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## Predicting hybrid value in bread wheat: biometric modelling based on a “top-cross” design

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**Abstract** Multi-environmental experimentation made it possible to compare 311 hybrids and their 59 parental lines for five characters: yield, two yield components (number of grains per m<sup>2</sup> and 1000-grain weight), height and date of heading. At all three sites, average high-parent heterosis exceeded 6%, and our results confirm that hybrids in general head as early as the earlier parent does and are as high as the taller parent. For the five characters studied ecovalences were significantly lower in the F1 than in the parents, indicating a higher level of homeostasis for hybrids. The experimental model, based on a “top-cross” design comprised of 55 lines used as females and four testers, made it possible to implement different hybrid-value prediction models. For yield, by far the most important character to predict, the predictor based on the general combining ability and the *per se* value of the parents, appears to be the most interesting. The prediction remains, however, imperfect as specific combining ability (SCA) has a strong impact for this character. Attempting to take account of SCA in the prediction, by using a multiplicative model for “male×female” interaction modelling, did not prove convincing.

**Key words** Hybrid wheat · Heterosis · Combining ability · Multiplicative model

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### Introduction

Since the early 1980s, the development of efficient chemical hybridizing agents has made it possible to select for hybrid varieties in bread wheat (Oury et al. 1990a; Barbosa-Neto et al. 1996; Brears et al. 1988; Morgan et al. 1989; Borghi et al. 1988). Even though the yield heterosis levels cannot compare with those found in allogamous species such as maize, the agronomic value of hybrid wheats appears to be quite interesting: in particular the productivity of the F1 is often superior to that of the higher parent, due to better grain-filling capacities (Oury et al. 1993, 1995). Moreover, higher levels of homeostasis are expected for F1 varieties, even if presently available data does not show lower genotype-environment interaction for hybrids than for pure lines (Carver et al. 1987, Oury et al. 1990b; Peterson et al. 1997).

In F1 wheat selection programs predicting the hybrid value is a major problem. On the one hand, the number of lines which could potentially be used as hybrid parents makes it unfeasible to obtain all possible combinations [ $n(n-1)/2$  when  $n$  is the number of lines], and, on the other hand, in contrast to maize, heterotic groups of bread wheat have not as yet been identified. Various biometric predictors based on general combining ability (GCA) values obtained using a “top-cross” design, as well as on specific combining ability (SCA), have been employed in maize (Lefort-Buson et al. 1987; Charcosset et al. 1990, 1993). Even though such “top-cross” or diallel designs have been used to calculate GCA and SCA in bread wheat (Borghi et al. 1989; Perenzin et al. 1992; Borghi and Perenzin 1994), the predictive value of such GCAs has never been verified, and models including SCAs have never been used.

In this article we present the results of a multi-environmental experiment, which has made it possible for us to test hybrid-value prediction models based on combining abilities and *per se* value of the F1 parents. We have also studied genotype-environment interactions in order to compare the stability of the hybrids with that of the parental lines.

## Materials and methods

### Plant material

To develop a “top-cross” design, 55 lines of bread wheat ( $L_i$ ) were crossed with four testers ( $T_k$ ). Parentage relationships between these 59 genotypes are unknown; nevertheless, according to the diverse origins of this material (varieties of the French catalogue, and selected lines supplied by the Clermont and Rennes INRA centers as well as by private breeders Momont and Hybrinova) we can assume that it was representative of the diversity of North-European material.

Twelve F1 diallel crosses between the four testers were developed, along with 79 hybrids each having two genotypes taken from the 55 lines as parents. These 79 combinations, which represent a sampling from the  $55 \times 54 / 2 = 1485$  possible couples, were used to validate the different prediction models which were run.

The hybrids were chemically produced in 1993. They were included in experimentation along with the parental lines in 1994 at three sites: Clermont-Ferrand (CF), Le Moulon (LM) and Mons (MO). Quantities of F1 seeds were sometimes insufficient to allow sowing at all three sites, and certain hybrids which appeared to be impure (a high proportion of female lines on the plot) were eliminated from the study. Table 1 shows the samples which were available for each of the different sites.

### Experimental design

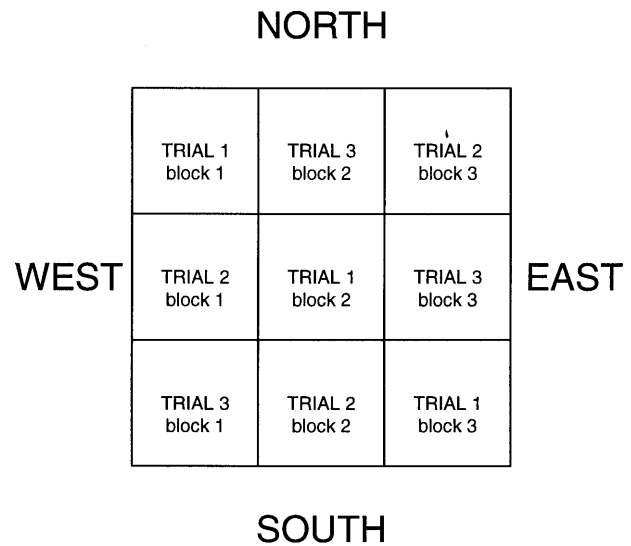
At each site the 55 lines and 299 hybrids resulting from the 55 lines were separated into three trials of three randomized complete blocks, in such a way that each hybrid was in the same trial as its parents. The 12 F1 between the testers were sown in one of the three trials. The four testers were included in each trial, as well as cultivar “Apollo” which served as a check for productivity. In view of the grouping of the three trials, the blocks were laid out so that the “trial” factor could be analyzed through the five common genotypes, taking into account field heterogeneity along two gradients (Fig. 1).

