Research Article

Turk J Agric For
33 (2009) 525-535
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doi:10.3906/tar-0901-8

Genetic analysis of some physical properties of bread wheat grain (*Triticum aestivum* L. em Thell)

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Received: 08.01.2009

Abstract: Very little information exists on the relative genetic architecture of the grain physical properties of wheat. The physical properties of grain have a direct or indirect influence on the milling and baking quality of wheat. Therefore, understanding the inheritance of grain physical properties will be useful to improve varieties with better quality. Five bread wheat cultivars were crossed in order to evaluate the mode of inheritance and combining ability and the correlation of the grain's physical properties. Analysis of variance for combining ability showed that both additive and non-additive gene actions were involved in controlling most of the traits. Magnitudes of general combining ability (GCA) for all features except grain weight (GW) and grain height (GH) were higher than those of specific combining ability (SCA) The effect of general combining ability was more prominent for 8 out of 10 traits in accordance with ratio of GCA:SCA. Path coefficient analysis showed that grain width (GWI), number of grains per spike (GS), and grain height (GH) had the highest significant direct and indirect effect on most of the other features. The results obtained from this study might be helpful for wheat breeders trying to develop new varieties with better grain features to improve the milling and baking quality of wheat.

Key words: Single kernel characteristics, diallel cross, regression and path coefficient analysis

Ekmeklik buğdayda (*Triticum aestivum* L. em Thell) danenin bazı fiziksel özelliklerinin genetik analizi

Özet: Buğdayda danenin fiziksel özelliklerinin genetik yapısı hakkındaki bilgiler sınırlıdır. Danenin fiziki yapısı, buğdayın öğütme ve pişirme kalitesi üzerinde doğrudan ya da dolaylı olarak etkiye sahiptir. Bu nedenle danenin fiziksel özelliklerinin kalıtımı hakkında bilgiler dane kalitesi daha yüksek çeşitlerin geliştirilmesinde faydalı olacaktır. Danenin fiziksel özellikleri arasındaki ilişkiler, kalıtım mekanizması ve uyum yeteneğini değerlendirmek için beş ekmeklik buğday çeşidi diallel olarak melezlenmiştir. Uyum yeteneği için yapılan varyans analizi, incelenen özelliklerin çoğu için hem eklemeli hemde epistatik gen etkisi tarafından kontrol edildiğini göstermiştir. Genel uyum kabiliyeti (GCA) değeri, dane yüksekliği (DY) ve dane ağırlığı (DA) haricindeki tüm özellikler için özel uyum kabiliyeti (SCA) değerinden daha yüksek bulunmuştur. GCA:SCA oranına göre incelenen on özelliğin sekizinde GCA daha fazla olmuştur. Path analizi sonuçlarına göre, dane genişliği (DG), başaktaki dane sayısı (BDS) ve dane yüksekliği (DY) diğer özellikler üzerinde doğrudan ve dolaylı etkisinin olduğunu saptanmıştır. Elde edilen bu sonuçlar, buğdayın pişirme ve öğütme kalitesini geliştirmek için, daha iyi dane özelliklerine sahip yeni çeşitleri geliştirmeye çalışan buğday ıslahçılarına faydalı olabilir.

Anahtar sözcükler: Tek dane özellikleri, diallel melezi, regresyon ve path analizi

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Introduction

Wheat is a major food crop worldwide and is used to produce a wide diversity of baked food products. The economic value of wheat is determined by the class, which in part depends on morphology, texture and size of grain. Grain morphology and texture are important quality traits because they influence the market value of wheat (Lyford et al., 2005).

The physical properties of grain have a direct or indirect influence on the milling and baking quality of wheat. Many researchers discovered that grain size had an influence on wheat milling and baking qualities (Marshall et al., 1984; Berman et al., 1996). Millers can obtain more flour per unit of weight from large, round, uniform and well-filled kernels. Similarly maltsters and brewers can obtain more extracts from large kernels (Dziki and Laskowski, 2005). Wheat grains of smaller size are considered harder than larger grain and have inferior milling and baking characteristics, whereas larger wheat grains generally have higher weight, which means more endosperm (Gaines et al., 1997). Marshall et al. (1986) reported that grain size, grain thickness, grain sphericity, endosperm size, and grain density are important factors that directly influence the milling yield. The authors also reported that an increase in grain weight and volume was usually due to an increase in grain length, rather than in grain width or height. The grain length, width, and area were associated with a 40% variation in the milling quality of Australian winter wheat cultivars (Berman et al., 1996). Dziki and Laskowski (2005) reported a positive correlation between grain size and grain sphericity. Grain shape and grain sphericity influence individual wheat grain as they pass through the mill (Marshall et al., 1984). The yield and quality of flour are also strongly related to wheat grain properties, which are taken into consideration during wheat milling evaluation. These properties depend on many factors, among which genetic heritage is most important. Therefore, it would be possible to use this information to increase the value of wheat marketed through breeders in developing new varieties with better grain features.

