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Genetic Mechanisms of Leaf Characteristics and Grain Yield in Maize under Normal and Moisture Stress Conditions

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Abstract: Eight inbred lines of maize were evaluated to determine the genetic mechanisms of leaf characteristics in maize inbred lines under different environments. The experimental material was planted under normal as well as water stress conditions. Data on yield and leaf characteristics revealed highly significant differences among inbred lines under both plantings. Graphical analysis revealed that additive gene action for soluble sugar content remained unchanged under water stress while over-dominance type of gene action for protein content, osmotic potential, stomata size and grain yield per plant under normal condition also remained unchanged under water stress whereas additive type of gene action for stomatal frequency under normal changed to over-dominance type of gene action under water stress.

Key words: Maize, diallel cross, genetic mechanisms, drought tolerance

INTRODUCTION

Maize production in Pakistan has increased from 353 thousand tons in 1947-48 to 1737 thousand tons in 2002-03[1]. This is more than a 400% increase and largely results from an increase in average yield from 987 to 1857 kg ha^{-1}[2]. However, this suggested that there is considerable potential for enhancing maize productivity in Pakistan. But still this average yield is very low as compared to the average yield (7077 kg ha^{-1}) of developed countries[3].

Now-a-days, Pakistan is facing a serious problem of water necessary for crops production and to fulfil the food, fuel and industrial material demands of its ever growing population. Due to the severe shortage of water, 24 million tons of maize grains are lost annually worldwide[4]. To formulate an efficient breeding program for developing drought tolerant varieties, it is essential to understand the mode of inheritance. The diallel cross developed by Hayman and Jinks[5,6], which is composed of all possible single crosses among a group of inbred lines, is a widely used method for investigating metrical traits in plant breeding and provide a handy technique to study the nature of gene action in quantitatively inherited traits.

Breeders are continually searching for lines tolerant to drought that can be used to enhance maize's adaptation to water deficient environments, though most of the selection is based only on grain yield. Perez *et al.*[7] studied 28 maize hybrids and their parents in 6 environments for grain yield. Additive effects were significant for all the studied traits. Chen *et al.*[8] studied inheritance of grain yield per plant in an eight parent diallel cross. Analysis of results showed that all the characters fitted into an additive-dominance model, except for grain yield per plant which exhibited high epistasis. Inheritance of grain yield per plant was controlled by dominant effects and epistasis. Gul *et al.*[9] studied maize synthetic varieties and recorded data on yield related traits. Mean square for grain yield was not significant. Joshi *et al.*[10] conducted the analysis in early maturing maize inbred lines for quality and yield components. Both additive and non-additive gene effects were present in the material under study. However, the ratio of additive and non-additive genetic variance revealed that there was a preponderance of non-additive gene action in the expression of yield per plant and protein content. Mathur *et al.*[11] studied seventy-eight single cross maize hybrids in normal and water stress environments. A preponderance of additive gene effects was observed in the expression of all the characters studied including grain yield per plant.

Dutu[12] derived information on phenotypic and genetic variances on grain yield in 56 simple hybrids from a diallel cross among 8 inbred lines. Analysis of the data indicated that additive gene action was predominant in the inheritance of grain yield. Vicente *et al.*[13] extracted 49 early maize lines from different CIMMYT populations and evaluated fewer than three water regimes, Normal Irrigation (NI), Intermediate Stress (IS) and Severe Stress (SS). Grain yield and other yield related traits were

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evaluated. Highly significant differences were detected among genotypes for all traits. The reduction in grain yield was 70 and 90% in IS and SS, respectively. Grain yield fluctuated between 0.30 t ha^{-1} (SS) and 2.41 t ha^{-1} (NI). The reduction for plant height was 36 cm in SS. Phutela *et al*.[14] concluded that osmotic adjustment under water stress differed in *Brassica juncea* cultivars. They studied plant water relations by using 5 genotypes and found Varuna having higher degree of adaptation to drought. Dass *et al*.[15] evaluated 166 genetically diverse lines of maize under different artificially given stress conditions, viz., control, mild stress, intermediate stress and severe stress and reported that hybrids were more tolerant as compared to inbred. Shabbir and Saleem[16] performed diallel analysis of six elite lines of maize and reported that all the characters being studied were under the control of over-dominance type of gene action, except protein percentage which showed additive type of gene action.

The under mentioned study was planned to know the effects of different planting conditions on some leaf traits reflecting quality and yield potential in term of the type of gene action. This information would be of great help to breed new maize inbred lines for drought related production situations in the country.

MATERIALS AND METHODS

Eight inbred lines (drought tolerant and susceptible) were planted in the field of the Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad and crossed in all possible combinations in a diallel fashion during April/May, 2002. Necessary measures were taken during the hybridization process to avoid contamination of the genetic material used. During the following season (August/September, 2002), all of the 56 F_1, S and eight parents were sown in the field using a Randomized Complete Block Design with three replications. The same experiment was also planted under water stress condition. All other agronomic and cultural practices were kept same except irrigation. Moisture stress was applied at the time of anthesis, silking, pollination and grain filling stages to water stress experiment. Data for stomata size, stomatal frequency, osmotic adjustment, soluble sugar content, protein content and grain yield per plant were collected and subjected to basic analysis of variance[17]. Graphical analysis for gene action and determination of genetic components of variation were also made following Hayman and Jinks[5,6].

RESULTS AND DISCUSSION

As regards stomata size, the highest (1364.2 μm^2) and the lowest (1003.3 μm^2) stomata size was recorded in inbred line F-149 and F-133, respectively, under normal condition while under water stress, same parental lines showed (Table 1) the largest and the smallest stomata size (1301.83 and 591.37 μm^2, respectively).

Among crosses (Table 1), stomata size ranged from 1023.10 μm^2 (SEL-8 x F-133) to 1376.4 μm^2 (F-141 x F-131) under normal, while under water stress experiment, stomata size ranged from 574.90 to 1300.0 μm^2 (F-128 x SEL-8 and F-131 x F-149, respectively). On average, a reduction of 19.93% was recorded for stomata size in all the genotypes under water stress.

It is obvious from the Table 1 that the parental line SR-402 showed maximum stomatal frequency (182.0) while a minimum value (155.0) was noted for F-133 under normal field. Under water stress, F-135 showed the highest (188.0) value and the genotype F-131 exhibited the lowest (177.0) value for this trait. Among crosses, the cross F-149 x F-128 exhibited maximum (184.3) stomatal frequency closely followed by the cross F-149 x F-131 (184.0) under normal condition while under water stress, the cross F-133 x SEL-8 had the highest (188.33) value followed by the cross F-128 x F-149 (187.67). A mean increase of 7.0% was recorded for stomatal frequency under water stress in all the genotypes. These results are in conformity with findings of Parkas and Rajethy[18] and Jones[19], who had also been reported an increase in stomatal frequency under water stress.

