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Variation in inheritance of resistance to sorghum midge, *Stenodiplosis sorghicola* across locations in India and Kenya

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Summary

Sorghum midge [*Stenodiplosis sorghicola* (Coquillett)] is an important pest of grain sorghum, and host plant resistance is one of the important components for the management of this pest. We studied the inheritance of resistance to this insect involving a diverse array of midge-resistant and midge-susceptible genotypes in India and Kenya. Testers IS 15107, TAM 2566, and DJ 6514, which were highly resistant to sorghum midge in India, showed a greater susceptibility to this insect in Kenya. The maintainer lines ICSB 88019 and ICSB 88020 were highly resistant to sorghum midge in India, but showed a susceptible reaction in Kenya; while ICSB 42 was susceptible at both the locations. General combining ability (GCA) effects for susceptibility to sorghum midge for ICSA 88019 and ICSA 88020 were significant and negative in India, but such effects were non-significant in Kenya. The GCA effects of ICSB 42 for susceptibility to sorghum midge were significant and positive at both the locations. The GCA effects were significant and positive for Swarna, and such effects for IS 15107 and TAM 2566 were negative at both the locations. GCA effect of DJ 6514 were significant and negative in India, but non-significant and positive in Kenya; while those of AF 28 were significant and positive during the 1994 season in India, but significant and negative in Kenya. Inheritance of resistance to sorghum midge is largely governed by additive type of gene action. Testers showing resistance to sorghum midge in India and/or Kenya did not combine with ICSA 88019 and ICSA 88020 to produce midge-resistant hybrids in Kenya. Therefore, it is essential to transfer location specific resistance into both parents to produce midge-resistant hybrids.

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is one of the most important cereal crops in the semi-arid tropics (SAT). It provides food, feed and forage, but grain yields on peasant farms are generally low, partly due to insect pest damage. Of the 150 insect pests that damage the sorghum crop, sorghum midge, *S. sorghicola* (Coquillett) is one of the most destructive insect pests of sorghum worldwide (Harris, 1976; Sharma, 1993). Nearly 15,000 sorghum germplasm accessions have been screened for resistance to sorghum midge at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India, and 25 lines have been identified as resistant to sorghum midge across seasons and locations in India (Sharma et al., 1993a). Most of the high-yielding midge-resistant genotypes developed at ICRISAT have been derived from DJ 6514. However, some of these lines have shown a susceptible reaction to sorghum midge at Alupe (Kenya), indicating the possibility of occurrence of a new biotype of sorghum midge in this region or the environment-induced breakdown of resistance mechanisms (Sharma et al., 1999a, b). Therefore, the present studies were planned to understand genotype x environment interactions on inheritance of resistance to sorghum midge.

Materials and methods

Plant material

Inheritance of resistance to sorghum midge was studied on two sorghum midge-resistant cytoplasmic male-sterile (CMS) lines (ICSA 88019 and ICSA 88020) (Agrawal et al., 1996) and two midge-susceptible commercial CMS lines (296 A and ICSA 42); and five midge-resistant (IS 8891 – landrace from East Africa, IS 15107 – landrace from West Africa, TAM 2566 – line from conversion program at Texas A & M (USA), AF 28 – landrace from Africa, and DJ 6514 – landrace from India) and two midge-susceptible (Swarna and ICSV 112) testers (Sharma et al., 1993a). Sterility of all the CMS females was based on Milo-cytoplasm. The CMS lines were crossed with the testers in a line x tester mating design.

At ICRISAT, Patancheru, India, a set of 28 F_1 hybrids and their parents (4 CMS lines and 7 testers) was evaluated for resistance to sorghum midge during the 1993 rainy and 1994 post-rainy seasons. The F_1 hybrids and their parents were sown in a randomized complete block design, and there were three replications. Each entry was planted on ridges in a two-row plot, 4 m long. Rows were 75 cm apart, and the plants were spaced at 10 cm within a row. The seeds were drilled with a four cone planter along with carbofuran 3G (@ 1.2 kg a.i. ha^{-1}) to protect the seedlings against the sorghum shoot fly *(Atherigona soccata* Rondani). No insecticide was applied during the reproductive phase of the crop. The crop was grown under rainfed conditions during the rainy season, and under irrigation during the post-rainy season.

