THE FEEDING AND REPRODUCTIVE BEHAVIOR OF GLOBAL HAPLOTYPES OF SUGARCANE APHID [MELANAPHIS SACCHARI (ZEHNTNER) (APHIDIDAE]

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Abstract

During the past four years, sugarcane aphid [*Melanaphis sacchari* (Zehntner)] has significantly impacted grain sorghum (*Sorghum bicolor* L.) production in the United States and Mexico. Currently, the origin and biology of *M. sacchari* (infesting sorghum) is not clearly understood but it is theorized that the host range expansion occurring in 2013 was caused by either A) emergence of a new *M. sacchari* biological type through mutation or recombination, B) U.S. introduction of an already previously evolved type, or C) possibly a change in aphid gut symbionts, virus, or other microorganism due to introduction to new habitats. A series of 3 experiments were initiated in 2016 investigating feeding and reproductive behaviors of this economically important pest, since there is a clear need to assess the role of antixenosis and colonization in genotypic reaction against *M. sacchari* to identify lines with different mechanisms of resistance to this pest. First: Potential host range was examined through 21 day no-choice studies of 54 graminous species. Second: Antixenosis to selected grasses was tested through a closed system multi-choice test of 16 selected grasses. Third: Aphid reproduction was compared by bioassay of 5 grass spp. Results from no-choice test identified grasses which supported temporary or long-term parthenogenic reproduction and of these 15 spp., 6 spp. in the genus *Miscanthus*, *Pennisetum, and Sorghum* were preferred by population $_{SI.WINN}$M.sach$_{04.2016}$ as hosts during the antixenosis test. Finally, results of reproductive test show that our isolated population has significantly greater reproductive potentials on sorghum versus the other grass treatments.

Introduction

Within the past few years in both Southern United States and Northern Mexico the overall occurrence of the Sugarcane Aphid [Melanaphis sacchari (Zethner, 1897) (Hemiptera: Aphididae)] on sorghum (Sorghum bicolor L.) has rapidly increased. In North America prior to 2013, population densities of *M. sacchari* attacking sugarcane were considered low and their economic impact in the region was just as unclear then as it is now (White 2001). However, during 2013, the aphid rapidly became an economically important insect pest in Mexico and the Southeastern United States attacking various cultivated varieties and types within the genus *Sorghum.* The aphid is historically considered to be an economically important pest of sorghum in the countries of China (Wang, 1961), Taiwan (Chang, 1981a), Japan (Setokuchi, 1973), India (Young, 1970), South Africa (van Rensburg, 1973a), and most recently in North America. The U.S. annually typically produces ~10-11 million metric tons of sorghum in an area of approx. 2-3 million hectares, compared to world annual production of 1-2 million metric tons in an area of approx. 40 million hectares (USDA, 2015). Since the United States produces much larger yields of sorghum within less arable space and the U.S. exports millions of bushels of grain sorghum annually, any yield losses resulting from *M. sacchari* attack can have significant affects globally. *M. sacchari* attack is not considered to be economically important in sugarcane; however the aphid is a transmitter of several persistent and non-persistent viruses, including sugarcane leaf virus (family Luteoviridae, genus Polerovirus, ScYLV) (Schenck and Lehrer 2000), which is very important to the sugarcane industry. The most common method for the management of these viruses is screening during micro propagation (Akbar, 2010) and the use of resistant varieties (Blackman and Eastop, 2000; Singh et. al., 2004). Since data on the identity, origin, and biological cycle of the *M. sacchari* / *sorghi* complex currently are insufficient and contradictory (Rodríguez-del-Bosque 2015) and since there is a need to assess the role of antixenosis and colonization in genotypic reaction against *M. sacchari* to identify the lines with different mechanisms of resistance to this pest (Sharma at. al 2014), it has been recommend that laboratory and field studies be conducted on topics such as holocycle, biotype, host transfer, and range of host plants.

In 2014, Nibouche et al. (2014) studied genetic diversity of samples identified as *M. sacchari* from many parts of the world. Using previously identified microsatellite markers and sequencing fragments of the mitochondrial cytochrome c oxidase I gene, they showed that *M. sacchari* has one of the lowest known rates of genetic diversity.

Within the 36 multilocus genotypes observed, 3 new distinct genetic groups (haplotypes) emerged. These three new haplotypes plus the two already available in GenBank from five Indian samples identified five haplotypes among 96 *M. sacchari* individuals. The five haplotypes were arbitrarily assigned the letters A, B, C, D, and E.

