Research Article

Preponderant of Dominant Gene Action in Maize Revealed by Generation Mean Analysis under Natural and Drought Stress Conditions

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Abstract | Generation mean analysis belongs to the quantitative biometric methods based on measurement of phenotypic performances of certain quantitative traits on as many as possible plant individuals in basic experimental generations. Initially, 108 inbred lines of maize were planted in two separate trails under water deficit and normal irrigation conditions in the experimental field of Department of Plant Breeding and Molecular Genetics. Selection of parents for further study was done with regards to grain yield and its component traits. Broad range of genetic diversity was shown by the inbred lines and displayed different levels of drought tolerance. Four inbred lines were selected i.e., VDR-51, DR3-126, DR-37 and 5CDR-53. Crosses were attempted between the selected inbred lines. Six generations as P_1, P_2, F_1, F_2, BC_1 and BC_2 were prepared for both the crosses for the estimation of gene action under generation mean analysis and planted in a triplicated Randomized Complete Block Design (RCBD) under split plot arrangement. Most of the traits in both the crosses under natural in addition to drought conditions were controlled by the dominance gene action as indicated by generation mean analysis. Five parameter model (mdhij) indicated that genes which control the grain yield were mostly dominate in nature but also influenced by the epistatic effects of additive genes under natural conditions. These results favoured that the hybrid breeding is the best option in the given set of inbreds to best exploit their potential.

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Introduction

Globally, the 3rd most utilized cereal after rice and wheat is maize (*Zea mays* L.). Growth and yield of several crops can be adversely effected by water deficit stress, as compared to other abiotic stresses it is the most detrimental abiotic stress yet known (Ribaut et al., 2012). Maize is the most productive under proper management and better environmental conditions, among cereals. Drought stress reduces grain yield in maize plant. However, these yield declines depend on stress intensity, term, and incidence at the crop stage. Usually 20-50% significant loss of yield is caused by the drought which occurs two weeks before and during silking phase (Said, 2014). Controlling different plant traits under drought stress requires understanding the

genetic mechanisms for adopting different breeding approaches (Ahsan et al., 2013).

Many studies expanded genetic models for estimation of different genetic effects (Adebayo et al., 2014). Though, most of genetic models are principally additive–dominance models or simply additive models. Non-allelic or epistatic interactions are mostly relinquished, so there exist basic explanation of genetic variation, however it has been recognized inter-allelic interaction which frequently occurs to control or continuous expression of genes in maize plant (Moharramnejad et al., 2016).

Generation mean analyses provides information on the relative importance of average effects of the genes (additive effects), dominance deviations and effects due to no allelic genetic interactions in determining genotypic values of the individuals and as a result, mean genotypic values of generations. For estimating gene effects for a polygenic trait a simple but useful technique of generation mean analysis is used, its greatest merit lies in ability to estimate epistatic gene effects such as additive × additive, dominance × dominance, and additive × dominance effects (Said, 2014).

Plant breeders can choose the breeding procedures which are suitable for the improvement of quantitative traits with the estimation of genetic effects. Due to high estimate of dominance effect, the breeding objective should be towards development of hybrids for commercial purpose. For the high estimate of epistatic component, more reliance should be placed on the selection between lines and families (Singh and Narayanan, 2013).

Therefore, the aims of our study were:

- To determine gene action through generation mean analysis under natural and water stress conditions.
- Selection of desirable inbred lines to initiate a hybridization program.

Materials and Methods

Based on screening under drought and normal conditions two sets of inbred lines (four inbred lines) were selected as parents i.e. drought tolerant and susceptible to drought. The selected parents were sown as multiple rows during mid of June, 2013 to perform crossing between genetically diverse parents at Faculty of Agriculture, University of The Poonch Rawalakot, Azad Jammu and Kashmir. The two crosses between diverse parents were as cross 1, VDR-51 x 5CDR-53 and cross 2, DR3-126 x DR-37. Selfing of the parents was also performed. The parents were sown at two dates of sowing to facilitate synchronization of late and early maturing parents.

For generation mean analysis multi-generations i.e., Parent 1, Parent 2, F_1, F_2, backcross with parent 1 (BC_1) and back cross with parent 2 (BC_2) were produced for two sets of combinations during 2014 at the experimental field of the Department of Plant Breeding and Molecular Genetics, Faculty of Agriculture, University of The Poonch Rawalakot, Azad Jammu and Kashmir. Parental 1 and 2 generations were maintained by self-pollination of 3-5 plants of each parent. Similarly, 5-6 plants of F_1 were selfed to obtain F_2 seed. Same number of F_1 plants were back crossed with both parents of the selected crosses to develop BC_1 and BC_2, segregating back cross generations.

All six generations that are F_1, F_2, back crosses with parents were planted at Faculty of Agriculture, University of The Poonch Rawalakot, Azad Jammu and Kashmir during Kharif, 2015. Trail was sown under split plot arrangement in a RCB Design with three replications under drought and rain-fed conditions. The trial was conducted in tunnel and drought treatments were covered with plastic sheet four weeks prior to flowering to impose drought stress one week before flowering and remained covered up to two weeks after flowering. The field selected deliberately for drought treatments consisted of terraces at least five feet to protect seepage of rain water as plastic sheet covering tunnel, slipped at least six feet down the ground level. For good stand, two seeds were planted per site. Single healthy seedling per site was kept after thinning. Non-experimental lines were planted to diminish edge border effect at the beginning and end of each replication. The spacing was kept 75 cm and 25 cm in row to row and plant to plant respectively. Standard dose of fertilizer was applied to each of the experimental unit. The treatments under natural conditions were not covered by plastic sheet i.e., they were kept under rain fed conditions. A total of 674.7 mm of rainfall was received by the treatments under natural conditions during the course of experiment while the treatments under drought conditions received 337.7 mm rainfall which is 50% less than the natural treatments. Environmental conditions regarding temperature and rainfall data during the course of experiment is mentioned in Tables 1 and 2.

The data concerning plant height, ear height, ear leaf

area, flag leaf area, days to pollen shed, days to silk emergence, anthesis-silking interval (ASI), shelling percentage, number of kernels per row, number of kernel rows per ear, 100-kernel weight, grain yield tons/ha, harvest index and biological yield tons/ha under control as well as water deficit conditions of each entry was recorded from 10, 50 and 100 randomly selected guarded plants for both parents and their F_1's, each of back cross and F_2, respectively.

