Influence of Sorghum Cultivar, Phenological Stage, and Fertilization on Development and Reproduction of Melanaphis sacchari (Hemiptera: Aphididae)

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Influence of sorghum cultivar, phenological stage, and fertilization on development and reproduction of *Melanaphis sacchari* (Hemiptera: Aphididae)

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Abstract

The sugarcane aphid, *Melanaphis sacchari* (Zehntner) (Hemiptera: Aphididae), is an invasive pest of grain sorghum, *Sorghum bicolor* (L.) Moench (Poaceae). Since its first outbreak in sorghum in 2013, severe infestations have spread throughout the southern USA, causing major economic losses. Whereas insecticide applications can mitigate some of the pest's impacts, a sustainable ecology-based management program is needed to reduce reliance on chemical control. Two greenhouse assays examined the influence of selected host plant characteristics on *M. sacchari* life table parameters. We studied the effects of silicon (rates equivalent to 0 and 3,360 kg silicon per ha) and nitrogen (rates equivalent to 0, 110, and 224 kg nitrogen per ha) on *M. sacchari* growth and reproduction on a susceptible cultivar (SP 7868) in 2 phenological stages (5-leaf stage and boot stage). A second experiment examined the same silicon and nitrogen treatments on resistant (DKS 37-07) and susceptible (DKS 38-88) cultivars of grain sorghum. We calculated *M. sacchari* life table parameters including the intrinsic rate of increase, finite rate of increase, doubling time, and mean generation time for each treatment. Aphid population growth parameters were greater for plants in the 5-leaf stage than in the boot stage. In both experiments, nitrogen fertilization had a positive effect on *M. sacchari* fecundity, but effects of nitrogen on other parameters were less consistent. Silicon had a negative effect on life table parameters on sorghum plants in the boot stage, but effects were not consistent across treatments. Sorghum cultivar DKS 37-07 showed a high level of resistance, because no aphids survived to adulthood. These results suggest that resistant sorghum cultivars and nitrogen management could have a role in integrated pest management of *M. sacchari*.

Key Words: sugarcane aphid, nitrogen; silicon; life table, host plant resistance

Resumen

El áfido de la caña de azúcar, *Melanaphis sacchari* (Zehntner) (Hemiptera: Aphididae), es una plaga invasora de grano del sorgo, *Sorghum bicolor* (L.) Moench. Desde su primer brote en el sorgo en el 2013, las infestaciones severas se han extendido por todo el sur de los Estados Unidos, causando grandes pérdidas económicas. Mientras que las aplicaciones de insecticidas pueden mitigar algunos de los impactos de la plaga, se necesita un programa de manejo sostenible basado en la ecología para reducir la dependencia en el control químico. Dos ensayos de invernadero examinaron la influencia de las características de la planta hospedera seleccionada sobre los parámetros de la tabla de vida de *M. sacchari*. Estudiamos los efectos del silicio (tasas equivalentes a 0 y 3,360 kg de silicio por hectárea) y nitrógeno (tasas equivalentes a 0, 110, y 224 kg de nitrógeno por hectárea) sobre el crecimiento y la reproducción de *M. sacchari* en cultivares susceptibles (SP 7868) en 2 etapas fenológicas (etapa de 5 hojas y etapa de arranque). Un segundo experimento examinó los mismos tratamientos de silicio y nitrógeno en cultivares resistentes (DKS 37-07) y susceptibles (DKS 38-88) del grano de sorgo. Calculamos los parámetros de la tabla de vida de *M. sacchari*, incluyendo la tasa intrínseca de aumento, la tasa finita de aumento, el tiempo de duplicación y el tiempo medio de generación para cada tratamiento. Los parámetros de crecimiento de la población de áfidos fueron mayores para las plantas en la etapa de 5 hojas que en la etapa de arranque. En ambos experimentos, la fertilización con nitrógeno tuvo un efecto positivo en la fecundidad de *M. sacchari*, pero los efectos del nitrógeno en otros parámetros fueron menos consistentes. El silicio tuvo un efecto negativo en los parámetros de la tabla de vida de las plantas de sorgo en la etapa de inicio, pero los efectos no fueron consistentes en todos los tratamientos. El cultivar de sorgo DKS 37-07 mostró un alto nivel de resistencia porque ningún áfido sobrevivió hasta la edad adulta. Estos resultados sugieren que los cultivares de sorgo resistentes y el manejo de nitrógeno podrían tener un papel en el manejo integrado de la plaga de *M. sacchari*.

