. In the Lepidoptera, there are only few studies on plant-volatile induction of pheromone release, probably because moths readily

Table 1. Examples of synergism of plant volatiles and aggregation pheromones

Host	Insect	Plant volatiles	Aggregation pheromone	Refs
Cotton	<i>Anthonomus grandis</i>	<i>Trans</i> -2-hexenol, <i>cis</i> -3-hexenol, <i>n</i> -hexanol	Grandisol, grandisal	[25]
Palm, sugarcane (<i>Saccharum officinarum</i>), pineapple, banana	<i>Metamasius hemipterus</i> <i>sericeus</i>	Ethyl esters	5-Methyl-4-nonanol, 2-methyl-4-heptanol	[67]
Apple, orange, stored grains, spices, seeds	<i>Carpophilus hemipterus</i>	Propanoic acid, butanoic acid, methanol, 2-propanol, <i>n</i> -heptanol, methyl butanoate, propanol	(2E,4E,6E,8E)-3,5,7-trimethyl-2,4,6,8-decatetraene	[68]
Cereal grain, flour	<i>Sitophilus oryzae</i>	Valeraldehyde, maltol, vanillin	Sitophinone	[69]
Palm	<i>Rhynchophorus phoenicis</i> , <i>Rhynchophorus vulneratus</i>	e.g. Alcohols and esters	3-Methyl-4-octanol, 4-methyl-5-nonanol (rynchophorol)	[70]
Palm	<i>Rhynchophorus cruentatus</i>	Ethyl acetate	5-Methyl-4-octanol (cruentol)	[71]
Wheat	<i>Carpophilus mutilatus</i>	Fermenting whole wheat bread dough	(3E,5E,7E)-5-Ethyl-7-methyl-3,5,7-undecatriene	[72]
Coconut, palm, banana	<i>Rhynchophorus palmarum</i>	Ethyl acetate	(2E)-2-Methyl-5-hepten-4-ol	[26]
Wheat	<i>Carpophilus obsoletus</i>	Propyl acetate	(2E,4E,6E,8E)-3,5,7-Trimethyl-2,4,6,8-undecatetraene	[73]
Palm	<i>Rhynchophorus phoenicis</i>	Palm tissue volatiles	Rhynchophorol	[64]
Palm	<i>Rhynchophorus ferrugineus</i>	Host plant volatiles	Ferrugineol (4-methyl-5-nonanol)	[74]
Oil palm (<i>Elaeis oleifera</i>)	<i>Oryctes rhinoceros</i>	Oil palm, fruit bunches	Ethyl-4-methyloctanoate	[75]
Coconut, palm, banana	<i>Rhynchophorus palmarum</i> , <i>Dynamis borassi</i>	Ethanol, ethyl acetate	Rhynchophorol	[27]
Palm, sugarcane	<i>Rhabdoscelus obscurus</i>	Ethyl acetate	2-Methyl-4-octanol, (2E)-6-methyl-2-hepten-4-ol, 2-methyl-4-heptanol	[76]
Fermenting aspen (<i>Populus tremula</i>) bark	<i>Drosophila borealis</i> , <i>Drosophila littoralis</i>	Host odors	Ethyl tiglate	[77]

deliver pheromone molecules even in the absence of host volatiles. Cases have been reported in which females are stimulated to release sex pheromones by the presence of pollen from the host [28] or by volatiles from the plant on which they then release the sex pheromone to attract males [29]. Some female moths deposit their pheromone on leaf surfaces, where they are adsorbed and then re-released [30]. Depositing pheromones on leaf surfaces can make the attractant signal easier to track for males by slowing down the release rate to the atmosphere and increasing the amplitude of the pheromone plume [30].

