



Original Article

Genetic control of bread wheat (*Triticum aestivum* L.) traits

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Abstract

Nine bread wheat genotypes were crossed under a partial diallel scheme, in which group 1 counted five lines and group 2 four lines. The 20 F₁'s and their parents were evaluated in randomized complete block design with three replications at the Field Crop Institute-Agricultural Experimental Station of Setif (Algeria) during the 2011/2012 cropping season. The results showed that the components associated with additive effects were more relevant than those associated with the dominance effects for these traits. Based on the K_D/K_R ratio, the dominant alleles are present in greater frequency in the first group of parents, while the opposite is true for the second group. Values of the gene proportion with positive and negative effects in the parents revealed an unequal distribution of dominant genes in the parents for almost all the traits except for number of grain per spike in the second group which showed an equal distribution.

Keywords: *Triticum aestivum* L., selection, partial diallel, genetic parameters, heritability

1. Introduction

Bread wheat (*Triticum aestivum* L.) is an important cereal crop in Algeria, whose production is well below the domestic demand. To keep pace with a growing population; it is essential to raise the productivity level. Since there is no possibility to increase the area under cultivation, the projected demand will have to be met by either using increased amount of inputs or by improving the genetic architecture of wheat plant. Actually the inputs are expensive and scarce, so more emphasis is to be made on genetic improvement (Fellahi

et al., 2013). The main objective of the wheat program is, therefore, to boost average national wheat grain yield. In this context, knowledge of the nature of gene action involved in the control of quantitative traits is important to identify the best parents and crosses and to make decisions about the appropriate selection strategies to manage progenies (Nazeer *et al.*, 2010; Aghamiri *et al.*, 2012). Yield and yield related attributes are complex quantitative traits controlled by multiple genes and are highly influenced by environmental conditions (Benmahammed *et al.*, 2010; Bendjama *et al.*, 2014); even though some yield related traits are less environmentally sensitive and have higher heritabilities than grain yield (Cuthbert *et al.*, 2008); inheritance studies of these traits are scarce and in some cases contradictory. Controversial results considering the same traits are reported in the litera-

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ture. Chowdhry *et al.* (2002) found that over dominance effects were more important for plant height, number of fertile tillers per plant, 1000-grain weight and grain yield per plant; while Ali *et al.* (1999) reported prevalence of additive genetic components. Basically, such information is important during planning and execution of a breeding program (Viana *et al.*, 1999).

One of the most accurate genetic designs to obtain information on the genetic control of characters is the diallel mating system, which has been used to study various traits in many crops such as wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), maize (*Zea mays* L.), cotton (*Gossypium hirsutum* L.), chickpea (*Cicer arietinum* L.) and soybean (*Glycine max* L.) (Babu *et al.*, 2003; Topal *et al.*, 2004; Wu *et al.*, 2004). Several methods have been proposed for diallel analysis (Jinks and Hayman, 1953; Hayman, 1954; Griffing, 1956). Plant breeders have often used Hayman's (1954) approach to investigate the genetic control of complex characters. This method allows genetic analysis of the F₁ and/or F₂ generations obtained from crosses involving homozygote parents (Khan *et al.*, 2009; Metwali *et al.*, 2014). The analysis is based on the knowledge of the nature of environmental and genetic statistics, such as means, variance and covariance, obtained from the diallel cross data (Silva *et al.*, 2010). Apart from additive and dominance gene effects, this method is efficient in detecting epistasis (Cruz, 2001). However, this procedure is not valid for a partial diallel. The adaptation of Hayman's method for partial diallel crosses, which represents, by definition, a set of crosses made between two distinct parents groups and where crosses between parents belonging to the same group are not of interest to the breeder, was worked out by Viana *et al.* (1999). The objective of the present research was to investigate the nature of gene actions involved in the genetic control of bread wheat agronomic traits by means of partial diallel analysis as outlined by Viana *et al.* (1999).

