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Hybrid performance and heterosis in spring bread wheat, and their relations to SSR-based genetic distances and coefficients of parentage

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Summary

Development of hybrids is considered to be a promising avenue to enhance the yield potential of crops. We investigated (i) the amount of heterosis observed in hybrid progeny, (ii) relative importance of general (GCA) versus specific (SCA) combining ability, and (iii) the relationship between heterosis and genetic distance measures in four agronomic traits of spring bread wheat. Eight male and 14 female lines, as well as 112 hybrids produced in a factorial design were grown in replicated trials at two environments in Mexico. Principal coordinate analysis based on Rogers' distance (RD) estimates calculated from 113 SSRs revealed three different groups of parents. Mid-parent heterosis (MPH) for grain yield averaged 0.02 t ha^{-1} (0.5%) and varied from -15.33% to 14.13%. MPH and hybrid performance (F1P) were higher for intra-group hybrids than for inter-group hybrids, with low values observed in inter-group crosses involving two non-adapted Chinese parents. Combined analyses of variance revealed significant differences among parents and among hybrids. Estimates of GCA variances were more important than SCA variances for all traits. Tight correlations of GCA with line *per se* performance, and mid-parent value with F1P were observed for all traits. In contrast, correlations of MPH with RD and coefficient of parentage were not significant. It was concluded that the level of heterosis in spring wheat was too low to warrant a commercial exploitation in hybrids. SSRs proved to be a powerful tool for the identification of divergent groups in advanced wheat breeding materials.

Introduction

In view of the growing need for wheat production worldwide, the International Maize and Wheat Improvement Center (CIMMYT) considers the development of hybrids as one promising tool in a multi-tiered strategy for breaking the yield barrier in wheat (Reynolds et al., 1996). Hybrid wheat has shown potential for enhanced yield performance and stability across diverse environments. For its successful implementation, three prerequisites are considered crucial: (i) a cost-effective system of seed production, (ii) adequate levels of heterosis, and (iii) the development of heterotic groups and patterns to ensure future progress through hybrid breeding (Lang, 1989). During the last four decades, hybrid wheat research has mainly focused on the introduction of male sterility and on acceptable cross-pollination characteristics (Pickett, 1993). The production of hybrids has been greatly enhanced by the discovery of effective chemical hybridizing agents (Pickett & Galwey, 1997). However, knowledge about hybrid performance, the relative importance of general (GCA) and specific (SCA) combining ability, and the genetic background of parental materials for maximum exploitation of heterosis in wheat, remains limited.

Quantitative genetic theory suggests that high heterosis can be expected in a hybrid if the source populations have (i) a high frequency of genes with partial or complete dominance and/or (ii) maximum differences in gene frequencies of overdominant loci (Hallauer et al., 1988). Consequently, for an optimum exploitation of heterosis, parents should be derived from genetically divergent germplasm pools, commonly referred to as heterotic groups (Melchinger & Gumber, 1998). Separate cultivation of populations of maize and other allogamous crops such as rye, facilitated their classification into heterotic groups according to their evolutionary history and geographic origin. In contrast, heterotic groups are not available or easily discernable in wheat, owing to its past breeding history. As for other autogamous crops, breeding of pure line cultivars has relied on deriving transgressive segregants from crosses between complementary parents obtained through a relatively widespread exchange of germplasm (Heisey et al., 2002). Furthermore, introgression of genes for new resistance or tolerance to various biotic and abiotic stresses from wild relatives into modern cultivars contributed to a mix of germplasm from diverse genetic origins.

The coefficient of parentage (COP) as well as phenotypic and molecular data have been used to study diversity among subsets of wheat germplasm (Souza et al., 1994). A linear association between marker-based genetic distance and heterosis was determined both in theory (Chacrosset & Essioux, 1994) and in numerous experiments with tropical maize (Reif et al., 2003) and other crops (Brummer, 1999). In wheat, a few studies applying RFLP or RAPD markers were carried out, but no clear relationship between molecular diversity and heterosis was observed (Liu et al., 1999; Corbellini et al., 2002). However, marker systems used in these studies were of limited use in wheat owing to a low degree of polymorphism or poor reproducibility. Currently, simple sequence repeats (SSRs) represent the most suitable marker system in wheat. They allow an even coverage of the genome, are abundant, genome specific, co-dominant in nature, and have been successfully used to characterize genetic diversity in advanced wheat breeding materials (Dreisigacker et al., 2004; Röder et al., 2002).

