Plant–Insect Interactions

Host Plant Effects on *Halyomorpha halys* (Hemiptera: Pentatomidae) Nymphal Development and Survivorship

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Abstract

*Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) is a highly polyphagous invasive species and an important pest of orchard crops in the United States. In the Mid-Atlantic region, wild hosts of *H. halys* are common in woodlands that often border orchards, and *H. halys* movement from them into orchards poses ongoing management issues. To improve our understanding of host plant effects on *H. halys* populations at the orchard–woodland interface, nymphal survivorship, developmental duration, and adult fitness (size and fresh weight) on apple (*Malus domestica* Borkh.), peach (*Prunus persica* (L.) Batsch), Tree of Heaven (*Ailanthus altissima* (Mill.) Swingle), and northern catalpa (*Catalpa speciosa* (Warder)) were examined in laboratory studies. Specifically, we investigated nymphal performance on the foliage and fruiting structures of those hosts and on single- versus mixed-host diets, as well as the effects of host phenology on their suitability. Nymphal performance was poor on a diet of foliage alone, regardless of host. When fruiting structures were combined with foliage, peach was highly suitable for nymphal development and survivorship, whereas apple, Tree of Heaven, and catalpa were less so, although nymphal survival on Tree of Heaven was much greater later in the season than earlier. Mixed-host diets yielded increased nymphal survivorship and decreased developmental duration compared with diets of suboptimal single hosts. Adult size and weight were generally greater when they developed from nymphs reared on mixed diets. The implications of our results to the dispersal behavior, establishment, and management of *H. halys* are discussed.

Key words: host plant suitability, brown marmorated stink bug, mixed diet, polyphagy, nymph

Plant species vary widely in their suitability as food for polyphagous insect herbivores (Scriber 1984) and can affect insect development and survival differently via their chemical (e.g., nutritional quality, allelochemicals) or physical (e.g., trichomes, tissue hardness) characteristics, which may vary with plant age and phenology (Bernays and Chapman 1994). Polyphagous insect herbivores may complete development on a single host, but their fitness is generally enhanced when they feed and develop on multiple plant species (Bernays et al. 1994, Hägge and Rowell-Rahier 1999, Miura and Ohnsaki 2004). For example, the polyphagous hemipteran, *Bemisia tabaci* (Gennadius), exhibited higher survivorship and increased fecundity on a mixed diet of cotton, cucumber, tomato, cabbage, and kidney beans than on any of those plants alone (Zhang et al. 2014). Earlier studies found that fitness advantages of mixed diets were associated with nutritional complementarity and/or the dilution of allelochemicals (Bernays et al. 1994, Hägge and Rowell-Rahier 1999).

Research on the relative suitability of plant species to polyphagous insect pests that utilize both cultivated and wild hosts has important implications for understanding aspects of pest biology and ecology, such as their movement in the landscape, host use patterns, and population dynamics, as well as the susceptibility of economic crops to attack (Panizzi 1997). Such studies have yielded beneficial information about basic pest biology, informed the development of ecologically based pest management options (Panizzi and Parra 2012), and are especially relevant to recently invasive economic pests, about which there are often important knowledge gaps regarding their biology and ecology in the invaded range. The brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), is a classic example of this.

*Halyomorpha halys* is an invasive pest from Asia that did not become a major pest until the late 2000s (Leskey et al. 2012a), following its initial detection in Allentown, PA, about a decade earlier (Hoebeke and Carter 2003). Since its widespread outbreak in the Mid-Atlantic region of the United States in 2010, *H. halys* has caused significant economic damage to various fruit, vegetable, and field crops (Rice et al. 2014). Its effects in Mid-Atlantic fruit orchards have been especially pronounced via reductions in fruit yield and quality and changed pest management practices (Leskey et al. 2012b) that have resulted in secondary pest outbreaks. *Halyomorpha halys* is reported to utilize well over 100 plant species...
as feeding or reproductive hosts (Rice et al. 2014), many of which are deciduous trees that grow in forested areas that often border commercial orchards in this region (Bakken et al. 2015). The abundance of wild hosts in these woodlands, the development of large H. halys populations on some, and the high dispersal capacity of H. halys adults and nymphs (Lee et al. 2014, Wiman et al. 2014, Lee and Leskey 2015) combine to create pest pressure in commercial orchards through most or all of the fruiting period (Joseph et al. 2015). Moreover, Funayama (2006) showed that fitness of H. halys nymphs was positively affected when they developed on a mixed diet.

