



Assessment of Development, Parasitism, and Predation of *Halyomorpha halys* (Hemiptera: Pentatomidae) in *Sassafras* (Lauraceae) in Southeastern US Agroecosystems

Authors: Tillman, P. Glynn, Kesheimer, Katelyn A., Hirsch, Katherine L., and Grabarczyk, Erin E.

Source: Florida Entomologist, 106(1) : 16-21

Published By: Florida Entomological Society

URL: <https://doi.org/10.1653/024.106.0103>

Assessment of development, parasitism, and predation of *Halyomorpha halys* (Hemiptera: Pentatomidae) in sassafras (Lauraceae) in southeastern US agroecosystems

P. Glynn Tillman^{1,*}, Katelyn A. Kesheimer², Katherine L. Hirsch², and Erin E. Grabarczyk¹

Abstract

The invasive brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), is a polyphagous pest that disperses from non-crop host plants into crops in search of food. Sassafras trees (*Sassafras albidum* (Nutt.) Nees; Lauraceae) are found commonly in woodland habitats in the southeastern US and may therefore be a potential host. The main objective of this 2-yr study was to determine if sassafras serves as a host plant for this pest in woodland habitats adjacent to crops in Prattville, Alabama, and Byron, Georgia, USA. Each yr pheromone-baited traps were deployed in the canopy of sassafras trees to capture *H. halys*. We also evaluated parasitism and predation of *H. halys* sentinel egg masses by native parasitoids and predators in sassafras. *Halyomorpha halys* adult males and females as well as second through fifth instars were captured in traps and observed in sassafras trees over the season at both locations each yr of the study. *Trissolcus euschisti* Ashmead (Hymenoptera: Scelionidae) (67.7%) and *Anastatus redivivus* (Howard) (Hymenoptera: Eupelmidae) (18.3%) were the primary parasitoid species that emerged from *H. halys* sentinel egg masses. Stylet sucking (62.3%) and chewing (32.0%) were the primary types of predation on *H. halys* eggs. We conclude that sassafras is a reproductive host plant for *H. halys*, and native natural enemies prey on and parasitize *H. halys* egg masses in this host plant.

Key Words: brown marmorated stink bug; non-crop host plant; sentinel egg mass; pheromone-baited trap

Resumen

La chinche hedionda invasora marrón marmorada, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), es una plaga polífaga que se dispersa de plantas hospedantes no cultivadas a los cultivos en busca de alimento. Se les encuentran en los árboles de sasafrás (*Sassafras albidum* [Nutt.] Nees; Lauraceae) comúnmente en hábitats boscosos del sureste de los EE. UU. y por lo tanto este puede ser un hospedero potencial. El objetivo principal de este estudio de 2 años fue determinar si el sasafrás sirve como planta hospedera para esta plaga en hábitats boscosos adyacentes a cultivos en Prattville, Alabama, y Byron, Georgia, EE. UU. Cada año, se colocaron trampas cebadas con feromonas en el dosel de los árboles de sasafrás para capturar *H. halys*. También evaluamos el parasitismo y la depredación de masas de huevos centinela de *H. halys* por parasitoides nativos y depredadores en sasafrás. Se capturaron machos y hembras adultos así como ninfas del segundo al quinto estadio de *Halyomorpha halys* en las trampas, y se observaron en árboles de sasafrás durante la temporada en ambos lugares cada año del estudio. *Trissolcus euschisti* Ashmead (Hymenoptera: Scelionidae) (67,7%) y *Anastatus redivivus* (Howard) (Hymenoptera: Eupelmidae) (18,3%) fueron las principales especies de parasitoides que emergieron de las masas de huevos centinela de *H. halys*. La succión por los estiletes (62,3%) y la masticación (32,0%) fueron las principales clases de depredación sobre los huevos de *H. halys*. Concluimos que el sasafrás es una planta hospedera reproductiva para *H. halys*, y los enemigos naturales nativos se alimentan y parasitan las masas de huevos de *H. halys* en esta planta hospedera.

Palabras Clave: chinche hedionda marrón marmorada; planta hospedera no cultivada; masa de huevos centinela; trampa cebada con feromonas

The invasive brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), is an economic pest in orchards, vegetables, row crops, vineyards, and ornamentals (Rice et al. 2014; Leskey & Nielsen 2018). This species oviposits and develops on a broad range of non-crop host plants that often are found in woodlands that border orchards and crop fields (Bakken et al. 2015; Bergmann et al. 2016). As a result, non-crop host plants near crops can be unmanaged sources of *H. halys*, as well as native stink bug species, that later dis-

perse into crops (Venugopal et al. 2014; Tillman & Cottrell 2016a). Thus, identifying host plants that occur commonly in woodlands near crops is important to link patterns of *H. halys* dispersal with local habitat composition. Sassafras (*Sassafras albidum* (Nutt.) Nees; Lauraceae) is a fruiting tree that grows commonly in woodland and marginal habitats of the southeastern US. Although sassafras has been listed as a wild host plant of *H. halys* (CABI 2022), very little information is available in the literature regarding development of stink bug species on this host.

