Generation mean analysis for important morpho-physiological traits in bread wheat (Triticum aestivum L.)

Bharat Bhushan, SS Dodake and PY Shinde

DOI: https://doi.org/10.22271/chemi.2021.v9.i1j.11315

Abstract
The present investigation consisted of six genetic populations i.e. P1, P2, F1, F2, BC1 and BC2 of six crosses which were evaluated during the rabi, 2015-16 season. The six populations (parents, F1, backcrosses and F2) of the two wheat crosses, (NIAW-34 X NIAW-343 and NIAW-917 X NIAW-2030) were grown under restricted irrigation at Post Graduate Institute Farm, Department of Botany, Mahatma Phule Krishi Vidyapeeth, Rahuri (MS). Mean performance of Parents, F1’s, F2’s, BC1 and BC2 for different morphological and physiological traits in wheat recorded significant differences among both the crosses. Analysis of variance showed significant variability for all the traits in both crosses. All the three individual scaling tests for viz., A, B and C were significant for four traits viz., Number of tillers per plant, Number of grains per spike, grain yield per plant and Chlorophyll stability index (CSI) in both the crosses indicating the inadequacy of additive-dominance model to explain inheritance. Additive as well as Dominant genetic effects were highly significant in both the crosses, for the Days for 50% flowering, Days to maturity, Number of tillers per plant, Number of grains per spike, grain yield per plant, Chlorophyll stability index (CSI) and Membrane injury index. The epistatic gene interactions (i, j and l) for Chlorophyll stability index (CSI) was highly significant. Additive x additive, additive x dominance and dominance x dominance was observed in both the crosses. Duplicate type of epistasis was observed in both the crosses for days to maturity, plant height, grain yield per plant, chlorophyll stability index (CSI) and membrane injury index.

Keywords: Bread wheat, gene action, generation mean analysis

Introduction
Wheat (Triticum aestivum L.) is the first important and strategic cereal crop for the majority of world populations. 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.

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.

Abiotic stresses, at any time of crop development, decrease leaf chlorophyll and photosynthesis and hasten senescence (Dulai et al. (2006) [5]. Drought stress during vegetative growth period of crop, decrease leaf area, number of tillers, plant height and biomass (Nouri et al. (2011) [15].

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) [2]. Nicolas et al. (1984) [14] reported a higher decline in wheat yield when high temperature and drought stresses were applied simultaneously at an early and late period of grain development stage (cell division) as compared to the independent stress.

To meet the ever increasing demand of wheat production, 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.
Knowledge of Generation mean analysis 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.

Material and Methods
The present investigation was conducted at Post Graduate Institute 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 which were obtained from ARS, Niphad) of each of the following two crosses (NIAW-34 X NIAW-343 and NIAW-917 X NIAW-2030). The experiment consisting of 12 treatments (Four parents, two f1’s, two f2’s, two B1’s and two B2’s) was conducted in Randomized Block Design with three replications. Among treatments two rows of parents and hybrids, backcrosses and F2’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 was applied and recommended agronomical practices were adopted to raise the good crop.

The observations were recorded on nine morphological characters of 10 randomly selected plants in non-segregating generations viz., P1, P2 and F1 and 10 plants in segregating generation viz., B1 and B2, and 20 plants in F2’s respectively of each of the cross in each replication and two physiological characters Chlorophyll Stability Index (CSI) and Membrane injury index (MII) was worked out by adapting procedures described by Koloyereas (1958) [11] and Sairam et al., (1997) [17] Respectively.

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 [16] and Estimation of population means and variances were recorded on the individual plant procedure as per given by Singh and Chaudhary (1999) [21]. Adequacy of additive-dominance model was tested by scaling test. Following three scales were calculated to determine the presence or absence of gene interaction using the formulae given by Singh and Chaudhary (1999) [21].