Investigation of the effects of different wild and cultivated host plants on H. halys development and survivorship in its invasive range should further our understanding of their relative contributions to local H. halys population densities and the risk to economic crops and may aid the development of ecologically based pest management tactics against this important pest. Here, we report laboratory experiments that examined the effects of selected wild and tree crops and may aid the development of large H. halys populations on some, and the high dispersal capacity of H. halys adults and nymphs (Lee et al. 2014, Wiman et al. 2014, Lee and Leskey 2015) combine to create pest pressure in commercial orchards through most or all of the fruiting period (Joseph et al. 2015). Moreover, Funayama (2006) showed that fitness of H. halys nymphs was positively affected when they developed on a mixed diet.

Materials and Methods

Insects

Adult male and female H. halys collected from natural overwintering aggregations in northern Virginia in April 2012 and February 2013 were placed in black, plastic bags with crumpled newspaper and held in a dark room at 4°C for 1 week before acclimation to room temperature. Each cohort of first instars on the egg mass was placed on or near the cage floor. All plants were transferred to cages as cohorts from each egg mass.

Cohorts of first instars, each with 10 adults and nymphs, were placed in an experiment between late May and early August 2013. Cohorts of first instars, each with ~28 instars, were assigned individually to seven replicates of each diet treatment. Each replicate was a complete randomized design with two factors, host plant species and the stage of development of each host plant in the field at the time each experiment was conducted. From early- to mid-June, immature apple and peach fruit (three to four per replicate) and foliage, Tree of Heaven flowers and foliage, and catalpa flowers and foliage were used. The volume of Tree of Heaven and catalpa flowers offered was comparable with the total volume of the apple and peach fruit offered. Later in the season,—one to two larger apple and peach fruit and foliage were offered. At that time, three catalpa seed pods (10.16–12.70 cm in length) and foliage and Tree of Heaven samaras and foliage were offered. The volume of seed pods and samaras offered was approximately the same as the other treatments.

The plant materials were washed thoroughly under running tap water to remove contaminants (e.g., fungicide residues, other arthropods, etc.). The foliage offered to nymphs included three terminal twigs of apples and peaches with—six to eight leaves (20.32–25.40 cm in length), two apical branches of catalpa with—two to three leaves (15.24–20.32 cm in length), and three compound leaves of Tree of Heaven (25.4–30.48 cm in length). All shoots offered, including those with flowers, samaras, or catalpa pods, were inserted into—two to four holes (8 mm diameter) in the plastic lid of plastic containers (8 cm height, 115 mm diameter) containing water, while peach and apple fruit were placed on the cage floor. All plant tissues were replaced—two to three times per week.

Single-Host Diets

A completely randomized design with two factors, host plant species and plant tissue (foliage versus foliage plus reproductive structures), was used in an experiment between late May and early August 2012. Cohorts of first instars, each with ~28 instars, were assigned individually to seven replicates of each diet treatment. Each cohort of first instars on the egg mass was placed on or near the plant material inside a 30.48 by 30.48 by 30.48-cm cage (BioQuip Products, Inc, Rancho Dominguez, CA) with ad libitum access to the food source and water. Water was provided in a plastic container with a cotton wick inserted through the lid. Cages were inspected daily for the presence of exuviae, which indicated the molt between instars, and the specific instars were identified following Hoebike and Carter (2003). As well, the numbers of live and dead nymphs and live adults were recorded. Stage-specific survivorship and nymphal developmental period were recorded for each diet treatment.

Host Plant Sources

‘Smoother Golden’ apple and ‘Redhaven’ peach trees growing at the AHSAREC were the sources of cultivated host plant material. These trees were treated with fungicides, but not insecticides, during the growing season. Northern catalpa (hereafter referred to as catalpa) and Tree of Heaven growing on or near the AHSAREC property were selected as the wild hosts, based primarily on their inclusion in the host list for H. halys (see StopBMSB.org) but also on reports by Bakken et al. (2015) and anecdotal observations of large populations of H. halys nymphs and adults on both species and the results of a census showing that Tree of Heaven was the most common deciduous tree species growing at the edge of woodlands adjacent to orchards in this region (Acebes-Doria, unpublished data). Like H. halys, Tree of Heaven is an invasive species from Asia (Kowarik and Sümel 2007) and catalpa is native to eastern North America (see http://dendro.cnre.vt.edu).

