

Generation Means Studies in Bread Wheat under Drought Condition

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ABSTRACT

Genetics of drought tolerance in bread wheat was investigated using the six basic generations (P₁, P₂, F₁, F₂, BC₁ & BC₂) of the crosses between Kohistan-97 (high yielding), Inqilab-91 (medium yielding) and Chakwal-86 (low yielding). Significant differences among generations for different traits indicated the presence of genetic variability between the parent varieties. The results showed that type of gene action varied with the traits, crosses and treatments. Study of generation means analysis revealed that additive, dominance and epistatic effects were involved in the inheritance of yield and yield components. The traits days to heading, spikelets per spike, grain weight per spike and harvest index were controlled by additive genes coupled with high heritability. Normal distribution of traits showed the presence of quantitative inheritance. The results suggested that it may be possible to obtain drought tolerance and high yielding lines with a relatively simple breeding procedure involving no progeny test. Transgressive segregation of the traits showed that the crossing of varieties may result into useful recombination for drought resistance.

Key Words: Wheat; Drought tolerance; Heritability; Inheritance; Pakistan

INTRODUCTION

The climate of Pakistan is characterized as arid to semiarid and deficient in water for potential crop production. It is estimated that one fifth of total cultivated and of Pakistan (4.9 millions hectares) is drought prone (Khan & Qayyum, 1986). Although the canal system of Pakistan is ranked best in the world, yet its agriculture is greatly dependent upon rains. Insufficient rain fall and lack of canal water are two major constraints in getting potential yields of crops. Development of wheat varieties with low moisture requirements and able to withstand moisture stress may cope well be an answer to come to grip with the on coming peril. This is because production will tend to be maximized as soon as the yield gap between irrigated and drought stress conditions will begin to narrow down. Evolution of drought resistance is a long, hard and complex process when the motive involved is the incorporation of grain yield into an otherwise desirable genotypic background adapted for drought situations. To identify ways to further traditional or empirical approach where selection is focus on yield, analytical approach for selection seeks out character other than yield that may have an agronomic edge under drought stress conditions.

Genetic improvement of drought tolerance in wheat requires search for possible phenological components for drought tolerance and the exploration/manipulation of variation (Blum *et al.*, 1983). Higher stomatal resistance reduces transpirational loss and hence can improve water use efficiency of the crop under water limited conditions. Significant genetic variation exists for these traits and has

been found to be related to drought resistance (Kirkham, 1980; Martin *et al.*, 1989). Semi-dwarf wheat varieties are better adapted to moist growing conditions than dry plain areas (Briggle & Vogel, 1968). Wallace *et al.* (1972) concluded that almost all biochemical and physiological processes in plants are relevant to physiological components of yield. Plant breeders have suggested the use of components traits as selection criteria for yield improvement (Misra *et al.*, 1994). However, the compensatory effects and negative correlation between these traits may nullify any improvement based on individual components.

For a successful breeding programme, the availability of genetic variability and knowledge of gene action to improve drought tolerance are essential, otherwise choice of breeding methods used may not result in appreciable improvement. This study reports the type of gene action for yield and yield components under drought conditions in two crosses of three wheat varieties.

MATERIALS AND METHODS

The experimental material comprised three wheat varieties viz Kohistan-97 (high yielding), Inqilab-91 (medium yielding) and Chakwal-86 (low yielding). High yielding wheat variety Kohistan-97 was crossed with medium yielding (Inqilab-91) and low yielding (Chakwal-86) to produce F₁s during 1997 - 98. Seed of the parents and F₁s were sown during 1998 - 99 to develop their back crosses (BC₁ & BC₂). All precautionary measures were adopted during the crossing operations to avoid contamination of the genetic material. The seed of used

parents, F_1 , F_2 , BC_1 and BC_2 were space planted in the field using the randomized complete block design in triplicate under drought condition during the wheat crop season (1999 - 2000). A single 5 m long row for each parent and F_1 generation, two rows for each back cross and three rows for each F_2 generation were planted. Plant to plant and row to row distance was 15 and 30 cm, respectively. Non-experimental lines were also planted at the start and end of each replication to eliminate edge effects. The field was irrigated for seed bed preparation. After sowing of seeds the experiment entirely depended upon natural precipitation and no surface irrigation was applied. All other operations were performed according to the standard practices. During 1999 - 2000 (July to June) 80.1 mm rainfall was received and out of which 22.6 mm was during the experiment i.e., November to April.

