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Review

Chemosensory systems in predatory mites: from ecology to genome

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Abstract

The reception of chemical cues in the environment is essential for the survival of almost all organisms, including phytoseiid mites. Compared with the progress made in the field of insect olfaction, the understanding of how predatory mites perceive chemical compounds and react to their surroundings is merely fragmentarily documented in past decades. In this review, we provide a guide in the field from chemoecology of herbivore-induced plant volatiles (HIPVs) as early as 1980s to the advances made in comparative genomics of predatory mites in 2019. We present from three aspects, i.e., chemosensory-guided feeding behavior, sensory structures and chemoreceptors predicted from genomes. The molecular principles of chemosensory system remain exciting areas for future research, since insights into the mechanisms underlying the sensing of chemical signals will not only contribute to a better understanding of predator behavior and physiology but may also open new avenues for the development of more specific and sustainable approaches to control pests by manipulating behaviors in predators. We then suggest three directions for future research: 1) chemoreceptor gene identification and function verification; 2) neural response circuit to stimuli and 3) application of chemoperception on feeding behavior. The potential methods and techniques are provided as well.

Key words: Phytoseiid mites, feeding behavior, chemoecology, chemoreceptors, genomic prediction, biological control

Introduction

As an important group of biological control agents, predatory mites (Acari: Phytoseiidae) are widely used in agricultural and horticultural crops to control various small pests and mites. Based on different feeding habits and lifestyles, phytoseiid mites are classified into four categories, including specialized predators of *Tetranychus* species, e.g. *Phytoseiulus persimilis*, selective predators of tetranychid mites, e.g. *Neoseiulus californicus*, generalist predators e.g. *Amblyseius swirskii*, and specialized pollen feeders or generalist predators e.g. *Euseius finlandicus* (McMurtry and Croft 1997; McMurtry *et al.* 2013).

To perceive the environments, predators may use a series of clues, such as chemical signals, temperature and humidity, visual and mechanical factors, either individually or collectively (Greany and Hagen 1981; Letourneau 1988). Among all these clues, chemoreception is recognized as the most important manner to locate appropriate foods, habitats, mating partners, oviposition sites and egg heaps. They perceive stimuli encountered in environments and tune behaviors to survive, not only to communicate in community but also compete among other natural enemies. Due to the low locomotive ability and insensitiveness to long distance odor, phytoseiid mites forage for close objects by frequent waving their front legs and then contact their prey by pedipalps (Jackson and Ford 1974; Sabelis 1981). This movement is considered as food selection by chemoreception that eventually results in different feeding habitats.

In the complicated process of chemoreception, predatory mites recognize a variety of infochemicals emitting from herbivorous pests or host plants (Fig. 1). Herbivore-induced plant volatiles (HIPVs) and surface substances in arthropod can manipulate foraging behavior of predators. For mechanism of chemosensory perception, chemical receptors have been successfully identified to recognize stimuli and tightly linked to chemoecological functions and behaviors in insects, although less is known in mites (Cande *et al*. 2013; Gadenne *et al*. 2016). To understand potential mechanism of chemoperception from stimuli to behaviors in predatory mites, we summarize the literature on the chemoecology of economically important phytoseiid mites, mainly *P. persimilis* and *Metaseiulus occidentalis*, from feeding behaviors, chemoperception structures to predicted receptor families in genomes. The accessibility of whole genomes of several phytoseiids facilitates the study of the molecular basis of mite chemosensory mechanisms, including functional genomics, sensory physiology and chemical ecology studies in Acari. The chemoecology of phytoseiids will serve to develop more efficient and sustainable approaches in biological control.