Freshly excised foliage and reproductive structures (flowers, fruit, or seed pods) of apples, peaches, Tree of Heaven, and catalpa were offered to nymphs. The reproductive structures used reflected the stage of development of each host plant in the field at the time each experiment was conducted. From early- to mid-June, immature apple and peach fruit (three to four per replicate) and foliage, Tree of Heaven flowers and foliage, and catalpa flowers and foliage were used. The volume of Tree of Heaven and catalpa flowers offered was comparable with the total volume of the apple and peach fruit offered. Later in the season,—one to two larger apple and peach fruit and foliage were offered. At that time, three catalpa seed pods (10.16–12.70 cm in length) and foliage and Tree of Heaven samaras and foliage were offered. The volume of seed pods and samaras offered was approximately the same as the other treatments.

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Single- Versus Mixed-Host Diets Early and Late in the Growing Season

The onset of these experiments coincided with two key points in the seasonal phenology of H. halys populations in the Mid-Atlantic region. Peak emergence of H. halys adults from overwintering sites occurs between approximately mid-May and early June (Bergh and Leskey, unpublished data), and F₁ generation adults are estimated to be reproducing in early to mid-August based on degree-day accumulations (Leskey et al. 2012b; Bakken et al. 2015). Experiments initiated in late May (early season) and mid-August 2013 (late season) included the following treatments in a completely randomized design with host plant as the factor: 1) apple, 2) peach, 3) Tree of Heaven, 4) catalpa, 5) apple plus Tree of Heaven, 6) apple plus Tree of Heaven plus peach, and 7) apple plus Tree of Heaven plus peach plus catalpa. Host plants in the mixed diet treatments were provided all at once. Hereafter, we refer to the diet treatments that consisted of three or four hosts as the three-host and four-host diet, respectively. All treatments included foliage and fruiting structures and each treatment was replicated four times.

As in the previous experiment, cohorts of ~28 H. halys first instars on the egg mass were placed individually in 30.48 by 30.48 by 30.48-cm rearing cages provisioned ad libitum with the diet treatment and water. Cages were checked daily to monitor the development and survivorship of nymphs from each egg mass. Stage-specific survivorship and nymphal developmental duration were recorded for nymphs from each cohort. Within 48 h after molting to the adult stage, the fresh weight of all adults produced was measured (nearest 0.1 mg) using a digital scale (AB54-S Mettler Toledo, Columbus, OH) and their prononum width was measured (nearest 0.01 mm) with a digital caliper (ROK International Industry Co., Ltd., Guangdong, China). Wild adult H. halys (n = 30) collected from Tree of Heaven trees at the AHSAREC in early September 2013 also were weighed and measured for comparison with adults obtained from the late-season laboratory experiments.

Data Analyses
All analyses were conducted using JMP® Pro version 11 (SAS Institute Inc., Cary, NC, 2007) and outcomes were considered significant at P < 0.05. Data that did not satisfy the assumptions of parametric tests were transformed using arcsine-square root for percentage data and log(x+1) for nymphal developmental duration and the prononum width and fresh weight. Two-way analysis of variance (ANOVA) was used to compare nymphal stage-specific survivorship and developmental duration among the diets that included foliage alone and foliage plus reproductive structures. One-way ANOVA was used to analyze the survivorship and developmental duration among the diets during the early- and late-season experiments. Student’s t-test was used to compare nymphal survivorship between the early- and late-season experiments for each diet. One-way ANOVA was used to compare the effect of host plant diet on the fresh weight and prononum width of the females and males that developed to the adult stage during the early- and late-season experiments, including measurements from the field-collected adult males and females, which were compared only with the adults reared from the late-season experiment. Student’s t-test was used to compare the fresh weight and prononum width, based on pooled data across all diet treatments. Multiple mean comparisons used Tukey’s post hoc honestly significant difference test.

Results

Single-Host Diets

In this experiment, 94.45 ± 1.39% of the eggs from each mass hatched. As first-instar H. halys do not feed on plant tissue, their survivorship was not significantly affected by diet treatment (Table 1). There were significant effects of host plant and the inclusion of reproductive structures on the survivorship of second through fifth instars (Table 1). In general, the percentage of nymphs that survived each of these instars was much higher on diets that combined foliage and reproductive structures than on foliage alone, although this effect was much less pronounced on Tree of Heaven, on which the fewest number of nymphs survived the second instar.

As the developmental duration of first instars was not significantly affected by diet treatment (F۷,۴۸ = 0.30, P = 0.95), the duration between the second instar and adult eclosion was compared. Moreover, as diets of foliage alone yielded very few adults, developmental duration was analyzed only for treatments that included fruiting structures. Among those, the developmental duration varied significantly among the treatments (Table 1) and was shortest on Tree of Heaven and significantly shorter on peach than on apple or catalpa, which did not differ from each other.

