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# Utilizing biodemographic indices to identify perennial bioenergy grasses as sugarcane aphid (Hemiptera: Aphididae) host plants

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## ABSTRACT

The sugarcane aphid [*Melanaphis sacchari* (Zehntner) (Hemiptera: Aphididae)] has been rapidly spreading in the United States and can cause devastating economic losses on sorghum [*Sorghum bicolor* (L.) Moench] when an effective management program is not utilized. Our objective was to determine if some of the most commonly used candidate bioenergy grasses can be alternative hosts of the sugarcane aphid. Host suitability was evaluated using aphid mortality and reproduction on each warm-season grass. An excised leaf bioassay was conducted for two continuous generations using eight bioenergy grasses and Johnsongrass [*Sorghum halepense* (L.) Pers.] as the control. Hosts that sustained multiple generations of the sugarcane aphid included Johnsongrass, energycane (*Saccharum* spp.), and giant miscanthus (*Miscanthus* x *giganteus or Miscanthus sinensis* x *M. sacchariflorus* Greef & Deuter ex Hodkinson & Renvoize). Poor hosts included the napiergrass [*Cenchrus purpureus* (Schumach.) Morrone] cultivar Merkeron, giant reed (*Arundo donax* L.), and switchgrass (*Panicum virgatum* L.) cultivar GA-001. *Erianthus arundinaceus* (Retz.) Jeswiet was a good host for first generation sugarcane aphids but a poor host for second generation aphids. Thus, the findings from the current study suggest that, if widespread planting of these bioenergy grasses were to occur, the plantings of napiergrass, giant reed, and switchgrass may prevent the further increase of the aphid population. Whereas the planting of the energycane and giant miscanthus may exacerbate sugarcane aphid damage on sorghum.

**KEYWORDS:** *Melanaphis sacchari*, mortality, daily nymph production, life span, alternative hosts.

## INTRODUCTION

The sugarcane aphid is a major pest of sorghum and sugarcane [*Saccharum officinarum* (L.)] worldwide, encompassing 33 countries [1]. In the United States, the sugarcane aphid had been limited primarily to infestations on sugarcane in Florida, Hawaii, and Louisiana [2- 4] but reports have described the sugarcane aphid on sorghum in Florida as early as 1922 [5, 6]. In the summer of 2013, the sugarcane aphid was found on grain sorghum near Beaumont, TX [7]. From the initial infestation in 2013 the sugarcane aphid spread and as of 2019 has been documented to be in 21 states and over 450 counties throughout the sorghum belt. In recent years, the sugarcane aphid has

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caused devastating reductions to sorghum yields due to plant death, delayed or no flowering [8, 9] and mechanical harvesting problems because of the stickiness of the honeydew produced by the aphids [7]. The adoption of early detection by scouting of sorghum fields, the use of hybrids with host resistance, and the use of insecticides are recommended to prevent yield loss.

The worldwide diversity of the sugarcane aphid has been examined from collections made from 2002 to 2009 and has been defined as five multilocus lineages with very low genetic diversity [10]. The distribution of the multlilocus lineages is strongly influenced by geography and not by host plant [10]. The multilocus lineages were defined as A-Africa, B-Australia, C-South America, the Caribbean, and the Indian Ocean including East Africa, D-USA, and E-China. The lineages A and C had a wide distribution and were defined as superclones. Since the 2013 invasion, sugarcane aphid samples collected from sorghum and Johnsongrass in the U.S. were found to be predominantly a single clone and this clone was designed as belonging to MLL-F [11-14]. Sugarcane aphids belonging to MLL-D were found after 2013 in the U.S. but only on sugarcane [14].

Reported hosts of the sugarcane aphid include *Saccharum* spp. and *Sorghum spp*. Additional hosts of the sugarcane aphid include bermudagrass (*Cynodon dactylon* L.), Chinese silvergrass (*Miscanthus sinensis* Andersson), rice (*Oryza sativa* L.), barnyard grass [*Echinochloa colonum* (L.) Link], Guinea grass (*Panicum maximum* Jacq.), hairy crabgrass [*Digitaria sanguinalis* (L.) Scop.], foxtail millet [*Setaria italica* (L.) P. Beauv.], wild sorghum [*Sorghum verticilliflorum* (Steud.) Stapf], and corn (*Zea mays* L.). Yet, colonization of corn has only been reported in a single country -Bhutan [1]. A host study using sugarcane aphids from sorghum in the U.S. found that these sugarcane aphids could not survive on field corn, Teff grass [*Eragrostis tef* (Zucc.)], proso millet (*Panicum miliaceium* L.), barley (*Hordeum vulgare* L.), or rye (*Secale cereale* L.), but could survive on Johnsongrass and sorghum [7].

Biofuels have the potential to replace a substantial fraction of the limited petroleum-based hydrocarbons [15]. Most renewable fuels in the U.S. are supplied by corn ethanol. However, a need exists to utilize crops for biofuels that are not used for human or animal consumption and, thus, production of corn ethanol has been capped at 57 billion L per year [16]. An additional 80 billion L per year is expected to be met by lignocellulosic biomass crops primarily from the southeastern U.S. [16]. Perennial $C_4$ grasses have high potential dry matter yields and many have rapid establishment. Candidate perennial grass biomass crops for the southeast include napiergrass, energycane, sugarcane, sweetcane (*S. arundinaceum*), giant miscanthus, giant reed, and switchgrass [16]. However, perennial bioenergy grasses that have been proposed as lignocellulosic bioenergy crops throughout the U.S. could also serve as new alternative hosts for the sugarcane aphid since many are related to sugarcane and sorghum.

Biodemography is defined as a sub-discipline that aims to understand the fundamental determinants of mortality, reproduction, aging, and life span of an insect in the entomological literature [17, 18], which is critical in determining whether a plant species could serve as the potential host of an invasive insect pest. In this study eight candidate grass biomass crops for the southeast were evaluated to determine if they could serve as possible hosts for the sugarcane aphid. Three key biodemographic indices (i.e., mortality, reproduction rate, and life span) were measured for two generations.

## MATERIALS AND METHODS

### Aphid source and culture of age-specific aphids for the experiments

The sugarcane aphids were collected from infested Johnsongrass on a roadside, near a creek, in Tifton, GA (LAT: N31°29’1.864”; LON: W83°29’43.15”) for each experiment. Aphids on Johnsongrass were collected, adults were then identified, and alates were excluded. To obtain age-specific aphids for each experiment, non-infested Johnsongrass leaf blades (the third leaf from the top of the plant) were cut into five, approximately 6-cm strips, and placed individually onto a Petri dish containing benzimidazole agar.

