Molecular and morphological evidence for resistance to sugarcane aphid (*Melanaphis sacchari*) in sweet sorghum [*Sorghum bicolor* (L.) Moench]

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Abstract

Aphids are one of the devastating pests affecting the productivity of sorghum in many countries. The aim of the present investigation was to identify sweet sorghum genotypes resistant to the sugarcane aphid, *Melanaphis sacchari* (Zehntner). A Sequence Characterized Amplified Region (SCAR) marker linked to an aphid-resistance gene (*RMES1*) was first used to prescreen for resistant genotypes in 561 sorghum accessions. Molecular assays indicated that 91 sorghum accessions in the collection had the *RMES1* resistance marker allele. Of those, 26 agronomically superior sweet sorghum accessions, along with three commercial cultivars and one susceptible check, were further evaluated in two locations (Antalya, a lowland province, and Konya, a highland province) under field conditions. These accessions were scored for resistance to aphid damage under natural aphid infestations. The number of aphids counted on the plant leaves and stalks in the accessions during the growing seasons was used to score resistant genotypes on a scale of 1–5, where 1 was highly resistant (plants having 0–50 aphids/plant) and 5 was highly sensitive (plants having 1000+ aphids/plant). Fumagine intensity on the leaves was also taken into consideration. Ten accessions from the lowland and one accession from the highland scored “1,” indicating a high resistance to aphid infestation. A further 13 accessions scored “1” or “2” in both environments. Only two accessions scored “4,” and no accession scored “5,” indicating the utility of the *RMES1* marker for prescreening purposes. One accession, BSS507, showed outstanding resistance to *M. sacchari*, with a score of “1” in both environments.

Keywords Bio-energy · Molecular marker · Aphid · Resistance · Selection

Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) is a C4 plant grown primarily for food and for fodder, fiber, and fuel (Anami et al. 2015). The crop is tolerant of high temperature and drought conditions (Assefa et al. 2010), and it has

a shorter growing period and a lower water consumption when compared to other industrial cereal crops. Sweet sorghum, with a fermentation ratio greater than 90% (Imam and Capareda 2011), is also an important source of bio-energy worldwide (Almodares and Hadi 2009). These features make this plant one of the most important cereal crops grown in more than 100 countries. The annual production is approximately 64 million tons, from a harvest area of 45 million ha across the globe (Food and Agriculture Organisation of the United Nations 2016).

When compared with other cereal crops, sorghum is more tolerant to drought (Fracasso et al. 2016), salinity (Almodares et al. 2007), and water logging (Promkhambut et al. 2010). Nevertheless, many biotic and abiotic stress factors still have negative effects on sorghum yield. Biotic stresses not only adversely affect the yield, but they also reduce grain quality and marketability (Kumar et al. 2014). Different species of aphids, including *Melanaphis sacchari*, *Schizaphis graminum*, *Rhopalosiphum maidis* (Wang et al. 2013), and

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Rhopalosiphum padi (Blackman and Eastop 2007), are recognized as important aphid pests of sorghum. Of these, the sugarcane aphid, *M. sacchari*, was the first to be identified on sorghum in the US (Wilbrink 1922).

The sugarcane aphid can cause serious and widespread economic losses due to its high reproductive rate and its production of copious amounts of honeydew. In addition, the sticky honeydew can accumulate on highly infested plants and create mechanical harvesting complications. In sorghum, extreme aphid infestations at the pre-flowering stage and infestations during grain development can decrease the yield through reduction in the number of heads, reduced seed weight, delayed development and maturity, and, ultimately, plant death (Bowling et al. 2016). These adverse effects of *M. sacchari* on agronomic attributes extend further to effects on quality traits, such as diastatic power, malt quality, and harvest index in sorghum (Van den Berg et al. 2003).

Management of sorghum insect pests includes cultural control methods, such as crop rotation, variety selection, early planting, seedbed preparation, and seed treatment (Teeles and Pendleton 2000). Chemical methods are available, but these have drawbacks due to the cost of the insecticides and their effects on the environment. Therefore, host-plant resistance against aphid infestation is an important concept in sweet sorghum grown as a bio-energy resource, since aphid feeding can result in a significant loss of nutritional content and can reduce the juice Brix (Knoll et al. 2018). However, evaluation of resistance by field assessment of aphid infestations in sorghum relies on aphid population counts and visual damage ratings in the plant. Under natural infestation conditions, achieving a uniform infestation of insects on test genotypes may be difficult. For this reason, breeding programs that integrate molecular markers are of great importance to increase the effectiveness of selection and to identify truly resistant plants.

