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ROLE OF GENETIC INTERACTIONS IN THE INHERITANCE OF GRAIN PROTEIN, TRYPTOPHAN AND LYSINE PERCENTAGE IN MAIZE (*ZEA MAYS* L.) UNDER CONTRASTING WATER REGIMES

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ABSTRACT

Maize is top most produced cereal and serves millions of people as their staple food globally. It is important source of nutrients like starch, protein and oil contents. However, normal maize varieties are deficient in essential amino acids of tryptophan and lysine. Understanding of genetic effects controlling the expression of these traits is important for development of maize varieties with favourable balances of protein and essential amino acids. In this study, generation mean analysis was used to understand the genetic effects responsible for these traits in different environmental conditions. Ten crosses and their subsequent generations F_1, F_2, back-cross 1 (BC_1) and back-cross 2 (BC_2) were developed and evaluated for genetic effects under normal irrigation supply and water stress conditions. Results of Hayman's six parameter model showed that additive effects, dominance effects and epistatic interactions played role in the inheritance of these traits. The significance of these genetic effects and interactions varied for different parental combinations under different water regimes. Thus, the information provided by this study can guide breeders to design specific strategies for particular parental combinations, aiming to improve protein, tryptophan and lysine percentages.

Keywords: generation mean analysis, Hayman's six parameter model, genetic effects, protein percentage, maize.

INTRODUCTION

The importance of maize is well realized as, with other cereals, it has been serving the dietary needs of human population since its domestication around 6000 BC in regions of southern America by Native American Indians (Accquaah, 2007). Production-wise, maize ranked top among cereals during 2013 with global production of 1,016 million tons followed by rice and wheat (www.faostat.fao.org). For more than three hundred million people in sub-Saharan Africa (Edmeadus, 2013) and several million people in other parts of world, maize is an important staple food who derive their daily energy and protein requirements from it (Vasal, 1999).

Maize is an important source of starch, protein and oil contents as maize kernels have these storage components in proportions of 70-75%, 8-10% and 4-5%, respectively (Boyer and Hannah, 2001; Werle *et al.*, 2014). However, normal maize varieties have drawbacks, that is, they are low in protein and they lack essential amino acids of lysine and tryptophan (Ikujenlola and Adurotoye, 2014). This deficiency of essential amino acids and its implications on human health strongly emphasizes on development of maize cultivars with an improved amino acid profile. In the 1960s and 1970s, the identification of different maize mutants like *opaque-2 (o2), floury-2 (fl2), opaque-7 (o7), opaque-6 (o6) and floury-3(fl3)* which exhibited higher lysine and tryptophan contents triggered the research and development of Quality Protein Maize (Vivek *et al.*, 2008).

Breeding for enhanced protein quality presents an up-hill task because of the complex and quantitative nature of protein concentration in the maize kernel (Blestsos and Goulas, 1999). It involves dealing with three distinct genetic systems; the recessive mutant alleles of *opaque* and *floury* genes being the first, second being alleles of endosperm hardness modifier genes (en-modifiers) and third being a distinct set of amino acid modifier genes (aa-modifiers) (Krivanek *et al.*, 2006).Therefore, knowledge about the nature of the gene action is essential for maize breeders enabling them to optimize their breeding programs better.

Generation mean analysis can prove useful is assessment of genetic effects involved in the expressions of quantitative traits in maize (Frank and Hallauer, 1997; Zdunic *et al.*, 2008). After its introduction by Anderson and Kempthron (1954) and Hayman (1958), generation mean analysis have been used in numerous studies in maize for understanding the gene actions for different important traits (Melchinger *et al.*, 1986). Frank and Hallauer (1997) studied the genetic effects for twin-ear penetrance and expressivity in maize using generation

means analysis. Similarly genetic effects of other important traits like grain yield (Azizi *et al.,* 2006, Zdunic *et al.,* 2008 and Haq *et al.,* 2013), kernels per row (Azizi *et al.,* 2006; Ishfaq 2011 and Haq *et al.,* 2013), kernel rows per ear (Azizi *et al.,* 2006 and Ishfaq 2011), grain weight (Azizi *et al.,* 2006; Ishfaq 2011 and Haq *et al.,* 2013), kernel depth, ear height, cob weight (Azizi *et al.,* 2006), plant height (Azizi *et al.,* 2006 and Iqbal *et al.,* 2010), anthesis (Azizi *et al.,* 2006; Ishfaq 2011 and Sher *et al.,* 2012), husk leaves (Ji and Brewbaker, 2007), starch contents in grain (Zdunic *et al.,* 2008), leaf area per plant (Iqbal *et al.,* 2010), days to 50% silking (Ishfaq 2011 and Sher *et al.,* 2012), anthesis silking interval (ASI), days to maturity (Sher *et al.,* 2012), days to 75% husk browning, ear length, ear diameter (Ishfaq 2011) were estimated using generation mean analysis. This study was designed to estimate genetic effects for protein, lysine and tryptophan percentages in maize under contrasting water regimes following the technique of generation mean analysis.

MATERIALS AND METHODS

Plant materials: Six maize inbred lines ($NCMLQ_1$, $NCMLQ_2$, $NCMLD_1$, $NCMLD_2$, $NCMLD_3$ and $NCMLD_4$) contrasting for traits like drought tolerance, protein, lysine and tryptophan percentages were selected as the result of screening during spring 2007, results of which are published in Hussain (2013). The crossing block was planted in spring 2008 and parental lines were crossed in ten combinations viz; $NCMLQ_1 \times NCMLQ_2$, $NCMLQ_1 \times NCMLD_1$, $NCMLQ_1 \times NCMLD_2$, $NCMLQ_1 \times NCMLD_3$, $NCMLQ_1 \times NCMLD_4$, $NCMLQ_2 \times NCMLD_1$, $NCMLQ_2 \times NCMLD_2$, $NCMLQ_2 \times NCMLD_3$, $NCMLQ_2 \times NCMLD_4$, $NCMLD_3 \times NCMLD_4$. In Kharif 2008, the F_1 plants were self-pollinated to produce F_2 and back-crossed with each of two parents of above crosses to develop back-cross generations BC_1 and BC_2 to constitute six generations of above crosses.