¹USDA-ARS, Southeast Watershed Research Laboratory, Tifton, Georgia 31793, USA; E-mail: Glynn.Tillman@usda.gov (P. G. T.), Erin.Grabarczyk@usda.gov (E. E. G.)

²Auburn University, College of Agriculture, Auburn, Alabama 36849, USA; E-mail: kak0083@auburn.edu (K. A. K.), klh0083@auburn.edu (K. L. H.)

*Corresponding author; E-mail: Glynn.Tillman@usda.gov

Therefore, the first step in our goal to understand the spatial and temporal dispersal and aggregations of *H. halys* in woodlands and crops in agroecosystems with sassafras, we examined the development of *H. halys* in sassafras in a woodland habitat adjacent to row crops.

Several studies have shown that pyramid traps baited with commercially available aggregation pheromones are highly attractive to capture of *H. halys* males, females, and nymphs in field settings (Khrimian et al. 2014; Weber et al. 2014; Leskey et al. 2015). The commercially available dual pheromone lures for *H. halys* include the aggregation pheromone of *H. halys*, a combination of stereoisomers (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 (PHER), and a synergist, methyl (2*E*,4*E*,6*Z*)-2,4,6-decatrienoate (MDT), the aggregation pheromone of *Plautia stali* (Scott) (Hemiptera: Pentatomidae). Stink bug nymphs do not enter traps randomly; instead they are attracted to traps that contain the synthetic aggregation pheromones attractive to their species (Khrimian et al. 2014; Weber et al. 2014; Tillman & Cottrell 2016b). Thus, pheromone-baited traps can be used to monitor adult and nymph populations of *H. halys*.

Knowledge of parasitism and predation of *H. halys* egg masses in host plants is essential to develop effective biocontrol tactics for this pest in southeastern US agroecosystems. Presently, several species of hymenopteran endoparasitoids, including *Anastatus redivivus* (Howard) and *Anastatus mirabilis* (Walsh & Riley) (both Hymenoptera: Eupelmidae), *Trissolcus euschisti* (Ashmead), *Trissolcus brochymenae* (Ashmead), *Trissolcus basalis* (Wollaston), *Trissolcus edessae* Fouts, *Telenomus podisi* Ashmead, and *Hadronotus obesum* Masner (all Hymenoptera: Scelionidae), and *Ooencyrtus* species Ashmead (Encyrtidae) have been reported to parasitize eggs of *H. halys* in the US (Cornelius et al. 2016; Herlihy et al. 2016; Ogburn et al. 2016; Dieckhoff et al. 2017; Jones et al. 2017; Morrison et al. 2018; Tillman et al. 2020). Recently, an adventive population of *Trissolcus japonicus* (Ashmead) (Hymenoptera: Scelionidae), a parasitoid of *H. halys* in its native range, has been confirmed in several US states (Talamas et al. 2015a; Milnes et al. 2016; Hedstrom et al. 2017). A diverse complex of chewing and piercing-sucking predators prey on *H. halys* eggs. Chewing predators consume prey whereas stylet sucking predators pierce prey and aspirate the egg content leaving the stylet sheath in the chorion of the egg (Yeagan 1979; Tillman 2011). Morrison et al. (2016) extended existing terminology to 4 characteristic patterns of predator feeding damage on stink bug eggs: complete chewing by Gryllidae and Tettigoniidae; incomplete chewing by Coccinellidae, Carabidae, and Dermaptera; stylet sucking by Anthocoridae and Pentatomidae; and punctured sucking by Salticidae. Also, removal of whole eggs from *H. halys* sentinel egg masses by ant species (Hymenoptera: Formicidae) has been detected in cotton and soybean (Tillman et al. 2020).

In this 2-yr study, our principal goal was to determine if sassafras serves as a host plant for *H. halys* in Alabama and Georgia. Pheromone-baited pyramid traps were used to capture stink bugs in the canopy of sassafras trees to provide estimates on seasonal abundance and the presence of nymphs as an indication of suitable host plant development. In addition, trees were examined visually for *H. halys* nymphs and adults. We also evaluated parasitism and predation of *H. halys* sentinel egg masses by native parasitoids and predators in sassafras over both seasons of the study.

Materials and Methods

SEASONAL TRAPPING

In 2019 and 2020, pheromone-baited traps were used to capture *H. halys* in the canopy of sassafras trees located in woodlands

