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Heterosis and Components of Genetic Variation for Protein and Lysine Content in some Grain Sorghums

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Summary. Twelve varieties representing six geographical regions and nine taxonomic groups from a World Collection of *Sorghum* were used in a diallel and line × tester analysis of the nature of genetic variation for protein and lysine content. In a majority of crosses, heterosis was negative for protein, and positive for lysine.

Analysis of combining ability indicated that both additive and non-additive variation were important for protein, while the non-additive component was predominant for lysine. Heterosis in *low* × *low* and *medium* × *low* crosses also indicated the presence of substantial non-allelic gene interactions for both the characters.

Associations between protein, lysine and yield in parents were significantly different from those in the hybrids indicating considerable scope for genetic manipulation. Negative correlations between protein and lysine (% protein) and between protein and grain yield were very low. The results indicated that a high level of protein and moderately high lysine may be incorporated in high yielding varieties of sorghum, by using Caudatum kaura, Roxburghii shallu and durra from Nigeria and Sudan in the hybridisation programme.

Introduction

The traditional areas of sorghum cultivation and consumption in Africa and Asia are also areas of low income and general malnutrition. The low level and poor quality of protein in *Sorghum* compared with other cereals like wheat, rice and maize (Swaminathan *et al.*, 1969), and the pellagragenic nature due to amino acid imbalance (Deosthale *et al.*, 1970), are two major problems which are amenable to solution by genetic manipulation, since genotypic differences for protein and lysine content exist both in the advanced cultivars and the World collections of *Sorghum* (Deosthale *et al.*, 1970; Tripathi *et al.*, 1971; Collins and Pickett, 1972a). The information on the protein and lysine levels in hybrid grain sorghums is limited to types used for feed rather than for human consumption (Liang *et al.*, 1968; Collins and Pickett, 1972b). An attempt has been made, therefore, to estimate the heterosis and nature of genetic variation for protein and lysine in some sorghums used for human consumption and representing the nine taxonomic groups in the World Collection of *Sorghum* classified by Murty *et al.* (1967) and Chandrasekhariah, Murty and Arunachalam (1969) using multivariate analysis.

Material and Methods

Twelve varieties with varying levels of protein (12% to 17.3%) and lysine content (1.43% – 2.13%) and representing six geographical regions were selected from the World Collection of *Sorghum* maintained at the Indian Agricultural Research Institute, New Delhi. Two varieties, IS 9837 (*roxburghii-shallu*) and IS 10526 (*caffrorum*), representing corneous and chalky endosperms, were crossed with the rest of the ten as male parents in a line × tester mating design (Table 1). Seven selected for different levels of protein were mated to obtain a diallel without reciprocals. All these crosses and their parents were planted in a randomized complete block design with two replications during the monsoon season, 1969, at New Delhi (29 °N). The plot was of a single row three metres long with 75 cm spacing between, and 15 cm within, rows. A fertilizer dose of 100 Kg N + 60 Kg P_2O_5 + 60 Kg K_2O per hectare was given. Nitrogen was applied in two split doses, the first half at the time of sowing and the other as top dressing 45 days after sowing. Protection against stem borer was provided by applying lindane granules.

A composite sample of grain from five randomly selected plants was analysed for protein and lysine. Nitrogen was determined by Kjeldahl's method and the value multiplied by 6.25 to obtain protein percent. Lysine was determined by an automated colorimetric method using a Technicon automatic lysine analyser (Schaiberger and Ferrari, 1960) and was expressed as per cent of protein and mg per 100 gm of grain (whole meal) on dry matter basis.

Heterosis was calculated as per cent increase over the superior and midparents. Combining ability analysis in the line × tester mating was done following Kempthorne (1957). Diallel analysis of combining ability was carried out according to Method-2 of Griffing (1956). Estimates of variances of general and specific combining ability in diallel and line × tester mating systems were obtained using the random effects model. In the diallel, the components of genetic variation, namely $\hat{D}$, $\hat{H}_1$, $\hat{H}_2$ and $\hat{F}$, were computed using the method of Hayman (1954). Correlations between protein, lysine and grain yield were estimated separately for parents and crosses and also pooled over all the entries.

