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Genetic Analysis of Protein, Lysine, Gluten and Flour Yield in Bread Wheat (*Triticum aestivum* L.)

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Abstract: The study was carried out to investigate the nature of gene action determining the inheritance pattern of protein, lysine, gluten and flour yield in eight wheat varieties (Pak 81, Pothowar 93, Parwaz 94, Shahkar 95, Suleiman 96, Chakwal 97, Kohistan 97 and MH 97) selected on the basis of phenotypic diversity. In order to ascertain the gene action involved in the inheritance of these characters, the techniques like analysis of variance of Hayman model and genetic component analysis were employed. The estimates of components of genetic variation showed that additive genetic effects controlled the expression of traits like protein contents and flour yield, however, non-additive gene effects were more important for lysine contents and gluten contents. Directional dominance was observed in case of protein contents, which indicated the possibility of further improvement in this particular trait. Protein contents and flour yield being controlled by additive genetic effects with partial dominance suggested that selection could be practiced in early segregating generations for improvement in these traits.

Key words: Wheat, gene action, quality traits, selection

INTRODUCTION

A great deal of research has been done in the domain of wheat breeding, which resulted towards significant breakthrough in the national wheat production. However, the importance of wheat quality remained ignored. Wheat is supreme among cereals largely due to fact, that its grain contains protein with unique chemical and physical properties. The bread making quality of bread wheat is determined by several factors of which the quantity and quality of gluten forming storage proteins is critical (Beitz, 1987).

The literature regarding the role of gene action controlling wheat quality traits is meager. However, different scientists have reported involvement of partial dominance type of gene action for protein contents like Bajwa *et al.* (1985) and El-Haddad *et al.* (1996). Over dominance type of gene action for economic yield per plant in the absence of non-allelic interactions was reported by Asif *et al.* (1999).

The magnitude and type of gene action in a particular population serves as criteria for selection of parents, which after hybridization are likely to produce the best recombinants for desirable traits. To improve leavened

bread-making quality, there is a need to improve both gluten strength and extensibility through the increased use of high quality bread wheat germplasm in the crossing programs (Abdalla *et al.*, 2006). Diallel crossing system has been widely used to ascertain the genetic reliability among the group of varieties/strains in F₁ generation. Diallel analysis, as developed by Hayman (1954 a,b) and Jinks (1954) provides a systematic approach for the selection of parents and crosses superior for the traits under investigation.

The main objective of the present study was to assess the nature of gene action determining the inheritance pattern of protein, lysine, gluten and flour yield in eight local bread wheat varieties, on the basis of which future wheat breeding programs could be made.

MATERIALS AND METHODS

The experimental material constituted eight promising wheat genotypes, which were selected for studying the inheritance pattern of quality attributes were obtained from National Agriculture Research Center (NARC), Islamabad, Pakistan. An 8×8 wheat parent diallel cross was conducted. Eight wheat varieties (Pak-81, Pothowar

93, Parwaz 94, Shahkar 95, Suleiman 96, Chakwal 97, Kohistan 97 and MH 97) were selected on the basis of phenotypic diversity and sown in the departmental farm of Plant Breeding and Genetics, University of Arid Agriculture, Rawalpindi, Pakistan during November 2000 with 2 sowing dates (5th and 20th November) in order to facilitate hybridization. Crossing of the varieties was performed during February/March 2001, whereas, the parent varieties were self-pollinated to maintain the true to type seed. At the time of harvesting, crossed spikes were individually harvested/threshed to have seed for raising F₁ generation.

The seeds of an 88 parent diallel (28 direct crosses and 28 reciprocal crosses) along with their parents were sown in the field on 3rd of November 2001. Randomized complete block design was followed in the experiment having 3 replications. Each treatment comprised of a single row of 5 m length in each replication. Inter row and inter plant distances were kept at 30 and 20 cm, respectively. Basal fertilizer dose of NPK was applied at the rate of 100-40-0 kg ha⁻¹ to meet the nutritional requirements of the crop.

Protein contents were determined by Kjeldhal's method of nitrogen estimation. After total nitrogen determination by the Kjeldahl procedure protein contents values were determined as N×6.25 and expressed as a % dry matter. Total lysine contents were estimated according to the method described by Miyahara and Jikoo (1967). The whole wheat flour was prepared by milling the wheat grains through Udy Cyclone Mill under laboratory conditions. Flour yield was calculated by separating bran from flour and then calculating flour percentage. Gluten contents were estimated by Martin process as described by Kent and Evers (1994). The data regarding protein contents, lysine contents, flour yield and gluten contents were recorded after harvest.

