

Inheritance Pattern of Important Quantitative Traits in Bread Wheat (*Triticum aestivum* L.)

Javid Ojaghi, Samira Salayeva and Roham Eshghi

Department of Agronomy and Plant Breeding,
Science and Research Branch, Islamic Azad University, Ardabil, Iran

Abstract: In this study the inheritance of important quantitative traits has been studied through a complete diallel cross (8×8) and generation mean analyzing design (two crosses) to choose an efficient breeding method for the improvement of these traits in doubled haploid bread wheat. The analyses of gene actions indicated that a large part of the total genetic variation observed for number of spikelets per spike, number of tillers and grain yield per plant was in the form of dominance genetic effects. In addition, duplicate type of epistasis observed in the expression of these traits. Thus, bi-parental mating, or diallel selective mating could prove a worthwhile approach for further improvement of these traits. Instead, dominance was partial and narrow sense heritability estimate for number of grains per spike and plant height was high, indicating the preponderance of the additive effects. To conclude, in order to improve these traits, selection in early generation is possible. In addition, in populations under study, these traits can be suitable indices for grain yield indirect selection.

Key words: Doubled haploid bread wheat • Quantitative traits • Heritability • Diallel analysis • Generation mean and variance analyses

INTRODUCTION

Cereal crops belong to the family *Gramineae* which is a large family and constituted by outstanding group of food plants, wherefrom, a majority of humanity meets its dietetic needs; amounting to an estimated 60% of calories and 50% of protein. Wheat (*Triticum aestivum* L.) is foremost among cereals and indeed among all food crops, as direct source of food and energy for human beings. The developments of improved varieties of wheat have always remained a focal point for wheat breeders all over the world [1].

Yield is a trait controlled by polygenes and is the result of interplay between many genetic and non-genetic components. Several studies in the recent past had identified QTLs for yield and its components such as number of tillers, number of grain per spike, plant height and number of spikelets per spike, in wheat. Gupta *et al.* [2] reported three QTLs on chromosomes 3A, 7A and 7B for number of tillers in cross PH132×WL711 (bread wheat). They also reported four QTLs on chromosomes 2A, 4B and 7A for number of grains per spike and three QTLs on chromosomes 2B, 4A and 6A for number of spikelets per spike. Maccaferri *et al.* [3] have identified 3 QTLs on

chromosomes 1B, 3A and 7A for plant height. Also Kuchel *et al.* [4] reported several QTLs on chromosomes 1B, 4D and 7D for grain yield in bread wheat. But bread wheat genomes is very large and consist of three set of chromosomes and in most cases QTLs analysis special for traits such as yield and its components which control with several genes and alleles will be not efficient. This analyzes mostly useful for investigation of resistance to pathogens for this crop.

The choice of selection and breeding procedures for genetic improvement of wheat or any other crop is largely depends on the knowledge of type and relative amount of genetic component and the presence of non-allelic interaction for different characters in the plant materials under investigations. Diallel cross technique is the one used most commonly to estimate inheritance and behaviour of quantitative characters. Application of Hayman [5] Jinks [6] and Griffing [7] models in F_1 generation provides information regarding nature and magnitude of the gene-action involved in the inheritance of a character. This information would be useful to plant breeders for two reasons viz. types of genetic variation in the traits for which selection is intended and rapid evaluation of yielding capacity by identifying crosses which will

produce superior genotypes. Generation mean analysis also is a simple but useful technique for estimating gene effects for a polygenic trait, its greatest merit lying in the ability to estimate epistatic gene effects such as additive \times additive [i], additive \times dominance [j] and dominance \times dominance [l] effects [8].

Thus in the present investigations, the inheritance of yield and its components has been studied through diallel cross and generation mean analyzing design to choose an efficient breeding method for the improvement of grain yield and its components.

MATERIALS AND METHODS

Diallel Analysis: The experimental material was composed of eight lines of doubled haploid wheat from CIMMYT (Table 1). The crosses were attempted in a diallel fashion including direct crosses and their reciprocals during crop season 2006-2007. The parents and F_1 s were sown in November 2007 in a randomized complete block design with three replications in Moghan region, Iran. The entries were assigned randomly to experimental units in each block having plant to plant and row to row distance 15 and 30 cm, respectively. At maturity, ten competitive plants were randomly selected to record data for number of spikelets per spike, number of tillers, number of grains per spike, plant height and grain yield per plant.

