

Effect of Soil Potassium Availability on Soybean Aphid (Hemiptera: Aphididae) Population Dynamics and Soybean Yield

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ABSTRACT Studies were conducted to examine the effect of potassium (K) on soybean aphid, *Aphis glycines* Matsumura, population growth. A laboratory feeding assay examined the effect of K-deficient foliage on life table parameters of soybean aphids, and field experiments were designed to determine the effect of three soil K treatment levels on aphid populations and their impact on soybean yields. The feeding assay found that life table parameters differed between aphids feeding on the K-deficient and nondeficient soybean leaves. Soybean aphids in the K-deficient treatment exhibited significantly greater intrinsic rate of increase (r_m), finite rate of increase (λ), and net reproductive rate (R_o) relative to aphids feeding on nondeficient leaves. No significant difference was observed in mean generation time (T) between the two treatments. However, the field experiment repeated over 2 yr showed no effect of K on soybean aphid populations. Soybean aphid populations were high in unsprayed plots and feeding resulted in significant yield losses in 2002 at all three K treatment levels: when averaged across 2001 and 2002, unsprayed treatments yielded 22, 18, and 19.5% less than the sprayed plots in the low, medium, and high K treatments, respectively. No significant interaction was observed between aphid abundance and K level on soybean yields in either year. This study therefore suggests that although aphids can perform better on K-deficient plants, aphid abundance in the field may be dependent on additional factors, such as dispersal, that may affect final densities within plots.

KEY WORDS *Aphis glycines*, soybean, life table, potassium deficiency

SOYBEAN APHID, *Aphis glycines* Matsumura, is native to much of eastern and southeastern Asia where it is a common perennial pest of soybean (Wang et al. 1962, 1994). The first documented observations of soybean aphids in Wisconsin and neighboring states were made during the 2000 growing season (Macedo et al. 2003). The soybean aphid has emerged as a major insect pest of soybean grown throughout north central United States (Ragsdale et al. 2004). Many commercial soybean fields have exhibited high soybean aphid populations and feeding damage has been widely reported.

Soybean aphid feeding on soybean can result in a reduction in photosynthetic capacity (Macedo et al. 2003) as well as cause leaf curling and stunted plant growth (Chung et al. 1980). Yield losses reported in literature from China routinely reach 20–30% (Dai and Fan 1991). Similarly, University of Wisconsin field trials have demonstrated yield losses resulting from aphid feeding can reach 1075 kg/ha (Grau et al. 2002). The result to the soybean producer is lost income due to yield reductions and/or increased cost of produc-

tion as insecticide applications are often warranted to control soybean aphid populations.

Since its appearance in Wisconsin, field observations of heavy soybean aphid infestations have suggested a potential link between potassium (K) deficiency in soybean and high aphid numbers. On-farm visits in 2000, indicated that many of the soybean fields most heavily infested with soybean aphids also were exhibiting symptoms of K deficiency (J.L.W., unpublished data). This observation generated concern among soybean growers that potassium deficiency could exacerbate soybean aphid problems and the resulting impact on soybean yields. Increased performance by aphids on K-deficient plants also has been documented on other crops. Havlickova and Smetankova (1998) demonstrated that barley grown in K-deficient soils were more suitable for bird-cherry oat aphid, *Rhopalosiphum padi* (L.), than were plants grown with an adequate K supply. Similarly, Marwat et al. (1985) found that cabbage aphid, *Brevicoryne brassicae* (L.) densities on sarsoon, *Brassica* spp., were negatively correlated with soil K levels. Thus, the potential exists for increasing aphid pressure on K-deficient plants.

The objectives of this study were to 1) evaluate the performance of aphids feeding on K-deficient and

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non-K-deficient soybean foliage, 2) examine the effect of variation of soil and soybean leaf K on soybean aphids under field conditions, and 3) to quantify the consequences for soybean yields. Gaining a better understanding of the relationship between soil fertility, plant nutrition, and insect pest management will be critical for developing aphid control recommendations for soybean growers, crop consultants, and pest managers. This study examines whether soybean pests and soil fertility issues can be viewed as independent management decisions or whether they interact and need to be considered in tandem.