The data were subjected to simple analysis of variance technique (Steel and Torrie, 1980), to establish the significant differences among parental lines and hybrids for various characters. Additive-dominance model of Hayman (1954 a, b) was used to study the basis of genetic variation in early generations like F₁ and it also provides the nature and magnitude of the genetic behaviour. The genetic parameters i.e., E, D, F, H₁ and H₂, h², H₂/4H₁, (H₁/D), ¹/₂KD/KR, h/H₂² and heritability estimates in narrow sense were computed using the formulae given by Mather and Jinks (1982).

RESULTS AND DISCUSSION

The mean squares of the analysis presented in Table 1 showed that genotypic differences for all the characters were highly significant (p<0.01). Therefore, the

data were arranged in diallel tables for formal analysis of variance. Hayman's analysis of variance was conducted for each character under study and is discussed as follows:

Protein contents: The analysis of variance of diallel data for protein contents (Table 2) exhibited significant differences for all the items except b₃. The significant a and b items indicated the role of additive and dominance properties of gene effects in the inheritance of protein contents. The components b₁ and b₂ were significant (p<0.05) suggesting the presence of directional dominance and asymmetrical distribution of genes. The non-significant b₃ item indicated the absence of specific gene action. The c and d items were significant at p<0.01 and p<0.05, respectively and it necessitated to retest a and b items against mean squares of c and d, respectively. After retesting, the significance of a item changed to non-significant which revealed that the genes with maternal effects masked the properties of additive genetic effects. Similarly, the significant b₁, b₂ and b items also changed to non-significant showing that the genes with reciprocal effects modified the effects of dominance genes. However, b₃ item remained unchanged.

The study of formal analysis of variance (Table 2) revealed that the item b was significant. The data were therefore subjected to analysis of Variance (Vr) and Covariance (Wr). To test the adequacy of data to the simple additive dominance model, uniformity of Wr-Vr and regression analysis were carried out. The results of both tests are given in Table 3. The regression coefficient (b) departed significantly from zero as well as from unity showing failure of assumptions. However, the uniformity test revealed the complete fulfillment of the assumptions.

Table 1: Analysis of variance of different quality traits in F₁ generation during the year 2001

Parameters	Genotypic mean squares	Replication mean squares	Error mean squares
Protein contents (%)	2.44**	11.46	1.13
Lysine contents (%)	1.24**	0.26	0.03
Flour yield (%)	18.49**	0.49	5.65
Gluten contents (%)	23.53**	72.15	11.70

**Highly significant

Table 2: Validity of hypothesis through two scaling tests

Parameters	Analysis of uniformity of Wr-Vr (t ²)	Joint regression analysis		
		Regression coefficient ± Standard error	Ho: b = 0	Ho: b = 1
Protein contents (%)	0.12	b = 0.66±0.26	2.57*	3.34*
Lysine contents (%)	0.76	b = 0.77±0.14	3.37*	3.75**
Flour yield (%)	0.01	b = 0.66±0.19	5.15**	0.62
Gluten contents (%)	1.04	b = 0.89±0.17	5.44**	3.63*

**,*Significant at 1 and 5% probability level, respectively

Table 3: Formal analysis of variance for protein contents in an 8×8 diallel cross of wheat

Source of variation	df	SS	MS	Variance ratio	Retested against	
					c	d
a [†]	7	18.23	2.61	3.05*	0.44	
b ₁ [‡]	1	9.88	9.88	21.86*		3.81
b ₂ [‡]	7	18.91	2.70	4.13*		1.04
b ₃ [‡]	20	39.36	1.96	1.30		0.75
b [‡]	28	68.16	2.43	1.93*		0.94
c [‡]	7	41.30	5.90	6.72**		
d [‡]	21	54.37	2.59	2.25*		
Blocks	63	182.06	2.88	2.17**		
B×a	14	11.96	0.85			
B×b ₁	2	0.91	0.45			
B×b ₂	14	9.14	0.65			
B×b ₃	40	60.30	1.51			
B×b	56	70.35	1.26			
B×c	14	12.28	0.88			
B×d	42	48.19	1.15			
Block interaction	126	142.78	1.13			

** Highly significant, * significant, a[†] = Additive effect, b[‡] = Dominance effect, b₁[‡] Directional dominance, b₂[‡] = Asymmetrical dominance, b₃[‡] Specific gene action, c[‡] Maternal effect, d[‡] = Reciprocal effects

