 © Springer-Verlag 1994

B. Borghi · M. Perenzin

Diallel analysis to predict heterosis and combining ability for grain yield, yield components and bread-making quality in bread wheat (*T. aestivum*)

Received: 2 May 1994 / Accepted: 10 June 1994

Abstract Combining ability for grain yield, yield components, and several agronomic and qualitative traits, was studied in a seven-parent diallel cross. The 21 F_1 hybrids and the seven parental cultivars were grown in replicated plot trials sown at normal seed density in three locations in the years 1992 and 1993. The effects of general combining ability (gca) were highly significant for all the traits measured with the exception of seeds per spikelet, while the specific combining ability (sca) effects were statistically significant for grain yield, plant height, heading time, for all the yield components, and for the Chopin alveographic parameters P and P/L ratio. For the majority of the traits measured gca was greater than sca. Standard heterosis (sh) for grain yield, i.e., the superiority of the hybrids over the best pure line cultivar (cv Eridano), was only 3.3%, confirming previous finding which indicate sh effects in the range of 10%. The most interesting hybrid derived from the cross Maestra×Golia revealed a yield level approaching that of the highest yielding cv Eridano but appeared more interesting because of its reduced plant height and superior bread-making quality, signifying a selling price 30% higher. It was concluded, therefore, that the first generation of hybrids, likely to appear on the market in the next few years, will be characterized by a yield potential only slightly superior to that of the best standard cvs but associated with other desirable traits, such as bread-making quality.

Key words Bread wheat · Heterosis · Grain yield
Bread-making quality · Diallel

Introduction

The prospect of introducing F_1 seed into practical agriculture, and thereby acquiring control of the seed market for a widely grown crop such as wheat, is very attractive and has led the commercial seed and agrochemical companies, in particular, to investigate this possibility. However, the current status of this research in the private sector is described only partially in the literature (Lucken 1986). The commercial exploitation of F_1 hybrid seeds in an autogamous, polyploid species characterized by a low seed-multiplication ratio and requiring a high seeding rate presents several problems but, apart from the practical aspect of production of F_1 seed on a large scale, the crucial question regards the yield advantage of the hybrids over the best conventional pure line cultivars (cvs).

Studies on heterosis and on combining ability for agronomic, productive and qualitative traits have been hampered in the past by the difficulty of producing substantial amounts of F_1 seed to be used for replicated plot trials sown at normal seed density. The majority of the investigations reported in the literature refer to experiments carried out with a limited number of hybrids, grown in small plots at very low density and evaluated for a limited number of years or in few locations (reviewed by Johnson and Schmidt 1968; Virmani and Edwards 1983; Lucken 1986; Pickett 1993). Because of these limitations the results were poorly correlated with performance in ordinary field conditions and were considered of limited practical or theoretical interest (Lucken 1986). It is a matter of fact that papers dealing with combining-ability effects on autogamous plants have been systematically refused in recent years by the leading scientific journals concerned with plant breeding.

The above mentioned limitations were partially overcome by the discovery of cytoplasmic male sterility and restorer genes; however, the manipulation of the genetic system, and the time required for the conversion of the desirable lines into male steriles, led to the production of hybrids which could not compete with the new cvs produced by conventional breeding methods owing to the low level of standard heterosis (sh) (reviewed by Pickett 1993).

The possibility of producing and testing hybrid wheats has been greatly enhanced by the discovery of effective chemical hybridising agents (CHAs). These chemicals,

Communicated by J. MacKey

B. Borghi (✉) · M. Perenzin
Istituto Sperimentale per la Cerealicoltura, Via Mulino No. 3, 20079 S. Angelo Lodigiano (MI), Italy

when applied to wheat plants at the appropriate growing stage, selectively induce male sterility. Although several technical and economic problems concerning the use of CHAs for the large-scale production of F_1 seed remain to be solved, it is now feasible to produce, on an experimental scale, hybrid combinations from a large number of parental cvs (Carver and Nash 1984; Edwards 1987; Borghi et al. 1989).

In the most important wheat growing area of the world, CHAs are being primarily used for the massive production of F_1 hybrid combinations to be tested against conventional cvs, in the hope of finding sh effects sufficient to cover the extra cost of hybrid-seed technology while leaving a sufficient margin for the farmers. Moreover, CHAs offer a unique opportunity to investigate the genetical basis of heterosis by producing F_1 hybrids according to special mating designs such as top-crosses or diallels.