Statistical Analysis: The data were subjected to component analyses according to Hayman [5, 9] and Jinks and Hayman [10]. The t^2 test and the analysis of regression coefficient test, which tests to overall assumption of diallel was performed according of the model with respect to non-allelic interaction.

Generation Mean and Variance Analysis: Generation mean analysis was carried out on P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 generations of two crosses (Cross I: Parent5 \times Parent7 and Cross II: Parent4 \times Parent8) to complement the genetic information from the diallel analysis. We used the parents of the respective crosses as the male parent and the F_1 generation as the female parent and effected back crosses to produce the BC_1 (F_1 back crossed to P_1) and BC_2 (F_1 back crossed to P_2) generation and the F_1 hybrids were selfed to obtain F_2 seeds. All these generation were produced during two cropping seasons and, as such, all the six generations had to be grown together in a randomized block design in three replications at the Moghan region in November 2007.

Table 1: Pedigree of parents

1-TEG/GANFRENCH/6/CMH79A.955/4/AGA/3/4*...
2-CMH80.638/CMH75A.411/...
3-CMH76.1084/2*CMH72A.429//ELVIRA/6/...
4-CMH81.794/4/CHEN/AEGILOPS (TAUS)...
5-VEE/CMH77A.917//VEE/3/ELVIRA/6/CMH79A...
6-CMH79A.955/CMH74A.487//CMH81A.744/3/...
7-STDS10/CIRCUS/6/CMH79A.955/4/AGA/...
8-CMH83.2578/GANFRENCH/6/CMH79A955/...

The plots were 2m long with a between-row spacing of 30cm and a within-row spacing of 15cm. The number of rows per plot and the number of analyzed plants per plot varied depending on the generation (three rows for the P_1 , P_2 and F_1 , 10 rows for the F_2 and 7 rows for the BC_1 and BC_2 generations and 10 plants for the P_1 , P_2 and F_1 , 70-75 plants for the F_2 and 15 plants in the BC_1 and BC_2 generations, respectively).

Statistical Analysis: The genetic model that best fit the data was found by the mean of joint scaling test [11] and the accuracy of the models was verified by chi-square test. Components within each model were evaluated for significance by t-test.

Broad-sense and narrow-sense heritabilities values calculated using the following formula [13]:

$$h_{b.s}^2 = \{VF_2 - [(VP_1 + VP_2 + 2VF_1)/4]\} / VF_2$$

$$h_{n.s}^2 = [VF_2 - (VBC_1 + VBC_2)/2] / VF_2$$

Variance components (additive, dominance and environment) were estimated as described by Kearsey and Pooni [12], using the following equations:

Environment variance:

$$V_{[g]} = (VP_1 + VP_2 + 2VF_1)/4$$

Additive variance:

$$V_{[d]} = 4VF_2 - 2(VBC_1 + VBC_2)$$

Dominance variance:

$$V_{[h]} = 4(VBC_1 + VBC_2 - VF_2 - V_{[g]})$$

Response to selection was estimated with 5% selection intensity (i) (selection differential, $K = 2.06$) as:

$$R = i \times h_{n.s}^2 \times \sqrt{VF_2}$$

The type of epistasis was determined only when dominance [h] and dominance \times dominance [l] effects were significant, when these effects had the same sign, the effects were complementary while different signs indicated duplicate epistasis [12].

RESULTS AND DISCUSSION

Diallel Analysis: The analysis of variance of means (parents and F_1 families) revealed highly significant difference for all of the traits under study (data not shown).

The estimates of genetics of variation in grain yield and its component are given in Table 2. Although D , H_1 and H_2 items were positive and significant for number of spikelets per spike, number of tillers and grain yield per plant, the greater magnitude of H_1 and H_2 than that of D revealed that genes with non additive effects were important. Also the ratio of $(H_1/D)^{1/2}$ was greater than unity for these traits. These results indicated that number of spikelets per spike, number of tillers and grain yield per plant were governed by over dominance gene action. Narrow sense heritability of number of tillers (0.154) and grain yield per plant (0.084) is very low while in number of spikelets per spike almost is medium enough (Table 2). Similar nature of gene action for grain yield has been reported by Chowdhry *et al.* [14] and Dere and Yildirim [15]. But Khan *et al.* [16] and Habib and Khan [17] reported partial dominance for this trait. Also the present results are in agreement with the works of Chowdhry *et al.* [18], Rahman *et al.* [19] and