adjacent to row crops at the Prattville Agricultural Research Unit in Prattville, Alabama, USA (32.4286°N, 86.4458°E) and in woodlands next to a pecan orchard at the USDA, ARS Fruit & Tree Nut Research Lab in Byron, Georgia, USA (32.3910°N, 83.4321°E). We note that the sassafras trees in this study were mature trees that flowered and produced fruit. A stink bug trap consisted of an insect-collecting device made from a 2.8 L clear plastic PET® jar (United States Plastic Corp., Lima, Ohio, USA) with a screw-cap lid (10.2 mm in diam) seated atop a 1.22 m tall yellow pyramid trap base (Cottrell et al. 2000). Each trap was baited with a commercial set of 2 aggregation lures: *H. halys* male aggregation pheromone (PHER) and the synergist (MDT) (Trécé BMSB DUAL lure; Trécé Pherocon, Adair, Oklahoma, USA). To eliminate the likelihood of stink bug escape, an insecticide kill strip (10% λ-cyhalothrin and 13% piperonyl butoxide) (Saber extra insecticide ear tags, Sagebrush Tags, De Smet, South Dakota, USA) was placed inside the insect-collection device of each trap (Cottrell 2001). Lures in traps were replaced bi-weekly, but kill strips were not replaced during a season. Once per wk, *H. halys* captured in traps were placed in zip top bags (US Plastics Corporation, Lima, Ohio, USA) and stored at the USDA Southeast Watershed Unit in Tifton, Georgia, USA, for identification, which was based on Rice et al. (2014) and his experience rearing a colony of this species. At the Prattville site, traps in 3 trees were sampled each wk from 24 Apr through 10 Oct in 2019, and traps in 2 trees were sampled from 10 Apr through 1 Oct in 2020. At the Byron site, 1 tree was sampled each wk from 24 Jun 2019 through 4 Nov 2020. A single trap was deployed in the canopy of each tree sampled. Observations on *H. halys* presence and feeding of *H. halys* on sassafras trees were noted when trap samples were collected. Seasonal means for the number of adult stink bugs per trap were calculated (PROC MEANS; SAS 2012). For the sassafras tree at the Byron site, trap capture was averaged by mo because data was collected over 18 mo.

SENTINEL EGG MASSES

Egg masses came from a *H. halys* colony reared in cages (27.9 cm long × 26.7 cm wide × 20.3 cm tall) on whole bean pods, apple slices, and raw peanuts at the USDA, ARS Southeast Watershed Unit in Tifton, Georgia, USA. Knit cloth (97% cotton, 3% spandex) (Jo-Ann Stores, LLC, Hudson, Ohio, USA) was used as a substrate for oviposition. Three cone-shaped knit cloths (12.7 cm²) were placed on the bottom of an ovipositional cage. A portion of the cloth with an egg mass was cut from the cloth. Any damaged eggs were gently removed from an egg mass when eggs were counted. Refrigerated egg masses (≤ 12 h old when placed in a refrigerator with a temperature range of 2.8 to 3.3 °C for 24 h) were used. Unlike frozen egg masses, refrigerated eggs retain typical shape and color when deployed in the field. Refrigerated eggs do not hatch, therefore eliminating the possibility of first instars feeding on parasitized eggs. At the Prattville site, paperclips were used to suspend the sentinel egg masses on stems of sassafras trees in a patch within the woodlands. In 2019, fifteen to 25 egg masses were deployed on 7 May, 11 Jun, 11 Jul, and 7 Aug. In 2020, 6 egg masses were deployed on 11 Jul, and 10 to 15 egg masses were deployed on 13 Aug, 21 Aug, and 2 Sep. The number of egg masses deployed on a particular date depended on the number of egg masses produced by the colony. Egg masses were retrieved after 72 h, and any predators present on the eggs at that time were noted. If a parasitoid female was detected on an egg mass during removal from sassafras, the female was collected and brought into the laboratory for identification.

Sentinel egg masses retrieved from the field were held in an environmental chamber (25 ± 2.0 °C; 50 ± 10% RH; 12:12 h (L:D))

photoperiod) until parasitoid emergence. Afterwards, each individual egg in an egg mass was dissected to check for dead immature parasitoids. At the same time, predation was assessed, and damage was divided into the 4 categories detected: (1) complete chewing; (2) stylet sucking; (3) punctured sucking; and (4) egg removal. Determination of parasitoid immature stages was based on descriptions of *Tr. basalis* immatures in Volkoff & Colazza (1992) and on descriptions of *Tr. basalis* and *An. redivii* every 24 h from oviposition in *H. halys* eggs to pupation (PGT, unpublished data). *Trissolcus* species adults were identified using the Talamas et al. (2015b) key. *Anastatus* species adults were identified using the Burks (1967) key. Voucher specimens of parasitoids are deposited in the Florida State Collection of Arthropods, Gainesville, Florida, USA.

