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Genetic Analysis of Yield Components in Durum Wheat: Gene Effects and Epistasis

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Genetic control of the number of heads per plant, spikelets per spike and grains per spike was studied in two durum wheat (*Triticum durum* Desf.) crosses, Inrat 69/Cocorit71 and Karim/Ben Bechir, respectively. Separate analyses of gene effects were done using means of four generations (parents P_1 and P_2, F_1, F_2, and the two reciprocal BC_1) at two sites. A three-parameter model was inadequate to explain all traits except number of heads per plant in Inrat 69/Cocorit 71 at one site. In most cases a digenic epistatic model explained variation in generation means. Dominance effects and dominance × dominance epistasis (l) were more important than additive effects and other epistatic components. Considering the genotype-by-environment interaction, the interactive model was applied and found adequate in all majority of cases except spiklets per spike and grains per spike in Inrat 69/Cocorit71. The results of this study indicate that maintenance of heterozygosity is useful for exploitation of epistatic effects and adaptability to varied environmental conditions for spiklets per spike and grain per spike in the cross Karim/Ben Bechir. Estimates of narrow-sense heritability indicated that the genetic effect was larger than the environmental effect. The additive effect was the largest component of genetic effects.

Key words: Genetic effects, epitasis, genotype-by-environment interaction, heritability, *Triticum durum*.

INTRODUCTION

Durum wheat (*Triticum durum* Desf.) is the most important cereal crop in Tunisia and is used primarily for couscous, macaroni and various types of bread (Bnejdi and El Gazzah, 2008). The development of high-yielding wheat cultivars is the major objective of breeding programs. Knowledge of the nature, magnitude of gene effects and their contribution to the control of metric traits is important in formulating an efficient breeding program for durum wheat genetic improvement. The inheritance of grain yield in wheat has been the subject of intensive studies (Grafius, 1959; Singh et al., 1985; Menon and Sharma, 1995; Sharma et al., 2002; Heidari et al., 2005; Rebetzke et al., 2006). Grain yield in wheat is determined by component traits and is highly complex. Reported heritability estimates indicate that certain morphological traits that influence grain yield in wheat are more heritable than yield itself. Ehdaie and Waines (1989)

reported direct positive effects of number of heads per plant and number of grains per head on grain yield. The inheritance of quantitative traits has been described as a 'moving target' since they are affected not only by the actions of multiple individual genes, but also by the interactions between genes and environmental factors (Lewis and John, 1999). Some genetic statistical models have been devised for plants and animals to estimate the parameters of genetic components (Mather and Jinks, 1982; Kearsey and Pooni, 1996; Lynch and Walsh, 1998; Chalh and El Gazzah, 2004). The method has been generally used to study quantitative trait inheritances and generation means analysis (Mather and Jinks, 1971), which allows testing the linear components of genotypic means. The present investigation of four generations (parental, F_1, F_2 and BC_1) studied gene action and heritability of four traits at two sites.

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MATERIALS AND METHODS

The study was carried out at two locations; El Kef characterized by

loam soil and a semi arid climate with an annual rainfall of about 400 - 500 mm and Tunis characterized by clayey soil and situated in the sub humid region with 600 - 700 mm under rain-fed conditions in 2005 - 2006. Parental lines were chosen for their different yield. Plants were grown in a randomised complete block design with two replications. From each plant the following data were obtained: number of heads per plant, spikelets per spike and number of grains per spike. The number of plants evaluated varied depending on the generation and was greater in generations with greater segregation, such as the F_2, BC_1P_1 and BC_1P_2.

Transforming the data by log, square root, arc-sine and arc-sine of square root had no effect on data distribution or in removing epistatic effects. Separate analysis of variance by population and by site using SAS Proc GLM (SAS, 1990) indicated that replication and generation × replications effects were not significant. Therefore generation means analysis was conducted without adjusting the data for replication.

