Economic injury levels for southern green stink bugs (Hemiptera: Pentatomidae) in R7 growth stage soybeans

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**A B S T R A C T**

Stink bugs, primarily southern green stink bug, Nezara viridula (Hemiptera: Pentatomidae), are a major pest complex of soybeans (Glycine max) throughout the southern United States. Densities sometimes peak during late R6 and R7 soybean growth stages when soybeans are approaching physiology maturity and the rate of injury from stink bugs is reduced. Field cage trials were conducted from 2005 to 2008 to examine the type and extent of soybean damage caused by southern green stink bugs during the R7 growth stage. The yield response was variable, but overall was not significant. The impact of southern green stink bugs on quality was more consistent. Test weight decreased, and heat damage and total damage increased as stink bug density increased. Based on these data, three economic injury models were developed using different assumptions. The model that assumes no yield loss, does not predict economic injury within the range of stink bug densities tested. However, if the statistically non-significant yield losses are accepted as real, then the models suggest that the southern green stink bug economic injury level and action threshold for soybeans during R7 stage is generally between nine and 15 stink bugs per row m.

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soybean reproductive development, but the vulnerability of soybeans to stink bug damage is not constant throughout this period. McPherson et al., 1979 confirmed earlier findings of Miner, 1966, that stink bug damage at R7 is much less than at earlier stages and concluded that chemical control should not be necessary after R6. Other research has shown that yield reductions only occur when stink bug infestations occur by R4, with quality damage continuing to occur through R6 (Yeargan, 1977). These studies indicate that the stink bug action threshold should be higher after R6 than during previous stages, but it is not clear what the action threshold should be during R7. This paper describes field cage trials conducted from 2005 to 2008 with southern green stink bugs during the R7 soybean development stage. The goal of these trials was to establish an action threshold for stink bugs during this period of high pest density and reduced crop vulnerability.

1. Materials and methods

1.1. All years

Soybeans were planted in 97-cm rows at the R. R. Foil Plant Research Center in Starkville, MS during 2005—2008 between 5 April and 5 May of each year (Table 1). Varieties planted ranged from a maturity group 4.6 in 2008 to 5.5 in 2005 (Table 1), which represented the maturities of the majority of soybeans currently grown in Mississippi. The field was conventionally tilled and managed uniformly for fertility and weed control each year using typical agronomic practices for the region. The field was monitored by a sweep net sampling for insects every 1—2 wk, and when insect pressure exceeded the recommended threshold (Catchot, 2008) for any pest prior to R7 stage, the entire field was treated with lambda-cyhalothrin (Karate Z 2.08 CS, Syngenta Crop Protection, Greensboro, NC) at the rate of 0.035 kg Al/ha (0.03 lb Al/ac). No more than one insecticide application was ever needed prior to R7 during any year of this trial. Field cages (6.1 m × 6.1 m × 1.8 m high) were erected when the soybeans were in the R6 stage. Field cages were made of 32-mesh Lumite® screen (Lumite Inc., Gainesville, GA), supported by an aluminum pipe frame. Six rows, each 6.1 m long were enclosed in each field cage. The bottom edges of each cage were buried under soil to prevent insect movement into or out of the cage. Insecticides were not applied within two weeks of the stink bug release. Stink bug adults and fourth and fifth instar nymphs were collected with a sweep net from nearby soybean fields and reared in cardboard containers covered with screen for up to one week on soybean pods. At least 75% of the stink bugs collected each year were southern green stink bugs with the remainder green and brown stink bugs. Immediately before stink bugs were released, 3 row-m of soybeans were sampled with a black drop cloth in each cage to estimate the natural stink bug species and density inside each cage. Previously collected stink bugs were then placed in the field cages at the beginning of the R7 stage by gently shaking them out of the cardboard containers while walking through the cage to evenly distribute them over the foliage. Infestation densities ranged from 0 to 16.4 stink bugs per row-m. When soybeans reached R8 stage (16—23 d after infestation), the final stink bug densities in each cage were estimated by sampling 3 row-m with a black drop cloth. The cages were then removed, and all plots were sprayed with lambda-cyhalothrin at the rate of 0.035 kg Al/ha (0.03 lb Al/ac) using a backpack sprayer. Plots were visually examined 1—2 days after insecticide application to verify that a high level of control had been achieved. In 2005, 2006 and 2007, two rows of each field cage were harvested at three different times (Table 1) with a combine modified for small plot research to evaluate whether there was an interaction between harvest timeliness and stink bug damage as measured in yield and seed quality. In 2008 the seed quality was poor at the initial harvest, so all six rows of the plots were harvested at the same time. Yield, moisture and test weight were measured for each cage during each harvest, except in 2005 when test weight was not measured. Approximately 700 g of seed from each harvest of each cage was sent to MidSouth Grain Inspection Service (Memphis, TN) for seed quality inspection, including stink bug damage, heat damage, splits and total damage. Seeds were considered damaged by stink bugs when soybeans showed an indentation or discoloration on the seed coat. Heat damaged kernels were those that were materially discolored and damaged by heat. Splits were soybeans with more than one-fourth of the bean removed that were not otherwise damaged (USDA GIPSA, 2004). Both stink bug and heat damage were confirmed by cross-sectioning the kernels. Total damage was the sum of all the other types of damage. As per standard protocol, only 25% of stink bug damage was counted as total damage (USDA GIPSA, 2004). Therefore non-stink bug damage was calculated by subtracting 25% of stink bug damage from total damage.