Table 1: *Rainfall data of Rawalakot during the course of experiment.*

Date	May-15	Jun-15	Jul-15	Aug-15	Sep-15	Oct-15
1	0.0	0.0	0.0	16.2	0.0	0.0
2	0.0	0.0	0.0	36.0	0.0	0.0
3	0.0	0.0	0.0	33.0	1.2	0.0
4	0.0	2.4	0.0	71.0	0.0	0.0
5	0.0	0.0	0.0	0.0	0.0	0.0
6	0.0	0.1	21.4	0.0	0.0	0.0
7	0.0	0.0	5.6	0.0	0.0	0.0
8	0.0	8.0	9.0	0.6	0.0	0.0
9	0.0	0.0	37.5	5.0	0.0	0.0
10	0.0	0.1	38.5	0.0	0.0	0.0
11	0.0	4.0	0.0	0.0	0.0	0.0
12	20.0	0.0	0.8	0.0	0.0	0.0
13	16.8	4.4	0.0	1.0	0.0	0.0
14	20.0	2.2	0.0	1.4	0.0	4.0
15	0.0	8.0	0.0	0.1	0.0	0.1
16	0.0	0.0	0.0	0.0	2.2	0.0
17	0.0	0.0	5.0	2.0	0.0	0.0
18	21.5	0.0	5.0	0.0	0.0	0.0
19	0.2	0.0	4.0	0.0	0.0	21.4
20	0.0	0.0	2.0	0.0	8.2	52.0
21	0.0	18.0	10.0	0.1	0.0	0.0
22	0.0	0.0	17.0	0.1	3.0	0.0
23	0.0	3.0	96.0	0.0	31.8	0.0
24	0.1	3.0	11.0	7.0	4.0	0.0
25	0.0	4.7	0.0	0.0	0.0	52.0
26	0.8	0.0	21.0	0.0	0.0	66.5
27	0.0	0.0	14.5	0.0	0.0	8.0
28	0.0	0.0	0.0	37.0	0.0	1.0
29	0.0	0.0	0.0	0.0	0.0	0.0
30	0.5	2.0	0.0	0.0	0.0	0.0
31	0.0	***	26.4	2.0	***	0.0
Total	79.9	59.9	324.7	212.5	50.4	205.0

Statistical analysis

Data were analyzed by using PAST V 217c and SPSS V 20. Genetic advance was computed by the formula stated by Falconer and Mackay (1996).

Table 2: *Data of minimum temperature of Rawalakot during the course of experiment.*

Date	May-15	Jun-15	Jul-15	Aug-15	Sep-15	Oct-15
1	***	13.6	20.1	22.2	16.7	12.5
2	12.5	15.0	22.2	20.0	17.2	12.2
3	12.5	16.4	21.4	21.7	18.3	12.3
4	15.3	16.0	24.6	***	16.7	12.8
5	16.7	16.4	28.0	21.9	17.5	13.6
6	17.2	13.9	20.7	23.6	18.1	13.5
7	19.4	17.5	21.8	23.3	16.4	13.7
8	18.6	17.5	22.7	23.1	16.9	13.3
9	20.7	18.1	20.3	22.8	***	12.8
10	16.7	20.2	19.5	23.7	15.2	13.1
11	19.7	16.7	***	22.2	15.7	15.5
12	16.1	19.8	21.3	23.7	15.7	16.7
13	14.6	17.2	20.0	22.8	15.9	17.6
14	14.0	15.3	21.4	22.8	17.6	17.3
15	13.6	16.8	25.0	22.3	19.1	13.0
16	15.7	16.5	25.5	21.2	18.1	12.2
17	19.4	18.9	22.5	19.7	16.7	13.3
18	15.9	21.1	21.5	19.2	16.3	13.9
19	15.6	22.9	22.0	20.8	17.0	13.1
20	14.5	22.2	23.0	24.0	16.1	10.8
21	17.4	18.9	22.0	21.5	15.9	12.8
22	18.1	21.2	22.0	22.2	16.7	10.0
23	20.0	17.0	22.0	20.8	16.0	10.2
24	17.5	16.8	22.0	18.5	13.7	10.7
25	13.3	17.2	21.5	17.5	16.0	8.0
26	15.0	16.9	21.1	18.6	***	8.2
27	17.7	17.2	20.6	19.4	***	8.1
28	17.2	17.2	21.1	16.4	13.5	5.4
29	21.1	24.2	22.8	17.8	14.7	5.9
30	16.8	17.3	23.6	18.6	12.2	6.3
31	16.1	***	21.9	18.3	***	7.8
Mean	16.6	17.9	22.1	21.0	16.3	11.8

Note: *** *means data is not available.*

$$Genetic\ advance\ (GA) = K.\ \sigma^2 p.\ h^2$$

Where;

K= Selection differential at 5% and 10% selection intensity; $\sigma^2 p$ = Standard deviation of the phenotypic variance of the population under selection; h^2= Heritability estimate.

Results and Discussion

Generation mean analysis

Generation mean analysis provide basic information to determine the inheritance pattern of quantitative traits in F1 and later generations. Therefore, data of P1, P2, F1, F2 and backcross (BC1 and BC2) populations were recorded for following plant traits.

Table 3: *Genetic effects for plant height, ear height, ear leaf area and flag leaf area in maize across different water regimes.*

Trait	Cross	M	D	H	I	J	l	χ^2
Plant height	VDR-51 × 5CDR-53 (N)	80.7**	----	355.6**	58.73**	-6.86**	-256.3**	1.31**
	DR3-126 × DR-37 (N)	223.2**	-5.26**	----	-85.37**	----	-34.8**	0.26**
	VDR-51 × 5CDR-53 (D)	71.04	-16.333	382.492	59.96	14.613	-233.1	0.92**
	DR3-126 × DR-37 (D)	132.6**	----	207.8**	24.8**	----	-121.4**	0.5**
Ear height	VDR-51 × 5CDR-53 (N)	40.61**	3.12**	192.01**	13.98**	----	-118.3**	1.56**
	DR3-126 × DR-37 (N)	41.11**	3.73**	207.13**	16.69**	----	-139.2**	0.96**
	VDR-51 × 5CDR-53 (D)	40.33**	2.87**	201.70**	12.98**	----	-123.1**	3.21**
	DR3-126 × DR-37 (D)	35.33**	1.87**	191.40**	8.92**	----	-134.4**	2.19**
Ear leaf area	VDR-51 × 5CDR-53 (N)	352.21**	----	448.35**	110.79**	----	----	0.81**
	DR3-126 × DR-37 (N)	278.59**	----	646.76**	171.39**	----	-132.17**	0.64**
	VDR-51 × 5CDR-53 (D)	336.31**	----	456.78**	118.46**	----	----	1.84**
	DR3-126 × DR-37 (D)	349.42**	----	423.92**	110.01**	----	----	5.38**
Flag Leaf Area	VDR-51 × 5CDR-53 (N)	96.88**	-13.87**	----	----	12.38**	131.55**	2.3**
	DR3-126 × DR-37 (N)	24.88**	----	208.89**	61.02**	----	----	3.76**
	VDR-51 × 5CDR-53 (D)	96.38**	-6.81**	----	----	----	133.26**	5.49**
	DR3-126 × DR-37 (D)	47.58**	8.05**	96.73**	40.01**	----	85.08**	2.35**