The plots had surfaces of 6 m<sup>2</sup> at LM, 6.5 m<sup>2</sup> at MO and 7.5 m<sup>2</sup> at CF. The agronomical practices used at the different sites corresponded to those commonly employed in intensive farming, with N-P-K fertilizing adjusted to a goal of high yield along with insecticide and fungicide treatments.

The characters under study were yield (YD), 1000-grain weight (TGW), height (HT) and the date of heading (DH). For each of these four variables measurements were taken for each of the three repetitions of each trial, except for the date of heading at Mons, where measurements were made on only one repetition. On the basis of yield and 1000-grain weight, we calculated the number of grains per m<sup>2</sup> (NG).

**Table 1** Samples which were available at all three sites for parental lines, tester hybrids, “top-cross” hybrids and validation hybrids. CF=Clermont-Ferrand ; LM=Le Moulon; MO=Mons.

Item	Potential size	Size without impure F1	Size of samples available at		
			CF	LM	MO
Testers	4	—	4	4	4
Female lines	55	—	55	54	55
F1 between testers	12	12	12	12	12
F1 with tester T <sub>1</sub>	55	49	49	47	49
F1 with tester T <sub>2</sub>	55	54	54	53	54
F1 with tester T <sub>3</sub>	55	42	42	39	41
F1 with tester T <sub>4</sub>	55	53	53	50	52
Validation F1	79	66	65	59	65



**Fig. 1** Experimental design used to take into account field heterogeneity along two gradients (North-South, West-East)

For all these characters we calculated mid-parent (MP) and high-parent (HP) heterosis expressed in percent.

### “Genotype-environment” interaction study

We used the following variance analysis model for the multi-environmental design:

$$Y_{ijl} = \mu + l_j + b_j(l_j) + g_i + \delta_{ij} + \epsilon_{ijl},$$

where  $\mu$  is the overall average,  $l_j$  is the effect of the site  $j$ ,  $b_j(l_j)$  the effect of block 1 hierarchized at site  $j$ ,  $g_i$  the effect of the genotype  $i$ ,  $\delta_{ij}$  the genotype-environment interaction and  $\epsilon_{ijl}$  an error term.

On the basis of the values of the interaction effects, we also calculated the ecovalences (Wricke 1962, cited in Becker and Léon 1988) as:

$$\text{ecov}_i = \sum_j (\delta_{ij})^2.$$

### Hybrid value prediction

Different predictors (labelled  $\tilde{Y}_{it}$ ) for the value of the F1 between lines  $L_i$  and  $L_t$  were calculated.

#### Predictor based on the per se value of the parents

Since the parental lines were tested at the same time as the hybrids, the first predictor was the value of the mid-parent:

$$\text{PSV} \tilde{Y}_{it} = \frac{L_i + L_t}{2}.$$

#### Predictor based on the general combining ability of the parents

We ran the following variance analysis model for the “top-cross” design:

$$Y_{ikl} = \mu + b_l + \alpha_i + \beta_k + \phi_{ik} + \delta_{li} + \delta_{lk} + \epsilon_{ikl},$$

where  $b_l$  is the effect of block  $l$ ,  $\alpha_i$  and  $\beta_k$  are the main effects of line  $i$  and tester  $k$ ,  $\delta_{li}$  and  $\delta_{lk}$  the “block×line” and “block×tester” interaction effects, and  $\phi_{ik}$  the “male×female” interaction effect corresponding to the specific combining ability between line  $i$  and tester  $k$ .

**Table 2** Data set used for the  $L_i \times L_i$  hybrid value prediction with the multiplicative model. The correspond to experimental data. The diallel table is completed symmetrically (\* in the table), assuming that  $T_k \times L_i$  crosses are identical to their reciprocals  $L_i \times T_k$ . There are two missing values (? in the table)

Item	T <sub>1</sub>	T <sub>2</sub>	T <sub>3</sub>	T <sub>4</sub>	L <sub>i</sub>	L <sub>i</sub> *
T <sub>1</sub>	+	+	+	+	*	*
T <sub>2</sub>	+	+	+	+	*	*
T <sub>3</sub>	+	+	+	+	*	*
T <sub>4</sub>	+	+	+	+	*	*
L <sub>i</sub>	+	+	+	+	+	?
L <sub>i</sub> *	+	+	+	+	?	+

Assuming that the testers are representative of the variability between the lines  $L_i$ ,  $\alpha_i$  can be considered as an estimate of GCA for the  $L_i$  lines. The following predictor can then be constructed:

$$GCA \tilde{Y}_{ii} = \hat{\mu} + \hat{\alpha}_i + \hat{\alpha}_i. \quad (1)$$

Due to the elimination of impure hybrids from the study, the GCAs are not estimated with the same level of precision for all  $L_i$  lines (most are estimated on four testers, but some on only three testers).

