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Comparison of the efficiency among half diallel methods in the genetic analysis of bread wheat *(Triticum aestivum* L.*)* under drought stress condition

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ABSTRACT

In order to compare the efficiency of different half-diallel methods in the analysis of bread wheat(Triticum aestivum L.), 15 genotypes from a six-parental diallel cross, excluding reciprocals, were grown in the field using a randomized complete block design (RCBD) with three replications under two different water regimes (irrigated and rainfed). Comparison of Griffing's model I, method II; Morley-Jones method; Gardner and Eberhar's method and Hayman's method indicated regardless of the restrictions of the Griffing model, it has the advantages of the definition of formulas for estimating the effects, their variances and the variances of contrasts of effects, as well as for the calculation of orthogonal sums of squares. Therefore, it is generally quite safe to use the Griffing model. Gardner and Eberhart appears to have the following advantages over the others: (1) it provides general combining ability (GCA) and specific combining ability (SCA), (2) information on the additive effects of varieties and their average and individual contribution to heterosis in crosses, (3) a clear-cut idea about the genetic aspect of heterosis by partitioning the total sum of squares of heterosis (h_{ij}) into different components, (4) since in this analysis parents are also included, and there is a simple relationship between heterosis (h_{ij}) and specific combining ability (s_{ij}) as $h_{ij} = (2\, s_{ij} - s_{ii} - s_{jj}) / 2$, heterosis can be easily calculated, (5) the results further indicated the possibility of dominance variance being confounded with the additive variance of general combining ability.

Keywords: Bread wheat; drought tolerance; different diallel methods; genetic analysis; heterosis.

INTRODUCTION

Drought is one of the most important abiotic stress factors, which affects almost every aspect of wheat crops (29, 35, 48). Genetic improvement of drought-related characters and selection or hybridization breeding program depends on precise estimates of genetic variation components

for the interested traits consisting of additive, dominance and non-allelic interaction effects, which may provide practical information to breeders during the development of drought-tolerant wheat varieties (15, 35, 37).

One of the several biometrical procedures available to plant breeders for evaluating and characterizing genetic variability existing in a crop species is diallel analysis. From the practical point of view, diallel mating designs provide a very simple and convenient method for the estimation of genetic parameters (44, 45). Among various diallel forms, the half diallel methods have certain advantages over others, giving maximum information about genetic architecture of a trait, parents and allelic frequency (12, 26). In addition, the diallel cross technique was reported to provide early information on the genetic behavior of these attributes in the first generation (46, 59).

There are several diallel methods for analyzing data from a set of p parents and their p(p-1)/2 single-cross progenies. Griffing used the half diallel analysis for combining ability while Gardner and Eberhart, using the set-up multiple regression approach, partitioning heterosis in terms of average, general and specific heterosis effects (20, 23). Morley-Jones extended the analysis of variance of a full diallel table to a half diallel table (36). The best-known methods for diallelic analysis are those developed by Hayman (24, 25), exclusively for homozygous parents (24, 25). Of these, the Griffing, Gardner and Eberhart methods are doubtless the most frequently applied (23, 20). The main reasons that justify the widespread uses of the Griffing method are its generality, since the parents can be clones, pure lines, inbred lines, or populations of a self-pollinated, cross-pollinated or intermediate species, and the ease of analysis and interpretation (23); the latter also characterizes the method developed by Gardner and Eberhart (20). The genetic interpretation of parameters in the Gardner and Eberhart and the Griffing models and the relationship between them have been discussed by Vencovsky, Cruz and Vencovsky, thereby making the methods more accessible to breeders (10, 62). The Hayman's method, on the other hand, may include statistical and graphical analyses of array variances and covariances, and the estimation of a number of genetic parameters (46).

This study was therefore, conducted to compare the efficiency of different half diallel methods in bread wheat (*Triticum aestivum* L.).

MATERIALS AND METHODS

Plant materials and experimental design

Six varieties of wheat (*Triticum aestivum* L.), namely: (1) Pishtase (drought sensitive), (2) CHAM-4DOVN-2ICW93-0001-AP-OL-1AP-2AP-OAP(semi-resistant),(3)Zagross (drought sensitive),(4) Ns732.HER//Darab (semi-resistant), (5) TEVEE S/KARAWAN "S" ICW93-0073-1AP-OL-8AP-OL (drought resistant) and URES/3//FURY//SLN/ALDAN "S"/4/NS732/HER ICW93-0531 (drought resistant) were crossed in a half diallel design at the Agricultural College of Razi University, Kermanshah, Iran (47° 20′ N, 34° 20′ Eand 1351. 6 m above sea level) during 2009 and 2010. Seeds of 28 F_1 along with their self-pollinated parents were sown in the field in November 2010 using a randomized complete block design with three replications under irrigated and rainfed conditions. Seeds were sown in 2.5 m rows and at 15 × 30 cm inter-plant and inter-row distances, respectively.

Traits evaluated

At harvest time, following the measurement of yield potential (Yp) in the irrigated condition and stress yield (Ys) in the rainfed condition, the following physiological characters were recorded from the rainfed condition.

