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Leila Hanifi-Mekliche, André Gallais. Heterosis, genetic effects and value of F2s and doubled-haploid lines in barley breeding. *Agronomie*, 1999, 19 (6), pp.509-520. hal-00885949

HAL Id: hal-00885949

<https://hal.science/hal-00885949>

Submitted on 11 May 2020

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Heterosis, genetic effects and value of F_2 s and doubled-haploid lines in barley breeding

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(Received 19 May 1998; accepted 16 May 1999)

Abstract – To study the potential of F_1 , F_2 and doubled-haploid lines in six-row barley, three connected experiments were developed: i) study of a complete 8×8 diallel; ii) comparison of F_1 , F_2 and their parents for three crosses from the diallel; iii) comparison of 53 doubled-haploid lines from a cross to their parents, F_1 and F_2 . In the diallel experiment, the average of all F_1 for grain yield was equal to the average of the parents. The best cross was only 3.2 % better than the best parent. However, for main ear grain weight mean heterosis was 13 %. It was negative (–11 %) for straw yield. There was a great variation among crosses. General combining ability (GCA) was a main component of such a genetic variation for all traits studied. Resistance to mildew, thousand grain weight and heading date were the most additive and grain and straw yield the least additive traits. The study of F_2 showed that, for grain yield, heterosis was reduced more than expected. This is interpreted as being mainly the result of intergenotypic competition between F_2 plants. However, epistasis is possible, and it was detected for yield and its components, by the comparison of DH lines to their mid-parent. The comparison of DH lines with F_1 showed that the genetic advantage obtained in F_1 for grain yield and its components can be fixed at the level of doubled-haploid lines. Nevertheless, the possible negative effect of recombination and epistasis can lead to the use of haplodiploidisation after the F_1 generation. (© Inra/Elsevier, Paris.)

barley / heterosis / F_2 / doubled haploid / competition / epistasis

Résumé – Hétérosis, effets génétiques et valeur des F_2 et des lignées haplodiploïdes chez l'orge (*Hordeum vulgare* L.). Pour étudier l'intérêt comparé des hybrides F_1 , des F_2 et des lignées chez l'orge à six rangs, trois expériences ont été réalisées: un croisement diallèle complet entre huit parents, une comparaison de trois F_2 à leur F_1 et l'étude de 53 lignées obtenues par haplodiploïdisation à partir d'un croisement. Au niveau du diallèle, le rendement en grains des F_1 était en moyenne égal à celui des parents. Le rendement du meilleur hybride n'a été supérieur que de 3.2 % au meilleur parent. Pour le rendement en grain du maître brin, l'hétérosis a été de 13 %. Il a été négatif pour le rendement en paille (–11 %). Une grande variation est apparue entre croisements. L'aptitude générale à la combinaison (AGC) est la com-

Communicated by André Gallais (Gif-sur-Yvette)

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posante majeure de cette variation pour tous les caractères étudiés. La résistance à l'oïdium, le poids de mille grains et la précocité d'épiaison apparaissent comme les caractères les plus additifs et le rendement en grain et en paille comme les moins additifs. La comparaison de la F_2 à la F_1 et au parent moyen a montré que l'hétérosis pour le rendement, était plus réduit qu'attendu. Cela est interprété comme étant principalement le résultat de la compétition entre génotypes au sein de la génération F_2 . Cependant cela peut être dû à des effets d'épistasie, d'ailleurs détectés pour le rendement et ses composantes, par la comparaison des lignées HD et de leurs parents. La comparaison des lignées HD avec la F_1 montre que l'hétérosis obtenu en F_1 , peut être fixé pour le rendement et ses composantes. Cependant, l'effet négatif possible de la recombinaison et de l'épistasie peut conduire à envisager l'haplodiploidisation après la génération F_1 . (© Inra/Elsevier, Paris.)

orge / hétérosis / F_2 / haplodiploidisation / compétition / épistasie

1. Introduction

In autogamous plants, heterosis is less important than in allogamous plants, but it can still be relatively important. In barley (*Hordeum vulgare* L.), some results show that the grain yield heterosis can reach from 20 % [8] to more than 100 % [6, 21] according to the material used [24], the type of sowing (dense sowing or space-planted) and the environment (high or poor fertility) [20].