#### Predictor based on a breakdown of the “male×female” interaction using a multiplicative model

The multiplicative (or bi-additive) model of Mandel (1971) consists in breaking down the interaction into a sum of multiplicative terms, which make it possible to estimate specific parameters for each of the interacting factors. In the case of our “top-cross” design, the model is:

$$Y_{ik} = \mu + \alpha_i + \beta_k + \sum_{m=1}^M \gamma_{m(i)} \theta_m \lambda_{m(k)},$$

where  $M$  is the number of multiplicative terms,  $\gamma_{m(i)}$  and  $\lambda_{m(k)}$  are the specific parameters of levels  $i$  and  $k$  of the two factors for the  $m$ th multiplicative term, and  $\theta_m$  a normalization factor. For a design with  $K$  testers, from 1 to  $K-1$  multiplicative terms can be introduced.

In predicting hybrid value, using such a model only makes sense if one works on a diallel-type data range (otherwise symmetry is not respected and it is impossible to compare  $\gamma_m$  and  $\lambda_m$ ). Too much data is missing from the diallel table of the 59 lines studied for the estimation to have any significance. Elementary diallels are therefore used (Charcosset et al. 1993), for which a general scheme is given in Table 2.

Using the estimates of the model parameters the following predictor can be constructed:

$$MM \tilde{Y}_{ii} = \hat{\mu} + \hat{\alpha}_i + \hat{\alpha}_i + \sum_{m=1}^M \hat{\gamma}_{m(i)} \hat{\theta}_m \hat{\gamma}_{m(i)}. \quad (2)$$

However, due to the two missing data items in these elementary diallels, estimates of the parameters can result in aberrant predictions for the two empty spaces (for a detailed explanation see Denis and Baril 1992). To solve this problem we used the solution offered by Denis and Baril (1992), which consists in running the multiplicative model for each diallel only after having replaced the two missing data items with estimates of their values resulting from the additive model. It must be noted that when estimations from the additive model are used to fill the  $L_i \times L_i$  and  $L_i \times L_i$  spaces in the elementary diallels, modelling of the “male×female” interaction is biased because, due to the construction, the interactions in these two spaces are given as zero and are, therefore, underestimated.

INTERA software (Decoux and Denis 1991) was employed in making all of these estimates.

Remark: for the same reason as in the GCA case, the multiplicative model sometimes was run for elementary diallels with only

three testers (instead of the usual four). Results for two predictors will be given: the one requiring a sole multiplicative term ( $MM_1 \tilde{Y}_{ii}$ ) and the other using the maximum number of multiplicative terms ( $MM_{K-1} \tilde{Y}_{ii}$ ); that is to say, two for diallels with three testers and three for diallels with four testers.

Even though equations (1) and (2) both show the term “ $\hat{\mu} + \hat{\alpha}_i + \hat{\alpha}_i$ ”, this term was not calculated in the same way in the two cases. For the predictor based on the GCA, parameters  $\mu$ ,  $\alpha_i$  et  $\alpha_i$  were estimated for the global “top-cross” design set, whereas for the predictor based on the multiplicative model these parameters were estimated using the elementary diallels (one for each  $L_i \times L_i$  hybrid).

#### Predictor quality

For each of the predictors the  $\tilde{Y}_{ii}$  was calculated for the  $L_i \times L_i$  crosses corresponding to validation hybrids. Prediction quality was, hence, evaluated by the coefficient of determination ( $R^2$ ) corresponding to the relationship between the predicted values and the observed values, for those validation hybrids which constitute a sample of the F1 which are independent of those used in parameters estimation.

## Results and discussion

Analysis of the five varieties common to all three trials showed no significant “trial” effect for the diverse characters in the three sites. We therefore grouped the three trials at each site.

#### Heterosis for the five characters studied

Table 3 shows:

- (1) Heterosis for yield, with values in the order of 10% for MP heterosis and in the order of 6% for HP heterosis. Even though the MP heterosis for NG is significant, the superior yield of the hybrids is mainly due to heterosis for TGW, which reaches values in the order of 7% for MP heterosis and of 2% for HP heterosis.
- (2) Heterosis for height, with values in the order of 7% for MP heterosis and of 2% for HP heterosis.
- (3) Negative values for heterosis for heading date, which corresponds to the fact that hybrids usually head as early as the earlier heading parent.

These results on heterosis values for the different characters are comparable to those previously published by various authors (Borghi et al. 1988; Morgan et al. 1989; Oury et al. 1990a, b, 1993; Barbosa-Neto et al. 1996) based on experimentation carried out with chemically produced F1s and, hence, under conditions close to those of agricultural practice. They confirm the agronomical interest of this varietal type.

#### Hybrid stability

Variance analysis shows significant genotype-environment interaction for all characters, both for lines and for

**Table 3** Average values for mid-parents, hybrids, relative MP and HP heterosis (with the result of the Student test comparing F1 average value to the average value of mid-parents or high-parents). Y=yield; NG=number of grains per m<sup>2</sup>; TGW=thousand-grain