The objectives of our research were to (i) determine the genetic diversity among 22 spring bread wheat lines representing widely grown landmark cultivars or successful breeding lines from CIMMYT, (ii) investigate the level of heterosis in hybrids produced from these lines, (iii) assess the relative importance of general *vs.* specific combining effects in the hybrids, and (iv) examine the relationship between heterosis and genetic distances based on COP and SSR markers.

Materials and methods

Genetic materials

Twenty parents were chosen from a set of widely grown landmark cultivars and successful breeding lines from CIMMYT, to represent contrasting phenotypes and diverse genetic backgrounds for production of hybrids (Table 1). In addition, one Chinese wheat and one CIMMYT cross with Chinese ancestry (hereafter referred to as "Chinese lines") were used as male parents. Fourteen hand-emasculated female lines were crossed with

Table 1. Name, abbreviation, year and country of release, as well as average grain yield evaluated at two environments in Mexico of 22 spring bread wheat lines used in the production of hybrids

Wheat line	Abbreviation	Parent	Year of release	Country of release	Grain yield (t ha^{-1})
Sonora 64	SN	Female	1964	Mexico	4.21
Sonalinka	SKA	Female	1973	Bangladesh	4.94
Jupateco F 73	JUP	Female	1973	Mexico	6.02
Yecora Rojo 76	YRR	Female	1975	USA	3.24
UP 262	UP	Female	1978	India	4.51
Debeira	DEBA	Female	1982	Sudan	5.68
HUW 234	HUW	Female	1984	India	5.41
Prointa Federal	PIFED	Female	1989	Argentina	5.37
Nesser	NESSER	Female	1990	Jordan	5.43
BAW 898	BAW	Female	1996	Bangladesh	5.29
Alucan/Ducula[a]	AL1	Female	–	Mexico	4.44
Chum18/5 × BCN[a]	AL2	Female	–	Mexico	6.23
Tilhi	TIL	Female	2003	Mexico	7.00
Heilo	HEI	Female	2003	Mexico	5.55
Kalyansona	KAL	Male	1967	India	5.41
Pavon F 76	PVN	Male	1976	Mexico	6.18
HD2329	HD	Male	1985	India	5.26
Inqalab 91	IQB	Male	1991	Pakistan	5.40
Tobarito M 97	TOB	Male	1993	Mexico	5.89
Baviacora M 92	BAV	Male	1997	Mexico	7.38
SW89.5124 × 2/Fasan[a]	SW89	Male	–	Mexico	4.06
SW90.1057	SW90	Male	–	China	4.94

[a] Advanced breeding lines from CIMMYT.

eight male parents to produce 112 hybrids in a factorial mating design during the 2001 and 2002 winter seasons at Ciudad Obregon, Sonora, Mexico.

SSR analyses

Genomic DNA of the parental lines was extracted from bulked leaves harvested from seven to ten young plants using the modified CTAB procedure described in CIMMYT's manual of laboratory protocols (CIMMYT, 2001). A set of 113 SSRs (60 genomic- and 52 expressed sequence tag (EST) derived SSRs) was employed covering the three (A, B, and D) wheat genomes. Four to eight SSRs were located on each chromosome, and the map locations of five SSRs were unknown. The genomic-derived SSRs were developed by M. Röder at the Institute of Plant Genetics and Crop Plant Research in Gatersleben, Germany, and by the Wheat Microsatellite Consortium Agrogene in France. The EST-derived SSRs were developed at DuPont, Wilmington, USA. In addition, the SSR marker 'Taglgap' developed by Devos et al. (1995) was used. The SSRs were multiplexed for maximum efficiency. Information on map location, repeat type, annealing temperature, fragment sizes, number of alleles, and polymorphic information content (PIC) for each SSR is available at http://www.cimmyt.org/english/web/support/publications/support_materials/ssr_mwl.htm. PCR amplification and allele detection were performed using an ABI-Prism Sequencer$^{\text{TM}}$377 in combination with computer software GeneScan 3.1 and Genotyper 2.1 (Perkin Elmer Biotechnologies), as described in detail by Dreisigacker et al. (2004).