Results and Discussion
Analysis of variance
Mean performance of Parents, f1’s, f2’s, B1 and B2 for different morphological and physiological traits in wheat recorded significant differences among both the crosses (Table 1). The range for 50 per cent flowering was 55.20 (NIAW-34 X NIAW-343) to 62.66 (NIAW-917) with mean days for 50 per cent flowering was 58.03. Among the treatment, F1 hybrids, NIAW-34 X NIAW-343 (96.73 days) matured early, whereas, NIAW-917 took maximum days to maturity (108.73 days) with 102.22 mean days to mature.

NIAW-2030 recorded maximum (84.53 cm) and NIAW-34 recorded minimum (59.33 cm) plant height with mean 68.19 cm. The F1 hybrids, NIAW-917 X NIAW-2030 and NIAW-34 produced the maximum (11.25) and minimum (8.8) tillers per plant, respectively. Back cross (NIAW-917 X NIAW-2030) X NIAW-917 recorded highest spike length (9.60) followed by NIAW-917 X NIAW-2030(9.30) whereas, NIAW-343 had the minimum (8.03 cm) spike length.

The F1 hybrids, NIAW-34 X NIAW-343 had the maximum number of grains per spike (44.50) however; NIAW-917 had the lowest number of grains per spike (36.40) with average 40.83. NIAW-917 X NIAW-2030 had the maximum 1000-seed weight (35.60g) while NIAW -217 recorded lowest 1000 seed weight (29.12 gm) amongst all generations. The F1 hybrids, NIAW-917 X NIAW-2030 exhibited higher (14.30g) whereas, NIAW-34 had the lowest grain yield per plant (7.46g) with general mean of 11.08 gm.

The general mean for CSI was 63.15 The parent NIAW-2030 recorded minimum CSI (57.47), while NIAW-34 recorded maximum CSI (69.86). The general mean for MII was 28.08. The parent NIAW-343 recorded minimum MII (28.00), while NIAW-917 recorded maximum MII (33.99).

Highly significant differences for all the quantitative characters studied were observed due to genotypes indicating the presence of considerable amount of variability.

Table 1: Analysis of variance for parents, f1’s, f2’s, B1 and B2 for different characters in wheat

| Sr. No. | Characters                         | Mean Sum of Square |
|---------|-----------------------------------|--------------------|
|         | Replication (d.f. 2) | Treatments (d.f. 11) | Error (df. 22) |
| 1.      | Days to 50% flowering             | 0.752              | 21.99**           | 1.880 |
| 2.      | Days to maturity                  | 3.070              | 60.62**           | 1.296 |
| 3.      | Plant height (cm)                 | 4.191              | 166.97**          | 4.624 |
| 4.      | No. of tillers/plant              | 0.02               | 2.51**            | 0.016 |
| 5.      | Spike length (cm)                 | 0.008              | 0.309**           | 0.032 |
| 6.      | No. of florets/plant              | 188.69             | 5197.7**          | 596.9 |
| 7.      | No. of grains/panicle             | 0.004              | 18.73**           | 0.015 |
| 8.      | 1000 seed weight (g)              | 1.863              | 23.68**           | 4.431 |
| 9.      | Grain yield per plant (g)         | 0.013              | 15.76**           | 0.015 |
| 10.     | Chlorophyll stability index       | 1.449              | 60.652**          | 0.521 |
| 11.     | Membrane injury index             | 0.033              | 58.699**          | 0.217 |

