Characterizing Damage of Brown Marmorated Stink Bug (Hemiptera: Pentatomidae) in Blueberries

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ABSTRACT Brown marmorated stink bug, Halyomorpha halys (Stål) (Hemiptera: Pentatomidae), is a severe economic pest of growing importance in the United States, Canada, and Europe. While feeding damage from H. halys has been characterized in tree fruit, vegetables, and agronomic crops, less is known about the impacts of stink bugs on small fruits such as blueberries. In this study, we examined H. halys feeding on two representative early and late ripening blueberry cultivars in Oregon and New Jersey. This research examined how different densities of H. halys confined on blueberry clusters for week-long periods affected fruit quality at harvest. After fruit were ripe, we stained and quantified the number of salivary sheaths on berries as an indication of feeding pressure. Feeding by H. halys damaged the fruits by causing increased levels of external discoloration, and internal damage in the form of tissue necrosis. Exposure of berries to H. halys was also associated with decreasing berry weights and lower soluble solids in fruits. However, the different cultivars did not respond consistently to feeding pressure from H. halys. Weekly variability in feeding pressure of two of the cultivars as quantified by the number of stylet sheaths per berry was largely accounted for by environmental variables. We conclude that H. halys does have potential to severely damage blueberries and may become an important economic pest. Characterization of damage is important because correct identification of insect damage is key for successful management.

KEY WORDS BMSB, Vaccinium, stink bug, feeding damage

Brown marmorated stink bug, Halyomorpha halys (Stål) (Hemiptera: Pentatomidae), is an invasive pest in the United States, Canada, and Europe. After becoming established in Mid-Atlantic states in the mid 1990s, this insect has become a major agricultural pest and urban nuisance (Leskey et al. 2012a, Rice et al. 2014). Stink bug damage and impacts have been characterized in tree fruit crops (Woodside 1950, Brown 2003, Funayama 2004, Nielsen and Hamilton 2009, Leskey et al. 2012b), tree nuts (Yates et al. 1991, Jones and Caprio 1994, Hedstrom 2014), agronomic crops (Boethel et al. 2000, Depieri and Panizzi 2011, Medrano et al. 2011), and vegetables (Lye et al. 1988, Kuhar et al. 2012, Huang et al. 2014). These crops have historically had problems with pentatomid pests, or are currently affected by H. halys. Halyomorpha halys is known to attack blueberries in the Mid-Atlantic United States, but its potential to cause feeding damage is unknown (Leskey et al. 2012a). Since becoming problematic on the East Coast of the United States, H. halys has continued to spread to other U.S. states with blueberry production such as Michigan, Washington, Oregon, and California (Leskey et al. 2012a). Blueberry production regions in Canada (Gariepy et al. 2014) and Europe may also be affected by H. halys in the future (Wermelinger et al. 2008, Haye et al. 2014).

Compared with more specialized Hemiptera, Pentatomidae use diverse feeding strategies that allow them to feed from a wide range of plant structures including vegetative structures such as stems and leaves, and reproductive plant structures such as seeds, nuts, pods, fruits, and vegetables (Panizzi et al. 2000). The strategies used to feed from this diversity of plant structures may include stylet-sheath feeding, lacerate and flush feeding, macerate and flush feeding, and osmotic pump feeding (Cobben 1978, Backus 1988). Stink bug feeding can damage crops in different ways depending on whether the vegetative or reproductive plant structures are attacked. In general, feeding damage from Heteroptera can be classified into five categories: localized wilting and necrosis, abscission of fruiting forms, morphological deformation of fruits and seeds, modified vegetative growth, and tissue malformation (Strong 1970, Tingey and Pillimer 1977). Stink bug feeding can damage crops in different ways depending on whether the vegetative or reproductive plant structures are attacked. In general, feeding damage from Heteroptera can be classified into five categories: localized wilting and necrosis, abscission of fruiting forms, morphological deformation of fruits and seeds, modified vegetative growth, and tissue malformation (Strong 1970, Tingey and Pillimer 1977). All plant-sucking Heteroptera are potential vectors for plant disease, and the lesion left behind at the feeding site can facilitate secondary infections of plant pathogens (Mitchell 2004).

