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Source: Journal of Economic Entomology, 114(2) : 757-768

Published By: Entomological Society of America

URL: <https://doi.org/10.1093/jee/toab013>

# Evaluating Sugarcane Aphid, *Melanaphis sacchari* (Hemiptera: Aphididae), Population Dynamics, Feeding Injury, and Grain Yield Among Commercial Sorghum Varieties in Alabama

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Subject Editor: Kristopher Giles

Received 2 June 2020; Editorial decision 11 January 2021

## Abstract

The sugarcane aphid, *Melanaphis sacchari* (Zehntner), emerged as a severe pest of sorghum, *Sorghum bicolor* (L.), in Texas and Louisiana in 2013 and currently threatens nearly all sorghum production in the United States. Proper management of populations is critical as sugarcane aphid has a high reproductive potential and can rapidly damage plants, resulting in extensive yield losses. The overall objective of this work was to investigate sugarcane aphid population dynamics, and subsequent sorghum injury and grain yield on commercially available grain sorghum varieties in Alabama. This research includes three-site years of data that show variation in plant injury, physiological maturity, and yields among varieties tested. Although performance of each variety was variable among locations, potentially due to abiotic factors, four varieties including DKS 37-07, 1G588, 1G855, and 83P17 exhibited characteristics consistent with resistance and corroborates reports of resistance from other states.

**Key words:** sugarcane aphid, sorghum, varieties, host plant resistance

The sugarcane aphid, *Melanaphis sacchari* (Zehntner), is a cosmopolitan pest whose distribution closely follows that of sugarcane, *Saccharum officinarum* (L.), and sorghum, *Sorghum bicolor* (L.), production (Singh et al. 2004). The sugarcane aphid was first introduced to the continental United States in Florida in 1977 (Mead 1978) and eventually established as a minor pest of sugarcane (Mondor et al. 2006). In 2013 (Villanueva et al. 2014), a newly identified sugarcane aphid haplotype (Harris-Shultz et al. 2017; Medina et al. 2017; Nibouche et al. 2014, 2018) emerged as a major pest of grain sorghum for the first time in Texas, Louisiana, and Mexico (Bowling et al. 2016a). Within 2 yr, the new 2013 haplotype had spread to nearly all (≥98%) sorghum production regions in the United States, the world's largest producer of grain sorghum (Bowling et al. 2016a, USDA NASS 2016). Phloem feeding stresses plants and causes chlorosis, leaf curl/wilt, and necrosis, and high populations also produce copious amounts of honeydew, which promotes black sooty mold, reduces photosynthesis of affected leaves, and can clog harvest equipment (Singh et al. 2004, Bowling et al. 2016a). Sugarcane aphid was also reported as a vector of sugarcane yellow leaf virus (Luteoviridae: *Polerovirus*) in sorghum (Wei et al. 2016), but the implications of virus infection on sorghum are not presently understood.

The timing and severity of sugarcane aphid infestations is variable among locations and years (Brewer et al. 2017; Szczepaniec 2018a, b; Zapata et al. 2018), and the biotic and abiotic factors underlying source-sink dynamics related to timing and direction of spread are not understood. Sugarcane aphid populations are able to withstand cold temperatures but require live plant tissue to overwinter because they are anholocyclic and do not undergo diapause in the United States (Bowling et al. 2016a, Michaud et al. 2018); populations have been reported to overwinter on Johnson grass, *Sorghum halepense* (L.), in southern Alabama and Georgia (Haar et al. 2019). Warm, dry weather promotes population increases (Bowling et al. 2016a), and doubling times of 4–12 d have been reported (Singh et al. 2004, Bayoumy et al. 2016, Brewer et al. 2017). Populations disperse when host plant quality declines, and dispersal is believed to be wind mediated due to the rapid expansion of this pest across the United States (Bowling et al. 2016b).

The dispersal ability and rapid population growth potential of sugarcane aphid greatly increase severity of plant injury risk and impact scouting and management decisions for grain sorghum (Chang et al. 1982, Singh et al. 2004, Bowling et al. 2016b). Brewer et al. (2017) identified that aphid-density, cumulative aphid-days, and leaf injury all increased steadily for susceptible hybrids once populations

exceeded 900 aphids per leaf. Additional studies reported significant yield losses in excess of 50% and economic losses of \$25–\$175 per acre once populations exceeded 250–300 aphids per leaf and have entered exponential growth (Bowling et al. 2016b, Brewer et al. 2017). As a result, economic thresholds for foliar insecticide sprays on susceptible varieties may be recommended when populations exceed as few as 50 aphids per leaf for 20% of plants to account for population growth potential between detection and management intervention (Bowling et al. 2016a, Brewer et al. 2016, Szczepaniec 2018b).

Host plant resistance is an economical and reliable management tool (Painter 1951, Starks and Schuster 1976, Teetes 1996) that has been widely adapted for sorghum aphid pests like the greenbug, *Schizaphis graminum* Rondani (Hemiptera: Aphididae) (Schuster and Starks 1973, Morgan et al. 1980, Starks et al. 1983, Dixon et al. 1990), and more recently, sugarcane aphid (Armstrong et al. 2015, 2017; Bowling et al. 2016b; Mbulwe et al. 2016; Brewer et al. 2017; Szczepaniec 2018a,b; Haar et al. 2019; Hayes et al. 2019; Lahiri et al. 2019; Paudyal et al. 2019). Resistant varieties provide a baseline of protection against insects by suppressing population growth rates and reducing plant injury and yield losses. Host plant resistance that decreases populations and/or population growth has been identified in several grain sorghum breeding lines (Armstrong et al. 2015, 2017; Mbulwe et al. 2016; Hayes et al. 2019) and commercial varieties (Bayoumy et al. 2016; Brewer and Gordy 2016; Brown and Kerns 2016; United Sorghum Checkoff Program 2016; Brewer et al. 2017; Kelley 2017; Michaud and Zuckoff 2017; Szczepaniec 2018a, b; Haar et al. 2019; Lahiri et al. 2019; Paudyal et al. 2019), but performance of these varieties is geographically variable. The underlying mechanisms responsible for sorghum resistance to sugarcane aphid are currently unknown (Szczepaniec 2018a); however, research has shown that the phenological stage and nutrient content during initial infestation can significantly influence sugarcane aphid fecundity on resistant varieties (Lama et al. 2019). Although host plant resistance alone does not prevent populations from reaching damaging levels, suppression of plant injury or population growth rates of sugarcane aphids may increase economic threshold levels for sorghum varieties with high resistance (Ahrens et al. 2014, Bowling et al. 2016a, Brewer et al. 2016, Szczepaniec 2018b, Trostle et al. 2018). This may give farmers a longer treatment window to make a foliar insecticide application, potentially reduce the number of insecticide sprays, and promote efficacy of biological control agents (Bowling et al. 2016a; Colares et al. 2015a, b; Haar et al. 2018, 2019; Lahiri et al. 2019).

Although grain sorghum is not grown on a large number of acres in Alabama and other parts of the southeast, it is an important rotation crop. Sugarcane aphid was first reported in Alabama in August of 2014. At the time of this study, there was limited information from any state about management options. This study reports results from a series of field experiments conducted to investigate host plant resistance for sugarcane aphid management in grain sorghum production regions of Alabama. The specific objective of this study was to compare aphid population dynamics, feeding injury, and grain yield among commercially available sorghum varieties.

## Materials and Methods

### Field Sites and Experimental Design

In 2015, small plot replicated sorghum experiments were conducted at the Brewton Agricultural Research Unit in Brewton, AL, the Wiregrass Research and Extension Center in Headland, AL, and the Prattville Agricultural Research Unit in Prattville, AL. Experiments

were performed using a randomized complete block design with four replicates per treatment. Research plots were four rows wide by 6.1 m long, except at Prattville where rows were 9.1 m long, and spaced 0.91 m apart. Plots were seeded at a rate of approximately 148,263 seeds per hectare on 15 June in Headland and 17 June in Brewton and Prattville. These planting dates fall within the conventional planting times for sorghum in central and southern Alabama (Mask et al. 1988). All fields were managed for weeds and fertilized per commercial recommendations. No insecticide applications for nonaphid pests were made at any location. Lateral move irrigation was implemented for the variety trial at Headland, whereas all other trials in this study were performed under dryland conditions.