Relative water content (RWC): The fresh weight (FW) of five flag leaves (0.5 g) was weighed. Segments were then placed in distilled water for 24 h and reweighed to obtain turgor weight (TW). Thereafter the leaf segments were oven dried for 48 h at 72°C and re-weighed to obtain dried weight (DW). RWC was calculated using the following formula (13):

$$RWC(\%) = \left[\frac{FW - DW}{TW - DW}\right] \times 100$$

Chlorophyll fluorescence (CHF): Three flag leaves were selected from each genotype in each replication and the quantum yield was recorded after dark adaptation using a MINI-PAM instrument according to the following equation (21):

Quantum yield = Fv/Fm

where Fv and Fm are variable and maximum fluorescence, respectively.

Cell membrane stability (CMS): CMS was determined according to the method described by Sullivan (1972)(58). For this purpose, young leaves were selected at anthesis stage from each genotype and each replication. Twenty leaf discs (1 cm in diameter) were cut from leaves and washed with deionized water to remove the solution from the injured cells. For desiccation treatment, ten leaf discs were flooded in 10 ml of 30% PEG-6000 in test tubes for 24 h at 10 °C and for control treatment then leaf discs were flooded in distilled water. Then the leaf discs were washed with deionized water. Next, 10 ml of deionized water was added to tubes, and they were maintained for 24 h at 10 °C. After that, the conductivity of the solutions was determined. Finally, the tubes were boiled in a water bath for 30 min, cooled to room temperature, and the conductivity of the solutions was read again. CMS of leaf tissues was calculated using the following equation:

$$CMS(\%) = 100 - \left[1 - (1 - T_1 / T_2)/(1 - C_1 / C_2) \times 100\right]$$

T1 and T2 are the first and second (after boiling) measurements of the conductivity of solutions and C1 and C2 are the respective values for the controls.

Relative chlorophyll content (RCC): The chlorophyll content in the flag leaf was determined using a chlorophyll meter (SPAD-502, Japan). Three flag leaves of each genotype grown in both rainfed and irrigated conditions were measured after anthesis stage. Three measurements at random locations in the middle of the flag leaf were made for each plant, and the average sample was used for analysis.

Stomatal conductance (SC): Using three points of a flag leaf in each plot SC was measured by a Porometer.

Grain yield and stress tolerance index (STI): At maturity, after separation of border effects from each plot, yield potential (Yp) and stress yield (Ys) were measured. Stress tolerance index (STI) was calculated using the formula suggested by Fernandez (19):

$$STI = \frac{(Ys)(Yp)}{\overline{Y}p}$$

Where Ys = the yield of cultivar under stress, Yp = the yield of cultivar under irrigated, and $\overline{Y}_p$ is the mean of all cultivars under non stress conditions.

Biological yield (BY) and days to maturity (DTM): Data were collected on number of days to maturity (DTM) from day of planting to maturity and the biological yield per plant (average weight of five sampled plants).

Biometrical genetic analyses

Griffing - Mode I, Method 2: This method was calculated by following model:

$$Xij = u + g_i + g_j + s_{ij} + \frac{1}{b}\sum_k e_{ijk}$$

Where, u = the population mean, g_i = the general combining ability effect of the i^{th} parent, g_j = the general combining ability effect of the j^{th} parent, s_{ij} = the specific combining ability effect of the cross between i^{th} and j^{th} parents such that $s_{ij} = s_{ji}$ and e_{ijk} the environmental effect associated with ijk^{th} observation.

Morley-Jones model: This analysis was performed as:
$Y_{ij} = m + 2\ J_i - (p\text{-}1)\ l - (p\text{-}2)\ l_i$ for parents and $C_{ij} = m + J_i + J_j + l + l_i + l_j + l_{ij}$ for single cross progeny. Where m = grand mean, J_i = mean deviation from the grand mean due to the i^{th} parent = "a" component, l = mean dominance deviation = b_1, l_i = further dominance deviation due to the i^{th} parent = b_2 and l_{ij} = dominance deviation that is unique to each F_1 and unexplained by above two dominance deviations = b_3. Also $b_1 + b_2 + b_3 = b$.

Statistical analysis of Morley-Jones and Hayman performed by MSTAT-C version 1.42, SPSS ver 17 and Dial 98 statistical packages to estimate genetic parameters.

Gardner and Eberhart model II analysis: The analysis II proposed by Gardner and Eberhart was used by Excel package to estimate several types of heterosis, as described by the following model (20):

$$Yij = \mu v + (vi + vj)/2 + \varphi\ hij = \mu v + (vi + vj)/2 + \varphi\ (h + hi + hj + heij)$$

where Yij = mean of a parent when i = j, or mean of a single cross when $i \neq j$; μv = mean of all parents; vi, vj = effect of parent i or j, measured as deviation from μv, so that Σvi or Σvj = 0; hij = heterosis of the cross vivj, estimated as the difference between the cross and the average of its two parents, so that Σhij = 0; h = mean heterosis, estimated by the difference between the average of all crosses and μv; hi, hj = mean heterosis of vi or vj in all crosses, also named

varietal heterosis, measured as deviations from h, so that Σhi or Σhj = 0; heij = specific heterosis of the cross vi vj, estimated as the difference hij – (h+hi+hj), so that Σheij = 0; φ = zero when i = j, or = 1 when i ≠ j. Heterosis with respect to the best parent (hbp) was estimated by the difference between the cross vivj and the highest parent mean.