A dominant gene for resistance to *M. sacchari* was detected in the Chinese grain sorghum variety “Henong 16” and designated as *RMES1* (Resistance to *Melanaphis sacchari*) and subsequently mapped to chromosome 6 (Chang et al. 2006, 2012; Wang et al. 2013). An SCAR marker developed for the *RMES1* gene (Chang et al. 2012) now allows the selection of aphid-resistant sorghum genotypes by following a marker-assisted selection scheme. In the present investigation, a sorghum collection consisting of 561 accessions from different worldwide origins was screened for the SCAR marker for sugarcane aphid resistance, and this resistance was further confirmed under field conditions in a selected subset of sweet sorghum accessions grown in lowland and highland areas.

Materials and methods

Genetic material

The genetic material used in this study consisted of 551 sorghum accessions with diverse origins and ten commercial cultivars registered in Turkey (Table S1). Of the 551 accessions, 242 were provided by the United States Department of Agriculture (USDA) and 309 were from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) gene banks. The sweet sorghum accession encoded BSS320 was found to suffer significant aphid damage in initial trials and was used as a susceptible check for the insect bioassays. This susceptible accession showed such severe aphid damage and fumagine intensity that obtaining an appreciable yield was extremely difficult.

Experimental design

In 2013, the 551 sweet sorghum accessions and ten cultivars registered in Turkey were screened for the SCAR marker (Chang et al. 2012). The sweet sorghum accessions that carried the *RMES1* allele were further evaluated in the field conditions. Field experiments were conducted in Antalya (a lowland province; 36°52'N and 30°50'E, 41 m above sea level) and Konya (a highland province; 37°34'N and 32°47'E, 1016 m above sea level) in two growing seasons (2014 and 2015). The plants, including 26 sweet sorghum accessions with the *RMES1*-resistance allele, three registered cultivars and a susceptible check, were planted in a randomized complete block design with three replications in both locations. Each genotype was sown in four rows 5 m in length, with inter- and intra-row distances of 0.7 m and 0.2 m, respectively. Plant residues were removed before sowing, and furrow irrigation was applied during the growing season. After plowing, fertilizer was applied at the rate of 80 kg N, 80 kg P₂O₅, and 80 kg K₂O per hectare and the field was harrowed twice. The highland sites were irrigated three times and the lowland sites were irrigated five times. The genotypes were sown on the 14th and 21st of May in 2014 and 2015, respectively. No insecticides or herbicides were applied during the growing seasons. Weeds were controlled by inter-row harrowing and by hand removal. The climatic conditions of the lowland and highland locations are summarized in Table 1.

Morphological scorings under natural aphid infestation

Resistance scorings against *M. sacchari*, diagnosed by an expert on Hemiptera systematic and taxonomy at the Directorate of Plant Protection Central Research Institute in

Table 1 Climatic conditions of lowland and highland locations

Months	Average temperature (°C)						Total rainfall (mm)					
	2013		2014		2015		2013		2014		2015	
	Lowland	Highland	Lowland	Highland	Lowland	Highland	Lowland	Highland	Lowland	Highland	Lowland	Highland
April	17.8	11.9	16.6	12.4	15.5	8.8	66.4	41.6	38.6	11.7	12.4	7.6
May	22.6	18.4	20.1	15.4	21.3	16.0	60.4	54.8	44.0	55.6	3.6	53.2
June	25.5	21.6	25.4	19.5	24.1	18.8	1.6	8.8	2.0	63.4	8.8	42.0
July	28.7	23.2	27.8	24.7	28.6	24.0	0.0	0.9	1.8	13.8	0.0	8.6
August	29.7	23.5	29.2	24.9	29.5	24.6	0.0	0.0	5.2	2.2	0.6	17.2
September	25.6	18.6	25.5	18.3	26.3	22.0	7.0	4.0	45.5	56.5	165.2	31.4

