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REVIEW PAPER

The ethological significance and olfactory detection of herbivore-induced plant volatiles in interactions of plants, herbivorous insects, and parasitoids

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Abstract

Tritrophic interactions play a pivotal role in maintaining a functional agroecosystem. After damaged by phytophagous insects, host plants release a blend of odorants called herbivore-induced plant volatiles (HIPVs) that are attractive to natural enemies including arthropod predators and, in particular, parasitoids. In the last three decades, the identities of HIPVs have been meticulously characterized in a variety of tritrophic systems by gas chromatography–mass spectrometry (GC–MS) analysis. A plethora of HIPV components have been physiologically screened by gas chromatography-electroantennogram detection (GC-EAD) and single sensillum recording (SSR). The effects of induced odorants on behavior of herbivores and parasitoids have been investigated using Y-tube olfactometer assays and wind tunnels in the laboratory and bait trap tests in the field. Given the potential utility of parasitic wasps for pest control, the understanding of olfactory mechanisms of how HIPVs are detected by herbivores and parasitic wasps could facilitate the exploitation of parasitoids as bio-control agents. As the advent of the genome sequencing and transcriptome analysis, a large repertoire of chemosensory protein genes including odorant receptors and odorant binding proteins has been identified in herbivores and parasitic wasps, providing an unprecedented opportunity to debunk the molecular basis of olfaction-based interactions. In this review, we will summarize the recent progresses in characterization of HIPVs, the studies of olfactory mechanisms underlying tritrophic interactions with a focus on parasitoids, Lepidopteran pests, and related host plants.

Keywords Herbivore-induced plant volatiles · Herbivore · Odorant binding proteins · Odorant receptors · Parasitoid

Retrospect of researches on herbivore-induced plant volatiles (HIPVs) in a tritrophic context

The theory of tritrophic interactions was envisioned by Price et al. (1980) to describe the mutual communications between three modalities: plants, herbivores, and the associated natural enemies including arthropod predators and parasitoids (Price et al. 1980). Since then, the effects of herbivore-induced plant volatiles (HIPV) have been extensively investigated for the attraction of predators and parasitoids of the inducing herbivores. Pioneering studies using lima bean plants–spider mites–carnivorous mites (*Phaseolus lunatus* [L.] Fabaceae-*Tetranychus urticae* Koch, Acari, Tetranychidae-*Phytoseiulus persimilis* Athiot, Mesostigmata, Phytoseiidae) (Dicke 1986, 1988), tomato–corn earworm–parasitoid wasps (*Solanum lycopersicon* [L.] Solanaceae-*Helicoverpa zea* Boddie, Lepidoptera, Noctuidae-*Trichogramma pretiosum* Riley, Hymenoptera, Trichogrammatidae) (Nordlund et al. 1985, 1987, 1988), and cotton–tobacco budworm–parasitoid wasps (*Gossypium hirsutum* [L.] Malvaceae-*Heliothis virescens* Fab, Lepidoptera, Noctuidae-*Campoletis sonorensis* Cameron, Hymenoptera, Ichneumonidae) (Vinson et al. 1984, 1987) provided substantial chemi-ecological underpinnings for indirect defenses of plants in tritrophic interactions. Two seminal works systematically identified the blend of volatiles emitted by herbivore-infested plants that actively recruit natural enemies of the herbivores, predatory mite *P. persimilis* (Dicke et al. 1990), and parasitoid *Cotesia marginiventris* Cresson (Hymenoptera, Braconidae) (Turlings

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et al. 1990b), providing the add-on chemical evidence for tritrophic interactions. From 1990 onward, numerous tritrophic systems have been studied in depth, unleashing an avalanche of reports about "infochemicals" that actively attract parasitoids to the host-infested plants (Turlings et al. 1995; Vet and Dicke 1992; Turlings and Tumlinson 1992; De Moraes et al. 1998; Kessler and Baldwin 2001; D'Alessandro and Turlings 2006; Hare 2011; Lucas-Barbosa et al. 2011; Clavijo McCormick et al. 2012; Aartsma et al. 2017; Turlings and Erb 2018). Meanwhile, the enhancement of performance of predators and parasitoids by host plants volatiles galvanized pest control researchers as an indirect defense approach of plants (Dicke and Sabelis 1987; Turlings et al. 1990a; Baldwin 1998; Karban et al. 1999; Paré and Tumlinson 1999; Thaler 1999; Loon et al. 2000; Kessler and Baldwin 2001, 2002; Dicke et al. 2003, 2009; Kessler et al. 2004; Arimura et al. 2005; Bruinsma and Dicke 2008; Heil 2008; Dicke and Baldwin 2010; Hare 2011; War et al. 2012; Dicke 2016).

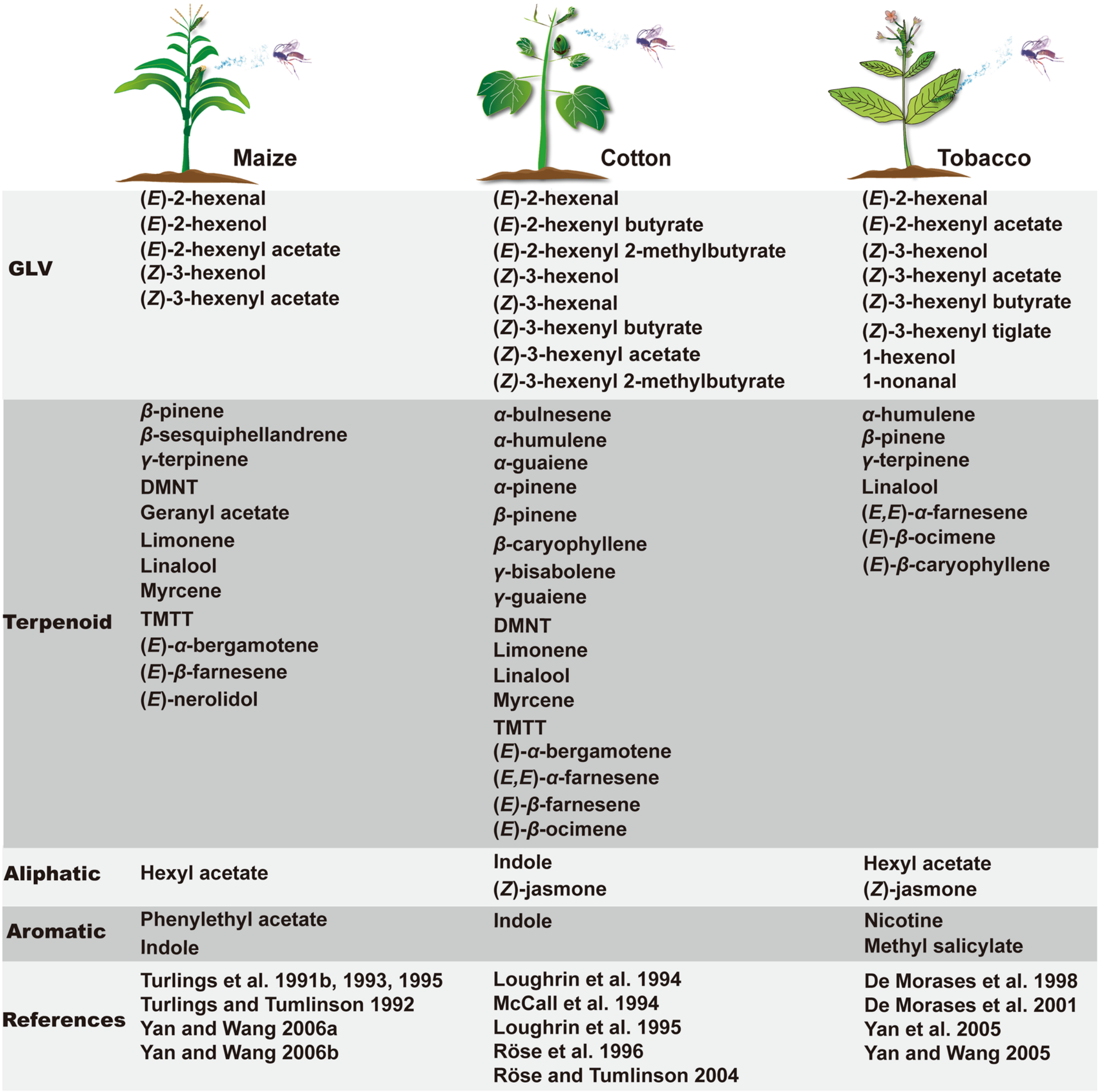
Parallelly, the studies of the molecular pathways triggering plant defense systems to release HIPVs have been carried out (Kessler and Baldwin 2002; Dicke et al. 2009; Arimura et al. 2009; Wu and Baldwin 2009; Holopainen and Gershenzon 2010; Baldwin 2010; Erb et al. 2012; Aljbory and Chen 2018). Volicitin [*N*-(17-hydroxylinolenoyl)-ʟ-glutamine], a fatty acid–amino acid conjugate, is one of important elicitors of plant resistance identified from the regurgitant of the beet armyworm *Spodoptera exigua* Hübner (Lepidoptera, Noctuidae) (Alborn et al. 1997; Turlings et al. 2000). Other elicitors encompassing enzymes (lipase, pectinase, β-glucosidase, and glucose oxidase), fatty acid–amino acid conjugates (FACs), peptides, esters, disulfooxy fatty acids, and debris of cell walls have been uncovered (Alborn et al. 1997, 2007; Doss et al. 2000; Kessler and Baldwin 2002; Schmelz et al. 2006; Erb et al. 2012; Aljbory and Chen 2018). The activation of nitric oxide and phytohormones, such as salicylic acids (Klessig et al. 2000; Bari and Jones 2009), jasmonic acid (Thaler et al. 2002; Schmelz et al. 2003a; Lou and Baldwin 2003; Lou et al. 2005; Bari and Jones 2009; Xin et al. 2012), and ethylene (O'Donnell et al. 1996; Kahl et al. 2000; Bari and Jones 2009; Lu et al. 2014), by the aforementioned elicitors results in the synthesis and emission of HIPVs. From late 1990s, field tests also provided ample evidence for the existence of tritrophic interactions, and the application of elicitors to enhance plant resistance in agriculture has been envisioned and discussed (Scutareanu et al. 1997; De Moraes et al. 1998; Thaler 1999; Kessler and Baldwin 2001; Poelman et al. 2009).

