

Inheritance of Grain Mold Resistance in Grain Sorghum without a Pigmented Testa

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ABSTRACT

The improvement of grain mold resistance in sorghum [*Sorghum bicolor* (L.) Moench] has been difficult, presumably because of the complex inheritance of the trait. The objective of this study was to determine the inheritance of grain mold resistance by generation means analysis. The F₁, F₂, and backcross generations of a cross between 'Sureño' (a dual-purpose food grain and forage variety, resistant to grain mold) and 'RTx430' (a widely adapted inbred line, highly susceptible to grain mold) were evaluated in eight different field environments. Significant differences in grain mold incidence between the generations evaluated in this study were observed in all environments. Combined analysis detected a significant generation five-environment interaction indicating that the genotypes reacted differently to each environment. Generation means analysis of transformed grain mold scores detected additive effects in all eight environments, and dominance effects were detected in seven of eight environments. Epistatic effects were detected in only two of eight environments, but combined analysis indicated that higher order interactions were important when evaluated across environment. Broad-sense heritability estimates ranged from 0.46 to 0.82, while narrow-sense heritability estimates ranged from 0.39 to 0.59. At least four to 10 genes were estimated to contribute to grain mold resistance. The results of this study indicate that selection in specific environments is useful for enhancing resistance to mold in these environments, but it may not be as effective in providing grain mold resistance across a wide range of environments.

IN MANY REGIONS OF THE WORLD where sorghum is produced, grain mold is a serious disease that reduces grain quality and utilization. The term *grain mold* is used to describe the diseased appearance of sorghum grain resulting from infection by one or more parasitic fungal species (Williams and Rao, 1981). Grain mold is most commonly caused by *Fusarium moniliforme* J. Sheld. and *Curvularia lunata* (Wakk.) Boedjin (Esele et al., 1993), although many other species also cause grain mold. This disease is especially severe when grain development coincides with wet and warm weather conditions.

Grain mold on sorghum reduces yield and seed quality with effects ranging from cosmetic deterioration of the pericarp to substantial deterioration of the endosperm and embryo (Rooney and Serna-Saldivar, 1991). In some cases, yield losses can reach 100% in highly susceptible cultivars (Williams and Rao, 1981). Qualitatively, grain mold discolors both the inside and outside of the grain, softens the endosperm, and reduces its acceptability by food and feed processors (Rooney and

Serna-Saldivar, 1991). In addition to reducing the nutritional value, fungi that cause grain mold in sorghum may also produce mycotoxins (Castor and Frederiksen, 1980). For these reasons, grain mold is listed as the most limiting factor in using sorghum as a food grain (Rosenow et al., 1995).

Breeding to improve grain mold resistance in sorghum has had limited success because of an incomplete understanding of the genetics of sorghum grain mold resistance. Sorghum geneticists have long suspected that both qualitative and quantitative loci influence grain mold resistance. Esele et al. (1993) showed that several qualitatively inherited pericarp traits such as color and pigmented testa influence the level of grain mold resistance. Menkir et al. (1996) determined that hard endosperm types were more resistant to grain mold. Menkir et al. (1996) and Esele et al. (1993) both demonstrated that the presence a pigmented testa layer is very effective in increasing grain mold resistance.

While several qualitative loci affect grain mold resistance, they do not account for all the variation observed for grain mold resistance in sorghum. Therefore, resistance to grain mold in sorghum is considered a quantitatively inherited trait. Using a diallel design, Dabholkar and Baghel (1980a) found that general and specific combining ability components of variation for grain mold resistance were highly significant. Murty and House (1984), using generation means analysis for evaluation of resistance to sorghum grain mold found that the F₁ hybrid was more resistant to *C. lunata* and *F. moniliforme* than the mid-parent, indicating that grain mold resistance exhibited dominance effects.

Much of the research on grain mold resistance has focused on sorghums with a pigmented testa, but the pigmented testa contains high amounts of tannins (Menkir et al., 1996). The presence of tannin in grain sorghums is usually an undesirable trait for both food and feed processors. Therefore, the use of tannin sorghums to reduce grain mold is not acceptable. Further research to improve grain mold resistance should focus on traits and genes that do not reduce the food and feed quality of the grain. The objectives of this study were (i) to determine the inheritance of the grain mold resistance in sorghum with non-pigmented testa, (ii) to estimate heritability and number of genes contributing to grain mold resistance, and (iii) to determine heterotic and extranuclear effects on grain mold resistance.