In this paper we present the results of combining ability for grain yield, yield components, and several agronomic and qualitative traits in a seven-parent diallel cross. Although numerous papers on diallel analysis in wheat have been published, this is, to our knowledge, the first case of a diallel sown at normal seed rate and grown in several locations in large replicated plot trials.

Materials and methods

The seven bread-wheat cultivars listed in Table 1, selected on the basis of their yield potential and high general combining ability (gca) previously evaluated by mean of top-crossing experiments (Borghi et al. 1989), were used to produce a 7×7 diallel cross without reciprocals. The cvs 1, 4, 5, 6 and 7 were bred in Italy; at present cv 1 is the most productive, cv 4 has superior bread-making quality (class 1) while cv 7 has a very short-straw high protein content, a high harvest index and medium high quality. The cvs 2 and 3, bred in East Europe, are both characterized by very poor bread-making quality and were included in the diallel because in previous experiments they revealed interesting combining effects for yield with the Italian germplasm.

F_1 hybrids were produced in 1991 using CHA technology as previously described (Borghi et al. 1988). The chemical compound MON-8164 was kindly provided by Hybritech.

The 21 F_1 hybrids plus the seven parental cvs were grown in replicated-plot trials in the Po Valley (North Italy) at two locations in 1992 and at one location in 1993.

The experimental design was a randomized complete block with three replications; the elementary plot of 6 m^2 was composed of eight rows, 17 cm apart. The contiguous plots were separated by an empty path of 34 cm and were bordered at both edges by the short-straw cv Golia sown perpendicularly to the direction of the plots in order to minimize intergenotypic competition and edge effects (Romani et al. 1993).

The agronomic practices were those recommended for high yields, including sowing with 400 germinating kernels m^{-2}, seed dressing, chemical control of weeds, 150 kg ha^{-1} of Nitrogen applied in three top-dressings, and without application of growth regulators or fungicides and pesticides.

Agronomical characteristics, grain yield, yield components, protein content (N×5.7) and SDS sedimentation tests were determined on each plot. Rheological analyses with the Chopin alveograph and the Brabender farinograph were carried out at two locations on seed samples from the blend of the replications, according to the standard procedures as previously described (Perenzin et al. 1992).

Standard analysis of variance was applied to all data; combining-ability analysis was carried out according to Design 2 of Comstock and Robinson (1950). The diallel cross was analysed according to Griffing (1956) method 2 model 1 (fixed effects) using the MSTAT-C package.

Results

The main characteristics and the performance of the parental cvs are reported in Table 1. In this experiment, cv Eridano was the highest yielding of the Italian cultivars but was surpassed by SK 7, which was very tall and produced grain of poor bread-making quality, in spite of the fact that all the other cvs revealed qualitative values higher than usual.

The results of the diallel analysis for grain yield, plant height, heading time, hectolitre weight, protein content, and SDS sedimentation value, concerning three locations, are reported in Table 2. The effects of gca were highly significant for all the traits measured with the sole exception of seeds per spikelet; specific combining ability (sca) effects were statistically significant for grain yield, plant height, heading time, for all the yield components and for the alveographic parameters P and P/L ratio. For several traits, gca and sca effects varied between locations as indicated by the significant interactions with locations.

The largest gca effects for grain yield were contributed by the two highest-yielding cvs 1 (Eridano) and 2 (SK-7); the relatively small variance of sca effects found in both these cvs suggests that yield potential was uniformly transmitted to all their hybrids. Moreover, the cvs carry additive genes for increasing plant height, but in the case of cv 1 the large variance of sca effects indicates that this negative trait will be transmitted only to some of the hybrids. The very short-straw cv 7 (Golia), on average, decreased the plant height of the hybrids by 7.7 cm with positive effects on the majority of their hybrids; in fact sca variance, statistically significant, was the second lowest after that of cv 2.

Significant sca effects for earliness were evident in the two hybrids 6×7 and 2×6 derived from cv 6, which was 5 days later than the earliest cv 3, and in the hybrid 3×4; but the largest sca and gca effects where of 1 day only.