Results

SEASONAL TRAPPING

The mean total number of *H. halys* captured in traps varied across the season and by yr and site. At the Prattville site, only adults were captured in tree traps in sassafras early season; 3 wk before mid-May in 2019 and 5 wk before mid-May in 2020 (Fig. 1A). Second instars were detected first in traps on 16 May 2019 and 15 May 2020. At the Byron site, low numbers of *H. halys* adults were detected in traps during early spring of 2020, but numbers of adults began to increase in traps by mid-May, and second instars were captured in traps on 6 May 2020 (Fig. 1B). Altogether, these data suggest that *H. halys* females entered sassafras trees and then began ovipositing on their leaves around late Apr to early May. Then, third, fourth, and fifth instars were captured in traps from late-May through early to mid-Sep at each site each yr, and subsequently new adults were captured in traps over time, a strong indication that *H. halys* nymphs developed into adults on sassafras. Each of the developmental stages of *H. halys* collected in traps were observed to feed on either leaves, stems, or fruit of sassafras when trap samples were collected. Later in the season as sassafras began to senesce, mainly only adults were captured in traps. In Prattville, the peak number of late season *H. halys* adults was 393 on 26 Sep 2019 and 229 on 25 Sep 2020 (Fig. 1A). In Byron, the peak number of late season *H. halys* adults was 61 and 22 on 15 Sep 2019 and 16 Sep 2020, respectively (Fig. 1B). Many of these late season *H. halys* were red in color and presumably was the fall overwintering population of this stink bug species at these sites. Thus, at each site for both yr of the study, *H. halys* adults entered sassafras early in the season and nymphs developed to adults on this host plant throughout the summer with adults peaking in Sep. Most adults were present in overwintering sites by mid-Nov at the Byron site. We conclude that 1 expanded generation develops in sassafras over the season.

SENTINEL EGG MASSES

Trissolcus euschisti (67.7%) and *A. redivii* (18.3%) were the primary parasitoid species that emerged from *H. halys* sentinel egg masses. *Telenomus podisi* (5.3%), *Ooencyrtus* sp. (4.0%), *Tr. basalis* (2.4%), and *Tr. brochymenae* (2.3%) also emerged from these egg masses. Females of each of these parasitoid species were observed ovipositing in *H. halys* sentinel eggs in sassafras based on identification of females on field egg masses in which adult parasitoids of the same species emerged. In 2019, parasitism per egg mass ranged from 0.2 to 14.3% (Table 1). In 2020, parasitism tended to be higher than in 2019, ranging from 32.3 to 39.2%.

Stylet sucking by Pentatomidae (62.3%) and chewing by Gryllidae and Tettigoniidae (32.0%) were the primary types of predation detected for *H. halys* sentinel egg masses in sassafras. Egg removal by Formicidae (5.2%) and punctured sucking feeding damage by Salticidae (0.5) also were detected on *H. halys* sentinel egg masses. During removal of *H. halys* sentinel egg masses from sassafras, mostly *H. halys*, including second through fifth instars and adults, were observed feeding on the egg masses. Occasionally, a grasshopper was observed chewing on an egg mass. In 2019, predation per egg mass ranged from 18.8 to 69.4% (Table 1). In 2020, predation per egg mass ranged from 3.3 to 41.0%. In both yr of the study, total percent mortality tended to increase over time resulting in relatively high mortality in Aug.

Discussion

Here, we show that sassafras is a reproductive host for *H. halys* in woodland habitats in the southeastern US. In this region, at least 1 extended generation began developing on sassafras in May and continued throughout the summer with late season adults eventually dispersing from senescing sassafras. As far as the authors are aware, this is the first study to document seasonal growth and development of *H. halys* on this host plant. Unlike many other non-crop host plants, sassafras can be a full-season host. There are earlier season host plants of *H. halys* in this region, such as peach and pear, but they generally mature earlier in the season than sassafras (Grabarczyk et al. 2022). As a non-crop host of *H. halys* in woodlands, there is a high probability that sassafras can be a source of *H. halys* from mid-Jun through Aug resulting in high density concentrations of this pest in nearby crops as reported in other studies (Joseph et al. 2014; Venugopal et al. 2014; Blaauw et al. 2016; Bergh et al. 2021; Grabarczyk et al. 2022).

Four of the parasitoid species that emerged from *H. halys* egg masses in this study, *A. redivii*, *Tr. euschisti*, *Tr. brochymenae*, and *Ooencyrtus* sp., and each type of chewing predation has been reported previously for *H. halys* egg masses in sassafras at the Prattville site (Tillman et al. 2020). The dominant parasitoid species emerging from these egg masses over these 4 yr has been *A. redivii*. The 2 *Trissolcus* species were detected first in sassafras in 2018. In 2017 at this site, a rare parasitoid, *Trissolcus solocis* Johnson (Hymenoptera: Scelionidae), emerged from *H. halys* frozen egg masses in sassafras and nearby cotton (Tillman et al. 2020), but has not been detected at the site since then. *Trissolcus basalis* is a dominant egg parasitoid of *Nezara viridula* (L.) (Heteroptera: Pentatomidae) egg masses, and *Te. podisi* is a dominant egg parasitoid of *Euschistus servus* (Say) (Heteroptera: Pentatomidae) (Tillman 2011). Interestingly, both parasitoid species emerged from *H. halys* egg masses in 2019 and 2020. Total mortality was relatively high in 2019 and 2020. However, the increase in total mortality was likely due to a steady increase in predation, not parasitism. The decrease in predation and parasitism in Sep likely was due to the reduction in oviposition during this time period as seen in Figures 1 and 2. This, along with the increased diversity of egg parasitoids at the site, suggests that conservation biological control could enhance the effectiveness of native biological control agents of *H. halys* in or near non-crop habitats adjacent to crops in the southeastern US. For example, nectar-producing sources at habitat interfaces can be planted to preserve or support populations of stink bug natural enemies (Tillman 2017). Also, wildflower plantings are known to increase biological control of prey in adjacent blueberry fields (Blaauw & Isaacs 2015).