***Hayman's graphical analysis*:** Hayman' s graph (Vr-Wr graph) is drawn with the help of variances of arrays (Vr) and covariances (Wr) between parents and their offspring. The array refers to the crosses in which a particular parent is common. The Wri values are estimated fo all the arrays by the formula: $Wri = (Vri \times VOLO)^{1/2}$ where, Vri is the variance of r^{th} array and VOLO is the variance of parents. The Wri values are plotted against Vr values to draw the limiting parabola. The Wrei values are obtained by the formula: Wrei = Wr- bVr + bVri for drawing regression line, where, Wr is array mean of variances, Vr array mean of covariances and b = regression coefficient. The position of regression line on Vr-Wr graph provides information about average degree of dominance. (a) When the regression line passes through the origin, it indicates complete dominance ($D=H_1$). (b) When it passes above the origin, cutting the Wr axis, it shows that there is par tial dominance ($D>H_1$). (c) When it passes above the origin, cutting Wr axis and touching the limiting parabola it suggests the absence of dominance. (d) But when it passes below the origin, cutting the Wr axis, it denotes the presence of ovedominance. The position of parental point along the regression line indicates the dominance order of parents. The parents with more dominant genes are located closer to the origin, while those with more recessive genes fall farther from the origin. The parents with equal frequencies of dominant and recessive genes occupy the intermediate possition (14, 47, 52, 53).

RESULTS AND DISCUSSION

Analysis of variance (ANOVA)

Analysis of variance (Table 1) revealed significant differences among parents and hybrids for Yp, Ys, STI, RWC and SC indicating the presence of genotypic variability, different responses of genotypes to water deficit and possible selection of drought tolerant genotypes. No significant difference was found for BY, RCC, CMS and CHF (Table 1). Genetic variability was found for Yp, Ys, RWC, STI and CMS in wheat (15, 16). RWC, STI, SC and CMS were shown as screening techniques for discrimination of drought tolerance genotypes in wheat, barley, maize and chickpea (18, 7, 39). In fact the development of any plant breeding program is dependent upon the existence of genetic variability, the efficiency of selection and expression of heterosis in the plant population (44, 45, 52, 53).

Griffing analysis of variance

Knowledge of the relative importance of additive and non-additive gene action is essential to a plant breeder for the development of an efficient hybridization program. The concept of combining ability as a measure of gene action refers to the capacity or ability of a genotype to transmit superior performance to its crosses. The value of an inbred line depends on its ability to produce superior hybrids in combination with other inbreds. Combining ability analysis helps in the evaluation of inbreds in terms of their genetic value, and in the selection of suitable parents for hybridization (22, 34, 52, 53). Mean square of the genotypes was partitioned into general and specific combining abilities (GCA and SCA) (Table 2). Mean squares of GCA and SCA were significant for RWC and SC indicating the involvement of additive and non- additive gene action

in their inheritance. As GCA was not significant for RWC and SC and SCA was significant, hence RWC and SC are predominantly controlled by non-additive (dominance and epistasis) gene action. The improvement of such characters warrants a breeding methodology which capitalizes on additive as well as non-additive genetic variance. In this situation bi-parental mating offers good prospects for increasing the frequency of genetic recombinants hastening the rate of genetic improvement. Population breeding is also suggested in the form of bi-parental mating between selected recombinants to exploit the additive and non- additive effects. In the case of non-additive gene action (RWC and SC), it may be necessary to resort to heterosis breeding (11, 26 , 66).

The ratio of MSgca/MSsca (Table 2) displayed the relative importance of additive gene action. This ratio was significant for DTM, therefore it is predominantly controlled by additive gene effects hence, the pedigree method of selection can be used for DTM improvement. For any breeding program, the choice of parents to be used in the crossing program is of paramount importance and constitutes the basis for the success of the breeding program. Combining ability analysis helps in identifying superior parents and cross combination used in the breeding program (5, 60). The best general combiner with positive effects, for Yp, SC, DTM, and CHF was parent 1, for Ys and RWC was parent 2, for CMS and CHF was parent 3 and for STI was parent 6 (Table 3).

Accordingly parents 6 is the best general combiner for improvement of drought tolerance and high grain yield under rainfed and irrigated conditions. Specific combining ability effects are presented in Table 4. The best specific combination with heterobeltiosis over the best parents for improvement of Yp, Ys, STI, RWC, CMS, SC, DTM and CHF were the crosses 1×2, 3×5, 3×6, 1×4, 1×3, 4×5, 3×4 and 3×4, respectively indicating that parents of these crosses are genetically diverse. The expression of positive heterosis in these hybrids reveals the preponderance of additive gene action. According to Topall et al. (2004), compared to other type of gene effects for a specific trait, additive gene action will increase success in selection for that trait.

Morley-Jones analysis of variance

The model proposed by Morley-Jones considers the homozygous varieties as taken at random from some base population about which the conclusion are to be drawn. Consequently, his model is concerned with variances and not the estimates of genetic constants (17, 51).

If reciprocal differences are absent and only one of each pair of reciprocal crosses is raised then this half-diallel data can be analysed following Morley-Jones (1965). In this model the sum of squares corresponding to a, b_1, b_2 and b_3 can be obtained. The general ANOVA in half-diallel analysis will take the form as given in Table 5 (43).

