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Combining ability under drought stress relative to SSR diversity in common wheat

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Summary

Eight-parental diallel cross and SSR molecular markers were used to determine the combining ability of common wheat lines grown under well-watered (WW) and water-stress (WS) conditions. Analysis of variance of yield indicated highly significant differences among the progenies. General combining ability (GCA) determined most of the differences among the crosses. Specific combing ability (SCA) was also significant but less important. The estimates of GCA effects indicated that one line was the best general combiner for grain yield under drought. Nei's genetic distance, measured using SSR markers, differed from 0.20 to 0.48 among the eight genotypes. The correlation of Nei's genetic distance with SCA for grain yield and heterosis ranged from 0.4 to 0.5. These results indicate that the level of SCA and heterosis depends on the level of genetic diversity between the wheat genotypes examined. Microsatellite markers were effective in predicting the mean and the variance of SCA in various cultivars combinations. However, selection of crosses solely on microsatellite data would miss superior combinations.

Introduction

Common wheat (*Triticum aestivum* L.) is the major source of calories and protein for a large segment of the world population (Harlan, 1995), and is the most important grain crop in Egypt. Wheat production in many regions of the world is below average because of adverse environmental conditions. A recent increase in Egyptian wheat production is not sufficient to meet the demands of a growing population. Water-stress issues are increasing, especially in newly reclaimed lands, sandy soils in some areas and shortages of water in the land located at the tails of irrigation canals. In wheat breeding programs, the choice of parents is the most important step in the development of varieties adapted to water-stress conditions.

The diallel technique developed by Griffing (1956) lends itself to detailed genetic analysis after only one generation. It can provide valuable knowledge about the nature of genetic variances and the magnitude of each of its components. Significant levels of heterosis have been reported in a number of self-pollinated crops, and were first observed in wheat by Freeman (1919). The magnitude of the heterotic effect is determined by the performance of both the parents and hybrids. Given that parental performance will differ between environments, the magnitude of heterosis may also show similar variation (El-Haddad, 1975; Uddin et al., 1992). Briggle (1963) summarized the results of earlier studies which indicated the occurrence of significant mid and high-parent heterosis for yield and various agronomic traits.

One of the important applications of DNA markers is the prediction of heterosis in hybrids. Evaluation of hybrids for heterosis or combining ability in the field is expensive and time-consuming (Sant et al., 1999).

For this reason, other parameters such as pedigree information, qualitative and quantitative traits (Smith et al., 1990; Wang et al., 1992) and biochemical data (Leonardi et al., 1991) are being used to study heterosis. DNA markers have also been extensively used to correlate genetic diversity and heterosis in several crops such as maize (Smith et al., 1990; Ajmone Marsan et al., 1998; Parentoni et al., 2001), rice (Xiao et al., 1996; Zhang et al., 1994; Zhao et al., 1999), oat (Moser & Lee, 1994; O'Donoughue et al., 1994), barley (Melchinger et al., 1990) and chickpea (Sant et al., 1999). In wheat, Martin et al. (1995) found a significant association only between pedigree-based genetic distance and heterosis only for kernel weight and protein concentration. Barbosa-Neto et al. (1996) investigated heterotic effects in 722 wheat hybrids evaluated in replicated trails over several locations and found that genetic distances based on restriction fragment length polymorphism and coefficient of parentage were weakly correlated with the heterotic effect. Corbellini et al. (2002) estimated the correlations between genetic similarities using molecular markers with general and specific combing ability effects for yield and related traits. The estimates were in several cases statistically significant but too low to be predictive.