For effective improvement of quality and yield of wheat, a plant breeder must have knowledge of inheritance of quality and agronomic traits. Until now, many wheat breeders studied heterosis and combining ability of F_1 generation of different agronomic and quality characters in wheat (Barnard et al., 2002; Sharma et al., 2005; Kamaluddin et al., 2007; Dağüstü 2008), but little is known about the physical properties of wheat grain. For the first time, Topal et al. (2004) studied durum wheat for the inheritance pattern of some physical properties, such as grain length, height, width, grain area, and sphericity. To the best of our knowledge, there has been no previous report on the inheritance pattern and genetic architecture of the physical properties of bread wheat grain; therefore, it is important to know the heritability and correlation of different grain features of wheat in order to develop varieties with better grain features and quality. Our aim was therefore to describe the gene effect and combining ability of kernel characteristics of bread wheat, and to find a correlation among different physical traits of grain by linear regression analysis and path coefficient analysis.

Materials and methods

Five cultivars of spring bread wheat (*Triticum aestivum* L. em. Thell) were crossed in a diallel design, including reciprocals. These 5 parents were selected because of the diversity of their grain characteristics. The parents, Genç99, Balatilla, Sagitario, Pandas, and Adana99, have been widely used as commercial cultivars. All possible 20F_1 hybrids, together with the 5 parents, were planted on December 5, 2006, according to a randomized completely blocked design with 3 replications at the Research and Implementation Area of the Department of Field Crops, Faculty of Agriculture, University of Çukurova, Adana, Turkey. Plots of F_1 hybrids and their parents consisted of 3 rows 1 m long containing 10 plants that were spaced 10 cm within the rows. Spacing between rows was 20 cm.

The soil used in this study was classified as a clay soil in the upper 0-30 cm profile, which contained an average 1.3% organic matter with pH 7.11, 478 K mg kg^{-1}, 15 P mg kg^{-1}, 0.69 Zn mg kg^{-1}, 12.4 Mn mg kg^{-1}, 1.26 Cu mg kg^{-1}, and 9.6 Fe mg kg^{-1}. Total precipitation of the growing season (sowing to physiological maturity) was 294 mm, which was less than the average of long years (468 mm). Agronomic and plant protection measures were kept normal for the entire experiment. Before heading time, the main shoots of 15 plants from each plot were marked with plastic clips.

Ten competitive plants from the parents and F_1's were sampled randomly from the 15 marked plants from each plot. Plants were harvested when grain moisture was about 13 (Zadoks–94) by hand on 5-8 June, 2007. Data on different spike characteristics such as spike length, number of spikelets per spike, number of grains per spike, grain yield per spike were recorded from the 10 marked main stems of plants in each plot, according to method described by Zadoks et al. (1974) and Bell and Fisher (1994).

The data on different physical properties of grain were also collected from the main stem spikes of the same 10 marked plants of each genotype/cross. For uniformity, spikes of the main stem were divided into 3 parts: central, apical, and basal, according to the number of spikelets per spike; grains from each of the portions of spikes were separated manually. Five grains were randomly selected from each of the central, apical, and basal portions of the spike in order to measure different grain physical properties. In total, 11,250 grains were analyzed: 15 grains (5 grains from each part of spike of the main stem) of each of 10 randomly selected plants from each of 25 genotype/crosses with 3 replications. Grain weight was calculated from the total of 15 grains, 5 from each of apical, central, and basal part of the spike, and was averaged to 1. Grain length (mm), grain width (mm), and grain height (mm) were calculated by using a micrometer adjusted to an accuracy of 0.01 mm. The equivalent diameter as the geometric means of 3 dimensions was calculated using the formula [$(De) = (LWH)^{1/3}$]. This equivalent diameter was used to calculate degree of sphericity (Φ) as described by Mohsenin (1996) by using the formula [$(\Phi) = (De/L)\ 100$]. Grain area (mm^2), which was calculated according to the formula [$(GA) = 13/11\ (W + H)\ L$] as described by Kachru et al. (1994), where W, H, and L stand for grain width, grain height, and grain length, respectively.

A separate analysis of variance for all examined characters was performed using the general linear model (PROC GLM) procedure of Statistical Analysis System software (SAS 2002, The SAS system for Windows, release 9.0, SAS Institute Inc, Cary, NC, USA). Separation of the means was determined according to Duncan's multiple range test (SAS 2002). Associations among traits were calculated by the 'CORR' procedure of the SAS program. Stepwise multiple regression analysis was also performed using the REG procedure of the SAS program. Path coefficient analysis was performed on genotype correlation coefficients: grain yield per spike as a dependent variable; other characteristics were taken as independent variables. The analyses of variance for general combining ability (GCA) and specific combining ability (SCA) and reciprocal effects (REs) were carried out using Griffing's (1956) Method 1 and Model 1 (including parents, F_1 and reciprocals) using the TarPopGen Statistical Package Program developed by Özcan (1999).

