

Chemical ecology of *Halyomorpha halys*: discoveries and applications

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Abstract There have been notable and significant advances in elucidating the chemical ecology of the invasive *Halyomorpha halys* (Hemiptera: Pentatomidae), brown marmorated stink bug. This highly destructive and polyphagous pest is originally from Korea, China, and Japan, but was accidentally introduced into North America and Europe. Prior to its invasion into these regions, little was known about its chemical ecology. However, since then, researchers have identified and synthesized its aggregation pheromone, documented its synergism with the pheromone of another Asian stink bug, *Plautia stali*, developed monitoring traps of various designs, and lures with reliable attractants have become commercially available. Furthermore, plant volatiles have been shown to have attractive, neutral, and repellent effects on attraction and retention of *H. halys*, and *H. halys*-derived volatiles have been shown to play a role in recruiting natural

enemies. Finally, management strategies based on pheromone-based technology have been evaluated, including insecticide applications based on a cumulative threshold of adult captures in pheromone-baited traps, and the use of intensively baited trees in an attract-and-kill strategy to manage this pest. This review summarizes the available literature on the chemical ecology of *H. halys* and concludes with several research areas that should be explored in future research.

Keywords Pheromone · Allomone · Cross-attraction · Plant volatiles · Natural enemies · Insect dispersal · IPM · Monitoring · Attract-and-kill · Hemiptera · Pentatomidae · Brown marmorated stink bug

Key messages

- The male-produced aggregation pheromone of *H. halys* can be combined with the pheromone of *Plautia stali* for reliable attraction throughout the growing season.
- This combination affords monitoring and potentially attract-and-kill suppression.
- Nymphs and adults emit diverse volatiles functioning as allomones, antifungal agents, and kairomones for natural enemies that can potentially be used to detect adults in cargo and elsewhere.
- *H. halys* is polyphagous and highly mobile, thriving on mixed diets, and not strongly attracted by plant volatiles alone.

Introduction

The brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), native to eastern Asia, has invaded North America (first identified in Pennsylvania

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in 2001; Hoebeke and Carter 2003) and has been found in 43 US states and 4 Canadian provinces (Northeastern IPM Center 2017). It has also invaded Europe and is now established in Switzerland, France, Germany, Italy, Austria, Liechtenstein, Hungary, Serbia, Romania, Bulgaria, Greece, and Georgia (Haye et al. 2015b; Haye and Wyniger 2016). In its native and introduced range, *H. halys* feeds on a very broad variety of plants including many crops (Lee et al. 2013), and, not surprisingly, it has become a significant agricultural pest in the USA and parts of Europe (Leskey et al. 2012a, b; Haye et al. 2015b), in addition to its nuisance status as an invader of homes and other buildings for overwintering (Northeastern IPM Center 2017; Inkley 2012).

Stink bugs (Pentatomidae) are named for their characteristic volatiles, which arise from various acrid compounds, including straight-chain unsaturated aldehydes, which are considered allomones (defensive compounds) used against members of other species such as predators and parasitoids. Pentatomid males produce pheromones which are, depending on species, attractive only to females (sex pheromones) or attractive to both adult sexes (aggregation pheromones) (Weber et al. 2017). Of the 32 species in 22 genera which are known, about half of the pheromones discovered fall into each category. Those that are aggregation pheromones have all proven attractive to nymphs as well as to adults, when nymphal attraction has been investigated (Weber et al. 2017). Several stink bug aggregation pheromones elicit cross-attractive responses from other stink bug species, as is the case for *H. halys*, as both receiver and sender. Natural enemies may also exploit allomones or pheromones, and there are examples for egg parasitoids and predators of *H. halys*. Plant volatiles may be important in host-finding for phytophagous pentatomids, including *H. halys*, or they may function as repellents. A single semiochemical or co-emitted blend may have multiple functions, and therefore may function as a pheromone, allomone, kairomone, or synomone, depending on the relationship between sender and receiver. All of these relationships are considered below for *H. halys*.

Semiochemicals discovered for *H. halys* offer great opportunities for pest management. Various iterations include tools for monitoring and detection, decision making, and management strategies such as attract-and-kill, trap plants, and trap crops. Each of these tactics involves detailed considerations of attractant selection, dose, purity, controlled release, and distribution in, around, or outside the focal agroecosystem or target area to be monitored and/or protected. While this review focuses on the chemical signals associated with *H. halys*, it is important to bear in mind that other sensory inputs are also very important, particularly visual cues and short-range vibrational (substrate-borne) signals which mediate mate location (Čokl

and Millar 2009; Millar et al. 2010). For example, Leskey et al. (2015c) investigated and reviewed *H. halys* response to light stimuli, Polajnar et al. (2016) characterized the intraspecific vibrational communication for *H. halys*, and Mazzoni et al. (2017) found a specific *H. halys* vibrational signal to be attractive and arrestive to conspecific males. However, for the purposes of this review we limit ourselves to a review of olfactory stimuli (pheromones, allomones, synomones, kairomones, and plant volatiles).

Insect volatiles

Cross-attraction of *Halyomorpha halys* to the pheromone of *Plautia stali*

Asian researchers discovered that *H. halys* is attracted to methyl (2*E*,4*E*,6*Z*)-2,4,6-decatrienoate (hereafter, *EEZ*-MDT; Tada et al. 2001a, b; Lee et al. 2002), the aggregation pheromone of the brown-winged green stink bug, *Plautia stali* Scott (Sugie et al. 1996), which is sympatric with *H. halys* in northeast Asia. This cross-attraction was confirmed in the USA after *H. halys* became established (Aldrich et al. 2007; Khrimian et al. 2008). Although this compound partially isomerizes under field conditions, Khrimian et al. (2008) demonstrated that about 80% of *EEZ*-MDT could be preserved on rubber septum dispensers if the dispensers were shielded from direct sunlight. However, further field studies showed that preventing isomerization of *EEZ*-MDT was not essential, because *H. halys* adults and nymphs were still attracted to mixtures of methyl 2,4,6-decatrienoate isomers, indicating that other *cis-trans* isomers were not antagonistic. Furthermore, methyl (2*Z*,4*E*,6*Z*)-2,4,6-decatrienoate and methyl (2*E*,4*Z*,6*Z*)-2,4,6-decatrienoate (pheromone of pentatomid *Thyanta* spp.) attracted *H. halys*, possibly through isomerization to the (2*E*,4*E*,6*Z*)-MDT isomer. Alternatively, either or both of these other isomers may be attractive in their own right.

Halyomorpha halys does not emit *EEZ*-MDT or its isomers. But, before the actual pheromone was identified, *EEZ*-MDT was the primary lure used in traps to monitor *H. halys* after it became established in the USA (Leskey et al. 2012c). However, the lures were attractive almost exclusively in the late season in both Japanese and American studies, limiting their value for monitoring during a major part of the growing season, especially early in the season when population densities are lower and injurious populations are difficult to detect (Funayama 2008; Leskey et al. 2012c). Funayama (2008) assessed the nutritional status of captured *H. halys* and hypothesized that *H. halys* might be eavesdropping on *P. stali* pheromone as an indirect method of host location. Intriguingly, he found a strong response in

early season to methyl *EEZ*-MDT only during a single year (2001) of high populations and scattered early season response in years of moderate populations (2002 and 2006). One dataset of three in Weber et al. (2014) also showed low numbers of adults attracted to *EEZ*-MDT in early season (April). However, the two other datasets of that study, and the vast majority of studies in the USA (including Leskey et al. 2015a), and a replicated study in South Korea (Morrison et al. 2016b), did not show any early season attraction even during outbreak years (Leskey et al. 2012c). It is possible that the attractive effects of *EEZ*-MDT could be explained by male aggregation and subsequent pheromone production in the vicinity of *EEZ*-MDT-baited traps, possibly in response to vibratory signals from conspecifics, as Miklas et al. (2003) demonstrated for *Nezara viridula* (L.).

Aggregation pheromone discovery and synthesis

Khirmian et al. (2014a) identified the male-produced aggregation pheromone of *H. halys* as a 3.5:1 mixture of two stereoisomers, (3*S*,6*S*,7*R*,10*S*)-10,11-epoxy-1-bisabol-3-ol and (3*R*,6*S*,7*R*,10*S*)-10,11-epoxy-1-bisabol-3-ol (hereafter referred to as “SSRS” and “RSRS,” respectively, and shown in Fig. 1). The basic structure of these stereoisomers was first identified by comparison to spectral data from mixtures of the stereoisomers generated during pheromone identification for the harlequin bug, *Murgantia histrionica* (Zahn et al. 2008, 2012). The specific SSRS and RSRS stereoisomers produced by *H. halys* males were then identified by development of synthetic stereoisomeric libraries of 10,11-epoxy-1-bisabol-3-ols, and screening those on two enantioselective gas chromatography (GC) columns (Khirmian et al. 2014a, b).