MATERIALS AND METHODS

Germplasm Development

Several familial generations from the cross of Sureño × RTx430 were used in this study. Sureño is a dual-purpose

Abbreviations: BE, Beeville; CC, Corpus Christi; CW, College Station with sprinkler irrigation; CD, College Station without sprinkler irrigation.

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grain and forage sorghum cultivar, with resistance to grain mold (Meckenstock et al., 1993). Sureño does not have pigmented testa and is known for excellent grain quality, both for food and feed purposes. RTx430 is a widely adapted inbred line with excellent combining ability, and it is a common restorer line in many U.S. grain sorghum hybrids (Miller, 1984). RTx430 has yellow endosperm, and it does not have a pigmented testa. RTx430 is highly susceptible to grain mold. In the summer of 1994, crosses of Sureño × RTx430 and its reciprocal were made at Lubbock, TX, by hand-emasculated panicles. In the winter of 1994, an F₂ population of Sureño × RTx430 was made by self-pollinating F₁ plants grown in Puerto Rico. The backcross populations (BC₁Tx430 and BC₁Sureño) were created with the F₁ plant as a pollinator and A3 male-sterile versions of RTx430 and Sureño as female parents.

The six generations (Sureño, RTx430, the F₁, F₂, BC₁Sureño, and BC₁Tx430) were evaluated in a total of eight environments over 3 yr. In 1995, the test was planted in Beeville (BE95) and College Station (CW95) Texas. At CW95 sprinkler irrigation was used during grain development to enhance the grain mold incidence. In 1996, the test was planted at College Station, TX, under two different conditions. Sprinkler irrigation was used to enhance grain mold in one experiment (CW96), while the other was exposed to natural conditions (CD96). The reciprocal F₁ (RTx430 × Sureño) was added to the experiments in 1996. In 1997, the test was planted at four environments: Beeville (BE97), Corpus Christi (CC97), and College Station, TX, (under the same environments used in 1996, CW97, and CD97). Analysis of data from 1995 and 1996 indicated that epistatic factors were not consistently significant, so only four generations (parents, F₁, and F₂) were evaluated in 1997. Inoculation was not necessary because the climatic conditions in all locations were conducive for the development of grain mold. Standard agricultural practices for these experiments were used. Plants were grown at each location in a randomized complete block design with two replications. Experimental units were three rows for homogeneous populations (parents and F₁), six rows for backcrosses and twenty rows for the F₂ generation. Plots were 6.3 m in length, with a row spacing of 0.76 m. To avoid bias in grain mold rating due to maturity, plants of similar maturity were tagged at anthesis, and grain mold ratings were taken approximately 40 d after anthesis. In each experiment, 25 plants from homogeneous generations, 80 plants from each backcross generation and 200 plants from the F₂ generation were evaluated for grain mold incidence using a 1-to-5 rating scale (Frederiksen et al., 1991). This scale is a progressive rating with 1 indicating the absence of grain mold and increasing numbers indicating higher levels of grain mold infection up to 5, which indicates that the grain was completely infected and destroyed by grain mold. To stabilize the variances before analysis, the data were transformed with the arcsine of the square root (Lentner and Bishop, 1993).

Analysis of Variance

The data were analyzed by environment with generation as the main effect. A combined analysis across environments was conducted including environment, generation and generation × environment as random effects in the model using SAS Proc GLM (SAS Institute, 1990).

Gene Effects

A joint-scaling test was performed (using data from the parents, F₁, F₂, BC₁Sureño, and BC₁Tx430) to provide estimates for the mean, additive effects, and dominance effects.

Those estimates were derived by the procedure of weighted least squares using as a weight the inverse of the variance of generation means. The joint-scaling test also evaluated the goodness of fit of the three parameter model [mid-parent (*m*), additive (*d*), and dominance (*h*) effects] to the observed data by assuming that the sum of squared deviations weighted with the appropriate coefficients follows a chi-square distribution with three degrees of freedom. Lack of fit implies the existence of non-additive gene effects other than dominance (Cavalli, 1952).

When the three-parameter model did not show good fit, a six-parameter scaling test to determine the adequacy of a digenic epistatic model was performed. This test, which requires a minimum of six family means, *m*, *d*, and *h*, also provides estimates of three epistatic parameters; additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*k*). The three and six-parameter scaling tests are described in detail by Mather and Jinks (1982). The calculations were completed using the JNTSCALE software (Ng, 1990).