Plant height: The estimates of joint scaling test and magnitude of genetic components of variation for plant height were given in Table 3. The results demonstrated the insufficiency of the additive dominance model for describing genetic variation and five parameter model was adequate. In VDR-51 × 5 CDR-53 under natural condition five parameters deviated significantly from the zero whereas one parameter was non-significant. Dominance effects were positive showing incline of F_1 towards parent with more plant height (P_1). Under water stress conditions additive dominance model was also insufficient to elucidate the gene action and six parametric model was found sufficient (Table 3).

In inter generation comparison, maximum plant height was observed in BC_2 (212.57 cm) under natural conditions followed by BC_1 (205.7 cm) while, lowest plant height was observed in P_2 (135.4 cm) Whereas under drought stress highest plant height (190.4 cm) was recorded in F_1 followed by BC_2 (189.8 cm) and lowest plant height was observed in P_1 (84.33) (Figure 1).

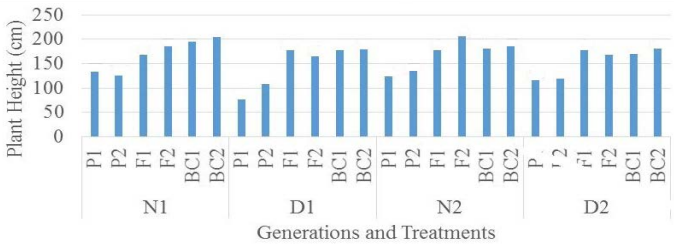

Figure 1: *Mean values of various generations of maize for plant height.*

However, in case of the cross DR-3-126 x DR-37 under natural conditions four parametric model (m, d, I, l) was found suitable for explaining gene action. Additive x additive interaction was significant with positive sign revealing the association (coupling) of interacting genes (Table 3). In cross DR-3-126 x DR-37 maximum plant height (214. 1 cm) was observed in F_2 population under natural conditions while in F_1 it was 189cm under water deficit stress conditions however lowest plant height under natural and drought conditions was observed in P_1 (132.2 cm) and P_1 (124.6 cm) respectively (Figure 1).

Ear height: Genetic variation and estimates of joint scaling test for ear height are mentioned in Table 3. Ear height was not only explained by additive dominance model but also by epistatic effects as inferred from table 04. Under controlled conditions ear height in cross VDR-51 × 5 CDR-53 was governed predominantly by dominance gene action as 'h' estimates were high. There was duplicate type of epistasis as sign of 'i' and 'h' were contradictory. Similar gene action with high dominance effects and low additive effects was observed in cross VDR-51 × 5 CDR-53 under drought stress conditions. Opposite signs of "i: (additive x additive) and "l" (dominance x dominance) represents that duplicate type of di-genetic non allelic interaction was present. Comparison of generation means showed that in cross VDR-51 × 5 CDR-53 lowest ear height (61 cm) was observed in P_2 and maximum ear height was observed

in BC_1 (113.1 cm) under natural conditions whereas under drought stress P_2 gave minimum ear height (34 cm) and maximum ear height was observed in BC_1 (95.8 cm) (Figure 2).

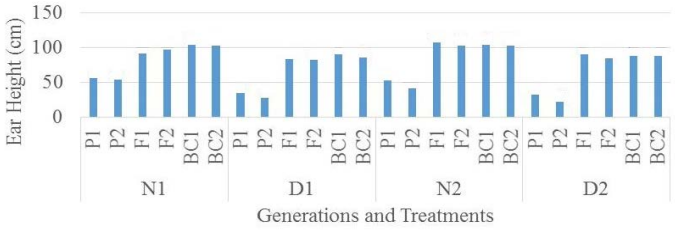

Figure 2: *Mean values of various generations of maize for ear height.*

In cross DR3-126 × DR-37 additive dominance model was inadequate to describe genetic variability for ear height under natural as well as drought conditions. Presence of epistasis was indicated by insufficiency of the model and it was observed that variability for ear height in this cross was properly explained by five parametric model (m, d, h, I, l). Dominance effects were more than the additive effects which showed that dominance genes were playing greater role in controlling the ear height. Similarly, higher values of 'l' and 'i' represented that dominance × dominance and additive × additive type of epistasis was also playing role. These parameters were opposite in both natural and drought stress conditions which indicated existence of duplicate type of epistasis (Table 3). While comparisons of generation means indicated that under natural conditions F_1 had the highest value (114.3 cm) whereas P_2 had the lowest ear height (50 cm). Under water deficit condition the lowest and highest values were recorded for the same generation i.e. P_2 (28.6 cm) and F_1 (99 cm) was significantly lower than their counterparts in the natural conditions (Figure 2).

Ear leaf area: Joint scaling test and different components of generation means for ear leaf area were given in the (Table 3). The results indicated that additive dominance model was not sufficient to explain the inheritance of ear leaf area in cross VDR-51 × 5 CDR-53. Three parameter model (mhi) was found sufficient to explain the genetic composition of ear leaf area. It indicated that the genes controlling the ear leaf area were mostly dominant in nature as was evident from the significant effects of parameter 'h' but also influenced by the epistatic effects of additive genes 'i' under natural as well as water stress conditions. Dominance effects were higher than the additive effects. Also sign of 'h' was positive which showed that ear leaf area was more inclined to parent with more ear leaf area i.e.VDR-51 under control as well as water stress conditions (Table 3). Whereas, generation mean comparisons showed that lowest ear leaf area and highest ear leaf area in drought as well as natural conditions was found in P2 and F1.

