Spatiotemporal Dynamics of the Invasive *Halyomorpha halys* (Hemiptera: Pentatomidae) in and Between Adjacent Corn and Soybean Fields

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J. Econ. Entomol. 108(5): 2231–2241 (2015); DOI: 10.1093/jee/tov188

ABSTRACT Knowledge on movement and spatial patterns of insect pest populations among preferred hosts aids in the development of effective pest management strategies. In this study, we quantified the spatiotemporal dynamics of the invasive brown marmorated stink bug, *Halyomorpha halys* (Stål 1855), in relation to field corn, *Zea mays* L., and soybean, *Glycine max* (L.), crop phenology. We also examined the potential role of corn as a source of stink bugs in adjacent soybean. The highest density of stink bugs in each crop coincided with blister to milk-dough stages in corn (R2–R3/R4), and beginning seed to full seed (R5–R6) stages in soybean. In entire fields of adjacent corn and soybean, *H. halys* was found in very low density ($<0.5/m^2$) or absent beyond 25 m from the field edge. Inverse distance weighted interpolations of *H. halys* densities suggest potential dispersal of *H. halys*, particularly adults and large nymphs, from corn into soybean, coinciding with the end of dough stage in corn and beginning of soybean seed development stage. These findings have important implications for managing *H. halys* through location and timing of scouting efforts, consideration of crop arrangement, and decisions on management interventions. Repeated scouting of field corn to assess *H. halys* densities, particularly from blister stage onwards, could inform decisions on management interventions for preventing or mitigating *H. halys* colonization into soybean. Where *H. halys* is an economic problem, reducing the extent of boundary shared between corn and soybean could reduce dispersal into soybean.

KEY WORDS spatiotemporal dynamics, crop phenology, *Halyomorpha halys*, field crop, pest management

Heterogeneity of available habitats within agricultural ecosystems influence the dispersal and habitat selection of herbivorous insect pests, thereby affecting their population dynamics (Carrière et al. 2006, 2012). Vagile, generalist insect pests disperse between available crop hosts at the preferred phenological stages in the landscape (see Lamp and Zhao 1993, Kennedy and Storer 2000). Therefore, the seasonal availability and suitability of source and recipient crops in relation to the life stages of the pest influence the dispersal dynamics of pests from sources to recipient crops. Thus, knowledge on insect pest population dynamics vis-à-vis availability of noncrop and crop hosts at preferred growth stages within dispersal distance in the farmscapes may aid the development of effective pest management strategies.

In the mid-Atlantic United States, stink bugs were only recently considered serious pests of crops. Until the past decade, the most common stink bugs in agricultural fields in the mid-Atlantic were *Chinavia hilaris* (Say 1832) and *Euschistus servus* (Say 1832), but these species have had little economic impact in the region (Hooks 2011, Nielsen et al. 2011). The recent explosion in populations of the invasive brown marmorated stink bug, *Halyomorpha halys* (Stål 1855), however, has led to significant economic and ecological impacts. Since the accidental introduction in 1996 and discovery of this Asian stink bug near Allentown, Pennsylvania, USA (in 2001), *H. halys* has been detected in 41 states, and the insect has also been detected in Europe (CAB International [CABI] 2014, Rice et al. 2014). This polyphagous stink bug has a wide range of host plants including tree fruits, vegetables, field crops, ornamental plants, and native vegetation in its native and invaded ranges (Bergmann et al. 2014). Since 2010, serious economic losses have been reported for tree, fruit, ornamental, and row crops including field corn, *Zea mays* L., and soybeans, *Glycine max* (L.), in the mid-Atlantic region (Leskey et al. 2012, Rice et al. 2014).

Many Pentatomid species show specific feeding habits in relation to the local sequence of host plants available (Panizzi 1997). For example, host plant sequence for *Nezara viridula* (L. 1758) in Louisiana differed from that in South Carolina, and consequently the spatial dynamics of stink bugs were different (Newsom et al. 1980, Jones and Sullivan 1982). In the United States, stink bugs typically colonize soybean in late summer, and require other host species such as corn (Jones and Sullivan 1982, Tillman 2010) or wheat, *Triticum aestivum* L., (Reay-Jones 2010, 2014) for feeding during the spring and summer, during which time they

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build up population sizes (Schumann and Todd 1982, Leskey et al. 2012).

Corn and soybean fields are planted in high acreage throughout the United States (USDA National Agricultural Statistics Service 2014), often adjacent to each other, and corn is one of the earliest row crops available to stink bugs in the mid-Atlantic region. Hence, quantifying the spatial dynamics of stink bugs in corn would help in management of stink bugs in the region (Tillman 2010). As *H. halys* is considered an economic pest of many legumes (particularly soybean) both in its native and introduced areas (Leskey et al. 2012, Lee et al. 2013), soybean adjacent to corn provides a potential opportunity for outbreaks. The sequence of crop planting dates in which soybean is planted later than corn in adjacent fields makes soybean a suitable host (at seed filling stages R5 & R6; Nielsen et al. 2011, Owens et al. 2013) for *H. halys* to disperse in and between adjacent corn and soybean. Quantifying the temporal and spatial dynamics of stink bugs in adjacent crops will therefore improve the understanding of its build up in each crop, and the potential for movement to other neighboring crops (Tillman et al. 2009). Currently available studies documenting spatial and temporal dynamics of stink bugs in farmscapes with heterogeneous crops all pertain to the southern portion of the United States, while the population dynamics of stink bugs in adjacent corn and soybean of the mid-Atlantic region has not yet been addressed (Nielsen et al. 2011, Owens et al. 2013).