Materials and Methods

Laboratory Cohort Life Table Experiment. Laboratory experiments were conducted to evaluate the performance of *A. glycines* on K-deficient and healthy soybean leaf material. Within a field at the University of Wisconsin Arlington Agricultural Research Station (ARS) (Columbia County, 43° 17.79 N, 89° 23.12 W), leaves were collected from soybean plants within two "treatment" categories to be fed to aphids: 1) plants showing K-deficient symptoms (yellowing at margins, stunted appearance), and 2) leaves from plants with normal or healthy appearance. Leaf material was collected from the same treatments on three dates (15, 21, and 24 July 2003) for K content analysis. Five trifoliates were removed from the upper portion of the soybean plant in each treatment per sampling date for these assays. A portable ion meter (Horriba Instruments U.S. Inc., Irvine, CA; $\pm 10\%$ measurement accuracy) was used to quantify the K levels in leaf tissue sap for both treatments. Additionally a single composite soil sample and a leaf tissue sample consisting of five trifoliates was taken from both treatments on 21 July and analyzed for K content by the University of Wisconsin Soil and Plant Analysis Laboratory (Madison, WI) (Liegel et al. 1980).

Soybean aphids used in this experiment were the progeny of field-collected aphids from soybean plants grown at the Arlington ARS in 2003. Soybean foliage infested with soybean aphids was taken from a soybean field with adequate soil fertility on 14 July 2003. Adult aphids were monitored for production of offspring, and the neonate aphids produced were used in this life table experiment. Neonate aphids (<24 h old) were placed individually on leaves from the each of two treatments ($n = 10$ replicates each), and aphids were maintained in 9.0-cm petri dishes with a double layer of moistened 9.0-cm-diameter filter paper (Fisher Co., Bridgewater, NJ). Distilled water was added daily to keep the filter paper disks saturated. Petri dishes were closed with lids and stacked to maintain high relative humidity inside the dish and to help prevent desiccation of leaf material. Petri dishes containing leaves and aphids were placed in an insect-rearing chamber at a constant temperature of 22°C and a photoperiod of 16:8 (L:D) h. The petri dishes were removed from the growth chamber at 24-h intervals so that aphid growth stages (nymphs versus adults), survivorship, and number of offspring could be recorded.

After nymphs molted to adults, daily fecundity of each female was determined, and offspring were removed from the petri dishes daily. Aphids were carefully transferred to freshly collected leaves from the two treatments three times weekly.

Life table statistics were calculated for the aphid cohorts reared on the two K treatments by using PopTools 2.5 (Hood 2003). The intrinsic rate of increase (r_m), net reproductive rate (R_0), and mean generation time (T) were calculated for the populations in both treatments. Randomization tests (Monte Carlo analysis, 1000 iterations) were performed (Hood 2003) to determine statistical significance between the life table parameters calculated on the two K treatments and jackknife estimates of parameters were used to construct 95% confidence intervals (Meyer et al. 1986).

Field K Manipulation Experiment. Small plot field experiments were established at the University of Wisconsin Arlington ARS during the 2001 and 2002 growing seasons. Two fields were used in this study and were planted with corn during the previous growing season on Plano silt loam soil (Typic Argiudoll). The soybean variety used in this experiment was Asgrow 2001 RR (glyphosate resistant). Soybean was planted on 10 May 2001, and on 9 June 2002, in 0.76-m (30-in.) rows at a rate of $\approx 328,700$ plants per hectare. Individual plots measured 3.05 m (four rows) by 6.71 m (22 feet). Both corn and soybean were grown using a no-tillage production system.

The fields used for this experiment contained plots with three potassium soil test K levels (high, medium, and low). Potassium treatments were established for a previous study using three rates of K fertilizer applied as a surface broadcast application of KCl. Potassium fertilizer applications were made from 1998 to 2000, but they were not continued when these fields were used in this experiment. The fertilizer applications consisted of a low K treatment (no K application), a medium K treatment of 46 kg/ha K applied annually equivalent to a 1 \times crop grain removal rate, and a high K treatment of 92 kg/ha K applied annually equivalent to a 2 \times crop grain removal rate. Crop removal rates were based on a soybean yield of 3360 kg/ha removing 56 kg K/ha annually (Kelling et al. 1998).

An insecticide spray treatment also was established to test for aphid effects on yields.