^aLowland is Antalya^bHighland is Konya

Ankara, Turkey, were conducted at the two locations under natural aphid infestations. A total of four resistance scorings were made in July and August during the vegetation period of the crop. The number of aphids during the growing seasons was used to score resistant genotypes, employing a 1–5 scoring scale (He et al. 1991), where 1 is highly resistant (plants having 0–50 aphids/plant); 2 is resistant (plants having 51–300 aphids/plant); 3 is moderately resistant (plants having 301–700 aphids/plant); 4 is sensitive (plants having 701–1000 aphids/plant); and 5 is highly sensitive (plants having 1000+ aphids/plant). Plant leaves and stalks were used for resistance scorings and fumagine intensity in the leaves was also taken into consideration (Fig. 1).

Molecular analyses

Leaf samples of the 551 accessions and ten commercial cultivars were collected from three plants per plot. The DNA of each sample was extracted using the CTAB protocol (Doyle and Doyle 1990). The quality and quantity of DNA were checked against λ DNA in 1% agarose gel electrophoresis and by spectrophotometry.

The PCR reaction was optimized to include 2 μ L of 10 $\times$ PCR buffer, 0.4 mM dNTPs, 2.5 mM MgCl₂, 10 μ M forward and reverse primers, 1 unit of Taq DNA polymerase, and 2 μ L genomic DNA templates in a final volume of 20 μ L. A programmable thermo cycler (Thermo Fisher) was used to amplify the products using forward (5'-AATTCCTGCAAG ACCATTT-3') and reverse (5'-CACAATGGTTCTAGG CATC-3') primers for the SCAR marker associated with the *RMES1* gene (Chang et al. 2012). The cycling program was 94 °C for 5 min, 30 cycles of 94 °C for 45 s, 52 °C for 45 s, and 72 °C for 1 min, followed by extension at 72 °C for 10 min. A total of 12 μ L PCR product was run at 75 V on 2.5% agarose gel stained with ethidium bromide. The PCR products were also checked using a high-resolution capillary Fragment Analyzer™ system (Advanced Analytical

Fig. 1 Natural *M. sacchari* infestation and fumagine intensity on sorghum leaves

Technologies, Heidelberg, Germany). The Array-DNF-900 reagent kit was used for qualitative analysis of DNA fragments ranging from 35 to 500 bp in an automated capillary system. Normalization was provided by the marker showing 35–500 bp fragments. Raw data were handled with PROSize™ software (Version 1.2.1.1) (Advanced Analytical Technologies, AMES, IA, USA).

Results

Molecular analyses of the *RMES1* gene

Molecular marker analyses were conducted to screen for *M. sacchari* resistance in the 561 sorghum accessions. The

SCAR marker was used to score genotypes in agarose gels following PCR amplification. The SCAR marker distance to the *RMES1* gene is 10 cM and the selective efficiency within the specific population developed for this marker was reported as approximately 88% (Chang et al. 2012). Therefore, the marker was helpful for prescreening the sweet sorghum germplasm and selecting 91 accessions carrying the *RMES1*-resistance allele.

The resolution power of the 2.5% agarose gel was not sufficient for discriminating the *RMES1* alleles originating from the resistant and susceptible accessions, as the relevant PCR fragment sizes were in the range of ~350–355 bp (Fig. 2a). Therefore, electrophoretic separation was conducted with the Fragment Analyzer™, which provided up to 3 bp resolution (Fig. 2b). The bio-imaging results of the SCAR marker

Fig. 2 Representative gel pictures of 2.5% agarose gel (**a**) and Fragment Analyzer™ (**b**) **a** 2.5% agarose gel shows the monomorphic appearance in the marker region. **b** Fragment Analyzer™ shows the ability to discriminate resistant/susceptible accessions in the marker region

indicated that 91 accessions had the *RMES1* resistance fragment (~355 bp), while 470 accessions had the susceptible fragment (~350 bp) (Table S1).