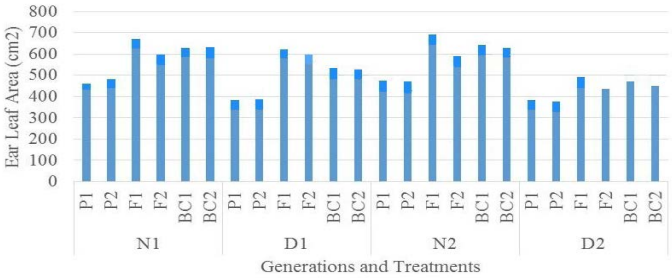

Figure 3: *Mean values of various generations of maize for ear leaf area.*

Under natural conditions four parameter model (mhil) was found satisfactory to explain the inheritance pattern in Cross DR3-126 × DR-37 for ear leaf area. Dominance effects were highest showing the main contribution of the dominance genes in controlling the ear leaf area. However, epistasis also played role in modifying the action of dominance genes via 'l' parameter. As the sign of dominance × dominance (l) and dominance (h) type of epistasis were opposite this indicated the presence of duplicate type of epistasis. However, under drought stress conditions three parametric model (mhi) was found sufficient to describe the genetic behaviour of ear leaf area for this particular cross. As the value of 'h' was high which represented that dominant genes have more role in controlling ear leaf area but significant contribution was also offered by additive genes via 'i' type of epistasis (Table 3). Under natural conditions the generation mean comparison showed similar results as were observed in above cross highest mean by F1 and lowest by DR-37. However, under drought stress conditions BC1 (503.69 cm^2) showed the highest generation mean and P2 showed lowest generation mean (353.9 cm^2) (Figure 3).

Flag leaf area: The estimates of joint scaling test (Table 3) represented that variability in flag leaf area could not be explained by additive dominance model alone. Hence it was concluded that the flag leaf area in cross VDR-51 × 5 CDR-53 was also influenced by epistatic gene action. Higher values of 'd' showed that the flag leaf area was mainly controlled by additive genes but higher value of 'l' alongside also indicated a strong influence of dominance genes in governing flag leaf area under natural conditions. Negative sign of 'd' indicated that additive genes controlling flag leaf area had negative impact on it. Similar results were

observed with drought stress. Comparing generation mean it was seen that maximum flag leaf area under drought as well as natural conditions was observed in F_1 generation (150 and 178 cm^2 respectively) whereas lowest flag leaf area was recorded in VDR-51 under control as well as water deficit conditions (Figure 4).

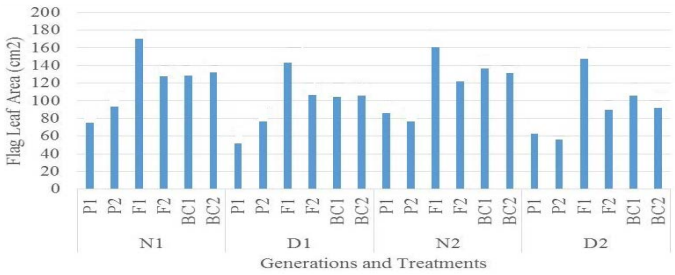

Figure 4: *Mean values of various generations of maize for flag leaf area.*

Additive dominance model was not suitable to describe the genetic effects for flag leaf area in DR3-126 × DR-37 cross. Three parametric model (mhi) was found sufficient to describe the inheritance pattern of Cross DR3-126 × DR-37 for flag leaf area. Dominance effect was higher indicating the role of dominant genes interaction in controlling flag leaf area. Not only dominance gene action but also the additive gene action via 'i' was also playing role in modifying the action of dominance genes under natural conditions (Table 3). Under drought stress conditions five parametric model (mdhil) was found significant for controlling the inheritance pattern of flag leaf area in DR3-126 × DR-37 cross. Dominance effects were highest among other parameters indicating that the trait was mostly governed by the dominance effects. As 'h' was positive it represented that the flag leaf area was more inclined towards parent with high flag leaf area (P_1). As the sign of 'h' and 'i' were same it showed the presence of supplementary epistasis. With respect to generation mean comparison it was observed that under natural and drought stress conditions highest flag leaf area was observed in F_1 and lowest flag leaf area was recorded in DR-37 (Figure 4).

Days to tasseling: The estimate of joint scaling test and components of genetic variation for days to tasseling were listed in Table 4. To explain days to 50 % pollen shed the additive dominance model was insufficient as indicated by results. Hence 03 parametric model (mhj) was found sufficient to explain the genetic variability in the cross VDR-51 × 5CDR-53 for days to 50 % pollen shed under natural conditions. Dominance played predominant role in controlling the inheritance pattern of days to 50% pollen shed and was influenced by additive × dominance type of epistasis. However, under alter deficit condition only additive × dominance type of epistasis was playing a role in governing days to 50% pollen shed (Table 2). Mean comparison showed that F_2 generation took minimum days (65) to 50% pollen shed whereas F_1 took highest number of days (73.3). However, under drought stress conditions lowest days to 50% pollen shed was recorded for P_2 (59.3 days) and highest were recorded for F_1 (70.35 days) (Figure 5).

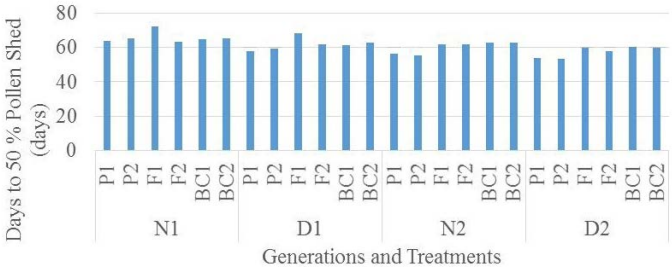

Figure 5: *Mean performance of different generation of maize for days to 50% pollen shed.*

In case of Cross DR3-126 × DR-37 it was observed that under natural conditions, it was governed only by additive × dominance type of epistasis. 2 parametric model (mh) was observed significant for it. Under drought stress condition days to 50% pollen shed was also controlled by similar set of genes as was indicated by the Table 04. Negative sign of 'j' indicated that this type of epistasis was affecting the days to 50% pollen shed negatively (Table 2). In mean comparison as was given in (Figure 3), it was observed that under natural conditions generation mean of BC_2 and F_1 was comparable and was highest among other generation i.e. 64.54 and 64.12 days respectively. Under drought stress conditions highest mean value was that of BC_1 (62.23 days). Lowest days to 50 % pollen shed were taken by P_2 plants (Figure 5).