1.2. 2005

All cages were infested with 16.4 stink bugs per row-m at the beginning of R7. The day following infestation, cages were sprayed using a backpack sprayer with one of the following treatments: insecticide (lambda-cyhalothrin, Karate® Z 2.08 CS @ 0.035 kg Al/ha (0.03 lb Al/ac)), fungicide (azoxystrobin, Quadris® 2.08F (Syngenta Crop Protection, Greensboro, NC) @ 0.224 kg Al/ha (0.2 lb Al/ac)), insecticide + fungicide (lambda-cyhalothrin and azoxystrobin @ 0.035 kg Al/ha and 0.224 kg Al/ha, respectively), and an untreated control. There were three replicates of each of the four treatments. As a result of the treatments and natural variation in reproduction, there was a range of stink bug densities in the cages at the end of the experiment.

1.3. 2006

Three field cages were sprayed with an insecticide (lambda-cyhalothrin, Karate Z 2.08 CS @ 0.035 kg Al/ha (0.03 lb Al/ac)) at the

<table>
<thead>
<tr>
<th>Year</th>
<th>Variety</th>
<th>Planting Date</th>
<th>Stink Bugs</th>
<th>Harvest Dates</th>
<th>Growth Rate ε</th>
<th>Green S γ</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>Asgrow 5501</td>
<td>5 May</td>
<td>2 Sept.</td>
<td>14 Oct.</td>
<td>46% ab</td>
<td>82% ε</td>
</tr>
<tr>
<td>2006</td>
<td>Asgrow 4703</td>
<td>5 April</td>
<td>5 Aug.</td>
<td>21 Sept.</td>
<td>76% a</td>
<td>100% υ</td>
</tr>
<tr>
<td>2007</td>
<td>Asgrow 4703</td>
<td>23 April</td>
<td>22 Aug.</td>
<td>1 Oct.</td>
<td>−15b</td>
<td>76%</td>
</tr>
<tr>
<td>2008</td>
<td>Dekalb 4651</td>
<td>21 April</td>
<td>20 Aug.</td>
<td>NA</td>
<td>−43c</td>
<td>75%</td>
</tr>
</tbody>
</table>

NA—not applicable.

ε Change in density from beginning to end of the trial. Back-transformed from log ([final density — initial density] / [initial density + 1]) averaged over all cages. Values with the same letter are not significantly different (LSD test with α = 0.05).

γ Includes green and southern green stink bug species at the end of cage experiment.

υ Unsprayed plots only.
time of infestation. The remaining nine cages were infested with 0, 3.3, 6.6, 9.8, 13.1, 13.1, 14.8, 16.4 and 19.7 stink bugs per row-m and not sprayed with pesticide to obtain a range of stink bug densities.

1.4. 2007 and 2008

No cages were sprayed with insecticide at the time of infestation. Cages were infested with 0, 3.3, 6.6, 9.8, 13.1 and 16.4 stink bugs per row-m, with three cages infested at each density.

