

Life History of the Invasive Species *Halyomorpha halys* (Hemiptera: Pentatomidae) in Northeastern United States

ANNE L. NIELSEN¹ AND GEORGE C. HAMILTON

Department of Entomology, Rutgers University, 93 Lipman Drive, New Brunswick, NJ 08901

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ABSTRACT Host plant use by nymphs and adults of the nonnative species *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) was investigated proximal to the location of its introduction, Allentown, PA. The seasonality of *H. halys* in the United States had not been thoroughly studied before this work. It is reported to have ≈ 300 host plants in its native range that could make control and identification of small populations difficult. Weekly beat samples were conducted beginning at petal fall (mid-April) in *Pyrus* spp. until the first frost (mid-October) from 2005 to 2007 on a variety of ornamental trees, shrubs, and agricultural crops. Egg masses were first observed on *Paulownia tomentosa* Thunb. the first week of June. In 2006 and 2007, *Fraxinus americana* L. was an important mid- and late season host for adults. Nymphal abundance differed seasonally. *P. tomentosa* supported high densities during the early season, whereas *Viburnum opulus* variety *americanum* Aiton was the preferred mid-season host, and *Viburnum prunifolium* L. and *Rosa rugosa* Thunb. had the highest densities of nymphs during the late season. Abundance of nymphs was strongly associated with maturing fruit or pods. All plants surveyed supported populations of *H. halys*, suggesting a large host range. In late August, a large adult population peak was observed (850–1,000 degree days [DD]), shortly after the DD accumulation for development to imaginal eclosion, supporting hypotheses that *H. halys* is likely univoltine in this region. Relative to native pentatomid species, *H. halys* was by far the predominant species collected in samples on ornamental and cultivated crops.

KEY WORDS *Halyomorpha halys*, population biology, seasonal dynamics, host plant

Halyomorpha halys (Stål) (Hemiptera: Pentatomidae) is an introduced species native to Japan, China, and Korea (Hoebeke and Carter 2003). In its native range, it is considered an occasional pest of fruit trees and soybean, *Glycine max* (L.) Merr. (Fabales: Fabaceae), as well as a nuisance pest during the winter (Takahashi 1930, Hoffman 1931, Saito et al. 1964, Kobayashi and Kimura 1969, Chung et al. 1995, Funayama 1996, Watanabe 1996, Choi et al. 2000, Tada et al. 2001, Funayama 2002). Its presence in the United States was first reported to Lehigh County Cooperative Extension in Allentown, PA, in 1996; however, it was not properly identified until 2001 (Hoebeke and Carter 2003). Allentown, PA, is the believed population epicenter based on homeowner reports and blacklight data (G.C.H. and A.L.N., unpublished). Since 2001, *H. halys* populations have increased to high densities in multiple states and represent a potential agricultural pest and overwintering adults create a homeowner nuisance throughout the Mid-Atlantic states.

H. halys overwinters as adults, commonly in artificial structures (Watanabe et al. 1994). As daily

temperatures and photoperiod increase, the adults (herein referred to as “spring adults”) emerge from these sites around mid-March to April. Females are believed to be reproductively immature at this stage (A.L.N., unpublished), resulting in a delay before reproduction while they accumulate enough degree days (DD) to complete maturity. After maturation, the spring females start to oviposit eggs on the underside of leaves (Takahashi 1930) in clusters containing 28 eggs, with 244 eggs laid over the life span of a female (Bernon 2004, Nielsen et al. 2008). The nymphs undergo five stadia before reaching the adults stage (Takahashi 1930). Fourth and fifth instars are sensitive to diapause induction, which is both temperature and photoperiod dependant (Niva and Takeda 2003). The adult generation (hereafter “fall adults”) enters overwintering sites in the fall in reproductive diapause. *H. halys* requires 538 DD to complete development (egg to adult) and an additional 148 DD for female maturation (Nielsen et al. 2008) and can have up to five generations per year in tropical climates (Hoffman 1931). It is predicted to be univoltine in the Mid-Atlantic states because of the delay before reproduction.

The term “host plant” has been used in different contexts. Here, we use the term as a plant that supports

¹ Corresponding author and current address: Department of Nematology, University of California, Davis, CA 95616-8584 (e-mail: alnielsen@ucdavis.edu).

consecutive nymphal stages for multiple years. Like most phytophagous pentatomids, *H. halys* is polyphagous with a wide host range encompassing ornamental shrubs, hardwood trees, and cultivated crops, such as soybean, apple (*Malus* spp.), pear (*Pyrus* spp.), cherry (*Prunus* spp.), and peach (*Prunus* spp.) (Hoffman 1931, Hoebeke and Carter 2003, Bernon 2004). Both adults and nymphs prefer to feed on plant reproductive structures (McPherson and McPherson 2000), although *H. halys* feeding sites differ for some host plants, such as the princess tree, *Paulownia tomentosa* (Thunb.) (Scrophulariales: Scrophulariaceae), on which feeding occurs primarily on vegetative structures (Bernon 2004). Host plant species occur among a wide range of plant families, but among reported hosts, the families of Fabaceae and Rosaceae are commonly cited (Hoebeke and Carter 2003, Bernon 2004).