Elicitation of a pheromone behavior by plant volatiles: synergism

Host plant volatiles can also evoke a positive effect on the behavior of insects responding to sex pheromones released in association with the host plant. This effect can result in synergism in which the response to the mixture of pheromone and plant volatiles is greater than the combined responses to the individual components. Synergism between plant semiochemicals and pheromones can contribute to more successful mate finding and therefore it is likely to play an important role in reproductive isolation. Host odor enhancement of attraction responses to pheromones occurs in several insect orders (Tables 1,2). In the Coleoptera, enhancement of an insect pheromone response by green leaf volatiles (GLVs) (blends of six-carbon alcohols, aldehydes and esters produced by plants as a result of oxidative degradation of surface lipids) was first reported in 1989 [25]. There was a remarkable increase in catches of the boll weevil *A. grandis* when traps were baited with *trans*-2-hexen-1-ol, *cis*-3-hexen-1-ol or 1-hexanol paired with the boll weevil aggregation

pheromone. Moreover, *trans*-2-hexen-1-ol also extended the longevity of attractiveness of pheromone-baited traps [25]. Males and females of *Anaglyptus subfasciatus* (Cerambycidae), one of the most harmful forest pests in Japan, are attracted to the Japanese cedar *Cryptomeria japonica* and the Japanese cypress *Chamaecyparis obtuse* for feeding [31]. Mixtures of one of the host floral constituents, methyl phenyl acetate, with the male-released pheromone were significantly more attractive to females than the pheromone or the ester alone.

Bark beetles convert host plant terpenes into oxygenated products that can serve as aggregation pheromones [32]. When host kairomones (chemicals released from one organism that induce an adaptively favorable response by an individual of another species) are released in combination with these pheromones, there can be a synergistic or additive effect. One of the first reports of such an effect is the synergistic action of α -pinene, a major host monoterpene in southern yellow pine (*Pinus* spp.), on frontalin, the primary component of the aggregation pheromone of the southern pine beetle *D. frontalis*, to stimulate mass attack [33]. Other cases have also been found (Table 1). In the European cockchafer, *Melolontha melolontha*, the sex pheromone toluquinone *per se* was not attractive to males in funnel traps. However, when it was mixed with GLVs mimicking the bouquet of mechanically damaged leaves, the activity of the lure was synergistically enhanced [34]. This is the first report in which a sex pheromone of a scarab beetle required the concomitant presence of GLVs to be active.

In the Lepidoptera, several cases of synergism have been noticed both in the laboratory and in the field (Table 2). For instance, mixtures of GLVs from cabbage (*Brassica oleracea*)

Table 2. Examples of synergism of plant volatiles and sex pheromones

Host	Insect	Plant volatiles	Sex pheromone	Refs
<i>Zea mays</i>	<i>Helicoverpa zea</i>	(Z)-3-hexenyl acetate	(Z)-11-hexadecenal, (Z)-11-hexadecenol, (Z)-9-hexadecenal, (Z)-7-hexadecenal, hexadecanal	[78]
<i>Zea mays</i>	<i>Cydia pomonella</i>	(Z)-3-hexenyl acetate	(E,E)-8,10-dodecadienol (codlemone)	[78]
<i>Beta vulgaris</i>	<i>Spodoptera exigua</i>	Linalool, myrcene benzaldehyde	(Z,E)-9,12-tetradecadienyl acetate, (Z)-9-tetradecenol	[79]
<i>Prunus padus</i>	<i>Rhopalosiphum padi</i>	Benzaldehyde	Nepetalactol	[80]
Japanese cedar (<i>Cryptomeria japonica</i>), Japanese cypress (<i>Chamaecyparis obtuse</i>)	<i>Anaglyptus subfasciatus</i>	Methyl phenyl acetate	(R)-3-hydroxy-2-hexanone, (R)-3-hydroxy-2-octanone	[31]
<i>Brassica oleracea</i> subsp. <i>capitata</i>	<i>Plutella xylostella</i>	(Z)-3-hexenyl acetate, (E)-2-hexenal, (Z)-3-hexenol	(Z)-11-Hexadecenal, (Z)-11-hexadecenyl acetate, (Z)-11-hexadecenol	[36]
Pine	<i>Pissodes nemorensis</i>	Pine bolt odors	Grandisol, grandisal	[81]
Papaya	<i>Toxotrypana curvicauda</i>	Host fruit odors	2-Methyl-6-vinylpyrazine	[82]
Cotton, tobacco, tomato	<i>Heliothis virescens</i>	(Z)-3-Hexenyl acetate	(Z)-11-Hexadecenal, (Z)-9-tetradecenal, hexadecanal, tetradecanal	[83]