The agar plate leaflet bioassay method has been used for life table monitoring of the Russian wheat aphid development on barley [19], to assess the role of plant growth regulators in preventing black pecan aphid [*Melanocallis caryaefoliae* (Davis) (Hemiptera: Aphididae)]-elicited leaf chlorosis [20], to assess the role of pecan [*Carya illinoinensis* (Wangenh.) K Koch] leaves with chlorotic feeding injury on black pecan aphid settling and nymphal development [21], and to assess fall armyworm [*Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) feeding on maize and sorghum genotypes [22]. Three Petri dishes containing benzimidazole agar were used. Four apterous adults were placed onto each leaflet for a total of 20 adult aphids per Petri dish. The Petri dishes with aphids were sealed with Parafilm M (Bemis, Oshkosh, WI) and placed in an I-30 BLL incubator (Percival Scientific, Perry, IA) at 25 °C with a photoperiod of 12:12 (L:D). The adult aphids were removed in 24 h and only the age-specific nymphs (produced within the 24-h period) were reared on Johnsongrass leaflets for either 3 (Trial 1) or 4 d (Trial 2) before they were used to initiate the leaflet bioassay experiments. Only apterous nymphs were used for the experiment.

**Leaf tissue of potential hosts**

Leaf blades of the eight perennial bioenergy grasses (i.e., all entries except Johnsongrass in Table 1) used as biofuel feedstocks were obtained from established field plots in Tifton, GA from 24 April 2015 to 2 July 2015. The bioenergy grass entries included two energycane cultivars ‘Ho 06-9001’ and ‘Ho 02-147’ and one sugarcane cultivar ‘Ho 95-988’ (planted Sept. 2007) [23]. Cultivar ‘Ho 06-9001’, a $BC_1$ between sugarcane and wildcane (*S. spontaneum*-wildcane is the recurrent parent), is a Type II energycane that produces primarily lignocellulosic biomass and very little free sugar. Cultivar ‘Ho 02-147’, an $F_1$ hybrid between sugarcane and wildcane, is also a Type II energycane that has slightly higher free sugar content than ‘Ho 06-9001’ but is also grown primarily for lignocellulosic biomass. Cultivar ‘Ho 95-988’ is from a complex pedigree of *Saccharum* species (*Saccharum officianarum*, *S. robustum* Brandes & Jeswiet ex Grassl, *S. spontaneum* L., *S. barberi* Jeswiet, and *S. sinense* Roxb. amend. Jeswiet) [24]. In addition, five other perennial bioenergy grasses were also examined as potential sugarcane aphid hosts. The five additional grasses were: *Erianthus*

**Table 1.** List of the eight bioenergy grasses and Johnsongrass (a known host) evaluated as potential hosts of the sugarcane aphid.

| Entry | Common name | Genus | Species | Genotype | Pedigree |
|---|---|---|---|---|---|
| 1 | Energycane | *Saccharum* | hybrid | Ho 06-9001 | *S. spontaneum* (*S. officinarum x S. spontaneum*) |
| 2 | Energycane | *Saccharum* | hybrid | Ho 02-147 | *S. officinarum x S. spontaneum* |
| 3 | Napiergrass | *Cenchrus* | *purpureus* | Merkeron | |
| 4 | Giant reed | *Arundo* | *donax* | | |
| 5 | Sugarcane | *Saccharum* | hybrid | Ho 95-988 | Complex - see ‘materials and methods’ |
| 6 | Johnsongrass | *Sorghum* | *halepense* | | |
| 7 | Switchgrass | *Panicum* | *virgatum* | GA-001 | |
| 8 | Sweetcane | *Erianthus* | *arundinaceus* | | |
| 9 | Giant miscanthus | *Miscanthus x* | *giganteus* | | *M. sinensis x M. sacchariflorus* |

*arundinaceus* (formerly *Saccharum arundinaceum Retz.*) and giant miscanthus that are both close relatives of *Saccharum*, switchgrass cultivar 'GA-001', napiergrass cultivar 'Merkeron' [25], and giant reed. Johnsongrass which is a known host for sugarcane aphids was used as the control for the experiment (Table 1, Entry 6). The perennial bioenergy grasses were fertilized in the spring with recommended applications for each species and harvested in the late fall of each year.

**Excised leaflet bioassay - First generation**

The experiment was performed using the leaflet bioassay that has been used for multiple aphid species [19-21]. To assess the inter-generational effect of a host plant on aphid biology, the aphids on the same host were evaluated continuously for two generations. The aphid survival, mortality, and reproduction were recorded daily for the two trials of the two continuous aphid generations on a host. The experiment was conducted between April 24 and July 2, 2015 in a growth chamber as described previously. For each potential host used in the experiment, the third leaf blade from the top of a plant was randomly sampled by removing the leaf blade at the leaf collar near the sheath and one leaf blade was used per Petri dish. Five leaf pieces of approximately 6-cm per leaf blade were placed on benzimidazole agar in a Petri dish. One aphid was placed on each leaf piece (a total of five age-specific aphids per Petri dish). The reason for using 3-4 d old nymphs in the experiment was to minimize mortality or injury caused by transferring nymphs with a camel-hair brush, which would be confounded with the mortality caused by an unsuitable host. For each entry, five leaf blades from five plants (one leaf blade per plant) were sampled and were used to make the five replicates (5 Petri dishes) for each trial of the experiment. Leaf pieces used in a trial were replaced every three days or earlier to ensure green leaflets were available at all times for aphid feeding. All efforts were made to maintain green leaf pieces in the agar Petri dishes to minimize possible reduced nutritional value of the excised leaves. Once the infested aphids started reproducing, the number of live and dead adults, as well as the number of newly produced nymphs per leaf piece, was recorded and the nymphs were then removed from the experimental leaf pieces daily until all of the adults had died in the petri dish.