Moreover, the association between HIPVs and rewards, such as oviposition success, provides an unprecedented opportunity for studying associative learning using parasitoids as model organisms (Vet and Groenewold 1990; Vet and Dicke 1992; Turlings et al. 1993; Vet et al. 1995). Unambiguously, olfaction plays an essential role in fulfilling tritrophic interactions. However, the molecular dissection of neuronal substrates in the olfactory detection of HIPVs in herbivores and parasitoids are much lagged behind. In this review, we will summarize the progresses in investigations on the ethological significance and the olfactory detection of HIPVs with a focus on herbivorous insects and parasitoids.

The chemistry of HIPVs

The identities of HIPVs have been characterized for many host plant species, especially some crops, such as maize, cotton, and tobacco, by using gas chromatography-mass spectrometry (GC–MS) analysis (Table 1) (Turlings et al. 1990b, 2005; Loughrin et al. 1994, 1995; McCall et al. 1994; Röse et al. 1996; Yan et al. 2005; Yan and Wang 2006a). Different plant species and varieties release distinctive HIPV profiles after infestation by herbivores (Buttery et al. 1988; Chang et al. 1988; Loughrin et al. 1990; Turlings et al. 1990b, 1993, 1995; McCall et al. 1994; Yan et al. 2005; Röse and Tumlinson 2004; Addesso et al. 2010; Silva et al. 2017). HIPVs are typically composed by green leaf volatiles (GLVs), terpenoid, aliphatic and aromatic compounds. GLVs are a series of volatile components produced by green plants as a result of oxidative degradation of leaf lipids, encompassing a variety of 6-carbon alcohols, aldehydes, and esters (Dudareva 2004; Hassan et al. 2015). GLVs are not strictly HIPVs, since they are also constitutively released from healthy and mechanically damaged plants and the release is typically not an induced response (Loughrin et al. 1994; Holopainen 2004). Three kinds of GLVs, (*Z*)-3-hexenol, (*Z*)-3-hexenyl acetate, and (*E*)-2-hexenal, are shared in this group of HIPVs emitted by maize, cotton, and tobacco. Terpenoids are usually considered to be a major group of chemicals released from damaged plants. Tobacco infested by caterpillars emitted a different spectrum of terpenoids compared with the ones released from infested maize and cotton (McCall et al. 1994; Loughrin et al. 1995; Yan et al. 2005; Yan and Wang 2006a, b) (Table 1). The tremendous diversity and variability of terpenoids in the emissions released by different plant species and even different cultivars/varieties of the same plant species may serve as a hallmark for parasitoids to efficiently locate the appropriate host-infested plants (Turlings and Ton 2006; Mumm et al. 2008). For instance, (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) is released from damaged plants of maize, cotton, lima bean, and pepper plants in large quantity (Turlings et al. 1993; Loughrin et al. 1995; Arimura et al. 2000; Yan and Wang 2006a; Addesso et al. 2010; Tamiru et al. 2015). Around one quarter of total amount of HIPVs released by maize *Zea mays* (L.) 'Zhongdan-306' (Poaceae) after infestation by the larvae of *Helicoverpa armigera* Hübner or *Mythimna separata* Walker (Lepidoptera, Noctuidae) is DMNT (Yan and Wang

Table 1 Classification of compounds of herbivore-induced plants volatiles released by maize infested by larvae of *Spodoptera exigua* (Turlings and Tumlinson 1992; Turlings et al. 1991b, 1993, 1995), *Mythimna separata* (Yan and Wang 2006a), *Pseudaletia separata* (Yan and Wang 2006b) and *Helicoverpa armigera* (Yan and Wang 2006b); cotton plants infested by larvae of *Helicoverpa zea* (McCall et al. 1994; Röse and Tumlinson 2004) and *Spodoptera exigua* (Loughrin et al. 1994, 1995; Röse et al. 1996); tobacco infested by *Helicoverpa zea* (De Moraes et al. 1998), *Heliothis virescens* (De Moraes et al. 1998, 2001), and *Helicoverpa armigera* (Yan et al. 2005)



	Maize	Cotton	Tobacco
GLV	(*E*)-2-hexenal (*E*)-2-hexenol (*E*)-2-hexenyl acetate (*Z*)-3-hexenol (*Z*)-3-hexenyl acetate	(*E*)-2-hexenal (*E*)-2-hexenyl butyrate (*E*)-2-hexenyl 2-methylbutyrate (*Z*)-3-hexenol (*Z*)-3-hexenal (*Z*)-3-hexenyl butyrate (*Z*)-3-hexenyl acetate (*Z*)-3-hexenyl 2-methylbutyrate	(*E*)-2-hexenal (*E*)-2-hexenyl acetate (*Z*)-3-hexenol (*Z*)-3-hexenyl acetate (*Z*)-3-hexenyl butyrate (*Z*)-3-hexenyl tiglate 1-hexenol 1-nonanal
Terpenoid	*β*-pinene *β*-sesquiphellandrene *γ*-terpinene DMNT Geranyl acetate Limonene Linalool Myrcene TMTT (*E*)-*α*-bergamotene (*E*)-*β*-farnesene (*E*)-nerolidol	*α*-bulnesene *α*-humulene *α*-guaiene *α*-pinene *β*-pinene *β*-caryophyllene *γ*-bisabolene *γ*-guaiene DMNT Limonene Linalool Myrcene TMTT (*E*)-*α*-bergamotene (*E,E*)-*α*-farnesene (*E*)-*β*-farnesene (*E*)-*β*-ocimene	*α*-humulene *β*-pinene *γ*-terpinene Linalool (*E,E*)-*α*-farnesene (*E*)-*β*-ocimene (*E*)-*β*-caryophyllene
Aliphatic	Hexyl acetate	Indole (*Z*)-jasmone	Hexyl acetate (*Z*)-jasmone
Aromatic	Phenylethyl acetate Indole	Indole	Nicotine Methyl salicylate
References	Turlings et al. 1991b, 1993, 1995 Turlings and Tumlinson 1992 Yan and Wang 2006a Yan and Wang 2006b	Loughrin et al. 1994 McCall et al. 1994 Loughrin et al. 1995 Röse et al. 1996 Röse and Tumlinson 2004	De Moraes et al. 1998 De Moraes et al. 2001 Yan et al. 2005 Yan and Wang 2005

DMNT: (*E*)-4,8-dimethyl-1,3,7-nonatriene; TMTT: (*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene; *GLV* green leaf volatiles

2006a). However, DMNT is not found in the emissions of caterpillar-infested tobacco *Nicotiana tabacum* (L.) 'K326' (Solanaceae) (De Moraes et al. 2001). Moreover, *β*-pinene and linalool are the shared two terpenoids in HIPVs of different cultivars of maize, cotton, and tobacco damaged by noctuid caterpillars. However, they appear to have different valences to cause the behavioral changes as linalool is attractive to the generalist parasitoid *Campoletis chlorideae* Uchida (Hymenoptera, Ichneumonidae), but *β*-pinene is not (Loughrin et al. 1994; Yan et al. 2005; Yan and Wang 2006b). Interestingly, *β*-pinene is effective in orienting the specialist parasitoid, *Microplitis croceipes* Cresson (Hymenoptera, Braconidae), to infested cotton, *G. hirsutum* 'max 9' (Morawo and Fadamiro 2016). This suggests that sympatrically occurring parasitoid species indeed differentially read the same HIPV component to find their respective host larvae-infested plants.