Aphid spp. fall into two categories; obligated to a single plant spp. or genera and highly polyphagous aphid species; however polyphagus spp. account for less than 1% of all aphid spp. (Inaizumi, 1980). Recent field and laboratory tests, including genetic diversity analysis within spp. level, hypothesized that populations of *M. sacchari* showed host specialization and stated that aphid genetic structures should be closely linked to host plant. In 2015, the CIRAD laboratory analyzed the effect of host plant (wild sorghum or sugarcane) for haplotype C by performing laboratory cross-bioassay experiments to detect fitness benefits based upon host plant in combination with diversity analysis of multilocus genotypes. Their study revealed strong host specialization despite low genetic differentiation (Nibouche et. al., 2015), however with 19 total spp. documented as a host to *M. sacchari*, literature review revealed a host list that doesn't seem to follow the typical obligate relationship (Table 1).

The Poaceae is a large and nearly ubiquitous family of monocotyledonous flowering plants which are commonly called grasses. Within the grasses there are two highly supported and distinct groups: the BOP clade, representing grasses utilizing C^3 photosynthesis, (families Oryzoideae, Bambusoideae, and Pooideae); and the PACMAD clade, representing grasses utilizing C^4 photosynthesis, (Aristidoideae, Panicoideae, Arundinoideae, Micraioideae, Danthonioideae, and Chloridoideae). In a recent study of both frequency and timing of the evolution of the C^4 photosynthetic pathway, a maximum likelihood tree was created to represent the phylotaxonomy of grasses. This tree identified 12 subfamilies, 51 tribes, and 80 subtribes, with 41% of the 12,074 graminous spp. utilizing the C^4 photosynthetic pathway with results also revealing evolutionary distributions worldwide. While considered to be mainly parthenogenic (Blackman and Eastop, 2008), the *M. sacchari* have been documented to also possess a sexual (or oviparous) reproductive cycle on 3 of the 19 hosts identified during literature review; *Miscanthus*, *Saccharum*, and *Sorghum* (Wang 1961, Yadava 1966, Setochuki 1974, van Rensburg and van Hamburg 1975). These three grasses were identified as being phylogenetically similar in the previously mentioned study, are C4 grasses, and share a common ancestor; where ~3.8 to 4.6 million years ago the Sorghum lineages diverged from (Changsoo 2014). Since these three graminous spp. are well documented (Table 1) as being a host to *M. sacchari* and because they are phylogenetically similar, we primarily focused on the use of these three grasses throughout our study and conducted no-choice tests utilizing phylogenetically related and non-related grasses.

Since there is not enough genetic differentiation to warrant a new spp. identification (Nibouche et al. 2014), which the authors of Aphids on the Worlds Crops R.L. Blackman and V.F Eastop would prefer (Burnett 1990 Margaritopolous et al 2013), the identification of virulent and fit biological types within the *M. sacchari* complex will be determined with well-established and compared methods for the designation of biotype. The combination of no-choice, intrinsic rate of increase, with antixenosis testing has been successfully used towards this goal. The intrinsic rate of increase is defined as a basic parameter which an ecologist can establish reproductive rates for an insect population in an unlimited environment and effects of increasing density do not need to be considered, id est the rate of increase per head under specified physical conditions (Birch, 1948). Intrinsic rate of increase (*rm*) values clearly indicate that biotypes have a greater reproductive potential depending on the host spp., and the function of both reproductive days (*d*) and generation time (*Md*) and for the cultivar comparisons follow *Md* more closely than *d*. Resistance to insects has been characterized into three components as antixenosis (non-preference), antibiosis, and tolerance (Painter, 1951; Horber, 1980; Smith, 1989; Smith et al., 1994) and both antixenosis and antibiosis resistance to *M. sacchari*, in sorghum, does not differ with plant age (Teetes, 1980). Antixenosis values clearly separate differences in host preference and host tolerance and are extensively used in the designation of greenbug and Russian wheat aphid biotypes (Porter, 1982; Webster, 1984, Kinder, 1986; Niassy, 1992).