**Excised leaflet bioassay - Second generation**

To further assess if sugarcane aphids can complete a life cycle on the perennial grass hosts, an additional experiment was initiated to continuously assess aphid survival and nymph production of the second aphid generation on the same bioenergy grass hosts. When the aphids were 13 d old on the experimental hosts during the first-generation bioassay, the bioassay for the second generation of sugarcane aphids was initiated. The nymphs produced within 24 h on day 13 were used to start a new experiment by placing the nymphs on new Petri dishes with the same corresponding host tissue following the same procedure as described for the first-generation experiment. The number of live and dead adults and nymphs produced was recorded daily starting when the aphids were 3 d old to match with the data collected from the first-generation bioassay. The second-generation experiment was repeated twice with only six host plants, because sugarcane aphids died or failed to produce nymphs on day 13 for three bioenergy grasses, as described in Table 1.

**Biodemographic parameter assessments**

Three critical biodemographic parameters were recorded in this study to demonstrate whether a perennial warm season grass could serve as an alternative host of the sugarcane aphid; they are mortality, reproduction rate (measured by daily nymph production), and life span. The daily percent mortality was calculated by a simple formula of (5-the number of live aphids)/5, because the experiment was started with five age-specific aphids per Petri dish. In a similar manner, daily nymph production was calculated by the daily record of the number of nymphs divided by the daily number of live adult aphids per Petri dish throughout the experimental period. The life span data were collected based on the daily live aphid record. Since live aphids were recorded daily per Petri dish based on the five age-specific aphids used to initiate the experiment, and all nymphs were recorded and removed daily, the life span of an aphid that was used to initiate

the experiment can be extracted from daily live aphid counts throughout the experiment period. The life span of an aphid would be the number of days when one less aphid (maximum of five aphids per Petri dish) was recorded per Petri dish in a daily aphid sampling.

### Experimental design and data analysis

The experiment utilized a split plot design with two trials considered as the main plots, while the grass entries were considered as the subplot. For the first trial (first generation bioassay) there were nine host plants used as treatment factors and five replications of treatments used as a block factor within a randomized complete block design, while for the second trial (second generation bioassay) there were six host plant treatments and five replications used as the block factor. All mortality and nymph production data were subjected to an analysis of variance (ANOVA) using the PROC MIXED procedure with a REPEATED (Measures) statement of the SAS statistical software v. 9.3 (SAS Institute, Cary, NC) according to [26]. Means were separated using Fisher's Protected LSD test ($P < 0.05$). The data graphs were generated using SigmaPlot software v. 13 (Systat Software Inc., San Jose, CA) or Microsoft Excel 2013 (Microsoft Corp, Redmond, WA).

## RESULTS

### Aphid bioassay data - The first generation

**Aphid reproduction:** The data from the two trials for the first-generation experiment were combined and overall daily nymph production and adult mortality on all grasses were compared. For the first-generation experiment, aphid age had a significant effect on nymph production averaged over all grass genotypes ($F = 41.55$; df = 31, 231; $P < 0.0001$) (Fig. 1). Overall daily nymph production peaked when the aphids were 7 to 14 d old producing on average of 5-6 nymphs per aphid per day and reproduction declined over time until it ceased on day 31 (Fig. 1).

Daily nymph production and mortality were further examined for each warm-season grass (see Supplementary Fig. 1A). Age ($F = 56.11$; df = 31, 231; $P < 0.0001$), genotype ($F = 40.69$; df = 8, 72; $P < 0.0001$), and age by genotype interaction ($F = 5.13$; df = 152, 732; $P < 0.0001$)

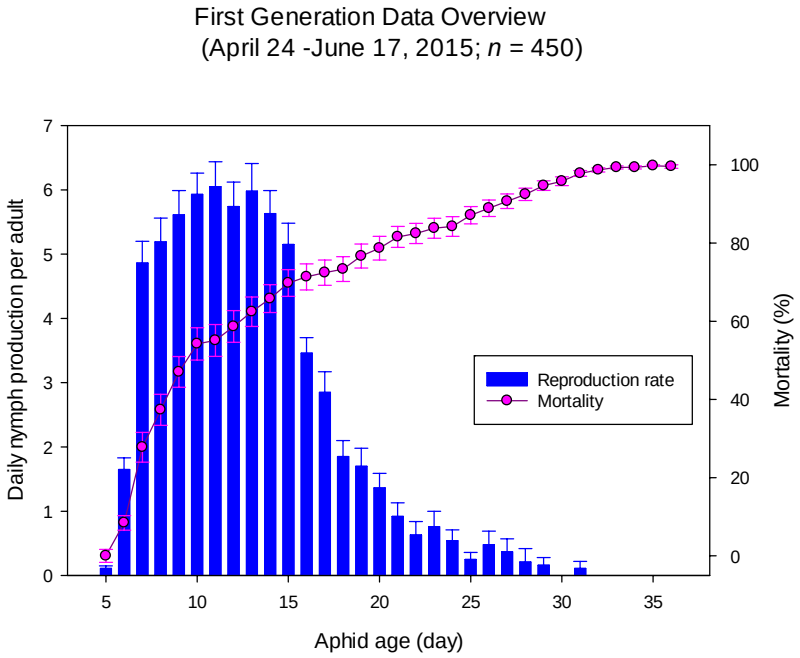


**Fig. 1.** Daily nymph production and adult mortality of the first-generation aphid bioassay combined over all nine grasses listed in Table 1.

significantly affected nymph production. The highest number of nymphs produced per adult per day was observed on Johnsongrass (10 nymphs/d), followed by giant miscanthus (8 nymphs/d), Ho 95-988 (7 nymphs/d) and Ho 06-9001 (6 nymphs/d). This rate of high reproduction lasted 8 to 10 d and occurred when the aphids were 6-14 d old on Johnsongrass (5-10 nymphs/d), 6-14 d old on giant miscanthus (5-8 nymphs/day), 6-16 d old on Ho 95-988 (5-7 nymphs/d), and 6-14 d old on Ho 06-9001 (5-7 nymphs/d). Aphids feeding on Ho 02-147, Merkeron, and sweetcane displayed two peaks in reproduction at 6 and 9 d (4 nymphs/d), at 6 and 8 d (4 nymphs/d), and 13 and 22 d (5 and 6 nymphs/d), respectively. Nymph production was lowest on giant reed and switchgrass cultivar GA-001 with a single peak producing 1 and 2 nymph/d at age 6 and 7 d old, respectively. Reproduction cessation for all grasses examined ranged from 9 to 31 d (Supplementary Fig. 1A). Nymph production stopped the earliest on switchgrass cultivar GA-001 and lasted the longest for sweetcane. Aphid age of reproduction cessation ranged from 26-29 d on *Saccharum* spp., giant miscanthus, and Johnsongrass. Reproduction cessation for napiergrass cultivar Merkeron and giant reed was 12 d (Supplementary Fig. 1A).