Field Experiment: Metrological data of 30 years guided us to plant these trials involving imposed drought stress in spring season as rainfall pattern showed minimal occurrences of rainfalls in the months of April-June in Islamabad. Coupled with temperature hikes during these months, it was possible to impose water stress by withdrawing irrigation 1 week before initiation of flowering to 2 weeks after its completion as it affects most of the pollination and early kernel development. However, rain gauge and thermometer were installed in field to record daily temperature and rainfall during induced-stress period (Figure 1).

Seed of all six generations, i.e. F_1, F_2, back crosses along with parents of crosses $NCMLQ_1 \times NCMLQ_2$, $NCMLQ_1 \times NCMLD_1$, $NCMLQ_1 \times NCMLD_2$, $NCMLQ_1 \times NCMLD_3$, $NCMLQ_1 \times NCMLD_4$, $NCMLQ_2 \times NCMLD_1$, $NCMLQ_2 \times NCMLD_2$, $NCMLQ_2 \times NCMLD_3$, $NCMLQ_2 \times NCMLD_4$, $NCMLD_3 \times NCMLD_4$ were planted in research area of Maize, Sorghum and Millet Programme in March, 2009. Randomized complete block design was followed having three replications. A single row for parental lines and F_1 hybrids, two for each backcross and six for F_2 progenies were planted in each replication. The length of each row laid out was four meter with row to row and plant to plant distances at 75 cm and 25 cm, respectively. The experiment was maintained in two separate trials i.e. one trial was managed at normal level of irrigations needed for raising commercial maize crop while in the second trial, the irrigation was stopped to induce moisture stress one week prior to the anthesis up to two weeks after completion of flowering.

Data Recording: For data recording, 10 guarded plants from each replication of parental lines and F_1, 15 plants from each replication of back crosses and 70 plants from each replication of F_2 were taken into account.

a) **Protein Percentage:** Maize flour was prepared by milling the maize grains through Udy Cyclone Mill from 25-30 maize kernels, after removing embryos. Crude protein percentages were determined by Kjeldhal's method of nitrogen estimation as described by Pearson (1976).

b) **Tryptophan Percentage:** Photo-spectrometer readings for tryptophan percentages were made on 560 nm, were in fact the percentages of tryptophan in protein solution, not in protein. Tryptophan percentages in protein for specific genotypes were determined by Quality Index (QI) as per formula (Vivik *et al.,* 2008):

$$\text{Quality Index (QI)} = \frac{\text{Photo – spectrometric reading at 560 nm}}{\text{Protein percentage of the specific genotype}} \times 100$$

Samples contained 25-30 kernels screened on light table for determination of tryptophan, of which embryos were removed prior to the laboratory analysis. Tryptophan percentages determination was specified by HPLC according to the methods described in the Quality Protein Breeding Manual by Vivik *et al.* (2008).

c) **Lysine Percentage:** Lysine percentages determination was specified by HPLC according to the methods described in the Quality Protein Breeding Manual by Vivik *et al.* (2008).

Statistical and Biometrical Analysis: Six parameter model for estimation of components of generation mean given by Hayman (1958) and later refreshed by Sing and Chaudhary (2004) was used for analysis in this study. This analytical approach has two main steps viz; testing of non-allelic interactions and estimation of gene effects along with other variances.

a) **Analysis of Variance:** Analysis of variance was performed for mean of generations of each cross individually to establish variation among generation of that cross for all traits separately.

b) **Scaling Tests for simple additive-dominance or epistatic interactions:** For generation mean analysis Singh and Chaudhary (2004) illustrated four individual scaling tests:

A= $2mBC_1 - mP_1 - mF_1$
B= $2mBC_2 - mP_2 - mF_1$
C= $4mF_2 - 2mF_1 - mP_1 - mP_2$
D= $2mF_2 - mBC_1 - mBC_2$,

Where, mP_1, mP_2, mF_1, mF_2, mBC_1 and mBC_2 are means of Parent-1, Parent-2, F_1, F_2, BC_1 and BC_2 respectively.

Variances of these estimates were calculated as:

$\mathbf{V_A}= 4V(mBC_1) + V(mP_1) + V(mF_1)$
$\mathbf{V_B}= 4V(mBC_2) + V(mP_2) + V(mF_1)$
$\mathbf{V_C} = 16V(mF_2) + 4V(F_1) + V(mP_1) + V(mP_2)$
$\mathbf{V_D}= 4(VmF_2) + V(mBC_1) + V(mBC_2)$

Computation of A, B, C and D types of epistasis was followed by estimation of variances for above epistatic types. Standard errors were calculated by taking square roots of the respective variances. Then by dividing A, B, C and D effects by their standard errors individually, t-values were calculated. Significance of each was tested against 't-value' at ($P \leq 0.05$). The calculated values when exceeded from 1.96, imparted effect as significant or otherwise. Inadequacy of simple additive-dominance model and presence of epistatic interactions was depicted by the significance of specific scale such as:-

a) If A and B are significant, then all types of non-allelic interactions additive × additive, additive × dominance and dominance × dominance were existent.
b) If C significant, then dominance × dominance interaction was prevalent.
c) If D significant, then additive × additive interaction was established.
d) If both C and D are significant, then additive × additive and dominance × dominance type of gene action was ascertained.

c) **Parameters of Generation Mean:** Following components of generation mean were computed according to the six parameter model:-

m= Mean= mF_2
d= Additive effects = $mBC_1 - mBC_2$
h= Dominance effect= $mF_1 - 4mF_2 - (0.5)mP_1 - (0.5)mP_2 + 2mBC_1 + 2mBC_2$
i=Additive × additive type of gene interaction = $2mBC_1 + 2mBC_2 - 4mF_2$.
j=additive × dominance type of gene interaction = $mBC_1 - (0.5)mP_1 - mBC_2 - (0.5)mP_2$
l=Dominance × dominance type of gene interaction = $mP_1+mP_2-2mF_1+4mF_2-4mBC_1-4mBC_2$, and their variances:

V(m) = $V(mF_2)$
Vd = $V(mBC_1) + V(mBC_2)$
V(h) = $V(mF_1) + 16V(mF_2) + (0.25)VmP_1 + (0.25)VmP_2 + 4VmBC_1 + 4VmBC_2$
V(i) = $4V(mBC_1) + 4V(mBC_2) + 16V(mF_2)$.
V(j) = $V(mBC_1) + (0.25)VmP_1 + V(mBC_2) + (0.25)VmP_2$
V(l) = $V(mP_1) + V(mP_2) + 4V(mF_1) + 16V(mF_2) + 16V(mBC_1) + 16V(mBC_2)$

The standard errors just as normal rule were square roots of the respective variances of each component. The "t" value was computed by dividing the genetic parameters by respective standard errors, thus, the calculated value was compared with 1.96, the tabulated value at ($P \leq 0.05$) to establish significance or non-significance.

