EFFECT OF TEMPERATURE ON THE DEVELOPMENT OF SUGARCANE APHID, *Melanaphis sacchari,* ON SORGHUM

by

Philip Osei Hinson

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ABSTRACT

The sugarcane aphid, *Melanaphis sacchari* (Zehntner), is a pest of sorghum, *Sorghum bicolor* (L.) Moench, and sugarcane, *Saccharum officinarum* L., in tropical and subtropical regions of the world. Sugarcane aphids have severely damaged sorghum in the United States since 2013. Abiotic factors, especially temperature, affect development of insects including aphids. Understanding aphid developmental rates at different temperatures is important for evaluating and developing sorghums with durable resistance.

Fecundity and longevity of sugarcane aphids were assessed in clip cages on susceptible 'ATx399 x RTx430' sorghum at four alternating temperatures of 11:24, 16:29, 21:34, and 26:39 ^{o}C (night:day) and a relative humidity of 65% in an incubator. A photoperiod of 11:13 dark:light hours corresponded with daily cool and warm temperatures. In total, 48 sugarcane aphids in clip cages were used for each temperature. The birth date of the first nymph per clip cage was recorded. The nymph was retained and allowed to mature.

Temperature greatly affected the lengths of the pre-reproductive, reproductive, and post- reproductive periods, as well as total longevity, fecundity, reproductive rate, intrinsic rate of increase, and mean generation time of the sugarcane aphids. The pre-reproductive period was 2.4, 1.3, 1.0 and 1. 5 days at 11:24, 16:29, 21:34 and 26:39 ^{o}C, respectively, and more than twice as long at 11:24 as at 21:34 ^{o}C.

The maximum number of reproductive days was about 20 at the cool temperature of 11:24 ^{o}C but decreased slowly to about 15 days at the warm temperature of 21:34 ^{o}C. At the hot temperature of 26:39 ^{o}C, the duration of the reproductive period was only 0.12 that at the cool temperature of 11:24 ^{o}C. Increasing temperature from cool to hot decreased the length of the post-reproductive period from about 23 days to 1 day. The aphids lived as long as 45 days at the cool temperature of 11:24 ^{o}C, but survived only 5 days at the hot temperature of 26:39 ^{o}C. From cool to moderate temperature of 16:29 ^{o}C, the lifespan of the aphid decreased by 27.6 %. However, from the warm (21:34 ^{o}C) to hot temperature (26:39 ^{o}C), the percentage of decrease in the lifetime of the aphids was as much as 79.8%. The aphid produced a maximum number of nymphs 3 days earlier at the moderate (16:29 ^{o}C) than at the cool temperature (11:24 ^{o}C). However, maximum average daily fecundity occurred 1 day earlier at the warm temperature of 21:34 ^{o}C than at the moderate temperature of 16:29 ^{o}C. Total fecundity per was greatest at 16:29 ^{o}C, with fewest nymphs produced at 26:39 ^{o}C.

The 'intrinsic rate of increase" of the population was greatest (33%) at the warm temperature of 21:34 ^{o}C and least (1%) at the hot temperature of 26:39 ^{o}C. The cool (11:24 ^{o}C) and hot (26:39 ^{o}C) temperatures decreased the growth rate of the sugarcane aphid populations on sorghum. The mean generation time was 3.2, 1.8, 1.3 and 2.1 days for sugarcane aphids at the cool, moderate, warm and hot temperatures, respectively. The most favorable temperature for development of sugarcane aphids on sorghum was 16:29 ^{o}C (moderate temperature), demonstrated by the comparatively large total fecundity and reproductive rate.

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APPROVED:

Dr. Bonnie Pendleton Chairperson, Thesis Committee	Date
Dr. Bob Stewart Member, Thesis Committee	Date
Dr. Marty Rhoades Member, Thesis Committee	Date
Dr. Lance Keith Head of Department	Date
Dr. Dean Hawkins Dean of Agriculture and Natural Sciences	Date
Dr. Angela Spaulding Dean, Graduate School	Date

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CHAPTER 1

INTRODUCTION

Background to the study

Sorghum [*Sorghum bicolor* (L.) Moench] is an important cereal crop worldwide that is grown for grain for human food, and stalks for fodder and building materials in developing countries. It is used primarily in developed countries as animal feed and in sugar, syrup, and molasses industries (Li and Gu 2004, Liu et al. 2009, Guo et al. 2011). Its many uses, efficient C4 photosynthesis system, high yield potential, and tolerance to abiotic stresses make sorghum an increasingly important crop for dealing with shortages of natural resources and climate change (Jackson et al. 2008, Paterson et al. 2009). Therefore, sorghum is an important cereal crop in Asia, Africa, Australia and the Americas. For production, sorghum was the fifth most important cereal crop worldwide, and was third behind wheat (*Triticum aestivum* L.) and maize (*Zea mays* L.) in the United States (FAOSTAT 2016).

Sorghum in the United States is grown in more than 30 states but predominantly on the southern Great Plains. Approximately 3,423,236 hectares of sorghum with an economic value of more than $2 billion were grown in the United States in 2015 (USDA-NASS 2015). Texas is second only to Kansas as the largest producer of sorghum in the U.S. In 2015, about 1.1 million hectares with an economic value of $742.7 million were grown in Texas (USDA-NASS 2015).

Sorghum contains large amounts of sugar that attracts not only people, but also pathogens and insects. One of the greatest threats to increasing sorghum yield potential is damage by insects. Insect pests such as the sugarcane aphid, *Melanaphis sacchari* (Zehntner) (Hemiptera: Aphididae), attack sorghum. In addition to sucking sap and killing sorghum, the sugarcane aphid is a vector of sugarcane yellow leaf virus that causes yellow leaf disease in sugarcane [*Saccharum officinarum* (L.)]. The aphid is distributed in Africa, Asia, Australia and the Americas (Nibouche et al. 2015).

The sugarcane aphid has a history of infesting sugarcane in Florida (Mead 1978, Denmark 1988) and Louisiana (Hall 1987, White et al. 2001) and has been a common pest of sugarcane in the U.S. since the late 1970's (Nibouche et al. 2015). In the summer of 2013, the sugarcane aphid was detected in sorghum fields near Beaumont, TX, and thereafter discovered in sorghum throughout the eastern half of the state of Texas including north-central Texas, the Gulf Coast and Lower Rio Grande Valley in South Texas, Louisiana, Mississippi and Oklahoma (Villanueva et al. 2014). Since 2013, sugarcane aphids have caused serious economic damage and threatened sorghum in the southern states of the U.S. (Nibouche et al. 2015, Zapata et al. 2016). The aphid was confirmed in 12 and 17 states in 2014 and 2015, respectively. In 2015, the 17 states with confirmed sugarcane aphids infesting sorghum accounted for 97% (2,996,697 ha) of the hectarage and 98% (15,247,593 metric tons) of the total sorghum production in the U.S. (USDA-NASS 2015). Because of rapid increase in abundance, great dispersion capacity, and few insecticides available to control the sugarcane aphid, the aphid is capable of causing substantial damage to sorghum. Wind-aided movement of aphid alates might be the reason for the rapid expansion of the sugarcane aphid (Bowling et al. 2016).

Sugarcane aphid infests sorghum during all plant growth stages, but significant economic damage usually occurs late (van Rensburg 1973a, Teetes et al. 1995), especially during flowering and grain filling when environmental conditions are unfavorable and plants are moisture stressed (Raetano and Nakano 1994). In North America, sugarcane aphids feed on sorghum species in the spring and summer and the same host that persists through fall and winter months (Bowling et al. 2016). The amount of damage the sugarcane aphid causes to sorghum depends on such factors as aphid abundance and duration of infestation. The aphid prefers to feed on the under surface of older leaves of sorghum plants, and the infestation progresses upward. Nymphs and adults suck sap from leaves resulting in drying and stunted plant growth or death when infestation by aphids is severe. While feeding, the aphid produces copious amounts of sticky honeydew that can clog combine harvesters and substantially reduce yield potential. The honeydew produced by the insect also supports the growth of fungus that can inhibit plant growth (Balikai 2007, Villanueva et al. 2014, Zapata et al. 2016). The sugarcane aphid also affects sorghum grain quality in terms of diastatic power, malt loss and abrasive hardness index. This results in poor sorghum grain and milling quality. Reduced grain hardness as a result of feeding by sugarcane aphids might result in loss of flour during milling (van den Berg et al. 2003, Sharma et al. 2014).

Statement of the problem

Abundance and population dynamics of insect pests, which are poikilothermic, are affected by temperature and might be influenced by climate change primarily by the greenhouse effect (Kiritani 2013). Weather factors such as temperature, relative humidity, rainfall, wind and photoperiod directly impact insect population dynamics.

Karuppaiah and Sujayanad (2012) considered temperature to be the most important weather factor. Changes in weather can affect the status of insect pests and enable them to cause more damage to crops (Sharma 2013). As a result of climate change, many insect species might move into new areas where they find more suitable environmental niches and could threaten crop production and food security (Jaba and Sharma 2016). For example, the sugarcane aphid has moved into new sorghum areas in the U.S.

Bionomics of aphids is considerably influenced by temperature (Asin and Pons 2001). Temperature affects population dynamics, rates of development, reproduction, mortality, survival and seasonal occurrence of aphids (Dixon 1977, 1987; Kuo et al. 2006). Sugarcane aphids like other insects are ectothermic organisms with physiological processes sensitive to temperature. Information is inadequate on the biology and growth rates of sugarcane aphids at different temperatures on sorghum. Therefore, this research focused on studying the effects of different cycling temperatures on the development of sugarcane aphids on sorghum.

Objectives of the study

The specific objectives of the research were to study the biology, growth, and development of sugarcane aphids on sorghum at different temperatures to determine the:

a. number of days before the first aphid nymphs were produced (pre-reproductive period)
b. number of days nymphs were produced (reproductive period)
c. number of days between the production of the last nymph and the death of the aphid (post-reproductive period)
d. number of days each sugarcane aphid lived (longevity)

e. number of nymphs produced per day (daily fecundity)

f. total number of nymphs produced (total fecundity) and total reproductive rate

g. percentage of increase in the abundance of sugarcane aphids (intrinsic rate of increase)

h. number of days between each sugarcane aphid generation (mean generation time)

Significance of the study

The research is important because results of the study can be used to predict when sugarcane aphids are expected to arrive in sorghum fields and to predict aphid development, time of damaging infestations, and biological control needed. The study provides valuable knowledge and contributes to literature on the biology and increase in abundance of sugarcane aphids on sorghum. Understanding developmental rates at different temperatures would aid in understanding population dynamics and increase in abundance of sugarcane aphids at late stages of sorghum growth. Understanding the biology and population growth rate of the aphid at different temperatures is necessary for development of integrated pest management strategies to control the aphid. Quantification of potential population growth rates of the sugarcane aphid under different temperature regimes would aid in developing computer forecasting models. Knowledge of sugarcane aphid biology and how the aphid develops under different alternating temperatures would help in developing sorghum with durable resistance against this serious insect pest of sorghum.

CHAPTER 2

LITERATURE REVIEW

Sorghum and its importance

Sorghum is a grass in the family Poaceae, tribe Andropogoneae, subtribe Sorghinae¸ and genus *Sorghum* (Smith and Frederiksen 2000). Cultivated sorghum is classified as *Sorghum bicolor* (L.) Moench. Sorghum is believed to have been domesticated in Ethiopia and surrounding African countries, commencing about 4000-3000 BC (Doggett 1970), then spread to other parts of Africa, India, Asia, Australia, and the United States (Smith and Frederiksen 2000, FAO 2007). Sorghum is a small-grain cereal grown between 40^{o}N and 40^{o}S of the equator (Doggett 1988). Globally, it is a vital cereal crop grown primarily in semi-arid and arid regions. Sorghum is the fifth most important cereal crop after wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), maize (*Zea mays* L.), and barley (*Hordeum vulgare* L.) (Prasad and Staggenborg 2009, FAOSTAT 2016). Sorghum is usually grown for food, fiber, forage, and production of ethanol and sugar (Li and Gu 2004, Liu et al. 2009). It is one of the most drought-tolerant cereal crops currently cultivated. This enables farmers to grow the crop in areas with limited water.

