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REVIEW

Relationship between phenotypic and genetic diversity of parental genotypes and the specific combining ability and heterosis effects in wheat (*Triticum aestivum* L.)

K. Krystkowiak · T. Adamski · M. Surma · Z. Kaczmarek

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Abstract The purpose of the study was to evaluate the relationship between the genetic distances (GD) and phenotypic distances (PD) of parents and the specific combining ability (SCA) and heterosis effects. The experiment comprised 18 parental genotypes of wheat (*Triticum aestivum* L.) and 76 F_2 hybrids, obtained after crossing in a line × tester scheme. Parents and hybrids were examined in a field experiment conducted in a block design with three replications. SCA as well as mid-parent heterosis effects were estimated for selected morphological and technological traits. PDs and GDs were investigated between pairs of parental genotypes. GD between parental genotypes was evaluated by using randomly amplified polymorphic DNA markers. Heterosis was observed in all hybrids, and protein content exhibited the highest heterosis among the seven examined traits. The relationship between PD and GD as well as the SCA and mid-parent heterosis effects were evaluated using correlation coefficient. The correlation between PD, SCA and heterosis were low and not significant for the examined traits, whereas the correlation between SCA, heterosis and GDs were significant for protein content and rheological properties. The results indicate that GDs between parents can be used to predict performance of hybrids for selected technological traits.

Keywords *Triticum aestivum* · Combining ability · Genetic distance · Heterosis · Line × tester analysis · Phenotypic distance · Randomly amplified polymorphic DNA

Introduction

The choice of appropriate components for crossing is the first and foremost step in the creation of new crop cultivars. Knowledge on the effects of general combining ability (GCA) and specific combining ability (SCA) is useful in the selection of parental genotypes. The main goal of hybrid wheat breeding is the identification of parents with high SCA for technological quality and agronomic traits. Such data facilitate the choice of pairs of parental genotypes with a high probability of heterosis in their F_1 progeny.

The breeding value of genotypes, including combining ability, is evaluated on the basis of the analysis of hybrids produced in appropriate crossing schemes. Most frequently diallel or factorial (line × tester) crossing is applied (Marciniak et al. 2003; Ahuja and Dhayal 2007). In case of self-pollinated crops these methods require a large number of manual crossings, which make them time consuming and expensive

K. Krystkowiak (✉) · T. Adamski · M. Surma · Z. Kaczmarek
Institute of Plant Genetics, Polish Academy of Sciences, Strzeszyńska 34, 60-479 Poznan, Poland
e-mail: kkry@igr.poznan.pl

(Sant et al. 1999; Shen et al. 2006). Thus, the selection of parental genotypes in wheat breeding based on the combining ability is seldom used.

Heterosis effect has been used in breeding of open-pollinated plants, such as maize or rye. At present, hybrid breeding is also being focused on self-pollinated plants, including wheat (Liu et al. 1999; Pomaj 2002; Weißmann and Weißmann 2002). Even though the yield heterosis level in wheat cannot compare with those found in allogamous species such as maize, the agronomic value of wheat hybrids appears to be promising (Oury et al. 2000). However, knowledge about hybrid performance, the relative importance of GCA, SCA and genetic background of parental materials for exploitation of heterosis in wheat, remains limited. A few studies applying restriction fragment length polymorphism (RFLP), randomly amplified polymorphic DNA (RAPD) or simple sequence repeat (SSR) markers were carried out, but no clear relationship between molecular diversity and heterosis was observed (Liu et al. 1999; Corbellini et al. 2002; Dreisigacker et al. 2005). Along with advances in studies facilitating the identification of quantitative trait loci (QTLs) it has become possible to know the genetic aspects of heterosis in combination with the role of an individual QTL and their interactions. Three types of QTL interactions causing heterosis have been described previously: Over-dominance in maize (Stuber et al. 1992), dominance in rice (Xiao et al. 1995) and epistasis in rice (Yu et al. 1997; Li et al. 2001).

Molecular techniques in combination with biometrical methods have opened new possibilities to evaluate input materials in terms of their suitability as parents. The initial studies were associated with the search for a relationship between the genetic diversity of parents, evaluated with molecular techniques, and their hybrid performance. Different methods have been used to assess the diversity of plant materials. This information can be obtained by studying pedigree, morphological traits, isozymes and DNA analysis (Cox et al. 1985; Shamsuddin 1985; Chan and Sun 1997). DNA markers are most suitable for genetic diversity estimations (Plaschke et al. 1995; Sun et al. 2003). RAPD analysis is simpler than some other molecular techniques so RAPD markers have also been proposed as an approach to assess genetic divergence among genotypes (Jain et al. 1994). RAPD has also been attempted to develop a method to select crossing components based on genetic distance (GD) between genotypes. Such studies have been conducted, among others, on sunflower, wheat and maize (Melchinger et al. 1990; Cheres et al. 2000; Corbellini et al. 2002). In heterosis breeding this approach was found on the simultaneous evaluation of both GCA and SCA as well as GD (Cox and Murphy 1990; Boppenmaier et al. 1993; Bernardo 1994; Martin et al. 1995; Barbosa-Neto et al. 1996; Diers et al. 1996; Burkhamer et al. 1998; Corbellini et al. 2002). In wheat, Martin et al. (1995) found a significant relationship between pedigree-based GD and heterosis for protein content and grain weight. On the basis of experiments conducted in different environments with 722 wheat hybrids, Barbosa-Neto et al. (1996) showed the occurrence of a weak relationship between GD based on RFLP and coefficient of parentage (COP) and heterosis effects. In turn, Corbellini et al. (2002) investigated the relationship between genetic similarity and GCA and SCA for yield and its components in wheat and found it unfeasible to apply these relationships to predict heterosis effects.

However, it needs to be stressed that phenotypic variation of parental forms was not taken into consideration in those studies. Occurrence of heterosis and transgression effects can be expected in the progenies of crosses between genotypes with dispersion of alleles controlling a given quantitative trait in their genomes, manifested in phenotypic similarity but genetic diversity of parents (Jinks and Pooni 1976; Mather and Jinks 1982; Kuczyńska et al. 2007).

The objectives of this study were as follows: (i) to assess genetic diversity based on RAPD markers of selected wheat cultivars; (ii) to estimate GCA, SCA and heterosis effects; (iii) to correlate the estimated parental genetic diversity with SCA and heterosis effects.

