Using *Cucumis sativus*, *Acalymma vittatum*, *Celatoria setosa*, and generalist pollinators as a case study for plant–insect interactions

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Abstract

Showcasing how semiochemicals are both multifunctional and can influence a community of organisms is a constant frontier shared by chemical ecologists and applied entomologists alike. As researchers in these fields continue to share broad and overlapping interests, converging on one system could allow for a better understanding of community interactions and the chemical substances that mediate them. Cucurbit systems are strategically positioned to study these types of interactions because they combine the elements of plant–herbivore, plant–predator, and plant pollinator into one model and are systems where researchers can pursue both basic and applied questions. In this review, we propose *Cucumis sativus* [cucumber], *Acalymma vittatum* [striped cucumber beetle], *Celatoria setosa* [a natural enemy], and generalist pollinators as a system for continued investigation into semiochemicals, their multifunctional roles, and their influence on both target and nontarget organisms. We believe this system is ripe for further exploration at the frontiers in chemical ecology and applied entomology.

Keywords *Cucumis sativus* · *Acalymma vittatum* · *Celatoria setosa* · Semiochemicals · Chemical ecology · Multitrophic interactions

Introduction: Why coalesce on a system?

Plants, insects, and their natural enemies account for an abundance of diverse and ecologically important interactions. Driving these interactions are *semiochemicals*—substances that provide the framework for cross-taxa communication and behavior. Despite these abundant and diverse interactions, some substances are repeatedly used as an important chemical signal between and across multiple organisms (Raguso 2016). Investigating how semiochemicals have wide effects and influence a community of organisms, including target and nontarget *receivers*, have remained of interest especially against the backdrop of agroecosystems (Theis et al. 2009; Mallinger et al. 2011; Barber et al. 2012;

Shapiro et al. 2012; Theis and Adler 2012; Theis et al. 2014; Reviewed in Raguso et al. 2015; Brzozowski et al. 2016; Filgueiras et al. 2016; Davis et al. 2019; Helms et al. 2019; Brzozowski et al. 2020). And since many chemical ecologists and applied entomologist share broad and overlapping interests coalescing on one system could allow for a deeper understanding of plant–insect interactions, especially if that system could combine the elements of plant–herbivore, plant–predator, and plant–pollinator interactions into one. Cucurbit systems are strategically positioned to study plant–insect interactions and the semiochemicals that influence them. Cucurbits are diverse and grown across the globe (Chomicki et al. 2020), require insect pollination (McGregor 1976), are subjected to diverse above- and below-ground herbivory (Mondal et al. 2020), suffer insect vectored pathogens (Review in Rojas et al. 2015), recruit natural enemies (Agrawal et al. 2002; Grunseich et al. 2020), and produce unique secondary defense compounds (Metcalf et al. 1980). In this review, we propose *Cucumis sativus* [cucumber], *Acalymma vittatum* [striped cucumber beetle], *Celatoria setosa* [a natural enemy], and generalist pollinators as such a system. Our goal in this review is to showcase that this proposed system is interesting and eminently useful in

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pursuing frontier questions in chemical ecology and applied entomology.

The system: a brief overview

We believe *Cucumis sativus* [cucumber], *Acalymma vittatum* [striped cucumber beetle], *Celatoria setosa* [a natural enemy], and generalist pollinators when combined are an interesting model system for exploring the boundaries in chemical ecology and applied entomology (Fig. 1).

Cucumbers (*Cucumis sativus*) are a widely grown and economically important annual crop (Chomicki et al. 2020) pollinated by *Apis mellifera* [honey bees] and various species of bumblebees, such as *Bombus impatiens* (Stanghellini et al. 2002a, b). Cucumbers have also been repeatedly been used to pursue frontiers in chemical ecology, such as investigating chemical defenses and the recruitment of natural enemies using herbivore-induced plant volatiles (HIPVs) (Da Costa and Jones 1971; Howe et al. 1972; Gould and Massey 1984; Takabayashi 1994a, b; Agrawal et al. 1999; Agrawal et al. 2002; Balkema-Boomstra et al. 2003; Kappers et al. 2011; Grunseich et al. 2020) or links between above- and below-ground processes (Barber et al. 2011, 2012). In addition, the genome of *C. sativus* was also completed in 2009 (Huang et al. 2009) paving the way for future research with genetic applications, such as novel gene discovery (Shang et al. 2014), important signaling molecules in induced responses (Liu et al. 2019), transcriptome adaptations in response to herbivory (He et al. 2020), and insights into diversification of cucurbit lineages (Qi et al. 2013; Chomicki et al. 2020).