Days to silk emergence: Additive dominance model was inadequate to explain the genetic behaviour of days to silk emergence and four parameter model (mhjl) was found appropriate to explain the genetic architecture of days to silk emergence in cross VDR-51 × 5CDR-53 under natural conditions. The estimates of dominance were high showing the preponderance of dominance genes in governing the inheritance pattern of this trait. Presence of epistasis was also explained as additive dominance model was insufficient. Two types of epistasis 'l' and 'j' were also governing days to silk emergence. As the sign of 'l' and 'h' were of same nature it indicated that there existed a duplicate nature of epistatic effects under natural conditions. However, under drought stress

conditions five parametric model (mdhil) was found sufficient to describe the genetic behaviour of days to silk emergence. Degree of dominance effects was high but negative sign indicated that the dominance was playing very crucial role in controlling the behaviour of this trait. However, days to silk emergence was more inclined to the parent which taken less number of days to pollen shedding. The epistasis was again of duplicate nature due to the contrary sign of 'h' and 'l' (Table 4). Comparing generation means it was observed that under natural conditions lowest days to silk emergence were taken by F_2 (65 days) and highest were observed with BC_2 (76.2 days) However, under drought stress least days to silk emergence were recorded in VDR-51(59.6 days) and maximum number of days to silk emergence was observed in F_1 (70.36 days) (Figure 6).

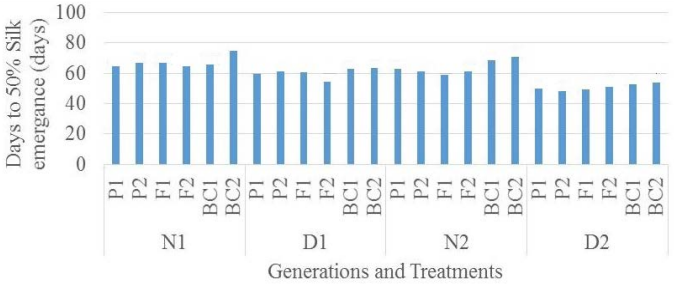

Figure 6: *Mean performance of different generation of maize, days to silk emergence.*

On the other hand in cross DR3-126 × DR-37 additive dominance model was not sufficient to describe inheritance pattern for days to silk emergence under natural conditions and three parametric model (mhj) was found enough. The estimate of 'h; was high but with negative value showing that days to silk emergence in this cross were more inclined to parent having less days to silk emergence. Although epistasis also played significant role in governing the trait via additive × dominance type of interactions. Under water deficit stress only additive dominance model was adequate showing no involvement of epistasis in controlling the days to silk emergence (Table 4). Over all generation means under drought stress were low as compared to control. Under controlled environment lowest mean was recorded in F_1 (60.3 days) and highest mean was of BC_2 (73.13 days). Under drought stress conditions however, lowest mean (51.31 days) and highest mean (59.34 days) were observed with DR3-126and BC_2 respectively (Figure 6).

Anthesis-silking interval: Joint scaling test and genetic components for anthesis-silking interval were listed in Table 4. The results showed that additive dominance model was inadequate to describe inheritance pattern of ASI in VDR-51 × 5CDR-53 cross under natural conditions. However, four parametric model (mijl) was found sufficient for explaining the genetic behaviour of ASI. ASI in this cross was mainly governed by epistatic interactions. However, under drought stress conditions only additive dominance model was found enough to explain genetic behaviour of ASI with preponderance of additive genes as 'h' was non-significant and 'd' was highly significant (Table 4). Generation means was highest in F_1 (1.5 days) and lowest in P_1 (0.67 days). However, under drought stress conditions highest ASI was observed in BC_2 (2.13 days and lowest in P_1 (1.13 days) (Figure 7).

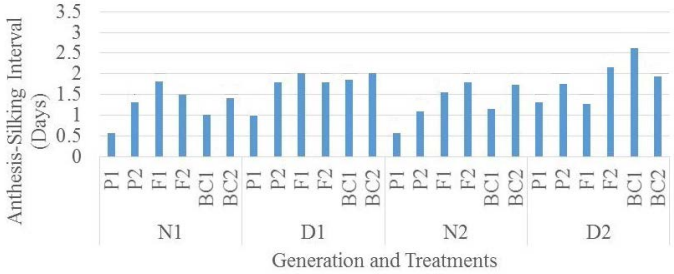

Figure 7: *Mean performance of different generation of maize for anthesis-silking interval (days).*

Additive dominance was also not suitable to describe the genetic behaviour of cross DR3-126 × DR-37 for ASI under drought stress as well as natural conditions (Table 4). Under natural conditions ASI was governed by additive interactions and dominance × dominance types of epistasis whereas under drought stress it was governed by additive × additive type of epistasis alone (Table 2). Generation means comparison indicated that highest ASI of 1.92 days under natural conditions was observed in $F_2$and lowest was observed in P_1 (0.71 days) however under drought stress it was lowest in F_1 (1.43 days) and highest in BC_1 (2.76 days) (Figure 7).

Shelling percentage: Shelling percentage in both crosses under natural as well as water deficit conditions except DR3-126 × DR-37 under natural conditions was governed by three parameter model (mhj) and additive dominance model was found inefficient in explaining the genetic behaviour. The cross DR3-126 × DR-37 under natural conditions was governed by three parameter model with the exception that it contains 'i' type of epistasis rather than 'j' type. It was observed that the dominance was the main factor in both crosses under both water conditions and mainly governed the inheritance pattern of this trait. However, epistasis 'j' (additive × dominance) type and

Table 4: *Genetic effects for days to 50% pollen shed, days to silk emergence, anthesis-silking interval and shelling % in maize across different water regimes.*