2. Materials and Methods

The experimental material consisted of nine bread wheat (*Triticum aestivum* L.) genotypes *viz.* Acsad₉₀₁,

Acsad₈₉₉, Acsad₁₁₃₅, Acsad₁₀₆₉ and Ain Abid used as female parents (group 1), and Mahon-Demias, El-Wifak, Hidhab and Rmada, which were used as male parents (group 2) (Table 1).

Compared to parents belonging to group 2, those of group 1 exhibited shorter plant height (-5.1 cm), lighter 1000-kernel weight (-2.6 g), and higher number of grains per spike (+6.3 grains); but didn't differed significantly for earliness and grain yield (Fellahi *et al.*, 2013). The nine parents were crossed in a partial diallel cross fashion, establishing all possible hybrids between the two groups of parents, without reciprocals to produce 20 F₁ hybrids. Hybrids along with their parents were sown in a randomized complete block design with three replications at the Field Crop Institute, Setif Agricultural Research Station (36°12'N, 05°24'E), during the 2011/2012 crop season. Experimental plot was a single row, 2.5 m long; with an inter-row distance of 30 cm. Plant to plant distance was maintained at approximately 15 cm. The locally recommended agronomic and plant protection practices were followed from sowing till harvest.

At maturity, observations were made on five random plants from each row for above ground biomass per plant (BIO, g plant⁻¹), number of spikes per plant (SN), number of grains per spike (GN), and grain yield per plant (GY, g plant⁻¹). Data obtained were submitted to an analysis of variance to test genotype effect according to Steel and Torrie (1984). The means of the parents and their hybrids were analyzed following the method of Hayman (1954) modified by Viana *et al.* (1999) to determine average degree of dominance, ratio of dominant to recessive alleles, number of effective factors, and the broad and narrow-sense heritability. Before carrying out the genetic analysis, however, it was considered advisable to test the adequacy of the data set to the additive-dominance model. To do so, examination of the regression Wr on Vr was carried out. According to Singh and Chaudhary (1985), the regression coefficient of Wr on Vr is expected to be significantly different from zero but not from unity for a fulfillment of the required assumptions. The statistical procedures adopted for the analysis of variance involved the partitioning of the genotype source of variation into the parents, crosses and the parent vs. crosses. The comparison of means was made through the means grouping method of

Table 1. Name, cross origin and pedigree of the parental material used in the diallel crosses.

Genotype	Code	Group	Origin/Pedigree
Acsad ₉₀₁	P ₁	1	Acsad ₅₂₉ /4/C _{182.24} /C _{168.3} /3/Cno* ² /7C//CC/Tob-1s
Acsad ₈₉₉	P ₂	1	Acsad ₅₂₉ /4/C _{182.24} /C _{168.3} /3/Cno* ² /7C//CC/Tob-0s
Acsad ₁₁₃₅	P ₃	1	Prl/Vee ₆ //Myna/Vul/3/Prew
Acsad ₁₀₆₉	P ₄	1	Zahrai I-14//HD ₂₁₆₉₉ /Bow's
Ain Abid	P ₅	1	Cultivar introduced from Spain (syn AS _{8189'A})
Mahon-Demias	P ₆	2	Algerian selection from a land race introduced from Baleares
El-Wifak	P ₇	2	K ₁₃₄ /4/Tob//Bman/Bb/3/Cal/5/Bucc. CM. X ; ITGC selection
Hidhab	P ₈	2	HD ₁₂₂₀ /3*/ Kal/Nac. CM. X ; ITGC selection
Rmada	P ₉	2	Vee's/Bow's//Alondra's/Pavon's CM. X ; ITGC selection

Table 2. Analysis of variance of the traits measured on the two bread wheat parents groups and their hybrids.

Source of variation	df	Mean squares			
		BIO	GN	SN	GY
Blocks	2	212.8	152.2	13	62
Treatments	28	238.7*	152.8*	23.4*	39.7*
Parents	8	317.1*	279.1*	29.9*	42.7*
G ₁	4	400.5*	135.0*	28.1*	65.5*
G ₂	3	300*	475.0*	37.2*	25.8*
G ₁ vsG ₂	1	34.4 ^{ns}	267.6*	15.1*	2.2 ^{ns}
Hybrids	19	179.3*	107.6*	19.6*	33.8*
Parents vs Hybrids	1	743.3*	2.3 ^{ns}	44.5*	129.0*
Error	56	90.6	31.4	3.4	6.5

df: degrees of freedom, BIO: Biomass per plant (g), GN: Number of grains per spike, SN: Number of spikes per plant, GY: Grain yield per plant (g). ns, *, **: non-significant and significant at 5% and 1% of probability, respectively.