Aphid populations were allowed to develop undisturbed in the unsprayed treatments, whereas insecticide applications were made on sprayed treatments when aphids were first observed in the field, and at 7–10-d intervals thereafter. Insecticides were applied as a foliar spray using a carbon dioxide (CO₂) powered backpack sprayer at 2.81 kgf/cm² (40 psi) and spray volume of 93.5 liters/ha. Applications of Warrior (λ -cyhalothrin) were made at a rate of 33.6 g (AI)/ha. Insecticides were applied on 10, 15, 27, and 31 July and 9 August in 2001; and on 17, 23, and 30 July and 6 August in 2002. Thus, the experimental design consisted of three soil test K levels crossed with two spray treatments (sprayed and unsprayed) in a randomized complete block design with six treatments per block.

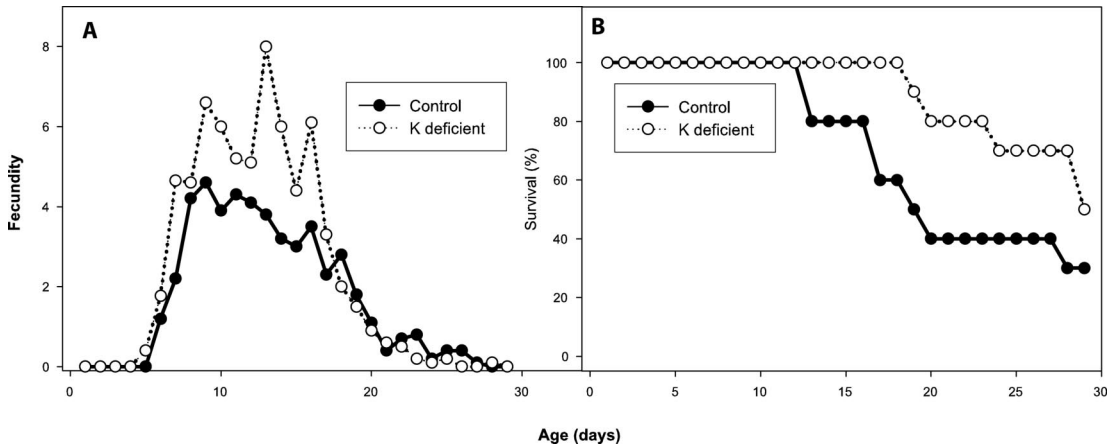


Fig. 1. Soybean aphid fecundity (A) and survivorship (B) on K-deficient and control (adequate K) treatments.

Four and six replications were used in 2001 and 2002, respectively.

Aphid populations were sampled in treatment plots during both years. Aphid counts and soybean yield estimates were taken from the middle two rows of each plot, with individual plots separated by at least 2 m. Aphid counts were taken on three dates in 2001: 11 and 25 July and 1 August, and in 2002, sampling was expanded to five dates: 18, 24, and 31 July, and 7 and 16 August. The aphid sampling protocol differed for the 2 yr of this experiment. Aphid counts in 2001 were based on a 0–6 rating scale: 0, no aphids were found on a plant; 1, 1–10 aphids/plant; 2, 11–25 aphids/plant; 3, 26–50 aphids/plant; 4, 51–100 aphids/plant; 5, 101–200 aphids/plant; and 6, >200 aphids/plant. An average rating for each plot was calculated based on 20 plants. Actual numbers of aphids per plant were estimated in 2002 (average of 10 plants per plot) on all sampling dates.

Soil and leaf tissue samples were taken on 10 July 2001 and 8 July 2002 to quantify the K soil test level in the field and plant tissue for the three K treatments (high, medium, and low). Soil samples were taken from each plot by combining 10 core samples composed of $\approx 500 \text{ cm}^3$ of soil each and mixing them together in a bucket. A composite sample (also $\approx 500 \text{ cm}^3$) was then taken from the soil mixture from each plot. Leaf tissue samples were taken according to the protocol outlined by the UW-Soil and Plant Analysis Laboratory. The fourth petiole and trifoliolate were removed from 20 R1 stage plants in each plot. Leaf tissue and soil samples were analyzed by the UW-Soil

and Plant Analysis Laboratory. The center two rows of each plot were harvested using a two-row plot combine reported grain yields were adjusted to 13% moisture.

