Evaluation of Late Vegetative and Reproductive Stage Soybeans for Resistance to Soybean Aphid (Hemiptera: Aphididae)

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ABSTRACT   The soybean aphid, *Aphis glycines* Matsumura, has become the most significant soybean [*Glycine max* (L.) Merrill] insect pest in the north central soybean production region of North America. The objectives of this research were to measure selected genotypes for resistance to the soybean aphid in the later vegetative and reproductive stages under field conditions, and confirm the presence of tolerance in KS4202. The results from 2007 to 2011 indicate that KS4202 can support aphid populations with minimal yield loss at levels where significant yield loss would be expected in most other genotypes. The common Nebraska cultivar, 'Asgrow 2703', appears to show signs of tolerance as well. None of the yield parameters were significantly different between the aphid infested and noninfested treatments. Based on our results, genotypes may compensate for aphid feeding in different ways. Asgrow 2703 appears to produce a similar number of seeds as its noninfested counterpart, although the seeds produced are slightly smaller. Field evaluation of tolerance in KS4202 indicated a yield loss of only 13% at 34,585–53,508 cumulative aphid-days, when 24–36% yield loss would have been expected.

KEY WORDS   host plant resistance, tolerance, *Aphis glycines*

The soybean aphid, *Aphis glycines* Matsumura, has become the most significant soybean [*Glycine max* (L.) Merrill] insect pest in the north central soybean production region of North America (Ragsdale et al. 2011). Since its initial detection in the United States in 2000 (Alleman et al. 2002), the soybean aphid has spread to 30 states and several Canadian provinces (Hartman et al. 2001, Alleman et al. 2002, Venette and Ragsdale 2004, Beckendorf et al. 2008, NAPIS 2011). The soybean aphid has caused considerable economic damage to soybean since its introduction.

Soybean aphid exhibits a heteroecious and holocyclic life cycle (Ragsdale et al. 2004). The primary hosts of the soybean aphid in North America consist of *Rhamnus* spp., the most suitable being common buckthorn, *Rhamnus cathartica* L.; Alder buckthorn, *Rhamnus alnifolia* L'Héritier; lanceleaf buckthorn, *Rhamnus lanceolata* Pursh; and glossy buckthorn, *Frangula alnus* Miller, also have been indicated as possible hosts (Ragsdale et al. 2004, Voegtlin et al. 2004, Voegtlin et al. 2005, Hill et al. 2010). The secondary host is soybean, *Glycine max* (L.) Merrill, (Hill

et al. 2004a, McCornack et al. 2004, Ragsdale et al. 2004). The soybean aphid does not generally appear on soybeans in Nebraska (NE) until late June to mid-July. Because of this, the soybean aphid is not usually reported in Nebraska until soybeans are in their reproductive stages (Brosius et al. 2007).

Initial infestations of soybean aphid in soybean are typically found on the undersides of young, tender leaves, but as the plant matures and aphid numbers increase, aphids can be detected throughout the soybean canopy on leaves, petioles, stems, and pods (Blackman and Eastop 2000, Ragsdale et al. 2004). Soybean aphid feeding directly affects the plant by removing photosynthates that thereby reduces photosynthesis (Ostlie 2002). Although that is the case, the soybean aphid resistant KS4202 soybean has shown the ability to tolerate relatively high levels of aphid feeding by upregulation of detoxification mechanisms, such as peroxidases and faster regulation of RuBP (ribulose-1,5-biphosphate) (Pierson et al. 2011). Indirect injury results from the transmission of viral diseases, such as soybean mosaic virus (*Potyviridae, Potyvirus,* SMV), and honeydew accumulation resulting in sooty mold (Clark and Perry 2002, Ostlie 2002). These direct and indirect effects reduce soybean growth and yield by reducing the number of pods, number of seeds per pod, and individual seed weight (Myers et al. 2005, Beckendorf et al. 2008). Yield losses of up to 50% have been reported (Wang et al. 1994, DiFonzo and Hines 2002, Ragsdale et al. 2004, Mensah et al. 2005). The severe and widespread

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damage caused by the soybean aphid has driven the development of a suite of pest management tools and strategies, including chemical, biological, host plant resistance, and cultural control (Wang and Ba 1998, Wang et al. 2000, Ostlie 2002, Hill et al. 2004b, Wu et al. 2004, Rutledge and O'Neil 2005, Brosius et al. 2007). Although chemical control is currently the primary method for soybean aphid management, the widespread adoption of aphid-resistant soybean varieties could reduce foliar insecticide use throughout the North Central region.

Over the past decade, several screening studies have identified resistant soybean genotypes (Hill et al. 2004b; 2006a,b; Li et al. 2004; Mensah et al. 2005; Diaz-Montano et al. 2006; Kim et al. 2008). More recent studies have focused on measuring soybean germplasm for resistance to the two different soybean aphid biotypes, the Illinois isolate (biotype 1) and the Ohio isolate (biotype 2). It is important to note that the above screening studies were conducted during the early seedling stages (Hill et al. 2004b, Diaz-Montano et al. 2006, Mian et al. 2008).