RESULTS

Analysis of variance: Significant differences were observed among generations of all crosses under normal and water-stress conditions for all traits, except for crosses $NCMLQ_1 \times NCMLQ_2$ (under both normal and drought conditions), $NCMLQ_2 \times NCMLD_3$ (under normal irrigation) and $NCMLQ_1 \times NCMLD_4$ (under drought conditions) for lysine percentage (Tables 1, 2). Hence these crosses were not considered for further biometrical analysis. Significant difference among generations not only depicted appropriate choice of parental lines but also suggested presence of diversity among the generations of these crosses under contrasting water regimes. This existence of genetic variation among generations enabled estimation of genetic parameters through generation mean analysis.

Scaling tests (A, B, C and D) to test adequacy of simple additive-dominance model: Individual scaling test A, B, C and D were carried out for all traits under normal irrigation and water stress conditions to check adequacy of simple additive-dominance model or presence of non-allelic interactions (Table 3).

Protein percentage: The results showed that values for A test were significant in 30% and 100% crosses for protein percentage under normal and drought conditions, respectively. Values for B were significant in all the crosses across both water regimes. C component was also significant in 80% and 100% crosses for protein in normal and water stress conditions. However, the values for D were non-significant for all crosses except for $NCMLQ_1 \times NCMLD_4$ which were significant under normal as well as drought conditions.

Tryptophan percentage: For tryptophan percentage, A was significant for 90% and 70% of the crosses under normal and drought conditions respectively. B was observed significant for all the crosses under both water regimes except for $NCMLD_3 \times NCMLD_4$ under normal irrigation. Only 30% crosses i.e $NCMLQ_1 \times NCMLD_1$, $NCMLQ_1 \times NCMLD_4$ and $NCMLQ_2 \times NCMLD_4$ showed significance for C under normal conditions, however, 80% were significant under drought. Values for D remained significant for 70% crosses under normal supply of irrigation and 80% crosses under water-stress conditions.

Lysine percentage: Significance of all four scaling tests was observed for lysine percentage for all crosses evaluated in contrasting water supplies except for the cross $NCMLQ_2 \times NCMLD_4$ which stood significant for B and D under normal water supply but was non-significant for all scaling tests under water deficit conditions. Hence, the cross was not considered for further analysis through six parameter model for this particular trait.

Genetic Effects for protein, tryptophan and lysine percentage: The significance of any one of the four individual scaling tests A, B, C and D evidenced the presence of non-allelic interactions. Hence, simple additive-dominance model was not adequate to explain the genetic effects governing protein, tryptophan and lysine percentages in maize. Using Hayman's six parameter model, genetic effects for these traits were estimated under normal and water deficit conditions and results are presented in table 4 and table 5.

Protein Percentage: The mean effects [m] were significant for protein percentage for all crosses under normal as well as water limited conditions. The additive genetic effects [d] were significant for 60% of the crosses under normal and drought conditions. However, the dominance effects [h] showed significance only for $NCMLQ_1 \times NCMLQ_2$ under normal irrigation and $NCMLQ_1 \times NCMLD_4$ under both irrigation levels. The additive × additive interaction [i] was significant for 30% crosses i.e $NCMLQ_1 \times NCMLQ_2$, $NCMLQ_1 \times NCMLD_4$, and $NCMLQ_2 \times NCMLD_4$ under normal and for the cross $NCMLQ_1 \times NCMLD_4$ under drought conditions. The additive × dominance [j] interactions were significant for most of the crosses except $NCMLD_3 \times NCMLD_4$ across both water regimes. However, the dominance × dominance interaction [l] was significant for only 30% crosses under normal water supply.

Tryptophan Percentage: For tryptophan percentage, the mean effects [m] were significant for all crosses across both water regimes. 80% and 90% crosses showed significance for additive effects [d] under normal and limited water supply, respectively. Only 40% crosses showed significance for dominance genetic effects [h] for this trait under normal conditions; however, this interaction was significant for 90% crosses under drought conditions except $NCMLQ_2 \times NCMLD_1$. Additive × additive [i] interactions were significant for 60% crosses under normal irrigation and 80% crosses under water deficit condition. Almost similar to the protein percentage, the additive × dominance [j] interaction was significant for all the crosses except $NCMLD_3 \times NCMLD_4$ which showed non-significance for this interaction under normal water supply. 100% crosses showed significance for dominance × dominance interaction [l] except three crosses viz; $NCMLQ_1 \times NCMLQ_2$, $NCMLQ_1 \times NCMLD_2$ and $NCMLQ_2 \times NCMLD_1$ under normal irrigation.

Lysine Percentage: Because of non-significance of all four scaling tests for lysine percentage under drought conditions, the cross $NCMLQ_2 \times NCMLD_4$ was not considered for estimation of genetic effects controlling lysine percentage. However, the mean effects [m] were significant for remaining six crosses under both normal and deficient water supply. The additive effects [d] were significant only for $NCMLQ_1 \times NCMLD_2$ across both water regimes. Only two and three crosses showed significance for dominance effects [h] under normal and water-stress conditions, respectively. Three crosses demonstrated significance for additive × additive interactions [i] under normal as well as drought stress. Additive × dominance interactions [j] were significant for crosses $NCMLQ_1 \times NCMLD_2$, $NCMLQ_1 \times NCMLD_3$ and $NCMLD_3 \times NCMLD_4$under normal and limited water supply. The crosses $NCMLQ_1 \times NCMLQ_2$ and $NCMLD_3 \times NCMLD_4$ showed significance for dominance × dominance interactions [l] under normal water supply, whereas crosses $NCMLQ_1 \times NCMLD_2$ and $NCMLQ_1 \times NCMLD_3$ expressed significance for this interaction under scarce water conditions.