As regards osmotic potential (Table 1), highest value of 0.8343 MPa and the lowest value of 0.5757 MPa were recorded for parental lines F-135 and F-141 under normal condition, respectively; while under water stress, the parent, F-149 had the highest (1.1300 MPa) osmotic potential and F-133 had the minimum value (0.8333 MPa) for this trait. Among crosses, osmotic potential ranged from 0.5627 MPa (SEL-8 x SR-402) to 0.9080 MPa (F-149 x SR-402) under normal trial, whereas under water stress, this range was 0.8100 to 1.4000 MPa (F-133 x F-128, F-128 x F-141 and F-131 x F-135, respectively). Table 1 showed an overall increase of 27.1% in all genotypes in osmotic potential under water stress. These findings are similar with those of Rehman *et al*.[20] Sojka *et al*.[21] and Premachandra *et al*. [22], who also provided the evidence of increase in osmotic potential under water stress, while these findings are different with those of Begg and Turner[23] and Jovanovic *et al*. [24], who

Table 1: Means, LSD values and CV % of stomata size, stomatal frequency, osmotic potential and osmotic adjustment of maize in an 8x8 diallel cross under normal and water stress conditions

Parental lines /crosses	Stomata size (μ m²)		Stomatal frequency		Osmotic potential (MPa)		Osmotic adjustment (MPa)
	Normal	Water stress	Normal	Water stress	Normal	Water stress	
F.133	1003.3	591.37	155.00	186.33	0.6533	0.8333	0.1800
F.141	1034.2	716.53	174.00	184.67	0.5757	0.9800	0.4043
F.128	1218.4	716.33	174.00	181.00	0.6460	0.9333	0.2873
F.131	1266.7	757.90	170.00	177.00	0.60.67	0.9667	0.3600
F.135	1298.2	1102.37	163.00	188.00	0.8343	1.1033	0.2690
SR.402	1266.7	1101.40	182.00	183.67	0.8257	1.0500	0.2243
F.149	1364.2	1301.83	178.00	185.00	0.7863	1.1300	0.3437
SEL.8	1292.4	1232.00	173.00	177.67	0.7033	0.9167	0.2133
F.133 x F.141	1248.5	1195.63	157.00	182.33	0.6273	1.0800	0.4527
F.133 x F.128	1122.5	1034.73	155.67	182.33	0.5970	0.8100	0.2130
F.133 x F.131	1230.20	1201.63	157.00	181.33	0.7487	1.0300	0.2813
F.133 x F.135	1297.20	1206.17	163.00	186.00	0.7640	1.0667	0.3027
F.133 x SR.402	1270.30	1065.70	161.00	183.33	0.7740	0.9400	0.1660
F.133 x F.149	1303.30	1100.67	160.00	185.33	0.7680	0.8900	0.1220
F.133 x SEL.8	1100.20	1033.93	168.00	188.33	0.8070	1.0167	0.2097
F.141 x F.133	1242.40	1198.87	153.00	182.67	0.7437	0.8800	0.1363
F.141 x F.128	1120.60	1097.87	175.00	178.00	0.6290	0.8633	0.2343
F.141 x F.131	1376.40	1096.73	173.33	184.33	0.6560	0.9967	0.3407
F.141 x F.135	1218.00	1069.00	168.00	181.00	0.6347	1.0067	0.3720
F.141 x SR.402	1171.80	1166.90	160.00	180.33	0.5663	0.9733	0.4070
F.141 x F.149	1305.20	1066.47	173.00	182.33	0.5943	1.0700	0.4757
F.141 x SEL.8	1207.80	1002.70	167.00	185.33	0.6253	0.9800	0.3547
F.128 x F.133	1171.80	646.47	159.00	186.00	0.7080	1.0467	0.3387
F.128 x F.141	1150.10	678.90	175.00	178.33	0.6220	0.8100	0.1880
F.128 x F.131	1205.80	1198.03	174.00	180.67	0.7683	0.9867	0.2183
F.128 x F.135	1115.50	1035.47	168.33	182.67	0.6137	1.1033	0.4897
F.128 x SR.402	1071.40	1000.93	173.00	180.00	0.7943	0.9567	0.1623
F.128 x F.149	1130.60	1124.90	177.33	187.67	0.6153	1.0333	0.4180
F.128 x SEL.8	1271.23	574.90	171.67	181.33	0.7423	0.8900	0.1477
F.131 x F.133	1169.30	1099.40	158.00	183.67	0.7483	0.9833	0.2350
F.131 x F.141	1327.00	843.87	170.00	184.00	0.6500	0.9267	0.2767
F.131 x F.128	1230.30	765.03	175.33	184.00	0.8063	1.0900	0.2837
F.131 x F.135	1297.20	858.00	172.00	184.33	0.7577	1.4000	0.2423
F.131 x SR.402	1111.00	713.47	171.00	182.00	0.7813	0.9600	0.1787
F.131 x F.149	1315.50	1300.00	182.00	184.67	0.7870	0.9333	0.1463
F.131 x SEL.8	1257.10	1132.53	175.00	181.33	0.7450	1.1300	0.3850
F.135 x F.133	1303.30	1299.70	157.33	183.67	0.7303	0.8800	0.1497
F.135 x F.141	1266.80	1096.17	173.00	183.00	0.5720	0.9500	0.3780
F.135 x F.128	1090.10	777.63	171.67	183.00	0.7247	1.0333	0.3087
F.135 x F.131	1132.20	795.90	168.00	182.33	0.7940	1.0033	0.2093
F.135 x SR.402	1205.80	1198.90	176.00	185.33	0.8193	1.0733	0.2540
F.135 x F.149	1208.40	1204.57	165.00	183.33	0.7690	1.1033	0.3343
F.135 x SEL.8	1193.70	678.33	174.00	180.00	0.7803	0.9900	0.2097
SR.402 x F.133	1199.80	1102.17	166.00	186.33	0.7753	0.8733	0.0980
SR.402 x F.141	1157.10	619.87	159.00	181.33	0.6113	0.9567	0.3453
SR.402 x F.128	1065.80	738.07	180.00	187.00	0.7350	0.9400	0.2050
SR.402 x F.131	1130.40	966.87	175.00	183.33	0.7457	1.0233	0.2777
SR.402 x F.135	1126.70	796.07	175.00	179.33	0.7737	0.8567	0.0830
SR.402 x F.149	1138.20	651.30	180.00	184.67	0.8387	1.0900	0.2513
SR.402 x SEL.8	1224.10	777.63	176.00	185.00	0.6423	0.9000	0.2577
F.149 x F.133	1321.60	1201.93	156.00	183.00	0.7860	0.8767	0.0907
F.149 x F.141	1358.10	671.8	173.00	181.67	0.6203	1.0100	0.3897
F.149 x F.128	1159.70	846.07	184.30	185.67	0.7890	1.0100	0.2210
F.149 x F.131	1224.10	1132.27	184.00	184.67	0.7793	1.1533	0.3740
F.149 x F.135	1220.20	1202.63	166.67	182.00	0.8390	1.0333	0.1943
F.149 x SR.402	1171.40	1102.10	176.00	183.67	0.9080	1.0367	0.1287
F.149 x SEL.8	1141.40	797.13	174.33	178.33	0.7670	1.1700	0.4030
SEL.8 x F.133	1023.10	774.07	165.67	186.00	0.7953	0.8700	0.0747
SEL.8 x F.141	1278.90	1100.83	165.00	183.67	0.6203	0.9800	0.3597
SEL.8 x F.128	1238.90	779.10	176.00	181.00	0.6270	1.1167	0.4897
SEL.8 x F.131	1263.20	783.53	173.30	177.67	0.7390	0.8967	0.1577
SEL.8 x F.135	1281.30	1104.07	174.00	183.00	0.7590	0.9900	0.2310
SEL.8 x SR.402	1151.20	759.43	177.00	181.67	0.5627	0.9467	0.3840
SEL.8 x F.149	1138.90	803.87	175.00	180.33	0.8650	1.0633	0.1983
Grand mean	1206.04	965.63 (-19.93%)	169.97	182.84 (+7.0%)	0.7199	0.9874 (+27.1%)	0.2675
CV %	2.89	5.28	2.11	1.74	3.8100	10.3000	38.6800
LSD	47.27	69.11	4.87	4.32	0.0370	0.1380	0.1400