Habib and Khan [17] that found over dominant type of inheritance for number of spikelets per spike. Although Kashif *et al.* [20] and Khan and Habib [21] reported similar finding for number of tillers, additive effects for this trait have been reported by Awan *et al.* [22]. As the magnitude of H_1 is greater than H_2 therefore distribution of negative and positive alleles were unequally distributed in the parents and further proof of this unequal distribution of alleles over loci is provided by the ratio $H_2/4H_1$, which is lesser than its maximum value 0.25 (Table 2). Positive value of F in number of spikelets per spike, number of tillers and grain yield per plant suggested that dominant alleles were more abundant than the recessive alleles in the parents and its claim was supported by the ratio of $[(4DH_1)^{1/2} + F / (4DH_1)^{1/2} - F]$ which is more than one in these traits. Correlation analysis of the genotypes showed recessive gene control for number of tillers. However, this analysis showed dominant gene control for number of spikelets per spike and grain yield per plant (Table 2).

The genetic components of variation for number of grains per spike and plant height revealed that genes with additive properties influenced the inheritance of these characters (Table 2). Although in number of grains per spike only value of additive component (D) was significant, in plant height both of D and H_1 were significant, but D value was more than H_1 . The lesser ratio of $(H_1/D)^{1/2}$ from unity indicated partial dominance occurring in the inheritance of these traits. The estimate of narrow sense heritability is 0.513 and 0.711 for number of grain per spike and plant height, respectively.

Table 2: Components of diallel variance and their estimates for different traits in doubled haploid wheat

Parameters	N.S.S	N.T	N.G.S	P.H	G.Y.P
D	0.437** \pm 0.61	0.929** \pm 0.05	75.37** \pm 6.73	25.04** \pm 1.66	5.39** \pm 1.94
F	0.031 ^{n.s} \pm 0.27	1.48** \pm 0.125	38.05 ^{n.s} \pm 15.91	2.620 ^{n.s} \pm 3.93	8.10 ^{n.s} \pm 4.60
H_1	0.799** \pm 0.26	2.12** \pm 0.122	28.40 ^{n.s} \pm 15.48	13.88** \pm 3.82	21.97** \pm 4.48
H_2	0.634** \pm 0.23	1.351** \pm 0.10	22.30 ^{n.s} \pm 13.47	5.150 ^{n.s} \pm 3.320	17.73** \pm 3.89
h^2	0.92 ^{n.s} \pm 0.150	0.19** \pm 0.071	8.310 ^{n.s} \pm 9.030	20.75** \pm 2.23	-1.56 ^{n.s} \pm 2.61
E	0.41** \pm 0.035	1.13** \pm 0.018	15.03** \pm 2.24	5.05** \pm 0.550	3.88** \pm 0.649
Proportion of components of variance					
$(H_1/D)^{1/2}$	1.352	2.278	0.614	0.744	2.020
$H_2/4H_1$	0.189	0.159	0.196	0.093	0.202
$[(4DH_1)^{1/2} + F / (4DH_1)^{1/2} - F]$	1.070	3.230	2.390	1.150	2.185
R ($W_r + V_r, Y_r$)	-0.265	0.602	-0.335	-0.691	-0.651
$h^2_{b.s.}$	0.519	0.647	0.645	0.769	0.572
$h^2_{n.s.}$	0.334	0.154	0.513	0.711	0.084

N.S.S: Number of spikelets per spike, N.T: Number of tillers, N.G.S: Number of grains per spike, P.H: Plant height, G.Y.P: Grain yield per plant, D: additive variance, H_1 and H_2 : dominance genetic variance and corrected dominance genetic variance, F: product of additive by dominance, h^2 : square of difference P vs All, E: environmental variance, whole, $(H_1/D)^{1/2}$: average of degree dominance, $H_2/4H_1$: Proportion of genes with positive and negative effects in parents, $[(4DH_1)^{1/2} + F / (4DH_1)^{1/2} - F]$: Proportion of dominant and recessive genes in parents, R ($W_r + V_r, Y_r$): correlation between parental measurement (Y_r) and W_r+V_r values, $h^2_{b.s.}$: Heritability for diallel in a broad sense, $h^2_{n.s.}$: Heritability for diallel in a narrow sense
n.s, * and **: non significant, significant at 5% and 1% of probability levels, respectively