Hectolitre weight appeared to be controlled by additive genes, cv 4 contributed genes with positive effects (+1.3 kg hl^{-1}) and cv 5 genes with negative effects (–2.2 kg hl^{-1}).

The analysis of yield components presented in Table 3 shows, in the case of seeds per spike and seeds per spikelet, sca effects of the same magnitude as, or greater than, the gca effects. The positive gca effects found for grain yield in cv 1 (see Table 2) appear to be the consequence of positive gca effects for spikes m^{-2} (+37.5); in the case of cv 2, yield increase was associated with positive gca effects on kernel weight (+4.1 mg). The high sca effects for grain yield found in the hybrid 3×4 (+0.63 t ha^{-1}) depend on the positive sca effects for kernel weight (+2.9 mg) and spikes m^{-2} (+21.8). It is likely that cvs 3 and 4 carry genes

Table 1 List of the parental cultivars, main agronomic and qualitative characters (mean values of three and two locations respectively), composition in high-molecular-weight (HMW) glutenin subunits, quality score according to Pogna et al. (1989), and marketing class

Character	1 Eridano	2[a] SK 7	3 1418-2	4[a] Maestra	5 Pegaso	6 Etruria	7 Golia	lsd (P= 0.05)
Grain yield (t ha^{-1})	7.75	8.13	6.82	6.46	6.66	6.49	6.98	0.45
Plant height (cm)	88.1	93.6	87.7	88.6	77.7	81.0	69.9	2.7
Harvest index (%)	45.7	48.8	44.7	44.9	46.3	49.9	51.2	3.8
Heading (days from 4–1)	42.2	43.4	40.9	42.1	42.9	45.4	42.0	0.5
Hectolitre weight (kg hl^{-1})	74.4	73.6	71.3	74.3	68.9	72.2	72.9	3.5
Protein content (%)	10.8	12.1	10.1	12.4	12.1	10.7	13.0	0.6
SDS Sedimentation volume (cc)	61.6	56.2	47.1	54.1	72.6	56.4	61.1	3.9
Chopin alveograph – W (joule 10^{-4})	298	126	113	350	312	186	338	71
– P/L (ratio)	0.68	0.95	0.41	0.57	0.50	0.53	0.85	0.15
Brabender farinograph – Stab. (s)	390	180	210	810	1110	210	945	403
– Soft. (FU)	60	150	80	30	20	65	25	36
HMW Subunit composition – A1	1	N	N	2*	N	2*	1	
– B1	7+8	7+9	7+9	7+9	7+9	7+9	17+18	
– D1	2+12	2+12	2+12	5+10	5+10	2+12	2+12	
Quality score	9	9	9	16	13	12	11	
Marketing class[b]	2	3	3	1	1–2	2	1–2	

[a] Cultivars with a 1B/1R translocation
[b] 1 Improver wheat; 2 direct for bread-making; 3 for animal feeding or biscuit

Table 2 Analysis of variance and estimates of gca and sca effects for agronomic and qualitative characteristics in a seven-parent diallel cross