The data were recorded on the competitive plants for each character at maturity except days to heading, fourth and flag leaf area and stomatal frequency for which observations were made when the plants were green and leaves were in fully expanded condition. Five plants were selected randomly for data recording from each row for each parent F_1 , back cross and ten plants for F_2 generations in each replication. Data on individual plant basis for days to heading, flag leaf area, tillers per plant, spike length, grains per spike, grain weight per spike, 1000-grain weight, grain yield per plant, biomass per plant and harvest index were recorded. Analysis of variance was used to assess significant difference between generations means technique given by Steel and Torrie (1980). Generation means analysis was performed following the procedure of Mather and Jinks (1982). Standard errors (SE) of generation means were computed by performing a nested analysis of variance (Snedecor & Cochran, 1989) with partitioning of total variation into (i) between replications (ii) between rows within replication and (iii) between plants within rows in each replication. The significant mean square were divided by the total number of plants in rows and replications (N) to obtain the variance of generation means and its square root provided the standard error of means. Pooling of non-significant means was done wherever required. A weighted least square analysis of variance (σ^2) was also performed as described by Mather and Jinks (1982). Pooled variance between plants within rows and within replications for each generation were used for successive model fitting. Narrow sense heritability estimates (h^2) for infinity generation were calculated from the components of variance of the best fitting model. The formulae used were: $h^2 (F_2) = 0.5D/(0.5D+E)$; $h^2 (F_{\infty}) = D (D + E)$, where D = additive genetic component and E = environment components.

RESULTS AND DISCUSSION

There were significant differences among generations for different traits indicating the presence of sufficient genetic variability. Shalaby *et al.* (1988), Nabipour *et al.*

(2002), Hassaan (2003) and Kazmi *et al.* (2003) reported genetic variability for various traits. Variety Kohistan-97 performed better in most of the yield and its related traits, while Chakwal-86 remained at the bottom except grains per spike, spike length, days to heading and flag leaf area. Variety Kohistan-97 scored the higher tillers per plant, grain yield, biomass per plant and harvest index indicating the over compensatory effects of these characters. This was an obvious choice to use as a parent for further breeding for drought stress and other environment. Hybrid vigor was observed in most of the yield and its related traits, except harvest index of the cross Kohistan-97 x Chakwal-86, while flag leaf area, grain yield per plant and biomass per plant of the cross Kohistan-97 x Inqilab-91 (Table I & II). Misra *et al.* (1994) also reported hybrid vigor for most of these characters. Genotypes giving high yield under drought conditions indicated that they had the genetic conditions to stress by maintaining higher values of grains per spike, 1000-grain weight etc. So, these components can be used as selection criteria for future breeding program for drought tolerance/resistance. Generation means analysis showed the presence of additive, dominance and epistatic genetic effects in the inheritance of the characters. Senapati *et al.* (1994) and Chaudhry *et al.* (1992) reported additive, dominance and epistasis genetics in the inheritance of different traits. The traits with no genetic effects indicated that all the variability was attributed by environment. A five parameter model [mdhij] provided the best fit for 1000-grains weight, while [mhijl] model for biomass per plant in the cross Kohistan-97 x Chakwal-86 (Table III). The [mdhil] model gave the best fit for grains per spike, while [mdhj] model worked well for 1000-grain weight in the cross Kohistan-97 x Inqilab-91 (Table IV). The signs of [h] and [l] provided evidence of duplicate non-allelic interactions produced similar data (Shreekant *et al.*, 1999). In general the dominance components being greater than the additive components suggested the presence of unidirectional dominance and existence of gene dispersion, which can not be directed from the analysis of generation means. Two parameter model [md] provided the best fit for spikelets per spike in the cross Kohistan-97 x Chakwal-86 and days to heading in the Kohistan-97 x Inqilab-91 (Table III & IV). It revealed that additive effects were prominent for these traits exhibiting the simple inheritance.

Additive and dominance genetic effects were pronounced for days to heading and tillers per plant in Kohistan-97 x Chakwal-86. The model fitting using generation variance showed the adequacy of either a model incorporating both D (additive) and E (environmental components) or a model incorporating E (environmental components) only. The significant and large D components revealed that for various traits all increasing alleles are not associated in one parent but existed with decreasing alleles in the same parents. This is perhaps the cause of the higher magnitudes of heterosis of same traits and for the relatively higher magnitude of [h] than [D] (Table V & VI).