Sorghum is principally a rain-fed crop in dry areas of the tropics and sub-tropics and a post-rainy season crop grown on residual soil moisture, particularly in India. It is also grown in more temperate climates such as the U.S. and China. Sorghum grows on a wide range of soils (low fertility, moderately acidic or very alkaline) at altitudes from sea

level to 3,000 m (Kimber 2000), but it is not tolerant of frost, shade, or sustained flooding (Clark 2007, FAO 2012).

Sorghum is a C4 annual self-pollinating plant with high photosynthetic efficiency. It is short-day plant (Dial 2012) that varies from 0.5 to 6 m tall, usually with a large erect stem terminating in a panicle of variable compactness (Kimber 2000). A sorghum leaf has a prominent midrib; typical leaf blades are 8-12 cm wide and 50-90 cm long. The leaf sheath and stem are often covered with waxy bloom (Prasad and Staggenborg 2009). Sorghum has an extensive fibrous root system as deep as 3 m (Prasad and Staggenborg 2009) that contributes to drought resistance (Kimber 2000).

Sorghum is classified into four groups by its intended purpose: grain sorghum, sweet sorghum, broom sorghum, or grass sorghum (Vinall et al. 1936). Grain sorghum is used as subsistence food in tropical areas and often as raw material for alcoholic beverages, sweets, and glucose. Sweet sorghum is used for syrup. Broom sorghum is used to make brooms, while grass sorghum is grown for green feed and forage. Sorghum grain has a high nutritive value, with 70-80% carbohydrate, 11-13% protein, 2-5% fat, 1-3% fiber, and 1-2% ash (Prasad and Staggenborg 2009). The protein in sorghum grain is gluten free, and is therefore food for people who suffer from celiac disease and diabetes. Sorghum is an excellent crop for the production of renewable fuels (Dahlberg et al. 2011).

Approximately 50% of sorghum is consumed by humans worldwide, however in the United States more than 90% is consumed as livestock feed. Leading producers of sorghum in the world include the United States, Mexico, Nigeria, India and Ethiopia (FAO 2014). Sorghum was introduced into the United States in the eighteenth century

(Smith and Frederiksen 2000) and is currently the third most important cereal crop behind wheat and maize. Sorghum in the United States is grown in more than 30 states, but mostly on the southern Great Plains. Grain sorghum is a multi-billion dollar crop with an economic value of more than $2 billion for 3,423,235 hectares planted in 2015 in the United States (USDA-NASS 2015). Kansas and Texas have been the main two sorghum-producing states. In 2016, about 768,903 hectares of sorghum with an economic value of approximately $388 million were grown in Texas (USDA-NASS 2016).

Aphids on sorghum

Aphids are serious pests of many agricultural crops and ornamental plants worldwide. They are categorized as phytotoxic and non-phytotoxic based on the intensity of damage done directly to the plant tissue and altering the physical characteristics. Depending on the species, they can remove large volumes of plant sap, secrete abundant amounts of honeydew, vector numerous plant diseases, and use salivary compounds to subvert normal plant metabolism, with potentially fatal consequences for plants (Dixon 2000, Quisenberry and Ni 2007, Bayoumy et al. 2015). Blackman and Eastop (1984) reported 14 aphid species that attack sorghum: common dogwood-grass aphid, *Anoecia corni* (Wilson); root aphid, *Forda orientalis* (George); rusty plum aphid, *Hysteroneura setariae* (Thomas); *Melanaphis sacchari*; corn leaf aphid, *Rhopalosiphum maidis* (Fitch); bird cherry oat aphid, *Rhopalosiphum padi* (Linnaeus); *Pseudaphis sijui* (Eastop); greenbug, *Schizaphis graminum* (Rondani); yellow sugarcane aphid, *Sipha flava* (Forbes); corn leaf aphid, *Sipha maydis* (Pesserini); *Sitobion africanum* (Lambers); banded cereal aphid, *Sitobion leelamaniae* (David); *Sitobion miscanthi* (Takahashi); and

rice root aphid, *Tetraneura nigriabdominalis* (Sasaki). Before sugarcane aphids became abundant, the greenbug and corn leaf aphid were the aphids that most commonly infested sorghum in the central Great Plains of the United States (Bayoumy et al. 2015).

Greenbug is a major aphid pest of small grains and sorghum (Teetes et al. 1983, Teetes and Pendleton 2000, Pendleton et al. 2009). The aphid is widely distributed in Asia, Africa, Australia and America. Greenbug infestation of sorghum in the United States was first documented in 1916. However, it was not until 1968 that greenbug became a serious and persistent pest of sorghum (Pendleton et al. 2009). The greenbug can be distinguished from other aphids by its pale green color, dark green mid-dorsal stripe, and black distal leg segments, antennae, and cornicle tips. Greenbug adults are approximately 1.6 mm long and can be winged or wingless (Teetes et al. 1983). Eleven biotypes of greenbug, designated A through K, have been identified in the United States. Biotypes of greenbugs are identified based on the responses of certain lines (differentials) of small grains and sorghum to damage by greenbugs (Pendleton et al. 2009).

Greenbug infests the stem and leaves at the base of the sorghum plant first and moves upward as the lower leaves die (Hoelscher et al. 1987). Infestations can occur from the time plants are seedlings until they mature. Seedlings are most vulnerable to damage by greenbugs. Greenbugs also colonize sorghum plants at the late-whorl stage and potentially persist until flowering (Michaud 2015). Infestations of sorghum are detectable by the appearance of reddish spots on the leaves caused by toxin the greenbugs inject into the plant. The leaves begin to die, turning brown from the outer edges. The aphid feeds in colonies on the underside of the foliage and produces an abundance of

honeydew. Greenbugs also transmit maize dwarf mosaic virus and may predispose sorghum to charcoal rot, *Macrophomina phaseolina* (Tassi) Goid.

Greenbugs tolerate a wide range of temperatures but prefer 24 to 29^{o}C for optimum reproduction (Hoelscher et al. 1987). Temperatures cooler than 4.5 or warmer than 35^{o}C significantly reduce the activity and fecundity of greenbugs. Pendleton et al. (2009) studied the effect of temperature on the fitness of different biotypes of greenbug. They reported that the greenbug pre-reproductive period, total fecundity, and longevity did not differ among temperature regimes except at the warmest temperature of 22-35 ^{o}C at which all parameters were greater for biotype E than biotype I greenbugs. They also stated that greenbugs produced a maximum average of 3.3 more nymphs per day at warmer than cooler temperatures. When weather conditions are favorable, greenbugs can increase 20-fold but the normal rate is five-to six-fold per week in sorghum fields (Teetes et al. 1983).

The corn leaf aphid is cosmopolitan in distribution, occurring between latitudes 40^{o}N and 40^{o}S in all sorghum-growing areas of the world. The aphid is Asiatic in origin (Teetes et al. 1983; Blackman and Eastop 1984, 2000). A corn leaf aphid can be identified by its dark bluish-green color with black legs, cornicles and antennae. The adult aphid is approximately 2 mm long and can be winged or wingless (Teetes et al. 1983). Blackman and Eastop (1984) reported that corn leaf aphid "apterae are rather elongate with short antennae and short, dark cornicles (siphunculi); yellow-green to dark olive green or bluish green, at times dusted with wax. Alates have a yellow-green to dark green abdomen without dark dorsal marking anterior to the cornicles (siphunculi). Apterae and alatae are about 0.9-2.4 mm."

The corn leaf aphid is most commonly found deep in whorl of the middle leaf, but also on the underside of leaves, on stems, or in panicles of sorghum (Teetes et al. 1983). Nymphs and adults suck plant juice from leaves which causes yellowish mottling and may cause marginal leaf necrosis. Corn leaf aphids often become abundant in the whorl of sorghum during the vegetative growth stages, but rarely cause economic damage.

Nomenclature of sugarcane aphid

The taxonomic name of the sugarcane aphid, *Melanaphis sacchari* (Zehntner 1897) (Hemiptera: Aphididae), has been changed frequently. The sugarcane aphid has been classified as *Aphis sacchari* (Zehntner) (Zimmerman 1948), *Melanaphis sorghi* (Theobald), and *Longiunguis sacchari* (Zehntner) (Eastop 1965). Detailed history on the nomenclature of the sugarcane aphid dates to 1917 when van der Goot renamed the genus of *Aphis bambusae* as *Melanaphis*. He also renamed the genus for *Aphis sacchari* (Zehntner) as *Longiunguis*. Van der Goot distinguished the two genera mainly by the ratio of the length of the antenna to the body and that of the siphunculi to the cauda. In 1920, Baker considered both genera synonymous with *Aphis* because the characteristics considered by van der Goot for separation of the two genera were too variable in large samples of either an individual species or even different species.

Lambers (1947) described *Longiunguis luzulella*. He considered *Longiunguis* as different from *Melanaphis*. Eastop (1958) also considered *Melanaphis* and *Longiunguis* as two distinct genera. In 1966, Lambers after studying the types of *Melanaphis* and *Longiunguis* stated the latter should be regarded as a synonym or at most a subgenus of the former. Although prior to Lambers, Eastop (1961) had stated that *Longiunguis* should be regarded as a subgenus of *Melanaphis*, he recorded *sacchari* as belonging to

the genus *Longiunguis*. Raychaudhuri and Banerjee in 1974 officially synonymized both *Longiunguis sacchari* and *Aphis sacchari* as *Melanaphis sacchari* (Zehntner) which unified the nomenclature. *Melanaphis sorghi* was also regarded as a synonym of *M. sacchari* by Remaudièrè and Ramaudièrè (1997).

Geographical distribution of sugarcane aphid

The sugarcane aphid is widely distributed on poaceous hosts (Blackman and Eastop 2006). The geographical distribution of the aphid is closely associated with sorghum- and sugarcane-producing countries. *M. sacchari* are found predominantly in Africa (Angola, Botswana, Egypt, Ethiopia, Kenya, Nigeria, South Africa, Sudan, Tanzania, Uganda and Zimbabwe), Asia (Bhutan, China, India, Indonesia, Japan, Pakistan, Philippines, Taiwan and Thailand), North America (Haiti, Jamaica, Mexico and United States of America), South America (Argentina, Brazil, Colombia, Ecuador, Peru, Trinidad and Tobago, and Venezuela) and Australia (Singh et al. 2004).

The aphid is an economically important pest of sorghum in China (Wang 1961, Singh et al. 2004), India (Young 1970), Japan (Setokuchi 1973), South Africa and Botswana (van Rensburg 1973a), and Taiwan (Chang 1981a, b; Pi and hsieh 1982a). In the U.S., it occurs on sugarcane in Hawaii (Pemberton 1948, Zimmerman 1948), Florida (Mead 1978, Summers 1978, Denmark 1988), and Louisiana (Hall 1987, White et al. 2001). Sugarcane aphid has become a major insect pest of sorghum in Mexico (Rodriquez-del-Bosque and Teran 2015) and the U.S.A. (Villanueva et al. 2014) since 2013.

History of sugarcane aphid in the United States

The sugarcane aphid has a documented history of infesting sugarcane in Florida (Mead 1978, Denmark 1988) and Louisiana (Hall 1987, White et al. 2001) and has been a common pest of sugarcane since the late 1970's (Nibouche et al. 2015). Earlier infestations were characterized by summer outbreaks followed by a decrease in abundance during the winter. No previous occurrences resulted in permanent infestation of sorghum by the pest, and there was no indication, at those times, that the aphid was able to successfully adapt to more temperate environments (Zapata et al. 2016).