Results

The analysis of variance indicated significant differences among parents and their F_1 hybrids for all characters except grain height (Table 1). The mean values of 5 parents and their 20 F_1 hybrids for all characteristics under consideration are presented in Table 2.

Analysis of variance for combining ability showed that general combining ability (GCA) and specific combining ability (SCA) were highly significant different for all traits except GCA for grain weight and grain height and SCA for the number of grains per spike, grain height, and grain sphericity (Table 3). Thus, both types of gene action were present in controlling the inheritance of most of the traits studied. Variance of GCA was higher for all traits except grain weight and grain height. GCA:SCA ratio favored GCA for most of the traits except grain weight and grain height, which showed that additive gene action was prominent in controlling most of the traits. Grain weight and grain height were primarily controlled by non-additive gene action in accordance with the lowest values of GCA:SCA ratios as 0.34 and 0.42, respectively. REs were significant for the number of spikelets per spike, the number of grains per spike ($P < 0.05$), and grain weight, grain length, and grain sphericity ($P < 0.01$).

Table 1. Analysis of variance for some spike and grain physical properties in 5 × 5 diallel crosses of bread wheat.

Character	Mean squares			
	Replication	Genotype	Error	CV (%)
d.f.	2	24	48	
Spike length	0.297	1.734**	0.288	4.60
Spikelets per spike	0.021	5.554**	0.980	4.36
Grains per spike	5.315	82.251**	28.733	7.97
Grain yield per spike	0.451	0.274**	0.116	12.36
Grain weight	35.026	40.430**	11.078	8.06
Grain height	0.102	0.051^{ns}	0.036	5.96
Grain length	0.025	0.280**	0.033	2.73
Grain width	0.059	0.051*	0.024	5.57
Grain area	14.251	31.373**	12.950	7.60
Grain sphericity	16.573	12.359**	2.769	2.85

*, **: Significant at P < 0.05, P < 0.01 probability level, respectively;
^{ns}: non-significantly; d.f.: degree of freedom; CV: coefficient of variation.

Table 2. Means of some spike and grain physical properties of parents and their F_1 progeny in 5 × 5 diallel cross of bread wheat.