The volatile blend of the same plant species, when infested by closely related herbivory species, usually shows a high degree of similarity in constituted components, but the proportions of the shared components have differences (Turlings et al.1993; Ngumbi et al. 2009). For instance, the composition of HIPVs is not qualitatively different between *H. virescens*-infested and *S. exigua*-infested cotton plants, but significant differences in the ratios of HIPV components have been discovered (Ngumbi et al. 2009). However, (*Z*)-jasmone, (*E*)-*β*-farnesene, and (*E,E*)-*α*-farnesene are released by cotton plants damaged by *S. exigua* (Loughrin et al. 1995) but not emitted by cotton plants infested by *H. zea* (McCall et al. 1994). Such differences may derive from the different cultivars of *G. hirsutum* 'McNair 235' and 'Delta Pineland 90' used in the two aforementioned studies. The HIPVs emitted from different cultivars or varieties of the same plant species could be quite distinctive in quality and quantity (Loughrin et al. 1995; Degen et al. 2004, 2012; Hare 2007; Schuman et al. 2009; Tamiru et al. 2011; Bruce 2014). For instance, the total emissions of HIPVs profoundly vary among 31 maize (*Z. mays*) inbred lines, with the 20-fold difference between the two extreme lines (Degen et al. 2004). On the other hand, the HIPV signatures are also exceedingly diversified. The emission of *α*-farnesene is detected in maize lines F2 and F7, but is completely absent in the HIPVs of other lines (Degen et al. 2004). Another great variety occurs in the ratios of HIPV components. Although (*E*)-*β*-caryophyllene is widely released by all maize lines, the ratios of this compound to the total emission vary by more than 40-fold between the two extremities (Degen et al. 2004). Similar phenomena are found in the different inbred lines of cotton (Loughrin et al. 1995) and rice (Lou et al. 2006). Terpinene is only detected in the HIPVs of cotton line TX2259 that has a propensity to release higher amount of HIPVs, including (Z)-3-hexenyl acetate, (*E*)-*β*-caryophyllene, (*E*)-*β*-ocimene, and myrcene (Loughrin et al. 1995). In addition, the proportions of (*E*)-*β*-caryophyllene range from 17 to 59% from different insect-damaged tobacco cultivars (Hare 2007). This enormous intraspecific variability of HIPV emissions provides great opportunities for plant breeders to cultivate new crop varieties with traits of attracting parasitoids to control herbivores.

The emission of HIPV components follows a diurnal rhythm (Loughrin et al. 1994; Turlings et al. 1995). The release of induced terpenes, such as (*E*)-*β*-farnesene, (*E*)-*β*-ocimene, and DMNT from *S. exigua* larvae-infested cotton plants, peaks during the late afternoon and wanes during the late night and morning (Loughrin et al. 1994). GLVs, such as (*Z*)-3-hexenal, (*E*)-2-hexenal, and (*Z*)-3-hexenol do not follow this diurnal pattern and are released instantaneously after larval infestation (Loughrin et al. 1994; Turlings et al. 1995). Some terpenoids, like *α*-pinene and (E)-*β*-caryophyllene, are also released right after the larval infestation on cotton plants, but the larvae-infested corn does not release any kind of terpenoid instantly (Loughrin et al. 1994; Turlings et al. 1995). Those on-site released compounds could be synthesized beforehand and stored in resin ducts, glandular trichomes, and vacuoles, and released transiently from bursting storage structures (Turlings and Tumlinson 1992; Paré and Tumlinson 1997; Becker et al. 2015). The emissions of terpenoids, like DMNT, (*E*)-*β*-farnesene, (*E*)-*β*-ocimene, and (*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT) from larvae-infested cotton plants, are not detected within several hours after larval infestation, presumably because those terpenoids needs to be de novo synthesized in response to larval infestation, and then the emission starts to increase and persist to several days independent of larval infestation (Loughrin et al. 1994; Turlings et al. 1995). These emission patterns ensure the maximal protection for plants by extending the lifetime of HIPV presence.

The effects of HIPVs on the physiology of herbivores and parasitoids

A wealth of bioactive HIPV components have been physiologically studied by EAD (electroantennogram detection), GC-EAD (gas chromatography-electroantennogram detection), and SSR (single sensillum recording). On the second tropical level, the antennal responses of Lepidoptera pests to HIPVs have been studied in depth. Female antennae of the Egyptian cotton leafworm moth, *Spodoptera littoralis* Boisduval (Lepidoptera, Noctuidae), show strong GC-EAD responses to HIPV components of cotton plants *G. hirsutum* 'Delta Pineland 90', *β*-myrcene, *β*-ocimene, (*Z*)-3-hexenyl acetate, linalool, and (*Z*)-jasmone, and to a less extent, *α*-pinene, *β*-pinene, (*E*)-hexenal, (*Z*)-3-hexenol, TMTT, and indole (Jönsson and Anderson 2002). In addition, following SSR recordings confirm the results of GC-EAD results (Jönsson and Anderson 2002). Later on, a similar work largely recapitulates those results (Zakir et al. 2013). Mated females of *Helicoverpa assulta* Guenée (Lepidoptera, Noctuidae) show strong GC-EAD responses to the components of headspace volatiles of tobacco flower *N. tabacum* 'NC89,' (*E*)-*β*-ocimene, octanal, (*Z*)-3-hexenyl acetate, (*Z*)-3-hexe-1-ol, nonanal, (*Z*)-3-hexenyl-2-methyl butyrate, linalool, and (*E*)-*β*-caryophyllene (Sun et al. 2012). The sensilla responsive to those chemicals have also been characterized by SSR (Sun et al. 2012). On the third trophic level, GC-EAD technique have been applied to compare the antennal responses of the specialist parasitoid, *M. croceipes*, and the generalist parasitoid, *C. marginiventris,* to cotton volatiles, *G. hirsutum* 'max 9', induced by the infestation of *H. virescens* and *S. exigua* (Ngumbi et al. 2009). The generalist, *C. marginiventris* bends the GC-EAD responses toward GLV components, e.g., (*Z*)-3-hexenal, (*E*)-2-hexenal, and (*Z*)-3-hexenal, while the specialist *M. croceipes* is predisposed to be more sensitive to terpenoid components, like linalool, DMNT, indole, (*Z*)-jasmone, *α*-farnesene, *α*-humulene (Ngumbi et al. 2009). These differences in the responsive pattern may foreshadow the distinct foraging strategies adopted by specialist and generalist parasitoids. In *Microplitis mediator* Haliday (Hymenoptera, Braconidae), a detailed GC-EAD analysis reveals that three principle HIPV components, namely DMNT, (Z)-3-hexenyl acetate and nonanal, emitted by *H. armigera* infested cotton plants, trigger the responses in antennae (Yu et al. 2010). The follow-up Y-tube olfactometer assays confirm the attractiveness of these three compounds to *M. mediator* (Yu et al. 2010). Finally, field cage studies indicate that the application of DMNT to the cotton plants dramatically augment the parasitism of *H. armigera* larvae by *M. mediator* (Yu et al. 2010). Although the local field potential recorded by EAD and SSR does not necessarily end up with behavioral changes (Wei and Kang 2006), it nevertheless provides valuable information for sifting out chemicals for behavioral tests.

