

Genetic analysis of quantitative traits in wheat (*Triticum aestivum*)

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INTRODUCTION

Wheat (*Triticum aestivum* L. em. Thell) is the most important cereal crop of the world. It is the main staple food of the rapidly increasing population of Pakistan that is why it occupies a prominent position in the cropping pattern of the country. Grain yield is a complex trait made up of the interaction between different yield components and environmental effects. Because of these complex interactions it is difficult to improve yield through breeding (especially in the early generations) if yield is the only factor recorded, suggesting that component traits should also be used as selection criteria for yield improvement. This is the reason why it is necessary to know the genetic architecture of yield components (Misra *et al.*, 1994).

Generation mean analysis provides information on the relative importance of average effects of the genes (additive effects), dominance deviations, and effects due to non allelic genic interactions, in determining genotypic values of the individuals and, consequently, mean genotypic values of families and generations (Viana 2000). Generation mean analysis 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 x additive (aa), dominance x dominance (dd) and additive x dominance (ad) effects (Singh and Singh, 1992).

Besides gene effects, breeders would also like to know how much of the variation in a crop is genetic and to what extent this variation is heritable, because efficiency of selection mainly depends on additive genetic variance, influence of the environment and interaction between genotype and environment.

The research reported in this paper was carried out to provide information about gene effects and available genetic variability for the most important quantitative traits of wheat (*Triticum aestivum* L.).

MATERIAL AND METHODS

We used winter wheat (*Triticum aestivum* L.), Falat (a wheat cultivar that cultivated in Iran) and Line 30 (a advanced line). The six basic generations (parent cultivars (P1, P2), first and second filial generations (F1, F2), first and second backcrosses (BC1, BC2)) of crossings (Falat/Line30) were planted in a randomized block design in three replicate plots at Research Farm of University of Tehran in Karaj during the autumn season of 2004/2005. The plots were 2 m long with a between-

row spacing of 20 cm and a within-row spacing of 10 cm. The number of rows per plot and the number of analyzed plants per plot varied depending on the generation.

The traits assessed were: plant height (cm); number of head per plant; number of grains per spike of the longest culm; spike length of the longest culm (cm); peduncle length of the longest culm (cm); 1000-seed weight (g); grain yield per plant (g) and above-ground biomass (g). The mean values standard errors and variances of the different generations were subjected to weighted least squares analysis using the joint scaling test (Mather and Jinks, 1982) to estimate gene effects and the maximum likelihood method (Hayman, 1960) to estimate variance components to fit models of increasing complexity until an adequate description of the observed means were found as shown by non-significance in the Chi-square test. The significance of genetic parameters was tested by t-test. The type of epistasis was determined only when dominance (d) and dominance x dominance (dd) effects were significant; when these effects had the same sign the effects were complementary while different signs indicated duplicate epistasis (Kearsey and Pooni, 1996).

Additive, dominance and environmental variance components were estimated using the maximum likelihood method with the observed variances of the six basic generations being used as the initial weights ($df/2*s^2 + 2$) until the Chi-square test values reached a minimum (Lynch and Walsh, 1998).

Broad sense heritability (h^2b) and narrow-sense heritability (h^2n) were calculated as follows:

$$h^2b = V_{F2} - ((V_{P1} * V_{P2})^{0.5} / V_{F2})$$

$$h^2n = 2V_{F2} - ((V_{BC1} + V_{BC2}) / V_{F2})$$

All statistical analyses were carried out using the STAT module and PROC REG procedure of the SAS software (SAS Institute, 1996).

RESULTS AND DISCUSSION

The mean values, their standard errors for the analyzed traits are presented in Tables 1. The parents differed with respect to plant height and peduncle length of the longest culm, although for the F1 generation only the means for the 1000-seed weight and grain yield per plant were greater than the better parent. For the other traits, differences were not so conspicuous and consistent.