Source of variation	*df*	Grain yield (t ha^{-1})		Plant height (cm)		Heading (days from 4–1)		Hectolitre weight (kg hl^{-1})	Protein content (%)		SDS sedim. volume (cc)	
gca	6	6.66**		1454**		26.76**		105.68**	22.86**		926.2**	
sca	21	1.30**		102**		2.57**		23.23	0.84*		38.3**	
gca/sca		5.1		14.3		10.4		4.6	27.2		24.3	
Locations	2	213.86**		11741**		675.04**		25.34	8.82		28.6	
L×gca	12	0.74**		40**		2.32**		33.11**	0.85*		27.1	
L×sca	42	0.46**		11		0.62**		20.18	0.64		16.6	
Error	162	0.23		8		0.28		14.39	0.46		17.7	
CV%		6.7		3.3		1.2		5.2	5.9		7.4	
Cultivars		gca eff.	sca var.	gca eff.	sca var.	gca eff.	sca var.	gca eff.	gca eff.	sca var.	gca eff.	sca var.
1 Eridano		0.42**	0.07	2.7**	15**	–0.2*	0.10*	0.5	–0.4**	0.01	0.8	2.8*
2 SK 7		0.33**	0.05*	3.6**	2*	0.3**	0.21	0.5	0.3**	0.02	0.2	0.3
3 1418/2		–0.10	0.10**	2.5**	14**	–0.8**	0.07*	0.1	–0.6**	0.00	–4.9**	0.6
4 Maestra		–0.11	0.21**	3.0**	12**	–0.3**	0.19**	1.3**	0.3**	0.02	–1.1*	0.0
5 Pegaso		–0.42**	0.09**	–3.6**	8**	0.2**	0.11*	–2.2**	0.2**	0.05	6.2**	5.4**
6 Etruria		–0.02	0.19**	–0.5	15**	1.0**	0.80**	–0.8	–0.6**	0.10*	–1.9**	3.9*
7 Golia		–0.09	0.06*	–7.7**	5**	–0.3**	0.16**	0.6	0.8**	0.07	0.8	3.4*
SE		0.06		0.33		0.07		0.42	0.07		0.44	
+ sca effects		3×4	0.63**	1×5	4.6**	5×7	0.3		3×7	0.4	3×4	2.7
		4×7	0.42*	3×6	4.0**	3×5	0.3		1×2	0.3	2×5	2.0
		1×6	0.38*	1×6	3.4**	5×6	0.3		6×7	0.3	3×7	1.5
		4×6	0.35	1×4	2.3*	2×4	0.2		2×7	0.3	6×7	1.1
		1×3	0.24	2×5	2.2	1×4	0.2		1×3	0.2	1×2	1.1
– sca effects		5×7	–0.58**	5×7	–3.2*	6×7	–0.9**		5×7	–0.5*	5×7	–4.0*
		3×5	–0.40**	1×2	–2.0	2×6	–0.7**		1×7	–0.4	1×6	–3.2*
		1×2	–0.39*	3×5	–0.3	3×4	–0.7**		4×6	–0.4	5×6	–2.0
		2×4	–0.34			1×6	–0.6		1×6	–0.3	1×7	–1.6
		2×3	–0.24			1×5	–0.5		2×6	–0.3	3×5	–1.6
SE			0.16		0.97		0.20			0.21		1.2
General mean		7.22		87.8		42.2		73.4	11.4		57.3	

Table 3 Analysis of variance and estimates of gca and sca effects for yield components in a seven-parent diallel cross