Results

Parental Performance and Heterosis: The significant differences observed among parents were also reflected in the variation among hybrids for protein and lysine (Table 2 and 3). The difference between the average performance of parents and hybrids was small but significant with negative heterosis for pro-

Table 1. *Parental performance for three quality characters in Sorghum*

Parents*	Geographical origin	Classificatory status	Protein %	Lysine (% protein)	Lysine (mg/100 gm grain)
1. IS 3922	U.S.A.	*Caffrorum feterita*	11.98	2.015	241.5
2. IS 3924	U.S.A.	*Caffrorum feterita*	14.85	1.865	277.5
3. IS 9837	Sudan	*Roxburghii shallu*	16.42	1.705	280.5
4. IS 10525	U.S.A.	*Caffrorum*	12.54	1.765	228.5
5. IS 10526	U.S.A.	*Caffrorum*	13.76	1.605	221.5
6. IS 10670	Nigeria	*Caudatum kafir*	12.54	1.960	247.0
7. IS 10890	U.S.A.	*Caffrorum*	14.23	1.935	276.0
8. IS 3703	Ethiopia	*Milo kaura*	14.96	1.720	257.5
9. IS 8191	India (Assam)	*Caffrorum birdproof*	17.27	2.130	368.5
10. IS 9985	Nigeria	*Caudatum kaura*	16.28	1.430	234.0
11. IS 10202	Egypt	*Durra*	16.07	1.765	284.0
12. IS 10521	U.S.A.	*Milo*	15.98	1.770	284.0
Low (L)			<13.00	<1.80	<260
Medium (M)			13.00–16.0	1.80–2.00	260–300
High (H)			>16.0	2.00	>300

* 1 to 7 diallel parents; IS 9837 and IS 10526 – female parents and rest of the 10 – male parents in line × tester mating.

Table 2. *Analysis of variance for protein and lysine in Sorghum*

Source	DF	Mean sum of squares		
		Protein %	Lysine (% of protein)	Lysine (mg/100 gm grain)
Replications	1	0.03	0.01	178.0
Entries	42	3.60**	0.15**	3103.2**
Parents	11	6.08**	0.07*	3097.2**
Hybrids	30	2.72**	0.17**	3197.0**
Parents Vs Hybrids	1	2.77*	0.13*	355.0
Error	42	0.57	0.03	821.6
Parental Mean		14.74	1.81	266.7
Hybrid Mean		14.34	1.90	271.2

* Significant at 5%, ** Significant at 1%.

tein percentage and positive heterosis for lysine (% protein). However, both positive and negative heterosis were observed for protein and lysine depending on the cross combination (Table 3). Crosses with high protein (>16%) were low in lysine (% protein) while high lysine (>2.0%) crosses were generally low in protein content.

Combining Ability Analysis: Significant differences among males were observed in their general combining ability (*gca*) for protein and lysine as per cent of protein in line × tester crosses, while differences in *gca* were significant only for protein in the diallel (Table 4). Significant variation for specific combining ability was found for lysine in both the mating designs, with a predominance of non-additive variation.

Components of Genetic Variance: Among the estimates of variance components in the diallel using Hayman's method (1954), additive ($\hat{D}$) and heterosis ($\hat{H}_1$) components were significant for protein, while only heterosis components were significant for lysine (Table 5). Partial dominance for protein was evident while over-dominance was indicated for lysine. The proportion of positive and negative genes among the parents as reflected by $\hat{H}_2/4\hat{H}_1$ was unequal for protein but equal for lysine percentage. The ratio of $\hat{h}^2/\hat{H}_2$ indicated three blocks of genes controlling protein and one block of genes controlling lysine. The intensity of non-allelic gene interactions for lysine appears to have resulted in an underestimate of the number of genes.

The values of $(4\hat{D}\hat{H}_1)^{0.5} + \hat{F}/(4\hat{D}\hat{H}_1)^{0.5} - \hat{F}$ revealed that the proportion of dominant genes in the parents was slightly higher than of recessive genes for protein and lysine % of protein. The high negative correlation between parental order of dominance and parental measure for protein indicated that negative genes were mostly recessive and the improved protein content was due to dominance of positive genes and therefore could be exploited in a hybrid sorghum programme.

General Combining Ability Effects: The general combining ability effects of parents revealed that IS 9985 (*caudatum kaura*) and IS 10670 (*caudatum kafir*) were better combiners for protein and IS 8191

Table 3. *Average performance of hybrids and heterosis ovar superior (SP) and mid-parent (MP) for protein and lysine in Sorghum*