Pierson et al. (2010) measured selected genotypes during their reproductive stages for resistance to the soybean aphid under greenhouse conditions and documented the categories of aphid-resistant soybean. Based upon damage ratings and yield parameters, three genotypes (KS4202, K-1639–2, and K1621) were considered moderately resistant. No choice studies documented antibiosis in K-1639–2 and tolerance in KS4202. This was among the first reports of resistance to the soybean aphid in reproductive-stage soybeans.

Although many resistant sources have been identified, very few studies have focused on identifying tolerant soybeans and characterizing their resistance mechanisms. In addition, over the past decade, most resistance screening studies have been conducted on the seedling stages, although in many regions the aphid does not colonize soybean until later vegetative stages, or even reproductive stages (e.g., NE). Because of this, and evidence of a differential physiological response between reproductive and vegetative soybeans to soybean aphid feeding (Macedo et al. 2003), it is important to expand the research to more mature soybean. The objectives of this research were to further measure selected genotypes for resistance to the soybean aphid in the later vegetative and reproductive stages under field conditions and confirm the presence of tolerance in KS4202, tolerance being the ability of the plant to withstand or recover from injury without adverse effects to the attacking arthropod (Smith and Clement 2012).

Materials and Methods

2007 Field Study. Six soybean genotypes were measured for resistance to soybean aphid in a field study at the University of Nebraska Northeast Research and Extension Center Haskell Agricultural Laboratory, Concord, NE. The genotypes selected for evaluation had unknown resistance ('Asgrow 2703', MG II), reported resistance in the seedling stage ('Dowling', MG VIII; 'Jackson', MG II; K-1621, MG IV; and K-1639–2, MG V), or susceptible in the seedling stage (KS4202, MG IV) (Hill et al. 2004b, Diaz-Montano et al. 2006). Soybean Asgrow 2703 is commercially available, commonly grown, and used in northeastern Nebraska (Pierson et al. 2010, 2011). Genotypes were planted with each replication containing an aphid infested and an aphid-free treatment.

Standard agronomic practices for northeastern Nebraska were used to maintain experimental plots. Fields were disked twice in the spring before planting. Soybeans were planted under the traditional corn–soybean rotation in an Alcester-silt loam soil. Soybeans were irrigated six times by an overhead lateral irrigation system during the growing season (2.5 cm of water each time). Pursuit (DG) (BASF Corp., Research Triangle Park, NC) and Cobra (Valent USA Corp., Walnut Creek, CA) herbicides were used to control weeds.

Experimental design was a randomized complete block with six replications. Plots were three rows wide and 1.5 m long. Because of limited seed quantity, the center of the center row was planted with nine seeds of the designated genotype in the middle of 0.46 m. The two outer rows, as well as the outer portions of the center row, were planted with Asgrow 2703 to serve as a buffer. Soybeans were planted on 6 June 2007.

Because natural soybean aphid colonization was light and sporadic, the center row of each plot was artificially infested on 4 August 2007 with leaflets containing 10–50 aphid nymphs and adults that were obtained from buffer rows. An infested leaflet was placed on the upper node of one soybean plant in the middle and at each end of the center (experimental) rows. The foliar insecticide lambda-cyhalothrin at 28.0 g ([AI]/ha) (Warrior, Syngenta Crop Protection, Inc., Greensboro, NC) was applied to the aphid-free plots on 16 July 2007, to prevent aphid colony development.

Three plants from each plot were chosen at random on a weekly basis from 12 July to 6 September 2007 for nondestructive evaluation. Aphids were counted and plants were assigned a damage rating. Damage ratings were based on a 1–5 damage scale where one is ≤10% yellowing discoloration; 2–11-30% yellowing discoloration; 3–31-50% yellowing discoloration; 4–51-75% yellowing discoloration; and five is ≥76% of leaf area with yellowing discoloration or dead tissue (Heng-Moss et al. 2002, 2004, Hill et al. 2004b; Pierson et al. 2010). Plant height and the growth stage (vegetative or reproductive) also were recorded (Fehr et al. 1971). As the season progressed, data collection was limited to the first four of the six replications because of time constraints.

A more informative measure of aphid pressure than peak aphid number is cumulative aphid-days (CAD), which is a measure of aphid pressure over time. Aphid-days are calculated from the equation

$$\text{aphid-days} = ((N_1 + N_2)/2)*T \qquad [1]$$

where N_1 is the number of aphids per plant on the previous sampling date, N_2 is the numbers of aphids per plant on the following sampling date, and T is the

number of days in between the two sampling dates (Hanafi et al. 1989, Ragsdale et al. 2007). To gain a better understanding of the total aphid pressure over the growing season, CAD were calculated for each genotype.

Soybean harvest occurred on 25 October 2007. All plants from each treatment (4–10 plants per plot) from the four replications sampled throughout the study were cut at the soil line and wrapped in brown wrapping paper for later processing. Plant material was oven-dried and yield components then were measured to determine the effect of soybean aphid injury to yield: number of pods per plant, number of seeds per pod, average dry seed weight, average dry pod weight, dry weight of stem, and total plant biomass (Hill et al. 2004b, Svehla 2007, Beckendorf et al. 2008).