A straightforward route to all stereoisomers of 1,10-bisaboladien-3-ol and 10,11-epoxy-1-bisabol-3-ol was developed (Khirmian et al. 2014a) via the rhodium-catalyzed asymmetric addition of trimethylaluminum (Siewert et al. 2007) to diastereomeric mixtures of cyclohex-2-enones, which were synthesized from commercially available (*R*)- and (*S*)-citronellals. Thus, a 1,4-conjugate addition of (*R*)-citronellal to methyl vinyl ketone mediated by diethylamino(trimethyl)silane, followed by intramolecular cyclization with potassium hydroxide catalyzed by tetrabutylammonium hydroxide (Hagiwara et al. 2002) provided cyclohexenone **1** (Fig. 1). Addition of trimethylaluminum to ketone **1** in the presence of chloro(1,5-cyclooctadiene)rhodium(I) dimer ([Rh(cod)Cl]₂) and (*R*)-BINAP (Fig. 1) yielded two stereoisomers, **2** and **3**, as major and minor products, respectively. Alcohol **2** was stereoselectively dihydroxylated with AD-mix-β, and the resulting triol **4** was converted to SSRS epoxybisabol-3-ol,

the main pheromone component of *H. halys* (Khirmian et al. 2014a) and *M. histrionica* (Khirmian et al. 2014b).

Addition of trimethylaluminum to ketone **1** in the presence of [Rh(cod)Cl]₂ and (*S*)-BINAP (Fig. 1) led to the stereoisomers **5** and **6**. The minor *trans*-stereoisomer **6** was dihydroxylated with AD-mix-β, and triol **7** was converted as described above to RSRS epoxybisabol-3-ol, the minor component of the *H. halys* pheromone blend. The synthesis of *trans*-bisaboladien-3-ol **6**, and thus RSRS epoxybisabol-3-ol, was recently improved by achieving a higher yield through introduction of chirality into the cyclohexenone molecule (i.e., ketone **1**), then non-stereoselectively adding methyl lithium and capitalizing on easy separation of *cis*- and *trans*-1,10-bisaboladien-3-ols (Khirmian et al. 2016).

The identifications of aggregation pheromone components of *H. halys* and *M. histrionica* were accomplished by careful matching of GC retention times of components in aeration extracts of male bugs with standards of known relative and absolute stereochemistries from the stereoisomeric library of 10,11-epoxy-1-bisabol-3-ols, on two enantioselective columns (Chiraldex G-TA and Hydrodex β-6TBDM; Khirmian et al. 2014a, b).

Patterns of pheromone emission by male *H. halys*

Harris et al. (2015) found that, under laboratory conditions, adult males began emitting pheromone at a mean age of ~13 days. When housed singly, males produced a mean of 843 ng of pheromone per day, in amounts that varied ~fivefold in daily volatile collections. There was a strong negative response to male density, such that males in groups emitted <10% of pheromone per bug per day as did lone males. This is consistent with other studies of pentatomids, e.g., Zahn et al. (2008) for *M. histrionica*. Males emitted pheromone primarily during the day.

Field attractiveness: combinations and ratios of pheromone components

In initial field bioassays, both the major component (SSRS) and the minor component (RSRS) attracted adult *H. halys* of both sexes, and nymphs. SSRS was more attractive than RSRS, whereas the mixture at the natural 3.5:1 ratio was more attractive than either component alone (Khirmian et al. 2014a). The ratio of SSRS/RSRS active stereoisomers in a synthetic mixture now used as the commercial attractant is approximately 1:1.7, in contrast to the 3.5:1 ratio in male bug pheromone emissions. Weber et al. 2017 (unpublished data) compared field captures in pyramid traps using these ratios of pure synthetic isomers, contrasted with SSRS and RSRS isomers alone and a blank control. They found the highest captures for male adults

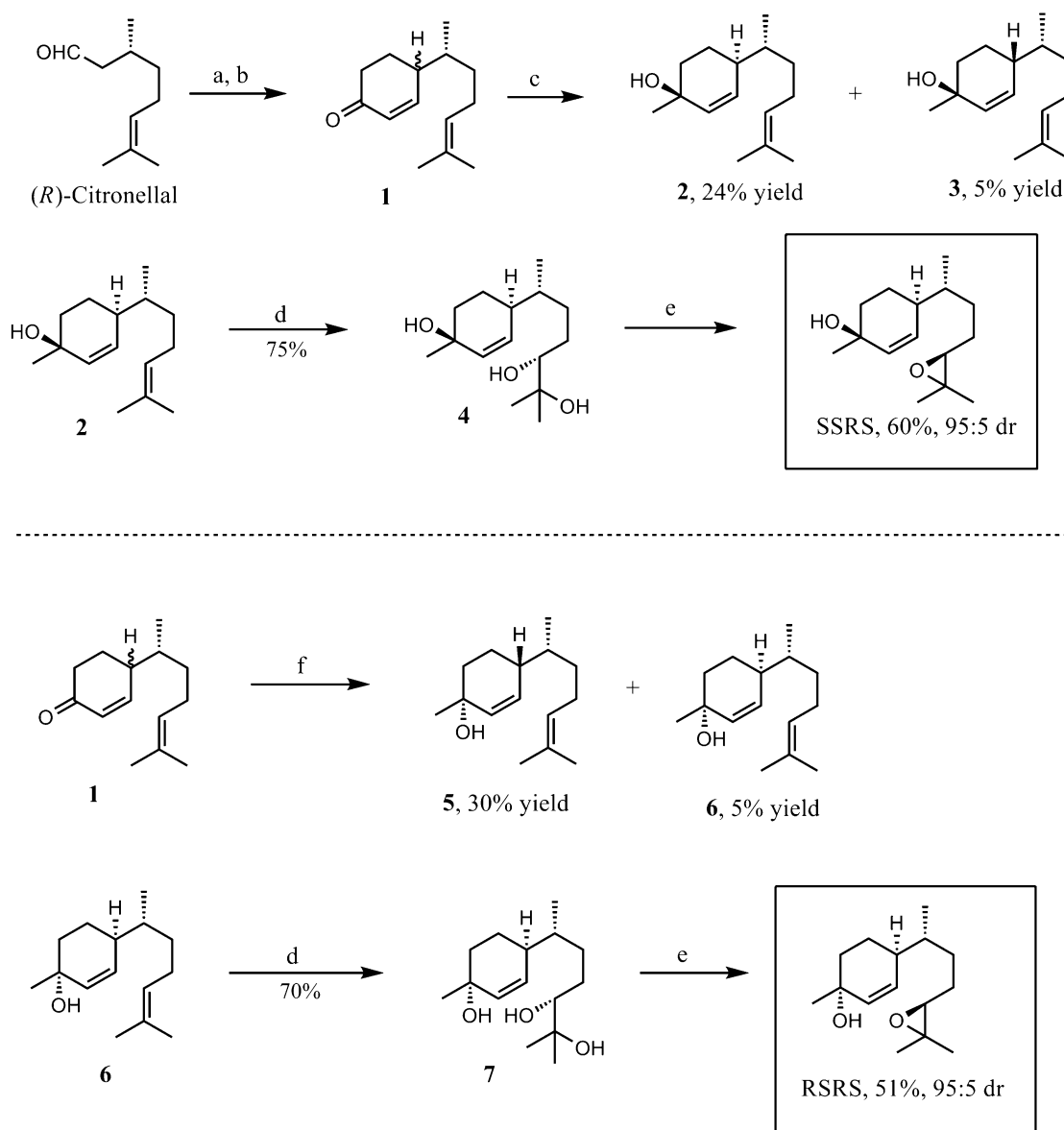


Fig. 1 Synthesis of (3*S*,6*S*,7*R*,10*S*)-10,11-epoxy-1-bisabolene-3-ol and (3*R*,6*S*,7*R*,10*S*)-10,11-epoxy-1-bisabolene-3-ol, *Halyomorpha halys* pheromone components (dr = diastereomeric ratio):

a MeC(O)CH = CH₂/(Et)₂NSi(Me)₃; **b** KOH/Bu₄NOH; **c** Me₃Al/([Rh(cod)Cl]₂/(*R*)-BINAP); **d** AD-mix-β; **e** NaOH/MeOH; **f** Me₃Al/([Rh(cod)Cl]₂/(*S*)-BINAP)

and nymphs in response to either blend, compared to the pure SSRS major component. Female adult captures were highest using the natural blend (3.5:1), which attracted more than either the 1:1.7 SSRS/RSRS blend or the pure SSRS. The RSRS minor isomer alone, unlike in the initial trial, did not attract significantly more bugs than the blank; these were different bug populations in different years, but the inconsistency of results suggests possible variability in response to the RSRS isomer. These results suggest that mixtures containing both pheromone components should be referenced by their content of the major pheromone component SSRS. The majority of research published to date has been done with lures (typically rubber septa)

containing an estimated 2 mg of SSRS (summary and citations in Table 1), but several other dispenser types are now being deployed.