Materials and Methods

Iso-linear Populations

The isolated population identified as $_{SI.WINN}$M.sach$_{04.2016}$ was utilized during each of the following experiments. It was established by sampling one leaf from a randomly chosen sorghum leaf blade in a protected overwintering plot of ratooned grain sorghum in Winnsboro, LA February 2016 and carefully transferring 3 apterous adult aphids to another potted sorghum plant of the same variety (M75GB39) which was then placed into growth chamber. Growth chamber settings were kept at 12:12 photoperiod, at 27°C, with 30-40% relative humidity to replicate early season growing conditions for both insect and pest spp. at 31° Latitude. All of the adult aphids were removed from plant

upon the birth of one 1st instar larvae, which was then allowed to progress to adulthood. Progeny from this fundatrix established working colony. This population was subjected to genetic diversity analysis by sequencing fragments of the mitochondrial cytochrome c oxidase I gene sing primers designed by Folmer et al. COI fragments were amplified with LCO1490 and HCO2198 (Folmer, 1994). PCR was carried out using well established protocol (Kim and Lee 2008). Population $_{SI.WINN}$M.sach$_{04.2016}$ was identified as belonging to the same COI as haplotypes A, B and E. Study conducted at the Macon Ridge Research Station in Winnsboro, LA. Environmentally controlled chamber used was Percival Scientific model E-41L2. Research conducted between June and September 2016.

No-Choice

The test is a factorial design with 54 various grass spp. against attack by $_{SI.WINN}$M.sach$_{04.2016}$, replicated 4 times. Sealed containers were used for these studies are 2.5 inch radius x 10 inch height enclosed plastic cylinders with lids, modified using hot glue to attach two container lids together; forming a 20 inch tall container. Three 4 inch ventilation holes added to containers top half using screen mesh and hot glue to manage moisture within container. Approximately, 1 kg of (1:3) native soil and potting soil mix per container served as the soil mixture and plants watered as needed with a 24-12-16 fertilizer solution. Plant seedlings transferred from 3 x 3 x 3 inch pots to modified containers at 3rd leaf stage, approximately 9 days prior to experiment. After plants established, at 5th leaf stage, infestation of aphids was achieved by adding a single sorghum leaf carrying 100-250 aphids to each container. Host determination was measured by recording initial aphid population, counting aphids occupying plants at 2, 7, 14 and 21 days after infestation, counts made in increments of 5. Plant injury was scored on a 1-9 scale where 1 = no injury and 9 = dead plant (Porter et al., 1982; Puterka et al., 1982; Webster & Starks, 1984). Population data for entries was subjected to ANOVA and compared (P = 0.05) by Tukey's post hoc test (SAS Institute, 1985).

Antixenosis

Plant varieties representing cultivated crops and wild spp. were used to evaluate antixenosis (non-preference) against $_{SI.WINN}$M.sach$_{04.2016}$. Sorghum isolates reared on sorghum variety M75GB39 for 1 month prior to test. Experiment replicated 3 times. In 8 equidistant rows, plants were established from seed into 12 x 24 x 12 in flats filled with (1:3) native soil and potting soil mix with 25 seeds planted per row, thinned to 10 plants per row upon germination. Flats watered, as needed, by hand can including a 24-12-16 nutrient solution. Once plants have reached the 5 leaf stage, each flat was infested with $_{SI.WINN}$M.sach$_{04.2016}$ isolates by shaking 250 aphids from cultured plants onto inside of box lid. Then lid placed over the flat and taped to allow aphid selection and prevent escape. This method randomly allowed for host selection through aphid preference. After aphids select host plants, counts of total aphids per plant were made 24 hours and 7 days after infestation and at two additional injury points. Plant injury scored on a 1-9 scale where 1 = no injury and 9 = dead plant (Webster & Starks, 1984). The first injury reading made when an entire row of a susceptible entry rated an average of 7-8. Second injury rating made when entire row of graminous spp., not identified in the first reading, rates an average of 7-8. All varieties within flats are rated in each reading. Each plant in a row individually rated to estimate mean injury rating per variety (Porter et al., 1982; Puterka et al., 1982; Webster & Starks, 1984). Mean comparisons (P = 0.05) made by least significant differences (LSD) method (SAS Institute 1985). Population data for entries was subjected to ANOVA and compared (P = 0.05) by Tukey's post hoc test (SAS Institute, 1985). Two readings analyzed separately by an ANOVA and mean injury ratings separated (P = 0.05) by LSD method (SAS Institute 2007).