Palabras Clave: pulgón o áfido de la caña de azúcar; nitrógeno; silicio; tabla de vida; resistencia de la planta hospedera

The sugarcane aphid, *Melanaphis sacchari* (Zehntner) (Hemiptera: Aphididae) is widely distributed among tropical and subtropical regions of the world including Asia, Africa, Australia, North America, and South America (Singh et al. 2004; Zapata et al. 2016). In the continental US, it was first reported in Florida in 1977 and in Louisiana in 1999 (White et al. 2001). *Melanaphis sacchari* remained a sporadic pest of sugarcane, but was not reported as a pest of sorghum in the US until 2013. In that year, a major outbreak in sorghum occurred in Texas, then spread to the surrounding states of Louisiana, Oklahoma, and Mississippi (Villanueva et al. 2014; Bowling et al. 2015). By 2015, it had been reported attacking sorghum in 17 states, and is now considered an important economic pest of sorghum throughout the southern US and Mexico

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(Bowling et al. 2015). *Melanaphis sacchari* injures sorghum by piercing plant tissues with its stylet and sucking the phloem sap, thereby causing nutrient loss (Singh et al. 2004). Furthermore, the aphids secrete honeydew that can later result in black sooty mold covering leaf surfaces and reducing photosynthetic area (Blackman & Eastop 2000; Singh et al. 2004). These problems can reduce the yield of sorghum by 46 to 78% (Van den Berg 2002; Bowling et al. 2015), and in some instances have resulted in complete crop loss (Sharma et al. 1997; Bowling et al. 2015). The economic value of sorghum in 2015 was approximately US $2 billion, which was the highest in recent years. However, both area and production of sorghum in the US have declined from 2015/2016 to 2016/2017 by 21.6% and 19.5%, respectively (USDA 2017). This production decline frequently is attributed to increased input costs associated with *M. sacchari* management. Management of *M. sacchari* in sorghum is focused principally on chemical control and resistant cultivars (Singh et al. 2004; Armstrong et al. 2015), with little emphasis on the effects of agronomic practices on aphid biology. Previous studies have documented positive effects on development and reproduction of insect herbivores, including aphids, with increasing available nitrogen in host plants (Awmack & Leather 2002). Thus, understanding the impact of nitrogen fertilization on *M. sacchari* biology will improve our understanding of how infestations respond to various nitrogen content levels in the host plant.

Silicon is a micronutrient which can affect plant physiology and influence herbivore populations. Silicon is known to induce plant defense mechanisms by enhancing physical resistance to feeding or increasing plant chemical defenses (Gomes et al. 2005; Goussain et al. 2005, Reynolds et al. 2009; Rodrigues & Datnoff 2015). Physical resistance can occur as a mechanical barrier resulting from the deposition of silicon in the form of amorphous silica in leaf tissue, which may impede stylet penetration (Gomes et al. 2005; Moraes et al. 2005). Chemical defense mechanisms involving silicon include induced production of defense enzymes or plant volatiles (Reynolds et al. 2009). Despite considerable research being done on the effects of silicon on plant resistance in various crops, including sorghum, there has been no study of its effect on *M. sacchari*. However, studying the level of resistance provided by the addition of silicon could aid in developing a sustainable integrated pest management (IPM) program for *M. sacchari*.

The overall objective of this study was to examine the influence of host plant characteristics, including sorghum cultivar, phenological stage, and nitrogen and silicon fertilization on *M. sacchari* life table parameters.

Materials and Methods

APHIDS AND PLANTS

The sugarcane aphid colony used in these experiments was founded from a single apterae field-collected from sorghum at the Louisiana State Agricultural Center Dean Lee Research Station, Alexandria, Louisiana, USA, in Jul 2014 by J. A. Davis. This colony, designated LSU-SCA14, is maintained on Pioneer 85G85 (Pioneer Hi-Bred International, Inc., Johnston, Iow, USA) planted in 10-cm diam plastic pots containing sterile potting mix (Sun Gro Horticulture, Beausejour, Manitoba, Canada) and 5 g Osmocote (14-14-14), a slow-release fertilizer (The Scotts Company, Marysville, Ohio, USA). Plants are grown in Percival E-36L2 Plant Growth Chambers (Percival Scientific, Perry, Iowa, USA) held at 25 ± 0.2 °C, 50 ± 5% RH, and a 14:10 h (L:D) photoperiod.

Two experiments were conducted hereafter referred to as the "phenology experiment" and the "cultivar experiment." Plants for the phenology experiment were grown from seeds of a susceptible cultivar (SP 7868) in the greenhouse on the campus of Louisiana State University (Baton Rouge, Louisiana, USA) in plastic pots (6.06 L) with a soil mixture (2 parts autoclaved river silt + 1 part peat + 1 part sand). Silicon was incorporated into the soil as Wollastonite (CaSiO3 23% silicon; Vanderbilt Minerals, LLC, Norwalk, Connecticut, USA) at a rate of 17 g per pot applied to half of the pots prior to planting. This rate corresponds to 3,360 kg silicon per ha at a plant density of 197,000 seeds per ha (Lanclos et al. 2007). Wollastonite contains calcium in addition to silicon, so 9.58 g per pot of lime (CaO; Northcoast Horticultural Supply, McKinleyville, California, USA) was incorporated in all the control pots to offset any potential effects of calcium. The experiment included sorghum at the 5-leaf and boot stages. Seeds were planted on 25 Feb 2017 (for boot stage) and 26 Mar 2017 (for 5-leaf stage). Five seeds were planted initially to ensure sufficient plant establishment, and 4 of the seedlings were removed after emergence. Nitrogen was applied to pots 3 wk after planting at rates of 0.0, 0.75, and 1.51 g per plant, which corresponds to 0, 110, and 224 kg nitrogen per ha, respectively, at a plant density of 150,000 plants per ha. Urea ($(NH_2)_2CO$; Alpha-chemicals, Cape Girardeau, Missouri, USA) was applied on wet soil around the plants by making a round furrow, and then covered by soil to avoid nitrogen loss by volatilization. All pots were irrigated as needed to maintain sufficient soil moisture. Thus, 2 silicon treatments, 3 nitrogen treatments, and 2 sorghum phenological stages resulted in 12 factorial (silicon × nitrogen × phenology) treatment combinations. The experiment was conducted using a completely randomized design with 5 replications. Life table assays were initiated on 26 Apr 2017 and concluded on 27 Jun 2017.

