

GENETIC DETERMINATION OF YIELD RELATED ATTRIBUTES IN BREAD WHEAT

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ABSTRACT

The present study was conducted in the Department of Plant Breeding and Genetics, University of Arid Agriculture, Rawalpindi during 2000-2002. Inheritance mechanism was studied in a complete 8x8 diallel involving indigenous wheat varieties. Gene action studies were made on some yield contributing attributes like days to heading, days to maturity, plant height, number of tillers m^{-2} , flag leaf area and grain filling period. The average degree of dominance for days to maturity (2.061), plant height (1.915), flag leaf area (1.679) and grain filling period (1.081) indicated the presence of over dominance gene action controlling these yield attributes. However, for number of tillers m^{-2} (1.00), the value suggested role of complete dominance governing it. These results revealed that selection for these traits in early generation is difficult. The selection process will have to be delayed till F_2 segregating population. Whereas 0.659 value for degree of dominance suggested additive type of gene action for days to heading, proposing the possibility of selection in early generation (F_1).

Key words: Gene action, Bread wheat, Yield traits

INTRODUCTION

Wheat being the staple diet for the human population occupies a unique position among all prevalent crops of the country. Being the major food crop of Pakistan, it has always been an object of extensive research. The basic aim of all wheat breeding programmes is to boost yield.

The basic knowledge of genetics is useful for the development of new varieties. Different morphological traits of wheat plant play a critical role in increasing its yield. The unit leaf area is the basis of measuring productivity in different plant species during their growth and development under a particular environmental condition prevailing over the season (Larcher, 1995). As the leaf area increases, a greater photosynthetically active surface area becomes available. At spike development, flag leaf is the major contributor of the seed yield (Kozkowski, 1992). Production of tillers number $plant^{-1}$ also depends on leaf number $main\ tiller^{-1}$, which also contributes to final grain yield (Camble and Davidson, 1979).

The diallel cross technique as advocated by Hayman (1954 a,b) and Jinks (1954) offers a method especially in self fertilized crops like wheat to assess the crosses in F_1 generation and provides the necessary genetic information on the plant characters. Subhani and Chowdhry, (2000), Chaudhry *et al.* (2001), Khan *et al.* (2000) and Kashif *et al.* (2003) have reported the role of partial dominance and overdominance gene action in controlling various economic traits in wheat.

The present study was designed to ascertain the mechanism of gene action responsible for the development of yield related traits of wheat. Such

information would be helpful for future crop improvement programmes.

MATERIALS AND METHODS

Eight wheat varieties viz. Pak-81, Pothowar 93, Parwaz 94, Shahkar 95, Suleiman 96, Chakwal 97, Kohistan 97 and MH 97 were sown during November, 2000 with two sowing dates (5th and 20th November) in order to facilitate hybridisation. The varieties were selected based on their promising features of yield related traits. Crossing of the varieties was performed during February/March 2001, whereas, the parent varieties were self-pollinated to maintain the true to type seed.

The seeds of 28 direct crosses and 28 reciprocal crosses along with their parents were sown in the field on 3rd of November, 2001. Randomised complete block design was followed in the experiment having three replications. Each variety was sown in single row of five-meter length in each replication. Inter row and inter plant distances were kept at 30 cm and 20 cm respectively.

Data regarding days to heading, days to maturity, grain filling period, plant height (cm), number of tillers m^{-2} and flag leaf area (cm^2) were recorded during the cropping season. The data were analysed to ascertain the significant differences among mean values of genotypes following Steel and Torrie (1980).

Additive-dominance model of Hayman (1954 a,b) is widely used technique to study the basis of genetic variation in early generations like F_1 and it also provides the nature and magnitude of the genetic behaviour. In this technique, the total sum of squares

is partitioned into various components, namely, a (additive), b (non-additive, which is further subdivided into b_1 , b_2 and b_3), c (maternal) and d (reciprocal differences other than c).

Significance of test of item 'a' suggests the significance of additive effects of genes and of item 'b', the dominance effects. Significance of ' b_1 ' indicates that the dominance is unidirectional. Asymmetry of gene distribution is indicated by the item ' b_2 ', whereas item ' b_3 ' tests that part of dominance deviation which are not attributable to ' b_1 ' and ' b_2 '. Item 'c' tests the presence of maternal effects whereas item 'd' tests the reciprocal differences other than 'c'. Further analysis of data using Vr (Variance), Wr (Covariance) approach of Hayman (1954 a) is valid only when 'b' item is significant.

