Host Plant Resistance to Insects in Sorghum: Present Status and Need for Future Research

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Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is an important cereal crop in Asia, Africa, the Americas, and Australia. Grain yields on farmers' fields in the semi-arid tropics (SAT) are generally low (500 to 800 kg ha^{-1}) mainly due to insect pest damage. Nearly 150 insect species have been reported as pests on sorghum, of which sorghum shoot fly (*Atherigona soccata* Rond.), stem borer (*Chilo partellus* Swin.), armyworm (*Mythimna separata* Walk.), shoot bug (*Peregrinus maidis* Ashmead), aphid (*Melanaphis sacchari* Zehnt.), sorghum midge (*Stenodiplosis sorghicola* Coq.), earhead bug (*Calocoris angustatus* Leth.), and head caterpillars (*Helicoverpa, Eublemma*, and *Cryptoblabes*) are the major pests (Sharma 1993). Annual losses due to insect pests in sorghum have been estimated to be over $1089 million in the SAT.

Host plant resistance

Techniques to screen for resistance to insect pests. The ability to develop insect-resistant cultivars, use of marker-assisted selection, and development of transgenic plants with insect resistance depends on the precision of resistance screening techniques. Infester row, cage and leaf disc screening techniques have been standardized to evaluate sorghum germplasm, breeding material, and mapping populations for resistance to insect pests under field and greenhouse conditions (Sharma et al. 1992, 2003). However, several of these techniques are being used in the sorghum improvement programs only sparingly because of lack of resources or lack of enthusiasm on the part of the scientists involved. Lack of infrastructure for insect rearing could be an impediment to screening for resistance to stem borer, but infester row and no-choice cage techniques developed to screen for resistance to shoot fly, midge, and head bugs do not require much investment. There is a need to standardize the techniques to screen for resistance to aphids – an emerging pest problem. One of the problems in selecting for resistance to stem borer is the relative importance of foliar injury, deadhearts, stem tunneling, exit holes, and tiller production (Singh 2002). The effects of different damage parameters on grain yield loss are not fully understood. Another important question is whether the material should be screened in each generation, alternate generations, or only after the material has become homozygous in $F_5 - F_6$ generations. Extensive studies at ICRISAT have indicated that the material subjected to borer infestation in F_2 to F_5 generations had greater frequency of resistant progenies than the material exposed to borer infestation in the F_5 generation only. Such information needs to be generated for different insect pests.

Identification and utilization of sources of resistance to insect pests. Host plant resistance should form the backbone of pest management in sorghum. Over the past five decades, a large proportion of the world sorghum germplasm collection has been evaluated for resistance to insect pests, and a number of lines with resistance to major insect pests have been identified (Sharma et al. 1992, 2003). Large-scale screening of the sorghum germplasm at ICRISAT has resulted in identification of several lines with reasonable levels of resistance to shoot fly, stem borer, midge, and head bugs (Table 1). Sources of resistance to insects in sorghum have been used in the breeding program, and many varieties with resistance to insect pests have been developed (Table 2). However, cultivars with resistance to insect pests are cultivated by farmers only on a limited scale due to an overemphasis by national programs on grain yield as a criterion for release of cultivars. Since sorghum varieties and hybrids with a yield potential of over 10 t ha^{-1} are already available in the market, it is important that insect and disease resistance be used as a criterion to identify varieties and hybrids for use by farmers for sustainable crop production.

Diversification of the cytoplasmic male-sterile systems with resistance to insect pests. Most of the hybrids grown in India are based on *milo* cytoplasm (A_1 cytoplasm), which is highly susceptible to sorghum shoot fly (Dhillon 2004) (Fig. 1). Extensive use of the A_1 cytoplasm as a source of cytoplasmic male-sterility (CMS) has resulted in narrowing of the genetic base of sorghum hybrids currently being cultivated by farmers, and this might increase the vulnerability of this crop to biotic and