The cultivar experiment was conducted with 2 silicon treatments, 3 nitrogen treatments, and 2 sorghum cultivars resulting in 12 factorial (silicon × nitrogen × cultivar) treatment combinations. All the treatment rates and methodologies were consistent with the first experiment, except that only 1 stage of sorghum (flag leaf stage) was used. In this experiment, a resistant cultivar (DKS 37-07; Dekalb®, Monsanto, St. Louis, Missouri, USA) and a susceptible cultivar (DKS 38-88 Dekalb®, Monsanto, St. Louis, Missouri) were planted on 13 Jul 2017. Life table assays were initiated on 13 Aug 2017 and concluded on 15 Sep 2017. The temperatures for both studies were maintained at 26 °C during the d and 21 °C during the night at 65 ± 5% RH and a 14:10 h (L:D) photoperiod.

LEAF TISSUE ANALYSIS

Leaf tissue analysis was conducted in the cultivar experiment to determine effects of treatments on nitrogen and silicon content. One leaf nearest to the leaf with the caged aphid was excised from each plant for analysis of nutrient composition. Nitrogen content analysis of leaf tissues was conducted on 30 Aug 2017 at the Louisiana State University AgCenter Soil and Plant Analysis Lab (Baton Rouge, Louisiana) using the Dumas Dry-Combustion method (Horneck & Miller 1998). Similarly, the silicon content was determined by oven-induced digestion and silicon colorimetric procedures (Kraska & Breitenbeck 2010).

MELANAPHIS SACCHARI LIFE TABLE ASSAYS

To determine the effect of treatments on population growth parameters of *M. sacchari*, no-choice life table assays were conducted following the methods defined by Carey (1993) and Davis et al. (2006). A single adult wingless aphid (5 aphids per treatment) was enclosed in a 1.2-cm diam clip cage on the abaxial surface of the third fully expanded leaf below the whorl of each plant and was left to larviposit for 24 h. After nymphs were deposited, the adult and all but a single first instar nymph were removed from each cage. Aphid survival and reproduction were monitored daily. Aphid development and reproduction param-

eters were recorded including age (*x*) in d, age-specific survival (*lx*), d to reproductive adult, fecundity (*mx*), and age-specific fecundity (*lxmx*). Lifespan was recorded as the d from birth of the aphid to its death. Life table parameters such as intrinsic rate of increase (r_m), mean generation time (*TG*), finite rate of increase (λ), and doubling time (*DT*) were calculated using Equations 1 to 4 of Birch (1948) and Carey (1993).

Intrinsic rate of increase (r_m):	e^{-rm} *lxmx* = 1	[Eq. 1]
Finite rate of increase (λ):	$\lambda = e^{rm}$	[Eq. 2]
Net reproductive rate (R0):	R0 = Σ lxmx	[Eq. 3]
Generation time (T_G):	$T_G = ln\ (R0)/r_m$	[Eq. 4]
Doubling time (DT):	DT = ln (2)/r_m	[Eq. 5]

DATA ANALYSIS

Pre-reproductive period, total fecundity, and lifespan data from the phenology experiment were analyzed with using mixed model analyses (Proc Mixed) (SAS Institute 2011) which included nitrogen fertilization, silicon amendment, sorghum phenology, and the interactions as fixed effects. Nitrogen and silicon content from the cultivar experiment were analyzed using mixed model analyses (Proc Mixed) (SAS Institute 2011) which included nitrogen fertilization, silicon amendment, sorghum cultivar, and the interactions as fixed effects. In the cultivar experiment, none of the aphids on DKS 37-07 survived long enough to collect data for any of the parameters. Thus, only data from the susceptible cultivar were analyzed. In all analyses, the Kenward-Roger method was used for calculation of error degrees of freedom and Tukey's HSD (α = 0.1) was used for mean separation. For both experiments, the jackknifing technique was employed to estimate means and 95% CI (confidence interval) for all life table parameters. This technique is done by repeated calculation of the parameter estimates by excluding 1 sample in turn as described by Meyer et al. (1986), and used in the studies of Maia et al. (2000), Zamani et al. (2006), Hosseini et al. (2010), Rostami et al. (2012), and Eini et al. (2017).