Each environment was evaluated independently for goodness of fit, and the appropriate model was used for estimating the effects. A combined analysis of data from the 1995 and 1996 experiments estimated genetic effects in those environments. Data from the four environments in 1997 were also combined to estimate genetic effects. Two combined analyses were used because six generations were evaluated in 1995 and 1996, and only four generations were evaluated in 1997.

Heritability

Broad-sense heritability on a single-plant basis was estimated according to the equation

$$H^2 = \hat{\sigma}_g^2 / (\hat{\sigma}_g^2 + \hat{\sigma}_e^2)$$

The estimate of the genetic variance ($\hat{\sigma}_g^2$) is equal to the variance of the F₂ generation ($\hat{\sigma}_{F_2}^2$) minus the environment variance ($\hat{\sigma}_e^2$). In this formula, $\hat{\sigma}_e^2 = [n_{p1}\hat{\sigma}_{p1}^2 + n_{p2}\hat{\sigma}_{p2}^2 + n_{F1}\hat{\sigma}_{F1}^2] / Ne$, where the terms n_{p1} , n_{p2} , n_{F1} refer to the number of plants of Sureño, RTx430 and the F₁ generation, respectively. The terms $\hat{\sigma}_{p1}^2$, $\hat{\sigma}_{p2}^2$, and $\hat{\sigma}_{F1}^2$ are the variance estimates of Sureño, RTx430, and the F₁ generation, respectively. The term, *Ne*, refers to the effective population size, where $Ne = n_{P1} + n_{P2} + n_{F1}$ (Wright, 1968). The standard error of broad-sense heritability was calculated as suggested by Dickerson (1969) where $SE(H^2) = 2SE(\hat{\sigma}_g^2) / (2\hat{\sigma}_g^2 + \hat{\sigma}_p^2 + \hat{\sigma}_{we}^2)$ where $SE(\hat{\sigma}_g^2)$ is the square root of the genetic variance, and $\hat{\sigma}_p^2$, $\hat{\sigma}_{we}^2$ refer to the genetic, between plot, and within plot variances, respectively.

The method used to estimate narrow-sense heritability on a single-plant basis was adapted from Fehr (1991)

$$h^2 = [2(\hat{\sigma}_{F_2}^2) - (\hat{\sigma}_{BC1P1}^2 + \hat{\sigma}_{BC1P2}^2)] / \hat{\sigma}_{F_2}^2$$

where $\hat{\sigma}_{F_2}^2$ is the variance among F₂ plants of the population, $\hat{\sigma}_{BC1P1}^2$ and $\hat{\sigma}_{BC1P2}^2$ are the variance among plants from the backcrosses of the single cross F₁ to Sureño and RTx430, respectively. The numerator of the equation represents additive genetic variance, and $\hat{\sigma}_{F_2}^2$ in the denominator represents the phenotypic variance among plants. A standard error for h^2 was derived as the square root from Ketata et al. (1976)

$$\hat{\sigma}(h^2) = 2 \{ [(\hat{\sigma}_{BC1P1}^2 + \hat{\sigma}_{BC1P2}^2) / df_{F_2}] + [(\hat{\sigma}_{BC1P1}^2) / (df_{BC1P1})] + [(\hat{\sigma}_{BC1P2}^2) / (df_{BC1P2})] \} / (\hat{\sigma}_{F_2}^2)^2$$

where $\hat{\sigma}_{F_2}^2$, $\hat{\sigma}_{BC1P1}^2$ and $\hat{\sigma}_{BC1P2}^2$ are the variance estimates of the F₂, backcross to Sureño and backcross to RTx430, respectively. The terms df_{F_2} , df_{BC1P1} and df_{BC1P2} refer to degrees of freedom associated with $\hat{\sigma}_{F_2}^2$, $\hat{\sigma}_{BC1P1}^2$ and $\hat{\sigma}_{BC1P2}^2$, respectively.