Table 2: Means, LSD values and CV % of soluble sugar content, protein content and grain yield per plant of maize in an 8x8 diallel cross under normal and water stress conditions

Parental lines /crosses	Soluble sugar content (%)		Protein content (%)		Grain yield per plant (g)	
	Normal	Water stress	Normal	Water stress	Normal	Water stress
F.133	5.96	9.21	7.53	8.05	183.00	148.00
F.141	8.13	10.81	6.57	8.28	139.30	123.00
F.128	4.01	12.83	6.00	7.92	168.00	86.00
F.131	5.69	11.08	6.50	7.33	142.30	69.30
F.135	4.61	8.89	7.70	9.49	226.00	147.70
SR.402	9.82	10.01	6.73	8.05	145.70	134.70
F.149	5.97	9.52	7.00	8.30	163.00	138.30
SEL.8	9.10	12.43	7.43	8.70	144.70	70.00
F.133 x F.141	6.20	11.47	6.77	8.10	232.70	156.30
F.133 x F.128	5.32	9.89	6.00	8.83	225.70	146.00
F.133 x F.131	5.77	10.91	7.50	8.01	212.30	139.00
F.133 x F.135	5.92	10.98	7.17	9.41	235.30	129.70
F.133 x SR.402	7.97	10.77	7.47	8.19	243.00	144.70
F.133 x F.149	5.32	10.24	7.43	8.52	244.70	140.00
F.133 x SEL.8	10.46	10.51	7.57	8.39	235.70	150.30
F.141 x F.133	6.01	10.13	6.97	8.75	241.30	151.70
F.141 x F.128	7.13	11.01	7.20	7.24	201.70	94.30
F.141 x F.131	7.75	10.07	7.10	8.46	243.30	119.70
F.141 x F.135	7.31	11.08	7.37	7.80	230.70	119.30
F.141 x SR.402	8.16	8.67	7.10	7.50	187.30	114.00
F.141 x F.149	8.29	8.37	7.43	7.90	177.30	152.70
F.141 x SEL.8	7.67	10.10	6.53	9.50	180.00	142.70
F.128 x F.133	5.20	9.66	6.63	8.70	236.30	146.30
F.128 x F.141	7.14	10.50	7.63	8.46	198.00	99.70
F.128 x F.131	5.24	10.49	7.13	7.57	181.00	122.30
F.128 x F.135	4.78	10.63	8.13	9.34	182.70	127.70
F.128 x SR.402	7.73	8.90	7.53	9.27	200.30	132.70
F.128 x F.149	4.40	9.79	7.57	9.54	241.00	131.70
F.128 x SEL.8	6.61	11.23	7.33	8.73	176.00	111.30
F.131 x F.133	5.47	10.00	7.57	8.14	205.00	135.00
F.131 x F.141	7.54	11.18	7.17	7.62	248.30	118.30
F.131 x F.128	5.00	10.71	7.17	7.79	185.00	110.00
F.131 x F.135	7.04	10.45	7.17	9.02	198.70	147.30
F.131 x SR.402	8.93	9.32	6.97	7.44	168.70	106.30
F.131 x F.149	7.68	9.27	8.03	8.55	203.70	139.70
F.131 x SEL.8	7.33	11.83	7.07	7.42	161.00	85.70
F.135 x F.133	5.22	8.75	7.40	9.08	240.00	130.30
F.135 x F.141	7.23	9.41	7.70	8.95	239.00	136.70
F.135 x F.128	4.63	12.60	8.13	9.08	180.00	136.00
F.135 x F.131	7.13	11.09	7.43	9.01	195.30	144.30
F.135 x SR.402	7.33	12.57	7.97	8.89	205.70	121.00
F.135 x F.149	4.72	9.62	7.87	8.51	188.70	131.00
F.135 x SEL.8	7.28	11.03	7.57	8.49	171.00	108.70
SR.402 x F.133	7.56	9.89	7.77	8.18	238.70	142.70
SR.402 x F.141	8.67	11.48	7.57	8.21	194.00	124.70
SR.402 x F.128	7.78	10.58	7.13	8.33	209.70	142.00
SR.402 x F.131	8.55	11.85	6.90	8.62	174.70	112.00
SR.402 x F.135	7.68	10.04	8.20	9.15	205.00	103.30
SR.402 x F.149	9.79	10.15	7.53	8.36	181.70	156.30
SR.402 x SEL.8	9.22	11.79	6.73	7.92	169.00	128.00
F.149 x F.133	5.67	9.17	7.47	8.77	249.30	131.00
F.149 x F.141	8.72	11.19	7.73	8.28	181.00	126.70
F.149 x F.128	4.99	10.53	7.50	8.50	238.30	125.70
F.149 x F.131	7.55	9.96	8.10	8.80	206.00	148.30
F.149 x F.135	4.89	8.86	7.97	8.56	187.00	156.70
F.149 x SR.402	9.32	9.56	7.40	8.30	183.70	150.30
F.149 x SEL.8	6.97	12.47	7.43	9.09	181.00	95.30
SEL.8 x F.133	10.32	10.94	8.07	8.96	234.70	147.00
SEL.8 x F.141	7.64	10.17	6.40	8.92	170.00	136.30
SEL.8 x F.128	6.79	10.03	7.40	8.68	180.70	106.70
SEL.8 x F.131	7.02	11.30	7.30	8.98	167.00	75.70
SEL.8 x F.135	8.15	10.20	7.67	9.56	169.30	118.70
SEL.8 x SR.402	9.23	10.81	6.77	8.60	171.70	129.70
SEL.8 x F.149	6.74	10.40	7.57	9.08	181.00	96.30
Grand mean	7.02	10.46 (+ 32.9%)	7.33	8.50 (+13.76%)	198.10	126.50 (-36.1%)
CV %	3.06	12.94	1.24	4.72	1.56	4.14
LSD	0.29	1.84	0.123	0.54	4.19	7.09