Materials and methods

Plant materials and field experiments

Material for the studies included 18 winter wheat cultivars (*Triticum aestivum* L.) of different origin (Table 1), belonging to different bread quality classes, and their 76 F_2 hybrids that had been obtained after crossing in a line × tester scheme. Two

Table 1 List of cultivars studied including pedigree and country of origin

Cultivar name	Origin	Pedigree	General combining ability effects[1]
Alidos^{A}	Germany	Arkos/Hadmerslebener-00914-76; Cato//Lundi/Selkirk/3/Alcedo	GWE (0.21^{A}), GWP (-0.52^{A}),WA (-0.57^{A})
Aristos^{A}	Germany	No data	TGW ($2.92^{A)}$, GWE (0.11^{A}), GWP (1.18^{A}), WA (-0.77^{A}), DD (-0.05^{A}), PC (-0.24^{A})
Aron^{A}	Germany	Arkos/Compal	TGW (-1.98^{A}), GWE (-0.07^{A}), GWP (-0.30^{A}), DS (-1.14^{A}), PC (0.09^{A})
Batis^{B}	Germany	RPB-4945//Maris-Huntsman/Glanens/3/Urban	TGW(-1.97^{B}), WA (-0.76^{B}), DD (-0.24^{B}), PC (-0.18^{B})
Begra^{AB}	Poland	Grana/Bezostaya-1	GWE (-0.18^{B}), GWP (1.02^{B}, $-0.62^{A)}$, WA (0.70^{A}), DS. (-9.96^{A}), PC (0.25^{A})
Borenos^{A}	Germany	Alcedo//Dornburg-4065-67*2/Kenya-Civet/3/2*Alcedo; Kenya-Civet/2*Dornburg-Stamm-4056-67//3*Alcedo	TGE (-2.03^{A}), GWE (-0.21^{A}), GWP (-0.62^{A})
Bussard^{A}	Germany	Kranich/Maris-Huntsman//Monopol; Chinese-166/Strubes-Dickkopf// Pansar-III/3/Teutonen/Dhe-516 /4/ Heines-VII	TGW (-1.31^{A}), GWE (-0.09^{A})
Charger^{A}	England	Fresco/Mandate	TGW (-1.04^{A}), GWP (-1.28^{B}), WA(-0.84^{A}), DD (0.22^{B}), DS (-10.53^{B}), PC (0.28^{A}, $0.53^{B)}$
Carolus^{A}	Germany	Cama//Diplomat/Perseus	TGW (1.89^{A}), GWP (0.29^{A}), WA (1.30^{A}), PC (0.34^{A})
Dad76^{AB}	Poland	No data	TGW (1.39^{B},1.82^{A}), GWE (0.14^{B}, 0.22^{A}), GWP (0.88^{A}), WA (-1.41^{A}, -1.04^{B}), DS (15.09^{A},19.88^{B}), PC (0.59^{B})
Elena^{AB}	Poland	STH-1262/SMH-1320	TGW (-1.67^{A}), GWP (-0.55^{A}, 0.68^{B}), WA (1.61^{A},1.16^{B}), DD (0.18^{AB}), PC (0.34^{A}, -0.82^{B})
Flair^{AB}	Germany	Ares/Marabu; Ares/3/Rabe/Jubilar//Armada	TGW (-1.09^{A}, -1.29^{B}), DD (-0.23^{B}), DS (-8.45^{B}), PC (0.15^{A}, -0.77^{B})
Kobra^{AB}	Poland	Maris-Huntsman/Krasnodarskaya-39//Mironovskaya -808 / Luna	GWP (0.48^{A}), WA (-0.73^{B}), DD (0.29^{A}, -0.18^{B}), PC (-0.13^{A}, 0.34^{B})
Kornett^{B}	Germany	No data	TGW (3.17^{B}), GWE (0.08^{B}), WA (-1.04^{B}), PC (0.31^{B})
Kris^{AB}	Germany	No data	TGW (2.67^{A}, 1.11^{B}), GWP (-0.88^{B}), DD (-0.18^{A}), DS (6.92^{A}), PC (-0.35^{A}, 0.19^{B})
Mikon^{A}	Germany	Fakon//Gaines/3*Mironovskaya-808	TGW (-1.64^{A}), GWE (-0.21^{A}), PC (-0.52^{A})
Pegassos^{B}	Germany	RPb-49-75/3/Maris-Huntsman/Glaucus//Urban	GWE (-0.09^{B}), WA (1.23^{B}), DD (0.24^{B})
Rektor^{B}	Germany	Kormoran/Monopol; Monopol/Kormoran	GWP (-0.48^{B}), WA (0.56^{B}), PC (-0.12^{B})

For each cultivar the statistically significant general combining ability effects detected for seven agronomic and quality traits are also indicated

[1] Only the statistically significant ($P < 0.05$) GCA effects are reported. TGW-1,000 grain weight (g) GWE-grain weight per ear (g). GWP-grain weight per plant (g). WA-water absorption (%). DD-dough development (min). DS-degree of softening (BU). PC-protein content (%)

[A] Set A

[B] Set B

different sets of parents (males and females) were used: Set A containing 8 maternal genotypes (Begra, Charger, Dad76, Elena, Flair, Kobra, Kris, Mikon) and 6 testers (Alidos, Aristos, Aron, Borenos, Bussard, Carolus), and Set B containing 7 lines (Begra, Charger, Dad76, Elena, Flair, Kobra, Kris) and 4 testers (Batis, Kornett, Pegassos, Rektor).

The field experiments were carried out in 2004/2005 in a randomised block design with three replications. In each experiment seeds were sown on 4 m^2 plots, in 10 cm × 3 cm apart. Parents and their F_2 hybrids were examined in terms of morphological and technological traits. After harvesting thousand-grain weight (g), grain weight per ear (g) and per plant (g), and protein content in grain were recorded. In addition, rheological parameters were evaluated using the Brabender farinograph. Flour samples of 300 g each were taken for analysis. Water absorption (in %), dough development time (in min) and the degree of softening (in Brabender Units, BU) were tested.

PCR-RAPD procedure

300 RAPD (GENSET) primers were screened to identity these, producing relatively high number of polymorphic and repeatable fragments. To check reproducibility, each polymorphic primer was tested three times on the same sample in three independent PCR reactions (Rajora and Rahman 2003; Chen et al. 2005). Primers that consistently generated polymorphic amplicons were retained for molecular analysis. Thirty-four primers were selected and used for RAPD analysis of each studied cultivar. DNA was extracted from 2 mm^2 leaf discs (3-week-old seedlings), soaked for 15 min at 95°C in 200 ml TPS buffer (Thompson and Henry 1995). Amplification was performed in a reaction volume of 25 µl, containing 35 ng of primer, 1.5–4.5 ng DNA, 10 mM Tris–HCl, pH 8.3, 2 mM $MgCl_2$, 2.5 µg BSA, 10 µM of each dNTP, and 1.5 U of Taq DNA polymerase (Fermentas). PCR reactions were carried out in a PTC-200 thermocycler (MJ Research) and the cycling was performed as follows: 95°C/5 min, followed by 40 cycles of 94°C/1 min, 36°C/2 min, 72°C/2 min and final extension at 72°C for 10 min (Kuczyńska et al. 2001). Amplification products were analysed by electrophoresis for 1 h 45 min in 1.5% agarose gels containing TBE buffer and ethidium bromide. The 100 bp DNA Ladder Plus (Fermentas) was used for fragment length determination.