If heterosis is important, F_1 hybrids could be justified as type of cultivar, instead of inbred lines. Then, breeders could be interested in the prediction of the F_1 value in order to reduce the work required by the large number of crosses necessary to identify the best crosses. As heterosis is related to genetic distance [26], different indicators of genetic divergence could be used for the F_1 value prediction. Parental divergence, estimated by Mahalanobis D^2 from phenotypic data could be used. However, inconsistent results have been obtained. Guo et al. [16] obtained a highly significant correlation between D^2 and heterosis in common wheat over 2 years. In contrast, in maize, Moll et al. [29] found that heterosis manifested in crosses of the most genetically divergent varieties was lower than heterosis expressed between varieties considered to be less genetically distant. In wheat, Singh and Behl [35] and Picard et al. [32] did not find any correlation between heterosis and D^2 . Apparently, crosses between extremely divergent parents create a situation where the harmonious functioning of alleles is disrupted [17]. To

predict specific combining ability in *Pennisetum typhoides*, Marchais [27] used the Hanson and Casas distance [18], and showed a relatively close relationship between such a distance and specific heterosis for 11 out of 12 traits studied. However, the value of such a distance has not been confirmed in other studies [27]. The use of molecular markers could contribute to the improvement of the measurement of genetic distance and hence possibly to the prediction of heterosis [4]. This is clearly demonstrated by the results of Xiao et al. [38], showing a high correlation between heterosis and molecular distance in rice. In fact, the prediction of heterosis remains an open question.

A main problem for the development of hybrids in cereals, such as barley and wheat, will be the difficulty or cost of crossing control, either by nucleo-cytoplasmic male sterility, with good fertility restoration, or by the use of chemical hybridising agents. To avoid such a problem, it has already been proposed in wheat to exploit heterosis at the F_2 level [2, 24]. This will be justified if inbreeding depression from F_1 to F_2 is lower than expected. This could be the case for some crosses due to the effect of intergenotypic competition. Finally, it may be questioned whether the use of heterosis is justified in comparison to the development of pure lines.

Therefore, using six-rowed barley (*Hordeum vulgare* L.) as material, the objectives of the present study were:

- to see the potential value of F_1 and to analyse F_1 value and heterosis in terms of genetic effects;

– to study different predictors of cross values and heterosis, using per se value and the Hanson and Casas distance;

– to investigate on the one hand the possibility of using heterosis at the F_2 level, and on the other the possibility to derive pure lines as good as the best single-cross hybrids, through the study of doubled-haploid (DH) lines from one cross.

2. Materials and methods

2.1. Plant material and designs

Heterosis was studied with a F_1 8×8 diallel cross with reciprocal crosses and the parents. The cultivars used in this diallel were of different origins (*table 1*). Jaidor and Motan are issued from the same pedigree and Prato and CM67 are also related. The crosses studied to compare the magnitude of heterosis in F_1 and F_2 were Motan/CM67, Prato/CM67 and Apizaco/Prato. Fifty-three doubled-haploid (DH) lines were derived by the 'bulbosum' method from the cross Motan/CM67.

The F_1 were studied in 1986. The comparison of F_1 with F_2 was performed in 1988 for Prato/CM67 and Apizaco/Prato hybrids and in 1991 for Motan/CM67 cross. DH lines were studied in 1991. The parental cultivars were included in each trial. A randomised block design with three replicates was used at I.N.A. of Algiers in the three trials (1986, 1988 and 1991). Each plot consisted of a single row of 1 m in length with ten grains per row in 1986 and 30 grains per row in 1988 and 1991, for F_1 , parental and DH lines, while the F_2 were grown on three rows each. Overall, the 1988 and

1991 trials included 7 and 56 treatments, respectively. To compare F_1 and F_2 , the different means were calculated on the basis of 30 plants per block, for the parents and F_1 . For the F_2 , the mean was calculated on the basis of 46 plants/block/cross for the 1988 trial and 72–79 plants/block for the 1991 trial.

Such micro-plot designs were chosen owing to the small quantity of available seeds for F_1 crosses and DH lines. For F_1 , parents and DH lines, the evaluation of different quantitative traits, such as grain yield and related traits, in single-row micro-plots could be biased by effects of inter-row competition [15]; an acceptable agronomic estimation of grain yield would have required multi-row micro-plots of at least 2 m². The problem is different for the F_2 because it is an heterogeneous generation, and then intergenotypic competition within the row was present. The design was more justified for studying grain yield in the presence of competition than for a genetic interpretation of heterosis. For all generations, in such micro-plots, border effects have undoubtedly been important.

