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Inheritance of drought tolerance traits in bread wheat (*Triticum aestivum* L.) under restricted irrigation

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Abstract
The present investigations on "Inheritance of drought tolerance traits in wheat (*Triticum aestivum* L.)" were conducted during the period rabi 2015-16. Gene action of 5 morphological, 11 physiological characters were studied to know the genetics of drought tolerance in two wheat crosses under restricted irrigation condition. The materials consist of two crosses involving four parents (NIAW-34, NIAW-343, NIAW-917, NIAW-2030) with six generation. The difference due to different genotypes for all the sixteen characters were highly significant, indicating high degree of variability. The parameter 'm' was highly significant in all the crosses for all the characters under study. Additive as well as Dominant genetic effects were highly significant in both the crosses, except SPAD reading in cross NIAW-917 X NIAW-2030 for Additive as well as Dominant genetic effects and 1000 grain weight for Dominant genetic effects in NIAW-917 X NIAW-2030. The epistatic gene interactions (i, j and l) for Days for 50% flowering, NPR, TR, RLWC, Chlorophyll stability index (CSI), Chlorophyll 'b' and TCC were highly significant additive x additive, additive x dominance and dominance x dominance epistatic gene interactions observed in both the crosses. Duplicate type of epistasis was observed for Days to maturity, grain yield per plant, TR, RLWC, Chlorophyll stability index (CSI), DTI, and TCC in both crosses. Complementary type of epistasis was observed only for 1000 grain weight in cross NIAW-34 X NIAW-343 and cross NIAW-917 X NIAW 2030 recorded Complementary type of epistasis for NPR and SC.

Keywords: Bread wheat, gene action, drought tolerance traits

Introduction
Wheat (*Triticum aestivum* L.) is the first important and strategic cereal crop for the majority of world populations. It is the staple food crop of the world and second important crop of India after by rice. The improvement in its productivity has played a key role in making the country self-sufficient in food production. It accounts for half the area under *rabi* food grain of India and contributes nearly one third of the total food grain production.

Wheat belongs to the grass family Poaceae (Gramineae). The chromosome number sets (genomes) for wheat are diploids 14 (n=7), tetraploids 28 (n=14) and hexaploids 42 (n=21) chromosomes. Wheat contains more protein than other cereals. Wheat proteins are special significance in nutrition, they are principally concerned in providing characteristic substance "gluten" which is very essential for bakers. Wheat grain has relatively high content of niacin and thiamine. Wheat grain is deficient in essential amino acid such as lysine. Wheat is a widely adapted crop. The optimum temperature for wheat is 15°C. Wheat is a C3 plant and as such it thrives in cool environments. In India wheat is grown in almost all states, but some important wheat growing states are Punjab, Uttar Pradesh, Haryana, Rajasthan, Gujarat, Karnataka, Madhya Pradesh, Maharashtra and West Bengal. The productivity and yield of wheat is significantly influenced by selection of suitable varieties, soil and environmental conditions as well as the management factors. Most of the wheat growing areas of the world experience environmental stresses like drought (water stress), high temperature (heat stress), cold, and salinity. Among them, drought and high temperature are two important environmental factors that adversely affect performance and yield of wheat crop.

The drought (moisture) stress mostly caused by arid conditions, implicating hot temperature and inadequate water supply. Water stress is the most significant environmental stress in agriculture worldwide and improving yield under drought is a major goal of plant breeding (Cattivelli *et al.* (2008) [6]. All phases of plant growth are not equally vulnerable to water shortage. Whereas some phases can cope-up with water shortage very well, others are more vulnerable to water shortages that may result in serious yield losses. The moisture stress adversely affects the various physiological and morphological processes of the crop and as a result, the growth of the crop gets stunted and yields are adversely affected through reduction of inflorescences size fertilization and grain filling. Drought stress often occurs at anthesis causing greater loss of wheat yield. These abiotic stresses frequently occur simultaneously in dry land wheat areas. The combined effects of these stresses on crop performance and yield may be quite different than the individual stress, but there are limited studies on this aspect and need attentions.

To meet the ever increasing demand of wheat production and challenges to be faced for increasing productivity without scope of increasing the area, there is prime need to follow the advanced physiological tools, which may be useful in formulating the breeding programme. There is need to improve gain yield under limited irrigation using reliable physiological traits which may be dependable for selecting genotypes having higher tolerance to water. The moisture stress has the greatest effect on crop potential yield or quality or both.

Knowledge of gene action helps in the selection of parents for use in the hybridization programme and also in the choice of appropriate breeding procedure for the genetic improvement of various quantitative characters. Hence insight into the nature of gene action involved in the expression of various quantitative characters is essential. Drought is one of the major abiotic factor which affects productivity of wheat to a great extent. The physiological processes in the plant are affected due to the soil moisture stress and thereby resulting in reduced plant growth mainly due to the development of high osmotic pressure in the roots and shoots. Therefore, genetic improvement programme must be concentrated on combining high yield with resistance to stresses.

Material and Methods

The present investigations entitled " Inheritance of drought tolerance traits in bread wheat (Triticum aestivum L.) under restricted irrigation " was conducted at Post Graduate Instructional Farm, Department of Botany, Mahatma Phule Krishi Vidyapeeth, Rahuri during the Rabi 2015-16. The experimental material consists of six generation (P1, P2, F1, F2, B1 and B2) of each of the two crosses (NIAW-34 X NIAW-343) and (NIAW-917 X NIAW-2030). The salient Features of the parents involved in crosses are

Sr. No.	Parents	Traits
1.	NIAW-34	Recommended for cultivation in Maharashtra under late sown irrigated condition.
2.	NIAW-343	High yielding and bold grained.
3.	NIAW-917	Spreading growth habit (In early stage) and bold grained and having shining luster.
4.	NIAW-2030	Bold grained and relatively drought tolerant cultivar with higher yield.