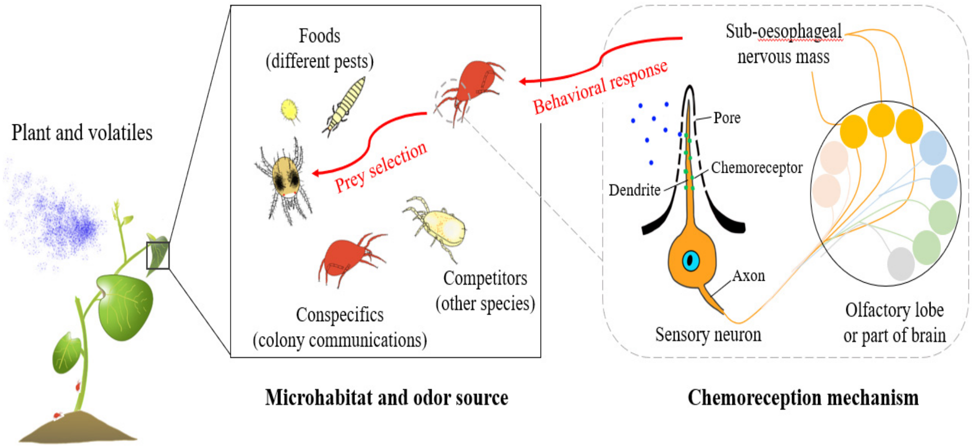

FIGURE 1. Schematic structure of chemoreception mechanism in phytoseiid mites from odor to predator behavior in their microhabitat.

Chemosensory-guided feeding and other behaviors

Phytoseiid mites have no eyes, yet they are able to detect and distinguish prey species using chemical cues deposited by spider mites, other preys and herbivore infested plants rather than visual cues (Azandémè-Hounmalon *et al*. 2016; Anja *et al*. 2021). As early as studies in 1980s, phytoseiid predators were found to be able to locate distant particular tetranychid species by specific kairomones (Sabelis and Vandebaan 1983). *P. persimilis* not only react to odors emanated directly by tetranychid preys (Dong and Chant 1986), but also perceived HIPVs produced by infested lima bean (*Phaseolus lunatus*) to locate their preys (Sabelis *et al*. 1984; Dicke and Sabelis 1987). Since then, an unprecedented research field has been established to study olfactory-guided feeding behavior of predatory mites in terms of tritrophic interactions.

Using chromatography and spectrometry, the HIPVs has been extensively identified and investigated for the role in attracting phytoseiid predators in biological control. HIPVs are typically composed of green leaf volatiles (GLVs), terpenoid, aliphatic and aromatic compounds. GLVs are a series of volatile components emitted by green plants through oxidative degradation of lipids in leaves, including a variety of 6-carbon alcohols, aldehydes and esters (Dudareva *et al*. 2004; Hassan *et al*. 2015). Strictly speaking, GLVs are not HIPVs because they can also be released from healthy or mechanically damaged plants and this process is typically not induced by herbivore infestation

(Loughrin *et al*. 1994; Holopainen 2004). However, some GLVs, e.g., *cis*-3-hexenyl acetate and *cis*-3-hexenol are found to be attractive to some parasitoid wasps (Reddy *et al*. 2002; Wei *et al*. 2007). Terpenoid is a major group of chemicals emitted by pest-damaged plants. *Tetranychus urticae*-infected Lima bean and cucumber often release 4,8-dimethylnona-1,3,7-triene (DMNT) and (*E*)-β-Ocimene (Dicke *et al*. 1990), while 4,8,12-trimethyltrideca-1,3,7,11-tetraene (TMTT), (*E*)-β-Caryophyllene and (*E*)-β-Ionone are major terpenoids of tomato's HIPVs (Silva *et al*. 2017). Methyl salicylate (MeSA), a ubiquitous aromatic compound in HIPVs, is often induced by herbivores (eg. mites, aphids and beetles) with different feeding habits (Bolter *et al*. 1997; Ament *et al*. 2004; Zhu *et al*. 2005; Salamanca *et al*. 2015). It is proved for effective attraction to beneficial arthropods including predatory mites, parasitoid wasps and phytophagous thrips (Shimoda *et al*. 2002; Shimoda *et al*. 2010; Salamanca *et al*. 2019).

