What is the Economic Threshold of Soybean Aphids (Hemiptera: Aphididae) in Enemy-Free Space?

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ABSTRACT Soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is the leading insect pest of soybean, *Glycine max* (L.) Merr., in the North Central United States. Soybean aphids are capable of reducing yields by up to 40% (Ragsdale et al. 2007). The current recommendation to prevent yield loss is an application of insecticide to foliage (Myers et al. 2005, Ragsdale et al. 2007) when aphid populations exceed 250 aphids per plant on >80% of the plants from the onset of flowering to early pod development (i.e., R1 to R5 stages; Fehr and Caviness 1977). This value serves as an economic threshold (ET) for an economic injury level ([EIL]: 674 aphids per plant) that was calculated from crop values and management costs typical for soybean growers in the midwestern United States. Ragsdale et al. (2007) calculated this ET based on the population growth rate of the aphid, allowing growers at least 7 d to prepare for the application of a foliar insecticide. This recommendation has been shown to reduce insecticide use and be more profitable than prophylactic management of the soybean aphid in which insecticides are applied based on the growth stage of the plant regardless of aphid population density (Johnson et al. 2009, Song and Swinton 2009).

Despite the large body of literature that indicates natural enemies regulate soybean aphid populations (Fox et al. 2004, 2005; Rutledge et al. 2004; Nielsen and Hajek 2005; Rutledge and O’Neil 2005, Costamagna and Landis 2006; Schmidt et al. 2007, 2008), economic outbreaks are common in North America. Why these outbreaks occur is unclear, although several factors can contribute to increasing the risk for soybean aphid outbreaks. Recent studies have shown the effects land use can have on natural enemy abundance in soybean (Gardiner et al. 2009a) and the biological control they provide for soybean aphids (Gardiner et al. 2009b). Landis et al. (2008) explored the impact of increased land use for corn (*Zea mays* L.)-based biofuel production on this ecosystem service. They argued that with increased incentives for corn production, corn acreage would increase, resulting in decreased biocontrol of the soybean aphid due to a simplified landscape (Landis et al. 2008, Gardiner et al. 2009b). Pesticide use in soybean also has increased since the introduction of the soybean aphid to the United States (NASS–USDA 1999, 2005). The primary insecticides to control the soybean aphid are broad spectrum in effect, reducing natural enemy populations along with aphid populations (Jeffries and Lawton 1984, Johnson et al. 2008, Ohnesorg et al. 2009). Removal of natural
enemies from an agroecosystem can lead to rapid recolonization by a pest and secondary outbreaks due to the creation of enemy-free space (Jeffries and Lawton 1984).

The ET developed by Ragsdale et al. (2007) for the soybean aphid was developed with at least a 7-day lag time between the ET and EIL that provides growers an opportunity to schedule an insecticide application to their fields. If aphidophagous arthropods diminish in the landscape, the growth rate of aphid populations in the field would increase. If the population growth rate increases during the critical time between 250 aphids per plant (ET) and 674 aphids per plant (EIL), the ET may need to be lowered to still provide a 7-d lag time and prevent yield loss from occurring. A recent study conducted under semiefield conditions with soybean plants artificially infested with aphids and grown within cages has suggested the ET should be reduced to as low as three aphids per plant (Catangui et al. 2009). The conditions under which the experiment was carried out excluded the impact of aphidophagous natural enemies, creating an enemy-free space. However, Catangui et al. (2009) did not compare the yield response of such a low threshold (e.g., no aphids) to that of Ragsdale et al. (2007). It is unclear whether yield loss or any impact to soybean plants will occur at either density of aphids.