Cross	Protein %		Lysine (% protein)		Lysine (mg/100 gm grain)	
	Hybrid mean	Heterosis (% SP)	Hybrid mean	Heterosis (% SP)	Hybrid mean	Heterosis (% SP)
1. IS 3924 × IS 3922	13.35	−10.10	1.86	− 7.69	248.5	−10.45
2. IS 3924 × IS 10525	14.82	−02.00	2.12	13.67	315.0	13.35
3. IS 3924 × IS 10526	14.36	− 3.30	2.04	9.38	295.0	6.31
4. IS 3924 × IS 10670	12.01	−19.19	1.43	−27.04	171.0	−38.38
5. IS 3924 × IS 10890	15.27	− 3.91	1.73	−10.59	259.5	− 6.49
6. IS 9837 × IS 3703	16.61	1.16	1.56	− 9.30	259.5	− 7.49
7. IS 9837 × IS 3922	13.06	−20.46	2.11	4.71	276.5	− 1.43
8. IS 9837 × IS 3924	14.38	−12.42	1.88	0.80	271.0	− 3.39
9. IS 9837 × IS 8191	13.76	−20.32	2.07	− 2.82	286.0	−22.39
10. IS 9837 × IS 9985	15.54	− 5.36	1.78	4.40	279.5	− 0.36
11. IS 9837 × IS 10202	13.98	−14.86	1.75	− 0.85	237.5	−16.37
12. IS 9837 × IS 10521	13.12	−20.09	2.07	16.95	270.5	− 4.75
13. IS 9837 × IS 10525	13.62	−17.05	1.91	8.21	260.5	− 7.37
14. IS 9837 × IS 10526	13.74	−16.32	1.97	15.54	271.0	− 3.39
15. IS 9837 × IS 10670	14.46	−11.94	1.72	−12.24	251.0	−10.51
16. IS 9837 × IS 10890	15.01	− 8.58	1.89	− 2.32	286.5	2.14
17. IS 10525 × IS 3922	13.30	6.06	2.15	6.70	288.0	19.25
18. IS 10525 × IS 10526	13.00	− 5.52	2.46	39.37	317.0	38.70
19. IS 10525 × IS 10670	14.96	19.30	2.27	15.82	341.5	38.26
20. IS 10526 × IS 3703	13.62	− 8.96	1.91	11.05	261.5	1.55
21. IS 10526 × IS 3922	15.46	−12.35	1.79	−11.17	277.5	14.91
22. IS 10526 × IS 8191	14.27	−17.37	2.07	− 2.82	296.0	19.67
23. IS 10526 × IS 9985	15.27	− 6.20	1.85	15.26	284.0	21.36
24. IS 10526 × IS 10202	13.99	−12.94	1.81	2.55	252.5	−11.09
25. IS 10526 × IS 10521	14.10	−11.76	1.87	5.65	264.0	− 7.04
26. IS 10526 × IS 10670	17.09	24.00	1.89	− 3.57	324.0	31.17
27. IS 10670 × IS 3922	14.32	14.19	1.90	− 5.21	273.0	10.53
28. IS 10890 × IS 3922	13.12	− 7.80	2.44	21.09	319.5	15.76
29. IS 10890 × IS 10525	16.73	17.57	1.04	−46.25	176.5	−36.05
30. IS 10890 × IS 10526	14.00	− 1.62	1.29	−33.33	182.0	−34.06
31. IS 10890 × IS 10670	14.87	4.49	2.11	7.65	313.0	13.41

Table 4. *Combining ability analysis for protein and lysine in diallel (D) and line × tester (L × T) crosses in Sorghum*

Source	DF	Mean sum of squares					
		Protein %		Lysine (% protein)		Lysine (mg/100 gm grain)	
a) Diallel crosses							
GCA	6	8.60*		0.05		133.00	
SCA	21	2.37		0.11**		2373.00*	
Error	27	3.08		0.03		951.00	
b) Line × Tester crosses							
Female effects	1	2.13		0.01		562.70	
Male effects	9	2.43*		0.12**		1524.53	
Female × Male interactions	9	1.55		0.11**		2205.25*	
Error	19	1.00		0.02		814.31	
		D	L × T	D	L × T	D	L × T
$\hat{\sigma}^2_{gca}$		0.69	0.10	−.01	0.00	−248.9	19.94
$\hat{\sigma}^2_{sca}$		0.83	0.27	0.10	0.40	1897.5	695.47
$\hat{\sigma}^2_{gca}/\hat{\sigma}^2_{sca}$		0.83	0.37	−.10	0.00	−0.13	0.02

* Significant at 5%, ** Significant at 1%.