abiotic stresses. In general, the CMS lines are more susceptible to sorghum shoot fly (*A. soccata*), sugarcane aphid (*M. sacchari*), shoot bug (*P. maidis*), and midge (*S. sorghicola*) than the maintainer lines, suggesting that the maintainer lines harbor the factors that influence expression of resistance to insects (Sharma et al. 2004b). Therefore, there is a need to develop a range of CMS, maintainer, and restorer lines with resistance to insect pests, and diversify the CMS systems in sorghum. The A_4M cytoplasm is slightly less susceptible to shoot fly than the other CMS systems. Recovery from shoot fly damage is better in A_4M, A_3, and A_2 cytoplasms than the A_1 cytoplasm. Shoot fly survival and development is also poor on A_4M and A_4VzM CMS systems. The A_4M cytoplasm being less susceptible to shoot fly and having better recovery resistance, can be exploited for developing shoot fly-resistant hybrids in future. However, as a first step, it may be better to transfer the traits associated with resistance to shoot fly into the hybrid parents in A_1 cytoplasm. Another alternative would be to explore opportunities for using male gametocytes and/or temperature and photoperiod-induced male-sterility for sorghum hybrid seed multiplication as these might allow exploitation of the favorable effects of normal maintainer line cytoplasm(s) on expression of resistance to insects in this crop. Of course, the simplest alternative would be to focus on open-pollinated varieties that do not require use of male-sterility for seed multiplication.

Development of CMS and restorer lines for resistance to insect pests. Much of the area under high-yielding sorghum cultivars is sown to hybrids in Asia, Australia, and the Americas. Therefore, it is apparent that for host plant resistance to be an important component of pest management in sorghum, we need to transfer the insect resistance genes into male-sterile, maintainer, and restorer lines that can be used by the public institutions and private seed industry to develop insect-resistant hybrids. The CMS, maintainer, and restorer lines with resistance to shoot fly, stem borer, midge, and head bugs have been developed at ICRISAT (Table 3). Much of this material has been shared with public institutions and private seed industry over the past decade for use in sorghum improvement, and for developing high-yielding hybrids with resistance to insects. To develop insect-resistant hybrids, the genes conferring resistance to insect pests need to be transferred into both CMS and restorer lines (Fig. 2a, b) (Sharma et al. 2004b). Hybrids based on resistant × resistant parents exhibit greater resistance than the hybrids based on other cross combinations (Sharma et al. 1996, Sharma et al. 2004b, Dhillon 2004). The hybrids

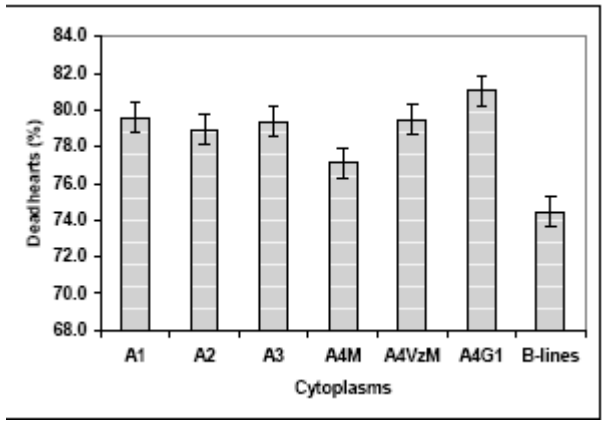

Figure 1. Relative susceptibility of different CMS systems to sorghum shoot fly, *Atherigona soccata*.

based on susceptible × susceptible parents are highly susceptible. The CMS lines showed a greater influence on the expression of resistance/susceptibility to shoot fly and sorghum midge than the restorer lines. Therefore, efforts should be made to transfer insect resistance genes into a diverse array of both CMS and restorer lines for developing hybrids with resistance to insect pests.