Considering the current simplification of the agricultural landscape and the increased use of insecticides for control of the soybean aphid, it is reasonable to assume that the biological control provided by aphidophagous arthropods will diminish. Previous studies have used cages to estimate the impact of predators on soybean aphid populations (Fox et al. 2004, Schmidt et al. 2007, Gardiner et al. 2009b). By comparing the growth of aphid populations within cages to those outside cages, several studies have observed a substantial decrease in aphid population growth when predators have access to aphids. However, growth of aphid populations within cages can be affected by other factors. For example, a previous study observed that the temperature inside a cage can vary from that outside (Fox et al. 2004). Temperature can have a dramatic impact on aphid developmental time and population growth rates (McCormack et al. 2004) and temperature-based models have been developed to predict A. glycines outbreaks (Venette et al. 2004).

Our goal was to evaluate the current recommended ET for the soybean aphid in a natural enemy-free environment (i.e., a cage). We hypothesized that in absence of the natural enemies, soybean aphid populations would reach the ET (250 aphids per plant) and exceed the EIL (674 aphids per plant) earlier than the seven days proposed by Ragsdale et al. (2007). We anticipated that within the cages, a temperature based model could predict when populations reached the EIL from the ET. Furthermore, we hypothesized that soybean aphid populations that reach the ET of 250 aphids per plant but do not exceed the EIL would not have an impact on the plant.

Materials and Methods
We conducted the following experiment during 2008 and 2009 at the Iowa State University Horticulture Research Station north of Ames, in Story Co., IA. We grew soybean in replicated plots (28 by 51 cm) kept 152 cm apart within six blocks. The ground in between plots was planted to foxtail Setaria spp. Foxtail was kept <0.6 m tall by mowing as needed. Plots were planted with commercially available soybean cultivars adapted for growing in the region. Five cultivars were used in 2008 with a sixth cultivar added in 2009. Six different pest treatments were established in a complete factorial design with each combination of treatment by cultivar present. A randomized complete block design was used in 2008 with six replications. The addition of a sixth cultivar in 2009 necessitated the use of a randomized incomplete block design with six blocks containing five replications of each treatment by cultivar combination. A subset of these treatments by cultivar combinations is reported here. This subset of treatment by cultivar combinations was part of a larger experiment conducted to evaluate the impact of multiple pests on soybean cultivars differing in seed composition characteristics. For the analyses presented here, two cultivars, ‘DK 27-52’ and ‘DK 28-52’ (Monsanto Company, St. Louis, MO) and three pest treatments were included. Planting occurred on 1 June and 19 May in 2008 and 2009, respectively. Planting density was 22 seeds per plot and plants were thinned to 10 evenly spaced plants per plot after emergence.

Three aphid population levels were established and randomly assigned to plots within each of six blocks. The first level was kept free of aphids, and is referred to as the control treatment throughout this document. The second level was a density of 250 aphids per plant and is referred to as the IPM treatment. The final infestation level consisted of allowing aphid populations to grow without limit, and is referred to as the unlimited treatment.

To control the density of aphids within each treatment, cages were placed around plots. Cages were constructed of white no-see-um mesh fabric (Quest Outfitters, Sarasota, FL) stretched over cage frames constructed of thin-walled polyvinyl chloride pipe (Charlotte Pipe, Charlotte, NC). Cages measured 1.1 by 0.8 by 0.6 m tall by mowing as needed. Plots were placed over plots after planting, at the VC-V1 growth stages (Fehr and Caviness 1977) and remained until after plots were harvested. For the remainder of this document, “cage” refers to both the plot and the physical cage surrounding the plot.