Table 1- Means and standard deviation of for quantitative traits

generation	plant height (cm)	number of head per plant	number of grains per spike of the longest culm	spike length of the longest culm (cm)	peduncle length of the longest culm (cm)	1000-seed weight (g)	grain yield per plant (g)	above-ground biomass (g)
Falati	83.29 $\bar{\pm}$ 3.81	5.91 $\bar{\pm}$ 1.64	68.29 $\bar{\pm}$ 8.4	10.51 $\bar{\pm}$ 0.65	25.29 $\bar{\pm}$ 2.21	27.29 $\bar{\pm}$ 2.91	10 $\bar{\pm}$ 2.16	22.21 $\bar{\pm}$ 5.43
Line 30	70.38 $\bar{\pm}$ 3.71	5.14 $\bar{\pm}$ 1.39	72 $\bar{\pm}$ 6.77	10.79 $\bar{\pm}$ 0.64	25.5 $\bar{\pm}$ 1.15	24.2 $\bar{\pm}$ 2.97	9.4 $\bar{\pm}$ 2.46	19.65 $\bar{\pm}$ 5.79
F1	77.62 $\bar{\pm}$ 4.34	5.29 $\bar{\pm}$ 1.62	62 $\bar{\pm}$ 8.79	10.42 $\bar{\pm}$ 0.83	20.64 $\bar{\pm}$ 2.34	29.67 $\bar{\pm}$ 3.58	9.96 $\bar{\pm}$ 4.58	21.22 $\bar{\pm}$ 7.18
F2	76.41 $\bar{\pm}$ 6.97	6.51 $\bar{\pm}$ 2.61	65.99 $\bar{\pm}$ 12.67	10.99 $\bar{\pm}$ 1.1	27.22 $\bar{\pm}$ 4.31	40.22 $\bar{\pm}$ 5.66	12.29 $\bar{\pm}$ 6.12	28.2 $\bar{\pm}$ 12.77
BC1	79.91 $\bar{\pm}$ 5.89	5.5 $\bar{\pm}$ 2.12	68.59 $\bar{\pm}$ 12.34	10.27 $\bar{\pm}$ 0.96	20.52 $\bar{\pm}$ 3.71	27.42 $\bar{\pm}$ 4.88	9.27 $\bar{\pm}$ 5.14	21.2 $\bar{\pm}$ 11.21
BC2	80.02 $\bar{\pm}$ 5.93	5.77 $\bar{\pm}$ 2.4	65.71 $\bar{\pm}$ 11.56	10.29 $\bar{\pm}$ 0.92	22.15 $\bar{\pm}$ 3.94	28.41 $\bar{\pm}$ 4.63	9.91 $\bar{\pm}$ 4.78	22.66 $\bar{\pm}$ 10.32

Table 2 - The estimates of gene effects for quantitative traits

traits	Mean [m]	Additive [d]	Dominance [h]	Additive x Additive [i]	Additive x Dominance [j]	Dominance x Dominance [l]	Chi-square [X2]
plant height (cm)	62.61 $\bar{\pm}$ 3.58***	6.45 $\bar{\pm}$ 0.58***	40.2 $\bar{\pm}$ 9.08***	14.23 $\bar{\pm}$ 3.53***	-12.12 $\bar{\pm}$ 2.66***	-25.19 $\bar{\pm}$ 5.88***	0.00 ^{ns}
number of head per plant	7.62 $\bar{\pm}$ 0.59***	0.23 $\bar{\pm}$ 0.21	-2.47 $\bar{\pm}$ 0.86***	-2.18 $\bar{\pm}$ 0.64***	-	-	3.05 ^{ns}
number of grains per spike of the longest culm	70.31 $\bar{\pm}$ 1.07***	-1.82 $\bar{\pm}$ 1.17	-7.86 $\bar{\pm}$ 2.1**	-	9.02 $\bar{\pm}$ 5.35	-	0.59 ^{ns}
spike length of the longest culm (cm)	13.33 $\bar{\pm}$ 0.57***	-0.09 $\bar{\pm}$ 0.08	-6.44 $\bar{\pm}$ 1.45***	-2.68 $\bar{\pm}$ 0.56***	-	3.55 $\bar{\pm}$ 0.96***	1.00 ^{ns}
peduncle length of the longest culm (cm)	14.29 $\bar{\pm}$ 2.24***	4.94 $\bar{\pm}$ 0.27**	25.49 $\bar{\pm}$ 5.72***	16.05 $\bar{\pm}$ 5.72***	-13.14 $\bar{\pm}$ 1.64***	-19.24 $\bar{\pm}$ 3.67**	0.00 ^{ns}
1000-seed weight (g)	44.29 $\bar{\pm}$ 2.89***	1.05 $\bar{\pm}$ 0.41***	-13.21 $\bar{\pm}$ 7.31	-9.13 $\bar{\pm}$ 2.85***	-	7.95 $\bar{\pm}$ 4.74	5.44 ^{ns}
grain yield per plant (g)	20.09 $\bar{\pm}$ 3.06***	0.21 $\bar{\pm}$ 0.33	-21.08 $\bar{\pm}$ 7.63**	-10.28 $\bar{\pm}$ 3.02	-	10.96 $\bar{\pm}$ 4.97*	0.61 ^{ns}
above-ground biomass (g)	46.33 $\bar{\pm}$ 6.5***	1.03 $\bar{\pm}$ 0.81	-47.41 $\bar{\pm}$ 16.41**	-25.33 $\bar{\pm}$ 6.44	-	22.31 $\bar{\pm}$ 10.52*	0.87 ^{ns}