Single- Versus Mixed-Host Diets Early and Late in the Growing Season: Survivorship

In this experiment, 93.61 ± 1.25% of eggs from each mass hatched. As in the previous experiment, diet treatment had no effect on the survivorship of first instars during the early- or late-season experiments (Table 2). In the early-season study, there were numerical, but not statistically significant, diet effects on second-instar survivorship, with the lowest survivorship on apple. In the late-season study, apple also resulted in second-instar survivorship that was significantly or numerically lower than on the other diets, which did not differ.

The early- and late-season experiments yielded significant diet effects on survivorship during the third through fifth instars (Table 2). In the early-season study, highest nymphal survivorship through the fifth instar was on peach, apple plus Tree of Heaven, and the three- and four-host diets; the lowest survivorship was on apple, Tree of Heaven, and catalpa. In the late-season study, apple and catalpa again yielded the lowest survivorship through the fifth instar, whereas the other diets yielded >69% survivorship. In both experiments, there was a pronounced decrease in survivorship on catalpa between the fourth and fifth instars that was not observed on the other diets.

Between the early- and late-season experiments, nymphal survival to the adult stage increased from 20 to 72% on Tree of Heaven (t = 6.32, df = 6, P = 0.001); survivorship to the adult stage on the other diets did not differ significantly between early- and late-season studies (apple: t = 2.34, df = 6, P = 0.06; peach: t = −2.19, df = 6, P = 0.07; catalpa: t = 0.66, df = 6, P = 0.54; apple plus Tree of Heaven: t = 0.79, df = 6, P = 0.46; three-host diet: t = −1.06, df = 6, P = 0.33; and four-host diet: t = 0.09, df = 6, P = 0.93).

Single- Versus Mixed-Host Diets Early and Late in the Growing Season: Developmental Duration and Adult Size and Fresh Weight

There was no effect of diet on the developmental duration of first instars (Table 3). Significant diet treatment effects on the developmental duration of second, fourth, and fifth instars were recorded during...
the early-season experiment, while in the late-season study, there were significant effects on second, third, and fifth instars. In the early season, total developmental period was significantly shorter on peach and the three- and four-host diets than on apple or catalpa, with intermediate durations on the others. The late-season study yielded similar results, with significantly shorter total developmental duration on peach, Tree of Heaven, and the four-host diet than on apple or catalpa, with intermediate periods among the other diets.

Based on pooled data across all diet treatments, mean adult pronotum width was significantly greater for females (7.95 ± 0.02 SE
Table 3. Stage-specific stadia and developmental duration (mean days ± SE) of *H. halys* nymphs on single- and mixed-host plant diets during the early- and late-season experiments, 2013

| Diet treatment (N) | Mean ± SE developmental duration (days) | Mean ± SE duration (days) from second instar to adult eclosion (N) |
|--------------------|-----------------------------------------|---------------------------------------------------------------|
|                    | First instar | Second instar | Third instar | Fourth instar | Fifth instar |
| Early season       |              |              |              |              |              |
| Apple (120)        | 5.25 ± 0.49a | 17.98 ± 0.9a | 20.12 ± 1.26a | 33.48 ± 3.7a | 44.71 ± 4.6ab | 91.79 ± 2.62a (10) |
| Peach (115)        | 5.26 ± 0.25a | 13.26 ± 0.50bc | 13.07 ± 0.71a | 17.61 ± 1.14b | 24.66 ± 2.06bc | 53.45 ± 2.70c (99) |
| Catalpa (103)      | 5.15 ± 0.25a | 13.09 ± 1.32c | 18.94 ± 6.11a | 28.46 ± 3.67ab | 51.25 ± 8.71a | 77.48 ± 8.66ab (10) |
| ToH (109)          | 5.32 ± 0.23a | 16.07 ± 0.82ab | 20.13 ± 2.82a | 22.90 ± 3.25ab | 19.00 ± 3.56c | 58.68 ± 4.98bc (22) |
| Apple + ToH (110)  | 5.19 ± 0.27a | 17.02 ± 0.86a | 18.98 ± 1.73a | 23.51 ± 1.49ab | 23.31 ± 1.74c | 62.59 ± 3.80abc (75) |
| Three-host (113)   | 5.20 ± 0.27a | 13.23 ± 0.62c | 14.27 ± 1.00a | 18.64 ± 1.59b | 19.34 ± 0.71c | 49.23 ± 2.80ac (101) |
| Four-host (114)    | 5.19 ± 0.36a | 12.99 ± 1.13c | 14.03 ± 1.17a | 19.84 ± 2.15ab | 23.54 ± 1.56c | 52.85 ± 2.56c (96) |
| One-way ANOVA      |              |              |              |              |              |
|                    | F<sub>6,21</sub> = 0.03 | F<sub>6,19</sub> = 4.04 | F<sub>6,19</sub> = 1.45 | F<sub>6,19</sub> = 3.92 | F<sub>6,19</sub> = 10.69 | F<sub>6,19</sub> = 7.43 |