Reproductive Behavior

Aphid reproduction potential was compared by bioassay of 5 hosts against $_{SI.WINN}$M.sach$_{04.2016}$: *Sorghum halepense* (wild), *Sorghum bicolor* (known susceptible), *S. drummundi*, *Sacchrum officinarum* (known susceptible), and *Miscanthus gigantus*. Test replicated 4 times in controlled greenhouse conditions at temperatures between 26-30°C. Containers used for this study were 2.5 in radius x 10 in height plastic cylinders with lids, modified using hot glue to attach two container lids together; forming a 20 in. tall container. Three 4 in. ventilation holes added to containers top half using screen mesh and hot glue to manage moisture within container. Plants watered as needed with available fertilizer solution. Seedling cores transplanted from 3 x 3 x 3 in pots into modified containers at 5th leaf stage, containers filled with 1 kg of (1:3) native soil and commercial potting soil mix per container. Computer fans were affixed with glue to the tops of each container to remove access humidity. After transplanting, 1-2 in. of course vermiculite was added to cover soil and basal portion of plant stems. Bioassays were performed with individual newborn nymphs with four replicates. Five nymphs were carefully placed on adaxial surface near the collar of lowermost leaf and observed until the appearance of fundatrix, at which point all other aphids were removed. Only one fundatrix per-plant was observed until natural mortality and differences in adult longevity and fecundity of $_{SI.WINN}$M.sach$_{04.2016}$ at temperature were tested for significance by analysis of variance (ANOVA) using general

linear model (PROC GLM, SAS Institute, 1989). Population growth statistics, including intrinsic rate of increase (*rm*), net reproductive rate (*Ro*), and mean generation time (*GT*) were calculated for populations at temperature using a computer program.

Results and Discussion

No-Choice

Results (Table 1) of the 43 spp. tested so far show us that $_{SI.WINN}$M.sach$_{04.2016}$ produced significantly larger populations occupying *Sorghum* sp. than other treatments. In addition to developing higher populations the aphid significantly injured both known resistant and susceptible Sorghum sp. to the point of mortality. During the 21 day no-choice test, host mortality was observed in 3 Sorghum spp. and 2 spp. of Pennisetum and then, within 30 days of termination of test, host mortality was observed in *Digitaria sanguinalis*, *Miscanthus gigantus*, 1 Sugarcane sp, and 1 Sorghum species. Treatment spp. *Digitaria sanguinalis*, *Urochloa ramosa*, and *Setaria italica* had at least one significant population time-point, are also phylogenetically related, are C4 grasses, and carried very low populations of *M. sacchari* for 21 days. Three non-native Echinochloa spp. carried non-significant populations for the duration of the experiment, are all C4 grasses, but there were no significant phytotoxic interactions. All of the grasses that survived the no-choice test were left to flower naturally and all grasses, except sugarcane, produced seed.

Antixenosis

Group 1 results (Table 2) show us that $_{SI.WINN}$M.sach$_{04.2016}$ preferred *Sorghum arundinaceaum* and a known susceptible *Sorghum bicolor* over the other 6 treatment grasses; both grasses reached the phytotoxic threshold of 7 at 28 days with mortality of entire row by 32 days and carried significant populations of aphids (>125). The second grass host to reach the threshold was a known susceptible *Pennisetum glaucum*; this grass reached the threshold at 32 days with mortality of entire row by 37 days after infestation. Group 2 results (Table 3) show us that *M. sacchari* preferred *Sorghum drumundii* over the other 7 treatment grasses; this host reached the phytotoxic threshold of 7 at 32 days with mortality of entire row by 35 days. Again, two grasses reached the susceptibility score at the same time, the next grass hosts to reach threshold was *Pennisetum orientale* and *Sorghum halepense*; these two grasses scored between 7-8 at 32 days with mortality of entire row by 34 and 45 days, respectfully, after infestation.

Reproductive

Results of analysis show that $_{SI.WINN}$M.sach$_{04.2016}$ had significantly greater generation time, mean nymph / generation, doubling time, intrinsic rate of increase, finite daily rate of increase, and more reproductive days on *S. bicolor* than the known susceptible sugarcane and *Miscanthus gigantus.* Additionally, *M. sacchari* had a significantly lower intrinsic rate of increase, finite daily rate of increase, mean nymph / generation, and generation time on treatment spp. *Sorghum halepense* than on *S. bicolor*.

Discussion

In the previously referenced genetic diversity analysis (2014) CIRAD identified that at least 5 gene groups (haplotypes) of *M. sacchari* exist on the worldwide scale and that genetic structure of the multilocus lineages were primarily influenced by geography and host plant. In the second study CIRAD published (2015) results from both field and laboratory tests supported their hypothesis of host plant specialization in *M. sacchari* populations (haplotype C), showed that genetic structures of *M. sacchari* were closely linked to host plants of sorghum and sugarcane. This genetic evidence combined with literature review, the results of our study, and consultations by relevant professionals globally reveal that *M. sacchari* is most likely not a polyphagous insect herbivore and more likely to be obligated to certain phylogenetically similar graminous genera.