** Significant at 1%
* Significant at 5%

Gene Action
Data obtained from the experiment were subjected to scaling test and components of generation mean analysis. 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 1 (Dominance x Dominance) type of gene interaction. The estimates of the scaling test in respect of eleven characters are given in Table 3. In the cross, NIAW-34 X NIAW-343 all the three individual scaling tests for viz., A, B and C were significant for six traits viz., Days for 50% flowering, Days to maturity, Number of tillers per plant, Number of grains per spike, grain yield per plant and Chlorophyll stability index (CSI) indicating the inadequacy of additive-dominance model to explain inheritance. In the cross NIAW-917 X NIAW-2030 all the three individual scaling tests for viz., A, B and C were significant for eight traits i.e. Plant height (cm), Number of tillers per plant, Number of florets per plant, Number of grains per spike, 1000 seed weight (g), grain yield per plant, Chlorophyll stability index (CSI) and Membrane injury index indicating the inadequacy of additive-dominance model to explain inheritance. In the cross, NIAW-34 X NIAW-343 only A test was significant in the result indicated to employ six-parameter model for estimation of gene effect involved in expression of plant height. Only Scale B was significant in NIAW-34 X NIAW-343 while all three individual scaling tests for Number of florets per plant were significant for number of florets in the cross NIAW-917 X NIAW-2030. Scale A and C were significant in NIAW-34 X NIAW-343 while all three individual scaling tests for 1000 seed weight (g) viz., A, B and C were significant in cross NIAW-34 X NIAW-2030 showing inadequacy of additive-dominance model for explaining gene action involved in both the crosses for expression of 1000 seed wt. (g). Scale A and B were significant in NIAW-34 X NIAW-343, while all three individual scaling tests viz., A, B and C were significant in cross NIAW-917 X NIAW-2030 showing inadequacy of additive-dominance model for explaining gene action involved in both the crosses for expression of MII. None of the three individual scaling tests for Spike length (cm) viz., A, B and C and x2 test were significant in cross NIAW-34 X NIAW-343 indicated adequacy of additive-dominance model and thus employ three parameter model of Jinks and Jones. In cross NIAW-917 X NIAW-2030 both scale B and scale C were significant indicated to employ six-parameter model for estimation of gene effects involved in expression of spike length in this cross. Spike length (cm), the non-significance of A,B,C scales and joint scaling test in the cross NIAW-34 X NIAW -343, indicated the adequacy of additive-dominance model. However, except ‘m’ none of monogenic gene action as well as epistatic gene interaction were significant for spike length in the cross NIAW-34 X NIAW -343.

In the cross, NIAW-34 X NIAW-343 all the three individual scaling tests for Days for 50% flowering viz., A, B and C were significant, while scaling test A and B were significant in cross NIAW-917 X NIAW-2030, indicating the inadequacy of additive-dominance model to explain inheritance of this trait. In the cross NIAW-34 X NIAW-343 all the three individual scaling tests for Days to maturity viz., A, B and C were significant while in 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 of days to maturity in both the crosses.