Field trials

The 112 hybrids, duplicate entries of the parents, and two local commercial checks (RAYON F 89 and KAMBARA 1) were sown in two yield trials arranged as randomized latinized 16 × 10 α-lattice designs with two replications. The trials were conducted in a dry, arid location near Ciudad Obregon (27°N, 40 m a. s. l.) in north-western Mexico during the winter season of 2002–2003 and at El Batan (19°N, 2640 m a. s. l.), a high rainfall site in the central Mexican highlands, during the summer season of 2003. The optimal planting dates at the end of Novermber at Ciudad Obregon and the end of May in El Batan, were used for each location. The experimental plots consisted of four rows of 3 m in length and were sown at a constant plant density of 200 seeds m^{-2} (corresponding to an average seeding rate of 50 kg ha^{-1}). The distance between rows within plots was 18 cm, and the distance between rows among plots was 50 cm. At both locations trials were irrigated according to a full-irrigation schedule. Fertilizers and pesticides were applied according to common station management practices. Grain yield (t ha^{-1}), plant height (cm), days to flowering and maturity in days after sowing were recorded on a plot basis.

Statistical analyses

For the grouping of germplasm, COP values of the parents were determined with fully expanded genealogical information extracted from the CIMMYT database IWIS version 4 (Payne et al., 2002). Rogers' (1972) distances (RD) based on the 113 SSR markers were calculated for all pairwise combinations of lines. Standard errors for RD estimates were obtained by using a bootstrap procedure with re-sampling over markers. A principal coordinate analysis (PCoA) was performed to group the parents based on RD estimates (Gower, 1966). Classification of the parents revealed by PCoA was used to determine the effect of genetic distance on intra- and inter-group hybrids.

For each hybrid the mid-parent value (MP), absolute mid-parent heterosis (MPH), relative mid-parent heterosis (MPH per cent), and relative better parent heterosis (BPH) were calculated as follows: $\text{MP} = (\text{P1} + \text{P2})/2$; $\text{MPH} = \text{F1P} - \text{MP}$; $\text{MPH}(\%) = (\text{MPH}/\text{MP}) \times 100$; $\text{BPH}(\%) = (\text{F1P} - \text{Pb})/\text{Pb} \times 100$, where P_1 and P_2 are the parents of the hybrid, F_1P the hybrid performance, and Pb the higher yielding, earlier, or taller parent. Mid-parent heterosis was tested for significance by an ordinary *t*-test. General (GCA) and specific combining ability (SCA) effects were estimated for all traits according to established methods (Hallauer & Miranda, 1988).

Combined analyses of variance were performed separately for the parents and hybrids for all traits, considering all effects as random. Sums of squares of hybrids were further partitioned into GCA and SCA effects. Because the classification of lines as male or female was arbitrary, GCA variance components were pooled with the following weights: $\sigma^2_{\text{GCA}} = 0.485\sigma^2_{\text{GCA male}} + 0.515\sigma^2_{\text{GCA female}}$. A corresponding subdivision was conducted on the hybrid × environment sums of squares. Parents and hybrids mean squares were tested for significance by F-tests using the corresponding interaction mean squares with environments. Parents × environment, hybrids × environment, GCA × environment, and SCA × environment mean squares were tested for significance by using the corresponding pooled error mean square in the denominator. From the genotypic and phenotypic variances among parents and hybrids, broad-sense heritabilities on an entry-mean basis were calculated.

Spearman correlation coefficients (*r*) were calculated for F_1P with MP, GCA with line *per se* performance (LP), RD with COP, as well as for MPH and F_1P with RD and COP. Analyses of variance were performed with software packages SAS (1988) and PLABSTAT (Utz, 1993). The PCoA was conducted using the software PLABSIM (Frisch et al., 2000), which is implemented as an extension of the statistical software R (Ihaka & Gentleman, 1996).

