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Combining Ability for Grain Yield, Percent Protein, and g Lysine/100 g Protein in a Nine-parent Diallel of *Sorghum bicolor* (L.) Moench[1]

F. C. Collins and R. C. Pickett[2]

ABSTRACT

Parents and one set of F_1 hybrids from a nine line diallel of *Sorghum bicolor* (L.) Moench were evaluated for combining ability for grain yield, percentage protein, and g L/100g P using the Griffing analysis. The ranges in performance were 31 to 159 q/ha for yield, 9.2 to 18.2% for protein and 1.74 to 2.74% for lysine in the protein. General (GCA) and specific (SCA) combining ability were found to be important for all three characters. The GCA:SCA ratio of mean squares indicated that additive gene action was more important for protein and less important for yield and g L/100g P. One parent had large GCA effects for all three characters. Several hybrids exhibited heterosis for yield, but only a few hybrids showed heterosis for percentage protein while no positive heterosis was observed for gL/100gP. Protein was negatively correlated with gL/100gP and yield. Yield and gL/100gP were positively associated.

Additional index words: Nutritional quality, Inheritance, Gene action.

RECENTLY, emphasis has been placed on improving the nutritional quality of sorghum which can be accomplished by increasing the level of protein and/or improving the quality of protein. Since lysine appears to be the most limiting amino acid in sorghum protein, the protein quality can be improved by simply increasing the level of the lysine. The world collection has been shown to be an excellent source of germplasm for relatively high levels of protein and lysine. In this experiment diverse lines of *Sorghum bicolor* (L.) Moench were selected for these characteristics and were crossed in all possible combinations to study combining ability for yield, protein, and lysine.

REVIEW OF LITERATURE

Numerous writers have reported general combining ability (GCA) and specific combining ability (SCA) for grain yield in sorghum, but little has been published on the combining ability for protein or lysine. Liang (3) found GCA for protein in a six parent diallel study. The hybrids in his study had significantly lower levels of protein than their better parents. In a later paper (4), he used the Jinks-Hayman method of analysis and concluded that protein content was partially dominant and that there was evidence of epistasis or correlated gene distribution or both. There was an indication that two groups of genes controlled protein content. Malm (5) crossed four male sterile testers with eight exotic lines which varied from 10.8 to 15.5% protein. He found significant amounts of GCA and SCA with GCA being 17.5 times greater than SCA; thus, the level of protein appeared to be due predominantly to additive gene action. Martin, one of the female parents, contributed more than the other females to the protein content of the hybrids. In an earlier paper (1), we reported finding significant amounts of GCA for yield, protein, and lysine; the SCA estimate was not significant for any of the three characters. The test consisted of parents and hybrids developed from crossing 12 exotic lines on to four male sterile testers. Again Martin, which was one of the female parents, contributed more than the other testers to high protein levels. Four crosses exhibited heterosis for percentage protein while percentage lysine in the hybrids never exceeded that of the higher parent. Percentage protein and yield were negatively correlated as was also shown by Malm. Lysine was negatively associated with protein while lysine and yield appeared unrelated.

MATERIALS AND METHOD

Nine parents selected for diversity in protein and lysine levels were crossed in all possible combinations. The F_1's were obtained mainly through hand emasculation and the use of male steriles. Only parents with restorer genes were crossed on to male steriles. The parents, a diallel set of 36 F_1 hybrids, and 'RS 610' (a check) were grown on the Purdue University Agronomy Farm during the summer of 1968. They were planted in a randomized complete block design which was replicated four times. Each plot consisted of four rows 75 cm apart and 4.5 m long. Plots were thinned to 225,000 plants per hectare. The soil type was a Chalmers silty clay loam which had 290 kg/ha of actual nitrogen (half as urea and half as ammonium nitrate) applied the week prior to planting. Grain yield was measured from 3 m of row harvested from each of the two center rows of a plot. Percentage protein (actually crude protein) was obtained by using the microkjeldahl technique to determine the proportion of nitrogen which was multiplied by 6.25 to obtain protein. Lysine, measured as gL/100 g protein (gL/100 gP), was determined from a hydrolyzed sample of the grain by ion-exchange chromatography. Protein and lysine, as well as yield, were measured on every plot. The data were analyzed statistically using "method 2 — model I" of the diallel analysis described by Griffing (2). Heterosis was calculated as the amount that a F_1 deviated above or below the range of the parents.

RESULTS AND DISCUSSION

The combining ability analyses of variance (Table 1) revealed significant levels of GCA and SCA for yield, percent protein, and gL/100gP. This was apparently the first time that SCA had been detected for gL/100gP. The ratio of GCA:SCA mean squares indicated that the additive gene action was probably

Table 1. Combining ability analyses of variance and coefficients of variability for yield, protein, and lysine.