The following six commercially available sorghum varieties were evaluated at all three locations: 84P80, 83P17 (DuPont Pioneer, Johnston, IA), DKS 37-07 (DeKalb Genetics Corporation, Dekalb, IL), SP6929 (Chromatin Inc., Chicago, IL), and 1G588 and 1G855 (Mycogen Corteva Agriscience, Indianapolis, IN). An additional four varieties were included in trial at Prattville only due to either space limitations on the research stations or limited seed availability: 1G741 (Mycogen Corteva Agriscience, Indianapolis, IN), KS585 (Chromatin Inc., Chicago, IL), and ATx2752RTx2783 and ATx2752RTx430 (Texas A&M University, College Station, TX). Commercial sorghum varieties reported as exhibiting resistance to the sugarcane aphid in previous studies include DKS 37-07, 1G855, and 83P17 in Kansas, Louisiana, and Texas (Anonymous 2016; Bowling et al. 2016a; Brewer et al. 2017; Brown and Kerns 2016; Kelley 2017; Michaud and Zuckoff 2017; Szczepaniec 2018a), and SP6929 in Louisiana (Brown and Kerns 2016).

Plots at each location were scouted for sugarcane aphid weekly after planting. Once infested, the total number of sugarcane aphid(s) was counted weekly from an upper fully expanded leaf (highest leaf below flag leaf) and lower leaf (second from the bottom, or lowest green leaf) of 10 random plants in the interior rows for each plot. Weekly aphid counts were made until populations on all varieties were naturally declining for two consecutive weeks. All plots were oversprayed with 0.0527 kg ai/ha Transform WG once populations crashed.

Plant growth characteristics were also evaluated. Plant stand counts were recorded from 1 m of both interior rows for each plot 14 d postemergence. Maturity was noted when 50% of plants from each plot had fully exerted panicles. Each plot was rated for final injury once populations declined using a 1–9 injury scale adapted from Starks and Burton (1977), Webster et al. (1991), Burd et al. (2006), Armstrong et al. (2015), and Paudyal et al. (2019): 1 = healthy, 2 = 173 1–5% injury and spotted, 3 = 5–20%, 4 = 21–35%, 5 = 36–50%, 6 = 51–65%, 7 = 66–80%, 8 = 81–95%, and 9 = 95–100% or dead. Varieties with injury ratings < 3.0 are considered to have high resistance, 3.0–5.0 have moderate resistance, 5.0–6.0 have low resistance, and >6.0 indicates susceptibility (Starks and Burton 1977; Armstrong et al. 2015, 2017; Mbulwe et al. 2016; Paudyal et al. 2019). Ratings were made on the interior rows of each plot during weekly aphid counts. The two interior rows of each plot were harvested for yield (tonnes/ha) with a small plot combine when grain moisture reached approximately 14%.

### Statistical Analysis

Prior to statistical analyses, the number of aphid-days per two-leaf sample was calculated for each evaluation period at each site-year following the equation developed by Ruppel (1983):

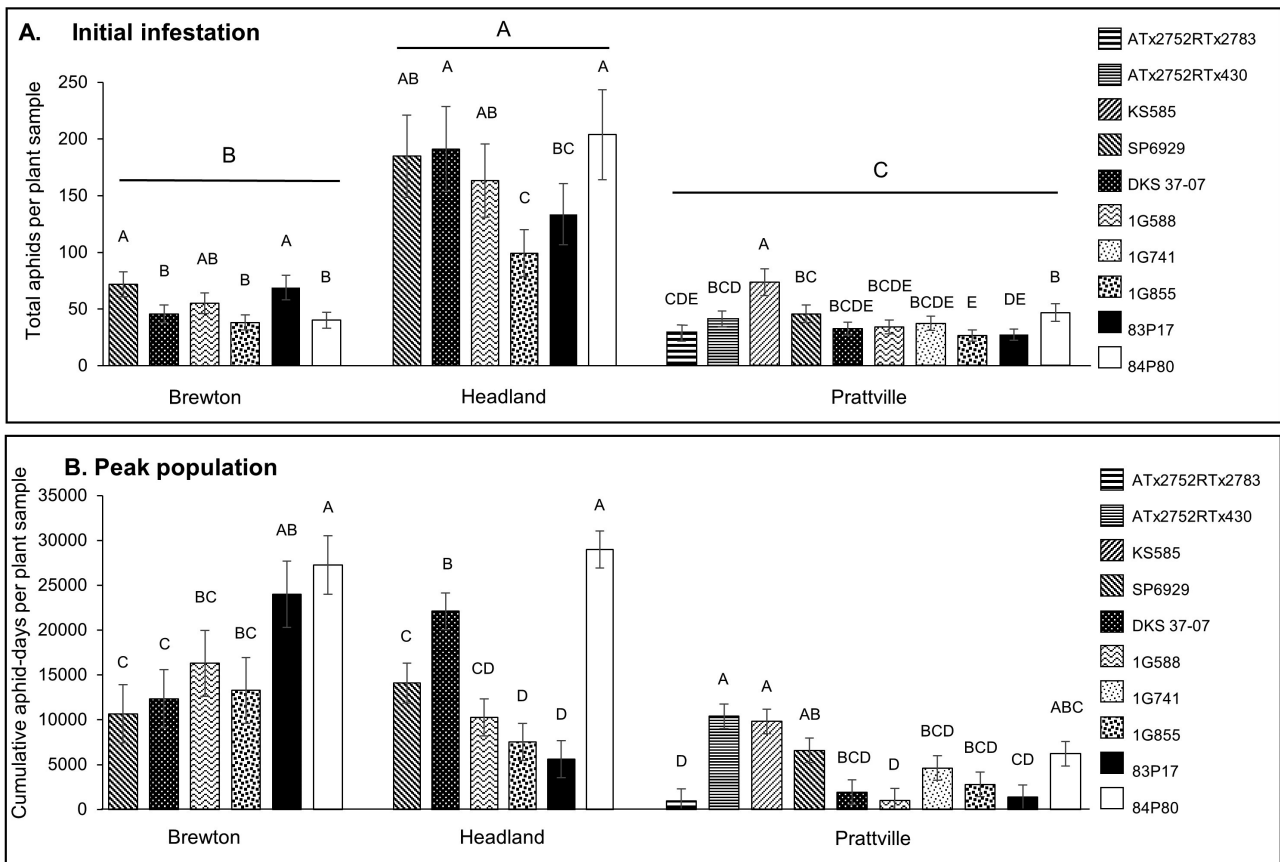
$$\text{Aphid-days} = (X_{i+1} - X_i) [(Y_i + Y_{i+1})/2]$$

in which  $X_i$  and  $X_{i+1}$  are two adjacent observation periods and  $Y_i$  and  $Y_{i+1}$  are the aphid densities corresponding to  $X_i$  and  $X_{i+1}$ . The aphid-days measurement is indicative of the severity of an insect attack and it takes into consideration the number of surviving aphids between time periods (Ruppel 1983, Kieckhefer et al. 1995, Brewer et al. 2017). Cumulative aphid-days were calculated by summing the number of aphid-days from each prior data collection period.

The average number of aphids per two-leaf sample was compared among varieties using ANOVA with PROC GLIMMIX (SAS 9.4, SAS Institute 2013). Means comparisons were performed with LS means at a  $P \leq 0.05$  level. Because the overall initial infestation level, irrespective of variety, significantly differed among locations (Fig. 1a; indicated by the three horizontal bars and mean comparisons significance letters overhead the varieties evaluated at each location), all means were compared among varieties in separate ANOVAs for each location. The average number of aphid-days, cumulative aphid-days, plant stand counts, final injury ratings, the number of days to 50% panicle exertion, and sorghum yields were compared separately among varieties using ANOVA in PROC GLIMMIX (SAS 9.4, SAS Institute 2013) with treatment as a main effect, and block, residuals, and plant (only for aphid-days analyses) as random effects; block was included as a random effect because it was not a significant main effect in preliminary analyses. Mean comparisons were conducted using LS means at a  $P \leq 0.05$  level. Analyses assessing data for plant stand count, plant injury, and days to 50% panicle exertion

were conducted using a Poisson distribution, whereas those assessing grain yield, aphid-days, and cumulative aphid-days were analyzed using a Gaussian distribution.