Late season

| Diet treatment (N) | Mean ± SE developmental duration (days) | Mean ± SE duration (days) from second instar to adult eclosion (N) |
|--------------------|-----------------------------------------|---------------------------------------------------------------|
|                    | First instar | Second instar | Third instar | Fourth instar | Fifth instar |
| Apple (112)        | 4.82 ± 0.72a | 22.39 ± 1.08ab | 22.73 ± 0.70a | 30.85 ± 2.05a | 53.91 ± 4.31ab | 105.21 ± 3.53a (32) |
| Peach (104)        | 5.90 ± 0.53a | 16.89 ± 1.05ab | 17.32 ± 0.33ab | 20.65 ± 1.28a | 27.96 ± 2.09c | 63.58 ± 2.94c (68) |
| Catalpa (82)       | 5.72 ± 0.32a | 22.33 ± 0.56ab | 22.80 ± 1.85a | 28.59 ± 3.69a | 61.72 ± 6.45a | 100.79 ± 4.64ab (12) |
| ToH (105)          | 5.32 ± 0.27a | 15.11 ± 2.60b | 14.17 ± 2.43b | 18.76 ± 3.97a | 32.22 ± 6.53c | 62.12 ± 11.92c (82) |
| Apple + ToH (110)  | 5.24 ± 0.19a | 18.61 ± 2.01ab | 18.01 ± 2.50ab | 25.59 ± 2.80a | 41.33 ± 3.72abc | 71.58 ± 4.14bc (85) |
| Three-host (113)   | 5.58 ± 0.28a | 23.21 ± 2.80a | 19.42 ± 1.15ab | 25.64 ± 1.99a | 34.36 ± 4.00bc | 68.03 ± 1.97bc (73) |
| Four-host (104)    | 5.75 ± 0.28a | 18.59 ± 0.69ab | 19.70 ± 0.15ab | 25.21 ± 2.51a | 31.15 ± 2.81c | 65.64 ± 1.45c (84) |
| One-way ANOVA      |              |              |              |              |              |
|                    | F<sub>6,21</sub> = 0.95 | F<sub>6,21</sub> = 3.32 | F<sub>6,21</sub> = 3.86 | F<sub>6,21</sub> = 2.32 | F<sub>6,20</sub> = 5.87 | F<sub>6,20</sub> = 7.23 |

**Notes:**
- a Total number of first instars at the outset of the experiment.
- b Total number of nymphs that developed to the adult stage. Second through fifth instars are the plant-feeding stages of juvenile *H. halys*.
- c ToH denotes Tree of Heaven.
- d The three-host diet consisted of the foliage and fruiting structures of apple, ToH, and peach.
- e The four-host diet consisted of the foliage and fruiting structures of apple, ToH, peach, and catalpa.

Means with the same letters under the same column and in the same experiment are not significantly different at α = 0.05.

mm) than males (7.17 ± 0.02 SE mm; t = −26.18, df = 878, P < 0.0001) and females were significantly heavier (109.37 ± 1.10 SE mg) than males (87.48 ± 0.86 SE mg; t = −15.61, df = 878, P < 0.0001). Diets that yielded fewer than three adult males or females were excluded from statistical comparisons. In both the early- and late-season experiments, the fresh weight and pronotum width of both sexes varied significantly among diets (Table 4). In the early season, Tree of Heaven and apple plus Tree of Heaven yielded females that were heaviest and had the largest pronotum width, while apple yielded the lightest and smallest females. The heaviest and largest males also were recorded from Tree of Heaven and apple plus Tree of Heaven, while the lightest and smallest males were from catalpa and apple. In the late-season study, the heaviest females and males were recorded from peach, although the three- and four-host diets also produced relatively heavy individuals of both sexes (Table 4). As in the early-season experiment, females and males from apple and catalpa were the lightest. The three- and four-host diets produced females with the largest pronotum width and smallest females were from catalpa and apple, while male pronotum width was largest from the four-host diet and smallest from apple. Field-collected females and males had statistically or numerically comparable fresh weights and pronotum widths to those from the three- and four-host diet treatments during the late-season experiment (Table 4).