Character	Mean squares†				
	GCA	SCA	Error	GCA:SCA	CV
Grain yield	10,037.66**	983.00**	85.85	10:1	12.1%
Protein	108.1496**	3.5381**	0.3788	31:1	5.0%
Lysine	0.7052**	0.1096**	0.0441	9:1	10.0%

† The mean squares of GCA, SCA, and error have 8, 36, and 132 degrees of freedom, respectively. ** Significant at the .01 level.

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Table 2. Means and estimates of SCA and GCA effects for grain yield of the parents and hybrids from a nine line diallel.

Parent	2319	0075	0508	Rdl	CK 60	Wht	8364	Mrt	1259	Mean of hybrids with a common parent
					Yield, q/ha					
2319	67	159	129	101	93	95	100	97	49	103
0075		85	110	102	96	94	100	91	43	99
0508			76	104	90	96	80	82	48	92
Rdl				72	68	65	62	63	47	76
CK 60					64	61	53	72	51	73
Wht						70	63	59	39	71
8364							55	58	50	71
Mrt								63	43	71
1259									31	46
Mean of RS 610 (check) = 66										
LSD (.05) = 13.0										Estimates of GCA effects
					Estimates of SCA effects					
2319	-45	46	23	7	3	5	14	9	-15	18
0075		-28	3	7	6	3	13	2	-23	19
0508			-24	16	6	12	-1	0	-10	13
Rdl				-4	-4	-7	-7	-6	1	0
CK 60					-4	-6	-11	6	9	-4
Wht						3	-2	-6	-3	-4
8364							-6	-4	11	-7
Mrt								-1	2	-6
1259									14	-29
SE a* = 12										SE = 4
SE b† = 12										

* Standard error of difference between effects of two crosses having one parent in common. † Standard error of difference between effects of two crosses having no parent in common.

more important for protein than it was for yield and gL/100gP; both of the latter appeared to be affected to a greater extent by nonadditive gene action. Since only a few fixed lines were used in this test, it was not possible to obtain valid estimates of the additive and nonadditive components of variance.

Grain yield varied considerably among entries; it ranged from 31 to 159 q/ha. Means and estimates of SCA and GCA effects for yield are reported in Table 2. The parental performance was a good indication of the variety's GCA; the higher yielding parents generally had higher yielding hybrids. However, the hybrids having IS 2319 as one parent were the highest yielding even though IS 2319 only had a medium level of yield. Heterosis was generally expressed by crosses among the higher yielding parents. All crosses involving IS 1259 had yields intermediate to those of their parents. The large negative SCA effects for the parental values of IS 2319, IS 0075, and IS 0508 show that these parents have the ability to combine better than expected based on their own yields. The magnitude of the estimates of their GCA effects indicate that it should be possible to select segregates from crosses among these parents which would be superior to the parents. This would be important in underdeveloped countries where facilities are not available for production and dissemination of hybrid seed. However, maximum utilization of the potential exhibited by the crosses would apparently require the growing of hybrids.

The means and estimates of SCA and GCA effects for protein are shown in Table 3. Protein varied from 9.2 to 18.2%. Hybrids of the higher protein parents, with the exception of IS 0075, generally had higher than average protein levels. The high protein of IS 0075 was not transmitted to its hybrids. Low levels of protein were found in most of the crosses involving IS 0508 — a low protein parent. Two of the hybrids exhibited heterosis for protein; one was a cross between the highest protein parent — IS 1259 — and another high protein parent — Martin. Martin's good GCA for protein in this experiment was consistent with its behavior in earlier studies reported by Malm

Table 3. Means and estimates of SCA and GCA effects for protein of the parents and hybrids from a nine line diallel.

Parent	1259	Mrt	2319	8364	Rdl	Wht	CK 60	0075	0508	Mean of hybrids with a common parent
					Protein, %					
1259	17.4	18.2	16.1	16.3	16.3	16.7	16.2	16.2	16.4	16.5
Mrt		12.8	12.8	13.5	12.5	12.2	11.7	11.9	10.3	12.9
2319			13.4	11.9	11.8	12.3	12.0	11.6	12.0	12.6
8364				10.7	12.6	11.3	11.9	11.2	9.3	12.3
Rdl					10.8	10.6	11.2	11.5	9.2	11.9
Wht						10.4	11.4	10.5	9.8	11.9
CK 60							10.5	10.3	9.5	11.8
0075								13.5	10.8	11.8
0508									10.1	10.9
Mean of RS 610 (check) = 11.0										
LSD (.05) = 0.9										
					Estimates of SCA effects					
1259	-2.9	1.5	-0.5	0.4	0.6	1.2	0.7	0.2	1.6	3.9
Mrt		-0.4	-0.3	1.2	0.3	0.2	-0.4	-0.6	-1.0	0.4
2319			0.5	-0.4	-0.2	0.4	0.1	-0.8	0.8	0.3
8364				-0.8	1.3	0.1	0.7	-0.5	-1.1	-0.5
Rdl					-0.3	-0.4	0.2	0.1	-1.1	-0.7
Wht						-0.4	0.6	-0.9	-0.3	-0.8
CK 60							-0.4	-0.6	-0.6	-0.8
0075								1.6	0.1	-0.3
0508									0.8	-1.5
SE_a* = 0.8										
SE_b† = 0.8										SE 0.3

* Standard error of difference between effects of two crosses having one parent in common. † Standard error of difference between effects of two crosses having no parents in common.