Source of variation	*df*	Kernel weight (mg)		Culm weight (g)		Yield spike^{-1} (g)		Spikelets spike^{-1} (no.)		Seeds spike^{-1} (no.)		Seeds spikelet^{-1} (no.)		Harvest index (%)	Spikes m^{-2} (no.)	
gca	6	200.0**		1.99**		0.42**		17.6**		56.7**		0.06		96.1**	332**	
sca	21	31.3**		0.33**		0.13**		5.4**		55.7**		0.14**		16.2	155**	
gca/sca		6.4		6.0		3.2		3.3		1.0		0.4		5.9	2.1	
Locations	1	140.7		19.56**		11.96**		323.1**		5781.8**		4.4**		1939.0**	651**	
L×gca	6	6.8		1.14		0.07		3.2		28.5		0.03		16.6	103	
L×sca	21	10.3		0.21*		0.07*		2.6		30.8		0.08		10.9	128**	
Error	108	7.5		0.11		0.04		1.8		19.4		0.07		11.3	6017	
CV%		6.9		10.8		12.8		7.9		11.6		11.7		7.0	17.2	
		gca eff.	sca var.	gca eff.	sca var.	gca eff.	sca var.	gca eff.	sca var.	gca eff.	sca var.	gca eff.	sca var.	gca eff.	gca eff.	sca var.
1 Eridano		−1.4**	1.0	−0.07	0.02	−0.02	0.02*	0.2	1.2**	0.9	7.4*			0.4	37.5**	20*
2 SK 7		4.1**	1.5	0.38**	0.00	0.18**	0.00	0.8**	0.0	0.8	0.5			0.0	−31.2**	0*
3 1418/2		−0.3	5.0**	−0.06	0.07**	−0.06*	0.03**	−0.7**	0.0	−1.3*	7.5*			−1.1*	9.8	17*
4 Maestra		−1.8**	6.8**	−0.01	0.03*	−0.06*	0.01	0.1	0.1	0.2	10.0			−1.8**	10.2	0
5 Pegaso		−0.6	2.0*	0.09	0.09**	0.02	0.04**	0.5**	0.6*	1.2*	14.6**			−0.6	−31.4**	43**
6 Etruria		0.4	3.3**	−0.08	0.01	−0.01	0.00	−0.5**	0.9**	−0.6	1.3			1.1*	−5.4	10
7 Golia		−0.4	7.6**	−0.24**	0.01	−0.06*	0.01	−0.5**	1.1**	−1.2	7.5*			2.1**	10.5	12
SE		0.35		0.04		0.03		0.18		0.58				0.43	10.74	
+sca effects		3×5	3.0*	3×5	0.61**	3×5	0.40**	5×7	1.8*	3×5	6.9**	3×5	0.33*		5×6	94.3*
		3×4	2.9*	2×4	0.26	1×7	0.13	1×6	1.6*	1×7	4.9*	1×7	0.18		1×3	47.4
		2×7	2.9*	1×6	0.20	5×7	0.13	1×7	0.8	5×7	4.2*	2×3	0.12		2×5	34.9
		6×7	2.4	1×5	0.20	1×6	0.13	3×5	0.7	2×4	2.9	1×5	0.09		4×7	24.2
		4×7	2.3	3×4	0.17	1×4	0.12	1×4	0.7	1×6	2.2	2×4	0.08		3×4	21.8
−sca effects		2×4	−1.4	5×6	−0.28	4×5	−0.16	4×7	−1.1	5×6	−4.7*	2×7	−0.22		3×5	−115.5*
		1×7	−1.3	4×5	−0.21	5×6	−0.16	5×6	−0.8	3×7	−3.6	4×5	−0.21		5×7	−57.3
		3×6	−1.2	3×7	−0.10	3×7	−0.08	2×5	−0.8	4×5	−3.6	3×7	−0.19		1×5	−55.5
		5×7	−0.9	2×5	−0.09	2×5	−0.06	2×3	−0.3	2×7	−2.9	6×7	−0.09		1×7	−43.5
		1×3	−0.8	3×6	−0.07	3×6	−0.06	3×7	−0.2	2×5	−2.3	1×3	−0.09		6×7	−38.9
SE			1.03		0.13		0.08		0.51		1.70		0.10			31.23
General mean		39.3		3.07		1.49		16.8		37.7		2.23		48.0	449	

Table 4 Analysis of variance and estimates of gca and sca effects for Chopin alveograph and Brabender farinograph parameters in a seven-parent diallel cross

Source of variation	*df*	Chopin alveograph							Brabender farinograph			
		G (%)	W (joule 10^{-4})	P (mm)		L (mm)	P/L		Develop. time (s)	Stability (s)	Degree of softening (FU)[a]	Water absorpt. (%)
gca	6	21.5**	409**	1167**		1867**	96**		4964**	7390**	6797**	47.1**
sca	21	2.9	15	38**		249	17**		512	519	547	1.9
gca/sca		7.4	27.3	30.7		7.5	5.6		9.7	14.2	12.4	24.8
Locations	1	13.9**	11**	25		1312*	18		789	196	457	30.8**
Error	27	1.8	11	8		195	5		620	382	297	1.2
CV %		5.5	15.1	4.5		11.3	12.8		20.3	30.8	17	1.9
Cultivars		gca eff.	gca eff.	gca eff.	sca var.	gca eff.	gca eff.	sca var.	gca eff.	gca eff.	gca eff.	gca eff.
1 Eridano		0.4	15	5.2**	24.9*	3.7	0.01	3	1	–69	4.8	1.0**
2 SK 7		–1.7**	–48**	–2.4**	8.1	–15.2**	0.08**	25**	31**	–134**	29.2**	1.7**
3 1418/2		–0.3	–65**	–11.4**	6.3	–2.8	–0.09**	0	–17**	–253**	17.5**	–1.4**
4 Maestra		1.2**	47**	2.6**	27.6*	11.5**	–0.04*	3	–2	77	–14.1**	0.7*
5 Pegaso		1.4**	27**	0.7	18.1*	12.7**	–0.05**	2	4	307**	–21.3**	–0.7**
6 Etruria		–0.9**	–31**	–7.4**	12.2	–8.5*	–0.03	4	–19**	–133**	4.2	–2.6**
7 Golia		–0.1	54**	12.8**	5.5	–1.4	0.11**	7	3	204**	–20.2**	1.4**
SE		0.29	7.51	0.65		3.05	0.01		5.44	42.66	3.77	0.24
+sca effects				6×7	5.7		6×7	0.12				
				1×4	4.2		5×6	0.05				
				5×6	2.6		5×7	0.03				
				3×5	1.5		1×4	0.03				
				3×4	1.3		3×4	0.02				
–sca effects				4×5	–8.9		2×7	–0.13				
				1×3	–6.2		2×5	–0.12				
				1×2	–4.9		2×6	–0.11				
				1×6	–4.8		1×6	–0.09				
				4×6	–4.7		2×4	–0.08				
SE					1.89			0.04				
General mean		24.5	227	65.9		122.9	0.55		123	635	49.6	56.3