The four parents and their two F_1's obtained from ARS, Niphad were raised during *rabi* 2014-15 so as to effect backcrosses as well as to obtain F_2 grains. The F_1's were backcrossed with both the parents involved in respective crosses. Simultaneously the parents of respective crosses were also crossed to obtain F_1 grains. The experiment consisting of 12 treatments (Four parents, two F_1's, two F_2's, two B_1's and two B_2's) was conducted in Randomized Block Design with three replications. Among treatments two rows of parents and hybrids, backcrosses and F_2's were planted with of 1.5 m row of each genotype with line spacing of 22.5 cm with 10 cm distance between plants to plant in a row. The recommended dose of fertilizer 120:60:40 NPK kg/ha was applied as a basal dose. The operation like gap filling, weeding and loosening of soil were carried out regularly in the experimental plots as per the need of the crop. The observational plants were selected randomly and marked by tagging their main axis with tag at top. The observations were recorded on five morphological characters days to 50% flowering, days to maturity, number of tillers per plan, 1000 grain weight (g) and grains yield plant^{-1} (g) on 10 randomly selected plants in non-segregating generations *viz*., P_1, P_2 and F_1 and 10 plants in segregating generation *viz*., B_1 and B_2, and 20 plants in F_2's respectively of each of the cross in each replication. The average value per plant was worked out. The Physiological characters, net photosynthetic rate, transpiration rate, stomatal conductance was recorded from flag leaf at 50% flowering and grain filling with the help of portable Infrared Gas Analyzer. Relative leaf water content (%) was estimated by using relative turgidity technique (Barrs and Weatherley, 1962) [3]. RLWC were estimated at 50% flowering and grain filling stage. SPAD index was estimated nondestructively, using SPAD-502 chlorophyll meter (Minolta Corp., Ramsey, NJ, USA) at 50% flowering and grain filling stage from flag leaf only. The observations were recorded during the day time between 11 a.m. to 14 p.m. The chlorophyll stability index (%) in the leaves was estimated by using a spectrophotometer at 50% flowering and grain filling stage. Membrane injury index was determined at 50% flowering and grain filling stage and was determined by recording the electrical conductivity of flag leaf leachets in double distilled water at 50 and 100ºC (Sairam *et al.*, 1997) [26]. Chlorophyll content (a, b and total) (mg g-1 fw) Chlorophyll a, chlorophyll b, and total chlorophyll content were estimated by using the method of Dhopte and Phadnawis (1989) [8] and Drought tolerance index was calculated as per the formula suggested by Fisher and Wood (1981) [9].

Table 1: Analysis of variance for parents, F_1's, F_2's, B_1 and B_2 for different characters in wheat

Sr. No.	Characters	Mean Sum of Square		
		Replication (d.f. 2)	Treatments (d.f. 11)	Error (d.f. 22)
1.	Days to 50% flowering	0.752	21.99**	1.880
2.	Days to maturity	3.070	60.62**	1.296
3.	No. of tillers/plant	0.02	2.51**	0.016
4.	1000 grain weight(g)	1.863	23.68**	4.431
5.	Grain yield per plant(g)	0.013	15.76**	0.015
6.	Net photosynthetic rate	0.156	4.66**	0.250
7.	Transpiration rate	0.0005	1.229**	0.005
8.	Stomatal conductance	0.000001	0.0091**	0.00001

9.	Relative leaf water content	0.671	76.974**	1.083
10.	SPAD reading	0.313	16.840**	4.019
11.	Chlorophyll stability index	1.449	60.652**	0.521
12.	Membrane injury index	0.033	58.699**	0.217
13.	Drought tolerant index	0.00001	0.009**	0.00002
14.	Chlorophyll 'a' content	0.001	0.026**	0.0008
15.	Chlorophyll 'b' content	0.00004	0.0025**	0.00002
16.	Total chlorophyll content	0.00081	0.176**	0.0008

**Significant at 1%
*Significant at 5%

Table 2a: Mean performance of Parents, F_1's, F_2's, B_1 and B_2 for different morphological characters in wheat