2.2. Traits studied in the trials

Grain yield/plant, straw yield/plant, harvest index, ear number/plant, main ear grain weight, grain number/ear, thousand grain weight, ear length, straw height and internode number were studied in all trials. Heading date was studied in 1986 and 1991 trials, whereas 'vertical' development of powdery mildew symptoms was only studied in 1986. Heading was noted when 50 % of ears reached the stage. For mildew, the scale of vertical progression varied from 0 to 5. All measurements or observations on different traits were made on individual plants.

Table 1. Origin of the parents used in the 8×8 diallel mating.

Parents	Origin	Pedigree
Jaidor	France	Rika.Baladi16 * Rika]33 / EMA 1038 // Robur
Motan	France	Rika.Baladi16*Rika]33 / EMA 1038 // Robur
Beecher	USA	Atlas/Vaughn (1940)
California Mariout 67 (CM67)	USA	2*California Mariout / CI237 // Club Mariout
Prato	USA	CM67 / 3 * Briggs / 4 / Briggs * 4 / 3 / Cali.
Apizaco	Mexico	Promesa / Toluca
Ensenada	Mexico	local cultivar
Saïda	Algeria	local cultivar

2.3. Analysis of general and specific heterosis of F₁ diallel

The Griffing analysis method 3, i.e. with reciprocal crosses but without parents [12], was first applied. According to this analysis, the average value of a cross between two lines *i* and *j* is broken down as follows:

$$Y_{ij} = \mu + g_i + g_j + s_{ij}$$

where g_i is the general combining ability (GCA) of line *i* and s_{ij} is the specific combining ability (SCA) of lines *i* and *j*.

Then, general and specific heterosis were studied according to the model developed by Eberhart and Gardner [5]:

$$Y_{ij} = v + 1/2 v_i + 1/2 v_j + h_{ij}$$

$$Y_{ii} = v + v_i$$

v is the mean of the parents and v_i the centred value of the line *i*.

$$h_{ij} = h + h_i + h_j + s_{ij}$$

where h is the average heterosis of all lines used in the trial, h_i and h_j are the general heterosis of lines *i* and *j*, respectively, and s_{ij} is the specific heterosis which is equal to the specific combining ability (SCA).

GCA can be related to h_i and v_i : $g_i = h_i + 1/2 v_i$ and thus, $h_i = g_i - 1/2 v_i$.

From this expression a *t*-test was developed for parental heterosis.

2.4. Determination of the F₁ value and heterosis components

The possibility of prediction of the F₁ value, GCA and SCA in the diallel was studied through correlations between F₁ and mid-parent, F₁ and GCA, general heterosis and GCA, general heterosis and per se value of parents (v_i), F₁ value and the Hanson and Casas distance (R^2_{ij}), specific heterosis and R^2_{ij} .

2.5. Comparative studies of F₁ and F₂, and DH lines

For traits where mid-parent heterosis was significant, F₂ was also compared to the parents. Finally, the scaling test $C = 2F_2 - F_1 - \bar{P} = 0$ was used to detect non-additivity [28]. Such a test has been developed to test epistasis. However, epistasis is the cause of significance of this test only if there is no competition. Competition can

generate interactions between genes, homologous or not, among different genotypes [9, 10]; in that case, it can simulate epistasis. Therefore, even in the absence of true dominance and true epistasis, the scaling test $C = 0$ can be significant due to competition. The comparison of the average of all DH lines to the mid-parent value is also a test for non-additivity. As this test is not affected by inter-genotypic competition, it will detect more probably the effect of epistasis.

3. Results

3.1. F₁ means, parental and specific heterosis

Heterosis was low on average. The more affected traits were harvest index (13.5 %), main ear grain weight (13 %), ear length (8.1 %), straw height (8.6 %) and thousand grain weight (6.9 %) (table II). For grain yield, the average of all F₁ was equal to the average of parents. Average mid-parent heterosis was also near zero for number of ears, internode number and heading date. It was negative for straw yield (-11.2 %) and ear number per plant (-15.3 %). This means a 'dominance' of the low yielding parent. In terms of the best parent, the results showed that for several traits the F₁ were, on average, less than the best parent.

However, there was a great variation between crosses for most of the traits except straw yield and ear number per plant for which no difference appeared among crosses. For the grain yield, the greater heterosis was 25.8 % in comparison to the mid-parent and 19.6 % in comparison to the best parent. Only one hybrid (Jaidor × Prato), showed a yield slightly higher (3.2 %) than that of the best cultivar used in this trial, Prato. The best hybrids involved parents which were highly geographically distant, i.e. from France and USA. Reciprocal effects were never significant whatever the traits. Considering only traits for which differences among crosses were significant, i.e. except for ear number, GCA was always highly significant. SCA was generally less significant and non-significant for resistance to powdery mildew (table III). Except for grain and straw yield, percentages of explained variation for GCA were higher than

Table II. Mid-parent heterosis in the 8 × 8 diallel.