Testing the validity of the hypothesis

Two scaling tests i.e. uniformity of Wr, Vr and joint regression analysis were conducted to ascertain the data sets for adequacy of the additive-dominance model. Wr-Vr is expected to be constant over arrays, if all assumptions of the analysis are fulfilled. Heterogeneity of Wr-Vr arrays indicates that one or more of the assumptions are not fulfilled for that character. The Wr-Vr values were calculated for each of eight arrays and their homogeneity was tested through the value of t^2 .

In joint regression analysis, the regression coefficient (b) of covariance (Wr) on variance (Vr) for each character is expected to be significantly different from zero, but not significantly different from unity (1), if all assumptions hold true (Jinks and Hayman, 1953).

Genetic parameters

The genetic parameters i.e. E (environmental variance from ANOVA), D (estimate of additive and some portions of additive x additive genetic variance), F (estimate of relative frequencies of dominant and recessive alleles in the parents), H_1 and H_2 (estimate of dominance and dominance x dominance interactions, respectively), h^2 (overall dominance effect), $H_2/4H_1$ (the proportion of genes with positive and negative effects in the parents), $(H_1/D)^{0.5}$ as the mean degree of dominance, KD/KR (the proportion of dominant and recessive genes in the parents) and heritability estimates in narrow sense were computed according to Mather and Jinks (1982).

RESULTS AND DISCUSSION

In present investigations, the data on days to heading, days to maturity, plant height, number of tillers m^{-2} , flag leaf area and grain filling period were analysed using ordinary analysis of variance technique. The mean squares of the analysis presented in Table I showed that genotypic differences for all the characters were highly significant ($P \leq 0.01$). Therefore, the data were arranged in diallel tables for formal analysis of variance. Hayman's analysis of variance was conducted for each character under study and is discussed as under:

Days to heading

The analysis of variance of diallel data (Table II) showed highly significant differences for most of the items except ' b_1 ' and 'c'. The significant 'a' and 'b' items indicated the role of additive and dominance properties of genes effects in the inheritance of days to heading. The component ' b_2 ' was found to be significant ($P \leq 0.05$) indicating asymmetrical distribution of genes, and similarly significant ' b_3 ' item revealed the importance of specific genetic effects.

The item 'c' was non-significant suggesting no need to retest 'a' item. As the item 'd' was significant ($P \leq 0.01$), thus there was need of retesting 'b' items against mean square of 'd'. After retesting the significance of ' b_1 ' item remained unchanged and showed the dominance of reciprocal effects. However, significant ' b_2 ', ' b_3 ' and 'b' items changed to non-significant which signified that properties of dominance were masked by the genes with reciprocal effects. Since Hayman's analysis of variance of diallel table showed that the item 'b' was significant for days to heading, the analysis of variance (Vr) and Covariance (Wr) was further carried out for this trait.

The two scaling tests i.e. uniformity of Wr and Vr and joint regression analysis were carried out to test the validity of data for analysis following additive dominance model (Table III). The uniformity of Wr and Vr (t^2 -test) validated the model for days to heading. Similarly the regression analysis completely fulfilled the assumptions. Thus, on the basis of the results of both tests the additive dominant model was found to be fully adequate for genetic analysis of F_1 data.

The results of this test (Table III) indicated that assumptions for days to heading were not fulfilled.

The uniformity of W_r and V_r (t^2 test) validated the model, but the regression analysis showed the partial failure of the assumptions. Earlier findings of Kearsey and Jinks (1968) and Daly and Robson (1969) pointed out that in studies of quantitative inheritance, complete validity of all the assumptions is unlikely. When a trait exhibits a partial failure of the assumptions, estimates of genetic parameters of that trait are still possible (Hayman, 1954a). Therefore, both the tests suggested that simple additive-dominance was adequate to determine genetic components of variation in days to heading.

The estimates of components of variation were computed for days to heading following Mather and Jinks (1982). The results presented in Table IV have shown significant values of D , H_1 and H_2 indicating the importance of both additive and non-additive gene action in the inheritance of this trait. However, the additive gene effects seemed to be more important than dominance genetic effects. This was supported by higher magnitude of component D than H_1 . Positive value of F revealed that dominant alleles were more frequent than the recessive ones. The degree of dominance $(H_1/D)^{0.5}$ with value of 0.659 indicated the presence of partial dominance. Asymmetrical gene distribution in the parents was apparent as $H_2/4H_1$ deviated from the expected value (0.25). The ratio of KD/KR suggested the presence of more dominant alleles in the parents for this trait. Similar results for days to heading were obtained by some earlier workers like Wagoire *et al.* (1998) and Pandey *et al.* (1999). This suggested that days to heading is an important attribute contributing towards yield and direct selection can be practiced in early segregating generations.