A two-factor analysis of variance (ANOVA) was used to evaluate the effects of K and spray treatments on K data (soil and leaf tissue, separately) using a mixed model (random block effects, PROC MIXED, SAS Institute 1990). Aphid sampling counts were analyzed as a repeated measures factorial design (PROC MIXED). Block and block by spray treatment by K treatment were entered into the model as random effects, and block by spray treatment by K treatment was entered as the within subject (repeated) effect. The within-subjects covariance was modeled using the first-order autoregressive [ar(1)] structure. Comparisons among treatment means were made using the least-squares mean method with a Dunn-Šidák (Ury 1976) adjustment of type I error rates (family-wide $\alpha = 0.05$).

Results

Laboratory Cohort Life Table Experiment

Field-Collected Soybean Leaves. Potassium levels (sap-extracted measured on handheld meter) of field-collected soybean leaves used in the aphid life table study were over twice as high in the control treatments (i.e., healthy plants $2,493 \pm 249 \text{ ppm}$) compared with K-deficient treatment plants ($1,004 \pm 100 \text{ ppm}$) for the three sample dates combined ($n = 15, t = 5.01,$

Table 1. Comparison of life table parameters between soybean aphids on healthy (control) and K-deficient soybean foliage

	<i>n</i>	λ (95%CI)	r_m (95% CI)	R_0 (95% CI)	T (95% CI)
Control	10	1.514 (1.491, 1.535)	0.415 (0.399, 0.428)	49.00 (42.78, 54.44)	7.66 (7.52, 7.88)
K-deficient	10	1.611 (1.591, 1.619)	0.477 (0.464, 0.482)	68.22 (65.72, 70.91)	7.09 (7.00, 7.39)
<i>P</i> value		0.0020	0.0020	0.0121	0.8652

n, number of females used in the analysis, λ , discrete rate of population increase, r_m , intrinsic rate of increase, R_0 , net reproductive rate, T, mean generation time. 95% CI, 95% confidence intervals constructed using jackknife estimates of parameters. *P* values comparisons are for within column mean comparisons ($P < 0.05$ was considered statistically significant).

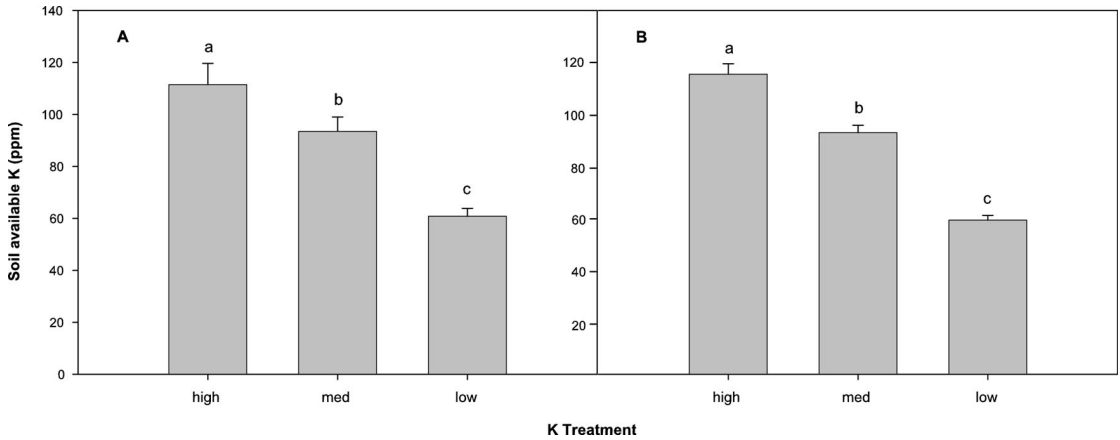


Fig. 2. Soil available K (mean \pm SEM) in soybean fields sampled in 2001 ($n = 8$) (A) and 2002 ($n = 12$) (B) with three fertility treatments. Means with the same letter do not differ significantly at the $P < 0.05$ level.

$P < 0.0001$, no date by treatment interaction). Leaf samples taken on 21 July and analyzed by the Soil and Plant Analysis Laboratory corroborated these results. Total leaf dry matter K content was 0.55 and 1.58%, whereas soil K measured 60 and 160 ppm for the K-deficient and control treatments, respectively.

Development and Survivorship. Aphids developing on K-stressed soybean performed significantly better than those on healthy soybean leaves. Aphids in both treatments reached adulthood at approximately the same time (5 d), and the majority of aphids in both treatments began producing nymphs within 24 h after reaching adulthood (Fig. 1A). However, aphids on K-deficient leaves produced significantly higher mean total number of nymphs than those on control treatments (Fig. 1A), yielding a 39% higher net reproductive rate (Table 1, R_0). Measurements of aphid population increase r_m (intrinsic rate of increase) and λ (finite rate of increase) were 15 and 6% significantly greater, respectively, in the K-deficient treatment. No

significant difference was observed in mean generation time (T) between the two treatments (Table 1).