Sr. No.	Name of Variety	Days to 50% Flowering	Days to Maturity	No. of tillers/Plant	1000 grain weight (gm)	Grain yield/plant (gm)	Net photosynthetic rate	Transpiration rate	Stomatal conductance
	Parents								
1.	NIAW-34	58.00	98.00	8.8	29.30	7.46	5.18	4.59	0.1572
2.	NIAW-343	58.20	99.00	8.8	30.12	8.00	7.82	3.84	0.1436
3.	NIAW-917	62.66	108.73	9.4	29.12	10.40	8.28	3.03	0.1180
4.	NIAW-2030	58.33	99.66	8.8	31.50	11.40	7.32	4.38	0.1498
	F1s								
5.	NIAW-34 X NIAW-343	55.20	96.73	10.53	34.44	10.73	6.52	3.24	0.1037
6.	NIAW-917 X NIAW-2030	56.23	102.00	11.25	35.60	14.30	8.46	4.08	0.3090
	F2s								
7.	NIAW-34 X NIAW-343	56.28	97.95	9.23	33.21	9.93	6.98	3.91	0.1283
8.	NIAW-917 X NIAW-2030	60.86	103.93	10.43	35.56	13.50	6.92	3.18	0.1366
	B1s								
9.	(NIAW-34 X NIAW-343) X NIAW-34	57.73	104.20	10.80	33.55	9.55	4.21	2.72	0.0862
10.	(NIAW-917 X NIAW-2030) X NIAW-917	57.20	105.66	11.20	34.51	12.56	6.48	3.43	0.1320
	B2s								
11.	(NIAW-34 X NIAW-343) X NIAW-343	56.80	105.20	10.13	31.11	10.66	5.89	3.27	0.1548
12.	(NIAW-917 X NIAW-2030) X NIAW-2030	58.90	105.66	10.65	32.67	13.53	7.48	4.64	0.1434
General mean		58.03	102.22	10.00	32.56	11.08	6.79	3.69	0.14
SE (±)		0.79	0.65	0.07	1.21	0.07	0.28	0.04	0.0015
CD at 5%		2.32	1.92	0.21	3.56	0.21	0.84	0.12	0.0045

Table 2b: 'Mean performance of Parents, F_1's, F_2's, B_1 and B_2 for different physiological characters in wheat

Sr. No.	Name of Variety	Relative leaf water content (%)	SPAD reading	Chlorophyll stability index (%)	Membrane injury index (%)	Drought tolerance index	Chlorophyll 'a' Content (mg/g)	Chlorophyll 'b' Content (mg/g)	Total Chlorophyll Content (mg/g)
	Parents								
1.	NIAW-34	58.54	55.86	69.86	31.13	0.5787	1.28	0.2973	2.40
2.	NIAW-343	62.80	51.82	63.80	28.00	0.6160	1.40	0.3193	2.54
3.	NIAW-917	61.85	51.01	69.35	33.99	0.5480	1.21	0.2700	2.53
4.	NIAW-2030	52.73	54.23	57.47	29.90	0.6260	1.37	0.2933	2.77
	F1s								
5.	NIAW-34 X NIAW-343	53.20	49.11	65.73	25.60	0.5747	1.09	0.2500	2.02
6.	NIAW-917 X NIAW-2030	49.46	52.02	61.86	26.30	0.6513	1.16	0.2280	2.35
	F2s								
7.	NIAW-34 X NIAW-343	50.16	53.95	60.18	33.50	0.5562	1.34	0.3023	2.42
8.	NIAW-917 X NIAW-2030	50.47	50.65	54.27	29.00	0.5797	1.28	0.2533	2.53
	B1s								
9.	(NIAW-34 X NIAW-343) X NIAW-34	56.50	47.40	62.10	26.50	0.5457	1.18	0.2510	1.97
10.	(NIAW-917 X NIAW-2030) X NIAW-917	58.91	50.08	62.86	22.86	0.5810	1.34	0.3110	2.74

	B2s								
11.	(NIAW-34 X NIAW-343) X NIAW-343	63.20	53.04	65.83	28.00	0.6340	1.33	0.2950	2.48
12.	(NIAW-917 X NIAW-2030) X NIAW-2030	59.33	50.39	64.46	21.46	0.5617	1.28	0.2555	2.53
	General mean	56.43	51.63	63.15	28.08	0.5877	1.27	0.27	2.44
	SE (±)	0.60	1.15	0.41	0.26	0.0023	0.016	0.0027	0.016
	CD at 5%	1.76	3.39	1.22	0.79	0.007	0.047	0.008	0.046

Table 3a: Estimates of scaling tests and joint scaling test for different characters for two crosses in wheat

Sr. No.	**Crosses / Characters**	**NIAW-34 X NIAW-343**	**NIAW-917 X NIAW-2030**
1.	Days to 50% flowering		
	A	2.26** ± 0.49	-9.26** ± 0.77
	B	4.20** ± 0.51	9.80** ± 0.73
	C	-1.46* ± 0.73	0.46 ± 1.39
	X^2	141.71**	785.92**
2.	Days to maturity		
	A	13.66** ± 0.61	0.60 ± 0.55
	B	14.66** ± 0.45	19.66** ± 0.53
	C	1.33* ± 0.86	3.33** ± 1.00
	X^2	2281.86**	1915.36**
3.	No. of tillers/plant		
	A	3.00** ± 0.35	2.47** ± 0.34
	B	1.66** ± 0.33	1.97** ± 0.23
	C	7.73** ± 0.51	2.47** ± 0.48
	X^2	249.06**	116.295**
4.	1000 grain wt.(g)		
	A	9.64** ± 1.68	8.74** ± 1.37
	B	-0.66 ± 1.45	-4.91** ± 1.75
	C	12.73** ± 1.58	11.70** ± 2.85
	X^2	100.12**	97.94**
5.	Grain yield per/ plant (g)		
	A	0.90** ± 0.26	0.93** ± 0.30
	B	2.60** ± 0.30	1.87** ± 0.28
	C	2.80** ± 0.50	10.47** ± 0.48
	X^2	96.11**	484.78**
6.	Net photosyn-thetic rate		
	A	-3.28** ± 0.13	-3.78** ± 1.106
	B	-2.55** ± 0.14	-0.82** ± 0.170
	C	1.88 ± 3.80	-4.84** ± 0.28
	X^2	900.31**	1359.49**
7.	Transpiration rate		
	A	-2.39** ± 0.12	-0.25** ± 0.160
	B	-0.54** ± 0.11	0.81** ± 0.12
	C	0.70** ± 0.19	-2.86** ± 0.24
	X^2	1355.42**	702.86**
8.	Stomatal conductance		
	A	-0.09** ± 0.005	-0.16** ± 0.013
	B	0.06** ± 0.006	-0.17** ± 0.013
	C	0.005 ± 0.009	-0.339** ± 0.026
	X^2	562.36**	175.44**