In summary, sassafras is a reproductive host plant as well as a source of food for *H. halys* adults in woodland habitat in the south-

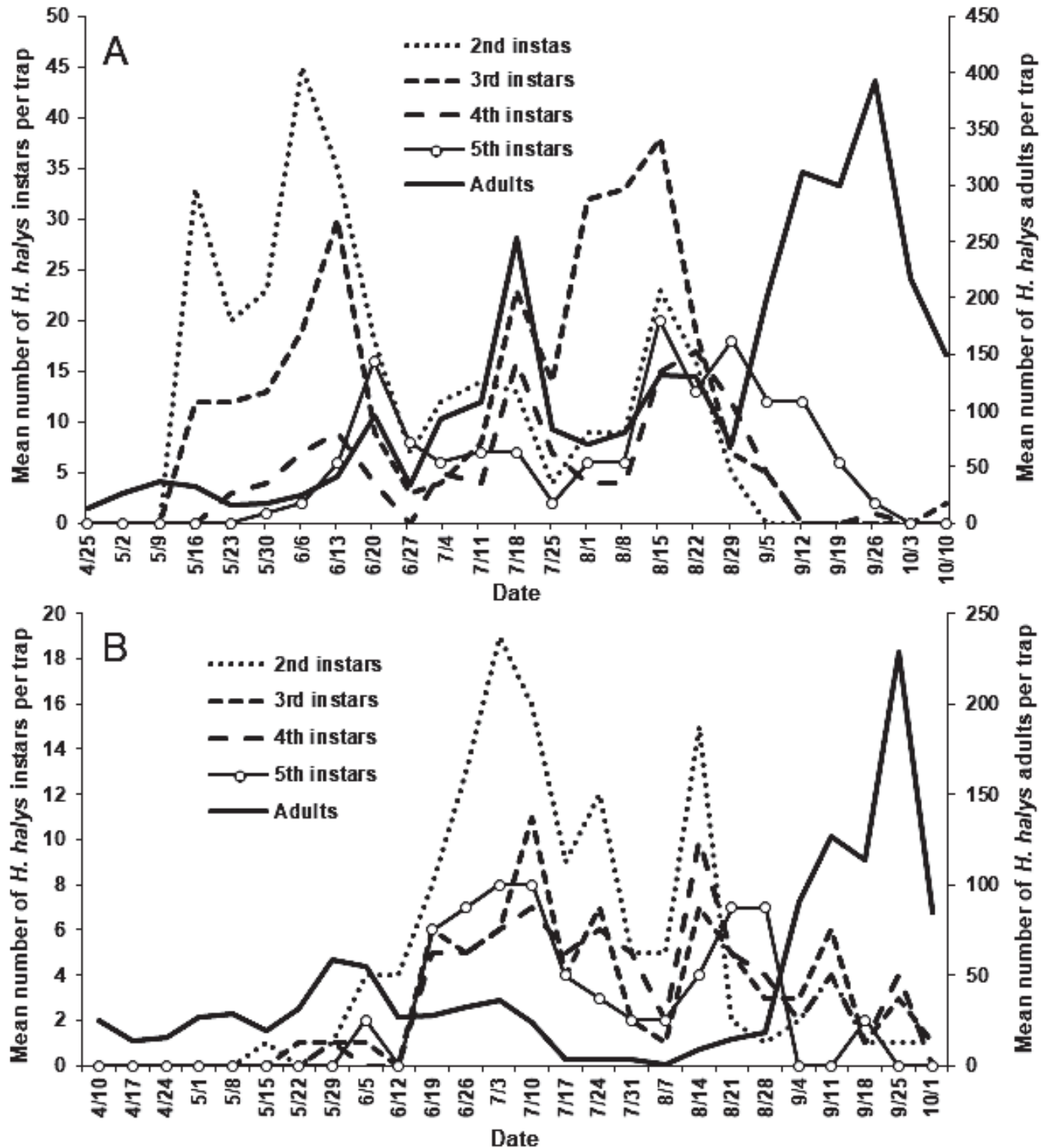


Fig. 1. Mean number of *Halyomorpha halys* adults and second through fifth instars captured per wk in pheromone-baited traps in the canopy of sassafras trees in woodlands in Prattville, Alabama, USA, in 2019 (A) and 2020 (B).

eastern US. Native natural enemies also are present and may serve as biological control agents of *H. halys* in this host plant. Thus, it is important to conserve these natural enemies and *Trissolcus japonicus* (Ashmead), if or when it arrives, by protecting them from insecticides and providing food for their survival and reproduction.

Acknowledgments

We thank Kristie Graham for excellent technical support. Mention of trade names or commercial products in this publication is

Table 1. Percent predation and parasitism of *Halyomorpha halys* sentinel eggs per egg mass in sassafras at the Prattville, Alabama, USA, site in 2019 and 2020.