Field K Manipulation Experiment

Soil and Leaf Tissue Analysis. Soil and leaf tissue level comparisons among K treatments were neither affected by spray treatment (leaf K 2001: $df = 1, 3; F = 1.10; P = 0.310$; soil K 2001: $df = 1, 3; F = 1.44; P = 0.248$; leaf K 2002: $df = 1, 5; F = 0.04; P = 0.838$; soil K 2002: $df = 1, 5; F = 0.09; P = 0.764$) nor spray by K treatment interaction (leaf K 2001: $df = 2, 3; F = 0.01; P = 0.986$; soil K 2001: $df = 2, 3; F = 3.12; P = 0.073$; leaf K 2002: $df = 2, 5; F = 0.64; P = 0.537$; soil 2002: $df = 2, 5; F = 0.73; P = 0.493$). Significant differences in both soil available K (Fig. 2, 2001: $df = 2, 5; F = 47.34; P < 0.001$; 2002: $df = 2, 5; F = 109.91; P < 0.001$) and leaf tissue K (Fig. 3; $df = 2, 3; F = 29.24; P < 0.001$; 2002, $df = 2, 5; F = 82.99; P < 0.001$) were measured among the three K treatment levels in both years of this study. Soil and leaf

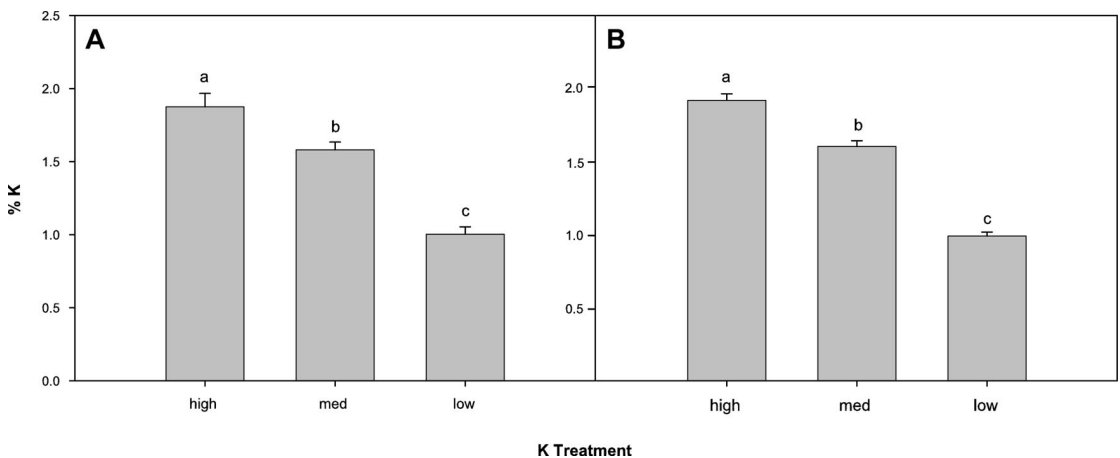


Fig. 3. Leaf tissue K (mean \pm SEM) in soybean fields sampled in (A) 2001 ($n = 8$) and (B) 2002 ($n = 12$) with three fertility treatments. Means with the same letter do not differ significantly at the $P < 0.05$ level for sprayed and unsprayed treatments separately.

