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Genetic analysis of grain mold resistance in white seed sorghum genotypes

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Summary

Grain molds in rainy season sorghums can cause poor grain quality resulting in economic losses. Grain molds are a major constraint to the sorghum production and for adoption of the improved cultivars. A complex of fungi causes grain mold. Information on genetics of grain mold resistance and mechanisms is required to facilitate the breeding of durable resistant cultivars. A genetic study was conducted using one white susceptible, three white resistant/tolerant sources, and one colored resistant source in the crossing programme to obtain four crosses. P_1, P_2, F_1, BC_1, and BC_2, and F_2 families of each cross were evaluated for the field grade and threshed grade scores, under sprinkler irrigation. Generation mean analyses and frequency distribution studies were carried out. The frequency distribution studies showed that grain mold resistance in the white-grained resistance sources was polygenic. The additive gene action and additive × additive gene interaction were significant in all the crosses. Simple recurrent selection or backcrossing should accumulate the genes for resistance. Epistasis gene interactions were observed in colored resistance × white resistance cross. Gene interaction was influenced by pronounced G × E. Pooled analysis showed that environment × additive gene interaction and environment × dominant gene interaction were significant. The complex genetics of mold resistance is due to the presence of different mechanisms of inheritance from various sources. Evaluation of segregating population for resistance and selection for stable derivatives in advanced generations in different environments will be effective.

Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) is grown in about 52 million ha in tropical, subtropical, and temperate environments. This crop is primarily grown in agroecological zones characterized with low rainfall and drought, predominantly by the subsistence farmers. In India, sorghum hybrids were developed from temperate × tropical crosses by manipulating the height and maturity genes, and the critical stages of growth (seedling, flowering, and grain filling) coinciding with the periods of assured rainfall. This resulted in quantum jump in productivity from 560 kg/ha in 1970 to 1020 kg/ha in 1996. Though grain yield/ha has increased, the area under cultivation has been decreasing. The decrease in the area of cultivation is due to low demand for sorghum, limited commercialization, limited yield increases, and grain mold susceptibility (Rana et al., 1997).

Most improved varieties and hybrids mature earlier than the local varieties, often before the end of rainy season. This results in increased exposure to grain molds, greatly limiting the adoption of these improved varieties and hybrids (ICRISAT and FAO, 1996). The grain molds are caused by complexes of fungi, predominantly by *Fusarium moniliforme, Curvularia lunata, F. semitectum*, and *Phoma sorghina* (Forbes et al., 1992). The molded grain is unfit for consumption and

marketing. Though the restorers of the current hybrids have good yield and some tolerance to pests and diseases, the male-sterile lines are poor yielders and highly susceptible to grain molds. Breeding grain mold resistant male-steriles and restorers is a prerequisite for planning an effective hybrid breeding programme aimed at durable resistance. Exploitation of any genotype in a resistance breeding programme or for commercial release should ideally be preceded by knowledge about the number, nature, and diversity of genes controlling the resistance in the genotype. The present study was undertaken to understand the genetics of grain mold resistance in the white seed sorghum genotypes.