Table 3: Best model fit estimates for generation mean parameters by weighted least squares analysis of various quantitative traits of the cross I and II

Traits	[m]	[d]	[h]	[i]	[j]	[l]	χ^2
Cross I							
Number of spikelets/spike	14.11±0.88**	0.24±0.09**	3.63±0.755**	-	-	-2.34±1.1*	0.49
Number of tillers	4.65±0.70**	0.16±0.07*	4.45±0.72**	-	-	-4.4±1.1**	0.1
Number of grains / spike	77.1±13.12**	8.2±0.95**	-	-	21.7±4.23**	-	3.9
Plant height	80.1±10.94**	-5.6±0.62**	-	-	16.5±3.1**	-	2.5
Grain yield / plant	16.4±3.28**	2.86±0.334**	17.26±8.11*	-	-9.23±2.1**	-13.11±4.43**	0.08
Cross II							
Number of spikelets/spike	14.1±2.3**	0.53±0.19**	5.7±2.38*	-	-	-	4.5
Number of tillers	5.35±0.85**	0.25±0.1*	4.75±2.2*	-	-	-4.7±1.14**	1.14
Number of grains / spike	70.15±11.6**	6.1±0.71**	-	-	-7.6±3.21*	-27.1±12.29*	2.8
Plant height	81.01±7.28**	-4.16±0.29**	-	-	5.82±1.71**	-	0.98
Grain yield / plant	15.71±4.27**	1.77±0.41**	18.91±9.38*	-	-	-	3.7

[m]: Mean, [d]: Additive effects, [h]: Dominance effects, [i]: Additive × additive effects, [j]: Additive × dominance effects, [l]: Dominance × dominance effects, χ^2 : Chi-square

*, **: Significant at 5% and 1% level of probability, respectively

Table 4: Estimates of variance components and heritability for quantitative traits in cross I and II

Traits	$V_{[d]}$	$V_{[h]}$	$V_{[e]}$	$(H/D)^{1/2}$	$h^2_{b.s}$	$h^2_{n.s}$	R
Cross I							
Number of spikelets/spike	0.011	0.035	0.013	1.78	0.47	0.21	0.43
Number of tillers	0.014	0.022	0.011	1.25	0.51	0.27	1.33
Number of grains / spike	15.34	1.570	1.74	0.32	0.82	0.78	6.10
Plant height	11.26	0.954	0.80	0.29	0.88	0.84	5.53
Grain yield / plant	0.148	0.798	0.25	2.32	0.52	0.14	0.95
Cross II							
Number of spikelets/spike	0.109	0.281	0.069	1.6	0.64	0.28	1.56
Number of tillers	0.015	0.042	0.022	1.67	0.45	0.19	1.21
Number of grains / spike	15.3	1.62	1.145	0.32	0.87	0.83	5.81
Plant height	6.74	0.275	0.271	0.2	0.92	0.91	4.50
Grain yield / plant	0.798	1.13	0.392	1.41	0.59	0.29	2.93

$V_{[d]}$: Additive variance, $V_{[h]}$: Dominance variance, $V_{[e]}$: Environmental variance, $(H/D)^{1/2}$: Average degree of dominance, $h^2_{b.s}$: Broad sense heritability, $h^2_{n.s}$: Narrow sense heritability, R: Genetic advance.

Chowdhry *et al.* [18] and Khan and Habib [21] showed similar results while studying plant height. Also Rahman *et al.* [19] and Habib and Khan [17] reported similar finding for number of grains per spike. The difference H_1-H_2 indicated the unequal distribution of genes for number of grains per spike and plant height and this claim is strengthened by the ratio of $H_2/4H_1$ which is lesser than 0.25 (Table 2). Ratio of $[(4DH_1)^{1/2} + F / (4DH_1)^{1/2} - F]$ more than unity for number of grains per spike indicated that dominant genes were more frequent. But in plant height this ratio was near unity and showed that frequency of dominance and recessive genes was equal. Correlation analysis of the genotypes showed dominant gene control, for number of grains per spike and plant height (Table 2).

Generation Mean Analysis: Analysis of variance for all the traits in two crosses showed significant difference among generations (data not shown). We were therefore, allowed to go ahead to study heredity and to analyze generation means.