2009 Field Study. The 2009 field study was similar to that of the 2007 field study with a few minor exceptions. Only four of the six genotypes were measured in the 2009 study: K-1621, K-1639–2, KS4202, and Asgrow 2703. Genotypes Dowling and Jackson are from higher soybean maturity groups that typically need a longer growing season for complete maturity. These two genotypes are usually grown south of Nebraska. Once again, two plots per genotype were planted in each replication, one infested and the other aphid-free. Planting occurred on 28 May 2009.

Standard agronomic practices for northeastern Nebraska were used to maintain the experimental plots. As with 2007, fields were disked twice in the spring shortly before planting. Soybeans were planted in a corn-soybean rotation in an Alcester-silt loam soil. Unlike 2007, experimental plots were not irrigated because the irrigation system was inoperative. Dual II Magnum and Resource herbicides were used to control weeds.

Experimental design was a randomized complete block with six replications. Plots were four rows wide and three meters long. The two center rows were planted with ≈100 seeds per row of the designated genotype. The outer two rows were planted with Asgrow DK 27–52 to serve as a buffer.

The level of aphid infestation in the field was again inadequate, so plots were artificially infested on 15 July 2009 using the technique described for 2007. The foliar insecticide lambda-cyhalothrin at 28.0 g ([AI]/ha) (Warrior) was applied to to the aphid-free plots

on 10 August 2009 to prevent aphid infestation. Unlike 2007, four plants were randomly selected from each plot for aphid and injury evaluation on a weekly basis from 1 July 2009–24 September 2009. After each evaluation, CAD were calculated. Each plant was assigned a damage rating using the previously described 1–5 scale. Plant height, vegetative and reproductive stage were recorded each week.

Harvest was completed on 5 November 2009. Ten plants were randomly selected from each plot. Each soybean sample was wrapped in brown wrapping paper and stored for later processing as described for 2007.

2011 Field Study. Through seed increases, enough seed was accumulated by 2011 to conduct a study to measure tolerance in KS4202. Planting occurred on 3 June 2011 into conventional tilled corn residue in an Alcester-silt loam soil. We adopted the same standard agronomic practices described for 2007 and 2009 evaluations. As with 2009, experimental plots were not irrigated. Pursuit, Flexstar, and Select Max herbicides were used to control weeds.

Experimental design was a randomized complete block with four replications. Plots were 3.0 m in width (four rows) by 15.24 m in length with 76.2-cm (30-in.) row spacing. Four target treatments of cumulative aphid-days (CAD) at 0, 3,000, 8,000, and 13,000 were evaluated, with the addition of an untreated control (=maximum CAD). Unlike the 2007 and 2009 studies, aphid populations developed without artificial infestation. The foliar insecticide lambda-cyhalothrin at 28.0 g ([AI]/ha) (Warrior) was applied to all plots in a given threshold by using ground equipment once a target aphid threshold, in terms of CAD, was met (average across the blocks). In all cases, insecticide was applied within two days after counts were completed. Five plants were destructively sampled per plot at each sampling date to enumerate the total number of aphids per plant. Data were taken out of the center two rows of each plot. Harvest was completed on 4 October 2011. Yield was estimated by harvesting the entire middle two rows of each plot and adjusting seed moisture to 13%.

Statistical Analysis. Damage ratings, aphid numbers, and yield components were analyzed using mixed model analyses (PROC MIXED, SAS Institute 2002). When there was a significant treatment effect ($P \leq$

Table 1.   Mean damage ratings and mean number of soybean aphids per plant for field experiments in 2007

Genotype	Mean damage rating (15 Aug.)[a]	Mean damage rating (24 Aug.)[a]	Mean no. of aphids (15 Aug.)[b]	Cumulative aphid days (15 Aug.)	Mean number of aphids (24 Aug.)[b]	Cumulative aphid days (24 Aug.)
Asgrow	1.6	1.7	254.9b	1,833.6	156.0a	3,682.8
K-1639-2	1.4	1.3	25.5c	149.7	25.9b	376.6
Dowling	1.3	1.3	17.2c	132.8	40.2b	390.8
Jackson	1.3	1.6	18.3c	126.7	30.4b	346.1
K-1621	1.2	1.5	106.3bc	1,839.1	48.8b	2,537.3
KS4202	1.1	1.3	578.6a	7,121.7	251.2a	10,855.6

Means within columns followed by the same letter are not significantly different ($P > 0.05$), LSD test.

[a] Genotype*date interaction effect: $F = 0.5$; df = 5, 36; $P = 0.8$; genotype main effect: $F = 1.4$; df = 5, 36; $P = 0.24$; date main effect: $F = 1.9$; df = 1, 36; $P = 0.18$; standard error = 0.2 (calculated by Proc Mixed).