Wild relatives of sorghum as sources of diverse genes for resistance to insect pests. Levels of resistance to sorghum shoot fly and stem borer in cultivated germplam are low to moderate (Sharma et al. 2003). Therefore, it may be important to identify wild relatives of sorghum with high levels of resistance to these pests. Wild relatives of sorghum have been evaluated for resistance to sorghum shoot fly at ICRISAT, and accessions belonging to *Parasorghum* (*S. australiense, S. purpureosericeum, S. brevicallosum, S. timorense, S. versicolor, S. matarankense,* and *S. nitidum*) and *Stiposorghum* (*S. angustum, S. ecarinatum, S. extans, S. intrans, S. interjectum,* and *S. stipoideum*) did not show any shoot fly damage under multi-choice conditions in the field (Venkateswaran 2003) (Table 4). *Heterosorghum* (*S. laxiflorum*) and *Chaetosorghum* (*S. macrospermum*) showed very low damage, while the species belonging to section wild races of *S. bicolor* subsp. *verticilliflorum* (*aethiopicum, arundinaceum, verticilliflorum,* and *virgatum*) were highly susceptible to shoot fly, as was *S. halepense*. Accessions belonging to *Heterosorghum*, *Parasorghum* and *Stiposorghum* showed little damage by the spotted stem borer under artificial infestation in the field, except for one accession of *Heterosorghum,* which showed 2% deadhearts (Venkateswaran 2003) (Table 5). In contrast, section *Chaetosorghum* (*S. macrospermum*) was highly susceptible to stem borer damage. Within the section

Sorghum, the four wild races of *S. bicolor* subsp. *verticilliflorum* (races *arundinaceum, aethiopicum, verticilliflorum,* and *virgatum*) were highly susceptible to stem borer damage. Sorghum midge females did not lay any eggs in the spikelets of *S. angustum*, *S. amplum*, and *S. bulbosum* compared to 30 eggs in spikelets of *S. halepense* under no-choice conditions. Odors from the panicles of *S. halepense* are more attractive to the females of sorghum midge than the odors from panicles of *S. stipoideum, S. brachypodum, S. angustum, S. macropsermum, S. nitidum, S. laxiflorum,* and *S. amplum* (Sharma and Franzmann 2001). The accessions belonging to the secondary gene pool with diverse mechanisms of resistance to insects can be crossed with cultivated sorghum, while those belonging to the tertiary gene pool may require application of embryo rescue techniques to transfer resistance genes from the wild relatives into the cultivated sorghums.

Marker-assisted selection. It takes five to six generations to transfer a trait within a species into high-yielding locally adapted cultivars through conventional breeding, and one has to evaluate a large number of progenies to be able to select the plants with the appropriate combination of traits. The use of DNA markers for indirect selection offers great potential gains for quantitative traits with low heritability, as these are the most difficult characters to work with in the field using direct phenotypic selection. The effectiveness of a marker-assisted selection (MAS) can only be as good as the quality of the phenotypic data on which the development of the marker was based. At ICRISAT, mapping populations have been phenotyped and genotyped for sorghum shoot fly (296B × IS 18551 and BTx 623 × IS 18551), and spotted stem borer, sorghum midge, and aphid (ICSV 745 × PB 15881-3). Genetic linkage maps based on these populations have been constructed to identify quantitative trait loci (QTLs) associated with resistance to these insects. Polymorphic simple sequence repeat (SSR) loci associated with resistance to shoot fly and the traits associated with resistance to this insect have been identified (Folkertsma et al. 2003). These QTLs are now being transferred into locally adapted hybrid parental lines via SSR based MAS. The QTLs associated with antibiosis and antixenosis mechanisms of resistance to sorghum midge (Tao et al. 2003), and tolerance to green bug (Nagaraj et al. 2005) have also been identified (Table 6). It is hoped that MAS will allow for rapid introgression of the resistance genes, and ultimately gene pyramiding, into the high-yielding varieties and hybrids.