Item		Average MP	Average F1	Average MP heterosis (%)	Average HP heterosis (%)
YD	CF	89.6 q/ha	99.2 q/ha	10.8***	6.9***
	LM	82.6 q/ha	90.4 q/ha	9.4***	6***
	MO	88 q/ha	96.5 q/ha	9.7***	6.5***
NG	CF	19709	20286	3***	-1.4
	LM	19466	19860	2.1***	-2.7
	MO	18942	19488	3***	-2.5
TGW	CF	45.8 g	49.1 g	7.3***	1.8***
	LM	42.8 g	45.8 g	7***	2.6***
	MO	46.9 g	49.7 g	6.1***	0.8
HT	CF	97 cm	105 cm	8.6***	2***
	LM	90 cm	97 cm	7.4***	1.8***
	MO	81 cm	86 cm	6.3***	-0.1
DH	CF	144 days after 01/01	142 days after 01/01	-1	-2.2
	LM	148 days after 01/01	145 days after 01/01	-2.1	-3.8
	MO	154 days after 01/01	152 days after 01/01	-1.4	-2.9

weight; HT=height; DH=date of heading; MP heterosis=heterosis with reference to the mid-parent; HP heterosis=heterosis with reference to the higher parent; \*\*\*=significant at the threshold of 0.1%

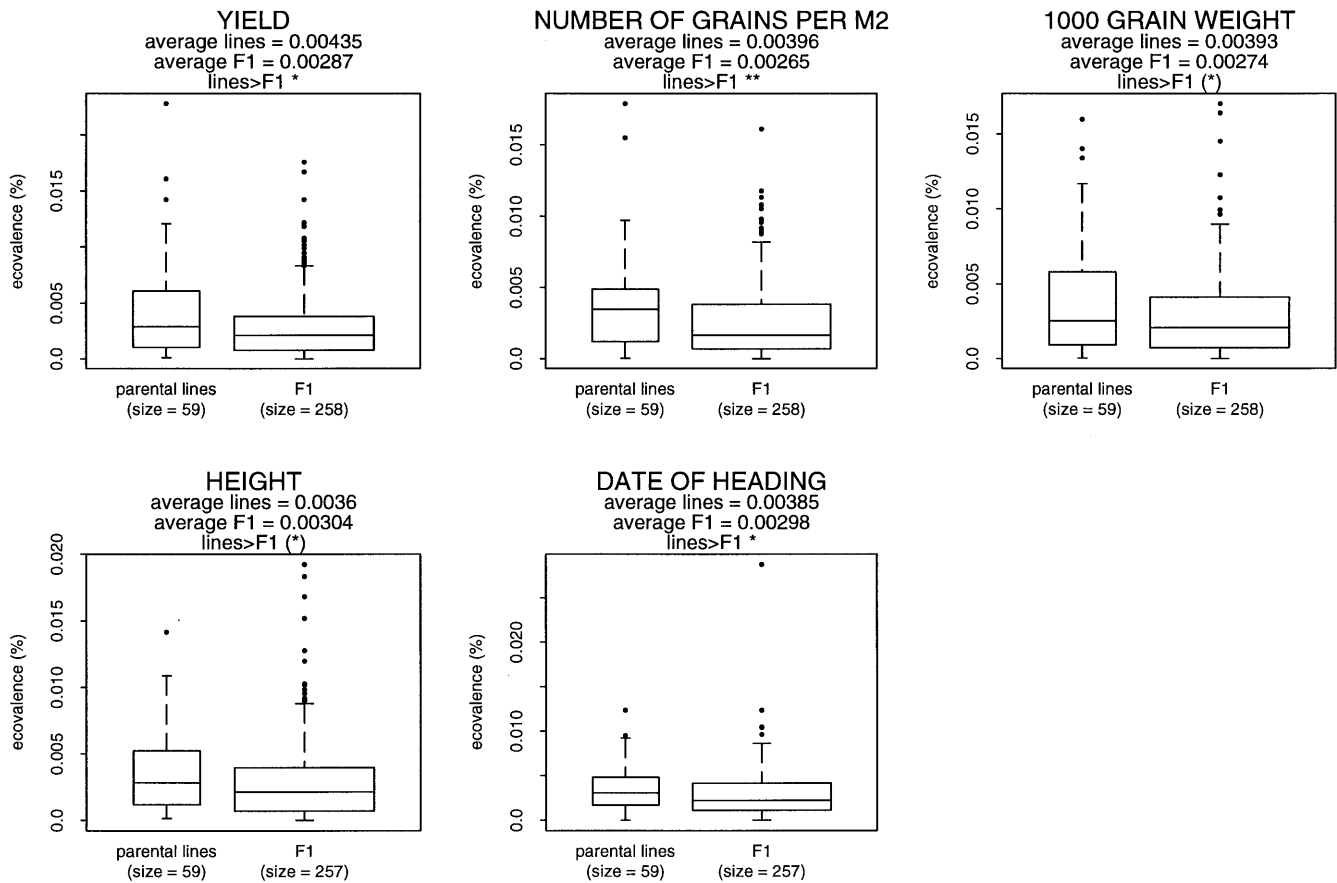
**Table 4** Variance analysis of the multi-environmental design for the five characters, covering the lines and the hybrids