Table 4: Estimates of genetic components of variation in protein contents

Parameters	Estimates
D	0.063±0.076*
F	0.150±0.182 ^{NS}
H ₁	0.146±0.177 ^{NS}
H ₂	0.127±0.154 ^{NS}
h ²	0.058±0.103 ^{NS}
E	0.021±0.025*
(H ₁ /D) ^{0.5}	2.308
H ₂ /4H ₁	0.165
KD/KR	0.256
Heritability (B.S.)	-0.319
r (Wr + Vr) Yr	-0.958
r ²	0.917
h ² /H ₂	-0.093

* Significant (when the value of a parameter divided by its standard error)
NS = Non significant

Both the tests suggested that simple additive dominance model partially adequate to determine the genetic components.

The significance of D component indicated the importance of additive gene action against non-significant dominance components i.e., H₁, H₂ and h² (Table 4). A positive value of F revealed that dominant alleles were more frequent than the recessive ones. Partial dominance was involved in this trait on the basis of (H₁/D)^{0.5} value. As the H₂/4H₁ deviated from its expected value of 0.25, therefore, the gene distribution was asymmetrical. The KD/KR ratio suggested that more number of dominant alleles were present in the parents for this character. These conclusions are quite in accordance with those of Bajwa *et al.* (1985) and El-Haddad *et al.* (1996) who reported the involvement of partial dominance type of gene action for protein contents. As it is held that by increasing yield we observe a considerable decrease in protein contents of wheat, which makes yield

Table 5: Formal analysis of variance for gluten contents in an 8×8 diallel cross of wheat

Source of variation	df	SS	MS	Variance ratio	Retested against	
					c	d
a	7	557.67	79.67	12.48**	3.66	
b ₁	1	32.19	32.19	11.18		2.41
b ₂	7	38.33	5.48	1.46		0.41
b ₃	20	399.81	19.99	4.82**		1.50
b	28	470.33	16.80	4.20**		1.26
c	7	152.33	21.76	4.84**		
d	21	279.67	13.32	2.81**		
Blocks	63	1460.00	23.16	5.07		
B×a	14	89.33	6.38			
B×b ₁	2	5.76	2.88			
B×b ₂	14	52.17	3.73			
B×b ₃	40	165.62	4.14			
B×b	56	223.54	3.99			
B×c	14	62.92	4.49			
B×d	42	199.08	4.74			
Block interaction	126	574.87	4.56			

** Highly significant, * Significant

improvement a difficult process to handle. The present study results indicated that improvement can be made in this particular character besides increase in yield.

Lysine contents: The results of formal analysis of variance of diallel data for lysine contents are given in Table 5. The significant (p≤0.01) a and b items exhibited the presence of additive and dominance effects in the genetic control of lysine contents. The non-significant b₁ item revealed the absence of directional dominance effects. As b₂ and b₃ items were significant (p≤0.01), the genes for lysine contents were distributed asymmetrically among the parents and specific gene effects were also present. Significant values of c and d items indicated the presence of maternal and reciprocal effects. Due to significant c and d items, mean square of item a was retested against c and mean squares of b, b₁, b₂ and b₃ items against d mean square. After retesting, the significance of a item reduced to non-significance and this showed that the additive genetic effects were masked by the maternal effects. Similarly, the values of b, b₁, b₂ and b₃ items also changed to non-significant after retesting against d item. This showed that the reciprocal effects influenced the dominance properties of the genes.

As the item b was significant for lysine contents, the analysis of Variance (Vr) and Covariance (Wr) was conducted for this trait. The perusal of both the scaling tests revealed the adequacy of data to the simple additive dominance model, uniformity of Wr-Vr and the regression analysis were carried out. The regression coefficient (b) departed significantly from zero as well as from unity showing failure of assumptions. However, the uniformity test completely fulfilled the assumptions. Both the tests suggested that simple additive dominance model adequates to determine the genetic components.

Table 6: Estimates of genetic components of variation in gluten contents

Parameters	Estimates
D	0.751±0.743*
F	1.783±1.765*NS
H ₁	1.734±1.717*
H ₂	1.509±1.494*
h ²	1.809±0.999*
E	0.251±0.249*
(H ₁ /D) ^{0.5}	0.649
H ₂ /4H ₁	0.847
KD/KR	-0.399
Heritability (B.S.)	0.461
r(Wr + Vr) Yr	-0.970
r ²	0.941
h ² /H ₂	1.260

* Significant (when the value of a parameter divided by its standard error exceeds 1.96), NS = Non significant