**Significant at 1%
*Significant at 5%

Table 3b: Estimates of scaling tests and joint scaling test for different characters for two crosses in wheat

Sr. No.	**Crosses / Characters**	**NIAW-34 X NIAW-343**	**NIAW-917 X NIAW-2030**
9.	Relative leaf water content (RLWC) (%)		
	A	1.26** ± 0.53	6.50** ± 1.54
	B	10.40** ± 0.62	16.46** ± 2.12
	C	-27.07** ± 1.11	-11.62** ± 2.93
	X^2	1396.17	120.77**
10.	SPAD reading		
	A	-10.18** ± 3.29	-2.86** ± 0.75

	B	5.15 ± 3.35	-5.46** ± 0.83
	C	9.88 ± 6.64	-6.66** ± 1.32
	X^2	616.49**	47.94**
11.	Chlorophyll Stability index (CSI) (%)		
	A	-11.39** ± 0.68	-5.48** ± 0.97
	B	2.13** ± 0.60	9.60** ± 1.20
	C	-24.39** ± 1.06	-33.47** ± 2.64
	X^2	894.22**	372.86**
12.	Membrane injury index (MII) (%)		
	A	-13.13** ± 0.62	-22.62** ± 0.64
	B	-7.00** ± 0.47	-21.33** ± 0.62
	C	4.86 ± 1.02	-16.59** ± 1.03
	X^2	879.05	2103.05**
13.	Drought tolerance index (DTI)		
	A	-0.02** ± 0.006	-0.23** ± 0.01
	B	0.117** ± 0.007	-0.25** ± 0.012
	C	-0.279* ± 0.014	-016** ± 0.02
	X^2	1056.34**	897.65**
14.	Chlorophyll ‘a’ content (mg/g)		
	A	-0.016 ± 0.03	0.30** ± 0.07
	B	0.24** ± 0.09	0.017 ± 0.07
	C	0.57** ± 0.11	0.23 ± 0.14
	X^2	48.761**	74.069**
15.	Chlorophyll ‘b’ content (mg/g)		
	A	-0.045 ± 0.004	0.124** ± 0.007
	B	0.021** ± 0.005	-0.010 ± 0.008
	C	0.093** ± 0.009	-0.006 ± 0.013
	X^2	380.70**	515.16**
16.	Total chlorophyll content (mg/g)		
	A	-0.48** ± 0.049	0.61** ± 0.04
	B	0.413** ± 0.041	-0.06** ± 0.033
	C	0.728** ± 0.096	0.11 * ± 0.054
	X^2	307.21**	255.47**

**Significant at 1%
*Significant at 5%

Table 4a: Estimates of gene effects in two crosses of wheat For different characters

Sr. No.	Character / Crosses	NIAW-34 X NIAW-343	NIAW-917 X NIAW-2030
1.	Days to 50% flowering		
	m	56.28**± 0.109	60.86** ± 0.12
	d	-1.06** ± 0.27	-7.36** ± 0.15
	h	5.03** ± 0.75	0.56** ± 0.87
	i	7.93** ± 0.69	0.06 ± 0.58
	j	-0.96** ± 0.30	-9.53** ± 0.34
	l	-14.40** ± 1.31	-0.60 ± 1.52
	Type of epistasis	Duplicate	--
2.	Days to maturity		
	m	97.95** ± 0.11	103.93** ± 0.15
	d	-1.00** ± 0.25	-5.00** ± 0.12
	h	25.23** ± 0.78	14.73** ± 0.76
	i	27.00** ± 0.69	16.93** ± 0.65
	j	-0.50 ± 0.30	-9.53** ± 0.35
	l	-55.33** ± 1.34	-37.20** ± 1.11
	Type of epistasis	Duplicate	Duplicate
3.	No. of tillers per plant		
	m	11.23** ± 0.05	10.43** ± 0.06
	d	0.67** ± 0.162	0.55** ± 0.09
	h	-2.06** ± 0.45	3.40** ± 0.38
	i	-3.07** ± 0.39	1.96** ± 0.32
	j	0.67** ± 0.19	0.25 ± 0.18
	l	-1.60 ± 0.82	-6.40** ± 0.62
	Type of epistasis	--	Duplicate
4.	1000 grain weight (gm)		
	m	34.44** ± 0.21	35.56** ± 0.37
	d	4.7** ± 0.96	1.85** ± 0.65
	h	-4.29** ± 2.21	-10.80 ± 2.32
	i	-3.76 ± 2.10	-7.86** ± 3.93

	j	5.15** ± 1.05	6.83** ± 0.76
	l	-5.21** ± 4.15	4.02 ± 3.86
	Type of epistasis	Complementary	--
5.	Grain yield per plant		
	m	9.93** ± 0.07	14.96** ± 0.09
	d	-1.12** ± 0.14	-0.97** ± 0.15
	h	3.70** ± 0.46	-4.7** ± 0.56
	i	0.70± 0.41	7.67** ± 0.48
	j	-0.85** ± 0.15	-0.47** ± 0.19
	l	-4.20** ± 0.74	4.86** ± 0.78
	Type of epistasis	Duplicate	Duplicate
6.	Net photosynthetic rate		
	m	6.98** ± 0.95	6.92** ± 0.07
	d	-1.68** ± 0.04	-0.99** ± 0.09
	h	-7.69* ± 3.80	0.88** ± 0.32
	i	-7.71* ± 3.80	0.23** ± 0.31
	j	-0.36** ± 0.097	-1.48** ± 0.09
	l	13.55** ± 3.80	4.37** ± 0.45
	Type of epistasis	Duplicate	Complementary