Statistical methods

The data were processed by the univariate analysis of variance (ANOVA) and multivariate analysis of variance (MANOVA). GCA and SCA effects for two line × tester sets of crosses for all morphological and technological traits were estimated according to Kaczmarek et al. (2005). Heterosis for a given trait was evaluated as the difference between F_2 hybrid performance and mid-parent value. Estimated GCA (the average performance of a parent in a series of crosses) and SCA (deviation in the performance of a cross from the performance predicted on the basis of GCA of its parents) effects and heterosis were tested by F-statistic, for each trait independently. In addition, for all traits jointly, SCA and heterosis effects were tested and described by F-statistic value (Kaczmarek and Krajewski 1996). Differences between the studied cultivars for all traits treated simultaneously were assessed by using Mahalanobis distance (*D*), which was treated as a measure of multivariate phenotypic distance (PD) between parents. Also, univariate PD was assessed with Euclides distances. GD for all pairs of cultivars were calculated according to the formula given by Nei and Li (1979): $GD = 1 - 2N_{ij}/(N_i + N_j)$, where N_{ij} is the number of alleles present in both compared lines, while N_i and N_j are numbers of alleles in line i and j, respectively.

The relationships between specific combining abilities, heterosis, and GDs and PDs were established by correlation coefficient for two set of crosses together and tested at $P = 0.05$ and 0.01.

Results

Parental genotypes

In Table 2, the mean values of the parental cultivars and hybrids for the analysed morphological and quality traits are reported. A wide discrepancy between parents may be observed in mean values of either group of characteristics. Water absorption of flour ranged from 52.2% in breeding line Dad76 to 58.2% in cv. Mikon. Dough development varied among cultivars; in Kris and Pegassos it was

Table 2 Mean values for analyzed morphological and technological traits of parental genotypes and their hybrids progenies

	Genotype	Water absorption (%)	Dough development (min)	Degree of softening (BU)	Protein content (%)	1,000-Grain weight (g)	Grain weight per ear (g)	Grain weight per plant (g)
Lines	Begra[AB]	56.7	2.0	76.0	13.4	46.8	1.9	10.7
	Begra hybrids	56.3	2.0	83.3	13.4	45.4	2.1	10.6
	Charger[AB]	54.4	2.7	83.3	13.6	43.1	2.0	10.8
	Charger hybrids	55.5	2.1	82.2	13.7	43.9	2.2	10.2
	Dad76[AB]	52.2	2.3	108.3	12.3	47.2	3.2	9.1
	Dad76 hybrids	54.5	2.1	104.3	13.6	46.5	2.4	11.1
	Elena[AB]	57.6	2.2	114.7	13.5	40.8	2.1	9.0
	Elena hybrids	57.2	2.3	88.1	13.2	43.4	2.2	10.5
	Flair[AB]	55.4	2.3	90.7	13.7	42.3	2.4	13.6
	Flair hybrids	55.9	2.0	82.9	13.1	43.7	2.2	10.8
	Kobra[AB]	53.7	2.3	91.3	13.4	45.1	2.1	11.4
	Kobra hybrids	55.5	2.3	84.1	13.4	44.8	2.2	10.9
	Kris[AB]	54.6	1.8	84.0	13.4	49.7	2.0	9.5
	Kris hybrids	55.3	2.0	88.8	13.2	46.9	2.2	10.1
	Mikon[A]	58.2	2.4	84.0	14.2	41.8	1.7	8.7
	Mikon hybrids	56.2	2.2	79.4	13.0	43.2	2.0	10.1
Testers	Alidos[A]	53.5	2.4	71.7	14.1	46.8	2.4	10.9
	Alidos hybrids	55.2	2.1	82.8	13.4	45.3	2.4	9.9
	Aristos[A]	54.9	2.2	71.7	12.7	50.9	2.4	11.6
	Aristos hybrids	55.0	2.2	85.2	13.2	47.7	2.3	11.6
	Aron[A]	55.6	2.6	76.7	13.1	39.5	1.9	10.1
	Aron hybrids	55.7	2.3	82.4	13.6	42.8	2.1	10.1
	Batis[B]	57.5	2.2	71.7	13.2	39.8	1.9	10.0
	Batis hybrids	55.0	1.6	93.8	12.9	42.9	2.2	10.9
	Borenos[A]	54.8	3.0	85.3	13.2	46.3	1.8	10.2
	Borenos hybrids	56.1	2.4	84.1	13.5	42.8	2.0	9.8
	Bussard[A]	54.7	2.8	85.0	13.0	42.7	1.8	10.4
	Bussard hybrids	55.5	2.2	84.0	13.4	43.5	2.1	10.3
	Carolus[A]	53.9	2.8	81.3	14.1	46.7	1.9	9.9
	Carolus hybrids	57.1	2.4	82.8	13.8	46.7	2.2	10.7
	Kornett[B]	57.0	1.8	76.0	13.2	49.7	1.7	9.0
	Kornett hybrids	54.8	1.7	94.1	13.4	48.1	2.3	11.2
	Pegassos[B]	56.3	1.8	78.3	13.6	39.7	1.7	8.0
	Pegassos hybris	57.0	2.1	92.6	13.1	44.1	2.1	10.9
	Rektor[B]	56.4	2.1	71.7	13.3	47.4	2.4	10.9
	Rektor hybrids	56.4	2.0	91.7	13.0	44.5	2.3	10.3

[A] Set A

[B] Set B

1.8 min., while in Borenos it was 3.0 min. Most parental genotypes exhibited dough softening below 92 BU. Breeding line Dad76 and cv. Elena were exceptions in this respect with 108.3 and 114.7 BU, respectively. Protein content was relatively high, ranging from 12.3% (Dad76) to 14.2% (Mikon). 1000-grain weight was between 39.8 (Batis) and 50.9 g (Aristos), grain weight per ear between 1.7

(Kornett, Mikon, Pegassos) and 3.2 g (Dad76), and grain weight per plant between 8.0 (Pegassos) and 13.6 g (Flair).

Phenotypic distances between parents

Estimated value of PD for morphological traits ranged from 0.74 to 10.29 (Table 3). The lowest Mahalanobis distance was found for cv. Carolus and Borenos (0.74) and Carolus-Begra (0.75), and the highest was revealed between cv. Mikon and Flair (8.12) and Flair-Kornett (10.29). PDs for technological traits were greater and ranged from 2.08 to 17.05 (Table 3). The most similar was cv. Batis and Kornett (PD = 2.08) and Charger-Flair (PD = 2.57) and the highest differences were revealed between Mikon-Aristos (PD = 17.01) and cv. Dad76 and Mikon (PD = 17.05).

Genetic distances between parents

Thirty-four primers that depicted very clear RAPD patterns were selected to amplify fragments from the DNA temples of 18 genotypes. Altogether, the primers used resulted in 268 amplification products, of which 145 (54%) were polymorphic. The number of polymorphic bands revealed by a single primer ranged from 3 to 8, with an average of 4.3. The size of amplification products ranged from 150 to 2,000 bp.

Values of GD between parents ranged from 0.24 to 0.55 (Table 3). The lowest GD was found for Begra-Kobra (0.24) and Kris-Kornett (0.25) cultivars, and the highest was shown for the cultivars Kobra and Kornett (0.55), as well as Charger-Pegassos (0.54).