An important advantage of Morley-Jones analysis of variance components is that it is free of the assumptions whether maternal or reciprocal effects are present or not and whether the parental lines are a fixed sample or a random sample of a population of inbred lines (16, 31). Here “a” signifies additive genetic variance in the absence of the b_2 item. If b_2 is significant, the “a” item will not measure additive variance unambiguously, but it will also be contaminated with non-additive variance. The b_1 item measures the mean deviations of the F_1's from the mid-parental values and becomes significant when the dominance effects at various loci are predominantly in

one direction. That is, there is a directional dominance effect. The absence of significance of this item in this case suggested an ambidirectional nature of dominance. The significance of the b_2 item indicated that the mean dominance deviation of the F_1's from their midparental values differed significantly over the F_1 arrays and these arrays differ if some parents contain more dominant alleles than others, implying asymmetry of gene distribution (i.e. $H_1 \neq H_2$; Hayman, 1954 a, b; Farshadfar et al., 2011b). That is, some parents contain considerably more dominant alleles than others. The "b_3" item tests residual dominance interaction coming from additive × additive, additive × dominance and dominance × dominance interaction effects that are not attributed to b_1 and b_2 and is unique to each F_1. The b_3 is equivalent to specific combining ability variance (50). In breeding jargon estimation of items (a) and (b) amounts to estimation of general combining ability and specific combining ability, respectively (43).

Highly significant differences were observed for additive ("a") effect for Y_p, STI, RWC, DTM and CHF in Morley-Jones method, while dominance ("b") item was significant for RWC, SC and CMS (Table 5) indicating that the inheritance of Y_p, STI, RWC, DTM and CHF was mainly controlled by additive gene effects, while SC and CMS by dominance type of gene action. Both ("a") and ("b") items were significant for RWC, accordingly RWC is controlled by both additive as well as dominance type of gene action. As (b_2) and (b_3) were not significant for Yp, Ys and CHF, hence interallelic interaction (epistasis) is not involved in their genetics. As the component (b_1) was significant for Y_p (Table 5), therefore dominance effects were due to directional dominance. Significant (b_2) item for STI, SC and DTM indicating imbalance of gene distribution for these traits. Significant (b_3) item for RWC, SC and CMS exhibited residual dominance effect (b_3) resulted from additive× additive, additive× dominance and dominance× dominance interaction effects (Table 5).

Gardner and Eberhart analysis

In view of considerable interest in inter-varietal hybrids (heterosis), Gardner and Eberhart (1966) proposed a statistical genetic model to obtain the maximum possible genetic information related to a fixed set of random mating varieties involved in a diallel set (20). They deduced three kinds of ANOVA (analysis 1, 2 and 3). Analysis 2 and 3 are mostly used by breeders. Analysis 2 is the same as Griffing ' s method 2 (half-diallel) except that heterosis is divided into three components (average, varieties and specific) (heterosis is shown as specific combining ability in Griffing' s model) (47). The existence of high significant differences between varieties (g_i) for Yp, Ys, RWC, DTM and CHF and Ys; SC, CMS, DTM and CHF for heterosis (Table 7) indicating different combining abilities of parents, different heterosis (h_{ij}) among individual crosses and involvement of additive and non-additive type of gene action in their inheritance that was thoroughly discussed in the previous methods. The heterosis source of variation (Table 7) is partitioned into variance arising from, (i) average heterosis ($\bar{h}$) which is parent *vs* hybrid single degree of freedom comparison, (ii) varieties heterosis (h_i) which is contributions of individual parents to heterosis, and (iii) specific heterosis (s_{ij}) which is differential interaction of parents in specific cross combination (40). The variances due to heterosis were significant for the characters Ys, SC, CMS, DTM and CHF suggesting the presence of non-additive gene action for these traits. Contribution of additive gene action was assessed by estimating variance due to varieties (the variance within parents). The estimates of variance due to average heterosis (parents *vs*. crosses) exhibited the direction of dominance for the characters (Table 7). Average heterosis was significant for Yp, SC and CHF indicating the unidirectional dominance for these

characters and the role of dominance and gene frequency among the parent (2, 40). The non-significant variance due to average heterosis for Ys, STI, RWC, RCC, CMS and DTM revealed unpredictable direction of dominance. Variety heterosis was estimated to judge overall contribution of a variety to its array heterosis. The variances due to variety heterosis were significant for all the characters except STI an RCC displaying the differences among the parental arrays for the heterosis of all the characters except STI an RCC. STI and RCC showed no difference among the parental arrays for heterosis.

Importance of total heterosis of the crosses was evaluated by the variance due to specific heterosis. The variances due to specific heterosis were significant for all the characters except STI an RCC. The present results explained that heterosis of a cross was usually contributed by average, variety and specific heterosis. Similar types of results also reported by Rahman and Akhter et al. in wheat(41, 2).As heterosis source of variation was not significant for Yp, STI, RWC and RCC therefore, GCA of each parent was independent of heterosis effects in these traits. Nevertheless, the non-significant values of heterosis in the present study do not allow us to conclude that there is an absence of dominance due to the possible cancelling of positive and negative genetic effects (6). Vencovsky postulates that if heterosis is not significant in dialleles of varieties, it must be concluded that variety means constitute the main information regarding GCA and varieties included must constitute a homogeneous group due to possible small genetic diversity among the parents for these traits (62). Average heterosis was not significant for the traits Ys, STI, RWC, RCC, CMS and DTM exhibiting that there is no significant difference between average heterosis and average of parents. As in the stress condition average heterosis was not significant for the traits Ys, STI, RWC, RCC, CMS and DTM but variety heterosis and specific heterosis were significant for these traits (except RCC), accordingly it can be concluded that directional dominance and interallelic interaction, enough dispersion of the genes in the parents and the complementary of the genes in the hybrids are not existed in monitoring these characters (3).