1.5. Data analysis

Stink bug density changed during the caged period and the change varied with the number released \( (F = 35.58; \text{df} = 1.45; P < 0.001) \) and with year \( (F = 7.66; \text{df} = 3.45; P < 0.001) \) (Table 1). To estimate a density that best reflected the mean density occurring in the unsprayed cages, a stink bug density was estimated from the mean of the number released plus sampled at the time of infestation (initial density) and the number sampled at the end of the infestation period (final density). First and second instars were not included in counts at the end of the infestation period because their impact on soybean damage would have been negligible (Simmons and Yeargan, 1988). Data were analyzed within each year using the mixed model procedure with an unstructured covariance (SAS Institute, 1999). Stink bug density was a fixed numerical factor and replicate was a random factor, so the results of stink bug density were interpreted as a regression. The three harvest dates were analyzed as a repeated measure for each cage. Degrees of freedom were estimated with the Kenwood-Rogers method. After initial analyses, data for heat damage, total damage, stink bug damage, non-stink bug damage, and harvest date were transformed in order to stabilize variance. Contrasts were made in 2005 to separate stink bug impacts from disease impacts. Differences were considered significant at \( a = 0.05 \).

The goal of this research was to evaluate the impact of southern green stink bug density on yield and seed quality during the R7 growth stage for varieties grown in the mid-southern region, so data from all years were also analyzed together. Even though the trial design and variety planted varied by year, stink bug infestation and removal times were consistent in relation to crop maturity. For the overall analysis, the mixed procedure was used with stink bug density as a fixed numerical factor, year and replicate as random factors, and harvest date as a repeated measure. Variety impacts were confounded with year impacts, so there was no attempt to determine whether differences among years were due to changes in variety or year. Soybean variety can impact the amount of stink bug damage (Jones and Sullivan, 1978; McPherson et al., 2007), influencing the results for any given year. Since the objective of this research was to estimate stink bug damage for varieties being commercially grown, different commonly grown varieties were used over time to be certain that the results were broadly valid for current soybean production. Quality measures were transformed for the overall analysis as in the individual year analyses.

1.6. Stink bug economic injury level

Three models were built using data collected from this trial combined with economic assumptions. For all models, the basic structure was based on the economic injury level (EIL) model described by Pedigo et al. (1986) where EIL = C/V/IDK and C is control costs, V is crop value, ID is damage per pest and K is the proportional reduction in pests from a control tactic. Soybean yield, value and insect control costs were drawn from 2009 budgets based on 2008 prices (MSU Ag Economics, 2008). Because high levels of control can be achieved with insecticides on southern green and green stink bugs (Smith and Catchot, 2008; Hood et al., 2009), K was given a value of one in all models. Model A (Table 2) assumes the yield loss and quality impacts were not affected by stink bugs unless differences were statistically significant. Model B (Table 2) uses four-year mean values of yield loss and quality factors, regardless of statistical significance. Model C (Table 2) uses the highest annual value for yield loss and quality factors recorded in 2005–2007. Values from 2008 were not used in model C because seed quality was poor regardless of stink bugs, and the estimates were large and imprecise compared to the other years. The mean loss of test weight from 2006–2008 was used in model C because the greatest test weight loss from stink bugs in 2006 and 2007 was less than the overall mean estimate from 2006–2008. Within each model, three scenarios are depicted, showing economic losses from stink bugs for an average situation, a higher profit and risk situation (high yield, high price, and poor seed quality before including stink bug impact), and a low-profit and risk situation (low yield, low price and good seed quality before including stink bug impact) (Table 3). Price discounts for seed quality were based on average rate schedules obtained from four grain purchasers for the 2008 soybean crop. Test weight was discounted when lower than 69.7 kg/hl (54 lb/bu), total damage was discounted when it exceeded 2.0%, and heat damage was discounted when it exceeded 0.25% (Table 4).