Development of insect-resistant transgenic sorghums. Given the wide host range of some of the insect pests, and low levels of resistance in the cultivated germplasm against stem borers, head bugs, and armyworms, it would be highly desirable to combine conventional plant resistance with novel genes from *Bacillus thuringiensis*, protease inhibitors or plant lectins. For plant resistance to be successful in integrated insect pest management, they have to substitute completely or partially for the use of insecticides and/or other methods of pest management, and result in improved economic returns and reduced environmental impact. In addition to the reduction in losses due to insect pests, the deployment of transgenic plants with insecticidal genes will also lead to: i) reduction in insecticide sprays, ii) reduced exposure of farm labour to insecticides, iii) reduction in harmful effects of insecticides on nontarget beneficial organisms, iv) increased activity of natural enemies, v) reduced amounts of pesticide residues in food and food products, and vi) a safer environment to live in. The first transgenic plants were developed in the mid-1980s (Vaeck et al. 1987). Since then, there has been a tremendous progress in development and deployment of transgenic plants for insect resistance (Sharma et al. 2002, James 2003). Toxins from *Bacillus thuringiensis* var *morrisoni* have shown biological activity against the sorghum shoot fly, *A. soccata*. The *B. thuringiensis* toxins Cry1Ac and Cry2A are moderately effective against spotted stem borer, *C. partellus*, while Cry1Ac is effective against *H. armigera* (Sharma et al. 2004a). Sorghum plants having *cry1Ac* gene have been developed at ICRISAT, and are presently being tested for resistance to spotted stem borer, *C. partellus* (Girijashankar et al. 2005). Combining transgenic resistance to insects with conventional plant resistance will render plant resistance an effective component for pest management in sorghum.

Genetic engineering of metabolic pathways. Many secondary plant metabolites such as flavonoids have been implicated in host plant resistance to insects in sorghum. Many compounds of the flavonoid biosynthetic pathway accumulate in response to biotic and abiotic stresses (Heller and Forkman 1993). Genetic engineering offers the opportunity to change the metabolic pathways to increase the amounts of various flavonoids that play an important role in host plant resistance to insect pests. Biotechnology also offers the opportunity to increase the production of secondary metabolites in plants to increase the levels of resistance to insect pests or inhibit the production of toxic metabolites such as HCN in forage sorghum.

Table 1. Germplasm accessions identified to be resistant to insect pests in sorghum.

Insect pest	Germplasm accessions (IS numbers)
Shoot fly	923, 1032, 1034, 1037, 1044, 1054,1071, 1096, 1104, 1119, 2122, 2123, 2146, 2162, 2168, 2195, 2205, 2265, 2269, 2291, 2309, 2312, 2394, 2681, 3461, 3962, 4224, 4273, 4646, 4663, 4664, 4835, 4881, 4981, 5075, 5076, 5078, 5210, 5429, 5469, 5470, 5480, 5484, 5490, 5511, 5538, 5566, 5571, 5604, 5613, 5619, 5622, 5636, 5648, 8064, 8100, 8320, 8571, 8721, 8811, 8887, 8891, 8918, 8922, 8988, 9009, 9692, 6566, 10711, 10795, 12150, 13674, 14108, 15437, 15896, 16235, 16357, 7726, 17742, 17745, 17747, 17750, 17948, 17966, 18274, 18325, 18366, 18368, 18369, 18371, 18476, 18551, 18580, 18635, 18662, 18700, 18733, 19485, 19569, 19706, 20064, 21871, 21877, 21969, 22039, 22114, 22121, 22144, 22145, 22148, 22149, 22196, 25744, and 26789.
Stem borer	923, 1044, 1051, 1082,1096, 1104, 2122, 2123, 2146, 2162, 2195, 2263, 2265, 2269, 2290, 2291, 2292, 2312, 2375, 2376, 3962, 4546, 4637, 4646, 4663, 4664, 4756, 4757, 4776, 4835, 4995, 5072, 5210, 5253, 5268, 5469, 5470, 5480, 5484, 5490, 5511, 5566, 5571, 5579, 5585, 5604, 5613, 5619, 5648, 8811, 5658, 6566, 7224, 8165, 8189, 8549, 8671, 12308, 13100, 17745, 17948, 18333, 18371, 18551, 18573, 18577, 18578, 18579, 18581, 18584, 18585, 18662, 18677, 21883, 22039, 22091, 22113, 22114, 22121, 22129, 22144, 22148, 22196, 22778, 23411, 23962 ,and 24027.
Midge	2290, 2292, 2579, 2687, 2739, 2830, 3461, 6283, 7005, 7134, 7138, 7151, 8100, 8151, 8190, 8196, 8198, 8204, 8577, 8671, 8721, 8729, 8751, 8887, 8891, 8918, 8922, 8988, 10712, 14380, 15107, 8849, 8884, 8946, 9021, 9045, 9107, 9112, 9608, 9807, 18563, 18573, 18695, 18696, 18698, 18733, 19474, 19476, 19512, 19955, 19957, 21006, 21031, 21211, 21871, 21873, 21879, 21881, 21883, 21883-1, 22400, 22464, 22471, 22806, 23748, 26789, 27103, 27466, 31626, 31635,and 31636.
Head bugs	2761, 8064, 14108, 14317, 14334, 14380, 16357, 17610, 17618, 17645, 18579, 19455, 19945, 19948, 19949, 19950, 19951, 19955, 19957, 20024, 20059, 20068, 20638, 20643, 20664, 20740, 21006, 21211, 21443, 21444, 21485, 21525, 21574, 22284, 22507, 23748, 24357, 25069, 25098, 25760, 21512, 25733, 25766, 27329, 27397, 27452, 27466, and 27477.