Microsatellites or simple sequence repeats (SSRs) are ubiquitous in eukaryotic genomes, and their study has been greatly facilitated by recent advances in PCR technology. A detailed genetic map of 279 microsatellite loci (Röder et al., 1998) and another map of 53 microsatellite loci (Stephenson et al., 1998) have been reported in common wheat. The latest version of a genetic/physical map containing over 1400 loci and primer (probe) details are available with GrainGenes web site (http://wheat.pw.usda.gov). In diversity studies, SSRs were shown to provide significant information on polymorphisms (Plaschke et al., 1995; Prasad et al., 1999). In wheat, the possibility of introducing hybrid seed production has been greatly enhanced by the discovery of effective chemical hybridizing agents. However, predicting F_1 common wheat hybrid performance using RFLPs and RAPDs to characterize the parental lines is not effective (Perenzin et al., 1998).

The present study was undertaken to identify superior parental lines that could be used as sources of drought tolerance in common wheat breeding programs. We also examined the relationship of genetic diversity measured using SSR markers with the amount of specific combining ability and heterosis under drought and irrigation conditions using eight wheat genotypes.

Materials and methods

A diallel was made among eight common wheat (*T. aestivum* L.) genotypes (Table 1). The F_1 seed was obtained by hand emasculation. The cross number and pedigree of the F_1 derived from the diallel is presented in Table 1. Ten plants per plot of the parents and the 28 F_1's were grown in a randomized block design with three replications at Nubaria Agricultural Research Station, Agriculture Research Centre, Egypt, in 1996

Table 1. The cross number and pedigree of the 28 F_1 hybrids derived from the diallel of eight common wheat (*Triticum aestivum* L.) parental genotypes

No.	Crosses (parent *i* × parent *j*)
1	Gemmiza1 × Giza164
2	Gemmiza1 × Giza167
3	Gemmiza1 × Sakha8
4	Gemmiza1 × Sids1
5	Gemmiza1 × Sids6
6	Gemmiza1 × Sakha69
7	Gemmiza1 × YecoraRojo
8	Giza164 × Giza167
9	Giza164 × Sakha69
10	Giza164 × Sakha8
11	Giza164 × Sids1
12	Giza164 × Sids6
13	Giza164 × YecoraRojo
14	Giza167 × Sakha69
15	Giza167 × Sakha8
16	Giza167 × Sids1
17	Giza167 × Sids6
18	Giza167 × YecoraRojo
19	Sakha69 × Sids6
20	Sakha69 × YecoraRojo
21	Sakha8 × Sakha69
22	Sakha8 × Sids6
23	Sakha8 × YecoraRojo
24	Sids1 × Sakha8
25	Sids1 × Sids6
26	Sids1 × Skha69
27	Sids1 × YecoraRojo
28	Sids6 × YecoraRojo

and 1997 under water-stress (WS) and well-watered (WW) conditions. The soil type was calcareous sandy. Irrigation was applied at approximately two-weekly intervals. The amount of applied irrigation water was determined by measuring soil water depletion before and after each irrigation. Soil moisture depletion is the amount of water measured in mm required to raise the soil-water content of the crop root zone to field capacity (Husman et al., 1999). The efficiency of surface irrigation at these experimental sites was determined to be 60%. Under WS conditions, a sowing irrigation of 70 mm was given, rainfall and supplementary irrigation made up the total of 310 mm of applied water. The total amount of applied irrigation water and rainfall for the WW treatment during the growing season was 695 mm. The irrigation interval was approximately every 12–15 days. Data were collected on grain yield per plant (GYP) in grams and mid-parent heterosis (MPH) was calculated.