and the pheromone [a mixture of (Z)-11-hexadecenal, (Z)-11-hexadecenyl acetate, (Z)-11-hexadecenol] induced a significantly higher attractant and arresting behavior in unmated males of the diamondback moth *Plutella xylostella* than the pheromone alone [35]. Field baits of (Z)-3-hexenyl acetate and the pheromone enhanced the number of females caught in traps severalfold over those baited with the natural attractant alone [36]. An important question remaining to be answered refers to the specificity of plant signals. Many of the compounds listed in Tables 1 and 2 are commonly found in different host and non-host plants. Therefore, it is expected that blends of these chemicals with specific pheromone components should have a precise composition to provide the required specificity to elicit a particular behavior on the insect. In any case, we know little about how insect responses to plant stimuli aid the insect in its efforts to mate and reproduce, but it is likely that these types of synergistic interactions are insect (male or female) strategies to optimize mating opportunities.

Semiochemically induced repellent effect

Host location is frequently the result of chemical and/or visual cues. This implies that insects are able to detect a suitable host while in flight and also that host selection can depend on a lack of repellency. Host compounds can also have an inhibitory or repellent effect in addition to their action as primary attractants, pheromone precursors and pheromone synergists. However, in contrast to the well documented attractant or synergistic nature of many chemicals, the repellent or inhibitory effects of other semiochemicals from the host have been largely overlooked and merit further investigation. A representative example is 4-allyl anisole, a common compound produced by loblolly pine (*Pinus taeda*) and other conifer species, which significantly reduced the response of *D. frontalis* to their own pheromone when simultaneously released with the natural attractant in the field [37].

Non-host GLVs have also been shown to inhibit the pheromone responses of several bark beetles [38–41]. The active non-host GLVs might act as negative signals at the habitat level for conifer bark beetles when they are seeking hosts. It is more beneficial for these beetles to be

able to recognize and avoid a general volatile signal that is commonly emitted by a wide range of non-host deciduous tree species than to recognize precise species-specific volatiles for each non-host species. In this way, several species of non-host trees with partially overlapping blends of common volatile compounds could be perceived and avoided during the host selection process [42]. A noteworthy example is shown by the pine shoot beetle *Tomicus destruens* (Coleoptera: Scolytidae), an important pine pest widely distributed throughout Europe. Benzyl alcohol, a semiochemical present in fennel extracts and in the callus of *Eucalyptus radiata* but completely absent from pine volatiles of leaves and twigs, induced beetles to bore a limited number of galleries when the chemical was deposited in the field on cut pine logs [43]. These results could have important implications for the control of pine shoot beetles by excluding them from potential hosts or regulating attack densities to unsuitable levels for tree colonization [43].

Plant volatiles released by attack of insect herbivores

The frass (solid larval insect excrement) or pheromones produced by herbivorous insects can provide predators and parasitoids with chemical signals that orient them to suitable hosts. Similarly, many parasitoids and predators orient towards plant odors, including specific chemical signals released following feeding by herbivores [44]. These compounds, which include monoterpenes, sesquiterpenes, homoterpenes, aromatic compounds and GLVs, often serve as a plant defense mechanism by attracting predators and parasitoids to the attacking pest species, thereby reducing further damage to the plant. For instance, (Z)-3-hexenyl esters that are emitted by tobacco after damage were found to deter female *Heliothis virescens* from laying eggs on injured plants [45], and some GLVs of cabbage attract the parasitoids *Trichogramma chilonis* and *Cotesia plutellae* and the predator *Chrysoperla carnea*, to the diamondback moth *P. xylostella*, an important cabbage pest, in a similar manner to the effect of the sex pheromone [35]. The major hosts of the bark beetles *I. pini* and *Ips grandicollis* (*Pinus resinosa*, *Pinus banksiana* and *Pinus strobus*) contain monoterpenes as their predominant phytochemical volatiles. Although