Simple linear regression analyses conducted with PROC REG (SAS 9.4, Freund and Littell 2000, SAS Institute 2013) were used to assess the rate of increase in aphid-days per two-leaf sample from the day of initial infestation until peak aphid-days for each sorghum variety evaluated at each location; a total of 22 simple linear regressions were performed including 6 for varieties at Brewton, 10 at Prattville, and 6 at Headland. Evaluation dates when populations were in decline for two consecutive weeks were omitted from these analyses. To test the null hypothesis that aphid population dynamics are similar among the varieties evaluated, the rate of population increase, or regression coefficients for each variety (i.e., slope) calculated from simple linear regression analyses, were compared with that of 84P80, a known susceptible variety using PROC REG (SAS 9.4, SAS Institute 2013). Interactions between the number of accumulated aphid-days and plant growth characteristics were investigated for each location using simple linear regression analysis with PROC REG (SAS 9.4, Freund and Littell 2000, SAS Institute 2013) to predict whether there were associations among (1) cumulative aphid-days and 1–9 injury rating per plot, (2) cumulative aphid-days and grain yield per plot, (3) 1–9 injury rating and grain yield per plot, (4) cumulative aphid-days and 1–9 injury rating per plot, and (5) cumulative aphid-days and days to 50% panicle exertion per



**Fig. 1.** Aphid populations on sorghum varieties evaluated in Brewton, AL, Prattville, AL, and Headland, AL. (A) The mean number of aphids per two-leaf sample during initial infestation that occurred on 7 July at Prattville, 8 July at Brewton, and 9 July at Headland. (B) The mean aphid-days accrued per two-leaf sample for varieties when populations reached peak size recorded on 29 July at Brewton, 30 July at Headland, and 24 August at Prattville. Multiple comparisons showing significant differences in the average number of aphids observed on all varieties among locations during the initial infestation is presented above each location (A). Means comparisons of the total number of aphids (A) or cumulative aphid-days (B) of each variety were conducted separately for each location. Bars with the same letter are not significantly different (LS means,  $P \leq 0.05$ ).

plot. For each analysis and location, two separate regression analyses were conducted: one for varieties that had final injury ratings < 6 and exhibited low to high levels of resistance, and the other for varieties that had final injury ratings  $\geq 6$  and exhibited susceptibility to aphid feeding (Starks and Burton 1977).

Multiple linear regressions were performed for each location using PROC ROBUSTREG (SAS 9.4, Chen 2002, SAS Institute 2013) to assess how maturation rate, injury rating, and cumulative aphid-days influenced grain yield. Robust regression was chosen to account for influential outliers that violated norms. Because the number of days until 50% panicle exertion for sorghum varieties was highly insignificant in the initial regression analysis, it was discarded to increase resolution.

## Results

### Aphid Population Dynamics

Sugarcane aphids were first detected in Prattville on 7 July, Brewton on 8 July, and Headland on 9 July. Average population densities of initial infestations, irrespective of sorghum variety, significantly differed among locations (Fig. 1a;  $F = 319.49$ ,  $df = 2, 690$ ,  $P < 0.0001$ ). The average number of aphids per two-leaf sample at Headland was 3.2- and 4.8-fold greater than at Brewton and Prattville, respectively. In Headland, the susceptible variety 84P80 had an average of 209.1 aphids per two-leaf sample, which was nearly five times more than reported in Brewton or Prattville (Fig. 1a). At all locations, 1G855 had the fewest aphids and was followed by 83P17 in Headland and Prattville; however, in Brewton, 84P80 had the second fewest aphids, whereas 83P17 had the second most aphids. No signs of phytotoxicity were observed at this time.

In Brewton, initial aphid populations were below economic threshold level but significantly differed among varieties (Fig. 1a;

$F = 6.78$ ,  $df = 5, 222$ ,  $P < 0.0001$ ); SP6929 and 83P17 had more aphids per two-leaf sample than 84P80, 1G588, and DKS 37-07. Aphid populations on all varieties increased and reached peak aphid-days within 3 wk on 29 July (Fig. 1b;  $F = 8.54$ ,  $df = 5, 133$ ,  $P < 0.0001$ ); SP6929, DKS 37-07, 1G588, and 1G855 had accumulated similar levels of aphid-days per two-leaf sample, and significantly less than 84P80 and 83P17, which did not vary from another. Simple linear regression analyses detected significant variation in rates of population increase from initial infestation to peak aphid-days among varieties (Fig. 2;  $F = 23.26$ ,  $df = 11, 27$ ,  $P < 0.0001$ ); relative to 84P80 (Fig. 2f), aphid populations increased slower on SP6929 (Fig. 2a;  $t = -4.18$ ,  $P = 0.0003$ ), DKS 37-07 (Fig. 2b;  $t = -3.72$ ,  $P = 0.0009$ ), 1G588 (Fig. 2c;  $t = -2.06$ ,  $P = 0.049$ ), and 1G855 (Fig. 2d;  $t = -2.76$ ,  $P = 0.0102$ ). The fastest overall population increase was observed on 83P17 (Fig. 2e;  $t = -0.31$ ,  $P = 0.7616$ ). SP6929 was the only variety to not have significant differences in aphid-days over time (Fig. 2a;  $F = 3.48$ ,  $df = 1, 5$ ,  $P = 0.1211$ ). Populations declined on all varieties by 4 August (Supp Table 1 [online only]).

In Headland, initial aphid populations were above economic threshold and the number of aphids per two-leaf sample significantly differed among sorghum varieties (Fig. 1a;  $F = 8.08$ ,  $df = 5, 222$ ,  $P < 0.0001$ ). Populations increased and reached their peak sizes on all varieties by 30 July and significant differences were detected (Fig. 1b;  $F = 38.89$ ,  $df = 5, 212$ ,  $P < 0.0001$ ); all varieties had accumulated fewer aphid-days per two-leaf sample than 84P80. Simple linear regressions elicited significant differences in aphid population growth rates from initial infestation to peak aphid-days among varieties (Fig. 3;  $F = 20.56$ ,  $df = 11, 77$ ,  $P < 0.0001$ ); relative to 84P80 (Fig. 3f), growth rates were similar on SP6929 (Fig. 3a;  $t = -1.35$ ,  $P = 0.1804$ ), and slower on DKS 37-07 (Fig. 3b;  $t = -2.20$ ,  $P = 0.0310$ ), 1G588 (Fig. 3c;  $t = -4.74$ ,  $P < 0.0001$ ), 1G855 (Fig. 3d;  $t = -5.26$ ,  $P < 0.0001$ ), and 83P17 (Fig. 3e;  $t = -5.75$ ,  $P < 0.0001$ ).