Combining abilities

Univariate analysis of variance showed significant variation of GCA for lines and testers in the case of the most analysed traits in both sets of crosses. However, the GCA variance for testers in dough development time and degree of softening in Set A as well as in degree of softening and grain weight per plant in Set B was an exception. SCA variance was significant for all the traits in Set A, whereas in Set B it appeared to be insignificant for 1,000-grain weight (Table 4). The SCA/GCA ratios in almost all the traits were lower than 1. An exception in both sets of crosses was recorded in the case of degree of softening; for this trait SCA variance was several times higher than GCA of testers. The statistically significant GCA effects for studied genotypes are presented in Table 1. The estimates of SCA effects are given in Table 5 and 6. Out of 76 cross combinations, significant SCA effects were detected in 15 crosses for 1,000-grain weight and grain weight per ear, in 30 for grain weight per plant, 16 crosses for water absorption, 13 for dough development time, 23 for degree of dough softening, and in 48 for protein content. For flour water absorption and dough development positive and significant SCA effects were recorded in about 7% of studied cross combinations. Advantageous (negative) SCA values were found for 16% of crosses in degree of dough softening. A high rate of positive SCA effect was recorded for protein content and grain weight per plant for which SCA appeared to be significant in approximately 18% and 32% analysed cross combinations, respectively. The SCA values for particular traits showed that for water absorption the best combination was Elena × Alidos, for dough development Begra × Batis, Kris × Batis for degree of softening and Mikon × Alidos for protein content. In term of analysed technological properties, the best cross combinations appeared to be Elena × Alidos that exhibited positive SCA effects for water absorption and protein content, and negative for dough softening. For this cross combination significantly

Table 3 Mean and range of genetic and phenotypic distances between parental lines and testers in two wheat sets of line × tester crosses

Distance	Set A		Set B	
	Mean	Range	Mean	Range
Genetic distance	0.38	0.24–0.52	0.40	0.24–0.55
Phenotypic distance for morphological traits	3.81	0.74–8.12	4.43	1.20–10.30
Phenotypic distance for technological traits	8.02	2.82–17.05	5.78	2.08–11.66

Table 4 Analysis of variance for morphological and technological traits of two wheat sets of line × tester crosses

Source of variation	Degrees of freedom	Mean square						
		Water absorption	Dough development	Degree of softening	Protein content	1,000-Grain weight	Grain weight per ear	Grain weight per plant
Set A								
GCA lines	7	16.36**	0.53**	1,054.27**	1.80**	48.20**	0.25**	4.74**
GCA testers	5	13.53**	0.22	28.11	0.94**	105.88**	0.55**	10.60**
SCA (line × tester)	35	6.89**	0.24*	436.14**	0.89**	10.27**	0.07**	3.08**
Error	96	19.80	0.14	98.63	0.06	4.92	0.03	0.58
$\text{SCA/GCA}_{\text{L}}$		0.42	0.45	0.41	0.49	0.21	0.28	0.65
$\text{SCA/GCA}_{\text{T}}$		0.51	1.09	15.52	0.95	0.10	0.13	0.29
Set B								
GCA lines	6	9.03**	0.34*	1,462.99**	3.75**	12.04**	0.12*	8.04**
GCA teestrs	3	17.35**	0.55**	25.69	1.21**	103.32**	0.12*	2.67
Error	56	2.03	0.11	158.63	0.04	3.02	0.04	1.06
SCA (line × tester)	18	7.96**	0.24*	1,064.58**	0.94**	5.18	0.10**	8.75**
$\text{SCA/GCA}_{\text{L}}$		0.88	0.71	0.73	0.25	0.43	0.83	1.09
$\text{SCA/GCA}_{\text{T}}$		0.46	0.44	41.44	0.78	0.05	0.83	3.38

* $P < 0.05$, ** $P < 0.01$

$_{\text{L}}$—Lines

$_{\text{T}}$—Testers

negative SCA for grain weight per plant was recorded.

As a result of MANOVA, multivariate SCA was evaluated for both groups of traits (F-statistic values in Tables 5 and 6). In the case of morphological characters, multivariate SCA effects were significant in 42 out of 76 cross combinations. For technological properties these effects were significant for 72 cross combinations. It may be seen from Table 5 that for all the traits treated simultaneously, SCA effects were frequently significant even though for individual traits they were insignificant (e.g. Kris × Aristos, Kris × Aron).

Heterosis

Heterosis effects evaluated in relation to mid-parent values are presented in Tables 5 and 6. These effects were observed in all the analysed traits but the degree of heterosis showed variation from trait to trait. The lowest number (14%) of significant heterosis effects was observed for 1,000-grain weight. For this trait, heterosis effect was ranged from 5.71 g for hybrid Begra × Borenos to 4.13 g for Dad76 × Carolus. The highest number of heterosis effect (66%) was found for protein content and ranged from 1.80% for Flair × Rektor to 1.32% for Dad76 × Borenos. Heterosis effects for water absorption, grain weight per plant and grain weight per ear were observed in approximately 30% of analysed hybrids. For water absorption, most of the heterosis effects were positive, and the highest was observed in Kobra × Carolus (4.37%). Dough development time in hybrids was generally similar to the mean value of this parameter for parental genotypes and only in 18% of cross combinations the heterosis effect was significant and negative, and ranged from 0.45 min for Flair × Rektor and Kobra × Kornett to 0.87 min for Charger × Carolus. No significant positive effect was found for that trait. For degree of softening 25% hybrids exhibited heterosis; positive and negative effects exhibited a similar rate. In the case of protein content, most of the analysed hybrids (two-third) differed significantly from the mid-parent values; however, these differences were relatively small and generally did not exceed 1%. A high rate (34%) of positive effects was found for grain yield per ear. For this trait negative effects were found only for a small number of hybrids (3%). For 1,000-grain weight and grain weight per plant a similar rate of hybrids differed from mid-parent values. The

Table 5 SCA and heterosis effects for pairs of parental genotypes in two wheat sets of line × tester crosses for technological traits