Results

LEAF TISSUE ANALYSIS

Leaf nitrogen content (Fig. 1) was affected by nitrogen fertilizer (F = 8.17; df = 2, 44; P = 0.001), silicon amendment (F = 15.25; df = 1, 44; P = 0.03), and cultivar (F = 4.65; df = 1, 44; P = 0.03), but no interactions were detected. Leaf silicon content (Fig. 2) was affected by silicon amendment (F = 149.22; df = 1, 47; P < 0.001) and nitrogen fertilization (F = 10.07; df = 2, 47; P < 0.001), but not by sorghum cultivar or any of the interactions.

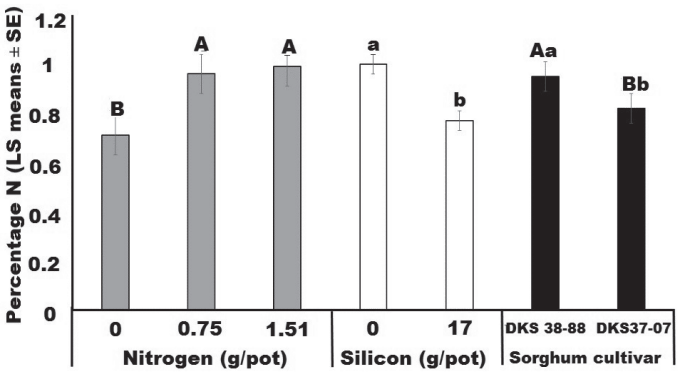

Fig. 1. Nitrogen content in leaf tissues as affected by N-fertilization (grey bars), Si-amendment (white bars), and sorghum cultivar (black bars). Bars of the same color followed by the same letter are not significantly different (P > 0.05).

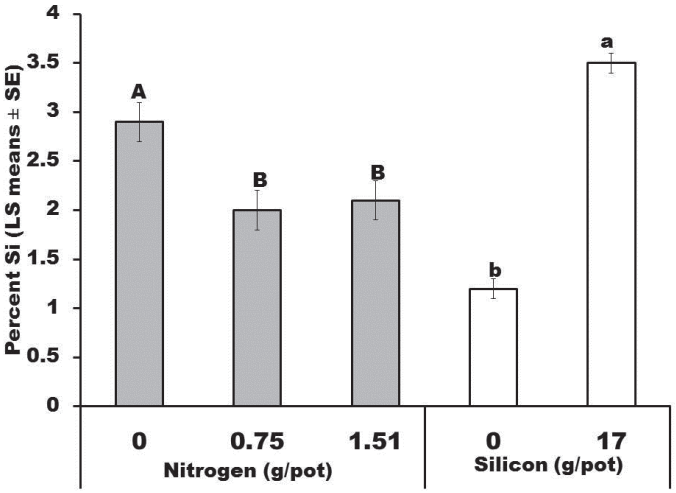

Fig. 2. Silicon content in leaf tissues as affected by N-fertilization (grey bars) and Si-amendment (white bars). Bars of the same color followed by the same letter are not significantly different (P > 0.05).

PHENOLOGY EXPERIMENT

The pre-reproductive period (Fig. 3A) of *M. sacchari* was greater in the boot stage than in the 5-leaf stage (F = 3.93; df = 1, 48; P = 0.053), but was not affected by either nitrogen fertilization, silicon amendment, or their interactions. The fecundity of *M. sacchari* (Fig. 3B) was greater in plants which received nitrogen fertilization than those that did not (F = 7.60; df = 2, 48; P = 0.001), but was not influenced by silicon, phenology, or any of the interactions. The lifespan of *M. sacchari* (Fig. 3C) was greater in plants which received nitrogen fertilization (F = 11.77; df = 2, 48; P = 0.001) and plants in the 5-leaf stage (F = 3.41; df = 1, 48; P = 0.07), but no effects of silicon or any of the interactions were detected. Nitrogen affected the intrinsic rate of increase (r_m), finite rate of increase (λ), doubling time (*DT*), and generation time (T_G) of *M. sacchari* in the 5-leaf stage, but only T_G and DT were affected in the boot stage (Table 1). Silicon had a variable effect on parameters during boot and the 5-leaf stage (Table 1). Sorghum phenology affected r_m, λ, and T_G with higher rates of increase in the 5-leaf stage than the boot stage (Table 2).

CULTIVAR EXPERIMENT

No aphids survived to reproduction on resistant cultivar DKS 37-07 regardless of nitrogen or silicon treatments. Dead aphids were replaced with new nymphs a total of 5 times for each plant of DKS 37-07. Nymphs survived only 2 d on average, and none lived greater than 4 d. Therefore, we were not able to generate data for analysis from this cultivar. The results presented below are from aphids which were fed on susceptible cultivar DKS 38-88.