In Oregon, H. halys has only recently begun to threaten agriculture, although nuisance problems have
been occurring for several years (Shearer and Wiman 2014, Wiman et al. 2014), while New Jersey has experienced economic damage to a variety of crops (e.g., apples, peaches, and soybeans) from the pest for a number of years (Nielsen and Hamilton 2009, Nielsen et al. 2011). Pentatomidae have not been a big problem in blueberries in Oregon and are not mentioned in the blueberry pest management guidelines (DeFrancesco et al. 2013). For New Jersey, *H. halys* is a relatively recent addition to the pest management guide for blueberries (Oudemans et al. 2013). Cultivated blueberries are an increasingly important crop in the United States, which is the world's largest producer, accounting for 214,685 metric tons in 2012, a crop worth approximately US$782 million. In Oregon there are 7,900 acres in production as of 2012, an increase of 200% since 2000, with a farm-gate value of US$107.6 million. In New Jersey there are 7,500 acres, which has been a steady level since 2000, with a farm-gate value of US$80.8 million (U.S. Department of Agriculture–National Agricultural Statistics Service [USDA NASS] 2013).

In this study, we examined potential for *H. halys* to damage fruits of blueberry cultivars (*Vaccinium* spp.) in the Willamette Valley in Oregon and in central New Jersey. This research examined how different levels of feeding pressure from *H. halys* applied at different times would affect quality of the fruit at harvest. We controlled the rate of feeding pressure and the timing of feeding by confining different densities of *H. halys* on berry clusters for week-long periods as berries matured. The purpose was to determine how feeding by *H. halys* would affect fruit from different cultivars in the two growing regions.

**Materials and Methods**

**Establishment of Sleeve Cages.** Experiments were conducted in 2013 on research farms using cultivars planted in a complete randomized block design at the Oregon State University Lewis Brown Horticulture Research Farm near Corvallis, and at the Rutgers University Philip E. Marucci Center for Blueberry and Cranberry Research and Extension near Chatsworth, NJ. In each location, a midseason or early maturing variety and a late maturing variety were selected for the study. In Oregon, the early variety was 'Duke,' and the late variety was 'Aurora.' In New Jersey, the earlier maturing variety was 'Bluecrop,' and 'Elliott' was used as the late maturing variety. Just after fruit set, clusters of berries were covered with sleeve cages, which consisted of 6.5 by 10 in (16.5 by 25.4 cm) white organza fabric bags (Your Organza Bag, Los Angeles, CA). If necessary, berry clusters were thinned to have approximately 10 berries per cluster in order to standardize cluster size before placement of the bag. There were 7–10 clusters on each bush that were bagged after fruit set, and *H. halys* were added to one of the bags at densities of 0 (control), 2, 5, or 10 individuals. Each week, insects within each bag were transferred to a new bag, and the bag was replaced over the cluster. Dead insects were replaced during the transfer to maintain the correct density of *H. halys*. The goal was to have 10 replications for each of the four *H. halys* density treatments for each week of the study. The period of time from fruit set to berry ripening differed between cultivars, so the number of weeks over which the study was conducted depended on the cultivar under study.

**Experimental Insects.** *Halyomorpha halys* were collected in the field using beat sheets in the Willamette Valley, OR, and from the area around Chatsworth, NJ. The insects were collected from ornamental and wild host plants. Adults were used exclusively in the OR studies, and late-instar nymphs (Elliott) and adults (Bluecrop) were used in the NJ studies because nymphs were easier to obtain during the first trial in this region. Insects were stored in the laboratory up to 24 h (22°C, photoperiod of 16:8 [L:D] h, 70% relative humidity) before they were placed within the experimental bags. Occasionally, limited collection success meant that dead or escaped *H. halys* in the sleeves couldn't be replaced, resulting in the loss of individual replicates for the week.