Days to maturity

The analysis of variance of diallel data (Table II) showed highly significant differences for days to maturity in case of 'b₂', 'b₃' and 'b' while 'a' and 'b₁' showed non-significant results. The non-significant 'a' and 'b₁' items indicated the absence of additive and directional dominance effects in the inheritance of days to maturity. The significant 'b' item suggested the role of dominance properties of gene effects. The component 'b₂' was found to be significant ($P \leq 0.01$) indicating asymmetrical distribution of genes and similarly significant 'b₃' item revealed the importance of specific genetic effects.

As 'd' item was significant ($P \leq 0.05$), thus there was need of retesting 'b' items against mean square of 'd'. After retesting the 'b₁' item remained non-significant showing the absence of directional dominance.

However, the significant 'b₂', 'b₃' and 'b' items reduced to non-significant which signified that properties of dominance genes were masked by the genes with reciprocal effects. The perusal of the Table II revealed that the item 'b' was significant for days to maturity, the analysis of variance (V_r) and Covariance (W_r) was therefore conducted.

The results of two scaling tests given in Table III revealed that for days to maturity, both the uniformity of W_r and V_r (t^2 -test) and regression analysis completely fulfilled the assumptions therefore; the additive dominance model was adequate to account for the data.

Both additive and non-additive types of gene actions were involved in the inheritance of this character as indicated by the significant additive and non-additive variances (Table IV). Dominance genetic effects (H_1 and H_2) however, were found to play an important role in the expression of this character due to higher magnitude of components H_1 and H_2 than D . Over dominance was detected for this trait on the basis of $(H_1/D)^{0.5}$ ratio. Asymmetrical gene distribution in the parents was observed, as $(H_2/4H_1)$ deviated from its expected value. The ratio KD/KR suggested the excess of dominant alleles among the parents for this character. The present results for days to maturity are in accordance with those of Kathiria and Sharma (1996) who reported over dominance type of gene action for the same trait. The over dominance type of gene action indicated that effective selection in the early segregating generations would be difficult.

Plant height

The genetic analysis for plant height presented in Table II revealed that item 'a' was highly significant ($P \leq 0.01$) and showed the presence of additive genetic effects for this character. The highly significant ($P \leq 0.01$) 'b' item indicated the importance of dominance effects of genes. The highly significant ($P \leq 0.01$) 'b₁' item revealed the presence of directional dominance effects. The genes were distributed asymmetrically among the parents as the item 'b' was highly significant. Item 'b₃' was also highly significant ($P \leq 0.01$) indicating the presence of specific gene action controlling plant height. The maternal and reciprocal effects were present in the genetic control of this character as 'c' and 'd' items were shown to be significant ($P \leq 0.01$).

Since 'c' item was significant, therefore, 'a' item was retested against 'c' as suggested by Mather and Jinks (1982). After retesting, significance of 'a' item was reduced to non-significant suggesting the masking role of maternal effects. Similarly 'b₁', 'b₂', 'b₃' and 'b' were retested against 'd'. After retesting the

significance of 'b₁' and 'b' items remained unchanged, however items 'b₂' and 'b₃' which were previously significant against their block interactions reduced to non-significant. Further analysis of variance (Vr) and Covariance (Wr) of the data sets was taken up as the item 'b' was found to be significant for plant height.

The results indicated that for plant height the uniformity of Wr and Vr tests validated the model but regression analysis showed that partial failure. Kearsey and Jinks (1968) and Daly and Robson (1969) pointed out that in studies of quantitative inheritance, complete validity of assumptions is unlikely. Estimation of genetic parameters of such data sets is still possible according to Hayman (1954a).

The estimates of components of variation D, H₁, H₂, E, F and h² are given in Table IV. The magnitude of H₁ was more pronounced than D, therefore dominance genetic effects were observed in controlling this character. The estimates of H₂ were less than H₁ which exhibited the presence of unequal proportion of negative and positive alleles in the parents. The unequal gene frequencies in the parents were evidenced by H₂/4H₁ value (1.207). The F value exhibited relative frequency of dominant alleles in the parental lines and variation in the dominance level over loci. Positive value of F ratio obtained from KD/KR (2.133) revealed that dominant genes for plant height were more frequent than recessive ones. Average degree of dominance (H₁/D)^{0.5} was more than unity, which pointed out the over dominance type of gene action. The degree of narrow sense heritability was 0.129. The high value of h² (135.305) indicated the dominance effect summed over all heterozygous loci. The findings of Hassan *et al.* (1996) and Sabour *et al.* (1996) supported the present results indicating the involvement of over dominance gene action for the trait. The presence of over dominance has made selection more difficult.