Aphids caged on plants with no nitrogen fertilization took longer (F = 3.60; df = 2, 24; P = 0.043) to reach the reproductive stage than aphids caged on plants which received higher rates of nitrogen fertilization (Fig. 4A). No effect of silicon or the interaction was seen on the pre-reproductive period. The fecundity of *M. sacchari* (Fig. 4B) was more than 2-fold greater in plants fertilized with nitrogen than unfertilized plants (F = 19.81; df = 2, 24; P < 0.001), but no effects of silicon or the interactions were detected. Lifespan of *M. sacchari* (Fig. 4C) was

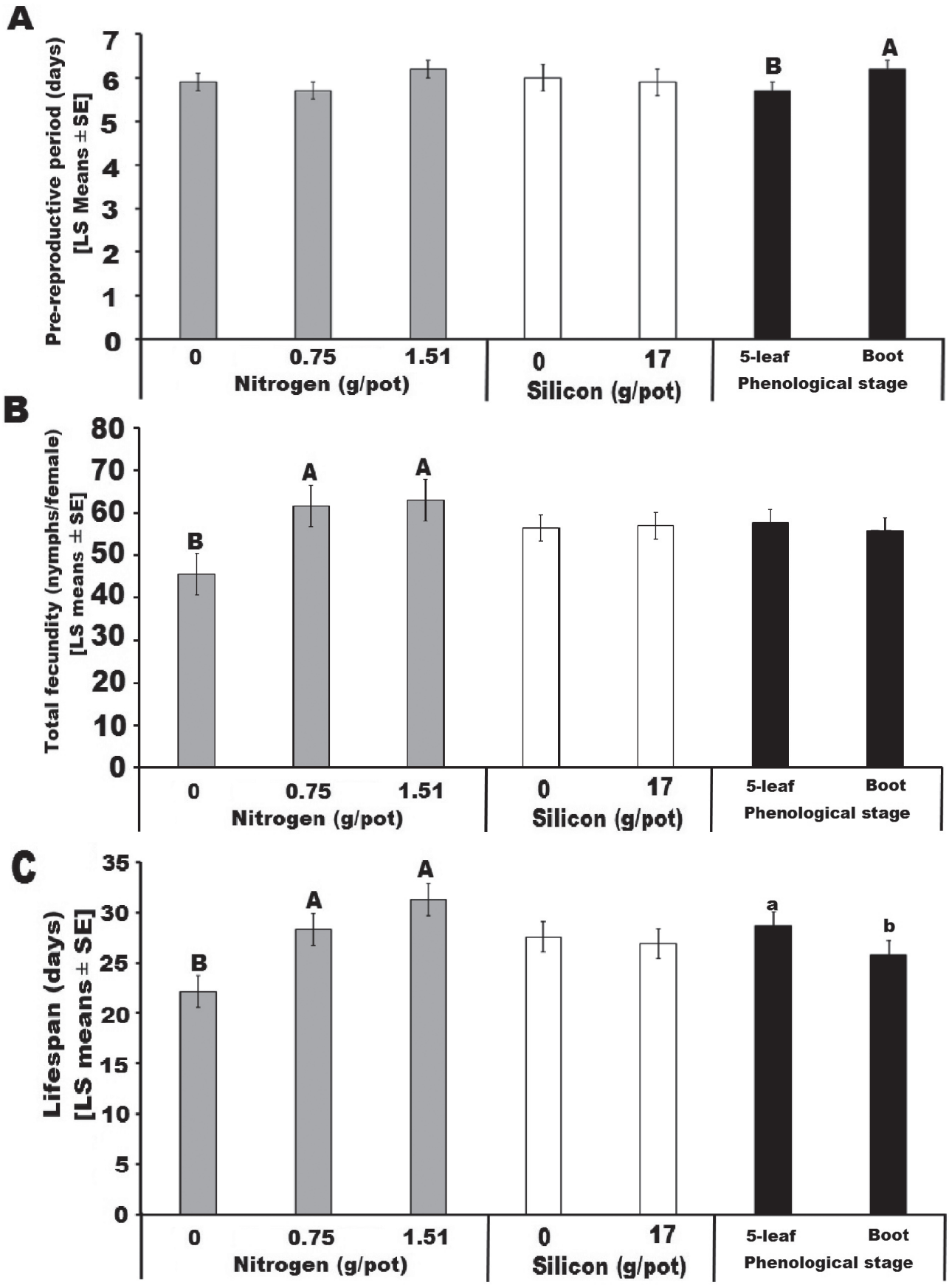

Fig. 3. *Melanaphis sacchari* pre-reproductive period (A), total fecundity (B), and lifespan (C) as affected by N-fertilization (grey bars), Si-amendment (white bars), and phenological stage (black bars) in the phenology experiment. Bars of the same color followed by the same letter are not significantly different ($P > 0.10$).

Table 1. Effect of different N and Si fertilization levels on life table parameter estimates of *M. sacchari* in the phenology experiment. Jackknife estimates (means) and associated 95% CI.