Our objective was to investigate the relationship of *H. halys* with its host plants. Alternative host plants are significant for stink bug development and can be essential for population buildup before dispersing to agricultural crops (Panizzi 1997). Identification of early and alternate host plants can be used to develop farm-scale control programs aimed at *H. halys*. We sampled ornamental host plants, fruit trees, and soybean for 2–3 yr and included plants native to Pennsylvania and nonnative plants, primarily of Asian origin. Our efforts concentrated on plants that were believed to support *H. halys* development. Because *H. halys* adults are attracted to blacklight traps (Tada et al. 2001, Lee et al. 2002), flight activity was documented using a blacklight trap located at a commercial farm where cultivated crops were sampled.

Materials and Methods

Seasonal Phenology. Weekly beat samples were collected during 2005–2007 at the Rodale Working Tree Farm (“Rodale”) in Allentown, PA, an organically managed 40.5-ha (100-acre) arboretum located near the believed epicenter of the population. Rodale has both native and exotic trees and shrubs in small homogenous clusters of approximately five to 10 plants throughout the middle and perimeter of the property. In 2006 and 2007, sampling in fruit trees and soybean also occurred at Lichtenwalner Farms in Macungie, PA, 4.7 km from the Rodale site. Beat sampling at both sites was initiated in mid-April when pear was in bloom and continued until mid-October or the first frost. The entire fruit tree or woody shrub was sampled except for *P. tomentosa*, which due to the large size of the trees, was sampled per branch, to standardize sample sizes. Each tree limb was tapped sharply three times at a height of 1.5–3.0 m with a rubber bat to dislodge insects into a canvas beat sheet (71 by 71 cm, BioQuip, Rancho Dominguez, CA). All dislodged pentatomid species were collected and taken to the laboratory for species identification and life stage determination. Soybean was sampled biweekly from early June until frost using a 38-cm sweep net (BioQuip, Rancho Dominguez, CA) in six 10-m rows, ranging 10–70 m from the edge of the plot, which is equiv-

alent to the recommended samples required to establish population densities.

A 110-V blacklight trap (Gempler’s, Madison, WI) was run at Lichtenwalner Farms from 1 May to 1 October to supplement beat sampling assessment of population density and flight activity of stink bugs in 2006 and 2007. The blacklight trap was placed in an open area of the farm in front of a shed or shilo; emptied biweekly; and all stink bugs collected were identified and recorded.

Visual surveys (≈ 1 min per branch) were conducted for unhatched egg masses and first instars. Unhatched egg masses are light green and are well camouflaged on the underside of leaves. First instars aggregate around an egg mass at least until they molt to the second instar (Aldrich et al. 1991). If first instars were found during beat sampling, a visual assessment was done on the host plant to look for egg masses. Preliminary sweep net sampling of wild grasses did not indicate the presence of *H. halys* and were not sampled further.

Degree day (DD) accumulations began on 31 May of each year, which is just before the time of the first egg mass found on *P. tomentosa* and when adults are consistently found in blacklight traps. Daily maximum and minimum temperature data obtained from the National Weather Service for Allentown International Airport was used to calculate daily accumulations. Daily accumulations were derived by taking the average of the maximal and minimal temperature (Celsius) and subtracting the minimum developmental temperature threshold ($T_0 = 14.17^\circ\text{C}$) (Nielsen et al. 2008).

Host Plant Survey. In 2005, an initial survey of 13 plant species that included native and exotic plants was conducted at Rodale to document seasonality and identify potential host plants. Results from the 2005 survey were not statistically analyzed due to the inability to calculate variance estimates; totals are provided for reference only. The plants selected had fruit or pods with various maturation times, and most had been documented previously as supporting populations of *H. halys* (Bernon 2004). The plants sampled were princess tree; pear (*Pyrus* sp.) (Rosales: Rosaceae); Russian olive, *Elaeagnus angustifolia* L. (Rhamnales: Elaeagnaceae); blackhaw viburnum, *Viburnum prunifolium* L. (Dipsacales: Caprifoliaceae); American cranberrybush, *Viburnum opulus* variety *americanum* Aiton (Dipsacales: Caprifoliaceae); Asian pear, *Pyrus pyrifolia* (Burm. f.) Nakai (Rosales: Rosaceae); rugosa rose, *Rosa rugosa* Thunb. (Rosales: Rosaceae); eastern hemlock, *Tsuga canadensis* (L.) Carrière (Pinales: Pinaceae); raspberry (*Rubus* spp.) (Rosales: Rosaceae); sweet gum (*Liquidambar* spp.) (Saxifragales: Altingiaceae); Tartanian honeysuckle, *Lonicera tatarica* L. (Dipsacales: Caprifoliaceae); white ash, *Fraxinus americana* L. (Lamiales: Oleaceae); and Siberian pea shrub, *Caragana arborescens* Lam. (Fabales: Fabaceae) (USDA 2008).

