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Grain mould resistance and associated characters of sorghum genotypes

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Summary

Twenty-two sorghum genotypes were evaluated for grain mould response, 13 morphological and biochemical traits thought to contribute to resistance, and 3 agronomic traits related to utilization. Measurements of grain mould (field grade score, threshed grade score, ergosterol content, and percentage germination) were strongly correlated with one another. Highly significant correlations between measures of grain mould and seed hardness, seed phenol content in acid methanol extract, and glume colour indicated that they strongly affected grain mould response. Harder grain, higher levels of seed phenols, and darker glumes contributed to grain mould resistance. Weaker and less consistent correlations between measures of grain mould and seed colour, seed flavan-4-ol content, glume phenol and flavan-4-ol contents, and glume cover indicated relatively less effect of these traits on grain mould response. Genotype means indicated that combinations of several traits are required to achieve resistance. Germplasm lines, including coloured-seeded lines IS 14375, IS 14387, IS 18144, and IS 18528, and white-seeded lines IS 21443, IS 24495 and IS 25017, showed greatest grain mould resistance. Improved lines generally had poorer grain mould resistance than these landraces. However, the best improved lines were comparable in resistance to white-seeded landraces. B58586, IS 14375 and IS 14387 are hard-seeded guinea sorghum lines that can be used as sources of grain mould resistance for West Africa. SP 33316, SP 33349 and GM 15018 are agronomically elite lines that can be used as sources of grain mould resistance for further improvement of white-seeded sorghum for South Asia and other regions.

Abbreviations: %G-COV – percentage glume cover; %GER – Germination percentage; DF – Days to 50% flowering; ERGO – Ergosterol content; FGS – Field grade score; G-FLAV – Glume content of flavan-4-ol; GI – Glume index; GLCL – Glume colour; G-PHEN – Glume content of total phenols; G-PHEN$^+$ – Glume phenol content in acid methanol extract; HT – Plant height; SDCL – Seed colour; S-FLAV – Seed content of flavan-4-ol; S-HRD – Seed hardness; S-PHEN – Seed content of phenols; S-PHEN$^+$ – Seed content of phenols in acid methanol extract; TGS – Threshed grade score; YD/PL – grain yield/plant.

Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) is a staple food crop in semiarid tropical areas of Africa and India. It is also an important feed and forage crop in other parts of the world. In India, the development of short-duration and short-statured sorghum hybrids resulted in a quantum jump in grain productivity from 560 kg ha^{-1} in 1970 to 1020 kg ha^{-1} in 1996. However, yield potentials of short-duration sorghum hybrids are often not fully realized as they mature before the end of the rainy season and are highly susceptible to grain moulds, which not only cause yield loss but also reduce grain quality and market value. In Africa, absence of grain mould resistance has been cited as a constraint to adoption of improved cultivars (Mukuru, 1992). Aflatoxin, which can cause harmful toxic effects to humans, has been associated with

grain moulds. Hence, breeding grain mould resistant cultivars may help improve sorghum production and profitability, extend the use of improved cultivars to new areas, as well as contribute to enhanced health of consumers.

Breeding grain mould resistant sorghum hybrids and varieties requires identification of useful resistance gene(s) in the germplasm or defining other sources of such genes (Sharma, 1994). The next step is to identify the defence mechanisms (morphological and biochemical) operating in the resistance sources against pathogen invasion (Sharma, 1994). Knowledge of the resistance mechanisms and their inheritance allows breeders to pyramid the genes of different, possibly complementary, mechanisms to produce greater or more stable resistance.

The present investigation was undertaken with the following objectives: (1) to evaluate in detail the grain mould responses of selected sorghum genotypes; (2) to evaluate the same genotypes for morphological and biochemical characters associated with mould resistance; and (3) to estimate correlations between grain mould resistance, and morphological and biochemical characters, in order to identify the likely resistance mechanisms.

Materials and methods

Two experiments were conducted during the 1994 rainy season at the Directorate of Oil Seeds Research, Rajendranagar, Hyderabad (India). Twenty-two sorghum genotypes, including released and pre-released varieties, restorers and non-restorers, advanced breeding lines, and germplasm lines, obtained from the National Research Centre for Sorghum (NRCS), the All India Co-ordinated Sorghum Improvement Project (AICSIP) and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) were utilised (Table 1). Seeds of 22 sorghum genotypes were sown in 4-m long rows (two rows each) on ridges 0.75 m apart, in June 1994, in a randomised complete block design in both experiments. Experiment 1 was conducted under sprinkler irrigation with three replications to evaluate the genotypes for grain mould resistance and other related characters. Experiment 2 was conducted under rainfed conditions in two replications for recording grain yield per plant and plant height of the genotypes. Standard recommended agronomic practices were followed throughout the duration of the crop. Land was prepared by deep ploughing, discing and harrowing. Ridges were 75 cm apart. Atrazine® at a rate of 1 kg ha^{-1} of active ingredient was applied after sowing but before emergence. A basal fertiliser dose of 42 kg N ha^{-1} and of 42 kg P_2O_5 ha^{-1} was applied. Seedlings were thinned 20 d after emergence to 10 plants m^{-1} row length. Three weeks after emergence, the crop was weeded mechanically beween rows and by hand within rows. The crop was top-dressed with 46 kg N ha^{-1} 25 d after emergence.