**Aphid mortality:** Aphid age significantly affected adult mortality ($F$ = 76.27; df = 33, 277; $P < 0.0001$). The daily change in mortality was high (7-17 %) for aphids aged 4 to 9 d, and the largest increase in daily mortality was when the aphids were 6 d old (17.3 %) (Fig. 1). After day 9, daily mortality increased at a low and steady rate (0-4%) until all adults were dead on day 36 (Fig. 1).

Age ($F$ = 206.50; df = 33, 277; $P < 0.0001$), genotype ($F$ = 339.72; df = 8, 72; $P < 0.0001$), and age by genotype interaction ($F$ = 7.01; df = 264, 2207; $P < 0.0001$) significantly affected adult mortality. The day that all adult aphids died for each warm-season grass host ranged from 9 (switchgrass cultivar GA-001) to 36 d (Ho 06-9001) (Supplementary Fig. 1B). All adult aphids on giant reed and napiergrass cultivar Merkeron died in 13 d. The remainder of the grasses, sweetcane, *Saccharum* spp., giant miscanthus, and Johnsongrass had 100% mortality at 26-36 d (Supplementary Fig. 1B). Among the three *Saccharum* spp., cultivar Ho 02-147 had the highest mortality per day.

**Aphid reproduction and morality per grass entry:** Nymph production and mortality per warm-season grass was compared by pooling data from all sampling dates (Figs. 2A, B). Nymph production was significantly different among the nine grass genotypes ($F$ = 9.02; df = 8, 72; $P < 0.0001$). Sugarcane aphids with the highest nymph production (3-4 nymphs/d) were from Johnsongrass, Ho 06-9001, Ho 95-988, and giant miscanthus leaf blades. Aphids that developed on H0 02-147, napiergrass, and sweetcane had 2-3 nymphs/d. Conversely, sugarcane aphids that developed on switchgrass cultivar GA-001 and giant reed leaf blades had the lowest reproduction (0-1 nymphs/d).

Similarly, when all data from all sampling dates were combined, adult mortality significantly differed among the nine grass genotypes ($F$ = 102.14; df = 8, 72; $P < 0.0001$) (Fig. 2B). Adult mortality was the lowest on the Johnsongrass, Ho 95-988, and giant miscanthus (Fig. 2B). Adult mortality was significantly higher on Ho 02-147 and Ho 06-9001 than Ho 95-988. The aphids had significantly higher mortality on sweetcane than on *Saccharum* hybrids Ho 01-147 and Ho 06-9001. The highest adult mortality was observed on switchgrass cultivar GA-001switchgrass, giant reed, and napiergrass cultivar Merkeron (Fig. 2B).

**Aphid bioassay data - The second generation**

**Aphid reproduction:** The second-generation bioassay trials lasted 31 and 35 d in length. When data for all grass genotypes was combined, age had a significant effect on nymph production ($F$ = 44.78; df = 32, 233; $P < 0.0001$). Overall nymph production for all of the second-generation aphids, which had only been maintained on the putative host grass, was highest when the aphids were 5 to 13 d old (5-8 nymphs/d) with peak reproduction at day 7 (8 nymphs/d) (Fig. 3).

Reproduction for the second-generation aphids on a bioenergy host was significantly affected by age ($F$ = 47.53; df = 32, 233; $P < 0.0001$), genotype ($F$ = 30.07; df = 5, 34; $P < 0.0001$), and age by genotype interaction ($F$ = 5.37; df = 103, 535; $P < 0.0001$). Similar to the first-generation