Sharma et al. (1992, 2003).

Table 2. Sorghum varieties with resistance to insect pests, developed at ICRISAT.

Insect pest	Improved lines with resistance to insects (ICSV numbers)
Shoot fly	700, 701, 702, 705, 707, 708, 711 to 714, 717, 726, 89013, 89018, 89025, 93093, and 25001 to 25055.
Stem borer	700, 708, 711, 714, 717, 89008, 89010, 93046, and 25056 to 25162.
Midge	197, 239, 305, 313, 385 to 395, 563, 564, 573, 693, 729 to 758, 804, 830 to 832, 835, 836, 843, 88006, 88013, 88014, 88028, 88032, 88035, 88041, 89001, 89010, 89031, 89034 to 89039, 89042 to 89044, 89049 to 89054, 89057, 89058, 90001 to 90010, 90014, 90016, 90018, 91015, 91025, 92011 to 92013, 92015 to 92018, 92020, 92021, 92023, 92024, 93001to 93026, 93035, 93046, 93057, 93059, 93065 to 93067, 93069, 95071 to 93093, 95080, 95123 to 95125, 96009 to 96011, 96027, 96031,96062 to 96082, and 25163 to 25244,.
Head bugs	25245 to 25263.

Agarwal BL, Sharma HC, Taneja SL, Reddy BVS, and Stenhouse JH (unpublished).

Table 3. Cytoplasmic maintainer and male-sterile lines with resistance to insect pests, developed at ICRISAT.

Shoot fly	Stem borer	Midge	Head bugs
ICSB 415, ICSB 416, ICSB 417, ICSB 418, ICSB 419, ICSB 422, ICSB 423, ICSB 425, ICSB 428, ICSB 429, ICSB 432, ICSB 433, ICSB 434, and ICSB 435	ICSB 464, ICSB 467, ICSB 468, ICSB 469, ICSB 472, ICSB 473, and ICSB 474	ICSB 488, ICSB 493, ICSB 494, ICSB 502, ICSB 505, ICSB 508, ICSB 512, ICSB 513, ICSB 516, ICSB 518, ICSB 520, ICSB 524, ICSB 527, and ICSB 541	ICSB 547, ICSB 548, ICSB 550, ICSB 552, ICSB 553, ICSB 555, ICSB 557, and ICSB 563

Reddy BVS, and Sharma HC (unpublished).

Table 4. Relative susceptibility of wild relatives of sorghum to shoot fly, *Atherigona soccata.*

Section	Species	Accession	Deadhearts (%)		Adult emergence (%)
			Field conditions	No-choice conditions	
Chaetosorghum	*Sorghum macrospermum*	TRC 24112	6.7	61.5	-
Heterosorghum	*S. laxiflorum*	IS 18958	0.0	7.4	6.2
Parasorghum	*S. australiense*	IS 18954	0.0	10.1	4.2
	S. matarankense	TRC 243576	0.0	0.0	-
	S. purpureosericeum	IS 18943	0.0	50.3	-
	S. nitidum	TRC 243514	0.0	9.7	-
	S. timorense	TRC 243498	0.0	21.1	-
	S. versicolor	IS 23177	0.0	6.2	-
Stiposorghum	*S. angustum*	TRC 243499	0.0	4.0	0.0
	S. ecarinatum	TRC 243574	0.0	3.5	-
	S. intrans	TRC 243571	0.0	1.1	-
	S. extans	TRC 243601	0.0	0.0	-
	S. interjectum	TRC 243461	0.0	1.2	-
	S. stipoideum	TRC 243399	0.0	0.0	-
Sorghum	*S. aethiopicum*	IS 27584	88.9	-	99.5
	S. virgatum	IS 18808	92.2	-	89.0
	S. bicolor	CSH 1I	96.7	-	-
		S 18551	30.6	70.2	50.8
LSD (P 0.05)			5.8	19.6	18.9

Venkateswaran (2003).