Discussion

The survivorship and developmental duration of laboratory-reared *H. halys* nymphs were significantly affected by host plant tissue, host plant species, host phenotype, and diet mixing. Like other pentatomid species, such as the southern green stink bug, *Nezara viridula* (L.), and the Neotropical brown stink bug, *Euschistus heros* (F.) (Panizzi 2000), *H. halys* nymphs have been known to feed on nonreproductive parts of plants such as the stem (Martinson et al. 2013) and foliage (Hoebeke and Carter 2003). For all plants examined, we found that diets consisting only of stems and foliage were unsuitable, and that most nymphs did not survive the second instar on them.

Martinson et al. (2015) showed that the presence of fruit on ornamental trees in a nursery strongly influenced the abundance of *H. halys* nymphs and adults and that fruit removal had a profound negative effect on *H. halys* counts. Complementing their results, we found that combining foliage and fruiting structures of peach dramatically increased *H. halys* nymphal survivorship and reduced their developmental duration compared with foliage alone. For apple and catalpa, we also showed that fruiting structures and foliage only led to marginal improvements in nymphal survivorship both early and late in the season. Tree of Heaven foliage plus samaras produced the same result early in the season, but nymphal survivorship on that diet increased in the late-season study.

With regard to the cultivated plant species offered as single-host diets that combined foliage and fruit, the relatively poor suitability of apple for *H. halys* nymphs concurs with Funayama (2002), who reported that nymphs reared on apple had low survivorship and developed poorly. In our study, we consistently found that nymphal survivorship was higher and their developmental duration was shorter on peach than on apple, indicating a clear difference in the suitability of these two economically important hosts for nymphal
development. The high suitability of peach for nymphal development and survival conforms to field observations that peach can support large H. halys populations from late May through harvest (Nielsen and Hamilton 2009) and often incurs higher levels of injury early in the growing season than apple (Leskey et al. 2012b, Joseph et al. 2015), this may be associated more with transient visits and feeding bouts by adults and nymphs than by resident populations; Morrison III et al. (2015) used harmonic radar to show that tagged H. halys adults remained on apple trees for only ~3.5 h.

A survey of 78 species of native and invasive trees and herbaceous shrubs in urban, rural, and forested areas in the eastern United States by Bakken et al. (2015) revealed that catalpa and Tree of Heaven were among the species that consistently yielded comparatively high counts of H. halys adults and nymphs. In China, Tree of Heaven is considered a preferred host of P. subastris (Huang), reared on diets of two, four, and six suboptimal hosts also showed higher survivorship compared with those on a diet of a single suboptimal host (Miura and Ohsaki 2004). The survivorship of P. subastris nymphs reared on all mixed diets of suboptimal hosts was statistically equivalent to that on single diets of the superior hosts, as was the case for H. halys reared on mixed diets of suboptimal hosts versus those on peach alone.

Overall, total developmental durations from the second through fifth instars were considerably longer than reported from H. halys rearing studies under similar environmental conditions by Nielsen et al. (2008) and Medal et al. (2012). Both previous studies used a bean, peanut, corn, and carrot diet, resulting in 34-d and 37-d developmental durations from the second through fifth instars, respectively. The underlying reasons for the differences between the present and previous experiments are unknown, but may be associated with differences in the nutritional quality of the diets used.

### Table 4

| Diet treatment | Early season | Late season | Females | Males |
|----------------|-------------|-------------|---------|-------|
|                | N    | Weight (mg) | Pronotum width (mm) | N    | Weight (mg) | Pronotum width (mm) |
| Apple          | 3    | 70.53 ± 7.76d | 6.98 ± 0.34d | 7    | 67.44 ± 5.91c | 6.62 ± 0.10c |
| Peach          | 51   | 111.84 ± 2.50c | 7.72 ± 0.04c | 48   | 96.87 ± 1.66ab | 7.11 ± 0.04b |
| Catalpa        | 2    | 97.00 ± 22.40* | 7.67 ± 0.53* | 8    | 59.44 ± 4.10c | 6.60 ± 0.11c |
| ToH*           | 7    | 138.04 ± 4.41a | 8.50 ± 0.09a | 15   | 107.47 ± 2.66a | 7.55 ± 0.05a |
| Apple + ToH*   | 33   | 132.38 ± 3.25a | 8.39 ± 0.06a | 42   | 102.80 ± 1.70a | 7.47 ± 0.04a |
| Three-hostb    | 55   | 121.11 ± 2.02bc | 8.09 ± 0.04bc | 46   | 93.21 ± 1.96b  | 7.20 ± 0.05b  |
| Four-hostc     | 50   | 118.04 ± 2.27c | 8.04 ± 0.04c | 46   | 96.62 ± 2.07ab | 7.27 ± 0.04b  |
| One-way ANOVA  | F<sub>5, 193</sub> = 13.32 | F<sub>5, 193</sub> = 28.23 | P < 0.0001 | F<sub>6, 205</sub> = 28.84 | F<sub>6, 205</sub> = 20.93 | P < 0.0001 |

*ToH denotes Tree of Heaven.  
b The three-host diet consisted of the foliage and fruiting structures of apple, ToH, and peach.  
c The four-host diet consisted of the foliage and fruiting structures of apple, ToH, peach, and catalpa.  
* Treatment excluded from analyses due to sample size.