Table 1. Analysis of variance for protein, tryptophan and lysine percentages to partition variation among generations under normal irrigation.

Combinations		Source	df	Protein Percentage			Tryptophan Percentage			Lysine Percentage		
				SS	M.S	F-value	SS	M.S	F-value	SS	M.S	F-value
$NCMLQ_1$	×	Generations	5	0.73	0.145	29.81**	0.0050	0.001	29.81**	0.14	0.028	1.39ns
$NCMLQ_2$		Error	10	0.05	0.005		0.0051	0.0005		0.2	0.02	
$NCMLQ_1$	×	Generations	5	3.52	0.704	15.73**	0.0200	0.004	15.73**	1.3	0.26	11.55**
$NCMLD_1$		Error	10	0.45	0.045		0.0103	0.0010		0.22	0.022	
$NCMLQ_1$	×	Generations	5	2.53	0.506	51.4**	0.0200	0.004	51.4**	0.36	0.073	3.47*
$NCMLD_2$		Error	10	0.1	0.01		0.0019	0.0002		0.21	0.021	
$NCMLQ_1$	×	Generations	5	3.67	0.734	45.72**	0.0250	0.005	45.72**	1.02	0.205	4.76*
$NCMLD_3$		Error	10	0.16	0.016		0.0015	0.0002		0.43	0.043	
$NCMLQ_1$	×	Generations	5	2.46	0.492	18.12**	0.0200	0.004	18.12**	0.29	0.057	3.66*
$NCMLD_4$		Error	10	0.27	0.027		0.0051	0.0005		0.16	0.016	
$NCMLQ_2$	×	Generations	5	2.46	0.491	15.93**	0.0050	0.001	15.93**	0.71	0.142	8.39**
$NCMLD_1$		Error	10	0.31	0.031		0.0024	0.0002		0.17	0.017	
$NCMLQ_2$	×	Generations	5	3.47	0.694	6.52**	0.0150	0.003	6.52**	0.59	0.118	18.89**
$NCMLD_2$		Error	10	1.07	0.107		0.0035	0.0004		0.06	0.006	
$NCMLQ_2$	×	Generations	5	3.87	0.773	30.46**	0.0200	0.004	30.46**	0.44	0.089	2.68ns
$NCMLD_3$		Error	10	0.25	0.025		0.0024	0.0002		0.33	0.033	
$NCMLQ_2$	×	Generations	5	1.23	0.245	91.99**	0.0150	0.003	91.99**	0.46	0.092	16.28**
$NCMLD_4$		Error	10	0.03	0.003		0.0076	0.0008		0.06	0.006	
$NCMLD_3$	×	Generations	5	0.8	0.159	30.28**	0.0100	0.002	30.28**	1.36	0.271	6.91**
$NCMLD_4$		Error	10	0.05	0.005		0.0081	0.0008		0.39	0.039	

** = significant (P≤0.01), * = significant (P≤0.05) and ns = non significant

Table 2. Analysis of variance for protein, tryptophan and lysine percentages to partition variation among generations under drought conditions.

Combinations		Source	df	Protein Percentage			Tryptophan Percentage			Lysine Percentage		
				SS	M.S	F-value	SS	M.S	F-value	SS	M.S	F-value
$NCMLQ_1$	×	Generations	5	5.25	1.05	130.25**	0.0450	0.009	130.25**	0.16	0.032	2.23ns
$NCMLQ_2$		Error	10	0.08	0.008		0.0038	0.0004		0.14	0.014	
$NCMLQ_1$	×	Generations	5	6.79	1.359	64.28**	0.0350	0.007	64.28**	0.88	0.177	14.44**
$NCMLD_1$		Error	10	0.21	0.021		0.0051	0.0005		0.12	0.012	
$NCMLQ_1$	×	Generations	5	3.82	0.763	58.78**	0.0250	0.005	58.78**	0.34	0.068	4.68*
$NCMLD_2$		Error	10	0.13	0.013		0.0040	0.0004		0.15	0.015	
$NCMLQ_1$	×	Generations	5	6.36	1.271	154.28**	0.0100	0.002	154.28**	0.79	0.159	6.52**
$NCMLD_3$		Error	10	0.08	0.008		0.0047	0.0005		0.24	0.024	
$NCMLQ_1$	×	Generations	5	2.93	0.586	20.13**	0.0200	0.004	20.13**	0.16	0.031	2.9ns
$NCMLD_4$		Error	10	0.29	0.029		0.0026	0.0003		0.11	0.011	
$NCMLQ_2$	×	Generations	5	6.09	1.218	41.51**	0.0450	0.009	41.51**	0.41	0.082	9.71**
$NCMLD_1$		Error	10	0.29	0.029		0.0020	0.0002		0.08	0.008	
$NCMLQ_2$	×	Generations	5	6.6	1.321	14.2**	0.0200	0.004	14.2**	0.54	0.108	26.54**
$NCMLD_2$		Error	10	0.93	0.093		0.0051	0.0005		0.04	0.004	
$NCMLQ_2$	×	Generations	5	7.6	1.52	114.94**	0.0250	0.005	114.94**	0.36	0.072	3.88*
$NCMLD_3$		Error	10	0.13	0.013		0.0045	0.0004		0.19	0.019	
$NCMLQ_2$	×	Generations	5	3.05	0.61	58.62**	0.0150	0.003	58.62**	0.25	0.05	13.42**
$NCMLD_4$		Error	10	0.1	0.01		0.0043	0.0004		0.04	0.004	
$NCMLD_3$	×	Generations	5	3.04	0.608	132.79**	0.0100	0.002	132.79**	0.87	0.174	6.88**
$NCMLD_4$		Error	10	0.05	0.005		0.0088	0.0009		0.25	0.025	

** = significant (P≤0.01), * = significant (P≤0.05) and ns = non significant

Table 3. Scaling test for protein, tryptophan and lysine percentages under normal irrigation and water stress conditions.