Minimum Number of Genes Controlling Grain Mold Resistance

The minimum number of genes controlling grain resistance was estimated using the equation (Lande, 1981)

$$N = [(P_1 - P_2)^2/8] \times (\hat{\sigma}_{F_2}^2 - \hat{\sigma}_{(P_1, P_2, F_1, \text{pooled})}^2)$$

where P_1 refers to the mean of Sureño, P_2 refers to the mean of RTx430, $\hat{\sigma}_{F_2}^2$ is the variance of the F_2 generation, and $\hat{\sigma}_{(P_1, P_2, F_1, \text{pooled})}^2$ is the pooled variance of Sureño, RTx430, and the F_1 generation, respectively.

Reciprocal Effects and Heterosis

The maternal inheritance pattern of extranuclear genes contributing to grain mold resistance was estimated from the comparison of reciprocal F_1 progeny Sureño \times RTx430 vs RTx430 \times Sureño at CW96 and CD96. The formula to compare the means using a large number of samples was (Sincich, 1992)

$$T = [(X_1 - X_2) - (md)] / [(s_1^2/n_1) + (s_2^2/n_2)]^{0.5}$$

with degrees of freedom equal to $(n_1 + n_2) - 2$. In this formula, X_1 and X_2 refer to the sample mean of Sureño \times RTx430, and RTx430 \times Sureño, respectively, and s_1^2 and s_2^2 refer to the sample variance of Sureño \times RTx430, and RTx430 \times Sureño, respectively. The terms n_1 and n_2 refer to the number of plants of Sureño \times RTx430, and RTx430 \times Sureño, respectively. The term md refers to the means difference in the null hypothesis. In this case, the null hypothesis was that there was no difference between population means, thus, $md = 0$.

Mid-parent heterosis was determined as the performance of the F_1 (Sureño \times RTx430) compared with the average performance of its parents (Fehr, 1991).

RESULTS AND DISCUSSION

Analysis of Variance

Significant differences among generations were detected in all eight environments. As expected, the two parental lines were consistently different, and the range in grain mold ratings of these two lines accurately reflected the variable level of grain mold pressure encoun-

Table 1. Grain mold incidence (non-transformed) data for Sureño and RTx430 at eight environments in Texas. These genotypes were the parental lines used for the generation means analysis of grain mold resistance in sorghum. The grain mold ratings are using the scale described by Frederiksen et al., (1991) where a rating of 1 indicates the absence of mold to 5 which indicates grain was completely destroyed by grain mold.

Environment	Sureño	RTx430
1995 College Station - Sprinkle Irrigation (CW95)	2.59 [†]	4.44 ^b
1995 Beeville (BE95)	2.76 ^a	4.29 ^b
1996 College Station - Sprinkle Irrigation (CW96)	3.85 ^a	4.91 ^b
1996 College Station (CD96)	3.92 ^a	4.96 ^b
1997 College Station - Sprinkle Irrigation (CW97)	2.29 ^a	4.51 ^b
1997 College Station (CD97)	2.17 ^a	4.41 ^b
1997 Beeville (BE97)	1.68 ^a	4.71 ^b
1997 Corpus Christi (CC97)	1.98 ^a	4.71 ^b
Combined Across Environments	2.66 ^a	4.62 ^b

[†] Letters a, b indicate that the mean of Sureño and RTx430 are significantly different at $P < 0.01$.

tered in each environment (Table 1). In the combined analysis, the environment and generations were significant sources of variation ($P > 0.001$) for grain mold ratings. In addition, a significant generation \times environment interaction ($P > 0.001$) was detected, indicating that generations reacted differently to each environment. However, Sureño was always more resistant than RTx430 in each environment. The interaction was due to a change in magnitude of the differences between the two parental lines rather than a reversal of grain mold reaction. Nonetheless, these observations suggest that selection and evaluation should be completed in an array of environments if reliable grain mold resistance is to be obtained.

Gene Effects

In six of eight environments, the variation among generation means for grain mold resistance was sufficiently explained by a simple additive-dominance model (Tables 2 and 3). The best approximation of additive and dominance effects can be obtained from the three-parameter additive-dominance model because these effects are unbiased due to the absence of epistasis (Hay-

Table 2. Estimates of additive, dominance and epistatic effects (and the standard errors) from the joint scale test for grain mold incidence[†] on Sureño, RTx430 and their F_1 , F_2 , BC₁Sureño and BC₁RTx430 grown in Texas in 1995 and 1996. The four environments were College Station with sprinkle irrigation in 1995 and 1996 (CW95 and CW96), College Station without sprinkle irrigation in 1996 (CD96) and Beeville in 1995 (BE95). The data were transformed using the arcsine transformation prior to analysis.