The spread of sugarcane aphid on sorghum has been rapid and covered a wide geographical range in North America. In June 2013, an outbreak of the aphid was detected in sorghum fields near Beaumont, TX, and thereafter discovered in sorghum throughout the eastern half of the state of Texas including north-central Texas, the Gulf Coast and Lower Rio Grande Valley in South Texas, Louisiana, Mississippi and Oklahoma (Villanueva et al. 2014). During the 2014 sorghum-production season, the aphid survived the winter in the northern state of Tamaulipas, Mexico, and in South Texas where it eventually moved north into Arkansas, more northern latitudes of Oklahoma, south-central Kansas, and as far west as Hale Center, TX (Armstrong 2015). The aphid infested grain and forage sorghum in 12 states, as far as Tennessee, Georgia, Florida in 2014 (Colares 2015). A 25% increase from 2014 was reported in the occurrence of sugarcane aphids in 2015. The occurrence of the aphid on sorghum was observed in 417 counties in 17 states by the end of the 2015 sorghum-growing season (Bowling et al. 2016). In 2015, the 17 states with confirmed sugarcane aphids on sorghum accounted for 97% (2,996,697 hectares) of the sorghum hectarage and 98% (14, 231,177 metric tons) of the total sorghum production in the U.S. (USDA-NASS 2015).

Description and biology of sugarcane aphid

Sugarcane aphids are small, oval-shaped, soft-bodied insects that have piercing-sucking mouthparts for sucking juice from plant tissues (Guo et al. 2011). They are yellow to buff in color (Teetes et al. 1983). Unlike other aphid species that feed on sorghum, their entire tarsi and cornicles at the rear of the abdomen are dark (Villanueva et al. 2014). The aphids are predominantly found at the axils of the lower leaves, but large colonies extend over the entire leaf (Blackman and Eastop 2006).

Comprehensive study of the biology, description, and life history of the sugarcane aphid has been on sorghum in South Africa (van Rensburg 1969, 1973ab, 1976), India (Raychaudhuri and Banerjee 1974), and China (Guo et al. 2011), and on sugarcane in India (Varma et al. 1978) and Japan (Setokuchi, 1980, 1988). According to Varma et al. (1978), the insect multiplies by parthenogenesis, that is, females without mating give birth to live nymphs that molt four times before becoming adults. Adults are alate (winged) or apterous (wingless). Varma et al. (1978) stated:

i. The first-instar nymph of a sugarcane aphid has: a cylindrical light-brown body, head and thorax not well marked, legs and flagellae of antennae pale yellow, black and conspicuous eyes, cornicles short and not well defined, and no cauda. The stage lasts for 2 or 3 days with a mean of 2.1 days.

ii. The second-instar nymph has a complete body demarcation with a visible thorax. The color of the head and thorax of the instar becomes darker, cornicles are black and well defined, and a cauda is not well developed. The stage lasts for a day.

iii. The third-instar nymph has a darker body and is larger than the first and second instars. Wing buds appear in those individuals that will develop into alates. The stage lasts for 1 or 2 days with a mean of 1.1 day.

iv. The fourth-instar nymph has integument more sclerotized and hence darker than the previous three instars. A cauda is under-developed. The stage finally changes into an adult within 1 or 2 days with a mean of 1. 4 day.

v. The adult (apterous) resembles the previous instar in all aspects except the bigger size and fully developed cauda. At this stage, a sugarcane aphid can produce nymphs. It reproduces parthenogenetically and lives for 10-14 days. The adult (alate) has a pair of wings that are conspicuous. The head and thorax are demarcated by a prominent constriction. An alate adult usually lives for 2-4 days and reproduces parthenogenetically. The body is smaller and darker than that of an apterous adult.

Raychaudhuri and Banerjee (1974) studied numerous apterous and alate viviparous females on several host plants including sorghum and described:

i. Apterous viviparous female: Has a body about 1.52-1.66 mm long and 0.44-1.34 mm wide. The head is pale with ill-developed lateral frontal tubercles and median frontal prominence. Thoracic tergites are usually pale, but sometimes broken brownish patches in a broken polygonal pattern are noticed between the mesothorax and metathorax. The dorsum of the abdomen is pale but often irregular brown to dark brown patches are developed in spinal and pleural areas. Hairs on the anterior half of the genital plate usually vary between seven and nine, but sometimes the number of hairs can be as few as two or as many as 11. Femoral hairs are short with acuminate apices. Legs are pale with the tips of the tibiae and whole tarsi dark brown.

ii. Alate viviparous female: Has a body about 1.3-1.84 mm long and 0.56-0.9 mm wide. The head is completely dark brown with tiny stipples on the dorsum of the head. Mesothoracic lobes are well-developed. The genital plate has five to nine long, fine hairs

on the anterior half. Mid and hind femora are brown to dark brown except the extreme base which is pale. The fore femora are pale brown with the base and apex still pale. All femora are smooth dorsally and with spinulose striae ventrally. The tibiae are pale with apices brown to dark brown and smooth. Tarsi are brown to dark brown. Wing venation is normal and wing veins are moderately thick and bordered brown.

Van Rensburg (1973a) studied the duration of immature stages as well as longevity and reproduction of adults. He reported that the mean duration of the four immature stages of apterous *M. sacchari* on young grain sorghum were 1.1, 1.4, 1.5 and 1.0 day, respectively, and the corresponding number of days on mature sorghum were 1.0, 1.1, 2.1 and 1.0, respectively, at a maximum temperature of 31.5 ^{o}C and a minimum temperature of 22.2 ^{o}C. He stated that the mean developmental time on young versus mature sorghum did not differ. Also, he stated that mean longevities of wingless sugarcane aphids on young and mature sorghum were 28.0 and 28.1 days, respectively, and the difference was not significant. Aphids on young and mature plants produced averages of 85.6 and 96.2 nymphs, respectively, at a maximum temperature of 32.0 ^{o}C and a minimum of 21.1 ^{o}C.

According to research by other scientists, the aphid has four nymphal stadia completed in 4.3-12.4 (Chang et al. 1982) or 5 days (Manthe 1992). Meksongesee and Chawanapong (1985) reported that under crowded conditions or when host plants were stressed, sugarcane aphids produced winged forms (alates) that molted five times before becoming adults. Sugarcane aphids form colonies of apterae and alate individuals on the abaxial surface of basal leaves of a sorghum plant. Some alates have patterned black

markings along the dorsal scleritis (Eastop 1955, Blackman and Eastop 1984, Singh et al. 2004).

The aphid is a parthenogenic and anholocyclic species. This means that reproduction by sugarcane aphids is predominantly asexual with adults being either apterae or alate viviparous females. In North America, all aphids are female and produce live young asexually, with the exception of one report of egg production by female aphids collected from three Mexican states (Bowling et al. 2016, Peña- Martinez et al. 2016). David and Sandhu (1976) stated that sexual reproduction by sugarcane aphid was also known to occur on sorghum; however, the environmental conditions under which sexual reproduction takes place have not been reported.

Studies have shown that the temperature when sugarcane aphids were most active ranged from 11.4 to 34.7 ^{o}C (Narayana et al. 1982, Mote and Kadam 1984, Waghmare et al. 1995, Balikai 2001b). Adults normally survive for 10-16 (Meksongsee and Chawanapoong 1985, Sharma et al. 2014), 14-37 (Chang et al. 1982), or 28 days (van Rensburg 1973a), and produce as many as 68 nymphs per female, with an average of 34 (Meksongsee and Chawanapoong 1985), 45-89 (Chang et al. 1982), 60-100 (Sharma et al. 2013), or 96 nymphs at 18.0-31.0 ^{o}C (van Rensburg 1973a).

Sugarcane aphids produce more than 10 generations per year, and 19-20 generations per year might occur depending on weather conditions (Singh et al. 2004, Guo et al 2011). In a screenhouse, sugarcane aphids developed 51-61 generations with an average of 56 annually (Chang et al. 1982). The life span of each generation is shorter in summer than in winter. The number of days for nymphal development increased with a decrease in longevity and fecundity of aphids reared on sorghum at 25.0 ^{o}C and a

photoperiod of 16:8 light:dark hours (Kawada 1995, Singh et al. 2004). Besides sugarcane and cultivated sorghum, the aphid overwinters parthenogenetically on ratoon sorghum and wild alternate hosts such as *Sorghum verticilliflorum* (Steud.) Stapf., *Sorghum halepense* (L.) Pers., *Panicum maximum* Jacq., and *Setaria* spp. (van Rensburg 1973a). Dispersal of alates throughout the year ensures that young cultivated sorghum is infested soon after germination. Environmental conditions (temperature and humidity) determine the length of life cycle of sugarcane aphids (Guo et al. 2011).

The seasonal history of the sugarcane aphid has been described in two phases: (i) exponential increase in numbers during the early season is terminated by dispersal in mid-season, and is responsible for considerable loss in yield; and (ii) late-summer phase, during which natural enemies regulate aphids and keep abundance less than sub-economic levels for the remainder of the season (van Rensburg and van Hamburg 1975, Singh et al. 2004). A sugarcane aphid colony has a relatively narrow time during which to increase in abundance. Physiological and biological changes occurring during sorghum plant development can cumulatively affect the exponential development growth rates during early and mid-season, reaching as many as 30,000 aphids on a single plant (van Rensburg 1973a, Setokuchi 1977). However, the aphids quickly decrease in abundance 2-3 weeks after peak abundance, and factors influencing the decrease are dispersal of alates and unsatisfactory condition of a host plant (van Rensburg 1973b, Singh et al 2004).

In India, Fang (1990) reported a significant increase in abundance of the aphid on sorghum from booting to soft-dough stages (40-70 days after planting) in the spring, and panicle formation (60-100 days after planting) in autumn. Also, Waghmare et al. (1995)

observed an increase and peak in abundance during January in India, when the post-rainy sorghum crop was between flowering and milk stages, and a decrease thereafter until maturity.

Increase in abundance of the sugarcane aphid is significantly affected by plant growth stage and temperature. Dispersal occurred within 6-10 days at a temperature regime of 15.1 and 31.0 ^{o}C (Balikai 2001), 16.0 and 29.0 ^{o}C (Mote and Kadam1984), 18.0-31.0 ^{o}C (van Rensburg 1973a, b), 19.5 and 34.7 ^{o}C (Narayanana et al. 1982), and 22.5 and 32.5 ^{o}C (AICSIP 1979, 2003), but the aphids died at 35.0 ^{o}C (Behura and Bohidar 1983).

In addition to temperature, cloudy weather and increasing humidity resulted in aphid colonies covering the abaxial surface of all leaves of sorghum plants (Mote 1983). The greatest rate of increase in abundance was between 94 and 43% relative humidity and 11.4 and 30.0 ^{o}C temperature in the morning and afternoon, respectively (Waghmare et al. 1995). Occurrence of sugarcane aphids on sorghum at the milk stage of kernel development did not affect the grain yield severely, but fodder quality deteriorated (Balikai 2001).

Nature of damage and crop loss

The amount of damage to sorghum depends mainly on the abundance of sugarcane aphids. However, the number of aphids necessary to reduce sorghum yield potential varies based on the plant stage and interval between and duration of infestation (Singh et al. 2004). Abundance of sugarcane aphids and damage to plants were correlated (Hagio 1992, Sharma et al. 2013), and both winged and wingless forms preferred susceptible varieties of sorghum (Kawada 1995, Sharma et al. 2014). The

degree of moisture stress with which sorghum is grown as well as the induction of stress because of infestation by the aphid play significant roles in the amount of damage sorghum can tolerate. Drought can stress and might intensify damage to sorghum by sugarcane aphids (Singh et al. 2004). Flatter (1982) reported that sugarcane aphids usually caused more damage to sorghum grown in soil with more clay than in sandy soil, especially during dry periods.

The sugarcane aphid infests sorghum during all plant growth stages, but infestation of economic significance usually occurs during the late growth stages (van Rensburg 1973a, Teetes et al. 1995), especially during flowering and grain filling when plants are moisture stressed and environmental conditions are unsuitable (Raetano and Nakano 1994). The importance of sugarcane aphid as a pest of sorghum results from its colonization when plants are 2-3 weeks old. Early in the infestation cycle, sugarcane aphids colonize the lower surfaces of the more mature, lower leaves of sorghum plants. The aphids gradually move upward and might eventually colonize even the panicles (Villanueva et al. 2014). Nymphs and adults of the aphid suck sap from phloem (Douglas 1998) of the abaxial surface of leaves (Sharma et al. 2014). Feeding by sugarcane aphids causes both sides of leaves to turn yellow or brown (Zapata et al. 2016), followed by necrosis, stunting, delay in flowering, and poor grain filling, including loss in quality and quantity of grain.