reported the reduction in osmotic potential under water stress.

Osmotic adjustment is calculated under water stress and not in normal condition. The highest value of 0.4043 MPa was obtained in the parent F-141 and the least value (0.1800 MPa) in the parent F-133. While the Crosses SEL-8 x F-128 and F-128 x F-135, each had the maximum value (0.4897 MPa) and SEL-8 x F-133 possessed the least (0.0747 MPa) value of osmotic adjustment.

Maximum soluble sugar content of 9.82% was recorded in parental line SR-402 followed by SEL-8 (9.10%) under normal experiment while highest SSC (12.83%) were recorded in F-128 followed by 12.43% in SEL-8, under water stress. Among crosses, the F-133 x SEL-8 and its reciprocal cross SEL-8 x F-133 showed the maximum soluble sugar content of 10.46 and 10.32% under normal field, respectively. The cross F-135 x F-128 had maximum 12.60% soluble sugar content followed by the cross F-135 x SR-402 (12.57%) under water stress (Table 2). Soluble sugar content showed an overall mean increase of 32.9% in all genotypes under water stress. These results are in accordance with Premachandra *et al.*[22] who also reported similar findings in soluble sugar content under water stress.

As apparent from the Table 2, F-135 had the maximum protein content (7.70%) followed by F-133 (7.53%) under normal condition, while under water stress, the maximum protein content (9.49%) was observed in F-135 followed by SEL-8 (8.70%). Among the crosses, protein content ranged from 6.00 (F-133 x F-128) to 8.20% (SR-402 x F-135) under normal and 7.24 (F-141 x F-128) to 9.56% (SEL-8 x F-135) under water stress. All the genotypes showed a mean increase of 13.76% for protein content under water stress condition. These findings are in agreement with those of Barlow *et al.*[25] who also reported an increase in protein content under water stress.

In case of grain yield per plant, parental line F-135 produced the highest yield (226.0 g) under normal condition and F-133 gave the highest yield (148.0 g) under water stress closely followed by the parent F-135 (147.7 g). Among crosses, F-149 x F-133 showed highest value of 249.3 g under normal condition, whereas the cross F-149 x F-135 showed the highest value (156.7 g) closely followed by two cross combinations F-133 x F-141 and SR-402 x F-149 (156.3 g) under water stress experiment. All genotypes showed a mean reduction of 36.1% for grain yield per plant under water stress. The results are in accordance with those of Hall *et al.*[26], Bolanos and Edmeades[27] and Vicente *et al.*[13], who also reported a reduction in grain yield per plant under water stress.

The exposure of the breeding material to the water stress circumstances, significantly affected the growth of maize plant as expressed in terms of altered morphological, physiological and biochemical traits studied.

Scaling test: To test the adequacy of the data for additive-dominance model, two types of scaling tests (regression analysis and analysis of variance of Wr + Vr and Wr - Vr) were carried out separately for the data under normal and water stress conditions (Table 3). Results of the scaling tests displayed complete adequacy of the data for stomatal frequency under both conditions while soluble sugar content and protein content depicted completely adequacy for the model under water stress only. Data for stomata size and grain yield per plant under both planting conditions showed partial adequacy due to the failure of analysis of arrays variance. Osmotic potential and osmotic adjustment also showed partial adequacy for the model due to failure of one of the two scaling tests. Thus, whole of the data under normal and water stress conditions, including data showing partial

Table 3: Test of adequacy of additive-dominance model for the traits with significant variation

		Regression analysis		Analysis of array variances		
Traits	Conditions	b = 0	b = 1	Wr+Vr	Wr-Vr	Model
Stomata size	Normal	2.56*	0.105	12.21**	3.52*	Analysis of Array made partial adequate
	Water stress	3.72**	1.76	27.34**	9.01**	---" ----
Stomatal frequency	Normal	2.50*	1.66	4.20**	2.66	Adequate
	Water stress	2.88*	0.31	1.71	1.02	"
Osmotic potential	Normal	2.57*	0.999	33.30**	5.90**	Analysis of Array made partial adequate
Osmotic adjustment	Water stress	2.14	1.40	1.47	1.01	Regression made partial adequate
Soluble	Normal	4.64*	1.15	44.65**	9.86**	Analysis of Array made partial adequate
sugar content	Water stress	2.77*	0.45	0.77	1.24	-------Adequate-------
Protein content	Normal	2.51*	1.35	23.99**	51.62**	Analysis of Array made partial Adequate
	Water stress	3.42*	0.06	1.26	1.16	------Adequate-------
Grain yield per plant	Normal	2.72*	1.94	108.37**	57.77**	Analysis of Array made partial adequate
	Water stress	12.39**	1.44	67.34**	6.56**	"

* = Significant at $p \leq 0.05$, ** = Significant at $p \leq 0.01$, b = Regression coefficient, Wr = Covariance of array and parental values, Vr = Array variance

Table 4: Genetic components of variation for studied traits in an 8 x 8 diallel cross of maize