2. Results and discussion

2.1. 2005

There was a yield loss of 9.5 ± 3.1 kg/ha for each increase of one southern green stink bug per row-m \( (F = 9.33; \text{df} = 1, 8.29; P = 0.015) \) (Fig. 1), and seed quality was reduced by stink bugs as indicated by increased stink bug damage \( (F = 45.58; \text{df} = 1, 8.52; P = 0.001) \) (Fig. 1). The use of stink bugs in the seed test weight, and heat damage units resulted in an overall economic loss to soybean production of $33.00, $22.00, and $44.00, respectively.
< 0.001) (Fig. 2), heat damage ($F = 5.56; \text{df} = 1, 8.48; P = 0.045$) (Fig. 3), and total damage ($F = 34.57; \text{df} = 1, 8.14; P < 0.001$) (Fig. 4) at higher stink bug densities. Delayed harvest had no impact on any quality parameters except splits ($F = 7.25; \text{df} = 2, 9; P = 0.013$), with more splits at later harvests than at the first harvest. The fungicide treatment had no impact on any measured parameters, either alone or in interaction with stink bugs or harvest time (data not shown). Weather was dry from the beginning of R7. Yield loss in 2005 was statistically significant each year. Over all years, stink bug density was a significant factor of stink bug damaged seed ($F = 28.29; \text{df} = 1, 35.5, P < 0.001$), with the square root of damaged seed increased by 0.0323% for each stink bug/row m.

caused soybean damage not normally associated with stink bugs. Delayed harvest reduced yield ($F = 27.27; \text{df} = 2, 8.03; P < 0.001$) and seed quality as shown by reduced test weight ($F = 27.09; \text{df} = 2, 6.75; P < 0.001$) and increased total damage ($F = 16.91; \text{df} = 2, 8.07; P = 0.001$) and non-stink bug damage ($F = 34.57; \text{df} = 2, 8.14; P < 0.001$). Stink bug damage was not affected by delayed harvest ($F = 2.51; \text{df} = 2, 7.55; P = 0.146$). Splits decreased at later harvests ($F = 204.02; \text{df} = 2, 8.03; P < 0.001$), likely because most of the split beans harvested at the first harvest fell from the pods before later harvest, reducing yield.

2.2. 2007

The yield response to stink bug density was not significant ($F = 0.91; \text{df} = 1, 10.3; P = 0.362$), even though the estimated yield loss value of 9.9 ± 10.4 kg/ha for each increase of one stink bug per row m was comparable to 2005 (Fig. 1). Significant seed quality factors in 2006 were increased stink bug damage ($F = 23.38; \text{df} = 1, 9.16; P = 0.001$) (Fig. 2) and total damage ($F = 7.26; \text{df} = 1, 10.3; P = 0.022$) as stink bug density increased (Fig. 4). Non-stink bug damage also increased ($F = 7.60; \text{df} = 1, 10.2; P = 0.020$) at higher stink bug densities, possibly indicating that stink bugs directly or indirectly

### Table 4

Price discounts (¢/kg) used to calculate economic losses from changes in soybean quality. Values based on an average of the discounts reported by four grain purchasers during 2008. Discounts for soybeans with poorer quality than shown in the table are negotiable.

<table>
<thead>
<tr>
<th>Test weight (kg/ha)</th>
<th>Discount %</th>
<th>Total Damage</th>
<th>Heat Damage</th>
</tr>
</thead>
<tbody>
<tr>
<td>$&gt;69.4$ (53.9)</td>
<td>0.00</td>
<td>$&lt;-2.1$</td>
<td>$&lt;-0.3$</td>
</tr>
<tr>
<td>$68.2$–$69.4$ (53.0–53.9)</td>
<td>2.43</td>
<td>2.1–2.5</td>
<td>0.3–0.5</td>
</tr>
<tr>
<td>$66.9$–$68.1$ (52.0–52.9)</td>
<td>3.97</td>
<td>2.6–3.0</td>
<td>0.6–1.0</td>
</tr>
<tr>
<td>$65.6$–$66.8$ (51.0–51.9)</td>
<td>5.73</td>
<td>3.1–3.5</td>
<td>1.1–1.5</td>
</tr>
<tr>
<td>$64.4$–$65.5$ (50.0–50.9)</td>
<td>7.28</td>
<td>3.6–4.0</td>
<td>1.6–2.0</td>
</tr>
<tr>
<td>$63.1$–$64.3$ (49.0–49.9)</td>
<td>9.04</td>
<td>4.1–4.5</td>
<td>2.1–2.5</td>
</tr>
</tbody>
</table>

### Fig. 1

Soybean yields and annual trend lines from mean yield of 1st and 2nd harvests in 2005–2008 for cages infested with various southern green stink bug rates at the beginning of R7. Yield loss in 2005 was statistically significant, but other years were not. Overall, yield was not significantly impacted by stink bugs ($F = 1.05; \text{df} = 1, 15.2; P = 0.322$).