Crosses	Protein Percentage								Tryptophan Percentage								Lysine Percentage							
	A		B		C		D		A		B		C		D		A		B		C		D	
Under Normal Irrigation																								
Q1 × Q2	0.04	±0.13	1.16	±0.34*	0.45	±0.34	-0.38	±0.29	-0.02	±0.004*	0.08	±0.018*	0.02	±0.051	-0.02	±0.026	-	-	-	-	-	-	-	-
Q1 × D1	0.11	±0.41	2.20	±0.54*	2.09	±0.40*	-0.11	±0.18	-0.04	±0.016*	0.05	±0.019*	-0.16	±0.059*	-0.09	±0.030*	-0.55	±0.163*	-0.77	±0.139*	-1.28	±0.192*	0.02	±0.103
Q1 × D2	-0.62	±0.14*	1.44	±0.26*	0.75	±0.29*	-0.04	±0.19	-0.06	±0.011*	0.10	±0.017*	0.08	±0.051	0.02	±0.026	-0.37	±0.102*	0.25	±0.086*	-0.26	±0.157	-0.07	±0.082
Q1 × D3	-0.40	±0.25	1.89	±0.38*	1.34	±0.31*	-0.08	±0.19	-0.05	±0.008*	0.12	±0.017*	-0.06	±0.053	-0.06	±0.027*	-0.33	±0.082*	0.49	±0.147*	0.42	±0.192*	0.13	±0.132
Q1 × D4	-0.92	±0.11*	0.81	±0.18*	-1.55	±0.19*	-0.72	±0.13*	-0.05	±0.010*	0.07	±0.019*	-0.18	±0.058*	-0.10	±0.030*	-	-	-	-	-	-	-	-
Q2 × D1	-0.08	±0.41	1.78	±0.44*	1.96	±0.49*	0.13	±0.30	-0.02	±0.014	0.07	±0.019*	0.05	±0.053	0.00	±0.027	-0.37	±0.150*	-0.61	±0.126*	-1.33	±0.181*	-0.17	±0.108
Q2 × D2	0.17	±0.51	2.16	±0.58*	1.96	±0.65*	-0.18	±0.35	-0.04	±0.014*	0.10	±0.018*	-0.05	±0.056	-0.06	±0.028*	-0.48	±0.168*	-0.26	±0.134	-1.20	±0.194*	-0.23	±0.094*
Q2 × D3	-0.01	±0.45	2.14	±0.51*	2.16	±0.56*	0.01	±0.33	-0.03	±0.011*	0.13	±0.018*	-0.09	±0.056	-0.10	±0.028*	-	-	-	-	-	-	-	-
Q2 × D4	-0.64	±0.29*	0.93	±0.22*	-0.22	±0.36	-0.25	±0.27	-0.04	±0.012*	0.06	±0.019*	-0.18	±0.058*	-0.10	±0.030*	-0.12	±0.089	-0.31	±0.088*	-0.05	±0.142	0.19	±0.086*
D3 × D4	0.29	±0.17	0.66	±0.23*	0.46	±0.21*	-0.25	±0.16	0.03	±0.010*	0.04	±0.018	-0.09	±0.058	-0.08	±0.030*	0.22	±0.122	-0.61	±0.075*	-0.10	±0.161	0.15	±0.113
Under Water Stress Conditions																								
Q1 × Q2	1.65	±0.14*	2.68	±0.31*	3.84	±0.31*	-0.25	±0.24	0.13	±0.007*	0.27	±0.018*	0.31	±0.015*	-0.04	±0.010*	-	-	-	-	-	-	-	-
Q1 × D1	1.40	±0.38*	3.09	±0.50*	4.67	±0.38*	0.09	±0.18	0.05	±0.016*	0.21	±0.018*	0.06	±0.022*	-0.10	±0.012*	-0.43	±0.164*	-0.54	±0.141*	-1.25	±0.199*	-0.15	±0.109
Q1 × D2	0.87	±0.13*	2.40	±0.27*	3.33	±0.29*	0.03	±0.21	0.04	±0.011*	0.17	±0.018*	0.24	±0.016*	0.01	±0.012	-0.22	±0.112	0.38	±0.100*	-0.29	±0.167	-0.23	±0.092*
Q1 × D3	1.04	±0.24*	2.98	±0.36*	4.12	±0.30*	0.05	±0.18	0.01	±0.009	0.13	±0.018*	-0.02	±0.018	-0.08	±0.012*	-0.11	±0.095	0.63	±0.149*	0.48	±0.189*	-0.02	±0.130
Q1 × D4	0.64	±0.11*	2.19	±0.18*	1.58	±0.19*	-0.62	±0.12*	0.01	±0.011	0.15	±0.019*	-0.07	±0.022*	-0.11	±0.014*	-	-	-	-	-	-	-	-
Q2 × D1	1.36	±0.36*	2.88	±0.42*	4.76	±0.46*	0.27	±0.26	0.14	±0.013*	0.25	±0.018*	0.36	±0.015*	-0.02	±0.009	-0.27	±0.155	-0.38	±0.131*	-1.22	±0.194*	-0.28	±0.115*
Q2 × D2	1.52	±0.45*	3.02	±0.54*	4.74	±0.57*	0.10	±0.32	0.10	±0.014*	0.18	±0.020*	0.14	±0.020*	-0.07	±0.012*	-0.41	±0.171*	-0.17	±0.139	-1.26	±0.209*	-0.34	±0.107*
Q2 × D3	1.33	±0.39*	3.18	±0.46*	4.83	±0.47*	0.16	±0.28	0.13	±0.011*	0.20	±0.019*	0.11	±0.020*	-0.11	±0.012*	-	-	-	-	-	-	-	-
Q2 × D4	0.79	±0.23*	2.22	±0.20*	2.70	±0.29*	-0.16	±0.22	0.07	±0.014*	0.16	±0.020*	-0.01	±0.027	-0.12	±0.014*	0.02	±0.105	-0.05	±0.105	0.08	±0.150	0.05	±0.097
D3 × D4	1.37	±0.15*	1.84	±0.22*	2.93	±0.19*	-0.14	±0.14	-0.001	±0.012	0.08	±0.020*	-0.10	±0.025*	-0.09	±0.012*	0.29	±0.130*	-0.36	±0.092*	-0.03	±0.169	0.02	±0.120

A = mid-parental value; B = additive effects; C = dominance effects; D = additive × additive interaction.
* = significant at ($P \leq 0.05$)

Table 4. Gene effects for protein and tryptophan percentages under normal irrigation and water stress conditions.