**Postharvest Fruit Evaluation.** Berry clusters were harvested by clipping the branch below the bag after the feeding periods were completed at the end of 5 wks for Elliott and Bluecrop, 7 wks for Duke, and 10 wks for Aurora. Harvested fruit was stored at 10°C before being processed. For each cluster, the number of berries on the branch and the number that had detached were recorded. For the varieties Duke and Aurora evaluated in OR, each individual berry from each cluster was weighed. For the varieties Bluecrop and Elliott evaluated in NJ, berry clusters were weighed. Pentatomids, and other Hemiptera, produce two types of saliva. The sheath saliva is proteinaceous and develops into a hardened sheath that surrounds the mouthparts as they are inserted into the food. The stylet sheaths were selectively stained pink by soaking berries in acid fuchs in for 20 min (Bowling 1979, 1980; Hollay et al. 1987). This protein-positive stain made it easier to quantify the number of *H. halys* stylet sheaths on each berry. Acid Fuchsin stain was made with 1 liter of water, 200 ml EtOH, and 1.25–2.5 g of acid fuchsin powder. After soaking, the berries were strained from the acid fuchsin dye and allowed to dry before further examination. Berries were sliced into two hemispheres, and each was examined individually under a dissecting microscope. A quadrat system was used to score discoloration of berries and internal tissue necrosis on each berry hemisphere. Each quadrant was scored for presence or absence of discoloration or necrosis. Total percent damage from these defects on each berry was calculated as the sum of the positive scores from eight quadrants where each quadrant represented damage of 12.5% of the berry. Thus, the percent of the fruit damaged was classified 0, 25, 50, or 100% in either defect category. However, the presence of the defect in any quadrant resulted in the berry being classified as discolored or necrotic. Discoloration was considered to be a surface defect of a different color than the remainder of the fruit. Necrotic internal tissue was indicated by dead tissue with lost cell structure, often dark in color,
similar to corking damage that characterizes *H. halys* feeding on pome fruits (Leskey et al. 2012a). After the number of stylet sheaths per berry was quantified by totaling counts of stylet sheaths on the exterior of each hemisphere, discoloration was scored. Then the hemisphere was flipped to expose the internal fruit tissues to score necrosis. After the damage assessment for Duke and Aurora, a random subsample of clusters (n = 61–65) of fruit from each density treatment were blended together and tested with an ocular refractometer (IW Scientific CTL-REFM-BR32, Source Medical Equipment). A smaller sample of clusters of (n = 4) per density treatment were also analyzed for Bluecrop. Brix data were plotted using Tukey boxplots.

**Data and Analysis.** All data analysis and plotting were performed in the open-source statistical environment R (R Core Team 2013). One-way ANOVA was used to test the null hypothesis that there were no differences in the mean number of stylet sheaths per berry or the proportion of discolored or necrotic berries per cluster at harvest within each cultivar for each density of *H. halys*. Proportional data were converted to percentage for plotting. Significant ANOVA analyses for stylet sheaths, discoloration, necrotic berries, berry weight, and brix at harvest were followed by LSD tests to determine differences between the density treatments. ANOVA was also used to test the null hypothesis that the timing of the feeding period would affect the number of stylet sheaths per berry. Stepwise regression used to predict feeding pressure (stylet sheaths) based on environmental variables was performed using the function “stepAIC” in the package MASS, using minimization of Akaike Information Criterion (AIC) to select the best model (Venables and Ripley 2002). Environmental data for the Lewis Brown Horticulture Farm near Corvallis Oregon were obtained from the WVCO KVCO weather station (1.9 km from experiment site). Weather data for the Philip E. Marucci Center near Chatsworth, NJ, were obtained from the weather station MKQ56, located at the research station. Environmental predictive variables used in the analysis were temperature, humidity, wind-speed, precipitation, and cloudcover.

**Results**

**Stylet Sheaths.** The density of *H. halys* within sleeve cages was associated with significant differences in the mean number of stylet sheaths per berry at harvest in all cultivars (Elliott: $F = 4.87$, df = 3,125, $P = 0.003$; Bluecrop: $F = 15.39$, df = 3,155, $P < 0.001$, Duke: $F = 23.23$, df = 3,235, $P < 0.001$, Aurora: $F = 21.28$, df = 3,330, $P < 0.001$). For Elliott, there were no differences in mean stylet sheaths between the density treatments greater than two *H. halys* per cluster, but for most of the cultivars, increasing density of *H. halys* tended to result in significant increases in mean stylet sheath number (Fig. 1; LSD tests, $P < 0.05$). Bluecrop appeared to have the highest feeding pressure, while Elliott had the lowest, but differences in experimental conditions prevented direct statistical comparison of the different cultivars.