Phenological Stage	Fertilization treatment	r_m	λ	*DT* (days)	T_G (days)
5-leaf	Nitrogen (g)				
	0	0.25 ± 0.06 b	1.29 ± 0.02 c	2.75 ± 0.12 a	10.53 ± 0.52 a
	0.75	0.35 ± 0.06 a	1.36 ± 0.02 b	2.13 ± 0.23 b	9.37 ± 0.43 b
	1.51	0.40 ± 0.09 a	1.43 ± 0.02 a	1.96 ± 0.12 b	9.16 ± 0.41 b
	Silicon (g)				
	0	0.25 ± 0.06	1.29 ± 0.02 b	2.75 ± 0.22 a	10.53 ± 0.92
	17	0.31 ± 0.09	1.36 ± 0.03 a	2.24 ± 0.20 b	9.80 ± 0.79
Boot	Nitrogen (g)				
	0	0.21 ± 0.04	1.27 ± 0.02	3.25 ± 0.18 a	13.77 ± 1.22 a
	0.75	0.20 ± 0.06	1.24 ± 0.07	3.24 ± 0.24 a	13.62 ± 0.89 a
	1.51	0.25 ± 0.08	1.28 ± 0.03	2.88 ± 0.20 b	10.43 ± 0.76 b
	Silicon (g)				
	0	0.31 ± 0.04 a	1.37 ± 0.02 a	2.68 ± 0.28 b	9.96 ± 1.03 b
	17	0.21 ± 0.04 b	1.24 ± 0.01 b	3.31 ± 0.10 a	13.42 ± 1.20 a

Non-overlapping 95% CI corresponds to a significant treatment effect (α = 0.05) which are denoted by separate letters (Maia et al. 2000).

not affected by either nitrogen fertilization, silicon, or the interaction. Intrinsic (r_m) and finite (λ) rates of increase were higher in plants that received the highest rate of nitrogen (Table 3). No effect of nitrogen was observed on generation time (T_G), and the longest average T_G of 9.31 d was recorded for *M. sacchari* with no nitrogen fertilization. Silicon did not affect any of the life table parameters in the cultivar experiment.

Discussion

In our study, we illustrated the effects of sorghum cultivar, phenology, nitrogen, and silicon content on *M. sacchari* life table parameters. Sorghum cultivar exerted the greatest influence on *M. sacchari* biology because no aphids survived to reproductive adults on resistant cultivar DKS 37-07. This effect is considerably greater than impacts of resistant cultivar KS 116B which reduced the intrinsic rate of increase by approximately 60% in life table studies (Bayoumy et al. 2016), suggesting DKS 37-07 possesses higher levels of resistance than other resistant cultivars. Although mechanisms of resistance were not examined in this study, the lower nitrogen content in leaves of DKS 37-07 relative to DKS 38-88 suggests resistance may be related to nutritional content. Although our data show DKS 37-07 has high resistance to *M. sacchari*, field studies have shown an intermediate level of resistance to this pest (Michaud & Zukoff 2017). The same cultivar reduced field infestations by approximately 50 to 75% relative to a susceptible cultivar, suggesting its resistance is variable under field conditions (Szczepaniec 2018). The discrepancy between our findings and those from field studies likely results from the exceedingly high inoculum present under high pest pressure (> 1000 aphids per plant) in the field compared to the greenhouse. Findings from life table assays should be re-evaluated under conditions in which high pest pressure can overcome resistance.

Table 2. Effect of sorghum phenology on life table parameter estimates of *M. sacchari*. Jackknife estimates (means) and associated 95% CI.

Phenological stage	r_m	λ	*DT*	T_G
5-leaf	0.31 ± 0.03 a	1.34 ± 0.02 a	2.37 ± 0.14	10.53 ± 1.15 b
Boot	0.24 ± 0.02 b	1.28 ± 0.02 b	3.07 ± 0.11	13.77 ± 1.30 a

Non-overlapping 95% CI corresponds to a significant treatment effect (α = 0.05) which are denoted by separate letters (Maia et al. 2000).