Traits		Heterosis %	
		$\bar{F}_1 - \bar{P}$	$(\bar{F}_1 - \bar{P}) / \bar{P}$ Ave $(F_{1ij} - \bar{P}_{ij}) / \bar{P}_{ij}$ ¹
Grain yield	(g/plant)	-0.2 ns	-1.1
Straw yield	(g/plant)	3.2**	-11.2
Harvest index		0.05***	13.5
Ear number per plant		-1.7***	-15.3
Main ear grain weight	(g)	0.3***	13.0
Number of grains per ear		3.4 ns	5.1
Thousand grain weight	(g)	3.0***	6.9
Ear length	(cm)	0.7***	8.4
Straw height	(cm)	6.4***	8.7
Internode number		-0.1 ns	-1.6
Heading date	(day)	-0.2 ns	-0.2
Mildew resistance		3.4*	8.6

*, **, *** Significant at 0.05, 0.01, 0.001, respectively.

¹ Ave $(F_{1ij} - \bar{P}_{ij}) / \bar{P}_{ij}$ means the average of the relative heterosis of each cross *ij*.

Table III. F- statistics from the analysis of variance of the 8 × 8 diallel according to Griffing method 3.

Traits	GCA	SCA	Reciprocal effects	
			general	specific
Grain yield	4.7***	2.5**	0.1 ns	0.2 ns
Straw yield	3.9***	2.3**	0.8 ns	0.4 ns
Harvest index	2.9**	1.3 ns	0.8 ns	0.8 ns
Ear number per plant	1.7 ns	1.2 ns	1.2 ns	0.8 ns
Main ear grain weight	24.0***	3.2***	1.1 ns	1.0 ns
Number of grains per ear	50.5***	11.2***	1.1 ns	1.1 ns
Thousand grain weight	32.2***	3.9***	0.8 ns	1.3 ns
Ear length	21.0***	4.5***	4.3**	0.6 ns
Straw height	39.5***	4.5***	0.6 ns	0.9 ns
Internode number	23.7***	2.4**	3.1**	1.7 ns
Heading date	46.4***	5.5***	1.7 ns	1.3 ns
Mildew resistance	48.9***	0.7 ns	0.5 ns	0.8 ns

*, **, *** Significant at 0.05, 0.01, 0.001, respectively; ns: non significant.

those for SCA, showing a more important role of GCA than SCA in the variation among crosses (table IV). From this criterion resistance to mildew and thousand grain weight appeared to be the most

additive traits, whereas grain and straw yield are the least additive. The greater mid-parent heterosis and SCA values were associated with crosses involving at least a low performing parent, mainly

for grain yield, harvest index, straw height, ear length and internode number.

Some parents, for some traits, have a high GCA associated with a low variation in SCA (data not shown). Such a behaviour may be due to favourable dominant genes. This is the case for Jaidor for the resistance to mildew, Motan for ear length,

Ensenada for thousand grain weight, and Prato for grain yield and grain weight from main ear.

3.2. Determination of the F_1 value and heterosis components

3.2.1. Relationships between F_1 value with mid-parent value, GCA and SCA

Most of the correlations found between F_1 and mid-parent for different traits were positive and significant except for straw yield and harvest index (table V). However, except for thousand grain weight, internode number and heading date, the other correlations were lower than 0.70. The mid-parent explained a maximum of 43.9 % of the variation in the resistance to powdery mildew.

For all the traits given in table V, the F_1 value was positively and highly significantly correlated with the GCA of parents. The correlation was higher than that with mid-parent and it is even significant for harvest index and straw yield, traits for which the correlation F_1 -mid-parent was not significant. Except for grain yield and straw yield the correlations were equal or greater than 0.75, i.e. GCA explained at least 56 % of the variation among crosses. SCA explained about 64 % of F_1 variation for grain and straw yield, 43 % for straw

Table IV. Variation components for combining ability in the 8×8 diallel.