Table 4b: Estimates of gene effects in two crosses of wheat For different characters

Sr. No.	**Crosses** / **Character**	**NIAW-34 X NIAW-343**	**NIAW-917 X NIAW-2030**
7.	Transpiration rate		
	m	3.91** ± 0.025	3.18** ± 0.02
	d	-0.55** ± 0.024	-1.20** ± 0.04
	h	-4.61** ± 0.14	3.80** ± 0.17
	i	-3.64** ± 0.11	3.42** ± 0.13
	j	-0.93** ± 0.081	-0.53** ± 0.09
	l	6.58** ± 0.217	-3.99** ± 0.28
	Type of epistasis	Duplicate	Duplicate
8.	Stomatal conductance		
	m	0.12** ± 0.001	0.137** ± 0.001
	d	-0.07** ± 0.002	-0.011** ± 0.001
	h	-0.078** ± 0.007	0.18** ± 0.014
	i	-0.03** ± 0.006	0.004 ± 0.005
	j	-0.07** ± 0.003	0.004 ± 0.003
	l	0.057** ± 0.012	0.331** ± 0.027
	Type of epistasis	Duplicate	Complementary
9.	Relative leaf water content (RLWC)		
	m	50.16** ± 0.22	50.47** ± 0.57
	d	-6.70** ± 0.31	-0.42** ± 1.14
	h	31.26** ± 1.14	26.77** ± 3.36
	i	38.73** ± 1.01	34.60** ± 3.24
	j	-4.57** ± 0.36	-4.98** ± 1.16
	l	-50.39** ± 1.67	-57.57** ± 5.42
	Type of epistasis	Duplicate	Duplicate
10.	SPAD reading		
	m	53.95** ± 0.21	50.67** ± 0.21
	d	-5.64** ± 0.19	-0.31 ± 0.39
	h	-19.64** ± 3.42	-2.27 ± 1.59
	i	-14.91** ± 0.93	-1. 66 ± 1.15
	j	-7.66** ± 0.41	1.29** ± 0.46
	l	19.94** ± 6.68	9.99** ± 2.04
	Type of epistasis	Duplicate	--
11.	Chlorophyll stability index (CSI)		
	m	60.18** ± 0.19	54.27** ± 0.54
	d	-3.73** ± 0.37	-1.60** ± 0.54
	h	14.03** ± 1.14	36.04** ± 2.54
	i	15.13** ± 1.08	37.58** ± 2.42
	j	-6.76** ± 0.38	-7.54** ± 0.57
	l	-5.86** ± 1.08	-41.70** ± 3.42
	Type of epistasis	Duplicate	Duplicate

Table 4c: Estimates of gene effects in two crosses of wheat For different characters

Sr. No.	Character / Crosses	NIAW-34 X NIAW-343	NIAW-917 X NIAW-2030
12.	Membrane injury index (MII)		
	m	33.50** ± 0.19	29.00** ± 0.17
	d	-1.50** ± 0.28	1.40** ± 0.30
	h	-19.56** ± 1.01	-24.95** ± 0.99
	i	-25.00** ± 0.96	-27.36** ± 0.92
	j	-3.06** ± 0.34	-0.64 ± 0.39
	l	45.13** ± 1.52	71.33** ± 1.61
	Type of epistasis	Duplicate	Duplicate
13.	Drought tolerance index (DTI)		
	m	0.49** ± 0.003	0.58** ± 0.004
	d	-0.08** ± 0.003	-0.03** ± 0.005
	h	0.31** ± 0.014	-0.27** ± 0.02
	i	0.37** ± 0.013	-0.33** ± 0.02
	j	-0.07** ± 0.004	0.008 ± 0.007
	l	-0.47** ± 0.018	0.82** ± 0.03
	Type of epistasis	Duplicate	Duplicate
14.	Chlorophyll ‘a’ content		
	m	1.34** ± 0.012	1.28** ± 0.014
	d	-0.15** ± 0.009	0.06** ± 0.015
	h	-0.55** ± 0.07	-0.04 ± 0.09
	i	-0.34** ± 0.05	0.09 ± 0.06
	j	-0.131** ± 0.045	0.144** ± 0.017
	l	0.11 ± 0.116	-0.41** ± 0.15
	Type of epistasis	--	--
15.	Chlorophyll ‘b’ content		
	m	0.30** ± 0.002	0.25** ± 0.002
	d	-0.04** ± 0.002	0.05** ± 0.002
	h	-0.17** ± 0.009	0.07** ± 0.01
	i	-0.117** ± 0.009	0.12** ± 0.009
	j	-0.033** ± 0.003	0.07** ± 0.005
	L	0.142** ± 0.013	-0.23** ± 0.016
	Type of epistasis	Duplicate	Duplicate
16.	Total chlorophyll content		
	m	2.42** ± 0.02	2.53** ± 0.008
	d	-0.517** ± 0.02	0.21** ± 0.018
	h	-1.24** ± 0.10	0.14** ± 0.053
	i	-0.79** ± 0.09	0.44** ± 0.05
	j	-0.44** ± 0.03	0.33** ± 0.024
	l	0.86** ± 0.14	-0.98** ± 0.09
	Type of epistasis	Duplicate	Duplicate

**Significant at 1%
*Significant at 5%

Statistical analysis

Analysis of variance (ANOVA)

The data collected on individual character were subjected to the statistical analysis as per the procedure given by Panse and Sukhatme, 1989 [25].