In 2006 and 2007, host plants were selected based on the 2005 preliminary survey and host phenology. The sampling period was divided into 5–6-wk “seasons”

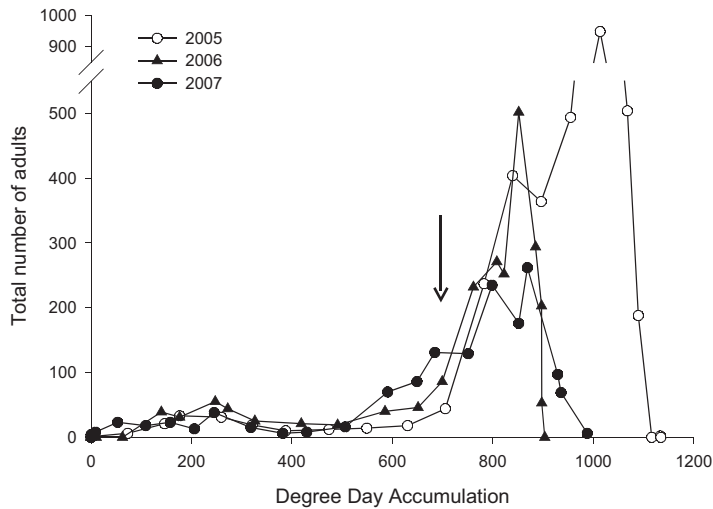


Fig. 1. Seasonality of *H. halys* adults on ornamentals from 2005 to 2007 in Allentown, PA. Arrow indicates the degree day accumulation for a complete generation (female maturation plus nymphal development, 685 DD) from 31 May.

based on periods of activity and host phenology: pre-oviposition, early, mid-, and late season. The sampling periods did not overlap. Preoviposition included mid-April to the last week of May, early season included the last week of May until the first week of July, mid-season included the end of the first week in July to the second week in August, and late season spanned the second week in August to mid-October. Pentatomid species, abundance, and life stage were recorded for individual plants, except for *P. tomentosa*, for which individual branches were sampled. Sampling was restricted to *P. tomentosa*, *Pyrus* spp., *E. angustifolia*, *V. prunifolium*, *V. opulus* variety *americanum*, *P. pyrifolia*, *R. rugosa*, *F. americana*, and *C. arborescens*. A hedge row that was located 100 m from the *P. tomentosa* containing garlic mustard, *Alliaria petiolata* (M. Bieb) Cavara & Grande (Capparales: Brassicaceae); Japanese stilt grass, *Microstegium vimineum* (Trin.) Camus (Cyperales: Poaceae); raspberry; Japanese honeysuckle, *Lonicera japonica* Thunb. (Dipsacales: Caprifoliaceae); and multiflora rose, *Rosa multiflora* Thunb. (Rosales: Rosaceae) was sampled weekly in 2006 and 2007. This section was sampled by beat sampling three 10-m stretches of the hedge. Cultivated hosts—apple, *Malus domestica* Borkh. (Rosales: Rosaceae), *P. pyrifolia*, *Pyrus* sp. and soybean—were sampled weekly from mid-April until frost. Fruit trees were sampled using methods identical to those done at Rodale. At each location, all pentatomid species collected were recorded and identified to document the relative abundance of native species compared with *H. halys*.

Statistical Analysis. The 2005 population data were not statistically analyzed due to the inability to calculate mean or variance estimates; sampling totals are provided for reference only. *H. halys* abundance on host plants did not meet the assumptions of normality and was Wilcoxon rank transformed and then analyzed with a one-way analysis of variance (ANOVA)

and Tukey's multiple comparison at $P \leq 0.05$. Samples were analyzed as nymphs and adult. To compare the relative abundance of *H. halys* to other phytophagous pentatomid species, data for each species was summed over each year's sampling period and $\sqrt{x + 1}$ transformed to account for temporal differences in abundance. All analyses were done using SAS, version 9.1 (SAS Institute 2002–2003). Results are presented as untransformed means.