Table 3-Estimates of variance components and heritability and for quantitative traits

traits	Genetic variance [VG]	Additive variance [VA]	Dominance variance [VD]	Environmental variance [VE]	Broad sense [HB]%	Narrow sense [HN]%
plant height	73.69	54.46	19.23	16.49	66	56
number of head per plant	9.61	6.8	2.81	2.46	64	50
number of grains per spike of the longest culm	300.72	70.19	230.53	67.7	58	22
spike length of the longest culm (cm)	1.34	1.31	0.03	0.55	54	44
peduncle length of the longest culm (cm)	41.3	15.63	25.67	4.3	77	42
1000-seed weight (g)	47.66	37.35	10.31	10.74	66	58
grain yield per plant (g)	74.76	51.48	23.28	6.03	84	68
above-ground biomass (g)	298.69	187.81	110.88	41.48	75	58

*, **, *** = statistically significant at p = 0.95, p = 0.99 and p = 0.999 respectively

The estimates of the main and first order interaction gene effects and Chi-square values are presented in Table 2. For plant height and peduncle length of the longest culm complementary epistasis was found. For the number of heads per plant a digenic epistatic model

was applicable, with dominance effects and additive x additive epistasis. For the spike length of the longest culm digenic epistatic model was adequate, with dominance effects, dominance x dominance epistasis and additive x additive epistasis being most important.

For the number of grains per spike of the longest culm a digenic epistatic model adequately explained variation between generations, although only dominance effects were significant. For grain yield per plant and above-ground biomass a digenic epistatic model adequately explained variation between generations, with dominance effects and dominance x dominance epistasis being most important. For 1000-seed weight a digenic epistatic model adequately explained variation between generations, although only additive effects were significant.

The estimates of the different variance components and narrow-sense heritability (h^2_n) are presented in Table 3. The additive variance (VA) was larger than dominance variance (VD) for plant height, number of head per plant, spike length of the longest culm, 1000-seed weight, grain yield per plant and above-ground biomass. The highest (68%) and lowest (22%) narrow sense heritability were obtained for grain yield per plant and number of grains per spike of the longest culm, respectively. These heritability values are in accordance with those reported by other authors (Sidwell, 1978; Baric, 1996 and Drezner, 1996).

Mean and additive components for plant height, peduncle length of the longest culm, 1000-seed weight were significant, and so indicate that selection in early generation is effective (Hayman, 1958). Higher values [d] comparing whit [h] which is observed for number of head per plant, number of grains per spike of the longest culm, spike length of the longest culm, 1000-seed weight, grain yield per plant and above-ground biomass showing the gene correlation (i.e. the genes that increase traits are in the same parent and vice versa). In other words a parent has genes with high performance while another one has genes with low performance.

For the plant height, spike length of the longest culm, peduncle length of the longest culm and grain yield per plant the components of [d] and [l] have the opposition marks, showing the presence of digenic epistasis. In the majority of traits additive x additive epistasis was significant indicating the importance of this component. These results are in agreement with Novoselovic, *et al.*, 2004; Singh and Singh, 1992 and Yadava, *et al.*, 1995. The sign of [d] and [j] depend on which parent is P1 or P2 and therefore the sign of [j] in most of cases varies while the sign of others remain unchanged. The minus sign of [h] indicates that there is partial dominance for low performance.

Although varying depending on trait, in most cases the variation in the generation means fitted a digenic epistatic model which indicates that improving the traits studied would be moderately difficult as compared to the situation pertaining had an additive-dominance model (best from a breeders point of view) providing the best fit. These findings correspond with the results published by other authors (Pawar *et al.*, 1988; Singh and Singh, 1992; Misra *et al.*, 1994; Singh *et al.*, 1998). This

situation is even more complicated when dominance effects are more important than additive effects, as was the case in this experiment. To identify whether a cause of the model failure is the presence of higher order interactions or linkage effects further analyses needs to be carried out with enough generations to fit a full trigenic interaction and linkage model. In respect of epistatic effects, additive x additive effects were more important than dominant x dominant effects and only complementary epistasis was observed. This situation is more favorable than the presence of dominant x dominant effects and/or duplicate epistasis due to a greater chance of breeding success, and partially explains why heterosis was not as frequent as might be expected from the fact that dominance effects were more important than additive effects.

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