Estimation of population means and variances

The mean, variances, variance of mean and standard error of parent, F1, F2 and backcross generations were estimated from the observations recorded on the individual plant procedure as per given by Singh and Chaudhary (1999) [31].

Scaling test

Adequacy of additive-dominance model was tested by scaling test. Following three scales were calculated to detect the presence or absence of gene interaction using the formulae given by Hayman and Mather (1955) [12].

Joint scaling test (Cavalli, 1952)

Inadequacy of additive-dominance model was also confirmed by joint scaling test (Cavalli, 1952) and Estimates of mean (m), additive (d), dominance (h), additive x additive (i), additive x dominance (j) and dominance x dominance (l) gene effects were calculated using the means of six generations i.e. P1, P2, F1, F2, B1 and B2 as per six parameter model given by Hayman (1958) [13].

Results and Discussion

Analysis of variance

The analysis for variance was carried out for various characters studied. Mean squares are given in Table 1 Mean sum of squares due to replications were non-significant for all the characters. Mean sum of squares due to treatments (genotypes), parents, hybrids as well as segregating generations (F_2, B_1 and B_2) were highly significant for all the characters. This indicated considerable genetic diversity among parents, hybrids, F_2’s and backcrosses with regards to characters under investigation. The mean performance of four parents, F_1’s, F_2’s, B_1 and B_2 generations for sixteen different characters studied were averaged over replications and presented in Table 2a and 2b. The general mean for days to 50 per cent flowering was 58.03 days. Among all the treatments F_1 hybrids, NIAW-34 X NIAW-343 was the earliest (55.20 days) followed by NIAW-917 X NIAW-2030 (56.23 days). The general mean for days to maturity was 102.66 days. The F_1 hybrids, NIAW-34 X NIAW-343 (96.73 days) matured early and NIAW-917 was late for maturity (108.73 days). The general mean for number of tillers per plant was 10.00. Among the treatment F_1 hybrids, NIAW-917 X NIAW-2030 produced the maximum (11.25) tillers followed by, (NIAW-917 X NIAW-2030) X NIAW-917. The general mean of 1000 grain weight was 32.56 g. Among the F_1 hybrids, NIAW-917 X NIAW-2030 had the maximum 1000-grain weight (35.60g). In F_2 generation, NIAW-917 X NIAW-2030 produced maximum (35.56g). The general mean of grain yield per plant was 11.08 g. The highest grain yield per plant was recorded by F_1 hybrids, NIAW-917 X NIAW-2030 (14.30g).

Among the parents NIAW-34 measured minimum Net photosynthetic rate (5.18) followed by B2s (NIAW-917 X NIAW-2030) X NIAW-2030. The general mean for Stomatal conductance (mol H_2O m^{-2} s^{-1}) was 0.14. Among the twelve treatment In B_1 generation, (NIAW-34 X NIAW-343) X NIAW-34 measured lowest SC (0.0862) whereas NIAW-917 X NIAW-2030 measured maximum SC (0.3090). The general mean for RLWC was 56.43%. Among the treatments F_1 hybrids, NIAW-34 X NIAW-343 measured minimum RLWC (50.16%) followed by parent NIAW-2030 (52.73%) whereas B_2 generation, RLWC in (NIAW-34 X NIAW-343) X NIAW-343 was maximum (63.20%). Among the treatment B_1 generation, (NIAW-34 X NIAW-343) X NIAW-34 measured minimum SPAD (47.40) followed by B_2 generation, (NIAW-917 X NIAW-2030) X NIAW-2030 whereas NIAW-34 measured maximum SPAD (55.86). The general mean for CSI was 63.15. F_2 (NIAW-917 X NIAW-2030) was minimum Chlorophyll stability index (54.27%) while parent NIAW-34 recorded maximum CSI (69.86) among all the treatments. Membrane injury index (%) ranged from 21.46% to 33.99%. B_2, (NIAW-917 X NIAW-2030) X NIAW-2030 recorded minimum Membrane injury index (%) and maximum recorded by NIAW-917 (33.99%). The general mean for DTI was 0.5877. The parent NIAW-917 recorded minimum DTI (0.5480), while F_1, NIAW-917 X NIAW-2030 recorded maximum DTI (0.6513). The general mean for Total chlorophyll content was 2.44 (mg/g). Among the treatment B_1 generation, (NIAW-34 X NIAW-343) X NIAW-34 recorded minimum TCC (1.97 mg/g) while parent NIAW-2030 recorded maximum TCC (2.77 mg/g) followed by F_1 generation, (NIAW-917 X NIAW-2030)X NIAW-917 (2.74 mg/g).