Results

Seasonal Phenology. These data support hypotheses that *H. halys* is univoltine in eastern Pennsylvania. Although there are enough DD for two generations, there is a delay between spring adult activity and oviposition that is likely the time required for female ovarian development. Adult *H. halys* were first found on ornamental and cultivated host plants in late April. A small peak in adult abundance coincided with the observation of the first egg masses in mid-June each year at ≈ 100 –230 DD (Fig. 1). The first egg masses were found at 104, 82, and 53 DD for 2005, 2006, and 2007, respectively, which was just past the time that *P. tomentosa* was fully leafed out. The shortened time in successive years could be due to warmer winter and spring temperatures or improved scouting ability. First instars were found on *P. tomentosa* (2005–2007; $n = 1,258$), *F. americana* (2005–2007; $n = 52$), *Liquidambar* spp. (2006; $n = 25$), *V. opulus* variety *americanum* (2007; $n = 28$), *V. prunifolium* (2007; $n = 6$), *Pyrus* sp. (2006; $n = 27$), and *P. pyrifolia* (2006–2007; $n = 99$). The number of egg masses and first instars may be skewed in favor of *P. tomentosa* because the large leaves made observation of egg masses easier than on smaller denser host plants; however, if first instars were found during beat sampling on any host plant, branches were observed for egg masses and other first instars. *P. tomentosa* is also a known host

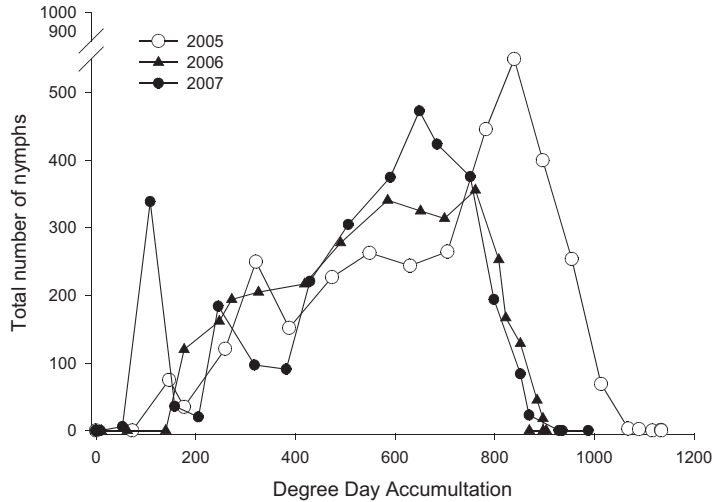


Fig. 2. Seasonality of *H. halys* nymphs on ornamentals from 2005 to 2007 in Allentown, PA.

plant of *H. halys* in China and Japan and may be a preferred oviposition site. In 2007, a large peak in nymphal abundance occurred at 100 DD (13 June 2007) when high numbers of first instars were observed (Fig. 2). A large population peak of fall adults was apparent from 800 to 1,000 DD (early-mid August through early September) (Fig. 1).

Adults were first found in blacklight traps beginning 31 May 2007, indicating that the adult populations were active. The application of the accumulated DD required to complete development (female maturity plus total development is 685 DD) beginning on 31 May confirms laboratory estimates that *H. halys* is univoltine in Allentown, PA (Fig. 1) (Nielsen et al. 2008). The population decreased dramatically at the beginning of October (900–1,100 DD), just before frost, when the adults migrate to overwintering sites. The similar rapid decline in the nymph population is due either to fifth instars molting to the adult stage or mortality due to frost (Fig. 2).

Host Plant Survey. Plants that supported consecutive nymphal stages for multiple years were considered as host plants. Although most of the plants surveyed conform to this definition, the survey was narrowed in 2006 and 2007 to represent varying plant phenologies at Rodale and agricultural crops were added to determine seasonal dynamics in an agroecosystem. Preoviposition hosts were identified as *V. prunifolium* and *M. domestica*. However, due to the low abundances on these plants, the results were not analyzed statistically. There was no difference in adult density on early season hosts ($F = 0.76$; $df = 11, 88$; $P = 0.68$) (Table 1), but densities of nymphs were significantly more abundant on *P. tomentosa* than the other hosts sampled ($F = 3.24$; $df = 11, 88$; $P < 0.001$) (Table 2).

H. halys adults and nymph populations varied through time. *F. americana* and *V. opulus* variety *americanum* had the highest mid-season adult populations ($F = 3.80$; $df = 13, 109$; $P < 0.001$). Nymph

Table 1. Mean \pm SE number of *H. halys* adults on ornamental and cultivated hosts (2006–2007)