**Necrosis.** The effect of *H. halys* density on the percentage of berries from a cluster exhibiting necrotic internal tissues depended on the cultivar. Elliott did not exhibit any increase in necrotic berries for any of the density treatments (Fig. 2; $F = 0.75$, df = 3,136, $P = 0.523$), and only the highest density of *H. halys* (10) caused a significant increase in the proportion of necrotic berries in Bluecrop ($F = 3.36$, df = 3,156, $P = 0.024$; LSD tests, $P < 0.05$). In Duke, there were major *H. halys* density effects on the proportion of necrotic berries ($F = 23.21$, df = 3,227, $P < 0.001$). With a density of two *H. halys*, there were 23% necrotic berries, and this level increased significantly to 38% with the density increased to five insects. The increase in *H. halys* from 5 to 10 did not lead to further increase in the percentage of berries that were necrotic, however (Fig. 2). There was also a significant density treatment effect in Aurora ($F = 15.73$, df = 3,330, $P < 0.001$). Unlike Duke, a density of two insects was enough to cause 21% necrotic berries, but increasing the density to five insects did not cause further increase in necrosis. At the highest density of
H. halys (10), there were 35% necrotic berries in Aurora at harvest.

**Discoloration.** With the exception of Elliott, the proportion of berries from clusters that had any level of discoloration on the surface of the fruit tended to be affected by the density of H. halys (Bluecrop: $F = 2.70, \text{df} = 3,156, P = 0.047$; Duke: $F = 4.40, \text{df} = 3,242, P = 0.005$; Aurora: $F = 5.15, \text{df} = 3,330, P = 0.002$). Comparison at the density level for these cultivars indicated that the low and intermediate density levels did not affect discoloration compared with controls, but a significant increase in the proportion of discolored berries occurred when there were 10 H. halys (Fig. 3).

**Timing of Feeding.** In the cultivars tested in Oregon, Aurora, and Duke, there was a significant interaction between the week of the exposure period and the density of H. halys on the number of stylet sheaths per berry (Aurora: $F = 1.82, \text{df} = 27,293, P = 0.009$; Duke: $F = 4.27, \text{df} = 18,215, P < 0.001$). Suggesting that feeding pressure from H. halys changed over the different exposure periods within the densities of H. halys that were tested. From follow-up analyses within densities, the number of stylet sheaths per berry was not dependent on the week of exposure for Aurora within the 0 and 2 density levels of H. halys, but it did depend on the week within the densities of 5 or 10 H. halys (density = 0: $F = 0.70, \text{df} = 9,76, P = 0.701$; density = 2: $F = 1.59, \text{df} = 9,74, P = 0.133$; density = 5: $F = 2.75, \text{df} = 9,77, P = 0.008$; density = 10: $F = 3.16, \text{df} = 9,66, P = 0.003$). Probing activity within density levels for Duke was significantly different between weeks for all densities except for in the bags that did not contain H. halys (density = 0: $F = 0.80, \text{df} = 6,57, P = 0.573$; density = 2: $F = 4.38, \text{df} = 6,49, P = 0.001$; density = 5: $F = 10.85, \text{df} = 6,55, P < 0.001$; density = 10: $F = 7.35, \text{df} = 6,54, P < 0.001$). In the cultivars tested in New Jersey, Elliott and Bluecrop, there were no significant effects of the timing of the exposure period of H. halys on the number of stylet sheaths per berry (Elliott: $F = 1.25, \text{df} = 4,124, P = 0.295$; Bluecrop: $F = 0.46, \text{df} = 6,218, P = 0.768$).

**Brix.** H. halys feeding resulted in a reduction in sugar levels of berries at harvest for both Duke ($F = 9.91, \text{df} = 3,249, P < 0.001$) and Aurora ($F = 5.63, \text{df} = 3,220, P < 0.001$) in Oregon. With Duke, each increase in density of H. halys resulted in lower brix at harvest, whereas in Aurora, all densities of H. halys had the same effect on brix (Fig. 4). In New Jersey, there was no effect of H. halys density on berry cluster weight for Bluecrop ($F = 0.95, \text{df} = 3,28, P = 0.429$), but there was for Elliott ($F = 3.43, \text{df} = 3,55, P = 0.023$).