Model [‡]	Environments			
	CW95	BE95	CW96	CD96
Three parameter				
m	1.19 \pm 0.01**	1.21 \pm 0.01**	1.42 \pm 0.01**	1.39 \pm 0.01**
d	-0.14 \pm 0.01**	-0.12 \pm 0.01**	-0.11 \pm 0.01**	-0.14 \pm 0.01**
h	-0.14 \pm 0.02**	-0.15 \pm 0.02**	-0.18 \pm 0.02**	-0.11 \pm 0.16
χ^2	0.56	0.79	10.51*	20.71*
Six parameter				
m			1.31 \pm 0.05**	1.33 \pm 0.06**
d			-0.14 \pm 0.01**	-0.15 \pm 0.01**
h			0.35 \pm 0.14**	0.01 \pm 0.16
i			0.06 \pm 0.05	0.06 \pm 0.06
j			0.13 \pm 0.04**	0.20 \pm 0.05**
k			-0.47 \pm 0.09**	-0.04 \pm 0.11

*, ** Indicates the term is significant at $P < 0.05$ and $P < 0.01$, respectively.

[†] Grain mold ratings use a scale where 1 indicates the absence of mold, and 5 indicates the grain is completely destroyed by mold (Frederiksen et al., 1991).

[‡] m = mid-parent effect, d = additive effect, h = dominance effect, i = additive \times additive effect, j = additive \times dominance effect, and k = dominance \times dominance effect.

Table 3. Estimates of additive and dominance effects (and their standard errors) from the joint scale test for grain mold incidence† on Sureño, RTx430 and their F₁ and F₂ generations grown in Texas in 1997. The four environments were College Station with sprinkle irrigation (CW97), College Station without sprinkle irrigation (CD97), Beeville (BE97), and Corpus Christi (CC97). The data were transformed using the arcsine transformation prior to analysis.

Three parameter model‡	Environment			
	CW97	CD97	BE97	CC97
<i>m</i>	1.19 ± 0.03**	1.17 ± 0.03**	1.20 ± 0.04**	1.18 ± 0.04**
<i>d</i>	-0.18 ± 0.03**	-0.16 ± 0.03**	-0.23 ± 0.04**	-0.18 ± 0.04**
<i>h</i>	-0.14 ± 0.04**	-0.17 ± 0.05**	-0.22 ± 0.05**	-0.16 ± 0.06**
χ ²	0.34	0.15	0.62	0.42

** Indicates the term is significant at $P < 0.01$.

† Grain mold ratings use a scale where 1 indicates the absence of mold, and 5 indicates the grain is completely destroyed by mold (Frederiksen et al., 1991).

‡ *m* = mid-parent effect, *d* = additive effect, *h* = dominance effect.

man, 1958). In the remaining two locations (96CW and 96CD), evidence for epistatic interactions was detected (Table 2). These data from these environments will be discussed later by means of the six-parameter model.

In the 1995 and 1997 locations, both the additive and dominance effects were significant (Tables 2 and 3). Because lower ratings are more resistant, the negative estimates for the dominance effects indicate that dominance contributed to increased grain mold resistance. The presence of significant additive effects in these locations indicates that selection for increased grain mold resistance should be effective with the performance of progeny predictable on the basis of the reaction of parents (Carson, 1995).

In the 1996 experiments, the additive and dominance model was not sufficient to explain the genetic variation for grain mold resistance (Table 2). Therefore, the six-parameter model was used to determine the type and magnitude of gene action involved in the inheritance of grain mold resistance. At CW96, all the effects were significant except for the additive × additive effects (*i*). In contrast, at CD96 only the additive (*d*) and the additive × dominance (*j*) effects were significant (Table 2). At CW96 the sign of the dominance effect (*h*) was positive while the sign of dominance × dominance effect (*i*) was negative (Table 2). This suggests that duplicate types of gene interactions were present confirming the importance of dominance effects (Grewal, 1988). At the 1996 locations, there was unusually heavy rainfall for ten days shortly after the physiological maturity of the grain. These environmental conditions resulted in extremely severe grain mold pressure, even on the most resistant lines. This caused the data to be skewed toward high grain mold scores. This reduction in the differentials between the resistant and susceptible lines as well as the different type of grain mold pressure could be the cause of the differential response seen in 1996 versus 1995 and 1997 environments.