Field attractiveness: purity of pheromone components

Lures with 8- or 16-way mixtures of stereoisomers also were attractive (Khrimian et al. 2014a; Weber et al. 2014; Leskey et al. 2015a, b), demonstrating that presence of non-pheromone stereoisomers does not seem to hinder attraction of *H. halys*. This is significant because it allows effective use of isomer mixtures of the aggregation

Table 1 Selected pheromone formulations used in trapping *H. halys*

Study	Pheromone components (mg)			Other isomers of murgantiol ^c and purity	<i>H. halys</i> response
	Lure ^a	SSRS ^b	RSRS ^b		
Khrimian et al. (2014a)	A	4.0	1.1	90% <i>de</i> ^d for both isomers	Adults: A > B > C > blank; nymphs: A, B > C, blank; lure A captured >40× adult and >12× nymphs versus blank
	B	4.0	–		
	C	–	4.0		
Weber et al. (2014)	BMSB1	2.0	0.7	(7 <i>R</i>) isomers, 3:1 <i>cis:trans</i> , 10.7 mg total murgantiol	Adults and nymphs strongly attracted to BMSB1 or BMSB2, especially in combination with <i>EEZ</i> -MDT; combined lures captured 40–111× adults & 12–31× nymphs versus blank
	BMSB2 (AgBio sachet)	2.0	4.0 ^e	(7 <i>R</i>) isomers, 1:2 <i>cis:trans</i> result from synthesis, 31 mg total murgantiol	
	SSRS + RSRS	3.1	0.9	90% <i>de</i> for both isomers	
Leskey et al. (2015a)	2012A = BMSB1	2.0	0.7	See BMSB1 above	Adults and nymphs strongly attracted; ~11× more adults and ~6× more nymphs captured versus blank
	2013A = BMSB2	2.0	3.2	See BMSB2 above	Adults and nymphs strongly attracted, esp. with <i>EEZ</i> -MDT; combined lures captured 24–40× more adults, and 11–17× more nymphs
Leskey et al. (2015b)	#3	–	–	(7 <i>S</i>) isomers, 3:1 <i>cis:trans</i> , 10.7 mg total murgantiol	Adult captures 2–6× blank and nymphal captures >blank; dose response demonstrated
	#6	2.0	0.8	see BMSB1 above	Adults and nymphs captures 7–19× and 1.2–4× versus blank, respectively; dose response with and without <i>EEZ</i> -MDT
	#8	2.0	–	All 4 <i>cis</i> -(7 <i>R</i>) isomers, total 8 mg	Adult and nymphal captures similar to #6
	#9	–	2.5	All 4 <i>trans</i> -(7 <i>R</i>) isomers, total 8 mg	Adult and nymphal captures not different from blank
	#11	2.0 ^f	3.2 ^f	See BMSB2 above	Adult and nymphal captures similar to #6, #13, #14, >10× versus blank
	#12	2.0	0.8	Similar to BMSB1 above, but less pure	Adult captures similar to #6 and #11, >10× versus blank
	#13	2.0 ^f	3.2 ^f	All 16 isomers with one chromatographic purification	Adult and nymphal captures similar to #11 and #14
	#14	2.0 ^f	3.2 ^f	All 16 isomers with no chromatographic purification	Adult and nymphal captures similar to #11 and #13
Morrison et al. (2015)	BMSB1	2.0	0.7	See BMSB1 above	Adults & nymphs strongly attracted in combination with <i>EEZ</i> -MDT with a range of different trap types (large and small pyramids, deployed variously; blanks not run)
Morrison et al. (2016a) and Morrison et al. (unpublished)	Gray septa	2.0	3.2	See #11 above	Dose-dependent increase in attraction of adults & nymphs, deployed with <i>EEZ</i> -MDT; area of arrestment ~2.5 m
	High-dose lure (Chem-Tica tea bag)	34.1 ^f	7.9 ^f	<i>cis</i> -(7 <i>R</i>) stereoisomeric mixture	Effective in attract-and-kill baited tree when combined with <i>EEZ</i> -MDT: resulted in a multiple-fold decrease in damage in attract-and-kill protected blocks compared to grower standard blocks
Short et al. (2016)	Gray septa	2.0	3.2	See #11 above	Used with <i>EEZ</i> -MDT to effectively trigger sprays in management regime while decreasing insecticide applications

^a Gray rubber septa, except as noted. Lure names as listed or specified in published studies

^b Loading to nearest reported 0.1 mg. SSRS denotes (3*S*, 6*S*, 7*R*, 10*S*)-10,11-epoxy-1-bisabolene-3-ol, and RSRS is (3*R*, 6*S*, 7*R*, 10*S*)-10,11-epoxy-1-bisabolene-3-ol

^c Murgantiol = 10,11-epoxy-1-bisabolene-3-ol (all isomers collectively)

^d *de* = diastereomeric excess

^e Reported as 4.0, but batch results range from 1:1.5 to 1:2 ratio of *cis:trans*, reflecting the 3.2 mg reported for RSRS in subsequent publications

^f Approximate values

pheromone for *H. halys* management without costly purification, or isomer-specific synthesis. Leskey et al. (2015b) reported a synthesis of “technical grade” pheromone from either (*R*)- or racemic citronellals using only one distillation and without chromatographic purification through the whole synthesis; the resulting mixtures of isomers attracted bugs in field bioassays, with or without the synergist *EEZ*-MDT (see Table 1 and below). Eight-isomer mixtures of synthesized (*R*)-citronellal were successfully used to monitor populations of *H. halys* in ten states across the USA (Leskey et al. 2015a). Although systematic studies of lure dose and formulations are still underway, rubber septa impregnated with 10.7 mg of more purified pheromone, or about 31 mg of the unpurified mixture of eight isomers produced from the large-scale synthesis from (*R*)-citronellal (both containing ~2 mg of SSRS) remained attractive for 2–3 weeks in field trials (Leskey et al. 2015a, b).

Synergy of the combination of *H. halys* pheromone and *EEZ*-MDT

The identification of the pheromone produced by *H. halys* males offered the opportunity to compare attraction by *EEZ*-MDT with synthetic *H. halys* pheromone preparations as well as with combinations of the two semiochemicals. Weber et al. (2014) found that a combination of a mixed-isomer preparation of the *H. halys* pheromone with *EEZ*-MDT acted synergistically. In season-long trials using pyramid traps, traps with both the *H. halys* pheromone and *EEZ*-MDT lures caught 1.9–3.2 times more adults, and 1.4–2.5 times more nymphs, than would be expected from additive effects of the compounds deployed individually. The pattern of captures of males and females was similar. This pheromone mixture was derived from (*R*)-citronellal and contained 2 mg SSRS isomer, and the *EEZ*-MDT lure was reported to contain 66 mg AI. Captures also increased with dose for the mixed-isomer lures with and without accompanying 66 mg *EEZ*-MDT (Leskey et al. 2015b). Morrison et al. (2016b) found that Korean populations of *H. halys* were similarly attracted synergistically to the combination of mixed-isomer pheromone and *EEZ*-MDT. Intriguingly, *P. stali* was cross-attracted to traps baited with *H. halys* pheromone mixture, but its attraction to the combination of *H. halys* pheromone and its own pheromone, *EEZ*-MDT, was not evaluated.

In all North American locations and in Korea, there is a marked seasonality in relative attractiveness of *H. halys* pheromone and *EEZ*-MDT when presented alone. In general, *EEZ*-MDT is attractive to adults in the late season and to nymphs season-long, whereas the pheromone is attractive to adults and nymphs season-long (see Weber et al. 2014; Leskey et al. 2015a; Morrison et al. 2016b).

However, the attractiveness of the combination of pheromone with *EEZ*-MDT has been shown in these studies always to be at least equal, and more often to significantly exceed, that of either attractant presented individually. Thus, the commercially marketed *H. halys* lures developed by several semiochemical companies consist of both components, known, respectively, as the pheromone (typically an eight-isomer pheromone mixture derived from (*R*)-citronellal) and its “synergist” (*EEZ*-MDT).

Cross-attraction presumably benefits the heterospecific pheromone receiver of the sender’s pheromone, which in this case functions as a kairomone or synomone, the latter if it benefits also the sender. Where they are sympatric in Asia, *H. halys* and *P. stali* pheromones (presented individually) are reciprocally cross-attractive (Morrison et al. 2016b), suggesting that both pheromones may qualify as synomones, but the selective benefits remain to be studied. Several benefits have been proposed for pentatomid cross-attraction resulting in aggregation: (1) location of food (Tada et al. 2001a; Endo et al. 2006), (2) location of overwintering sites (Khrimian et al. 2008), and (3) density-based protection from dipteran parasitoids (Aldrich et al. 2007). Pheromone cross-attraction between pentatomid species is a widespread phenomenon (Tillman et al. 2010; Weber et al. 2017). It may account at least in part, for the common observation of mixed-species occurrence while feeding (e.g., in soybeans, Owens et al. 2013; Tuelher et al. 2016), and in pre-overwintering and overwintering aggregations, including those of *H. halys* (Ueno and Shoji 1978, unpublished observations in USA by T. Leskey and T. Kuhar).