Morphological scorings for aphid resistance under natural field infestation

Of the 91 accessions carrying the *RMES1*-resistance allele, 26 agronomically superior accessions (based on high sugar content, biomass, plant height, yield, etc.) were further evaluated in the two locations. Three commercial cultivars with the *RMES1* resistance allele and one susceptible check were also used in field trials, along with the 26 sweet sorghum accessions. The highland and lowland locations were chosen to allow observation of the actual performances of the sweet sorghum accessions as well as reactions to aphid infestation in different environments.

Insect bioassays conducted in the fields indicated that ten accessions from the lowland location and one accession from the highland location had a rating score of 1, indicating high resistance to aphid infestation based on the 1–5 scoring scale. Furthermore, 13 accessions had scores of “1” or “2” resistance ratings in both environments. Only two accessions had scores of “4,” indicating a mild pest infestation. None of the 26 accessions had infestations as severe as the susceptible check, which had a score of “5.” These data confirmed the overall utility of the *RMES1* marker for prescreening.

In the lowland location, the accessions encoded as BSS55, BSS78, BSS246, BSS314, BSS402, BS423,

BSS473, BSS474, BSS507, and BSS510 were rated highly resistant to aphids (scores of “1” on the scale of 1–5). By contrast, accessions BSS5, BSS27, BSS59, BSS82, BSS505, BSS508, and Akdarı supported greater numbers of *M. sacchari* (50–301 aphids/plant) and were regarded as resistant (scores of “2”). In total, seven accessions showed a moderate level of resistance (scores of “3”) and the remaining four accessions were rated as susceptible (scores of “4”) to aphid infestation. The susceptible check had the highest number of aphids, at more than 1000 aphids/plant, and had a score of “5” (Table 2).

In the highland location, only one accession, BSS507, showed high resistance to *M. sacchari* (a score of “1”). This accession also scored “1” in the lowland location. Overall, 13 accessions were classified as resistant (scores of “2”), while 11 genotypes were evaluated as moderately resistant (scores of “3”). The remaining four accessions were rated as susceptible (scores of “4”).

BSS507 was the only sweet sorghum accession that showed high resistance to *M. sacchari* according to all the environment and molecular assays, indicating its outstanding resistance to aphids when compared to the other resistant accessions.

Discussion

Early planting is one strategy for avoiding sorghum aphid infestations, because sorghum is beyond the vulnerable stage at the time when these insects become abundant

Table 2 Field testing results against the aphid damage

Accession no.	USDA/ICRISAT ID	Rating		Accession no.	USDA/ICRISAT ID	Rating	
		Lowland	Highland			Lowland	Highland
BSS5	PI144134	2	2	BSS410	IS18039	3	3
BSS27	PI154988	2	3	BSS423	IS20679	1	2
BSS55	PI196049	1	2	BSS456	IS24453	4	3
BSS59	PI21812	2	3	BSS473	IS26222	1	2
BSS78	PI586541	1	2	BSS474	IS26484	1	2
BSS79	PI641807	3	2	BSS496	IS29187	3	3
BSS80	PI641810	4	4	BSS497	IS29233	4	4
BSS82	PI641817	2	2	BSS505	IS29358	2	3
BSS83	PI641821	4	4	BSS507	IS29441	1	1
BSS100	PI155746	3	3	BSS508	IS29468	2	2
BSS246	PI33028	1	2	BSS510	IS29565	1	2
BSS314	IS602	1	2	Akdarı ^a	Cultivar	2	3
BSS325	IS2389	5	4	E Sumac ^a	Cultivar	3	3
BSS376	IS1619	3	3	Nes ^a	Cultivar	3	3
BSS402	IS15744	1	2	BSS320 ^b	IS2379	5	5

^aCheck varieties

^bHighly susceptible control to *M. sacchari*

enough to cause damage (Teetes and Pendleton 2000). Reducing insect damage is also possible by altering the planting time so that the insect larval stage is incompatible with the plant development stage (Guo et al. 2011). Crop rotation is another common practice that can reduce the buildup of insects on sorghum in the same field (Guo et al. 2011). Of the several strategies for combatting aphid infestation, however, the most economical and ecological, without a doubt, is the use of resistant cultivars.