Table I. Generation means and standard errors of yield and its related traits of cross Kohistan-97 (P₁) x Chakwal-86 (P₂)

Traits	P ₁ Mean ± S.E	P ₂ Mean ± S.E	F ₁ Mean ± S.E	F ₂ Mean ± S.E	BC ₁ Mean ± S.E	BC ₂ Mean ± S.E	Probability
Days to heading	104.00 ^c ± 0.218	108.80 ^a ± 0.200	108.26 ^{ab} ± 0.330	107.05 ^{cd} ± 0.260	106.40 ^d ± 0.414	107.43 ^{bc} ± 0.373	0.0000**
Flag leaf area	29.13 ^c ± 0.583	34.16 ^{ab} ± 0.541	34.50 ^{ab} ± 0.491	35.67 ^a ± 0.710	33.18 ^{ab} ± 0.983	31.32 ^{bc} ± 1.032	0.0150*
Tillers per plant	11.93 ^{ab} ± 0.182	9.66 ^c ± 0.035	12.33 ^a ± 0.211	12.24 ^a ± 0.321	11.00 ^{ab} ± 0.310	10.70 ^{bc} ± 0.386	0.0141*
Spike length	13.10 ^c ± 0.839	13.80 ^b ± 0.203	14.19 ^a ± 0.125	14.16 ^a ± 0.127	13.74 ^b ± 0.102	13.12 ^c ± 0.064	0.0001**
Grains per spike	54.86 ^d ± 1.036	77.26 ^b ± 2.101	64.26 ^{bc} ± 1.367	68.48 ^b ± 1.267	60.23 ^{cd} ± 1.643	57.03 ^d ± 1.595	0.0001**
Grain weight per spike	2.16 ^c ± 0.041	2.86 ^a ± 0.093	2.51 ^b ± 0.886	2.58 ^{ab} ± 0.059	2.35 ^{bc} ± 0.098	2.17 ^c ± 0.079	0.0046**
1000-grain weight	39.16 ^a ± 0.421	35.96 ^{bc} ± 0.230	37.54 ^{ab} ± 0.384	35.14 ^c ± 0.544	35.02 ^c ± 0.299	36.65 ^{bc} ± 0.350	0.0092**
Grain yield per plant	22.68 ^a ± 0.186	21.08 ^{ab} ± 0.298	22.58 ^a ± 0.383	22.44 ^{ab} ± 0.729	20.21 ^b ± 0.182	17.84 ^c ± 0.401	0.0059**
Biomass per plant	54.26 ^a ± 0.492	53.40 ^{ab} ± 0.567	59.40 ^a ± 0.748	58.93 ^{ab} ± 1.824	51.76 ^b ± 0.676	46.76 ^{bc} ± 0.783	0.0055**
Harvest index	41.83 ^a ± 0.457	39.49 ^b ± 0.497	38.04 ^b ± 0.552	38.09 ^b ± 0.406	39.13 ^b ± 0.774	38.06 ^b ± 0.675	0.0155*

Table II. Generation means and standard errors of yield and its related traits of cross Kohistan-97 (P₁) x Inqlab-91 (P₂)

Traits	P ₁ Mean ± S.E	P ₂ Mean ± S.E	F ₁ Mean ± S.E	F ₂ Mean ± S.E	BC ₁ Mean ± S.E	BC ₂ Mean ± S.E	Probability
Days to heading	105.13 ^{ab} ± 0.215	103.00 ^d ± 0.239	104.26 ^{bc} ± 0.182	104.01 ^{cd} ± 0.236	105.50 ^a ± 0.321	104.53 ^{abc} ± 0.335	0.0055**
Flag leaf area	29.23 ^a ± 0.406	28.73 ^{ab} ± 0.450	26.62 ^b ± 0.271	23.99 ^c ± 0.607	27.84 ^{ab} ± 0.818	26.70 ^b ± 0.969	0.0099**
Tillers per plant	11.46 ^a ± 0.401	10.13 ^{ab} ± 0.306	10.53 ^{ab} ± 0.192	10.05 ^b ± 0.257	9.86 ^b ± 0.373	8.23 ^c ± 0.286	0.0113*
Spike length	12.77 ^c ± 0.136	13.31 ^{bc} ± 0.181	13.77 ^{ab} ± 0.151	13.56 ^b ± 0.108	13.89 ^{ab} ± 0.203	14.29 ^a ± 0.236	0.0072**
Grains per spike	56.53 ^c ± 0.256	60.00 ^{ab} ± 0.276	59.06 ^{bc} ± 0.430	57.92 ^{bc} ± 0.968	59.20 ^{bc} ± 0.699	62.70 ^a ± 1.205	0.0255*
Grain weight per spike	2.21 ^c ± 0.033	2.54 ^{ab} ± 0.041	2.46 ^{ab} ± 0.027	2.40 ^{bc} ± 0.043	2.39 ^{bc} ± 0.064	2.67 ^a ± 0.068	0.0313*
1000-grain weight	36.48 ^b ± 0.316	40.17 ^a ± 0.577	41.74 ^a ± 0.395	40.11 ^a ± 0.455	40.01 ^a ± 0.529	42.29 ^a ± 0.771	0.0201*
Grain yield per plant	20.45 ^a ± 0.230	20.43 ^a ± 0.282	18.89 ^{ab} ± 0.206	19.16 ^{ab} ± 0.541	17.54 ^{bc} ± 0.841	15.84 ^c ± 0.736	0.0107*
Biomass per plant	53.20 ^a ± 0.618	50.06 ^{ab} ± 0.258	45.93 ^{bc} ± 0.452	46.95 ^b ± 1.323	46.53 ^b ± 2.398	40.70 ^c ± 1.771	0.0066**
Harvest index	38.54 ^c ± 0.719	40.84 ^{ab} ± 0.616	41.21 ^a ± 0.693	40.99 ^{ab} ± 0.418	37.89 ^c ± 0.645	39.09 ^{bc} ± 0.835	0.0145*