Table 1. The sorghum genotypes evaluated for grain mould response during 1994

S.No	Genotype	Origin	Source[1]	Grain mould response[2]
1	AKMS 14B	India	AICSIP	S
2	296B	India	AICSIP	S
3	AKR 150	India	AICSIP	S
4	MS 422B	India	NRCS	S
5	R 1413	India	NRCS	S
6	IS 14375	Zimbabwe	ICRISAT	R
7	IS 14387	Zimbabwe	ICRISAT	R
8	IS 18144	Lebanon	ICRISAT	R
9	IS 18528	Lebanon	ICRISAT	R
10	IS 24495	S. Africa	ICRISAT	R
11	IS 25017	Sudan	ICRISAT	R
12	SP 33316	India	ICRISAT	M
13	SP 33349	India	ICRISAT	M
14	SP 33487	India	ICRISAT	M
15	GM 15018	India	ICRISAT	M
16	GM 15375	India	ICRISAT	M
17	TNS 30	India	AICSIP	M
18	B58586	India	AICSIP	R
19	GMRP 13	India	AICSIP	M
20	IS 21443	Malawi	AICSIP	M
21	SPV 462	India	AICSIP	S
22	SPV 475	India	AICSIP	S

[1] AICSIP = All India Coordinated Sorghum Improvement Project, NRCS = National Research Centre for Sorghum, ICRISAT = International Crops Research Institute for the Semi-Arid Tropics.
[2] S = Susceptible; R = Resistant; M = Moderately resistant.

A third experiment was carried out in 1995 to investigate further the correlation of glume and seed traits with FGS and TGS. The P_1, P_2, F_1, F_2, $BC_1$and BC_2 families of a cross between a straw-glume line (AKMS 14) and a purple-glume line (IS 14375) were grown at Patancheru and screened for grain mould resistance. The experiment was grown in randomized complete block design with three replications using the agronomic practices mentioned above. The

parental lines, F_1, BC_1 and BC_2 were grown in single-row plots of 4 m length, and the F_2 was grown in 4-row plots of 4 m length. In each replication observations were recorded on 10 plants each from the parental lines and F_1, 15 plants from BC_1 and BC_2, and 75 plants from the F_2. The F_2 data was used to calculate correlations between FGS, TGS and grain and glume traits.

Field screening technique for grain moulds. The screening technique of Bandyopadhyay & Mughogho (1988), using overhead sprinkler irrigation to increase grain mould pressure, was followed. The test plots were sprinkled for 1 h in the morning and for an additional hour in the evening, if it did not rain during the previous 10-12 h. Overhead sprinkler irrigation was provided for 54 d after anthesis, when panicles were harvested for evaluation. Observations were recorded on the following variables.

Field grade score (FGS). Five panicles from each replication of each test entry were scored visually for mould severity on the panicle surface at harvest, using a 1 to 5 scale, where 1 = no mould visible on the panicle; 2 = scant superficial mould growth up to 10% of the panicle surface covered by mould; 3 = moderate mould growth and 11–25% of the panicle surface moulded; 4 = considerable mould growth with 26–50% of the panicle surface moulded; and 5 = extensive mould growth with more than 50% of the surface moulded.

Threshed grade score (TGS). Five panicles from each replication of the 22 genotypes were harvested 14 d after maturity (54 d after 50% bloom) and threshed. A sample of 35 g of threshed grain from each panicle was spread in a 9-cm-diameter petri plate and scored visually for mould severity on the seed surface. Like FGS, TGS was recorded on a 1 to 5 scale, where 1 = no mould and 5 = more than 50% of the seed surface covered by mould.

Germination percentage (%GER). One hundred grains from each of the five panicles from each replicate that were scored for TGS, were incubated in petri dishes lined with wet filter paper for 4 d at 30 °C, and number of germinated seed was counted.

Ergosterol content (ERGO). Ergosterol content was determined according to the modified method of Jambunathan et al. (1991). From each entry, 3 panicles were chosen at random and dried. Grains from dried panicles were removed and mixed thoroughly. A 25 g sample of the mixed grain was ground in a Udy Cyclone mill. Ergosterol was extracted in hexane and methanol. Ergosterol was determined in a SHIMADZU LC-6A high performance liquid chromatograph with manual loading. The extract was loaded on a reverse-phase column [3 μm particle size, 6 mm $\times$ 8 cm] consisting of two 4 cm Zorpax Reliance Cartridges (DuPont). The mobile phase was methanol-water (96:4 v/v) at a flow rate of 1.2 ml min^{-1}. The column temperature was maintained at 50 °C, and the absorbance of eluted ergosterol was detected at 282 nm. The standard ergosterol (Sigma) had a retention time of 8.3 min. The standard ergosterol was loaded in 2.5, 5.0, 7.5, and 10.0 mg concentration for calibration of the instrument every time and directly gave ergosterol content of the sample in μg g^{-1}.

Estimation of total phenols. The Folin-Ciocalteau's method (Kaluza et al., 1980) was followed for estimation of total phenols in glumes (G-PHEN and G-PHEN$^+$) and seeds (S-PHEN and S-PHEN$^+$) of sorghum. Developing sorghum panicles were tagged at 50% flowering and harvested 30 d after flowering. At each time of sampling, three panicles from each replicate were collected and oven dried soon thereafter. Glumes and seeds from oven dried panicles were removed separately. About 2 g of each of glume and seed samples were ground in a Udy Cyclone mill to pass through a 0.4 mm screen. The glume and seed powders were defatted with n-hexane and air dried. Duplicate 250 mg samples of defatted glume and seed materials were extracted twice with 5 ml methanol and twice with 5 ml methanol-HCl. Readings for absorbance were recorded at 560 nm against a reagent blank using a spectrophotometer (Spectronic 21, Bausch and Lamb, USA). Using the standard curve, the quantity of phenol as mg tannic acid equivalent (g sample)$^{-1}$ was calculated.

Estimation of flavan-4-ols. The procedure of Butler (1982) was followed for estimation of flavan-4-ols in glumes (G-FLAV) and seeds (S-FLAV). An 0.5 ml aliquot of the methanol-HCl extract, prepared as described above, was taken and 7 ml of water-saturated butanol was added. Simultaneously a blank was prepared by mixing methanol, water-saturated butanol and 0.1N acetic acid in a 70:15:15 ratio v/v. The tubes along with the blank were rotated in the test tube rotator for 1 h. The absorbance was read at 550nm in a

spectrometer. Results were calculated as A_{550} g^{-1} dry sample.