In the CIRAD study, aphid genotypes identified as A and E, which originated from Africa and Asia, showed the most significant genetic divergence from other aphid samples, were almost all collected from *Sorghum bicolor*, and both haplotypes have had historically significant impact on sorghum production in their associated regions. Beginning in the late 1940's, the aphids obvious impact on sorghum in Asia (haplotype E) and Africa (haplotype A) was similar to what currently being observed in North America, id est the rapid expansion of host range and severe economic impact by a pest which was historically considered to be a low impact pest of sugarcane, therefore these two haplotypes must have a narrow physiological relationship with sorghum. Haplotype C, originating from East Africa, South America, and Caribbean, prefer both sugarcane and wild sorghums and the aphid does not economically impact grain sorghum production; this haplotype must have a broad physiological relationship with both sorghum and sugarcane. Haplotype B, originating in Australia, has a strong preference for sugarcane with no

significant activity on sorghum and as well as haplotype D, originating in Hawaii and North America, has preference for sugarcane and has been present in North America for nearly 100 years and has never impacted grain sorghum production; these two haplotypes must have a narrower biological relationship with Sugarcane and little-to-no preference for grain sorghum.

It is our belief that population $_{SI.WINN}$M.sach$_{04.2016}$ belongs to haplotype A (from Africa) for three primary reasons: firstly because this population of aphids was identified as belonging to the same COI as haplotype A and E which are well known to attack sorghum; secondly because modern micro-propagation certifications for sugarcane cultivars screen for numerous insects and pathogens so a shipping route of invasion by a sexually reproductive sugarcane type (haplotype B or C) is unlikely, and thirdly because of significant trade-wind activity during the summer of 2012, the year prior to rapid expansion. To our lab, the high altitude invasion is the most logical route specifically because the National Ocean and Atmospheric Administration recorded 4 significant events in the summer of 2012 (Hurricane Ernesto, Tropical Storm Florence, Tropical Storm Helene, and very large dust storm), during periods alate dispersal periods with each storm being a potential alate deposition event with trajectories that tracked from the coast of West Africa (haplotype A) towards the Greater Indies, Florida, and coast of Mexico. Our laboratory is currently seeking collaborations with other host nations in order to perform this series of tests in order to formally introduce the biotype nomenclature within the *M. sacchari* complex by detecting fitness benefits based upon host plant in combination with diversity analysis of different multilocus genotypes.

Summary

Just recently in North America sorghum production has become constrained by attack from the sugarcane aphid, even though this exotic pest of near global distribution has had economic impacts on both sorghum and sugarcane cropping systems worldwide for more than 50 years. Because literature on *Melanaphis sacchari* in North America is limited and since sorghum production can be heavily constrained by aphid feeding, the objectives are to observe ecological and biological aspects of known genetic types of *M. sacchari* to better mitigate economic impacts on worldwide sorghum production and to better understand various biological interactions. The hypothesized long term goal for our laboratory is to compare the reproductive and feeding behavior of different sugarcane aphid haplotypes on the worldwide scale to determine if there are enough physiological differences to warrant biotype designation. It is our option that biotype designation is critical to reducing confusion for the rapid throughput of resistant cultivars. Results of the no-choice test revealed a potential host range for $_{SI.WINN}$M.sach$_{04.2016}$ that includes grasses in the genus Digitaria, Echinochloa, Miscanthus, Pennisetum, Urochloa, Saccharum, and Sorghum. The confirmed primary host range for our population includes grasses in the genera Miscanthus, Pennisetum, and Saccharum, and Sorghum. Results of our antixenosis test revealed that $_{SI.WINN}$M.sach$_{04.2016}$ prefer 4 spp. of Sorghum, 2 spp. of Pennisetum, and 1 spp. Miscanthus to sugarcane and other documented grasses. Our reproductive test revealed that this population has significantly greater reproductive potential on grain sorghum (*S. bicolor*) than other treatments, including a wild sorghum spp., with significant fitness differences between sorghum and sugarcane in mean nymph per generation, generation time, doubling time, as well as both finite and intrinsic rates of increase.

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Table 1. Documented host range of the sugarcane aphid, *M. sacchari* and 2 popular synonyms, *Aphis sacchari* and *Longinunis sacchari* (Zehnt.), reported from different countries and years.