Infestations by sugarcane aphids can kill seedling sorghum. Infestation of pre-boot sorghum can result in significant grain loss, and infestation during kernel development can reduce yield. Large infestations can stunt plant growth and result in uneven panicle emergence from the boot (Bowling et al. 2016). Damage caused by the

aphid can reduce plant biomass, grain yield, and grain quality (van den Berg et al. 2003, Singh et al. 2004).

Leaves below the infested ones are often coated with sooty mold that grows on the honeydew produced by the aphids (Narayana 1975). The entire plant, including the inflorescence and stalk may be covered in abundant honeydew and sooty mold. Honeydew is composed primarily of plant sugars and water (Bowling et al. 2016). The abundant honeydew produced turns leaves and stalks sticky and shiny. This clogs combines and makes harvesting and machine maintenance difficult (Villanueva et al. 2014) and compounds the economic loss caused by sugarcane aphids (Armstrong 2015). Sticky leaves and stalks prevent separation of the kernels from the plants. Combines might require service to wash off the honeydew and remove stalks and panicles (Bowling et al. 2016). Honeydew and mold accumulation also can reduce photosynthesis by inhibiting light absorption. Honeydew can hamper transpiration (Villanueva et al. 2014) and also reduce effectiveness of insecticides and herbicides (Bowling et al. 2016).

Sugarcane aphid affects sorghum grain quality in terms of diastatic power, malt loss, and abrasive hardness index. This results in poor quality of sorghum beer and milling quality. Reduced grain hardness as a result of feeding by sugarcane aphids also can increase flour loss during the milling process (van den Berg et al. 2003, Sharma et al. 2014). Sorghum stressed by sugarcane aphids might be more susceptible to stalk rots (Bowling et al. 2016). On sugarcane, the sugarcane aphid is considered to be the most common and most efficient vector of sugarcane yellow leaf virus that causes yellow leaf disease (Schenck et al. 2000, Rott et al. 2008) of worldwide economic importance (Nibouche et al. 2014).

There are scanty information and data on the amount of sorghum grain lost to sugarcane aphids in most parts of the world. Sorghum yield losses ranging from minor to severe were reported in Botswana (Anonymous 1974, Flattery 1982) and Zimbabwe (Page et al. 1985). In South Africa, where sorghum production is intensive and use of hybrids is common, losses to sugarcane aphid ranged from 24 to 78% annually (van Rensburg and van Hamburg 1975, van Rensburg 1979, Teetes et al. 1995, van den Berg 2002). In India, Balikai (2007) reported that early sowing (3 September) resulted in 15 and 13% loss in grain and fodder yield, respectively, while late sowing (3 October) resulted in 30 and 35% loss in grain and fodder yield, respectively. In Mexico, yield losses of sorghum were reported to be 50-100% (Villanueva et al. 2014).

In 2014, some fields in the Lower Rio Grande Valley of Texas that were not treated had 30 to 100% loss of grain (Zapata et al. 2016), and 50-100% was reported in Louisiana (Villanueva et al. 2014). Catchout et al. (2015) summarized potential yield loss caused by sugarcane aphids on sorghum with 20% infestation at different growth stages. They reported that percentages of yield loss with no treatment at the pre-boot, boot, panicle emergence, and soft-dough stages were 81-100, 52-69, 67, and 21%, respectively.

Host plant range

The sugarcane aphid is a minor pest of several crops, but has increased rapidly (Singh et al. 2004) and become a major pest of sugarcane and sorghum in tropical regions around the world (Zapata et al. 2016). The genus *Melanaphis* infests 20 species of Poaceae (Blackman and Eastop 1984). The host range of the sugarcane aphid is

restricted mostly to species of the genera *Saccharum*, *Sorghum*, *Oryza*, *Panicum*, and *Pennisetum* (Denmark 1988).

Plant resistance

Resistance to insects has been characterized into three mechanisms of antixenosis (non-preference), antibiosis, and tolerance (Painter 1951, Horber 1980). Plant resistance to insects is rarely totally dependent on a single mechanism; invariably, overlapping mechanisms as well as morphological and biochemical factors of resistance are noticed (Balikai 2001). Plant resistance bred into crop varieties is an important component of aphid management and can be aided by biological control (Fuentes-Contreras and Niemeyer 1998, Qureshi et al. 2006). Considering the intimate physiological interactions between aphids and their host plants, it is not surprising that plant resistance is often an effective management tool for protecting crop plants (van Emden 2007, Bayoumy et al. 2015). Identification of sugarcane aphid-resistant sorghum hybrids contributes to reduce yield loss and the possible negative effects of the aphid on grain quality as well as contributing to optimizing input costs in sorghum production (van den Berg 2002).

Efforts have been made to identify sources of resistance to the sugarcane aphid pest. Sorghums resistant to the aphid have been found in China (Chang 1981, Chang and Fang 1984), Taiwan (Hsieh and PI 1982, Pi and Hsieh 1982a), Japan (Setokuchi 1976, Hagio et al. 1985, Hagio and Ono 1986), and India (Mote and Kadam 1984; Mote et al. 1985; Sharma et al. 2013, 2014). Aphid abundance and plant damage with natural infestation have been used to select resistant sorghum genotypes in the greenhouse and field (Setokuchi 1976, Pi and Hsieh 1982a, Hagio and Ono 1986). Both alate and apterous virginoparous sugarcane aphid adults preferred susceptible sorghum (Kawada

1995) and Johnson grass rather than *M. sinensis* (Singh et al. 2004). Sharma et al. (2014) evaluated a diverse array of sorghum genotypes under natural and artificial infestation and identified lines EC 434430, CSH 16, 9728, ICSB 215, ICSB 323, ICSB 724, ICSR 165, ICSV 12001, ICSV 12004, and IS 40615 to be moderately resistant to sugarcane aphids in India (Sharma et al. 2014) while the genotypes ICSV 112, ICSV 197, and ICSV 745 were reported to show moderate amounts of resistance to the aphid and few alates. Bhagwat et al. (2014) reported that lines SLB 80, ICSV 93046, and SLR 31 were durable, improved, and moderately resistant sources against sugarcane aphid.

In North America, efforts are being made to evaluate parental lines and commercially available hybrids for resistance to sugarcane aphid (Bowling et al. 2016). Several mechanisms and sources of resistance have been reported. Bowling et al. (2016) stated that high levels of resistance to sugarcane aphid in greenhouse and field tests were expressed in Texas A&M sorghum lines and hybrids Tx2783, Tx3408, Tx3409, B11070, AB11055-WF1-CS1/RTx436, and AB11055-WF1-CS1/RTx437. They also stated that high level of resistance to the aphid was found in sorghum parental types SC110 and SC170.

TAM 428 was reported to have both antixenosis and antibiosis resistance to sugarcane aphids in sorghum (Teetes et al. 1980, Xu 1982, Manthe 1992) and hence, is a widely used source of resistance (Bhagwat et al. 2014). Antixenosis for adult colonization was noticed in TAM 428, IS 1144C, IS 1366C, IS 1598C, IS 6416C, IS 6426C, IS 12661C, and IS 12664C. Among them, IS 1144C and IS 12664C were preferred less than the resistant check, TAM 428. Setokuchi (1988) reported that sugarcane aphids failed to establish on resistant lines under field conditions although the

resistant sources served as a suitable hosts in confined studies, which indicated the involvement of both antixenosis and antibiosis mechanisms of resistance. High levels of antibiosis were expressed in TAM 428, IS 1144C, IS 5188C, IS 12609C, and IS 12664C for the least number of days of reproduction, and in TAM 428, IS 12609C, and IS 12664C for greater mortality and shorter longevity of sugarcane aphid adults and production of fewer or no nymphs (Teetes et al. 1995). Genotypes ICSB 323, ICSB 215, ICSV 12004, ICSR 125, IS 40615, ICSV 12001, ICSB 321, and ICSB 724 resulted in low rates of increase in sugarcane aphids in clip cages as well as little damage under field conditions, and indicated antibiosis as the mechanism of resistance (Sharma et al. 2013). Genotypes PAN 8446, PAN 8564, SNK 3939, and NS 5511 were tolerant to damage by sugarcane aphids in South Africa (van den Berg 2002).

Plant resistance to sugarcane aphid is extensively characterized in sorghum (Singh et al. 2004) more than in sugarcane (Akbar et al. 2010). Nymphal development in addition to reduced fecundity and longevity of sugarcane aphids were prolonged in resistant sorghums (Liu et al. 1990, Kawada 1995, Sharma et al. 2014). Teetes (1980) found that antixenosis and antibiosis mechanisms of resistance to sugarcane aphid in sorghum did not differ with plant age. Evaluation of seedling and mature plants showed similar results (Pi and Hsieh 1982a, Hagio and Ono 1986), but seedlings were preferred for easy handling and control of amounts of infestation (Teetes 1980). Tolerance to sugarcane aphid injury in sorghum increased greatly with a slight increase in plant height, and has inherent advantage over antibiosis and antixenosis because it does not impose selection pressure on aphids to become resistant, and thus might be more permanent. There is a need to assess the role of antixenosis and tolerance mechanisms of resistance

to the sugarcane aphid to identify sorghum germplasm with diverse mechanisms or genes for resistance (Sharma et al. 2014).

Plant resistance to herbivores, especially aphids, can depend on accessibility and nutritional value of host tissues, and hence there is a need to understand the role of biochemical components of a host plant in conferring resistance to the sugarcane aphid and the effect of damage by aphids on the stalk and juice quality of sweet sorghums and fodder, or grain quality of dual-purpose sorghums (Sharma et al. 2014). Host suitability to various phloem-feeding Hemiptera has frequently been related to amounts of nitrogen in host plants. Hsieh (1988) stated that the presence of p-hydroxybenzaldehyde during hydrogen cyanide or hydrocyanic acid release from sorghum leaves because of aphids feeding at the seedling stage might be important to repel further attack. The average hydrocyanic acid content of F_1 hybrids produced from crosses between genotypes with large or small amounts of hydrocyanic acid usually had correlation intermediate between those or the parents or lines that were closer to the parent with a large amount of hydrocyanic acid. Aconiteic acid has been shown to have anti-feedant effect on aphids (Rustamani et al. 1992).

Mote and Shahane (1994) observed that genotypes with large amounts of phosphorus, potassium, and polyphenols were less preferred by aphids and also showed less development of sugary exudate from leaves. Increase in aphid abundance and sugary exudation was more pronounced in sorghum genotypes having more nitrogen, sugar, and chlorophyll in the leaves (Mote and Jadhav 1993, Mote and Shahane 1994). Amounts of nitrogen, phosphorus, potash, total sugars, and chlorophyll in sorghum can be less because of infestation by sugarcane aphids (Balikai 2001).

In sorghum, some morphophysiological traits such as genotypes with small, narrow, and fewer leaves, and low leaf bending at the seedling stage (Mote and Kadam 1984), greater plant height and longer distance between two leaves and the presence of waxy lamina (Mote and Shanane 1994), and epicuticular wax on the ventral surface of the leaves were associated with less susceptibility to the sugarcane aphid (Pi and Hsieh 1982a, b). However, Balikai (2001) stated that there was no significant relationship between morphological characteristics such as plant height, number of leaves per plant, distance between two leaves, leaf angle, leaf color, and waxy character, with infestation by sugarcane aphids.