Aphids have negative effects on the quality and quantity of seeds and on the juice Brix in sorghum (Knoll et al. 2018). Prior to the identification of the dominant *RMES1*-resistance gene against *M. sacchari* on chromosome 6 (Chang et al. 2006), the use of aphid resistance as a way to reduce insect damage was limited by the lack of knowledge related to its genetic mechanism. The development of the SCAR marker in that chromosome region was, therefore, a significant advancement, and its selective efficiency was determined as 86.8, 91.1, and 86.3% in the BC₁, F₂, and F_{2,3} populations, respectively (Chang et al. 2012). Our use of this linked marker and our confirmative field tests at two locations allowed the identification of 13 resistant sweet sorghum accessions (scored “1” or “2” in both environments) within our sorghum collection. A further eight accessions and three commercial cultivars also showed a moderate resistance to the aphid when growing under the same conditions in which the susceptible check was infested with more than 1000 aphids on the leaves and stalk.

The BSS507 accession appears to be an exceptionally resistant source, as it showed high resistance in both locations. The information provided here will be useful for examining the mechanism of resistance as well as for pyramiding the resistance. Of the resistant sources identified in the present study, 7 originated in Africa, mostly in Ethiopia and Lesotho. Manthe (1992), Teetes et al. (1995), and Van den Berg (2002) also identified aphid resistance in genotypes originating from Africa. The first domestication of this crop in Africa (Kimber 2000) may, therefore, have introduced several resistance sources from this continent.

The resistance to sugarcane aphid can vary at different plant growth stages during natural infestations (Elliott et al. 2015). Moreover, a positive correlation is also observed between aphid-induced injury and the sensitivity of the plant growth stage (Elliott et al. 2015). In our study, intense aphid infestations were observed to start on lower leaves. In general, during the first field invasion, as the populations increase, the foliage remains green despite the presence of aphids under the leaves. When the aphid population increases, the leaves change color to yellow, purple, and ultimately brown (Bowling et al. 2016). Aphid populations increase and peak between the flowering and milky stages (Waghmare et al. 1995), as well as during the boot to soft dough stage and the heading to harvesting stage in

spring and autumn (Fang 1990), thereby confirming environmental differences in aphid populations (Balikai 2001).

Several studies have examined aphid resistance in sorghum. For example, Sharma et al. (2014) conducted a field study to evaluate 102 grain sorghum genotypes under natural and artificial infestation and identified seven lines with moderate levels of resistance to aphid damage and lower losses in grain yield. Similarly, Sharma et al. (2013) observed moderate resistance to aphids in a few genotypes in a sorghum germplasm collection. The resistant lines included CSH 16, EC 434430, and 9728, which are commonly grown in India (Ghuguskar et al. 1999), as well as PAN 8446, SNK 3939, and NS 5511, which are grown in South Africa (Van den Berg 2002). The sorghum collection used in our study now provides additional aphid-resistant genotypes to expand the genetic diversity to allow selection for other desirable traits.

To our knowledge, no previous reports in the literature have looked for resistance to sugarcane aphid (*M. sacchari*) in sweet sorghum types. Sharma et al. (2014) indicated that aphid numbers increased at a faster rate on genotypes with high contents of nitrogen, sugar, free amino acids, and total chlorophyll (Mote and Shahane 1994; Tsumuki et al. 1995), whereas genotypes with high phosphorus, potassium, and polyphenol contents were less preferred by aphids (Mote and Shahane 1994). Sweet sorghum stalks are juicy and sweet, so the sweet types are more likely to be attacked by the sugarcane aphid. Indeed, sweet sorghum is more suitable than sugarcane for supporting the population growth of sugarcane aphids (Lopes-da-Silva et al. 2014). Therefore, determining resistant sweet sorghum sources is relatively difficult. However, the molecular and morphological evidence presented here, in two different environments, revealed more than ten different resistant sources and identified one sweet sorghum accession, encoded BSS507, which was an outstanding novel source for aphid resistance. These sources will be useful for breeding sweet sorghum genotypes for aphid resistance and may help in studies of the role of biochemical components that confer resistance to the sugarcane aphid, *M. sacchari*.

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Author contributions B. Uzun conceived and planned the experiments. B. Guden and E. Yol carried out molecular analysis. C. Erdurmus assisted with field experiments. B. Uzun, C. Ikten, E. Yol and B. Guden discussed the results and contributed to the final manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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