The effects of HIPVs on the behavior of herbivores

The effects of HIPVs to herbivores' behavior seem to be bimodal. HIPVs either act as herbivore repellents (Landolt 1993; De Moraes et al. 2001; Signoretti et al. 2012; Reisenman et al. 2013) and/or work as attractants to herbivores (Anderson and Alborn 1999; Rojas 1999; Shiojiri and Takabayashi 2003; Sun et al. 2014). The recent progresses of HIPVs' effects on the behavior of major herbivorous pests are summarized in Table 2. A large array of HIPV components have been ethologically characterized by, e.g., using oviposition bioassays, wind tunnels, Y-tube olfactometer assays, field bait traps. Linalool emitted from *Nicotiana attenuata* Torr. ex S. Watson (Solanaceae) upon infested by caterpillars of *Manduca quinquemaculata* Haworth (Lepidoptera, Sphingidae) significantly reduces the oviposition efficiency (Kessler and Baldwin 2001). Similarly, linalool emitted by damaged tea plants are repellent to *Ectropis obliqua* Prout (Lepidoptera, Geometridae) (Sun et al. 2014). Homoterpene DMNT significantly impairs the chemotaxis behavior of *S. littoralis* in wind tunnels (Hatano et al. 2015). Moreover, indole strongly repels both larvae and adults of *S. littoralis* (Veyrat et al. 2016). Conversion of (*Z*)-3-hexenyl acetate to (*E*)-2-hexenyl acetate trigged by the feeding of tobacco hornworm *M. sexta* on sacred *Datura wrightii* Regel (Solanaceae) plants changes the ratio of these compounds, which act as an alarm signal for the oviposition decision of *Manduca* moths (Allmann et al. 2013). Moreover, farnesene isomers released from damaged maize and cotton plants inhibits the oviposition of mated female *H. assulta* (Wu et al. 2018).

On the other hand, nerolidol and geranyl acetate have been shown to be attractive to *H. assulta* by using Y-tube olfactometer tests (Cui et al. 2018). Benzyl alcohol, (*Z*)-3-hexenyl hexanoate, and (*Z*)-3-hexenal emitted by infested tea plants (*Camellia sinensis* [L.] Kuntze, Theaceae) are attractive to *E. obliqua* (Sun et al. 2014). (*Z*)-jasmone, one of HIPV components released from herbivore damaged cotton and tobacco, is attractive to the caterpillar of *H. armigera* (Sun et al. 2018). Larvae of *H. armigera* are variably attracted by (*Z*)-3-hexenol, (*Z*)-3-hexenyl acetate, (*Z*)-3-hexenyl butyrate, caryophyllene, linalool, limonene, myrcene, ocimene, and (*Z*)-jasmone when tested separately by two-choice behavior assays in 9-cm disposable Petri dishes (Di et al. 2017). A blend of two HIPV components released from apple seedlings (*Malus* sp. [L.] Rosaceae), benzyl nitrile and acetic acid is attractive to the light brown apple moth, *Epiphyas postvittana* Walker, and the eye-spotted bud moth, *Spilonota ocellana* Denis & Schiffermüller (Lepidoptera, Tortricidae) (El-Sayed et al. 2016). Both (*Z*)-3-hexenyl acetate and TMTT are strong attractants to *Aphis gossypii* Glover (Hemiptera, Aphididae), while DMNT is not effective in eliciting of any behavioral modifications in the aphid (Hegde et al. 2011). The bimodal effects of some constitutes of HIPVs on the behavior of different herbivores, such as linalool that attracts larvae of *H. armigera* but reduces the oviposition rate of *M. sexta*, may reflect different survival strategies adopted by different insects. Swarming feeding could maximally exploit the nutrients of host plants, but also could dramatically increase the conspecific competitiveness (Prokopy and Roitberg 2001). Insects have to make a trade-off and adopt gregarious living or solitary living depending on the natural stress from their respective ecology niches. In this case, same chemical information that is used by gregarious insects as an aggregation signal could be employed by solitary insects as a dispersal signal. Moreover, different chemical dosages of HIPVs were used in different studies and different behavioral observations, like foraging, oviposition, and feeding preference, were investigated, which could lead to diverging conclusions and make the comparisons tenuous.

The effects of HIPVs on the behavior of parasitoids

More than 30 parasitoid species have been shown to be attracted by HIPVs, including several representatives of Braconidae (Hymenoptera): *Cotesia glomerate* L. (Geervliet et al. 1996), *Cotesia rubecula* Marshall (Geervliet et al. 1996), *Cotesia kariyai* Watanabe (Ozawa et al. 2004), *Cotesia marginiventris* Cresson (D'Alessandro et al. 2009), *Cotesia plutellae* Kurdjumov (Shiojiri et al. 2000); *Cotesia sesamiae* Cameron (Tamiru et al. 2015), *Diaeretiella rapae* McIntosh (Cascone et al. 2018), *Microplitis croceipes* Cresson (Turlings et al. 1990b), *Microplitis rufiventris* Kokujev (Ngumbi et al. 2009), and *Microplitis mediator* Haliday

Table 2 Valence of the odorant receptors of herbivorous insects tuned to salient herbivore-induced plant volatiles (HIPV)

Odor (HIPV)	Insect species	Effect (bioassay)	OR	References
Caryophyllene	*Helicoverpa armigera*	Attractant (Chemotaxis, Petri dish)	U	Di et al. (2017)
DMNT	*Spodoptera littoralis*	Deterrent (Chemotaxis, wind tunnel)	OR3	Hatano et al. (2015); Fouchier et al. (2017)
(*E*)-2-hexenal	*Manduca sexta*	Deterrent (Oviposition preference, field test)	U	Allmann et al. (2013)
(*E*)-*β*-farnesene	*Spodoptera exigua*	U	OR3	Liu et al. (2014)
Farnesene isomer	*Helicoverpa assulta*	Deterrent (Oviposition preference, cage)	OR23	Wu et al. (2018)
Geranyl acetate	*Helicoverpa assulta*	Attractant (Chemotaxis, Y-tube olfactometer)	OR40	Cui et al. (2018)
Indole	*Spodoptera littoralis*	Deterrent (Chemotaxis, Petri dish) (Oviposition preference, cage)	OR27	Veyat et al. (2016); Fouchier et al. (2017)
Limonene	*Helicoverpa armigera*	Attractant (Larval choice, Petri dish)	U	Di et al. (2017)
Linalool	*Maduca quinquemaculata*	Deterrent (Oviposition preference, field test)	U	Kessler and Baldwin (2001)
Methyl salicylate	*Helicoverpa armigera*	Attractant (Chemotaxis, two-choice olfactometer)	U	Gregg et al. (2010)
Myrcene	*Helicoverpa armigera*	Attractant (Chemotaxis, Petri dish)	OR31	Di et al. (2017)
Nerolidol	*Helicoverpa armigera*	Attractant (Chemotaxis, Y-tube olfactometer)	OR40	Cui et al. (2018)
Ocimene	*Helicoverpa armigera*	Attractant (Chemotaxis, Petri dish)	U	Di et al. (2017)
TMTT	*Aphis gossypii*	Deterrent (Chemotaxis, four arm olfactometer)	U	Hedge et al. (2011)
(*Z*)-3-hexenol	*Helicoverpa armigera*	Attractant (Chemotaxis, Petri dish)	OR60	Di et al. (2017)
(Z)-3-hexenyl acetate	*Helicoverpa armigera*	Attractant (Chemotaxis, Petri dish) (Chemotaxis, two-choice olfactometer)	OR42	Di et al. (2017); Gregg et al. (2010)
(*Z*)-3-hexenyl butyrate	*Helicoverpa armigera*	Attractant (Chemotaxis, two-choice olfactometer)	U	Gregg et al. (2010)
(*Z*)-jasmone	*Helicoverpa armigera*	Attractant (Chemotaxis, Petri dish)	OR41	Di et al. (2017)

DMNT E)-4,8-dimethyl-1,3,7-nonatriene, *TMTT* (*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene, *OR* odorant receptor, *U* uncharacterized behaviors/odorant receptors