Results

SSR and COP data

The 113 SSRs amplified a total of 420 alleles across all parents. RD estimates ranged from 0.26 to 0.62, with a mean of 0.46. Pedigrees of the two Chinese parents SW89 and SW90 were not available and, therefore, could not be considered for the estimation of COPs. For the remaining 20 parents, COP values ranged from 0.06 to 0.35, with a mean of 0.17. The correlation between RD and COP values was significant ($P < 0.05$) but low ($r = 0.24$).

In the PCoA based on RD estimates, the first three principal coordinates (PC) explained 11.4%, 9.8%, and 7.6% of the total variation, respectively (Figure 1). In the graph, the parents clustered in three distinct groups as can be seen by eye, although Group III contains only the two Chinese parents.

Hybrid performance and heterosis

Four hybrids produced with Chinese line SW90 expressed hybrid necrosis and were excluded from subsequent analyses. Hybrids showed a significantly ($P < 0.05$) higher grain yield and plant height than the corresponding MP, combined with earlier flowering and maturity. MPH per cent for grain yield was on average

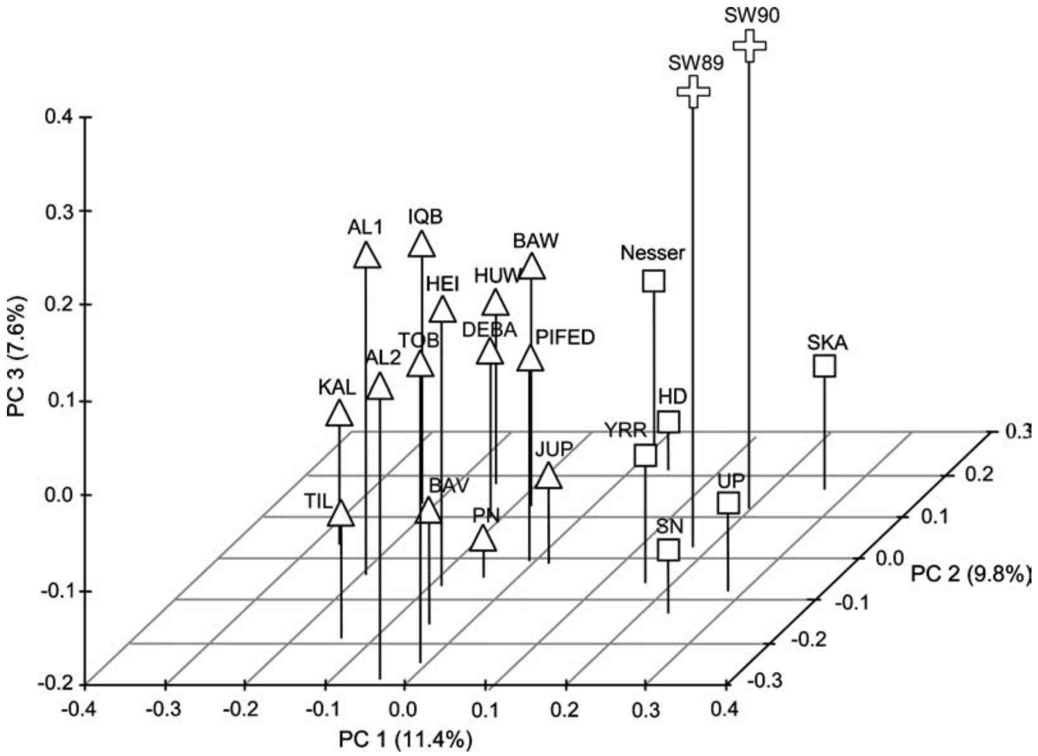

Figure 1. Principal coordinate analysis of 22 spring bread wheat lines performed with Rogers' distance estimates calculated from 113 SSRs. Abbreviation of the line names refer to Table 1. Different groups of germplasm are designated with triangles (Group I), squares (Group II), and crosses (Group III).

-0.15% at Ciudad Obregon and ranged from -27.98% for hybrid PRIFED × SW89 to 22.98% for hybrid BAW × HD. At El Batan MPH per cent for grain yield was on average 0.62% and ranged from -25.67 for hybrid AL1 × KAL to 18.15% for hybrid UP × SW89. Over both locations, MPH per cent for grain yield averaged -0.02% and ranged from -15.33% for hybrid TIL × KAL to 14.13% for the top yielding hybrid BAW × BAV (Table 2). Differences between the hybrid and the better parent were not significant, and the average BPH was negative.