Parents and crosses [a]	SL (cm)	SS (number)	GS (number)	GYS (g)	GW (mg)	GH (mm)	GL (mm)	GWI (mm)	GA (mm^2)	GSH (Φ)
Genç 99 (1)	11.3 def	20.7ef	72.4 abc	2.99abc	41.4b-f	3.18a-d	6.88 bc	2.72 cd	48.0a-f	56.8d-g
Balatilla (2)	11.6 c-f	21.4de	69.5a-e	2.58b-e	40.4b-f	3.27abc	6.21g	2.83a-d	44.8c-f	62.1 ab
Sagitario (3)	9.8 g	19.1 f	63.7b-g	2.12e	38.7c-g	2.99bcd	6.51d-g	2.61 d	43.0a	56.9d-g
Pandas (4)	10.8 fg	22.8a-d	61.7d-g	2.72a-e	45.8 ab	3.33ab	7.25 a	3.03 ab	54.5 a	57.7 c-g
Adana 99 (5)	13.1 a	23.8abc	71.7a-d	3.13 abc	41.4b-f	3.20a-d	6.31fg	2.73 bcd	44.2def	60.4 abc
1 × 2	11.0 ef	19.6 f	58.5fg	2.47cde	42.4a-e	3.13a-d	6.32 fg	2.67cd	43.5 def	59.3b-f
1 × 3	10.8 fg	22.6bcd	69.3a-e	2.97abc	45.1abc	3.17a-d	6.0 b-e	2.66 cd	47.1b-f	56.6efg
1 × 4	12.3 a-d	24.3 ab	72.7ab	2.56b-e	35.5fg	2.93cd	6.53 d-g	2.70 cd	43.5 def	57.1c-g
1 × 5	12.0 b-e	22.5bcd	73.2 ab	3.24 ab	44.1 abc	3.31ab	6.61 c-f	2.79a-d	47.7 a-f	59.6a-f
2 × 1	10.7 fg	22.0 cde	69.3a-e	2.53cde	36.6efg	3.14a-d	6.67 cde	2.67cd	45.8 c-f	57.3c-g
2 × 3	11.0 ef	22.8a-d	62.0c-g	2.59b-e	40.6b-f	3.26abc	6.51d-g	2.80 a-d	46.7 b-f	60.0 a-d
2 × 4	12.0 b-e	23.7abc	67.4b-g	2.61b-e	36.6efg	3.13a-d	7.22 a	2.74 bcd	50.1 a-f	54.8 g
2 × 5	11.8 b-e	23.0a-d	72.9 ab	2.85a-d	36.8d-g	3.15a-d	6.51 d-g	2.60 d	44.3def	57.8 c-g
3 × 1	11.0 ef	23.1a-d	70.3 a-e	2.70a-e	40.4b-f	3.11a-d	6.75 b-e	2.63 d	45.8 c-f	56.4fg
3 × 2	11.3 c-f	23.4abc	66.0b-g	2.87abc	44.8abc	3.33ab	6.76b-e	2.95 abc	50.2 a-e	59.8a-e
3 × 4	12.3 abc	24.7 a	63.0b-g	2.98abc	43.3a-d	3.28abc	6.83bcd	2.95abc	50.4 a-d	59.3b-f
3 × 5	11.9 b-e	23.8abc	69.1a-e	3.09abc	46.3 ab	3.30abc	6.68 cde	2.97 abc	49.5 a-f	60.3 abc
4 × 1	12.3 a-d	23.9abc	64.4b-g	3.00abc	41.7a-f	3.20a-d	7.03 ab	2.69 cd	49.0 a-f	55.8g
4 × 2	12.2a-d	22.9a-d	69.6a-e	2.82a-d	48.1 a	3.40a	7.05 ab	3.05 a	53.7 ab	59.3 b-f
4 × 3	11.3 c-f	22.9a-d	61.1d-g	2.57b-e	42.9a-e	3.14a-d	7.31 a	2.82 a-d	51.5 abc	54.9 g
4 × 5	12.2 a-d	22.6bcd	57.9 g	2.18de	38.7c-g	3.08a-d	6.64c-f	2.71cd	45.5c-f	57.4c-g
5 × 1	12.8 ab	24.2 ab	79.0 a	3.33 a	41.3b-f	3.27abc	6.63c-f	2.79a-d	47.5a-f	59.2b-f
5 × 2	12.0 b-e	22.0cde	60.9efg	2.60b-e	41.3b-f	3.35ab	6.22 g	2.83 a-d	45.4 c-f	62.6 a
5 × 3	12.2 a-d	22.7bcd	66.4b-g	2.86abc	45.1 abc	3.25abc	6.70b-e	2.91 a-d	48.9 a-f	59.5a-f
5 × 4	12.3 a-d	23.1abcd	68.7a-f	2.49cde	33.4 g	2.87d	6.45 efg	2.75 bcd	42.9 f	57.5c-d

[a]: SL: spike length, SS: spikelets per spike, GS: grains per spike, GYS: grain yield per spike, GW: grain weight, GH: grain height, GL: grain length, GWI: grain width, GA: grain area; GSH: grain sphericity. Φ: degree of sphericity

Table 3. Analysis of variance for combining ability of some spike and grain physical properties in bread wheat.

Physical properties	Mean squares				
	GCA	SCA	Reciprocal	Error	GCA/SCA
d.f.	4	10	10	48	
Spike length	1.947**	0.491**	0.118ns	0.096	3.97
Spikelets per spike	2.653**	2.572**	0.809*	0.327	1.03
Grains per spike	54.239**	18.553ns	25.553*	9.578	2.92
Grain yield per spike	0.144*	0.123**	0.039ns	0.039	1.17
Grain weight	5.120ns	15.277**	15.019**	3.693	0.34
Grain height	0.010ns	0.024ns	0.013ns	0.012	0.42
Grain length	0.304**	0.060**	0.042**	0.011	5.07
Grain width	0.027*	0.020*	0.010ns	0.008	1.35
Grain area	18.586**	14.064**	3.600ns	4.317	1.32
Grain sphericity	12.259**	1.568ns	3.416**	0.923	7.82

*, ** : Significant at P < 0.05, P < 0.01 probability level, respectively; ns: non-significant, d.f.: degree of freedom.

Estimates of GCA revealed that parent Adana99 was the best general combiner for SL. and GYS. The next best combiners were SS, GS, and GSH. Similarly, Pandas was one of the best general combiners for SS, GL, GWI, and GA, while Genç99 was the best combiner for GS, as well as a good-to-average combiner for GYS. Parent Balatilla was a good combiner for GSH, whereas Sagitario was a good combiner for GW (Table 4).

Estimates of specific combining ability (SCA) of the crosses are given in Table 4. The Sagitario × Adana99 (3 × 5) combination can be used to develop desirable progenies for GW, GWI, GA, and GSH, whereas Balatilla × Pandas (2 × 4) can be used for desirable progenies for GS, GL, and GA. Genç99 × Adana99 (1 × 5) and Sagitario × Adana99 (3 × 5) produced positive SCA effects for all traits, whereas Genç99 × Pandas (1 × 4) produced significant SCA values for SL and SS. Similarly, Genç99 × Sagitario (1 × 3) worked well for SS and GS. Balatilla × Sagitario (2 × 3) for SS, GA, and GSH were other good combinations. Sagitario × Pandas (3 × 4) showed positive SCA values for all characteristics except for GS.