monoterpenes by themselves do not attract predators, some of them significantly affect predator attraction to aggregation pheromones. This is the case for α -pinene, which enhanced the attraction of some predators to the pheromone of their corresponding *Ips* prey [46]. Moreover, the predator responses can be modulated by the absolute configuration of the monoterpene, and thus (+)- α -pinene synergized predator responses to the pheromone of *I. pini*, whereas (-)- α -pinene synergized responses to the pheromone of *I. grandicollis* [46]. These results appear to confirm the proposal that the chiral specificity of bark beetle pheromones might have evolved partly as a response to predator recognition [47].

In many cases, the volatile compounds emitted from leaves as a result of insect damage allow insect parasitoids and predators to distinguish between infested and uninfested plants, and therefore help to locate hosts or prey [48]. This is the case for Lima bean (*Phaseolus lunatus*) plants and apple trees, which produce volatiles that attract predatory mites when damaged by spider mites [49], and for corn and cotton plants, which release substances when damaged that attract hymenopterous parasitoids that attack larvae of several species of Lepidoptera [50].

In all plants reported so far, there are remarkable similarities in the structure of VOCs that are emitted from insect-damaged leaves [51]. This structural uniformity suggests the activation of a common set of biosynthetic pathways shared by a wide range of plants, and that the products are detectable by a broad spectrum of insect parasitoids and predators. The ability of host-seeking insects to recognize and respond to such chemical cues and to distinguish them from background odors indicates that herbivory-injured plants emit volatiles that are clearly distinguishable from those released in response to other types of damage or those released from undamaged plants. Therefore, the plant's ability to differentiate between herbivore damage and a general wound response suggests the presence of elicitors associated with insect feeding [51]. In many plants (e.g. cotton, tobacco), these elicitors induce the emission of higher concentrations of induced volatiles that are synthesized in response to caterpillar feeding than to mechanical damage alone. Only two oral secretion products from chewing insects have been identified so far. A β -glucosidase present in the regurgitant of *Pieris brassicae* caterpillars has the same effect on mechanically damaged cabbage leaves as the caterpillar feeding – the emission of a similar bouquet of volatiles and the attraction of the parasitoid wasp *Cotesia glomerata* [52]. The protein appears to be an elicitor of the defense response of cabbage plants to herbivory injury, inducing the emission of volatiles that are used by parasitoids of the herbivore to locate their victim. Similarly, a fatty acid derivative of glutamine, N-[17-(*S*)-hydroxylinolenoyl]-L-glutamine (also called volicitin) has been identified from oral secretions of beet armyworm *Spodoptera exigua* caterpillars that induces corn seedlings to release the same blend of volatile terpenoids and indole as when they are damaged by caterpillar feeding [53]. This blend of chemicals attracts females of the parasitic wasp *Cotesia marginiventris*, natural enemies of the armyworm caterpillars, to the damaged corn plants.

Although larval feeding is known to elicit VOCs in many plants, herbivore oviposition has only recently been shown to induce VOCs as an indirect defense mechanism. In elm, oviposition by the elm leaf beetle *Xanthogaleruca luteola* (Coleoptera: Chrysomelidae) induces the release of volatiles that are attractive to the egg parasitoid *Oomyzus gallerucae* [54]. Neither artificial damage nor damage by feeding of non-ovipositing elm leaf beetles induces elm leaves to produce volatiles that attract the parasitoid. The nature of the elicitor has not been identified but jasmonic acid (JA), a known mediator of plant responses induced by feeding of herbivorous insects [44], has been demonstrated to mediate production of chemicals that attract the egg parasitoid [54]. A novel type of indirect defense response in peas has been elicited by bruchins, long chain diols esterified as 3-hydroxypropanoates. These compounds are found in pea and cowpea weevils, and elicit neoplastic growth at the oviposition site in certain genotypes of peas [55]. The neoplastic growth expels the recently hatched larvae out of the oviposition site and forces them to re-burrow into the pea pod. The young larvae are then exposed to predators, parasites and desiccation.