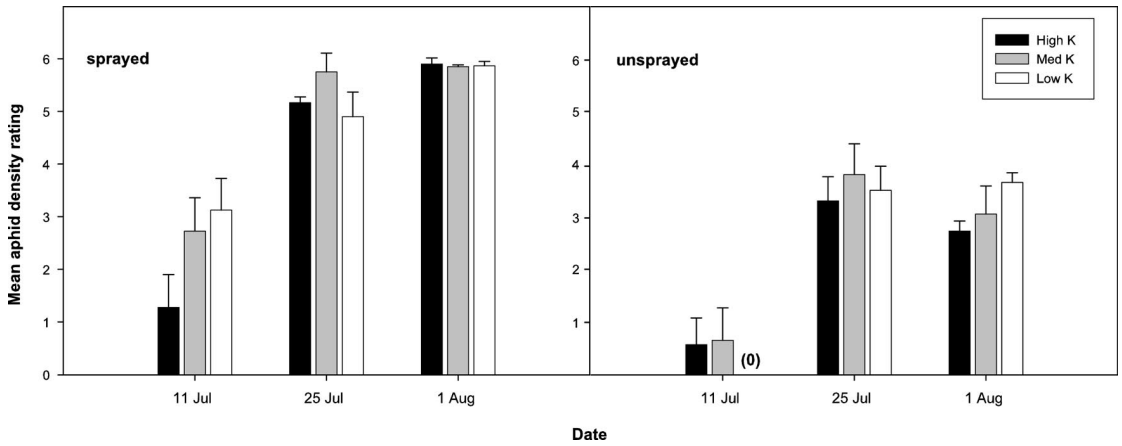


Fig. 4. Soybean aphid numbers per plant based on density ratings during the 2001 growing season (mean ± SEM, n = 4). Ratings were 0, 0; 1, 1–10; 2, 11–25; 3, 26–50; 4, 51–100; 5, 101–200; and 6, 200+ aphids per plant.

tissue K was highest in the high K treatment plots and lowest in the low K plots (Figs. 2 and 3).

Aphid Sampling. Multiple foliar insecticide applications (spray treatments) were effective at reducing aphid numbers yet they did not completely eliminate aphids in either year (Figs. 4 and 5; Table 2, significant spray effect). In contrast, aphid populations in the unsprayed treatments increased rapidly on soybean plants (Table 2, significant date by spray interaction) in all three K treatments in both years reaching peak numbers during late July to early August (Figs. 4 and 5). However, neither K treatment nor spray by K treatment had a significant effect on aphid densities in either 2001 or 2002 (Figs. 4 and 5; Table 2).

Soybean Yields

During the 2001 growing season, both spray (Fig. 6A; df = 1, 3; F = 14.00; P < 0.001) and K treatment (df = 2, 3; F = 6.79; P < 0.001) had a significant effect on harvested grain yields (no spray by K interaction: df = 2, 3; F = 0.33; P = 0.724). Soybean yield tended

to decrease in both K limited and unsprayed treatments (Fig. 6A). On average soybean yields in low K treatments was significantly lower (2,493.2 kg/ha) than the high K treatment (3,247.4 kg/ha). Sprayed treatments yielded ≈20.5% more than their unsprayed counterparts (2,622.3 kg/ha versus 3,299.8 kg/ha).

The effect of spray and K treatments on yield in 2002 were similar to the patterns found in 2001 in that both spray (Fig. 6B; df = 1, 5; F = 35.15; P < 0.001) and K treatment (df = 2, 5; F = 136.88; P < 0.001) effects were significant (no spray by K interaction: df = 2, 5; F = 0.29; P = 0.753). In 2002, yield differences attributable to K deficiency were significant among each of the three K levels. Additionally, on average insecticide treated plots yielded 18.2% more than the corresponding unsprayed treatments (Fig. 6B, 2,581.7 versus 2,113.1 kg/ha).

Discussion

Results from our laboratory experiments showed that soybean aphid populations feeding on K-deficient