At Alupe, Kenya, 15 hybrids and their parents (3 CMS lines and 5 testers) were evaluated for resistance to sorghum midge during the 1993 short rainy season. The seed of F_1hybrids was produced during the 1992/93 post-rainy season at ICRISAT Center, India. Because of rejection of seed samples in the quarantine, hybrids based on 296A male-sterile line, and IS 8891 and ICSV 112 were not tested at Alupe, Kenya. The material was planted in a randomized complete block design, and there were three replications. Each entry was planted in a single row, 4 m long. The rows were 75 cm apart, and the plants were thinned to a spacing of 15 cm within the row at 15 days after seedling emergence. Normal agronomic practices were followed for crop cultivation. No insecticide was applied in this crop during the reproductive stage of the crop.

Insect infestation

Sorghum midge damage under natural conditions varies over space and time because of day-to-day variation in sorghum midge density and the staggered flowering of the sorghum genotypes. The sorghum midge females in general emerge every morning, mate, lay eggs in the flowering sorghum panicles between 0800 and 1100 hr, and mostly die by afternoon. As a result, sorghum midge emergence and oviposition varies over seasons and locations depending on sunrise, temperature, and relative humidity. Therefore, in addition to the natural infestation, the test material was also screened using no-choice headcage technique at ICRISAT, Patancheru, India (Sharma et al., 1988). Three panicles were infested with sorghum midge females under headcage in each replication. The panicles were covered with muslin cloth bags at panicle emergence to avoid natural midge infestation. Before infestation with the sorghum midges, the spikelets at the tip portion of the panicle, which had flowered the previous day, and the spikelets at the lower portion of the panicle, which may not flower over the next 2 days were removed with scissors. Wire-framed cages were then tied around the sorghum panicles, which were covered with blue colored cloth bags (Sharma et al., 1988). Sorghum midge females were collected in plastic bottle aspirators between 0800 and 1000 hr from flowering sorghum panicles, and 40 midge females were released inside each cage. Each panicle was infested with midge females for two consecutive days as the sorghum midges lay eggs only in spikelets at flowering stage (flowering in caged panicles was completed in 2 days). The cages were removed 15 days after infestation.

At Alupe, Kenya, the material was evaluated under natural infestation as sorghum midge population at this location remains quite high, because of continuous emergence of midges from wild relatives of sorghum (*Sorghum sudanense*), and staggered flowering of sorghum in this region during the long- and short-rainy seasons. At maturity, the test material was evaluated for sorghum midge damage (damage rating, DR) on a 1 to 9 scale (where $1 = <10\%$, and $9 > 80\%$ midge damaged spikelets) (Sharma et al., 1992).

Statistical analysis

Data on sorghum midge damage were subjected to analysis of variance. Significance of differences between the treatment means was judged by the F-test, and the treatment means were compared using least significant difference (LSD) at $P < 0.05$. The combining ability analysis was carried out according to Kempthorne (1957). The sum of squares (SS) due to F_1 hybrids was partitioned into SS due to lines, testers, and their interaction. The F-test was applied to test the significance of line x tester interaction, and if significant, mean squares for line x tester interaction were used to test the significance of lines and testers. If line x tester interaction was non-significant, error mean square was used to test the significance of lines and testers. The main effects of the lines and testers are equal to general combining ability (GCA), and female interaction with a specific tester is equivalent to specific combining ability (SCA) (Hallauer & Miranda, 1981). Standard error of GCA for the lines and testers were calculated to test the significance of these effects.

Results

Susceptibility of parental lines and F_1 hybrids to sorghum midge

The genotypes IS 8891, IS 15107, TAM 2566, AF 28, and DJ 6514 have shown a resistant reaction to sorghum midge (DR 1.0 to 3.8) in India, of which DJ 6514 showed a susceptible reaction in Kenya (Table 1). Swarna showed a susceptible reaction at both locations. In Kenya, IS 15107, TAM 2566, and AF 28 showed moderate levels of resistance to sorghum midge (DR 4.5 to 5.0 compared with a DR and 9.0 in the susceptible check). The maintainer lines (of the CMS lines) ICSB 88019 and ICSB 88020 showed a resistant reaction to sorghum midge (DR 2.5 to 4.7, except a DR of 6.0 in ICSB 88019 during the 1993 season under no-choice headcage screening) in India, and a susceptible reaction in Kenya (DR 7.0 to 8.0) (Table 1), while ICSB 42 showed a susceptible reaction at both the locations. In India, F_1 hybrids based on ICSA 88019 and ICSA 88020 showed a resistant reaction to sorghum midge (DR 3.5 to 4.7), while the hybrids based on ICSA 42 and 296A showed a susceptible reaction (DR 5.8 to 8.4) (Table 1). However, most of the F_1 hybrids showed a susceptible reaction to midge in Kenya (DR 7.0 to 9.0).