Crosses	Protein Percentage												Tryptophan Percentage									
	[m]		[d]		[h]		[i]		[j]		[l]		[m]		[d]		[h]		[i]		[j]		[l]	
Under Normal Irrigation																								
$Q_1 \times Q_2$	10.17	±0.038*	-0.47	±0.11*	0.82	±0.31*	0.76	±0.27*	-0.56	±0.23*	-1.96	±0.56*	1.02	±0.013*	-0.04	±0.009*	0.03	±0.054	0.04	±0.054	-0.05	±0.009*	-0.11	±0.062
$Q_1 \times D_1$	10.06	±0.068*	-0.50	±0.32	0.15	±0.71	0.22	±0.69	-1.05	±0.33*	-2.54	±1.34	0.93	±0.015*	-0.02	±0.012	0.11	±0.063	0.18	±0.063*	-0.04	±0.013*	-0.19	±0.076*
$Q_1 \times D_2$	9.65	±0.052*	-0.44	±0.12*	-0.07	±0.33	0.07	±0.31	-1.03	±0.17*	-0.89	±0.55	0.98	±0.013*	-0.02	±0.010*	-0.08	±0.054	-0.04	±0.054	-0.08	±0.010*	0.00	±0.064
$Q_1 \times D_3$	9.69	±0.051*	-0.46	±0.21*	-0.01	±0.48	0.15	±0.46	-1.14	±0.24*	-1.65	±0.89	0.94	±0.013*	-0.03	±0.009*	0.10	±0.056	0.13	±0.056*	-0.08	±0.010*	-0.20	±0.064*
$Q_1 \times D_4$	9.04	±0.032*	-0.42	±0.09*	0.95	±0.23*	1.44	±0.22*	-0.87	±0.12*	-1.33	±0.40*	0.92	±0.014*	-0.02	±0.009*	0.13	±0.060*	0.19	±0.060*	-0.06	±0.011*	-0.20	±0.069*
$Q_2 \times D_1$	9.95	±0.067*	-0.48	±0.24	-0.30	±0.59	-0.26	±0.55	-0.93	±0.31*	-1.43	±1.09	0.99	±0.013*	-0.02	±0.011*	-0.03	±0.057	0.00	±0.057	-0.04	±0.012*	-0.06	±0.069
$Q_2 \times D_2$	10.03	±0.090*	-0.50	±0.32	0.55	±0.78	0.36	±0.74	-1.00	±0.38*	-2.69	±1.44	0.94	±0.014*	-0.02	±0.011	0.09	±0.060	0.12	±0.060	-0.07	±0.012*	-0.18	±0.072*
$Q_2 \times D_3$	9.95	±0.069*	-0.48	±0.27	0.10	±0.66	-0.02	±0.61	-1.07	±0.35*	-2.11	±1.23	0.94	±0.014*	-0.03	±0.010*	0.18	±0.059*	0.19	±0.059*	-0.08	±0.011*	-0.29	±0.069*
$Q_2 \times D_4$	9.39	±0.024*	-0.43	±0.09*	0.23	±0.27	0.50	±0.21*	-0.78	±0.21*	-0.78	±0.52	0.92	±0.014*	-0.02	±0.010*	0.16	±0.061*	0.21	±0.061*	-0.05	±0.012*	-0.23	±0.071*
$D_3 \times D_4$	9.04	±0.027*	-0.42	±0.12*	0.35	±0.27	0.49	±0.25	-0.18	±0.15	-1.44	±0.51*	0.90	±0.014*	-0.02	±0.009*	0.12	±0.060*	0.15	±0.059*	0.00	±0.012	-0.22	±0.068*

Under Water Stress Conditions																						
$Q_1 \times Q_2$	9.81	±0.037*	-0.45	±0.11*	0.49	±0.30	0.49	±0.26	-0.51	±0.20*	-4.83	±0.54*	1.00	±0.003*	-0.04	±0.009*	0.04	±0.022*	0.08	±0.022*	-0.07	±0.010*	-0.48	±0.038*
$Q_1 \times D_1$	9.64	±0.064*	-0.47	±0.30	-0.33	±0.66	-0.18	±0.64	-0.84	±0.31*	-4.31	±1.24*	0.90	±0.005*	-0.02	±0.012	0.17	±0.031*	0.21	±0.031*	-0.08	±0.013*	-0.47	±0.051*
$Q_1 \times D_2$	9.28	±0.049*	-0.42	±0.11*	-0.32	±0.32	-0.06	±0.30	-0.76	±0.17*	-3.21	±0.54*	0.96	±0.003*	-0.03	±0.009*	-0.08	±0.023*	-0.02	±0.022	-0.07	±0.012*	-0.19	±0.041*
$Q_1 \times D_3$	9.30	±0.048*	-0.44	±0.19*	-0.33	±0.45	-0.11	±0.43	-0.97	±0.22*	-3.91	±0.83*	0.92	±0.004*	-0.03	±0.009*	0.14	±0.024*	0.16	±0.023*	-0.06	±0.011*	-0.31	±0.040*
$Q_1 \times D_4$	8.71	±0.031*	-0.40	±0.09*	0.77	±0.22*	1.24	±0.21*	-0.77	±0.11*	-4.06	±0.39*	0.90	±0.005*	-0.03	±0.009*	0.21	±0.027*	0.23	±0.026*	-0.07	±0.012*	-0.38	±0.043*
$Q_2 \times D_1$	9.54	±0.065*	-0.45	±0.23	-0.78	±0.55	-0.53	±0.52	-0.76	±0.28*	-3.70	±1.01*	0.97	±0.003*	-0.03	±0.011*	0.02	±0.026	0.03	±0.026	-0.06	±0.012*	-0.42	±0.046*
$Q_2 \times D_2$	9.65	±0.088*	-0.47	±0.30	-0.31	±0.73	-0.20	±0.69	-0.75	±0.35*	-4.34	±1.33*	0.92	±0.004*	-0.03	±0.011*	0.11	±0.027*	0.14	±0.027*	-0.04	±0.013*	-0.41	±0.048*
$Q_2 \times D_3$	9.53	±0.065*	-0.46	±0.25	-0.32	±0.60	-0.33	±0.57	-0.93	±0.31*	-4.18	±1.12*	0.92	±0.004*	-0.03	±0.010*	0.18	±0.027*	0.22	±0.026*	-0.03	±0.011*	-0.55	±0.044*
$Q_2 \times D_4$	9.05	±0.023*	-0.41	±0.09*	0.10	±0.25	0.32	±0.21	-0.72	±0.18*	-3.33	±0.47*	0.89	±0.005*	-0.02	±0.010*	0.24	±0.029*	0.24	±0.027*	-0.04	±0.012*	-0.47	±0.047*
$D_3 \times D_4$	8.70	±0.026*	-0.40	±0.11*	0.19	±0.26	0.29	±0.24	-0.24	±0.14	-3.50	±0.48*	0.88	±0.004*	-0.03	±0.009*	0.20	±0.026*	0.18	±0.024*	-0.04	±0.011*	-0.26	±0.044*

