The Association of Genes Controlling Caryopsis Traits with Grain Mold Resistance in Sorghum

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ABSTRACT

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Four parental cultivars with distinct characteristics and gene markers for caryopsis traits were used as a base population to generate F_1, F_2, and BC_1 populations at College Station, TX. These populations were evaluated for grain mold resistance at College Station, TX, in 1990, and at Namulonge and Serere Research Stations in Uganda, in 1991. The presence of a pigmented testa (B_1-B_2-), a red pericarp (*R*-*Y*-), a thin mesocarp (*Z*-), and an intensifier gene (*I*-) were all dominantly inherited. A pigmented testa was the single most important trait conferring grain mold resistance. The red pericarp trait also conferred grain mold resistance, though not as greatly. The effect of a red pericarp was enhanced by the presence of the intensifier gene. The effects of both a pigmented testa and a red pericarp were additive. Mesocarp thickness did not play a significant role in grain mold resistance. College Station and Serere were suitable locations for grain mold evaluation.

Grain mold is one of the most serious biotic constraints in the production of grain sorghum (*Sorghum bicolor* (L.) Moench). Many fungal genera are associated with grain mold, and most of these are facultative parasites or saprophytes. The predominant species vary with locations, seasons, or years; *Fusarium moniliforme* J. Sheld. and *Curvularia lunata* (Wakk.) Boedijn are the most important species worldwide (1–5,7,15,22). The most obvious symptom of grain mold is pink, orange, gray, white, or black discolorations on the grain surface, depending on the fungal species present. *F. moniliforme* produces a pinkish-white mycelium that appears powdery in the early stages and later appears fluffy. *C. lunata* appears as shiny, velvety black, fluffy growth on the grain surface (2). The increased use of photoperiod-insensitive cultivars that mature under humid weather conditions has increased the prevalence of grain mold infection (22). Losses caused by grain mold are both quantitative and qualitative. Quantitatively, grain mold causes a decrease in actual grain yield. At

ICRISAT Center, Hyderabad, India, grain yield losses of up to 100% in highly susceptible cultivars have been experienced (22). In Texas, unusually heavy rains at grain maturity in 1976 affected 400,000 ha of sorghum and caused a $46 million loss (5). The disease also causes a reduction in seed viability, kernel size, volume weight, and 1,000-kernel weight (5,7,15,22). Preharvest sprouting also may occur during prolonged rainfall, high humidity, and alternating wetting and drying conditions (5,7). Qualitatively, grain mold results in a loss of market value (1,5,7,18,22) as well as reductions in processing and nutritional values (2,7,18,22).

Limited information is available on the genetics of grain mold resistance in sorghum. Because many fungal genera and several plant and caryopsis traits are involved, the resistance is thought to result from an additive effect of many genes (6,14,15,22). Glueck and Rooney (8) showed that certain structural features of the sorghum kernel may play an important role in limiting movement of water and entry of microorganisms into the kernel. However, the actual association of various caryopsis traits with grain mold resistance is not clear. This knowledge would be of use to sorghum-breeding programs aimed at the improvement of food and feed quality.

Genes at seven loci are known to be responsible for the different characteristics affecting caryopsis traits: *R*, *Y*, *I*, *Z*, B_1, B_2, and *S* genes (16,18–20). The *R* and *Y* genes determine pericarp color. If both genes are dominant (*R-Y-*), then the pericarp is red. When the *Y* gene is homozygous recessive (*R-yy* or *rryy*), the pericarp is colorless or white regardless of the *R* gene. A lemon-yellow pericarp is found when the *R* gene is homozygous recessive and the *Y* gene is dominant (*rrY-*). The intensifier gene (*I*) modifies the color of the pericarp to appear bright when dominant (*I-*) and dull when recessive (*ii*). The B_1 and B_2 genes determine the presence or absence of pigmentation in the testa. When the complementary B_1 and B_2 genes are dominant (B_1-B_2-), testa pigmentation is present, and when either or both genes are homozygous recessive (B_1-b_2b_2, $b_1b_1B_2$-, or $b_1b_1b_2b_2$), pigmentation is absent. The color of the pigmented testa is controlled by another gene (*Tp*) in which brown is dominant to purple. The spreader gene (*S*) allows the brown color of a pigmented testa to be present in the epicarp (*S-*). The mesocarp is thin when the *Z* gene is dominant (*Z-*) and thick when the gene is recessive (*zz*). Pigmentation, controlled by *R*, *Y*, *I*, B_1, B_2, and *S* genes, is associated with the presence of phenolic compounds that could be antifungal, conferring grain mold resistance (4,10,17,18,21). A thin mesocarp, determined by the amount of starch granules present, is also thought to confer grain mold resistance (8,18).