Traits	GCA ¹	SCA ²	GCA/SCA
Grain yield	17.8	22.3	0.8
Straw yield	17.1	28.9	0.6
Harvest index	$2.9 \cdot 10^{-3}$	$1.46 \cdot 10^{-3}$	2.0
Ear number per plant	0.58	0.49	1.2
Main ear grain weight	0.46	0.17	2.7
Number of grains per ear	261.5	170.3	1.5
Thousand grain weight	108.1	4.1	26.2
Ear length	0.98	0.60	1.6
Straw height	146.5	47.6	3.1
Internode number	0.27	0.05	5.3
Heading date	42.2	7.9	5.3
Mildew resistance	462.6	5.9	77.4

¹ $2 \sum g_i^2 / 7$.

² $\sum s_{ij}^2 / 20$.

Table V. Determination of F_1 value and heterosis components in the 8×8 diallel.

Traits	$F_1 - \bar{P}$	$F_1 - GCA$	Correlation $F_1 - SCA$	$GCA - v_i$	$h_i - v_i$	$s_{ij} - R^2_{ij}$
Grain yield	0.58***	0.68***	0.78***	0.86**	-0.02 ns	-0.41 ns
Straw yield	0.33 ns	0.57**	0.81***	0.58 ns	-0.01 ns	-0.36 ns
Harvest index	0.33 ns	0.76***	0.64***	0.37 ns	-0.39 ns	-0.25 ns
Ear number per plant	0.13 ns	0.29 ns	0.69 ns	0.21 ns	-0.85*	-0.02 ns
Main ear grain weight	0.55***	0.85***	0.46*	0.74*	-0.23 ns	0.25 ns
Number of grains per ear	0.59**	0.82***	0.44*	0.72*	-0.08 ns	0.01 ns
Thousand grain weight	0.82***	0.89***	0.44*	0.96***	-0.01 ns	0.04 ns
Ear length	0.56**	0.79**	0.52**	0.42ns	-0.51 ns	-0.50**
Straw height	0.61***	0.75***	0.66***	0.64 ns	-0.61 ns	-0.15 ns
Internode number	0.74***	0.87***	0.49*	0.85**	-0.51 ns	0.15 ns
Heading date	0.82***	0.91***	0.39*	0.95***	-0.26 ns	0.05 ns
Mildew resistance	0.64***	0.96***	0.26 ns	0.71*	0.17 ns	0.09 ns

*, **, *** Significant at 0.05, 0.01, 0.001, respectively; ns: non significant

height and less than 25 % for other traits. The correlation F_1 -SCA was not significant for resistance to mildew.

3.2.2. Relationships between *per se* value, GCA and parental heterosis

The correlation between GCA and line *per se* value (v_i) was significant for seven traits out of 11 (table V). It was not significant for straw yield, harvest index, plant height and ear length. For grain yield, thousand grain weight, internode number and heading date the *per se* value explains more than 70 % of variation, while for main ear grain weight, grain number and resistance to powdery mildew it explained about 50 % of total variation. The correlation between parental heterosis (h_i) and *per se* value of parents was generally not significant.

3.2.3. Relationships between SCA and Hanson and Casas distance

The correlation between the Hanson and Casas distance (R^2_{ij}) and the F_1 value was not significant for all traits except for the internode number (0.61**) (table V). The correlation between R^2_{ij} and specific heterosis (h_{ij}) was also not significant except for ear length (-0.50*).

3.3. Inbreeding depression from F_1 to F_2

This study was developed with crosses Motan/CM67, Prato/CM67 and Apizaco/Prato. The loss of heterosis in F_2 is expected to be 50 %. For 11 cross and trait combinations for which the heterosis measured by the difference between F_1 and mid-parent was significant, five showed an inbreeding depression from F_1 to F_2 in agreement with expectation (table VI). This was the case for all traits exhibiting heterosis with the Apizaco \times Prato cross. It was also the case for straw yield, harvest index and grain weight from main ear, whatever the cross. For the six significant situations, the depression in F_2 was always greater than expected; this was in particular the case for grain yield for the two crosses Prato \times CM67 and

Motan \times CM67. The scaling test $C = 2F_2 - F_1 - \bar{P}$ corresponds in fact to the comparison of observed to expected depression in F_2 . It was then significant for grain yield for Prato \times CM67 and Motan \times CM67, for grain number per ear and ear length for Prato \times CM67, and for thousand grain weight and straw height for Motan \times CM67. This means either a competition effect or epistasis or both.

3.4. Comparison between F_1 and DH

This study was developed from the cross Motan \times CM67. The average of all DH lines was equal to mid-parent value only for straw yield, harvest index, number of ears and grain weight from main ear (table VII). For the eight other traits, the difference between the two averages was highly significant, showing a situation of non-additivity of locus effects, which can be due to epistasis or competition. This was in particular the case for grain yield. For five out of these traits, the difference was negative, showing a negative effect of recombination. However, a great variation was observed among DH lines. For most traits studied, DH lines statistically higher or equal to F_1 were obtained. However, for thousand grain weight, all the DH lines obtained are statistically lower than F_1 .