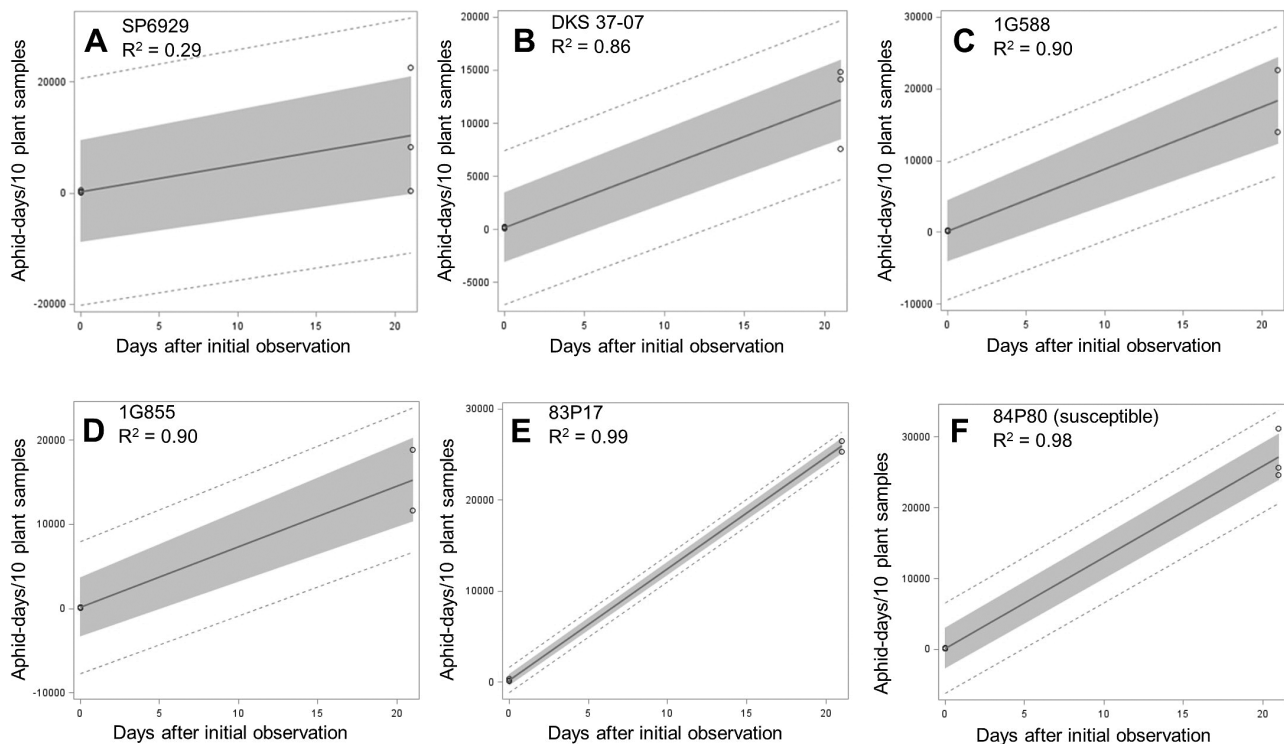


Fig. 2. Scatterplots with regression lines from simple linear regression analyses showing the relationship between the mean aphid-days and days after initial infestation for each variety evaluated in Brewton, AL.

Populations declined on all varieties by 6 August (Supp Table 2 [online only]).

Initial aphid populations for all sorghum varieties at Prattville were below economic threshold and significantly less than at Brewton or Headland (Fig. 1a;  $F = 13.62$ ,  $df = 9$ ,  $378$ ,  $P < 0.0001$ ). Aphid populations increased and reached peak levels about 7 wk later on 24 August. Varieties accumulated significantly different numbers of aphid-days per two-leaf sample (Fig. 1b;  $F = 10.56$ ,  $df = 9$ ,  $378$ ,  $P < 0.0001$ ). Simple linear regressions detected significant differences in rates of aphid population increase from initial infestation to peak aphid-days among varieties (Fig. 4;  $F = 10.23$ ,  $df = 19$ ,  $252$ ,  $P < 0.0001$ ); relative to 84P80 (Fig. 4j), populations increased slower on ATx2752RTx2783 (Fig. 4a;  $t = -3.09$ ,  $P = 0.0022$ ), DKS 37-07 (Fig. 4e;  $t = 2.67$ ,  $P = 0.0082$ ), 1G588 (Fig. 4f;  $t = -3.15$ ,  $P = 0.0018$ ) and 83P17 (Fig. 4i;  $t = -2.88$ ,  $P = 0.0043$ ), but similarly on KS585 (Fig. 4c;  $t = 0.47$ ,  $P = 0.6363$ ), SP6929 (Fig. 4d;  $t = 0.29$ ,  $P = 0.7733$ ), 1G741 (Fig. 4g;  $t = -1.32$ ,  $P = 0.1865$ ) and 1G855 (Fig. 4h;  $t = -1.95$ ,  $P = 0.0519$ ). ATx2752RTx430 (Fig. 4b;  $t = 2.27$ ,  $P = 0.0242$ ) was the only variety that had populations increase faster than 84P80, whereas SP6929 was the only variety in which the rate of increase was not significant over time (Fig. 4d;  $F = 0.93$ ,  $df = 1$ ,  $34$ ,  $P = 0.3409$ ). Populations declined on all varieties by 31 August (Supp Table 3 [online only]).

### One to Nine Injury Rating

Final plant injury ratings recorded during peak infestations significantly differed among varieties at each location. At Brewton, average injury ratings were high ( $>4$ ) among varieties (Fig. 5, Supp Table 4 [online only]); DKS 37-07 and 1G855 had injury ratings of 4.5 and 5.0, respectively, which were significantly lower than 84P80, which had a final injury rating around 8 but similar to SP6929, 1G588, and 83P17. Regression analysis failed to detect a significant relationship between cumulative aphid-days and 1–9 injury ratings per

plot when varieties were evaluated collectively ( $R^2 = 0.03$ ,  $F = 0.63$ ,  $df = 1$ ,  $21$ ;  $P = 0.4361$ ), or grouped by final injury ratings  $> 6$  (Fig. 6a;  $F = 2.88$ ,  $df = 1$ ,  $10$ ,  $P = 0.1204$ ) or  $< 6$  (Fig. 6a;  $F = 0.13$ ,  $df = 1$ ,  $6$ ,  $P = 0.7295$ ), although the slope for varieties with ratings  $> 6$  was nearly 10-fold greater than those with ratings  $< 6$ .

In Headland (Fig. 5, Supp Table 4 [online only]), varieties showed moderate injury levels. Three varieties, including 84P80, SP6929, and DKS 37-07, exhibited the highest final injury ratings of approximately 6 and 7. Varieties 1G855, 1G588, and 83P17 exhibited lower injury levels between 3 and 4, which were significantly less than 84P80. Regression analysis failed to detect a significant relationship between cumulative aphid-days and 1–9 injury ratings per plot for varieties grouped by injury ratings  $> 6$  (Fig. 6b;  $F = 1.47$ ,  $df = 1$ ,  $10$ ,  $P = 0.2532$ ) or  $< 6$  (Fig. 6b;  $F = 1.74$ ,  $df = 1$ ,  $10$ ,  $P = 0.2169$ ), and the slopes for both varieties  $> 6$  and  $< 6$  were approximately the same. However, when all varieties were analyzed collectively, a strong and significant positive relationship was observed ( $R^2 = 0.54$ ,  $F = 26.24$ ,  $df = 1$ ,  $22$ ,  $P < 0.0001$ ).

In Prattville (Fig. 5, Supp Table 4 [online only]), varieties exhibited significantly different injury ratings, albeit overall injury levels were low ( $<4$ ). Means comparison tests failed to detect significant differences among the individual varieties. The variety 1G741 exhibited a final injury rating near 1, whereas ATx2752RTx2783, DKS 37-07, and 1G588 had final ratings around 2. The remaining varieties had injury ratings around 3 or 4 and began to discolor and accumulate honeydew. Simple linear regression analysis failed to detect a relationship between cumulative aphid-days and 1–9 injury ratings per plot for all varieties (Fig. 6c;  $R^2 = 0.19$ ,  $F = 3.09$ ,  $df = 1$ ,  $38$ ,  $P = 0.0868$ ).

### Panicle Exertion

The number of days it took for each variety to go from plant emergence to  $\geq 50\%$  panicle exertion significantly differed among varieties at each