The general and specific combining ability (GCA and SCA, respectively) analysis was conducted following Griffing's Model 1 Method 2 (Griffing, 1956). All calculations were performed using the MSTAT-C package (1991). Mid parent heterosis (MPH) was computed as percent deviation from mean values of the parents. DNA from 7-day-old seedlings of the parental cultivars was extracted according to modified CTAB procedure (Murray & Thompson, 1980). SSR analysis was performed as described by Röder et al. (1998). Reproducibility of amplification profiles was tested on two randomly chosen cultivars; only clear and stable bands were considered. Forty SSRs developed and provided by Dr. P. Cregan, USDA-ARS, Maryland, USA were used to create the molecular marker data presented in Table 2. The SSR primer information and chromosome location can be found on the U.S. Wheat and Barley Scab Initiative web site http://www.scabusa.org/pdfs/BARC_SSRs_011101.xls. Only SSR bands polymorphic in at least two genotypes were considered in the analysis. Nei's (1972) genetic distance was calculated to measure genetic diversity among the eight wheat genotypes using NTSY-pc software, version 2.02 (Rohlf, 1993). Cluster analysis of parental genotypes was based on Nei's values using the unweighted pair-group method with arithmetical average (UPGMA) and the relationships among cultivars were visualized using a dendogram. MPH and SCA for agronomic and quantitative traits of the 28 hybrids under WW and WS were correlated with the genetic diversity estimates based on SSR markers.

Table 2. Primers used for SSR analysis

Primer pair ID[a]	MOTIF
BARC004	(TTA)15
BARC012	(TAA)28
BARC017	(TAA)12
BARC018	(TAA)20
BARC024	(TCA)10+(TAA)9
BARC042	(TTA)12
BARC048	(TATC)11
BARC052	(ATCT)5
BARC062	(TAGA)8
BARC065	(TAGA)9
BARC066	(TC)8(TAGA)5
BARC069	(TATC)15
BARC072	(CT)4(TCTA)8(TC)8
BARC074	(GA)13(GATA)7(GA)9
BARC076	(TATC)7
BARC077	(ATCT)6+18
BARC078	(TC)27(TATC)43
BARC079	(TAGA)10+(TC)9
BARC080	(GAA)12
BARC093	(TTC)10+3
BARC001	(TAA)8
BARC003	(CCT)17
BARC005	(TTA)5+8
BARC006	(TTA)24
BARC007	(TTC)6+3
BARC008	(TTA)15+11
BARC009	(TAA)3+3+(TTG)6
BARC010	(GAA)13
BARC011	(TAA)9+(TTA)12
BARC013	(TTC)5+3+2
BARC014	(TAA)18+12
BARC016	(TTG)9
BARC019	(TAA)18
BARC020	(TAA)21
BARC021	(TAA)19
BARC023	(TAA)9
BARC025	(TAA)22+(GAA)10
BARC026	(ATT)8
BARC027	(TAA)8
BARC028	(ATT)9

[a]www.scabusa.org/pdfs/BARC_SSRs_011101.xls.

Results

Analysis of variance of grain yield in the diallel experiment indicated significant differences due to genotypes under well-watered and water-stress conditions. The genotype × water level and genotype × year interactions were not significant. Grain yield of the parental genotypes ranged from 17.8 to 28.8 grams per plant under WW (Table 3). Yield reduction under water-stress ranged from 18% for Sakha8 to 58% for Sids6. The heterosis of grain yield per plant (GYP) in F_1 under WW and WS exceeded their mid-parents in crosses numbered 11 and 19 of the 28 hybrids, respectively (Figure 1). The highest significant heterosis under WW was observed in crosses 18 (Giza167 × YecoraRojo) and 25 (Sids1 × Sids6). Highest heterosis for GYP under WS was found in crosses 19 (Sakha69 × Sids6) and 14 (Giza167 × Sakha69). Highly negative heterosis was observed in Sids1 × Sakha8 (cross 24) and Gemmiza1 × Sakha69 (cross 6) under WW and in Giza164 × Sids6 (cross 12) under WS (Figure 1).

Analysis of variance indicated that GCA and SCA mean squares were highly significant for yield under WW and WS conditions. The highest SCA for GYP under WW was observed in crosses 13 (Giza164 × YecoraRojo), 22 (Sakha8 × Sids6) and 18 (Giza167 × YecoraRojo) (Figure 1). The highest SCA under WS was estimated in crosses 18 (Giza167 × YecoraRojo) and 16 (Giza167 × Sids1) (Figure 1). Highly negative SCA was found in Gemmiza1 × Giza167 (cross 2) under WW and in Sids1 × Sakha8 (cross 24) under WS.