Intra-group hybrids outperformed inter-group hybrids for grain yield (Figure 2) and other traits (data not shown). F_1P for grain yield was largest in intra-group hybrids of Group I and smallest in inter-group hybrids involving the two Chinese parents of Group III.

Table 2. Mid-parent value (MP), hybrid performance (F_1P), absolute (MPH) and relative mid-parent heterosis (MPH percent) and relative better-parent heterosis (BPH percent) observed for four agronomic traits of 22 spring bread wheat lines and 108 wheat hybrids evaluated at two environments in Mexico

Statistic	Grain yield ($t\,ha^{-1}$)	Plant height (cm)	Flowering date (days)	Maturity date (days)
		MP		
Mean[a]	5.41	80.8	70.7	108.0
Min.	3.64	65.1	63.7	98.9
Max.	7.20	89.6	78.1	113.2
$LSD_{5\%}$	0.82	7.7	3.9	5.2
		F_1P		
Mean	5.44	81.7	69.3	107.5
Min.	3.44	60.7	61.5	100.8
Max.	7.32	95.7	77.7	112.9
$LSD_{5\%}$	0.98	2.4	3.9	1.7
		MPH		
Mean	0.02^{*}	0.9^{**}	-1.4^{**}	-0.4^{**}
Min.	−0.80	−8.3	−7.6	−7.5
Max.	1.00	11.1	4.5	6.9
$LSD_{5\%}$	0.82	10.1	3.9	6.6
		MPH (percent)		
Mean	−0.02	0.8	−2.1	−0.4
Min.	−15.33	−13.7	−11.8	−7.5
Max.	14.13	12.21	6.1	6.5
		BPH (percent)		
Mean	−9.3	6.5	1.8	2.8
Min.	−37.26	−5.0	−7.8	−6.4
Max.	14.12	28.0	11.9	17.2

*,**Significant at the 0.05 and 0.01 probability levels, respectively.
[a] Values represent averages across environments.
Min. = Minimun, Max. = Maximum, $LSD_{5\%}$ = Least square difference at $\alpha = 0.05$.

Table 3. Components of variance (σ^2) and heritability (h^2) for four agronomic traits determined form the combined analyses of variance of 22 spring bread wheat lines and 108 hybrids grown at two locations

		Grain yield		Plant height		Flowering		Maturity	
Source	df	($t\,ha^{-1}$)	S.E.[a]	(cm)	S.E.	(days)	S.E.	(days)	S.E.
				Parents					
σ^2_{G}	21	0.71^{**}	0.26	74.1^{**}	24.0	9.4^{*}	5.7	18.5^{**}	6.7
$\sigma^2_{G\times L}$	21	0.33^{**}	0.10	13.6^{**}	4.0	16.1^{**}	4.7	0.9^{*}	2.3
h^2		0.81		0.9		0.5		1.9^{**}	
				Hybrids					
σ^2_{GCA}	20	0.20^{**}	0.11	18.9^{**}	8.0	4.5^{**}	2.0	7.7	1.6
σ^2_{SCA}	87	0.04^{**}	0.02	3.0^{**}	1.1	0.6^{*}	0.3	0.8	0.4
$\sigma^2_{GCA\times L}$	20	0.86^{**}	0.09	2.3^{**}	1.2	0.9	0.5	2.8^{**}	0.9
$\sigma^2_{SCA\times L}$	87	0.11	0.02	6.8	1,0	2.3	0.3	2.8	0.4
h^2		0.78		0.8		0.9		0.7	

*,**Significant at the 0.05 and 0.01 levels of probability, respectively.
[a] S.E.=standard error.

The combined analyses of variance revealed significant ($P < 0.05$) genetic variation among parents and among hybrids for all traits (Table 3). Estimates of genotypic variance were twice as large among the parents than among the hybrids for all traits. Estimates of GCA and SCA variances were significant ($P < 0.05$) for all traits, with the former being three to four times greater than the latter. The largest GCA effect over both locations for grain yield was observed for male parent BAV ($0.92\,t\,ha^{-1}$), the lowest for female parent YRR ($-0.96\,t\,ha^{-1}$).