Seed hardness (S-HRD). Seeds were equilibrated to a moisture content of 6.5 ± 1.0% by keeping the samples in an oven at 37 °C for 3–4 d, before hardness determinations were made. The seed hardness was tested by measuring resistance to grinding by the Stenvert hardness tester (Glencreston, Stanmore, England). The grinding resistance offered by 18 g of sorghum grains in a micro hammer-cutter mill was measured in seconds to obtain a fixed volume of flour (Pomeranz et al., 1985).

Number of days to flowering (DF), plant height (HT) and grain yield per plant (YD/PL). Data on flowering, plant height (cm) and grain yield per plant (g) were recorded on 10 random plants in two replications of each genotype.

Percentage glume cover (%G-COV). Percentage cover by the glume was recorded visually as 25% glume cover, 50% glume cover, 75% glume cover, 90% glume cover and 100% glume cover.

Glume colour (GLCL). Visual scores of 1 to 5 were given to glume colours, where 1 = straw glume, 2 = light red glume, 3 = red glume, 4 = dark purple glume; and 5 = black glume.

Seed colour (SDCL). Visual scores given to seed colour were 1 = white seed, 3 = red seed, and 5 = brown seed.

Glume index (GI). Glume index was calculated as length of glume/breadth of glume.

Means, coefficients of variation (CV), standard errors (SE) and correlations were calculated using the GENSTAT 5 statistical package (GENSTAT 5, 1993). Correlations were estimated between FGS, TGS, and different biochemical and morphological characters in Experiments 1 and 2 and between FGS, TGS and seed and glume traits in the F_2 generation of Experiment 3.

Results and discussion

The means of the 22 genotypes for the recorded variables are shown in Table 2 and the phenotypic correlations between the traits are shown in Table 3. To add further information on correlations between traits, the 22 genotypes were grouped on seed colour, glume colour, and seed hardness (Table 4) and the correlations of FGS and TGS with other characters were computed within different groups. The estimates of these intragroup correlations are shown in Tables 5 and 6. Similarly, correlations were calculated for several characters observed in the F_2 generation of a cross between straw-glumed AKMS 14B and purple-glumed IS 14375. These results are shown in Table 7.

Measures of grain mould response

Four variables (FGS, TGS, germination percentage, and ergosterol content) represent measures of grain mould response. FGS and TGS are direct visual ratings of the presence of grain mould on the complete panicles and threshed grain, repectively. Dennis and Girard (1977) found that grain germination was so closely related to grain moulds that resistant genotyes could be identified from germination tests. Ergosterol is a steroid that is very much specific to fungi. The quantity of ergosterol in a grain sample is an index of fungal mass (Seitz et al., 1977) and is another criterion for measuring grain mould damage. The correlations between these traits were uniformly high and statistically highly significant (Table 3).

Williams & Rao (1981) reported that FGS could be misleading because some cultivars developed mould on the rachis and glume but maintained clean seed, and vice versa. Castor & Frederiksen (1980) also found that field ratings on natural and *Fusarium* inoculated heads would have permitted some susceptible sorghum lines to escape detection as mould growth was hidden by the glumes and visible only after threshing. In this study, FGS and TGS were strongly correlated ($r = 0.93$, $p < 0.01$). TGS was slightly higher on average than FGS, but only SP 33487 showed marked discrepancy between the two.

Seed viability and germination were shown to decrease with increasing infection by mould-causing fungi (Mahalinga et al., 1988; Singh & Agarwal, 1989; Forbes et al., 1989). In the present study also, FGS showed strong negative correlation with germination percentage ($r = -0.84$, $p < 0.01$) confirming that germination percentage falls dramatically with increased grain mould infection.

Forbes et al. (1989) and Jambunathan et al. (1991) reported that the quantity of ergosterol was highly correlated to visual grain mould. They found that the concentration of ergosterol was 10-fold higher in susceptible than in resistant genotypes. In the present

Table 2. Means of 18 variables measured in 22 sorghum genotypes

Genotype	FGS	TGS	%GER	ERGO (μg/g)	G-PHEN	G-PHEN$^+$	S-PHEN	S-PHEN$^+$	G-FLAV (A_{550}/g)	S-FLAV (A_{550}/g)
AKMS 14B	4.9	4.9	28	71	113	70	42	67	0.0	0.0
296B	5.0	5.0	6	254	73	82	40	37	0.0	0.0
AKR 150	4.6	4.7	35	170	106	90	77	87	0.0	0.0
MS 422B	4.8	4.7	53	92	217	187	117	91	0.0	0.0
R 1413	4.6	4.8	18	134	167	117	73	83	0.0	0.0
IS 14375	1.4	1.9	90	14	123	187	160	167	0.1	0.1
IS 14387	1.6	1.9	95	6	147	240	333	230	0.0	0.0
IS 18144	2.0	2.2	90	11	200	233	580	175	0.1	0.1
IS 18528	2.4	2.5	84	18	170	203	288	200	0.3	0.3
IS 24495	3.0	3.1	81	12	117	130	74	80	0.0	0.0
IS 25017	2.8	3.0	89	45	143	100	77	77	0.0	0.0
SP 33316	3.2	3.3	68	41	217	217	53	90	0.2	0.0
SP 33349	3.1	3.6	78	16	310	223	127	127	0.2	0.2
SP 33487	2.7	4.5	46	39	310	217	177	180	0.0	0.0
GM 15018	3.1	3.5	63	56	200	167	52	60	0.0	0.0
GM 15375	3.6	4.2	35	30	177	152	87	97	0.0	0.0
TNS 30	3.7	4.2	57	45	193	117	90	93	0.0	0.0
B58586	2.7	3.0	84	25	47	33	77	77	0.0	0.0
GMRP 13	3.8	4.7	27	110	150	152	60	67	0.0	0.0
IS 21443	3.1	3.3	85	34	63	43	47	75	0.0	0.0
SPV 462	4.8	5.0	45	102	96	103	63	122	0.0	0.0
SPV 475	4.5	4.9	22	178	173	137	58	80	0.0	0.0
Mean	3.4	3.8	58	68	160	144	125	107	0.0	0.0
SE	0.14	0.16	6.2	19.0	20.3	23.5	17.8	19.4	0.17	0.05
CV(%)	6.8	7.4	18	48	22	28	25	31	62.8	50.3