Variety heterosis of the parents

Parent 1 (V1= drought sensitive), parent 3 (V3= drought sensitive) and parent 6 (V6= drought resistant) contribute more to the genetic diversity of the parents, because heterosis variety effect in these parent was significant and positive for most of the characters (Table 8). The specific heterosis of the crosses were not estimated because they are the same as SCA effects estimated in method of Griffing (Table 4).

Hayman numerical analysis

The parameters H_1 and H_2 were significant for the characters SC, CMS and DTM which confirms the existence of dominance in the inheritance of all the traits, but as component D was also significant for DTM, hence simultaneous effect of additive and dominant gene action is involved for DTM. Difference between (H_1-H_2) was positive for SC, CMS and DTM accordingly the frequency of dominant and recessive alleles over all the loci was not equal for these traits. The component *F* was not significant but positive for SC, CMS and DTM exhibiting that the distribution of alleles in the parents is unknown. As the ratio of $\sqrt{H_1/D}$ is greater than one for SC, CMS and DTM, hence, overdominance is involved in the genetic of these traits.

The proportion of genes with positive and negative effects in the parents is estimated as ($H_2/4H_1$). If positive and negative alleles are symmetrically distributed this ratio equals 0.25 (52). Estimates of the proportion of positive and negative genes ($H_2/4H_1$) in the parents ranged from 0.159 for DTM to 0.249 for CMS. As this ratio for CMS is close to 0.25 (Table 6) hence, positive and negative alleles are symmetrically distributed in this trait. This reconfirms that H_2 was not different from H_1 in this trait.

The variation observed between the genotypes for the characters studied revealed that selection may be effective for the improvement of drought tolerance, however selection efficiency is related to the magnitude of heritability (30). Solomon and Labuschagne (2004) reported that high estimate of heritability (greater than 0.5; Stanfield) for all the traits studied may be probably for the involvement of few major genes in the control of inheritance of these traits. High broad-sense heritability observed for SC, CMS and DTM confirmed that these traits are more genetic, but because of low narrow-sense heritability the rule of additive part is low. Broad-sense heritabilities of all true-sense heritability, or the proportion of additive variance out of the total variance of accessions composed of mainly additive and environmental variation, is viewed as eventual heritability (61). In our results, true-sense heritability of all traits ranged from 0.429 for CMS to 0.847 for DTM. High true-sense heritability in DTM suggests that additive variance would dominate this trait in advanced generation.

Hayman graphical analysis

Hayman graphical analysis was conducted to asses the genetic relationship among the parents. Graphic analysis of the mode of inheritance varied from additive to overdomince for the characters investigated. The position of regression line on Vr-Wr graph provides information about the average degree of dominance (52, 53). Regression line passes below the origin cutting Wr axis in the negative region (intercept=a<0(negative)) for CMS and SC indicating the presence of overdominance while DTM was under the control of partial-dominance (Fig.1).

High difference between regression line and regression line with slope of one for SC, suggesting the presence of non-allelic interaction therefore, selection through selfing is not effective for improvement of SC (15). Non-allelic interaction related to a number of interacting genes, lead to in efficient selection, but if the number of interacting genes reduced, selection will be efficient. Detection of epistasis suggested that variation for SC was higher under oligo-or polygenic control. Thus it is conceivable that independent alleles at two or more loci could be pyramided into a single family for increasing or decreasing SC (42). Dispersion of parents around the regression line for CMS showed that parents 6 and 3 are close to the origin of coordinate, accordingly have the most dominant genes. Dispersion of parents around regression line for DTM exhibited that parents 1 and 4 have the most dominant genes.

Interrelationships among different diallel methods

1- *Griffing vs Gardner and Eberhart*

The estimates of all genetic constants in Griffing's method are dissimilar to those from the other methods.The main characteristics of Griffing method is its generality, since it can be used for any species, and the easiness of analysis and interpretation. The latter also characterizes the method developed by Gardner and Eberhart (20). If the diallel's parents are not a sample from a population, i.e., when the model is fixed, then the parametric restrictions associated with the

statistical model must be addressed. The statistical models for combining ability analysis of a population group are obligatorily restricted. The restrictions $\sum_{j=1\leq}^{N}\sum_{j`=1}^{N} s_{jj`} = 0$ and $s_{jj} + \sum_{j`=1}^{N} s_{jj`} = 0$ for all j, of the model proposed by Griffing (1956) (method 2, model 1) do not satisfy the parametric values of SCA effects. A consequence of the restrictions of the Griffing (1956) model is to allow the definition of formulas for estimating the effects, their variances and the variances of contrasts of effects, as well as for the calculation of orthogonal sums of squares. In conclusion, it is generally quite safe to use the Griffing model (23, 63).