Inheritance of resistance to sorghum midge across locations in India and Kenya

Mean squares for the parents, parents versus crosses, lines, testers, and lines x testers (except for the 1993

Table 1. Sorghum midge damage rating (DR)[1] under natural infestation and no-choice headcage screening in seven testers, and four B-lines in sorghum

	Patancheru, India					Hybrid means*		
	Natural infestation		Headcage conditions			Patancheru, India		
Testers/lines	1993	1993/94	1993	1993/94	Alupe, Kenya 1993	Natural infestation	Headcage conditions	Alupe, Kenya 1994
Testers								
IS 8891	2.0	1.5	3.1	1.5	–	4.1	5.2	–
IS 15107	3.0	3.5	1.8	1.8	4.5	6.2	6.9	8.5
TAM 2566	2.0	2.0	3.5	2.1	5.0	4.1	4.3	7.2
AF28	2.5	1.5	3.8	1.5	5.0	5.5	5.6	7.0
DJ 6514	2.5	1.0	2.2	1.4	8.0	4.1	4.2	8.0
Swarna	9.0	9.0	4.5	8.5	9.0	7.3	7.7	9.0
ICSV 112	4.5	6.5	5.3	8.8	–	5.7	6.3	–
B-lines								
ICSB 88019	2.5	3.5	6.0	3.5	8.0	4.1	3.6	7.6
ICSB 88020	4.0	3.5	3.3	3.3	7.0	4.2	4.7	7.7
ICSB 42	8.5	8.5	3.8	9.0	9.0	6.8	7.8	8.6
296B	7.5	8.0	8.3	9.0	–	6.5	6.8	–
SE	± 0.94	± 0.66	± 1.90	± 0.65	80.49	± 0.57	± 1.01	± 0.49

[1]Sorghum midge damage rating (1 $\leq$ 10% midge damage, and 9 $\geq$ 80% midge damage).
*Hybrid means across the CMS lines, and/or testers.

Table 2. Analysis of variance and mean squares for sorghum midge damage for parents, lines, testers and lines x testers across locations

		Patancheru, India				Alupe, Kenya	
		Natural infestation		No-choice head cage conditions		Natural infestation	
Source of variation	df	1993	1994	1993	1994	df	MS
Parents	10	14.4**	28.9**	14.4*	23.6**	7	8.0**
Parents vs. crosses	1	12.4**	54.9**	60.2**	32.7**	1	12.4*
Lines	3	10.5**	79.9**	33.8**	69.9**	2	4.6**
Testers	6	29.7**	16.6**	15.6*	19.9**	4	3.9**
Lines x testers	18	2.8	6.7**	3.2	4.9**	8	1.3*
Error	76	1.72	1.36	7.01	0.85	44	0.6

*,** = Mean squares significant at P equal to 0.05 and 0.01, respectively.

rainy season in India) were significant at both locations, indicating the presence of variability among the hybrids and their parents for susceptibility to sorghum midge (Table 2). The general combining ability (GCA) effects for some of the midge-resistant lines and testers were significantly different across seasons in India and Kenya. In India, the GCA effects for susceptibility to sorghum midge were significant and negative for the midge-resistant CMS lines ICSA 88019 and ICSA 88020, while such effects for the midge-susceptible CMS lines (ICSA 42 and 296A) were significant and positive (Table 3). However, in Kenya, the GCA effects for ICSA 88019 and ICSA 88020 were negative, but non-significant. The GCA effects for ICSA 42

Table 3. General combining ability (GCA)* effects of four CMS lines and seven testers for sorghum midge damage in sorghum