Acalymma vittatum [striped cucumber beetle] (SCB) is a specialist herbivore and major pest of all cucurbits including *C. sativus* (Ellers-Kirk and Fleischer 2006). SCB are highly destructive pests that feed above- and below-ground in larval and adult stages, respectively, use an aggregation pheromone (*vittatalactone*) to increase congregation onto their host plant (Smyth and Hoffmann 2003; Morris et al. 2005), and can phytophagously vector *Erwinia tracheiphila*, the pathogen cause of bacterial wilt (Reviewed in Rojas et al. 2015). SCB are obligate herbivores to cucurbits and as a consequence their behavior and biology are strongly influenced by cucurbit chemistry including secondary defense metabolites, blossom volatiles, and foliar volatiles (Metcalf et al. 1980; Lewis et al. 1990; Metcalf et al. 1995; Andrews et al. 2007; Shapiro et al. 2012; Theis et al. 2014; Brzozowski et al. 2020).

Celatoria setosa (Colliquet) [Diptera: Tachinidae] is a small and elusive parasitoid fly that is perhaps the best above ground natural enemy of SCB. *Celatoria setosa* has been found in Illinois, Maryland, and New York, Ohio, and Pennsylvania and has been shown capable of parasitizing

nearly half the wild SCB population (Walton 1914; Houser and Baldud 1925; Bussart 1937; Fischer 1983; Smyth and Hoffmann 2010; Coco et al. 2020). When combined these organisms create a unique model system that can be used for all fronts of plant–insect interactions. Although some of these organisms have also been extensively researched like *C. sativus*, other organisms like *Celatoria setosa* remain largely unexplored and provide new and exciting opportunities to investigate the influence of semiochemicals and their multifunctional nature.

Semiochemicals in the system

In this section, we highlight important characteristics of our proposed system and why it is a useful model for continued investigations of plant–insect interactions and the multifunctional nature of semiochemicals. We also highlight relevant semiochemicals and their effects and influences on other organisms. Finally, we touch on the recent discoveries within our system and discuss unexplored areas and opportunities for future research.

Toxic terpenoids: chemical defense in *C. sativus*, kairomones in striped cucumber beetle, and effects on nontarget organisms

Cucurbits chemically defend themselves against herbivory by producing a class of secondary defense compounds called cucurbitacins. Cucurbitacins are nonvolatile oxygenated tetracyclic triterpenoids that also are highly toxic. Cucurbitacins are well-studied and have a range of adverse effects on organisms that consume them including general cytotoxicity, cell-growth inhibition (Revi, digestive irritation, insect molting disruption, and feeding and oviposition deterrence (Chambliss and Jones 1966; Da Costa and Jones 1971; Reviewed in Jeffery 1980; Metcalf et al. 1980; Stowesand et al. 1985; Metcalf 1986; Tallamy and Gorski 1997; Tallamy et al. 1997; Dinan et al. 1997; Reviewed in Metcalf and Lampman 1989; Agrawal et al. 1999; Tallamy et al. 2000; Agrawal et al. 2002; Balkema-Boomstra et al. 2003). Cucurbitacins also function as an important karimone and phagostimulant in SCB, in both larvae and adults. For example larvae have been shown to grow larger and faster when reared on bitter diets as compared to nonbitter diets (Tallamy and Gorski 1997; Smyth et al. 2002) and adults displays clear preferences for cucurbit varieties that are higher in cucurbitacin concentration (Ferguson and Metcalf 1985; Tallamy and Gorski 1997; Smyth et al. 2002) although these preferences were found to be affected by age, sex, and previous feeding history (Smyth et al. 2002). SCB adults and larvae have also been shown to sequester cucurbitacins in various tissues including hemolymph, elytra, and adipose

Fig. 1 A graphical representation of our proposed system consisting *Cucumis sativus* [cucumber], *Acalymma vittatum* [striped cucumber beetle], *Celatoria setosa* [a natural enemy], and generalist pollinators with arrows indicating various semiochemicals and their multi-functional interactions within a community of organisms. Solid arrow indicates direct influences of a semiochemical or blend of semiochemicals supported by evidence, whereas dashed arrows indicate suspected semiochemical influence where more research is needed. The lettering “AG” and “BG” represent aboveground or below-ground respectively

tissue (Ferguson et al. 1983, 1985; Ferguson and Metcalf 1985).

Despite the wealth of knowledge surrounding cucurbitacins in both *C. sativus* and SCB, there are still a lot of unanswered questions regarding cucurbitacins and the greater role they play in the ecology of SCB and other non-target organisms that come in contact with cucurbitacins indirectly (Fig. 1). For example, sequestration of these toxic secondary metabolites has been shown to increase defense against some predators (Ferguson and Metcalf 1985), but other natural enemies, such as *Celatoria setosa* appear largely unaffected. *C. setosa* has been shown to parasitize really high percentages of SCB (upwards of 57% of a population sample) (Bussart 1937) and is orders of magnitude smaller than the predator (*Tenodera aridifolia sinensis*) used by Ferguson and Metcalf in their 1985 experiment. Although no study has directly compared the concentration of cucurbitacins in beetles parasitized by *C. setosa* it would seem that this parasitoid can tolerate some level of concentrations of cucurbitacins. Investigating how these predators deal with a toxic host would provide new insight into our understanding of indirect effects of plant defenses and the broader effects of cucurbitacins on beneficial organisms.