(Yu et al. 2010); and Ichneumonidae (Hymenoptera): *Campoletis sonorensis* Cameron (Elzen et al. 1984), *Campoletis chlorideae* Uchida (Yan and Wang 2006a), *Diadegma semiclausum* Hellén (Houshyani et al. 2013), and *Diadegma fenestrale* Holmgren (Gols et al. 2012). Although host larvae-infested plants are largely attractive to parasitoids, the composition of HIPVs needed to elicit strong chemotaxis behavior of parasitoids seems to be variable. A blend of four volatiles [*n*-heptanal, *α*-pinene, sabinene, and (*Z*)-3-hexenyl acetate] released by *Plutella xylostella* (L.) (Lepidoptera, Plutellidae)-infested cabbage plants *Brassica oleracea* (L.) (var. capitata, cv. Shikidori) is necessary to elicit a strong chemotaxis behavior of the parasitoid, *Cotesia vestalis* (Haliday) (Hymenoptera, Braconidae), while none of those compounds alone shows attractiveness (Shiojiri et al. 2010). Moreover, attraction of parasitoids *C. sonorensis* and *M. rufiventris* is correlated with nonanal, *α*-pinene, (*E*)-*β*-ocimene, DMNT, (*S*)-linalool, and (*E*)-*β*-farnesene (Sobhy et al. 2018). On the other hand, single HIPV, linalool, acts as a potent attractant to a parasitoid *Anagrus nilaparvatae* Pang & Wang (Xiao et al. 2012) and *C. sesamiae* (Tamiru et al. 2015). (*Z*)-3-hexenol alone could effectively lure wasps *Opius dissitus* Muesebeck (Hymenoptera, Braconidae) towards lima bean plants damaged by the leafminer *Liriomyza huidobrensis* Blanchard (Diptera, Agromyzidae) (Wei et al. 2007). (*Z*)-jasmone acts as a strong attractant to *C. chlorideae* tested in both a Y-tubes olfactometer test and in a cage (Sun et al. 2018). Application of (Z)-jasmone to tobacco plants dramatically increases the parasitism rate of *H. armigera* by *C. chlorideae* (Sun et al. 2018). Several lines, including GC/MS quantification and forging behavior assays, suggest that DMNT is a potent attractant for certain species of parasitoids whose host larvae feed on cotton, maize, pepper, and cowpea. First, DMNT is an abundantly and promiscuously released HIPV component from various damaged plants, e.g., cotton (*G. hirsutum*) seedlings (McCall et al. 1994; Röse et al. 1996), maize (*Z. mays*) (Turlings and Tumlinson 1992; Yan and Wang 2006a), pepper (*Capsicum annuum* [L.] Solanaceae) (Addesso et al. 2010), and cowpea (*Vigna unguiculata* [L.] Walp, Fabaceae) (Turlings et al. 1993). Second, DMNT has been experimentally shown to be a strong attractant to several parasitoid species (Turlings et al. 1995; Kappers et al. 2005; D'Alessandro et al. 2009; Yu et al. 2010; Tamiru et al. 2011, 2015). DMNT alone shows the same attractiveness for *M. mediator* as does the blend of HIPVs (Yu et al. 2010). Most of conducted behavioral assays only compare the attraction of single HIPV component versus solvent, which efficiently identify the behavior-relevant components, but could inadvertently ignore the synergism between compounds (Hu et al. 2018). Additionally, the importance of identified compounds should be scrupulously reconsidered, because the attractiveness of blends has not been tested in parallel.

The components of HIPVs are not always attractive to parasitoids (Yan and Wang 2006a; Snoeren et al. 2010). For instance, parasitoid *C. chlorideae* has shown to be indifferent to (*E*)-2-hexenal and (*Z*)-3-hexenol even though they are one of major constitutes of HIPVs from *M. separata*-infested maize (Yan and Wang 2006a). Moreover, methyl salicylate has been reported to negatively affect the attraction of parasitoid *D. semiclausum* (Snoeren et al. 2010). This is seemingly counterintuitive since methyl salicylate is found in emissions of many pest-infested plants, such as tobacco (Yan et al. 2005), tomato (Ament 2004), and Lima bean (Dicke et al. 1990). However, the aversive components in HIPVs could be important as some parasitoids can take advantage of them to avoid non-host pests.

Genetically tractable plant, *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae) not only has prodigiously contributed to the unraveling of signal transduction in indirect defense (Poecke et al. 2001; Poecke and Dicke 2004) but also has been demonstrated to be an ideal tool to study the modulation of behavior in parasitoids by HIPV components (Schnee et al. 2006; Houshyani et al. 2013; Zhang et al. 2013b). A maize terpene synthase gene, *tps10*, is responsible for the formation of several terpenoids, including (*E*)-α-bergamotene and (*E*)-β-farnesene, the major components of HIPVs of *S. littoralis* larvae-infested maize plants (Schnee et al. 2006). Overexpression of *tps10* in *A. thaliana* results in an emission that is a mimicry of the HIPV blend of infested maize (Schnee et al. 2006). Unambiguously, the parasitoid *C. marginiventris* learns to exploit the tps10-expressing *A. thaliana* over the control, elegantly demonstrating the importance of terpenoids, in particular, (*E*)-α-bergamotene and (*E*)-β-farnesene, in the recruitment of the parasitoid *C. marginiventris* (Schnee et al. 2006). Moreover, *A. thaliana* that is genetically tailored to release higher amount of nerolidol outwits the control plants in terms of attracting the parasitoid *D. semiclausum* (Houshyani et al. 2013). Those examples clearly showcase the feasibility of genetic manipulation in studying correlations between HIPVs and the behavior of parasitoids.

Learning of parasitoids

Besides an innate preference of HIPVs, generalist parasitoids can leverage associative learning to distinguish most suitable host plant species from others after they have learned the association between host pests and plants (Turlings et al. 1990a; Geervliet et al. 1998; Steidle 1998; Peñaflor et al. 2011). Other than that, many specialist parasitoids also have a keen ability to learn to respond to HIPVs (Kaiser and Cardé 1992; Fukushima et al. 2001; Takasu and Lewis 2003; Peñaflor et al. 2011). For instance, the landing frequency of experienced females of the specialist parasitoid *C. kariyai* on the aphid-infested corn (*Z. mays*) is 60%, which is significantly higher than that of naïve females (12%), indicating initial host searching experiences greatly enhance the subsequent flight orientation to the herbivore-infested plants (Fukushima et al. 2001). Several lines of evidence indicate that the specialist parasitoids and the generalist parasitoid display different associative learning abilities (Vet and Dicke 1992; Simons et al. 1992; Geervliet et al. 1998; Bleeker et al. 2006; Ngumbi et al. 2012). The two closely related parasitoids, the generalist *Cotesia glomerata* (L.) (Hymenoptera, Braconidae) and the specialist *C. rubecula*, find their hosts by responding to HIPVs, but differ profoundly in olfactory learning: *C. glomerata* instantly changes its congenital preference for white cabbage *Brassica oleracea* (L.) convar. Capitate var. alba (Brassicaceae) towards brussels sprouts *Brassica oleracea* (L.) var. *gemmifera* (Brassicaceae) after a single oviposition experience, while the preference of *C. rubecula* for the cabbage remain unchanged even after 5 rounds of oviposition training (Geervliet et al. 1998). Moreover, one associative learning experience instills a strong and long-lasting memory in the generalist parasitoid, *C. glomerata*, whereas one oviposition experience only induces a short-lived memory trace in the specialist parasitoid, *C. rubecula* (Bleeker et al. 2006). Furthermore, a comparative study of learning abilities between the generalist *C. marginiventris* and the specialist *M. croceipes* to four behavior-related HIPV components, (*E*)-2-hexanal, *α*-pinene, (*Z*)-3-hexenyl butyrate, and (*E,E*)-*α*-farnesene, reveals that trained generalist parasitoid quickly associates all four odorants to sugar water, whereas the trained specialist only establishes the association of *α*-pinene and (*E,E*)-*α*-farnesene with the reward (Ngumbi et al. 2012). However, some caveats should be considered regarding the differential learning abilities of generalist and specialist parasitoids. Two congeneric parasitoid species, the specialist *D. semiclausum* and the generalist *D. fenestrale,* show similar behavior responses to HIPVs regardless of experience treatments (Gols et al. 2012). Taken together, both generalist and specialist parasitoids can locate their hosts with competitive efficiency and accuracy through associative learning irrespective of myriads of odorants released from non-host larvae-infested plants (Vet and Groenewold 1990; Turlings et al. 1993; Giunti et al. 2015). However, the associative learning seems to confer greater adaptive value to the generalist parasitoids than the specialist parasitoids (Vet and Groenewold 1990; Vet and Dicke 1992; Ngumbi et al. 2009).