### Fig. 2

Stink bug damage and annual trend lines in 2005–2008 for cages infested with various southern green stink bug rates at the beginning of R7. Data were statistically significant each year. Over all years, stink bug density was a significant factor of stink bug damaged seed ($F = 28.29; \text{df} = 1, 35.5, P < 0.001$), with the square root of damaged seed increased by 0.0323% for each stink bug/row m.

### Fig. 3

Heat damage and annual trend lines in 2005–2008 for cages infested with various southern green stink bug rates at the beginning of R7. Heat damage was not significantly affected by stink bug density in any year, but over all years, stink bug density was a significant factor of heat damaged seed ($F = 12.49; \text{df} = 1, 46.8, P < 0.001$), with the square root of damaged seed increased by 0.015% for each stink bug/row m.
and total damage \((F = 5.91, df = 1, 15, P = 0.028)\) (Fig. 4) as stink bug density increased. No other parameters were significantly impacted by stink bug density. Delayed harvest impacted all parameters of yield and seed quality, especially the third harvest which was 36 days later than the first harvest, many of them with rain. Yield was reduced \((F = 21.01, df = 2, 12.4, P < 0.001)\) (Fig. 6), test weight declined \((F = 35.67, df = 2, 15, P > 0.001)\) (Fig. 6), heat damage increased \((F = 3.74, df = 2, 14.4, P = 0.049)\), total damage increased \((F = 41.29, df = 2, 15, P < 0.001)\) (Fig. 6), splits increased \((F = 28.12, df = 2, 14.8, P < 0.001)\), and non-stink bug damage increased \((F = 25.32, df = 2, 14, P < 0.001)\) when harvest was delayed. Stink bug damage was higher at the second harvest than the first \((t = 3.82, df = 14.8, P = 0.002)\), but stink bug damage levels at the first and third harvest were similar \((t = 0.45, df = 16, P = 0.660)\). This was the only year stink bug damage was statistically impacted by harvest time, so it is unlikely that the interaction between stink bug damage and harvest time is an important management consideration.

### 2.4. 2008

Tropical storm ‘Fay’ followed by hurricanes ‘Gustav’ and ‘Ike’ in late August and early September kept fields very wet for several weeks during the R7 development period when the field cages were infested with stink bugs. The excessive moisture caused seeds to sprout in the pods and disease was rampant. Furthermore, the cooler weather slowed maturation, so the cages were on the plants for four days longer than any other year. At the first harvest, seed quality was much poorer than in previous years, regardless of stink bug density. The impact of stink bugs on yield was inconsistent, so while the best fit value was a yield loss of 45.8 ± 31.2 kg/ha for each increase of one stink bug per row-m, this value was not statistically

\[\text{Yield (kg/ha)}
\]

\[\text{Test weight (kg/hl)}
\]

\[\text{% Total Damaged Seed}
\]

\[\text{Stink bugs / row m}
\]
significant \((F = 2.16, df = 1, 16, P = 0.161)\) (Fig. 1). Similar to other years, total damage increased as stink bug density increased \((F = 6.70, df = 1, 14.5, P = 0.021)\) (Fig. 4). However the impact of stink bugs on stink bug damage was not significant \((F = 2.22, df = 1, 16, P = 0.155)\) (Fig. 3), probably because stink bug damage was obscured by other quality problems. Test weight was poor overall, but stink bugs reduced test weight even further \((F = 8.21, df = 1, 16, P = 0.011)\) (Fig. 5). All beans were harvested at one time so there was no evaluation of harvest dates.