4. Discussion

As a whole, the amount of heterosis for grain yield was relatively low in this experiment. Generally, greater heterosis was associated with a low mid-parent performance. The specific heterosis values obtained show a large variability for all the traits allowing the selection of superior F_1 hybrids. The best heterosis for grain yield, harvest index, thousand grain weight and ear length was given by the hybrids resulting from geographically different lines. This suggests a good gene complementarity between these cultivars. Johnson and Whittington [22] have already underlined that the divergence between parents (European cultivars \times American cultivars) increases the level of heterosis. On the

Table VI. Comparison of generation means F_1 , F_2 and \bar{P} for three crosses.

Traits	Year	Cross ¹	F_1	$F_1 - \bar{P}$	$F_1 - F_2$	$(F_1 - \bar{P})/2$	$F_2 - \bar{P}$	C^2
Grain yield (g/plant)	1988	Pra × CM67	10.2	4.9***	4.4	2.4	0.6 ns	**
	1988	Api × Pra	6.2	-0.1 ns	0.4	0.0	-0.05 ns	ns
	1991	Mot × CM67	10.0	0.5 ns	2.9	0.2	-1.5 ns	***
Straw yield (g/plant)	1988	Pra × CM67	12.0	3.5**	3.4	1.7	0.1 ns	ns
	1988	Api × Pra	8.4	-1.3 ns	-0.4	-0.6	-0.4 ns	ns
	1991	Mot × CM67	8.1	-0.9 ns	0.1	-0.4	-1.0 ns	ns
Harvest index	1988	Pra × CM67	0.46	0.08***	0.1	0.04	0.03 ns	ns
	1988	Api × Pra	0.43	0.03 ns	0.0	0.01	0.04 ns	ns
	1991	Mot × CM67	0.49	-0.02 ns	0.0	-0.01	-0.06 ns	ns
Main ear grain weight (g)	1988	Pra × CM67	2.9	1.1 ns	0.8	0.5	0.3 ns	ns
	1988	Api × Pra	2.6	0.7 ns	0.3	0.3	0.4 ns	ns
	1991	Mot × CM67	3.2	1.4 ns	0.9	0.7	0.4 ns	ns
Ear number per plant	1988	Pra × CM67	4.6	1.0 ns	0.9	0.5	0.0 ns	ns
	1988	Api × Pra	3.3	-0.7 ns	-0.4	-0.3	-0.3 ns	ns
	1991	Mot × CM67	3.8	-1.9 ns	-0.6	-1.0	-1.4 ns	ns
Grain number per ear	1988	Pra × CM67	67.8	16.8***	13.7	8.4	3.1 ns	*
	1988	Api × Pra	63.2	11.9*	7.3	6.0	4.7 ns	ns
	1991	Mot × CM67	62.1	17.7***	2.9	8.8	14.8***	ns
Thousand grain weight (g)	1988	Pra × CM67	43.0	10.1***	6.0	5.0	4.1 ns	ns
	1988	Api × Pra	39.5	2.60 ns	0.0	1.3	2.6 ns	ns
	1991	Mot × CM67	51.2	11.7***	14.0	5.8	-2.2 ns	***
Straw height (cm)	1988	Pra × CM	77.6	8.8***	0.1	4.4	8.7 ns	ns
	1988	Api × Pra	76.7	3.8 ns	-2.6	1.9	1.2 ns	ns
	1991	Mot × CM	91.7	4.9 ns	12.4	2.5	-7.3***	***
Ear length (cm)	1988	Pra × CM67	8.3	1.5***	1.4	0.8	0.2 ns	**
	1988	Api × Pra	7.4	0.5*	0.6	0.3	-0.0 ns	ns
	1991	Mot × CM67	7.4	1.3 ns	-0.0	0.6	1.3 ns	ns
Internode number	1988	Pra × CM	6.7	0.3 ns	0.2	0.1	0.1 ns	ns
	1988	Api × Pra	6.3	-0.2 ns	0.2	-0.1	0.2 ns	ns
	1991	Mot × CM	5.7	-0.3 ns	0.1	-0.1	-0.4 ns	ns

*, **, *** Significant at 0.05, 0.01, 0.001, respectively; ns: non significant.