Aphids used in this experiment came from a laboratory colony maintained at Iowa State University. The laboratory colony was established from field populations collected from central Iowa in 2004 and maintained on commercially available aphid susceptible soybean cultivars. The colony was supplemented with field populations from central Iowa each summer from 2005 to 2008.
Treatments that received aphids (IPM and unlimited) were infested by randomly selecting one plant per cage and infesting it with five soybean aphids on the second trifoliate at the V3-V4 growth stage. Initially infested plants were marked by tying a strip of fluorescent flagging tape to the stem at soil level. Aphid infestations occurred on 3 July in 2008 and on 23 June in 2009. Aphid populations were counted twice a week by counting all aphids (immature and adult stages) on the initially infested plant. Care was taken not to damage plants during the counting of aphids. If a plant was damaged during counting, it was removed from aphid growth rate analyses. The remaining plants in each cage were infested when cages reached 50 aphids on the initially infested plant. The secondary infestation was accomplished by clipping leaves with ≈50 aphids onto the newest expanded trifoliate. The initial infestation was followed to determine the population growth rate of aphids within the cages. The secondary infestation was performed to obtain aphid infestations that were more uniform in spatial pattern throughout a cage for the purpose of collecting yield data in response to varying aphid densities. IPM treatment cages received a single application of λ-cyhalothrin (Warrior with Zeon Technology, Syngenta Crop Protection, Greensboro, NC) when populations reached 250 aphids per plant. Insecticides were applied using a backpack sprayer and Teejet (Springfield, IL) twinjet nozzle (TJ 11002) with 20 gal/acre at 40 lb/inch² pressure. Nets were opened and lowered to ground level and plots were wrapped with a spray shield (117- by 117-cm laminated paper) during insecticide application to ensure adequate insecticidal drift. Immediately after insecticide application, nets were raised and closed again. Populations in the unlimited treatment were counted on the initially infested plant twice each week until the populations reached >1,000 aphids per plant. Populations were then measured once each week until all aphid populations had declined from the previous sampling date.

The effect cages had on temperature and relative humidity were measured using HOBO micro stations equipped with Temperature/RH smart sensors (Onset Computer Corporation, Bourne, MA). Two stations were positioned at opposite ends of the field (37 m apart). Each station was equipped with four sensors. Each sensor recorded both temperature and relative humidity. One sensor was positioned outside of a cage. The other three sensors were placed inside the three nearest cages to the outside sensor. Sensors inside the cage were attached to one of the support legs ≈1.0 m off the ground. Sensors recorded temperature and relative humidity every 30 min for the duration of the experiment.

Yield was measured by hand harvesting all ten plants in each cage. Seed was dried to a uniform moisture content to <8%. Total seed weight was then measured for each cage.

**Data Analysis. Temperature and Relative Humidity.** Sensors inside and outside of cages were used to collect temperature and relative humidity data starting 7 d after cages were infested with aphids and until aphid populations declined. Daily maximum and minimum temperatures were used to calculate the accumulated degree-days (DD) for a single day using the following equation:

\[ DD = \frac{(\text{max temp} - \text{min. temp})}{2} \]

where the developmental threshold is set at 8.6°C and the upper developmental threshold is set at 34.9°C in accordance with previous studies on soybean aphid development (Hirano et al. 1996, McCormack et al. 2004). The degree-day equation was used as outlined by Pedigo and Rice (2008). We summed degree-days for the entire season to calculate the cumulative degree-days from the temperatures recorded by the sensors inside and outside of cages. Average relative humidity was calculated for each day from each sensor and was used to compare the relative humidity inside and outside the cages.

**Aphid Population Growth.** Aphid population data from the cages assigned the unlimited treatment was used to determine how quickly soybean aphids reach the EIL from the ET in enemy-free space. The effects of year and cultivar and their interaction were tested using a mixed model (PROC MIXED, SAS Institute, Cary, NC). Block was set as a random effect in the model. The rate of population growth of aphids in each cage (total of 22 cages) was estimated. The linear relationship for the density of aphids over time was estimated using regression analysis. The density of aphids was log transformed to control for heteroscedasticity. This rate of growth per day was estimated during a period of time that began when populations reached 250 aphids per plant and ended 10 d later.

We used the rate of growth calculated from each cage to determine how many days were required for a population to grow from the ET to the EIL. We accomplished this by plotting the aphid density (ln aphids/plant) on the y-axis and time (in days) on the x-axis. The following equation was then solved:

\[ y = mx + b \]

where \( y = \ln674 \) (the current EIL), \( m \) is population growth rate for an individual cage, and \( b = \ln250 \) (the current ET). The equation could then be solved for \( x \), giving the time it took the aphids in an individual cage to increase in density from the ET to the EIL.