Trait	Cross	M	d	H	I	J	L	χ^2
Days to pollen shed	VDR-51 × 5CDR-53 (N)	54.3**	----	-3.99**	----	-4.34**	----	4.91**
	DR3-126 × DR-37 (N)	53.28**	----	----	----	-3.93**	----	1.32**
	VDR-51 × 5CDR-53 (D)	50.15 **	----	-9.9**	-4.32**	-1.39**	----	2.32**
	DR3-126 × DR-37 (D)	49.32 **	----	----	----	-2.10**	----	3.15 **
Days to silking	VDR-51 × 5CDR-53 (N)	55.1**	----	-7.12**	----	-4.27**	-11.23**	5.23**
	DR3-126 × DR-37 (N)	53.9**	----	-5.23**	----	-5.32**	----	3.23**
	VDR-51 × 5CDR-53 (D)	52.2**	1.94**	-11.12**	-6.23 **	----	7.95**	1.93**
	DR3-126 × DR-37 (D)	51.23**	----	-4.21**	----	----	----	4.78**
Anthesis-silking interval	VDR-51 × 5CDR-53 (N)	0.82**	----	----	-0.13**	0.37**	0.31**	1.51**
	DR3-126 × DR-37 (N)	0.62**	0.23**	----	----	----	0.12**	2.91**
	VDR-51 × 5CDR-53 (D)	2.05**	----	0.32**	----	----	----	1.31**
	DR3-126 × DR-37 (D)	1.91**	----	----	-0.31**	----	----	0.21**
Shelling %	VDR-51 × 5CDR-53 (N)	83.2**	----	6.23**	----	-2.32**	----	3.12**
	DR3-126 × DR-37 (N)	80.66**	----	5.92**	3.92**	----	----	0.99**
	VDR-51 × 5CDR-53 (D)	81.59**	----	6.12**	----	-2.92**	----	1.53**
	DR3-126 × DR-37 (D)	80.61**	----	1.92**	----	0.95**	----	3.29**

Table 5: *Genetic effects for number of kernel per row, number of kernel rows per ear, 100-kernel weight, grain yield tons/ha, biological yield tons/ha and harvest index in maize across different water regimes.*

Trait	Cross	M	d	H	I	J	L	χ^2
Number of kernel per row	VDR-51 × 5CDR-53 (N)	11.40**	----	3.43**	----	0.47**	----	3.45**
	DR3-126 × DR-37 (N)	11.56**	----	3.16**	----	----	----	7.78**
	VDR-51 × 5CDR-53 (D)	10.65**	----	----	-0.89**	----	4.91**	0.73**
	DR3-126 × DR-37 (D)	9.52**	----	4.64**	----	----	----	2.29**
Number of kernel Rows per ear	VDR-51 × 5CDR-53 (N)	23.01**	----	37.01**	----	----	-12.87**	1.96**
	DR3-126 × DR-37 (N)	28.19**	----	20.12**	-5.98**	1.39**	----	0.54**
	VDR-51 × 5CDR-53 (D)	18.35**	----	10.60**	----	----	----	1.74
	DR3-126 × DR-37 (D)	22.81**	----	----	-1.91**	-0.85**	5.26**	2.52**
100-Grain weight	VDR-51 × 5CDR-53 (N)	17.53**	-0.55**	29.20**	3.12**	----	-15.93**	0.47**
	DR3-126 × DR-37 (N)	23.2**	2.46**	7.04**	----	-3.37**	5.82**	0.03**
	VDR-51 × 5CDR-53 (D)	14.01**	----	15.91**	1.81**	----	-4.78**	2.525**
	DR3-126 × DR-37 (D)	16.55**	----	7.01**	----	----	2.76**	2.45**
Grain yield tons/ha	VDR-51 × 5CDR-53 (N)	18.83**	15.01**	67.36**	7.98**	-18.9**	----	0.31**
	DR3-126 × DR-37 (N)	10.71**	----	60.35**	7.97**	----	58.27**	0.12**
	VDR-51 × 5CDR-53 (D)	25.63**	-0.48**	58.87**	-14.49**	----	----	3.64**
	DR3-126 × DR-37 (D)	71.04**	-16.33**	382.49**	59.96**	14.61**	-233.13**	0.36**
Biological yield tons/ha	VDR-51 × 5CDR-53 (N)	83.2**	----	6.23**	----	-2.32**	----	3.12**
	DR3-126 × DR-37 (N)	80.66**	----	5.92**	3.92**	----	----	0.99**
	VDR-51 × 5CDR-53 (D)	81.59**	----	6.12**	----	-2.92**	----	1.53**
	DR3-126 × DR-37 (D)	80.61**	----	1.92**	----	0.95**	----	3.29**
Harvest Index	VDR-51 × 5CDR-53 (N)	49.21**	----	----	----	5.70**	----	33.38**
	DR3-126 × DR-37 (N)	43.21**	-1.99**	11.65**	8.54**	----	-17.13**	39.41**
	VDR-51 × 5CDR-53 (D)	50.31**	----	----	-3.29**	2.91**	----	43.21**
	DR3-126 × DR-37 (D)	44.23**	-1.87**	11.21**	6.81**	-2.21**	----	31.32**

'i' also influenced the 'h' in final shaping of the genetic architecture of both the crosses under natural and water stress conditions. Dominance effects 'h' had positive sign which indicated that shelling % age was inclined towards the parent with high shelling % age P_1 (Table 4) Highest shelling % in natural and drought stress conditions in VDR-51 × 5CDR-53 cross was observed in F_1 (85.4% and 70.3% respectively). However, lowest shelling %age of 76.4% and 65.1% in natural and drought stress conditions was observed in P_2 and P_1 respectively (Figure 8). In case of Cross DR3-126 × DR-37 lowest shelling % under natural and drought stress was observed in F_2 (80.45%and 64.5% respectively). However, highest shelling % was observed in F_1 (83.4%) and P_2 (69.2%) in natural and drought conditions respectively (Figure 8).

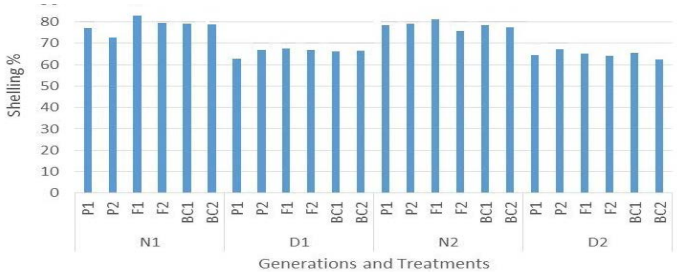

Figure 8: *Mean values of various generations of maize for shelling (%).*

Number of kernals row $^{-1}$: The joint scaling test and genetic components for kernels per row are listed in Table 5. Results represented that additive dominance model was insufficient to explain the genetic behaviour of kernels per row in VDR-51 × 5CDR-53 cross under natural as well as water deficit conditions. Under natural conditions the trait was governed by dominance effects as 'h' was higher than the additive components 'i'. Also the epistatic effects were present 'j' (additive × dominance) and influenced the behaviour of dominance genes. Under drought stress conditions neither additive nor dominance effects were significant instead epistatic effects were playing crucial role in governing the kernels per row. Two epistatic components 'l' (dominance × dominance) and 'i' (additive × additive) were found significant in controlling kernels per row. While comparing generation mean it was observed that in general kernels per row were negatively affected by drought stress. Under natural conditions 5CDR-53 had the lowest kernels per row (23) whereas F_1 had the highest kernels per row (47.25). Under water deficit condition both the parents had lowest number of kernels per row (18.4) and highest number of kernels per row was observed in F_1 (29) (Figure 9).