In this study we quantified the spatiotemporal dynamics of *H. halys* population density between corn and adjacent soybean, and examined the potential role of corn as a source of stink bugs in adjacent soybean. It represents the first effort to examine the influence of the reproductive corn growth stages on the density of *H. halys*, and the population densities and growth stage preferences in adjacent crops for *H. halys*. The experimental design addresses the following questions: 1) When is the peak density of *H. halys* in relation to corn and soybean reproductive development? 2) How does *H. halys* age structure differ in corn and soybean through time? 3) How does density of *H. halys* spatially vary through the season, within adjacent corn and soybean fields? 4) How does population density of *H. halys* in corn affect density in soybeans? We hypothesized that initial population buildup in corn would reach peak density during grain development stages (Leskey et al. 2012, CABI 2014, Rice et al. 2014). We expected the typical crop sequence and timings prevalent in the mid-Atlantic region to facilitate the dispersal of *H. halys* from corn to soybean during the seed filling stages of soybean.

Materials and Methods

Field Sampling. The study was conducted at the USDA Beltsville Agricultural Research Center at Beltsville, MD, and University of Maryland Research and Education Center facilities at Beltsville and Keedysville, MD. Stink bug populations were monitored at these two sites during 2012 and 2013 in a total of seven fields with adjacent corn and soybean and of varying dimensions. At each site, corn (76.2-cm row spacing) and full season soybean (17.8-cm row spacing) fields were planted within 10 m apart using standard agricultural practices (see Table 1 for field details), and shared at least 50 m of boundary interface. The soybean portion of each field bordered wooded regions, which are reported to influence *H. halys* abundance (Venugopal et al. 2014), that harbored many *H. halys* host plants including tree of heaven (*Ailanthus altissima* Swingle), princess tree (*Paulownia tomentosa* Baill.), and black cherry (*Prunus serotina* Ehrhart). Visual counts of stink bugs were recorded at geo-referenced points within each field that were spaced 15 m apart in all directions, except at the corn–soybean interface where samples were taken at each crop boundary interface. The total number of the sampling points in corn and soybean varied among fields and study sites (Table 1).

Stink bugs were counted at each sampling point in corn by carefully examining 10 consecutive plants and converted to densities using field level planting density information (see Table 1) to standardize across the different sizes and shapes of fields. For soybean, stink bugs were counted in all plants within two semicircular plots of 0.5 m radius each. Data were recorded for adults, small nymphs (2nd and 3rd instars), large nymphs (4th and 5th instars), and egg masses of *H. halys*, and densities were converted to stink bugs/m^2. The crop growth stage was also recorded based on samples from five corn or soybean plants at each point. Sampling commenced at the onset of silking through grain maturity of corn (R1–R6; Hanway 1963) during mid-July. In soybean, sampling commenced at the beginning pod stage (R3) during mid-July and continued till the physiological maturity of soybean seeds (R7; Fehr et al. 1971) in late September.

In addition to sampling entire fields of adjacent corn and soy, five soybean field edges adjacent to corn fields were also monitored for stink bugs using transect sampling (Table 1). At edges of soybean fields adjacent to corn, sampling sites along four transects spaced 15 m apart were marked at distances 0, 1.5, 3, 4.5, 6, 9, 12, and 15 m from the edge to field interior (total of 32 samples). Stink bugs were enumerated in all plants within a semicircular area of 0.5 m radius (1.57 m^2) from mid-August–late September coinciding with the seed development stages of soybean (R4–R7), which are associated with high *H. halys* abundance (Nielsen et al. 2011).

Statistical Analysis. The influences of crop phenology on the density of *H. halys* was analyzed by generalized linear mixed models (GLMMs) based on Laplace approximation, with a Poisson-lognormal error distribution and log link function (Elston et al. 2001, Bolker et al. 2009). Separate GLMMs for corn and soybean were performed, and each analysis treated density of *H. halys* as response variable, crop stage (phenology) as fixed effect with fields as replicates and points within the fields as subsamples. The fields were used as a random factor, as they were sampled repeatedly and mixed effects models with unit of measurement as random effect are also used to account for repeated measurement (Pinheiro and Bates 2000). The significance of

Table 1. Details on the corn and soybean fields, and soybean fields for edge sampling in Beltsville and Keedysville, MD, during 2012 and 2013

Study	Site	Year	ID	Location	Crop	Area (Ha)	Points	Planting date	Planting density/Ha	Variety	Sampling dates	Sampling frequency (d)
Corn–soy fields	Beltsville	2012	1	39.02 N, 76.87 W	Corn	0.63	28	7-May	113,311	Hubner 5582VT3	July 26–Sept. 6	7–10
					Soy	0.41	28	6-June	60,703	Channel 3806	July 26–Sept. 26	7–10
			2	39.04 N, 76.89 W	Corn	0.42	28	7-May	11,331	Hubner 5582VT3	July 18–Sept. 20	7–10
					Soy	0.42	28	6-June	60,703	Channel 3806	July 18–Sept. 26	7–10
			3	39.03 N, 76.82 W	Corn	0.72	32	3-May	11,331	Channel 207-13VT3P	July 16–Sept. 6	7–10
					Soy	0.66	32	6-June	60,703	Channel 3806	July 16–Sept. 27	7–10
			4	39.00 N, 76.85 W	Corn	0.53	32	27-April	11,331	Channel 210-61VT3	July 18–Sept. 6	7–10
					Soy	0.53	32	7-June	60,703	Channel 3806	July 18–Sept. 26	7–10
		2013	1	39.02 N, 76.87 W	Corn	0.63	28	6-May	11,331	Hubner 5582VT3	July 30–Sept. 6	7
					Soy	0.41	28	6-June	60,703	Channel 3806	July 30–Sept. 6	7
	Keedysville		5	39.50 N, 77.74 W	Corn	0.19	19	24-April	10,522	Pioneer 5K09AM1	July 26–Sept. 6	7
					Soy	0.43	35	22-May	72,844	Seed Consultants SCS9360RR	July 26–Sept. 24	7
			6	39.50 N, 77.72 W	Corn	0.47	28	25-April	10,522	Doebler's 633HXR	July 26–Sept. 6	7
					Soy	0.48	28	27-May	72,844	Seed Consultants SCS9360RR	July 26–Sept. 24	7
Soy edge	Beltsville	2012	1	39.02 N, 76.82 W				8-May	62,951	Pioneer 93Y91	Aug. 16–Sept. 6	7
	Keedysville		2	39.51 N, 77.73 W				4-June	72,844	Doebler's 3809RR	Aug. 16–Sept. 26	7
			3	39.50 N, 77.73 W				4-June	72,844	Doebler's 3809RR	Aug. 16–Sept. 26	7
	Beltsville	2013	4	39.02 N, 76.83 W				8-May	62,951	Pioneer 93Y91	Aug. 16–Sept. 16	7
	Keedysville		5	39.51 N, 77.74 W				27-May	72,844	Seed Consultants SCS9360RR	Aug. 16–Sept. 18	7