Estimates of reciprocal effects (Table 4) of the crosses showed that SS was significant in Balatila × Genç99 (2 × 1) and Adana99 × Genç99 (5 × 1), but worked negatively in Panda × Sagitario (4 × 3) and Adana99 × Sagitario (5 × 3). GS was significantly affected in Balatila × Genç 99 (2 × 1) and Adana99 × Pandas (5 × 4), but was negatively affected in the cross Adana99 × Balatila (5 × 2). Similarly, Pandas × Balatila (4 × 2) and Pandas × Genç99 (4 × 1) had significant positive reciprocal effects for GW, whereas Balatila × Genç99 (2 × 1) showed negative reciprocal effects. Pandas × Genç99 (4 × 1) and Pandas × Sagitario (4 × 3) showed positive REs for GL. A positive reciprocal effect on the percentage of GSH was observed in Pandas × Balatila (4 × 2) and Adana × Balatila (5 × 2), whereas a significant negative effect was evident in Pandas × Sagitario (4 × 3).

Correlation coefficient for different physical parameters showed that significant and positive correlations exist between most of the traits (Table 5); therefore, linear regression analysis was performed to see whether selection for stability in one characteristic affected the stability of other characteristics. There were significant positive correlations between all features (data not shown), whereas a significant negative correlation existed only between GL and GSH (data not shown).

Correlation analysis for different physical properties revealed that grain yield per spike is an important characteristic in wheat breeding and had a

Table 4. Estimation of general combining ability (GCA), specific combining ability (SCA) and resiprocal effect (RE) in the F_1 generation for some spike and grain physical properties in bread wheat.

Parents and Crosses	SL	SS	GS	GYS	GW	GL	GWI	GA	GSH
GCA									
Gençç99 (1)	-0.152	-0.351*	2.930**	0.124*	-0.316	0.017	-0.080**	-0.745	-0.867**
Balatilla (2)	-0.151	-0.467**	-0.679	-0.104	-0.502	-0.128**	0.012	-0.416	1.188**
Sagitario (3)	-0.518**	-0.286	-1.770*	-0.068	1.257*	0.041	0.007	0.285	-0.272
Pandas (4)	0.157	0.669**	-2.409**	-0.089	-0.118	0.260**	0.064**	2.204**	-1.179**
Adana 99 (5)	0.663**	0.435**	1.927*	0.137*	-0.320	-0.190**	-0.003	-1.329*	1.130**
gi[a] (0.05)	0.172	0.318	1.715	0.110	1.066	0.059	0.049	1.152	0.533
gi (0.01)	0.220	0.405	2.188	0.140	1.360	0.075	0.063	1.470	0.680
SCA									
1 × 2	-0.541**	-1.080**	-5.609**	-0.275*	-0.964	-0.088	-0.049	-1.527	-0.382
1 × 3	-0.119	0.754*	1.412	0.023	0.471	0.022	-0.064	-0.426	-0.697
1 × 4	0.575**	1.090**	0.814	-0.008	-2.274*	-0.190*	-0.074	-2.577*	0.135
1 × 5	0.196	0.571	4.046*	0.272*	2.060	0.101	0.089	2.358	0.784
2 × 3	0.171	1.189**	-0.784	0.145	0.620	0.030	0.071	1.249	0.663
2 × 4	0.418*	0.415	4.353*	0.156	1.683	0.306**	0.038	2.760*	-1.272*
2 × 5	-0.255	-0.171	-1.565	-0.062	-1.400	-0.015	-0.078	-0.773	-0.433
3 × 4	0.513**	0.720*	-0.999	0.175	0.638	0.074	0.033	1.094	0.213
3 × 5	0.240	0.384	0.385	0.154	3.435**	0.145	0.152**	2.936*	0.729
4 × 5	-0.277	-0.960**	-3.460	-0.467**	-4.818**	-0.222**	-0.118*	-4.055**	-0.848
si[b] (0.05)	0.355	0.653	3.538	0.225	2.197	0.165	0.102	2.374	1.098
si (0.01)	0.453	0.833	4.513	0.288	2.803	0.210	0.130	3.028	1.400
RE									
2 × 1	-0.153	1.195**	5.388*	0.032	-2.888*	0.177*	-0.002	1.178	-0.993
3 × 1	0.125	0.237	0.458	-0.133	-2.352	-0.025	-0.015	-0.613	-0.105
4 × 1	-0.018	-0.195	-4.112	0.218	3.115*	0.255**	-0.005	2.755	-0.647
5 × 1	0.455*	0.885*	2.903	0.047	-1.403	0.010	0.002	-0.083	-0.178
3 × 2	0.167	0.305	2.013	0.140	2.098	0.125	0.072	1.712	-0.060
4 × 2	0.098	-0.403	1.068	0.107	5.733**	-0.087	0.155*	1.832	2.265**
5 × 2	0.082	-0.500	-6.013**	-0.125	2.262	-0.147	0.113	0.548	2.377**
4 × 3	-0.520*	-0.917*	-0.952	-0.205	-0.170	0.240**	-0.065	0.527	-2.160**
5 × 3	0.160	-0.570	-1.375	-0.117	-0.552	0.012	-0.028	-0.282	-0.425
5 × 4	0.042	0.265	5.388*	0.158	-2.613	-0.097	0.018	-1.303	0.035
rji[c] (0.05)	0.429	0.792	4.288	0.272	2.664	0.147	0.123	2.879	1.331
rji (0.01)	0.548	1.010	5.470	0.348	3.398	0.188	0.158	3.673	1.698