[b] Genotype*date interaction effect: $F = 2.9$; df = 5, 36; $P = 0.03$; standard error = 55.4 (calculated by Proc Mixed).
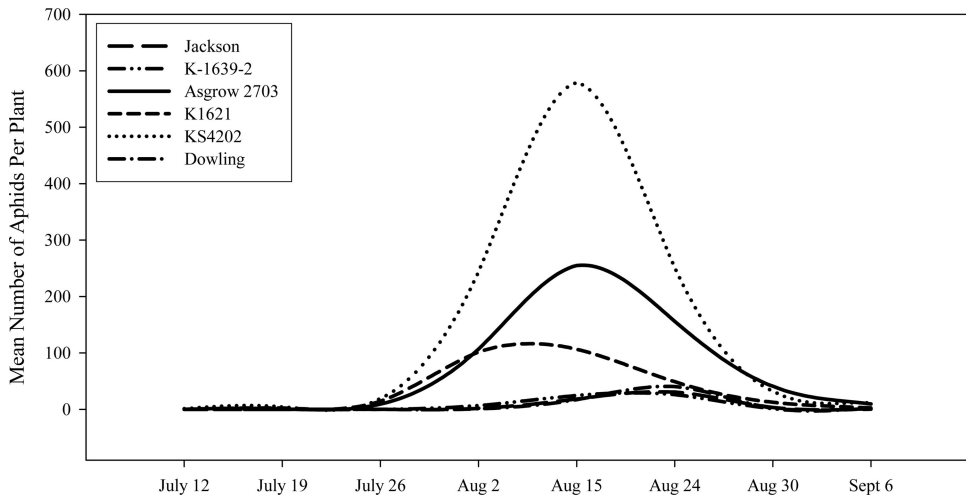
Fig. 1. Mean aphid numbers for each genotype during weekly counts in 2007.

0.05), means were separated using Fisher LSDs (LSD) procedures (**PROC MIXED, SAS** Institute 2002). Linear regression (**PROC REG, SAS** Institute 2002) was used to relate yield to CAD and percentage yield reduction to CAD in the 2011 field study.

Results and Discussion

Aphid Numbers 2007 and 2009. Overall aphid pressure was higher in 2009 than in 2007, and data for each year were analyzed separately. The current economic threshold for the soybean aphid on soybeans is 250 aphids per plant with populations increasing (Ragsdale et al. 2007). In 2007, most genotypes did not reach the economic threshold, let alone yield damaging levels. Genotype KS4202 was the only genotype to exceed the economic threshold and had more than twice as many aphids as Asgrow 2703 on 15 August 2007, the day of peak aphid population (Table 1; Fig. 1). In 2009, all genotypes exceeded the economic threshold, and KS4202 had the highest level of aphids throughout the season (Table 2; Fig. 2).

In 2007, KS4202 accumulated just under 12,000 CAD by 6 September, whereas Asgrow 2703 accumulated just under 4,500 CAD (Fig. 3). Genotype K-1621 had 2,537 CAD, whereas the remaining genotypes did not

even reach 1,000 CAD. Genotypes Jackson, Dowling, and K-1639–2 accumulated an average of 527.2 aphids per plant during the entire growing season, whereas KS4202 had an average of 578.6 aphids per plant on the peak aphid day of 15 August 2007 (Table 1; Figs. 1 and 3).

In 2009, all genotypes exceeded 15,000 CAD by 24 September (Fig. 4). Genotype KS4202 accumulated over 28,000 CAD during 2009, which was nearly double that of 2007 (Figs. 3 and 4), and nearly double that of Asgrow 2703, K-1621, and K-1639–2 in 2009 (Fig. 4). There were significant differences in mean aphid number between genotypes (Tables 1 and 2).

Damage Ratings 2007 and 2009. In 2007, damage ratings were fairly consistent from one week to the next. This is not surprising because aphid numbers were very low for most of the genotypes tested. KS4202 was the only genotype in 2007 to exceed the economic threshold and reach population levels where significant injury would be expected. Even though KS4202 had relatively high aphid numbers, it maintained the lowest damage ratings throughout the growing season (Table 1).

In 2009, damage ratings were higher for all infested genotypes when compared with 2007. Asgrow 2703, KS4202, and K-1621 soybean damage ratings remained

Table 2.   Mean damage ratings and mean number of soybean aphids per plant for field experiments in 2009

Genotype	Mean damage rating (27 Aug.)[a]	Mean damage rating (3 Sept.)[a]	Mean no. of aphids (27 Aug.)[b]	Cumulative aphid days (27 Aug.)	Mean no. of aphids (3 Sept.)[b]	Cumulative aphid days (3 Sept.)
Asgrow	2.1	2.0	621.5a	10,353.9	342.2ab	13,726.9
K-1639-2	2.9	3.5	617.5a	12,886.9	175.3a	15,661.8
K-1621	2.4	2.0	556.2a	11,556.1	204.4ab	14,217.8
KS4202	2.3	2.4	1,058.5b	18,903.1	488.6ab	24,317.9