**Table 2: Mean performance of Parents, f1’s, f2’s, B1 and B2 for different morphological characters in wheat**

| Sr. No. | Name of Variety | Days to 50% Flowering | Days to Maturity | Plant Height at maturity (cm) | No. Of tillers /Plant | Spike length (cm) | No. Of Florets /plant | No. Of grains /spike | 1000 seed weight (gm) | Grain yield/ Plant (gm) | Chlorophyll stability index (%) | Membrane injury index (%) |
|---------|-----------------|-----------------------|-----------------|-------------------------------|---------------------|-------------------|---------------------|---------------------|----------------------|------------------------|-----------------------------|-----------------------------|
| 1.      | NIAW-34         | 58.00                 | 98.00           | 59.33                         | 8.8                 | 8.06              | 571.53              | 36.80               | 29.30               | 7.46                   | 69.86                       | 31.13                       |
| 2.      | NIAW-343        | 58.20                 | 99.00           | 67.16                         | 8.8                 | 8.03              | 559.46              | 38.00               | 30.12               | 8.00                   | 63.80                       | 28.00                       |
| 3.      | NIAW-917       | 62.66                 | 108.73          | 70.33                         | 9.4                 | 8.38              | 560.73              | 36.40               | 29.12               | 10.40                  | 69.35                       | 33.99                       |
| 4.      | NIAW-2030       | 58.33                 | 99.66           | 84.53                         | 8.8                 | 8.80              | 652.86              | 38.53               | 31.50               | 11.40                  | 57.47                       | 29.90                       |
| 5.      | NIAW-34 X NIAW-343 | 55.20               | 96.73           | 64.15                         | 10.53               | 8.66              | 631.60              | 44.50               | 34.44               | 10.73                  | 65.73                       | 25.60                       |
| 6.      | NIAW-917 X NIAW-2030 | 56.23               | 102.00          | 64.36                         | 11.25               | 9.50              | 660.23              | 42.20               | 35.60               | 14.30                  | 61.86                       | 26.30                       |
| 7.      | NIAW-34 X NIAW-343 | 56.28               | 97.95           | 64.15                         | 9.23                | 8.50              | 591.05              | 42.50               | 33.21               | 9.93                   | 60.18                       | 33.50                       |
| 8.      | NIAW-917 X NIAW-2030 | 60.86               | 103.93          | 81.25                         | 10.43               | 9.30              | 650.20              | 41.05               | 35.56               | 13.50                  | 54.27                       | 29.00                       |
| 9.      | (NIAW-34 X NIAW-343) X NIAW-34 | 57.73               | 104.20          | 64.43                         | 10.80               | 8.50              | 596.46              | 44.16               | 33.55               | 9.55                   | 62.10                       | 26.50                       |
| 10.     | (NIAW-917 X NIAW-2030) X NIAW-917 | 57.20               | 105.66          | 69.53                         | 11.20               | 9.60              | 633.80              | 42.80               | 34.51               | 12.56                  | 62.86                       | 22.86                       |
| 11.     | (NIAW-34 X NIAW-343) X NIAW-343 | 56.80               | 105.20          | 65.30                         | 10.13               | 8.30              | 556.90              | 41.56               | 31.11               | 10.66                  | 65.83                       | 28.00                       |
| 12.     | (NIAW-917 X NIAW-2030) X NIAW-2030 | 58.90               | 105.66          | 63.80                         | 10.65               | 9.33              | 660.76              | 41.48               | 32.67               | 13.53                  | 64.46                       | 21.46                       |
| General |                |                       |                 |                               |                     |                   |                     |                     |                     |                       |                             |                             |
| SE (±)  | 0.79            | 0.65                  | 1.24            | 0.07                          | 0.10               | 14.07             | 0.07                | 1.21               | 0.07                | 0.41                   | 0.26                        |                             |
| CD at 5%| 2.32            | 1.92                  | 3.64            | 0.21                          | 0.30               | 41.36             | 0.20                | 3.56               | 0.21                | 1.22                   | 0.79                        |                             |

**Joint Scaling Test**

Significance of one or more individual scaling test either individually or simultaneously was observed for almost all the characters in both the crosses, indicated the inadequacy of additive-dominance model to explain inheritance of these traits except for spike length in cross NIAW-34 X NIAW-343, where all the three scales were non-significant in their expression which indicated adequacy of additive-dominance model. The result of individual scaling tests were also confirmed and supported by joint scaling test. The
The adequacy/inadequacy of additive-dominance model were confirmed by performing joint scaling test in respect of all the characters in both the crosses (Table 4).

Table 3: Estimates of scaling tests and joint scaling test for different characters for two crosses in bread 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         |
| X²      | 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       |
| X²      | 2281.86**           | 1915.36**           |
| 3.      | Plant height at maturity |                 |                      |
| A       | 5.34** ± 1.04       | 4.36** ± 1.43       |
| B       | -0.75 ± 0.87        | -21.29** ± 1.37     |
| C       | 1.72 ± 1.38         | 41.40** ± 2.75      |
| X²      | 29.86**             | 3240.73**           |
| 4.      | No. Of tillers/plant |                     |                      |
| A       | 3.00** ± 0.35       | 2.47** ± 0.34       |
| B       | 1.66** ± 0.33       | 1.97** ± 0.23       |
| C       | -0.18 ± 0.37        | -0.70* ± 0.35       |
| X²      | 249.06**            | 116.295**           |
| 5.      | Spike length (cm)   |                     |                      |
| A       | -0.29 ± 0.23        | 0.24 ± 0.23         |
| B       | -0.32 ± 0.22        | -0.88* ± 0.23       |
| C       | -0.18 ± 0.37        | -0.70* ± 0.35       |
| X²      | 3.660               | 21.80**             |
| 6.      | No. Of florets/ plant |                   |                      |
| A       | -12 ± 27.70         | 113.80** ± 29.12    |
| B       | -57.53* ± 23.71     | 75.60** ± 25.00     |
| C       | -30.53 ± 35.48      | 281.06** ± 54.83    |
| X²      | 9.475*              | 30.41**             |
| 7.      | No. Of grains/ spike |                     |                      |
| A       | 11.26** ± 0.35      | 7.00** ± 0.31       |
| B       | 4.86** ± 0.24       | 2.23** ± 0.25       |
| C       | 14.66** ± 0.40      | 4.87** ± 0.48       |
| X²      | 92.806**            | 545.42**            |
| 8.      | 1000 seed 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      |
| X²      | 9.475*              | 30.41**             |
| 9.      | 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      |
| X²      | 96.11**             | 484.78**            |
| 10.     | 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     |
| X²      | 894.22**            | 372.86**            |
| 11.     | 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     |
| X²      | 879.05              | 2103.05**           |