Estimation of GCA effects showed different trends and a few cases were significant (Table 3). Giza164 gave the highest significant positive GCA effect followed by Sids1 under WW, whereas Sids1 and YecoraRojo showed significant positive GCA under WS (Table 3). All hybrids exhibited either significant positive or negative SCA effects under WW conditions. The crosses leading to positive SCA effects resulted from combinations involving Sakha8, Sakha69, Sids1, Gemmiza1 and Giza167, which also showed positive GCA under WW (Table 3).

A total of 112 alleles were detected by the 40 microsatellites markers evaluated on the eight genotypes. This represented an average of 2.8 alleles per locus with a range of two to five alleles detected by a single SSR locus. Nei's genetic distance (GD) was measured using the 112 polymorphic SSR alleles. The GD for each genotype combination ranged from 0.20 to 0.48 (Figure 2). The relationship of heterosis and SCA for GYP with genetic distance, measured using SSR markers, for the diallel is presented Table 4. The amount of heterosis and SCA were significantly correlated with Nei's GD under WS and WW. Heterosis was also significantly correlated with SCA under both WS and WW.

Table 3. Mean parental yields (g/plant) over two years, standard deviation (±S.D.) and general combining ability effects (GCA) for yield under water-stress and well-watered conditions

	Mean ± S.D.		GCA	
Genotype	WS	WW	WS	WW
Sakha8	20.52 ± 5.6	24.99 ± 3.4	0.230	0.368
Sakha69	20.14 ± 4.8	27.12 ± 2.1	−0.428	1.491*
Sids1	21.45 ± 3.9	28.78 ± 2.2	1.433**	1.730**
Sids6	8.59 ± 2.2	20.65 ± 3.0	−1.473**	−4.551**
Gemmiza1	20.93 ± 3.5	26.54 ± 3.3	0.755	0.297
YecoraRojo	15.61 ± 2.7	22.14 ± 2.8	1.151**	−1.491*
Giza164	15.84 ± 2.6	19.23 ± 2.7	0.658	2.309**
Giza167	14.39 ± 2.9	17.79 ± 3.3	−3.026**	−0.753

Discussion

The present investigation was carried out to identify parental common wheat genotypes and hybrids that have good performance for grain yield under well-watered and water-stress conditions. Approximately 55% of the area sown to wheat in the developing countries is periodically affected by drought stress (Trethowan et al., 2002). The development and cultivation of varieties that are tolerant to drought is the most effective means of water shortage management for wheat farmers. A diallel among eight cultivars was made to study the general combing ability, heterosis

Table 4. Pearson correlations among Nei' genetic distances (Nei' GD), heterosis (H_) and specific combing ability (SCA_) for grain yield per plant (GYP) under water-stress (WS) and well-watered (WW) conditions

	Nei's GD	H_WS	H_WW	SCA_WS	SCA_WW
Nei's GD	1.000				
H_WS	0.462**	1.000			
H_WW	0.503**	0.512**	1.000		
SCA_WS	0.417**	0.360*	0.687**	1.000	
SCA_WW	0.514**	0.689**	0.509**	0.596**	1.000