Plant family	Common name ^a	Plant species	Early season ^{b,c}	Mid-season ^b	Late season ^b
Rosaceae	Asian pear ^a	<i>Pyrus pyrifolia</i>	0.49 \pm 0.12a	0.25 \pm 0.14ab	1.77 \pm 0.42abc
Rosaceae	Asian pear ^a	<i>Pyrus pyrifolia</i> (cultivated)	0.46 \pm 0.22a	0.43 \pm 0.24ab	1.17 \pm 0.26abcd
Rosaceae	Apple	<i>Malus domestica</i> (cultivated)	0.25 \pm 0.11a	0.08 \pm 0.05ab	0.37 \pm 0.13cde
Rosaceae	Pear	<i>Pyrus</i> spp.	0.75 \pm 0.20a	0.13 \pm 0.07b	3.50 \pm 0.70ab
Rosaceae	Pear	<i>Pyrus</i> spp. (cultivated)	0.41 \pm 0.21a	0.32 \pm 0.11ab	1.06 \pm 0.58bcde
Rosaceae	Rugosa rose ^a	<i>Rosa rugosa</i>	0.52 \pm 0.24ab	0.79 \pm 0.23cde	
Oleaceae	White ash	<i>Fraxinus americana</i>	0.44 \pm 0.30a	0.93 \pm 0.36a	3.54 \pm 0.73a
		Uncultivated hedge		0.00 \pm 0.00b	0.58 \pm 0.35cde
Caprifoliaceae	Highbush cranberry	<i>Viburnum opulus</i> var. <i>americanum</i>	0.64 \pm 0.25a	0.88 \pm 0.28a	1.65 \pm 0.29abc
Caprifoliaceae	Blackhaw viburnum	<i>Viburnum prunifolium</i>	0.30 \pm 0.09a	0.31 \pm 0.12ab	2.08 \pm 0.45abc
Scrophulariaceae	Princess tree ^a	<i>Paulownia tomentosa</i>	0.17 \pm 0.04a	0.15 \pm 0.08b	2.97 \pm 0.56ab
Elaeagnaceae	Russian olive	<i>Elaeagnus angustifolia</i>	0.25 \pm 0.07a	0.06 \pm 0.03b	1.80 \pm 0.46abc
Fabaceae	Soybean ^a	<i>Glycine max</i> (cultivated)		0.00 \pm 0.00b	0.19 \pm 0.05e
Fabaceae	Siberian pea shrub	<i>Caragana arborescens</i>	0.28 \pm 0.03a	0.20 \pm 0.04ab	0.21 \pm 0.04de

^a Indicates Asian origin (USDA 2008).

^b Untransformed means are shown. Columns with the same letters have rank transformed means that are not significantly different ($P \leq 0.05$; Tukey's test).

^c If plant was flowering or did not have leaves during the early season period, it was not sampled.

Table 2. Mean ± SE number of *H. halys* nymphs on ornamental and cultivated hosts (2006–2007)

Plant family	Common name ^a	Plant species	Early season ^{b,c}	Mid-season ^b	Late season ^b
Rosaceae	Asian pear ^a	<i>Pyrus pyrifolia</i>	0.19 ± 0.12ab	1.12 ± 0.60de	0.77 ± 0.21ab
Rosaceae	Asian pear ^a	<i>Pyrus pyrifolia</i> (cultivated)	0.27 ± 0.25b	0.33 ± 0.14e	1.04 ± 0.38ab
Rosaceae	Apple	<i>Malus domestica</i> (cultivated)	0.00 ± 0.00b	0.09 ± 0.07e	0.06 ± 0.05b
Rosaceae	Pear	<i>Pyrus</i> spp.	0.40 ± 0.38b	0.63 ± 0.19de	0.87 ± 0.22ab
Rosaceae	Pear	<i>Pyrus</i> spp. (cultivated)	0.01 ± 0.01b	0.30 ± 0.14e	0.18 ± 0.10b
Rosaceae	Rugosa rose ^a	<i>Rosa rugosa</i>		4.54 ± 1.22ab	2.59 ± 0.55a
Oleaceae	White ash	<i>Fraxinus americana</i>	0.44 ± 0.11ab	6.60 ± 1.35ab	2.42 ± 1.17ab
		Uncultivated hedge		1.25 ± 0.16cde	1.00 ± 0.33ab
Caprifoliaceae	Highbush cranberry	<i>Viburnum opulus</i> var. <i>americanum</i>	1.12 ± 0.68ab	9.40 ± 1.83a	3.62 ± 1.36ab
Caprifoliaceae	Blackhaw viburnum	<i>Viburnum prunifolium</i>	0.36 ± 0.26ab	5.09 ± 1.29abc	3.82 ± 0.92a
Scrophulariaceae	Princess tree ^a	<i>Paulownia tomentosa</i>	2.80 ± 1.00a	2.00 ± 0.52bcd	1.76 ± 0.45ab
Elaeagnaceae	Russian olive	<i>Elaeagnus angustifolia</i>	0.18 ± 0.18b	1.10 ± 0.94e	3.58 ± 1.12ab
Fabaceae	Soybean ^a	<i>Glycine max</i> (cultivated)		0.17 ± 0.09e	0.53 ± 0.13b
Fabaceae	Siberian pea shrub	<i>Caragana arborescens</i>	0.12 ± 0.08b	1.07 ± 0.17cde	0.80 ± 0.24ab

^a Indicates Asian origin (USDA 2008).

^b Untransformed means are shown. Columns with the same letters have rank transformed means that are not significantly different ($P \leq 0.05$; Tukey's, test).