In the combined analysis of the 1995 and 1996 data, the three-parameter model was not sufficient to account for the genetic variation of grain mold resistance (Table 4). In the six-parameter model, significant effects for the additive, dominance, additive × dominance (*j*) and dominance × dominance (*k*) were detected (Table 4). The combined analysis of the 1997 data did fit a three-parameter model, but the χ² was close to statistical significance (Table 4). When analyzed individually, each environment in 1997 easily fit a three-parameter model,

but combined analysis did not have as good a fit. The data indicate that epistatic effects may be important when data are combined as compared to the results from individual environment analysis.

The type of inheritance reported for grain mold resistance in previous studies has been inconsistent (Mukuru, 1992). There are some reports that additive effects are very important for grain mold resistance (Ibrahim et al., 1985; Dabholkar and Baghel, 1980b; Shivanna et al., 1994). In contrast, some authors indicated that dominance (Murty and House, 1984; Kataria et al., 1990) or additive and dominance effects (Dabholkar and Baghel, 1983) were the most important on grain mold resistance. Possible explanations for this inconsistency are (i) most of these studies were conducted at few locations (less than three), (ii) sorghum germplasm of different genetic backgrounds were used, and (iii) minimal and different types of inoculum were used. However, when grain mold incidence is seen as a complex of fungi and analyzed at multi-location trials, resistance to grain mold may be the result of many different loci with both additive and dominance effects that are influenced by many different environmental factors. Consequently, the same trait may be inherited quite differently in specific environ-

Table 4. Estimates of additive and dominance effects (and their standard errors) from the combined joint-scale tests for grain mold incidence† on Sureño, RTx430, and their F₁, F₂, BC₁Sureño, and BC₁RTx430 grown in Texas in 1995, 1996, and 1997. Because six generations were evaluated in 1995 and 1996, and four generations were evaluated in 1997, these two groups of combined data are presented.

Model‡	1995 and 1996 (four environments)	1997 (four environments)
Three parameter		
<i>m</i>	1.39 ± 0.01**	1.21 ± 0.01**
<i>d</i>	-0.14 ± 0.01**	-0.12 ± 0.01**
<i>h</i>	-0.11 ± 0.16	-0.15 ± 0.02**
χ ²	20.71**	6.12
Six parameter		
<i>m</i>	1.30 ± 0.04**	
<i>d</i>	-0.14 ± 0.01**	
<i>h</i>	-0.16 ± 0.08**	
<i>i</i>	0.06 ± 0.06	
<i>j</i>	0.18 ± 0.05**	
<i>k</i>	-0.19 ± 0.08**	

** Indicates the term is significant at $P < 0.01$.

† Grain mold ratings use a scale where 1 indicates the absence of mold, and 5 indicates the grain is completely destroyed by mold (Frederiksen et al., 1991).

‡ *m* = mid-parent effect, *d* = additive effect, *h* = dominance effect, *i* = additive × additive effect, *j* = additive × dominance effect, and *k* = dominance × dominance effect.

ments or genotypes. The data from this study suggest that both additive and dominance effects are important, but epistasis may be a factor when multiple environments are considered.

Heritability

Broad-sense heritability (H^2) averaged 0.70 over eight environments with a range of 0.46 to 0.82 (Table 5). The moderate to high values found in this study suggest that improvement for grain mold resistance can be realized through breeding if some of this genetic variation is additive in nature. Narrow-sense heritability (h^2) averaged 0.47 over four environments with a range from 0.39 to 0.59 (Table 5), indicating that additive variance is important for grain mold resistance. Relatively high values for narrow-sense heritability ($h^2 > 0.50$) for grain mold resistance have been reported previously (Dabholkar and Baghel, 1983; Ibrahim et al., 1985). The moderate to high values for narrow-sense heritability found in the present study suggest that conventional pedigree and early generation selection methods should be effective for initial improvements in grain mold resistance in sorghum.