¹ Pra = Prato, Mot = Motan.

² $C = 2F_2 - F_1 - P$

whole, it appears that the mid-parent heterosis for grain weight from main ear was higher than that for yield components. Such results are in accordance with those of Lefort-Buson [25] on rape and

with those found on bread wheat [1, 20, 31, 35]. This superiority of yield heterosis might result from accumulation of heterosis effects observed for the various simple traits such as grain number

Table VII. Comparison of generation means F_1 , F_2 and DH for the cross Motan \times CM64.

Traits	F_1	F_2	\overline{HD}	$\overline{HD} - \overline{P}$	$F_1 - \overline{HD}$	$F_2 - \overline{HD}$
Grain yield (g/plant)	10.0	7.0	6.7	-2.7**	3.3***	1.2 ns
Straw yield (g/plant)	8.1	8.0	8.7	0.3 ns	-0.6 ns	-0.76 ns
Harvest index	0.49	0.45	0.42	-0.10 ns	0.08**	0.04 ns
Ear number per plant	3.8	4.3	4.8	-0.9 ns	-0.9 ns	-0.4 ns
Main ear grain weight (g)	3.2	2.2	1.8	0.09 ns	1.3***	0.4**
Grain number per ear	62.1	59.2	54.5	10.1***	7.6**	4.6 ns
Thousand grain weight (g)	51.2	37.2	33.9	-5.5***	17.2***	3.2 ns
Ear length (cm)	7.3	7.4	7.4	1.3***	-0.0 ns	0.0 ns
Straw height (cm)	91.7	79.3	75.2	-11.5***	16.4***	4.1*
Internode number	5.7	5.6	5.5	-0.5***	0.2 ns	0.1 ns
Heading date (days)	117.3	117.3	122.4	2.5 **	- 5.0***	- 5.0***
Mildew resistance	44.9	44.9	44.8	- 18.2***	0.2 ns	0.0 ns

*, **, *** Significant at 0.05, 0.01, 0.001, respectively; ns: non significant.

per ear and thousand grain weight. In this case, the improvement of complex traits such as grain yield could be obtained by the improvement of the yield components which display more additivity.

The correlation between F_1 and mid-parent value was significant for different traits. However, the mid-parent value did not allow prediction of the F_1 value with enough accuracy for grain yield. The fact that the correlation between F_1 and GCA was higher than the correlation between F_1 and the mid-parent, shows that dominance or epistatic effects may exist. In the case of additivity, it can also be the result of a greater accuracy on GCA than on the parental value. This was in particular clearly the case for mildew resistance, a trait which does not show SCA, but also for main ear grain weight and grain number, two traits for which the correlation F_1 -SCA was low. In fact, such an effect of low accuracy on per se value must affect more or less all traits, even those showing a preponderant role of SCA, such as grain and straw yield which are also traits known to be greatly influenced by environment. It appears then, that grain weight of the main ear and its components (grain number and thousand grain weight), heading date and resistance to mildew are the more additive traits and grain and straw yield are the less addi-

tive. As a consequence for the plant breeder, it will be possible to select the parent on the basis of their earliness and grain yield components of main ear.

Several arguments are in favour of a possible fixation of heterosis. Indeed, the role of dominance appeared at different levels. First, the coexistence of a high additivity with heterosis, with a high F_1 -mid-parent correlation, could be due to partial to complete dominance. The fact that large SCA values were associated with crosses involving at least a low performing parent is also in favour of dominance. Furthermore, for several traits, it was observed that parents with good GCA transmitted their quality to their offspring, probably because of dominant genes. Finally, the best argument in favour of possible fixation of heterosis is the fact that for most of the traits, the best F_1 was nearly equal to the best parent. In the presence of a major role of dominant genes, a negative correlation between parental heterosis and per se value was expected. Such a correlation has already been estimated as significantly negative in different species [3, 11, 19]. In our experiment, the correlation was negative but non-significant; the non-significance perhaps due to a lack of accuracy at the level of per se value.