2.5. Overall analysis

When analyzing data from all years together, yield was not significantly impacted by stink bugs infested at R7 \((F = 1.05, df = 1, 15.2, P = 0.322)\) (Fig. 1). However, seed quality was impacted by stink bugs as measured by several parameters. The trend of losing test weight with increased stink bug pressure was consistent in all three years it was measured, so test weight was significantly reduced by stink bug density when the data were combined \((F = 4.26, df = 1, 27.7, P = 0.049)\) (Fig. 5). Stink bug damage \((F = 28.29, df = 1, 35.5, P = 0.001)\) (Fig. 2), heat damage \((F = 12.49, df = 1, 46.8, P < 0.001)\) (Fig. 3), and total damage \((F = 18.25, df = 1, 24.6, P < 0.001)\) (Fig. 4) all increased with increased stink bug densities. Heat damage was likely impacted by stink bugs due to misidentification of stink bug feeding symptoms. Test weight, heat damage and total damage are factors that directly impact the value of soybeans in the market, so it is clear there are economic implications from stink bug feeding during the R7 growth stage. While stink bug density did not significantly impact yield, harvest time did \((F = 52.66, df = 2, 70.8, P < 0.001)\), with later harvests yielding less than timely harvests. Stink bug damage was not affected by harvest time \((F = 1.97, df = 2, 40.3, P = 0.153)\), but late harvests had more total damage \((F = 137.37, df = 2, 49.2, P < 0.001)\). While stink bug density and harvest time both were significant factors of yield and/or seed quality, there was no evidence of a consistent interaction between these two factors on any yield or seed quality parameters.

2.6. Stink bug economic injury level

The primary objective of this study was to determine the EIL for stink bug feeding on R7 stage soybeans. Based on data collected in this and other studies (Thomas et al., 1974; Yearygan, 1977), there was not a significant yield loss from stink bug feeding at R7 stage overall, so a model built only on quality losses can be justified (Model A). However, there was a significant yield loss in 2005 and a yield loss trend from stink bugs in 3 of the 4 years, so including yield loss may be necessary to estimate a more realistic EIL (Models B & C). A small yield loss is biologically reasonable because some seeds are still immature during R7. The values for the yield and quality losses used in models A, B and C are shown in Table 2.

Based on Model A, which assumes no yield loss, the EIL for the most sensitive scenario (high yield, low quality, and high price) is greater than 20 stink bugs per row-m, so experimental conditions did not go high enough to reach the EIL (Fig. 7). However, when some yield loss is predicted (Models B, C), then an EIL is often reached within the range of infestation levels tested. Using Model B assumptions, the EIL is between 9.9 and 25.5 stink bugs per row-m, depending on yield, price and initial seed quality assumptions (Fig. 7). Model C estimates an EIL between 7.7 and 19.8 stink bugs per row-m (Fig. 7). Even using the highest risk scenario for the most conservative model (C), the economic injury level of 7.7 stink bugs per row-m is more than twice as high as the recommended threshold of 3.3 stink bug/row m (Catchot, 2008). Based on models B and C, the economic injury level in most soybean fields will fall between 9 and 15 stink bugs/row-m, which is 2.5 to 4.5 times higher than the currently recommended threshold.

The EIL was calculated in this trial, whereas an economic threshold is needed to prevent damage from reaching the EIL (Stern et al., 1959). This requires an understanding of the population dynamics of the pest. Where populations are rapidly growing, the economic threshold needs to be lower than the EIL, but where populations are more stable, the economic threshold and EIL can be the same. Peak oviposition of southern green stink bug occurs during R3 to R5 stages (Schumann and Todd, 1982), with peak densities normally occurring during R5 to R7 stages. Since the peak density normally occurs before or during R7, population growth during R7 is not common. There was no population growth in two of the four years in this trial (Table 1). Similarly, Thomas et al., 1974 and Schumann and Todd, 1982 observed little to no population growth during R3 to R5 stages.
growth when soybean pods were turning yellow. There was some population growth inside the cages during 2005 and 2006, but it was relatively slow given the cages were on for more than 2 wk. If the stink bugs had been free to leave these senescing plants, it is likely that growth would have been further reduced. Because there is little expectation of substantial population growth during R7 for southern green stink bugs, the economic threshold can be established at the same level as the EIL.

Southern green stink bugs can reduce seed quality during the R7 stage, which reduces the value of the crop. However, price discounts based on quality reductions alone are not severe enough to make an insecticide application economically viable at any realistic stink bug densities (Model A), unless the quality of the seed is already compromised due to other factors. Yield losses attributed to stink bug feeding were not statistically significant in three of the four years in this study, nor when all years were analyzed together. However, if the small trend in yield loss observed was real, then the EIL is low enough that it is occasionally reached in Mississippi and other southern states (Models B & C). Therefore a threshold is still needed for stink bugs on R7 stage soybeans, but it should be at least twice as high as current thresholds used during earlier reproductive stages.

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