Other *H. halys* volatiles

Stink bugs emit a wide variety of hydrocarbons, aldehydes, oxo-aldehydes, and other volatile organic compounds in abundance from the dorsal abdominal glands of nymphs, and the metathoracic glands of adults (see, e.g., Lopes et al. 2015). (*E*)-2-alkenals are typically abundant and are considered allomones, i.e., defensive compounds, which prompt avoidance by generalist predators (e.g., Noge et al. 2012), though there is some evidence that trap-making species such as spiders can circumvent this defense (Morrison et al. 2017a). However, these compounds also have antifungal and antibacterial properties (Lopes et al. 2015; Sagun et al. 2016). They may also be exploited by parasitoids and predators (see Table 2 in Weber et al. 2017).

Kitamura et al. (1984) identified the common volatiles in male and female adult *H. halys* (then *H. mista*) as including *n*-alkanes and aldehydes, the most abundant of which were *n*-tridecane, *n*-dodecane, decenal and oxohexenal, without disclosing structures of the latter two. These

are common components of pentatomid metathoracic secretions, and these authors also found all four of these volatiles in *P. stali*, *Menida disjuncta* (Uhler) (Hemiptera: Pentatomidae) and *Megacopta punctatissima* (Montandon) (Hemiptera: Plataspidae). Harris et al. (2015) also detected and quantified tridecane and (*E*)-2-decenal emitted by both sexes and by third-instar nymphs. The latter compound is considered an allomone and alarm pheromone (see Weber et al. 2017), and its distinctive odor, which is shared with the cilantro plant (= coriander, *Coriandrum sativum* L. (Apiales: Apiaceae)), is capable of tainting wine made from grapes infested at harvest, depending on abundance and specific wine-making processes (Mohekar et al. 2017a, b). However, (*E*)-2-decenal does not transfer to cow milk when it is ensiled with cattle fodder (Baldwin et al. 2014). Harris et al. (2015) found that (*E*)-2-decenal was much more abundant in emissions from nymphs (mean >3 µg/day) versus single females (mean 422 ng/day) or males (mean 99 ng/day).

Several studies have investigated *H. halys* volatiles for detection of bugs in the various settings including cargo and in overwintering sites. Nixon et al. (unpublished) sampled headspace from diapausing and diapause-disrupted aggregations of *H. halys* using volatile collection traps and solid phase microextraction, and found that the predominant compounds included tridecane, 4-oxo-(*E*)-2-hexenal, and (*E*)-2-decenal. In addition, stink bugs in diapause readily emitted these compounds, suggesting that they may be of use for monitoring international shipments for the presence of *H. halys*-infested cargo. This result was not surprising, based on the successful training of canine detectors to signal the presence of diapausing *H. halys* in a variety of settings (Lee et al. 2014a). Following the lead of Bromenshenk et al. (2015), a New Zealand group has found that honeybees are very sensitive to several compounds emitted by *H. halys* and related pentatomids (Mas et al. 2014). Bees have successfully been trained to exhibit proboscis extension reflex behavior and open field searching to these volatiles (Russell et al., in prep.). A. Harper et al. (unpublished) found that the emissions from *H. halys* varied in quantity and ratio depending on whether the bugs were alive or dead, which may have implications for the detection of live bugs when trained on dead ones. Interestingly, Zhang et al. (2016) found that the combination of (*E*)-2-decenal and tridecane resulted in strong feeding deterrent activity for *H. halys* in laboratory trials.

Tridecane emissions, in contrast to the pattern with (*E*)-2-decenal, were especially high in crowded males, increasing ~9-fold when males were in groups versus alone, and Harris et al. (2015) stated that tridecane inhibited pheromone production by individual males; however, Figs. 4 and 5 of Harris et al. (2015), which purport to show

this effect, are not convincing nor statistically analyzed. Lockwood and Story (1985, 1987) had earlier reported that tridecane acts as a nymphal aggregation pheromone at low doses but as an alarm pheromone at high doses in *Nezara viridula* (L.) (Hemiptera: Pentatomidae). Fucarino et al. (2004), however, were not able to replicate results of Lockwood and Story (1987), probably because doses used by Lockwood and Story were well above the biologically relevant range. Thus, it remains unclear whether the reported responses to linear hydrocarbons including tridecane represent biologically relevant responses. Authors beginning with Calam and Youdeowei (1968) suggested that such hydrocarbons function as solvents or carriers, rather than as inherently bioactive compounds, to mediate the efficient evaporation of aldehydes and other active compounds on the structurally specialized thoracic scent efferent system common to many pentatomoids (Kment and Vilimova 2010), providing a reason for the relatively large quantities found in stink bug glands.

H. halys volatiles and entomopathogenic fungi

Aldehydes produced abundantly by *H. halys*, including (*E*)-2-decenal and (*E*)-2-octenal, are fungistatic and inhibit spore germination in entomopathogenic fungi in the genera *Metarhizium*, *Beauveria*, and *Isaria* (Pike 2014). (*E*)-2-decenal has been investigated for this effect in the context of other stink bug species. Borges et al. (1993) showed inhibition of the entomopathogen *Metarhizium anisopliae* (Metschnikoff) Sorokin (Hypocreales: Clavicipitaceae) by aldehydes produced by *N. viridula*, (*E*)-2-decenal and (*E*)-2-hexenal, when tested individually or combined. Sosa-Gomez et al. (1997) also showed that (*E*)-2-decenal was strongly fungistatic on *N. viridula* cuticle against *M. anisopliae* but not against *Beauveria* and *Paecilomyces* spp. Da Silva et al. (2015) found that synthetic versions of (*E*)-2-hexenal, (*E*)-2-octenal, and (*E*)-2-decenal inhibited spore germination, growth, and sporulation of *M. anisopliae* strain CG168, a commercially marketed entomopathogen in Brazil. Lopes et al. (2015) found that the volatiles from “fungus-resilient” species of pentatomids tested showed a strong fungistatic effect, and a somewhat less-pronounced fungicidal effect, on *Beauveria bassiana* (Balsamo) Vuillemin (CG1105) conidia, with individual compounds (*E*)-2-hexenal, (*E*)-2-octenal, and (*E*)-2-decenal showing also dose-dependent inhibition of spore germination, but with tridecane showing zero effect on spore germination. These authors concluded that, because the effective levels of single aldehydes were significantly higher than those present in pentatomids tested, the observed fungistasis and fungal mortality were most likely effected by a combination of the compounds present, and that these acted both through the gaseous phase (as

volatiles) and through direct contact. There is a continuing necessity in studies with stink bug volatiles and pathogenic fungi to demonstrate that concentrations and arenas used are realistic compared to bugs in field settings.

Use of *H. halys* semiochemicals by natural enemies

Pentatomid natural enemies exploit the volatile chemicals produced by their hosts as kairomones to locate them (see review by Weber et al. 2017). The compounds exploited can include host allomones, pheromones, or other host-associated compounds such as frass, exuviae, and host “footprints.” In egg parasitoids, primarily the scelionid wasps of genera *Telenomus* and *Trissolcus*, many results support the importance of (*E*)-2-alkenals to locate their preferred pentatomid hosts (Borges and Aldrich 1992; Pareja et al. 2007; Laumann et al. 2009; Vieira et al. 2014). There may also be other compounds involved, depending on host species (Weber et al. 2017). Morrison et al. (2017b) provided evidence that native natural enemies do not use the *H. halys* aggregation pheromone to find this bug’s egg masses. Rondoni et al. (2017) detected attraction of the native European parasitoids *Anastatus bifasciatus* (Geoffroy) (Hymenoptera: Eupelmidae) and *Ooencyrtus telenomicida* (Vassiliev) (Hymenoptera: Encyrtidae), but not *Trissolcus basalis* (Wollaston), to *H. halys* males in Y-tube bioassays.