Scientific name	Common name	Country from which reported	Reference
Anthistiria coromandeliana		India	Raha (1979)
Arthraxon hispidus (Thunb.) Makino	*Small carpetgrass*	India	Raychaudhuri (1980)
Cynodon dactylon L.	Bermuda grass, Burmagrass, Common stargrass, Devilgrass,	Taiwan	Wilbrink (1922)
Echinochloa colona L. (*Panicum colonum* L.)	Jungle Rice	Florida and Taiwan	Denmark (1988) and Wilbrink (1922), Behura (1963)
Eleusine coracana	African finger millet	Africa	Aphids on the Worlds Crops
Echinochloa crus-galli (L.) P. Beauv.	Barnyard grass	Florida and Taiwan	Denmark (1988) and Wilbrink (1922)
Hordeum vulgare L.	Barley	India	(Despande, 1938)
Iseilema laxum Hack.	Musal grass	India	(Behura, 1963)
Miscanthus sinensis L.	Ornamental grass, Japanese silvergrass	Japan	Setokuchi (1973) and Kawada (1995), Halbert (2000)
Oryza sativa L.	Paddy, Rice	China and USA (Florida)	Miao and Sunny (1987) and Denmark (1988)
Panicum maximum Jacq.	Jacquin Hamilgrass Guineagrass	Botswana and Zimbabwe	van Rensburg (1973a)
Panicum sp.	unknown	India	Raychaudhuri (1980)
Phragmites australis (Cav.) Trin. Ex Steud.	Common reed	Iraq	Hayder and Nassreen (2012)
Poa sp. L.	Bluegrass	India	Raychaudhuri (1973)
Digitaria sanguinalis (L.) Scop. Syn. *Paspalum sanguinale* Lamarck	Hairy crabgrass	USA (Florida)	Wilbrink (1922)
Pennisetum glaucum L.	Pearl millet	India	Akhtar and Dey (2011)
Pennisetum spp.	Fountaingrass	USA (Florida) India	Denmark (1988), Raychaudhuri (1980)
Saccharum officinarum L.	Sugarcane	Australia, Argentina, USA (Florida, Louisiana, and Hawaii), India (Sikkim), India (Tamil Nadu), India (Uttar Pradesh), India (West	Delfino (1985), Mead (1978), Denmark (1988), Pemberton (1948), Agarwala et al. (1983), Alexander and Madhusudhanrao (1977), Shuja-Uddin (1975), Edward (1937) Varma et al. (1978), Akhtar and Dey (2011), Agarwala et al. (1983), White et al. (2001), Hamid (1983), Rueda and Catling (1978), Wilbrink (1922)

		Bengal), Jamaica, Pakistan, Philippines, and Taiwan	
Setaria italica (L.) P. Beauv	Boar millet, Foxtail millet, German millet,	South Africa, USA (Florida)	van Rensburg (1973a, b), Wilbrink (1922)
Sorghum bicolor (L.) Moench Syn: *S. vulgare* Pers.; *Andropogon sorghum* (L.) Brot. Andropogon vulgare L.)	Sorghum	Australia, Argentina US (Florida) India (Karnataka), India (Kashmir), India (Maharashtra), India (Punjab), Japan, South Africa, USA (Florida) Taiwan,) Thailand, Uruguay, Venezuela	Delfino (1985) Wilbrink (1922) and Denmark (1988), Patil (1992) and Balikai (1997), Bhagat (1981), George (1927) Behura (1963), Mote (1983) and Mote and Kadam (1984), David and Sandhu (1976) and Akhtar and Dey (2011), Setokuchi (1973), Hagio et al. (1985), and Hagio and Ono (1986) van Rensburg and van Hamburg (1975) van Rensburg and Malan (1983), Chang (1981a, b), and Chang and Fang (1984) Banzoger (1976) Delfino (1985) Sanchez and Cermeli (1987), and Aponte et al. (1988)
Sorghum halepense (L.) Pers.	Aleppo grass, Cuba grass, Johnson gras	Japan South Africa India	Kawada (1995) van Rensburg (1973a), Bhagat (1981)
Sorghum verticilliflorum (Steud.) Stapf.	Wild Sudangrass	South Africa	van Rensburg (1973a), and van Rensburg and van Hamburg (1975)
Thysanolaena latifolia (Roxb. ex Hornem.) Honda	Tiger grass	India	Chakrabarti et al., (1988) and Chakrabarti and Sarkar (2001)
Triticum sp.	Wheat	Unknown	CABI (2014), Plantwise Knowledge Bank (2016)
Zea mays (L.)	Maize	Bhutan India	Agarwala (1985), Chakrabarti (1972) and Raychaudhuri (1978)

Table 2. Results of no-choice, combined mean population counts and phytotoxicity scores for each grass. Asterisk (*) designates results of ANOVA was significant, with $P < 0.05$. A box (□) designates phytotoxic scores greater than 7 exceed our susceptibility threshold of 6. Cross (†) represents non-infested control.