The molecular basis of olfactory detection of HIPVs

Compared with the numerous reports on the identification and behavioral studies of HIPVs, the mechanisms underlying olfactory detection of HIPVs remain largely unexplored. However, the holistic view of insect olfactory signal transduction pathways has been obtained in fruit flies and mosquitos (Diptera) (Vosshall and Stocker 2007; Masse et al. 2009, Su et al. 2009; Ray 2015; Joseph and Carlson 2015). The detection of odorants in insects is orchestrated by a series of chemosensory proteins, including odorant binding proteins (OBPs), olfactory receptors (ORs), and odorant degrading enzymes (ODEs) (Vogt 2003; Leal 2013) (Fig. 1). OBPs bind to odorants, ferry the odorants across antennal lymph, and release them in the vicinity of ORs that are embedded in the membrane of olfactory receptor neurons (ORNs) (Su et al. 2009; Leal 2013) (Fig. 1). Insects OBPs are a class of small soluble proteins with a length of about 150 amino acids, and are mainly structured in 6 *α*-helix that are folded to form a hydrophobic binding pocket (Pelosi et al. 2006). Insect ORs are seven transmembrane proteins with an intracellular N terminus and extracellular C terminus, bearing no sequence similarities with their vertebrate counterparts (Clyne et al. 1999; Vosshall et al. 1999; Gao and Chess 1999; Benton et al. 2006). Insect ORs previously considered as a heterodimer (Sato et al. 2008; Wicher et al. 2008), but recent structure analysis favors a heterotetramer consisting of two subunits of tuning OR and two subunits of odorant receptor co-receptors (ORco) (Butterwick et al. 2018) (Fig. 1). Other than ORs, inotropic receptors (IRs) that are located to coeloconic ORNs are a special detector for amines and acids (Benton et al. 2009). Sensory neuron membrane protein 1 (SNMP1), a CD36-like protein (Rogers et al. 1997; Benton et al. 2007; Jin et al. 2008), along with pheromone binding proteins (PBPs) (Vogt and Riddiford 1981; Guo et al. 2012a) and pheromone receptors (PRs) (Nakagawa et al. 2005; Jiang et al. 2014; Yang et al. 2017), is located to the trichoid sensilla and essential for pheromone detection. A large array of basiconic sensilla are usually responsive to general odorants, including HIPVs. The concentrations of OBPs in the antennal lymph are staggeringly

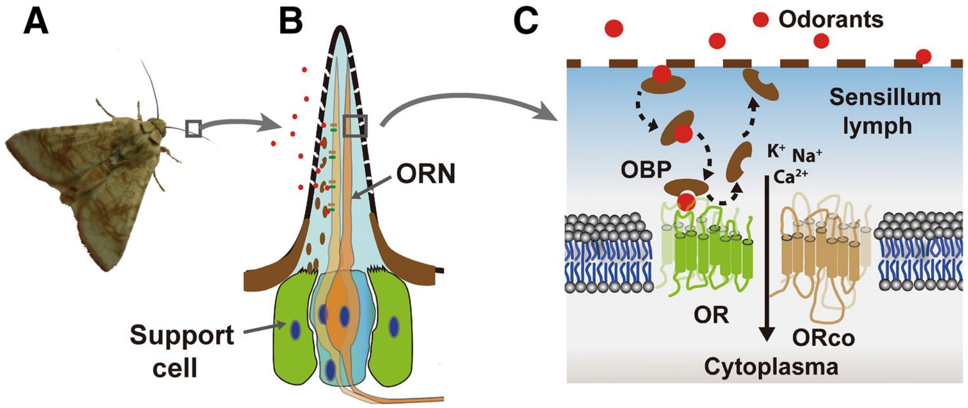


Fig. 1 Peripheral detection of odorants on the insect antennae. **a** Antennae are the major olfactory organ of insects and are decorated by the hair-like structure termed sensillum (Hansson and Stensmyr 2011). **b** The olfactory sensillum is multiporous and morphologically diverse. The dendrites of olfactory receptor neurons (ORNs) are bathed in the aqueous sensillum lymph. Odorant binding proteins (OBPs) are synthesized and secreted by support cells (Vogt 2003; Pelosi et al. 2006; Leal 2013). **c** Once upon diffusion into the sensillum through the pores, odorants are captured by OBPs and transferred to the vicinity of odorant receptors (ORs). The transient interaction between ligand and OR activates the channel which is formed by a predicted heterotetramer consisting of two subunits of tuning OR and two subunits of odorant receptor co-receptors (ORco) (Sato et al. 2008; Wicher et al. 2008; Butterwick et al. 2018)

high (~ 10 mM) (Vogt et al. 1989). The numbers of *OBP* genes in a given species are lower that the numbers of ORs revealed by the numerous antennal transcriptome analysis (Zhang et al. 2015; Du et al. 2018). Those characteristics of OBPs imply the importance of OBPs for odorant detection. However, the competitive fluorescence binding assay reveals that OBPs equip some degree of odorant selectivity, but definitely cannot account for the specificity of ORNs. Instead, many lines of evidence support that ORs are major determinants of response patterns of ORNs (Hallem et al. 2004; Hallem and Carlson 2006). The chemical information generated by the ORs is relayed to the glomeruli located in antennal lobes where the olfactory information is preliminarily sorted and integrated (Galizia and Rössler 2010). The sorted information is further processed in mushroom bodies for associative learning and is decoded in the lateral horn for innate behavior (Su et al. 2009). Insects usually employ two coding paradigms to detect ecologically relevant odorants either by recruiting multiple ORN types (combinatorial coding) or by activating a single narrowly tuned ORN (labeled line) (Kaupp 2010). Highly relevant negatively acting odorants are tended to be sensed by a dedicated repulsion-inducing ORN type (Stensmyr et al. 2012).

Olfactory detection of HIVPs by herbivorous insects

The selectivity of OBPs has been widely tested by using competitive fluorescence binding assays. In *Chilo suppressalis* Walker (Lepidoptera, Crambidae), OBP8 displays high binding affinities to nerolidol, but also show somewhat equal bindings to non-HIPV compounds, such as *β*-Ionone, farnesol, and 2-hexanone (Yang et al. 2016). OBP1 of *S. exigua* shows higher binding capacities to (*E*)-*β*-caryophyllene over other tested odorants, such as farnesol and acetophenone (Liu et al. 2017). OBP6 of *E. obliqua* indiscriminately binds to a group of terpenoids, such as *α*-caryophyllene, *α*-terpinene, nerolidol, *α*-farnesene (Ma et al. 2018). Other reports about high selectivity of OBPs derive from the studies of OBP3 of two aphid species (Qiao et al. 2009; Vandermoten et al. 2011). OBP3 from the pea aphid *Acyrthosiphon pisum* (Harris) (Hemiptera, Aphididae) and the English grain aphid *Sitobion avenae* (Fabricius) (Homoptera, Aphididae) are highly conserved and both of OBPs show a specific binding affinity to (*E*)-*β*-farnesene, the alarm pheromone of aphid (Qiao et al. 2009; Vandermoten et al. 2011). Largely, OBPs bind to multiple odorants without appreciative discrimination. This fact complicates the conclusion on the roles of OBPs in detection of HIPVs.

Since ORs are the major determinants of response patterns of ORNs, functional characterizations of ORs are of paramount importance towards understanding the olfactory coding of odorants (Hallem et al. 2004). The recent deorphanized ORs are listed in Table 2. Using heterologous expression in *Xenopus* oocytes coupled with two-electrode voltage-clamp, many ORs tuning to salient HIPVs are deorphanized in herbivores. SexiOR3 in *S. exigua* has been reported to be narrowly tuned to *E*-*β*-farnesene (Liu et al. 2014). The counterpart of SexiOR3 in *H. assulta*, HassOR23 is also tuned to (*E*)-*β*-farnesene (Wu et al. 2018). OR12 conserved in *H. armigera, H. assulta*, and *H. virescens* shows strong responses to (−)-linalool, linalool, and (*Z*)-2-hexenyl acetate (Cao et al. 2016), whereas the OR12 from *S. exigua* is exclusively tuned to (*Z*)-3-hexenyl acetate (Zhang et al. 2013a). In *H. assulta*, OR40 has been shown to be a detector for nerolidol and geranyl acetate (Cui et al. 2018). In *H. armigera*, OR42 is tuned to both phenylacetaldehyde and (*Z*)-3-hexanyl acetate (Di et al. 2017). Although HarmOR60 shows detectable responses to many volatiles, the best ligand to it is (*Z*)-3-hexenol (Di et al. 2017). HarmOR41 is strongly activated by (*Z*)-jasmone, to a less extent, by benzaldehyde (Di et al. 2017). In *Bombyx mori* (L.) (Lepidoptera, Bombycidae), the detection of (*Z*)-jasmone is specially attributed to OR56 (Tanaka et al. 2009). However, it is not known whether (*Z*)-jasmone is constitutively or inductively released in mulberry leaves (*Morus* sp. [L.] Moraceae), the exclusive food of *B. mori*.