Means with the same letters under the same column and in the same category are not significantly different at α = 0.05.

Diet mixing was clearly beneficial to the survivorship of H. halys nymphs. Funayama (2006) reported similar results when carrots were added to a peanut and soybean diet for H. halys nymphs; indeed, mixed diets for rearing H. halys have been universally adopted (Medal et al. 2012, Leskey and Hamilton 2014). In the early-season study in 2013, the diet that combined apple and Tree of Heaven, both of which were suboptimal as single hosts, yielded improved nymphal survivorship through the fifth instar, although this effect was not found for the same diet in the late-season study, perhaps due to the apparently increased suitability of Tree of Heaven. Nymphs of the polyphagous grasshopper, Parapodisma subastris (Huang), reared on diets of two, four, and six suboptimal hosts also showed higher survivorship compared with those on a diet of a single suboptimal host (Miura and Ohsaki 2004). The survivorship of P. subastris nymphs reared on all mixed diets of suboptimal hosts was statistically equivalent to that on single diets of the superior hosts, as was the case for H. halys reared on mixed diets of suboptimal hosts versus those on peach alone.

### Table 4

| Diet treatment | Early season | Late season | Females | Males |
|----------------|-------------|-------------|---------|-------|
|                | N    | Weight (mg) | Pronotum width (mm) | N    | Weight (mg) | Pronotum width (mm) |
| Apple          | 3    | 70.53 ± 7.76d | 6.98 ± 0.34d | 7    | 67.44 ± 5.91c | 6.62 ± 0.10c |
| Peach          | 51   | 111.84 ± 2.50c | 7.72 ± 0.04c | 48   | 96.87 ± 1.66ab | 7.11 ± 0.04b |
| Catalpa        | 2    | 97.00 ± 22.40* | 7.67 ± 0.53* | 8    | 59.44 ± 4.10c | 6.60 ± 0.11c |
| ToH*           | 7    | 138.04 ± 4.41a | 8.50 ± 0.09a | 15   | 107.47 ± 2.66a | 7.55 ± 0.05a |
| Apple + ToH*   | 33   | 132.38 ± 3.25a | 8.39 ± 0.06a | 42   | 102.80 ± 1.70a | 7.47 ± 0.04a |
| Three-hostb    | 55   | 121.11 ± 2.02bc | 8.09 ± 0.04bc | 46   | 93.21 ± 1.96b  | 7.20 ± 0.05b  |
| Four-hostc     | 50   | 118.04 ± 2.27c | 8.04 ± 0.04c | 46   | 96.62 ± 2.07ab | 7.27 ± 0.04b  |
| One-way ANOVA  | F<sub>5, 193</sub> = 13.32 | F<sub>5, 193</sub> = 28.23 | P < 0.0001 | F<sub>6, 205</sub> = 28.84 | F<sub>6, 205</sub> = 20.93 | P < 0.0001 |

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* Treatment excluded from analyses due to sample size.

Means with the same letters under the same column and in the same category are not significantly different at α = 0.05.
viridula (Kester and Smith 1984) and B. tabaci (Zhang et al. 2014) found that nymphs reared on mixed diets produced longer-lived adults and more fecund females. These results suggest that the larger and heavier adult H. halys from nymphs reared on suitable diets, whether of single or mixed hosts, may also have improved longevity and fecundity. The size and weight of adults from nymphs reared on mixed diets in the late-season study in 2014 did not differ significantly from field-collected adults in September 2013, which had likely also developed from nymphs that had fed on a range of host plants. As well, Todd’s (1989) finding of higher overwintering survivorship in larger than smaller N. viridula adults suggests that the bigger and heavier H. halys adults from nymphs reared on mixed diets or peach later in the season also may be better able to overwinter successfully.

Further investigation of the mechanisms behind the relative suitability of the different host plants in our study and the benefits of diet mixing on H. halys development and survival may further improve our understanding of its host-utilization at the orchard–woodland interface. Toward the end, Acebes-Doria (unpublished data) quantified the nutrient content in the adults from this study that had developed from nymphs reared on the different diets, revealing new information about host plant effects on H. halys nutrition.