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 (P₁, P₂, F₁, F₂, B₁ and B₂) according to the procedure given by Hayman (1958) [9] 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 and 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, for the Days for 50% flowering, Days to maturity, Number of tillers per plant, 

The $x^2$ values were found significant for all the characters in both the crosses except for spike length (cm) and Membrane injury index (MII) in F₁ (NIAW-34 X NIAW-343).
Number of grains per spike, grain yield per plant, Chlorophyll stability index (CSI) and Membrane injury index. Both additive and dominance gene effects were significant with relative greater magnitude of dominance component for days for 50 per cent flowering in the cross I. Both the crosses showed significant additive as well as dominance gene effect with higher magnitude of dominance component for days to maturity. These findings are in conformity with Singh et al. (2002) [20]. Both additive as well as dominant gene action were significant in both the crosses studied with relative higher magnitude of dominance gene effect for number of tillers per plant, similar result was also reported by Shekhawat et al. (2000) [18] who reported the preponderance of dominance and epistatic effects in Number of tillers per plant. As regards the epistatic gene interactions (i, j and l) for Days for 50% flowering, Chlorophyll stability index (CSI) and Membrane injury index, highly significant additive x additive, additive x dominance and dominance x dominance was 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 and Chlorophyll stability index (CSI), are highly significant additive x additive, additive x dominance and dominance x dominance was observed in NIAW-917 X NIAW 2030. Additive x dominance was significant in cross II for days to 50% flowering, In plant height, additive gene effects were significant in only cross II for this trait, while the significant dominance gene effects was observed in both the two crosses. Similar results were reported by Kaur et al. (2003) [12].