In a similar scenario, it is very likely that the pathogen vectored by SCB, *Erwinia tracheiphila*, is also coming into contact with dietary cucurbitacins. Populations of SCB have been shown to become increasingly infected with *Erwinia tracheiphila* throughout the growing season (Brust 1997) and *Erwinia tracheiphila* cells have been shown to adhere to and persist in SCB digestive tracts for as long as 30 days (Garcia-Salazar et al. 2000). As populations of SCB consume and metabolize cucurbitacins, *Erwinia tracheiphila* cells in infected SCB beetles are likely coming into contact with cucurbitacins. It is not known if this association between SCB and *Erwinia tracheiphila* is mutualistic or parasitic, but it does present an interesting opportunity to use *C. sativus* and *A. vittatum* to investigate interactions of cucurbitacins with an agriculturally important pathogen, *Erwinia tracheiphila*. Microbial chemical ecology is already an emerging frontier (Reviewed in Schmidt et al. 2019) and any interaction would be evidence of chemically mediated tri-trophic relationship. It may be possible that *Erwinia tracheiphila* is more parasitic in nature to SCB, and that SCB feeds on cucurbitacins to self-medicate against an infection. Self-medication behavior by consuming plant secondary metabolites has been shown in other systems including beetles *Drosophila* to (Milan et al. 2012) and Lepidopterans (Singer et al. 2009; Povey et al. 2014) to defend against parasitism but used against a pathogen is relatively novel.

***Cucumis sativus* recruits natural enemies above- and belowground**

When plants are damaged by herbivores, they release specific volatile organic compounds, commonly referred to as herbivore-induced-plant volatiles or (HIPVs), and these substances have been thoroughly studied across multiple systems (Reviewed in Turlings and Erb 2018). HIPVs can also serve as important chemical cues mediating plant insect interactions, such as priming plant defenses (Thaler 1999; Yi et al. 2009; Helms et al. 2019), deterring subsequent herbivory (Kessler and Baldwin 2001; Mallinger et al. 2011; Grunseich et al. 2020) or recruiting natural enemies (Kessler and Baldwin 2001; Kappers et al. 2011; Mallinger et al. 2011; Grunseich et al. 2020).

Aboveground, *C. sativus* has been shown to release HIPVs that help recruit natural enemies. For example *C. sativus* leaves were found to release four terpenes (E)- β -ocimene, (3E)-4,8-dimethyl-1,3,7-nonatriene, (E,E)-TMTT, and (E,E)- α -farnesene, as well as methyl salicylate when attacked by spider mites (Takabayashi et al. 1994a, b; Agrawal et al. 2002; Kappers et al. 2011). Damaged *C. sativus* plants were also found to be highly attractive to predatory mites and other insect herbivores (Agrawal et al. 2002; Kappers et al. 2011) and highlight a classic example of the semiochemical multifunctionality in which spider mite natural enemies using HIPVs as a karimonal cue. In addition, some of these compounds have been shown to recruit natural enemies in other systems such as (E)- β -ocimene and (3E)-4,8-dimethyl-1,3,7-nonatriene recruiting insect herbivore predators in cotton (Röse et al. 1998) and methyl salicylate recruiting predators in soybeans (Mallinger et al. 2011). In addition, a study published in 2012 found that *C. pepo texana* infected with *E. tracheiphila* released a blend of volatile compounds including terpenes like ocimene and nonatriene that were found to attract SCB adults (Shapiro et al. 2012). Specific and blended HIPVs from damaged cucurbit foliage likely function as an important cue for SCB host selection as well but more research is needed to fully understand this relationship.

Cucumbers also can release HIPVs belowground. In a recent study investigating belowground HIPVs in response to SCB larva feeding on *C. sativus* seedlings, researchers found that *C. sativus* seedlings released three monoterpenes [camphene, α -pinene, and sabinene] (Grunseich et al. 2020). Seedlings that were damaged were more attractive to entomopathogenic nematodes, suggesting that *C. sativus* recruits below ground predators too (Grunseich et al. 2020). In addition, SCB larva display preference for undamaged seedlings as compared to damaged seedlings that suggests these belowground HIPVs could also function as a subsequent herbivore deterrent or cue that predators are nearby. No study has looked at specific foliar HIPVs in response to

SCB herbivory, nor attractiveness of SCB damaged foliage to aboveground natural enemies such *Celatoria setosa*. Similar to recruitment of other predators it is likely that *C. setosa* uses *C. sativus* HPIVs as cue, but more research would be needed to determine which compound or blends of compounds are attractive.