Table 4. Means and estimates of SCA and GCA effects for lysine of the parents and hybrids from a nine line diallel.

Parent	0508	2319	0075	CK 60	8364	Wht	Rdl	Mrt	1259	Mean of hybrids with a common parent
					Lysine, gL/100 g protein					
0508	2.74	2.16	2.18	2.56	2.48	2.32	2.37	2.07	1.92	2.26
2319		2.64	2.11	2.26	2.15	1.91	2.11	2.22	1.88	2.10
0075			1.87	2.02	1.98	2.30	2.16	2.09	1.90	2.09
CK 60				2.45	1.98	1.95	1.95	2.13	1.78	2.08
8364					2.20	2.10	1.98	2.01	1.82	2.06
Wht						2.21	2.01	1.93	1.74	2.04
Rdl							2.02	1.98	1.74	2.04
Mrt								1.91	1.74	2.02
1259									2.04	1.82
Mean of RS 610 (check) = 2.18										
LSD (.05) = 0.29										Estimates of GCA effects
					Estimates of SCA effects					
0508	0.17	-0.28	-0.11	0.17	0.15	0.01	0.09	-0.18	-0.20	0.24
2319		0.34	-0.05	0	-0.05	-0.24	-0.04	0.10	-0.11	0.11
0075			-0.14	-0.09	-0.07	0.27	0.16	0.12	0.06	-0.04
CK 60				0.25	-0.17	-0.18	-0.14	0.06	-0.16	0.06
8364					0.11	0.03	-0.06	0	-0.06	0.00
Wht						0.15	-0.01	-0.06	-0.12	-0.02
Rdl							0.03	0.03	-0.09	-0.05
Mrt								-0.01	-0.06	-0.08
1259									0.37	-0.21
SE_a* = 0.28										
SE_b† = 0.27										SE 0.09

* Standard error of difference between effects of two crosses having one parent in common. † Standard error of difference between effects of two crosses having no parents in common.

(5) and ourselves (1). The gene(s) controlling the high protein of IS 0075 must be recessive and different from those in the other parents since its expression was repressed in F_1's.

Means and estimates of SCA and GCA effects for gL/100gP are given in Table 4. Hybrids having the highest gL/100gP had a high lysine parent and *vice versa*. The hybrids which had IS 0075 as one parent had higher values of gL/100gP than expected. Crosses involving IS 1259 were uniformly very low. Although the hybrid value was usually equal to the mid-parent value, there were a few cases of negative heterosis. None of the hybrids exceeded their better parents. It is interesting that most of the estimates of SCA effects for the parents were positive. It appeared that the parents were unable to exhibit their lysine potential in the F_1's. Evidently, selection would be effective in the improvement of gL/100gP in inbred lines but

Table 5. Phenotypic, genotypic, and environmental correlations among yield, protein, and lysine measured from the nine parent diallel.

Characters correlated	Correlation coefficients		
	Phenotypic	Genotypic	Environmental
Yield and percent protein	-0.60**	-0.61**	-0.22*
Yield and g L/100g P	0.40**	0.47**	-0.12
Protein and g L/100g P	-0.65**	-0.73**	-0.12

* Significant at the .05 level. ** Significant at the .01 level.

care should be exercised in choosing hybrids from this material since they tended to be low in lysine.

Correlation coefficients are presented in Table 5. The genotypic correlations between protein and yield and between protein and gL/100gP were highly significant and negative. Although these correlations are a reflection of the genotypes grown in this experiment, it would appear that selection for the highest levels of protein would be done at the expense of yield and protein quality. Yield and gL/100gP were positively correlated, but selection for high yield would not always result in concurrent increases in protein quality. Environmental influences tended to increase yield while decreasing protein and *vice versa*, but it did so to a lesser degree than the genotypic effects.

CONCLUSIONS

Based on these results, it appears that IS 2319 would probably be the best overall parent from this material in a breeding program. It was effective in transmitting very high yields and better than average protein and gL/100gP levels to F_1's. If IS 0508 were used, the F_1's would be high yielding and the grain would have fairly good protein quality, but the grain would probably be low in protein. If IS 1259 were used, the hybrids would have a very high level of protein but protein quality and yield would be sacrificed.

The levels of GCA and SCA expressed in this experiment indicate that additive and nonadditive gene action were important in the control of these characters. The performance of IS 2319 for all three characters should provide encouragement for the development of homozygous lines, particularly in areas lacking technology for hybrid seed production. However, the full ultilization of the genetic variability exhibited by these parents may depend on the use of hybrids in order to capitalize on the variability due to nonadditive gene action. With careful selection of the parents, it appears possible to develop high yielding hybrids whose grain is superior in protein quantity and quality to that of standard varieties.

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