			2 DAI		7 DAI		14 DAI		21 DAI	
Plant	Entry	Initial count	Score	Count	Score	Count	Score	Count	Score	Count
Sorghum bicolor †	K 73-J6	0	1	0	1	0	1	0	1	0
Avena sativa	LA9906	150	1	75	1	0	1	0	1	0
Bouteloua curtipendula	Native	150	1	35	1	0	1	0	1	0
Bromus hordeaceus	PI 469232	150	1	20	1	0	1	0	1	0
Bromus unioloides	Local	150	1	25	1	0	1	0	1	0
Buchloe dactyloides	Native	125	1	0	1	0	1	0	1	0
Cymbopogon citratus	Commercial	100	1	0	1	0	1	0	1	0
Cynadon dactylon	Commercial	200	1	100	1	45	5	5	3	0
Digitaria sanguinalis	Native	200	2	100	3	135 *	6	165 *	6	70
Echinochloa colona	PI 664492	150	1	50	1	75	2	35	2	20
Echinochloa esculenta	PI 315699	150	1	75	1	35	1	50	1	40
Echinocloa crus-galli	PI 664493	150	1	75	1	50	1	20	1	0
Echinocloa muricata	PI 649370	150	1	20	1	0	1	0	1	0
Elymus canadensis	Native	100	1	50	1	0	1	0	1	0
Elymus lanceolatus	PI 518498	100	1	5	1	0	1	0	1	0
Eriochloa sericea	Native	100	1	35	1	0	1	0	1	0
Hordeum vulgare	on order	100	1	0	1	0	1	0	1	0
Lolium multiflorum	JSS988.30	200	1	100	1	0	1	0	1	0
Panicum virgatum	Blackwell	150	1	50	1	0	1	0	1	0
Pascopyrum smithii	Native	100	1	0	1	0	1	0	1	0
Paspalam notatum	Pensecola	150	1	0	1	0	1	0	1	0
Pennisetum glaucum	JSS187.32	250	3	125 *	6	150 *	9	0	9	0
Pennisetum glaucum	Millex BMR	250	1	75	2	50	2	0	2	0
Pennisetum glaucum	Millex 32	250	1	100	1	15	1	0	1	0

Pennisetum orientale	PI 600996	150	1	80	1	195 *	7	225 *	9	0
Phalaris caroliniana	Native	100	1	0	1	0	1	0	1	0
Saccharum officinarum	L 01-299	150	1	50	1	25	1	0	1	0
Saccharum officinarum	HO/CP 96-540	150	1	35	1	0	0	0	1	0
Saccharum officinarum	Exp 13 7000	250	1	175 *	2	325 *	6	400 *	8	550 *
Secale cereale	JSS968.32	100	1	20	1	20	1	0	1	0
Setaria italica	NSL 6636	150	1	120 *	2	150 *	3	80	3	50
Sorghum arundinaceaum	JSS1455.26	250	2	250 *	8	575 *	9	0	9	0
Sorghum bicolor	K 73-J6	250	2	265 *	7	450 *	9	0	9	0
Sorghum drumundii	BMR2826G	250	2	175 *	8	550 *	9	0	9	0
Sorghum halepense	Native	250	1	200 *	7	225 *	8	375 *	8	460 *
Sporobolus indicus	Native	150	1	65	1	0	1	0	1	0
Tridens flavus	Native	100	1	50	1	0	1	0	1	0
Tridens albescens	Native	100	1	25	1	0	1	0	1	0
Tripsacum dactyloides	PMK-24TX	125	1	50	1	0	1	0	1	0
Triticum aestivum	LA06146	200	1	100	1	0	1	0	1	0
Urochloa ramosa	Lot 472	150	1	55	2	125 *	4	65	5	85
Zea mays	DK2508	200	1	75	1	50	2	35	2	0

Table 3. Mean population counts and Phytotoxicity scores of Group 1, means for three replications. Asterisk (*) designates results of ANOVA were significant, with $P < 0.05$. A box (□) designates phytotoxic scores greater than 7, which we considered the susceptibility threshold. [R] = known resistant [S] = known susceptible