m= mid-parental value; d = additive effects; h = dominance effects; i = additive × additive interaction; j = additive × dominance interaction; l = dominance × dominance interaction.
* = significant at ($P \leq 0.05$)

Table 5. Gene effects for lysine percentage under normal irrigation and water stress conditions.

Crosses	[m]		[d]		[h]		[i]		[j]		[l]	
Under Normal Irrigation												
$NCMLQ_1 \times NCMLQ_2$												
$NCMLQ_1 \times NCMLD_1$	3.63	±0.027*	0.08	±0.09	-0.55	±0.22*	-0.04	±0.20	0.11	±0.11	1.36	±0.39*
$NCMLQ_1 \times NCMLD_2$	3.83	±0.023*	-0.09	±0.04*	0.02	±0.14	0.14	±0.13	-0.31	±0.06*	-0.02	±0.23
$NCMLQ_1 \times NCMLD_3$	4.08	±0.022*	-0.05	±0.04	0.05	±0.14	-0.26	±0.12*	-0.41	±0.10*	0.11	±0.25
$NCMLQ_1 \times NCMLD_4$	-	-	-	-	-	-	-	-	-	-	-	-
$NCMLQ_2 \times NCMLD_1$	3.64	±0.024*	0.01	±0.07	0.07	±0.19	0.35	±0.18	0.12	±0.10	0.63	±0.35
$NCMLQ_2 \times NCMLD_2$	3.44	±0.025*	0.03	±0.09	0.21	±0.22	0.47	±0.20*	-0.11	±0.10	0.27	±0.39
$NCMLQ_2 \times NCMLD_3$	-	-	-	-	-	-	-	-	-	-	-	-
$NCMLQ_2 \times NCMLD_4$	-	-	-	-	-	-	-	-	-	-	-	-
$NCMLD_3 \times NCMLD_4$	3.78	±0.020*	-0.04	±0.04	-0.51	±0.13*	-0.29	±0.11*	0.41	±0.08*	0.68	±0.22*
Under Water Stress Conditions												
$NCMLQ_1 \times NCMLQ_2$	-	-	-	-	-	-	-	-	-	-	-	-
$NCMLQ_1 \times NCMLD_1$	3.46	±0.023*	0.08	±0.08	-0.13	±0.21	0.29	±0.19	0.05	±0.11	0.67	±0.38
$NCMLQ_1 \times NCMLD_2$	3.66	±0.016*	-0.09	±0.04*	0.34	±0.13*	0.45	±0.11*	-0.30	±0.07*	-0.61	±0.24*
$NCMLQ_1 \times NCMLD_3$	3.92	±0.011*	-0.05	±0.04	0.24	±0.13	0.04	±0.09	-0.37	±0.10*	-0.56	±0.25*
$NCMLQ_1 \times NCMLD_4$	-	-	-	-	-	-	-	-	-	-	-	-
$NCMLQ_2 \times NCMLD_1$	3.50	±0.019*	0.01	±0.07	0.35	±0.18	0.56	±0.16*	0.05	±0.10	0.09	±0.34
$NCMLQ_2 \times NCMLD_2$	3.30	±0.022*	0.02	±0.08	0.46	±0.21*	0.68	±0.18*	-0.12	±0.11	-0.10	±0.38
$NCMLQ_2 \times NCMLD_3$	-	-	-	-	-	-	-	-	-	-	-	-
$NCMLQ_2 \times NCMLD_4$	-	-	-	-	-	-	-	-	-	-	-	-
$NCMLD_3 \times NCMLD_4$	3.63	±0.010*	-0.04	±0.03	-0.24	±0.11*	-0.04	±0.08	0.32	±0.09*	0.10	±0.22

m = mid-parental value; d = additive effects; h = dominance effects; i = additive × additive interaction; j = additive × dominance interaction; l = dominance × dominance interaction.
* = significant at ($P \leq 0.05$)