The restrictions $\sum_{j`=1}^{N} S^{*}_{jj`} = 0$ ($j` \neq j$), for all j, of the Gardner and Eberhart model do not satisfy the parametric values of the specific heterosis effects (20). Consequently, the estimators of the effects of variety heterosis, specific heterosis and their variances differ from those of the unrestricted model. Analyses using the unrestricted and the Gardner and Eberhart models should lead to the same inferences, at least in the assessment of population effects expressed as deviations from the average effect, the heterosis, the average heterosis and the variety heterosis (the correlation between the estimates of the two models is 1) (20). The use of the unrestricted model is limited by the lack of formulas for calculating the sums of squares and the variance estimates for estimable functions, although this does not exclude the possibility of developing the appropriate software for analysis. In conclusion, it is generally quite safe to use the Gardner and Eberhart model (20, 64).

2- Griffing, Gardner and Ebehart and Morley-Jones

The estimates of mean squares for GCA of Griffing's method-2 are equal to V_i of Gardner and Eberhart and equivalent to "a" of Morley-Jones(20). The value of "a" was three times that of GCA, i.e. "a" = 3 × GCA, since GCA value is based on mean of three replications. Both parameters measure additive variance.

Mean squares for "b" of Morley-Jones are equivalent to Griffing's method-2 and " h_{ij}" of Gardner and Eberhart, i.e., "b" = 3 × SCA = 3 × $h_{ij.}$ All these parameters measure dominance or heterosis components (20).

Mean squares of "b_1" of Morley-Jones are equivalent to parents vs. crosses (P vs F_1) contrast of completely randomized block analysis, and both are equivalent to **($\bar{h}$)** of Gardner and Eberhart, i.e., "b_1" = 3 × $\bar{h}$; because the M.S. values were based on the means of 3 replications (20) . All these parameters measure average heterosis or average dominance.

Mean squares for "b_2" of Morley-Jones are equivalent to "h_i" of Gardner and Eberhart. These items estimate the difference between genetic constants of Hayman. i.e. H_1 and H_2 (H_1-H_2), indicating the asymmetry in the gene distribution and / or parental contribution to variety heterosis (20).

Mean squares for "b_3" of Morley-Jones are equivalent to "S_{ij}" of Gardner and Eberhart (20). These items measure specific dominance / combining ability. In the model of Gardner and Eberhart , the variance due to gca effects (h_i = parental heterosis) is equivalent to b_2 which

estimate asymmetrical gene distribution or parental contribution towards variety heterosis(20). and average heterosis (**$\bar{h}$**) is equivalent to b_1, l and parents vs F_1's and the SCA variance (s_{ij}) is equivalent to b_3/l_{ij}.

3- Griffing and Hayman

Hayman approach is based on estimation of components of varianc while, Griffing approach is based on estimates of combining ability and effects. Hayman approach provides information about six components, i.e., D, H_1, H_2, E, F, and h^2 while, Griffing approach provides information about D and H components through GCA and SCA variances. In Hayman approach various genetic ratios can be worked out from above components while, in Griffing approach calculation of genetic ratios is not possible. In Hayman approach analysis is not possible without parents while, in Griffing approach analysis is possible even when parents are not included. Hayman approach does not help in the identification of superior cross combination while, Griffing approach helps in the identification of superior cross combination (52).

4- Griffing, Hayman and Morley-Jones

The advantage of analysis of variance components (36**)** (Table 5) is its validity irrespective of whether there are maternal or reciprocal differences among the progeny families and whether the parental lines are a fixed sample or a random sample of a population of inbred lines (31).

The approaches of Griffing, Morley-Jones and Hayman are statistically similar, in their analyses of variance (13). The Griffing's general combining abilities (GCA) is mathematically identical to Morley-Jones's additive component. Griffing employs one specific combining ability (SCA) and one reciprocal effect component, while Hayman and Morley Jones subdivides these into three dominance components (b_1, b_2 and b_3), and two reciprocal effect components(c and d), respectively. They differ, however, in the genetic assumptions, information and interpretation which are associated with them.. In general, the Morley-Jones and Hayman's method appears to extract more genetic information than the Griffing's method does from the same data set. The Griffing's method involves only analysis of variance and estimation of GCA and SCA effects, while Morley-Jones and Hayman's method includes statistical and graphical analyses of array variances and covariances, and estimation of a number of genetic parameters. The "b_3" component in Morley-Jones's is equivalent to specific combining ability variance of Griffing approach.

According to Mather and Jinks and Singh and Chaudhary the "a" item primarily tests the significance of the additive effects of the gene, while the "b" item the non-additive effects(31, 53). Yates, on the other hand, described that GCA may be sometimes called additive genetic component or main effect, while SCA may be referred to as non-additive genetic component or dominance component or interaction effect (65).

The parameter "a" appears to contain some portion of a dominance components for "a" = D-F+H_1-H_2 (Hayman, 24, 25), and when the " b_2" item [$b_2 = H_1-H_2$] is significant, "a" gets confounded with the dominance mean square.