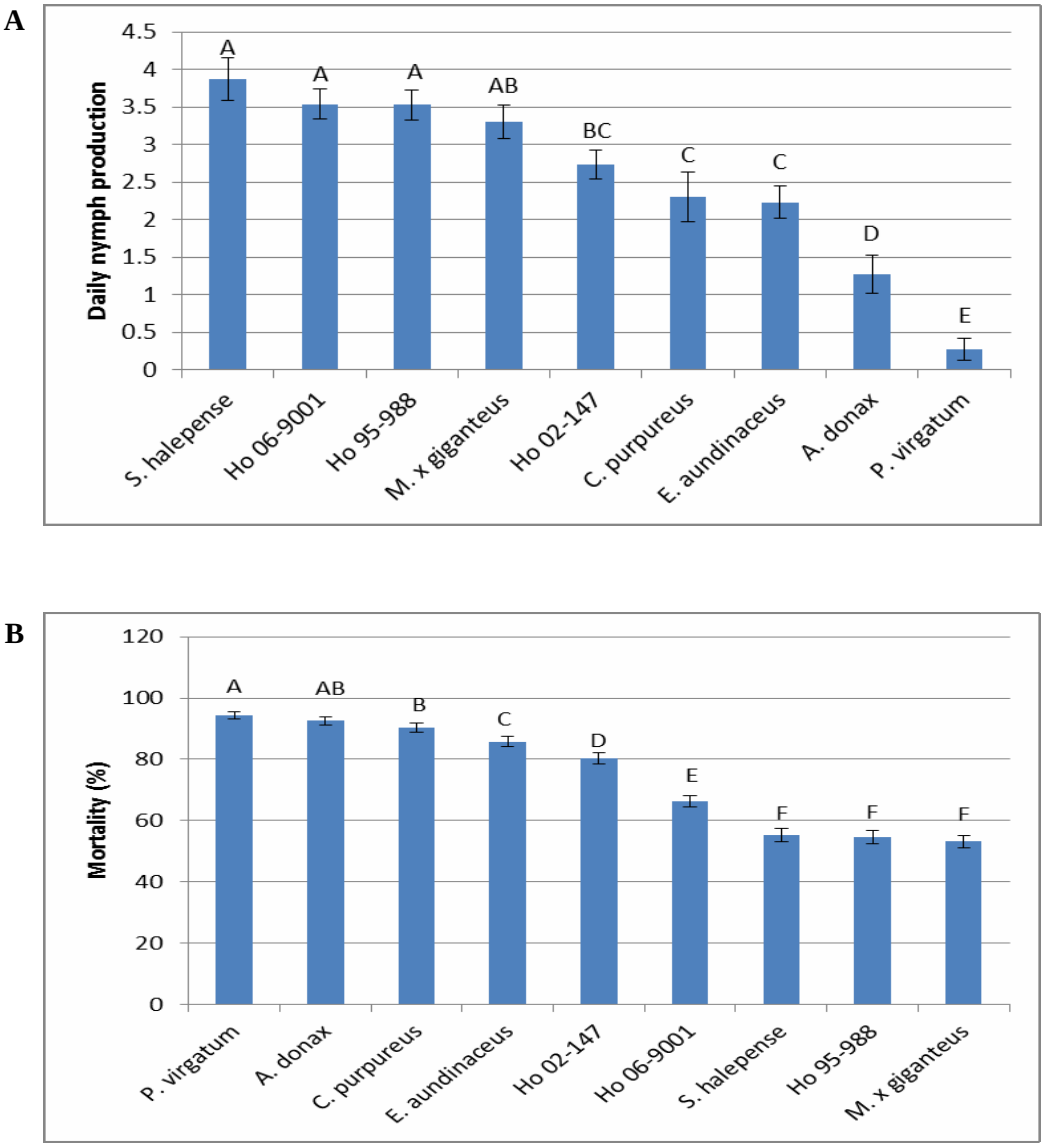


**Fig. 2.** Overall (all days combined) nymph production (A) and adult mortality (B) for the first-generation aphids fed each warm-season grass.

data, the largest number of nymphs produced for a given day was from aphids on Johnsongrass (10 nymphs at 6 d old). Aphids, 4-10 d old, on Johnsongrass produced 7 to 10 nymphs per day (Supplementary Fig. 2A). Aphids on giant miscanthus and Ho 95-988 had very similar patterns of nymph production per day where peak nymph production (5 to 8 nymphs/d) was observed from 5 to 14 d. Peak nymph production (8 nymphs/d) was at 9 and 12 d for giant miscanthus and Ho 95-988, respectively. Adult aphids on Ho 06-9001 had the highest nymph production at 6 to 14 d (5-8 nymphs/d) with peak nymph production (8 nymphs/d) at 7 d of age. Aphids on hosts Ho 02-147 and sweetcane had very low nymph production and the highest number of nymphs produced was only 2 and 5 per day at 8 and 6 d, respectively (Supplementary Fig. 2A).

**Aphid mortality:** Combined over genotypes, a significant age effect on adult mortality was observed ($F$ = 44.43; df = 33, 277; $P$ < 0.0001). In contrast to the first generation of sugarcane

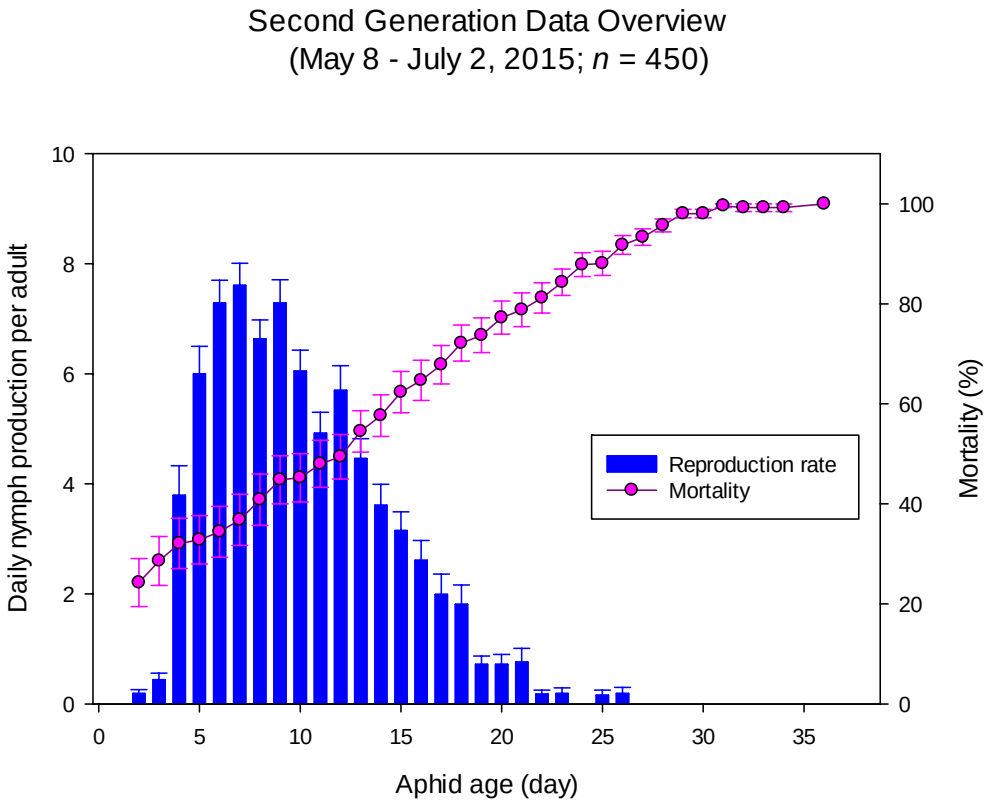


**Fig. 3.** Daily nymph production and mortality of the second-generation aphid bioassay combined over all grasses listed in Table 1, except switchgrass, napiergrass, and giant reed.

aphids on these grasses, there was not a large increase in aphid mortality at specific ages. Rather, mortality increased at a relatively steady rate (0-5%; Fig. 3).

Adult aphid mortality was significantly affected by age ($F$ = 82.59; df = 33, 277; $P$ < 0.0001) and genotype ($F$ = 274.41; df = 5, 36; $P$ < 0.0001), as well as age by genotype interaction ($F$ = 5.41; df = 164, 1087; $P$ < 0.0001). For the second-generation aphids, a separation for aphid mortality was observed among the warm season grasses (Supplementary Fig. 2B). Aphids developed on Ho 02-147 and sweetcane had much higher mortality than aphids developed on Johnsongrass, Ho 95-988, Ho 06-9001, and *M.* x *giganteus*.

**Aphid reproduction and mortality per grass:** Nymph production of second-generation sugarcane aphids was affected by the six grass genotypes ($F$ = 8.85; df = 5, 34; $P$ < 0.0001) when data from all sampling dates were combined for each grass entry (Fig. 4A). Ho 95-988, Johnsongrass, giant miscanthus, and Ho 06-9001 had the highest overall reproduction with 3-4 nymphs produced per day. Conversely, sugarcane aphids developed on Ho 02-147 and sweetcane leaf blades had the lowest overall reproduction with one or fewer aphids produced per day.