FGS = Field grade score, TGS = Threshed grade score, %GER = Germination, ERGO = Ergosterol, G-PHEN = Glume phenol, G-PHEN$^+$ = Glume phenol in acid methanol, S-PHEN = Seed phenol, S-PHEN$^+$ = Seed phenol in acid methanol, G-FLAV = Glume flavan-4-ols, S-FLAV = Seed flavan-4-ols, S-HRD = Seed hardness, DF = Days to flower, HT = Plant height, YD/PL = Yield/plant, %G-COV = Glume cover, GLCL = Glume colour, SDCL = Seed colour, GI = Glume index.

study, FGS and TGS showed strong positive correlations with ergosterol content (r = 0.78, $p < 0.01$ and r = 0.74, $p < 0.01$ respectively).

Agronomic traits

Three important agromonic traits of sorghum cultivars (days to 50% flowering, plant height and grain yield plant^{-1}) were measured on the test genotypes. Days to 50% flowering (DF) was not correlated to any of the measures of grain mould, in agreement with the findings of Ibrahim et al. (1985), Mukuru (1988) and Menkir et al. (1996b). Plant height (PH) and grain yield plant^{-1} (YD/PL) were both significantly correlated to all four measures of grain mould response (Table 3). Greater plant height and lower grain yield were associated with greater grain mould resistance.

Grain mould associated traits

The phenotypic correlations between associated traits and measures of grain mould response are shown in Table 3. Seed hardness, glume colour and seed phenols in acid-methanol extract showed highly significant correlations with FGS, TGS, germination percentage and ergosterol content. Similarly, seed phenols in methanol extract and seed colour were significantly correlated with all four measures of grain mould response but at a lower level of significance for some. Glume phenols in acid-methanol extract, glume flavan-4-ols, seed flavan-4-ols, and glume cover showed significant correlation with one or more measure of grain mould reaction but not with all.

Considering the magnitude of the phenotypic correlations, their statistical significance, and consistency across the four measures of grain mould resistance,

Table 2. Continued

Genotype	S-HRD (sec)	DF (days)	HT (cm)	YD/PL (g)	%G-COV	GLCL	SDCL	GI
AKMS 14B	4.2	56	139	56	25	1	1	1.5
296B	3.1	66	129	71	25	1	1	1.1
AKR 150	3.6	60	142	72	50	1	1	2.2
MS 422B	4.6	61	156	79	50	4	1	2.6
R 1413	4.0	72	152	74	25	1	1	2.6
IS 14375	6.5	69	295	60	50	5	3	1.6
IS 14387	6.8	61	250	56	50	5	5	2.4
IS 18144	4.7	59	222	40	75	5	3	2.5
IS 18528	5.1	58	203	37	75	5	5	2.5
IS 24495	5.4	51	218	30	25	1	1	2.0
IS 25017	5.7	73	286	79	50	5	1	1.6
SP 33316	4.9	60	178	59	25	3	1	1.6
SP 33349	5.7	58	176	53	50	3	3	1.5
SP 33487	4.1	62	133	78	50	2	5	1.6
GM 15018	4.6	59	163	90	25	2	1	1.3
GM 15375	5.0	57	159	52	25	4	1	1.3
TNS 30	4.3	69	215	69	50	1	1	1.0
B58586	6.0	67	296	60	50	1	1	2.0
GMRP 13	3.8	70	219	92	40	1	1	1.6
IS 21443	5.2	63	266	50	90	1	1	1.3
SPV 462	4.2	70	237	107	25	1	1	1.6
SPV 475	3.1	70	195	85	50	1	1	1.3
Mean	4.7	63	201	66	44	2.3	1.6	1.8
SE	0.36	1.0	11.2	6.5	4.0	0.36	0.28	0.11
CV(%)	13.3	3	8	14	42	73.3	79.0	28.9

FGS = Field grade score, TGS = Threshed grade score, %GER = Germination, ERGO = Ergosterol, G-PHEN = Glume phenol, G-PHEN^{+} = Glume phenol in acid methanol, S-PHEN = Seed phenol, S-PHEN^{+} = Seed phenol in acid methanol, G-FLAV = Glume flavan-4-ols, S-FLAV = Seed flavan–4-ols, S-HRD = Seed hardness, DF = Days to flower, HT = Plant height, YD/PL = Yield/plant, %G-COV = Glume cover, GLCL = Glume colour, SDCL = Seed colour, GI = Glume index.

when calculated for the complete set of 22 genotypes, we conclude that seed hardness, glume colour and seed phenols in acid methanol extract are the strongest determinants of grain mould reaction. Harder seed, darker glumes and higher levels of seed phenols led to higher grain mould resistance.

Seed colour and content of seed phenols in methanol extract were also significantly correlated with each of the four measures of grain mould reaction, but with lower level of significance in the case of germination percentage and ergosterol content. Both appear to be reliable predictors of grain mould reaction, with darker seeds and higher phenol contents giving greater grain mould resistance.

Seed phenol content in both methanol and acid-methanol extracts, seed flavan-4-ol content and seed colour are highly positively correlated (Table 3). Seed phenol content in acid-methanol extract appears to be the most predictive of grain mould reaction among these related traits.