the fixed effects was determined by Wald χ^2 tests, and the coefficient of determination (R^2) for the fixed effects was also calculated (Nakagawa and Schielzeth 2013). Significant differences in the estimated means of stink bug density between the different crop stages were identified through Tukey's HSD pair-wise comparisons.

Seasonal dynamics in *H. halys* population structure in relation to crop phenology were visualized through area charts. Differences in *H. halys* population structure between corn and soybean was investigated through Fisher's exact test on overall count data (pooled over sampling dates) for each of the fields sampled. The spatial heterogeneity in *H. halys* density was characterized using Inverse Distance Weighted (IDW) interpolation technique. IDW utilizes values from geo-referenced points to predict densities for points not sampled, and values from the geo-referenced points close to the target point carried larger weight than those further away (Webster and Oliver 2007). The exponent or power value for the IDW was set to the commonly used value of two (Webster and Oliver 2007), and a search radius based on input from 12 points was used. The primary rationale for using IDW for the interpolation was that *H. halys* is predominantly distributed at the edges of field crops (Venugopal et al. 2014) and IDW is reported to be appropriate for such aggregated data. Previous studies have characterized spatial variation in the density of other aggregated insect species, including stink bugs, using IDW (Beckler et al. 2004, Rhodes et al. 2011, Tillman 2011). For each field and sampling date, observed *H. halys* densities were converted to density / m^2 and interpolations were performed with the converted data.

H. halys density in soybean field edges adjacent to corn was compared between Beltsville and Keedysville using GLMM based on Laplace approximation with a Poisson-lognormal error distribution and log link function (Elston et al. 2001, Bolker et al. 2009). GLMM were performed with stink bug density as response, study site as the fixed effect, and sampling field as random variable to account for differences in conditions at the field level. The significance of the fixed effects was determined by Wald χ^2 tests. Significant differences in the GLMM estimated means of stink bug density between the study sites were identified through Tukey's HSD pair-wise comparisons.

All statistical analyses were performed in R program (R Development Core Team 2014) and associated statistical packages. GLMMs were performed with package lme4 (Bates et al. 2014) and Tukey's HSD comparisons of means for GLMMs were computed with package "multcomp" (Hothorn et al. 2013). Coefficient of determination (pseudo R^2) for the GLMM fixed effects was calculated with package MuMin (Bartoń 2013). IDW interpolations were performed and visualized using package "gstat" (Pebesma and Graeler 2013).

Results

The total number of *H. halys* recorded was 90 (corn) and 348 (soybean), in the four fields that were sampled at Beltsville during 2012. Stink bug populations were significantly lower at Beltsville in 2013, with only 7 (corn) and 6 (soybean) *H. halys* recorded at one of the fields. At Keedysville during 2013, a total of 1,157 (corn) and 2,154 (soybean) *H. halys* respectively, were recorded in two fields sampled. As data from the Beltsville sites were too few for any meaningful analyses, only the 2013 data from Keedysville were used for statistical analyses. However, to depict the general population density trend at the Beltsville fields, interpolated density map for each sampling date was generated for the field with highest stink bug observation in both 2012 and 2013.

GLMMs relating corn and soybean phenology to *H. halys* densities showed significant results (corn—Wald $\chi^2 = 106.7$, df = 6, $P < 0.001$, fixed effects *psuedo*-$R^2 = 0.48$; soybean—Wald $\chi^2 = 238.2$, df = 8, $P < 0.001$, fixed effects *psuedo*-$R^2 = 0.43$). Generally higher density of *H. halys* was observed during earlier stages of corn maturity (R2 blister–R3/R4 milk/dough), than the later maturity stages (R5 dent–R6 physiological maturity). In soybean, highest density was observed at begin-full seed (R5/R6; Fig. 1B) stages, and higher stink bug densities were observed during seed filling stages (R5–R6) than the begin pod (R3) or physiological maturity (R7) stages.

The seasonal dynamics in the density and age structure of *H. halys* differed between corn and soybean. In the corn portion of Field 5 and 6 at Keedysville, proportions of small nymphs and adults were greater than that of large nymphs (Figs. 2A and 3A, respectively). Also, there was a steep decline in total number of stink bugs observed in both fields beyond the dough stage of corn (Figs. 2A and 3A). This decrease coincided with corresponding increase in observed stink bug density in soybean, particularly at the full pod to early seed development stages (R4–R5). Also, higher proportion of large nymphs than small nymphs or adults was observed in soybean (Figs. 2B and 3B). The difference in age structure of *H. halys* between corn and soybean with respect to the relative proportions of large nymphs to small nymphs was statistically significant for both Fields 5 and 6 in Keedysville ($P < 0.001$, Fisher's exact test).