Components	Stomata size		Stomatal frequency		Osmotic potential	Osmotic adjustment
	Normal	Water stress	Normal	Water stress	Normal	
D	16450.7100±2285.86*	73884.3900±5060.15*	68.787±10.70*	14.122±2.06*	0.00980±0.0015*	0.00185±0.00130
H_1	38111.7900±5254.85*	164832.4500±11632.50*	86.989±24.59*	14.476±4.73*	0.01620±0.0035*	0.00549±0.00302
H_2	22539.5200±4571.72*	88157.4100±10120.30*	66.804±21.39*	8.888±4.12*	0.01150±0.00303*	0.00663±0.00263*
F	28531.9300±5400.73*	133147.9400±11955.5*	-3.632±25.27	16.930±4.86*	0.00596±0.00358	-0.00514±0.00310
h^2	397.4900±3065.99	2255.4800±6787.10	3.387±14.35	-1.504±2.76	0.00090±0.00203	-0.00064±0.00176
E	401.2800±777.04	868.4700±1720.12	4.481±3.64	3.464±0.70*	0.00025±0.0005*	0.00435±0.00045*
$(H_1/D)^{0.5}$	1.5221	1.4936	1.125	1.013	1.28500	1.72100
Heritability (%) narrow sense	22.4300	27.5400	68.610	19.650	57.90000	32.77000
Heritability (%) broad sense	94.8400	97.2500	93.360	51.050	96.96000	51.32000

Table 4: Continue

Components	Soluble sugar content		Protein content		Grain yield per plant	
	Normal	Water stress	Normal	Water stress	Normal	Water stress
D	4.4440±0.3198*	1.5280±0.182*	0.3452±0.0617*	0.343±0.044*	893.70±153.30*	1148.17±51.96*
H_1	3.3510±0.7352*	0.6190±0.419	0.8927±0.1418*	0.396±0.100*	3236.40±352.41*	1294.55±119.45*
H_2	3.2590±0.6396*	0.2560±0.364	0.6957±0.1233*	0.360±0.087*	2452.69±306.60*	1064.32±103.92*
F	0.5650±0.7556	1.4740±0.430*	0.3805±0.1457*	0.092±0.103	820.07±362.20*	918.43±122.77*
h^2	0.5150±0.4290	-0.1910±0.244	0.6141±0.0827*	0.202±0.058*	4814.38±205.62*	555.10±69.69*
E	0.0153±0.1087	0.6310±0.062*	0.0027±0.0210	0.053±0.015*	3.20±52.11	9.21±17.66
$(H_1/D)^{0.5}$	0.8685	0.6370	1.6080	1.074	1.90	1.06
Heritability (%) narrow sense	70.52	23.5800	31.4200	50.080	41.00	46.00
Heritability (%) broad sense	99.46	30.8000	98.9500	81.380	99.69	98.18

* The value of variance is significant (*) when the value exceeds 1.96 after dividing it with its standard error

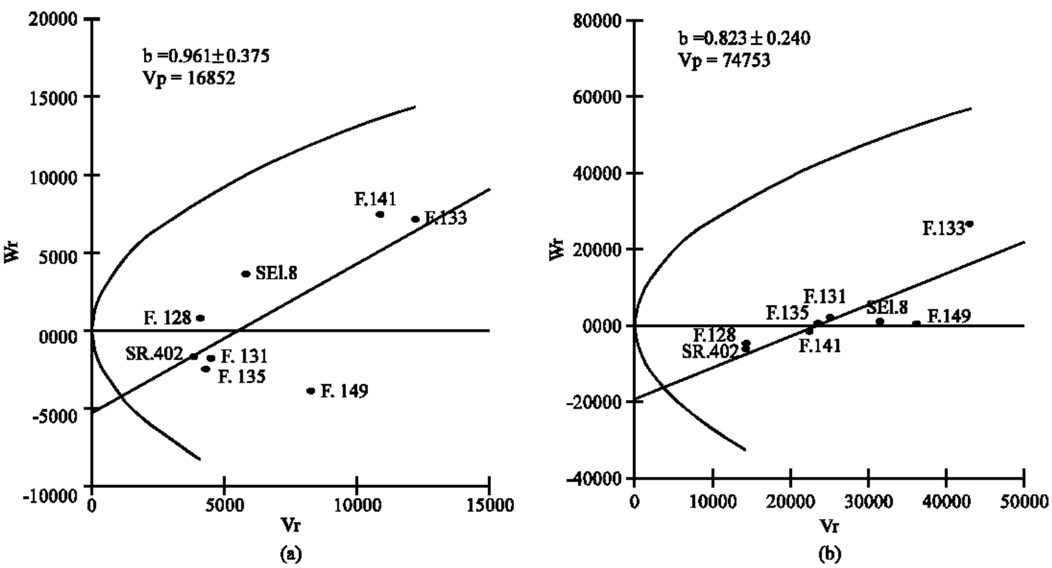

Fig. 1: Vr/Wr graph for stomata size under a) normal and b) water stress conditions

adequacy were analyzed further for the determination of genetic information.

Stomata size: A study of Table 4 displays that both additives as well as dominant gene effects were important for stomata size under both plantings. However, unequal distribution of dominant and recessive genes among the parents was indicated by unequal values of H_1 and H_2 under both planting conditions. F was positive and significant, signifying the greater frequency of dominant genes under both planting situations. However, effects of heterozygous loci (h^2) were not important in any case.

Average degree of dominance (1.522 and 1.493) revealed an over-dominance type of gene action for the expression of stomata size with low narrow-sense heritability (22.43 and 27.54%) under normal and water stress conditions, respectively.

Graphical presentation of the data (Fig. 1a and b) also depicted an over-dominant type of gene action governing stomata size under both sowing conditions.

The regression line cut the Wr-axis below the origin in both cases. Distribution of array points displayed that under normal condition SR-402 and F-128 contained the most dominant genes for stomata size while F-133 had the lowest number of dominant genes. In case of water stress, F-128 kept the highest dominant genes and F-133 had the lowest dominant genes.

Stomatal frequency: The significant values of D and H components for stomatal frequency under both planting conditions (Table 4), showed that the expression of this trait was conditioned by both additive and dominance gene effects. The H_1 components were dissimilar to H_2 providing the information that dominant and recessive alleles were present in unequal proportion.

Value of F was negative and non-significant under normal condition, but was positive and significant under water stress indicating the greater frequency of dominant genes for the expression of this character. The effects of heterozygous loci among the parents under both conditions were not important as revealed by the non-significant item h^2. Environmental effect was non-significant under normal condition but it had a significant contribution for the expression of stomatal frequency under water stress.

The average degree of dominance under normal planting showed an over-dominance gene action with a moderate heritability (68.61%). Graphical presentation of the data (Fig. 2a and b) also confirmed the presence of over-dominance type of gene action. The results are dissimilar with those of Sharma and Bhalla[28] who reported additive type of gene action for stomatal frequency.