Item		Lines			Hybrids		
		SS	df	F-value	SS	df	F-value
YD	Site	4431	2	175***	32069	2	1222***
	Block (site)	783	6	10.3***	2378	6	30.2***
	Genotype	15348	58	20.9***	29411	276	8.12***
	Genotype* site	4422	115	3.04***	13815	533	1.98***
	Error	5318	420		20789	1585	
NG	Site	66×10 <sup>6</sup>	2	19.6***	262×10 <sup>6</sup>	2	117***
	Block (site)	230×10 <sup>6</sup>	6	22.7***	549×10 <sup>6</sup>	6	82.1***
	Genotype	1311×10 <sup>6</sup>	58	13.4***	3313×10 <sup>6</sup>	276	10.8***
	Genotype* site	431×10 <sup>6</sup>	115	2.22***	1245×10 <sup>6</sup>	533	2.1***
	Error	702×10 <sup>6</sup>	415		1750×10 <sup>6</sup>	1570	
TGW	Site	1577	2	130***	7059	2	889***
	Block (site)	365	6	10***	1362	6	57.2***
	Genotype	7549	58	21.5***	18093	276	16.5***
	Genotype* site	1761	115	2.52***	4945	533	2.34***
	Error	2517	415		6252	1575	
HT	Site	22869	2	1818***	151423	2	9048***
	Block (site)	228	6	6.03***	947	6	18.9***
	Genotype	39887	58	109***	82279	276	35.6***
	Genotype* site	2885	115	3.99***	13391	530	3.02***
	Error	2635	419		13272	1586	
DH	Site	9187	2	8361***	40082	2	53806***
	Block (site)	2.2	6	0.67NS	3.9	6	1.74NS
	Genotype	13467	58	423***	32710	276	318***
	Genotype* site	948	115	15***	3149	531	15.9***
	Error	231	420		597	1604	

hybrids (Table 4). Ecovalences (computed for the global design: lines+F1) are on average lower for hybrids (Fig. 2) no matter what the character. Interaction effects are, thus, less pronounced for the F1 than for their parents.

Unlike previous studies (Carver et al. 1987; Oury et al. 1990b; Peterson et al. 1997) our work covered a large number of wheat hybrids. Under these conditions, we observe a higher level of homeostasis for the F1 than for

their parents. The difference, however, is not large and one finds a result for stability analogous to that found for heterosis: hybrid wheats appear to be superior to their parents, although there is no great gap between the two varietal types, as is the case, for example, for an allo-gamous species like maize.



**Fig. 2** “Box-plot” presentation of the distribution of ecovalences for the five characters studied, covering parental lines and F1. Also shown are the average values of these ecovalences for the F1 and for the lines, as well as the result of the Mann-Whitney-Wilcoxon test comparing the average value of the F1 ecovalences with that of the lines. (\*)=significant at the threshold of 10%; \*=significant at the threshold of 5%; \*\*=significant at the threshold of 1%

**Table 5** Values of the coefficients of determination for the correlations between locations, for the five characters

Item	YD	NG	TGW	HT	DH
CF-LM	0.56	0.39	0.59	0.84	0.92
CF-MO	0.47	0.32	0.52	0.65	0.80
LM-MO	0.6	0.34	0.50	0.81	0.82

### Predicting hybrid value

In spite of the genotype-environment interactions, which have been shown to be significant (Table 4), the correlations between locations for the different characters are high (Table 5), suggesting that the three locations can be considered together for breeding purpose. Therefore, the predictions have been made on data averaged over the three environments.

### Prediction based on the *per se* value of the parents

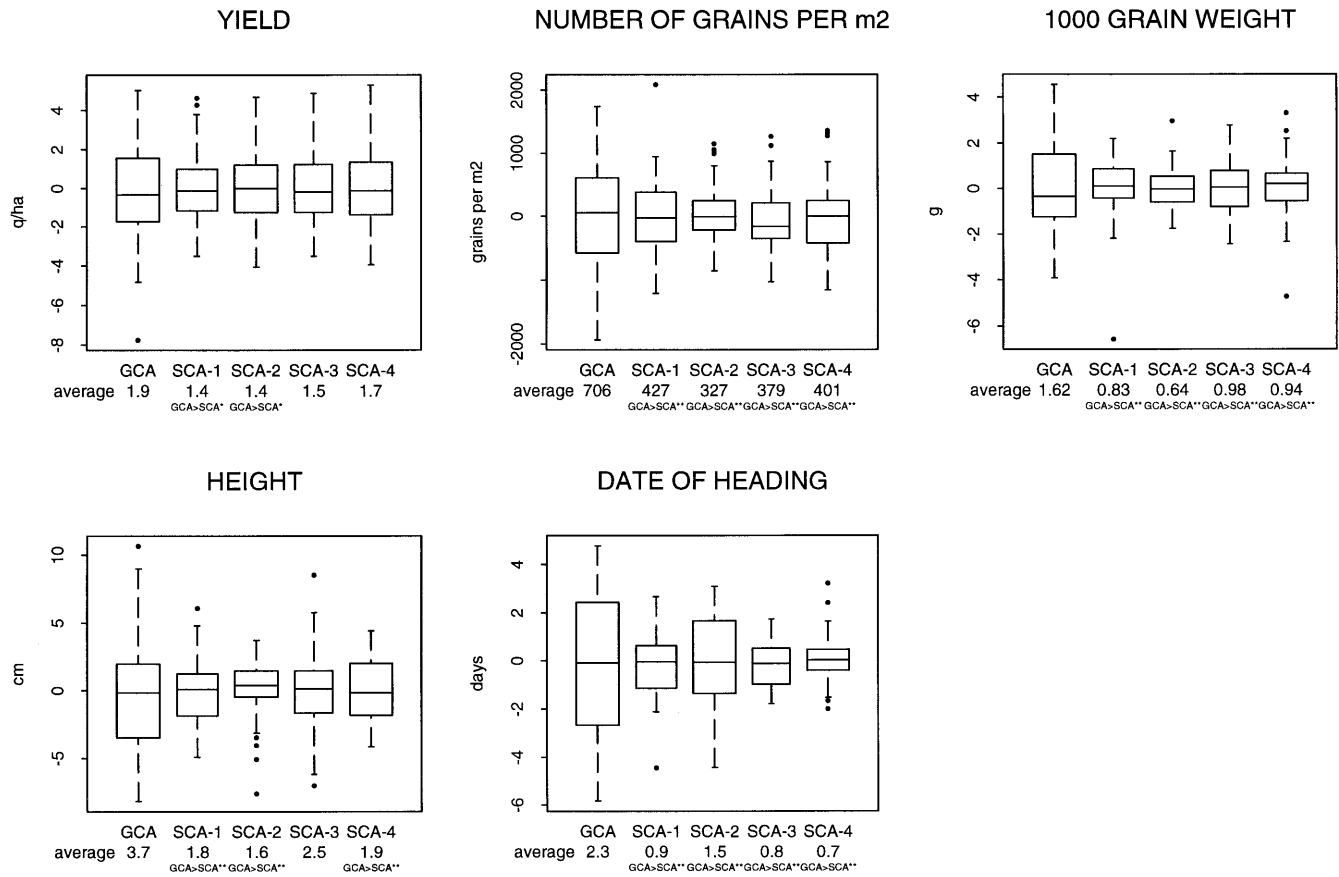
For the  $PSV\tilde{Y}_{ii}$  predictor we evaluated prediction quality not only on the F1 validation sample, but on the global F1 set as well. In this case  $R^2$  is estimated with a much higher level of precision because it is computed over a much larger number of units. The  $R^2$  values for the validation hybrids were computed so as to permit their comparison with the other predictors.