Materials and methods

Sorghum genotypes, viz., elite nonrestorer lines MS 422B (S_1) and AKMS 14B (S_5), two colored resistant sources, IS 14375 (R_1) and IS 14387 (R_2), and a white resistant source IS 25017 (R_3) were grown under sprinkler irrigation and evaluated for grain mold resistance during 1995 and 1996. A genetic study was conducted using one white susceptible genotype MS 422 B (S_1), three white resistant/tolerant sources, IS 25017 (R_3), IS 30469-6 (R_6), and IS 24495 (R_{16}), and one colored resistant source, IS 14387 (R_2) in the crossing programme to obtain four crosses viz. $S_1 \times R_3$, $S_1 \times R_6$, $S_1 \times R_{16}$, and $R_2 \times R_3$ (Table 1). These genotypes were selected from the world germplasm collection for crossing on the basis of evaluations in 1994 (Audilakshmi, 1997; Audilakshmi et al., 1999). Out of the four crosses, two crosses $S_1 \times R_3$ and $R_2 \times R_3$ were studied during 1995 and 1996, and the crosses $S_1 \times R_6$ and $S_1 \times R_{16}$ were studied during 1996 (Table 1). The F_1 hybrids and the parental lines were raised during the 1994 and 1995 postrainy seasons and additional crosses were made to generate six families (P_1, P_2, F_1, BC_1, BC_2, and F_2) in each cross. The crosses and families were grown separately during the 1995 and 1996 rainy seasons at ICRISAT, Patancheru, Andhra Pradesh, India. The six families of each cross were grown in a randomized complete block design with three replications. The plot size varied for different families. The parental lines, F_1, BC_1, and BC_2, were grown in single-row plots and F_2s were grown in four-row plots of 4 m grown on ridges with 0.75 m between ridges. The experimental materials were screened for grain mold resistance under sprinkler irrigation. In each replication, observations were recorded on 10 random plants from P_1, P_2, and F_1, on 15 plants from BC_1 and BC_2, and on 70–75 plants from F_2 in 1995 and 65 plants from F_2 in 1996.

Field screening technique for grain molds

The screening technique followed was that of Bandyopadhyay and Mughogho (1988). Sprinklers were arranged in a sequence grid pattern, the shortest distance between any two sprinklers being 12 m. The test plots were sprinkled for 1 h in the morning if it did not rain the previous night and same morning and for an additional 1 h in the evening if it did not rain throughout the day. Overhead sprinkler irrigation was provided on this basis from flowering to grain maturity (black layer formation) and up to 2 weeks later when the panicles were harvested.

Grain mold damage was evaluated after the harvest as field grade score (FGS) and threshed grade (TGS) scores. Panicles/threshed seeds from the plants of different families indicated above were scored visually for mold severity at 54 days after 50% flowering. FGS and TGS were recorded on a scale of 1–9, where 1 = free from mold, 2 = 5% of the panicle molded, 3 = 10% of the panicle molded, 4 = 15% of the panicle molded, 5 = 30% of the panicle molded, 6 = 40% of the panicle molded, 7 = 50% of the panicle molded, 8 = 60% of the panicle molded, and 9 $\geq$ 70% molded.

Generation mean analyses were determined using the original and square root transformed data. Genetic effects of the generation means were estimated by a weighted least square regression (WLSR) analysis

Table 1. Parents and crosses used in the study

	IS 25017 (white-grained) R_3	IS 14387 (colored-grained) R_2	IS 30469-6 (white-grained) R_6	IS 24495 (white-grained) R_{16}
MS 422 B S_1 (white-grained)	[1]		[2]	[2]
IS 25017 R_3 (white-grained)		[1]		

[1]Crosses studied during 1995 and 1996.
[2]Crosses studied during 1996.

(Cavalli, 1952; Hayman, 1958) using the notation and definition of Mather and Jinks (1977, pp. 36–67), where m = mean, d = additive effects, h = dominance effects, i = additive × additive interactions, j = additive × dominance interactions, l = dominance × dominance interactions.

Since the generation means of the parents and progenies were estimated with equal precision, each generation was weighted by the variance of the mean for that generation. The equation fitted for Least Square Regression was

$$\underset{-}{Y} = \underset{\wedge}{X}\,\underset{-}{B} + E$$

Y = Vector of generation means = [P_1, P_2, F_1, F_2, BC_1, BC_2]′; X = Coefficient matrix; B = Vector of parameter = [$m\ d\ h\ i\ j\ l$]′; E = Enov vector.

The coefficient matrix is

Generations	Parameters					
	[m]	[d]	[h]	[i]	[j]	[l]
P_1	1	1.0		1.00		
P_2	1	−1.0		1.00		
F_1	1		1.0			1.00
F_2	1		0.5			0.25
BC_1	1	−0.5	0.5	0.25	−0.25	0.25
BC_2	1	−0.5	0.5	0.25	−0.25	0.25

Estimates of the genetic parameters were derived from the equation

$$\underset{\wedge}{B} = (X^{\mathrm{T}}W^{-1}X)^{-1}(X^{\mathrm{T}}W^{-1})Y$$

Where X^T = Transpose of X; B = Vector of estimates of parameter; W = Diagonal matrix for weights, diag[$S^2_{P_1}$, $S^2_{P_2}$, $S^2_{F_1}$, $S^2_{BC_1}$, $S^2_{BC_2}$, $S^2_{F_2}$]; W^{-1} = Inverse of weight matrix, W.