The study was designed to elucidate the effects and relationship of the various grain characteristics on the development of grain mold, to confirm gene action controlling these characteristics, and to determine characteristic-inheritance patterns.

MATERIALS AND METHODS

Four inbred cultivars with different characteristics and distinct gene markers for testa presence, pericarp color, mesocarp thickness, and known mold reaction were selected for this study, RTx2536, SC103-12E, BTx3197, and BTx378 (Table 1). Diallel crosses including reciprocals were made, using hand emasculation, to generate 12 F_1, 12 F_2, and 24 BC_1 populations at College Station, TX. One-third of the seeds from the parentals and crosses were planted at College Station. The remaining two-thirds were divided and planted at Namulonge and Serere Research Stations, Uganda. Grain mold was evaluated on these populations and on the parental populations at College Station during April–July 1990 and at Serere and Namulonge Research Stations during April–July 1991. Grain mold reaction was evaluated on field inoculated plants. A mixture of *F. moniliforme* and *C. lunata* spores was used as an inoculum source. Both fungi frequently occur together on molded grain and are the most important grain mold causal organisms. The mixture was prepared as described by Bandyopadhyay and Mughogho (3). *F. moniliforme* and *C. lunata* were isolated from naturally infected grain in each location and were cultured separately on potato-dextrose agar at 30 C for 10–14 days. The fungal cultures were comminuted in distilled water using a blender (Waring 700, model 33BL79, New Hartford, CT) and were filtered through a double layer of cheesecloth. Suspensions of the two fungi were made separately. Equal quantities of the suspensions were mixed and appropriately diluted with distilled water to make a mixture of 1×10^6 spores per milliliter to form the inoculum. A few drops of Tween 20 were added as a wetting agent. The panicles were inoculated at 50% anthesis by spraying the spore suspension on panicles until run-off. The inoculated panicles were bagged in pollinating paper bags (Lawson Kraft, No. 400, Northfield, IL) for 4–7 days to maintain high humidity.

Inoculated plants were planted in 6-m row plots in a completely randomized design with two replications. The nonsegregating P_0, F_1, and BC_1 generations were planted in single-row plots; the segregating F_2 generations were planted in five-row plots per replication. The data collected at each location included grain mold rating, phenotypic classification (testa presence, mesocarp thickness, and pericarp color), and genetic ratios. Rooney and Miller (18) were used as a reference in phenotypic classification. These data were recorded on at least 50 plants in each of the nonsegregating generations (P_0, F_1, and BC_1) and on at least 250 plants in the segregating generations (F_2) per replication. In each location, every individual plant in F_2 and BC_1 was considered an experimental unit. Studies on gene dominance and inheritance patterns were carried out on the F_2 and BC_1 progeny. Grain mold was evaluated on mature plants (at harvest stage) in the field by visually estimating severity, based on a 1–5 rating scale: 1 = no mold; 2 = 1–10% molded grain; 3 = 11–25% molded grain; 4 = 26–50% molded grain; and 5 = over 50% molded grain in panicles. The frequency of the occurrence of each individual fungus was not considered. An analysis of variance was used to determine location and genotype effects. Fisher's LSD test was used to determine differences among the means. Genetic ratios were evaluated for goodness-of-fit by a chi-square test of the observed to the expected number of genotypes within each of the F_2 and BC_1 populations (SAS Institute, Inc., Cary, NC).