For the overall character set, the parent *per se* value appears to be a relatively good predictor of hybrid value (Table 6). Indeed, even in the case of yield, for which the  $R^2$  values are relatively low, variability of the mid-parents explains at least 30% of the variability of the hybrids. Variability of the mid-parents explains about 50% of the F1 variability as far as NG is concerned and at least 65% as far as TGW is concerned. For HT and DH the high  $R^2$  values show that the variability of the mid-parents explains in large part the variability of the hybrids (at least 70% for HT and at least 80% for DH).

### Prediction based on the general combining ability of the parents

As far as yield is concerned, the  $GCA\tilde{Y}_{ii}$  predictor based on the GCA of the parents is not very efficient as it explains less than 30% of the F1 variability (Table 6). For the other characters, by contrast, it is possible in large part to ex-





**Fig. 3** “Box-plot” presentation of the distribution of GCA and SCA with testers, for the five characters. Also shown are the averages of GCA and SCA absolute values, as well as the result of the Student test comparing the average of the GCA absolute values to the averages of the SCA absolute values with the different testers. SCA-k=SCA with tester  $T_k$ ; \*=significant at the threshold of 5%; \*\*=significant at the threshold of 1%

plain the hybrid variability (at least 60% for NG, about 70% for HT, and about 80% for both TGW and DH). For NG and TGW this GCA-based predictor makes it possible to substantially improve prediction quality compared to the predictor based on the *per se* value.

The character-based differences in predictive value can be explained by the GCA and SCA relative parts. Indeed, even though variance analysis indicates highly significant “male”, “female” and “male×female” effects for

all five characters at all three sites (Table 7), Fig. 3 shows that for NG, TGW, HT and DH, the GCAs are significantly higher in absolute value than the SCAs, whereas for yield the SCAs are of the same scale as the GCAs. These results concerning the comparative importance of SCA and GCA for the diverse characters are similar to those of Borghi et al. (1989) and Borghi and Perenzin (1994). They show that, for bread wheat, if only GCA is taken into account, it will not be possible to make a good prediction of a character like yield for which specific effects are important.

#### Prediction based on the multiplicative model

Table 7 shows highly significant “male×female” interaction for all five characters. Consequently, we tried to

**Table 6** Values of the coefficients of determination for the relationships between predicted values and observed values, for the different types of predictors and for the five characters

Predictor		YD	NG	TGW	HT	DH
$PSV\tilde{Y}_{ii'}$	All hybrids	0.31	0.54	0.64	0.72	0.80
	Validation hybrids	0.42	0.46	0.72	0.77	0.81
$GCA\tilde{Y}_{ii'}$		0.28	0.63	0.82	0.69	0.79
$MM\tilde{Y}_{ii'}$	One multiplicative term	0.47	0.61	0.78	0.83	0.84
	K-1 multiplicative terms	0.50	0.61	0.79	0.78	0.83
$GCA_{dial}\tilde{Y}_{ii'}$		0.46	0.63	0.81	0.75	0.82
$PSV+GCA\tilde{Y}_{ii'}$		0.43	0.62	0.80	0.76	0.82