Number of tillers m⁻²

The results of formal analysis of variance of diallel data for number of tillers m⁻² are given in Table II. The highly significant (P≤0.01) 'a' item exhibited the presence of additive genetic effects in the genetic control of number of tillers m⁻². The non-significant 'b₁' and 'b₂' items revealed the absence of directional dominance and unequal distribution of dominance. The significant 'b₃' and 'b' items indicated the presence of specific gene action and dominance effects. As the item 'b' was significant for this particular character under study, the analysis of

variance (Vr) and Covariance (Wr) was further carried out.

The diallel assumptions of Hayman (1954) were fulfilled for number of tillers m⁻². Both the scaling tests i.e. the uniformity of Wr and Vr (t²-test) and the regression analysis fully validated the data sets for additive dominant model.

Estimates of additive (D) and non-additive genetic effects (H₁, H₂, h²) were significant (Table IV). The value of H₁ was almost similar that of D showing the dominance genetic effects. Negative and significant value of F in the table showed a preponderance of recessive alleles in the expression of the character. Complete dominance was indicated for this trait on the basis of (H₁/D)^{0.5} value (1.00). A low value of H₂/4H₁ revealed that genes were distributed asymmetrically among the parents. The ratio of KD/KR suggested the presence of more recessive alleles in the parents for this trait. The findings of earlier researchers Malik *et al.* (1989), Alam *et al.* (1990) and Chowdhry *et al.* (1992) are in accordance with the results of the present study.

Flag leaf area

The analysis of variance of diallel data (Table II) showed significant (P≤0.01) differences for all the items except 'b₁' and 'd'. Both additive and dominance properties of genes effect were playing important role in the inheritance of flag leaf area as the items 'a' and 'b' were significant. The non-significant 'b₁' item indicated the absence of directional dominance. The significant (P≤0.05) 'b₂' and 'b₃' items revealed the presence of asymmetrical distribution of genes and importance of specific gene action.

The 'c' item was significant (P≤0.05), thus there was need of retesting 'a' item against mean square of 'c'. After retesting the significance of 'a' item changed to non-significant, which showed that the genes with maternal effects masked properties of additive genetic effects. The item 'd' was non-significant. The significance of item 'b' permitted the data for analysis of variance (Vr) and Covariance (Wr).

The results of the two scaling tests given in Table III revealed that the data for flag leaf area fulfilled the assumptions in both the cases (uniformity of Wr and Vr (t²-test) and regression analysis). Therefore, further analysis of genetic components can be carried out.

The results that are mentioned in Table IV suggested that the estimates of additive and non additive genetic variances were significant, indicating the importance

of both additive and dominance types of gene actions for this character. Higher values of H_1, H_2 and h^2 showed the importance of non-additive type of gene action. Positive value of F exhibited the presence of more number of dominant alleles than the recessive ones. Over dominance gene action was evidenced, as the average degree of dominance $(H_1/D)^{0.5}$ value exceeded the unity. Low value of $H_2/4H_1$ manifested that positive and negative alleles were unequally distributed at the loci exhibiting dominance in the parental genotypes. The ratio of KD/KR suggested that more dominant alleles than the recessive were controlling the character. Over dominance was also reported by Iqbal *et al.* (1991), Chowdhry *et al.* (1992) and Mohyuddin and Shahzad (1998) for flag leaf area. The character thus seems difficult to fix and the progress in selection will be inherently slow.

Grain filling period

The formal analysis of variance of grain filling period (Table II) showed that all the items were highly significant ($P \leq 0.01$) except 'b₁' item which was non-significant and 'b₂' which was significant ($P \leq 0.05$). The significant 'a' and 'b' items revealed the presence of both additive and dominance genes for grain filling period. The non-significant 'b₁' item indicated the absence of directional dominance. The significant ($P \leq 0.05$) 'b₂' item revealed the presence of unequal distribution of genes.