Glume flavan-4-ol content and glume cover were significantly correlated with FGS, TGS and germination percentage but not with ergosterol content. Other characters were only weakly correlated (glume phenol content and seed flavan-4-ol content) or not at all correlated (glume index) with grain mould response measures and appear to contribute relatively little to grain mould reaction. Glume phenol content, glume flavan-4-ol content and glume colour are also highly correlated with one another.

Earlier studies showed that sorghum kernels with more corneous endosperm and hard seed are more resistant to grain moulds than those with floury endosperm (Ibrahim et al., 1985; Jambunathan et al.,

Table 3. Phenotypic correlations between different variables in 22 sorghum genotypes

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	FGS	1.00																	
2	TGS	0.93**	1.00																
3	%GER	–0.84**	–0.91**	1.00															
4	ERGO	0.78**	0.74**	–0.83**	1.00														
5	G-PHEN	–0.17	0.04	–0.04	–0.27	1.00													
6	G-PHEN^{+}	–0.51**	–0.40	0.31	–0.40	0.76**	1.00												
7	S-PHEN	–0.60**	–0.61**	0.49*	–0.42*	0.26	0.64**	1.00											
8	S-PHEN^{+}	–0.68**	–0.60**	0.52**	–0.54**	0.35	0.72**	0.77**	1.00										
9	G-FLAV	–0.45*	–0.49*	0.42*	–0.37	0.30	0.51**	0.37	0.52**	1.00									
10	S-FLAV	–0.40	–0.43*	0.39	–0.34	0.27	0.45*	0.41	0.55**	0.92**	1.00								
11	S-HRD	–0.79**	–0.83**	0.86**	–0.81**	–0.04	0.26	0.30	0.48*	0.31	0.30	1.00							
12	DF	0.14	0.25	–0.23	0.37	–0.22	–0.30	–0.24	–0.17	–0.26	–0.26	–0.17	1.00						
13	HT	–0.60**	–0.60**	0.70**	–0.48*	–0.42*	–0.14	0.18	0.23	0.09	0.08	0.67**	0.38	1.00					
14	YD/PL	0.50*	0.63**	–0.51**	0.53**	0.01	–0.18	–0.46*	–0.34	–0.50*	–0.47	–0.47*	0.62*	–0.12**	1.00				
15	G-COV	–0.50*	–0.50*	0.56**	–0.36	0.04	0.15	0.52**	0.45*	0.36*	0.43	0.28*	0.03	0.45	–0.39	1.00			
16	GLCL	–0.75**	–0.73**	0.61**	–0.56**	0.24	0.61**	0.66**	0.69**	0.57**	0.52**	0.62**	–0.12	0.35	–0.44*	0.33*	1.00		
17	SDCL	–0.66**	–0.53**	0.42*	–0.44*	0.43*	0.70**	0.68**	0.92**	0.55**	0.63**	0.39	–0.23	0.07	–0.36	0.45*	0.62**	1.00	
18	GI	–0.19	–0.29	0.26	–0.17	0.04	0.33	0.55**	0.46*	0.25	0.28	0.23	–0.19	0.02	–0.25	0.20	0.25	0.36	1.00

* $p < 0.05$, ** $p < 0.01$.

FGS = Field grade score, TGS = Threshed grade score, %GER = Germination, ERGO = Ergosterol, G-PHEN = Glume phenol, G-PHEN^{+} = Glume phenol in acid methanol, S-PHEN = Seed phenol, S-PHEN^{+} = Seed phenol in acid methanol, G-FLAV = Glume flavan-4-ols, S-FLAV = Seed flavan-4-ols, S-HRD = Seed hardness, DF = Days to flower, HT = Plant height, YD/PL = Yield/plant, %G-COV = Glume cover, GLCL = Glume colour, SDCL = Seed colour, GI = Glume index.

1992; Mukuru, 1992; Kumari & Chandrashekar, 1992). Brown coloured seed with testa and high phenolic acid content was the most influential combination of seed characteristics affecting grain mould reaction in several studies (Ellis, 1972; Hahn et al., 1983; Hahn & Rooney, 1985; Jambunathan et al., 1986; Jiminez & Vallejo, 1986; Esele et al., 1993). Harris & Burns (1973), Doherty et al. (1987) and Menkir et al. (1996a) also reported a strong association between phenols and mould resistance. However, Menkir et al. (1996a) found that resistance was not always associated with corneous endosperm in white sorghums and that resistance to grain mould was not always associated with a high concentration of tannin in brown sorghums. They further reported that higher levels of resistance to moulding seemed to arise from

Table 4. Grouping of sorghum genotypes based on morphological characters

Genotype	Seed colour[1]	Glume colour[2]	Seed hardness[3]
AKMS 14B	–	–	–
296B	–	–	–
AKR 150	–	–	–
MS 422B	–	+	–
R 1413	–	–	–
IS 14375	+	+	+
IS 14387	+	+	+
IS 18144	+	+	–
IS 18528	+	+	+
IS 24495	–	–	+
IS 25017	–	+	+
SP 33316	–	+	–
SP 33349	+	+	+
SP 33487	+	+	–
GM 15018	–	+	–
GM 15375	–	+	+
TNS 30	–	–	–
B58586	–	–	+
GMRP 13	–	–	–
IS 21443	–	–	+
SPV 462	–	–	–
SPV 475	–	–	–

[1] Seed colour: + = coloured seed, – = white seed.
[2] Glume colour: + = coloured glume, – = straw glume.
[3] Seed hardness: + = hard seed, - = soft seed.

the combined effects of tannin and flavan-4-ols. High content of flavan-4-ol content in seeds had been found to correlate strongly with grain mould resistance (Butler, 1982; Jambunathan et al., 1991; Martinez et al., 1994). There is little in the literature on the effects of glume colour although Mansuetus et al. (1988) found that glumes with darker colour had increased levels of phenolic acid and that high levels were associated with resistance. Similarly, for glume cover, Mansuetus (1990) found grain mould score had significant negative correlations with glume cover, glume length and glume area when the cultivars were inoculated, but correlations were not significant when the cultivars were not inoculated. The present study confirms the important role of grain hardness and seed phenol content in determining grain mould response and suggests, for the first time, an important role for glume colour. It suggests relatively minor effects of glume phenol content, seed and glume flavan-4-ol contents, and glume cover on grain mould response compared to the effects of grain hardness, seed phenol content and glume colour.