**Table 7** Variance analysis for the five characters at all three sites

Item		CF			LM			MO		
		SS	df	F-value	SS	df	F-value	SS	df	F-value
YD	Block	217	2	9.51***	823	2	34.9***	682	2	31.8***
	Female	6479	57	9.94***	3067	57	4.56***	6013	57	9.84***
	Male	1459	3	42.51***	1957	3	55.3***	705	3	21.9***
	Female*male	4413	149	2.59***	2973	140	1.8***	2982	147	1.89***
	Female*block	2091	114	1.6***	1606	114	1.2NS	1939	113	1.59**
	Male*block	57	6	0.83NS	137	6	1.93NS	144	6	2.24*
	Error	3386	296		3194	271		3046	284	
NG	Block	24×10 <sup>6</sup>	2	13.1***	337×10 <sup>6</sup>	2	126***	5.6×10 <sup>6</sup>	2	4.94**
	Female	823×10 <sup>6</sup>	57	15.6***	522×10 <sup>6</sup>	57	6.88***	481×10 <sup>6</sup>	57	14.9***
	Male	143×10 <sup>6</sup>	3	51.4***	269×10 <sup>6</sup>	3	67.3***	492×10 <sup>6</sup>	3	289***
	Female*male	292×10 <sup>6</sup>	149	2.12***	308×10 <sup>6</sup>	140	1.65***	181×10 <sup>6</sup>	147	2.16***
	Female*block	128×10 <sup>6</sup>	114	1.21NS	168×10 <sup>6</sup>	114	1.11NS	180×10 <sup>6</sup>	113	2.8***
	Male*block	2.7×10 <sup>6</sup>	6	0.49NS	11×10 <sup>6</sup>	6	1.41NS	8.3×10 <sup>6</sup>	6	2.43*
	Error	272×10 <sup>6</sup>	294		349×10 <sup>6</sup>	262		161×10 <sup>6</sup>	284	
TGW	Block	31.2	2	7.35***	805	2	80.3***	88.3	2	16.8***
	Female	3798	57	31.4***	2875	57	10***	2389	57	16***
	Male	964	3	151***	411	3	27.3***	2190	3	278***
	Female*male	963	149	3.05***	1541	140	2.19***	970	147	2.52***
	Female*block	352	114	1.46**	674	114	1.18NS	833	113	2.81***
	Male*block	18.8	6	1.47NS	42.1	6	1.4NS	38.3	6	2.43*
	Error	624	294		1339	267		745	284	
HT	Block	22.2	2	2.82NS	23	2	1.72NS	606	2	23.1***
	Female	19562	57	87.4***	13471	57	35.2***	10147	57	13.6***
	Male	2781	3	236***	1143	3	56.8***	2451	3	62.3***
	Female*male	5681	147	9.84***	3969	140	4.23***	4433	147	2.3***
	Female*block	424	114	0.95NS	976	114	1.28NS	1536	113	1.04NS
	Male*block	38.7	6	1.64NS	28.6	6	0.71NS	138	6	1.75NS
	Error	1139	290		1858	277		3736	285	
DH	Block	1.3	2	3.4*	3.8	2	2.06NS			
	Female	2861.9	57	269***	6255	57	118***			
	Male	1539.9	3	2747***	3994	3	1427***			
	Female*male	710.6	148	25.7***	1600	140	12.25***			
	Female*block	16.8	114	0.8NS	99.3	114	0.93NS			
	Male*block	3.3	6	2.9**	5.59	6	1NS			
	Error	54.9	294		257	276				

**Table 8** Relationships between the different predictors for the five characters. The values are those of the coefficients of determination (which all correspond to positive correlations)

Predictor	YD	NG	TGW	HT	DH
$PSV\tilde{Y}_{ii'}/GCA\tilde{Y}_{ii'}$	0.48	0.56	0.81	0.84	0.91
$MM_1\tilde{Y}_{ii'}/MM_{K-1}\tilde{Y}_{ii'}$	0.94	0.99	0.98	0.96	0.99
$GCA_{Adial}\tilde{Y}_{ii'}/MM_1\tilde{Y}_{ii'}$	0.90	0.97	0.97	0.93	0.99
$GCA_{Adial}\tilde{Y}_{ii'}/MM_{K-1}\tilde{Y}_{ii'}$	0.97	0.98	0.98	0.98	1
$GCA_{Adial}\tilde{Y}_{ii'}/PSV+GCA\tilde{Y}_{ii'}$	0.96	0.98	0.99	0.99	1

model these interactions using the multiplicative model for the five variables.

Table 8 shows a strong correlation between predictors obtained using a sole multiplicative term and those using the maximum of multiplicative terms, even in the case of yield, where  $R^2$  values are slightly lower. This strong correlation results in equivalent prediction qualities for the corresponding two types of multiplicative models (Table 6).

Even though we do not have statistics making it possible to test whether the growth in  $R^2$  values is significant, the multiplicative model appears to be especially interesting in the case of yield (Table 6). By explaining about a half of the F1 variability, it represents an appreciable improvement over predictors based on *per se* value or GCA. The bi-additive model also makes it possible to improve prediction quality for height, for which one reaches an explanation level of about 80% for hybrid variability. For DH, by contrast, very little progress can be observed. For NG and TGW, for which the GCA-based model had permitted improved levels of prediction, no progress is made using the multiplicative model.

The question remained as to whether the results obtained using the bi-additive model really corresponded to SCA modelling using multiplicative terms, or whether they were caused by the difference in the way of computing the  $\hat{\mu} + \hat{\alpha}_i + \hat{\alpha}_j$  term corresponding to the GCA (cf. Materials and methods). To provide an answer, we considered the predictor based on the GCA but computed

using the elementary diallels (this  $GCA_{dial}\tilde{Y}_{ii'}$  predictor is therefore the equivalent of the additive part of the multiplicative model). It became obvious that the multiplicative terms have very little impact on the predictors based on the bi-additive model as there is a strong correlation between the  $MM\tilde{Y}_{ii'}$  and  $GCA_{dial}\tilde{Y}_{ii'}$  predictors (Table 8), with, however, somewhat lower  $R^2$  values for the relationship between  $GCA_{dial}\tilde{Y}_{ii'}$  and  $MM\tilde{Y}_{ii'}$  in the case of HT and, especially, YD. This strong correlation leads to very similar prediction qualities between the multiplicative model and the GCA-based model when calculations are made using the elementary diallels (Table 6). The only cases in which modelling SCA slightly improves prediction quality are that of HT (when only a sole multiplicative term is taken into account) and YD (when all the multiplicative terms are taken into account).