The study of inbreeding depression from the F_1 to F_2 shows that, for some traits (grain yield, thousand grain weight, number of grains per ear, plant height), in competition conditions, the heterosis can be reduced by more than one half, which is what is expected with additivity of locus effects. Such deviations from expected values can be due to epistasis or to competition. It is probable that in our condition of high density, intergenotypic competition may have played a great role at the F_2 level. Indeed, a performance of a plant depends on two types of parameters: its producer or direct effect and the associate effects of its neighbours [9, 10, 13]. As a plant is simultaneously producer and partner, with a positive association between direct and associate effect, i.e. when the more productive plants are also the more competitive, the value of the F_2 can be greater than expected. On the contrary, if there is a negative association between the two parameters, the value of the F_2 can be lower than expected. This could be the case with high difference in tillering, tillering ability being a trait related to aggressiveness of forage grasses very often negatively related to biomass in dense sward. It seems that it was such a situation in our experiment at least in the Motan \times CM67 cross. In this cross, the F_2 plants were shorter than expected. This can be explained by a negative correlation between vegetative tillering and plant height. Then, by competition, high tillering/low yielding plants tend to dominate low tillering/high yielding plants, with the correlated negative effect on thousand grain weight, because there was a positive correlation between thousand kernel weight and plant height. In fact this may be due to difference in earliness and to a drought stress which affected late plants. In such conditions, high tillering/low yielding plants were late and the low tillering/high yielding ones were early. For the other cross, Prato \times CM67, the situation was not so clear because F_2 plants tended to be taller than expected, although not significantly; however, grain yield, ear length and grain number per ear were lower than expected. In this situation, competition and epistasis could explain the observed results. Our results are not in accordance with those of Singh and Mishra [36] who obtained in one hybrid con-

siderable heterosis and a very low inbreeding depression for grain yield in F_2 . However, they show that deviations from expected depression depend on the cross and on environmental conditions which can affect competitive ability of genotypes.

The comparison of DH lines to the mid-parent in one cross showed that for several important traits recombination has an unfavourable effect. As there is no intergenotypic competition within F_1 and DH plot, i.e. no competition between different genotypes, such a result may be due to epistatic effects. This means that recombination has destroyed some genic equilibrium. The comparison between the average of DH lines and mid-parent values is a more powerful test of epistasis than the test $C = 2F_2 - F_1 - \bar{P}$. This confirms the result from this test for grain yield, thousand grain weight and plant height. The unfavourable effect of recombination appears clearly at the F_2 level but is not so obvious at the DH level, owing to heterozygosity. In addition, for the Motan \times CM67 cross, epistasis must be also considered superimposed with a competition effect. Strong epistatic effects have also already been detected by Goldringer et al. [14], in wheat, by studying genetic variance components among DH lines. To understand the unfavourable effect of recombination it is necessary to consider simultaneously epistasis and the distribution of genes between the parents. According to Snape and Simpson [37], this unfavourable effect could be due to duplicate epistasis and excess of coupling or to complementary epistasis and excess of repulsion. In such a case, it will be better to derive DH from generations after F_1 . Recombination after the first meiosis will tend to correct unfavourable effects.

In spite of such an unfavourable effect of haplodiploidization, it appears that the genetic advantage obtained in F_1 can be fixed by the doubled-haploid method. For all traits, except thousand grain weight, it was possible to observe some lines equal to the F_1 . This tends to confirm our conclusion from the diallel analysis that heterosis will be fixable. Such a conclusion was already derived by Kasha [23], Reinbergs et al. [33] and Fedak [7], from the study of DH lines. However, the probabil-

ity of transgression depends on several parameters: the difference between the F_1 value and the DH mean, the variance among DH lines and the heritability values concerning the DH lines. Considering the variance, again the effect of distribution of genes among the parents must be considered, even without epistasis. With an excess of coupling, the variance among DH lines will be maximum with haplodiploidisation at the F_1 level, and if there is an excess of repulsion it will be maximum with haplodiploidisation in later generations. Taking into account the quite different origins of the parents it is probable that, in our cross, there was an excess of coupling. Then, haplodiploidisation at the F_1 level will be justified. The study of the probability of transgression shows that it would be necessary to study at least 100 to 150 DH lines to have some chance of detecting several good lines (2–5).

In the material studied, it can clearly be seen that F_1 superiority is not large enough to produce hybrid seed profitably. Rousset [34], Brears et al. [2] and Oury et al [30] consider that about 12 % gain is required to compensate for the high cost of hybrid seed production. In the material studied, it does not appear justified to develop F_1 hybrids. Even if there was a sufficient advantage of F_1 there does not appear to be any benefit in using F_2 , perhaps owing to a strong negative effect of competition. Then, taking into account the results of the present study, one of the most efficient strategies of variety development in barley could be to develop doubled-haploid lines which allow the development of lines as good as F_1 .

Acknowledgements: We are very grateful to Dr Felicity Vear and Louis Jestin, Inra (Clermont-Ferrand, France) for their helpful comments on the manuscript.

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