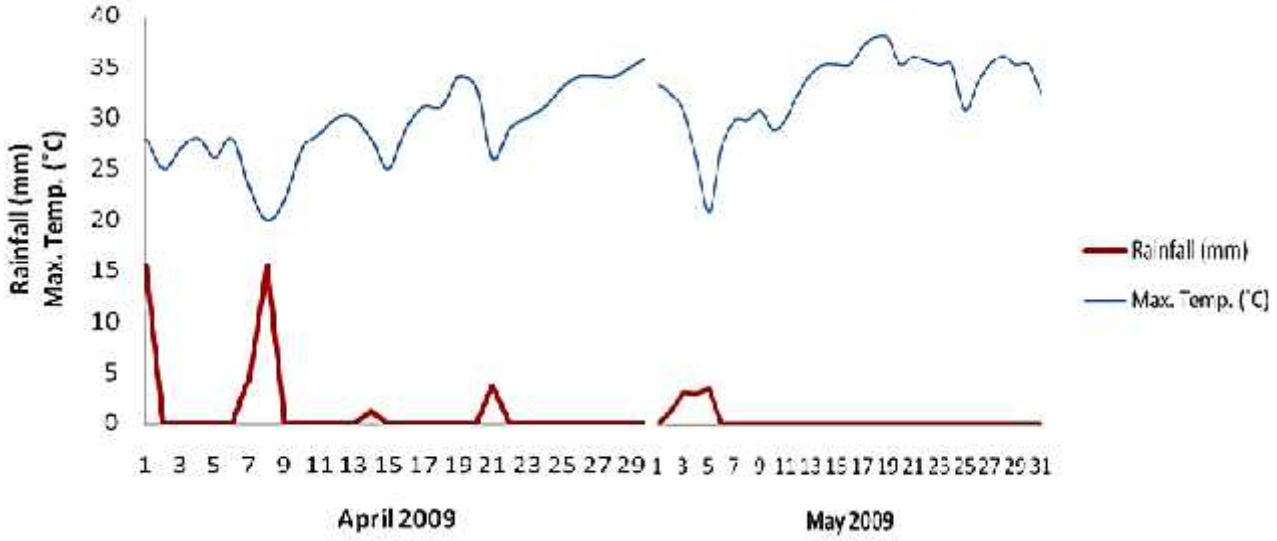

Figure 1. Meteorological data recorded for the drought induced period during April and May, 2009

DISCUSSION

Genetic diversity among parents and their subsequent generations F_1, F_2, BC_1 and BC_2 for protein, tryptophan and lysine percentages was established through analysis of variance. Presence of non-allelic interactions governing these biochemical traits in maize under optimum and limited water supply were evidenced through significance of individual scaling tests (A, B, C and D). Therefore, simple additive-dominance model was not enough to explain genetic effects controlling these traits in maize. To understand genetic effects for protein and its components; tryptophan and lysine, Hayman's six parameter model was used.

Significance of the mean effects [m] for protein percentage in all the crosses under drought as well as normal conditions indicated quantitative nature of this trait (Magda, 2013). The additive effects [d] were significant in more number of crosses as compared to dominance effects [h], however, higher values for dominance effects [h] suggest the role of dominance more important than additivity in maize for this trait (Iqbal *et al.*, 2010). Some studies suggested the prevalence of over-dominance for protein content (Agrawal *et al.*, 2015). Most values for [h] were positively significant indicating that the parental material have decreasing alleles for this trait. Hence, for improvement in grain protein percentage in maize, selection could prove effective (Magda, 2013). Under normal water supply, the additive × dominance [j] epistatic interaction was observed in most of the crosses (90%) as compared to other interactions; additive × additive [i] and dominance × dominance [l]. The negative sign for this interaction showed the dispersion of genes in the parents meaning genes from both parents contribute in expression of this trait in maize (Lyimo *et al.*, 2011; Magda, 2013). However, under water-stress conditions, significant values were observed for most of the crosses for additive × dominance [j] and dominance × dominance [l] interactions reinforcing the role of dominant genes. The negative sign for dominance × dominance values [l] points out the scope of heterosis breeding for development of improved maize germplasms with high protein percentages.

For tryptophan percentage, the role of dominance effects [h] was evidenced through higher significant values as compared to those of additive effects [d] under normal water supply as well as under restricted irrigation (Jatothu *et al.*, 2013). Complete to over-dominance have been reported by Agrawal *et al.*, (2015) for tryptophan contents in maize kernels. The lower magnitude of additive effects [d] suggested that selection in early generations will not be effective (Akhshi *et al.*, 2014). This role of dominance in the inheritance of tryptophan percentage was further consolidated by the significance of additive × dominance [j] and dominance × dominance [l] effects in most of the crosses under contrasting water regimes which shows that dominance or dominance type of epistatic interactions could have been involved in expression of this trait in maize (Iqbal *et al.*, 2010). The signs for the dominance [h] and dominance × dominance [l] estimates were opposite indicating duplicate epistasis, suggesting that selection may be delayed until high level of gene fixation is achieved. Intermating between promising lines may also prove useful in accumulating favourable genes (Azizi *et al.*, 2006).

Results showed that in addition to additive and dominance effects, epistatic interaction were also contributing to the genetics of lysine in maize under

drought and normal irrigation conditions. However, their relative magnitude varied according to the environment and parents involved in individual crosses. One possible explanation for these peculiar genetic interactions for this trait can be the contribution of unique combinations of genes in inheritance of this trait in specific crosses (Azizi *et al.,* 2006). Under normal conditions, additive effects [h] were significant for only one cross $NCMLQ_1 \times NCMLD_2$ with negatively significant additive × dominance [j] interaction, suggesting dispersion of genes in the parents (Magda, 2013).Whereas, negatively significant dominance effects [h] for $NCMLQ_1 \times NCMLD_1$ and $NCMLD_3 \times NCMLD_4$ with their corresponding significant but positive estimates of dominance × dominance [l] suggested presence of duplicate epistasis for this trait (Iqbal *et al.,* 2010). This type of epistatic interaction normally hinders the improvement through selection; hence, selection may be delayed till later generations (Azizi *et al.,* 2006).

Under water deficit conditions, additive effects [d] were significant but lower in magnitude from dominance effects [h] for $NCMLQ_1 \times NCMLD_2$ emphasizing the role of dominance effects in inheritance of this trait in this parental combination. Inter-allelic interactions controlling this trait were evidence by the significance of additive × additive [i], additive × dominance [j] and dominance × dominance [l] estimates varyingly depending on cross-combinations. In such case, different breeding methods can be applied involving particular parental combinations under water stress environment. For example, the cross $NCMLQ_2 \times NCMLD_2$ had significant estimates for dominance effects [h] and additive × additive [i] interactions suggesting the role of dominant genes having small additive effects in control of this trait. Hence, in this case where preponderance of additivity is obvious, pedigree method involving these particular parents can prove fruitful for improving this trait (Jatothu *et al.,* 2013).

Conclusion: In the light of the present study, it can be inferred that both additive and dominance effects along with the epistatic interactions play role in the inheritance of protein, tryptophan and lysine percentages in maize. These effects and epistatic interactions vary according to the parental combination used and environmental conditions. However, both additivity and dominance are of essential importance to breeder to predict the gene expression and design suitable breeding strategy under different environments for improvement of protein and these essential amino acid percentages in maize.

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