RESULTS

The inheritance of testa pigmentation and pericarp color were examined in the RTx2536 (P_1) × SC103-12E (P_2) cross and its

TABLE 1. Sorghum cultivars used to determine grain mold response, known genotypes, and resulting phenotypes

	Genotype					
Cultivar[v]	Mold reaction[w]	Pericarp color[x]	Intensifier[y]	Spreader	Testa[z]	Mesocarp
RTx2536	S	*RRyy* (W)	*ii* (NO)	*SS*	$b_1b_1b_2b_2$ (U)	*ZZ* (thin)
SC103-12E	R	*RRYY* (RE)	*II* (I)	*SS*	$B_1B_1B_2B_2$ (P)	zz (thick)
BTx3197	MR	*RRyy* (W)	*ii* (NO)	*SS*	$b_1b_1B_2B_2$ (U)	zz (thick)
BTx378	S	*RRYY* (RE)	*II* (I)	*SS*	$b_1b_1B_2B_2$ (U)	zz (thick)

[v] Source is Raab (17).
[w] S = susceptible; R = resistant; and MR = moderately resistant.
[x] W = white, and RE = red.
[y] NO = No intensifier, and I = intensifier.
[z] U = Unpigmented, and P = pigmented.

progeny (Table 2). All the F_1 progeny had pigmented testae and red pericarps. F_2 populations segregated in the expected 27:9:21:7 ratio for pigmented testa with red pericarp, pigmented testa with red pericarp, unpigmented testa with red pericarp, and unpigmented testa with white pericarp, respectively. $F_1 \times P_1$ progeny segregated in the expected 1:1:3:3 ratio for similar gene combinations. $F_1 \times P_2$ progeny all had pigmented testae and red pericarps. These ratios showed that the B_1, B_2, and Y genes were inherited in a dominant manner. Moreover, B_1 and B_2 interacted in a dominant complementary fashion.

The F_1 population (Table 3) was resistant to mold, with a rating of 1.1, which was lower (though not significantly) than that of SC103-12E (1.2), the resistant parent. This indicated that resistance was completely dominant. In the F_2 and BC_1 populations, phenotypes that possessed both gene combinations in their dominant conditions (B_1-B_2-RRY-: pigmented testa present with red pericarp) had the lowest mean grain mold ratings (1.1–1.3), indicating high levels of resistance. Genotypes B_1-b_2b_2RRyy, $b_1b_1B_2$-$RRyy$, and $b_1b_1b_2b_2RRyy$ (unpigmented testa with white pericarp) had the highest mean grain mold ratings (highest susceptibility). Genotype B_1-B_2-$RRyy$ (pigmented testa with white pericarp) and genotypes B_1-b_2b_2RRY-, $b_1b_1B_2$-RRY-, and $b_1b_1b_2b_2RRY$- (unpigmented testa with red pericarp) showed moderate resistance. Genotypes with a pigmented testa and white pericarp were more resistant than those with an unpigmented testa and red pericarp. This indicated that although both a pigmented testa and a red pericarp conferred grain mold resistance, the presence of a pigmented testa conferred greater resistance than a red pericarp. However, there seemed to be an additive effect, because when both traits were present, higher levels of resistance were observed.

The inheritance of pericarp color in combination with the intensifier gene was studied in the BTx378 (P_1) × RTx2536 (P_2) cross and its progeny (Table 4). All the F_1 progeny had red pericarps with intensifiers ($RRYyIi$). The F_2 population segregated

TABLE 2. Chi-square analysis of the inheritance of testa pigmentation and pericarp color from the RTx2536 (P_1) × SC103-12E (P_2) cross at College Station, TX, and at Namulonge and Serere, Uganda