Statistical analysis

Gene effects

The means of different generations were analyzed by a joint scaling test using the weighted least squares method (Mather and Jinks, 1982; Kearsey and Pooni, 1996; Lynch and Walsh, 1998). The observed generation means were used to estimate the parameters of a model consisting only of mean (m), additive and dominance genetic effects. The estimated parameters were used in turn to calculate the expected generation means. The goodness-of-fit between observed and expected was tested; a significant chi-squared value indicated a significant difference between the observed and expected generation means, which implied that a simple additive model did not explain the data. When the additive-dominance model was found to be insufficient, then additive × additive, additive × dominance and dominance × dominance digenic epistatic parameters were added. If a digenic epistatic parameter was not significant then it was omitted and the best fit model was applied. The weighted least-squares model that incorporates additive, dominance and digenic epistatic effects is (Hayman, 1958; Mather and Jinks, 1982; Kearsey and Pooni, 1996; Lynch and Walsh, 1998):

$$X = (C'WC)^{-1} (C'WY)$$

where X is the vector of mean, additive, dominance, additive × additive, additive × dominance and dominance × dominance parameters. W is the diagonal matrix of weights (that is, the reciprocals of the variance of generation means) and Y is the vector of generation means. The variances of the parameter estimates can be obtained from the diagonal elements of $(C'WC)^{-1}$. The expected means of the six generations were calculated using the parameter estimates, the goodness-of-fit of the observed generation means was tested with the chi-squared statistic. The significance of each parameter was determined by t-test.

Genotype-by-environment interaction

The weighted least squares method was also used to estimate environmental and genotype-by- environment interactions. This technique was applied to parents and F_1 only (Mather and Jinks, 1971). The analysis was done in three stages by three different models: the no-interactive model, the interactive model and the best-fit model.

The no-interactive model: this model involves four parameters mean (m), additive (d), dominance (h) and environmental (e) effects. If the chi-squared test revealed that the simpler model was

inadequate then the interactive model was applied. This model involves an interactive-parameter model and two genetic environment interactions; additive × environment interactions (ed) and dominance × environment (eh). When additive × environment interaction (ed) or dominance × environment interaction (eh) were not significant by t-test in the interactive model, then it was omitted and the best-fit model was applied.

Heritability

Additive variance is a component of the total genetic variance and cannot easily be distinguished from the dominance variance and environmental components. However, an estimate of the additive variance can be obtained using F_2 and backcross generations' data to calculate narrow-sense heritability:

$$\sigma^2{}_A = 2\,\sigma^2{}_{F2} - (\sigma^2{}_{BC1P1} + \sigma^2{}_{BC1P2})$$

Narrow-sense heritability (h^2) was estimated using F_2 and backcross generations' variance components as described by Warner (1952).

$$h^2 = [2\sigma^2{}_{F2} - (\sigma^2{}_{BC1P1} + \sigma^2{}_{BC1P2})]/\ \sigma^2{}_{F2}$$

Dominance variance was estimated as:

$$\sigma^2{}_D = (\sigma^2{}_{BC1P1} + \sigma^2{}_{BC1P2}) - \sigma^2{}_{F2} - \sigma^2{}_E$$

The environmental variance was estimated as

$$\sigma^2{}_E = (\sigma^2{}_{P1} + \sigma^2{}_{P2} + 2\,\sigma^2{}_{F1})\ /4\ \text{(Wright, 1968).}$$

RESULTS

Parental means and their variances in both environments are given in Table 1. In all cases, depending on the site, the means of the parents in each cross showed a tendency to be more extreme. The means of backcrosses BC_1P_1 and BC_1P_2 tended to be located close to those of their respective recurrent parents. These results con-firmed the choice of parents for the present study. For most traits, F_1 generation means were higher than the mid-parent value. The F_1 and F_2 generations' means were not significantly different in the majority of cases for grains per spike and spikelets per spike. For number of heads per plant, the F_2 generation mean was significantly different from the F_1 generation mean in the majority of cases.