Natural enemies

Natural enemies, although sometimes unable to prevent increase in damaging numbers of sugarcane aphids even in early season, play an important role in the population dynamics (van Rensburg and van Hamburg 1975) and often help to maintain abundance of the sugarcane aphid below the economic threshold level in sorghum (van Rensburg 1973b; Anonymous 1978; Chang 1981a, b; Meksongsee and Chawanapong 1985). Sugarcane aphids are attacked by indigenous, locally adapted, aphidophagous arthropods. For example, a recent field study in central Kansas before natural arrival of sugarcane aphids demonstrated that sorghum plants infested with either sugarcane aphids or greenbugs recruited a similar diversity of natural enemies at similar rates (Colares et al. 2015).

More than 47 species of natural enemies attack sugarcane aphids worldwide. Zimmerman (1948) reported *Aphelinus maidis* Timberlake parasitizing the sugarcane aphid in Hawaii. The parasitoids *Enrischia comperei* Ashm. in Australia (Gilstrap 1980)

and *Lioadalia flavomaculata* (DeGeer) in South Africa (van Rensburg 1973b) have been recorded.

Several predators suppressed sugarcane aphid abundance on sorghum, with lady beetles (Coleoptera: Coccinellidae), lacewings (Neuroptera: Chrysomelidae and Hemerobiidae), and hover flies (Diptera: Syrphidae) reported as killing most sugarcane aphids. Bowling et al. (2016) assessed species of natural enemies of sugarcane aphids on sorghum in South and Central Texas in 2015 and found nine species of lady beetles: *Cocciella septempunctata* L., *Coleomegilla maculata* (Degeer), *Cycloneda sanguinea* Casey, *Harmonia axyridis* Pallas, *Hippodamia convergens* Guèrin-Mèneville, *Olla v-nigrum* (Mulsant), and three morphospecies of dusky lady beetles (Coccinellidae: Scymninae). They also detected green lacewings (Neuroptera: Chrysopidae) and brown lacewings (Neuroptera: Hemerobidae) as well as three species of hover flies: *Allograpta oblique* (Say), *Pseudodoros clavatus* (Fabricius), and *Eupodes americanus* (Wiedemann). The hover fly species *Allograpta exotica* (Wiedemann 1830) in Florida (Hall 1987) and *Xanthogramma aegyptium* in Lousisiana (White 1987) played an important role by preying on sugarcane aphids.

The parasitoid *Aphelinus* sp. *varipes* group (Hymenoptera: Aphelinidae) and the hyperparasitoid, *Syrphophagus aphidivorus* (Mayr) (Hymenoptera: Encyrtidae), were detected in sugarcane aphid colonies (Bowling et al. 2016). Hall (1987) found the entomogenous fungus *Verticillium lecani* (Zimm.) Viegas to be an important biological control agent in the U.S.A. (Florida). Ants are notorious in interfering with the beneficial activities of aphid predators and/or parasites, and the sugarcane aphid might sometimes benefit from symbiotic association with certain species of ant.

Chemical control

According to Bowling et al. (2016), foliar insecticides often used in sorghum for the control of other pests have been unpredictable in their performance against the sugarcane aphid. Effectiveness of insecticides depends on factors such as the rate of application, plant growth stage, application method, and time of application.

Sulfoxaflor (Transfrom^{TM} 50 WG, Dow AgroSciences, Indianapolis, IN) and flupyradifurone (Sivanto^{TM} 200SL, Bayer CropScience, Leverkusen, Germany) were very effective for controlling sugarcane aphids in the U.S.A. (Knutson et al. 2015). Buntin and Roberts (2016) reported that Sivanto and Transform significantly reduced sugarcane aphid abundance at 3, 6 and 14 days after treatment. Gordy et al. (2015) evaluated the efficacy of eight insecticides or insecticide combinations against sugarcane aphid in three field experiments. They reported that Sivanto, Transform WG, Centric 40WDG, and Lorsban Advanced had reduced aphid abundance by 7 and 14 days after treatment, compared to Baythroid XL and non-treated plots.

Steckel and Stewart (2016) evaluated selected insecticides for control of sugarcane aphids on sorghum. They reported that Sivanto at a rate of 511.5 ml per hectare reduced aphid abundance more than did Sivanto at a rate of 292.3 ml per hectare and Transform 50WG (73.0 and 109.6 ml per hectare) at 3 days after treatment. They also stated that both rates of Sivanto controlled sugarcane aphids better than did the other insecticide treatments (Lorsban Advanced 3.755 F, Lorsban Advanced 3.755 F + dimethoate 4 EC, Transform 50WG + dimethoate 4 EC) at 13 days after application. Transform 50 WG (109.6 ml per hectare) had fewer aphids than dimethoate or Lorsban Advanced 3.755 F + dimethoate 4 EC mixture at 13 days after treatment.

Besides being effective at controlling sugarcane aphids, another important advantage of Transform and Sivanto is their low toxicity to aphid-specific natural enemies (Michaud et al. 2016). Although insecticides are effective at controlling aphids, application of insecticide is expensive, especially when large rates of chemicals are required.

CHAPTER 3

MATERIALS AND METHODS

Plant material

The sorghum hybrid ATx399 X RTx430 developed by the Texas Agricultural Experiment Station was used for the study because it is susceptible to aphids. For each experiment at different temperatures, 10 seeds were planted in Miracle-Gro Enriched Potting Mix with Miracle-Gro Plant Food (Miracle-Gro Lawn Products, Inc., Port Washington, NY) in each of six perforated Azalea plastic pots with diameter and height of 10.1 and 14 cm, respectively, in a greenhouse at West Texas A&M University, Canyon. Each of the Azalea plastic pots was placed into a clear plastic saucer (diameter of 12.6 cm and height of 9.2 cm) filled to the brim with water. This was done to ensure capillary flow of water to wet the planted seeds and the soil surface.

The water in each clear plastic saucer was drained after the soil surface was wet. The sorghum seedlings were watered from the saucer at the bottom of the pot when the soil surface was somewhat dry. Sorghum seedlings were thinned to four plants per pot when the plants reached the three true-leaf stage to reduce interplant competition for resources (nutrients, water, and space). The four experimental plants per pot were watered when necessary and maintained in the greenhouse for the establishment of vigorous and healthy plants until they reached the seven true-leaf stage.

Infestation by sugarcane aphids and experiments

When the experimental plants reached the seven true-leaf stage, each was infested with two sugarcane aphids from a pure culture maintained on ATx399 x RTx430 sorghum in the greenhouse. Active apterous adult sugarcane aphids of similar age and weight were selected from a pure culture maintained in the greenhouse. A fine, camel-hair brush was used to gently place a single sugarcane aphid (F_0 generation) into a clear plastic clip cage that was clipped onto a leaf of a sorghum plant. The clip cage was a plastic box used to confine the sugarcane aphid to one location on the sorghum plant. The length, width and height of the clip cage were 2.6 cm, 2.4 cm and 2.0 cm, respectively. The clip cage was modified to allow air circulation by drilling a 10 mm-diameter hole into each of two sides of the plastic box and covering the holes with organdy cloth attached with hot glue. A permanent marking pen was used to number the clip cages. Two clip cages with single aphids were attached to leaves of each of the four sorghum plant in a pot, for a total of eight sugarcane aphids per pot. Six pots of four sorghum plants were used at each temperature. In total, 48 sugarcane aphids (replications) in clip cages were used in a completely randomized design for each temperature. A sample size of 48 sugarcane aphids per treatment was used for the study to ensure greater statistical power to detect differences among treatments, increase precision of estimates, as well as maximize resource utilization.

The six pots of infested sorghum plants were transferred to a Precision model 818 Microprocessor Controlled Low Temperature Illuminated Incubator (Precision, Winchester, VA). Four sets of cycling temperatures of 11:24, 16:29, 21:34, and 26:39 ^{o}C were used for the study in the incubator to simulate as much ambient temperature in the field as possible as well as cover the temperature range for activity of the aphid (Table 1).

Table 1. Alternating temperatures used to study the development of sugarcane aphids on sorghum in an incubator in 2016

Temperature (^{o}C)	Date of infestation
11:24 (Cool)	4 December
16:29 (Moderate)	27 October
21:34 (Warm)	2 August
26:39 (Hot)	5 October

The regimes represented daily minimum and maximum temperatures. The difference between daily maximum and minimum temperatures for the four treatments was 13 ^{o}C because it was the average daily maximum and minimum temperature difference recorded during the sorghum-growing season near College Station in Central Texas in 2015 (National Weather Service 2015). The incubator was set for a photoperiod of 11:13 dark:light hours that corresponded with daily cool and warm temperatures, respectively. Relative humidity of 65% was used for the study. Humidity was maintained by water in a flat pan on a shelf of the incubator.

The original sugarcane aphids (F_{0}-generation) in each clip cage was monitored daily and discarded after it produced a nymph (F_{1}- generation). The birth date of each nymph of the F_1 generation was recorded, and the nymph was retained in the clip cage and allowed to mature. Each day, the positions of the pots were changed in a circular pattern to ensure that all plants and sugarcane aphids received an equal amount of light in the incubator. The experiment was done once at each of the four temperature regimes.

Fecundity and longevity

When the F_{1}-generation aphid in each clip cage matured and began producing offspring, the nymphs produced per day were counted and removed by using a fine, camel-hair brush. Each aphid in a clip cage was examined daily until death. Pre-reproductive period, reproductive period, post-reproductive period, daily fecundity, total fecundity, as well as longevity of sugarcane aphids were assessed on the sorghum at the different temperatures. The pre-reproductive period was considered as the time (days) between birth of the aphid of the F_{1}-generation until production of its first nymph. The reproductive period was the time (days) between the first and the last nymph produced by

the F_1-generation aphid. The post-reproductive period was the time (days) after the last nymph was produced and the death of the F_1-generation aphid. Daily fecundity was the number of nymphs produced per F_1-generation aphid per day. Total fecundity was the total number of nymphs produced per F_1-generation aphid. Longevity was the number of days each F_1-generation aphid lived.

Intrinsic rate of increase and mean generation time

Intrinsic rate of increase (r_m) is a measure of the ability of a population to increase exponentially in an unlimited environment. According to Ong et al (2016), the intrinsic rate of increase is an appropriate measure for describing population dynamics of insects. Mean generation time (T_d) is defined as the time (days) interval between two consecutive generations. The intrinsic rate of increase and mean generation time for each sugarcane aphid were calculated using equations developed by Wyatt and White (1977) for studying biological and ecological characteristics of aphids and mites. The intrinsic rate of increase was calculated for each aphid by using the formula:

$$r_m = 0.738 (\log_e M_d)/d$$

where

r_m = intrinsic rate of increase

d = pre-reproductive period

M_d = number of young produced in a reproductive period equivalent to the pre-reproductive period (d).

The mean generation time was calculated for each aphid by using the formula:

$$T_d = d/0.738$$

where

T_d = mean generation time and

d = pre-reproductive period.

The equation applies the assumption that 95% of the intrinsic rate of increase of an aphid or mite is achieved during twice the amount of time needed for the pre-reproductive period (d).

Statistical analysis

Data on average pre-reproductive period, reproductive period, post-reproductive period, daily fecundity, and total fecundity, as well as longevity were collected for all temperature treatments. Intrinsic rate of increase and mean generation time were calculated for all temperature regimes. Each factor was analyzed using Statistical Analysis System software (SAS) version 9.4 (SAS Institute, Cary, NC). All data were tested for assumptions of normality (Shapiro-Wilks test) and equality of variance (Levene's test) before analysis of variance (ANOVA). The Mixed procedure of SAS was used for ANOVA ($P \leq 0.05$). The least significant difference test at $P = 0.05$ was used to separate means.

CHAPTER 4

RESULTS AND DISCUSSION

Pre-reproductive period

The time (days) before sugarcane aphids began to reproduce decreased as temperature increased from cool (11:24ºC) to warm (21:34ºC). The average number of days before each sugarcane aphid produced its first nymph was longest at the cool temperature and shortest at the warm temperature. At the cool temperature, the pre-reproductive period of sugarcane aphids ranged from 2 to 3 days (Table 2). At the warm temperature, the pre-reproductive period was 1 day or less. The range in the number of days before each sugarcane aphid started producing at the moderate (16:29ºC) and hot (26:39ºC) temperatures was 1 to 3 and 1 or 2 days, respectively. Sugarcane aphids started producing nymphs within a narrower range of days at the cool, warm, or hot temperature than at the moderate temperature. The coefficient of variation at the cool, moderate, warm, and hot temperatures was 20.5, 39.0, 14.7, and 32.6, respectively. This means that the standard deviation of the mean was greatest at the moderate temperature and least at the warm temperature.