Visual inspection of the interpolated density of *H. halys* in Field 5 at Keedysville showed initial distribution and buildup of population restricted to corn (Fig. 4; 26 July) and higher densities in corn (15–20/m^2) along the corn–soy interface (31 July and 7 August). After August 7, densities in corn diminished and stink bugs were observed in soybean adjacent to corn (20 August–12 September) and at the other end of the field adjacent to woods (5–10/m^2), while not at the center of the soybean field. Also, nymphs comprised a high proportion of stink bugs in soybean adjacent to corn on 6 September (3–5/m^2). Spatial pattern of density in Field 6 at Keedysville was similar to that of Field 5, with high density in corn along corn–soy interface (31 July–7 August; 10–12/m^2) gradually diminishing to show increasing density in adjacent soybean (14 August–6 September; Fig. 5). In Beltsville, however, very few stink bugs were observed overall and there was no buildup of populations in corn in both

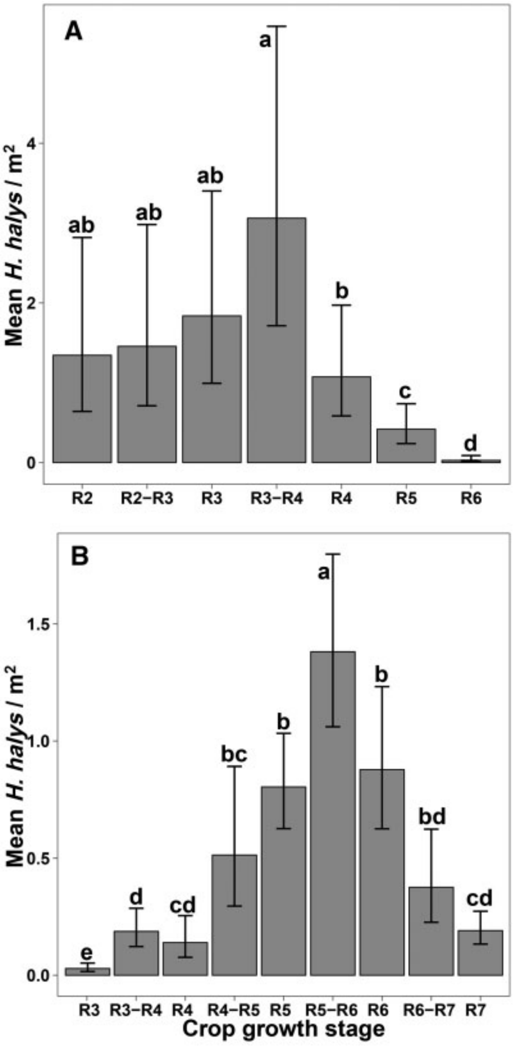

Fig. 1. GLMM comparisons of *H. halys* densities at different phenological stages of field corn (A) and soybean (B) at Keedysville, MD, during 2013. The vertical lines represent 95% confidence interval. Means with the same letter above bars are not significantly different ($\alpha = 0.05$, Tukey's HSD).

years at Field 1 (Fig. 6). The highest density of stink bugs was observed later in the season, in soybean (20 August–30 August 2012; 8/m^2 and 29 August 2013; 8/m^2). In Beltsville, stink bug density in corn–soy interface was close to zero, and the highest density of stink bug was observed directly in soybean edges bordering woods (Fig. 6; 20–31 August 2012 and 29 August 2013) during the R5-R6 stage.

Results comparing densities at soybean field edges adjacent to corn were similar to the site level differences in the stink bug spatial dynamics as observed from the interpolated maps. In soybean edges adjacent to corn, GLMM and Tukey's HSD showed significantly less *H. halys* density/m^2 ($\chi^2 = 33.3$, df = 1, $P < 0.001$)

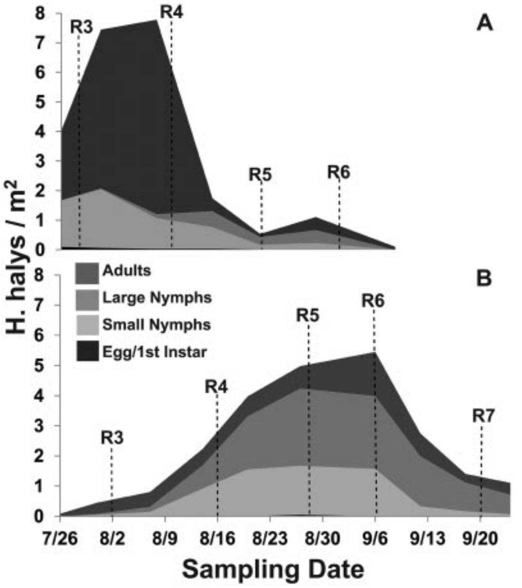

Fig. 2. Seasonal dynamics and life stage densities of *H. halys* in relation to growth stages of adjacent corn (A) and soybean (B) in Field 6 at Keedysville, MD, during 2013.