The North America tobacco plant *Nicotiana attenuata* shows a massive metabolic commitment to nicotine production in response to herbivorous attack, particularly from the specialized tobacco hornworm *Manduca sexta*. The nicotine is produced and distributed throughout the plant in a manner that optimizes plant fitness [56]. Nicotine is one of the most broadly effective plant defense metabolites known because it poisons acetylcholine receptors and is thus toxic to most heterotrophic organisms with neuromuscular junctions. When attacked by a nicotine-tolerant insect, the plant 'recognizes' the attack, as evidenced by an endogenous JA burst that is propagated through the damaged leaf ahead of the rapidly foraging herbivore [57]. JA treatment dramatically increases direct defenses, including the production of toxins (e.g. nicotine, phenolics, flavonoids), antidigestive proteins (e.g. proteinase inhibitors) and antinutritive enzymes (e.g. polyphenol oxidases), and, in addition, the plant emits a range of VOCs as an indirect defense [58]. Nicotine is biosynthesized from the polyamine putrescine, and putrescine *N*-methyltransferase (PMT) catalyzes the *N*-methylation of putrescine in the first, probably regulatory, step of nicotine biosynthesis. The wound-induced transcription of two *N. attenuata* PMT genes (*NaPMT1* and *NaPMT2*) is suppressed by the attack of *Manduca* larvae but the release of VOCs is maintained [59]. Accumulation of nicotine is also suppressed and the defense process is mediated by a dramatic burst of ethylene. Ethylene directly suppresses biosynthesis of nicotine, reduces the fitness cost of JA-induced resistance and optimizes resource allocation [60].

Herbivore-induced indirect defenses are not only a laboratory phenomenon. A recent study in nature on *N. attenuata* plants growing in natural conditions demonstrated that the VOCs *cis*-3-hexenol, linalool and *cis*- α -bergamotene increased egg predation rates by a generalist predator, whereas linalool and the complete blend of VOCs decreased lepidopteran oviposition rates. As a result, the release of VOCs, which mediates both effects

(predator attraction and oviposition avoidance), is estimated to reduce potential herbivore attacks by more than 90% [61].

Conclusions

The behavior of herbivorous insects is often integrated with their host plants in a range of ways. This integration can be apparent from the effects induced by host plants on insect physiology and behavior, including reproduction, and by the plant defense responses to an attacking insect. Particularly important are the effects of host plants on pheromone behavior, which appear to be part of male strategies (to maximize encounters with females) as well as female strategies (to gain access to new feeding and oviposition sites). The enhancement of sex attraction induced by host odors suggests that more effective traps can be devised for the management of insect pests. Lures based solely on synthetic pheromones are unlikely to be fully competitive with signals emanating from food or plants. Based on this strategy, the development of new lures for the Japanese beetle [62], the dried-fruit beetle *Carpophilus lugubris* [63], the palm weevil *R. phoenicis* [64] and several species of bark beetles [65] is worthy of note. Moreover, it has been suggested that mating disruption dispensers could be developed for certain moth species using small amounts of expensive active pheromonal ingredients by adding small amounts of selected inexpensive plant volatiles to the pheromone blend [66]. However, to our knowledge, this possibility has not yet been experimentally proved. In addition, the synergism between insect pheromones and plant odors can increase the attraction of natural enemies, offering new strategies for biological control. New research in this area will shed light on this and other issues relevant for the development of more effective and reliable pest control programs.

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