Temperature significantly affected the duration of the pre-reproductive period of sugarcane aphids ($F_{3, 186} = 87.63$; $P < 0.0001$) (Table 3).

Table 2. Descriptive statistics on the pre-reproductive period (days) of sugarcane aphids on sorghum at different temperatures

Temperature (^{o}C)	n	Mean ± SE	Minimum	Maximum	CV
Cool (11:24)	48	2.4 ± 0.06	2	3	20.5
Moderate (16:29)	48	1.3 ± 0.07	1	3	39.0
Warm (21:34)	48	1.0 ± 0.02	0	1	14.7
Hot (26:39)	46	1.5 ± 0.07	1	2	32.6

n = number of observations.

CV = coefficient of variation.

Table 3. Effect of temperature on the mean (±SE) length of the pre-reproductive period and percentage of the pre-reproductive period relative to the longevity of sugarcane aphids on sorghum

Temperature (^{o}C)	n	Mean (±SE)
	Pre-reproductive period (days)	
Cool (11:24)	48	2.4 ± 0.06d
Moderate (16:29)	48	1.3 ± 0.07b
Warm (21:34)	48	1.0 ± 0.02a
Hot (26:39)	46	1.5 ± 0.07c
	Percentage of lifetime	
Cool (11:24)	48	5.30 ± 0.15a
Moderate (16:29)	46	3.97 ± 0.24a
Warm (21:34)	46	3.96 ± 0.09a
Hot (26:39)	44	30.00 ± 1.32b

Means followed by the same lowercase letter in a column are not significantly different (P = 0.05, LSD).

n = number of observations.

The pre-reproductive period of sugarcane aphids was twice as long at the cool temperature than at the warm temperature. These results agreed with other studies of aphids that found that cooler temperatures resulted in longer pre-reproductive periods than did warmer temperatures. The longer pre-reproductive period at the cool temperature was because of slow biological processes that ultimately resulted in slower development. A delay in development at the cool temperature might also have been caused by suboptimal feeding by the aphids.

Jeffs and Leather (2014) reported that aphids reared at cooler temperatures had slower metabolic rates and required longer periods to complete development relative to aphids reared at warmer temperatures. However, at the hot temperature, the pre-reproductive period was 1.5 times longer than at the warm temperature. This showed that temperature warmer than the ecologically relevant temperature range of sugarcane aphids prolonged the duration of the pre-reproductive period. This is in agreement with a study by Rouault et al. (2006) who stated that temperatures warmer than the specific optimum range resulted in slower development, decreased growth rates, reduced fecundity, and increased rates of mortality for many insect species.

Although there are studies on the effect of temperature on other aphids on cereal crops, there are few published studies on the effect of alternating temperatures on the development of sugarcane aphids on sorghum. Pendleton et al. (2009) studied the effect of alternating temperatures on biotypes of greenbug on sorghum. They found the pre-reproductive period was longest at the coolest temperature of 10-23 ^{o}C and shortest at the warmest temperature of 22-35 ^{o}C for both biotypes E and I greenbugs. Kuo et al. (2006) studied temperature effects on the life history of the corn leaf aphid on maize in Taiwan

and reported that the duration of the pre-reproductive period decreased with increasing temperature.

Despite varying lengths of pre-reproductive periods reported for many aphids reared at different temperatures, generally an increase in temperature decreased the length of the pre-reproductive period and resulted in more rapid growth. However, extremely warm temperature prolonged the duration of the pre-reproductive period of aphids as shown in this study.

The percentage of the length of the pre-reproductive period relative to longevity differed significantly by temperature ($F_{3, 180}$ 396.90; $P < 0.0001$) (Table 3). Except at the hot temperature, the aphids at cool, moderate, or warm temperature spent less than 6% of the lifetime in the pre-reproductive phase. At the cool temperature of 11:24ºC, the sugarcane aphid spent 5.3% of its lifetime before it produced the first nymph. At the moderate temperature, the length of the pre-reproductive period decreased to 3.97% of total longevity. As the temperature warmed, the time spent before sugarcane aphids produced their first nymphs decreased slightly to 3.96% of the lifetime of the aphid. But, at the hot temperature, a sugarcane aphid spent 30% of its lifetime before producing the first nymph. This meant that the percentage of the pre-reproductive period relative to longevity was 26% more at the hot temperature than at the warm temperature. The percentage of the pre-reproductive period relative to longevity at the hot temperature also significantly differed from the percentage of the pre-reproductive period relative to longevity at the cool, moderate, or hot temperature.

Reproductive period

Temperature had a negative effect on the duration of the reproductive period. An increase in temperature resulted in a decrease in the length of the reproductive period. The maximum number of reproductive days was about 20 at the cool temperature but decreased slowly to about 15 days at the warm temperature. At the hot temperature, the duration of the reproductive period was only 0.12 that at the cool temperature. From cool to moderate temperatures, the percentage of decrease in the duration of the reproductive period was 16.6%. However, from warm to hot temperature, the percentage of decrease in the length of the reproductive period was 84%. The length of the reproductive period ranged from 18 to 22, 14 to 19, 14 to 17, and 2 to 3 days at cool, moderate, warm, and hot temperatures, respectively (Table 4). The coefficient of variation was 6.15, 7.47, 4.94 and 20.60 at cool, moderate, warm, and hot temperatures, respectively. Of the 48 sugarcane aphids studied at the cool temperature, most (33.3%) produced nymphs for 19 days. A greatest frequency (28.26%) was recorded at the moderate temperature for a reproductive period of 17 days. At the warm temperature, most (50%) aphids produced nymphs for 15 days. At the moderate temperature, sugarcane aphids had the widest range of reproductive period. The aphids had the narrowest range of reproductive period at the hot temperature.

The duration of the reproductive period of the sugarcane aphids on sorghum was significantly affected ($F_{3,180} = 2701.00$; $P < 0.0001$) and decreased with increasing temperature (Table 5). The length of the reproductive period of sugarcane aphids reared at the cool temperature of 11:24ºC was an average of 19.9 days, and this was the longest reproductive period. At the hot temperature of 26:39ºC, the average length of the reproductive period was 2.4 days and was the shortest among the four temperatures.

Table 4. Descriptive statistics on the reproductive period (days) of sugarcane aphids on sorghum at different temperatures

Temperature (^{o}C)	n	Mean ± SE	Minimum	Maximum	CV
Cool (11:24)	48	19.9 ± 0.18	18	22	6.15
Moderate (16:29)	46	16.6 ± 0.18	14	19	7.47
Warm (21:34)	46	15.1 ± 0.11	14	17	4.94
Hot (26:39)	44	2.4 ± 0.07	2	3	20.6

n = number of observations.

CV = coefficient of variation.

Table 5. Effect of temperature on the mean (±SE) reproductive period and percentage of the reproductive period relative to the longevity of sugarcane aphids on sorghum

Temperature (^{o}C)	n	Mean (±SE)
	Reproductive period (days)	
Cool (11:24)	48	19.9 ± 0.18d
Moderate (16:29)	46	16.6 ± 0.18c
Warm (21:34)	46	15.1 ± 0.11b
Hot (26:39)	44	2.4 ± 0.08a
	Percentage of lifetime	
Cool (11:24)	48	44.02 ± 0.37a
Moderate (16:29)	46	50.76 ± 0.39b
Warm (21:34)	46	59.92 ± 0.41c
Hot (26:39)	44	48.00 ± 1.26ab

Means followed by the same lowercase letter in a column are not significantly different (P = 0.05, LSD).

n = number of observations.

The reproductive period at the cool temperature was eight times longer than at the hot temperature. At the intermediate temperatures, the lengths of the reproductive periods were similar to each other, 16.6 and 15.1 days at moderate and warm temperatures, respectively.

Generally, an increase in temperature decreased the duration of the reproductive period of the sugarcane aphids. However, the length of the reproductive period at the warm temperature was about 13 days longer than at the hot temperature (Table 5). Hot temperature had a harmful effect on the length of the reproductive period of the aphids. This was consistent with a study by De Conti et al (2010) who reported reproduction and created a fertility life table of three aphid species at different temperatures in Brazil. They asserted that excessively hot temperatures shortened the reproductive period of aphids. Mehrparvar and Hatami (2007) also stated that temperatures warmer than optimum for reproduction resulted in deleterious effects on various biological parameters, including the reproductive period.

The percentage of the reproductive period of sugarcane aphids relative to longevity differed significantly by temperature ($F_{3, 180} = 97.91$; $P < 0.0001$) (Table 5). Regardless of the temperature, the aphid spent a significant percentage of its lifetime in the reproductive phase. The aphids at the cool temperature spent 44% of the lifetime in the reproductive phase, which was the shortest reproductive period relative to longevity. The sugarcane aphids spent about 60% of their lifetime in the reproductive phase at the warm temperature, which was the largest percentage of reproductive period relative to longevity. About 51% of the lifetime of sugarcane aphids at the moderate temperature was spent during the reproductive period, which did not differ significantly from the 48%

of total longevity spent during the reproductive period at the hot temperature. Also, the percentage of the reproductive period relative to longevity at the cool temperature was not significantly different from that at the hot temperature.

Post-reproductive period

The minimum numbers of days during the post-reproductive periods were 20, 13, 8, and 0 at cool, moderate, warm, and hot temperatures, respectively (Table 6). The maximum numbers of days during the post-reproductive periods were 26, 17, 12, and 2 at the cool, moderate, warm and hot temperatures, respectively. At the cool temperature, sugarcane aphids had the widest range (6 days) of post-reproductive period. The aphids had the narrowest range (2 days) of post-reproductive period and died quickly at the hot temperature. The coefficient of variation ranged from 5.74 to 39.76 and increased with increasing temperature.

Temperature significantly affected the length of the post-reproductive period of sugarcane aphids ($F_{3, 180} = 3857.13$; $P < 0.0001$) (Table 7). The length of the post-reproductive period dramatically decreased as temperature increased from cool to hot. Increasing temperature from cool to hot decreased the length of the post-reproductive period from about 23 days to 1 day. This meant that the average number of days the aphid lived after producing its last nymph was longest at the cool temperature and shortest at the hot temperature. The post-reproductive period of sugarcane aphids on sorghum at the cool temperature was 8 days longer than at the moderate temperature, 13 days longer than at the warm temperature, and 21 days longer than at the hot temperature. Comparatively, the average number of days the aphid lived after producing its last nymph was eight times longer at the warm temperature than at the hot temperature.

Table 6. Descriptive statistics on the post-reproductive period (days) of sugarcane aphids on sorghum at different temperatures

Temperature (^{o}C)	n	Mean ± SE	Minimum	Maximum	CV
Cool (11:24)	48	22.9 ± 0.19	20	26	5.74
Moderate (16:29)	46	14.8 ± 0.14	13	17	6.20
Warm (21:34)	46	9.1 ± 0.16	8	12	11.91
Hot (26:39)	44	1.1 ± 0.07	0	2	39.76

n = number of observations.

CV = coefficient of variation.

Table 7. Effect of temperature on the mean (±SE) days of the post-reproductive period and the percentage of the post-reproductive period relative to the longevity of sugarcane aphids on sorghum

Temperature (^{o}C)	n	Mean (±SE)
	Post-reproductive period (days)	
Cool (11:24)	48	22.9 ± 0.19d
Moderate (16:29)	46	14.8 ± 0.14c
Warm (21:34)	46	9.1 ± 0.16b
Hot (26:39)	44	1.1 ± 0.07a
	Percentage of lifetime	
Cool (11:24)	48	50.66 ± 0.33d
Moderate (16:29)	46	45.26 ± 0.31c
Warm (21:34)	46	36.11 ± 0.42b
Hot (26:39)	44	22.00 ± 1.22a

Means followed by the same lowercase letter in a column are not significantly different (P = 0.05, LSD).

n = number of observations.