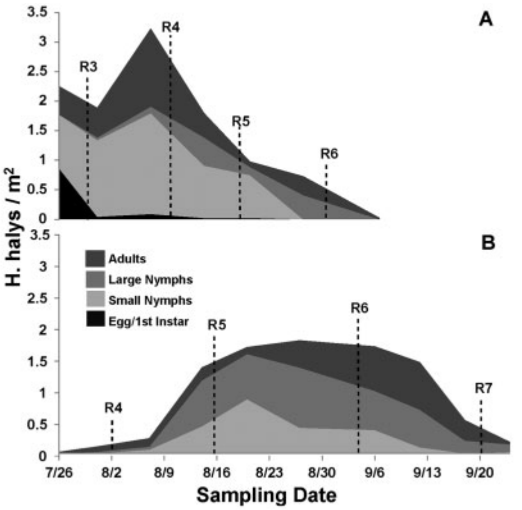

Fig. 3. Seasonal dynamics and life stage densities of *H. halys* in relation to growth stages of adjacent field corn (A) and soybean (B) in Field 5 at Keedysville, MD, during 2013.

in Beltsville [mean (95% CI)–0.05 (0.02–0.0.11)] than Keedysville [0.91 (0.52–5.00)].

Discussion

H. halys is a generalist feeder that utilizes multiple hosts within the farmscape. Our results suggest that *H. halys* exhibits edge-mediated dispersal from corn into soybean at sites with higher initial population in corn, and that the timing of movement is highly dependent on the presence of preferred crop growth stages. Such dispersal between available crops at preferred stages in the farmscape has been recorded for various agricultural pests including mites (Kennedy and Margolies 1985), thrips (North and Shelton 1986), lygus bugs (Sevacherian and Stern 1975, Sivakoff et al. 2013), soybean aphids (Bahlai et al. 2010), potato leafhoppers (Lamp and Zhao 1993), and European corn borers (Umeozor et al. 1986). We found that while crop growth stages influenced stink bug population densities, the role of adjacent corn as a source of *H. halys* invading soybean varied with site.

The edge-centric behavior by *H. halys* observed in our study conforms to existing reports (Blaauw et al. 2014, Venugopal et al. 2014, 2015). Likewise, the preference for fruiting bodies by *H. halys* is similar to that of many other North American stink bug species (Jones and Sullivan 1982, Panizzi and Slansky 1985, Kennedy and Storer 2000, Tillman et al. 2009, Reay-Jones 2010, Reeves et al. 2010). *H. halys* densities on corn and soybean are related to seed development stages. Adults and older nymphs feed primarily on developing corn ears by penetrating the husk leaves with their feeding stylets to suck tissue from the developing kernels (P. D. V., personal observation). They also feed on the developing seeds in soybean pods in a similar way. The nutritional quality of developing corn kernels and soybean seeds likely explains the high density of *H. halys* during these stages of crop growth. The moisture and sugar content in corn grain peaks just around the blister stage (Ingle et al. 1965, Ritchie et al. 1993). The various nitrogenous materials including protein, soluble nitrogen, amino acid, RNA, DNA, and soluble nucleotides increase steadily during milk stage (Ingle et al. 1965). While the sugar content continues to decrease after blister, amino acid content, soluble nucleotides and RNA all which peak around the dough stage, also begin to decline steeply as the grain hardens and matures (Ingle et al. 1965).

In soybean, seed weight increased rapidly during the pod filling stages (R4–R6), to 90% of total by R6, providing continuous consumable food resources for stink bugs. Peak abundance of stink bugs were observed between R5–R6 stages which represent the stages with increasing seed dry weight, protein, oil, and sugar content (Rubel et al. 1972, Dornbos and McDonald 1986, Kim et al. 2006). Overall free sugar content, particularly sucrose, raffinose, and stachyose, increased sharply between R5–R6 during which the fatty acid content, especially oleic and linoleic acids, also accumulates rapidly (Dornbos and McDonald 1986, Kim et al. 2006). In both corn and soybean, the high density of stink bugs observed was probably associated with the nutritional quality of the fruiting bodies at these stages. Corn blister to dough stages and soybean seed filling stages represent the period of availability of both carbonaceous and nitrogenous material in high proportions for the stink bugs.

Stink bug infestations vary between corn and soybean in relation to the duration of fruiting bodies at preferred stages. The longer period for which high density of stink bugs was observed in soybean than in corn could be attributed to the duration of kernel and