Scott and Knott (1974) at a 5% probability. All statistical analyses were performed using the GENES software (Cruz, 2013).

3. Results and Discussion

3.1 Mean performances

The analysis of variance indicated significant treatment effect for the measured traits, (Table 2). Partitioning the treatment effect indicated significant differences between the parents as a whole for the measured traits. The partitioning of the parent effect indicated also significant differences between genotypes within each group of parents. The best performing parents in group 1 were no significantly different from those belonging to group 2 for BIO (Acsad₁₁₃₅ and Mahon-Demias), GN (Acsad₉₀₁ and Ain Abid) and SN (Acsad₁₁₃₅ and Mahon-Demias) (Table 3).

Similarly, the least performing parents, in group 1, were no significantly different from those belonging to group 2 for BIO and SN (Acsad₉₀₁ and Rmada). Mahon-Demias, from the group 2, exhibited the lowest GN. The Scott-Knott means grouping test suggested the presence of significant differences between genotypes within group 1 and within group 2, for grain yield per plant (GY). Acsad₉₀₁ and Ain Abid from group 1 and Rmada from group 2 showed the lowest GY; while Acsad₁₁₃₅ and El-Wifak presented the highest GY, with mean values of 21.7 and 20.5 g/plant, respectively (Table 3). The contrast G1 vs G2 indicated that significant differences existed between groups of parents for number of gains per spike (GN) and number of spikes per plant (SN) but not for above ground biomass and grain yield (GY) per plant

Table 3. Summary of the Scott-Knott cluster analysis (P<5%) of the partial diallel cross parents.

Genotypes	BIO	GN	SN	GY
Acsad ₉₀₁	28.67 ^b	55.17 ^a	7.87 ^b	10.52 ^b
Acsad ₈₉₉	52.47 ^a	44.97 ^b	13.67 ^a	20.05 ^a
Acsad ₁₁₃₅	58.13 ^a	44.47 ^b	15.00 ^a	21.74 ^a
Acsad ₁₀₆₉	44.47 ^a	49.96 ^b	11.80 ^a	18.82 ^a
Ain Abid	38.67 ^b	60.09 ^a	8.80 ^b	13.78 ^b
Mahon-Demias	56.27 ^a	26.33 ^c	16.80 ^a	17.38 ^a
El-Wifak	49.60 ^a	47.68 ^b	14.13 ^a	20.45 ^a
Hidhab	48.47 ^a	55.05 ^a	12.40 ^a	18.80 ^a
Rmada	32.67 ^b	49.32 ^b	8.40 ^b	13.58 ^b
G ₁ mean	45.49	48.11	12.10	17.24
G ₂ mean	44.48	50.93	11.43	16.98
Parents mean	46.75	44.59	12.93	17.55
Hybrids mean	51.80	48.53	13.64	19.91

BIO: Biomass per plant (g), GN: Number of grain per spike, SN: Number of spikes per plant, GY: Grain yield per plant (g). Means followed by the same letter are not significantly different at 5% probability level by the Scott-Knott test.

(Table 2). Group 1 had significantly more grains per spike while group 2 had more spikes per plant (Table 3). The hybrids effect indicate significant differences between hybrids for all the measured traits while the contrast hybrids vs parents did not indicated significant difference between parents and hybrids for the number of grains per spike (Table 2). Hybrids had greater above ground biomass, spike number, and grain yield (Table 3).

3.2 Genetic parameters

The presence of genetic variability, among the parents and their hybrids, as suggested by the analysis of variance of BIO, GN, SN, and GY, which showed significant genotype effect, allows the estimation of genetic parameters for the crossed parents, as suggested by Singh and Chaudhary (1985). The results of scaling test based on regression coefficient of W_r on V_r , indicated that the hypotheses of the genetic analysis were largely satisfied for grain number and spike number of group 1 and for grain number, spike number and grain yield of group 2 (Table 4).