[a]: Critical differences between GCA effects of parents.
[b]: Critical differences between SCA effects of the ijth F_1 hybrid.
[c]: Critical differences between reciprocal effects of the jith F_1 hybrid.

Table 5. Correlation coefficients among spike and grain physical properties in bread wheat.

Property[a]	SS	GS	GYS	GW	GH	GL	GWI	GA	GSH
SL	0.62**	0.33**	0.33**	-0.05ns	0.08ns	-0.05ns	0.13ns	0.03ns	0.16ns
SS	-	0.37**	0.45**	0.12ns	0.18ns	0.31**	0.27*	0.32**	-0.00ns
GS	-	-	0.55**	-0.02ns	0.13ns	-0.00ns	0.04ns	0.06ns	0.08ns
GYS	-	-	-	0.56**	0.58**	0.23*	0.49**	0.50**	0.36**
GW	-	-	-	-	0.75**	0.38**	0.71**	0.73**	0.44**
GH	-	-	-	-	-	0.26*	0.80**	0.78**	0.72**
GL	-	-	-	-	-	-	0.42**	0.78**	-0.43**
GWI	-	-	-	-	-	-	-	0.86**	0.59**
GA	-	-	-	-	-	-	-	-	0.23*

[a]: SL: spike length, SS: spikelets per spike, GS: grains per spike, GYS: grain yield per spike, GW: grain weight, GH: grain height, GL: grain length, GWI: grain width, GA: grain area; GSH: grain sphericity.

*, **: Correlation coefficient is significant at $P < 0.05$ and $P < 0.01$ respectively. ns: Non-significant.

significant positive association with all other traits; hence, it should be further analyzed. Because of this, path coefficient analysis was performed to see the direct and indirect effects of all grain physical features on grain yield per spike (Table 6). The highest direct effect on grain yield per spike was through grain height (28.7%), followed by grain width and grains per spike (25.9% and 23.9%, respectively). Grain sphericity and grain area had a direct negative effect on grain yield per spike. The number of grains per spike was an important feature that had the highest indirect effect (29%) on grain yield per spike via grain height. Grain sphericity, grain weight, grain area, and grain width also had important indirect effects on grain yield per spike through grain height as 27.2%, 26.3%, 24.5%, and 23.1%, respectively. Spikelets per spike (25.7%), grain area (24.4%), spike length (23.1%), grain weight (22.1%), grain height (20.4%), and grain sphericity (19.9%) are also important characteristics that had important indirect effects on grain yield per spike via grain width.

Discussion

The diallel analysis between 5 bread wheat cultivars was performed in order to evaluate the mode of inheritance and combining ability of grain's physical properties and some spike characteristics. This study is in agreement with previously established literature, which reported significant differences between genotypes for different spike characteristics (e.g. Borghi and Perenzin, 1994; Li et al., 1997; Pecetti et al., 2001; Sharma et al., 2003; Joshi et al., 2004; Singh et al., 2004; Dağüstü, 2008). However, we did not find any studies describing the inheritance of the physical properties of bread wheat grains except Topal et al. (2004), who reported heterosis, combining ability, and correlations of grain physical properties in durum wheat. In the present study, it is clear that both additive and non- additive gene effects were important, but a large part of the total genetic variation observed for 8 out of the 10 characteristics was associated with genes that are additive in nature, since the variance in GCA was higher than that in SCA. The present findings thus supported the data presented by several previous studies (e.g. Bhatti, 1970; Borghi and Perenzin, 1994; Joshi et al., 2004; Sharma et al., 2005; Kamaluddin et al., 2007). They also showed that additive genetic variation was the main source of genetic control for most of the economic traits in bread wheat. Sharma et al. (2003) reported that additive gene effects were significant for spike length in all cases, Joshi et al. (2004) also explained the predominance of additive gene effects for spike length, number of grains per spike, and grain yield per spike, as well as a report by Ekiz et al. (1998)

Table 6. Path coefficient analysis of grain yield per spike and other physical properties among different bread wheat genotypes/crosses.