HIPV profiles highly vary depending on plant species, temporal diurnal rhythm, infested herbivores with different feeding strategies and other abiotic factors (Arimura *et al*. 2008; Hare and Sun 2011; Ozawa *et al*. 2012; Wei *et al*. 2014; Rim *et al*. 2019). Researchers tested 30 compounds from HIPVs to identify the key component that attracts predatory mite *P. persimilis*. However, only three compounds are significantly attractive to the mites: octan-1-ol, not involved in indirect defense, and *cis*-3-hexen-1-ol and MeSA, which are both induced by herbivory but not specific (van Wijk *et al*. 2008). Many studies have consistently pointed to MeSA, the only compound of HIPVs to attract predatory mites (de Boer and Dicke 2004, 2006; Azandémè-Hounmalon *et al*. 2016). Interestingly, when MeSA combined with other four artificial chemicals (TMTT, DMNT, (*E*)-β-Ocimene and cis-3-hexenyl acetate) or under lima bean background odor, the attraction of mixtures to *P. persimilis* is lower than MeSA alone. However, lima bean odors can improve the attractiveness of these five compounds while all the compounds released by *T. urticae*-infested plants were reported to be somehow equal to MeSA attractiveness (Shimoda 2010), suggesting that predatory mite attraction to HIPVs may not be a consequence of attraction to individual compounds, but to the whole mixtures (van Wijk *et al*. 2011). Since not all components in HIPVs can be detected by electroantennography, which is an efficient tool to identify physiological active compounds releasing receptor potentials in olfactory neurons (Ngumbi *et al*. 2009; Sun *et al*. 2020), physiological effects of any component from HIPVs on predatory mites have not been investigated yet so far.

Predatory mites with different feeding habits can consistently follow the trails of spider mites to locate prey colonies (Zhang and Sanderson 1992; Yano and Osakabe 2009). In addition to locating prey by odors, contacting and tasting preys is an essential recognition process for natural enemies, while predatory mites, in particular, often encounter conspecific or heterospecific species in nature. Cuticular hydrocarbons (CHCs) are reported to play important roles when predators recognize close objects. By touching with the tips of the chelae fingers, *Androctonus australis* can respond to cuticle extracts of dead insect before feeding (Krapf 1986). The parasitic mite *Varroa destructor* can also exploit the differences of CHCs of European honeybee (*Apis mellifera*) for an accurate selection (Piccolo *et al*. 2009). However, the effect of CHCs on food selection of predatory mites has not been undertaken yet. We deduce that infochemicals also most likely be involved in mating and oviposition behaviors of predatory mites. Because deutonymphal females of *Macrocheles muscaedomesticae* and *Metaseiulus occidentalis* can secrete non-volatile pheromone over their body surface to trigger precopulatory mate guarding behavior in males, so that mate immediately after the females matured (Hoy and Smilanick 1979; Yasui 1992). To select an appropriate oviposition sites, predatory mites can discriminate own, conspecific or heterospecific eggs to avoid food competition, cannibalism and intraguild predation (Schausberger and Croft 1999; Faraji *et al*. 2000; Walzer *et al*. 2006).

The responses of predators to chemical clues vary according to environmental factors, previous experiences, and physiological state (Zhang and Sanderson, 1993; Krips *et al*. 1999; Drukker *et al*. 2000; de Boer *et al*. 2004). For example, response to the odors or preys depends on the state of satiety

(Zhang and Sanderson 1993). Satiated *P. persimilis* with different rearing histories responded variably to uninfested plant volatiles (Takabayashi and Dicke 1992). *P. persimilis* can learn associate odors with reward, but the memory to this association wanes after being starved for 24 hours (van Wijk *et al*. 2008). Interestingly, prenatal or embryonic experiences can affect postnatal foraging behavior in *N. californicus* (Quesada and Schausberger 2012), suggesting predators may respond to odorants in coordination with different physiological and developmental states. Likewise, early experience of aversive hexane extracts produced from thrips body reduced thrips predation by *A. swirskii*, but early experience of water extracts enhanced predation on thrips (Schausberger *et al*. 2020). Most likely, food selective responses to any sensory cue would be an energy investment if physiology of predatory mites were not ready for the final behavioral output.