Year	Date	% Predation	Predation type ^a	% Parasitism	Parasitoid species ^b	% Total mortality
2019	7 May	18.8	CH, ER	3.6	Ar	22.4
	11 Jun	27.7	CH, SS	14.7	Te, Ar, Oo, Tp, Tba	42.4
	11 Jul	45.7	CH, SS	0.2	Te	46.0
	7 Aug	69.2	CH, SS	9.0	Te, Ar, Oo	78.2
2020	11 Jul	3.6	CH, SS	36.3	Te	39.9
	13 Aug	40.4	CH, SS	36.4	Te, Ar	76.8
	21 Aug	39.5	CH, SS	32.8	Te, Ar, Tp	72.4
	2 Sep	11.6	CH, SS, PS	41.3	Te, Ar, Oo, Tbr	53.0

^aCH = complete chewing; ER = egg removal; SS = stylet sucking; PS = punctured sucking.

^bAr = *Anastatus reduvii*; Oo = *Ooencyrtus* sp.; Tba = *Trissolcus basal*; Tbr = *Trissolcus brochymenae*; Tp = *Telenomus podisi*; Te = *Trissolcus euschisti*.

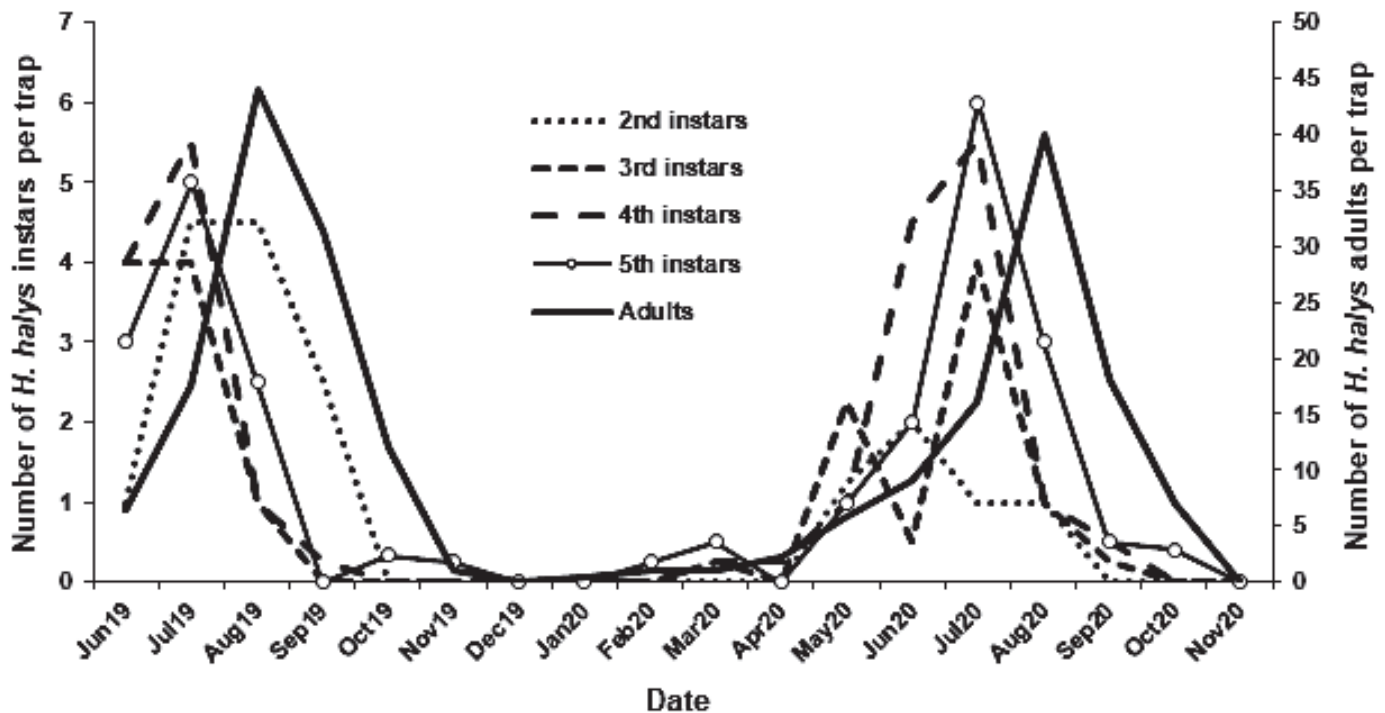


Fig. 2. Mean number of *Halyomorpha halys* adults and second through fifth instars captured per mo in pheromone-baited traps in sassafras in Byron, Georgia, USA, in 2019 to 2020.

solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA or any other author affiliated institution.