**Correlation is significant at $P = 0.01$ (two-tailed).

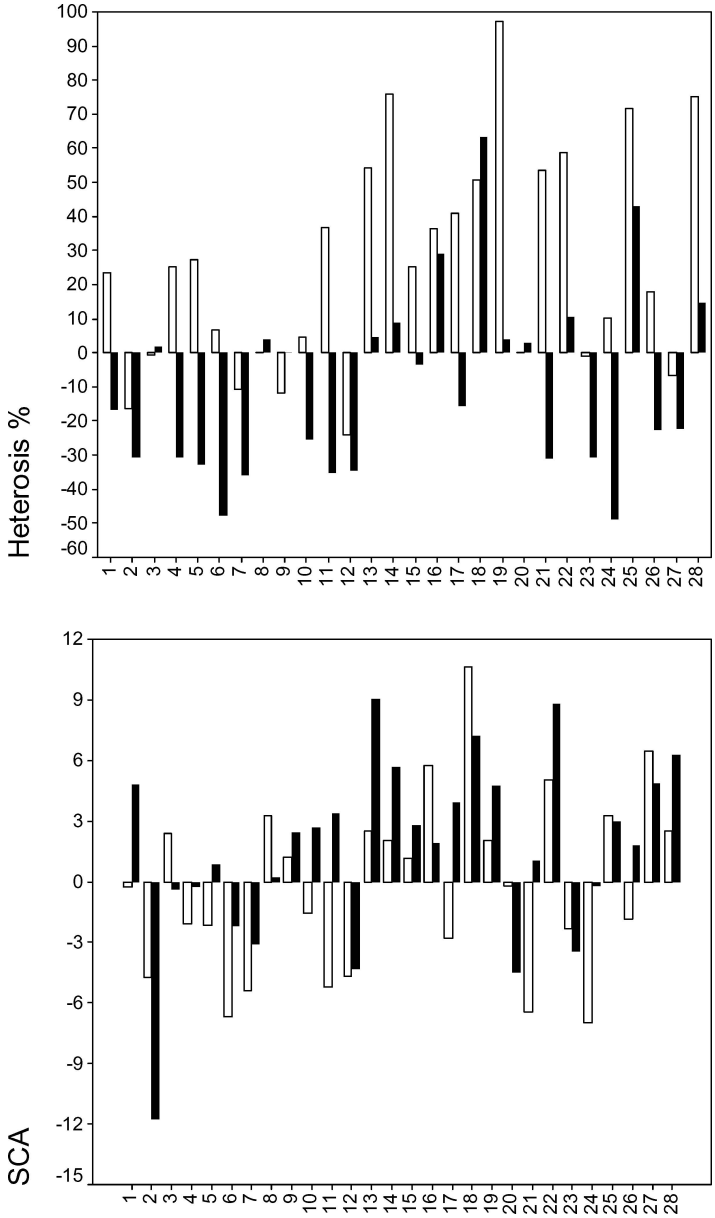

Figure 1. Percent heterosis and SCA of GYP (y-axis) in 28 crosses (x-axis) developed from eight genotypes of common wheat (*T. aestivum* L.). Solid bars represent well-watered and white bars represent water-stress conditions.

and specific combing ability in relationship to SSR diversity.

The diallel crosses revealed significant differences in both the phenotypic value of the F_1 hybrids and the amount of heterosis among the genotype combinations. The heterosis trend was positive for grain yield per plant for many crosses under water-stress, indicating that genetic gain from simple breeding should be obtainable (Nanda et al., 1983). The results suggested that grain yield per plant is controlled by loci with both additive and non-additive gene effects under both conditions, and support earlier findings (Sayed, 1978; Abul-Nass et al., 1986; Singh, 1988). This study suggests that hybrids such as Sakha69 × Sids6 and Giza167 × YecoraRojo provide a worthwhile degree of heterosis under both stressed and well-watered conditions. Combining ability has been shown to be an inherited character (Satter et al., 1992). Our