[a] FU Farinograph unit

contributing positive sca effects for yield, as is suggested by the significant variance of sca for grain yield and kernel weight. In the hybrids 5×7, and 3×5 the negative sca effects for grain yield could be related to a specific yield component, namely spikes m^{-2}. In the case of the hybrid 2×4, the negative sca effects on grain yield, derived from the negative effects on kernel weight (–1.4 mg), were tempered by a greater number of seeds per spike (+2.9). Compensation between yield components was a very common phenomenon as exemplified by the hybrid 3×5 which was characterised by positive sca effects on kernel weight, culm weight, yield per spike, spikelets per spike, seeds per spike and seeds per spikelet, and the largest negative effect on spikes m^{-2} (–115.5).

The mean values of the qualitative characteristics recorded at two locations are reported in the last two columns of Table 2 and in Table 4. Quality traits appeared to be mainly under the control of additive gene action. In fact the highest gca effect for protein content (0.8% in cv 7) was twice that of the largest sca effect found in the combination 3×7. Similar results were obtained from the SDS sedimentation test: cv 5 increased the value by 6.2 cc while the largest sca effect in the combination 3×4 was only 2.7 cc.

The storage-protein composition of the parents should be taken into account in order to explain the effects on bread-making quality of the hybrid progeny. For example, the peculiar behaviour of SK 7, which, as in previous experiments, presented positive gca effects for protein content coupled with negative effects for dough viscoelastic properties, is likely to be due to the presence of rye secalins coded by the 1BL/1RS translocation (Perenzin et al. 1992). In fact this translocated chromosome was found by Zeller et al. (1982) to cause a decrease in bread-making quality (sticky dough). On the other hand, cv 3, characterized by the same low quality score (9) but without the 1B/1R translocation, revealed gca negative effects for all the qualitative traits (including protein content) as great, in the case of alveographic W and farinograph stability, as those observed for the line with the 1B/1R translocation.

Positive gca effects on bread-making quality (alveograph W, farinograph stability and degree of softening) were contributed by cv 4 (Maestra), another cv carrying the 1B/1R translocation but characterized by an optimal HMW-subunit composition as indicated by the highest quality score. The largest gca effects for bread-making quality were, however, contributed by cv 7 (Golia), which had a relatively low quality score (11 as against 16 of the best cv Maestra). It is likely that the positive gca effects on alveograph W (+54 joule 10^{-4}), farinograph stability (+204 s), and degree of softening (–10.2 FU), derived from the increase in protein content induced by cv 7 in its hybrids (gca effect +0.8%).

Discussion and conclusions

In a recent review on hybrid wheat Pickett (1993) found at least 36 published studies on combining ability in wheat. For the majority of the traits measured, gca was of greater importance than sca, the latter being more important in spaced planting (Virmani and Edwards 1983; Lucken 1986). The few papers based on large-scale trials (Borghi et al. 1989; Brears and Bingham 1989; Morgan et al. 1989; Perenzin et al. 1992), including the present study, confirmed the greater importance of gca. Large sca effects were observed in our experiment only in some yield components; however, these effects can hardly be exploited, in terms of grain-yield increase, because of the reciprocal compensation between traits. On the other hand, the largest positive sca effects for grain yield were found in the combinations 3×4 (0.63 t ha^{-1}) and 4×7 (0.42 t ha^{-1}), both derived from parents characterized by negative gca values, and, therefore, the two hybrids did not out-yield Eridano, the best cv.