	Patancheru, India				
	Natural conditions		Headcage conditions		Alupe, Kenya
Lines/testers	1993	1994	1993	1994	1993
Lines					
ICSA 88019	−0.7*	−1.4*	−1.7*	−2.5*	−0.30
ICSA 88020	−0.8*	−1.5*	−0.9	−1.2*	−0.25
ICSA 42	0.9*	1.8*	1.8*	2.4*	0.55*
296A	0.5	1.1*	0.8	1.3*	–
SE (gi)	0.35	0.22	0.71	0.25	0.17
SE (gi-gj)	0.50	0.31	1.00	0.35	0.55
Testers					
IS 8891	−2.6*	0.3	−1.3	0.1	–
IS 15107	0.1	1.4*	0.2	2.1*	0.93*
TAM 2566	−1.0*	−1.9*	−1.1	−1.7*	−0.73*
AF 28	0.1	0.6*	−0.3	0.0	−0.90*
DJ 6514	−1.3*	−0.5	−0.7	−2.3*	0.10
Swarna	3.2*	0.3	2.8*	1.1*	0.77*
ICSV 112	1.5*	−0.2	0.4	0.8*	–
SE (gi)	0.46	0.29	0.94	0.33	0.37
SE (gi-gj)	0.66	0.41	1.32	0.46	0.44

*GCA effects significant from zero at $P < 0.05$. SE (gi) = SE for comparing significance of differences amongst the lines tested. SE (gi-gj) = SE for comparing the significance of differences between any two lines.

were significant and positive at both locations. Testers IS 15107 and Swarna showed significant and positive GCA effect both in India and Kenya, while the GCA effects for TAM 2566 were significant and negative at both the locations. However, the GCA effects for AF 28 in India were significant and positive during the 1994 season under natural infestation, while such effects were significant and negative in Kenya. The GCA effects for DJ 6514 were significant and negative in India, but non-significant and positive in Kenya. In India, the specific combining ability (SCA) effects in general were low and non-significant (data for cross combinations with significant SCA effects discussed in the text) in India. The SCA effects for ICSA 88019 × IS 8891, ICSA 42 × DJ 6514, ICSA 42 × Swarna, ICSA 42 × ICSV 112, 296A × IS 15107, and 296A × TAM 2566 were negative for susceptibility to sorghum midge. The SCA effects for ICSA 88019 × DJ 6514, and ICSA 42 × TAM 2566 were positive. In Kenya, the SCA effects for midge damage were non-significant (except for ICSA 88020 × IS 26789 during the 1993 season).

Discussion

TAM 2566 and DJ 6514 have been found to be stable for resistance to midge across seasons in India, while AF 28 and IS 8891 have shown resistance to sorghum midge both in India and Kenya (Sharma et al., 1999a, b). However, sorghum midge damage in these lines is greater in Kenya than that observed in India. DJ 6514 and ICSV 197 (which is derived from DJ 6514; Agrawal et al., 1987), which are highly resistant to sorghum midge in India, have shown a susceptible reaction in Kenya (Sharma et al., 1999a). In the present studies, IS 15107, TAM 2566, and AF 28 showed moderate levels of resistance to sorghum midge in Kenya, while DJ 6514 (which was highly resistant to sorghum midge in India) showed a susceptible reaction in Kenya. There is also evidence of breakdown of resistance in some of the sources of resistance to sorghum midge in Yemen, except in AF 28 (Sharma, H.C.; unpublished).

The maintainer lines (B-lines) ICSB 88019 and ICSB 88020 showed a resistant reaction to sorghum midge in India, but a susceptible reaction in Kenya, while the commercial check ICSA 42, showed a susceptible reaction at both the locations. Several hybrids showed a resistant reaction to sorghum midge in India, but most of the hybrids showed a susceptible reaction in Kenya. Male-sterile lines showed a greater influence on the resistance or susceptibility of F_1 hybrids to sorghum midge in India, but such effects were not apparent in Kenya. The testers showing resistance to sorghum midge in Kenya did not combine with the midge-resistant CMS lines ICSA 88019 and ICSA 88020 to produce midge-resistant hybrids. Therefore, it is essential to transfer location specific resistance into both parents to produce hybrids with resistance to this insect. The GCA effects of ICSA 88019 and ICSA 88020 have earlier been observed to be significant and negative in India (Sharma et al., 1996), while the GCA effects were found to be non-significant in Kenya. Resistance to sorghum midge was predominantly governed by additive type of gene action in India (Agrawal et al., 1988; Sharma et al., 1996). Similar results have also been reported from the USA (Widstrom et al., 1984; Boozaya-Angoon et al., 1984). However, additive type of gene action for resistance to sorghum midge was not evident in Kenya.