Fruit flies *Drosophila* sp. Fallén (Diptera, Drosophilidae) empty neuron in which the endogenous *OR22a* is deleted has emerged as a faithful system to deorphanize ORs from other insect species (Hallem and Carlson 2006; Fouchier et al. 2017). A total of 24 *ORs* from the herbivorous pest *S. littoralis* were expressed in the ab3A neurons and the odorant detection spectrum against a panel of 51 volatiles was investigated (Fouchier et al. 2017). SlitOR4 was narrowly tuned to (±)-linalool, SlitOR17 to methyl salicylate, SlitOR27 to indole, and SlitOR28 to (*Z*)-3-hexenyl acetate. SlitOR24 and SlitOR36 were equally activated by three GLVs, (*Z*)-3-hexenol, (*E*)-2-hexenol, 1-hexanol. SlitOR29 was strongly activated by both (*E*)-*β*-ocimene and *β*-myrcene and, to a less extent, by DMNT and (*Z*)-3-hexenyl acetate (Fouchier et al. 2017). Although the best ligand to SlitOR3 was DMNT, the response was moderate (~ 90 spikes*s − 1) compared with the strong responses of other ORs to their best ligands (~ 200 spikes*s − 1) (Fouchier et al. 2017). DMNT is a potent herbivore deterrent for *S. littoralis* (Hatano et al. 2015). The activation of glomeruli by DMNT in antennal lobe is not detected by using optical calcium imaging, which leads to a conclusion that DMNT exerts its deterrent effects by attenuating the responses to (*Z*)-9-(11)-tetradecenyl acetate (the main sex pheromone component) and to (*Z*)-3-hexenyl acetate (a major plant volatile), but not by activation of dedicated ORNs (Hatano et al. 2015). This result is contradictory to the fact that SlitOR3 and SlitOR29 are tuned to DMNT, albeit with a moderate sensitivity (Fouchier et al. 2017). This incongruity may arise from different detection sensitivities of the two methods, as two-electrode voltage-clamp technique directly records the activation of ORs by ligands and the channel current is amplified preceding the conversion of acquired data, whereas optical calcium imaging indirectly monitors the fluctuations of cytosolic calcium concentrations by a calcium-sensitive dye (Wu et al. 2013, 2015).

Olfactory detection of HIPVs by parasitoids

Our knowledge of olfactory coding mechanism underlying parasitoid olfaction is very skimpy. Through genome sequencing and antennal transcriptome analysis, a slew of *OBP* genes has been identified in at least 10 parasitoid species, but most of them has yet functionally characterized (Vieira et al. 2012; Nishimura et al. 2012; Wang et al. 2014, 2015, 2018; Farias et al. 2015; Li et al. 2015; Zhou et al. 2015; Sheng et al. 2017; Liu et al. 2018). The binding patterns of seven OBPs of a solitary endoparasitoid *M. mediator* have been characterized (Zhang et al. 2011). All OBPs show somewhat binding affinities to a variety of odorants. MmedOBP4 shows binding to some aromatic compounds, like benzaldehyde and its derivatives (Zhang et al. 2011). The binding abilities of MmedOBP4 and MmedOBP6 are skewed to several terpenoids, like α-pinene, β-pinene, α-humulene, β-humulene, β-myrcene, nerolidol, limonene, and geraniol (Zhang et al. 2011), implying these two OBPs are involved in the olfactory detection of terpenoids.

Concurrently, a myriad of *OR* genes is found in multiple parasitoid species by genome sequencing or RNAseq (Robertson et al. 2010; Zhang et al. 2014; Sheng et al. 2017; Wang et al. 2017a, b; Liu et al. 2018; Sun et al. 2018). By mining the transcriptome of male and female antennae of *C. chlorideae*, 211 *OR* transcripts, with 95 being full length, were identified (Sun et al. 2018). The expression of *OR14, OR52, OR53, OR60, OR62, OR63,* and *OR70* is female biased, implying that those *ORs* may be necessary for some female specific behaviors, such as the location of hosts (Sun et al. 2018). Among them, *OR62* is exclusively expressed in female antennae. Indeed, *OR62* co-expressed with *ORco* in *Xenopus* oocytes shows an exclusive response to (*Z*)-jasmone, a strong attractant to *C. chlorideae* (Sun et al. 2018) (Fig. 2). The (*Z*)-jasmone receptors in *H. armigera* and *B. mori* are OR41 and OR56, respectively. However, pairwise comparisons of the amino sequence of CchlOR62, HarmOR41, and BmorOR56 reveal the identities between them are merely 15%, suggesting ORs tuned to (*Z*)-jasmone in different insect species are evolutionarily divergent. Extensive RNAi screens coupled with EAG measurements and preference essays collectively demonstrates OR35 as a detector of oviposition attractants β-caryophyllene and (*E*)-α-farnesene in *Anastatus japonicus* Ashmed (Hymenoptera, Eupelmidae), the parasitic wasp of litchi pest *Tessaratoma papillosa* Stål (Heteroptera, Pentatomidae) (Wang et al. 2017b). However, most of OBPs and ORs in parasitoids remain uncharacterized, which is a major hindrance for the understanding of olfactory mechanisms of trophic interactions between host plants and parasitoids.

The numbers of *OR* genes found in different parasitoid species are strikingly variable, ranging from 21 *OR* genes found in pupal parasitoid of the oriental fruit fly, *Spalangia endius* Walker (Zhang et al. 2014) to 301 *OR* genes in the jewel wasp *Nasonia vitripennis* Walker (Hymenoptera, Pteromalidae) (Robertson et al. 2010), which may reflect the complexities of chemical space different parasitoids encounter. *C. chlorideae* is an endoparasitoid of the generalist herbivore *H. armigera* that can feed on more than 200 plants species across 60 families (Wang et al. 2004; Han et al. 2013). In nature, *C. chlorideae* need to faithfully and efficiently extract the most meaningful olfactory information against the bombardment of the myriads of non-relevant volatiles in order to locate its host larvae. The large number of OR repertoire may confer *C. chlorideae* with a strong associative learning ability expanding the odorant spectrum it can detect.

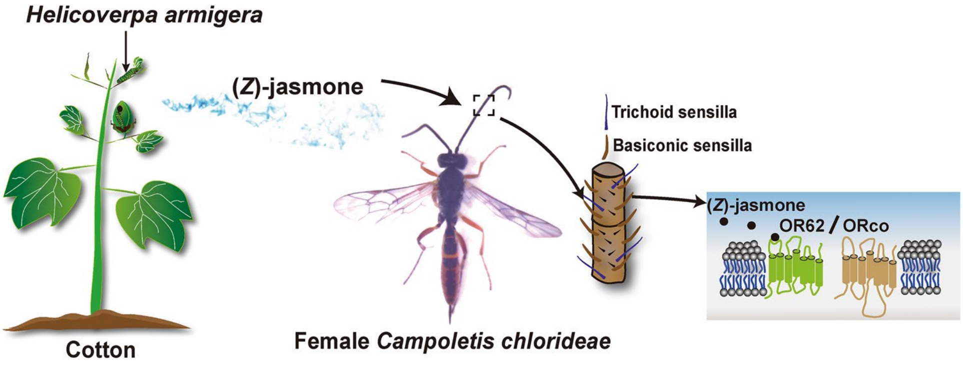


Fig. 2 Schematic cascade of olfactory detection of (*Z*)-jasmone in female *Campoletis chlorideae*. (*Z*)-jasmone is released by cotton plants infested by the larvae of *Helicoverpa armigera* and attracts the female parasitoid *C. chlorideae* towards the infested plants. Female parasitoids detect (*Z*)-jasmone through OR62-expressing ORNs ensheathed in the antennal basiconic sensilla (Sun et al. 2018)