Means within columns followed by the same letter are not significantly different ($P > 0.05$), LSD test.
[a] No significant date*genotype interaction ($P = 0.4524$); genotype main effect: $F = 5.6$; df = 3, 40; $P = 0.003$; date main effect: $F = 0.14$; df = 1, 40; $P = 0.7$; genotype standard error = 0.3 (calculated by Proc Mixed); date standard error = 0.2 (calculated by Proc Mixed).
[b] No significant date*genotype interaction ($P = 0.6618$); genotype main effect: $F = 4.5$; df = 3, 40; $P = 0.008$; date main effect: $F = 23.0$; df = 1, 40; P = <0.0001; standard error = 121.21 (calculated by Proc Mixed).
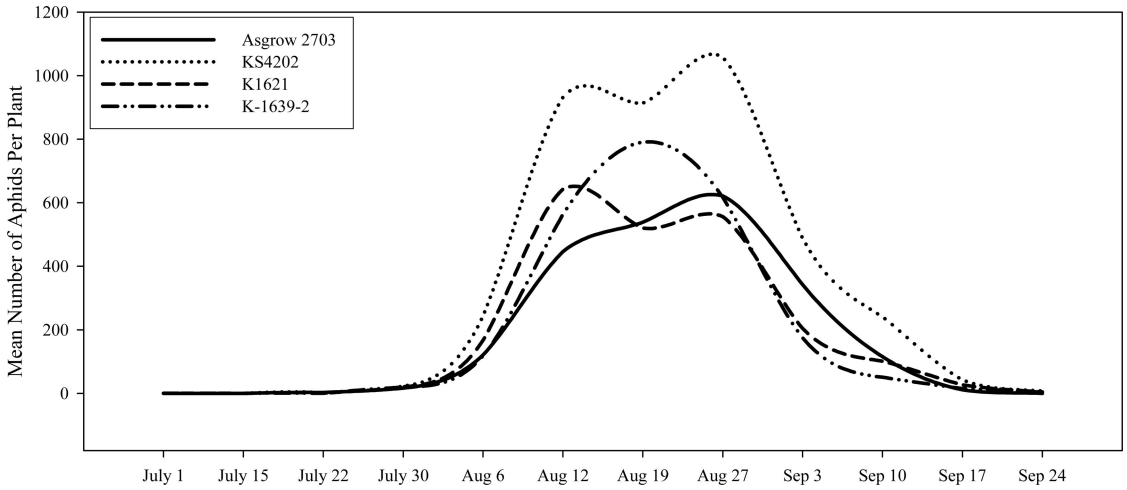
Fig. 2. Mean aphid numbers for each genotype during weekly counts in 2009.

fairly consistent or reduced from the week of peak aphid number to the next week (Table 2). Genotype K-1639–2 was the only genotype to have an increase in damage from the peak aphid week to the next week (Table 2).

Plant Stage 2007 and 2009. In 2007, aphids initially were observed in mid-July when the soybeans were in vegetative stages V5-V9. Aphid populations reached their peak in mid-August. For Dowling and Jackson, aphid peak occurred at stages V11-V17 with some plants entering the R1 stage (beginning bloom). The remaining genotypes all peaked in the reproductive stages with K-1639–2 peaking in reproductive stage R1, K-1621 peaking in R2, KS4202 peaking in R2-R3 (full bloom–beginning pod set), and Asgrow 2703 peaking in R4-R5 (full pod set–beginning seed set). Peak aphid populations occurred on 27 August 2009 with plant stages at R4-R6 for Asgrow 2703 and

KS4202, R2-R4 for K-1621, and R1-R2 and V9-V15 for genotype K-1639–2.

In 2007, aphids had little to no effect on plant development. Infested soybeans were generally in the same growing stages as their noninfested controls. In 2009, plant stages varied by as much as one reproductive stage.

Yield 2007 and 2009. In 2007, there were no significant differences between aphid infested and noninfested control treatments for each genotype for any of the yield parameters tested: total biomass, average seed weight and total seed weight, number of seeds per plant, number of pods per plant, or number of seeds per pod. This is not surprising because the genotypes did not reach economic injury levels (**EILs**), or indeed, exceed the economic threshold with the exception of KS4202. Genotype KS4202 did surpass the economic threshold and reached CAD levels where
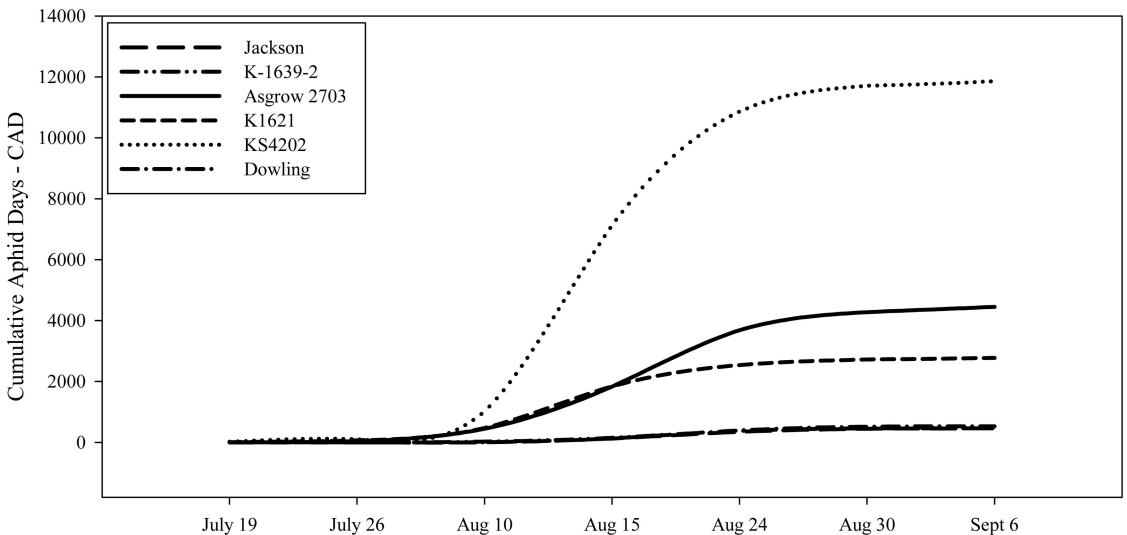