Minimum Number of Genes Controlling Grain Mold Resistance

The estimated minimum number of genes controlling grain mold resistance averaged 5.7 genes with a range of 3.1 to 10.5 (Table 5). However, it is likely that the real number of genes conferring grain mold resistance is higher than five. Several plant and caryopsis traits are known to improve grain mold resistance in sorghum. Physical kernel properties such as a high proportion of corneous to floury endosperm, pericarp structure, thick surface wax of the grain and kernel density are associated with grain mold resistance (Glueck and Rooney, 1980). Plant traits like panicle shape (Castor, 1981), plant height, glume structure (Rao and Rana, 1989), and tan plant color (Murty, 1975) have been also associated with grain mold resistance. Phenolic compounds (Waniska et al., 1992), proteins, prolamine (Kumari and Chandrashekar, 1992), and antifungal proteins (Seeth-

Table 5. Broad (H^2) and narrow (h^2) sense heritability estimates, and estimates for the minimum number of genes conferring grain mold resistance in grain sorghum. The estimates were made using generation means analysis of generations from the cross of Sureño \times RTx430 that were evaluated in eight environments in Texas from 1995 to 1997.

Environments	H^2	h^2	Minimum no. of genes
1995 College Station - Sprinkle Irrigation (CW95)	0.67 \pm 0.05	0.47 \pm 0.13	4.7
1995 Beeville (BE95)	0.46 \pm 0.09	0.44 \pm 0.23	3.4
1996 College Station - Sprinkle Irrigation (CW96)	0.70 \pm 0.14	0.59 \pm 0.05	3.1
1996 College Station (CD96)	0.65 \pm 0.13	0.39 \pm 0.15	4.5
1997 College Station - Sprinkle Irrigation (CW97)	0.82 \pm 0.25		10.5
1997 College Station (CD97)	0.69 \pm 0.21		10.0
1997 Beeville (BE97)	0.82 \pm 0.16		5.6
1997 Corpus Christi (CC97)	0.82 \pm 0.16		4.3

araman et al., 1996) have been related with grain mold resistance as well. In the current study, some traits that influence grain mold infection are not segregating in the cross between Sureño and RTx430 and this will reduce the total number of estimated genes. Another factor that will influence this estimate is genetic linkage (Rao and Rana, 1989). Presence of linkage may result in an underestimation of the real number of genes conferring grain mold resistance, but relatively few genes or blocks of genes controlling grain mold resistance should allow for modest gain from selection.

Reciprocal Effects and Heterosis

No significant difference existed between mean of grain mold incidence on the F_1 (Sureño \times RTx430) and its reciprocal F_1 (RTx430 \times Sureño) in the environment CW96. In contrast, in the environment CD96, a significant reciprocal difference did exist. In 1996, the College Station experiments were exposed to excessive moisture and humidity because of heavy rains after physiological maturity of the grain. Grain molding was worse in the CW96 environment because sprinkler irrigation was applied weekly during grain development. It is possible that excess moisture in CW96 masked any difference between reciprocal F_1 s. No reports of reciprocal differences for grain mold incidence exist in the literature, and additional studies are needed to determine the generality of our findings.

Mid-parent heterosis ranged from 7.2 to 18.7%, indicating that heterosis influences the expression of grain mold resistance (Table 6). These data support the conclusion that dominance is involved in the expression of grain mold resistance. Heterosis can be expressed when the parents of a hybrid have different alleles at a locus, and there is some level of dominance among those alleles (Falconer and Mackay, 1996).

CONCLUSIONS

At each individual environment, analyses of genetic effects, heritability, and gene number indicated that a simple additive-dominance model accounted for most of the genetic variation for grain mold resistance, but combined analyses across environments indicated that the genetic effects may have been more complex. It appeared that each environment favored environmentally specific mechanisms of grain mold resistance. Consequently, genotypes may have reacted differently across

Table 6. Estimates of mid-parent heterosis for grain mold incidence in the cross of Sureño \times RTx430 in eight environments in Texas. Mean comparisons were performed with data transformed by the arcsine.

Environment	Heterosis
1995 College Station - Sprinkle Irrigation (CW95)	13.5
1995 Beeville (BE95)	12.3
1996 College Station - Sprinkle Irrigation (CW96)	17.6
1996 College Station (CD96)	7.2
1997 College Station - Sprinkle Irrigation (CW97)	11.9
1997 College Station (CD97)	14.1
1997 Beeville (BE97)	18.7
1997 Corpus Christi (CC97)	15.4

a range of environments. This type of interaction would make the selection of stable grain mold resistance much more difficult and it would explain why the improvement of grain mold resistance in sorghum has been so slow, even though many genetic studies have indicated that grain mold resistance is moderately to highly heritable.

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