^c If plant was flowering or did not have leaves during the early season period, it was not sampled.

densities were significantly highest on *V. opulus* variety *americanum* ($F = 17.35$; $df = 13, 109$; $P < 0.001$). Based on the mid-season abundance of immatures (Fig. 3), it is possible that *H. halys* uses different host plants at various times of the year and possibly by different life stages. It is unclear at this point whether nymphs are more apparent on host plants at different times of the year or whether nymphs will move between host plants. Adult den-

sities were highest on *F. americana* during late season sampling ($F = 11.45$, $df = 13, 178$, $P < 0.001$) and *R. rugosa* and *V. prunifolium* both supported significantly higher nymphal densities than other hosts during late season ($F = 3.24$; $df = 11, 88$; $P < 0.001$). Use of host plants is consistent with the timing of fruit or pod development. For both *G. max* and *C. arborescens* (Fabaceae), population peaks occurred at the pod-fill stage.

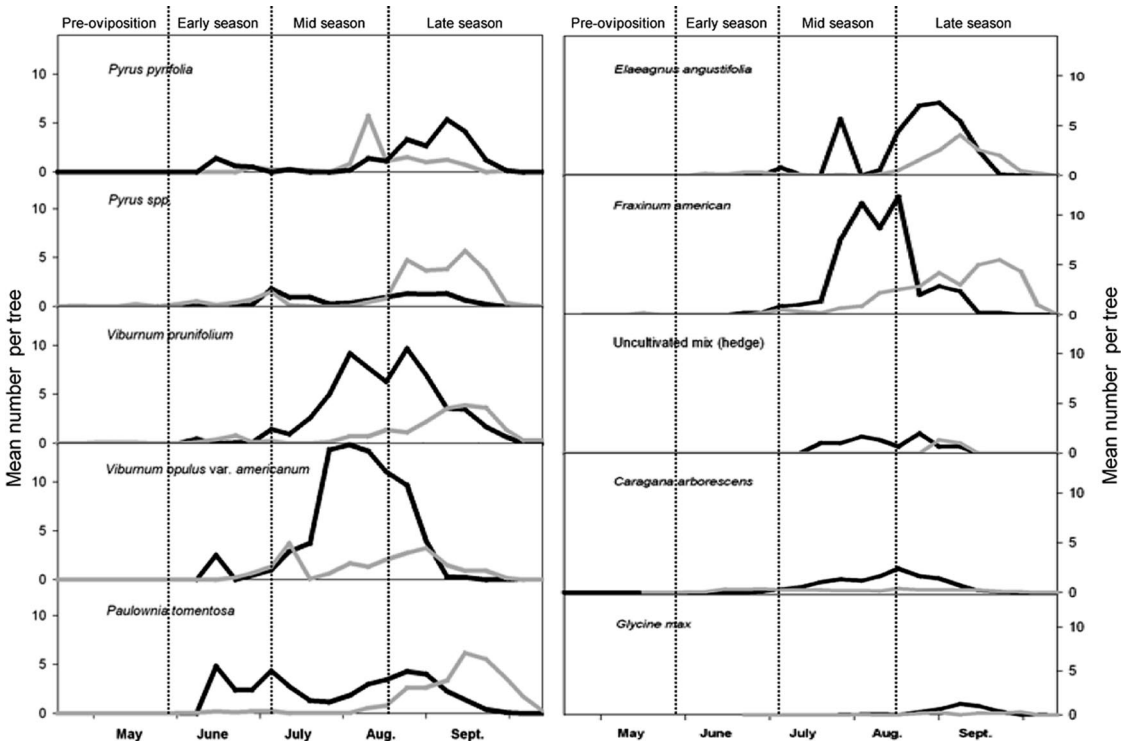


Fig. 3. Mean ± SE number of *H. halys* on host plants, 2006 and 2007. Nymphal populations are indicated with a black line, adult populations with a gray line. The different sampling periods (preoviposition, early, mid-, and late season) are designated.