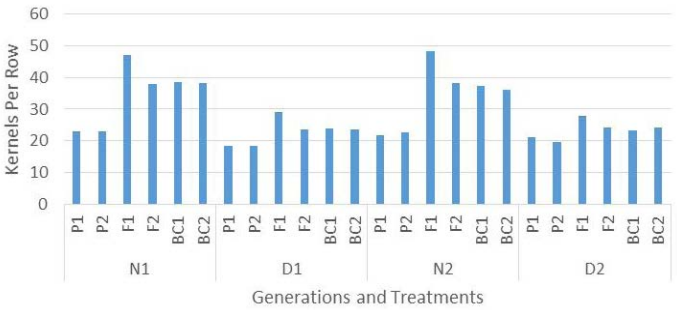

Figure 9: *Mean values of various generations of maize for kernels row^{-1}.*

However, in Cross DR3-126 × DR-37 under natural conditions additive dominance model was found sufficient to explain genetic architecture of kernels per row. Results represented that only dominant genes were governing the expression of kernels per row and no contribution of additive genes directly or via epistasis was found. Similar results were also observed for the above mentioned cross under drought stress conditions as dominant genes were governing inheritance pattern of this trait. Only 'h' was found significant and rest of the parameters were non-significant. Lowest kernels per row (22) were observed under natural conditions in DR3-126 whereas under drought conditions in P_2 (19.5) whereas, highest kernels per row under natural as well as drought conditions were observed in F_1 (48.3 and 26.3 respectively) (Figure 9).

Number of kernal rows ear $^{-1}$: Additive dominance model was not enough to describe genetic inheritance of kernel rows per ear in the cross VDR-51 × 5CDR-53 under natural conditions. The three parametric model (mhl) was found enough to explain genetic variability present in kernel rows per ear. Results showed prevalence of dominant genes in governing the inheritance pattern as value of 'h' was high. However, it was influenced by epistatic interaction 'l'. As the sign of 'l' and 'h' was opposite it showed presence of duplicate epistasis. Under drought stress conditions however additive dominance model was sufficient in explaining genetic variability present in kernel rows per ear. Dominance have predominant role in controlling the inheritance pattern (Table 5). Highest kernel rows were found in F_1 (13.6 and 14.5) under drought as well as natural conditions.

In cross DR3-126 × DR-37 four parameters model (mhij) was found significant for explaining the genetic architecture of kernel rows per ear under natural and water deficit conditions. Dominance effects were more important in controlling trait under natural conditions, which were also supported by epistatic

effects. However, under drought stress conditions neither dominance nor additive effects played role instead different types of epistatic effects (i, j and l) were governing the trait (Table 5). Highest effects were observed with 'l' indicating that dominance × dominance type of interaction is governing the trait. Maximum kernel rows per ear under drought as well as natural conditions were observed with F_1 and lowest kernel rows per ear under control conditions were observed in P_1 whereas under stress conditions in P_2(Figure 10).

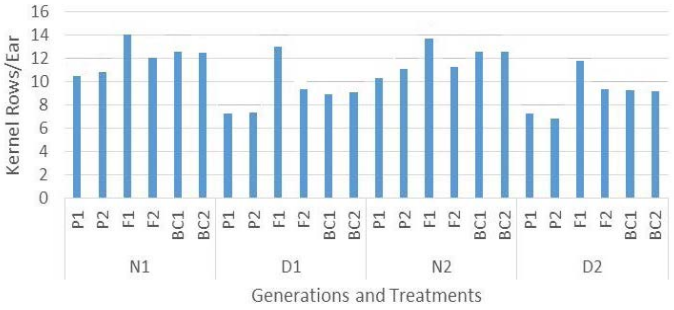

Figure 10: *Mean values of various generations of maize for kernel rows ear^{-1}.*

Present study revealed that for kernel rows per ear, the dominance gene action was accounted for most of observed variability, but the additive and epistatic effects can also be considered important.

100-grain weight: The estimate of joint scaling test and magnitude of genetic components of variation for hundred grain weight are given in Table 5. Results showed the inadequacy of the additive dominance model for describing the genetic variation and five parametric model (mdhil) was adequate. In the cross VDR-51 × 5 CDR-53 five parameters deviated significantly from the zero whereas one parameter [j] was non-significant under natural condition. Dominance effects were positive showing inclined of F_1 towards parent with more hundred grain weight (5 CDR-53). Epistasis was of duplicate type as was indicated by the contrary sign of l and h. Additive x additive interaction was significant with positive sign revealing the association (coupling) of interacting genes. Under water stress conditions additive dominance model was insufficient to describe gene action and four parametric model (mhil) was found sufficient (Table 2). Dominance effects were higher than the additive showing prevalence of dominant genes in governing plant height as was observed under natural conditions. Epistasis was of duplicate nature. Maximum hundred grain weight was observed in F_1 (30.8 g) under natural conditions and lowest hundred grain weight was observed in P_1 (20.6 g). Whereas, under drought stress highest hundred grain weight (25.13 g) was observed in F1 and lowest hundred grain weight was observed in P_1 (15.3 g) (Figure 11).