Under water stress condition, both degrees of dominance as well as graphical presentation displayed an over-dominant type of gene action for stomatal frequency.

Distribution of arrays points in the graphs depicted that under normal condition, the inbred line F-133 possessed the most dominant genes for stomatal frequency and F-149 kept the least dominant genes, whereas SR-402 attained the most dominant genes and SEL-8 had the most recessive genes for this trait under water stress. The remaining inbred lines were of intermediate constitution for both cases.

Osmotic potential or Osmotic adjustment: This trait is calculated as the difference of osmotic potentials under normal and water stress conditions.

Estimation of genetic components of variation (Table 4) displayed the significance of additive variation for osmotic potential while the same table revealed the significance of dominance (H) variation for osmotic potential under normal condition. Unequal values of H_1 and H_2 indicated the different distribution of dominant and recessive genes among the parents. Value of F and h^2 were non-significant, however, significant E displayed an important effects of environments on osmotic potential. Broad sense heritability was high (96.96%) but moderate heritability in the narrow-sense (57.9%) indicated almost equal amount of additive and dominance variation in the total inherited genetic variation. Average degree of dominance for osmotic potential under normal condition (1.285) and the graphical analysis (Fig. 3a and b) displayed the presence of over-dominance type of gene

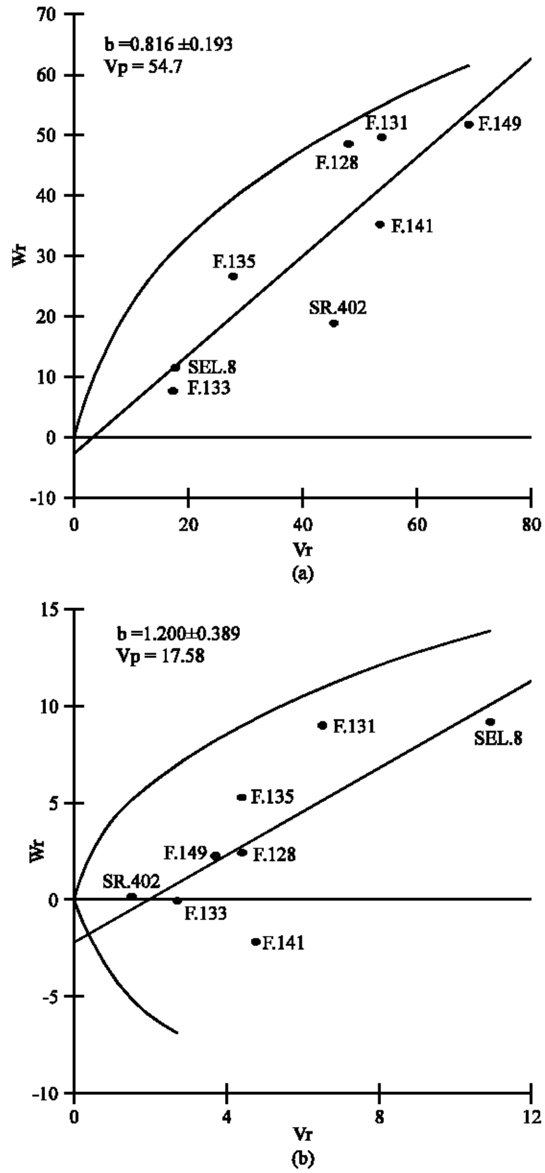

Fig. 2: Vr/Wr graph for stomatal frequency under a) normal and b) water stress conditions

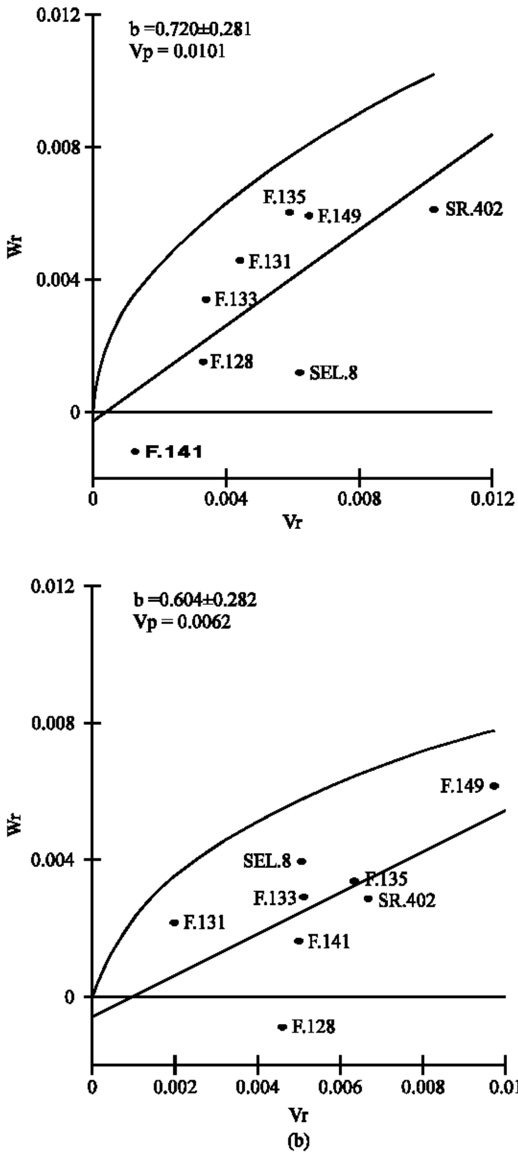

Fig. 3: Vr/Wr graph for a) osmotic potential under normal and b) osmotic adjustment under water stress conditions

action. Distribution of array points displayed the dominant gene distribution among the parents. It was noted that maximum dominant genes were contained in the inbred line F-141 while SR-402 contained minimum dominant genes for osmotic potential.

Genetic component for osmotic adjustment (Table 4) revealed that component D was non-significant, indicating that additive effects were not important. The dominance component H_1 was recorded as non-significant while H_2 was marked as significant. Unequal values of H_1 and H_2 showed the different distribution of dominant genes. The value of F was negative and non-significant displaying that the dominant genes were less in number. Component h^2 was negative but non-significant. However, the Environmental variance E was recorded to be significant, indicating the importance of environmental factors in the determination of osmotic adjustment. Narrow-sense heritability was recorded as 32.77%, showing that a greater proportion of the genetic variation transferred from the parent was of dominance nature. The degree of dominance was more than one (1.721) indicating over-dominance type of gene action for this trait. Graphical analysis of the data (Fig. 3b) also depicted an over-dominance type of gene action for osmotic adjustment. Distribution of arrays indicated that F-131 was indicated as having most dominant genes while F-149 contained the least dominant genes for osmotic adjustment.