Parental genotypes	Water absorption (%)		Dough development (min)		Degree of softening (BU)		Protein content (%)		F statistic for all traits jointly	
	SCA	Heterosis	SCA	Heterosis	SCA	Heterosis	SCA	Heterosis	SCA	Heterosis
Set A										
Begra × Alidos	0.93	1.77	0.07	−0.15	−4.45	−5.50	−0.11	−0.20	1.29	1.60
Begra × Aristos	−0.43	−0.53	−0.60**	−0.68*	3.09	4.50	0.36**	0.07	3.61**	2.44*
Begra × Aron	−1.48*	−1.22	0.11	−0.10	4.59	0.67	−0.13	0.45**	4.02**	1.57
Begra × Borenos	0.44	1.52	−0.06	−0.38	−10.78*	−17.33*	0.70**	1.08**	5.21**	11.36**
Begra × Budssard	−0.31	0.21	0.45*	0.08	−5.66	−12.17	−0.42**	0.05	7.18**	4.88**
Begra × Corolus	0.86	3.33**	0.03	−0.17	13.22**	7.33	0.32**	0.63**	3.02**	13.32**
Charger × Alidos	−2.69**	−2.27*	0.01	−0.48	−9.51	−5.83	−0.04	−0.22	2.40*	5.79**
Charger × Aristos	−0.46	−0.97	0.14	−0.22	6.37	12.50	0.39**	−0.05	2.83**	1.45
Charger × Aron	1.59	1.45	0.02	−0.47	0.20	1.00	0.33**	0.83**	2.90**	4.83**
Charger × Borenos	1.18	1.85	0.14	−0.45	−10.84*	−12.67	0.26*	0.57**	3.02**	3.74**
Charger × Bussard	2.77**	2.88**	0.09	−0.55	−10.05*	−11.83	0.11	0.50**	2.73*	4.25**
Charger × Corolus	−2.40**	−0.33	−0.39*	−0.87**	23.83**	22.67**	−0.28*	−0.50**	14.18**	7.57**
Dad76 × Alidos	0.38	1.35	0.23	−0.05	4.83	12.67	0.06	0.23	2.91**	6.85**
Dad76 × Aristos	−1.79*	−1.75	0.20	0.05	−0.63	9.67	0.14	0.83**	2.86**	5.37**
Dad76 × Aron	0.13	0.53	0.00	−0.27	3.53	8.50	−0.07	0.78**	0.14	3.69**
Dad76 × Borenos	1.55*	2.77**	−0.07	−0.45	−5.84	−3.50	0.66**	1.32**	3.25**	12.17**
Dad76 × Bussard	0.27	0.93	−0.13	−0.55	20.95**	23.33**	−0.25*	0.48**	4.16**	6.87**
Dad76 × Corolus	−0.53	2.08*	−0.24	−0.50	−22.84**	−19.83**	−0.54**	0.03	7.23**	2.82**
Elena × Alidos	2.83**	4.08**	0.15	0.18	−12.73*	−26.50**	0.77**	0.70**	18.16**	7.14**
Elena × Aristos	2.26**	2.58**	0.02	0.18	−0.19	−11.50	0.54**	1.00**	7.09**	9.11**
Elena × Aron	0.58	1.27	−0.14	−0.10	0.98	15.67*	0.27*	0.83**	2.95**	7.58**
Elena × Borenos	−2.67**	−1.17	−0.08	−0.15	0.20	−20.67**	−0.70**	−0.28	14.03**	6.98**
Elaena × Bussard	−2.35**	−1.40	−0.34	−0.45	−2.27	−21.50**	−0.85**	−0.35*	8.24**	6.35**
Elena × Corolus	−0.65	2.25*	0.38*	0.43	15.60**	−3.00	−0.04	0.30	5.91**	3.83**
Flair × Alidos	0.04	1.02	−0.03	−0.15	0.90	−9.50	−0.25*	−0.60**	3.81**	7.65**
Flair × Aristos	−0.16	−0.12	0.14	0.15	0.81	3.17	0.10	0.27	2.42*	1.75
Flair × Aron	0.19	0.60	0.38*	0.27	−2.35	−5.33	0.33**	0.65**	3.15**	4.35**
Flair × Borenos	0.91	2.13*	−0.32	−0.55	0.94	−4.67	0.09	0.22	3.06**	1.37
Flair × Bussard	−1.51*	−0.83	−0.38*	−0.65*	7.73	2.17	−0.36**	−0.15	3.12**	1.74
Flair × Corolus	0.53	3.15**	0.21	0.10	2.27	−2.67	0.08	0.13	4.91**	5.57**
Kobra × Alidos	−1.39*	0.17	−0.42*	−0.35	12.94*	12.83	−0.26*	−0.72**	3.31**	6.67**
Kobra × Aristos	0.77	1.40	0.21	0.42	−8.85	−6.50	0.22	0.28	2.60*	4.29**
Kobra × Aron	−1.04	−0.05	−0.51**	−0.43	8.98	6.00	−0.68**	−0.47**	7.40**	3.69**
Kobra × Borenos	−1.72*	0.08	0.25	0.22	0.60	−5.00	−0.55**	−0.53**	5.19**	2.39*
Kobra × Bussard	2.23**	3.48**	0.36	0.28	5.06	−0.50	0.86**	0.97**	14.23**	9.37**
Kobra × Carolus	1.16	4.37**	0.11	0.20	−18.73**	−23.67**	0.41**	0.35*	9.64**	15.77**
Kris × Alidos	0.05	0.58	−0.05	−0.20	5.33	17.17*	−1.04**	−1.72**	21.08**	22.45**
Kris × Aristos	−0.42	−0.82	−0.12	−0.13	7.20	21.50**	0.14	−0.02	2.81**	4.79**
Kris × Aron	0.63	0.60	0.25	0.12	−0.97	8.00	0.16	0.17	2.46*	3.09**
Kris × Borenos	−0.11	0.67	0.28	0.03	0.66	7.00	0.53**	0.33*	5.02**	1.66
Kris × Bussard	−0.46	−0.23	−0.01	−0.30	−4.22	2.17	0.18	0.07	5.14**	15.30**