Table 5. *Estimates of variance components for protein and lysine in diallel crosses in Sorghum*

	Protein %	Lysine (% protein)	Lysine (mg/100 gm grain)
$\hat{D}$	10.02* ± 0.67	0.004 ± 0.060	147.1 ± 1184.4
$\hat{F}$	11.03** ± 1.60	0.005 ± 0.143	965.3 ± 2821.2
$\hat{H}_1$	6.45** ± 1.62	0.398* ± 0.144	8744.5* ± 2846.4
$\hat{H}_2$	3.49* ± 1.43	0.373* ± 0.127	7892.6* ± 2512.5
h^2	9.62** ± 0.24	0.039 ± 0.085	4039.3 ± 1686.8
$(\hat{H}_1/\hat{D})^{0.5}$	0.802	9.845	7.709
$\hat{H}_2/4\hat{H}_1$	0.135	0.234	0.225
$\frac{(4\hat{D}\hat{H}_1)^{0.5}+\hat{F}}{(4\hat{D}\hat{H}_1)^{0.5}-\hat{F}}$	1.186	1.108	1.543
r	−0.917	0.073	−0.120
r^2	0.841	0.005	0.014

* Significant at 5%, ** Significant at 1%.

Table 6. *General combining ability effects of parents for protein and lysine in diallel and line × tester mating systems in Sorghum*

Sl. No.	Parent	Protein %		Lysine (% protein)		Lysine (mg/100 gm grain)	
		Diallel	L × T	Diallel	L × T	Diallel	L × T
1.	IS 3922	−0.55**	−0.02	0.13	0.06	10.60	5.40
2.	IS 3924	−0.25	0.09	−0.04	0.07	−9.80	11.40
3.	IS 9837	−0.24	−0.23	−0.03	−0.01	−0.50	− 3.75
4.	IS 10525	−0.21	−0.97	0.05	0.30**	13.20	17.15
5.	IS 10526	0.33**	0.23	−0.05	0.01	7.80	3.75
6.	IS 10670	0.35**	1.47*	0.02	−0.08	−7.60	15.90
7.	IS 10890	0.56**	0.22	−0.08	−0.29**	−13.70	−37.35
8.	IS 3703		−0.41		−0.15**		−11.10
9.	IS 8191		−0.25		0.18**		19.40
10.	IS 9985		1.13*		−0.06		10.15
11.	IS 10202		−0.56		−0.11		−26.60
12.	IS 10521		−0.67		0.08		− 4.35
	SE ($\hat{g}_i$)	0.18		0.04		9.75	

* Significant at 5%, ** Significant at 1%.

and IS 10525 were good combiners for lysine measured as per cent of protein, based on the results of both the diallel and line × tester experiments (Table 6).

Character Associations: The phenotypic and genetic correlations indicated a positive association between protein and lysine (mg/100 gm grain) accounting for nearly 52% of the genotypic variability in parents, but no such association was found in the hybrids (Table 7). The negative association of protein with grain yield in hybrids was not present in the parents. Other associations were very low, except the highly positive association between the two measures of lysine content. These contrasting results of association between the quality characters in parents vs hybrids indicate that adverse associations can be modified genetically in a favourable direction or neutralised in some recombinants.

Discussion

Sorghum is widely distributed all over the tropics in Africa and some of its diverse forms could have arisen by disruptive selection (Doggett, 1970). The collections from West and Central African countries and some Indian material represent mostly diverse and unselected bulk, while *caffrorums* and its derivatives from the United States are the products of intense human selection. The higher protein content observed in some African and Indian varieties in the World collection (Murty *et al.*, 1967) reveals that natural selection has preserved varieties with high protein while intense human selection in pursuit of higher grain yield has resulted in low protein types as observed in the *caffrorums* of the USA. Thus, groups like *roxburghii shallu, caudatum kaura* and *durra* from Africa are good sources of protein content and quality. IS 9985 (*caudatum kaura*) and IS 10670 (*caudatum kafir*) from Nigeria have shown better performance in hybrid combinations and thus are good combiners for protein. On the other hand, *caffrorum* and its derivatives provide a good source of lysine.

The crosses between *high* × *high*, *high* × *low* and *medium* × *low* parents did not show heterosis over

Table 7. *Phenotypic and genotypic (in parenthesis) correlation among three quality characters and grain yield in Sorghum*

	Lysine (% protein)	Lysine (mg/100 gm grain)	Grain yield
A. Parents			
Protein %	−0.234 (−0.268)	0.675* (0.721)	−0.156 (−0.261)
Lysine (% protein)		0.560 (0.481)	−0.179 (−0.085)
Lysine (mg/100 gm grain)			−0.253 0.454
B. Hybrids			
Protein %	−0.358 (−0.453)	0.134 (0.012)	−0.425* (−0.532)
Lysine (% protein)		0.870** (0.882)	0.048 (0.171)
Lysine (mg/100 gm grain)			−0.039 (0.238)
C. Parents + Hybrids			
Protein %	−0.304 (−0.353)	0.307* (0.284)	−0.470** (−0.569)
Lysine (% protein)		0.798** (0.772)	0.082 (0.201)
Lysine (mg/100 gm grain)			−0.051 (0.189)

* Significant at 5%, ** Significant at 1%.

the role of general and specific combining ability for protein in *Sorghum*. The predominance of the non-additive component and the high level of dominance for lysine impose severe limits on the progress of selection. However, the absence of a strong adverse association between protein and lysine content in this study is encouraging, so that lysine content can be improved without serious loss in protein content.