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, Days to maturity, plant height, Number of grains per spike, grain yield per plant, Chlorophyll stability index (CSI) and Membrane injury index. 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, plant height, Number of tillers per plant, grain yield per plant, Chlorophyll stability index (CSI) and Membrane injury index. Singh et al. (1998) [19] also reported similar findings for Days for 50% flowering. Singh et al. (2002) [20] observed preponderance of non-additive gene action in the inheritance of days to maturity. In plant height, similar results were also reported by Yadav and Narsinghani (1999) [22]. Among the epistatic gene interactions for Number of tillers per plant, significant additive x additive (i) and additive x dominance (j) effects were observed in the cross I, while significant additive x additive (i) and dominance x dominance (l) effects were observed in the cross II. Yadav and Narsinghani (1999) [22] reported similar findings in his studies. Duplicate type of epistasis was observed in the cross II with relative higher magnitude of dominance x dominance (l) gene action. Similar results were reported by Shekhawat et al. (2000) [18] and Kaur et al. (2003) [12]. In Number of grains per spike, among the epistatic gene interactions significant additive x additive (i) effects was observed only in the cross II. This indicated the predominance of additive and dominance gene effects in inheritance of this character. Similar results also reported by Chowdhry et al. (1991) [4]. 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]. Similarly, due to opposite signs of h and l components the duplicate epistasis was confined in cross I for Number of grains per spike. Similar results were also reported by Kaur et al. (2003) [12] thus conforming the present findings. However, except ‘m’ none of the monogenic gene action and epistasis gene interaction were observed significant in cross II. This may be due to presence of some higher order gene interaction or linkage. 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) [7]. All digenic gene interactions viz., additive x additive, additive x dominance and dominance x dominance were highly significant for this trait in NIAW-917 X NIAW 2030 cross, while additive x additive and dominance x dominance were significant for this trait in NIAW-34 X NIAW-343 for number of tillers per plant. Additive x additive (i) and additive x dominance (j) interactions were less in magnitude for Plant height (cm), than dominance x dominance (l) interactions indicating that genes were highly dispersed among the parents. Additive x dominance (j) gene interaction was highly significant in NIAW-34 X NIAW-343 for number of tillers per plant, and significant dominance x dominance (l) was observed significant in NIAW-917 X NIAW-2030. The non-allergic gene interaction i.e. Additive x dominance (j) was highly significant only in NIAW-917 X NIAW-2030 however, none of the epistatic gene interaction was significant in NIAW-34 X NIAW-343 for Spike length (cm). Additive as well as dominance gene effect for Number of florets per plant were observed significant in cross NIAW-917 X NIAW-2030 with higher magnitude of dominance gene effect in cross II. Significant additive and dominance gene effects were observed in the cross II similar results were reported by Chowdhry et al., (1991) [4] and Khan et al. (2000) [10]. However, none of the epistatic gene interaction were significant in NIAW-34 X NIAW-343 for this character. In Number of grains per spike, none of the epistatic gene interaction were significant in NIAW-917 X NIAW-2030 for this character except ‘m’. None of the monogenic gene action as well as epistatic gene interaction were significant for florets per plant in the cross NIAW-34 X NIAW-343. This may be due to presence of some higher order gene interaction or linkage. Additive as well as dominance gene effect in 1000 seed weight (g) were observed highly significant in cross NIAW-34 X NIAW-343 with higher magnitude of additive gene effect, while only additive gene effect was observed significantly in cross NIAW-917 X NIAW-2030. The non-allergic gene interactions i.e. Additive x additive (i) and additive x dominance (j) was significant in NIAW-917 X NIAW-2030, while non-allergic gene interactions i.e. Additive x dominance (j) and dominance x dominance (l) were observed significant in cross NIAW-34 X NIAW-343 for this character. Complementary type of epistasis was observed in the cross NIAW-34 X NIAW-343 due to presence of similar signs to dominance (h) and dominance x dominance (l) components. Kaur et al. (2003) [12] reported the similar results in 1000 seed weight (g). 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) [13] reported the similar results.
### Table 4a: 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 |
|---------|------------------|---------------------|----------------------|
| 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      |                      |
| I       | -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    | -9.83** ± 0.35      |                      |
| I       | -55.33** ± 1.34 | 12.70** ± 1.11      |                      |
| Type of epistasis | Duplicate | Duplicate |                      |
| 3.      | Plant height (cm) |                     |                      |
| m       | 64.15** ± 0.27  | 81.25** ± 0.28      |                      |
| d       | -0.86 ± 0.58    | 5.73** ± 0.37       |                      |
| H       | 3.803* ± 1.65   | -71.39** ± 1.85     |                      |
| I       | 2.86 ± 1.59     | -58.32** ± 1.36     |                      |
| J       | 3.05** ± 0.63   | 12.83** ± 0.49      |                      |
| I       | -7.46** ± 2.71  | 75.25** ± 3.13      |                      |
| Type of epistasis | Duplicate | Duplicate |                      |
| 4.      | 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         |                      |
| I       | -1.60 ± 0.82    | -6.40** ± 0.62      |                      |
| Type of epistasis | Duplicate | --                  |                      |
| 5.      | Spike length (cm) |                     |                      |
| m       | 8.48** ± 0.34   | 8.38** ± 0.04       |                      |
| d       | 0.013 ± 0.05    | 0.35** ± 0.10       |                      |
| H       | -1.59 ± 0.88    | 0.003 ± 0.30        |                      |
| I       | --              | 0.063 ± 0.25        |                      |
| J       | --              | 0.56** ± 0.14       |                      |
| I       | --              | 0.57 ± 0.53         |                      |
| Type of epistasis | -- | Duplicate |                      |
| 6.      | No. of florets per plant | |                      |
| m       | 591.05** ± 6.83 | 670.20** ± 10.54    |                      |
| d       | 28.56 ± 15.63   | -26.96* ± 20.10     |                      |
| H       | 26.90 ± 43.05   | -105.40* ± 61.68    |                      |
| I       | -39.46 ± 41.54  | -91.67* ± 58.27     |                      |
| J       | 22.53 ± 17.10   | 19.10 ± 22.44       |                      |
| I       | 109.46 ± 71.91  | -97.73* ± 99.40     |                      |
| Type of epistasis | -- | --                |                      |
| 7.      | No. of grains per spike | |                      |
| m       | 41.05** ± 0.09  | 46.75** ± 0.59      |                      |
| d       | 1.31** ± 0.16   | 0.067 ± 1.85        |                      |
| H       | 9.10** ± 0.52   | -7.50 ± 4.60        |                      |
| I       | 4.36** ± 0.50   | -7.00 ± 4.40        |                      |
| J       | 2.38** ± 0.19   | -1.10 ± 2.00        |                      |
| I       | -13.60** ± 0.80 | 3.20 ± 8.24         |                      |
| Type of epistasis | Duplicate | --                  |                      |
| 8.      | 1000 seed 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       |                      |
| I       | -5.21** ± 4.15  | 4.02 ± 3.86         |                      |