**Environmental Effects.** For Duke and Aurora, regression analysis suggested that environmental variables explained much of the variability in the mean number of stylet sheaths per berry of the treated fruit between the different weeks of the experiment. Stepwise regression with environmental predictive variables suggested a model that accounted for 59% of the variability in the mean number of stylets per berry per week, with weekly mean temperature, mean wind-speed, and mean cloud cover ($F = 17.22, \text{df} = 3,3, P = 0.021$; adj. $r^2 = 0.89$; Table 1, Fig. 6). For Aurora, less of the weekly variability in mean stylets per berry could be accounted for by environmental variables and different variables were selected ($F = 5.39; \text{df} = 3,6$).
Aurora ripened three weeks after Duke and mean weekly temperatures were relatively high and consistent over that extended period (Fig. 7). Predictive variables for stylets on Aurora were mean weekly precipitation and humidity.

### Discussion

This study demonstrated how feeding by *H. halys* can damage blueberries, and illustrated the potential importance of environmental conditions in determining feeding pressure. While there are unrealistic elements in any study that confines insects to feed in one place on a crop, there are not many viable alternatives that can be used to experimentally control feeding damage under field conditions. However, these studies are important because correct identification of insect damage and understanding potential for economic loss is key to properly selecting management tools. There were multiple symptoms of *H. halys* feeding damage on blueberries, including discoloration of the fruit surface, necrosis of internal tissues, weight loss of berries, and depletion of soluble solids. These results suggest that this invasive pest has potential to become a direct pest in commercial blueberries. However, our results also suggest that cultivars have different reactions to feeding damage from *H. halys*.

There did not appear to be a consistent relationship between the number of stylet sheaths and the level of damage to fruit between the different blueberry cultivars. For example, Bluecrop had some of the highest numbers of stylet sheaths, indicating high feeding pressure, yet there was relatively little damage to this cultivar in terms of necrosis, discoloration, or weight loss. Conversely, Aurora had relatively low feeding pressure.

**Table 1. Predicting the number of necrotic berries**

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Predictor</th>
<th>β</th>
<th>SE</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duke</td>
<td>Temperature</td>
<td>1.67</td>
<td>0.42</td>
<td>3.93</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Wind speed</td>
<td>2.06</td>
<td>0.36</td>
<td>5.73</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Cloud cover</td>
<td>3.44</td>
<td>0.58</td>
<td>5.97</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Aurora</td>
<td>Precipitation</td>
<td>6.84</td>
<td>0.38</td>
<td>3.35</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Humidity</td>
<td>−0.16</td>
<td>0.05</td>
<td>−3.40</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Fig. 5. The effect of *H. halys* feeding on the dissolved solids (sugar) in fruit at harvest. Levels connected by different letters were significantly different (LSD test, *P* < 0.05).

Fig. 6. Mean stylet sheaths per berry per week for berries that were exposed to brown marmorated stink bug and mean weekly temperature for Duke.

Fig. 7. Mean stylet sheaths per berry per week for berries that were exposed to brown marmorated stink bug and mean weekly temperature for Aurora.
at the different densities, yet some of the highest rates of necrosis. While cultivars may differ in host plant resistance or susceptibility to damage, there can also be problems with using stylet sheath counts as a proxy for feeding pressure. While stylet sheaths are often used as an index of feeding pressure, they are not indicative that the food has actually been penetrated by the mouthparts (Bowling 1979, 1980; Hollay et al. 1987, Brennan et al. 2001). Hemiptera begin to salivate while in the early phases of the feeding behavioral sequence, and a droplet of sheath saliva can oxidize and form an apparent sheath anytime the mouthparts contact the food. Feeding is often preceded by labial dabbing, where mouthparts are touched or dragged across the food item (Backus 1988). Some feeding strategies of pentatomoids are less reliant on stylet sheath formation, indicating potential for feeding to be underestimated by counting of sheaths. However, stylet sheath formation is typically associated with feeding on vascular tissue as opposed to feeding on seeds or nuts (Backus 1988, Mitchell 2004). A further consideration for inconsistent relationships between the stylet sheaths and density and stylet sheaths and damage is the possibility that sheaths were dislodged by the insects themselves (particularly in the high density treatments), or by the handling of fruit.