Studies in Maryland, USA, have shown that naturally laid eggs are more heavily parasitized than laboratory-sourced, artificially placed sentinel egg masses of *H. halys* (Jones et al. 2014). Presumably, this is due to the attachment of the egg mass to the plant and to footprints left by the female on leaf surfaces. Laboratory experiments (S. Boyle et al., U. Delaware, unpublished) show that these traces stimulate the host searching behavior of the Asian *Trissolcus japonicus* (Ashmead), allowing the parasitoid to more rapidly locate and parasitize *H. halys* egg masses. This species, and *Trissolcus cultratus* (Mayr), are the most important egg parasitoids of *H. halys* in Asia (Leskey et al. 2012a). In contrast to Asian species, native North American and European Scelionidae, which often abundantly attack *H. halys*, frequently fail to develop in the exotic host, thus representing a sink or “evolutionary trap” for these natural enemies (Haye et al. 2015a; Herlihy et al. 2016; Abram et al. 2014). Related studies have shown that egg dissections are important, because many of the eggs with no outcome contain undeveloped or developed nymphs or parasitoids (Cornelius et al. 2016). Molecular analysis has shown that DNA from several native parasitoid species is present in sentinel and field-collected *H. halys* egg masses in Ontario (Canada), including *Trissolcus thyantae* (Ashmead), *Trissolcus euschisti* (Ashmead), *Telenomus podisi* (Ashmead), and other *Telenomus* spp. (T. Garipey et al., unpublished). This indicates that, although they fail to complete

development, native parasitoids can locate and oviposit in naturally occurring and sentinel *H. halys* eggs. However, two scelionids native to California, *Trissolcus erugatus* Johnson and *Te. podisi*, are strongly repelled by aldehydes associated with *H. halys* eggs (hexadecanal, octadecanal, and eicosanal) in laboratory Y-tube choice assays (Tognon et al. 2016). Intriguingly, these longer-chain aldehydes were found in similar ratios also in the genital capsule extracts of *H. halys* males and may be transferred to the female during mating. Both *Tr. erugatus* and *Te. podisi* were attracted to methyl (2*E*, 4*Z*)-2,4-decadienoate, which is present on native *Euschistus conspersus* Uhler egg masses and is that species’ aggregation pheromone. Using field sentinel egg masses of *E. conspersus*, parasitism by *Tr. erugatus* and *Gryon obesum* Masner (Hymenoptera: Scelionidae) was higher on eggs washed and then re-treated with methyl (2*E*, 4*Z*)-2,4-decadienoate, than either on washed eggs or those washed then re-treated with the synthetic *H. halys* egg aldehyde blend odor of hexadecanal, octadecanal, and eicosanal (Tognon et al. 2016). This suggested that the olfactory cues from *H. halys* egg masses were, in this California environment, unattractive to native egg parasitoids, unlike the situation for sentinel *H. halys* egg masses in eastern USA or Europe, which were found heavily attacked, often unsuccessfully, by natives.

Interestingly, tridecane was emitted not only from *H. halys* nymphs and adults but also from bean pods previously damaged by *H. halys*, and it attracted predaceous minute pirate bugs, *Orius* spp., in greenhouse and field experiments (Fraga et al. 2017). Several studies with pentatomids have shown that egg parasitoids exploit herbivore-induced plant volatiles (HIPVs) to locate pentatomid host eggs. For example, *Te. podisi* exploited HIPVs indirectly to locate *Euschistus heros* (F.) eggs (Moraes et al. 2005, 2008; Michereff et al. 2011). Colazza et al. (2004) reported that *N. viridula* feeding on beans also elicited HIPVs that attracted the egg parasitoid *Trissolcus basalis* (Wollaston). Pentatomid oviposition may also induce plant volatiles or non-volatiles that attract and/or arrest egg parasitoids. Conti et al. (2010) demonstrated that with *M. histrionica* as host, a complex of host- and plant-produced compounds aided egg location by *Trissolcus brochymenae* (Ashmead). Rondoni et al. (2017) found that some native European parasitoids (*A. bifasciatus* and *Oo. telenomicida*), but not others (*Tr. basalis*), are attracted to volatiles emitted by host plants (fava bean, *Vicia faba* L.) oviposited upon by *H. halys*.

Plant volatiles and *H. halys*

Plant volatiles are recognized as important to trophic interactions in agriculture (e.g., Pliske et al. 1976; Turlings et al. 1990; Dudareva et al. 2013). In fact, a meta-analysis

has found that 75% of 374 unique plant volatile-insect herbivore interactions resulted in attraction, with an intermediate effect on herbivore abundance based on the mean effect size (Szendrei and Rodriguez-Saona 2010). While the role of stink bug pheromones in the chemical ecology of *H. halys* has been heavily explored, comparatively very little work has been performed on the role of plant volatiles in the foraging ecology of *H. halys* and tritrophic interactions of the pest. Because *H. halys* is highly polyphagous, feeding on >100 plant species, this may suggest one of two a priori possibilities. First, it is possible that the odor profile is relatively flexible as *H. halys* searches the environment, depending in part on its internal state and external conditions. Alternatively, it may be that *H. halys* is attracted to volatile compounds that are generally expressed across a wide range of taxa, such as green leaf volatiles (Schoonhoven et al. 1998; Bernays and Chapman 1994). We consider the evidence for both below.

Attraction and retention

The nymphs of *H. halys* have a robust capacity for walking and exhibit a strong response to the *H. halys* aggregation pheromone + synergist, traveling at least 20 m to reach the source (Lee et al. 2014b). In order to better understand how *H. halys* nymphs react to host plant volatiles, Blaauw et al. (2017) performed a replicated study evaluating host plant attraction of *H. halys* nymphs to, and headspace analysis of, four crops (Swiss chard, bell pepper, sweet corn, and soybean) throughout the crops' phenological stages. Nymphs readily dispersed from or remained on a sentinel host plant depending on the resources provided by the hosts, which changed throughout the season. Subsequently, host attraction, documented through host choice, was correlated with host plant phenology. Of the 17 volatile organic compounds that were common among the four host plants, five identified were expressed by plants when those plants were the most attractive to nymphs. Although preliminary, these five volatiles (caryophyllene, decanal, nonanal, phenol, and undecane) were unattractive individually to *H. halys* nymphs in laboratory trials but, when combined in a blend, attracted on average 10% more nymphs than the control. However, field evaluation of this blend at 1×, 5×, and 100× concentrations did not show enhanced attraction to plant volatiles by nymphs in a mark-release-recapture study (Blaauw and Nielsen unpublished data).

The distinction between attraction and retention (arrestment) is important, but often overlooked. Both contribute to population distribution, but semiochemicals and other environmental factors may be attractive but not arrestant, vice versa, or both. In the case of *M. histrionica*, for instance, Cabrera Walsh et al. (2016) found that pheromone lures hung above host collard plants were highly

attractive, but did not affect the retention of bugs on the treated plants. For *H. halys*, Blaauw et al. (unpublished) found a differential retention capacity between a trap crop of peppers and sunflower compared to a cash crop of bell peppers using harmonic radar and immunomarking with proteins. In that study, the authors only found 6% of adults doubly marked with both proteins, signifying minimal movement between the plant communities, and harmonic radar revealed that adults stayed for 1.5 times longer on trap crop plants than those in the cash crop. Morrison et al. (2017b) examined the effect of host stimuli augmented with plant volatiles and pheromone on the retention capacity and attraction of *H. halys*. That study evaluated the effect of mixtures of apple fruit, peach fruit, green leaf volatiles, or no plant volatiles, and found that supplemental volatiles provided a boost to the retention capacity of host plants for *H. halys*, but this was relatively small compared with the increase in retention capacity provided by adding pheromone and *EEZ*-MDT synergist. Green leaf volatiles were present in each of the blends, suggesting the importance of these cues in the arrestment of *H. halys*. Interestingly, deployment of plant volatiles resulted in potential inhibition of attraction by *H. halys* nymphs to pyramid traps that contained pheromone. Moreover, the host plant that *H. halys* was released on significantly affected the retention capacity, with non-host plants retaining adults for a shorter period of time (Morrison et al. 2017b). This suggests that there may be other host stimuli that are important for retention and attraction of *H. halys* to a location (e.g., visual, thermal, gustatory, auditory).

Plant-derived repellents

Plant-derived compounds may also play repellent roles (e.g., De Moraes et al. 2001; Hayes et al. 1994). Zhang et al. (2014) investigated nine essential oils, a ternary mixture of oils, as well as nine individual plant volatile components that exhibited coupled gas chromatography-electroantennographic detection (GC-EAD) activity for *H. halys*. The authors found that clove, lemongrass, spearmint, and ylang-ylang oil were the most effective at inhibiting attraction to traps baited with *EEZ*-MDT, while the most inhibitory plant volatile chemicals were eugenol, *l*-carvone, *p/l*-methone, and methyl salicylate (Zhang et al. 2014). Another study tested the preference of *H. halys* adults and nymphs for leaves treated with a commercial blend of essential oils (10% rosemary, 2% peppermint oil: EcoTec, EcoSmart Technologies, Inc.), kaolin (e.g., particle film, Surround), or nothing at all (Morehead et al. 2016; Morehead 2016). The study found that adults and nymphs interacted with leaves more in the presence of the essential oils, but avoided leaves with the kaolin clay relative to the control. In the field, weekly applications of the essential

oils did not result in a significant reduction in damaged bell peppers on three out of five harvests, though kaolin applications resulted in 76–90% reduction in damage (Morehead 2016). Another study found that a mixture of essential oils (0.25% rosemary, 0.25% peppermint, 0.25% thyme, and 0.25% clove oil) resulted in about 75% mortality of *H. halys* nymphs, but did not increase the mortality of adults when applied topically as a spray in laboratory trials (Bergmann and Raupp 2014). The plant-derived mosquito- and tick-repellent isolongifolenone (Zhang et al. 2009) have also shown activity as a strong feeding deterrent to *H. halys* adults and nymphs in the laboratory (Zhang et al. 2016). However, in both the case of isolongifolenone and the combination of secretion components of *H. halys* ((*E*)-2-decenal and tridecane), phytotoxicity has proven a challenge to translating the results to the field.