Several climatic and edaphic factors influence the expression of resistance to insects. In general, temperature has a negative effect on host plant resistance to insects (Kogan, 1975). Differences in susceptibility to greenbug *(S. graminum)* in sorghum increase with an increase in temperature (Schweissing & Wilde, 1978). However, susceptibility to sorghum midge decreases with an increase in maximum and minimum temperatures (Sharma et al., 2003). Maximum and minimum temperatures are lower by 4.5 and 5.5 °C at Alupe, Kenya, than at Patancheru, India during flowering and grain development in sorghum. Therefore, low temperatures in Kenya may be one of the factors resulting in greater susceptibility to sorghum midge. Photoperiod, which alters the physico-chemical characteristics of the plants, influences the interactions between the insects and their host plants, e.g., continuous high intensity light increases the susceptibility to cabbage looper [*Trichoplusia ni* (Walker)] in soybean (Khan et al., 1986). Susceptibility to sorghum midge in ICSV 197 has been found to be positively associated with sunshine hours (Sharma et al., 2003). The sorghum crop at Alupe (Kenya) is exposed to a constant photoperiod of 12 hr (since it is located at the equator), while the sorghum crop at Patancheru, India, is exposed to 7.3 sunshine hours during October during the rainy season and 9.4 sunshine hours during the post-rainy season. Therefore, longer daylength at Alupe may influence the flowering pattern in sorghum lines as flowering in sorghum has been found to vary over seasons (Sharma and Hariprasad, 2002). Flowering patterns have been reported to be associated with resistance to sorghum midge (Diarisso et al., 1998), although this phenomenon has not been confirmed later (Sharma and Hariprasad, 2002). However, these interactions might influence genotypic susceptibility to sorghum midge by inducing some physico-chemical changes in glume and grain characteristics associated with resistance to this insect.

Differences on mode of infestation in India and Kenya also might contribute to differences in genotypic reaction to sorghum midge. However, artificial infestation in India was used to overcome low levels of midge infestation under natural conditions (3–5 midges per panicle), while midge infestation in Kenya was quite high throughout the season (20–25 midges per panicle). And hence, there was no need of using artificial infestation in Kenya. High midge density in Kenya would result in similar levels of midge infestation as those obtained under headcage infestation in India.

Short, tight and hard glumes, faster rate of grain development, and tannin content of the grain are associated with resistance to sorghum midge (Rossetto et al., 1984; Sharma et al., 1990). Grain growth rate between 3rd and 6th day after anthesis is negatively associated with damage by the sorghum midge at Patancheru, India; but not at Alupe, Kenya (Sharma et al., 1999b). And therefore, such differences in association of grain growth rate with susceptibility to sorghum midge may lead to variation in genotypic susceptibility to sorghum midge in India and Kenya. Chemical composition of the sorghum grain is influenced by environment (Butler, 1982; Price et al., 1979), and these changes have been linked to the expression of resistance to sorghum midge (Sharma et al., 1993b).

Sorghum midge emergence and oviposition is also influenced by relative humidity (Fisher & Teetes, 1982). However, there is only a slight difference in maximum relative humidity between Patancheru (71.9%) and Alupe (67.3%) during the flowering of sorghum crop. However, minimum relative humidity at Alupe, Kenya (47.7%) is much greater than that at Patancheru, India (26.7%), and this may also contribute to greater midge activity and infestation at Alupe than at Patancheru. Thus, temperature, relative humidity, and possibly solar radiation may account for greater susceptibility of some of the midge-resistant genotypes in Kenya. However, AF 28 and IS 8891 have shown resistance to sorghum midge across locations, and hence factors other than the climatic differences may also be responsible for breakdown of resistance to sorghum midge (Sharma et al., 2003). Therefore, both climatic factors and difference in insect populations across these geographical regions may account for differences in nature of gene action governing host plant resistance to sorghum midge.

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