Generation	Phenotype[u]	Genotype	Ratio[v]	College Station[w]				Namulonge				Serere			
				O	E	χ^2	p[x]	O	E	χ^2	p	O	E	χ^2	p
P_1	White, unpigmented	$b_1b_1b_2b_2RRyy$	1	...[y]	...	...	...	...	...	...	...	...	...	...	...
P_2	Red, pigmented	$B_1B_1B_2B_2RRYY$	1	...	...	...	...	...	...	...	...	...	...	...	...
F_1	Red, pigmented	$B_1b_1B_2b_2RRYy$	1	...	...	...	...	...	...	...	...	...	...	...	...
F_2	Red, pigmented	B_1-B_2-RRY-	27	228	216.0			191	204.2			234	227.8		
	White, pigmented	B_1-B_2-$RRyy$	9	65	72.0			75	68.1			67	75.9		
	Red, unpigmented	$b_1b_1b_2b_2$, $b_1b_1B_2$-, or B_1-b_2b_2RRY-[z]	21	170	168.0			150	158.8			185	177.2		
	White, unpigmented	$b_1b_1b_2b_2$, $b_1b_1B_2$-, or B_1-b_2b_2RRyy	7	49	56.0	2.25	0.55	68	52.9	6.33	0.09	54	59.1	2.00	0.59
$F_1 \times P_1$	Red, pigmented	$B_1b_1B_2b_2RRYy$	1	17	13.3			5	12.3			12	12.3		
	White, pigmented	$B_1b_1B_2b_2RRyy$	1	15	13.3			16	12.3			8	12.3		
	Red, unpigmented	$b_1b_1b_2b_2$, $b_1b_1B_2b_2$, or $B_1b_1b_2b_2RRYy$	3	33	39.8			43	36.8			38	36.8		
	White, unpigmented	$b_1b_1b_2b_2$, $b_1b_1B_2b_2$, or $B_1b_1b_2b_2RRyy$	3	41	39.8	2.48	0.50	34	36.8	6.71	0.08	40	36.8	1.81	0.63
$F_1 \times P_2$	Red, pigmented	B_1-B_2-RRY-	1	...	...	...	...	...	...	...	...	...	...	...	...

[u] White, unpigmented = white pericarp, unpigmented testa; red, pigmented = red pericarp, pigmented testa, etc.
[v] Expected segregation ratio for the phenotypes in each generation.
[w] O = number of plants of the phenotype observed; E = number of plants of the phenotype expected.
[x] p = probability of a greater χ^2 value (3 df) under the null hypothesis of the segregation ratio.
[y] All plants observed were of the same phenotype, therefore no analysis was performed.
[z] All possible unpigmented testa genotypes were present with the listed pericarp genotype.

TABLE 3. Relationship of pericarp color and testa pigmentation with grain mold resistance in the RTx2536 (P_1) × SC103-12E (P_2) cross at College Station, TX, and at Namulonge and Serere, Uganda

Generation	Phenotype[w]	Genotype	Grain mold ratings[x]			
			College Station	Namulonge	Serere	Mean
P_1	White, unpigmented	$b_1b_1b_2b_2RRyy$	4.7	4.8	4.8	4.8 e[y]
P_2	Red, pigmented	$B_1B_1B_2B_2RRYY$	1.2	1.1	1.2	1.2 a
F_1	Red, pigmented	$B_1b_1B_2b_2RRYy$	1.1	1.1	1.3	1.1 a
F_2	Red, pigmented	B_1-B_2-RRY-	1.4	1.4	1.3	1.3 a
	White, pigmented	B_1-B_2-$RRyy$-	2.8	2.5	2.6	2.6 c
	Red, unpigmented	$b_1b_1b_2b_2$, $b_1b_1B_2$-, or B_1-b_2b_2RRY-[z]	2.1	1.8	1.9	1.9 b
	White, unpigmented	$b_1b_1b_2b_2$, $b_1b_1B_2$-, or B_1-b_2b_2RRyy	4.7	4.8	4.8	4.8 e
$F_1 \times P_1$	Red, pigmented	$B_1b_1B_2b_2RRYy$	1.2	1.0	1.1	1.1 a
	White, pigmented	$B_1b_1B_2b_2RRyy$	2.8	2.7	2.6	2.6 c
	Red, unpigmented	$b_1b_1b_2b_2$, $b_1b_1B_2b_2$, or $B_1b_1b_2b_2RRYy$	2.0	1.8	1.8	1.9 b
	White, unpigmented	$b_1b_1b_2b_2$, $b_1b_1B_2b_2$, or $B_1b_1b_2b_2RRyy$	4.4	4.0	4.3	4.2 d
$F_1 \times P_2$	Red, pigmented	B_1-B_2-RRY-	1.1	1.0	1.1	1.1 a
Mean			2.4 h	2.2 f	2.3 g	

[w] White, unpigmented = white pericarp, unpigmented testa; red, pigmented = red pericarp, pigmented testa, etc.
[x] Grain mold rating is based on a 1–5 scale: 1 = no mold; 2 = 1–10% molded grain; 3 = 11–25% molded grain; 4 = 26–50% molded grain; and 5 = over 50% molded grain.
[y] Means followed by the same letter are not significantly different at $P = 0.05$ using Fisher's LSD.
[z] All possible unpigmented testa genotypes were present with the listed pericarp genotype.

in the expected 9:3:3:1 ratio for red pericarp with intensifier, red pericarp with no intensifier, white pericarp with intensifier, and white pericarp with no intensifier, respectively. $F_1 \times P_1$ progeny all had red pericarps with intensifiers. The $F_1 \times P_2$ population segregated in a 1:1:1:1 ratio for similar gene combinations. These ratios showed that the genes for a red pericarp (*Y*) and the intensifier (*I*) were inherited in a dominant manner.