* P ≤ 0.05, ** P ≤ 0.01

Note: Means sharing the same letters are non-significant

Table III. Estimates of parameters of best fit model on generation means of yield and its related traits of cross Kohistan-97 x Chakwal-86

Traits	M ± S.E	[d] ± S.E	[h] ± S.E	[i] ± S.E	[j] ± S.E	[l] ± S.E	χ ² (df)
Days to heading	106.313 ± 0.303	2.403** ± 0.323	1.714** ± 0.614		-3.375** ± 0.944		0.687 (2)
Flag leaf area	34.416 ± 0.476	2.396** ± 0.500		-2.944** ± 0.736			6.385 (3)
Tillers per plant	10.718 ± 0.219	1.037** ± 0.219	1.473** ± 0.478				5.375 (3)
Spike length	13.490 ± 0.161					0.902** ± 0.342	3.037 (4)
Grains per spike	1.794 ± 0.041						1.420 (5)
Grain weight per spike	2.390 ± 0.113						4.983 (5)
1000-grain weight	32.053 ± 1.398	1.581** ± 0.402	5.338** ± 1.827	5.444** ± 1.491	-3.250** ± 0.900		0.782 (1)
Grain yield per plant	1.327 ± 0.634						1.017 (5)
Biomass per plant	69.808 ± 3.733		-33.10** ± 5.99	-15.94** ± 3.75	-6.348** ± 1.698	22.697** ± 2.504	0.713 (1)
Harvest index	38.030 ± 0.416	1.162* ± 0.452		2.620** ± 0.668			0.038 (3)

Table IV. Estimates of parameters of best fit model on generation means of yield and its related traits of cross Kohistan-97 x Inqlab-91

Traits	m ± S.E	[d] ± S.E	[h] ± S.E	[i] ± S.E	[j] ± S.E	[l] ± S.E	χ ² (df)
Days to heading	104.336 ± 0.201	1.042** ± 0.311					3.936 (4)
Flag leaf area	22.577 ± 1.494		4.195* ± 1.777	6.545** ± 1.592			4.225 (3)
Tillers per plant	8.884 ± 0.404			1.742** ± 0.630		1.890** ± 0.588	6.163 (3)
Spike length	13.532 ± 0.162						8.050 (5)
Grains per spike	51.879 ± 2.497	1.650** ± 0.355	15.441** ± 4.211	6.354* ± 2.522		-8.340** ± 1.966	1.059 (1)
Grain weight per spike	2.426 ± 0.083						2.731 (5)
1000-grain weight	38.556 ± 0.432	1.906** ± 0.469	3.594** ± 0.772		-3.949** ± 1.205		2.806 (2)
Grain yield per plant	20.453 ± 0.350		-6.566** ± 1.227			5.023** ± 1.145	1.916 (3)
Biomass per plant	1.684 ± 0.034						0.951 (5)
Harvest index	39.456 ± 0.380	1.187* ± 0.577			-3.583* ± 1.405	2.165* ± 0.931	5.032 (2)

m = Mean, [d] = Additive effects, [h] = Dominance effects, [i] = Additive x additive effects, [j] = Additive x dominance effects, [l] = Dominance x dominance effects.