		Population				Phytotoxicity			
Graminous spp.	Rep / Time (days)	1	7	28	32	1	7	28	32
Zea mays	A	10	45	90	425 *	1	1	1.2	3.4
	B	0	25	80	245 *	1	1	1	2.4
	C	10	50	20	325 *	1	1	1	1
Miscanthus gigantus	A	6	35	150	350 *	1	1	1.6	3.1
	B	9	24	150	175	1	1	1	1.2
	C	15	55	125	225 *	1	1	2.5	2.5
Sorghum arundinaceaum	A	100 *	300 *	3300 *	0	1	2.9	7.6	9
	B	90 *	475	3500 *	0	1	1.3	7.5	9
	C	100 *	515	3150 *	0	1	1.8	7.5	9
Sorghum bicolor [R]	A	20	65	475 *	825 *	1	1	3.85	4.6
	B	20	55	515 *	900 *	1	1.5	4.85	4.5
	C	10	20	475 *	675 *	1	1	4.1	4.35
Sorghum bicolor [S]	A	85 *	325 *	2875 *	0	1	2.3	7.35	9
	B	65 *	300 *	2450 *	0	1	1.5	7.5	9
	C	80 *	345 *	2500 *	0	1	1	7.1	9
Pennisetum glaucum	A	10	50	600 *	1000 *	1	1.5	2.1	7.85
	B	35	85	765 *	1050 *	1	1.8	4.5	7.6
	C	25	50	550 *	1200 *	1	1.2	3.8	7.4
Saccharum officinarum [S]	A	0	0	4	25	1	1	1	1
	B	5	5	20	10	1	1	1	1
	C	0	0	10	45	1	1	1	1
Triticum aestivum	A	0	0	0	5	1	1	1.1	2.3
	B	10	0	0	0	1	1	1	1
	C	0	0	0	0	1	1	1	1

Table 4. Population counts and Phytotoxicity scores of Group 2, means for three replications. Asterisk (*) designates results of ANOVA were significant, with $P < 0.05$. A box (□) designates phytotoxic scores greater than 7, which we considered the susceptibility threshold. [S] = known susceptible

		Population count				Phytotoxicity score			
Treatment	Rep / Time	1	7	32	35	1	7	32	35
Echinocloa crus-galli	A	20	50	85	150 *	1	2	4.3	4.7
	B	15	65	100	125	1	2	2.9	4.3
	C	45	65	95	125	1	2	4.6	5.4
Echinocloa muricata	A	30	30	15	20	1	1	2	1.3
	B	5	30	0	5	1	1	2	1.3
	C	30	30	15	20	0.2	1	2	1.3
Paspalam notatum	A	2	0	0	0	0	0	0	1
	B	15	10	0	0	0	1	1	0
	C	1	0	0	0	1	0	1	0
Pennisetum orientale	A	15	45	375 *	475 *	1	2.3	3.5	7.13
	B	0	15	245 *	645 *	1.3	2.3	3.5	7.6
	C	15	45	375 *	600 *	1	2.3	3.5	7.25
Setaria italica	A	0	10	45	45	1	1	1.9	2.6
	B	35	10	45	25	1	1	1.9	2.6
	C	0	10	45	45	0.2	1	1.9	2.5
Sorghum drumundii [S]	A	100	375 *	1600 *	0	1	3.3	7.3	9
	B	115	400 *	1800 *	0	1	3.3	7.7	9
	C	75	425 *	1900 *	0	1	3.3	7.5	9
Sorghum halepense	A	50	200	425 *	675 *	1	2.1	5.6	7.2
	B	75	265	785 *	1165 *	1.2	2.1	5.6	8.5
	C	50	275	450 *	1250 *	1	2.1	5.6	7.9
Urochloa ramosa	A	5	20	85	125	1	1.1	1.8	2.3
	B	0	5	65	200 *	1	1.1	1.9	2.2
	C	15	20	50	85	1	1.1	2.4	2.1

Table 5. Results of analysis of reproductive data. Intrinsic rate of increase rm = K*(LOG(Md))/d. Type III Tests of Fixed Effects (LS-means with the same letter are not significantly different.)

Graminous spp.	Generation time	Mean nymph / generation	Doubling time	Intrinsic rate of increase	Finite daily rate of increase	Reproductive days
	d	Md	DT	rm	λ	Lr
Sorghum bicolor [S]	6.62 c	40.87 a	3.89 b	0.17 a	1.19 a	16 a
Sorghum drumundii	7.37 b, c	26.25 b	5.01 b	0.14 a, b	1.15 a, b	14.37 a, b
Sorghum halepense	7.57 b	19.28 b, c	5.93 b	0.12 b, c	1.13 b, c	12.42 a, b
Saccharum officinarum [S]	9.87 a	15.62 b, c	8.38 a	0.08 c, d	1.09 c, d	10.5 b
Miscanthus gigantus	8.87 a, b	10.5 c	10.31 a	0.08 d	1.08 d	5.62 c
	P<.0001	*P*<.0001	*P*<.0019	*P*<.0001	*P*<.0001	*P*<.0001

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