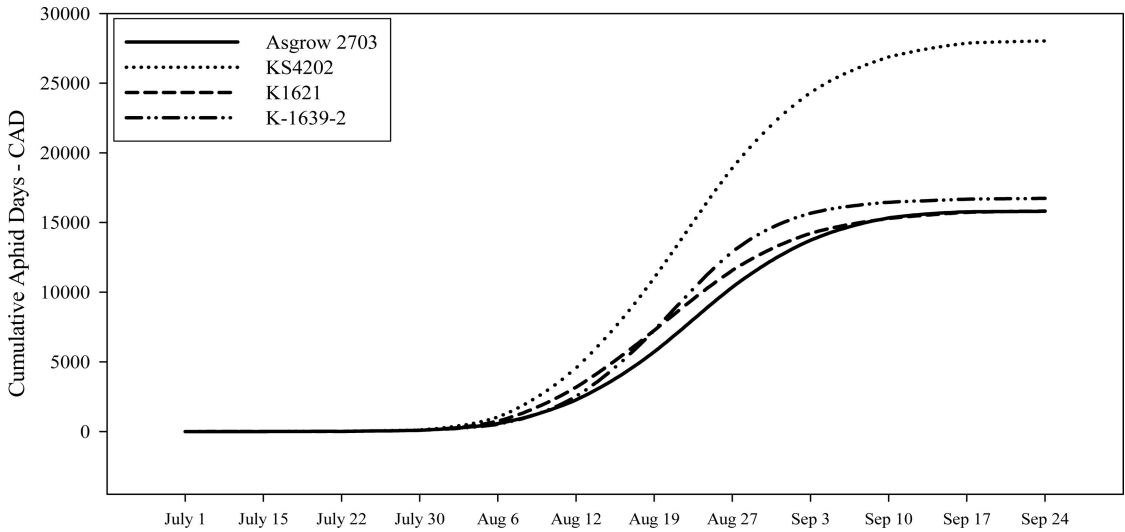**Fig. 3.** Cumulative aphid-days for each genotype in 2007.

Fig. 4. Cumulative aphid-days for each genotype in 2009.

yield loss would be expected, but there were no significant differences in yield parameters between the aphid infested and the aphid-free treatments.

Although aphid pressure reduced yield in 2009 (Figs. 2 and 4), results were similar to 2007. Most of the genotypes showed no significant differences in yield parameters except for a few yield parameters (Table 3). For KS4202, the average seed weight ($P = 0.0179$) and the average number of seeds per pod ($P = 0.0332$) for aphid infested treatments were significantly lower than their respective aphid-free treatments (Table 3). For K-1639–2, the number of pods per plant ($P = 0.0459$) and average number of seeds per pod ($P = 0.0453$) for aphid infested treatments were significantly lower than their respective noninfested controls (Table 3).

For KS4202, two of the six yield components were significantly different between control and infested plants in 2009, whereas in 2007, no significant differences were indicated. This could be because of the

difference in aphid numbers observed between the 2 yr. In 2007, the average number of aphids for KS4202 peaked at 578.6 aphids (Table 1; Fig. 1) with a CAD of nearly 12,000 by 6 September (Fig. 3), which is at a level where yield damage would be expected (Ragsdale et al. 2007). In 2009, the average peak number of aphids for KS4202 was nearly double that in 2007, reaching 1,058 aphids per plant (Table 2), and KS4202 accumulated nearly 28,000 CAD by 24 September (Fig. 4), which should easily result in significant yield loss. Similar patterns were also observed for the other genotypes (Tables 1 and 2). In 2009, the mean aphid numbers per plant were significantly higher for KS4202 when compared with the other genotypes. In fact, KS4202 had nearly twice as many aphids per plant than Asgrow 2703 (Fig. 2).