Variable[a]	Coefficient of correlation (r)	Direct effects		Indirect effects							
				SL		SS		GS		GW	
		p[b]	%	p	%	p	%	p	%	p	%
SL	0.33**	0.13	6.88	-	-	0.08	4.15	0.13	6.99	-0.02	1.22
SS	0.45**	0.12	3.54	0.08	2.26	-	-	0.15	4.25	0.05	1.44
GS	0.55**	0.39	23.99	0.04	2.51	0.05	2.80	-	-	-0.01	0.53
GW	0.56**	0.42	4.12	-0.01	0.06	0.01	0.14	-0.01	0.08	-	-
GH	0.58**	3.60	28.67	0.01	0.08	0.02	0.187	0.05	0.41	0.32	2.55
GL	0.23*	-0.50	6.43	-0.01	0.08	0.04	0.48	-0.01	0.01	0.16	2.07
GWI	0.49**	3.23	25.97	0.02	0.13	0.03	0.27	0.02	0.13	0.30	2.42
GA	0.50**	-4.22	37.03	0.01	0.04	0.04	0.34	0.02	0.20	0.31	2.72
GSH	0.36**	-3.61	37.84	0.02	0.21	-0.01	0.01	0.03	0.33	0.19	1.96

Variable[a]	r	Direct effects		Indirect effects									
				GH		GL		GWI		GA		GSH	
		p[b]	%	p	%	p	%	p	%	p	%	p	%
SL	0.33**	0.13	6.88	0.30	16.6	0.03	1.40	0.42	23.1	-0.15	8.43	-0.57	31.3
SS	0.45**	0.12	3.54	0.65	18.9	-0.15	4.46	0.89	25.7	-1.35	39.1	0.01	0.43
GS	0.55**	0.39	23.99	0.47	29.0	0.00	0.02	0.14	8.40	-0.24	14.8	-0.29	17.9
GW	0.56**	0.42	4.12	2.71	26.3	-0.19	1.85	2.28	22.1	-3.08	29.9	-1.59	15.4
GH	0.58**	3.60	28.67	-	-	-0.13	1.03	2.57	20.4	-3.27	26.0	-2.59	20.6
GL	0.23*	-0.50	6.43	0.93	11.9	-	-	1.36	17.3	-3.28	42.0	1.54	19.7
GWI	0.49**	3.23	25.97	2.87	23.1	-0.21	1.70	-	-	-3.63	29.2	-2.12	17.1
GA	0.50**	-4.22	37.03	2.80	24.54	-0.39	3.43	2.78	24.4	-	-	-0.84	7.33
GSH	0.36**	-3.61	37.84	2.59	27.2	0.21	2.25	1.90	19.9	-0.98	10.3	-	-

[a]: SL: spike length, SS: spikelets per spike, GS: grains per spike, GYS: grain yield per spike, GW: grain weight, GH: grain height, GL: grain length, GWI: grain width, GA: grain area; GSH: grain sphericity.

[b]: Path coefficient **: $P < 0.0.1$ *: $P < 0.05$

for kernel mass and Topal et al. (2004) indicating that GCA effects were dominant for kernel length, kernel area, kernel sphericity, and kernel mass in durum wheat. However, major gene effects in the inheritance of grains per spike was non-fixable (additive) in nature, as reported by Sharma and Sain (2004). The importance of dominance gene effects was reported by Gorjanovic and Balalic (2005), whereas equal roles of both additive and non-additive effects for inheritance for yield and its components were illustrated by Bhullar et al. (1979) and Ansari (2003).

The choice of appropriate components for crossing is the first and foremost step in the creation of a new crop cultivar. Breeders used combining ability to select those parents that have maximum potential of transmitting desirable genes in the progenies (Gorjanovic and Balalic, 2005). In wheat, where the ultimate objective is to develop pure line varieties, estimates of general combining ability are very important, because GCA represents additive gene effect and additive × additive interaction effects (Gallais 2003; Joshi et al., 2004) that can be fixed in further generations, whereas SCA represents dominance epistatis (Griffing, 1956). GCA:SCA ratio is also very important for determining the genetic architecture of traits. A GCA:SCA ratio with a value greater than 1 indicates additive gene action, whereas a GCA:SCA ratio with a value less than 1 shows dominant gene action (Singh et al., 1986). Grain sphericity and grain length have the highest additive gene effects in accordance with the GCA:SCA ratio. Therefore, selection for these traits in early generations may contribute to better end-use quality in a wheat breeding program.