Interactions between pollinators and herbivores and possible chemical cues

Researchers have used different combinations of cucurbit varieties, herbivores and pollinators to investigate multitrophic interactions. Discussing all of them beyond the scope of this piece, but two studies have used this proposed system (Barber et al. 2011, 2012) to investigate possible links between above- and below-ground processes with herbivores and pollinators. In one of these experiments researchers investigated the effects of above- and below-ground SCB herbivory on subsequent herbivory as well as flower production, floral resources, and pollination in *C. sativus* (Barber et al. 2011). The researchers found that honeybees spent more time probing *C. sativus* flowers on plants with root damage with less time spent probing plants with leaf damage (Barber et al. 2011). They also found that *C. sativus* plants with root herbivory produced fewer female flowers and had limited pollen production (Barber et al. 2011). In a similar study published a year later researchers found that SCB herbivory reduced honey bee and bumble bee visitations (Barber et al. 2012). Researchers also noticed the SCB were also less attracted to *C. sativus* with previous damage (Barber et al. 2012). Cucumbers typically produce more male flowers than female flowers and allocate more nectar to female flowers than male flowers (Collison 1973) so it is interesting that honeybees spend more time probing flowers with enhanced root damage but less time in flowers with leaf damage in Barber et al. 2011 experiments. Although the blend and ratio of volatiles can often be more important than the individual volatiles released (Reviewed in Raguso et al. 2015), it has been shown that cucumbers roots when damaged by SCB larva release the monoterpene α -pinene. α -pinene was also found to be a principal volatile compound released in cucumber flowers (Barber et al. 2012). Belowground volatile blends that contained α -pinene were also found to deter subsequent SCB larva herbivory as well as attract entomopathogenic nematodes (Grunseich et al. 2020). It is possible that both SCB and pollinating bees use α -pinene as an important chemical cue given that it is released by both roots and flowers but more research is needed to better understand this relationship.

In addition to α -pinene, *C. sativus* flowers have also been found to release other major floral fragrances including benzaldehyde, benzyl alcohol, 1,2-dimethoxybenzene, α -farnesene, and perhaps most relevant, linalool and its

metabolites (Barber et al. 2012; Wei et al. 2016). Linalool is a classic semiochemical found in many plant–pollinator and plant–herbivore systems and has a wide range of effects (Reviewed in Raguso 2016) wide range of effects further emphasizing how some semiochemicals have a diverse range. In *C. sativus* flowers, linalool serves as cue for pollinators (Barber et al. 2012) but the timing and concentration of released linalool and its metabolites may be more important for pollinators and perhaps herbivores too like SCB that are attracted as well. In fact, a recent study using *P. digitalis* and bumble bees, researchers showed under laboratory conditions only that bumble bees were able to discriminate among concentrations of linalool (Burdon et al. 2020). More work however is needed to better understand the relationship of pollinator signal discrimination and perhaps *C. sativus* and bumble bees would be a good model system to use. *C. sativus* flowers already allocate resources based on sex, such as female flowers producing significantly more nectar than male flowers (Collison 1973) and a recent study from 2016 showed that male and female flowers produce very different volatile profiles (Wei et al. 2016).

Final remarks

Cucumis sativus, *Acalymma vittatum*, *Celatoria setosa*, and generalist pollinators comprise a unique study system for chemical ecology that showcase how semiochemicals are both multifunctional and can influence a community of organisms. *C. sativus*, like other cucurbits, synthesizes extremely bitter triterpenoid compounds known as cucurbitacins. These compounds have shown to be effective chemical defenses for cucurbits and are also exploited by cucurbit specialist beetles as kairomones that provide important cues for their biology and behavior. Cucumbers also release blends of terpenes and other volatiles when under attack by herbivores that have been shown to recruit natural enemies above and belowground as well as deterring subsequent herbivory. The manner in which cucurbitacins mediate the interactions with predators and pathogens is a frontier both for this system and for chemical ecology in general. This is especially the case for investigations into the ecology of *Celatoria setosa*. In addition, using this model system to investigate above- and belowground multitrophic interactions remain an area for further exploration. The dynamic interactions between cucurbits, their herbivores, and their pollinators could piece together an entire story of chemically mediated interactions across a breadth of interactions.

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Declarations

Conflict of interest The authors listed below certify that they have no affiliation or involvement in any organization, individual, or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript. Text adopted by Elsevier <https://doi.org/10.1016/j.asjsur.2011.11.003>.

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