The change in other attributes as a result of selection for a desirable trait will depend on the magnitude and direction of genotypic correlations among them. Lysine and yield showed very low association so both these characters seem to be independent. Therefore, a high level of lysine can be incorporated in high yielding varieties, and breeding for high yielding protein lines with moderately high lysine is possible, using the Nigerian and Sudanese material with high gca effects such as the *caudatum kaura*, *roxburghii-shallu* and *durra* groups of the World collection.

It would appear that hybrid sorghums with a high level of protein using the above lines as one of the parents with the available male steriles could also be developed, utilizing both the additive and non-additive components of variation for protein and lysine, while inbred lines or varieties with high protein and moderate levels of lysine might also be isolated. Further collection and evaluation of these taxonomic categories from Sudan and Nigeria would be useful.

Table 8. *Mean and number of total heterotic crosses between different groups*

Group	Protein (%)		Lysine (% Protein)		Lysine (mg/100 gm grain)	
	Group mean	Heterotic/total crosses	Group mean	Heterotic/total crosses	Group mean	Heterotic/total crosses
H × H	14.43	0/3	—	—	—	—
H × M	14.73	1/3	2.07	1/3	286.0	0/1
H × L	14.15	0/8	2.04	2/5	295.0	1/1
M × M	—	—	1.76	0/3	265.0	0/5
M × L	13.93	0/7	1.79	3/9	243.2	6/17
L × L	14.69	7/10	1.90	10/11	299.1	7/7
Low (L)		<13.0	<1.80		260	
Medium (M)		13.00−16.00	1.80−2.00		260−300	
High (H)		>16.00	>2.00		>300	

the superior parent for protein (Table 8) and the group means of these crosses were also low, indicating negative heterosis. High lysine parents appear to give hybrids better in lysine, while all the *low* × *low* combinations were also heterotic for lysine.

The estimates of general combining ability effects (*gca*) in diallel and male effects in line × tester for protein have indicated the differences among parents for *gca* effects even in this limited number of parents. It should be possible to select better parents by further examination of the variation for these characters in *roxburghii* and *caudatum kaura* and *durras* from Sudan and Nigeria. Since the magnitude of $\hat{\sigma}^2_{gca}$ (0.69) is as high as $\hat{\sigma}^2_{sca}$ (0.83) for protein and the degree of dominance is low, both additive and non-additive gene action are important in selecting for high protein, as observed by Malm (1968) regarding

Our results are in contrast to the reports of a strong adverse association ($r = -0.64$) between protein and lysine content by Collins and Pickett (1972b) whose material consisted predominantly of *kafir* and *bicolor* types not normally used for human consumption. Their own earlier work (1972a), including 12 lines from the same World Collection assembled in India in crosses with four male steriles of *Kafir* type from the USA, indicated a lower negative association ($r = -0.34$) between protein and lysine and the absence of any significant association between yield and lysine, which are comparable to the results in our study. This is supported by the recent detection of two high-lysine lines from Ethiopia with 15.7 and

17.2 per cent protein from 62 floury endosperm lines from the same World Collection (Rameshwar Singh and Axtell, 1973), which are clear exceptions to the reports of a strong negative association between protein and lysine in Sorghum. The simple recessive nature of the high-lysine allele supports our conclusion from the diallel analysis that one block of genes is involved for lysine. The high-lysine lines have an altered amino-acid pattern with a leucine/isoleucine ratio slightly more favourable than their normal sibs, but similar in 100-seed lot. Thus it would appear that simultaneous improvement of protein, lysine and some yield components is possible.

The present investigation is based on different taxonomic groups with free gene exchange but possibly with different adaptive gene complexes. Therefore, it will be necessary to promote recombination by breaking the linkages and releasing the latent variability in crosses between them. As suggested by Doggett (1970), a programme of recurrent selection and hybridization using composites of two or more populations from material showing considerable heterosis would also be useful for protein improvement in Sorghum. Such a population breeding programme, involving the range of the three taxonomic groups found useful in this study would be advantageous for the development of varieties as well as hybrids between selections from them, instead of the traditional crossing involving a narrow range of genotypes hitherto used in Sorghum breeding.

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