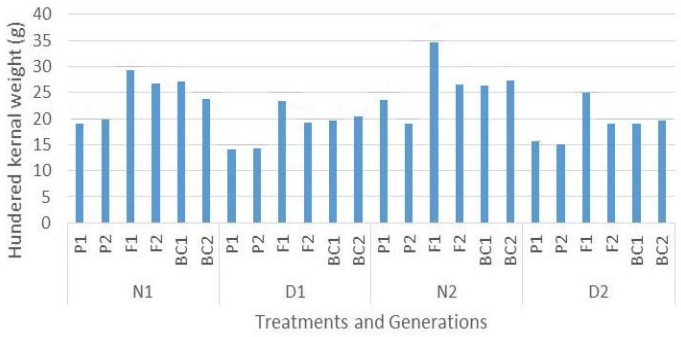

Figure 11: *Mean values of various generations of maize for 100-Grain weight.*

However, in case of the cross DR-3-126 x DR-37 five parametric model (mdhjl) was found sufficient for explaining gene action under natural conditions. Dominance effects were larger than additive effects, indicating role of dominance genes in controlling hundred grain weight. Epistasis was of complementary nature as the sign of 'i' and 'h' were same. Under water deficit conditions three parameter model with different parameters (mhl) was adequate. Dominance effects were prominent in controlling the gene action under water stress for hundred grain weight. Complementary type of epistasis was more prominent as was indicated by the same sign of 'l' and 'h' (Table 5). In cross DR-3-126 x DR-37 highest hundred grain weight of 36.1g and 26.3 g was observed in F_1 population under natural as well as drought conditions respectively, however lowest hundred grain weight under drought and natural conditions was observed in P_2 (20.73 and 16.2 g respectively) (Figure 11).

Grain yield: Joint scaling test and different components of generation means for grain yield tons/ha are given in the Table 5. The results illustrated that additive dominance model was not adequate to describe inheritance of grain yield tons/ha in cross VDR-51 × 5 CDR-53. Five parameter model (mdhij) was found sufficient to describe genetic composition of grain yield tons/ha. It indicated that the gene controlling the grain yield tons/ha were mostly dominance in nature as was evident from the significant effects of parameter 'h' but also influenced by the epistatic effects of additive genes 'i' and 'j' under natural conditions. Dominance effects were higher than additive effects (Table 4). Whereas generation mean comparisons showed that lowest grain yield tons/ha and highest grain yield tons/ha in drought as well as natural conditions was found in P_2 and F_1 (Figure 12). Under

natural conditions four parametric model (mhil) was found sufficient to explain the inheritance pattern in Cross DR3-126 × DR-37 for grain yield tons/ha. Dominance effects were highest showing the main contribution of the dominance genes in controlling the grain yield tons/ha. However, epistasis also played role in modifying the action of dominance genes via 'l' parameter. As sign of dominance × dominance 'l' and dominance 'h' type of epistasis was of same sign which indicated presence of complementary type of epistasis. However, under drought stress contribution six parametric model was found sufficient to describe the genetic behaviour of the grain yield for the particular cross. As the value of 'h' was high which indicated that dominance genes have more role in controlling grain yield but significant contribution was also offered by additive genes via 'h' type of epistasis. Duplicate epistasis existed as indicated by the opposite sign of 'h' and 'i' (Table 5). Under natural conditions the means comparison showed similar result as were observed in above cross highest grain yield by F_1 and lowest by P_2 under drought stress as well as natural conditions (Figure 12).

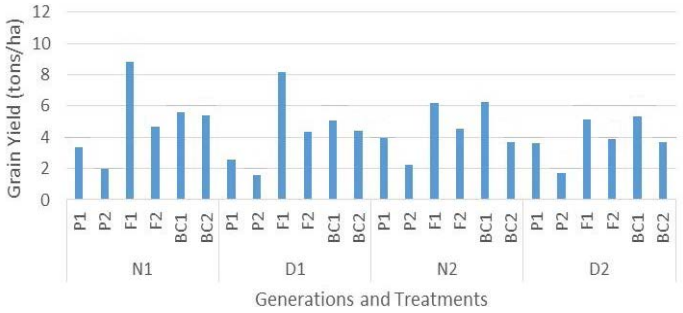

Figure 12: *Mean values of various generations of maize for grain yield tons/ha.*

Harvest index: Pattern of inheritance for VDR-51 × 5CDR-53 cross for harvest index was not governed by additive dominance model and was controlled by two parametric model (mj) under natural conditions. Only additive × dominance type of epistasis was governing harvest index under natural conditions. Under drought stress conditions three parametric model (mij) was found enough to describe genetics of harvest index. Two types of epistasis i.e. additive × additive and dominance × dominance were controlling the harvest index (Table 5). Highest harvest index was observed in F_2 and F_1 under drought and natural conditions (54% and 52.8%) respectively. Whereas, lowest harvest index was observed in P_2 under drought (47%) and natural conditions (43%) (Figure 13).

In Cross DR3-126 × DR-37 five parameter model (mdhil) was found sufficient to describe the genetic architecture of harvest index under natural conditions. The gene action was that of duplicate type as the sign of 'l' and 'h' was contrary. However, there was preponderance of dominance genes as 'h' effects were higher than the 'd' effects. However, positive sign of 'h' indicated that harvest index was inclined towards parent with high harvest index (P_1). Under drought stress conditions also five parametric model (mdhij) was found significant. Major contribution was that of dominance genes which were being influenced by additive × additive and additive × dominance type of epistasis (Table 5). Highest harvest index in drought and natural conditions was observed in BC_2 (48.4%) and F_1 (52%) (Figure 13).

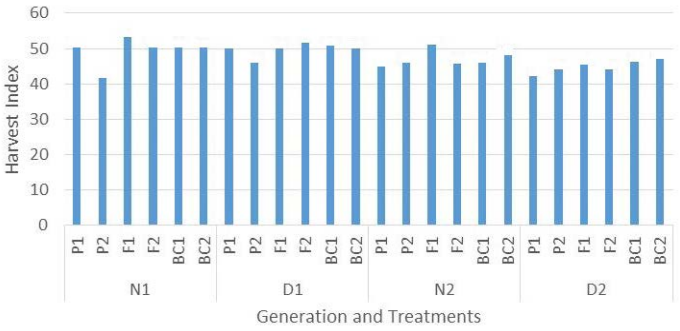

Figure 13: *Mean values of various generations of maize for harvest index.*

Conclusions and Recommendations

Mean performance for the grain yield and most of the yield related traits under both natural and drought stress conditions was high for the crossVDR-51 × 5CDR-53. Dominant type of gene action was depicted by generation mean analysis for most of the traits studied. Hence the crossVDR-51 × 5CDR-53 might be recommended as a drought tolerant single cross hybrid for the drought prone semi-arid areas of the country.

Novelty Statement

This study is important for plant breeders to select the desirable traits for crop improvement or in the future breeding program.

Author's Contribution

MI performed the experiments, wrote the paper. SAK designed the experiments. SIA analyzed the data. SR contributed in data collection. MRK, contributed reagents. WA modified the paper. RMMN contributed analysis tools. MMUK assisted in data collection and SH modified the paper.

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