The results given in (Table 6) revealed that both additive and non-additive genetic effects were significant. However, the dominance components (H₁, H₂) effects were more prominent. The H₂ component was found to be approximately equal to H₁, showing that positive and negative alleles were equal in proportion among the parents. Over dominance type of gene action controlled this character as indicated by (H₁/D)^{0.5} ratio. Asymmetrical gene distribution in the parents was apparent as H₂/4H₁ ratio deviated from its expected value. The ratio KD/KR suggested that dominance alleles were more frequent than those of recessive alleles. These results are in accordance with those of Raine *et al.* (1979) who also reported non-additive gene action for this trait. Lysine contents present a constant problem to breeders, that its content is very low in wheat. The present investigation also concluded that improvement in lysine is accompanied by decrease in yield.

Flour yield: Analysis of variance of F₁ data for flour yield showed significant differences (p≤0.01) for item a suggesting the presence of additive genetic effects in the manifestation of flour yield (Table 7). Highly significant b item indicated the presence of dominance effects of genes. The non-significant b₁ item showed the absence of any directional dominance effects. The parent's contained different numbers of dominant genes for flour yield as b₂ item was significant (p≤0.01). The significant b₃ (p≤0.01) revealed the presence of specific gene action. Maternal effects were also observed in the genetic control of flour yield as c item was significant (p≤0.01) whereas reciprocal effects were not absent as d item was non-significant. Since c item was significant, therefore a item was retested against mean square of c. After retesting a item reduced to non-significant showing that additive genetic effects were masked by the maternal effects.

The perusal of Hayman's analysis of variance of diallel tables showed that the item b was significant for

Table 7: Formal analysis of variance for lysine contents in an 8×8 diallel cross of wheat

Source of variation	df	SS	MS	Variance ratio	Retested against	
					c	d
a	7	12.88	1.84	39.14**	1.23	
b ₁	1	0.06	0.06	0.95		0.05
b ₂	7	2.18	0.31	5.65**		0.27
b ₃	20	28.39	1.42	44.34**		1.21
b	28	38.63	1.09	28.76**		0.94
c	7	10.43	1.49	33.08**		
d	21	24.52	1.17	38.93**		
Blocks	63	78.45	1.25	33.70**		
B×a	14	0.65	0.05			
B×b ₁	2	0.12	0.06			
B×b ₂	14	0.76	0.06			
B×b ₃	40	1.28	0.03			
B×b	56	2.18	0.04			
B×c	14	0.62	0.05			
B×d	42	1.25	0.03			
Block interaction	126	4.70	0.04			

** Highly significant, * Significant

flour yield, therefore the analysis of Variance (Vr) and Covariance (Wr) was further carried out. Two scaling tests were carried out to ascertain the adequacy of the additive dominance model for the data sets. The analysis of data revealed that uniformity of Wr-Vr test validated the results. Similarly, the regression analysis also completely validated the data for further genetic studies.

Both additive genetic component (D) and non-additive genetic components (H₁, H₂) were involved in the expression of this character (Table 8). The additive gene effects, however, seemed to be more prominent due to higher magnitude of component D than both of H₁ and H₂. A positive and significant F value indicated that dominant alleles were more frequent than recessive alleles. Partial dominance was indicated for this trait on the basis of (H₁/D)^{0.5} ratio. Lower value of H₂/4H₁ revealed asymmetrical distribution of gene. The ratio of KD/KR suggested the involvement of more dominant alleles in the parents for this trait. The findings of Haraska *et al.* (1979) are in agreement with the present results. This finding indicated that future breeding program should be aimed at improving flour yield besides yield increase as it is controlled by additive type of gene action and selection can be performed for this trait as early as first generation.

Gluten contents: The results of formal analysis of variance of diallel data regarding gluten contents are given in Table 9. The significant (p≤0.01) a and b items exhibited the presence of additive and dominance genetic effects for gluten contents. The non-significant b₁ item revealed the absence of directional dominance. The non-significant b₂ item indicated the symmetrical distribution of dominance genes among the parents. The component b₃ was significant (p≤0.01), which indicated the presence of specific gene action in the inheritance of this character.