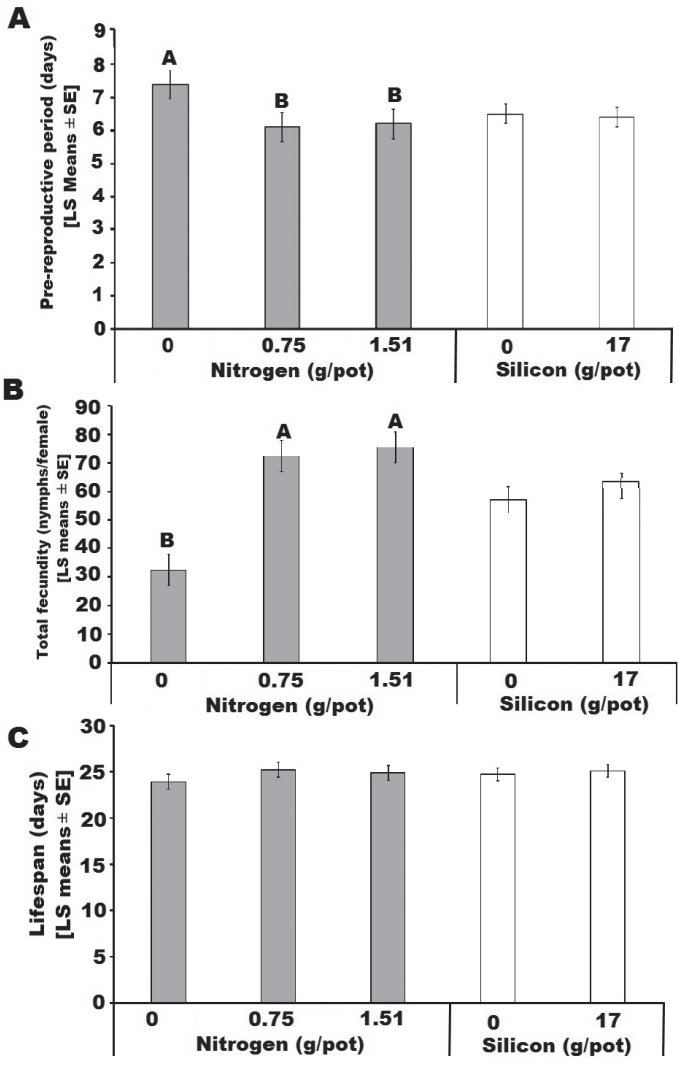

Fig. 4. *Melanaphis sacchari* pre-reproductive period (A), total fecundity (B), and lifespan (C) as affected by N-fertilization (grey bars) and Si-amendment (white bars) in the cultivar experiment. Bars of the same color followed by the same letter are not significantly different ($P > 0.10$).

Table 3. Effects of Si and N treatments on life table parameter estimates of *M. sacchari* in the cultivar study. Jackknife estimates (means) and associated 95% CI.

Fertilization treatment	r_m	λ	*DT*	T_G
Nitrogen (g)				
0	0.29 ± 0.04 b	1.34 ± 0.01 b	2.36 ± 0.19 b	9.31 ± 0.93
0.75	0.30 ± 0.18 ab	1.35 ± 0.05 b	2.30 ± 0.21 b	9.24 ± 1.29
1.51	0.50 ± 0.15 a	1.64 ± 0.06 a	1.39 ± 0.28 a	7.26 ± 1.09
Silicon (g)				
0	0.36 ± 0.04	1.43 ± 0.01	2.35 ± 0.21	9.06 ± 1.16
17	0.36 ± 0.05	1.43 ± 0.02	2.34 ± 0.21	9.03 ± 1.14

Non-overlapping 95% CI corresponds to a significant treatment effect (α = 0.05) which are denoted by separate letters (Maia et al. 2000).

Our study adds to a growing body of evidence that resistant cultivars can and do play a key role in integrated pest management programs for *M. sacchari* (Armstrong et al. 2015; Bayoumy et al. 2016; Brewer et al. 2017; Szczepaniec 2018). Several resistant germplasms now have been identified, including cultivars with cross resistance to greenbug, *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae) (Armstrong et al. 2015). Resistant cultivars are compatible with insecticide usage, naturally occurring biological controls, and cultural controls such as early planting (Szczepaniec 2018), and are a critical component of *M. sacchari* management strategies (Knutson et al. 2016; Michaud & Zukoff 2017). Aphid population growth was numerically greater in our cultivar study (DKS 38-88) than our phenology study (SP 7868), suggesting these cultivars differ in their levels of susceptibility. Continued investigation of resistant germplasm is required, because genetic variation exists among US populations of *M. sacchari* that could lead to the development of new biotypes able to overcome cultivar resistance (Medina et al. 2017; Nibouche et al. 2018).

The rates of development, fecundity, and population increase observed in our study are consistent with previous life table studies with *M. sacchari* on susceptible sorghums (Bayoumy et al. 2016; Michaud et al. 2017). However, greater rates of population growth were documented on other susceptible sorghums (Bayoumy et al. 2016; Michaud et al. 2017). These studies highlight the remarkable reproductive potential of this pest, and support the need for frequent pest scouting (Brewer et al. 2017) throughout the growing season. Our data suggest that sampling and management plans will be influenced by fertilization practices and infestation timing, in addition to sorghum cultivars, because these factors affect aphid population growth rates.