Most interesting from a practical point of view are the hybrids revealing high levels of sh and, therefore, able to perform better than the best pure line cvs. Even though sh effects higher than 88% are reported in the earlier literature (Walton 1971), in the most recent publications sh effects rarely exceed 10%, values which, according to Pickett (1993), are at best economically marginal. Our results confirm this finding: while the largest gca effect in cv 1 was 5.8%, and the largest sca effect in the combination 3×4 reached 8.7%, the best hybrid (1×6) surpassed Eridano, the best cv, by only 3.3%. Although, as previously mentioned, the current state of results concerning the performance of the thousands of F_1 wheat hybrids produced and tested in the main wheat-growing areas of the world is described only partially in the literature, it appears likely that no hybrids showing sh values significantly greater than those previously mentioned have been found.

The hybrids so far produced mainly derive from parental cvs produced by conventional breeding programmes (Lucken 1986). Basically, the putative parental cvs are first screened for their suitability for cross-fertilization (either as female or male parent), then evaluated for gca in top-crosses and, finally, the few cvs showing the largest gca values are included in diallel crosses in order to find the best hybrid combinations. Following this approach, we observed a positive trend in the yield potential of the hybrids produced in the last 10 years. In fact in the first set of 141 hybrids produced by crossing the available cvs at random, none produced 10% more than the controls and only 15% produced over 5% more than the controls. In the following set of top crosses, 50% of the hybrids surpassed the controls by 5% and 19% by more than 10%. Of the 21 hybrids originated from this diallel, 71% surpassed the controls by 5% and 5% by more than 10%. It appears evident that, with this approach, we increased the frequency of hybrids able to compete with the best cvs continuously produced by conventional breeding but did not increase the level of sh. These results indicate that, unless specific breeding programmes based on reciprocal recurrent selection and aimed at exploiting and accumulating sca effects are developed, we cannot expect to significantly enhance the advantage of the hybrids over the pure line cvs.

Therefore, it appears likely that the first generation of hybrids, which will be put on the market in the next few years, will not be characterized by a yield potential remarkably higher than that of the best standard cvs. In this case hybrid wheats will only appeal to farmers if they have interesting characteristics other than yield alone. For instance, stability of performance in different environments and seasons was observed by Wienhues (1968) and Stroike (1987), while Boland and Walcott (1985) and Borghi and Perenzin (1990) found that the yield stability of the hybrids was intermediate to that of the parents. Where resistance to disease is dominant and is expressed in the heterozygote, it could be quickly incorporated in the hybrids (Johnson and Schmidt 1968). Resistance genes could be accumulated in the hybrids (Stroike 1987). The hybrid-seed production system could be more flexible to match with the evolution of the parasite population (Driscoll 1981). According to Edwards (1987) the manipulation of quality traits best exemplifies the possibility offered by hybrids for trait complementation. For instance, in previous experiments (Perenzin et al. 1992) we observed that some hybrids derived from crosses between low quality-high yielding cvs and high quality-low yielding cvs, revealed a yield level (>7 t ha^{-1}) approaching that of the highest-yielding cvs coupled with a bread-making quality corresponding to the first class of the Italian market (W>250, P/L< 1). In our diallel only the three cvs Maestra, Pegaso and Golia produced grains with first class technological properties but their yield level was below that of the best cv, Eridano. By contrast, the three hybrids 1×5, 4×7 and 1×4, with similar positive qualitative characteristics, produced 7.3, 7.4 and 7.7 t ha^{-1} respectively, values not statistically different from that of Eridano, the best cv (7.7 t ha^{-1}) and corresponding to a yield advantage over the cvs of the first class of 9, 11 and 14% respectively. Moreover, the hybrid 4×7 was agronomically superior to Eridano because of its reduced plant height (cv Eridano is considered too tall and therefore susceptible to lodging) and superior grain quality, which represents a 30% higher selling price.