Alteration of plant volatiles by *H. halys*

In a diverse array of other species, it is not uncommon for herbivory to affect the emissions profiles from various plant taxa (e.g., Morrison et al. 2016c; Pierre et al. 2011; Conti et al. 2008). A recent study by Zhou et al. (2016) found that feeding on blueberries by *H. halys* altered the plant's chemistry, and that this changed the feeding frequency by conspecifics. While that study did not directly assess the plant volatiles produced, it did document a lower Brix, higher total phenolics, and a lower proportion of anthocyanins derived from malvidin after feeding by *H. halys*. The study also documented that fruit that were previously fed upon were less preferred to conspecifics than unfed fruit, and one possible explanation for this may be changes in the emissions of plant volatiles as a result of altered underlying chemistry. Altered plant chemistry and plant emissions may also have implications for the natural enemy community of *H. halys*, and the role of *H. halys*-induced-plant volatiles in tritrophic level interactions needs further investigation.

Research needs on the role of plant volatiles

Overall, it appears that host stimuli are important for foraging decisions and attraction of *H. halys* and potentially for their key natural enemies, but plant volatiles are just one component of this. Plant volatiles have been shown to be both mildly attractive and inhibitory of attraction in prior research. This has included field experiments assessing attraction to naturally emitted volatiles in headspace, but also crude mixtures of plant volatiles as a bait, as well as compounds that *H. halys* is not likely to encounter in the wild such as essential oils. At this point, it is hard to make generalizations, and therefore, more research is required on the foraging cues used by *H. halys* to gain a

more comprehensive understanding of the role that plant volatiles play in foraging decisions by this pest. Future work should especially focus on the volatile cues emitted by host plants at the height of their attractiveness to *H. halys* in the field, attempt to understand commonalities among those headspace profiles in order to relate it back to behavioral responses of *H. halys*, and elucidate how plant volatiles may be affecting its key natural enemies.

Movement and dispersal

Halyomorpha halys experience greater fitness when feeding on multiple host plant species compared with single host plant diets (Funayama 2002; Acebes-Doria et al. 2016) and this may explain their strong capacity to disperse at landscape scales. Coupled with this dispersal tendency, the lack of strong attraction to plant volatiles may indicate that movement is mediated first by random or explorative dispersal, followed by arrestment on preferred plant hosts and subsequent pheromone-mediated aggregation of bugs on these hosts. Based on flight mill studies, *H. halys* have the ability to fly 117 km/day, although average flights were ~2 km per day (Lee and Leskey 2015; Wiman et al. 2015). In the field, flight occurs during day and night and averages ~3 m/s (Lee and Leskey 2015; Rice et al. 2014). Actively foraging adults have greater dispersal capacity compared with overwintered adults (Lee and Leskey 2015). However, recent laboratory and field trials suggest overwintered *H. halys* undertake a dispersal flight upon diapause termination, before they are attracted to aggregation pheromone (Bergh et al. 2017; Morrison et al. 2017c). *Halyomorpha halys* nymphs also actively disperse and can move over 20 m in the field in 4–5 h (Lee et al. 2014b), and readily move vertically as well (Acebes-Doria et al. 2017).

Landscape factors such as available host plant species and overwintering shelters influence *H. halys* dispersal behavior (Venugopal et al. 2015a; Rice et al. 2016), whereas housing developments and railroads may facilitate human-mediated transport (Wallner et al. 2014). Several techniques have been used to quantify *H. halys* movement in the field including black light traps (Nielsen et al. 2013), harmonic radar (Morrison et al. 2016a), and protein markers (Blaauw et al. 2016; Blaauw et al. unpublished). Novel mark-release-recapture techniques using handheld focusable lasers provided nondestructive detection of fluorescent marked *H. halys* at a distance of 40 m allowing monitoring *H. halys* movement in forest canopies (Rice et al. 2015). Future studies of *H. halys* response to semiochemicals using marked individuals in the natural landscape may enable outstanding behavioral and chemical ecology questions to be addressed at landscape scales.

Use of lures and traps for monitoring and management

Lures for monitoring *H. halys*

The pheromone-based tools developed for *H. halys* may be employed for monitoring of the species. In the development of commercially viable lures, there are several important considerations. For example, unlike many species of Lepidoptera where highly purified pheromone is needed (reviewed in Ando et al. 2004), *H. halys* does not require highly purified pheromone; other stereoisomers of 10,11-epoxy-1-bisabolene-3-ol (murgantiol) do not elicit inhibition of response, and the species is even possibly attracted to stereoisomers not naturally found in the wild (Leskey et al. 2015b). This suggests that impure blends of the main pheromonal components may be used without impairment of biological activity. In addition, there is a dose-dependent response in attraction to both the aggregation pheromone (Morrison et al. 2016a) and *EEZ*-MDT (Leskey et al. 2012b), such that more pheromone results in greater number of adults and nymphs captured. Finally, it is important that a lure be long-lasting so that it requires little maintenance during the growing season. The original rubber septa lures used with *H. halys* pheromone for research purposes required changing every 2 weeks, whereas currently available commercially formulated lures with the *H. halys* aggregation pheromone recommend changing once every 4 weeks (AgBio, Inc.) or once every 12 weeks (Trécé, Inc), and a lure may be forthcoming in the near future that will remain attractive over the entire growing season for 16 + weeks (Short and Leskey, unpublished data). Prior work has demonstrated that commercially available *EEZ*-MDT lures last a maximum of four weeks (Joseph et al. 2013). Commercially available lures have demonstrated season-long attraction of *H. halys* throughout the USA when changed regularly (Leskey et al. 2015a), as well as in the species' native range in the Republic of Korea (Morrison et al. 2016b).

Trap design and positioning

In order for a lure to be effective, it must have a trap that is compatible with the focal pest's behavior. Work with native stink bugs, including *Euschistus* spp., has shown that yellow pyramid traps were effective in capturing individuals in apple and peach orchards in the eastern USA (Leskey and Hogmire 2005). Early work with *H. halys* in soybeans compared two sizes of yellow pyramid traps baited with *EEZ*-MDT, with the large size pyramid (142 cm height) having significantly higher numbers of *H. halys* (Nielsen et al. 2011). The smaller trap (81.3 cm

height) was attractive until the canopy covered the trap, blocking any visual cues to migrating adults. In comparison trials, Leskey et al. (2012b) found that darker-colored pyramid traps, including black wooden ones, were the most effective in capturing *H. halys*. Black pyramid traps outperformed hanging bucket traps and canopy-deployed pyramid traps in capturing adults and nymphs, and the proposed reason for this was that the pyramid traps may be a trunk-mimicking stimulus (Leskey et al. 2012b). When commercially available *H. halys* lures are paired with the black pyramid trap, there are reliable captures throughout the growing season when the lures are changed at regular intervals (Leskey et al. 2015a; Morrison et al. 2016b). In order to find a trap that is more compatible with current grower management practices in orchards, follow-up studies have investigated whether alternative trap designs can deliver biologically similar information to the black pyramid trap, while retaining sensitivity (e.g., Morrison et al. 2015; Rice et al. unpublished data, Leskey et al. unpublished data). Those studies have found that when effective lures containing the *H. halys* aggregation pheromone and *EEZ*-MDT are used, alternative trap styles such as clear sticky cards attached to wooden posts and small pyramid traps deployed in trees are also effective for season-long detection of *H. halys* though some of these may not be as sensitive as a corrugated plastic (coroplast), black pyramid trap. Figures 2, 3, and 4 illustrate the lure types, toxicant types, and trap designs tested by researchers in North America and Asia, while Table 2 gives commercially available products and duration of trap components.