Adult aphid mortality also significantly differed among the grass genotypes when data from all sampling dates were combined ($F$ = 84.80; df = 5, 36; $P$ < 0.0001) (Fig. 4B). The highest aphid mortality was observed on sweetcane followed by Ho 01-147. The lowest mortality was observed for aphids fed *M.* x *giganteus* followed by Ho 06-9001. Aphids on Johnsongrass and Ho 95-988 had significantly higher mortality than aphids on Ho 06-9001 but less mortality than aphids on Ho 02-147 (Fig. 4B).

**Aphid life span:** The pooled data showed that aphid life span was significantly different between the two generations ($F$ = 20.18; df = 1, 115; $P$ < 0.0001), among the nine genotypes

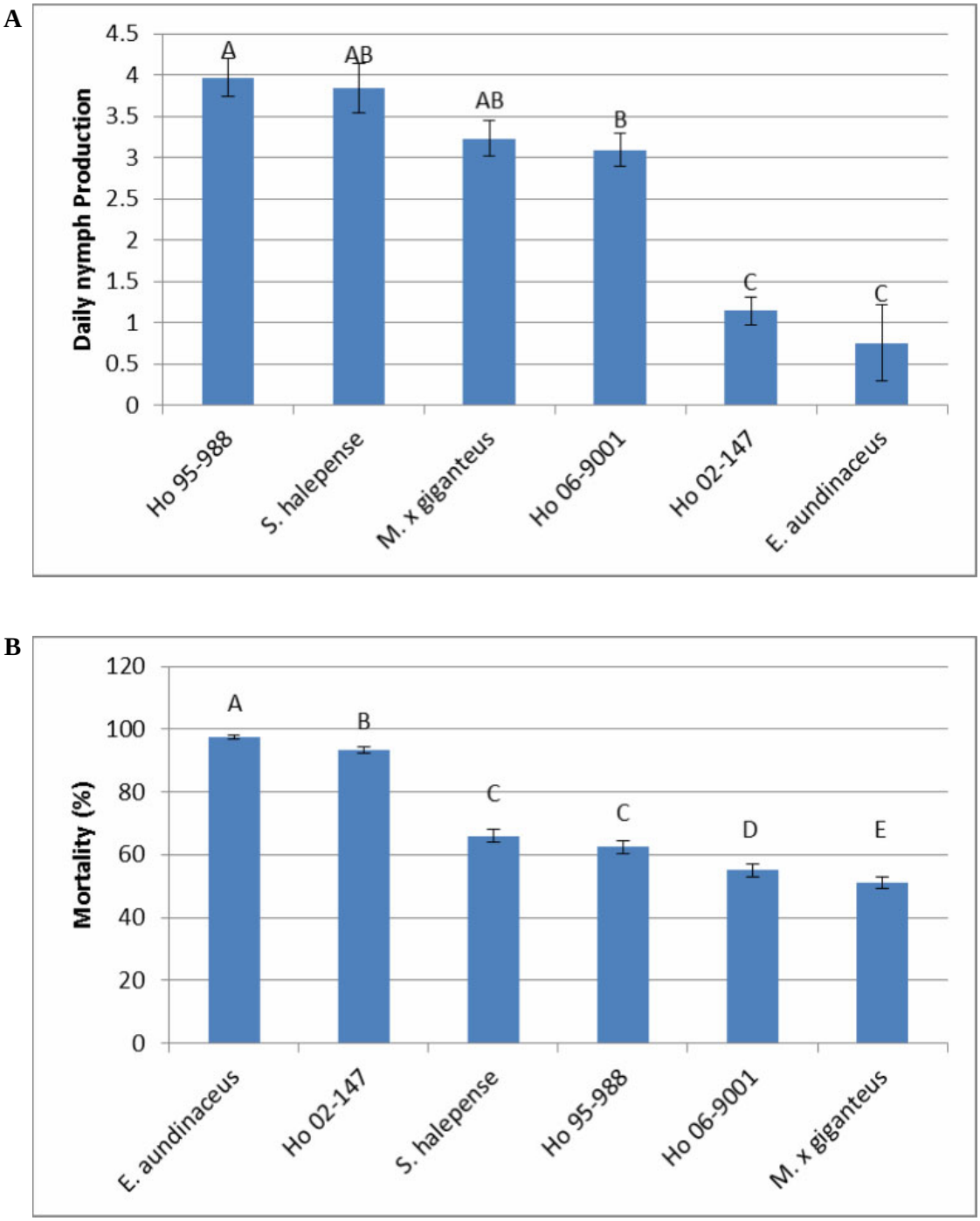


**Fig. 4.** Overall (all days combined) nymph production (A) and adult mortality (B) for the second-generation aphids fed each warm-season grass.

($F$ = 42.81; df = 8, 115; $P$ < 0.0001), as well as influenced by generation × genotype interactions ($F$ = 3.77; df = 5, 115; $P$ < 0.003). Aphid life span in the second generation (13.77 ± 0.83) was significantly greater than the first generation (12.20 ± 0.64). The data were further compared among the grass species within each generation (Table 2). In the first generation,

**Table 2.** Life span of *M. sacchari* on nine perennial grasses from two continuous generations using an excised leaflet bioassay

| Generation | Grass Tested[a] | *n*[b] | Life Span[c] |
|---|---|---|---|
| 1st | Ho 06-9001 | 10 | 14.86 ± 1.12 B |
| | Ho 02-147 | 10 | 10.46 ± 0.97 C |
| | *C. purpureus* | 10 | 7.2 ± 0.71 D E |
| | *A. donax* | 10 | 6.34 ± 0.52 E |
| | Ho 95-988 | 10 | 18.44 ± 0.94 A |
| | *S. halepense* | 10 | 18.6 ± 1.49 A |
| | *P. virgatum* | 10 | 5.88 ± 0.41 E |
| | *E. aundinaceus* | 10 | 8.66 ± 1.3 CD |
| | *M. x giganteus* | 10 | 19.36 ± 0.93 A |
| | | | |
| 2nd | Ho 06-9001 | 9 | 17.33 ± 1.67 A |
| | Ho 02-147 | 7 | 5.49 ± 1.24 B |
| | Ho 95-988 | 10 | 14.28 ± 1.02 A |
| | *S. halepense* | 10 | 14.74 ± 0.89 A |
| | *E. aundinaceus* | 3 | 3.87 ± 0.37 B |
| | *M. x giganteus* | 10 | 17.84 ± 1.09 A |

[a]: In the 2nd generation of the experiment, grass entries *P. virgatum*, *A. donax*, and *C. purpureus* were missing because no nymphs were available for the 2nd generation experiment.