Relationships of MPH and F_1P with genetic distance

Hybrid performance was significantly ($P < 0.01$) correlated with MP for all traits (Table 4). Correlation coefficients were highest for plant height ($r = 0.86$) and lowest for days to maturity ($r = 0.72$). A tight association also existed between GCA effects and LP for all traits. The correlation between F_1P and COP was not significant for all traits. Between F_1P and RD the correlation was significantly negative for grain yield, days to flowering and maturity, but of low magnitude. The correlations between MPH and COP or RD were generally of small magnitude and not significant for most traits. For Group I comprising the most promising parents for hybrid production, the correlation between MPH and RD was also low and not significant ($r = 0.06$).

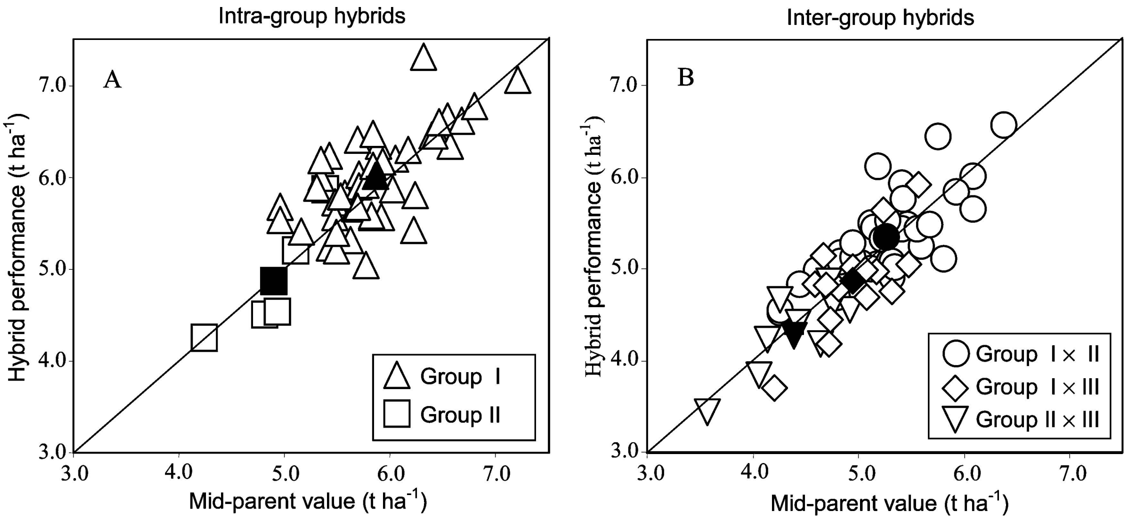

Figure 2. Hybrid performance *vs.* mid-parent value for grain yield of (A) intra-group and (B) inter-group hybrids evaluated in two environments in Mexico. Groups I to III refer to Figure 1 of this study and are based on groupings of 22 spring bread wheat breeding lines determined by principal coordinate analysis. Group means are designated by the corresponding filled symbols.

Table 4. Correlation coefficients of hybrid performance (F_1P) with mid-parent performance (MP), general combining ability (GCA) with line *per se* performance (LP), as well as F_1P and mid-parent heterosis (MPH) with coefficient of parentage (COP) and Rogers' distance (RD) based on 113 SSRs for four agronomic traits evaluated in wheat lines and hybrids grown at two environments in Mexico

r (x, y)		Grain yield	Plant height	Flowering date	Maturity date
x	y				
F_1P	MP[a]	0.75**	0.86**	0.83**	0.72**
GCA	LP	0.86**	0.92**	0.67**	0.85**
F_1P	COP	−0.08	−0.11	−0.04	−0.07
F_1P	RD	−0.29**	−0.11	−0.31**	−0.46**
MPH	COP	0.06	−0.31*	−0.14	−0.26*
MPH	RD	−0.06	−0.03	−0.05	−0.05

*,**Significant at the 0.05 and 0.01 probability levels, respectively.
[a]Correlation coefficients based on means across environments.