To understand the difference between the two GCA-based predictors ( $GCA\tilde{Y}_{ii'}$ , computed with the “top-cross”, and  $GCA_{dial}\tilde{Y}_{ii'}$ , using the elementary diallels) one should consider (Table 2) that each of the diallels includes results on both the hybrids (outside the diagonal) and the lines (on the diagonal). Additionally, it should be remembered that the information on testers is the same for all diallels. For this reason, computation of the  $\hat{\mu} + \hat{\alpha}_i + \hat{\alpha}_{i'}$  predictor using the elementary diallel results in simultaneously taking into account the *per se* value of the parents  $L_i$  and  $L_{i'}$  (through  $\hat{\mu}$ ) and their combining ability (through  $\hat{\alpha}_i$  and  $\hat{\alpha}_{i'}$ ).

This situation is confirmed by computation of another predictor taking into account both the *per se* value and the combining ability of the parents estimated for the overall “top-cross” design set:

$$PSV + GCA\tilde{Y}_{ii'} = \frac{L_i + L_{i'}}{2} + \hat{\alpha}_i + \hat{\alpha}_{i'}.$$

Table 8 clearly displays the similarity between the predicted values thus obtained and those supplied by the GCA-based model when the calculations are run using the elementary diallels. The hybrid-value prediction quality offered by these two models is, therefore, very similar for all the characters (Table 6). As far as YD is concerned, however,  $R^2$  values are slightly lower for the model based on *per se* value and the combining ability of the parents, with the result that here one finds only limited improvement over the model based solely on *per se* value.

It seems that “male×female” interaction in bread wheat is not structured in such a way as to be well described by multiplicative terms, and that the results obtained using the multiplicative model can be attributed mainly to the calculation mode used in the part of the model relative to the GCA. Indeed, through computation using the elementary diallels the *per se* value and the combining ability of the parents are simultaneously taken into account, which could lead to an increase in prediction quality if there was no correlation between the two predictors  $PSV\tilde{Y}_{ii'}$  and  $GCA\tilde{Y}_{ii'}$ . This situation holds true for yield (Table 8), whereas for TGW, HT and DH no improvement can be made to the level of prediction due

**Table 9** F1 proportions, in the case of yield, for which the values predicted by the different models and the observed values are found in the same superior segment of the distribution

Predictor	Superior fifth of the distribution	Superior quarter of the distribution
$PSV\tilde{Y}_{ii'}$	0.56	0.50
$GCA\tilde{Y}_{ii'}$	0.44	0.45
$MM\tilde{Y}_{ii'}$	0.56	0.55
One multiplicative term	0.69	0.60
K-1 multiplicative terms	0.69	0.60
$GCA_{dial}\tilde{Y}_{ii'}$	0.69	0.60
$PSV + GCA\tilde{Y}_{ii'}$	0.56	0.60

to the strong correlation between the predictors based respectively on *per se* value and on GCA.

#### Interest of these different prediction models for selection

From among the five characters studied, yield is the most interesting to predict in selecting hybrid wheats. In fact, the compensatory relationship between the two yield components makes it possible to obtain high productivity using genotypes with high NG and low TGW or genotypes with low NG and high TGW. Therefore, these two characters are usually not the object of selection. For both height and date of heading, selection according to the somewhat imperfect predictions based on wheat hybrid experimentation results seems sufficient: an F1 is usually as tall as or slightly taller than the taller parent and has a heading date as early, or earlier, than the earlier parent.

Yield is, unfortunately, the character for which the different models tested gave their lowest levels of prediction quality. However, the  $R^2$  values obtained (explanation of 30% to 50%) remain significant and, in the absence of any alternative, the proposed predictors at least make pre-selection of the hybrid crosses to be carried out possible. This fact becomes more evident if the center of attention is shifted from global prediction quality to the proportion of F1 for which predicted and observed values are both found in the same superior distribution segment. One then sees that this proportion varies from 45 to 70% depending on the predictor, when the top quarter or fifth of the distribution is considered (Table 9).

#### Conclusion

The quality of hybrid-value prediction depends heavily on the character in question. For TGW, HT, DH, and, to a smaller degree, NG, one or more of the proposed predictors can give a good quality prediction. For yield, by far the most important character to predict, hybrid-value prediction remains imperfect, as SCA has a strong impact on this character and the possibility of modelling “male×female” interaction using a multiplicative model appears to be limited for bread wheat.



For all the characters, it appears that the most simple predictor,  $^{PSV}\tilde{Y}_{ii}$ , is certainly the most efficient, as the quality of the predictions it gives is not very different from those of more sophisticated models and as it only needs an evaluation of the parental lines. If it is possible for breeders to implant a “top-cross” including the parents of the hybrids, the other predictors are worth using, the  $^{PSC+GCA}\tilde{Y}_{ii}$  predictor based on *per se* value and GCA of the parents being the easiest to calculate.

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