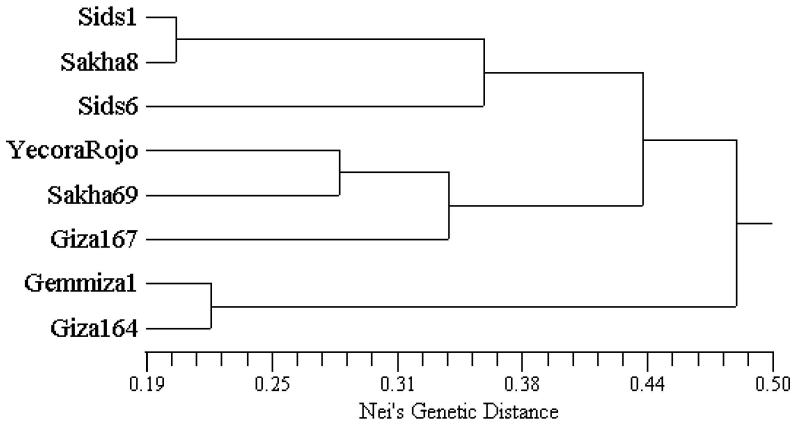

Figure 2. Dendrogram obtained from UPGMA cluster based on SSR data from the eight common wheat genotypes.

study demonstrated that, although the amount of heterosis was independent of yield values, it was larger in crosses between more distantly related parents compared with closely related genotypes.

In autogamous cereals RFLPs have been successfully used to group genotypes (Peterson et al., 1994; O'Donoughue et al., 1994; Zhang et al., 1995) but little information is available about relationships between genetic diversity and heterosis in wheat (Perenzin et al., 1998). If a simple, efficient, inexpensive and reliable method could be used to predict heterosis before expensive field testing, much of the field work associated with making crosses and field evaluation would be eliminated and hybrid breeding programs would be accelerated. For this reason, we focused on the relationship between heterosis and F_1 performance under well-watered and stressed conditions with the level of genetic diversity between the parents measured by microsatellite markers. The use of SSR for DNA fingerprinting and variety identification with emphasis on common wheat was reviewed by Gupta and Varshney (2000). Our results show that SSRs are useful in detecting a high level of polymorphism among wheat cultivars. The utility of these markers for detection of population differences agrees with previous reports in other species (Liu & Wu, 1998; Xiong et al., 1998; Sant et al., 1999; Agrama & Tuinstra, 2003).

The most important result obtained in the present study is that the amount of heterosis under well-watered and stress conditions, is positively correlated with the genetic distance between the genotypes used for the crosses. This is in disagreement with other results reported in wheat using RFLPs where the statistically significant heterotic effects found for several traits were only weakly correlated with the genetic distances between parental cultivars (Barbosa-Neto et al., 1996; Corbellini et al., 2002). Perenzin et al. (1998) also found that genetic diversity of the parental lines determined using RFLP and RAPD analyses do not appear helpful for predicting F_1 performance. A significant association between pedigree-based genetic distance and heterosis for wheat kernel weight and protein concentration only was found (Martin et al., 1995). However, high correlations between heterosis and DNA-based genetic distance have been reported in other crops (Smith et al., 1990; Melchinger et al., 1990, 1994; Zhang et al., 1994). The high correlations could depend on the higher levels of heterosis reported (Corbellini et al., 2002). However, while the correlation is significant, selection of crosses solely on microsatellite data would miss superior combinations. For instance, Giza167/YecoraRojo showed much higher heterosis than Giza164/Sakha8, even though the latter cross is much more diverse.

Heterosis is presumably caused by directionally dominant loci and/or reduced homozygosity at deleterious recessive loci (Falconer, 1989). The present study demonstrated that the degree of heterosis was significantly correlated with genetic distance of the parental cultivars, suggesting an effect of overall heterozygosity on the amount of heterosis. The negative values in the amount of heterosis observed in the genotype combinations with small genetic distances might be caused by individuals with similar genetic backgrounds.

The present study demonstrated that the amount of heterosis and specific combing ability in common wheat depends on the level of genetic diversity among the genotypes used for the crosses. Even though

seed of hybrid wheat is still relatively expensive, microsatellite markers are also useful for predicting the mean and the amount of heterosis in various genotype combinations under both well-watered and water-stressed conditions. The likelihood of a positive return is reduced in marginal environments. Pure-line systems are likely to be preferred for some time. However, selection of crosses solely on microsatellite data would miss the most superior combinations.

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