Discussion

SSR diversity and grouping of germplasm

The degree of polymorphism observed across the 22 lines was similar to the findings of Ahmad (2000) and Bryan et al., (1997), who analyzed 13 and 10 wheat cultivars, respectively. We had expected a somewhat higher degree of allelic variation in the present study, given the broad genetic base of the genotypes evaluated and the marker system used. However, the EST-SSR markers employed generally revealed a much lower degree of polymorphism than the genomic-derived SSRs used in other studies (Eujayl et al., 2002).

Principal coordinate analysis based on RD estimates confirmed the power of SSR markers to group breeding germplasm according to common ancestry and geographic origin. The separate grouping of the two Chinese parents was expected because wheat breeding programs in China have operated independently and under specific environmental conditions until the mid-1980s, making their germplasm quite unique compared to materials from other countries (He et al., 2001). The remaining lines tended to group according to chronological evolution through breeding, as Group I was composed mostly of more recently bred, high yielding lines, and Group II of the earlier released semi-dwarf wheats (Figure 1).

No clear grouping of the parents based on COPs was observed. COP values represent only an indirect measure of genetic diversity. The diverse genetic background of the parents resulted in a small range of COP values, which complicated the classification of the parents, whereas a large variation in the RD was observed. Furthermore, calculating COPs is based on simplifying assumptions regarding the relatedness of ancestors, parental contribution to the offspring, and absence of selection and genetic drift, most of which are not met under breeding conditions (Cox et al., 1985).

Exploitation of heterosis in wheat

The major goal in hybrid breeding is the exploitation of heterosis. While a large number of studies found significant heterosis in wheat, there is considerable variation in its magnitude. High MPH per cent of 92% for grain yield was reported by Walton (1971) and up to 46% by Bailey et al. (1980). In recent papers, lower levels of MPH per cent for grain yield were measured, which rarely exceeded 10% (Liu et al., 1999; Oury et al., 2001). Cukadar et al. (1999) evaluated 260 hybrids including CIMMYT advanced lines and reported BPH per cent between 3.5% and 6.5%. In the present study, MPH per cent for grain yield was generally small and on average BPH per cent was even negative. It is striking that most of the earlier studies reporting high levels of heterosis employed low seeding densities. With fewer plants to work with (which was caused by the smaller numbers that could be emasculated by hand), plants were sown at a lower density and heterosis estimates are most likely inflated due to improved growing conditions, leading, for example, to higher degrees of tillering and higher grain yield (Pickett, 1993). With the discovery of chemical hybridizing agents, it became feasible to produce sufficient quantities of F_1 seeds and to test a large number of hybrid combinations at normal seeding densities, which gives more realistic estimates of heterosis under common agricultural practices (Pickett & Galwey, 1997). Owing to hand emasculation, the seeding rate was reduced in our study, but it was still close enough to commercial seeding rates to avoid strong effects on the yield levels of either the hybrids, parental lines or checks. Hybrid seed was somewhat smaller than the parental seed, but no visible differences in vigour of plant development between hybrids and parents have been recognized.

Since wheat is an allopolyploid species with three ancestral genomes, substantial benefits from a high degree of intergenomic heterosis are expected. When we exclusively considered hybrids produced from parents released during the last decade, 50% outyielded the commercial pure line check RAYON F 89, but none of them outperformed KAMBARA 1, the most recently released check. Thus, the hybrid advantage over lines applied only to the parents but not to the newest released line cultivar. Earlier released parents mostly showed suboptimal performance and might have contributed alleles negatively affecting MPH per cent and BPH per cent in the hybrids.

The relative amount of heterosis also depends on environmental factors. MPH per cent for grain yield has been found to be smaller under optimum than under stress conditions in maize and sorghum (Betrán et al., 2003). This could be a further explanation for the low levels of MPH per cent observed in our study, because common, optimized agronomic practices were applied (e.g., full irrigation, complete fertilization, fungicide treatment) for achieving high yields.

Earliness is a desirable breeding goal, and hence the presence of negative heterosis for days to flowering and maturity, observed in this study, would favour hybrids. On the other hand MPH per cent for plant height was significant but on average only 0.9%. This would be of no concern for the release of wheat hybrids, because most of them fell within the range of their parents.