Field Evaluation of Tolerance. Actual CADs (CAD means) for target CAD treatments (0, 3,000, 8,000, 13,000, and untreated max CAD) were 164; 4,355;

Table 3. Yield parameters for soybeans grown in 2009

Genotype	Total plant biomass (g)			Average seed weight (g)		
	Aphid	No aphid	P value	Aphid	No aphid	P value[a]
Asgrow	13.70 ± 1.32	15.53 ± 1.32	0.3536	0.15 ± 0.00	0.16 ± 0.00	0.1874
KS4202	18.46 ± 2.53	22.41 ± 2.53	0.2948	0.13 ± 0.01	0.14 ± 0.01	0.0179
K-1621	23.60 ± 3.31	23.44 ± 3.31	0.9744	0.06 ± 0.00	0.06 ± 0.00	0.7984
K-1639-2	39.30 ± 8.39	55.87 ± 8.39	0.1924	0.02 ± 0.01	0.04 ± 0.02	0.2881
	No. of seeds/plant			No. of pods/plant		
Asgrow	54.83 ± 4.44	58.78 ± 4.44	0.5438	25.25 ± 1.86	26.12 ± 1.86	0.7483
KS4202	72.83 ± 10.50	81.87 ± 10.50	0.5566	35.58 ± 4.62	37.90 ± 4.62	0.7304
K-1621	128.82 ± 20.66	123.62 ± 20.66	0.8623	67.25 ± 9.31	67.41 ± 9.31	0.9910
K-1639-2	28.15 ± 33.04	116.69 ± 33.04	0.0874	77.11 ± 16.91	131.60 ± 16.91	0.0459
	Total seed weight/plant (g)			Average no. of seeds/pod		
Asgrow	8.42 ± 0.86	9.48 ± 0.86	0.4039	2.18 ± 0.05	2.25 ± 0.05	0.3499
KS4202	8.93 ± 1.29	11.52 ± 1.29	0.1840	2.00 ± 0.04	2.16 ± 0.04	0.0332
K-1621	8.29 ± 1.40	8.27 ± 1.40	0.9898	1.81 ± 0.10	1.70 ± 0.10	0.8323
K-1639-2	2.78 ± 3.11	9.05 ± 3.11	0.1844	0.15 ± 0.13	0.56 ± 0.13	0.0453

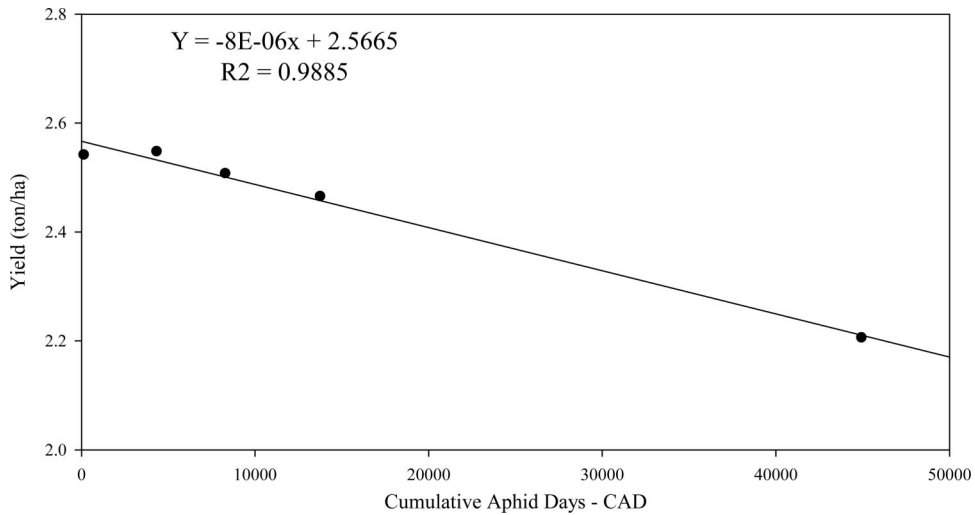[a] Significantly different at $P \leq 0.05$ by least significant difference.

Fig. 5. Relationship between cumulative aphid-days and KS4202 yield in 2011.

8,314; 13,777; and 44,959 (range, of 141–53,508 CAD), with mean yields of 2.54, 2.55, 2.51, 2.46, and 2.21 ton/ha, respectively. We used linear regression to relate CAD and KS4202 yield in different target CAD. Actual CAD was negatively correlated with yield ($F = 51.48$, df = 19, $P < 0.0056$, $R^2 = 0.9449$). However, the low yield loss for actual CAD treatments 164; 4,355; 8,314; 13,777 (≤ 0.08 ton/ha, or 3%), and the relatively low yield loss for 44,959 CAD (0.33 ton/ha, or 13%) indicates that KS4202 has tolerance to soybean aphid feeding (Fig. 5). These findings are consistent with results from field evaluations conducted by Pierson et al. (2010) that reported no significant differences in average seed weight or number of seeds per pod between the infested and control KS4202 plants.