Soluble sugar content: Regarding genetic parameters, under normal condition (Table 4), the value of D, the additive component was found to be significant, which indicated the importance of additive variation in defining the genetic behavior of this character. Dominance effects (H) were important under normal condition, whereas under water stress, these were not effective. Unequal values of H_1 and H_2 depicted the different distribution of gene among the parents. The value of F was positive but non-significant under normal condition, while it was positive and significant under water stress depicting the greater frequency of dominant or positive genes. Component h^2 was non-significant under both environments indicating the unimportant effects of heterozygous loci. The effects due to E were non-significant under normal but significant under water stress, suggesting the unimportant role of environment for the expression of soluble sugar content under normal planting but played a significant role in the development of this character under water stress condition.

Degree of dominance was less than 1 indicating additive type of gene action under both plantings. Additive type of gene action with partial dominance was also shown in the graphical presentation (Fig. 4a and b). The graph also indicated that the inbred line F-141 had the maximum dominant genes for this trait under normal as well as water stress conditions. A high and a low heritability estimates (70.52 and 23.58%) for the expression of this character under normal and water stress conditions, respectively was observed.

Protein content: The estimates of genetic components of variation (Table 4) indicated significant D and H

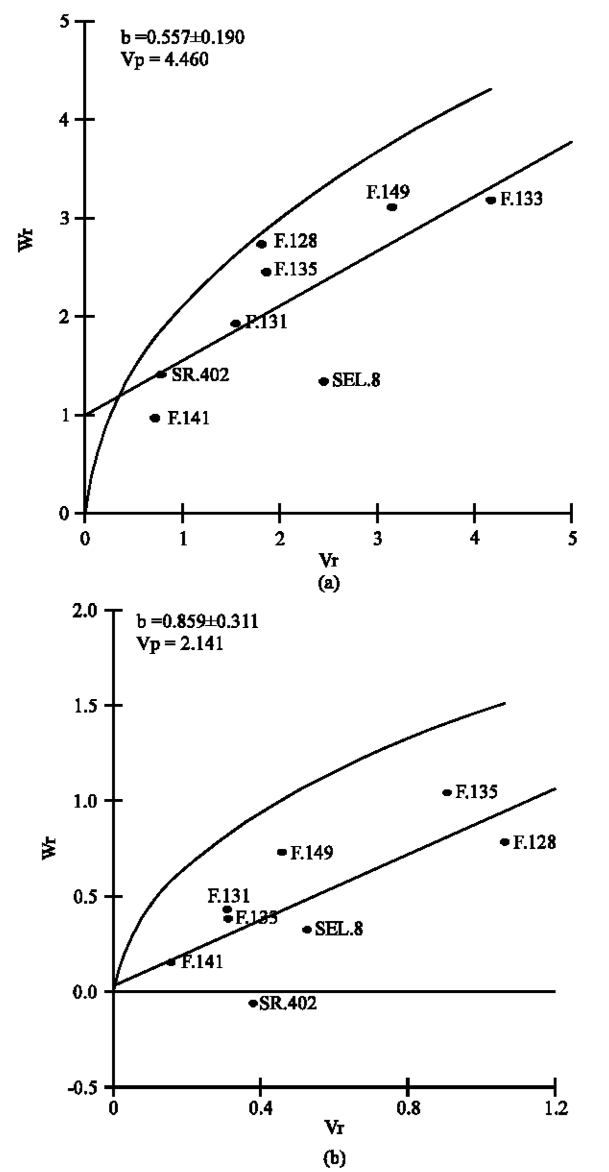

Fig. 4: Vr/Wr graph for soluble sugar content under a) normal and b) water stress conditions

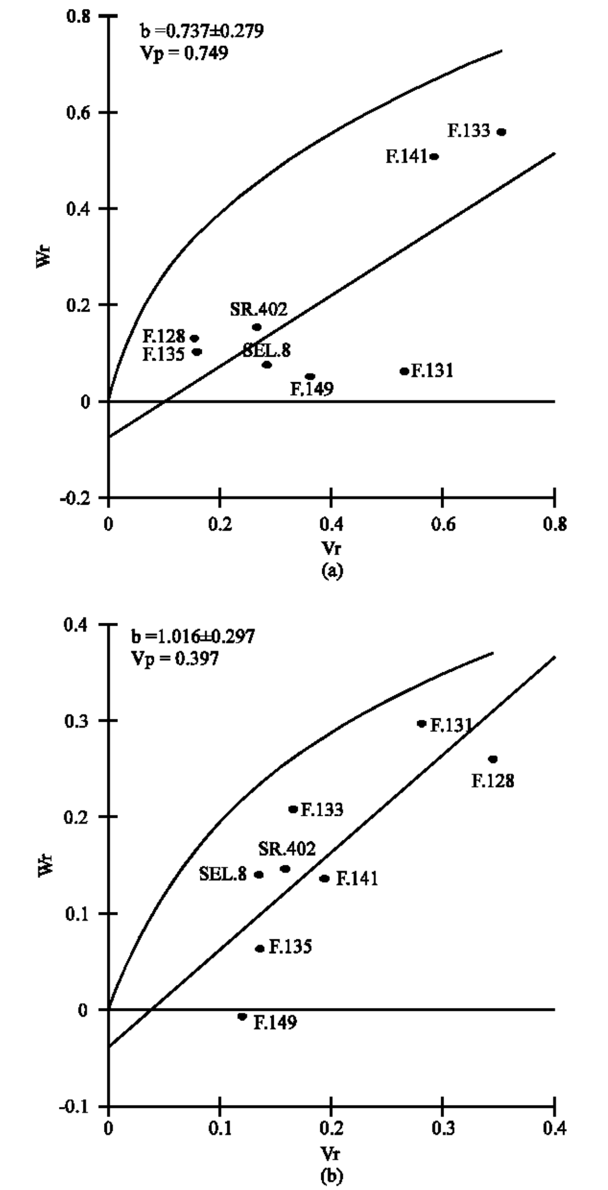

Fig. 5: Vr/Wr graph for protein content under a) normal and b) water stress conditions

components displaying that both additive and dominance effects of genes were important under both planting conditions. Unequal value of H_1 and H_2 revealed the different distribution of dominant genes under both plantings. The positive and significant value of F showed greater frequency of dominant alleles under normal sowing, while its value was non-significant under water stress condition. The significant h^2 components indicated the effects of heterozygous loci among the parents were very much important under both plantings. However, the environmental variation (E) was recorded to be non-significant and significant under normal and water stress, respectively. This indicated that environmental variation was more important under water stress than under normal condition.