There was no significant difference between the grain mold ratings for the P_1 parent, BTx378 (*RRYYII*), and the F_1, F_2, and BC_1 progeny that had at least one dominant allele at each locus (*R-Y-I-*) (Table 5). They all had low grain mold ratings (1.7–1.9), indicating dominance of resistance. Genotypes *RRyyI-* (white pericarp with intensifier) and *RRY-ii* (red pericarp no intensifier) showed moderate resistance (2.6–3.0), although *RRY-*

TABLE 4. Chi-square analysis of the inheritance of pericarp color and intensifier in the BTx378 (P_1) × RTx2536 (P_2) cross at College Station, TX, and at Namulonge and Serere, Uganda

				College Station[x]				Namulonge				Serere			
Generation	Phenotype[v]	Genotype	Ratio[w]	O	E	χ^2	p^y	O	E	χ^2	p	O	E	χ^2	p
P_1	Red, intensifier	*RRYYII*	1	...[z]	...	...	...	...	...	...	...	...	...	...	...
P_2	White, no intensifier	*RRyyii*	1	...	...	...	...	...	...	...	...	...	...	...	...
F_1	Red, intensifier	*RRYyIi*	1	...	...	...	...	...	...	...	...	...	...	...	...
F_2	Red, intensifier	*RRY-I-*	9	258	273.4			311	301.5			248	255.4		
	Red, no intensifier	*RRY-ii*	3	107	91.1			96	100.5			94	85.1		
	White, intensifier	*RRyyI-*	3	89	91.1			101	100.5			86	85.1		
	White, no intensifier	*RRyyii*	1	32	30.4	3.77	0.31	28	33.5	1.41	0.71	26	28.4	1.35	0.73
$F_1 \times P_1$	Red, intensifier	*RRY-I-*	1	...	...	...		...	...	...	...	...	...	...	...
$F_1 \times P_2$	Red, intensifier	*RRYyIi*	1	26	24.3			19	21.8			21	21.0		
	Red, no intensifier	*RRYyii*	1	22	24.3			24	21.8			17	21.0		
	White, intensifier	*RRyyIi*	1	28	24.3			26	21.8			25	21.0		
	White, no intensifier	*RRyyii*	1	21	24.3	1.35	0.72	18	21.8	2.06	0.58	21	21.0	1.52	0.69

[v] Red and white refer to the pericarp color.
[w] Expected segregation ratio for the phenotypes in each generation.
[x] O = number of plants of the phenotype observed; E = number of plants of the phenotype expected.
[y] p = probability of a greater χ^2 value (3 df) under the null hypothesis of the segregation ratio.
[z] All plants observed were of the same phenotype, therefore no analysis was performed.

TABLE 5. Relationship of pericarp color and intensifier with grain mold resistance in the BTx378 (P_1) × RTx2536 (P_2) cross at College Station, TX, and at Namulonge and Serere, Uganda

			Grain mold ratings[y]			
Generation	Phenotype[x]	Genotype	College Station	Namulonge	Serere	Mean
P_1	Red, intensifier	*RRYYII*	2.0	1.8	1.9	1.9 a[z]
P_2	White, no intensifier	*RRyyii*	5.0	4.7	4.8	4.8 e
F_1	Red, intensifier	*RRYyIi*	1.8	1.7	1.8	1.8 a
F_2	Red, intensifier	*RRY-I-*	1.8	1.8	2.0	1.9 a
	Red, no intensifier	*RRY-ii*	2.8	2.4	2.5	2.6 b
	White, intensifier	*RRyyI-*	3.0	2.8	2.8	2.9 c
	White, no intensifier	*RRyyii*	4.6	4.5	4.5	4.5 d
$F_1 \times P_1$	Red, intensifier	*RRY-I-*	1.8	1.6	1.8	1.7 a
$F_1 \times P_2$	Red, intensifier	*RRYyIi*	1.9	1.7	1.8	1.8 a
	Red, no intensifier	*RRYyii*	3.0	2.9	3.0	3.0 c
	White, intensifier	*RRyyIi*	3.1	2.8	3.0	3.0 c
	White, no intensifier	*RRyyii*	4.8	4.6	4.6	4.7 d
Mean			3.0 h	2.8 f	2.9 g	