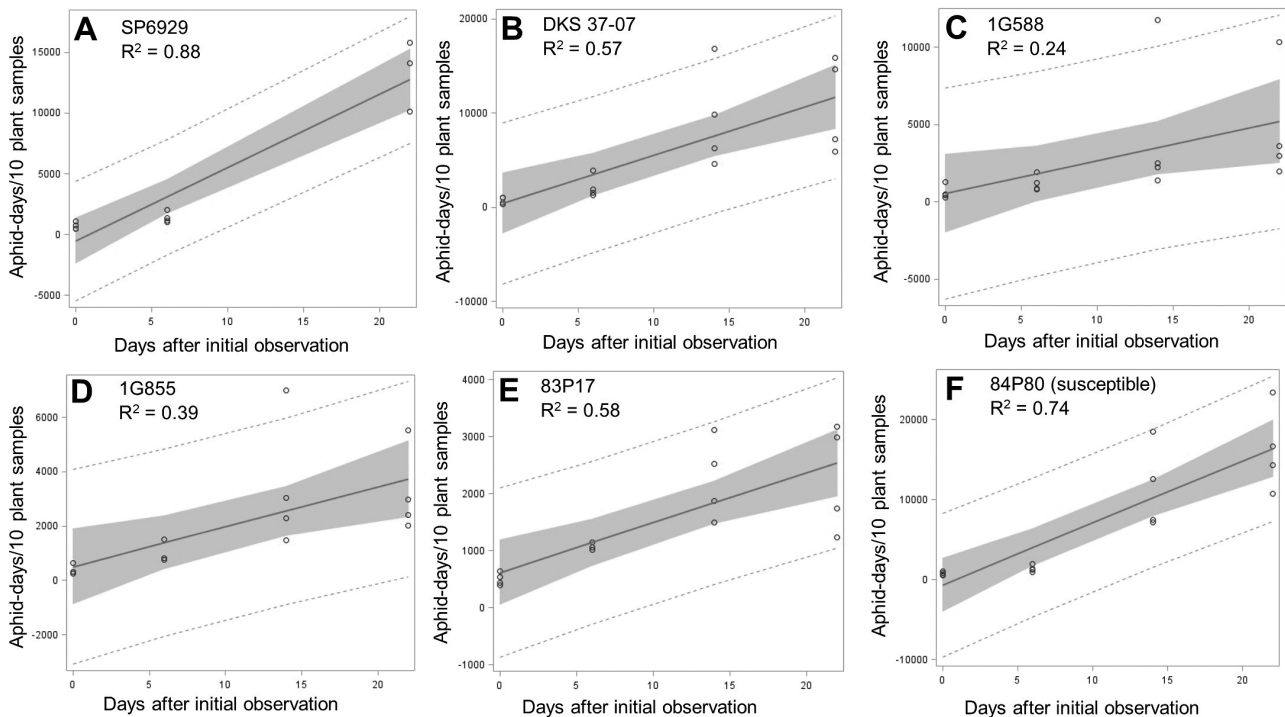
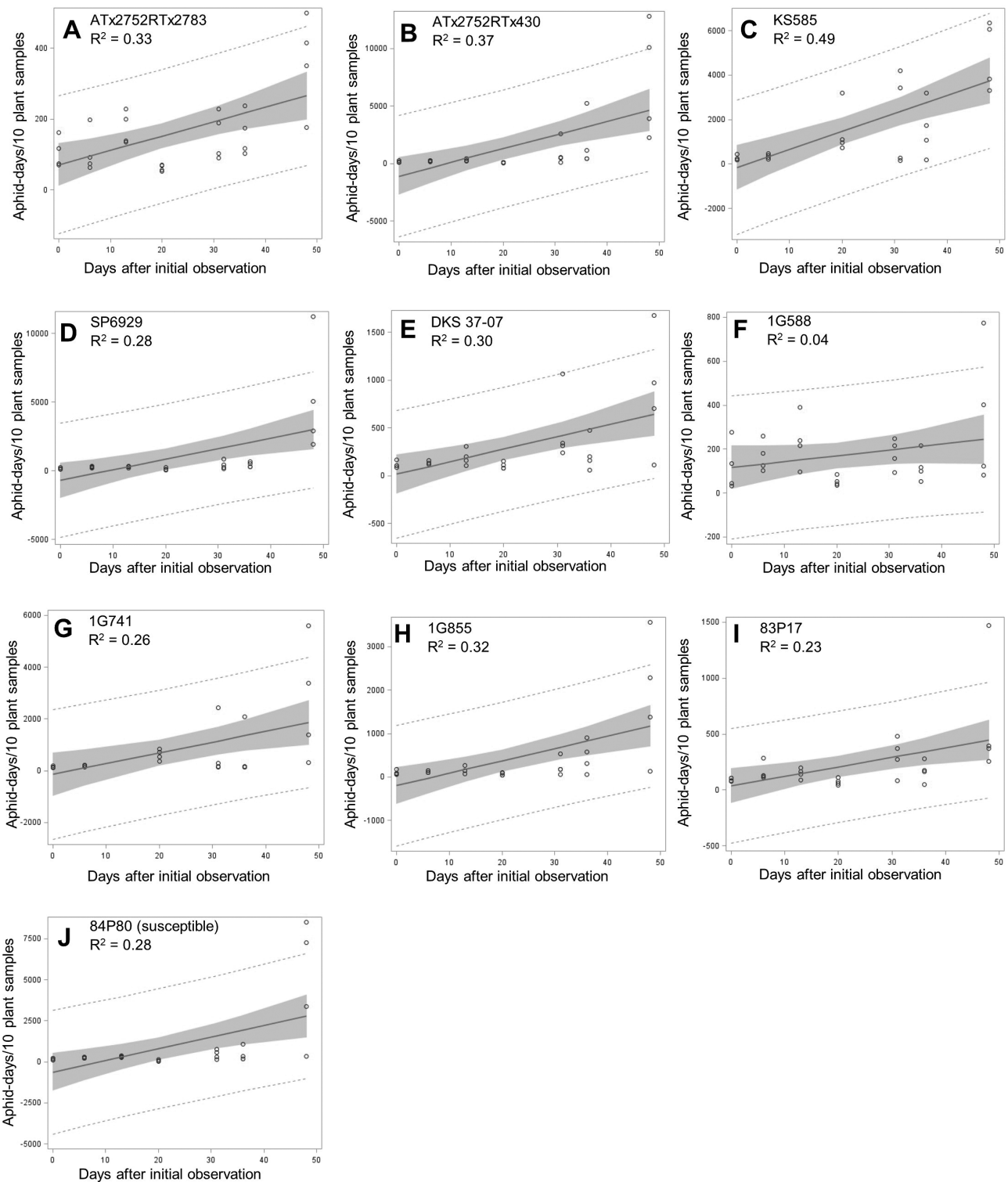


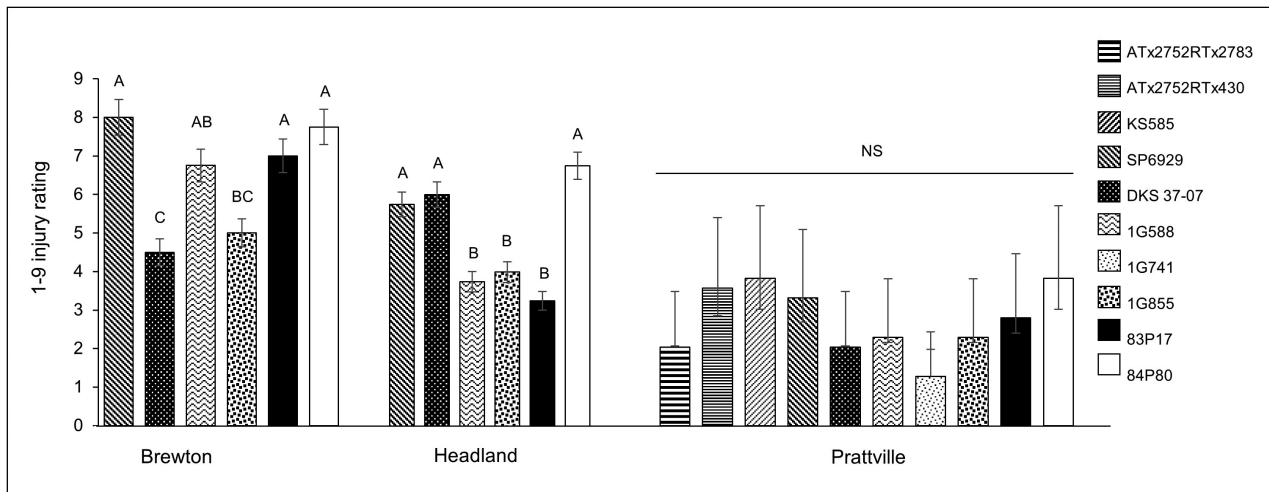
Fig. 3. Scatterplots with regression lines from simple linear regression showing the relationship between the mean aphid-days and time after initial infestation for each variety evaluated in Headland, AL.