The estimates of mean degree of dominance were more than one, signifying over-dominance for this trait under both planting conditions. This idea got the support from position of intercept being on the negative side of the Wr-axis (Fig. 5a and b). These results are different with those of Shabbir and Saleem[16] who reported additive gene action for protein content.

Narrow-sense heritability was recorded as 31.42 and 50.08%, under normal and water stress conditions,

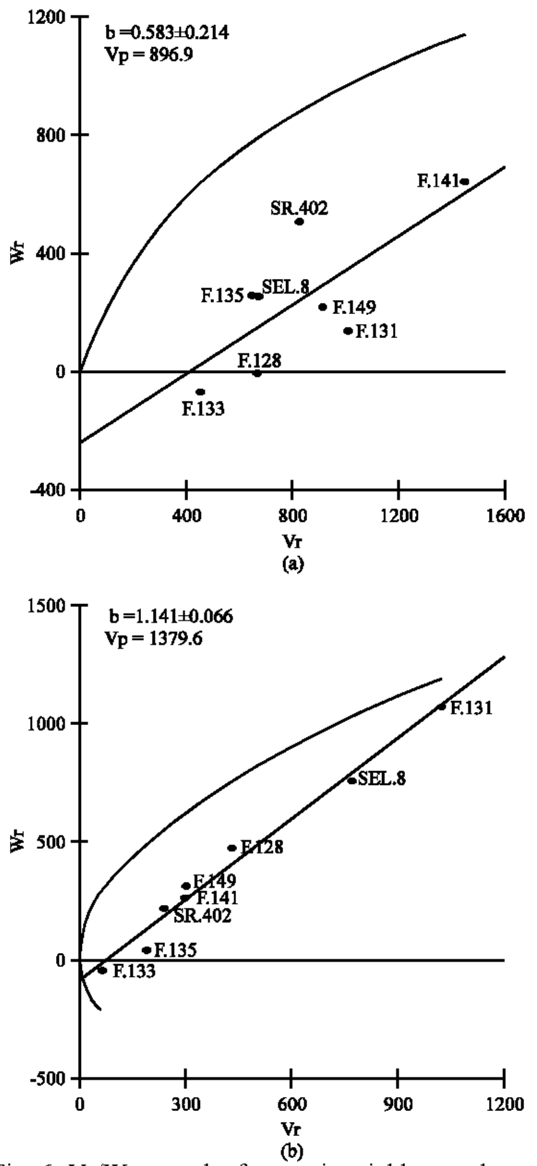

Fig. 6: Vr/Wr graph for grain yield per plant under a) normal and b) water stress conditions

respectively. This indicated that lesser amount of heritable additive variation was present for protein content under normal field but under water stress, both additive and non-additive variations were inherited in almost equal amount.

From the distribution of the array points along the regression line (Fig. 5), F-135 and F-149 appeared to contain the greatest number of dominant genes for protein contents under normal condition and water stress, respectively, while parental line F-133 and F-128, being farthest from the origin under normal and water stress, respectively appeared to carry maximum number of recessive alleles.

Grain yield per plant: The significant values of D and H components under both planting conditions displayed the importance of additive as well dominance effects for the control of grain yield per plant. Dissimilar values of H_1 and H_2 indicated the dissimilar distribution of dominant genes. Values of F were positive and significant displaying the greater frequency of dominant or positive genes under both environments. Components h^2 were also significant displaying the idea that heterozygous loci had an important role in the expression of grain yield per plant. Environmental variation (E) was also found non-significant under both sowing conditions. Narrow sense heritability was recorded as 41 and 46.0%, respectively. The average degree of dominance $(H_1/D)^{½}$ under both sowing conditions was more than one (1.90 and 1.06, respectively), indicating an over-dominance type of gene action for the control of this trait (Table 4).

Graphical presentation of the data (Fig. 6a and b) also depicted a similar gene action for this trait under normal as well as water stress. Results are similar with those of Shabbir and Saleem[16], who also reported over-dominance type of gene action while Dutu[12] and Mani *et al.*[29] reported additive gene action for this trait. Distribution of array points indicated that the inbred line F-133 contained maximum dominant genes for grain yield per plant under both environments. F-141 and F-131 had the least dominant genes under normal and water stress, respectively. The remaining inbred lines were of intermediate constitution.

On overall mean basis, a considerable reduction in stomata size and grain yield per plant was recorded under water stress condition as compared to normal planting except for osmotic potential, soluble sugar content, protein content and stomatal frequency which showed 27.1, 32.9, 13.76 and 7.0% increase under water stress condition, respectively. Stomata size showed a reduction of 19.93% while grain yield per plant, as a consequence of reduction in all its components, showed a maximum reduction of 36.1% under water stress.

The over all results indicated that scaling tests suggested the partial adequacy of the data for additive-dominance model due to analysis of arrays under both normal and water stress conditions for stomata size and grain yield per plant. Both scaling tests (regression analysis and analysis of variance of arrays) suggested the adequacy of the model only for stomatal frequency under both conditions whereas under water stress soluble sugar content and protein content proposed completely adequacy of the model. Data for osmotic potential, soluble sugar content and protein content under normal condition were considered partially adequate due to failure of analysis of variance of arrays.

Estimation of genetic components analysis revealed that under both (normal and water stress) conditions, components of both additive (D) and dominant (H) genetic variations were significant for stomata size, stomatal frequency, protein content and grain yield per plant while for osmotic potential and soluble sugar content, only additive variation (D) was found significant under both conditions. For osmotic adjustment, estimation of these components of variation depicted as non-significant.

Average degree of dominance (Table 4) under normal condition indicated that over-dominance type of gene action for stomata size, stomatal frequency, osmotic potential, protein content and grain yield per plant remained unchanged under water stress while additive type of gene action for soluble sugar content under normal condition also remained unchanged under water stress condition. It was also observed that parental genotypes shifted their position in the graph from dominant to recessive or the midway or vice versa, showing different genetic constitution for the same trait in response to environmental change.

On the basis of overall results of this study and performance of the genotypes, Inbred line F-133 was the best for stomata size under both conditions and performed also the best for stomatal frequency and grain yield under normal and water stress, respectively. It was also found that gene action for all the mentioned traits remained the same over environmental conditions (Normal and water stress conditions). Thus, the above mentioned inbred lines are suggested to be used in future breeding strategies for the production of drought tolerant maize genotypes.

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