The percentage of its total lifetime that a sugarcane aphid survived during the post-reproductive period differed significantly at different temperatures ($F_{3, 180} = 362.02$; $P < 0.0001$) (Table 7). The aphids at the cool temperature spent slightly more than one-half of the lifetime in the post-reproductive phase, which was the largest percentage of post-reproductive period relative to longevity. However, the aphids spent 22% of their lifetime in the post-reproduction phase at the hot temperature, which was the smallest percentage of post-reproductive period relative to longevity. The percentage of post-reproductive period relative to longevity differed significantly and sugarcane aphids survived about 9% longer at the moderate than at the warm temperature.

Longevity

Temperature had a negative relationship with the duration of the reproductive period, such that an increase in temperature resulted in a decrease in the life span of the aphids. The maximum longevity was about 45 days at the cool temperature but decreased drastically to only 5 days at the hot temperature. From cool to moderate temperature, the percentage of decrease in the lifetime of the aphid was as small as 27.6%. However, from warm to hot temperature, the percentage of decrease in the lifetime of the aphids was as much as 79.8%. Longevity ranged from 43 to 49, 30 to 35, 23 to 28, and 4 to 6 days at the cool, moderate, warm, and hot temperatures, respectively (Table 8). The aphids at the cool temperature lived the most days. The aphids lived for the fewest days at the hot temperature. The coefficient of variation ranged from 3.25 to 12.08 and increased with increasing temperature.

Table 8. Descriptive statistics on the longevity (days) of sugarcane aphids on sorghum at different temperatures

Temperature (^{o}C)	n	Mean ± SE	Minimum	Maximum	CV
Cool (11:24)	48	45.2 ± 0.21	43	49	3.25
Moderate (16:29)	46	32.7 ± 0.21	30	35	4.38
Warm (21:34)	46	25.2 ± 0.19	23	28	5.16
Hot (26:39)	44	5.0 ± 0.09	4	6	12.08

n = number of observations.

CV = coefficient of variation.

Temperature significantly affected the longevity of sugarcane aphids on sorghum ($F_{3,180} = 8045.90$; $P < 0.0001$) (Table 9). As the temperature warmed, the longevity of the sugarcane aphids decreased. The aphids lived as long as 45 days at the cool temperature, but survived only 5 days at the hot temperature. Hot temperature had an adverse effect on longevity and drastically shortened the life span of the aphid. At the moderate temperature, longevity of sugarcane aphids was 8 days longer than at the warm temperature. Several studies found that an increase in temperature decreased longevity of aphids. Michels and Behle (1989) studied the effects of temperature on development, reproduction, and intrinsic rate of increase of the Russian wheat aphid, *Diuraphis noxia* Kurdjumov. They found that longevity of Russian wheat aphids decreased significantly with an increase in temperature. Moiroux et al. (2013) also reported that the life span of aphids and other ectotherms typically decreased as temperature increased.

Daily fecundity

Curves for average daily fecundity for sugarcane aphids at the four temperatures were similar. Average daily fecundity initially increased gradually over time, then increased rapidly, remained stable for a while, and decreased (Fig. 1). At the cool temperature of 11:24 ^{o}C, sugarcane aphids produced means of 7.1, 8.3, 7.6 and 7.1 nymphs on the 10th, 11th, 12th and 13th days, respectively, after birth. Eight percent of sugarcane aphids at the cool temperature produced these numbers of nymphs per day at the cool temperature. At the cool temperature, sugarcane aphids produced nymphs from the 3rd until the 25th days after birth.

Table 9. Effect of temperature on mean (±SE) longevity of sugarcane aphids on sorghum

Temperature (^{o}C)	N	Longevity (mean days ± SE)
Cool (11:24)	48	45.2 ± 0.21d
Moderate (16:29)	46	32.7 ± 0.21c
Warm (21:34)	46	25.2 ± 0.19b
Hot (26:36)	44	5.1 ± 0.09a

Means followed by the same lowercase letter in a column are not significantly different (*P* = 0.05, LSD).

n = number of observations.

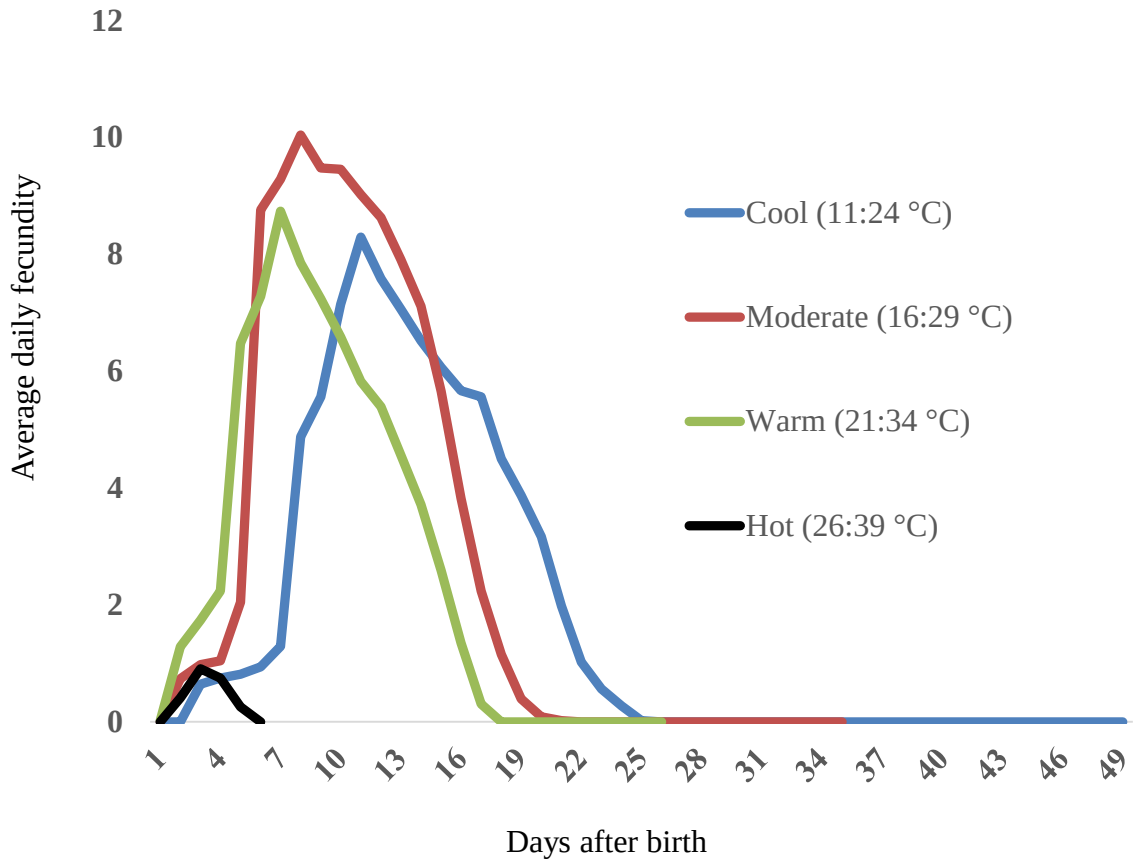

Fig. 1. Average daily fecundity of sugarcane aphids at different temperatures on sorghum.

The average number of nymphs produced per sugarcane aphid increased from 2 to about 9 on the 5th to 6th days after birth at the moderate temperature (Fig. 1). The aphids produced most nymphs (10) when they were 8 days old and produced nine nymphs each on the next 3 days. The aphids at the moderate temperature produced nymphs from the 2nd through the 21st days after birth. The number of nymphs produced per aphid per day increased greatly at the moderate temperature but for slightly fewer days than at the cool temperature.

Days 6 through 14 were the most productive period at the warm temperature, with a total of about 80 nymphs produced per aphid during that period (Fig. 1). At the warm temperature, the average number of nymphs produced per sugarcane aphid increased from 2.2 to 6.5 on the 4th and 5th days after birth. About nine nymphs per aphid, the greatest daily fecundity, were produced on the 7th day after birth at the warm temperature. At the warm temperature, the most productive period for the aphids was from the 5th to 10th days after birth, with a total of 44.2 nymphs produced per aphid during that period. At the warm temperature, the sugarcane aphid produced nymphs from the 1st through the 17th days after birth. At the hot temperature, the number of nymphs produced per sugarcane aphid per day was less than one, with a maximum of 0.9 nymph per aphid per day. The aphids at the hot temperature produced from the 2nd through the 5th days after birth.

The day on which the maximum number of nymphs was produced decreased with an increase in temperature. Maximum numbers of 8.3 nymphs at the cool temperature, 10.0 at the moderate temperature, 8.7 at the warm temperature, and 0.9 at the hot temperature were produced per aphid on the 11th, 8th, 7th, and 3rd days after birth,

respectively (Fig. 1). The mother aphid produced a maximum number of nymphs 3 days earlier at the moderate than at the cool temperature. However, maximum average daily fecundity occurred a day earlier at the warm temperature than at the moderate temperature.

Except at the hot temperature, the curves of cumulative average daily fecundity were similar. With the exception of the hot temperature, the curves of cumulative average daily fecundities at the cool, moderate, and warm temperatures were sigmoidal (Fig. 2). This indicated that at the cool, moderate, or warm temperature, the number of aphids produced over time initially increased slowly, then increased rapidly to approach an exponential growth rate, but then decreased in a negative acceleration phase until reaching a zero growth rate. The number of nymphs produced per day increased greatly at the moderate temperature but for slightly fewer days than by aphids at the cool temperature. Also, growth was zero on the 26^{th}, 22^{nd}, 18^{th}, and 6^{th} days after birth at the cool, moderate, warm, and hot temperatures, respectively.

Total fecundity

At the cool temperature, the minimum and maximum total fecundities per aphid were 74 and 96 nymphs, respectively (Table 10). The most frequent total fecundity per aphid was 89 nymphs at the cool temperature. Total fecundity ranged from 81 to 114 nymphs, with a mode of 93 per aphid at the moderate temperature. The minimum and maximum total fecundities per aphid at the warm temperature were 64 and 86 nymphs, respectively, and at the hot temperature were two and three, respectively. The most frequent total fecundities per aphid at the warm and hot temperatures were 72 and two nymphs, respectively.

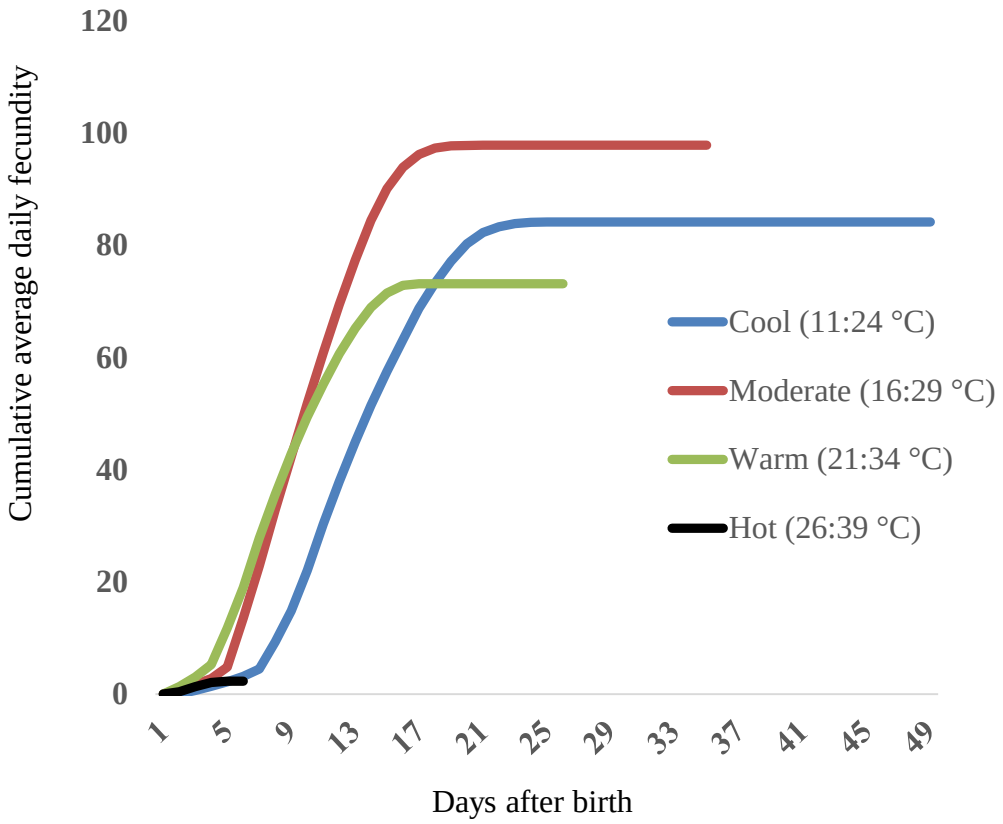

Fig. 2. Cumulative average daily fecundity of sugarcane aphids at different temperatures on sorghum.