The estimates of the main and first order interactions and the test of the fitness of models are presented in Table 2. The adequacy of models and the magnitude of gene action depended on the cross and experimental site. The joint scaling test indicated that the additive-dominance model (three-parameter model) was inade-quate to explain the nature of gene action for all traits, for both crosses at both sites, except for number of heads per plant in the Inrat 69/Cocorit 71 cross at Tunis, indicating that epistatic effects were involved in the inheritance of all traits studied.

For grains per spike at Tunis and spikelets per spike at El Kef, both models did not explain variation in generation

Table 1. Means and variances for all traits for different generations of Inrat 69/Cocorit 71 and Karim/Ben Bechir crosses grown at Tunis and El Kef sites from two replications in 2005 - 2006.

	Inrat 69/Cocorit 71		Karim/Ben Bechir	
Generation	El Kef	Tunis	El Kef	Tunis
Number of heads per plant				
P_1	6.45 ± 0.78 (20)[y]A	7.85 ± (20)A	9.35 ± 0.45 (20)A	10.15 ± 0.55(20)A
BC_1	6.02 ± 1.44 (50)AB	7.08 ± (50)B	7.82 ± 2.51(50)B	7.36 ± 0.92 (50)C
F_1	5.24 ± 1.10 (25)CD	6.44 ± (25)C	8.40 ± 1.58 (25)B	7.96 ± 1.20(25)B
F_2	5.69 ± 2.32 (72)BC	5.04 ± (72)DE	6.11 ± 3.42(72)C	6.11 ± 1.28(72)D
BC_2	4.86 ± 1.12 (43)D	4.76 ± (43)D	5.58± 1.78 (43)C	6.23 ± 0.84(43)D
P_2	4.04 ± 0.44 (21)E	4.28 ± 1.01 (21)E	5.66± 0.53 (21)C	5.23 ± 0.79 (21)E
Spikelets per spike				
P_1	23.00 ± 0.31(20)A	20.00 ± 0.42 (20)A	18.35 ± 0.55(20)A	20.40 ± 0.77 (20)A
BC_1	21.27 ± 1.45 (44)B	19.48 ± (35)AB	18.37 ± 0.75(40)A	19.26 ± 0.76 (50)B
F_1	20.15 ± 0.66(20)C	19.15 ± 0.97(20)B	18.30 ± 0.85 (20)A	19.30 ± 0.74 (20)B
F_2	20.51 ± 1.92(68)C	19.65 ± 2.76 (76)AB	18.28 ± 1.34 (50)A	17.90 ± 1.29 (74)C
BC_2	18.94 ± 0.91 (38)D	18.11 ± 1.91 (43)C	16.94 ± 1.31 (39)B	18.20 ± 0.86 (24)C
P_2	18.35 ± 0.97 (20)E	17.00 ± 0.42 (20)D	15.25 ± 0.82 (20)C	17.10 ± 0.72 (20)D
Grains per spike				
P_1	55.85 ± 7.71 (20)A	63.90 ± 12.83 (19)A	50.50 ± 13.21 (20)A	54.60 ± 6.88 (20)A
BC_1	51.42 ±14.90 (20)B	50.62 ± 43.09(50)A	45.70 ± 18.82 (50)B	49.76 ± 11.57(50)AB
F_1	53.72 ± 8.04(20)AB	57.00 ± 10.91 (25)CD	47.00 ± 11.58 (25)B	50.20 ± 22.08(25)AB
F_2	48.57 ± 18.24 (20)C	48.55 ± 57.64 (100)CD	42.18 ± 32.53 (100)C	47.26 ± 45.02(100)AB
BC_2	47.16 ± 39.57(20)C	46.53 ± 46.76 (52)D	45.15 ± 35.30(52)B	43.98 ± 40.68 (52)B
P_2	44.45 ± 6.36(20)D	49.10 ± 11.88(20)CD	37.10 ± 10.72(20)D	44.80 ± 7.74 (20)B

P_1 = better parent, P_2 = worse parent.
y = number of random plants for each generation in parentheses.
For each trait, means within a column with different letters (e.g. A, B, C, D or E) following them are significantly different using Duncan's multiple range test ($P < 0.05$).

means in the Karim/Ben Bechir cross. In the other cases the epistatic model adequately explained variation between generation means in the two crosses at both sites. The magnitude of dominance (h) and dominance × dominance (l) and additive × additive (i) when significant where more important than additive (d) effects.