With b_2 being significant the estimate of additive variance (a) could not be unbiased. It is to be mentioned that a = 3 × GCA. In fact, these two estimates would have been equal, had these been

estimated on the mean values over three replications. In the present case, however, "a" was estimated on the bases of totals over replications whereas GCA variance was estimated on means. The relationship between the "a" of Morley-Jones and GCA of Griffing's method-2 shows that the GCA is a direct function of "a" and, since the latter may be confounded with dominance variance, the GCA may also contain the dominance variance. The GCA variance being equal to "a" of the Morley-Jones model, it may contain some portion of dominance. Thus the belief that GCA is purley a function of additive variance appears to be contradicted (8, 27, 32). Jugeneheimer emphasized the need for more experiments to prove the validity of the assumption that GCA variance was due to additive variance only (27). Sokal and Baker have also demonstrated that when gene frequencies are not equal to one-half, dominance variance also contributes to GCA variance regardless of correlation between loci (55).

Table 1. Analysis of variance for the characters under investigation

		Mean squares									
S.O.V	**df**	**Yp**	**Ys**	**STI**	**BY**	**RWC**	**SC**	**RCC**	**CMS**	**DTM**	**CHF**
Replications	2	30.4	29.049	0.016	161.63	68.52	3870.694**	18.194	233.86	1.159	0.004**
Treatments	20	30.05*	12.620**	0.553*	61.61	86.15*	1026.712**	16.725	33.32	13.230**	0.001
Parents	5	13.64	14.781**	1.002	44.79	13.62	448.263	3.777	20.97	6.464	0.014
Cross	14	7.76	4.41	0.323	9.16	34.60	280.129	5.214	6.01	3.690	0.0002
Parents versus F1	1	424.07**	116.69**	0.002	880.09**	1170.52**	14371.12**	242.61**	477.36**	0.793	0.0001
Error	40	13.06	5.51	0.290	79.59	43.69	416.043	28.406	26.10	2.792	0.000
CV	--	24.54	24.59	12.03	32.15	8.77	22.45	12.01	5.83	1.02	2.43

Table 2. Griffing analysis of variance for significant traits in a six-parent diallel crosses of wheat

S.O.V	df	Mean Square							
		Y_p	**Y_s**	**STI**	**RWC**	**SC**	**CMS**	**DTM**	**CHF**
GCA	5	27.16	8.35	0.411	124.21	447.75	395.59	22.81**	0.00
SCA	9	22.45	16.70	0.454	98.24**	1105.21**	652.11	5.17	0.00
Error	28	8.96	24.67	0.300	42.39	455.88	303.50	3.41	0.00
GCA /SCA		1.210	0.5	0.905	1.264	0.405	0.607	4.412**	

*** significant at 1% probability level*

Table 3. General combining ability of parents in a 6×6 diallel design for significant traits

Parents	**characters**							
	Yp	**Ys**	**STI**	**RWC**	**SC**	**CMS**	**DTM**	**CHF**
1	2.85	-0.49	0.197	3.34	7.46	-1.19	-1.83	0.01
2	0.37	1.37	-0.18	3.39	0.07	0.52	1.33	0.00
3	-0.45	-0.43	-0.074	1.27	-0.23	0.96	-1.08	0.01
4	-0.56	-0.76	-0.199	-1.66	-6.16	-1.26	0.17	-0.01
5	-0.88	-0.38	0.024	-4.69	1.14	0.5	1.00	-0.01
6	-1.33	0.68	0.232	-1.65	-7.78	0.46	0.92	0.00

Table 4. Specific combining ability effects of the crosses for significant traits

Crosses	Characters							
	Yp	**Ys**	**STI**	**RWC**	**SC**	**CMS**	**DTM**	**CHF**
1×2	5.81	3.24	0.507	-1.28	-6.09	-0.12	-0.28	0.00
1×3	-2.12	-2.85	-0.489	0.20	32.07	3.22	0.8	0.00
1×4	-1.16	0.67	0.240	6.83	-7.47	-4.36	0.22	0.01
1×5	-0.35	-1.70	0.334	-1.87	-9.75	-0.55	-1.62	0.00
1×6	-2.19	0.65	-0.112	-3.87	-8.74	1.8	0.88	0.00
2×3	-2.92	0.95	-0.223	5.88	17.39	-2.3	1.88	0.01
2×4	-0.89	0.51	0.184	-11.3	-3.81	0.62	-1.03	-0.02
2×5	-1.19	-2.26	-0.254	0.85	-10.41	1.86	0.53	-0.01
2×6	-0.81	-2.43	-0.214	5.85	2.92	-0.07	-0.03	0.01
3×4	2.21	-1.77	-0.026	-0.53	-20.68	1.25	-0.28	1.00
3×5	0.53	3.35	0.116	-2.3	-14.52	-1.03	-0.78	-0.01
3×6	2.29	0.33	0.621	-3.25	-14.25	-1.15	-1.62	0.00
4×5	0.06	-0.12	0.091	-3.52	23.29	1.40	3.62	0.02
4×6	-0.23	0.72	-0.009	1.48	8.69	1.09	-0.53	-0.01
5×6	0.94	0.74	-0.287	-0.21	11.39	-1.68	1.30	0.00

Table 5. Morly-Jones analysis of variance for significant traits in the six-parent diallel crosses of wheat