These results suggested that additive-dominance model was adequate to determine genetic components of variation for these traits. Since the regression slope deviated significantly from zero but not from unity suggesting that epistasis was absent and genes were distributed independently among the parents for these characters. Above ground biomass of both groups and grain yield of group 1 did not meet the required assumptions, because the coefficient of regression was not significantly different from zero (Table 4). The determination of the genetic parameters of these characters was made, knowing that the results are less reliable. D_1 and D_2 measure the genetic variation due to additive genetic effects of group 1 and group 2, respectively; these genetic parameters were significant at 5% probability, for above ground biomass, grain number, spike number and grain yield indicating the importance of the additive component of genetic variance in the determination of these traits (Table 5).

The estimate [$D_1 - D_2$] was negative for GN and SN and positive for BIO and GY, suggesting that more variability was present in group 2 for the former two traits cited and in group 1 for the two last cited traits. Genetic components H_1 and H_2 are measures of variation due to dominance deviations, H_1 component was non-significant for the four traits under study, suggesting the absence of dominance effect in the group 1,

while H_2 component was significant for spike number and grain yield and non-significant for above ground biomass and grain number. Dominance effects were present in the control of these two characters (Table 5). F is a measure of the mean covariance between additive and dominant genetic effects. The absence of dominance effect was confirmed for above ground biomass and spike number in the group 1 for which $F_{(G1)}$ was not significant but not for grain number and grain yield which exhibited significant $F_{(G1)}$ (Table 5). The presence of dominance effect was not confirmed for spike number and grain yield in group 2 since $F_{(G2)}$ was not significant for these traits (Table 5). Significant estimates of F within group 1 suggested predominance of dominant alleles controlling above ground biomass in P2, P3 and P5; controlling grain number in P4 and P5, controlling spike number in P1, P2, P3 and P4 and controlling grain yield in P2 and P3. Within group 2, significant estimates of F indicated predominance of dominant alleles for above ground biomass in P6 ($F'1$) and P7 ($F'2$); for grain yield in P6 ($F'1$) and for grain number in P8 ($F'3$). Significant estimates of F revealed predominance of recessive alleles controlling above ground biomass in P9 ($F'4$), controlling grain number in P6 ($F'1$), in P8 ($F'3$) for spike number and in P9 ($F'4$) for grain yield (Table 5). Positive F -values suggested that dominant alleles were more abundant than the recessive ones in group 1 while group 2 showed more recessive than dominant alleles (Table 5).

Positive and significant value of the statistic h^2 was found for grain yield indicating that the direction of dominance was unidirectional from crosses towards parents and dominance of genes have increasing effect at most of the loci. The lack of significance for the other yield components showed that dominance was not unidirectional, suggesting that pedigree selection could be rewarding for these traits (Ali *et al.*, 2008). The environmental variation (E) was significant for SN, only, indicating important environmental effect on this trait. $\sqrt{h/d}$ represents a measure of the mean degree

Table 4. Regression of W_r on V_r test of the validity of the assumptions required for the additive-dominance model for above ground biomass (BIO), number of grains per spike (NGS), number of spikes per plant (NS) and grain yield (GY).

Groups	Traits	$b \pm se_b$	$b=0$ vs $b \neq 0$	$b=1$ vs $b \neq 1$
1	BIO	0.94±0.52	1.81 ^{ns}	0.12 ^{ns}
1	GN	1.43±0.24	5.96*	1.79 ^{ns}
1	SN	1.11±0.42	2.64*	0.26 ^{ns}
1	GY	0.21±0.84	0.25 ^{ns}	0.94 ^{ns}
2	BIO	0.99±0.39	2.53 ^{ns}	0.03 ^{ns}
2	GN	0.77±0.14	5.50*	1.64 ^{ns}
2	SN	0.64±0.20	3.20*	1.80 ^{ns}
2	GY	1.08±0.36	3.00*	0.22 ^{ns}

t: t -test levels of probability, ns, *: not significant and significant at 5% level of probability.