Suitability of the six parameter model which included i, j, l, digenic interaction terms, in addition to m, d, h was judged by its R^2 value and by the model-associated F-statistic, which indicates whether a statistically significant relationship exists between the genetic effects and the genetic means. Significance of the estimates of genetic parameters was tested by t-test. Stepwise regression was followed in an attempt to obtain the best possible regression for the given set of response and the explanatory variables. Similarly, the estimates of genotype × environment interactions were calculated by the weighted least square regression analysis, as described above, on the 2 years' pooled data of the three crosses. The family means and frequency distributions for FGS and TGS were calculated using GENSTAT 5 (GENSTAT 5, 1993). Segregation ratios for the crosses and families were obtained from the frequency distributions by classifying the scores of 1–4 as resistant and above 4 as susceptible.

Results and discussion

The genotypes and crosses studied were evaluated for both the field grade (FGS) and threshed grade (TGS) scores. However, the results obtained were not different for these two measures of grain mold reaction. Hence, only the results for TGS are presented and discussed. Sorghum genotypes were evaluated for TGS during the 2 years. Mean values for TGS of some of the sorghum genotypes raised during the 1995 and 1996 rainy seasons are given in Table 2. The mean values for TGS of the susceptible lines S_1 (MS 422B), and S_5 (AKMS 14B) were consistently high over the years. They ranged from 8.50 to 8.93 during 1995 and 8.40–8.57 during 1996 on a scale of 1–9 where 1 = no molds on seed surface and 9 = 75% molded (Table 2). Similarly, two colored resistant lines, R_1 (IS 14375) and R_2 (IS 14387) showed consistently low mean values for TGS over the 2 years. Their TGS varied from 2.27 to 2.67 during 1995, and 2.8–2.97 during 1996 (on a scale of 1–9).

The white resistant source, R_3 (IS 25017), which recorded low mean TGS during 1994 (Audilakshmi

Table 2. Mean performance of Sorghum genotypes for threshed grade score in 1995 and 1996

Genotype	MS 422B (white-grained) S_1		AKMS 14B (white-grained) S_5		IS 14375 (colored-grained) R_1		IS 14387 (colored-grained) R_2		IS 25017 (white-grained) R_3	
Year	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
1995	8.5	0.1	8.9	0.1	2.3	0.1	2.7	0.2	8.1	0.1
1996	8.4	0.1	8.6	0.2	3.0	0.1	2.8	0.2	5.7	0.2

et al., 1999) gave a susceptible reaction 8.05 during 1995. However, during 1996, R_3 showed low resistance of 5.6 score for grain molds. Rodriguez-Herrera et al. (2000) studied the grain mold incidence of the white resistant variety, Sureno and susceptible line, RTx430 in eight different environments. They found that, whereas susceptible RTx430 recorded consistently high grain mold incidence of 4.29–4.91, white resistant source recorded grain mold incidence of 1.68–3.92 in different environments. Bandyopadhyay and Mughogho (1988) reported that when the ambient humidity is low, sprinkler irrigation might be ineffective in maintaining sufficient humidity for the grain mold development. In their experiments using inoculation and bagging, they observed that response of a white seeded genotype (IS 14332) to mold changed over years. In the present study, the genotypes that showed inconsistent reactions to the grain molds were also white seeded, suggesting that the white-seeded resistant lines are particularly prone to the changes in reaction to the molds in different environments.