Inducible resistance to insect pests – gene switches. A wide range of inducible genes have been identified in plants based on endogenous chemical signals such as phytohormones, response to insect attack, or wounding. Chemically induced expression systems or "gene switches" enable the temporal, spatial, and quantitative control of genes introduced into crop plants, or those that are already present in the plants. The best-studied system utilizes pathogenesis-related protein-1a (*PR 1-a*) gene expression in tobacco (Uknes et al. 1993). *PR 1-a* mRNA levels can also be induced by exogenous application of salicylic acid (Ward et al. 1991). Peptide hormones also induce production of proteinase inhibitors. Systemically induced responses are modified through synthesis and action of jasmonic acid via its lipid precursor, e.g., linoleic acid in tomato. Application of exogenous jasmonate induces the production of proteinase inhibitors. Enhanced resistance in transgenic rice plants by application of methyl jasmonate and abscisic acid has been reported (Xu et al. 1993).

Dominant repressible lethal genetic system. Traditionally, the sterile insect technique has been employed to control several insect pests. However, this system depends on large-scale production of the target insect, and use of irradiation or chemical sterilization. Release of insects carrying a dominant lethal (RIDL) gene has been proposed as an alternative to the conventional techniques used for insect sterilization (Alphey and Andreasen 2001). This is based on the use of a dominant, repressible, female-specific gene for insect control. A sex-specific promoter or enhancer gene is used to drive the expression of a repressible transcription factor, which in turn controls the production of a toxic gene product. A non-sex specific expression of the repressible transcription factor can also be used to regulate a selectively lethal gene product. Insects produced through genetic transformation using this approach do not require sterilization through irradiation, and could be released in the ecosystem to mate with the wild population to produce sterile insects that will be self-perpetuating.

Need for future research

- Improvement in precision of screening and selection criteria for resistance to insect pests.
- Gene pyramiding and development of cultivars with multiple resistance to insect pests and diseases.
- Transfer of insect resistance genes into CMS, maintainer, and restorer lines, and exploitation of alternate CMS