The position of traps is also important for accurately monitoring a population, and placing traps in the appropriate location also depends on the focal pest movement patterns. In a variety of systems, *H. halys* is a perimeter-driven pest, with greatest pest abundance and highest damage on the borders of fields, including for orchard crops (Joseph et al. 2014; Blaauw et al. 2015, 2016), corn and soybeans (Venugopal et al. 2015a), woody nurseries (Venugopal et al. 2015b), grapes (Basnet et al. 2015), and vegetables (e.g., Soergel et al. 2015). In addition, some borders of fields are more at risk of invasion by *H. halys* populations, especially those surrounded by woodlands (Venugopal et al. 2014; Rice et al. 2016) or soybean (Venugopal et al. 2015b). However, there is also movement of *H. halys* into the interior of blocks (e.g., Blaauw et al. 2016). In addition, Sargent et al. (2014) placed pyramid traps baited with *EEZ*-MDT lures in community vegetable gardens infested with *H. halys*, and more bugs and greater damage were noted on tomato fruits near the traps. Similarly, *P. stali* injury to persimmon fruit in Japan, adjacent to poisoned eggplant trap plants baited with *EEZ*-MDT, was severely damaged (Yamanaka et al. 2011). Thus, judicious placement of traps relative to susceptible

crops is an essential consideration. There is little detailed knowledge for optimal trap placement except in tree fruit, where the ideal locations for traps to monitor *H. halys* are at the perimeter or within the border rows, and in an ancillary fashion, the interior of blocks but away from host plants, to understand whether individuals are moving into the interior of plantings and/or if reproduction may be occurring in situ (e.g., Short et al. 2016; Blaauw et al. 2016; Morrison et al. unpublished). Because of the spillover effects noted earlier, traps are not placed directly adjacent to crop plants, but rather between plants, which often ameliorates the spillover effects. Cropping systems, such as soybean, which have low profit margins may benefit from alternative sampling protocols such as the use of visual surveys instead of the use of traps and lures.

In addition to an appropriate lure and deployment device, there must be a mechanism to prevent escape of *H. halys*. In many prior studies, a 10% dimethyl 2,2-dichlorovinyl phosphate (DDVP)-infused kill strip has been included in the jar top of the pyramid traps discussed above (e.g., Leskey et al. 2015b; Morrison et al. 2015), which has been registered for use in some but not all US states as a toxicant in insect traps. These strips often require replacement every 2–4 weeks under field conditions, and prior work has shown that the numerically highest number of adults result from the use of fresh kill strips (Joseph et al. 2013). More recently, insecticide-infused netting, similar to that used to combat pathogen-carrying mosquitoes, has been employed with great success. For example, lining the base of jar tops on pyramid traps with this netting can result in season-long kill of *H. halys* without the need for replacement under field conditions (Kuhar et al. 2017). This shows promise in making pyramid traps less cumbersome to maintain through the season, but is not yet registered for use in insect traps.

Patterns and limitations of semiochemical-based monitoring

Generally, captures in the current standard black pyramid trap with commercially available lures (combination of aggregation pheromone and *EEZ*-MDT) peak in the late season (mid-August to late September), though in higher population years, there tends to also be an earlier peak in mid-June from overwintering populations (Leskey et al. 2015a). Captures are elevated season-long with the combined stimuli compared to either stimulus alone (Weber et al. 2014). There is a similar pattern of capture using the same system in Asia (Morrison et al. 2016b).

However, the current pheromone-based tools have some important limitations. For example, as *H. halys* seeks out overwintering sites around the autumnal equinox in the USA, adults cease to be responsive to their pheromone and then to *EEZ*-MDT as well. As a result, trap captures

rapidly decline. Likewise, in the late winter, the pheromones do not seem functional in monitoring *H. halys* inside buildings or in the wild (Morrison et al. 2017c). Another study has suggested that *H. halys* may require a spring dispersal flight before becoming responsive to its pheromone, as almost no marked bugs that were settled in overwintering structures out of thousands were captured in pheromone-baited pyramid traps in the direct vicinity (10 m away) from March to late June (Bergh et al. 2017). However, with those caveats, pheromone-baited traps generally capture *H. halys* from April to October, which includes the full growing season for most crops. As a result, the pheromone-based tools that are currently available meet the needs of growers and scouts, but do not meet the needs of homeowners, who typically are interested in trapping out all individuals invading their homes.

Overwintering traps

Beyond the standard growing season trap design discussed above, there is promise in the development of artificial overwintering structures for monitoring *H. halys* populations during the fall and winter. For example, in the Asian literature, some authors have employed apple crates packed with straw (Funayama 2003), paper (Yanagi and Hagihara 1980; Oda et al. 1982), or straw mats (Oda et al. 1982) and placed these adjacent to buildings known to have large overwintering populations. Wooden slit traps have also been used under the eaves and on the roofs of heavily infested locations (Watanabe et al. 1994). More recently, Bergh et al. (2017) presented one design composed of wood and cardboard, which are able to capture up to 3000 dispersing *H. halys* adults during the fall in the mid-Atlantic USA (Leskey et al. unpublished data). These trap designs can be used to intercept *H. halys* dispersing into buildings, but also to examine the emergence pattern of the species in the early spring. For example, Bergh et al. (2017) consistently found that there are two peaks of emergence in the early season over 3 years, one in early April and another in late May to mid-June. It is possible that adults in the early peak are responding to temperature cues in the environment, while the latter peak is responding to photoperiod cues (Bergh et al., unpublished data). If effective attractants during the fall and winter could be found, these could be combined with these shelters to create attract-and-kill sites for dispersing adults in the fall, both helping homeowners and growers in the subsequent season.

Use of monitoring for pest management decision making

Pheromone-based technology is already being employed in management studies for *H. halys*. For example, Short et al.

Lures

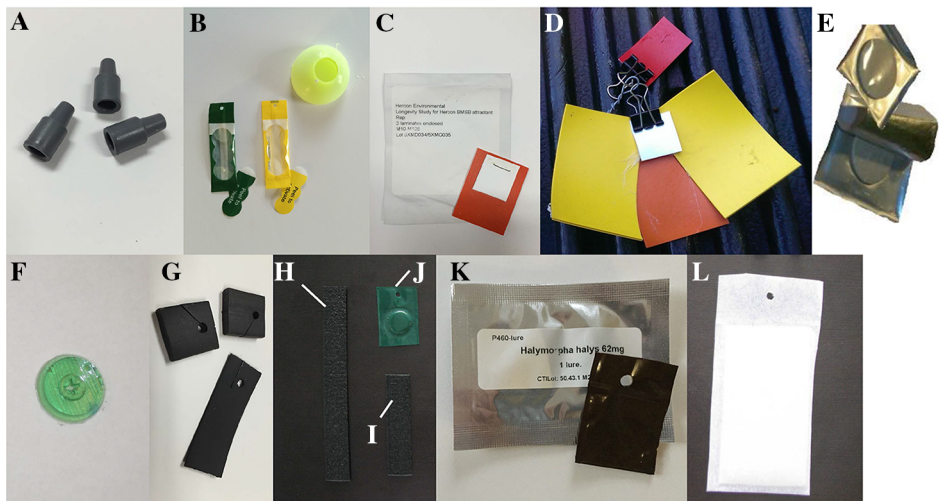
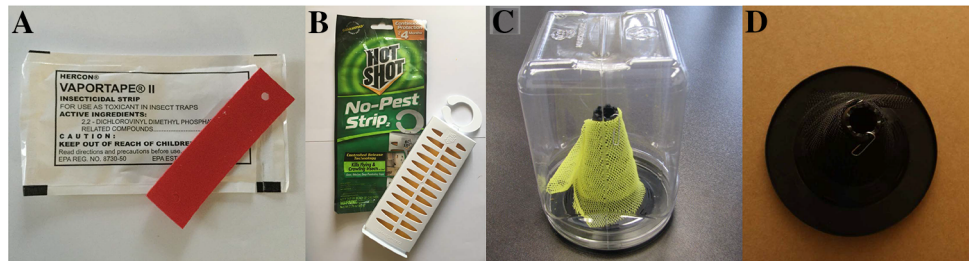


Fig. 2 Lures that have been used for monitoring and managing *H. halys*. Lures include **A** the original experimental rubber septa lures in the US, **B** commercially available Rescue lures (Sterling International), **C, D** Hercon-produced lures, **E** AlphaScents-produced lures, **F** Scentry-produced lures, **G, H, I** Trécé-produced lures, including current standard monitoring lures (2 MDT lures and one BMSB lure pictured), experimental high dose high-dose lure, and prior standard

monitoring lure, respectively, and **J, K, L** AgBio-produced lures, including a murgantiol monitoring lure, MDT-only lure, and a specially formulated high-dose “tea bag” aggregation pheromone lure, respectively. Pictures were contributed by Jay Abel, Samuel Brandt, John Cullum, Torri Hancock, Megan Herlihy, Rob Holdcraft, William R. Morrison III, Kevin Rice, Cesar Rodriguez-Saona, and Brent Short

Fig. 3 Toxicants and lure deployments that have been used for monitoring and managing *H. halys*. Toxicants include **A** Hercon-produced insecticide-infused strip, **B** Hot Shot™ insecticide-infused strip, as well as more recent **C, D** deltamethrin-infused insecticide netting (Vestergaard Frandsen, Inc.). Lure deployment can either be **E** outside the trap, or **F** inside the trap, with trap captures generally higher when the lure is placed outside the trap (Leskey et al., unpublished). Pictures were contributed by Torri Hancock, Megan Herlihy, and William R. Morrison III