In conclusion, the CHAs greatly facilitate the production on an experimental scale of a large number of hybrid combinations and represent a powerful tool for recurrent selection by eliminating the need for manual emasculation and pollination, thus opening new possibilities for the study of the basic and applied aspects of wheat hybrid vigour. More information is needed before an answer can be given to the crucial question concerning the economic convenience of the introduction of the hybrids into practical agriculture and it appears likely that, at first, productivity *per se* will not be the main or the only reason for hybrid cultivation.

References

Boland OW, Walcott JJ (1985) Levels of heterosis for yield and quality in an F_1 hybrid wheat. Aust J Agric Res 36:545–552

Borghi B, Perenzin M (1990) Yield and yield stability of conventional varieties and F_1 bread wheat hybrids. J Genet Breed 44:307–310

Borghi B, Perenzin M, Nash RJ (1988) Agronomic and qualitative characteristics of ten bread hybrids produced using a chemical hybridizing agent. Euphytica 39:185–194

Borghi B, Perenzin M, Nash RJ (1989) Combining ability estimates in bread wheat and performance on 100 F_1 hybrids produced using a chemical hybridizing agent. J Genet Breed 43:11–16

Brears T, Bingham J (1989) Exploitation of heterosis in hybrid wheat using gametocides. V für Pflanzenzücht 16:397–409

Carver MF, Nash RJ (1984) The future for hybrid cereals. Spain 2:64–65

Comstock RE, Robinson HF (1950) Estimation of average dominance of genes. In: Gowen JW (ed) Heterosis. Iowa State Univ Press, Ames Iowa, pp 494–516

Driscoll CJ (1981) New approaches to wheat breeding. In: Evans LT, Peacock WJ (eds) Wheat science today and tomorrow. University Press, Cambridge, pp 97–106

Edwards IB (1987) Baking quality of hard red winter and hard red spring wheat hybrids. In: Borghi B (ed) Hard wheat (*T. aestivum*): agronomic, technological, biochemical and genetic aspects. CEC Publ EUR 11172 EN, Brussels, Belgium, pp 215–224

Griffing B (1956) A generalised treatment of the use of diallel crosses in quantitative inheritance. Heredity 10:31–50

Johnson VA, Schmidt JW (1968) Hybrid wheat. Adv Agron 44: 179–190

Lucken KA (1986) The breeding and production of hybrid wheat. In: Genetic improvement in yield of wheat. CSSA Spec Pub No. 13. Crop Science Society of America and American Society of Agronomy. Madison, Wisconsin, pp 87–197

Morgan CL, Austin RB, Ford MA, Bingham J, Angus WJ, Chowdhury S (1989) An evaluation of F_1 hybrid winter-wheat genotypes produced using a chemical hybridising agent. J Agric Sci Cam 112:143–149

Perenzin M, Pogna NE, Borghi B (1992) Combining ability for breadmaking quality in wheat. Can J Plant Sci 72:743–754

Pickett AA (1993) Hybrid wheat – results and problems. Paul Parey Scientific Publishers, Berlin Hamburg, pp 259

Pogna NE, Mellini F, Beretta A, Dal Belin Peruffo A (1989) The high-molecular-weight glutenin subunits of common wheat cultivars grown in Italy. J Genet Breed 43:17–24

Romani M, Borghi B, Alberici R, Delogu G, Hesselbach J, Salamini F (1993) Intergenotypic competition and border effect in bread wheat and barley. Euphytica 69:19–31

Stroike JE (1987) Technical and economic aspects of hybrid wheat seed production. In: Hybrid seed production of selected cereal, oil and vegetable crops, FAO Plant Protection and Production paper 82, Food and Agriculture Organisation of the United Nations, Rome, pp 177–185

Virmani SS, Edwards IB (1983) Current status and future prospects for breeding hybrid rice and wheat. Adv Agron 36:145–214

Walton PD (1971) Heterosis in spring wheat. Crop Sci 11:422–424

Wienhues F (1968) Long-term yield analyses of heterosis in wheat and barley: variability of heterosis, fixation of heterosis. Euphytica 17:49–62

Zeller FJ, Gunzel G, Fischbeck G, Gerstenkorn P, Weipert D (1982) Veränderungen der Backeigenschaften des Weizens durch die Weizen-Roggen-Chromosomentranslokation 1B/1R. Getreide Mehl Brot 36:141–143