High rainfall was recorded during week nos. 10–13 of 1995 and during week nos. 3–6 of 1996. Figure 1 shows the postmaturity phases (30–50 days after anthesis) of sorghum genotypes superimposed on the rainfall patterns of 1995 and 1996, respectively. The postmaturity period of the white resistant source IS 25017 (R_3), coincided with the heavy rainfall weeks during 1995 and low rainfall weeks during 1996. The mean TGS of R_3 was high during 1995 and moderate during 1996. Heavy rains at grain maturity, especially during the critical period from 30 to 50 days after anthesis, induce maximum grain damage. It appears that the white resistant sources, in particular, are rather unstable and the TGS reaction of such genotypes depends on the level of ambient humidity during the postmaturity period.

The white susceptible × white resistant ($S_1 \times R_3$) and colored resistant × white resistant ($R_2 \times R_3$) crosses gave differential responses to mold during 1995 and 1996 (Table 3). Both the crosses involved IS 25017 (R_3) which showed contradictory grain mold reactions in different seasons. In $S_1 \times R_3$, the mean values of P_1 and P_2 were significantly different in both the years. The mean TGS of the F_1 and F_2 was equal to the midparent value during 1995, but tended toward the resistant parent (R_3) during 1996. In $R_2 \times R_3$, the mean value of F_1 tended toward the brown resistant parent (R_2) during 1995 and toward the midparent value during 1996. However in 1995, F_2 mean tended toward the midparent value and during 1996 it tended toward P_2.

In the two crosses, $S_1 \times R_{16}$ and $S_1 \times R_6$, studied during 1996, the F_1 mean TGS values were less than those of both the parents. In both these cases, the white grained parents R_6 and R_{16} showed marginally higher grain mold resistance than the susceptible line (S_1) but markedly inferior resistance compared to the colored

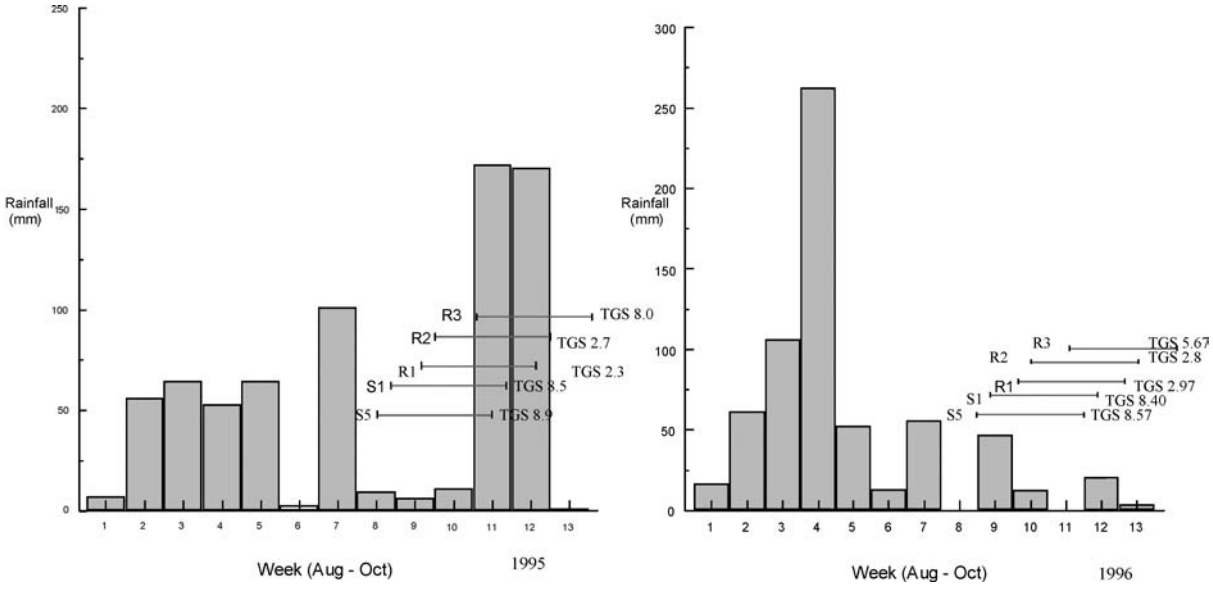

Figure 1. Postmaturity period of sorghum genotypes and rainfall pattern during 1995 and 1996. R1 = red resistant line, R2 = brown resistant line, R3 = White resistant line, S1 and S5 = White susceptible lines and TGS = Threshed grade score.