Table 5. Estimates of the component of genetic and environmental variation, their standard deviations (Est ± sd) and t-test values (t) for above ground biomass (BIO), number of grains per spike (GN), number of spikes per plant (SN) and grain yield per plant (GY).

Param	BIO		GN		SN		GY	
	Est ± sd	t	Est ± sd	t	Est ± sd	t	Est ± sd	t
D ₁	133.1±34	3.81*	44.6±11.8	3.78*	9.0±2.8	3.18*	21.5±4.7	4.54*
D ₂	99.6±34	2.85*	158.0±11.8	13.38*	12.0±2.8	4.25*	8.2±4.7	1.74*
D ₃	90.2±58	1.53	96.6±19.8	4.86*	9.0±4.7	1.89*	11.4±7.9	1.43
F 1	-140.6±103	-1.35	39.9±35.0	1.14	20.5±8.4	2.44*	6.1±14.0	0.44
F 2	272.6±103	2.63*	-30.8±35.0	-0.88	31.3±8.4	3.72*	24.9±14.0	1.78*
F 3	269.9±103	2.60*	24.0±35.0	0.68	19.6±8.4	2.33*	24.5±14.0	1.74*
F 4	50.2±103	0.48	129.4±35.0	3.69*	23.2±8.4	2.75*	17.3±14.0	1.23
F 5	205.5±103	1.98*	264.4±35.0	7.55*	7.2±8.5	0.84	29.1±14.0	2.07*
F' 1	252.4±104	2.41*	-97.2±35.4	-2.74*	6.7±8.5	0.78	41.0±14.2	2.89*
F' 2	219.5±104	2.09*	54.2±35.4	1.53	3.7±8.5	0.44	19.2±14.2	1.35
F' 3	44.7±104	0.42	67.0±35.4	1.89*	-32.9±8.5	-3.86*	-2.6±14.2	-0.19
F' 4	-233.7±104	-2.23*	6.0±35.4	0.17	13.9±11.7	1.19	-39.9±14.2	-2.81*
H1(1)	190.6±143	1.32	42.4±48.6	0.87	16.6±11.4	1.45	30.2±19.5	1.54
H1(2)	213.9±140	1.52	64.9±47.5	1.36	20.6±11.1	1.84*	43.5±19.0	2.28*
H2 1	210.7±137	1.53	39.9±46.5	0.85	5.6±11.1	0.50	29.8±18.6	1.60
H2 2	106.2±137	0.77	49.0±46.5	1.05	7.5±11.1	0.67	20.3±18.6	1.09
H2 3	161.7±137	1.17	41.1±46.5	0.88	6.7±11.1	0.6	34.1±18.6	1.83*
H2 4	140.6±137	1.02	37.5±46.5	0.80	7.9±11.1	0.70	23.4±18.6	1.25
H2 5	135.1±137	0.98	44.5±46.5	0.95	6.8±11.0	0.61	23.6±18.6	1.27
H2' 1	123.7±136	0.90	53.0±46.1	1.14	7.5±11.0	0.68	28.2±18.5	1.52
H2' 2	99.2±136	0.72	32.1±46.1	0.69	10.9±11.0	0.98	17.6±18.5	0.95
H2' 3	173.5±136	1.27	33.2±46.1	0.72	11.0±11.0	0.99	26.4±18.5	1.43
H2' 4	169.3±136	1.24	40.8±46.1	0.88	8.3±8.1	1.02	26.2±18.5	1.42
h ²	152.9±100	1.52	1.7±33.8	0.05	0.3±2.0	0.16	26.8±13.5	1.97*
E	0.3±24.6	0.01	0.3±8.3	0.03	16.1±6.7	2.40*	0.3±3.3	0.10
F(G ₁)	131.5±82	1.59	85.4±27.9	3.05*	-3.8±6.9	-0.54	20.4±11.2	1.82*
F(G ₂)	70.7±85	0.82	7.5±28.9	0.26	9.4±7.3	1.29	4.5±11.6	0.38
H ₂ medium	146.7±89	1.63	41.2±30.3	1.35	9.04±2.8	3.18*	25.5±12.1	2.09*

*: Estimate of the components significant at 5% probability when t value equals or exceeds 1.67.