The estimates of the effects of genetic, environment, genotype- by-environment interaction and the test of fitness of the model are given in Table 3. Due to the presence of allelic and non-allelic interactions analysis was invoked only in non-segregating generations. This study revealed that the non-interactive model was inade-quate in all cases. Therefore the interactive model was tested and found adequate in four cases. For the cross Inrat 69/Cocorit 71 the interactive model failed to explain variation in generation mean for spiklets per spike and grains per spike. Significant environment (e) type effect was observed for all the traits except number of heads per plant in the Karim/Ben Bechir cross. The additive × environment (ed) effect was present especially in the cross Inrat 69/Cocorit71. The environment × dominance interaction (eh) effect was present in the tow crosses for

spiklets per spike and grains per spike (Table 3). Estimates of variance components were used to calculate h^2 for both crosses and four traits (Table 4) . For all traits the additive variances were positive; 0.78 - 2.60 for number of heads per plant, 10.93 - 45.98 for grains per spike and 0.63 - 1.47 for spikelets per spike. Dominance variance was negative in the majority of cases. Environmental variance was 0.86 - 1.03 for number of heads per plant, 7.54 - 14.69 for grains per spike, and 0.65 - 0.77 for spikelets per spike. For all traits, h^2 was dependent upon the cross and site and ranged from moderate to high.

DISCUSSION

There were significant differences among generation means for the three analyzed traits in all cases, revealing genetic diversity for these attributes in the materials, thus validating the genetic analysis of the traits following the technique of Mather and Jinks (1982). The analysis of gene effects revealed that both additive and dominance

Table 2. Estimates of gene effects for three quantitative traits for Inrat 69/Cocorit and Karim/Ben Bechir crosses at Tunis and El Kef sites from two replications in 2005–2006.

Site	Cross	m	d	h	i	l	j	x^2 (df)
Number of heads per plant								
El Kef/	Inrat 69/Cocorit 71	5.32**	1.21**	0.15	-	-	-	4.48(3)
	Karim/Ben Bechir	5.22**	1.88**	0.36	2.27*	2.8*	-	1.53 (1)
Tunis/	Inrat 69/Cocorit 71	0.77	1.85**	10.28**	5.28**	-4.62**	-	0.84 (1)
	Karim/Ben Bechir	4.2**	2.46**	3.63**	3.44**	-	-2.68**	3.58 (1)
Grains per spike								
El Kef/	Inrat 69/Cocorit 71	40.08**	5.7**	12.75**	9.13**	-	-5.64*	0.69 (1)
	Karim/Ben Bechir	141.84**	6.7**	29.28**	12.98**	-13 .09*	-12.3**	-
Tunis /	Inrat 69/Cocorit 71	56.5**	7.4**	-32.23**	-	32.73**	-6.63*	0.810^{-3}(1)
	Karim/Ben Bechir	49.69**	5.02**	-10.76**	-	11.27**	-	0. 7 (2)
Spikelets per spike								
El Kef/	Inrat 69/Cocorit 71	22.29**	2.32**	-4.97*	-1.61**	2.82*	-	1.710^{-6}(1)
	Karim/Ben Bechir	19.31**	1.51**	-3.12	-2.51**	2.10*	-	0.24 (1)
Tunis/	Inrat 69/Cocorit 71	21.92**	1.48**	-6.28*	-3.42**	3.51*	-	0.13 (1)
	Karim/Ben Bechir	100.<u>75</u>**	1.65**	6.01**	3.31**	-2.15*	-119*	-

Mean (m), additive (d), dominance (h), additive × additive (i), additive × dominance (j) dominance × dominance (l) genetic effects for the model. $y = m + d + h + i + j + l$, where y is the generation mean.df: degrees of freedom, calculated as the number of generations minus the number of estimated genetics parameters.
*, ** indicates means and gene effects are statistically different from zero at $P < 0.05$ and $P < 0.01$, respectively.