The glume appears to be the plant's first defence mechanism against grain moulds (Waniska et al., 1992). Seeds completely covered in long papery glumes were found to show resistance to grain moulds (Williams & Rao, 1980). However, the same authors concluded that there was no apparent correlation between resistance and grain glume cover. Phenolic compounds in the glume increase 20 d after anthesis, especially in resistant and moderately resistant cultivars (Mansuetus et al., 1988; Waniska et al., 1992). There are no reports in the literature on glume flavan-4-ol contents. The results of the present study contradict those of Williams and Rao (1980) in finding a correlation between glume cover and grain mould reaction (significant for three out of four measures of grain mould response). Glume phenol content appears not to influence grain mould reaction, contradicting the findings of Mansuetus et al. (1988), while glume flavan-4-ol content appears to have a weak effect. Glume colour, which is highly significantly correlated to both glume phenol content (in both methanol and acid-methanol extract) and glume flavan-4-ol content, is more important in determining grain mould reaction.

Grain mould reactions of test genotypes

The grain mould reactions of the individual genotypes can be readily assessed from their means for FGS, TGS, germination percentage and ergosterol content (Table 2). Seven genotypes, IS 14375, IS 14387, IS 18144, IS 18528, IS 24495, IS 25017 and B58586, showed low FGS (1.4 to 3.0), low TGS (1.9 to 3.1), high germination percentage (over 80%), and low ergosterol content (6 to 45 mg (g seed)$^{-1}$) and were highly resistant to grain moulds. These results confirm earlier findings that these lines were resistant to grain moulds (Bandyopadhyay et al., 1988; Anonymous, 1995; ICRISAT, 1994).

A further seven genotypes, AKMS 14B, 296B, AKR 150, MS 422B, R 1413, SPV 462, and SPV 475, showed high FGS (over 4.5), high TGS (over 4.5), low germination percentage (less than 53%), and high ergosterol content (greater than 90 mg (g seed)$^{-1}$) and were consistently susceptible to grain moulds. Earlier reports (Anonymous, 1995) identified genotypes 296B, SPV 462, and SPV 475 as moderately resistant. The grain mould reactions of the other cultivars are reported for the first time. One reason for the conflicting

Table 5. Correlation matrix in different sorghum lines for Field Grade Score

Character	22 Lines	Lines with					
		coloured seed	white seed	straw glume	coloured glume	hard seed	soft seed
FGS	1.00	1.00	1.00	1.00	1.00	1.00	1.00
TGS	0.93**	0.85*	0.94**	0.94**	0.86**	0.94**	0.85**
%GER	–0.84**	–0.63	–0.84**	–0.83**	–0.77**	–0.74*	–0.75**
ERGO	0.78**	0.55	0.75**	0.73**	0.67*	0.51	0.72**
G-PHEN	–0.17	0.94**	0.00	0.32	0.45	0.08	–0.71**
G-PHEN$^+$	–0.51**	0.17	0.22	0.32	–0.45	–0.53	–0.83**
S-PHEN	–0.60**	–0.31	–0.04	0.10	–0.61*	–0.69*	–0.67*
S-PHEN$^+$	–0.68**	–0.57	0.04	0.00	–0.76**	–0.78*	–0.64*
G-FLAV	–0.45*	0.21	–0.22	0.00	–0.17	–0.20	–0.52
S-FLAV	–0.40	0.32	0.00	0.00	–0.21	–0.13	–0.60*
S-HRD	–0.79**	–0.61	–0.81**	–0.78**	–0.58	–0.76*	–0.52
DF	0.14	–0.65	0.09	0.13	–0.35	–0.29	–0.31
HT	–0.60**	–0.89*	–0.67**	–0.82**	–0.69*	–0.34	–0.26
YD/PL	0.50*	0.07	0.37	0.54	0.25	–0.14	0.38
G-COV	–0.50*	0.01	–0.30	–0.49	–0.60*	0.08	–0.50
GL-CL	–0.75**	–0.76	–0.46	0.00	–0.60*	–0.68*	–0.77*
SD-CL	–0.66**	0.03	0.00	0.00	–0.61*	–0.64	–0.63*
GI	–0.19	–0.35	0.17	0.08	–0.64*	–0.40	–0.03

* $p < 0.05$, ** $p < 0.01$

FGS = Field grade score, TGS = Threshed grade score, %GER = Germination, ERGO = Ergosterol, G-PHEN = Glume phenol, G-PHEN$^+$ = Glume phenol in acid methanol, S-PHEN = Seed phenol, S-PHEN$^+$ = Seed phenol in acid methanol, G-FLAV = Glume flavan–4-ols, S-FLAV = Seed flavan-4-ols, S-HRD = Seed hardness, DF = days to flower, HT = Plant height, YD/PL = Yield/plant, %G-COV = Glume cover, GLCL = Glume colour, SDCL = Seed colour, GI = Glume index.

results for 296B, SPV 462 and SPV 475 could be differences in the grain mould pressure between studies, as pressure is known to vary with season and location, particularly under natural infestation.