Penetration of the berry by the mouthpart and salivation are important for necrosis to occur because it allows the watery saliva to enter the fruit and break down tissues, and provides a pathway for pathogen introduction. The watery saliva contains the suite of digestive enzymes necessary to break down the plant tissues into a liquid form that can be imbibed (Hori 1975, Cohen 1993, Ramzi and Hosseininaveh 2010, Chapman et al. 2012, Peiffer and Felton 2014). This extra-oral digestion can cause the damage known as “corking” in fruits such as apples (Brown 2003). Saliva can also be toxic to plants and can cause a secondary reaction in plant tissue (Miles 1969, Hori 2000, Depieri and Panizzi 2011). Thus, the digestive action of watery saliva is likely a cause of necrosis in blueberries. However, another potential cause for the necrosis may be the action of pathogens either vectored by the insect itself, or by opportunistic invasion of microbes through the puncture wound of the berry. Pentatomidae are known to vector pathogens that can cause decay of plant tissues (Mitchell 2004, Medrano et al. 2009, Esquivel et al. 2010). In East Asia, *H. halys* is known to vector a phytoplasma of *Pseudotomento* spp., trees, which are valuable as ornamental, timber, and reforestation species (Okuda et al. 1998, Hiruki 1999). Thus, it is possible that stinkbug populations in different regions are vectors or facilitators of pathogens. This could potentially be an explanation of why necrosis was higher in Oregon blueberries compared with New Jersey berries in this study. Potentially, the damage caused by *H. halys* is dependent on pressure from pathogens in the local environment and may thus be tied to weather conditions, sanitation, or disease management practices.

There were other observed damage effects to the berries that were linked to the number of stink bugs confined on the clusters. Berry weight was one of these, and may have reflected shriveling, a variable that we did not quantify but we consistently observed. Highly shriveled berries were suffering from dehydration from being fed upon by *H. halys*. Duke had the largest and heaviest berries and was the most affected by *H. halys* feeding. *H. halys* feeding also affected sugar content of berries as quantified by Brix. This effect is probably due to the digestion of carbohydrate in the berries by salivary amylase enzymes in the watery saliva of *H. halys* and then the removal of the compounds during feeding (Peiffer and Felton 2014). The effect of reduced soluble solids may be pronounced on blueberries due to their small size, but this phenomenon could conceivably occur in other small fruits.

Environmental conditions can also influence feeding by *H. halys*, and week-to-week variability in feeding pressure was predicted by weekly environmental conditions in Oregon. Temperature has an important influence on probing activity of *H. halys* and optimum feeding temperature are thought to be approximately 17°C, with an upper threshold for feeding of 26.5–29.5°C (Wiman et al. 2014). In this study, the mean temperature over the weeks that the study was conducted was 16.7°C for Oregon and 23.7°C for New Jersey. This suggests that conditions were potentially more optimal for *H. halys* feeding in Oregon compared with New Jersey. In the current study, we found that temperature was an important predictor of feeding pressure for Duke, but temperature was not an important predictor for Aurora. However, some of the most consistent temperatures occurred over the period where Duke had already been harvested. Thus, it makes sense that temperature was not a good predictor for this period.

In conclusion, *H. halys* has the potential to negatively impact the quality of blueberries causing economic loss if densities of *H. halys* and environmental conditions are favorable. We found that there could be decreases in quantity of healthy fruit as levels of discolored, necrotic berries, and lighter, shriveled berries increased as a result of *H. halys* feeding. *H. halys* also has the potential to decrease berry quality due to a decrease in sugar content. Other potential impacts of the *H. halys* invasion on commercial blueberry production may be contamination of the crop with pathogens causing secondary infection, contamination of fruit by the defensive volatile compounds produced by *H. halys*, and contamination of the crop by nymphs and adults at harvest. These potential secondary effects need further investigation. It is likely that there will be increasing impact of *H. halys* on commercial blueberries as populations of this pest continue to invade new blueberry production regions. Data on blueberry crop infestation levels and retention rates from the field would be helpful to determine how potential damage effects manifest under natural conditions.

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