Table 5 continued

Parental genotypes	Water absorption (%)		Dough development (min)		Degree of softening (BU)		Protein content (%)		F statistic for all traits jointly	
	SCA	Heterosis	SCA	Heterosis	SCA	Heterosis	SCA	Heterosis	SCA	Heterosis
Kris × Carolus	0.30	2.48*	−0.35	−0.48	−8.01	−1.00	0.02	−0.25	3.61**	4.06**
Mikon × Alidos	−0.15	−0.37	0.05	−0.25	12.99**	13.83	0.87**	−0.42*	11.02**	2.06
Mikon × Aristos	0.22	−0.93	0.01	−0.15	7.80	−4.50	−0.39**	−1.15**	5.16**	9.37**
Mikon × Aron	−0.59	−1.38	−0.11	−0.40	−14.97**	−17.00*	−0.23	−0.83**	3.13**	8.92**
Mikon × Borenos	0.43	0.45	−0.15	−0.55	26.66**	22.00**	−1.00**	−1.80	24.12**	23.26**
Mikon × Bussard	−0.62	−1.15	−0.04	−0.48	−11.55*	−16.17*	0.72**	0.00	16.10**	2.95**
Mikon × Carolus	0.72	2.13*	0.25	−0.03	−5.34	−9.33	0.03	−0.85**	7.42**	14.66*
Set B										
Begra × Batis	1.08*	−0.70	0.53**	−0.03	−25.36**	−0.50	0.44**	−0.07	8.65**	0.62
Begra × Kornett	0.49	−1.32	−0.01	0.22	−8.93	14.00	0.03	0.02	3.08**	5.04**
Begra × Pegassos	−1.27**	−0.50	−0.02	0.10	40.83**	61.17**	−0.05	−0.62**	4.09**	10.59**
Begra × Rektor	−0.31	−0.22	−0.51**	−0.72**	−6.55	16.17	−0.42**	−0.90**	3.72**	9.64**
Charger × Batis	−0.73	−1.17	−0.04	−0.67**	−1.61	4.17	−0.76**	−0.70**	6.19**	6.94**
Charger × Kornett	0.35	−0.12	0.12	−0.15	3.15	7.00	−0.02	0.55**	0.21	4.55**
Charger × Pegassos	0.21	2.33**	−0.09	−0.03	−7.09	−5.83	0.44**	0.45**	8.16**	4.40**
Charger × Rektor	0.18	1.62*	0.01	−0.25	5.54	9.17	0.34**	0.43**	4.41**	2.84*
Dad76 × Batis	0.04	−0.73	−0.26	−0.80**	11.31	35.00**	−0.20**	0.50**	2.21*	7.03**
Dad76 × Kornett	−0.41	−1.22	0.07	−0.12	−8.93	12.85	−0.42**	0.78**	7.62**	7.72**
Dad76 × Pegassos	0.39	2.17**	0.10	0.23	−14.17*	5.00	0.21**	0.85**	3.26**	9.85**
Dad76 × Rektor	−0.01	1.08	0.08	−0.12	11.79	33.30**	0.41**	1.13**	7.19**	15.43**
Elena × Batis	0.34	−1.02	−0.34*	−0.80**	14.23*	21.80	0.51**	−0.75**	11.23**	11.16**
Elena × Kornett	−0.78	−2.17**	−0.01	−0.12	8.99	14.65	0.19**	−0.57**	2.91**	7.88**
Elena × Pegassos	0.06	1.25	−0.08	0.13	−9.58	−6.50	−0.75**	−2.07**	23.40**	37.70**
Elena × Rektor	0.39	0.90	0.43**	0.32	−13.63*	−8.20	0.05	−1.18**	3.01**	13.42**
Flair × Batis	−0.58	−1.88**	0.07	−0.84**	29.64**	33.83**	−0.06	−1.43**	4.12**	21.65**
Flair × Kornett	0.37	−0.97	−0.03	−0.58**	−12.27	−10.00	0.38**	−0.48**	5.16**	3.99**
Flair × Pegassos	0.31	1.55*	−0.14	−0.37	−9.17	−9.50	0.14	−1.28**	2.92**	18.15**
Flair × Rektor	−0.10	0.47	0.10	−0.45*	−8.21	−6.17	−0.46**	−1.80**	9.03**	29.30**
Kobra × Batis	−0.80	−2.07**	0.09	−0.77	−1.19	6.50	0.12	0.15	0.36	4.44**
Kobra × Kornett	0.75	−0.55	0.05	−0.45*	−6.43	−0.67	0.16*	0.70*	2.90*	6.05**
Kobra × Pegassos	0.31	1.60*	0.18	0.00	−5.00	−1.83	−0.31**	−0.33*	5.06**	3.71**
Kobra × Rektor	−0.25	0.35	−0.32*	−0.82**	12.62	18.17	0.03	0.08	2.81*	3.31**
Kris × Batis	0.66	−0.55	−0.06	−0.52*	−27.02**	−17.83	−0.06	−0.28*	3.92**	3.74**
Kris × Kornett	−0.76	−2.00**	−0.20	−0.30	24.41**	31.67**	−0.32**	−0.03	6.45**	4.59**
Kris × Pegassos	−0.02	1.32	0.06	0.28	4.17	8.83	0.34**	0.07	5.90**	1.79
Kris × Rektor	0.11	0.77	0.20	0.10	−1.55	5.50	0.04	−0.15	2.79**	2.73*

* $P < 0.05$, ** $P < 0.01$

highest heterosis effects were observed in Kobra × Bussard for water absorption, Elena × Alidos for degree of softening and Dad76 × Borenos for protein content. In the case of morphological characters, multivariate heterosis effects were significant in 40 out of 76 cross combinations. Whereas for technological properties these effects were significant for 75 cross combinations.

Table 6 SCA and heterosis effects in two wheat sets of line × tester crosses for morphological traits

Parental genotypes	1,000-Grain weight (g)		Grain weight per ear (g)		Grain weight per plant (g)		F statistic for all traits jointly	
	SCA	Heterosis	SCA	Heterosis	SCA	Heterosis	SCA	Heterosis
Set A								
Begra × Alidos	−1.13	−1.87	0.17*	0.41**	1.26**	−0.28	5.27**	6.90**
Begra × Aristos	1.04	0.67	0.06	0.21	−0.15	−0.38	0.84	1.58
Begra × Aron	1.69	2.10	0.18*	0.40**	1.35**	0.42	4.15**	4.24**
Begra × Borenos	−2.66*	−5.71**	−0.32**	−0.22	−0.60	−1.91**	7.11**	7.15**
Begra × Budssard	0.80	0.27	−0.09	0.17	−1.60**	−2.44**	5.08**	8.14**
Begra × Corolus	0.26	0.94	0.01	0.33**	−0.26	−0.05	0.70	3.82*
Charger × Alidos	0.25	−0.44	−0.10	0.09	0.18	−0.62	0.65	0.87
Charger × Aristos	−2.28*	−2.60	−0.12	−0.01	−0.95*	−0.43	4.22**	1.14
Charger × Aron	2.88**	3.32*	−0.11	0.07	−0.58	−0.78	4.05**	2.52
Charger × Borenos	−0.66	−3.67*	−0..01	0.05	−0.38	−0.95	0.25	3.26*
Charger × Bussard	−0.91	−1.40	0.13	0.34**	0.70	0.61	2.40	4.16**
Charger × Corolus	0.73	1.46	0.21*	0.49**	1.02**	1.51*	5.01**	7.03**
Dad76 × Alidos	−1.20	−1.06	0.04	0.35**	−0.25	0.49	0.89	4.14**
Dad76 × Aristos	−0.33	0.18	0.11	0.33**	1.34**	3.40**	4.16**	12.60**
Dad76 × Aron	−1.96	−0.68	−0.10	0.18	−0.62	0.74	2.02	1.48
Dad76 × Borenos	−0.35	−2.53	0.25**	0.42**	1.99**	2.97**	11.26**	14.21**
Dad76 × Bussard	1.27	1.61	−0.10	0.22	−1.19**	0.27	4.90**	1.36
Dad76 × Corolus	2.56*	4.13**	−0.20*	0.20	−1.28**	0.76	5.62**	2.91*
Elena × Alidos	1.69	1.56	−0.21*	−0.06	−1.80**	−2.42**	10.70**	6.62**
Elena × Aristos	−3.61**	−3.36*	0.03	0.09	0.11	0.79	4.31**	3.00*
Elena × Aron	−0.37	0.64	0.15	0.28	0.85*	0.82	4.16**	2.26
Elena × Borenos	1.21	−1.22	0.02	0.03	−0.12	−0.53	0.81	0.61
Elaena × Bussard	1.49	1.56	0.04	0.21	0.30	0.37	1.10	1.23
Elena × Corolus	−0.40	0.90	−0.02	0.21	0.67	1.32	1.91	2.31
Flair × Alidos	−0.99	−1.28	−0.05	−0.10	−1.76**	−4.02**	4.15**	16.10**
Flair × Aristos	2.43*	2.50	−0.21*	−0.35**	−0.59	−1.53**	2.73*	6.94**
Flair × Aron	−1.26	−0.42	0.05	−0.02	0.34	−1.31	1.03	1.72
Flair × Borenos	1.23	−1.38	0.13	−0.06	−0.21	−2.24**	1.32	5.05**
Flair × Bussard	−0.50	−0.60	0.15	0.12	0.99*	−0.57	4.01**	1.02
Flair × Corolus	−0.91	0.21	−0.06	−0.03	1.22**	0.25	5.60**	0.11
Kobra × Alidos	1.78	1.38	−0.08	0.08	1.66**	0.83	9.36**	0.85
Kobra × Aristos	0.64	0.61	0.07	0.13	0.17	0.66	0.18	0.71
Kobra × Aron	1.09	1.83	−0.19*	−0.06	−0.88*	−1.11	3.06*	2.01
Kobra × Borenos	0.93	−1.78	0.11	0.13	0.08	−0.51	1.02	1.62
Kobra × Bussard	−1.32	−1.52	0.00	0.18	0.11	−0.01	0.65	1.59
Kobra × Carolus	−3.13**	−2.11	0.10	0.34**	−1.14**	−0.68	4.93**	5.96**
Kris × Alidos	−2.74*	−3.01	−0.07	0.16	0.32	−0.26	2.90*	2.87*
Kris × Aristos	0.23	0.33	0.05	0.20	−0.44	0.30	0.98	1.04
Kris × Aron	−0.66	0.21	0.04	0.26**	−0.07	−0.05	0.12	1.92
Kris × Borenos	0.05	−2.53	−0.05	0.05	−0.01	−0.35	0.09	1.31
Kris × Bussard	0.80	0.72	−0.03	0.22	0.59	0.68	0.63	1.45
Kris × Carolus	2.33*	3.48*	0.06	0.39**	−0.36	0.35	2.72*	4.50**