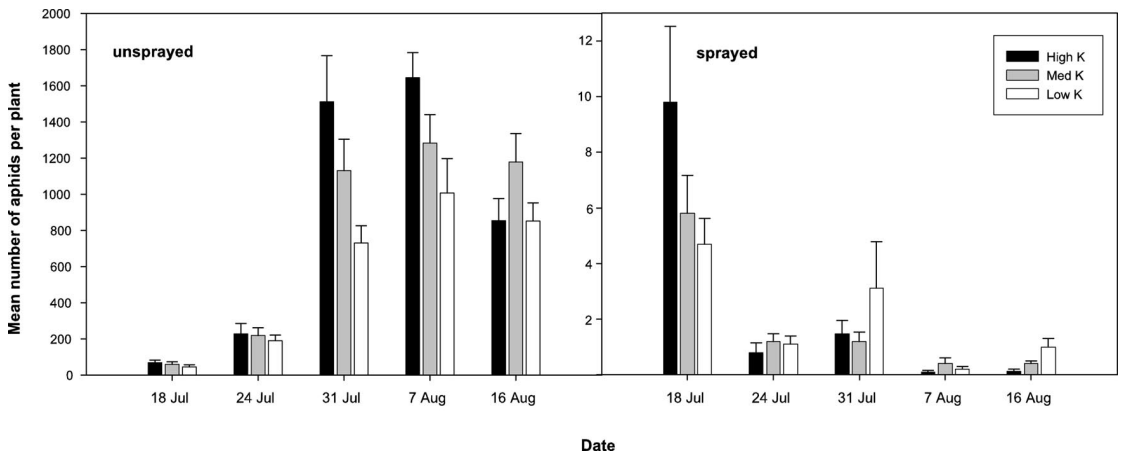


Fig. 5. Soybean aphid numbers per plant during the 2002 growing season (mean ± SEM, n = 6).

Table 2. Repeated measures ANOVA results for mixed model analysis for the fixed effects of Spray treatment, K treatment, date, and their interactions on soybean aphid numbers per plant in 2001 and 2002

Yr/source	df	ddf	F	P value
2001				
Spray treatment	1	15	78.83	<0.0001
K treatment	2	15	1.30	0.3004
Spray by K	2	15	1.10	0.3590
Date	2	36	129.98	<0.0001
Spray by date	2	36	3.79	0.0320
K by date	4	36	2.22	0.0865
Spray by K by date	4	36	0.57	0.6830
Covariance parameter estimates: block by spray by K = 0.3385, residual = 0.7137				
2002				
Spray treatment	1	25	678.93	<0.0001
K treatment	2	25	0.14	0.4564
Spray by K	2	25	0.30	0.4545
Date	4	120	57.10	<0.0001
Spray by date	4	120	149.06	<0.0001
K by date	8	120	1.55	0.4479
Spray by K by date	8	120	0.95	0.4354
Covariance parameter estimates: block by spray by K < 0.0001, residual < 0.0001				

soybean grew significantly more rapidly than those feeding on normal soybean. This response was primarily due to the substantially higher fecundity and greater survivorship of aphids feeding on K-deficient foliage (Fig. 1A). These results suggest that there may be nutritional differences between K-deficient and nondeficient soybean that influence soybean aphid population growth. The physiological basis for this effect is not well understood; however, important biochemical steps in protein synthesis are in part dependent on potassium, and deficiencies in K may lead to increased free amino-acid concentrations in soybean plant tissues (Marschner 1995).

Aphids and other phloem-feeding herbivores are known to be sensitive to variation in leaf N whereby

higher N results in increased insect developmental rates and higher fecundity (Awmack and Leather 2002). Honek (1991) showed that increasing the N supply to wheat and barley increased the performance of *Metopolophium dirhodum*. Janssen and Smilowitz (1986) showed that intrinsic rate of increase (*r*) of green peach aphid, *Myzus persicae* (Sulzer), is positively correlated with the concentration of free amino acids, and Cisneros and Godfrey (2001) found that increased N applied as fertilizer resulting in elevated leaf nitrate levels increased populations of cotton aphid, *Aphis gossypii* Glover on cotton. Thus, K-stressed soybean plants may positively affect aphid performance by enhancing N availability to these N-limited herbivores.

Despite the rapid-growth potential of soybean aphids on K-deficient leaves in the laboratory, we did not observe greater aphid populations on K-stressed soybean in the field (Figs. 4–5). The lack of aphid population response to K treatments occurred despite the fact that the K treatments established in this study resulted in soil K levels that current soil testing recommendations (Kelling et al. 1998) classify as high (101–120 ppm), optimum (81–100 ppm), and low (50–80 ppm) (Fig. 2). Leaf tissue recommendations (Schulte and Kelling 1999) classify leaf tissue analysis taken from high, medium, and low K treatments as sufficient, low, and deficient.

Aphid sampling data from both 2001 and 2002 failed to show any statistical differences between aphid populations in the three K treatments. The sampling protocol used in 2001 did not accurately reflect the total numbers of aphids per plant once aphid densities eclipsed 200 per plant. Field observations indicated that aphid populations were substantially higher than 200 per plant on the final two sampling dates. The sampling protocol used in 2002 provided a more accurate assessment of the soybean aphid populations in the experiment. Nevertheless, even with more accu-