**Fig. 4.** Scatterplots with regression lines from simple linear regression showing the relationship between the mean aphid-days and time after initial infestation for each variety evaluated in Prattville, AL.

location (Fig. 7, Supp Table 4 [online only]). In Brewton,  $\geq 50\%$  panicle exertion occurred within 78–84 d of planting (Fig. 7, Supp Table 4 [online only]). In Headland,  $\geq 50\%$  panicle exertion was observed 60–81 d after planting (Fig. 7, Supp Table 4 [online only]). In Prattville, varieties had exerted  $\geq 50\%$  panicles within 51–61 d after planting (Fig. 7, Supp Table 4 [online only]). Simple linear regression failed to detect a

relationship between the number of cumulative aphid-days and days to  $\geq 50\%$  panicle exertion for all varieties at Brewton ( $R^2 = 0.01$ ,  $F = 1.12$ ,  $df = 1,18$ ,  $P = 0.3041$ ), Prattville ( $R^2 = 0.02$ ,  $F = 1.90$ ,  $df = 1,38$ ,  $P = 0.1763$ ), and Headland ( $R^2 = 0.06$ ,  $F = 2.58$ ,  $df = 1,22$ ,  $P = 0.1226$ ), and when varieties were classified as having a final injury rating  $< 6$  or  $> 6$  at Brewton and Headland (data not shown,  $P > 0.05$ ).



**Fig. 5.** Mean 1–9 plant injury ratings after sugarcane aphid populations naturally declined for all varieties that were tested in Brewton, AL, Headland, AL, and Prattville, AL. Multiple comparisons were evaluated separately for each location and data bars with the same letter are not significantly different (LS means,  $P \leq 0.05$ ).

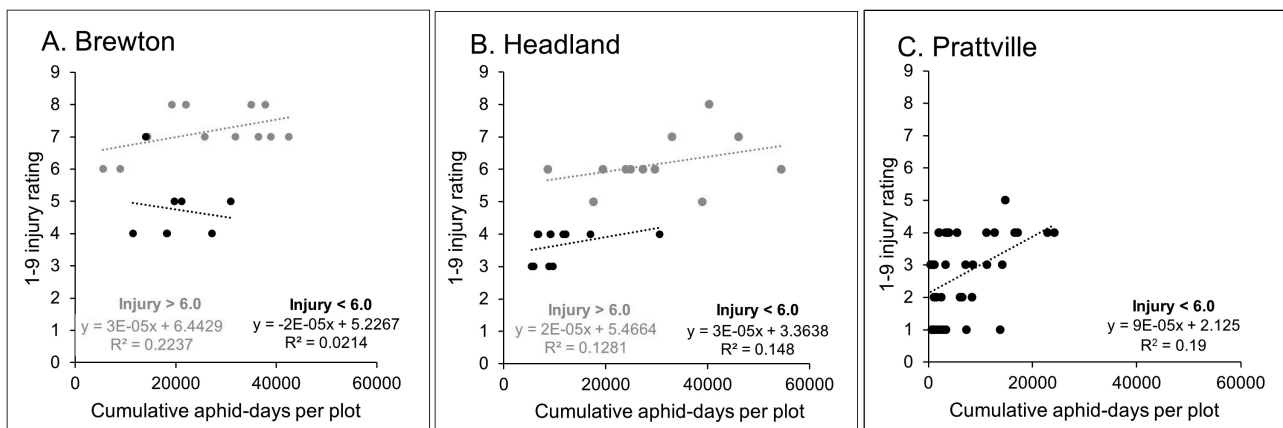
### Plant Stand Count and Grain Yield

Plant stand counts taken 14 d postemergence were similar among plots for all site-years and ranged from 13 to 17 plants per 1 row m at Brewton ( $F = 1.43$ ,  $df = 5, 15$ ,  $P = 0.2708$ ) and at Prattville ( $F = 0.69$ ,  $df = 9, 27$ ,  $P = 0.7102$ ), and 12–18 plants at Headland ( $F = 1.54$ ,  $df = 5, 15$ ,  $P = 0.2371$ ). It is unlikely that any variation observed in plant stand counts had an effect on yield. Grain yield was not recorded in Prattville as all plots accrued excessive bird feeding damage.

There were significant differences in yield among sorghum varieties at Brewton and Headland (Fig. 8, Supp Table 4 [online only]). In Brewton, DKS 37-07 was the highest yielding variety and produced 2,404 kg/ha more than the next best variety 1G855, which was similar to 84P80 and all other varieties (Fig. 8a, Supp Table S4 [online only];  $F = 33.43$ ,  $df = 5, 15$ ,  $P < 0.0001$ ). Simple linear regression analysis detected a negative, significant relationship between cumulative aphid-days and yield among varieties with injury ratings  $> 6$  (Fig. 9a;  $F = 7.11$ ,  $df = 1, 10$ ,  $P = 0.0236$ ), but not injury ratings  $< 6$  (Fig. 9a;  $F = 0.06$ ,  $df = 1, 6$ ,  $P = 0.8164$ ) or all varieties collectively ( $R^2 = 0.039$ ,  $F = 0.84$ ,  $df = 1, 21$ ,  $P = 0.3691$ ). Similar trends were observed among 1–9 injury rating and grain yield for all varieties collectively ( $R^2 = 0.49$ ,  $F = 19.92$ ,  $df = 1, 21$ ,  $P < 0.0002$ ), and for

varieties with final injury ratings  $> 6$  (Fig. 10a;  $F = 20.85$ ,  $df = 1, 10$ ,  $P = 0.0010$ ), but not injury ratings  $< 6$  (Fig. 10a;  $F = 0.76$ ,  $df = 1, 6$ ,  $P = 0.4167$ ), and the slope was nearly six times greater for varieties with injury ratings  $> 6$ . Robust multiple regression analysis showed a significant negative relationship among the amount of plant injury, accumulated aphid-days, and the resulting yield ( $R^2 = 0.49$ ,  $F = 9.72$ ,  $df = 1, 21$ ,  $P = 0.0011$ ). There was a significant correlation with injury rating ( $t = -4.23$ ,  $df = 22$ ,  $P = 0.0004$ ) and resulting yield; however, the number of accumulated aphid-days and grain yield did not significantly influence yield ( $t = -0.49$ ,  $df = 22$ ,  $P = 0.6276$ ).

In Headland, 1G855, 83P17, and 1G588 produced larger yields than 84P80, which performed similar to SP6929 and DKS 37-07, the latter of which was the top performing variety in Brewton (Fig. 8b, Supp Table 4 [online only]). Simple linear regression analysis detected a negative, significant relationship between cumulative aphid-days and yield for all varieties collectively ( $R^2 = 0.49$ ,  $F = 21.27$ ,  $df = 1, 22$ ,  $P = 0.0001$ ) and those with injury ratings  $< 6$  (Fig. 9b;  $F = 9.09$ ,  $df = 1, 10$ ,  $P = 0.0130$ ), but not injury ratings  $> 6$  (Fig. 9b;  $F = 0.30$ ,  $df = 1, 10$ ,  $P = 0.5948$ ). Simple linear regression analyses failed to detect significant relationships among injury ratings and grain yield for both varieties with injury ratings  $> 6$  (Fig. 10b;



**Fig. 6.** Scatterplots with regression lines showing the relationship between cumulative aphid-days and 1–9 injury ratings for susceptible (gray) and resistant (black) varieties as determined by final injury ratings in (A) Brewton, AL, (B) Headland, AL, and (C) Prattville, AL.



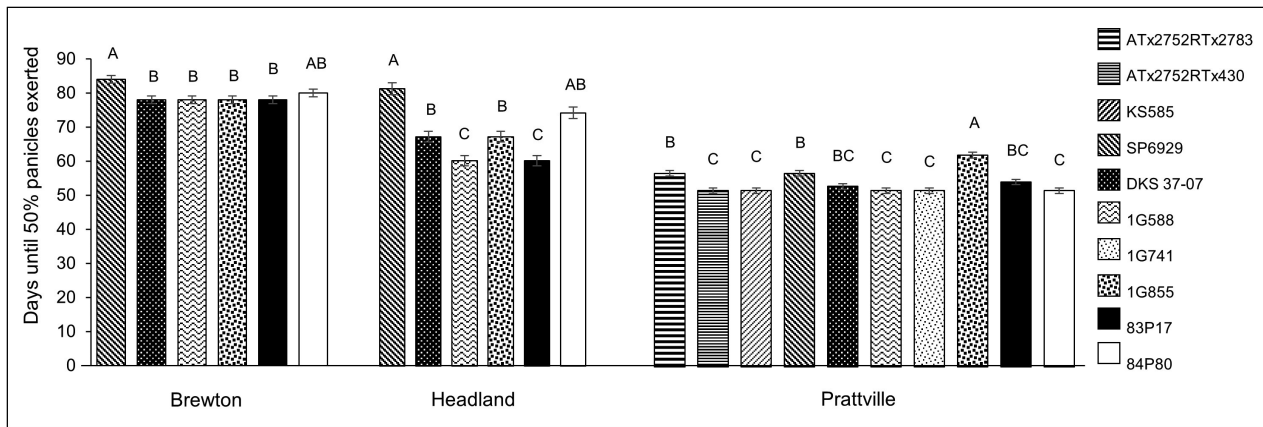


Fig. 7. Mean number of days for 50% panicle exertion for each variety evaluated in Brewton, AL, Prattville, AL, and Headland, AL. Multiple comparisons were evaluated separately for each location and data bars with the same letter are not significantly different (LS means,  $P \leq 0.05$ ).