Combining ability of parental lines and implications for hybrid breeding

The choice of parental combinations yielding superior hybrids is the most important aspect in hybrid breeding. Analysis of the relative importance of GCA and SCA effects provides an indication of the type of gene action involved in the expression of traits and allows inferences about optimum allocation of resources in hybrid breeding. In accordance with earlier studies in wheat, GCA variances were more important than SCA variances, indicating the predominance of additive effects. Theoretical and experimental results in maize show that SCA effects are of primary significance in intra-group crosses, whereas GCA effects are predominate in inter-group crosses (Melchinger & Gumber, 1998). Our findings in wheat are in contrast with these results for unknown reasons.

The tight correlations of GCA with LP and MP with F_1P (Table 4) suggest that the probability of obtaining superior hybrids is greater when crossing the highest yielding parents. Thus, hybrid wheat breeding should be relatively efficient based only on selection for parental performance and a relatively small number of testcrosses involving outstanding parental lines. Although the correlations depend on the material studied and were often reported to be lower in other studies, the use of MP as a predictor for F_1P was suggested earlier owing to its simple assessment and because reliable information about LP is readily available from line breeding programs (Oury et al., 2001).

Relationship between MPH and diversity measures

Quantitative genetic theory suggests a linear correlation between MPH and the squared modified Rogers' distance under certain simplifying assumptions (Falconer & Mackay, 1996). Because the parents were homozygous lines in our study, the squared modified Rogers' distance corresponds to the RD (Melchinger, 1993). Contrary to expectations, however, the observed correlation between MPH and RD was low for all traits. Four possible explanations include: (i) a poor association between heterozygosity estimated from the SSR data and heterozygosity at quantitative trait loci controlling the trait, (ii) a lack of association between heterozygosity and heterosis at quantitative trait loci in the crosses examined, (iii) existence of multiple alleles with similar effects on a given trait, and (iv) epistasis among the respective quantitative trait loci. Thus, molecular diversity represents relict diversity, most probably not related to fitness traits and is also of limited value for predicting performance. Providing that the existence of multiple alleles and epistasis among loci are absent, Melchinger (1999) pointed out that a correlation between MPH and molecular distance was more likely to be found in intra-group crosses than in inter-group crosses. This could not be confirmed in our study, presumably due to the lower levels of heterosis observed in inter-groups than in intra-group crosses.

A decrease in MPH and F_1P in extremely wide crosses with large RDs, as observed in hybrids with the Chinese parents from Group III, was also found in crosses between tropical and U.S. maize populations (Moll et al., 1965). The authors attributed this nonlinear relationship between geographic distance and heterosis to the lack of co-adaptation between both allelic and non-allelic combinations from the two parental genomes, which resulted in negative dominance and negative epistatic effects, respectively (Falconer & Mackay, 1996).

Prospects of hybrid breeding in wheat

In light of the low level of MPH per cent and BPH per cent observed in the present and other studies, the successful dissemination of hybrids in wheat cannot be considered promising, especially if the costs of hybrid seed production remain high. Agnus (1997) concluded that a yield advantage of 5% over the best conventional variety is required to compensate for the higher seed costs associated with male emasculation and cross fertilization, and to justify the additional expenses in breeding of hybrid wheat. Pickett & Galwey (1997) argued that 6–34% of MPH per cent is necessary to make wheat hybrids commercially viable. Thus, our estimates of MPH per cent and BPH per cent as well as the F_1P relative to the checks cannot be considered encouraging for large-scale development and global acceptance of hybrid wheats.

Owing to their better vigour, robustness and stress tolerance compared with pure line cultivars under more marginal conditions, the development of hybrids may be justified in marginal environments and where low seeding rates are used (Jordaan et al., 1999). Biotechnological approaches including the exploitation of apomixis might nurture hopes to facilitate seed production and make hybrid wheat an attractive alternative for niche environments in the future. Finally, genetic distances based on SSRs cannot be considered a promising tool to predict hybrid performance, but could be a powerful tool for identification of divergent groups in advanced wheat breeding materials.

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