References Cited

- Bakken A, Schoof S, Bickerton M, Kamminga K, Jenrette J, Malone S, Abney M, Herbert D, Reisig D, Kuhar T. 2015. Occurrence of brown marmorated stink bug (Hemiptera: Pentatomidae) on wild hosts in nonmanaged woodlands and soybean fields in North Carolina and Virginia. *Environmental Entomology* 44: 1011–1021.
- Bergh JC, Morrison WR, Stallrich JW, Short BD, Cullum JP, Leskey TC. 2021. Border habitat effects on captures of *Halyomorpha halys* (Hemiptera: Pentatomidae) in pheromone traps and fruit injury at harvest in apple and peach orchards in the Mid-Atlantic, USA. *Insects* 12: 419. doi: 10.3390/insects12050419
- Bergmann EJ, Venugopal PD, Martinson HM, Raupp MJ, Shrewsbury PM. 2016. Host plant use by the invasive *Halyomorpha halys* (Stål) on woody ornamental trees and shrubs. *PLoS One* 11: e0149975. doi: 10.1371/journal.pone.0149975
- Blaauw BR, Isaacs R. 2015. Wildflower plantings enhance the abundance of natural enemies and their services in adjacent blueberry fields. *Biological Control* 91: 94–103.
- Blaauw BR, Jones VP, Nielsen AL. 2016. Utilizing immunomarking techniques to track *Halyomorpha halys* (Hemiptera: Pentatomidae) movement and distribution within a peach orchard. *PeerJ* 4: e1997. doi: 10.7717/peerj.1997
- Burks BD. 1967. The North American species of *Anastatus* Motschulsky (Hymenoptera, Eupelmidae). *Transactions of the American Entomology Society* 93: 423–432.
- CABI – CAB International. 2022. Invasive Species Compendium. *Sassafras albidum* (common sassafras). <https://www.cabi.org/isc/datasheet/51270> (last accessed 8 Oct 2022).