Morphology and structure of chemosensory system

Foraging behavior of predatory mites requires the participation of olfactory and gustatory systems, as insect feeding habits are closely related to chemosensory proteins (Zhang *et al*. 2019b). Insects have developed a sophisticated sensory system consisting of olfactory and gustatory receptor neurons situated in sensilla on the antennae and mouthparts (Keil 1999). However, lacking eyes and antennae, phytoseiid mites move curvedly and tap the substrate by their front legs to resemble insect antennae during foraging, while the pedipalps frequently contact their prey before feeding (Jackson and Ford 1973; Sabelis 1981). Several setae at the distal ends of the first pair of legs and the pedipalps might be used to perceive chemical clues (Jackson 1974; Jagers op Akkerhuis *et al*. 1985).

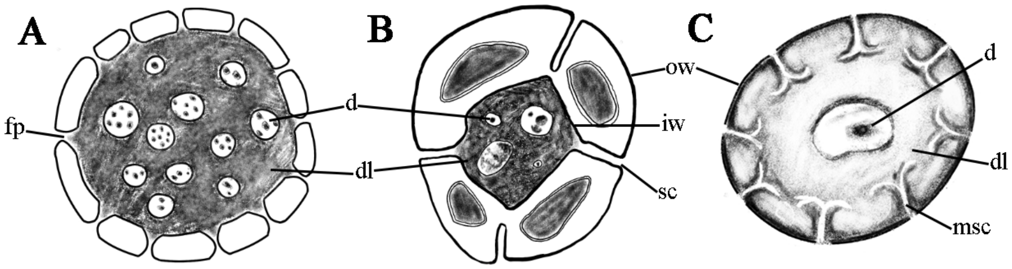

FIGURE 2. Cross-sections of setae on the tarsi of first legs in *P. persimilis* (after Jagers op Akkerhuis *et al*. 1985). (A) funnel-shaped pores in single-wall setae (fp: funnel-shaped pores, d: dendrites, dl: dentritic lumen); (B) spoke canals with cone-shaped connections in the second wall to the inner fluid (sc: spoke canals, ow: outer wall, iw: inner wall); (C) spoke canals with a mushroom-shaped connections in an incomplete second wall to the inner fluid (msc: mushroom-shaped spoke canals).

Scanning electron microscopy (SEM) and transmission electron microscopy (TEM) facilitate to discover the ultrastructure of pedipalpal and anterior tarsal setae in *P. persimilis* (Jackson 1974; Jagers op Akkerhuis *et al*. 1985). In short, the palp tarsal setae consist of 11–12 or 4–8 dendrites, while a crescent-shaped lumen and a rounded lumen are revealed in the cross-sections of these setae. Pores are below the tip of the palpal setae, where some blobs are presumed to be secreted by pores on the external wall. The structure of the palp tarsal setae is almost consistent with those described taste sensilla in insects and spiders. Similarly, the dorsal surface of the anterior tarsi contains long, tapering socketed setae or short, blunt setae with or without sockets in *P. persimilis*. Some of the short setae with several pores are innervated by dendrites and are divided into three types (Jagers op Akkerhuis *et al*. 1985): (1) funnel-shaped pores in single-wall setae (Fig. 2A); (2) spoke canals with cone-shaped connections in the second wall to the inner fluid (Fig. 2B); and (3) spoke canals with a mushroom-shaped connection in an incomplete second wall to the inner fluid (Fig. 2C). Even if these short setae are different from each other in pore structure and number of innervations, the ultrastructure of these setae are similar with the olfactory sensilla known in insects. Consistently, our recent study shows the similar numbers of palp tarsal setae and putative olfactory sensilla at the tip of first pair of legs in *P. persimilis, N. californicus* and *A. swirskii* by SEM.