Table 6 continued

Parental genotypes	1,000-Grain weight (g)		Grain weight per ear (g)		Grain weight per plant (g)		F statistic for all traits jointly	
	SCA	Heterosis	SCA	Heterosis	SCA	Heterosis	SCA	Heterosis
Mikon × Alidos	2.34*	1.73	0.30**	0.46**	0.38	0.23	4.86**	5.51**
Mikon × Aristos	1.88	1.64	0.03	0.09	0.50	1.67**	2.16	2.88*
Mikon × Aron	−1.40	−0.87	−0.02	0.10	−0.39	0.06	1.06	0.51
Mikon × Borenos	0.25	−2.68	−0.11	−0.10	−0.75*	−0.68	2.74*	1.30
Mikon × Bussard	−1.62	−2.03	−0.09	0.08	0.12	0.68	1.63	1.44
Mikon × Carolus	−1.44	−0.62	−0.10	0.13	0.13	1.27	1.13	1.98
Set B								
Begra × Batis	0.00	0.00	0.09	0.19	−2.35**	−0.79	9.55**	1.51
Begra × Kornett	−0.88	−0.68	0.11	0.43**	2.97**	5.39**	11.16**	19.11**
Begra × Pegassos	0.83	2.03	0.15	0.30*	−0.36	2.20**	1.60	4.82**
Begra × Rektor	0.05	−2.16	−0.34**	−0.39**	−0.26	0.36	3.22*	4.26**
Charger × Batis	1.79*	2.37	−0.04	0.16	−1.72**	−2.52**	3.86*	6.10**
Charger × Kornett	0.46	1.25	0.27**	0.69**	0.71	0.78	2.81*	9.94**
Charger × Pegassos	−0.23	1.54	0.03	0.28*	2.94**	3.15**	8.90**	7.26**
Charger × Rektor	−2.02*	−3.65**	−0.25**	−0.21	−1.92**	−3.67**	9.03**	11.57**
Dad76 × Batis	1.50	2.35	0.17	0.44**	1.60**	2.99**	7.61**	8.91**
Dad76 × Kornett	−1.47	−0.42	−0.17	0.32*	−0.87	1.39	2.41	2.83*
Dad76 × Pegassos	0.45	2.49	−0.25**	0.06	−2.42**	−0.02	10.23**	1.26
Dad76 × Rektor	−0.49	−1.85	0.25**	0.37**	1.70**	2.15**	6.91**	5.43**
Elena × Batis	0.20	2.69*	−0.04	0.22	0.65	2.71**	0.91	6.46**
Elena × Kornett	1.08	3.77**	−0.07	0.41**	−1.80**	1.11	4.98**	6.13**
Elena × Pegassos	−1.79*	1.90	0.03	0.34**	0.10	3.15**	2.77*	7.94**
Elena × Rektor	0.52	0.81	0.08	0.18	1.05*	2.16*	2.75*	3.24*
Flair × Batis	−0.12	0.51	−0.16	−0.07	0.00	−0.57	1.48	0.29
Flair × Kornett	−0.48	0.35	0.02	0.33**	0.10	0.38	0.11	2.22
Flair × Pegassos	−0.44	1.39	0.03	0.17	−0.01	0.43	0.27	0.92
Flair × Rektor	1.03	−0.56	0.12	0.05	−0.09	−1.61*	0.42	2.01
Kobra × Batis	−1.22	−1.19	−0.08	0.11	0.95	1.15	2.55	1.18
Kobra × Kornett	−0.46	−0.23	0.00	0.41**	−0.57	0.50	0.93	3.59*
Kobra × Pegassos	0.73	1.95	0.09	0.32*	0.72	1.93**	1.46	4.37**
Kobra × Rektor	0.95	−1.24	−0.01	0.02	−1.09*	−1.83*	2.81*	2.74*
Kris × Batis	−2.16**	−2.86*	0.07	0.29*	0.88	1.10	2.99*	3.86*
Kris × Kornett	1.75*	1.26	−0.16	0.27*	−0.54	0.55	2.80*	1.78
Kris × Pegassos	0.44	0.94	−0.07	0.19	−0.96*	0.27	2.74**	0.9
Kris × Rektor	−0.03	−2.94*	0.15	0.21	0.62	−0.11	1.21	2.98*

* $P < 0.05$, ** $P < 0.01$

Correlation between parental diversity and SCA and heterosis effects

Correlation coefficients between GD and SCA effects are presented in Table 7. GD was positively and significantly correlated with SCA for water absorption, dough development and protein content, and negative with dough softening. No correlations were found between GD and SCA for morphological traits. Similarly, heterosis effects were significantly correlated with GD only in the case of rheological properties. Univariate PDs were significantly correlated with SCA and

Table 7 Correlation coefficients between genetic (GD) and phenotypic distances (PD) of parents and specific combining ability and heterosis effects in morphological and technological trait

		Water absorpion	Dough development	Degree of softening	Protein content	1,000-Grain weight	Grain weight per ear	Grain weight per plant
GD	SCA	0.36**	0.37**	−0.30**	0.36**	−0.13	−0.13	−0.05
	Heterosis	0.32**	0.31**	−0.25*	0.24*	0.01	0.18	0.10
PD uniwariate	SCA	0.31**	−0.37**	−0.18	0.11	−0.11	−0.13	0.02
	Heterosis	0.34**	−0.43**	−0.01	−0.11	0.01	0.07	0.07
PD mulivariate	SCA	0.06	−0.15	−0.11	−0.03	−0.01	0.10	−0.02
	Heterosis	0.12	−0.13	−0.15	−0.09	0.13	0.05	0.04

* $P < 0.05$, ** $P < 0.01$

heterosis for water absorption (positively) and dough development (negatively). Multivariate PD was not significantly correlated with SCA and heterosis for analysed traits.