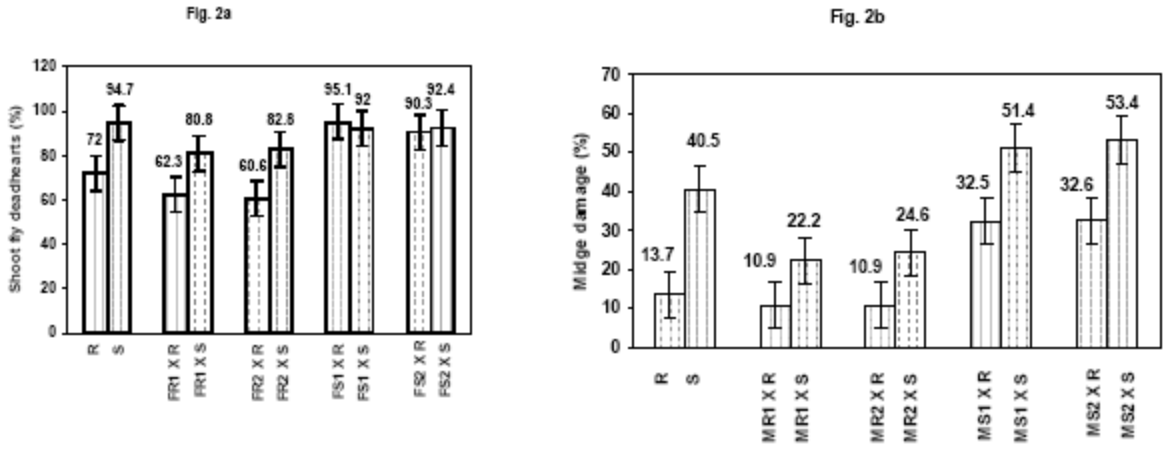

Figure 2. Insect damage in sorghum hybrids based on resistant (R) and susceptible (S) male-sterile and restorer lines. a: shoot fly, Atherigona soccata (FR1 = SPSFR 94006, FR2 = SPSFR 94007, FS1 = ATx623, and FS2 = CK 60A). b: sorghum midge, Stenodiplosis sorghicola (MR1 = ICSA 88019, MR2 = ICSA 88020, MS1 = 296A, and MS2 = ICSA 42). FR = Resistant female. FS = Susceptible female. MR = Resistant male. MS = Susceptible male. R = Resistant. S = Susceptible.
Sharma et al. (2004b).

Table 5. Relative susceptibility of wild relatives of sorghum to spotted stem borer, *Chilo partellus.*

			Deadhearts (%)		
Section	Species	Accession	Field conditions	Greenhouse conditions	Larvae recovered (%)
Chaetosorghum	*Sorghum macrospermum*	TRC 24112	72.9	-	-
Heterosorghum	*S. laxiflorum*	IS 18958	0.0	82.5	6.0
		TRC 243492	0.0	15.3	0.0
Parasorghum	*S. australiense*	IS 18955	0.0	10.5	0.0
	S. matarankense	TRC 243576	0.0	5.2	0.0
	S. nitidum	TRC 243514	0.0	0.0	0.0
	S. purpureosericeum	RN 285	0.0	11.1	0.0
	S. timorense	TRC 243498	0.0	0.0	0.0
	S. versicolor	IS 14262	0.0	0.0	0.0
Stiposorghum	*S. angustum*	TRC 243499	0.0	0.0	6.0
	S. ecarinatum	TRC 243574	0.0	0.0	0.0
	S. extans	TRC 243601	0.0	0.0	0.0
	S. intrans	TRC 243571	0.0	0.0	0.0
	S. interjectum	TRC 243461	0.0	0.0	0.0
	S. stipoideum	TRC 243399	0.0	0.0	0.0
Sorghum	*S. aethiopicum*	IS 27584	86.7	-	-
	S. virgatum	IS 18808	94.5	98.2	55.0
	S. bicolor	CSH 1I	95.5	98.4	90.0
		S 18551	58.0	96.8	40.0
LSD (P 0.05)			10.5	4.4	-

Venkateswaran (2003).

Table 6. Molecular makers identified to be associated with resistance to insect pests in sorghum.

Linkage group (LG)	Primers	Linked traits/mechanisms
Sorghum shoot fly, *Atherigona soccata*		
LG F	*Xtxp 258* (bp 190/230) *Xtxp 289* (bp 270/294)	Trichome density
LG G	*Xgap 1* (bp 180/254) *Xtxp 141* (bp 154/169)	Deadhearts, leaf glossiness, and trichome density
LG I	*IS 328* (bp 144/166) *IS 264* (bp 153/207)	Leaf glossiness
LG J	*IS 258* (bp 170/193) *Xtxp 65* (bp 125/134)	Deadhearts and leaf glossiness
Sorghum midge, *Stenodiplosis sorghicola*		
LG A	*RZ* 543 *ST* 698	Antixenosis mechanism of resistance
LG G	*ST* 1017 *SG* 14	Antixenosis mechanism of resistance
LG J	*TXS* 1931 *SG* 37	Antibiosis mechanism of resistance
Green bug, *Schizaphis graminum*		
LG 3	*Xtxp* 12 *Xcup* 20 *Sb1* 10	Tolerance mechanism of resistance
LG 5	*Xt xp* 43 *Xtxp* 85 *Xtxp* 335 *Xtxp* 204	Tolerance mechanism of resistance

Folkertsma et al. (2003), Tao et al. (2003), and Nagaraj et al. (2005).

systems that are less susceptible to insect pests.

- Identification of toxin genes for shoot fly, stem borer, and head bugs, and development of transgenic plants with resistance to insect pests.
- Identification of molecular markers associated with resistance to shoot fly, midge, stem borer, aphids, and head bugs for use in MAS.

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