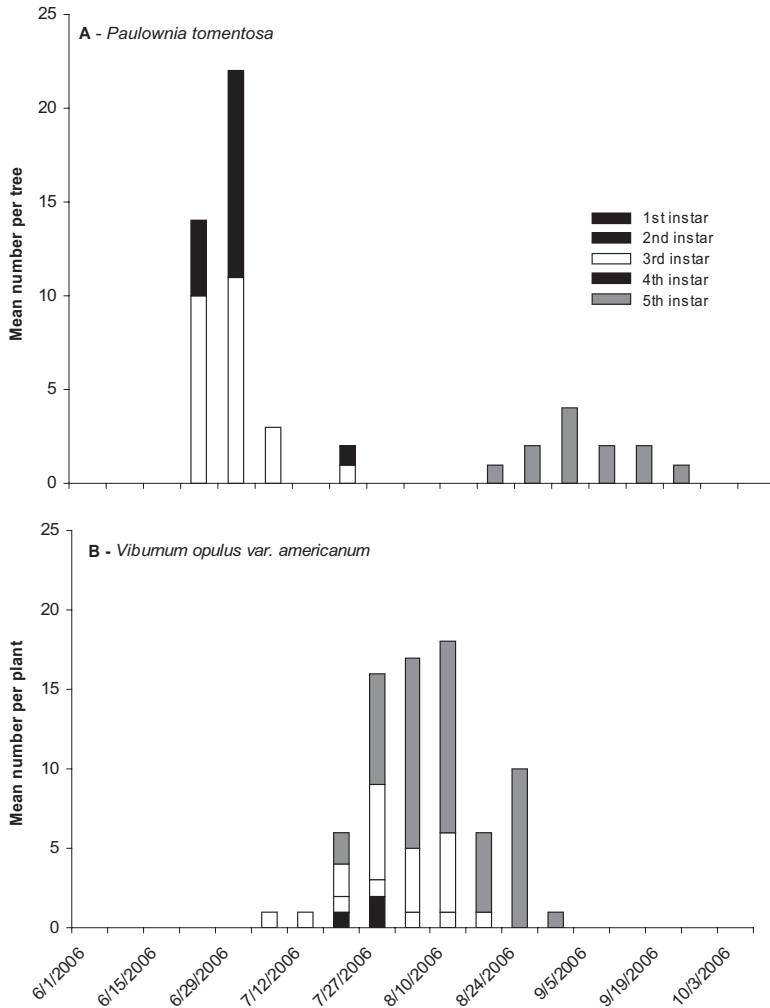


Fig. 4. Stage-specific association of *H. halys* nymphs with *P. tomentosa* and *V. opulus* variety *americanum* in 2006 in Allentown, PA.

Peaks in the nymphal seasonal dynamics were temporally separate between the exotic *P. tomentosa* and native *V. opulus* variety *americanum* in 2006 (Fig. 4), despite being >100 m apart. Although the two plants have different architecture and vary phenologically, peak abundance of nymphs on each host plant was consistent with leaf flush in *P. tomentosa* and maturing fruits in *V. opulus* variety *americanum*. Stage-specific differences were also evident. First, second, and fifth instars were abundant on *P. tomentosa*, whereas large populations of third, fourth, and fifth instars were present on *V. opulus* variety *americanum* (Fig. 4). Egg masses were not commonly observed on *V. opulus* variety *americanum*; however, beat sampling would dislodge second instars and indicate a recent oviposition event. This may indicate that *P. tomentosa* is a preferred oviposition site for females but an inferior plant for development or that third and fourth instars move upward into the canopy. Development on spe-

cific host plants and dispersal by nymphs between nearby host plants requires further study.

Relative Abundance. On host plants sampled from 2006 to 2007, *H. halys* was significantly more abundant than native pentatomid species in both ornamentals (2006: $F = 35.28$; $df = 9, 250$; $P \leq 0.0001$ and 2007: $F = 31.79$; $df = 8, 233$; $P \leq 0.0001$) and soybean (2006: $F = 11.82$; $df = 2, 75$; $P \leq 0.0001$ and 2007: $F = 11.55$; $df = 2, 69$; $P \leq 0.0001$) (Table 3). Assuming *H. halys* was introduced in 1996, there have been 14 generations in this region, during which it has become the predominant stink bug species in Allentown, PA, at the locations we sampled.

Flight Activity. Flight activity was monitored with a blacklight trap at Lichtenwalner Farms in 2006 and 2007 (Fig. 5). In 2006, the number of *H. halys* captured in blacklight traps throughout the season was higher than in 2007. Early season captures were low each year followed by a large peak at the beginning of August.

Table 3. Mean \pm SE number of pentatomid species found on ornamentals and in soybean

Species	2006		2007	
	Ornamental ^{a,b}	<i>G. max</i> ^{a,c}	Ornamental ^{a,b}	<i>G. max</i> ^{a,c}
<i>Halyomorpha halys</i>	206.23 \pm 39.51a	2.04 \pm 0.50a	300.38 \pm 66.59a	6.21 \pm 1.77a
<i>Euschistus servus</i>	1.00 \pm 0.36b	0.08 \pm 0.05b	0.31 \pm 0.14b	0.73 \pm 0.25b
<i>Euschistus tristigmus</i>	2.73 \pm 0.56b		1.15 \pm 0.30b	
<i>Euschistus variolarius</i>	0.23 \pm 0.10b	0.54 \pm 0.20b	0.00 \pm 0.00b	0.90 \pm 0.26b
<i>Euschistus</i> spp. ^d	4.92 \pm 0.10b		4.69 \pm 0.94b	
<i>Banasa</i> spp.	0.04 \pm 0.04b		0.39 \pm 0.21b	
<i>Thyanta</i> spp.	0.35 \pm 0.21b		0.04 \pm 0.04b	
<i>Acrosternum hilare</i>	14.15 \pm 3.08b		11.69 \pm 3.69b	
Other ^e	0.15 \pm 0.12b		1.58 \pm 0.47b	

^a Untransformed means are shown. Columns with the same letters have transformed means that are not significantly different ($P \leq 0.05$; Tukey's, test).