To produce good progeny, the use of those parents that are good general combiners for most of the characteristics is suggested in multiple crossing programs (Barnard et al., 2002). Pandas was the best parent for grain width, grain area, and spikelets per spike. Adana99 was the high combiner for spike length and grain yield per spike, while Genç 99 worked best for the number of grains per spike due to high GCA value. With regard to the importance of different parents in a breeding program for improving these traits, the results of this study showed that Adana99 could be one of the parents, as well as Pandas and Genç 99.

For self-pollinated crops like wheat, SCA based on heterotic effect is likely to have a small contribution toward the improvement of any particular trait (Joshi et al., 2004). The crosses having high SCA were higher yielding, and in most of the crosses one of the parents involved was a good general combiner, indicating that these combinations would yield desirable transgressive segregants (Joshi et al., 2004). Pandas and Adana99 proved to be the best parents for both GCA and SCA.

Significant REs on grain weight, grain length, and grain area ($P < 0.01$), and spikelets per spike, and grains per spike ($P < 0.05$) indicate the cytoplasmic influences for these traits. This might be due to the cytoplasmic influences of the female parents for these characters (Barnard et al., 2002; Topal et al., 2004; Dağüstü, 2008). For improvement of these characteristics, Adana99 and Pandas should be exploited as male and female parents.

Correlation between different traits is generally due to the presence of linked genes and the epistatic effect of different genes. Environment plays an important role in correlation. In some cases, environment affects both the traits simultaneously in the same direction or sometimes in different directions (Acreche and Slafer, 2005). Grain weight and grains per spike have significant positive correlations with grain yield per spike, but there is no correlation between grain weight and grains per spike. This contradicts the findings of Acreche and Slafer (2005), who found that grain weight decreased when the number of grains increased, due to genetic and environmental factors. Grain yield per spike had positive and significant correlations with all other traits. Previous researchers (Özkan et al., 1997; Acreche and Slafer, 2005; Dağüstü 2008) also observed that grain yield per spike is positively correlated with the number of spikelets per spike and number of grains per spike. The yield of wheat can be accelerated by using progenies selected for more grains per spike, grain weight, and grain height. Similarly, grain area had a significant positive correlation with all traits except the number of grain per spike and spike length. This is in agreement with the findings of Topal et al. (2004), who discovered a positive correlation between kernel area, kernel height, and kernel length in durum wheat. From the results of the correlation analysis, it could be concluded that the size of the wheat kernel can be improved by selecting progenies with higher width and length of kernels, whereas the effects of other features cannot be omitted.

Path coefficient analysis for different physical properties showed that the component with the highest correlation coefficient with grain yield per spike also had the maximum direct effect on spike yield. Other studies (Özkan et al., 1997; Dağüstü, 2008) suggested a similar conclusion. Grain width and grains per spike are important features that have a direct effect on spike yield. Grain width is also an important characteristic that has an indirect effect on most of the other characteristics. The parent Pandas (for grain width) and parent Adana99 and Genç99 (for grain per spike) produced significant GCA values. Therefore, they could be considered as one of the parents in a breeding program when better grain features are desired. Moreover, it could be possible to increase the yield of wheat through grain weight and grain per spike.

In this study, we observed that both additive and non-additive components of genetic variation were present in governing the inheritance of all physical properties, although additive gene action was prominent, except for grain weight and grain height. Therefore, good success can be achieved when selecting for grain sphericity, grain length, spike length, and number of grains per spike having a high value of GCA. Characteristics with a high SCA can be used for hybrid wheat production or application of double haploid production via anther culture on F_1 progenies. Thus, it is also suggested from these results that selection for the right characteristics will ensure improvement of more than one characteristic simultaneously, due to the correlation among different traits.

In some countries (e.g., the US, Australia, and Canada) a new cultivar must meet a prescribed minimum level of quality before it is recommended for registration for commercial production (Bushuk, 1998). Therefore, in these countries, a simple test known as 'single kernel wheat characterization system (SKCS)' has been widely used to test the quality of wheat grains (Martin et al., 1993). This test was developed to determine directly the physical properties of wheat grain, such as grain weight, size of grain, hardness, thickness, and length of grains that become prominent for end-use quality and for wheat importers throughout the world (Lyford et al., 2004). Moreover, the knowledge of mechanical properties of wheat grains is important for designing a machine for sowing, handling, milling, cleaning, storing, and conveying purposes. Milling sieves are designed according to dimensions of grains such as length, width, and height, while grain sphericity and grain area are important during storage and drying after harvest. This strategy might be helpful for wheat breeders to develop new varieties with better grain features to improve the milling and baking quality of wheat.

Acknowledgment

Thanks are due to TÜBİTAK for awarding a doctoral fellowship to Faheem Shehzad Baloch.

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