[b]: The sample size (*n*) was the number of Petri dishes used for data collection, and the life span data from each of the five aphids per Petri dish were collected, and the mean of the five aphids was used for ANOVA.

[c]: Column means followed by different capital letters are statistically different and were separated by the PROC MIXED procedure followed by Fisher's Protected LSD test ($P < 0.05$).

aphid life span was significantly different among the nine grasses ($F = 51.82$; df = 8, 72; $P < 0.0001$), as were the six grasses examined for the second generation ($F = 84.80$; df = 5, 36; $P < 0.0001$).

## DISCUSSION

The spread of sugarcane aphids on sorghum throughout the sorghum growing region of the United States has been at an alarming pace. Insecticide options for farmers to control the damage to sorghum are limited mainly to Sivanto (flupyradifurone; Bayer Crop Science, Research Triangle Park, NC) or Transform WG (sulfoxaflor; Dow AgroSciences, Indianapolis, IN), and seed treatments. Neonicotinoid seed treatments can provide protection at the seedling

stage but all of these insecticides are nicotinic acetylcholine receptor competitive modulators, increasing the possibility that the clonal sugarcane aphids will develop resistance. An integrated pest management (IPM) approach is needed to suppress this damaging pest. One aspect of IPM is the discovery and control of alternative hosts.

The results of the current experiment showed that Johnsongrass, energycane (*Saccharum* spp.), sugarcane, and giant miscanthus sustained ultiple generations of the sugarcane aphid with relatively low mortality, high reproduction rates (daily nymph production), and relatively long life spans. In fact, sugarcane aphids fed giant miscanthus and Ho 95-988 had as long as a lifespan as Johnsongrass and had similar levels of nymph production and mortality as Johnsongrass for both generations (Table 2; Figs 2A, 2B, 4A, 4B). Poor hosts included the napiergrass cultivar Merkeron, giant reed, and switchgrass cultivar GA-001. Sweetcane was a good host for first-generation sugarcane aphids but a poor host for second-generation aphids. Thus, if widespread planting of napiergrass, giant reed, and switchgrass occurs it may prevent the further increase of the aphid population. However, widespread planting of the energycane, sugarcane, and giant miscanthus may exacerbate sugarcane aphid damage on sorghum in sorghum growing areas. The current experiment also demonstrated that utilizing the three biodemographic parameters (mortality, reproduction rate, and life span) can be effective in identifying alternative hosts for the sugarcane aphid.

Although the sugarcane aphid is well documented for feeding on *S. officinarum* [1], this study has identified other *Saccharum* hosts. Ho 02-147 which is a cross between *S. officinarum* x *S. spontaneum*, Ho 06-9001which is a *S. spontaneum* (*S. officinarum x S. spontaneum*) cross, and Ho 95-988 which has a complex pedigree of five *Saccharum* species all served as hosts to the sugarcane aphid. Yet Ho 02-147 was a poorer host than Ho 06-9001 and Ho 95-988 (Table 2; Figs 2A, 4A, and 4B). Although sugarcane aphids are known to feed on *Miscanthus sinensis* [1], this study determined that giant miscanthus (*Miscanthus sinensis* x *M. sacchariflorus*) is also a host for sugarcane aphids. Furthermore, our field plots of giant miscanthus in Tifton, GA have been infested with sugarcane aphids from September 2015 - January 2016 as well as February 2019-currently. In conclusion, the widespread planting of sugarcane, energycane or giant miscanthus could cause increased aphid pressure on sorghum. Aphid infestations on these perennial grasses can influence aphid population densities in the sorghum fields near and far as aphids can migrate long distances facilitated by weather patterns, and commerce [27]. To minimize alternative perennial grass hosts on sugarcane aphid populations the planting of switchgrass, giant reed, and napiergrass may serve as better alternatives in regions where sorghum is grown.

## CONCLUSION

We sought to determine if candidate bioenergy grasses, many related to *Sorghum bicolor*, could serve as alternative hosts of the sugarcane aphid. Results from our multigenerational experiments indicate that as compared to the Johnsongrass control, adult aphids developed on the three *Saccharum* spp. and giant miscanthus had high rates of nymph production and low mortality and thus served as suitable hosts that could potentially build up large numbers of sugarcane aphids for infestations of other crops.