^b Seasonal mean number per tree.

^c Seasonal mean number of stink bugs per 10-m row sweep (as indicated under Materials and Methods). In soybean, only *E. servus*, *E. variolarius*, and *H. halys* were found consistently. Populations of *A. hilare* and *Thyanta* sp. were collected infrequently and at low numbers.

^d *Euschistus* nymphs were not identified to species.

^e Other phytophagous pentatomid species include *M. histrionica* and *Brochymena* spp., which were collected infrequently in the ornamentals.

Imaginal eclosion as indicated by DD accumulation (from 31 May) occurred at the large peak in flight activity observed in 2006 and 2007 (550 and 575 DD, respectively), suggesting that in an agroecosystems, recently eclosed fall adults move between hosts.

Discussion

Invasive species present a series of problems associated with their appearance in a new habitat (Lockwood et al. 2007). One approach to gauge potential pest status is to understand a species' host plant associations, seasonal dynamics, and distribution. These ecological factors are essential to implement future control methods. From the data presented here, it is evident that *H. halys* has a wide host range, a behavior that could make the presence of incipient populations difficult to detect until densities reach damaging levels.

There were apparent differences in the densities of adults and nymphs for each season. *P. tomentosus* was an early season host for nymphs and seemed to be a

preferred oviposition host. Nymphal population densities were consistent with host phenology, with *V. opulus* variety *americanum* and *R. rugosa* being preferred hosts in mid- and late season, respectively. A preference for early season hosts was not apparent for adults but in mid- and late season, adult densities were highest on *F. americana*.

We confirm that *H. halys* is univoltine in the Mid-Atlantic states with peak abundance occurring from late July through early September. The large population buildup we observed most likely results from the absence of natural enemies. Escape from natural enemies is hypothesized to be an important factor that permits invasive species to become significant pests in their new habitat (Williamson 1996). In China and Japan, egg parasitoids in the *Trissolcus* genus parasitize *H. halys* (Arakawa and Namura 2002). Although a different egg parasitoid species complex exists in the United States, preliminary studies suggests that parasitism of *H. halys* eggs by native *Trissolcus* spp. is low and may account for the large populations at the site

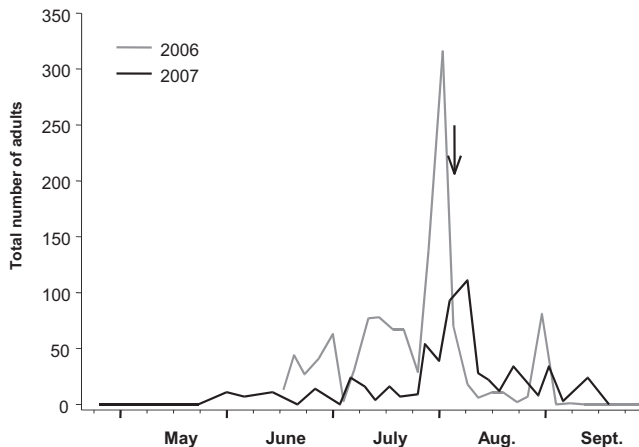


Fig. 5. Seasonal flight activity of *H. halys* as measured by captures of adults in a blacklight trap, Allentown, PA. Arrows (2006 —, 2007 —) indicate the degree day accumulation for imaginal eclosion (583 DD) from 31 May.

of introduction (K. Hoelmer, personal communication).

H. halys was the most abundant pentatomid species on all hosts sampled, although the ornamental host plants we selected for sampling may have biased the pentatomid species composition found. Native *Euschistus* spp., for example, are known to prefer mullein and uncultivated hosts plants to ornamental hosts and could account for the low population levels observed (Panizzi 1997, Krupke et al. 2001). *Euschistus* spp. are known pests of fruit trees and soybean, particularly in the southern states. However, in soybean, *H. halys* was found at significantly higher levels than both *Euschistus servus* (Say) and *Euschistus variolarius* (Palisot de Beauvois). *Acrosternum hilare* (Say) is believed to have a similar host range as *H. halys* (Bernon 2004); yet, we found significantly higher *H. halys* densities on all host plants sampled. Unlike other phytophagous pentatomid species, it does not seem that grasses play an important role in population buildups; instead, woody shrubs and hardwood trees may act as the desired alternate host species for *H. halys*.

M. domestica and *Pyrus* spp. have been shown here and in Japan to support spring adults and egg masses (Funayama 2004). Monitoring programs may be developed to focus on detecting small populations early in the season before reproduction and damage can occur. The data presented here demonstrated that a combination of beat samples and blacklight traps may allow detection of spring adults and accurate prediction of imaginal ecdysis, when most of the damage will occur. By increasing our understanding of *H. halys* life history, we can begin to develop monitoring programs and increase our understanding of traits for invasion success.

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