The significant 'c' and 'd' items showed the presence of maternal and reciprocal effects in the expression of this character. In case, 'c' and 'd' items become significant, the values of 'a' and 'b' items need to be retested against 'c' and 'd' items respectively as

suggested by Mather and Jinks (1982). After retesting 'a' and 'b' items situation had become quite different. The non-significant 'a' item indicated that maternal effects had masked the role of genes acting additively. Similarly 'b', 'b₁', 'b₂' and 'b₃' suggested the predominant role of reciprocal effects for the development of grain filling period.

Results shown in Table III revealed that for grain filling period the uniformity of W_r and V_r (t^2 -test) validated the model as well as joint regression analysis fulfilled the assumptions. Therefore, data can be further processed for genetic analysis.

Both additive and non-additive types of gene actions were involved in the inheritance of this character as indicated by their significant variances (Table IV). The dominance genetic variance was found to play an important role in the expression of this character as the magnitude of components H_1 was greater than D . Positive F value revealed that dominant alleles were more frequent than recessive ones. Over dominance type of gene action was shown by $(H_1/D)^{0.5}$ value. The proportion of genes with negative and positive effects among the parents was found to be less than 0.25 denoting asymmetry at the loci showing dominance as indicated by value of $H_2/4H_1$. The ratio of KD/KR suggested more dominant alleles in the parents for this character. Due to the presence of over dominance type of gene action selection of this trait in early generations will be difficult. Over dominance was also reported earlier by workers like Iqbal *et al.* (1991), Chowdhry *et al.* (1992) and Mohyuddin and Shehzad (1998).

Table I. Analysis of variance of different yield traits in F_1 generation of bread wheat

| Parameters | Genotypic mean squares | Replication mean squares | Error mean squares |
|-----------------------------------|------------------------|--------------------------|--------------------|
| Days to heading | 71.57** | 30.15 | 20.81 |
| Days to maturity | 255.06** | 196.29 | 33.57 |
| Plant height (cm) | 106.81** | 96.26 | 16.04 |
| Number of tillers m ⁻² | 3727.10** | 1723.60 | 420.10 |
| Flag leaf area (cm ²) | 87.77** | 34.60 | 15.99 |
| Grain filling period (days) | 288.44** | 105.77 | 57.25 |

** , * = Significant at 1% and 5% probability level, respectively.

Table II. Formal analysis of variance for various yield contributing traits in an 8 x 8 diallel cross of wheat

| Source of Variation | Days to heading | | Days to maturity | | Plant height (cm) | | Number of tillers m ⁻² | | Flag leaf area (cm ²) | | Grain filling period (days) | |
|---------------------|-----------------|----------|------------------|---------|-------------------|----------|-----------------------------------|------------|-----------------------------------|---------|-----------------------------|----------|
| | D.F. | M.S. | D.F. | M.S. | D.F. | M.S. | D.F. | M.S. | D.F. | M.S. | D.F. | M.S. |
| a | 7 | 311.36** | 7 | 21.46 | 7 | 64.59** | 7 | 25427.10** | 7 | 78.65* | 7 | 238.56** |
| b ₁ | 1 | 35.69 | 1 | 1.07 | 1 | 931.48** | 1 | 16444.00 | 1 | 218.94 | 1 | 28.58 |
| b ₂ | 7 | 22.30* | 7 | 62.20** | 7 | 56.11** | 7 | 4657.94 | 7 | 66.54* | 7 | 55.34* |
| b ₃ | 20 | 42.87** | 20 | 30.02** | 20 | 71.77** | 20 | 4464.08** | 20 | 27.25* | 20 | 68.58** |
| b | 28 | 37.47** | 28 | 37.03** | 28 | 98.56** | 28 | 4940.40* | 28 | 43.91** | 28 | 63.85** |
| c | 7 | 51.32 | 7 | 26.88 | 7 | 37.25** | 7 | 3140.20 | 7 | 36.98* | 7 | 136.20* |
| d | 21 | 36.72** | 21 | 25.34** | 21 | 38.29** | 21 | 1604.80 | 21 | 33.57 | 21 | 66.17* |
| Blocks | 63 | 69.19** | 63 | 30.28** | 63 | 67.88** | 63 | 5904.82 | 63 | 43.55** | 63 | 92.07** |
| B x a | 14 | 14.42 | 14 | 18.03 | 14 | 2.33 | 14 | 2378.20 | 14 | 18.57 | 14 | 40.21 |
| B x b ₁ | 2 | 9.95 | 2 | 0.54 | 2 | 0.06 | 2 | 4096.50 | 2 | 42.57 | 2 | 8.89 |
| B x b ₂ | 14 | 5.56 | 14 | 15.78 | 14 | 2.75 | 14 | 6588.30 | 14 | 16.24 | 14 | 19.36 |
| B x b ₃ | 40 | 10.21 | 40 | 12.40 | 40 | 4.89 | 40 | 1477.40 | 40 | 14.12 | 40 | 24.86 |
| B x b | 56 | 9.04 | 56 | 12.82 | 56 | 4.18 | 56 | 2848.70 | 56 | 15.67 | 56 | 22.92 |
| B x c | 14 | 25.11 | 14 | 24.49 | 14 | 3.99 | 14 | 1707.40 | 14 | 9.89 | 14 | 36.66 |
| B x d | 42 | 9.17 | 42 | 13.42 | 42 | 2.26 | 42 | 1493.10 | 42 | 19.27 | 42 | 30.76 |
| Block interaction | 126 | 11.47 | 126 | 14.90 | 126 | 3.31 | 126 | 2217.70 | 126 | 16.55 | 126 | 28.98 |