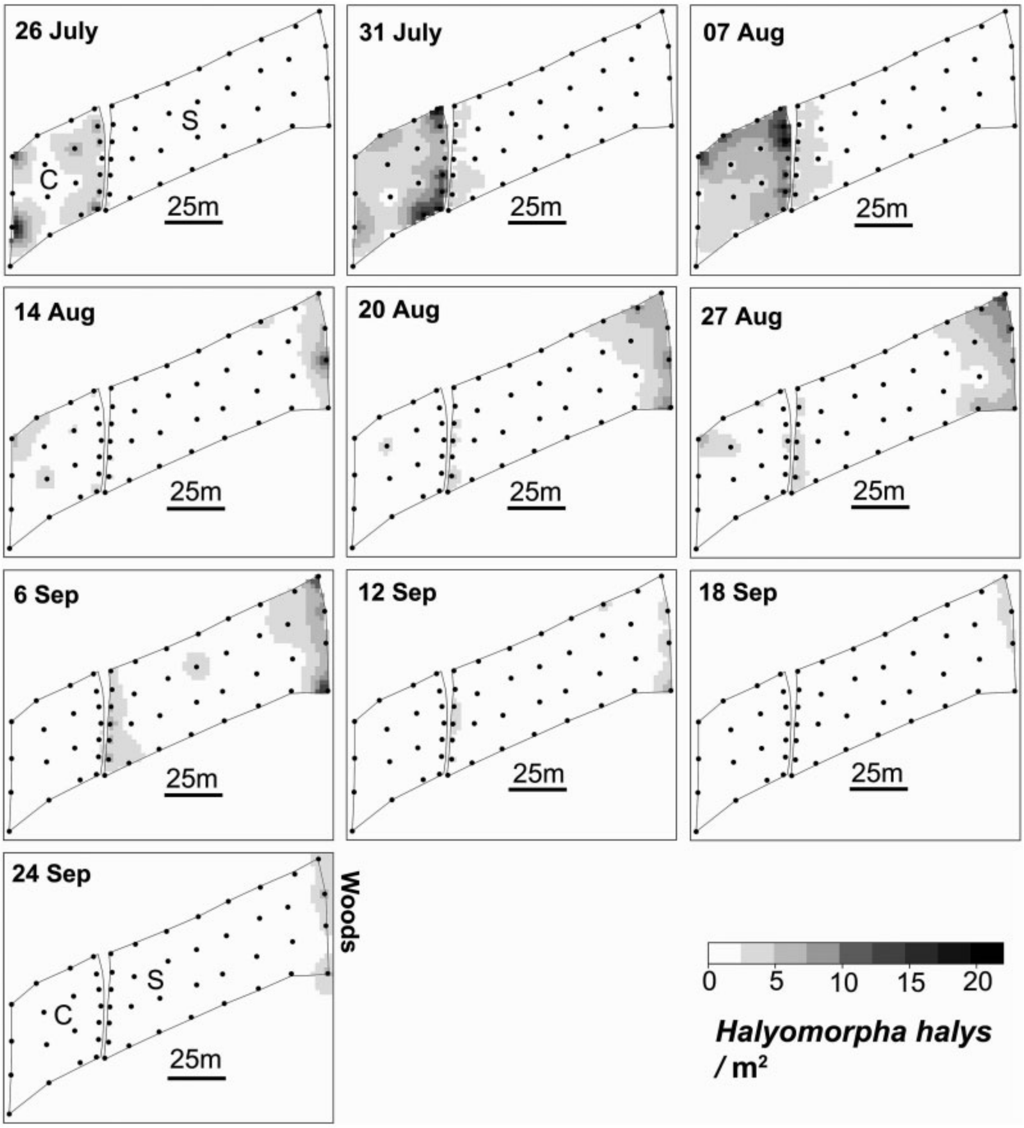

Fig. 4. Spatial interpolation of *H. halys* densities in adjacent corn (denoted by C) and soybean (S) across the 2013 growing season at Field 5 in Keedysville, MD. Extent of corn and soybean sampled is demarcated by black lines while the black circles represent the location of sample points, and the location of woods along field edges is also shown.

seed growth stages preferred by stink bugs in each crop. Beyond the dough stage, maturity of corn proceeds rapidly with grain hardening to maturity within 2 wk. However, the seed enlargement period in soybean occurs over an entire month. At Keedysville after the initial buildup of population in corn, the steep decline in *H. halys* density during the dent stage corresponded to the steep increase in soybean during the pod filling stages. Also, interpolation maps revealed high densities in soybean edge bordering corn (during 9 August–6 September) illustrating the potential dispersal of stink bugs from corn into soybean. The preference and dispersal of stink bugs into soybean during the reproductive stages has been well documented by earlier studies (Turnipseed and Kogan 1976, Jones and Sullivan 1982, Schumann and Todd 1982, Panizzi and Slansky 1985, Kogan and Turnipseed 1987, Todd 1989, Velasco and Walter 1992, McPherson et al. 1993, Bundy and McPherson 2000, Kennedy and Storer 2000, Olson et al. 2011, Herbert and Toews 2012).

Additionally, the age structure of *H. halys* within each crop was significantly different. Significantly higher numbers of small nymphs and adults compared to large nymphs were recorded in corn, whereas the relative proportions of these stages were reversed in soybean. This suggests potential dispersal of large nymphs from corn into soybean at the interface of these crops, particularly during the dent stage in corn.

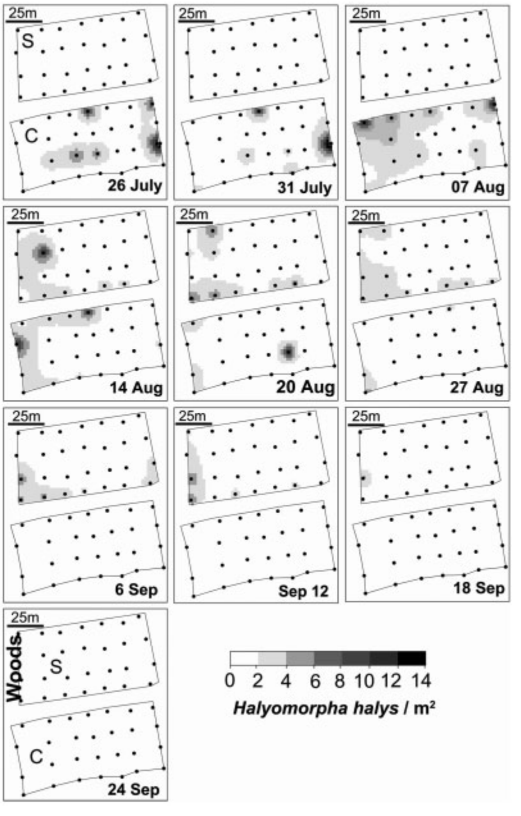

Fig. 5. Spatial interpolation of *H. halys* densities in adjacent corn (denoted by C) and soybean (S) across the 2013 growing season at Field 6 in Keedysville, MD. Extent of the corn and soybean sampled is demarcated by black lines while the black circles represent the location of sample points, and the location of woods along field edges is also shown.