**Aphid Growth Model.** We compared our observations of aphid population growth within cages to populations predicted by the temperature-based model Soybean Aphid Growth Estimator (SAGE) version 1.2 (McCornack and Ragsdale et al. 2004, Venette et al. 2004) using Student’s t-test. The SAGE model was designed using the soybean aphid growth parameters from McCormack et al. (2004). The SAGE model is available online free of charge through the University of Minnesota’s soybean extension website. The SAGE model is a management tool designed for farmers and crop advisors to predict future within field aphid pop-
ulation growth based on the current aphid population within a field and predicted temperatures.

The SAGE model predicts the aphid population over a 7-d period based on the daily minimum and maximum temperatures for the current day and the following 7 d. To determine predicted rates of population growth, we used the daily minimum and maximum temperatures recorded from sensors inside the cages. We added temperature data from our field sensors to SAGE (Venette et al. 2004). We used temperatures from the 7-d period when the aphids in the unlimited treatment were in the range of the ET to the EIL. The initial aphid population used in this model was 250 aphids per plant. The output from the model was a daily estimate of aphid density, which was log transformed, and a rate of growth was calculated. A unique rate was calculated from temperature data collected from each sensor. The average amount of time between the ET and EIL predicted by this model was estimated for each year.

Yield. We used two soybean cultivars within each treatment. To reduce the variation in yield across these cultivars, we calculated a ratio for each cultivar based on the yield measured in each treatment compared with the aphid-free control treatment. This resulted in the following equation:

\[
\text{yield ratio} = \frac{\text{yield of treatment plot}}{\text{yield of control plot}}
\]

The yield ratio analysis yielded 44 observations across the two cultivars and two aphid treatments. Four observations were not used due to missing yield data for either the treatment plot or aphid-free control plot.

The means of the ratios for the IPM and unlimited treatments are reported. Yield ratios were compared between the IPM and unlimited treatments using an analysis of variance (ANOVA) to determine the effect of insecticide treatment on yield. Our mixed model included the fixed effects of year, treatment, cultivar, and the interactions of cultivar by year, treatment by year, cultivar by treatment, and the three-way interaction of cultivar by treatment by year. Block was set as a random effect. The Student’s t-test was used to determine whether the yield ratio of the IPM treatment was significantly different from 1. This comparison determined if the aphid exposure experienced by plants in the IPM treatment was sufficient to reduce yield.

Results

Temperature and Relative Humidity. The average \(\pm\) SEM degree-days accumulated outside of the cages in 2008 and 2009 were 685 \(\pm\) 3.1 and 638 \(\pm\) 2.5, respectively. The average \(\pm\) SEM degree-days inside of cages were 703 \(\pm\) 1.8 and 675 \(\pm\) 7.8 in 2008 and 2009, respectively. For the 2 yr of this study, the temperatures within the cages were higher than those outside the cages, resulting in an average of 28 DD, or a 4% increase in degree-days experienced within the cages. The average daily relative humidity for the season in 2008 and 2009 was 81.6 and 82.8%, respectively. The average daily humidity inside cages was 79.1 and 79.9% in 2008 and 2009, respectively. Overall, we measured an average reduction of 2.7% in humidity within the cages during the 2 yr of our study.