Detailed molecular dissection of neural mechanisms of learning in bee and fruit flies reveal that the response plasticity of peripheral olfactory systems and the temporary neural connections concertedly contribute to the orchestration of associative learning in insects (Hammer and Menzel 1995; McGuire et al. 2005; Busto et al. 2010). Repeated odorant stimulation with subthreshold concentrations sensitizes the ORNs, whereas repeated stimulations with high concentrations desensitize the ORs (Getahun et al. 2013; Guo et al. 2017). Moreover, the long-term olfactory stimulation increases the volume of corresponding glomeruli, presumably by enhancing synapse connections (Devaud et al. 2001; Das et al. 2011). The Kenyon cells in mushroom body are necessary for forming an olfactory memory (Heisenberg et al. 1985; McGuire 2001). The classical learning mutant rutabaga, which is deficient in the activity of a type I adenylate cyclase, shows a strikingly compromised associative olfactory memory (Levin et al. 1992; Han et al. 1992; McGuire 2001). However, the aforementioned mechanisms implicated in insect learning have not been verified in parasitoids, and only a few of works have been sporadically reported (Vet et al. 1990). In the larvae parasitoid of fruit fly, *Leptopilina heterotoma* Thomson (Hymenoptera, Figitidae), a correlation between the associative learning and the attenuation of ORNs sensitivities to the odors of food substrate has been elaborated (Vet et al. 1990). This downregulation of olfactory sensitivity may be attributed to olfactory receptor desensitization (Guo and Smith 2017). It seems like that the modulation on peripheral sensitivities, at least, can partially account for associate learning. However, this modulation has not been tested in other parasitoid species. It is worthwhile to check for the sensitivities of the peripheral olfactory detection before and after conditioning in various parasitoid wasps. Rewarding experiences, such as an encounter with hosts or an oviposition, are essential for establishing the associative learning (Turlings et al. 1991a; Geervliet et al. 1998; Tamò et al. 2006; Costa et al. 2010). This posits a neural connection between rewarding circuits and olfactory processing circuits.

Beyond tritrophic levels

In order to fully understand the tritrophic interactions between host plants, herbivores, and parasitoids, other factors cannot be overlooked. Hyperparasitoids comprise a major component of the fourth trophic level and attack parasitoids in the third trophic level. The hyperparasitoid *Lysibia nana* Gravenhorst (Hymenoptera, Ichneumonidae) is indifferent to the odorants derived from the pupae of primary parasitoids in the genus *Cotesia* (Hymenoptera: Braconidae), while is strongly attracted by HIPVs (Poelman et al. 2012). These results favor the hypothesis that hyperparasitoids eavesdrop the release of HIPVs and exploit them to locate the pupae of primary parasitoids (Kaplan 2012; Poelman et al. 2012). However, the prevalence of this phenomenon merits future examinations. Researchers therefore should be cautious when they consider seeking out HIPVs to augment the recruitment of parasitoids because the imprudent application of HIPVs could literally reduce the parasitism of herbivores by exposing primary parasitoids to hyperparasitoids.

Polydnaviruses (PDV) including the bracovirus (BV) and ichnovirus (IV) are co-opted by parasitoids to suppress host immune responses (Herniou et al. 2013). PDV is characterized as multi-segmented double-stranded DNA with heterogeneous sizes (Stoltz et al. 1984). PDV particles replicate exclusively in virogenic stroma within the calyx cell nuclei of female wasps and are injected into the Lepidoptera hosts where virus multiplies and hijacks host cells to accommodate the development of wasps (Strand and Burke 2015). Recently, PDV infection is reported to be a suppressor of β-glucosidase enzyme activity in parasitized caterpillar regurgitant, resulting in a modified composition of HIPV that reveals the location of the parasitoid *C. glomerata* to the hyperparasitoids *L. nana* (Zhu et al. 2018). In another work, PDV of the parasitoid *M. croceipes* suppresses the activity of glucose oxidase in caterpillar saliva, an elicitor of immune defense responses in plants (Tan et al. 2018). These two studies elegantly explain how PDV modify the composition of HIPV, which further manipulate the phenotypes of wasps and herbivores down the road. Other than that microbial symbionts living in the bodies of herbivores have been reported to affect the interactions between herbivores and higher tropic levels either by interfering with the release of HIPVs to reduce the recruitment of parasitoids (Dicke and Baldwin 2010; Frago et al. 2017) or producing new chemicals that are attractive to parasitoids (Adams and Six 2008; Boone et al. 2008). Taken together, symbionts and PDV add another degree of intricacy to the interactions between tropical levels.

The emission of HIPVs in nature is modulated by multiple biotic factors, such as plant genotypes (Loughrin et al. 1995; Degen et al. 2004; Schuman et al. 2009; Bruce 2014), pathogens (Rostás et al. 2006; Dicke 2016), herbivory duration (Loughrin et al. 1994), and feeding guilds (Rodriguez-Saona et al. 2003; Rasmann and Turlings 2007; Zhang et al. 2013b). For example, fungal infection causes a plummeted emission of HIPVs from *S. littoralis*-infested maize (Rostás et al. 2006). Moreover, simultaneous infestation of cotton by silverleaf whitefly *Bemisia tabaci* Gennadius (Hemiptera, Aleyrodidae) and beet armyworm *S. exigua* dramatically suppresses the emission of HIPVs compared to the emissions of HIPV when infested by *S. exigua* alone (Rodriguez-Saona et al. 2003). In addition to the biotic factors, a series of abiotic impacts, such as ambient temperatures, air and soil humidity, light, the levels of CO_2 and ozone, and availability of nutrients, significantly regulate the emission dynamics of HIPVs (Schmelz et al. 2003b; Niinemets et al. 2004; Holopainen and Gershenzon 2010; Peñuelas and Staudt 2010; Holopainen and Blande 2013; Becker et al. 2015). Elevated ambient temperatures not only enhance the enzyme activities involved in synthesis of phytohormones, e.g., jasmonic acid, salicylic acid, and ethylene, but also change the physical structures of plants, such as the openness of stomatal aperture, resulting in an elevated emission of terpenoids (Niinemets et al. 2004; Gouinguene and Turlings 2002). Drought appears to increase the emission of HIPVs, most likely by boosting plant defense in the condition of water depletion (Gouinguené and Turlings 2002). The emission of HIPVs largely hinges on the light intensities, which coincides with the diurnal feeding rhythms of herbivores (Gouinguené and Turlings 2002). Moreover, elevated atmospheric CO_2 concentrations have been reported to compromise the plant defense response to herbivory (Vuorinen et al. 2004). Recent findings indicate that increased CO_2 concentrations enhance the salicylic acid pathway, and concomitantly suppress the jasmonic acid pathway, which would change the composition of HIPVs emitted from host plants, and in turn confound the foraging of herbivores and parasitoids (Guo et al. 2012b). O_3 has been reported to hamper the emission of terpenoids (Himanen et al. 2009) and mediate the degradation of GLVs and terpenoids (Pinto et al. 2007). Taken together, those aforementioned abiotic factors exert tangible effects on the emission of HIPVs, and they should be considered when the interactions between different tropic levels are studied.

Future perspectives

Over the last three decades, enormous strides have been made in the identification of HIPVs and the disentanglement of intricate chemical interactions between tropical levels. However, in the next decade, there are several questions needed to be addressed. First, the effects of mixtures to the behavior of herbivores and parasitoids should be further addressed. To date, most of HIPVs have been individually examined against solvent control in behavior tests. As such, we cannot fully leverage the full advantage of the HIPV-mediated recruitment of parasitoids. Second, the transformation of our knowledge obtained in the lab into commercially accessible products for pest control needs to be expedited. Third, the olfactory mechanisms underlying HIPV perception remain largely unknown. ORs tuned to behavior-relevant HIPVs in herbivorous insects and parasitoids await functionally characterized. We expect to see that, in the next decade, the ORs tuned to ecology-relevant odorants will be deorphanized, and taking a step further, the coding atlas of ethologically relevant odorants in the insect brain will be unveiled. The correlations between modulations of the responsive sensitivity of ORs and learning in parasitoids await further studies. These interdisciplinary efforts will concretely expedite the development of an economic and practical way to exploit parasitoids as an arsenal to curb the occurrence of pests.

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