Previous studies have documented fewer number of large nymphs in comparison to adults of *N. viridula* and *E. servus* in corn (Herbert and Toews 2011, 2012; Reisig et al. 2013). Like the adults, large nymphs of stink bugs including *H. halys* are capable of dispersal and observed to move between habitats (Tillman 2011, Lee et al. 2014). Taken together, the spatial dynamics and age structure within each crop at the Keedysville sites imply that the sequential movement of *H. halys* (particularly adults and large nymphs) between corn and soybean fields is strongly influenced by the availability of the preferred phenological growth stages. Such movement and aggregation of nymphs at the interface of peanut–cotton systems has been reported for *N. viridula* and *E. servus* (Tillman 2011). Shifting between host plants as the preferred phenological stages become available in other hosts is a prevalent behavioral characteristic of stink bugs (Toscano and Stern 1976, Jones and Sullivan 1982, Panizzi 1997, Tillman et al. 2009, Reay-Jones 2010, Olson et al. 2011, Reisig 2011, Tillman 2011).

Studies quantifying spatial dynamics of stink bugs have documented the movement and population increase between corn and other adjacent crops. Similar to our study, adult stink bugs were observed to move from senescing corn into peanut and cotton (Tillman 2011). High stink bug densities were observed in cotton adjacent to corn, and therefore, localized control methods in corn have been recommended to mitigate stink bug invasion in subsequent crops (Tillman 2011). Likewise our study identifies the potential role of corn as a source of stink bugs invading soybean but more research is needed to determine if managing stink bugs in corn will reduce the risk of infestations in soybean. The stink bug population density in late maturing crops such as soybean is heavily influenced by the extent of synchrony between dispersing adults and large nymphs, and availability of phenological stages of the crop preferred by stink bugs (Kennedy and Storer 2000). The seasonal occurrence of preferred soybean crop stage is largely determined by the planting date, cultivar of choice, and maturity group (Schumann and Todd 1982, Kennedy and Storer 2000). For the fields in this study, there was observed synchrony between the stink bug stages dispersing from corn and the preferred pod filling stages of adjacent soybean planted as a full season crop. However, the synchrony between the two crops may be different if the soybean fields were planted later as a double crop after small grains, which is a common practice in the mid-Atlantic region. Reports from crop advisors do indicate that the highest stink bug infestations in soybean have varied with respect to full season or double crop plantings (personal observation, Galen Dively).

At Beltsville, the spatial pattern of density did not suggest any dispersal of stink bugs from corn into soybean. Insect population dynamics and spatial patterns are affected by regional landscape context and species traits such as dispersal ability (Tscharntke and Brandl 2004), and distribution. Hence, the density of *H. halys* at a field may depend on habitat and other environmental characteristics at spatial scales greater than the local agricultural field (Thies et al. 2003, Tscharntke et al. 2005). These factors could explain the potential differences in *H. halys* density observed between study sites rather than any asynchrony in the availability of preferred crop growth stages at Beltsville, when stink bugs were probably moving among host plants during the mid to late summer. These results suggest potential differences between sites with differing overall *H. halys* population densities, in the role of corn as a source of *H. halys* invading soybean. Therefore, the combined results of the study help understand the potential role of corn as a source of *H. halys* that disperse (particularly adults and large nymphs) into soybean, when overall *H. halys* density is high. This has significant relevance for *H. halys* management in field crops especially given the high proportion of soybean fields that are planted adjacent to corn. While the invasion of *H. halys* into soybean from corn is observed only at sites with high overall population density, the ubiquity of adjacent soybean and corn plantings in the mid-Atlantic region does warrant attention with regards to managing *H. halys* in field crops.

Findings of this study have important implications for managing *H. halys* both at the regional and farm