** , * = Significant at 1% and 5% probability level, respectively.

Table III. Two scaling tests validating the additive-dominance model

| Parameters | Analysis of uniformity of Wr-Vr (t ²) | Joint Regression Analysis | | |
|-----------------------------------|---|---|-----------|-----------|
| | | Regression coefficient ± Standard error | Ho: b = 0 | |
| | | | Ho: b = 0 | Ho: b = 1 |
| Days to heading | 0.03 | b = 0.98 ± 0.11 | 9.13** | 1.16 |
| Days to maturity | 1.44 | b = 0.10 ± 0.40 | 2.47* | 1.10 |
| Plant height (cm) | 1.11 | b = 0.63 ± 0.19 | 3.36* | 4.98** |
| No. of tillers m ⁻² | 1.00 | b = 0.97 ± 0.28 | 5.45** | 0.50 |
| Flag leaf area (cm ²) | 0.05 | b = 0.74 ± 0.22 | 3.35* | 0.57 |
| Grain filling period (days) | 0.54 | b = 0.10 ± 0.18 | 3.45* | 1.11 |

** , * = Significant at 1% and 5% probability level, respectively.

Table IV. *Estimates of genetic components for some yield contributing traits in an 8 × 8 diallel cross of wheat*

| | Days to heading | Days to maturity | Plant height (cm) | Number of tillers m ⁻² | Flag leaf area (cm ²) | Grain filling period (days) |
|------------------------------------|-----------------|------------------|-------------------|-----------------------------------|-----------------------------------|-----------------------------|
| Parameters | Estimates | Estimates | Estimates | Estimates | Estimates | Estimates |
| D | 46.442 ± 1.882 | 6.004* ± 2.172 | 20.803* ± 5.576 | 1481.850* ± 144.152 | 10.255* ± 2.859 | 23.525* ± 3.766 |
| F | 24.182* ± 4.468 | 17.090* ± 5.155 | 28.835* ± 13.235 | -826.200 ± 342.136 | 17.246* ± 6.787 | 12.232 ± 8.940 |
| H ₁ | 20.169* ± 4.347 | 25.519* ± 5.015 | 76.361* ± 12.877 | 1498.530* ± 332.859 | 28.922* ± 6.603 | 27.529* ± 8.698 |
| H ₂ | 17.426* ± 3.782 | 13.983* ± 4.363 | 63.253* ± 11.203 | 1418.960* ± 289.595 | 16.921* ± 5.745 | 21.567* ± 7.567 |
| h ² | 3.552 ± 2.530 | -2.185 ± 2.919 | 135.305* ± 7.494 | 1801.080* ± 193.738 | 29.225* ± 3.843 | -0.424 ± 5.062 |
| E | 3.776* ± 0.630 | 5.352* ± 0.727 | 1.226 ± 1.867 | 91.130* ± 48.266 | 6.177* ± 0.957 | 10.498* ± 1.261 |
| (H ₁ /D) ^{0.5} | 0.659 | 2.061 | 1.915 | 1.005 | 1.679 | 1.081 |
| H ₂ /4H ₁ | 0.216 | 0.137 | 0.207 | 0.236 | 0.146 | 0.195 |
| KD/KR | 2.306 | 5.458 | 2.133 | 0.565 | 3.005 | 1.632 |
| Heritability (N.S.) | 0.605 | 0.024 | 0.129 | 0.728 | 0.194 | 0.351 |

* = Significant at 5% probability level.

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