Table 8: Estimates of genetic components of variation in lysine contents

Parameters	Estimates
D	0.231±0.046*
F	0.148±0.109 ^{NS}
H ₁	0.769±0.106*
H ₂	0.701±0.092*
h ²	0.002±0.061 ^{NS}
E	0.013±0.015 ^{NS}
(H ₁ /D) ^{0.5}	1.824
H ₂ /4H ₁	0.228
KD/KR	1.428
Heritability (B.S.)	0.948
r (Wr + Vr) Yr	-0.987
r ²	0.985
h ² /H ₂	0.003

* Significant (when the value of a parameter divided by its standard error exceeds 1.96) NS = Non significant

Table 9: Formal analysis of variance for flour yield in an 8×8 diallel cross of wheat

Source of variation	df	SS	MS	Variance ratio	Retested against c
a	7	269.60	38.51	8.43**	1.23
b ₁	1	1.90	1.90	0.17	
b ₂	7	139.12	19.87	4.40**	
b ₃	20	298.69	14.93	3.16**	
b	28	439.71	15.70	3.21**	
c	7	219.11	31.30	4.68**	
d	21	237.03	11.28	1.68	
Blocks	63	1165.44	18.49		
B×a	14	63.91	4.56		
B×b ₁	2	21.54	10.77		
B×b ₂	14	63.16	4.51		
B×b ₃	40	188.61	4.71		
B×b	56	273.32	4.88		
B×c	14	93.45	6.67		
B×d	42	281.48	6.70		
Block interaction	126	712.15	5.65		

** Highly significant, * Significant

The c and d items were significant ($p \leq 0.01$), therefore item a mean square was retested against c item and mean squares of b, b₁, b₂ and b₃ items against d. After retesting a item was reduced to non-significant indicating that additive genetic effects were masked by the genes with maternal effects. Similarly, the non-significant b, b₁, b₂ and b₃ items suggested the predominant role of reciprocal effects on the dominance genes for gluten contents.

Since Hayman's analysis of variance of diallel tables showed that the item b was significant for gluten contents, the analysis of Variance (Vr) and Covariance (Wr) was conducted for this trait. The two scaling tests i.e., uniformity of Wr-Vr and regression analysis were carried out to determine the fitness of data to the additive dominance model (Table 9). The uniformity of Wr-Vr completely fulfilled the assumptions, however, joint regression analysis showed failure i.e., b is significantly different from zero as well as from unity. Thus, on the basis of results of scaling test the simple genetic model was partially adequate to analyse the data.

Table 10: Estimates of genetic components of variation in flour yield

Parameters	Estimates
D	12.629±0.765*
F	13.459±1.816*
H ₁	10.330±1.767*
H ₂	6.755±1.537*
h ²	-0.535±1.028 ^{NS}
E	1.857± 0.256*
(H ₁ /D) ^{0.5}	0.904
H ₂ /4H ₁	0.163
KD/KR	3.868
Heritability (B.S.)	0.622
r(Wr + Vr) Yr	-0.544
r ²	0.296
h ² /H ₂	-0.079

* Significant (when the value of a parameter divided by its standard error exceeds 1.96), NS = Non significant

Both additive and non-additive types of gene actions were involved in the inheritance of gluten contents (Table 10). However, the non-additive genetic components (H₁, H₂, h₂) seemed to be more prominent due to their higher magnitude. Over dominance was indicated for this trait on the basis of (H₁/D)^{0.5} ratio. As the H₂/4H₁ ratio was very close to the expected value, hence suggested the symmetrical gene distribution among the parents. The KD/KR ratio revealed that recessive alleles were more frequent than dominant alleles. The research findings of Mandloi *et al.* (1974) are in accordance with the results of the study. Further improvement in this trait poses difficulties as it is predominantly controlled by non additive type of gene action. Selection for this character in early generation is difficult.

The results of validity test indicated the adequacy of the model for grain yield plant⁻¹, protein contents, lysine contents and gluten contents. For flour yield, the uniformity of Wr and Vr (t² test) validated the model, but the regression analysis showed the failure of the assumptions. Earlier findings of Kearsley and Jinks (1968) and Daly and Robson (1969) pointed out that in studies of quantitative inheritance, complete validity of all the assumptions is unlikely. When a trait exhibits a partial failure of the assumptions, estimates of genetic parameters of that trait are still possible (Hayman, 1954a,b).

The genetic analysis revealed that additive genetic effects were controlling protein contents and flour yield however, non-additive gene effects appeared to be more important for lysine contents and gluten contents. The comparison of these two components showed that genes acting non-additively were more pronounced than additively.

CONCLUSIONS

Based on these results, it could be stated that all modes of gene action i.e., additive, dominance and over dominance are responsible for the inheritance of protein,

lysine, gluten contents and flour yield in this diallel cross, selection for high quality wheat should be effectively practiced in future breeding programs involving wheat varieties used in this cross. There is wide scope available for the wheat breeders to address the problem of increase in wheat quality not compromising on its yield.

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