Table 3. Means of the families and estimates of gene effects for the threshed grade score in susceptible × resistant crosses of sorghum during 1995 and 1996

	$S_1 \times R_3$				$R_2 \times R_3$				$S_1 \times R_6$		$S_1 \times R_{16}$	
Year	1995		1996		1995		1996		1996		1996	
	M	S.E.	*M*	S.E.	*M*	S.E.	*M*	S.E.	*M*	S.E.	*M*	S.E.
P_1	8.5	0.1	8.4	0.1	2.7	0.2	2.8	0.2	8.5	0.1	8.2	0.2
P_2	8.0	0.1	5.7	0.2	7.4	0.1	5.6	0.2	7.4	0.2	7.1	0.2
F_1	8.2	0.2	6.1	0.2	2.8	0.2	3.7	0.1	7.0	0.1	6.2	0.2
BC_1	8.2	0.1	6.0	0.2	2.7	0.1	4.9	0.2	8.1	0.1	7.7	0.2
BC_2	8.0	0.1	5.5	0.1	5.5	0.3	5.3	0.2	8.0	0.1	7.7	0.2
F_2	8.2	0.2	5.8	0.1	5.9	0.2	5.9	0.1	7.9	0.1	7.6	0.1
Estimates of gene effects												
[*m*]	8.5*		6.0*		5.5*		6.4*		8.3*		9.0*	
[*d*]	0.5*		1.3*		−2.4*		1.7*		0.2*		0.6*	
[*h*]	–		–		−1.1*		–		–		−2.1*	
[*i*]	–		1.5*		−1.3*		−1.7*		0.4*		−0.6*	
[*j*]	–		1.6*		–		2.4*		–		–	
[*l*]	–		–		−2.0*		−1.3*		–		–	
R^2	95.2		92.4		90.0		90.7		96.1		97.9	

Note. M = Mean, S.E. = Standard error, *Significant at $p = 0.05$, [m] = mean, [d] = additive gene action, [h] = dominance gene action, [i] = additive × additive gene interactions, [j] = additive × dominance gene interactions, [l] = dominance × dominance gene interactions.

resistant sources (Table 3). The mean F_2 of both the crosses tended toward the midparent value suggesting polygenic nature of inheritance.

Generation mean analysis was conducted on a set of transformed square root data. Although this transformation produced a change in the scale of the observations, it did not seem to affect the interpretation of the data. Estimates of genetic effects on the original scale were comparable with those determined from the transformed scale, hence those based on original scale are presented. The estimates of the genetic effects for TGS are given in Table 3. Though the R^2 values obtained were very high (90–97%), the χ^2 values in some crosses were high indicating that the model was not a good fit. Similar results were reported by Torres et al. (1993); they chose the regression analysis method as the most adequate test for the generations derived from common parents; and discarded the χ^2 proposed by Mather and Jinks (1971) as the addition of F_2, F_3 mean values inflates the χ^2 value. We followed the same procedure to judge the goodness-of-fit.

In both the years, additive and additive × additive genetic effects were significant for the white susceptible × white resistant/tolerant crosses. In one cross $S_1 \times R_{16}$, the dominant gene effect was of higher magnitude. In the brown resistant × white resistant crosses, additive gene effect was significant in both the years but during 1995, dominance × dominance gene interaction and during 1996, the additive × dominance gene interaction were important. Murty & House (1984) and Kataria et al. (1990) reported large dominance effects besides significant additive and additive × additive interaction effects for grain mold resistance. In other studies, additive gene action was predominant in the inheritance of resistance (Narayana & Prasad, 1983) and both additive and nonadditive components of variance determined the expression of mold reaction (Dabholkar & Baghel, 1983)

The estimates of G × E interactions for the two crosses ($S_1 \times R_3$ and $R_2 \times R_3$) tested during 1995 and 1996 are given in Table 4. The two crosses, $S_1 \times R_3$ and $R_2 \times R_3$ showed significant additive and dominance gene effects. Environmental × additive and environmental × dominance components were significant and of lesser magnitude in the cross $R_2 \times R_3$. In the cross $S_1 \times R_3$, environmental effects, environment × additive ($e \times d$), and environment × dominance ($e \times h$) interactions were found to be significant and substantial.