Gene action

Data obtained from the experiment were subjected to scaling test and components of generation mean analysis. Data was analyzed by joint scaling tests (Cavalli, 1952) [6] as well as individual scaling test (Mather, 1949) [19] to detect the adequacy of additive-dominance model. To test the adequacy of additive and dominance model A, B and C scaling tests were applied, it is to be noted that, significance of A and B tests provides largely for presence of all the three types of interaction *viz*., additive x additive (i), additive x dominance (j) and dominance x dominance (l), while C test indicates l (Dominance x Dominance) type of gene interaction. The estimates of the scaling test in respect of sixteen characters are given in table 3a & 3b.

In the cross, NIAW-34 X NIAW-343 all the three individual scaling tests *viz.,* A, B and C were significant for Days for 50% flowering, Days to maturity, Number of tillers per plant, Grains yield per plant (g), Transpiration rate, Relative leaf water content (RLWC), Chlorophyll stability index (CSI), Drought tolerance index (DTI) and Total chlorophyll content (TCC) (mg/g).

In the cross, NIAW-917 X NIAW-2030 all the three individual scaling tests *viz.*, A, B and C were significant for Number of tillers per plant, 1000 grain weight, Grains yield per plant (g), Net photosynthetic rate, Transpiration rate, Stomatal conductance, Relative leaf water content (RLWC), SPAD reading, Chlorophyll stability index (CSI), Membrane injury index (MII), Drought tolerance index (DTI) and Total chlorophyll content (TCC) (mg/g).

In the cross, NIAW-34 X NIAW-343 scaling tests *viz.*, A, B significant for Net photosynthetic rate, Stomatal conductance and Membrane injury index (MII) indicating the inadequacy of additive-dominance model to explain inheritance for this traits.

In the cross, NIAW-917 X NIAW-2030 scaling tests A and B were only significant for Days for 50% flowering indicating the inadequacy of additive-dominance model to explain inheritance of this trait.

In NIAW-34 X NIAW-343 only scale B and C were significant for Chlorophyll ‘a’ content and Chlorophyll ‘b’ content also in cross NIAW-917 X NIAW-2030 scale B and C were significant. It reveals that additive-dominance model was inadequate to explain gene action involved in the expression.

Scale A and C were significant in NIAW-34 X NIAW-343 showing inadequacy of additive-dominance model for explaining gene action involved for expression of 1000 grain wt. (g).

Only Scale A and B were significant in NIAW-34 X NIAW-343 for net photosynthetic rate, stomatal conductance, and Membrane injury index (MII) showing inadequacy of additive-dominance model for explaining gene action involved.

Only Scale A was significant in NIAW-34 X NIAW-343 for SPAD reading and in cross NIAW-917 X NIAW-2030 for Chlorophyll ‘a’ content (mg/g) showing inadequacy of additive-dominance model for explaining gene action involved in both the crosses for these characters.

Joint scaling test

The adequacy/inadequacy of additive-dominance model was confirmed by performing joint scaling test in respect of all the characters in both the crosses (Table 3a & 3b). The x^2 values were found significant for all the characters in both the crosses except for Relative leaf water content (RLWC), and Membrane injury index (MII) in cross NIAW-34 X NIAW-343.

Estimation of gene effect (Components of generation mean)

Six genetic parameters m, d, h, i, j and l were estimated by using the mean of six generation (P_1, P_2, F_1, F_2, B_1 and B_2) according to the procedure given by Hayman (1958) for various characters in two crosses of wheat. The estimates of major genetic effects (d and h) and non-allelic epistatic interactions (i, j and l) for various characters are presented in Table 4a & 4b.

The parameter ‘m’ was highly significant in all the crosses for all the characters under study. Additive as well as Dominant genetic effects were highly significant in both the crosses, except SPAD reading in cross NIAW-917 X NIAW-2030 for

Additive as well as Dominant genetic effects and 1000 grain weight for Dominant genetic effects in NIAW-917 X NIAW-2030.

In cross NIAW-34 X NIAW-343 dominance gene effects were significant with relative greater magnitude of dominance component for days for 50 per cent flowering, days to maturity, grain yield per plant, relative leaf water content, CSI and DTI as well as in cross NIAW-917 X NIAW-2030 for days for 50 per cent flowering, days to maturity, number of tillers per plant, NPR, TR, SC, RLWC, CSI, Chlorophyll 'b' and TCC. Similar result was also reported by Shekhawat *et al.* (2000) [27] who reported the preponderance of dominance and epistatic effects in number of tillers per plant. Both the crosses showed significant additive as well as dominance gene effect with higher magnitude of dominance component for days for 50 per cent flowering and days to maturity. These findings are in conformity with Singh R P and Singh S. 1992 [29] observed preponderance of non-additive gene action in the inheritance of days to maturity.

As regards the epistatic gene interactions (i, j and l) for Days for 50% flowering, NPR, TR, SC, RLWC, SPAD reading, Chlorophyll stability index (CSI) Membrane injury index (Similar results reported by Kushwaha *et al*, (2011) [17]., DT, Chlorophyll 'b' and TCC were highly significant additive x additive, additive x dominance and dominance x dominance epistatic gene interactions observed in NIAW-34 X NIAW-343.

As regards the epistatic gene interactions (i, j and l) for Days to maturity, plant height, grain yield per plant, NPR, TR, RLWC, Chlorophyll stability index (CSI), Chlorophyll 'b' and TCC were highly significant additive x additive, additive x dominance and dominance x dominance epistatic gene interactions was observed in NIAW-917 X NIAW 2030. Similar results were reported by Kaur *et al.* (2010) [15].