- Cornelius ML, Dieckhoff C, Hoelmer KA, Olsen RT, Weber DC, Herlihy MV, Talamas EJ, Vinyard BT, Greenstone MH. 2016. Biological control of sentinel egg masses of the exotic invasive stink bug *Halyomorpha halys* (Stål) in mid-Atlantic USA ornamental landscapes. *Biological Control* 103: 11–20.
- Cottrell TE. 2001. Improved trap capture of *Euschistus servus* and vertical distribution of *Euschistus servus* (Say) and *Euschistus tristigmus* (Say) (Hemiptera: Pentatomidae) in pecan orchards. *Florida Entomologist* 84: 731–732.
- Cottrell TE, Yonce CE, Wood BW. 2000. Seasonal occurrence and vertical distribution of *Euschistus servus* (Say) and *Euschistus tristigmus* (Say) (Hemiptera: Pentatomidae) in pecan orchards. *Journal of Entomological Science* 35: 421–431.
- Dieckhoff C, Tatman KM, Hoelmer KA. 2017. Natural biological control of *Halyomorpha halys* by native egg parasitoids: a multi-year study in northern Delaware. *Journal of Pest Science* 90: 1143–1158.
- Grabarczyk EE, Cottrell TE, Tillman PG. 2022. Spatiotemporal distribution of *Halyomorpha halys* (Stål) across a fruit and tree nut agricultural ecosystem. *Environmental Entomology* 51: 824–835.
- Hedstrom C, Lowenstein D, Andrews H, Bai B, Wiman N. 2017. Pentatomid host suitability and the discovery of introduced populations of *Trissolcus japonicus* in Oregon. *Journal of Pest Science* 90: 1169–1179.
- Herlihy MV, Talamas EJ, Weber DC. 2016. Attack and success of native and exotic parasitoids on eggs of *Halyomorpha halys* in three Maryland habitats. *PLoS One* 11: e0150275. <https://doi.org/10.1371/journal.pone.0150275>
- Jones AL, Jennings DE, Hooks CRR, Shrewsbury PM. 2017. Field surveys of egg mortality and indigenous egg parasitoids of the brown marmorated stink bug, *Halyomorpha halys*, in ornamental nurseries in the mid-Atlantic region of the USA. *Journal of Pest Science* 90: 1159–1168.
- Joseph SV, Stallings JW, Leskey TC, Krawczyk G, Polk D, Butler B, Bergh JC. 2014. Spatial distribution of brown marmorated stink bug (Hemiptera: Pentatomidae) injury at harvest in mid-Atlantic apple orchards. *Journal of Economic Entomology* 107: 1839–1848.
- Khrimian A, Zhang A, Weber DC, Ho H-Y, Aldrich JR, Vermillion KE, Siegler MA, Shirali S, Guzman F, Leskey TC. 2014. Discovery of the aggregation pheromone of the brown marmorated stink bug (*Halyomorpha halys*) through the creation of stereoisomeric libraries of 1-bisabolen-2-ols. *Journal of Natural Products* 77: 1708–1717.
- Leskey T, Nielsen AL. 2018. Impact of the invasive brown marmorated stink bug in North America and Europe: history, biology, ecology, and management. *Annual Review of Entomology* 63: 599–618.
- Leskey TC, Agnello A, Bergh JC, Dively GP, Hamilton GC, Jentsch P, Khrimian A, Krawczyk G, Kuhar TP, Lee D-H. 2015. Attraction of the invasive *Halyomorpha halys* (Hemiptera: Pentatomidae) to traps baited with semiochemical stimuli across the United States. *Environmental Entomology* 44: 746–756.
- Milnes JM, Wiman NG, Talamas EJ, Brunner JF, Hoelmer KA, Buffington ML, Beers EH. 2016. Discovery of an exotic egg parasitoid of the brown marmorated stink bug, *Halyomorpha halys* (Stål), in the Pacific Northwest. *Proceedings of the Entomological Society of Washington* 118: 466–470.
- Morrison III WR, Mathews CR, Leskey TC. 2016. Frequency, efficiency, and physical characteristics of predation by generalist predators of brown marmorated stink bug (Hemiptera: Pentatomidae) eggs. *Biological Control* 97: 120–130.
- Morrison III WR, Blaauw BR, Nielsen AL, Talamas E, Leskey TC. 2018. Predation and parasitism by native and exotic natural enemies of *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) eggs augmented with semiochemicals and differing host stimuli. *Biological Control* 121: 140–150.
- Ogburn EC, Bessin R, Dieckhoff C, Dobson R, Grieshop M, Hoelmer KM, Mathews C, Moore J, Nielsen AL, Poley K, Pote JM, Rogers M, Welty C, Walgenbach JF. 2016. Natural enemy impact on eggs of the invasive brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), in organic agroecosystems: a regional assessment. *Biological Control* 101: 39–51.
- Rice KB, Bergh CJ, Bergmann EJ, Biddinger DJ, Dieckhoff C, Dively G, Fraser H, Garipey T, Hamilton G, Haye T. 2014. Biology, ecology, and management of brown marmorated stink bug (Hemiptera: Pentatomidae). *Journal of Integrated Pest Management* 5: A1–A13.
- SAS 2012. PROC FREQ, PROC MEANS, PROC GLIMMIX, SAS/STAT, v9.4. SAS Institute, Inc., Cary, North Carolina, USA.
- Talamas EJ, Johnson NF, Buffington M. 2015b. Key to Nearctic species of *Trissolcus* Ashmead (Hymenoptera, Scelionidae), natural enemies of native and invasive stink bugs (Hemiptera, Pentatomidae). *Journal of Hymenoptera Research* 43: 45–110.
- Talamas EJ, Herlihy MV, Dieckhoff C, Hoelmer KA, Buffington M, Bon M-C, Weber DC. 2015a. *Trissolcus japonicus* (Ashmead) (Hymenoptera, Scelionidae) emerges in North America. *Journal of Hymenoptera Research* 43: 119–128.
- Tillman G, Toews M, Blaauw B, Sial A, Cottrell T, Talamas E, Buntin D, Joseph S, Balusu R, Fadamiro H, Lahiri S, Patel D. 2020. Parasitism and predation of sentinel eggs of the invasive brown marmorated stink bug, *Halyomorpha halys* (Hemiptera: Pentatomidae) in the southeastern US. *Biological Control* 145: 104247. <https://doi.org/10.1016/j.biocontrol.2020.104247>
- Tillman PG. 2011. Natural biological control of stink bug (Heteroptera: Pentatomidae) eggs in corn, peanut, and cotton farmscapes in Georgia. *Environmental Entomology* 40: 303–314.
- Tillman PG. 2017. Ecosystem-based incorporation of nectar-producing plants for stink bug parasitoids. *Insects*. 8:65. <http://doi.org/10.3390/insects8030065>
- Tillman PG, Cottrell TE. 2016a. Density and egg parasitism of stink bugs (Hemiptera: Pentatomidae) in elderberry and dispersal into crops. *Journal of Insect Science* 16: 1–14.
- Tillman PG, Cottrell TE. 2016b. Attraction of stink bug (Hemiptera: Pentatomidae) nymphs to *Euschistus* aggregation pheromone in the field. *Florida Entomologist* 99: 678–682.
- Venugopal PD, Coffey PL, Dively GP, Lamp WO. 2014. Adjacent habitat influence on stink bug (Hemiptera: Pentatomidae) densities and the associated damage at field corn and soybean edges. *PLoS One* 9: e109917. doi: 10.1371/journal.pone.0109917
- Volkoff N, Colazza S. 1992. Growth patterns of teratocytes in the immature stages of *Trissolcus basalus* (Woll.) (Hymenoptera: Scelionidae), an egg parasitoid of *Nezara viridula* (L.) (Heteroptera: Pentatomidae). *International Journal of Morphology and Embryology* 21: 323–336.
- Weber DC, Leskey TC, Walsh GC, Khrimian A. 2014. Synergy of aggregation pheromone with methyl (E, E, Z)-2, 4, 6-decatrienoate in attraction of *Halyomorpha halys* (Hemiptera: Pentatomidae). *Journal of Economic Entomology* 107: 1061–1068.
- Yeargan KV. 1979. Parasitism and predation of stink bug eggs in soybean and alfalfa fields. *Environmental Entomology* 8: 715–719.