Table 3. Estimates of the genetic, environmental and genotype-by-environment interaction components of generation means.

Cross	m	d	h	e	eh	ed	x^2(df)
Number of heads per plant							
Inrat 69/Cocorit71	5.67***	1.47***	0.19	0.47***		0.29**	2.01(1)
Karim/Ben Bechir	7.58***	2.15***	0.56**			0.31***	2.95(2)
Spikelets per spike							
Inrat 69/Cocorit71	20.49***	1.92***	0.06	1.08***	0.41***	-0.58***	
Karim/Ben Bechir	17.76***	1.59***	1.03***	0.97***	0.47**	-	0.27(1)
Grain per spike							
Inrat 69/Cocorit71	58.32***	6.55***	2.03***	3.17***	0.85*	-1.53*	-
Karim/Ben Bechir	47.14***	5.25**	2.15**	2.53***	-1.63*	-	2.32(1)

m: mean, d: additive effect, h: dominance effects, e : environment effects, eh: environment dominance effects interaction, ed : environment additive effects interaction for the model $y = m + d + h + e + eh + ed$, where y equals the non-segregating generation mean. df: degrees of freedom, calculated as the number of generation minus the number of estimated genetic parameters.
* ** ***indicates means and gene effects are statistically different from zero at P <0.05, 0.01, 0.001 respectively.

effects were involved in the inheritance of most traits (Table 2). The dominance effects were greater in most cases than additive gene effects. This study also revealed a preponderance of dominance gene effects in the expression of all traits. The higher estimates for dominance than for additive effects, for the majority of

Table 4. Estimates of additive (σ^2_A), dominance (σ^2_D), and environmental (σ^2_E) variances, narrow-sense heritabilities (h^2) and genetic gain through selection (Gs) for three traits of Inrat 69/Cocorit 71 and Karim/Ben Bechir crosses at two sites (Tunis and El Kef) from two replications in 2005-2006.

Cross	Site	σ^2_A	σ^2_D	σ^2_E	h^2	Gs
Number of heads per plant						
Inrat 69/Cocorit 71	El Kef	2.08	–0.6	0.86	0.89	3.54
	Tunis	0.96	–0.17	0.90	0.56	1.64
Karim/Ben Bechir	El Kef	2.60	–0.21	1.03	0.76	4.42
	Tunis	0.78	–0.44	0.93	0.61	1.33
Grains per spike						
Inrat 69/Cocorit 71	El Kef	45.98	–13.96	7.54	1.16	78.18
	Tunis	25.42	20.57	11.63	0.44	43.22
Karim/Ben Bechir	El Kef	10.93	9.82	11.77	0.33	16.58
	Tunis	37.78	–7.46	14.69	0.83	64.23
Spikelets per spike						
Inrat 69/Cocorit 71	El Kef	1.47	–0.20	0.65	0.76	2.50
	Tunis	1.17	0.88	0.69	0.42	1.99
Karim/Ben Bechir	El Kef	0.63	–0.05	0.77	0.46	1.07
	Tunis	0.94	–0.4	0.75	0.73	1.61

Variance components calculated as follows: $\sigma^2_E = (\sigma^2_{P1} + \sigma^2_{P2} + 2\,\sigma^2_{F1})\,/4$; $\sigma^2_A = 2\,\sigma^2_{F2} - (\sigma^2_{BC1P1} + \sigma^2_{BC1P2})$;
$\sigma^2_D = (\sigma^2_{BC1P1} + \sigma^2_{BC1P2}) - \sigma^2_{F2} - \sigma^2_E.$
Heritabilities calculated as follows: $h^2 = [2\sigma^2_{F2} - (\sigma^2_{BC1P1} + \sigma^2_{BC1P2})]/\sigma^2_F.$
Genetic gain calculated as follows: $Gs = (1.76)\,(h^2)\,(\sigma^2_{F2}).$

traits, indicated that the parents were in dispersion phase and that there was an accumulation of dominant parental genes in the hybrids (Dhanda and Sethi, 1996).