Given the analogous structures of smell and taste sensilla between insects and phytoseiid mites (Jagers op Akkerhuis *et al*. 1985; Ma *et al*. 2016), we presume the similar processing circle from stimulus to response between Insecta and Chelicerata (Fig. 1). In insects, the odors penetrate into the pores of the cuticular and reach olfactory receptor neurons (ORNs) of dendrites through odorant binding proteins (OBPs). It then activates the odorant receptors (ORs), gustatory receptors or ionotropic receptors (GRs or IRs) and generates action potential (Jacquin-Joly and Lucas 2005; Wilson and Mainen 2006). Subsequently, the axons of the ORNs transmit the signal to the primary brain-antennal lobe (Anton and Homberg 1999). The olfactory neurons and the local interneurons are connected to each other, then to the projection neurons. Finally, the signal can be transmitted to the higher brain center, such as the mushroom body and the lateral protocerebrum (De Belle and Kanzaki 1999; Ito *et al*. 2014). However, some differences of nerve structures between insects and chelicerates contribute to the neurophysiological differences. In the absence of OBPs and ORs, odors perception may be achieved through other related proteins, such as Niemann-Pick Type C2 (NPC2), which was indicated as potential carriers for semiochemicals in chemical communication with GRs or IRs (Vizueta *et al*. 2018; Li *et al*. 2020). Although transient receptor potential (TRP) channels are involved in the process of heat and light perception (Hoy *et al*. 2016; Peng *et al*. 2016), they have also been implicated as chemosensory receptors (Ngoc *et al*. 2016; Zhang *et al*. 2019a). The olfactory lobes filled with glomerulus in *P. persimilis* play the same role as the antennal lobes in insects, due to only the first pedal nerve innervating the olfactory lobes (van Wijk *et al*. 2006a). Unlike the meticulous investigations on insect brains, the study of advanced nerve center is scarce in Phytoseiidae as well as in Acari.

The ratio of receptor cells to olfactory glomeruli varies in different organisms. In Drosophila, for instance, the ratio is about 30:1 (~13000 to ~43) (Lessing and Carlson 1999). However, the female adults of P. *persimilis* have approximately a 1:1 ratio that is about 14-21 olfactory receptor cells and olfactory glomeruli, respectively (van Wijk *et al.* 2006b). Even with a small peripheral olfactory system, P. *persimilis* still can detect a large group of HIPVs emitted from T. *urticae*-infested plants which consist of 124 genera and over 900 species (Bolland *et al.* 1998). Unfortunately, no further research was conducted on olfactory and nerve systems in phytoseiid mites after 2006.

Chemosensory receptors predicted from genome sequencing

As discussed above, different chemical stimuli are perceived by ORs, IRs, GRs, NPC2 and TRP in invertebrates. ORs expressed in insect antennae are considered as an expanded phylogenetic lineage from GRs, which were expressed in many nonantennal sensory organs (Missbach *et al*. 2014). GRs recognize both contact chemical cues and volatile compounds (Nei *et al*. 2008). IRs and the ionotropic glutamate receptors superfamily (iGluR) are involved in both volatile odorant and taste perception (Joseph and Carlson 2015). The advent of the high throughput sequencing used in Acari species facilitates our understanding of the molecular basis of predatory mite olfaction. We found striking variances among chemoreceptor families in Acariformes and Parasitiformes, including three phytoseiids *M. occidentalis* (Hoy *et al*. 2016), *Neoseiulus cucumeris* (Zhang *et al*. 2019a) and *P. persimilis* (Xu *et al*. unpublished data) (Table 1).

TABLE 1. Chemoreceptor information in Acari. The bolds point to phytoseiid mite species.