Aphid Populations and Growth Dynamics. Aphid populations reached the ET between 22 July and 25 July in 2008 and between 23 July and 28 July in 2009 (Fig. 1). This was 19–22 and 25–30 d after initial infestation in 2008 and 2009, respectively. In both years, these dates occurred during the R1–R3 growth stages of the plant. Aphid populations peaked in the unlimited treatment between 19 and 28 August in 2008 and between 12 and 20 August in 2009. In both years, these dates occurred during the R4–R5 growth stages of the plant. The average peak aphid population was 7,180 and 9,305 aphids per plant in 2008 and 2009, respectively.
We did not observe a difference in the population growth rate of aphids across years \( (F = 1.55; \text{df} = 1, 13; P = 0.235) \) or cultivars \( (F = 0.68; \text{df} = 1, 13; P = 0.4245) \) or an interaction between year and cultivar \( (F = 0.09; \text{df} = 1, 13; P = 0.7677) \). Therefore, data were pooled across years and cultivars to estimate an average growth rate. The average growth rate per cage was calculated to be \( 0.14 \pm 0.06 \) ln aphids per plant per day, with a 95% confidence interval.

The growth rate of aphids in each cage also was used to calculate the average number of days required for a population to grow from 250 aphids per plant to 674 aphids per plant. From the 19 cages used in this study, we observed populations reaching 674 in an average of 6.97 \( \pm 1.11 \) d (Fig. 2).

**Aphid Growth Model.** Daily high, low, and average temperatures for the 8 d in each year used in the model calculations are listed in Table 1. From these temperatures, we predicted the abundance of aphids (Fig. 3). The model predicted an average growth rate of \( 0.33 \pm 0.004 \) ln aphids per day. This was significantly greater than our observed growth rate of \( 0.14 (t = 236.79; \text{df} = 32; P < 0.0001) \). The model’s predicted growth rate resulted in an estimate of 2.8 and 3.3 d, respectively, for 2008 and 2009, for the time between the ET and EIL.

**Yield.** We report yield as the ratio of the seed weight for both the IPM and unlimited treatments to the control treatment (Fig. 4). No significant interactions were present between aphid treatment and cultivar \( (F = 0.42; \text{df} = 1, 27; P = 0.5244) \); aphid treatment and year \( (F = 0.60; \text{df} = 1, 27; P = 0.4448) \); cultivar and year \( (F = 0.04; \text{df} = 1, 27; P = 0.8494) \); or aphid treatment, cultivar, and year \( (F = 0.60; \text{df} = 1, 27; P = 0.4468) \). Neither cultivar \( (F = 0.11; \text{df} = 1, 27; P = 0.7424) \) nor year \( (F = 0.33; \text{df} = 1, 27; P = 0.5678) \) had a significant effect on yield ratios. Yields were then pooled across cultivars and years for all further analyses. We observed a significant difference of 46% between the yield ratios of the IPM and unlimited treatments \( (F = 13.65; \text{df} = 1, 27; P = 0.0009) \) (Fig. 4). We did not observe a difference in the yield ratio of the IPM treatment from a ratio of one \( (t = 0.01; \text{df} = 1, 27; P = 0.9948) \), indicating that the aphid densities in the IPM treatment did not significantly effect yield (Fig. 4).

**Discussion**

The growth of aphids was slower than what was predicted from a temperature-based model (Venette et al. 2004) of soybean aphid growth, which was created from developmental thresholds calculated by McCorrnack et al. (2004). McCorrnack et al. (2004) found the optimal temperature for development to be 26.7°C.
27.8°C. In our study, both external temperatures and internal cage temperatures oscillated above and below this threshold, often by as much as 7°C. The developmental thresholds of the soybean aphid were calculated based on the growth of populations in an environment with a constant temperature (McCornack et al. 2004). The difference in the predicted rate of soybean aphid growth to what we observed may be due to daily fluctuations of temperatures in the field which was not addressed by McCornack et al. (2004). Such fluctuations may prevent the populations from growing at their optimal rate.

This difference in the predicted versus the observed growth rate of aphid populations could be due to other abiotic factors such as rain and wind (Trumble 1982, Moran et al. 1987, Sanderson et al. 1994, Maudsley et al. 1996). Although we excluded predators and parasitoids from soybean aphids in this study, entomopathogenic fungi are a source of aphid mortality and would probably not be excluded by our cages.