The additive-dominance model was accurate for the number of heads per plant in one cross (Inrat 69/Cocorit 71) at Tunis, similar to results of Kashif and Khaliq (2003) in bread wheat. For digenic interaction, the model was adequate in the Inrat 69/Cocorit 71 cross at both sites. By contrast, in the Karim/Ben Bechir cross the digenic model failed to explain variation between generations in two cases (Table 2), indicating more complex mechanisms of genetic control. The presence of digenic interaction in durum wheat has been reported for spike length (Sharma et al., 2003), grains per spike (Sharma and Sain, 2004) and number of heads per plant (Singh et al., 1986). Epistasis has been reported for many traits in a number of crops: barley (Kularia and Sharma, 2005), maize (Melchinger et al., 1987), sorghum (Finkner et al., 1981), rice (Saleem et al., 2005) and durum wheat (Bnejdi and El Gazzah, 2008).

None of the models explained variation between generation means in the Karim/Ben Bechir cross for grains per spike at Tunis and spikelets per spike at El Kef, suggesting there were higher order interactions or linkage effects. To discover the cause of the model failure further analyses of more generations are necessary.

Trigenic interactions in durum wheat have been

reported for grains per spike (Sharma and Sain, 2004). In the present study, mostly the variation in generation means fitted a digenic epistatic model, depending on the cross and site. This indicates that improvements for these traits would be moderately difficult, compared to fitting an additive-dominance model (best from a breeder's point of view); however, this is better than the presence of trigenic interaction.

The majority of traits were largely influenced by dominance × dominance and additive × additive gene effects in both crosses and both sites, with dominance × dominance (l) effects being more pronounced than additive × additive (i) effects (Table 2). This finding is in accordance with those of Dhanda and Sethi (1996), but not Novoselovic et al. (2004) in bread wheat. Mostly the dominance × additive effect did not significantly contribute to the genetic control of these traits.

The non-segregating generations in the present study show that the estimates of genotype by environment interaction components were dependant upon the cross. For Inrat 69/Cocorit 71 the interactive model failed to explain variation of generation mean in tow cases, indicating the presence of more mechanism in the control of this traits. Therefore selection based on the cross Karim/Ben Bechir was better than the cross Inrat 69/Cocorit71.

For Karim/Ben Bechir cross environmental × dominance

(eh) effects are highly significant for spiklets per spike and grain per spike. By contrast, estimates of environment × additive (ed) effects were not significantly different from zero and indicated that for these traits the heterozygote show a greater interaction with the environment than do the homozygote (Table 4). This condition is more favorable than the presence of interaction of homozygote with environment; since homozygous populations are less adaptable than heterozygous populations to varied environmental conditions, as reported by Kaczamarek et al. (2002).

The present study revealed that both additive and non-additive components of genetic variances were involved in governing yield components; with dominance effects and dominance × dominance epistasis more important than additive effects or other epistatic components. However, the heterozygote showed greater interaction with the environment than the homozygote. Maintenance of heterozygosity can give two advantages, the exploita-tion of epistatic effects and adaptability to varied environmental conditions. Successful methods will be those that can map-up the gene, to form superior gene combinations interacting in a favorable manner and at the same time maintain heterozygosity. This objective can be achieved by restricted recurrent selection (Joshi 1979) and/or di-allele selective mating (Jensen, 1978) methods.

Narrow-sense heritability is important to plant breeders, because effectiveness of selection depends on the additive portion of genetic variation in relation to total variance (Falconer, 1960). In our results, moderate to high values for narrow-sense heritability suggested a considerable participation of genetics in the phenotypic expression of traits and that selection for all traits could be efficient.

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