Superorder	Order	Family	Species	GR	IR	iGluR	CSP	OBP-like	NPC 2	CD36-SNMP	Source	Reference
Acariformes	Trombidiformes	Tetranychoidea	*Tetranychus urticae*	469	5	14	0	4	47	13	Genome	Vizueta *et al*., 2018
	Sarcoptiformes	Acaridae	*Tyrophagus putrescentiae*	--	--	--	2	--	--	--	Transcripts (intact mite)	Qu *et al*., 2016
Parasitiformes	Mesostigmata	Phytoseiidae	*Metaseiulus occidentalis*	58	58	15	0	4	13	17	Genome	Vizueta *et al*., 2018
			Neoseiulus cucumeris	24	65	--	0	--	2	--	Genome	Zhang *et al*., 2019a
			Phytoseiulus persimilis	32	60	15	0	2	17	12	Genome	Xu *et al*., unpublished
		Dermanyssidae	*Dermanyssus gallinae*	0	6	5	--	8	6	5	Transcripts (forelegs and hindlegs)	Bhowmick *et al*., 2020
		Varroidae	*Varroa destructor*	3	46	--	0	5	8	8	Transcripts (intact mite)	Eliash *et al*., 2017
		Laelapidae	*Tropilaelaps mercedesae*	5	8	--	0	--	--	--	Genome	Dong *et al*., 2016
	Ixodida	Ixodidae	*Dermacentor variabilis*	3	2	27	--	1	--	0	Transcripts (forelegs and hindlegs)	Carr *et al*., 2017
			Ixodes scapularis	57	70	14	1	3	16	5	Genome	Vizueta *et al*., 2018

Predatory mites may rely on GRs and IRs for chemosensation from genomic clues (Vizueta *et al*. 2018). The identified GRs in Acari are highly divergent from insect GRs of known function, such as the sugar, fructose, carbon dioxide, and bitter taste receptors (Gulia-Nuss *et al*. 2016; Vizueta *et al*. 2018). Compared with 469 GRs identified in spider mites (Vizueta *et al*. 2018), about 24, 32 and 58 GRs are predicted from genomes of *N. cucumeris*, *P. persimilis* and *M. occidentalis* respectively (Table 1). Interestingly, these GR homologs showed different evolutionary relationships that 24 GR genes in *N. cucumeris* are clustered into three clans, while GR genes of *M. occidentalis* fall into two clans, one of which contains 50 GR genes as an intronless form (Hoy *et al*. 2016). The multiple duplications of this intronless ancestral gene may suggest the functional divergence of chemoperception in *M. occidentalis*. IRs, the biggest chemoreceptor family in Acari, are enriched in phytoseiid mites with approximate 60 homologs, which is over ten times more than that in spider mites. The number of chemoreceptor genes may indicate different chemosensory capacity in predatory mites, thus we speculate the importance of IR in chemical signal perception in further functional assignment.

ORs are thought to have originated with the appearance of flying insects for long distance communication (Arana *et al*. 2009; Vieira *et al*. 2011), thus it is plausible to be absent in Acari for weak dispersal capacity. However, OBP-like family with some sequence and structural similarity to insect OBPs is identified in Acari based on novel annotation method (Vizueta *et al*. 2018). The chemosensory proteins (CSPs) are also absent in most species of Acari with two exceptions, one *csp* gene in *I. scapularis* and two *csp* genes in *Tyrophagus putrescentiae* (Nuss *et al*. 2016; Qu *et al*. 2015). The CSPs are predicted to appear before the split of the Chelicerata and Pancrustacea lineages. In addition, other chemosensory receptors, such as NPC2 and CD36-SNMP (sensory neuron membrane proteins related to the CD36 receptor family) are predicted to play roles in sensory perception and conduction in Acari

(Vizueta *et al*. 2018). In *Neoseiulus barkeri*, there are three NPC2 genes, which might be involved in responding and binding to female sex pheromone (Li *et al*. 2020).

Interestingly, a gene family involving in olfactory long-term memory formation in *Drosophila*, oo18 RNA-binding protein 2 (ORB2) genes, have been found in *N. cucumeris* with two members, suggesting the potential genetic basis of learning ability in predatory mites (Zhang *et al*. 2019a). However, simple comparative analysis of genomic sequences does not allow inferring which specific members of already known chemosensory families are involved in which sensory modalities in Acari. Therefore, the assignment of specific functions requires further experimental evidence beyond the clues from multigenomic databases.