### 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 |
|---------|------------------|---------------------|----------------------|
| 6.      | No. of florets per plant | |                      |
| m       | 591.05** ± 6.83 | 670.20** ± 10.54    |                      |
| d       | 28.56 ± 15.63   | -26.96* ± 20.10     |                      |
| H       | 26.90 ± 43.05   | -105.40* ± 61.68    |                      |
| I       | -39.46 ± 41.54  | -91.67* ± 58.27     |                      |
| J       | 22.53 ± 17.10   | 19.10 ± 22.44       |                      |
| I       | 109.46 ± 71.91  | -97.73* ± 99.40     |                      |
| Type of epistasis | -- | --                |                      |
| 7.      | No. of grains per spike | |                      |
| m       | 41.05** ± 0.09  | 46.75** ± 0.59      |                      |
| d       | 1.31** ± 0.16   | 0.067 ± 1.85        |                      |
| H       | 9.10** ± 0.52   | -7.50 ± 4.60        |                      |
| I       | 4.36** ± 0.50   | -7.00 ± 4.40        |                      |
| J       | 2.38** ± 0.19   | -1.10 ± 2.00        |                      |
| I       | -13.60** ± 0.80 | 3.20 ± 8.24         |                      |
| Type of epistasis | Duplicate | --                  |                      |
| 8.      | 1000 seed 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       |                      |
| I       | -5.21** ± 4.15  | 4.02 ± 3.86         |                      |
Summary and Conclusions
Gene action for yield and its components
Highly significant differences for all the quantitative characters studied were observed due to genotypes indicating the presence of considerable amount of variability. All additive, dominance and epistatic gene effects were found operating in inheritance of almost all characters. Significance of one or more individual scaling test either individually or simultaneously was observed for almost all the characters in both the crosses, indicated the inadequacy of additive-dominance model to explain inheritance of these traits except for spike length in cross NIAW-34 X NIAW-343. 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. Therefore, selection should be delayed till virtual homozygosity is attained. 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 / transgressants. 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.

Generation mean analysis for physiological characters
Both additive and non-additive gene actions were involved in control of the plant mechanisms responsible for chlorophyll stability index (CSI) and Membrane Injury Index (MII) which have been least studied so far. For Chlrophyll Stability index (CSI) and Membrane Injury Index (MII), 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. 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. The multiple crosses, biparental mating, disruptive mating, transgressive segregation followed by effective selection in subsequent generations may be fruitful for bringing improvement in these traits.