Table 10. Descriptive statistics on the total fecundity of sugarcane aphids on sorghum at different temperatures

Temperature (^{o}C)	n	Mean ± SE	Minimum	Maximum	CV
Cool (11:24)	48	84.2 ± 0.81	74	96	6.68
Moderate (16:29)	46	97.9 ± 1.23	81	114	8.55
Warm (21:34)	46	73.2 ± 0.65	64	86	6.03
Hot (26:39)	44	2.3 ± 0.07	2	3	20.11

n = number of observations.

CV = coefficient of variation.

The coefficients of variation were 6.7, 8.6, 6.0 and 20.1 at the cool, moderate, warm and hot temperatures, respectively. In total, 4,040 nymphs were produced by all 48 aphids reared at the cool temperature. At the moderate temperature, 4,502 nymphs, the greatest total fecundity, was produced by the total number of 48 aphids. As temperature increased to the warm temperature, 3,368 nymphs were produced by the aphids. Total fecundity was only 101 nymphs produced at the hot temperature. This showed that exposure of sugarcane aphids to the hot temperature reduced fecundity more than did exposure to the cool temperature.

Temperature significantly affected the total number of nymphs produced per sugarcane aphid ($F_{3,180} = 2642.65$; $P < 0.0001$), with 84.2 nymphs produced at cool, 97.9 at moderate, 73.2 at warm, and 2.3 at hot temperatures (Table 11). Total fecundity per aphid was greatest at the moderate temperature and least at the hot temperature. Each sugarcane aphid produced about 14 more nymphs at the moderate than at the cool temperature. The total number of nymphs produced per aphid at the moderate temperature was 24 more than at the warm temperature. Total fecundity per aphid increased 16% from cool to moderate temperatures but decreased 25% from the moderate to warm temperature. The total number of nymphs produced per aphid decreased markedly, by about 97%, from the warm to the hot temperature.

Reproductive rate, defined as the ratio of total fecundity to the length of the reproductive period, was calculated for each aphid. The reproductive rate was significantly affected by temperature. As temperature increased from cool to moderate, the reproductive rate per aphid increased from 4.2 to 5.9 nymphs, respectively (Table 11). However, when the temperature increased from moderate to warm, the reproductive

Table 11. Effect of temperature on mean (±SE) total fecundity and reproductive rate of sugarcane aphids on sorghum

Temperature (ºC)	n	Mean ± SE
	Total fecundity	
Cool (11:24)	48	84.2 ± 0.81d
Moderate (16:29)	46	97.9 ± 1.23c
Warm (21:34)	46	73.2 ± 0.65b
Hot (26:39)	44	2.30 ± 0.07a
	Reproductive rate	
Cool (11:24)	48	4.2 ± 0.04d
Moderate (16:29)	46	5.9 ± 0.07c
Warm (21:34)	46	4.8 ± 0.04b
Hot (26:39)	44	1.0 ± 0.02a

Means followed by the same lowercase letter in a column are not significantly different (P = 0.05, LSD).

n = number of observations.

capability of each aphid decreased to 4.8 nymphs and further decreased sharply to only one nymph at the hot temperature.

Intrinsic rate of increase

The intrinsic rate of increase (r_m) of sugarcane aphids on sorghum was significantly affected by temperature ($F_{3,180} = 5.73$; $P < 0.0009$) (Table 12). The intrinsic rate of increase increased from the cool to warm temperature but decreased at the hot temperature. The intrinsic rate of increase was greatest (33%) at the warm temperature and least (1%) at the hot temperature. This meant that a sugarcane aphid population would increase 32% faster at the warm than at the hot temperature. Rates of increase of 8 and 29% were calculated for sugarcane aphids at cool and moderate temperatures, respectively. The intrinsic rate of increase at the outside temperatures (cool and hot) differed from each other, but the intermediate temperatures (moderate and warm) did not differ from each other. However, the intrinsic rate of increase at the cool temperature differed from that at the moderate temperature, and the intrinsic rate of increase at the warm temperature differed from that at the hot temperature.

Birch (1948) stated that the intrinsic rate of increase was a good indicator of the temperature at which growth of a population was greatest, because it reflected the overall effect of temperature on development, reproduction, and survival characteristics of a population. The intrinsic rate of increase explains the physiological characteristics of an aphid regarding its capacity to increase (Andrewartha and Birch 1954). The intrinsic rate of increase is a function of the length of the pre-reproductive period and effective fecundity (number of nymphs produced in a reproductive period equivalent to the pre-reproductive period). Hence, a longer pre-reproductive period results in slower

Table 12. Effect of temperature on mean (±SE) intrinsic rate of increase of sugarcane aphids on sorghum

Temperature (^{o}C)	n	Intrinsic rate of increase (mean ± SE)
Cool (11:24)	48	0.08 ± 0.02b
Moderate (16:29)	46	0.29 ± 0.06c
Warm (21:34)	46	0.33 ± 0.04c
Hot (26:39)	44	0.01 ± 0.10a

Means followed by the same lowercase letter in a column are not significantly different (*P* = 0.05, LSD).

n = number of observations.

population growth rate. Also, lower effective fecundity causes a smaller intrinsic rate of increase.

Data in Table 12 show that the intrinsic rate of increase was reduced at the cool temperature but significantly reduced at the hot temperature. The reason was a result of the relatively longer pre-reproductive period at the cool temperature but not at the hot temperature because of the negative effect of hot temperature on the fecundity of the aphids. This result confirmed research by Jeffs and Leather (2014) who studied the effect of extreme, fluctuating temperatures on life history traits of the English grain aphid, *Sitobion avenae* (Fabricius). They found that extreme hot or cold temperatures considerably reduced the intrinsic rate of increase of English grain aphids.

Mean generation time

Temperature significantly affected the mean generation time of sugarcane aphids on sorghum ($F_{3,186} = 87.49$; $P < 0.0001$) (Table 13). The estimated values of the mean generation time were 3.19, 1.75, 1.33 and 2.09 days for sugarcane aphids at the cool, moderate, warm and hot temperature, respectively. This meant that the mean generation time decreased gradually from 3.19 days at the cool temperature to an estimated minimum of 1.33 day at the warm temperature. However, the mean generation time increased to 2.09 days at the hot temperature. The time (days) interval between two consecutive generations was greatest at the cool temperature because of a relatively longer pre-reproductive period.

Table 13. Effect of temperature on the mean generation time of sugarcane aphids on sorghum

Temperature (^{o}C)	n	Mean generation time (mean days ± SE)
Cool (11:24)	48	3.19 ± 0.09d
Moderate (16:29)	48	1.75 ± 0.09b
Warm (21:34)	48	1.33 ± 0.03a
Hot (26:39)	46	2.09 ± 0.10c

Means followed by the same lowercase letter in a column are not significantly different (*P* = 0.05, LSD).

n = number of observations.

CHAPTER 5

SUMMARY, CONCLUSION AND RECOMMENDATIONS

Summary

At the cool temperature of 11:24 ºC, sugarcane aphids started producing nymphs when they were about 2.5 days old, produced for 20 days, and stopped producing nymphs 23 days before death. The aphids lived for 45 days at the cool temperature. At the cool temperature, the total number of nymphs produced by a sugarcane aphid was 84, with a reproductive capacity of 4.2 nymphs per reproductive day. The population growth rate of sugarcane aphids at the cool temperature was 8%, with a mean generation time of about 3 days.

At the moderate temperature of 16:29 ºC, the sugarcane aphids began producing nymphs when they were 1.3 day old, produced for 16.5 days, and ceased producing nymphs about 15 days before death. The aphids lived for about 33 days at the moderate temperature. Also, at the moderate temperature, each sugarcane aphid produced as many as 98 nymphs, with a reproductive capacity of about six nymphs per reproductive day. The intrinsic rate of increase at the moderate temperature was 29%, and the mean generation time was 1.75 day.

At the warm temperature of 21:34 ºC, the sugarcane aphids started producing nymphs when they were less than 1 day old, produced for 15.3 days, and stopped producing nymphs 9 days before death. The aphids lived for about 25 days. At the warm temperature, the total number of nymphs produced by a sugarcane aphid was 73, with a

reproductive capacity of 4.8 nymphs per reproductive day. The population growth rate of sugarcane aphids at the warm temperature was 33%, and the mean generation time was 1.3 day.

At the hot temperature of 26:39 ºC, the sugarcane aphids began producing nymphs when they were 1.5 day old, produced for 2.4 days, and ceased producing nymphs 1.1 day before death. The aphids lived 5.1 days at the hot temperature. At the hot temperature, each sugarcane aphid produced as few as 2.3 nymphs, with a reproductive capacity of 0.96 nymph per reproductive day. The intrinsic rate of increase at the hot temperature was 1%, and the mean generation time was 2.1 days.

Conclusion

Temperature greatly affected the lengths of the pre-reproductive, reproductive, and post- reproductive periods, as well as total longevity, fecundity, reproductive rate, intrinsic rate of increase, and mean generation time of sugarcane aphids on sorghum. The length of the pre-reproductive period decreased from the cool to warm temperatures but increased at the hot temperature. The lengths of the reproductive and post-reproductive periods and longevity decreased with increasing temperature. The daily fecundity, total fecundity, and reproductive rate were greatest at the moderate temperature. Exposure of the aphids to the hot temperature drastically reduced their fecundity, whereas the cool temperature did not. The warm temperature resulted in the greatest intrinsic rate of increase and the shortest mean generation time. The cool and hot temperatures decreased the growth rate of the sugarcane aphids on sorghum. This might be a result of slow development of the sugarcane aphids at the cool temperature and less fecundity at the hot

temperature. At the hot temperature, the aphids were barely able to survive and reproduce.

The most favorable or ideal temperature for development of sugarcane aphids on sorghum was 16:29 ºC (moderate temperature), demonstrated by the comparatively large total fecundity and reproductive rate, as well as second-greatest intrinsic rate of increase (not statistically different from the largest value) and the second-shortest mean generation time. The study also revealed that the lower developmental threshold (temperature where reproduction begins) of sugarcane aphid could be below the fluctuating temperature of 11:24 ºC, whereas the upper developmental threshold (temperature where reproduction ceases) of the sugarcane aphid was above the fluctuating temperature of 26:39 ºC. Importantly, sugarcane aphids even at the hot temperature were able to survive and produce nymphs for at least a brief period of time. This finding might help explain why sugarcane aphids are so adaptable that they could survive and recently quickly invade new sorghum areas in North and Central America.

Recommendations for future research

Recommended future research would be to:

1. assess the effect of temperature on different sorghum plant growth stages.
2. determine developmental thresholds (lower and upper) of sugarcane aphids on sorghum.
3. assess the effect of temperature on different sorghum cultivars.
4. evaluate the interaction of temperature and relative humidity on development of sugarcane aphids on sorghum.

5. evaluate the interaction of temperature and photoperiod on growth and development of sugarcane aphids on sorghum.

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