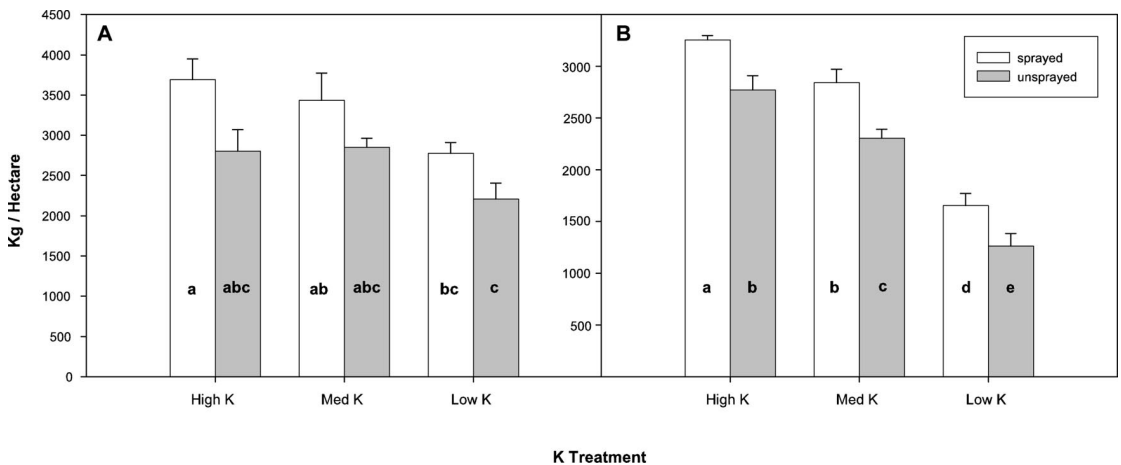


Fig. 6. Soybean grain yields (mean ± SEM) harvested in 2001 (*n* = 4) (A) and 2002 (*n* = 6) (B) with three fertility treatments. Means with the same letter do not differ significantly at the *P* < 0.05 level for comparisons made separately by year.

rate estimates of high aphid densities, we found no differences among K treatments.

Although our small plots did not show greater aphid populations on K-deficient plots, aphid densities observed in both years of this experiment were unusually high compared with other fields in the area. Most notably, soybean aphid numbers recorded in this experiment in 2002 (peak abundance in unsprayed plots 1,644 aphids per plant) far outnumbered aphid population densities observed in other fields surveyed throughout southern Wisconsin (average peak abundance 282 aphids per plant, $n = 5$ fields; S.W.M., unpublished data). This suggests that K deficiency within our small plots in this field contributed to the overall high soybean aphid populations that were observed. A possible mechanism for this is that soybean aphids were attracted to the leaf yellowing exhibited by K-stressed soybean. Yellow has been shown to be attractive for some aphid species (Eastop 1955) and can promote aphid colonization of plants (Havlickova and Smetankova 1998, Liburd et al. 1998). If aphids are attracted to the leaf yellowing symptoms of the K-deficient plants early, aphid migrants may initially prefer to colonize these plants and then spread throughout the field. Although our sampling results did not detect this trend, it may be that the small plots used for individual treatments in this experiment were not large enough (3.05 by 6.71 m) or were not separated by a large enough distance (0.76–1.0 m) from one another to detect differential colonization of aphids into K-deficient plots. Additionally, if aphid performance increases on K-deficient soybean, as the life table study demonstrates, K-deficient treatments may have provided a source for aphids for nearby non-K-deficient plots. Thus, the individual plot size used in this study may have hindered our ability to detect aphid population differences between soil and leaf K levels that were clearly established in the field.

Grain yield data indicated that both a lack of K and heavy infestations of soybean aphid infestations are capable of causing significant yield losses. However, there was no significant spray by K interaction on soybean yield, indicating that, at least in small plots, the combined effects of K deficiency and soybean aphid feeding do not act synergistically in reducing yield. Aphid densities in the unsprayed treatments reduced soybean yield by $\approx 19\%$, and soybean grown on soils that are deemed K-deficient (low K treatment) decrease soybean yield by an additional 32% compared with optimum K treatments.

So although it is clear that soybean aphid feeding and K stress both serve to impact soybean yield, it remains unclear whether K-deficient soybean plants promote soybean aphid outbreaks in the field. The life table study suggests that K deficiency may provide an advantage, perhaps a nutritional benefit to soybean aphid populations, allowing for increased reproductive rates. Additional work is needed to determine the mechanistic effect of K on soybean aphid reproduction as well as the impact of K on aphid populations on a larger spatial scale.

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