Table 6. Estimates of average degree of dominance ($\sqrt{h/d}$), average value of the allelic frequency products ($H_2/4H_1$), proportion between dominant and recessive genes (K_D/K_R), direction of dominance [$(K^+ - K^-)^2/K$], and heritability in broad (h_{bs}^2) and narrow (h_{ns}^2) senses in both groups of parents for biomass (BIO), number of grains per spike (GN), number of spikes (SN) and grain yield (GY).

Traits	Genetic Parameters									
	$\sqrt{h/d}(G_1)$	$\sqrt{h/d}(G_2)$	$H_2/4H_1(G_1)$	$H_2/4H_1(G_2)$	$K_D/K_R(G_1)$	$K_D/K_R(G_2)$	$(K^+ - K^-)^2/K$	h_{bs}^2	h_{ns}^2	
BIO	1.20	1.47	0.17	0.19	2.63	1.57	1.70	0.99	0.80	
GN	0.97	0.64	0.16	0.24	2.46	1.19	0.03	0.99	1.01	
SN	1.24	0.98	0.14	0.18	3.64	0.71	1.18	0.95	0.67	
GY	1.18	2.29	0.14	0.21	3.34	1.19	1.43	0.97	0.54	

of dominance at all loci. This ratio revealed that alleles controlling above ground biomass and grain yield in both groups and spike number in group 1 were over dominant

(Table 6). Complete dominance was evidenced in the expression of grain number in group 1 and spike number in group 2 while partial dominance was present for grain number in

group 2 (Table 6). Average value of the allelic frequency products ($H_2/4H_1$) was lower than 0.25 for all traits in both groups parents, suggesting unequal distribution of dominant and recessive alleles (Table 6). Similar findings have earlier been reported by Kashif *et al.* (2003) in wheat and Bouzerzour and Djakoune (1998), and Metwali (2014) in barley.

The ratio K_D/K_R estimating the proportion between dominant and recessive genes indicated that more dominant alleles were present in parents belonging to group 1 than those of group 2. Dominance acted in the direction of increasing value for above ground biomass, spike number and grain yield but was bi-directional for grain number as the genetic parameter $(K^+ - K^-)^2/K$ that estimates the direction of dominance had a value close to zero for this trait (Table 6). Broad sense heritability was high for all the traits under study, while, the narrow sense heritability was high for above ground biomass, number of grain per spike and number of spikes per plant, and just moderate for grain yield per plant, indicating that selection for improvement of these traits would be effective (Table 6). Nazir *et al.* (2014) also reported moderate to high narrow sense heritability estimates for yield related traits.

4. Conclusions

The results of the present study indicated sufficient variability in both parental groups to sustain genetic improvement for BIO, GN, SN and GY. More variability was present in G_2 for GN and SN and in G_1 for BIO and GY. The additive genetic component was important in the determination of the four traits, with absence of dominance effect in G_1 and presence of dominance effect in G_2 for SN and GY. The presence of dominance effect was partially confirmed by $F_{(G_1)}$ and $F_{(G_2)}$ values. F values indicated that dominant alleles were more abundant in G_1 , while G_2 had more recessive than dominant alleles. This was confirmed by the $H_2/4H_1$ ratio which suggested unequal distribution of dominant and recessive alleles for all traits in both groups and the K_D/K_R ratio which indicated that more dominant alleles were present in G_1 than in G_2 . Degree of dominance revealed over dominant inheritance for BIO and GY in both groups and for SN in G_1 , dominant inheritance for GN in G_1 and SN in G_2 , and partial dominant inheritance for GN in G_2 . Dominance acted in the direction of increasing value for BIO, SN and GY but was bi-directional for GN as indicated by $(K^+ - K^-)^2/K$ ratio. The narrow sense heritability was high to moderate for most the studied traits indicating better chance for improvement following selection.

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