[x] Red and white refer to pericarp color.
[y] Grain mold rating is based on a 1–5 scale: 1 = no mold; 2 = 1–10% molded grain; 3 = 11–25% molded grain; 4 = 26–50% molded grain; and 5 = over 50% molded grain.
[z] Means followed by the same letter are not significantly different at $P = 0.05$ using Fisher's LSD.

TABLE 6. Chi-square analysis of the inheritance of mesocarp thickness in the BTx3197 (P_1) × RTx2536 (P_2) cross at College Station, TX, and at Namulonge and Serere, Uganda

				College Station[x]				Namulonge				Serere			
Generation	Phenotype	Genotype	Ratio[w]	O	E	χ^2	p^y	O	E	χ^2	p	O	E	χ^2	p
P_1	Thick mesocarp	*zz*	1	...[z]	...	...	...	...	...	...	...	...	...	...	...
P_2	Thin mesocarp	*ZZ*	1	...	...	...	...	...	...	...	...	...	...	...	...
F_1	Thin mesocarp	*Zz*	1	...	...	...	...	...	...	...	...	...	...	...	...
F_2	Thin mesocarp	*Z-*	3	406	396.0			385	386.3			373	370.5		
	Thick mesocarp	*zz*	1	122	132.0	1.01	0.34	130	128.8	0.02	0.79	121	123.5	0.07	0.74
$F_1 \times P_1$	Thin mesocarp	*Zz*	1	28	29.0			30	28.0			34	31.5		
	Thick mesocarp	*zz*	1	30	29.0	0.07	0.74	26	28.0	0.29	0.60	29	31.5	0.40	0.54
$F_1 \times P_2$	Thin mesocarp	*Z-*	1	...	...	...	...	...	...	...	...	...	...	...	...

[w] Expected segregation ratio for the phenotype in each generation.
[x] O = number of plants of the phenotype observed; E = number of plants of the phenotype expected.
[y] p = probability of a greater χ^2 value (1 df) under the null hypothesis of the segregation ratio.
[z] All plants observed were of the same phenotype, therefore no analysis was performed.

ii had better resistance than had *RRyyI-*. Therefore, both *R-Y-* and *I-* genes conferred grain mold resistance individually, and their effects were additive when present together.

The effect of mesocarp thickness was studied in the progeny of the BTx3197 (P_1) × RTx2536 (P_2) cross (Table 6). All the F_1 plants had thin mesocarps (*Zz*). The F_2 population segregated in the expected 3:1 ratio, and $F_1 \times P_1$ progeny segregated in the expected 1:1 ratio for thin to thick mesocarp, respectively. All the $F_1 \times P_2$ progeny had thin mesocarps. These data demonstrated that the thin mesocarp characteristic was dominant over thick.

BTx3197 had lower mean grain mold ratings (3.4); RTx2536 and all the progeny had the highest (4.8–5.0) mean grain mold ratings (Table 7). Grain mold ratings of the F_1 and all the other progeny were higher than the average of the parents (4.9–5.0). Thus, all the progeny from this cross, whether segregating for thin or thick mesocarp, were highly susceptible to grain mold. This indicated a lack of relationship between resistance and mesocarp thickness. Grain mold severity at College Station, TX, and Serere, Uganda, were not significantly different, although College Station had numerically higher grain mold ratings than had Serere. Namulonge, Uganda, had the lowest disease ratings.

DISCUSSION

Identification of grain mold-resistant sorghum lines is difficult because numerous fungal species are involved, and several types of damage occur. Furthermore, many plant and caryopsis traits are thought to be involved in conferring the resistance. A broader understanding of the genetic control of the resistance will enhance the development of intermating programs designed to generate variability enabling scientists to combine resistance genes.