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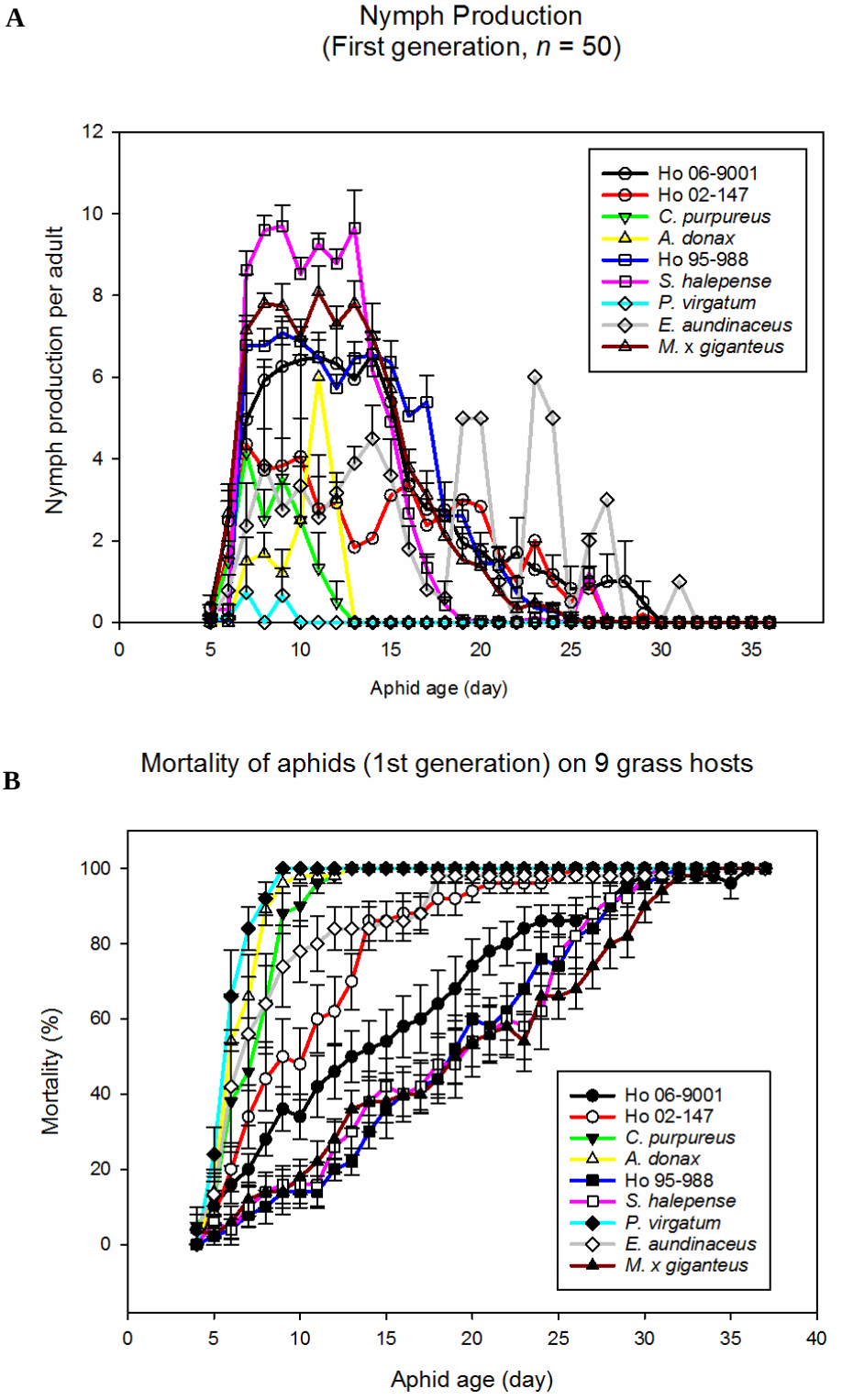
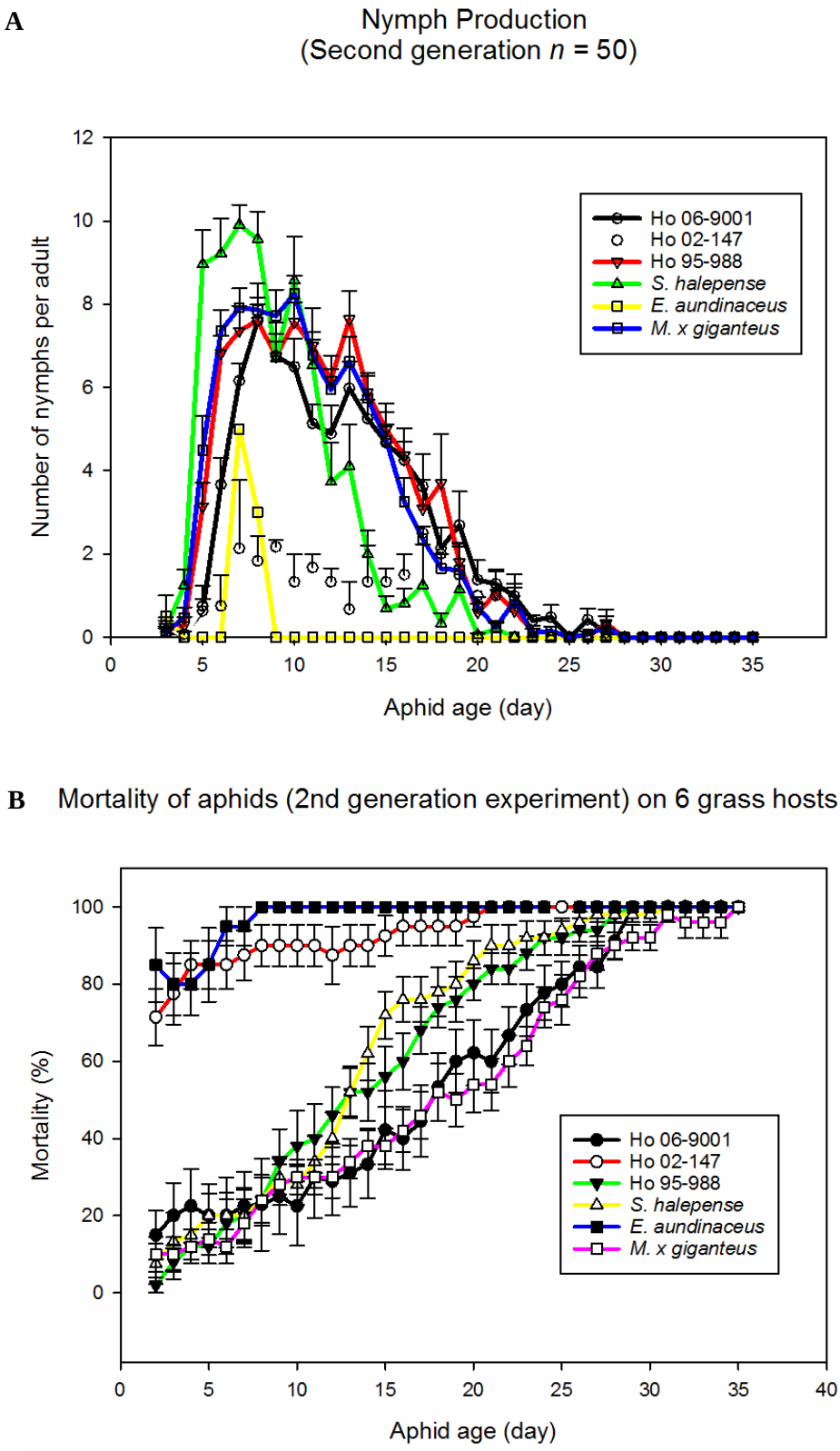
## CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

**SUPPLEMENTARY MATERIAL**




**Supplementary Fig. 1.** Daily nymph production (A) and adult mortality (B) of the first-generation aphid bioassay for each warm-season grass ($n$ = 50).




**Supplementary Fig. 2.** Nymph production (A) and adult mortality (B) of the second-generation aphid bioassay for each warm-season grass ($n$ = 50).

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