Reference
1. Amawate JS, Behl PL. Genetical analysis their relations to stress susceptibility index in several of some quantitative components of yield in bread wheat genotypes. BIBAN, 7(1):31-47. Wheat. Ind. J Genet 1995;55(2):120-125.
2. Cattivelli L, Rizza F, Badeck FW, Mazzucotelli E, Mastrangelo AM, Francia E et al. Drought tolerance improvement in crop plants: An integrated view from breeding to genomics. Field Crops Res 2008;105:1-14.
3. Cavalli LL. An analysis of linkage in quantitative inheritance. In Quantitative Inheritance, ed. E.C.R. Reeve, and C.H. Waddington. H.M.S.O., London 1952.
4. Chaudhari RR, Mandal AB. Association and path analysis for grain yield in wheat at different micro-environment, environment and ecology 1991;9(4):906-910.
5. Dulai S, Molnar I, Pronay J, Csernak A, Tarnai R, Molnar-Lang M. Effects of drought on photosynthetic parameters and heat stability of PSII in wheat and Aegilops species originated from dry habitats. Acta Biologica Szegediensis 2006;50:11-17.
6. FAO. FAOSTAT agriculture dat. Agricultural production. FAO, Rome 2012.
7. Gupta NK, Shukla DS, Pandey PC. Interaction of yield determining parameters in late sown wheat genotypes. Indian J Plan Physiol 2002;7(3):264-269.
8. Hayman BI, Mathur K. The description of genetics interaction in continuous variation. Biometrics 1955;11:69-82.
9. Hayman BI. The Separation of Epistatic from Additive and Dominance Variation in Generation Means. Heredity 1958;12:371-390.
10. Khan AS, Khan MKR, Khan TM. Genetic analysis of plant height, grain yield and other traits in wheat (Triticum aestivum L.). Intern. J Agri. Bio 2000;2:129-132.
11. Koloyereas AS. A new method of determining drought resistance. Plant Physiol 1958;33:232-233.
12. Kaur Satvindra, Singh Surjit, Mahal GS, Joshi Sunil. Genetics of leaf blight resistance in durum wheat. Crop Improvement 2003;30(2):159-163.
13. Misra SC, Rao VS, Dixit RN, Surve VD, Patil VP. Genetic control of yield and its components in breadwheat. Indian Journal of Genetics 1994;54:77-82.
14. Nicolas Marc E, Roslyn Gleadow M, Michael Dalling J. Effects of Drought and High Temperature on Grain Growth in Wheat. Aust. J Plant Physiol 1984;11:553-66.
15. Nouri A, Etminan A, Teixeira da Silva JA, Mohammadi R. Assessment of yield, yield-related traits and drought tolerance of durum wheat genotypes (Triticum turgidum var. Durum Desf.). Australion J Crop Sci 2011;5:8-16.
16. Panse VG, Sukhatme PV. Statistical methods for Agril. Workers, ICAR, New Delhi 1989.
17. Sairam RK, Deshmukh PS, Shukla DS. Increased antioxidant enzyme activity in response to drought and temperature stress related with stress tolerance in wheat genotypes, Abstract: National Seminar (ISSP), IARI, New Delhi 1997, 69.
18. Shekhawat US, Bhardwaj RP, Vijay Prakash. Gene action for yield and its components in wheat (Triticum aestivum L.). Indian J of Agri. Res 2000;34(3):176-178.
19. Singh G, Nanda GS, Sahu VS. Gene effect for grains per spike grain weight and grain perspikelets in a set of nineteen crosses of wheat. Indian J, of Gene and Plant Breeding 1998;58(1):83-89.
20. Singh SP, Kumar Rajendra. Genetic analysis of yield and its contributing traits in bread wheat (Triticum aestivum L.). Progressive Agri 2002;2(1):1-10.
21. Sing RK, Chaudhary BD. In: Biometrical methods in quantitative genetic analysis. First ed. Kalyani publishers, New Delhi India ISBN 1999, 81-7663.
22. Yadav RK, Narshinghani VG. Gene effects for yield and its components in wheat. Rachis newsletter 1999;18:79-81.