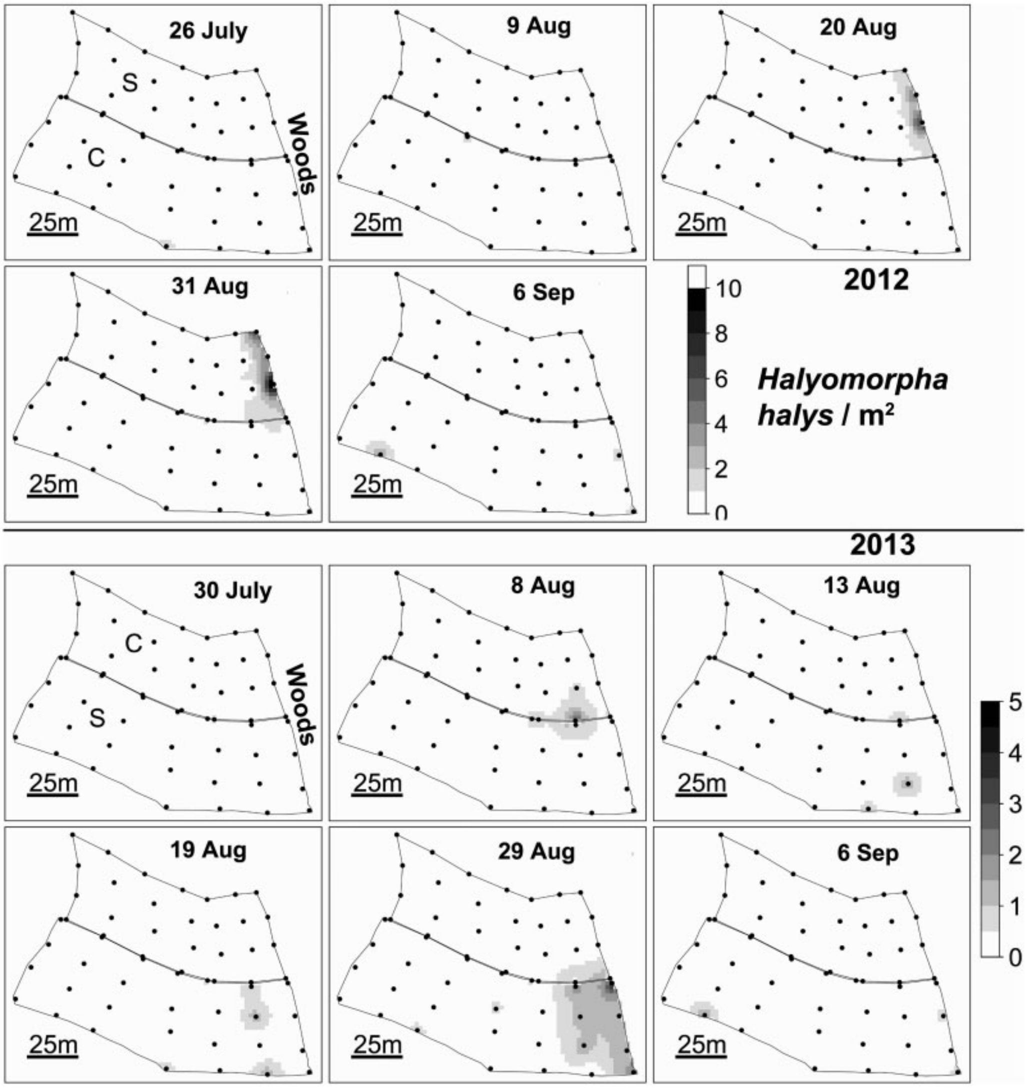

Fig. 6. Spatial interpolation of *H. halys* densities in adjacent corn (denoted by C) and soybean (S) during 2012 (top panel) and 2013 (bottom panel) growing seasons at Field 1 in Beltsville, MD. Extent of the corn and soybean sampled is demarcated by black lines while the black circles represent the location of sample points, and the location of woods along field edges is also shown.

levels. The economic thresholds for field corn are currently still being developed, and in general, higher stink bug density is associated with increased injury to corn kernels (Venugopal et al. 2014). Also, kernel quality loss due to *H. halys* is restricted to about 10 m from the field edge and currently growers in the mid-Atlantic region do not report yield losses and do not consider any management interventions for stink bugs in field corn. It should be noted that effective insecticidal treatment for stink bugs in field corn could be challenging due to the amount of foliage between the corn ear and the top of the plant (Reisig 2011). For soybean, density of stink bugs above the current tentative threshold of one to two stink bugs per foot row (Rice et al. 2014) only occurred at Keedysville, at the field edge bordering woods and at the interface of corn and soybean. The above threshold densities of *H. halys* observed is reported to have significant negative impacts on soybean pod development, seed damage, and yield, and is also associated with "stay-green" phenomenon, significant delay or failure in senescence due to stink bug feeding injuries, observed at the field edges (Rice et al. 2014, Venugopal et al. 2014).

Given this, management strategies may consider an area-wide manipulation of the phenology, placement, and suitability of selected types of vegetation and crops to counteract landscape-level processes supporting pest outbreaks (Lamp and Zhao 1993, Kennedy and Storer 2000, Jonsson et al. 2010). Particularly at high density sites, the timing of scouting in corn and soybean should coincide with the onset of preferred growth stages in each crop and focus at least initially on the interfaces of adjacent fields. Crop arrangement in the farmscapes, planting date, and cultivar, may also serve as possible options to desynchronize the timing for initial stink bug build up in corn and subsequent dispersal into soybean. Thus, strip planting of corn and soybean as a cultural practice associated with farm topography may represent a poor strategy for placement and arrangement of crops in the farm in terms of stink bug management tactics. In general, reducing the extent of boundary shared between corn and soybean could reduce migration into soybean where *H. halys* is an economic problem.

In the context of adjacent corn and soybean fields, our results suggest that the co-occurrence of crop stages favored by *H. halys* might exacerbate damage to soybeans. The problem could be solved by planting an early maturing variety of soybean that reach mature, less attractive seed stages before stink bugs move off trees or out of corn; conversely, using late soybean varieties with delayed maturation might avoid the greatest movement of stink bugs in mid to late July. It is noted that these recommendations are preliminary and their efficacy in preventing *H. halys* infestation needs detailed field evaluation. Repeated scouting of field corn to assess stink bug density levels, particularly from blister stage onwards, could inform decisions on management interventions for preventing or mitigating *H. halys* colonization into soybean. Our study identifies potential ways by which the management of spatial dynamics of *H. halys* may reduce losses incurred by this mobile, polyphagous pest.

Acknowledgments

The farm managers at each of the research facilities—Kevin Conover (Beltsville), Tim Ellis (Keedysville), and David Swain (USDA–BARC)—all extended excellent support and assistance for conducting the study. We thank Terry Patton for his help to identify sampling fields. We thank the summer technicians, Peter Coffey, Jesse Ditillo, Jessie Saunders, Jake Bodart, Taylor Schulden, Kyle Runion, and Emily Zobel for data collection. The study was funded by United Soybean Board, Maryland Soybean Board, Maryland Grain Producers Utilization Board, Cosmos Club Foundation, and Hatch Project #MD-ENTM-1016. Support for the principal investigator was provided by a United States Department of Agriculture, National Institute of Food & Agriculture - Sustainable Agriculture Research & Education graduate student grant (GNE12-047) and Gahan Fellowship from the Department of Entomology, University of Maryland. Comments from three anonymous reviewers improved the manuscript.

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Received 20 July 2014; accepted 12 June 2015.