Fig. 3. Predicted aphid population growth for 7 d beginning at the density of the economic threshold (250 aphids per plant). The 2008 and 2009 models were calculated using SAGE version 1.2 developed by Venette et al. (2004) and temperature data collected from inside cages. The observed values were calculated from the population growth rates observed during the experiment.

Fig. 4. Mean seed weight ratio of the two aphid treatments averaged over the two varieties and 2 yr of the study. Significant treatment differences determined using LSMEANS are represented with letters. Significant differences between a treatment mean and a ratio of 1 determined using Student’s t-test are represented with an asterisk and signify a yield loss due to the treatment.
Such fungi have been observed to reduce soybean aphid populations in North America (Baute 2003, Rutledge et al. 2004, Nielsen and Hajek 2005). However, we focused our estimates of aphid population growth, well before populations declined. Throughout the 2 yr of the experiment, we did not observe any evidence of fungal infection in the aphid populations. Furthermore, we did not observe a significant difference in relative humidity inside the cage to that outside the cages, suggesting that the cage did not affect an abiotic factor that could promote fungal growth.

Soybean aphids have been reported to be capable of doubling populations in as little as 1.5 d (McCornack et al. 2004). Ragsdale et al. (2007) reported an average doubling time of 6.8 d for naturally occurring populations in the field. In our experiment, for population densities between the ET and EIL, we observed an average population doubling time of 4.95 d. Our temperature model predicted aphid population doubling times to be 2.13 d. Ragsdale et al. (2007) proposed that the difference in doubling times observed in the field and those predicted by temperature models were due to “environmental resistance.” Environmental resistance includes natural enemies, weather, and immigration and emigration of winged aphids.

Our study suggests that for the period of time when aphid population densities are between the ET and EIL, natural-enemy-free space may more closely resemble field conditions than ideal conditions for aphids. Previous studies have shown natural enemies have a large impact on the regulation of soybean aphid populations (Fox et al. 2004, Costamagna and Landis 2006, Schmidt et al. 2007, Gardiner et al. 2009b). In all cases, these studies focused on the growth of initial populations of aphids at low densities (1–10 aphids per plant). Our study focused on populations of >250 aphids per plant. Our results suggest that at this point of a soybean aphid outbreak, natural enemies may not be as important a source of mortality as previously thought. Rather abiotic factors may play a larger than anticipated role in environmental resistance. The difference between the soybean aphid rates of growth we observed and the one predicted by the temperature-based model may be due to abiotic factors such as fluctuations in temperature and the protection of aphids from other abiotic factors such as rainfall and wind. Further research may be necessary to explore the role of these abiotic factors in regulating aphid population dynamics at the critical time between the ET and EIL.

A growing body of literature suggests that the level of natural enemy induced mortality of the soybean aphid may be diminishing due to agricultural practices (Landis et al. 2008, Ohnesorg et al. 2009, Schmidt et al. 2010). Olson et al. (2008) reported that the most commonly used insecticides for control of soybean aphids in the Midwest included Asana, Lorsban, Mustang, and Warrior; all are considered broad-spectrum in nature and reduce natural enemy populations in addition to aphids (Ohnesorg et al. 2009). The research presented here is the first step in analyzing how our current soybean aphid management practices will respond to the changing soybean agricultural ecosystem in the midwestern United States.

Our findings support the use of an ET of 250 aphids per plant recommended by Ragsdale et al. (2007) and supported by Johnson et al. (2009). Our data show that under cage conditions a treatment threshold of 250 aphids per plant provides yield protection from the soybean aphid. Our linear regression analysis also demonstrated that the observed aphid population growth rates in our study provided an average 7-d lag time from the ET to the EIL. This 7-d lag time is within the range proposed by Ragsdale et al. (2007). Our analysis also indicates that abiotic factors may have a larger than expected impact on aphid population during the period between the ET and EIL and further research may be necessary to enhance our understanding of these factors.

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References Cited


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