Of the remaining genotypes, SP 33487 gave contradictory responses, showing susceptible reactions according to TGS and percentage germination but resistant reactions according to FGS and ergosterol content. The other seven genotypes, however, gave relatively consistent intermediate reactions with different levels of resistance and susceptibility. SP 33316, SP 33349, GM 15018 and IS 21443 tended towards the resistant lines while GMRP 13, GM 15375 and TNS 30 tended towards the susceptible. These are the first published reports of the grain mould reactions of these lines. Several are new improved lines and indicate that progress is being made in breeding for grain mould resistance, particularly in the cases of SP 33316, SP 33349 and GM 15018.

Interestingly, white-grained lines IS 25017, IS 24495, IS 21443 and B58586 showed high mean seed germination levels (greater than 80%) although some of them showed moderate mean values for FGS and TGS (sufficient in the case of IS 21443 for us to drop it from the list of most resistant lines). This indicated that the discolouration on the seed was superficial and very little damage had occurred internally. Castor & Frederiksen (1980) reported similar results. It is likely that white-seeded sorghum is penalised in visual ratings of grain mould damage because mould is more visible on white grain than on coloured.

Mechanisms of resistance

The genotype means allow us to identify the traits for which individual genotypes are strong and which are contributing to their grain mould reactions. For example, among resistant genotypes, B58586, IS 25017 and IS 24495 have hard grain and this appears to be the main trait contributing to their high levels of resistance. B58586 has substantial glume cover, and IS 25107 also has substantial glume cover and coloured glumes. The relative ranking of the grain mould reactions of these genotypes support the idea that greater

Table 6. Correlation matrix in different sorghum lines for Threshed Grade Score

Character	22 Lines	Lines with					
		coloured seed	white seed	straw glume	coloured glume	hard seed	soft seed
TGS	1.00	1.00	1.00	1.00	1.00	1.00	1.00
%GER	–0.91**	–0.94**	–0.91**	–0.92**	–0.85**	–0.71*	–0.87**
ERGO	0.74**	0.87*	0.76**	0.75**	0.67*	0.57	0.65*
G-PHEN	0.04	0.94**	0.12	0.44	0.63*	0.26	–0.43
G-PHEN$^+$	–0.40	0.04	0.11	0.43	–0.34	–0.43	–0.70**
S-PHEN	–0.61**	–0.48	0.01	–0.08	–0.61*	–0.70	–0.74**
S-PHEN$^+$	–0.60**	–0.45	0.05	0.01	–0.56	–0.77*	–0.46
G-FLAV	–0.49*	–0.15	0.28	0.00	–0.35	–0.15	–0.72**
S-FLAV	–0.43*	–0.07	0.00	0.00	–0.31	–0.09	–0.76**
S-HRD	–0.83**	–0.66	–0.85**	–0.87**	–0.64*	–0.61	–0.62*
DF	0.25	–0.25	0.28	0.36	–0.16	–0.09	0.46
HT	–0.64**	–0.92**	–0.60*	–0.73**	–0.73*	–0.30	–0.32
YD/PL	0.63**	0.56*	0.51*	0.71*	0.44	0.11	0.54
G-COV	–0.51*	–0.30	–0.33	–0.51	–0.52	–0.06	–0.44
GL-CL	–0.73**	–0.97**	–0.35	0.00	–0.73*	–0.49	–0.84**
SD-CL	–0.53**	0.20	0.00	0.00	–0.34	–0.63	–0.31
GI	–0.29	–0.59	0.08	–0.00	–0.70*	–0.48	–0.19

* $p < 0.05$, ** $p < 0.01$

TGS = Threshed grade score, %GER = Germination, ERGO = Ergosterol, G-PHEN = Glume phenol, G-PHEN$^+$ = Glume phenol in acid methanol, S-PHEN = Seed phenol, S-PHEN$^+$ = Seed phenol in acid methanol, G-FLAV = Glume flavan-4-ols, S-FLAV = Seed flavan–4-ols, S-HRD = Seed hardness, DF = Days to flower, HT = Plant height, YD/PL = Yield/plant, %G-COV = Glume cover, GLCL = Glume colour, SDCL = Seed colour, GI = Glume index.

grain hardness combined with greater glume cover and/or glume colour lead to better grain mould resistance.

IS 14375, IS 14387 and IS 18528 have hard seed, coloured glumes and high levels of seed phenols in acid-methanol extract, all of which contribute to their high levels of grain mould resistance. IS 18144 has only moderately hard seed, but has dark glumes, high seed and glume phenol contents which give its high grain mould resistance. IS 25017 has hard seed and dark glumes contributing to its resistance. Similarly, among the moderately resistant genotypes, SP 33316 has moderately hard seed and coloured glumes with high glume phenols and flavan-4-ols, SP 33349 has hard seed, pigmented glumes and high seed and glume phenols, GM 15018 has moderately hard seed, pigmented glumes with high glume phenols, and IS 21443 has moderately hard seed only.

On the other hand, MS 422B has dark glumes but remains highly susceptible to grain mould. Similarly, SP 33487 has high glume and seed phenol contents and remains susceptible. The combined observations from resistant and susceptible genotypes show that combinations of favourable traits are required to obtain the highest possible levels of grain mould resistance.

The intragroup correlations shown in Tables 5 and 6 generally confirm these conclusions. In the white seeded and straw glumed groups, in which seed phenol and glume pigmentation mechanisms, respectively, are by definition limited in the role that they can play, only seed hardness is correlated significantly to FGS and TGS. In the coloured glume group, glume colour is significantly correlated to both FGS and TGS, while seed hardness is only correlated to TGS (Table 6). Similarly, in the soft seeded group, FGS is not significantly correlated with grain hardness but is significantly correlated with glume and seed phenol contents, seed flavan-4-ol content, and glume and seed colours. This shows that in the absence of one of the stronger factors affecting grain mould reaction, other factors become important and is entirely consistent with the idea that the effects of different traits on grain mould resistance are independent and additive.