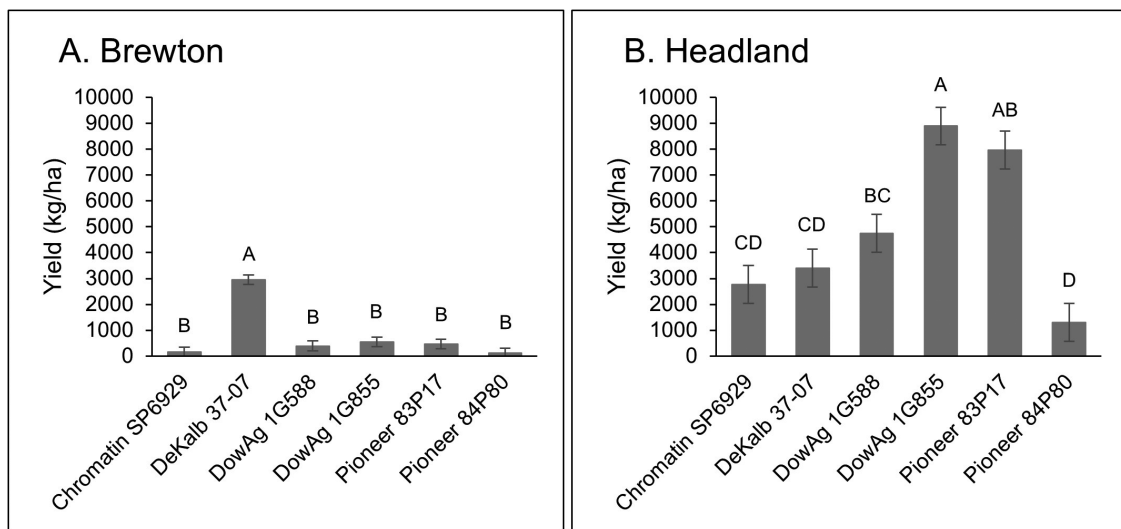


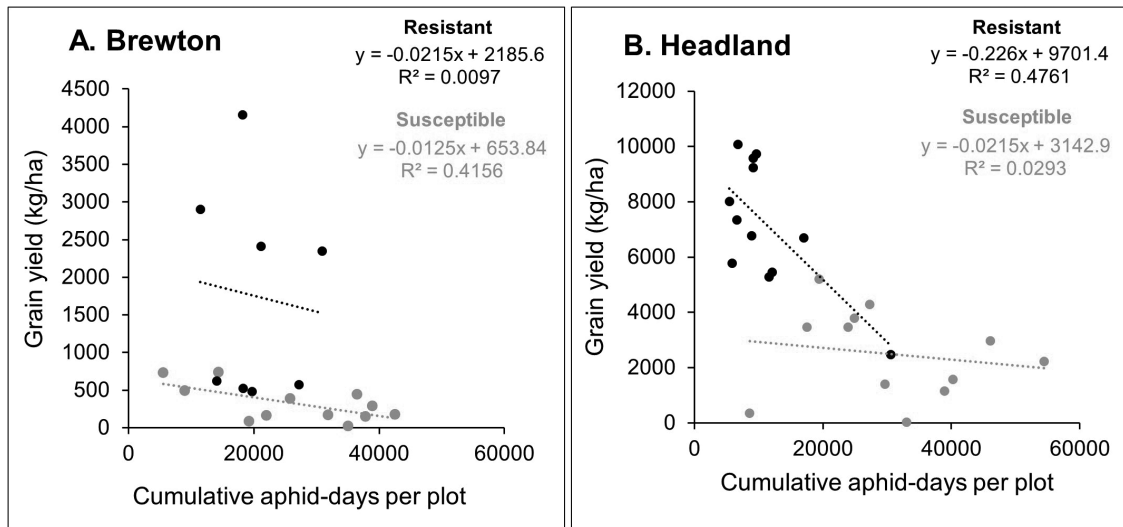
Fig. 8. Mean sorghum grain yield, reported in kilogram per hectare, for all sorghum varieties harvested when grain moisture reached 14% in (A) Brewton, AL, on 22 October, and (B) Headland, AL on 20 October. Multiple comparisons were evaluated separately for each location and data bars with the same letter are not significantly different (LS means,  $P \leq 0.05$ ).

$F = 0.58$ ,  $df = 1, 10$ ,  $P = 0.4652$ ) and injury ratings  $< 6$  (Fig. 10b;  $F = 0.15$ ,  $df = 1, 10$ ,  $P = 0.7084$ ), although the slope was three times greater for those with ratings  $> 6$ . However, all varieties collectively elicited a strong negative relationship ( $R^2 = 0.55$ ,  $F = 26.48$ ,  $df = 1, 22$ ,  $P < 0.0001$ ). Robust multiple regression analysis showed a significant strong negative relationship between the amount of plant injury and accumulated aphid-days and grain yield ( $R^2 = 0.60$ ,  $F = 15.72$ ,  $df = 2, 21$ ,  $P < 0.0001$ ). There was a significant correlation with injury rating ( $t = -2.38$ ,  $df = 22$ ,  $P = 0.0269$ ) and resulting yield, but not with the number of accumulated aphid-days and grain yield ( $t = -1.67$ ,  $df = 22$ ,  $P = 0.1090$ ).

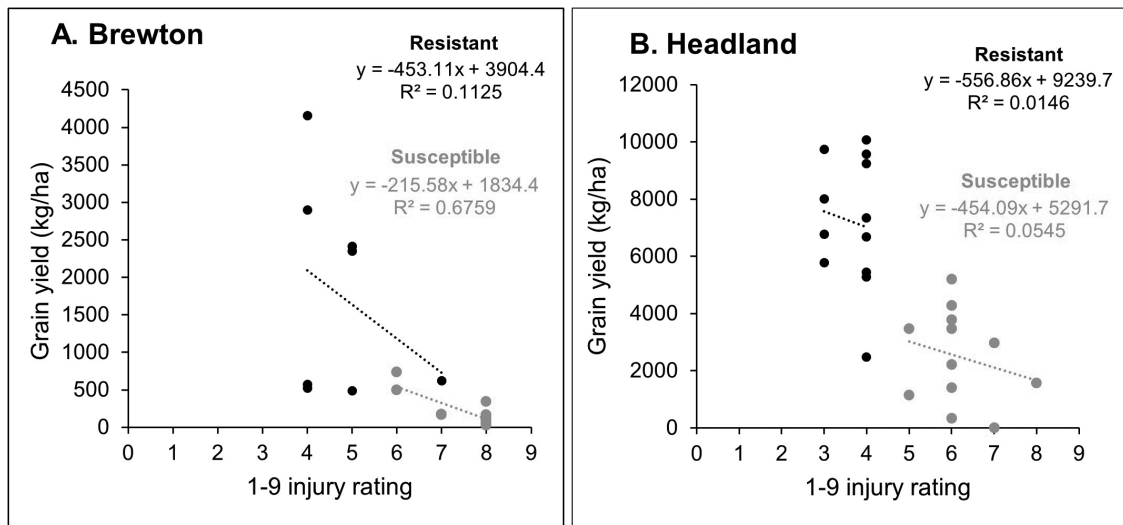
## Discussion

This study reports three-site years of data in which DKS 37-07, 1G588, 1G855, SP6929, and 83P17 generally exhibited resistance based on at least one of the following characteristics: (1) low to intermediate injury ratings ( $\leq 5$ ) indicative of moderate to high resistance (Starks and Burton 1977; Webster et al. 1991; Burd et al. 2006; Armstrong et al. 2015, 2017; Mbulwe et al. 2016; Paudyal