We also used linear regression to relate CAD and KS4202 percentage yield losses in different target aphid densities. The actual CAD values for 2011 were positively correlated with percentage yield loss ($F = 257.28$, df = 19, $P < 0.0005$, $R^2 = 0.9885$). Field studies completed by Ragsdale et al. (2007) assessed fourteen commercial soybean varieties in six U.S. states (including Nebraska), to determine the economic threshold and EIL. In general, yield (tons per hectare) was reduced by 6.88% for every 10,000 CAD. Nevertheless, in this study, the untreated control had an average of 44,959 CAD and a yield loss of ≈13% (Fig. 6), when we would have expected a yield loss of 24–36% (Ragsdale et al. 2007). These results confirm the tolerance response in KS4202.

Implications. Based on our results, genotypes may compensate for aphid feeding in different ways. When aphid numbers are high, KS4202 appears to tolerate severe aphid feeding without the expected severe
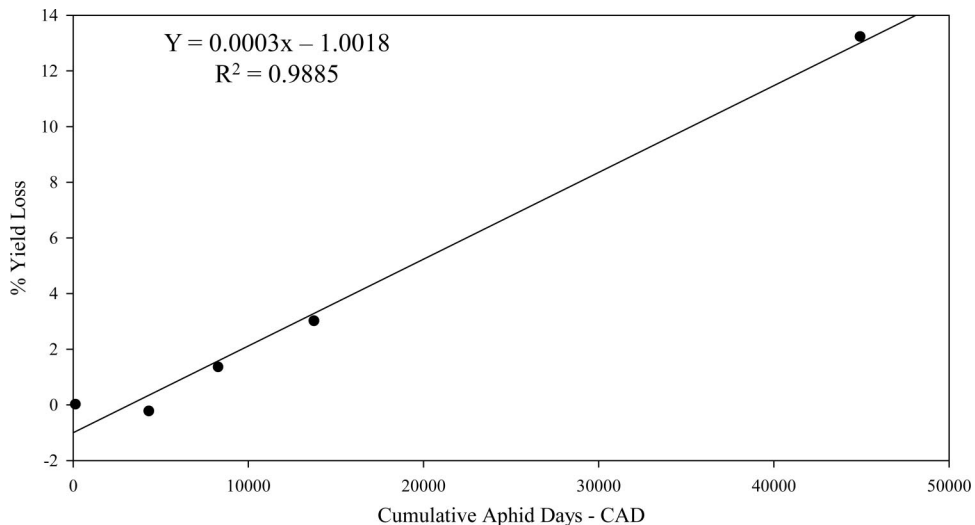

Fig. 6. Relationship between cumulative aphid-days and KS4202 percentage yield loss in 2011.

impact on yield. Further studies are necessary to fully describe the plant compensation for aphid feeding in KS4202. Asgrow 2703 appears to produce a similar number of seeds as its noninfested counterpart, although the seeds produced are slightly smaller. Genotype K-1621 tends to keep aphid numbers at moderate levels without allowing the aphid feeding to significantly reduce yield. Genotypes K-1639–2, Dowling, and Jackson appear to hinder aphid numbers by keeping them low; however, whether these genotypes are using antibiosis, antixenosis, or both to hold aphid populations down remains unclear. K-1639–2 may show some level of resistance, but that did not protect yield. The average number of pods per plant and the average number of seeds per pod were significantly lower when compared with the control (Table 3).

It is clear from the three field seasons that KS4202 is compensating for aphid feeding. Similar mechanisms of compensation are not only found in soybeans, but are common in other plant–insects systems as well. Resource reallocation is common in plants with insect herbivory. Some of the common methods to reallocate resources include mechanisms like tiller production, an increase or decrease in seed production, increased branching, smaller seed development, increased flowering, larger leaves, delayed senescence, and many others. Many of the mechanisms are often dependent on stress factors such as plant competition, water stress, interactions of nutrients, root damage, air pollution, and timing of defoliation (Morton and Watson 1948, Dixon 1971, Dyer and Bokhari 1976, Satoh et al. 1977, Inouye 1982, Kolodny-Hirsch and Harrison 1982, Lechowicz 1987, Benner 1988; Hendrix and Trapp 1989, Wisdom et al. 1989, Deregibus and Trlica 1990, Doak 1991, Reichman and Smith 1991, Swank and Oechel 1991, Trumble et al. 1993).

The results of this study support the findings by Pierson et al. (2010) and add evidence that KS4202 shows tolerance to soybean aphid feeding. The results from 2007 to 2011 indicate that KS4202 can support aphid populations without the significant and severe yield losses that would normally be expected (Ragsdale et al. 2007). The common Nebraska cultivar, Asgrow 2703, appears to show signs of tolerance as well. None of the yield parameters were significantly different between the aphid infested and noninfested treatments. Although not significantly different, seeds that were produced appeared slightly smaller, even in the 2009 field study where aphid numbers were high. Future studies should continue to focus on gaining a better understanding of the compensation mechanism exhibited by KS4202 and Asgrow 2703 in response to aphid feeding.

Acknowledgments

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