Perspectives

Chemoreceptor identification and function: Chemoreceptor repertories from genomic annotation and gene prediction provide the shortcut to study adaptive functions of species-specific genes related to stimuli perception and signal conduction. Particularly, high-throughput sequencing enables deep genome study of various predatory mites in a cheap and fast way. Thus, the development of computation methods is requisite for the identification and comparison of the entire gene repertoires in Acari. For complex structure and unconserved domain of diverse chemoreceptor family, more genes will be explored by advanced computational strategy and updated database. In previous research, chemoreceptor functions have been studied in a variety of heterologous systems, eg. Xenopus oocytes expression system, the insect cultured cell lines, *Drosophila* empty neuron system etc. The genetic engineering tools in vivo, TALENs system and CRISPR/Cas9 system, are thought to be more efficient and accurate ways to examine the function by knocking out the candidate genes. Fluorescence in-situ hybridization (FISH) can improve our knowledge of chemoreceptor location in chemosensory system in mites (Sumner-Kalkun *et al*. 2020). Further experimental verification of chemoreceptor function can be done in mites by advanced techniques.

Neural response to chemical compounds: Electrophysiology provides an efficient and effective way to study how chemical signaling transmits from olfactory sensilla to nervous system in phytoseiid mites. Although *P. persimilis* can respond to MeSA and DMNT involved in distant prey location (de Bruyne *et al*. 1991), the size of mites and technical difficulties limit the elaborateness of electrical potential in neuronal circuits that studies olfactory and nervous system of predatory mites were rarely reported in last decade. With the development of electroantennography and single-sensillum recording (SSR) techniques, tiny specimen can be handled by delicate manipulator, and combined with gas chromatography to measure the responses of sensory structure (*e.g.*, tips of the first pair of legs of phytoseiids) to MeSA and DMNT. In addition, some sophisticated methods used in insects offer the lessons to study mite electrophysiology (Olsson and Hansson 2013). For example, sensillum incision allows manipulation of the internal sensillum environment during SSR. Calcium imaging permits the visual monitoring of neural responses to odors in ensembles of neurons. Microinjection allows to study pharmacological effects on the response kinetics of olfactory sensory neurons.

Feeding behavior Manipulation: Despite the extensive practical use of phytoseiids for the biological control of pest species, much remains to be known about microhabitat and food preference for most of the species. By understanding the chemosensory mechanism of predatory mites, we can explain some fundamental questions in mite biology. What genetic factors affect the preference for different microhabitats and prey range? Why some taxonomic groups are much more diverse than others in terms of food or microhabitat preferences? Why some species are restricted to a narrow range of prey species or preferably resident in specific habitats? Once we know the underlying principle of "attractant-response-behavior" in mites, it is plausible to manipulate the feeding behaviors of predators, *e.g.*, to expand the prey range or change food habits by adding artificial compounds in ecosystems. We might also genetically modify key receptor genes (GRs/IRs) and potential channels of predatory mites to expand prey range of *P. persimilis* from only *Tetranychus* species to a wider range of tetranychid mites. Or, we could further limit prey range of *A. swirskii* and *N. barkeri* to improve predation efficiency of specific pest in certain greenhouses and to reduce the risk of interspecific predation or cannibalism.

Biological control application: Understanding the chemosensory capacity in phytoseiid species will facilitate better biological control in field application. For examples, what is the average or maximal dispersal distances of phytoseiids on fruit trees or vegetable stems? How to release those predators in a cost-effective way to manage target pests? Depending on different chemosensory capacities to some prey, predators can be released at an appropriate distance on stems or trees for better pest management. Additionally, although mint as a companion plant can attract *P. persimilis* (Togashi *et al*. 2019), we can add individual compound or the appropriate proportions of stimuli compounds at the same time to improve the efficiency of biological control by utilizing HIPVs in the predation process of phytoseiids. After clarifying the direction attraction mechanism of MeSA, DMNT and other stimuli, artificially releasing specific compounds to lure specific predators could be expected to improve foraging rates of predators and pest control in the field.

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