Discussion

The line × tester crossing scheme was used in this study to evaluate effects of SCA and heterosis in wheat. The same scheme to calculate combining ability effects in wheat and other species has been previously described (Narro et al. 2003; Shoran et al. 2003; Tuteja et al. 2003; Ahuja and Dhayal 2007). Combining abilities (GCA, SCA) may be estimated based on the data from the experiments with F_1 or F_2 hybrids (Cox and Murphy 1990; Oettler et al. 2001; Acquaah 2006). In this study, the F_2 hybrids were analysed as it was necessary to obtain sufficient amount of kernels to determine their rheological properties. As it is known in F_2 hybrids 50% of loci are in heterozygous state. Consequently, the difference between F_2 hybrids and mid-parent value is rather heterotic than heterosis effect.

The analysis of variance showed significant both GCA and SCA variances ($P < 0.01$). Generally, SCA variances were lower than GCA. It was observed especially for 1,000-grain weight and grain weight per ear. In experiments conducted in *Triticum durum*, Topal et al. (2004) also found larger variances for GCA than SCA for 1,000 kernel weight. Perenzin et al. (1998) in experiments with F_1 hybrids of bread wheat found significant SCA effects for agronomical traits but no statistically significant SCA effects were detected for quality traits. In their studies, statistically significant heterotic effects found for several traits had mostly weak correlation to GD between parental cultivars.

Results presented in this study indicate the complexity of inheritance for grain properties of analysed wheat genotypes. In most cases, the advantageous effect of a given parental genotype on progeny in terms of one of the analysed traits was not associated with an improvement of the other trait and frequently resulted in even further deterioration. Results confirm a well-known fact that the occurrence of the heterosis effect in relation to one of the traits does not have to be equivalent to the occurrence of the heterosis in relation to other traits. A heterosis effect in one hybrid may be both an increase in some traits and deterioration in others (Lefort-Buston et al. 1987). Wheat of good quality needs to meet specific criteria in relation to analysed technological properties. A failure to meet even one of them frequently results in a disqualification of a given cultivar as a variety with good technological value. It is one of the factors hindering breeding of good quality wheat cultivars.

One of the aims of this study was to determine whether there was a relationship between GDs and PDs of parental forms, evaluated on the basis of RAPD markers, SCA and heterosis effects. The results demonstrate that PDs were not significantly correlated with SCA and heterosis effects for all the analyszed traits but a positive significant correlation was found between SCA and GD for flour water absorption, dough development time and protein content in grain. Dependencies, equally advantageous from the point of view of breeding practice, were observed in case of dough softening. The correlation coefficient between GD and SCA for this trait had a negative and significant value. It needs to be stressed that high dough softening does not have an advantageous effect on technological quality of flour.

Results recorded for technological traits are promising for practical purposes. They show that in heterosis breeding the effectiveness of choosing pairs of parental genotypes based on GD and SCA effects may be similar. This conclusion is confirmed by the values of correlation coefficient between GD of parents, SCA and heterosis effects. A strong relationship was shown between GD and heterosis for flour water absorption and dough development ($P < 0.01$), as well as protein content ($P < 0.05$). In case of dough softening, the recorded correlation coefficient was significant but negative. The GD between cultivars may be defined on the basis of molecular and morphological (phenotypic) markers (Shamsuddin 1985; Melchinger et al. 1990; Diers et al. 1996). The investigation of distance based on phenotypic traits may be burdened with an error resulting from the dependence of the expression of these traits on environmental conditions. Molecular markers based on DNA analysis are independent of environmental factors and exhibit a high degree of polymorphism. Moreover, they appear to be a promising tool in the prediction of heterosis in other species; for example in maize (Boppenmaier et al. 1992; Melchinger et al. 1992), rice (Zhang et al. 1996), wheat (Martin et al. 1995), rape (Sheng et al. 2002) or oat (Moser and Lee 1994).

Because of the simplicity and low cost of the RAPD technique, it found a wide range of applications in breeding programs (Cao et al. 1998; Sun et al. 2003; Paczos-Grzeda 2004; Bhutta et al. 2006). In the current study, RAPD markers have been used to detect genetic diversity within analysed genotypes. The level of RAPD polymorphism has been relatively high (54%) but lower than in experiments considered by Joshi and Nguyen (1993) and Sun et al. (2003).

There have been several studies on the subject of the dependence between GD based on the COP, molecular or biochemical markers and the possibility to produce lines (in the classical breeding of self-pollinated plants) or hybrids (in hybrid breeding) exhibiting improved values of traits (Shamsuddin 1985; Cox and Murphy 1990; Melchinger et al. 1990; Dudley et al. 1991; Xiao et al. 1996; Cerna et al. 1997; Riaz et al. 2001; Yu et al. 2005; Kuczyńska et al. 2007). It is not defined a priori, which is the best method for estimating GDs because each of them has some limitations. Caution should be exercised; however, when discussing the possibility of applying the above-mentioned dependencies to develop a method of selecting crossing components. The possible application of RAPD markers in the selection of cross components in hybrid breeding of maize for yield has been reported earlier (Stuber et al. 1992; Wang et al. 1994; Betran et al. 2003). In contrast, other studies in maize did not showed any association between combining ability and GD (Melchinger et al. 1990, Dudley et al. 1991). Similar results were also reported by Lee et al. (1989), Goldshalk et al. (1990) and Shieh and Thseng (2002). Zhang et al. (1994) found a high correlation between grain yield in selected rice lines and the GD between parents based on RFLP markers. Studies conducted also on the same species by Xiao et al. (1996) showed a positive relationship between yield and GD based on RAPD markers. However, no such dependence was found by Diers et al. (1996) or Kwon et al. (2002). In addition, in case of rape, Riaz et al. (2001) showed a close relationship between GD based on sequence-related amplified polymorphism (SRAP) markers and the yield of hybrids and the heterosis effect. Varied opinions were also expressed on the possible application of molecular markers in the selection of components for crossing in wheat. Martin et al. (1995) showed the existence of a relationship between GD based on the pedigree of analysed cultivars and heterosis for grain weight and protein content. They stressed that the knowledge on the relationship between GD based on molecular markers and heterosis effects is insufficient for the development of a methodology of the choice of parents for crossing. Similar conclusions were reached by Barbosa-Neto et al. (1996) on the basis of experiments established in different environments with 722 wheat hybrids. These authors, when analysing yield and its components, showed only a weak relationship between GD and heterosis effects. In turn, Liu et al. (1999) were of the opinion that heterosis effects in progeny of wheat may not be predicted solely on the basis of genetic diversity evaluated by RAPD markers. Corbellini et al. (2002) found statistically significant correlation between GDs based on molecular markers and mid-parents heterosis value for grain yield, but authors noticed that these correlations were too low to be of predictive value.

Conclusions

Results recorded in this study may contribute to the development of an effective method to select components for heterosis breeding, combining elements of both quantitative and molecular genetics. Among all the analysed crosses, Elena × Alidos seems to be of special interest for breeders because of significant and positive SCA and heterosis effects for water absorption, degree of softening and protein content and relatively high (0.42) GD.

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