Kill Mechanisms



Lure Deployment



(2016) have deployed pheromone-baited pyramid traps to develop a cumulative threshold of ten adults per trap for apples in the eastern USA. Once the threshold is reached, it triggers two back-to-back alternate row middle sprays of the orchard over a two week period, and then the threshold is reset. In that study, two pyramid traps with the *H. halys*

aggregation pheromone and *EEZ*-MDT were deployed per orchard block [mean area, 0.32 ha ± 0.26 (SD)], and relative to blocks that were sprayed every week with an insecticide, threshold-managed blocks used 40% less insecticide, while delivering equivalent control of *H. halys* injury to apple trees. This approach significantly reduced

Traps



Fig. 4 Lures, kill mechanisms, trap types, and lure deployments that have been used for monitoring and managing *H. halys*. *Trap types* have included: **A** standard wooden 1.22-m pyramid, **B** lighter-weight coroplast 1.22-m pyramid, **C** smaller 0.29-m pyramid traps deployed on the ground, **D** on a limb in a tree, or **E** hanging from a branch, **F** the commercially available Rescue trap (Sterling International), **G** pipe trap, **H** the commercially available delta trap, **I** commercially available yellow sticky trap hung in a tree, **J** clear sticky trap

deployed on a stake, **K** Japanese-produced bucket trap, and **L** Japanese-produced pyramid trap deployed in a tree, **M** AlphaScents-produced pyramid trap, and **N** AlphaScents-produced clear panel trap. Pictures were contributed by Samuel Brandt, John Cullum, Torri Hancock, Tracy C. Leskey, William R. Morrison III, and Brent Short

the frequency of broad spectrum insecticides now often targeted for *H. halys* (Leskey et al. 2012b). Incorporating an action threshold is an economical approach based on pest biology and is compatible with existing grower management programs. However, as lure formulations change, and for different agroecosystems, this action threshold will need to be adjusted. Another unknown parameter is the optimal number of monitoring traps needed per acre to effectively monitor *H. halys* populations. Future research should resolve these open questions.

Attract-and-kill tactic to suppress *H. halys* populations

Morrison et al. (2016a) investigated the behavioral basis for an attract-and-kill tactic for *H. halys* in apple. In a 6-day period on a total of six trees, a total of almost 30,000 adults and 5000 nymphs were killed with trees baited with 1000 mg of aggregation pheromone (200 mg of SSRS and 70 mg of RSRS active isomers) and 66 mg of EEZ-MDT (Morrison et al. 2016a). These adults were killed with a contact insecticide (bifenthrin in this case) sprayed on the trees. By contrast, a typical trap capture in the same year with a pyramid trap and the combined stimuli at the normal lower loading rates (10 mg of mixed murgantiols containing 2 mg SSRS active isomer and ~119 mg of EEZ-MDT) averaged 10–16 adults and 12–18 nymphs (Leskey et al. 2015a). Baited attract-and-kill trees sprayed on a weekly basis with insecticides efficacious against *H. halys*

(e.g., Leskey et al. 2012d) in a research orchard resulted in a very small area of arrestment, with spillover of adults, nymphs, and damage mostly confined to the baited tree. A proof of concept for attract-and-kill in commercial orchards was conducted in 2015 and 2016, with attract-and-kill sites spaced every 50 m around the perimeter of an apple block on ten farms in five mid-Atlantic US states (Morrison et al. unpublished). This translates to roughly seven attract-and-kill sites for every 0.81 ha, depending on the configuration of the block; because these are deployed on borders only, the number of sites required per ha will likely decrease as the size of the block increases. Each attract-and-kill site had a baited tree with 840 mg of the aggregation pheromone (reached by adsorbing 420 mg of a 10% cis-(7R)-10,11-epoxy-1-bisabolene-3-ols onto a tea bag lure (Fig. 2L), and placing 20 lures in a tree) and 66 mg of EEZ-MDT (for details see Morrison et al. 2016a). Baited trees and neighboring perimeter trees within 5 m distance were sprayed with an efficacious insecticide (e.g., Leskey et al. 2012d) on a weekly basis. The study found equivalent or lower stink bug damage in attract-and-kill apple blocks compared to grower standard blocks throughout the season. While resulting in a 97% reduction in the area treated with an insecticide in an orchard, the main challenge for attract-and-kill is to overcome the increased cost of the lures, which amounts to ~\$900 US dollars per acre over the season. This cost might be ameliorated through less expensive synthesis and/or formulation, decreased amounts of lure provided per attract-and-kill site, by decreasing the

Table 2 Commercially available lures, traps, and killing devices for monitoring *H. halys* in US specialty crop production as of May 2017

Company	Product name	Claimed duration	Website for more information including pricing	Corresponding picture in Figs. 2 or 4
<i>Lures</i>				
AgBio, Inc.	Stink Bug Xtra Combo	4 weeks	http://www.agbio-inc.com/dead-inn-pyramid-trap.html	2J
Alpha Scents	HALHAL	4 weeks	http://www.alphascents.com/lures/lures1/lures1.html	2E
Hercon Environmental	BMSB Lure	8 weeks	http://www.herconenviron.com/index.html	2D
Sterling International	Rescue Stink Bug Attractant	7 weeks	http://www.rescue.com/product/rescue-stink-bug-attractant	2B
Trece, Inc.	Pherocon BMSB Lure	12 weeks	http://www.trece.com/PDF/Pherocon_Stink_Bug.pdf	2G
<i>Traps</i>				
AgBio, Inc.	4' Dead-Inn Grower Trap	Reusable	http://www.agbio-inc.com/dead-inn-pyramid-trap.html	4B
AgBio, Inc.	2' Dead-Inn Professional Trap	Reusable	http://www.agbio-inc.com/dead-inn-pyramid-trap.html	4C
AgBio, Inc.	16" Dead-Inn Homeowner Trap	Reusable	http://www.agbio-inc.com/dead-inn-pyramid-trap.html	–
AgBio, Inc.	6 × 28" Clear Sticky Trap	4–6 weeks	http://www.agbio-inc.com/dead-inn-pyramid-trap.html	–
Alpha Scents	Black pyramid trap	Reusable	http://www.alphascents.com/splash/splash3/splash3.html	4M
Alpha Scents	Black modified panel trap	Reusable	http://www.alphascents.com/docs/AlphaScents_Panel_Trap_Modified_for_Brown_Marmorated_Stink_Bug.pdf	–
Sterling International	Rescue Stink Bug Trap	Reusable	http://www.rescue.com/product/reusable-outdoor-stink-bug-trap	4F
Trece, Inc.	6 × 9" Clear Sticky Trap	4–6 weeks	http://www.trece.com/PDF/Pherocon_Stink_Bug.pdf	4J
Trece, Inc.	Funnel traps	~6 months	http://www.trece.com/PDF/Pherocon_Stink_Bug.pdf	–

number of attract-and-kill sites in total, and by evaluating whether a single attract-and-kill block can provide areawide suppression of *H. halys* populations.

Conclusions

Overall, there have been significant advances made in discovery of semiochemicals associated with *H. halys*, and their function in its ecology and behavior. The threat posed by *H. halys* has motivated research to develop pheromone-based tools and management strategies for appropriately dealing with invasions of North America and Europe. Prior to these invasions, very little was known about the most effective traps, lures, placement, or identity of or purity of aggregation pheromone required for optimal attraction. There are now reliable, commercially available monitoring traps and lures, and several different styles are effective throughout the growing season, including ground-deployed large pyramid traps and clear sticky cards. These traps can be used with thresholds in some crops to trigger management decisions, which ultimately reduce insecticide usage while increasing control of *H. halys* in an economical

manner. The deployment of pheromone at attract-and-kill sites can decrease insecticide applications even more substantially, though this technique still needs to be optimized for widespread adoption. These pheromone-based threshold and management strategies are most applicable in apple, as this has been one of the most severely affected crops, but are being expanded to other cropping systems. Ornamental systems are the least likely to require the use of pheromone-based tools because economic damage rarely occurs even though *H. halys* has been documented feeding on nursery plants (Bergmann et al. 2016).

Important future directions for research on the chemical ecology of *H. halys* include (1) evaluation of the role of semiochemicals in tritrophic interactions with natural enemies in its introduced and native range and their potential for manipulating the third trophic level for improved biological control, (2) clarification of the role that plant volatiles play in foraging decisions by *H. halys* and their prospects for incorporation into lures, (3) elucidation of the underlying ecological-evolutionary basis for attraction of both nymphs and adults to the *H. halys* aggregation pheromone, and for cross-attraction involving other species, (4) a fuller understanding of the role that

semiochemical cues (and those of differing modality) play in the overwintering aggregation behavior of the species as well as its emergence in the spring, (5) development of novel means for detection and location of bugs using the volatiles they emit; (6) insight into how different sensory modalities (particularly olfaction, vision, and vibrational communication) interact in bug behavior, and finally, (7) a more mechanistic understanding of olfactory signaling and olfaction by *H. halys* on the molecular level.

Author contribution

DCW and WRM organized the review based on contributions from all authors. DCW drafted the overall manuscript. All authors contributed to the writing of the manuscript and approved the final manuscript.

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