Following sorghum cultivar, nitrogen fertilization had the greatest influence on population growth of the factors examined in our study. The nutritional content of a host plant has an important influence on growth and reproduction of herbivores (Dixon 1977) with increases in nitrogen fertilizer generally enhancing insect growth and reproduction (Lu et al. 2007). Increased nitrogen content is reported to increase total amino acid content in plants that are key nutrients for aphid growth and reproduction (Sauge et al. 2010). In this study, nitrogen fertilization had the most consistent benefit to total fecundity, which was 1.5-fold and 2-fold greater in fertilized vs unfertilized plants in the phenology and cultivar experiments, respectively. The positive influence of nitrogen on the nymphal development rate observed only in the cultivar experiment, and the improved lifespan in the phenology experiment, indicate the influence of nitrogen on these parameters is more variable. This discrepancy may be the result of the different cultivars used in each experiment, DKS 38-88 (cultivar experiment) and SP 7868 (phenology experiment). These findings are similar to those from life table studies with other aphid species that demonstrated the greatest effect of nitrogen on fecundity with more variable effects on nymphal development and overall lifespan. For example, positive effects of nitrogen on fecundity and lifespan, but not nymphal development, were reported for the cotton aphid, *Aphis gossypii* Glover (Hosseini et al. 2010), and the cherry-oat aphid, *Rhopalosiphum padi* (L.) (both Hemiptera: Aphididae) (Aqueel & Leather 2011). Positive effects of nitrogen on aphid fecundity and nymphal development rates, but not on lifespan, have been reported for the cabbage aphid, *Brevicoryne brassicae* L. (Zarghami et al. 2010), and the rose-grain aphid, *Metopolophium dirhodum* Walker (both Hemiptera: Aphididae) (Gash 2012). The increased level of silicon in plants that did not receive nitrogen in our study may have further hindered aphid development, though no nitrogen by silicon interaction was detected in any parameter measured. Results from our study provided the first documentation of the beneficial influence of nitrogen fertilization of sorghum on population growth of *M. sacchari*, and add to literature supporting general positive effects of host plant nitrogen on aphid development. Future studies should examine influences of lower rates of nitrogen fertilization and determine how these affect *M. sacchari* infestations in the field.

In both of our experiments, silicon had no detectable effect on *M. sacchari* fecundity, d to reproductive adult, lifespan, and life table parameters despite silicon concentration being > 3-fold greater in plants that received the silicon amendment. In the phenology experiment, when only the boot stage is considered, silicon amendment affected r_m, λ, *DT*, and T_G, but the effect was not consistent across other treatments, and the opposite effect was observed at the 5-leaf stage. These results contrast with some of the other studies where silicon significantly reduced the fecundity and population growth of *S. graminum* in wheat, *Triticum* spp. L. (Goussain et al. 2005); *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae) in corn, *Zea mays* L. (Poaceae) (Moraes et al. 2005); *Sitobion avenae* (F.) (Hemiptera: Aphididae) in wheat (Dias et al. 2014), and *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) in zinnia, *Zinnia elegans* Jacq. (Asteraceae) (Ranger et al. 2009). This contradictory result of our study might be due to the different source of silicon used and the methods of application. The studies conducted by Goussain et al. (2005), Moraes et al. (2005), and Dias et al. (2014) used furnace slag, sodium silicate solution, and silica gel solution as a source of silicon, respectively. Although the Wollastonite amendments in our study effectively increased leaf tissue silicon content, the distribution of silicon within plant tissue may be influenced by the silicon source and method of application. Furthermore, in studies conducted by Goussain et al. (2005) and Moraes et al. (2005) aphid fecundity was reduced only in the treatment with soil plus foliar applications of silicon even though leaf silicon content in this treatment was not different from plants that received only 1 soil application of silicon. One possible explanation for this is that foliar application of silica solution improves the distribution of silicon in all plant parts (Moraes et al. 2005). Our results suggest that silicon amendment to sorghum plants does not reduce the reproductive potential of *M. sacchari*. Further, silicon amendment in our study resulted in reduced nitrogen content in leaf tissues, suggesting the amendments may be disruptive to other agronomic practices if used in a commercial setting. Whereas our study indicates

silicon amendment has limited potential as a *M. sacchari* management tactic, future examinations of other silicon sources and application methods may be warranted because of the negative effects of silicon amendment on aphid development in other aphid/host plant systems.

The influence of host plant phenology on aphid life table parameters was minimal in our study relative to effects of cultivar and nitrogen fertilization. Increased intrinsic (r_m) and finite (λ) rates of increase in the 5-leaf stage likely resulted from the increased rate of nymphal development and lifespan, because fecundity was not different between phenological stages. Field studies have shown *M. sacchari* infestations increased faster when they occurred in the boot stage relative to infestation, which occurred in the soft-dough stage (Szcsepeniac 2018), but younger sorghum plants were not examined in that study. Our study provides evidence that population growth may be greatest early in the growing season, and managing the pest in these stages is critical. Foliar insecticide applications to sorghum in the 5-leaf stage may not be needed, because widely used insecticidal seed treatments can protect plants for up to 6 wk after planting (Szczepaniec 2018).

Although our study provides insights into the effects of several factors on aphid population growth, field studies are needed to better understand how production practices affect *M. sacchari* management on commercial farms. Alternatives to chemical controls such as *M. sacchari* resistant cultivars are needed to reduce the input costs associated with pest management in commercial sorghum production. The ongoing infestation of sorghum throughout the southern US necessitates continued research into IPM strategies for *M. sacchari*.

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