Duplicate type of epistasis was observed in NIAW-34 X NIAW-343 due to presence of significant positive signs to dominance (h) and significant negative sign to dominance x dominance (l) component and vice versa for Days for 50% flowering. (Kaur *et al.* (2010) [15] also reported similar findings for this trait.), Days to maturity, grain yield per plant, NPR, TR (Similar results correlated with Kumar and Sharma (2007) [16]. SC (Similar results correlated with Hassan and Khaliq (2008) [11], RLWC, SPAD reading (These results are in line with those obtained by Tammam, 2005 [32]. and Amin, 2013 [2], Chlorophyll stability index (CSI) Membrane injury index, DTI, Chlorophyll 'a' and TCC (A similar result was reported by Amin 2013 [2]. As well as duplicate type of epistasis was observed in NIAW-917 X NIAW 2030 due to presence of significant positive signs to dominance (h) and significant negative sign to dominance x dominance (l) component and vice versa for Days to maturity (These findings are in conformity with Singh S. P. and Kumar Rajendra (2002) [30], Number of tillers per plant, grain yield per plant (Similar results correlated with Shekhawat *et al.* (2000) [28], TR, RLWC (similar results was reported by Amin (2013) [2]., Chlorophyll stability index (CSI) Membrane injury index, DTI (Similar results were reported by Yadav *et al.* (1999) [33], Chlorophyll 'b' and TCC. Singh *et al.* (1992) [29] also reported similar findings for Days for 50% flowering. Duplicate type of epistasis was observed in both the crosses with relative higher magnitude of dominance x dominance (l) gene action similar results were reported by Shekhawat *et al.* (2000) [28].Duplicate type of epistatis was also observed in above mentioned two crosses for different morpho – physiological traits in wheat Bharat Bhushan *et al.* (2021) [4].

Complementary type of epistasis was observed due to presence of significant positive signs to dominance (h) and significant positive sign to dominance x dominance (l) component and significant negative signs to dominance (h) and significant negative sign to dominance x dominance (l) component only for 1000 grain weight in NIAW-34 X NIAW-343 and as well as cross NIAW-917 X NIAW 2030 recorded Complementary type of epistasis for NPR and SC. results correlated with Zhang *et al.* (2000) [34]. However, additive (d) and additive x additive (i) and additive x dominance (j) gene effects were significant in cross II with higher magnitude of additive x additive (i) gene effects. Mishra *et al.* (1994) [20] reported the similar results.

The opposite signs of (h) and (l) components indicated the involvement of duplicate type of epistasis in the expression of grain yield. Similar results correlated with Amawate and Behl (1995) [1]. In Chlorophyll stability index (CSI), the opposite signs of h and l components indicated the involvement of duplicate type of epistasis in the expression of CSI in both the crosses. The opposite signs of h and l components indicated the involvement of duplicate type of epistasis in the expression of Membrane injury index (MII) in both the crosses. Similar results were reported by Gupta *et al.* (2002) [10].

Both additive as well as dominant gene action were significant in both the crosses studied with relative higher magnitude of dominance gene effect, similar result was also reported by Shekhawat *et al.* (2000) [27] who reported the preponderance of dominance and epistatic effects in number of tillers per plant.

Summary and Conclusions

Generation mean analysis for different characters

All additive, dominance and epistatic gene effects were found operating in inheritance of almost all characters. Selection should be delayed till virtual homozygosity is attained under drought, as both additive and non-additive gene actions were found predominant in the control of grain yield per plant and its components with duplicate type of epistasis in both the crosses. The plant mechanisms responsible for drought tolerance index, cell membrane injury, relative water content (RLWC%), chlorophyll stability index (CSI), Chlorophyll content (mg/g) and stomatal characters were governed by both additive and non-additive gene actions.

For drought tolerance index (DTI), both additive as well as non–additive gene action were significant in both the crosses except additive x dominance (j) epistasis gene interaction in cross NIAW-917 X NIAW-2030 with higher magnitude of dominance (h) and dominance x dominance (l) gene effect in both the crosses *viz.*, NIAW-34 X NIAW-343 and NIAW-917 X NIAW-2030.

In F1 transgressive segregants of (NIAW-917 X NIAW-2030) maximum drought tolerant index was found coupled with higher yield and early maturity characters and hence can be utilized for commercial purpose.

Thus, the present investigation revealed F_1 of cross NIAW-917 X NIAW-2030 can provide better opportunities for improvement for drought tolerance and yield and yield contributing character than other segregating and non-segregating generations of both the crosses. Though significant dominance and dominance x dominance (l) gene components were observed for many characters in the two crosses studied, it cannot be exploited because of presence of duplicate type of epistasis.

Based on above findings, it may be suggested that in those characters, additive and additive x additive gene effects were predominant, one should follow the simple selection in early segregating generations, whereas in those characters where dominance and dominance x dominance gene effects were significant indicated that these traits are predominantly under the control of non-additive gene action. Biparental mating / multiple crosses induced with pre pollination are suggested for improvement of these traits, in order to break the undesirable linkages and to generate desirable recombinants / transgrants. This would certainly enhance possibility that various recombinations may result in the accumulation of favourable genes in ultimate homozygous lines. Therefore, few cycles of recurrent selection followed by pedigree breeding approach can be suggested to improve the yield.

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