Different 3 to 5 parameter models showed the best fit to generation means of different traits and cross combination (Table 3). Additive effects were significant for all traits in both crosses. As is shown in Table 3, additive effects for plant height were negative in both crosses. The negative and positive signs for additive effects depend on which parent is chosen as P_1 [23, 24]. Generation variance analysis (Table 4) indicated additive variance was larger than dominance for plant height and

number of grains per spike in both crosses. Also the average degree of dominance was less than unity showed that partial dominance gene action for these traits. These results are in accordance with Awaad [25] and Akhtar and Chowdhry [26] who reported that additive gene effects were predominant for plant height in wheat. Also Awaad [25] reported similar finding for number of grains per spike. However, Akhtar and Chowdhry [26] reported dominance effects were important in cross Chakwal-86 \times V-8060 for number of grains per spike.

Dominance effects were positive and significant in cross I, for number of spikelets per spike, number of tillers and grain yield per plant. In cross II, dominance effects were significant for all traits, except plant height and number of grains per spike. The average of dominance as indicated over dominance towards the better parent for number of tillers, number of spikelets per spike and grain yield per plant in both crosses. Chowdhry *et al.* [27] reported additive and dominance components for genetic variance for number of tillers per plant. However, Chowdhry *et al.* [28] found non-additive type of gene action for this trait. Although Akhtar and Chowdhry [26] showed that in order to control the number of spikelets per spike in cross V-95199 \times PART – 73 the share of the dominance were more than additive effects, Sharma and Ahmad [29] and Walia *et al.* [30] reported that the estimated additive genetic effects were important for spikelets per spike. Also waial *et al.* [30], Chowdhry *et al.* [27] and Akhtar and Chowdhry [26] showed that dominance genetic effects were more important than additive gene action for grain yield per plant in wheat. But Kamboj *et al.* [31] reported that the additive genetic effects were important for this trait.

As it is shown in Table 3, different types of epistasis interaction effects were found for different trait and cross combinations. No additive \times additive [i] type of interaction was present in the genetic control of the studied traits. However, additive \times dominance [j] epistasis was positive and significant for plant height in both crosses and negative and significant for grain yield per plant in cross I and number of grains per spike in both crosses. Dominance \times dominance non-allelic interaction was significant and negative for number of spikelets per spike for cross I, number of grains per spike in cross II and number of tillers in both crosses. The dominance [h] and dominance \times dominance [l] gene effects showed opposite signs for number of spikelets per spike and grain yield per plant in cross I and number of tillers in both crosses, indicating the presence of duplicate dominant epistasis in the expression of these traits, which would

limit the range of variability. Since none of the signs of [h] were similar to the [l] type of epistasis, it was concluded that no complementary type of interaction was present in the genetic control of the studied traits. The presence of epistasis has important implication for any plant breeding program. Confounding epistatic effects in models suggested that inheritance of these traits is complex and polygenic. Novoselovic *et al.* [32] disclosed that plant height was governed by additive \times additive [i] gene interaction. Also Akhtar and chowdhry [26] reported different type of epistasis for number of tillers and number of spikelets per spike. Mehla *et al.* [33] reported that additive \times additive [i] and dominance \times dominance [l] type of epistasis were important for grain yield per plant in wheat.

Heritability estimates in each of broad and narrow sense were generally found to be high in magnitudes in the cross II comparative to cross I, except for number of tillers (Table 4). Difference between the genetic backgrounds of the two crosses may be to explain these ambiguous results.

The highest estimates of narrow sense heritability associated with highest genetic advance for plant height and number of grains per spike in two crosses, indicated sufficient improvement of their variability traits. These results are in agreement with diallel analysis. Dabholkar [34], stated that when additive effects are larger than the non additive, it is suggested that selection in early segregation generation would be effective. Low heritability with low genetic gain was found for number of tillers, number of spikelets per spike and grain yield per plant in both crosses. These results are conformity to the findings of diallel analysis. Straight forward selection from the segregation population of the characters does not seem to be possible, the genetic variation existed in these characters could be improved successfully following reciprocal recurrent selection. Furthermore, these characteristics in which over dominance was involved may advantageously to be utilized by the breeders to develop hybrid, as suggested by Chowdhry *et al.* [14], Dere and Yildirim [15] and Akhtar and chowdhry [26].

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