* P ≤ 0.05, ** P ≤ 0.01

Table V. Components of variance, D (additive), H (dominance), E (environmental) and narrow sense heritability of yield and its related traits of cross Kohistan-97 x Chakwal-86

Traits	(D) ± S.E	(H) ± S.E	(E) ± S.E	χ^2 (df)	h^2 (F ₂)	h^2 (F _∞)
Days to heading	11.18** ± 1.79		1.19** ± 0.25	1.76 (4)	82.47	90.39
Flag leaf area	90.61** ± 12.06		4.25** ± 0.89	0.93(4)	91.42	95.52
Tillers per plant	21.11** ± 2.65		0.59** ± 0.12	0.19(4)	94.75	97.28
Spike length	4.93** ± 0.88	-5.25** ± 0.90	0.30** ± 0.96	5.58(3)	60.57	94.30
Grains per spike	230.66** ± 41.16		33.50** ± 6.96	0.86(4)	77.49	87.32
Grain weight per spike	0.46** ± 0.10		0.10** ± 0.02	2.32(4)	69.34	81.89
1000-grain weight	7.332** ± 15.30	-87.32** ± 16.19	3.45** ± 0.73	0.10(3)	63.32	96.20
Grain yield per plant	164.31** ± 29.02	-143.56** ± 30.32	1.67** ± 0.35	8.27(4)	68.62	98.99
Biomass per plant	1126.8** ± 179.00	-1082.3** ± 180.5	6.57** ± 1.38	0.05(3)	67.03	99.42
Harvest index	0.003** ± 0.006		0.001** ± 0.0001	1.98(4)	75.00	85.71

Table VI. Components of variance, D (additive), H (dominance), E (environmental) and narrow sense heritability of yield and its related traits of cross Kohistan-97 x Inqlab-91

Traits	(D) ± S.E	(H) ± S.E	(E) ± S.E	χ^2 (df)	h^2 (F ₂)	h^2 (F _∞)
Days to heading	10.43** ± 1.45		0.63** ± 0.13	0.155(4)	89.06	94.27
Flag leaf area	77.49** ± 9.64		1.95** ± 0.41	1.916(4)	95.21	82.13
Tillers per plant	9.13** ± 1.58		1.22** ± 0.25	1.938(4)	80.33	88.24
Spike length	0.003** ± 0.007	-0.003** ± 0.001	0.004** ± 0.0001	2.613(3)	55.96	89.34
Grains per spike	143.13** ± 17.17		1.91** ± 0.40	6.957(4)	97.15	98.68
Grain weight per spike	0.36** ± 0.05		0.02** ± 0.004	4.343(4)	90.09	94.79
1000-grain weight	52.55** ± 7.18		2.91** ± 0.61	6.507(4)	90.66	94.75
Grain yield per plant	59.45** ± 7.15		0.82** ± 0.17	3.588(4)	97.31	98.64
Biomass per plant	390.80** ± 46.33		3.58** ± 0.76	9.449(4)	98.20	99.09
Harvest index	21.44** ± 6.36		8.11** ± 1.64	6.565(4)	56.92	72.55

** P ≤ 0.01

The generation variance analysis showed the additive genetic effects involved in the inheritance of yield and yield components. However, the generation means analysis showed both additive and dominance components but in some traits genetic interactions were involved in the inheritance. Deswal *et al.* (1996) also reported significant G x E interaction and its involvement in the inheritance. The inconsistencies may be due to the estimation precision of the two analyses. The generation variance analysis has been found more robust than the generation means analysis.

The narrow sense heritability estimates were higher for yield and other traits (Table V & VI). This indicated that high proportion of genetic component of variance that can be fixed by selection in segregating generations. Yadav *et al.* (1993) and Rana *et al.* (1999) reported high heritability estimates for yield and yield components. Frequency distribution of F₂ generation in both crosses showed normal distribution and transgressive segregation in all the traits. The normal distribution shows that the traits are quantitative in nature. The transgressive segregation shows the possibility of having better recombination by crossing these genotypes.

It also suggests that the selection possibilities with segregating generations substantiated by high heritability estimates exist. It may be concluded that some traits were controlled by additive and dominance genes, which are further supported by high heritability. Normal distribution of the traits shows the presence of quantitative inheritance. Transgressive segregation of the traits showed that the crossing of varieties may result better recombination for

drought tolerance/resistance.

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