When the inheritance of B_1, B_2, *R*, *Y*, and *I* genes was analyzed by chi-square, goodness-of-fit tests, the results agreed with the findings of earlier authors (13,15–17,19,20). Complete dominance was found when each locus was considered individually. As a result, a pigmented testa, red pericarp, thin mesocarp, and intensifier are all dominantly inherited.

Examination of the effects of the various gene combinations showed that higher resistance levels could be achieved by combining different genes. Generally, when genes at the loci were dominant for the presence of a pigmented testa (B_1-B_2-), red pericarp (*R-Y-*), and intensifier (*I-*), there was a substantial reduction in grain mold. Progenies with a pigmented testa had higher grain mold resistance than had those without a pigmented testa. A red pericarp conferred grain mold resistance, though not as greatly. The intensifier gene imparted higher levels of grain mold resistance when present than when absent. However, its effect was most apparent when combined with the *R-Y-* genes.

TABLE 7. Relationship of sorghum mesocarp thickness with grain mold resistance in the BTx3197 (P_1) × RTx2536 (P_2) cross at College Station, TX, and at Namulonge and Serere, Uganda

Generation	Mesocarp phenotype	Genotype	Grain mold ratings[y] College Station	Namulonge	Serere	Mean
P_1	Thick	*zz*	3.4	3.3	3.5	3.4 a[z]
P_2	Thin	*ZZ*	5.0	4.7	4.8	4.8 b
F_1	Thin	*Zz*	5.0	4.8	5.0	4.9 c
F_2	Thin	*Z-*	4.9	4.8	5.0	4.9 c
	Thick	*zz*	5.0	4.9	5.0	5.0 c
$F_1 \times P_1$	Thin	*Zz*	5.0	4.8	5.0	4.9 c
	Thick	*zz*	5.0	4.9	5.0	4.9 c
$F_1 \times P_2$	Thin	*Z-*	5.0	4.8	5.0	4.9 c
Mean			4.8 d	4.6 e	4.8 d	

[y] Grain mold rating is based on a 1–5 scale: 1 = no mold; 2 = 1–10% molded grain; 3 = 11–25% molded grain; 4 = 26–50% molded grain; and 5 = over 50% molded grain.

[z] Means followed by the same letter are not significantly different at $P = 0.05$ using Fisher's LSD.

White grain (*RRyy*) had lower grain mold resistance than had red grain (*RRY-*). The greatest resistance was seen when a red pericarp was combined with a pigmented testa (B_1-B_2-*RRY-*). These results have shown that it is possible to estimate the number of genes for resistance to grain mold. The exact number of the genes established will depend on the F_2 population being studied.

Our data agree with earlier reports of grain mold resistance determined by these genes (6,13,16–18). Ellis (6) studied the morphological characteristics indicating grain mold resistance and reported that a pigmented testa was the most influential seed characteristic affecting weathering resistance in the field. Furthermore, within a given genetic background and when a pigmented testa was absent, lines with red or lemon-yellow pericarps were more resistant than lines with white pericarps to grain mold. The ability of a pigmented testa to resist grain mold development is attributed to its high-tannin content. Tannins inhibit spore germination or mycelial growth (4,9,12,17,18). Similarly, sorghum plants with red pericarps contain high levels of flavan-4-ols (11) that confer grain mold resistance.

Sorghum plants with thick pericarps have many starch granules in their mesocarps. For this reason, Raab (17) and Rooney and Miller (18) reported that sorghum plants with thick pericarps are more susceptible to grain mold because they are more capable of supporting fungal growth. Sorghum plants with thin pericarps have few, if any, starch granules, so they are not thought to support fungal development. However, when crosses were made between BTx3197 (thick mesocarp) and RTx2536 (thin mesocarp), all the progenies in F_1, F_2, and BC_1, whether segregating for thin (*Z-*) or thick (*zz*) mesocarp, were susceptible to grain mold. Moreover, the levels of susceptibility of the progenies were higher than those of either parent. Also, the P_1 parent, BTx3197, with a thick mesocarp, was more resistant than RTx2536, with a thin mesocarp. This indicates that the factor(s) determining resistance was unrelated to mesocarp thickness.

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