Despite the reports (Bakken et al. 2015) and observations of Tree of Heaven and catalpa supporting large populations of H. halys in the eastern United States, our results suggest that H. halys nymphs may need to disperse from these trees during their development to find and feed on other plants. In the laboratory, Lee et al. (2014) demonstrated that H. halys nymphs can walk up to 41 m in 1 h and up to 8 m in 15 min on smooth horizontal and vertical surfaces, respectively. In a follow-up field experiment using pheromone-baited traps near a woodlot, Lee et al. (2014) found that marked nymphs walked over 20 m on a mowed grassy lawn within 4–5 h. Acebes-Doria et al. (2016) captured H. halys nymphs in traps designed to monitor their upward and downward movement on tree trunks. Results from Tree of Heaven revealed that second through fifth instars were captured walking up and down tree trunks, but that more nymphs were captured while walking up than down, leading them to speculate that nymphs may also disperse from the tree canopy by dropping (Acebes-Doria et al. 2016). Follow-up field studies using trunk traps have also examined seasonal patterns of the upward and downward walking dispersal of H. halys nymphs on cultivated and wild tree hosts at the orchard–woodland interface.

The relative suitability of available hosts may affect the extent to which H. halys nymphs disperse among hosts at the orchard–woodland interface. Our data suggest that nymphs from eggs laid on apple, catalpa, or Tree of Heaven early in the season would be more likely to disperse to other hosts than those on peaches. Host phenology and the presence and maturity of fruiting structures appear to strongly influence seasonal patterns of host use by adults and nymphs (Martinson et al. 2015). Moreover, Bakken et al. (2015) reported that among the 78 plant species surveyed, H. halys egg masses, nymphs, and adults were found on 34 species, including Tree of Heaven and catalpa, while only nymphs and adults were found on 41 species and none were detected on three species. These findings further support the likelihood that H. halys nymphs and adults disperse among available plants, that some species serve as its feeding and reproductive hosts, and that others are only feeding hosts or are unsuitable.

At the orchard–woodland interface, many known wild and tree fruit hosts of H. halys are commonly found growing close to one another (Acebes-Doria, unpublished data) and well within the dispersal distance of which nymphs are capable (Lee et al. 2014). Consequently, additional and very relevant questions that follow from the data reported here include: 1) how long do nymphs remain on a particular host, 2) do nymphs that disperse from one host species move to the same or different species, 3) do nymphs disperse from wild hosts into orchards, and if so, 4) how far into the orchard do nymphs move? Moreover, the potential geographic distribution of H. halys based on niche modeling indicates that much of the Eastern United States and portions of its Pacific coastal regions could be successfully colonized by this invasive species (Zhu et al. 2012). Our results indicate that within a particular ecosystem, available host plants also could have a major impact on the survivorship and population growth of H. halys, particularly if available hosts are suboptimal. The apparent need for diet mixing due to suboptimal hosts could limit H. halys establishment and build-up in areas that lack suitable host diversity. Indeed, some suboptimal hosts may be considered a “dead end” for nymphal survivorship and development if alternate hosts that provide additional nutritional benefits are not available nearby.

In summary, H. halys nymphs are commonly found on wild hosts adjacent to fruit orchards and have the capacity to disperse between the two habitats (Lee et al. 2014). Indeed, transects of pheromone-baited traps that extended from woodlots into apple orchards revealed highest captures of adults and nymphs in traps at the orchard and woodland edges (Bergh, unpublished data). In addition, field studies using trunk traps deployed on apple and peach trees and known tree hosts of H. halys at the orchard–woodland interface revealed movement of H. halys nymphs both up and down the trees during much of the growing season (Acebes-Doria, unpublished data). As well, more H. halys injury has been recorded from apples in trees at orchard edges adjacent to woodlands than from orchard interior trees (Leskey et al. 2012b, Joseph et al. 2014). These findings and our demonstration of the effects of host plant species and diet mixing on nymphal performance suggest the likelihood that H. halys nymphs move between these two habitats during much of the growing season and that effective management programs targeting H. halys in orchards next to woodlands might be perimeter-driven. Restricting applications of the most efficacious insecticides against H. halys to the orchard perimeter, whether via border sprays (Blauw et al. 2014) or sprays to pheromone-baited trees at intervals along the borders (“attract-and-kill”; Morrison et al. 2015), should translate to fewer secondary pest problems throughout the orchard and facilitate a return to the more ecologically and economically sustainable programs that were widely practiced before H. halys became an issue.

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