The correlations in Table 7 show that glume colour, the trait that is here directly implicated in grain mould

Table 7. Correlation matrix in F_2 of a cross AKMS 14B× IS 14375 in sorghum

1	FGS	1.00					
2	TGS	0.86**	1.00				
3	G-COV	–0.07	–0.14*	1.00			
4	SD-CL	–0.18**	–0.29**	0.09	1.00		
5	DF	–0.03	–0.01	0.01	0.04	1.00	
6	GL-CL	–0.40**	–0.49**	–0.02	0.16*	0.10	1.00
		1	2	3	4	5	6

* $p < 0.05$, ** $p < 0.01$

1. FGS = Field Grade Score, 2. TGS = Threshed Grade Score, 3. %G-COV = Percentage glume cover, 4. SDCL = Seed colour, 5. DF = Days to flower, 6. GLCL = Glume colour.

reaction for the first time, is also significantly correlated with FGS and TGS in the F_2 generation of the cross between straw-glumed AKMS 14B and purple-glumed IS 14375. This suggests that the significant correlations between glume colour and measures of grain mould reaction (Table 3) are not simply a consequence of the trait associations among the 22 genotypes. Glume colour either plays a direct role in determining grain mould reaction or the genes that control it are linked to genes that control grain mould reaction.

Implications for breeding for grain mould resistance

The four measures of grain mould response used in this study (FGS, TGS, percentage germination and ergosterol content) were very strongly correlated with one another. The precision with which FGS and TGS were measured was much higher than that for germination percentage and ergosterol content (Table 2). FGS and TGS also have advantages of speed and economy over measures of germination percentage and ergosterol content. FGS and TGS are therefore reliable and effective measures of grain mould reaction for evaluating sorghum lines in replicated experiments.

The difficulties reported by Williams and Rao (1981) who found that FGS could be misleading because some cultivars developed mould on the rachis and glume but maintained clean seed, and vice versa, were not generally found here (although FGS and TGS were contradictory for SP 33487). This could be a consequence of the panicle and glume types of the genotypes used in this study, which were less diverse than would be found in a wider selection of landraces. The effectiveness of FGS and TGS in evaluating segregating progenies or single plants was not tested in this study. *A priori*, we expect them to be less effective, particularly for evaluating single plants, where misclassification as described by Williams & Rao (1980) and Castor and Frederiksen (1988) could become important. However, measuring germination percentages and ergosterol contents on large numbers of breeding progenies would be expensive and time consuming. Therefore, selecting individual plants in the field on the basis of FGS and subsequent elimination of susceptible ones on the basis of TGS seems the most practical option for early generation segregating material.

The results presented above show clearly that very hard grain on its own can confer good levels of grain mould resistance in sorghum. However, hardness affects the end uses that can be made of grain and hence it is important to strike a balance between grain hardness and the requirements for local food preparations. In India, large soft grain as found in the postrainy season cultivar 'Maldandi' is preferred for making *chapati* with good texture and flavour. Similarly, in Sudan and Ethiopia, soft grain is preferred to produce *kisra* and *injera* of the correct texture and keeping quality. There is therefore little scope to increase grain mould resistance in cultivars for these regions by breeding for harder grains without seriously affecting consumer acceptability. In West Africa, on the other hand, many preferred landrace cultivars, particularly those of the guinea sorghum group, have very small and highly corneous grains that are highly acceptable for making *tô*, the stiff porridge for which most sorghum is used. Manipulating grain hardness therefore seems to be an option for ensuring high levels of grain mould resistance in improved cultivars for this region. IS 14375, IS 14387 and B58586 are guinea sorghum types that could be used as sources of grain hardness.

In areas where white grain is preferred, as in India, breeding for high seed phenol content is not an option as this is only found in coloured grain. However, breeding cultivars with pigmented glumes does offer scope for improving grain mould resistance. Glumes with intense red and purple colour have a tendency to stain the kernels in humid conditions (Rooney & Miller, 1982) and this in turn can lead to discolouration of food products and reduced acceptability to consumers. Most improved cultivars in India have been deliberately selected for straw glume colour to avoid this problem, which is particularly acute in white grained sorghum. However, the possibility of using light glume pigmentation, which causes no or minimal staining of the seed, in combination with moderate

grain hardness to produce improved levels of grain mould resistance in white grained cultivars has not been tested.

It is interesting to note that of three breeding lines in this study which combine white grain, coloured glumes and moderately hard grain (MS 422B, SP 33316, and GM 15018), two are moderately resistant to grain moulds (SP 33316 and GM 15018). These two lines were selected for grain mould resistance under artificial screening conditions and were not deliberately selected for glume pigmentation. They represent sources of resistance that will be useful in breeding for India. However, the fact that MS 422B combines essentially the same traits with comparable expression but remains susceptible shows that the effects of glume pigmentation on grain mould reaction are not fully clear and require further study.

For sorghum growing areas where coloured grain with high tannin content is preferred (e.g., much of eastern Africa where such sorghum is used for beer production), or tolerated (e.g., Sudan where chalky white feterita type sorghum with a high tannin content is favoured because of its bird resistance), achieving adequate levels of grain mould resistance is unlikely to present problems. Combining high grain phenol content and pigmented glumes will result in good levels of resistance, even in relatively soft grain cultivars.

The strong correlations between grain mould response and grain yield plant^{-1} and plant height were in unfavourable directions. These were undoubtedly a reflection of the trait combinations in the study materials. The resistant lines were predominantly tall, low-yielding germplasm lines (IS designations), whereas the short-statured, high yielding improved lines were generally highly susceptible. However, the existence of a number of improved lines which combine short stature, high yield and good levels of grain mould resistance show that these trait associations can be broken. These lines, e.g., SP 33316, SP 33349, and GM 15018, show that progress has been made in breeding for grain mould resistance and represent suitable source materials for future breeding efforts.

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