S.O.V	df	Mean Squares							
		Yp	**Ys**	**STI**	**RWC**	**SC**	**CMS**	**DTM**	**CHF**
a	5	63.18**	26.97	1.002*	137.50*	287.62	428.43	24.78**	0.02*
b	15	18.81	20.12	0.414	69.03**	1273.07**	516.36*	5.17	0.01
b_1	1	55.47*	22.85	0.075	13.54	1624.69	332.61	3.41	0.01
b_2	5	4.93	25.72	0.859*	27.57	1504.91**	308.76	4.41**	0.02
b_3	9	22.45	16.70	0.205	98.22*	1105.21*	652.10*	0.89	0.00
Error	40	13.23	19.01	0.290	137.50	416.04	268.28	0.09	0.01

Table 6. Hayman genetic parameters for significant traits in wheat genotypes

Genetic Parameters	SC	CMS	DTM
D	307.714	6.355	5.475*
H_1	1485.414**	1075.365**	12.194**
H_2	1114.024**	1069.282**	7.739**
F	680.793	14.416	5.670
H^2	279.437	4410.972**	1.036
E	140.549**	8.463	0.988**
$(H_1/D)^{0.5}$	2.197**	13.008	1.492**
(kd/(kd+kr)	0.752**	0.544**	0.674
(h^{2}/H_2)	0.294	4.950**	0.161
(h)	18.735*	-66.448	-1.241
(D/(D+E)) **(true sense heritablility)**	0.686**	0.429	0.847**
(H^2b)	0.658**	0.969**	0.804**
(H^2n)	-0.035	-0.004	0.422**
($H_2/4H_1$)	0.192**	0.249**	0.159**

D=Additive variance, H_1= Dominance variance, H_2= Dominance variance, F= Relative frequency of dominant and recessive allels, H^2= square of difference P vs. all, E= Environment variance, $(H_1/D)^{0.5}$=Average degree of dominance, (kd/(kd+kr)= Proportion of dominance genes, (h^{2}/H_2)= Number of effective factors, (h)=Average direction of dominance, (D/(D+E))= Heritability by parents or true sense heritablility, H^2b)= Broad-sense heritability, (H^2n)= Narrow-sense heritability, ($H_2/4H_1$)= Proportion of dominance and recessive genes

Table 7. Heterosis analysis based on Gardner and Eberhart model (analysis II)

S.O.V.	d.f.	Yp	Ys	STI	RWC	SC	RCC	CMS	DTM	CHF
Varieties (g_i)	5	21.41**	7.631**	0.47	45.827**	95.886	3.83	142.802	8.259**	0.0005**
Heterosis (h_{ij})	15	6.30	3.064*	0.47	23.014	424.361**	3.65	172.097**	3.126*	0.00025**
Average($\bar{h}$)	1	18.75**	0.001	0.16	4.521	541.543*	0.04	141.699	2.375	0.0004*
Variety (h_i)	5	916.98**	477.613**	0.10	29505.74**	42093.73**	5.23	28672.18**	139410.4**	3.0705**
Specific(s_{ij})	9	138.04**	51.786**	0.16	3276.171**	4617.922**	4.43	3464.992**	15314.16**	0.339**
Error	40	4.35	1.836	0.26	14.563	138.681	16.45	89.427	0.931	0.0001

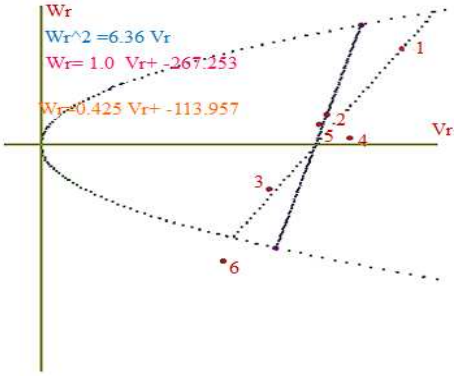

Fig. 1. Regression line and dispersion of parents around origin for CMS under drought condition

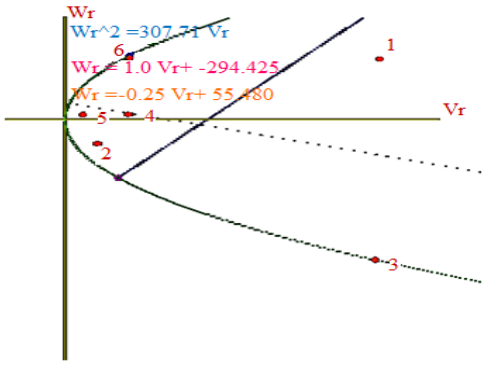

Fig. 2. Regression line and dispersion of parents around origin for SC under drought condition

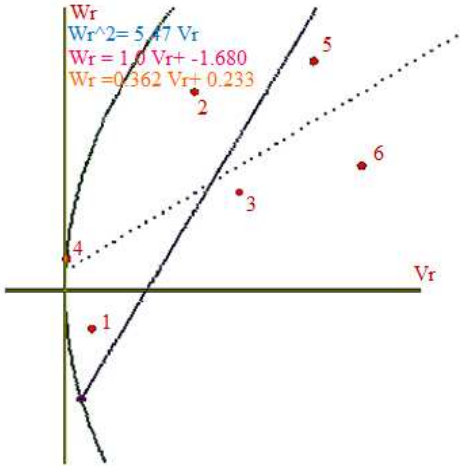

Fig. 3. Regression line and dispersion of parents around origin for DTM under drought condition

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