et al. 2019), (2) lower populations (Armstrong et al. 2015, 2017; Bayoumy et al. 2016; Szczepanec 2018a; Haar et al. 2019; Limaje et al. 2018; Paudyal et al. 2019) compared with a known susceptible variety, or (3) higher yield relative to a known susceptible variety (Armstrong et al. 2015, 2017; Szczepanec 2018a; Haar et al. 2019; Paudyal et al. 2019). Lower aphid populations and plant injury were reported on SP6929, but yields were similar to 84P80, probably because it is not regionally adapted to the southeast. Relative to 84P80, aphid populations increased three times slower on 1G588 at Headland and Prattville, and on SP6929 at Brewton. Cumulative aphid-days during peak population size, injury, and yield were variable among locations. DKS37-07 was the only resistant variety that had lower cumulative aphid-days, lower injury, and higher yield at Brewton than at Headland; it was the highest yielding variety at Brewton where it accrued 1.4-fold fewer cumulative aphid-days and yielded 1.2-fold more grain than at Headland. Other varieties exhibiting some form of resistance, SP6929, 83P17, 1G588, and 1G855, had relatively higher cumulative aphid-days, higher injury ratings, and lower yields at Brewton than at Headland. Varieties 83P17, 1G588, and 1G855 had 0.13- to 5.0-fold fewer cumulative



**Fig. 9.** Scatterplots with regression lines from robust regression analyses showing the relationship between cumulative aphid-days per plot and grain yield (kg/ha) for varieties classified as susceptible (gray) and resistant (black) as determined by final injury ratings in (A) Brewton, AL, and (B) Headland, AL.



**Fig. 10.** Scatterplots with regression lines from robust regression analyses showing the relationship between 1 and 9 injury rating and grain yield (kg/ha) for varieties classified as susceptible (gray) and resistant (black) as determined by final injury ratings in (A) Brewton, AL, and (B) Headland, AL.

aphid-days and yielded 10.0- to 19.8-fold more grain at Headland than at Brewton. The same relative changes were observed for the known susceptible, 84P80, but the magnitude of the differences was low. All of the varieties at Prattville, regardless of resistance or susceptibility, had relatively lower injury ratings < 4.0 and aphid populations compared with the other two locations.

These experiments were not designed to examine underlying causes of varietal performance. However, variable growing conditions and aphid pressure are two factors that may have influenced variation among observations at the three locations. Infestations may have originated from the same flight event given sugarcane aphids ability to disperse long distances via wind currents; following its initial report in Texas in 2013, sugarcane aphid was reported nearly 900 miles away by the end of the year (Bowling et al. 2016a). Initial infestations occurred the same week and at a time when plants were at a similar growth stage at each location. The initial numbers observed, however, were much higher at Headland compared

with Brewton or Prattville, with an average of over 200 aphids per two-leaf sample. Despite the higher initial infestation at Headland, however, yield was also higher at this location. Within 21 d of initial infestation, sugarcane aphid populations on 84P80 accrued  $33,625 \pm 3,744$  and  $39,321 \pm 2,643$  aphid-days at Brewton and Headland, respectively. Aphid pressure at Prattville was much lower than at the other two locations. Here, initial infestations were similar to those observed at Brewton, but 84P80 had  $11,528.3 \pm 1,921.3$  aphid-days, or 700 aphids, per two-leaf sample during peak which was 3.6–3.7 times less than at Brewton or Headland, respectively.

The three research stations are located in different growing regions of Alabama that differ in landscape features and environment. Average temperatures, including daily highs and lows, did not differ among locations by more than two degrees during the months of June–August when vegetative and reproductive development was completed, but precipitation and irrigation were different between Brewton, Headland, and Prattville. In Brewton, sorghum

was grown under dryland and drought-like conditions in 2015, and rainfall totaled 1.84” between the date of first detection and peak population size of aphids, which corresponded with early vegetative growth (approximately four true-leaf stage), and panicle initiation, respectively. In Headland, rainfall and irrigation totaled 3.94” between first infestation and peak population size, which corresponded to early vegetative and panicle initiation growth stages, respectively. In Prattville, which was under dryland conditions but received similar amounts of rainfall as Headland, all varieties matured nearly 3 wk sooner and exhibited much less injury than at Brewton. Approximately 70% of the final grain yield in sorghum develops during panicle initiation; any plant stress stemming from variety–environment interactions during this critical period reduces seed set and resulting yield (Gerik et al. 2003, Schnell et al. 2014, Trostle 2016, Szczepaniac 2018a, Haar et al. 2019). Variety–environment interactions are recognized to impact overall plant health and grain yields (Schnell et al. 2014, Trostle 2016, Szczepaniac 2018a), and abiotic factors influence aphid population dynamics (NOAA 2014, 2015; Bowling et al. 2016a; Zapata et al. 2018), but the impact of abiotic factors on performance of sugarcane aphid resistance in varieties has not been investigated. Although DKS 37-07, 1G588, 1G855, SP6929, and 83P17 exhibited some measure of resistance at each location, there was variation in aphid populations, injury, and yield among the three replications. These results suggest that abiotic factors including precipitation/irrigation are potentially influencing aphid suppression, injury, and yields of resistant varieties.

Predation and parasitism effects on sugarcane aphid population dynamics were not investigated during these studies; however, the presence of natural enemy species was recorded in parallel with aphid counts around peak population size at each site (data not shown). Seventeen natural enemy species were observed in Alabama: six Coccinellid species (Coleoptera: Coccinellidae) including *Coleomegilla maculata* DeGeer, *Cycloneda sanguinea* L., *Diomus terminatus* Say, *Harmonia axyridis* Pallas, *Hippodamia convergens* Guerin-Meneville, *Scymnus* sp. Kugelann; four syrphid species (Diptera: Syrphidae) including *Allograpta obliqua* Say, *Pseudodoros clavatus* F., *Syrphus* sp. F., *Toxomerus geminatus* Say; three lacewing species including *Chrysoperla carnea* Stephens and *Cereochrysa* sp. (Neuroptera: Chrysopidae) and *Hemerobius* sp. L. (Chrysopidae: Hemerobidae); the minute pirate bug, *Orius insidiosus* Say (Hemiptera: Anthocoridae); and three parasitoid species including two *Aphelinus* sp. Dalman (Hymenoptera: Aphelinidae) (identified by black or blue mummies) and *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae). These natural enemy species were also reported in Louisiana and Kansas (Colares et al. 2015a, b; Bowling et al. 2016a; Brewer et al. 2017). It is unlikely these species had a significant impact on aphid population reduction throughout these studies as the sugarcane aphid’s reproductive rate is much faster than any of the observed natural enemies.

In this study, varieties that consistently exhibited characteristics of resistance were identified even though there was variation in aphid population suppression, injury ratings, and yield among the three site-years of data. Additional research is needed to understand the potential for these varieties to promote biological control, reduce insecticide sprays, or alter economic threshold levels for sorghum varieties with high resistance (Ahrens et al. 2014, Bowling et al. 2016a, Brewer et al. 2016, Szczepaniac 2018b, Trostle et al. 2018). Future research investigating host plant resistance as a component of sugarcane aphid IPM should also consider the effects of variety × environment interactions on resistance characteristics related to sugarcane aphid population suppression, plant injury, and yield potential.

## Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

## Acknowledgments

We thank the E. V. Smith Plant Breeding Research Unit, Brewton Agricultural Research Station, Gulf Coast Research and Extension Center, Prattville Agricultural Research Station, and Wiregrass Research and Extension Center for providing assistance with planting, maintenance, and harvest of field plots. We thank Ian Ingram, Emily Ingram, Dylan Bartlett, Bruno Sausa-Viera, and Rafael De Almeida Leite for their assistance with data collection, and Charles Ray for assisting with identification. David Kerns, Pioneer, Dekalb, Chromatin, Inc., and Dow AgroSciences provided seed for these trials. Funding for these studies was provided by the United Sorghum Checkoff Program, Alabama Wheat and Feed Grain Producers, Alabama Farmers Federation, and the Alabama Agricultural Experiment Station.

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