The frequency distributions for TGS of P_1, P_2, F_1, BC_1, BC_2, and F_2 families grown during 1996 for a

Table 4. Estimates of G × E effects for threshed grade score in sorghum during 1995 and 1996

Cross	$S_1 \times R_3$	$R_2 \times R_3$
[*m*]	1.9*	5.1*
[*d*]	0.9*	−2.2*
[*h*]	−0.9*	2.0*
[*e*]	0.6*	–
[exd]	−0.4*	−0.8*
[exh]	0.9*	−0.9*
R^2	92.6*	91.3*

Note. *Significant at $P = 0.05$, [*m*] = mean, [*d*] = additive gene action, [*h*] = dominance gene action, [*e*] = environment effect, [exd] = environment × additive gene interaction, [exh] = environment × dominance gene interaction.

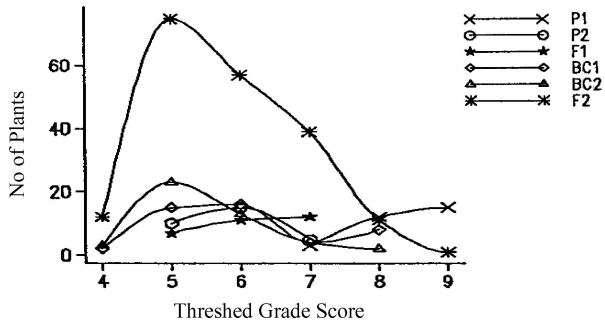

Figure 2. Frequency distributions of P_1, P_2, F_1, F_2, BC_1, and BC_2 families in cross, $S_1 \times R_3$ of sorghum for TGS (1996).

cross between $S_1 \times R_3$ are shown in Figure 2. The frequency distributions of the parents and F_1s generally confirmed the patterns shown by the family means (Table 3), with the F_1 more closer to the value of the resistant parent. The F_2 showed normal distribution. The BC_1 and BC_2 distributions were leaning toward the recurrent parents with some overlap.

In crosses of white-grained resistant and susceptible lines, in the absence of segregation for seed color (Audilakshmi et al., 1999 reported strong negative correlations between seed color and grain mold reaction in F_2 of a cross between white susceptible × colored resistant line), various dominant genes with moderate effects control the grain mold reaction. This is shown by the similarity of resistant parent and F_1 means, the normal distribution of grain mold reaction in F_2 progenies, mean F_2 tending toward midparent value, and the pronounced genotype × environment interactions shown by specific genotypes. In the present study, two white resistant sources, R_3 and R_{16} showed different gene actions. Rodriguez-Herrera et al. (2000) reported different gene action for the same cross in different environments. Breeding for grain mold resistance in the white grained sorghum lines and varieties is therefore likely to be difficult. Seed hardness, glume color, and glume cover in association with one another give high resistance to grain mold in the white genotype (Audilakshmi et al., 1999). Crossing between the resistant or moderately resistant lines endowed with different resistance mechanisms is likely to produce stable lines with useful traits. Simple recurrent selection or backcrossing should accumulate the resistance genes from different sources having different mechanisms. IS 25017 has been shown to have hard seed and colored glumes with high phenol content, both of which traits have been associated with grain mold resistance (Audilakshmi et al., 1999). Similarly, IS 24495 has hard seed. Alternatively, advancing grain mold resistant derivatives from segregating population and evaluating such advanced derivatives in different environments will lead to identification of stable resistant derivatives. Breeding the hybrids with grain mold resistance can take advantage of the dominance of resistance and dispersal of favorable genes among the diverse parents to permit the moderately resistant parent lines to produce more highly resistant hybrids.

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