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Mid-parent advantage and heterosis in F_1 hybrids of wheat from crosses among old and modern varieties

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SUMMARY

Twenty-eight F_1 hybrids of wheat and their parents were grown in field trials at Trumpington, Cambridge during 1986/87 and 1987/88. They were derived from crosses between seven 'modern' varieties, used as female parents, and either two 'old' (Squareheads Master and Partridge) or two 'modern' varieties (Bert and Motto), which were used as male parents. Grain yield, yield components, biomass and height were determined. The male parents were chosen to provide contrasting phenotypes and genetic backgrounds for the F_1 hybrids. Mid-parent advantage, the increase of a hybrid for a given character above the mean of its parents, and heterosis, the increase of a hybrid above the 'better' parent for that character, were calculated. Most F_1 hybrids showed mid-parent advantage for the characters studied. This tended to be greatest for hybrids derived from parents with the largest phenotypic differences in that character. In contrast, where heterosis occurred it tended to be greatest where the phenotypic difference between the parents was least. This suggests that the beneficial effects of hybridization, resulting from the dispersion of dominant genes between the parents, was insufficient to overcome the detrimental effects of other genes present where the 'less good' parent was substantially lower than the 'better' parent. Hybrids derived from the 'modern' male parents had greater heterosis for grain yield and mean grain weight than those from the 'old' parents. Of the yield components, positive heterosis for mean grain weight resulted in heavier seeds and was the most important yield component in determining heterosis in grain yield. Heterosis for the number of grains/ear was small or did not differ significantly from zero while number of ears/m² showed negative heterosis resulting in fewer ears/m² in the hybrids.

INTRODUCTION

Many studies have shown that F_1 hybrid wheat can yield significantly more than the mean of its parents (e.g. Fonseca & Patterson 1968; Gyawali *et al*. 1968; Walton 1971; review, Wilson & Driscoll 1983). In these studies, the contribution to grain yield from the different yield components (i.e. mean grain weight, number of grains/ear and number of tillers/m²) was variable, but all usually showed that the hybrid was better than the mid-parent value. Two main ways of expressing hybrid advantage have been used. First, it has been expressed as mid-parent advantage, the increase in yield or other character of the hybrid compared to the mean of the parents and is an estimate of the mean directional dominance (potence) of the alleles for a given character. Second, it has been expressed as heterosis, the increase in yield or other character of the hybrid compared to that of the 'better' parent for that character. Heterosis implies that there is dispersion for dominant alleles between the parents which may increase or decrease the character. In this paper, both of these methods of expressing hybrid advantage for a character will be considered.

Because wheat is a naturally self-pollinating crop, all the F_1 hybrids used in early experiments were produced either by emasculation followed by hand-pollination or by utilizing cytoplasmic male sterility (Wilson & Ross 1962; Hughes & Bodden 1978). Both of these methods are time-consuming and only limited amounts of seed can be produced. As a consequence, most early studies were carried out using spaced plants in small plots. More recently, however, it has been possible to produce F_1 hybrid seed on a large scale by using chemical hybridizing agents (CHAs) thus enabling drilled field trials to be carried out which more closely approach normal agronomic practices. Results of such trials have been reported by

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Table 1. *Yields and yield components, biomass, harvest index, height and date of ear emergence for wheat hybrids in 1987 and 1988*

	Mean of all hybrids			
	1987	S.E. (83 D.F.)	1988	S.E. (83 D.F.)
Grain yield (g/m²)	593	2·65	815*	2·74
Mean grain weight (mg)	46·3	0·17	49·9*	0·16
Grain number/ear	38·5	0·30	40·3	0·46
Number of ears/m²	348	2·67	438	3·28
Biomass (g/m²)	1439	8·15	1896*	8·79
Harvest index	0·42	0·002	0·43	0·002
Height (cm)	84·1	0·32	114·1	0·30
Ear emergence (June)	3·99	0·13	12·4	0·08

* Values adjusted using covariate analysis with the difference between a plot and the mean height of its neighbouring plots as covariate.

Morgan *et al*. (1989) and Borghi *et al*. (1988). In these trials the mid-parent advantage for grain yield was small and usually less than that reported for trials grown at lower densities. Morgan *et al*. (1989) showed that heterosis for grain yield was less where the parents were higher yielding and suggested that the parental lines, used in the trials, already had many of the genes beneficial for yield fixed in the homozygous state and so were unable to show much heterosis.

Experiments with maize hybrids (Moll *et al*. 1962, 1965; Smith & Smith 1992) have shown that heterosis is positively correlated with the genetic diversity of the parents as measured by the number of marker alleles which differ between the parents, although extreme genetic diversity may result in less heterosis. Similar results for wheat have been obtained by Zhang *et al*. (1985). The F_1 hybrids used in the trials described by Morgan *et al*. (1989) and Borghi *et al*. (1988) were produced from varieties and advanced breeding lines within contemporary large-scale breeding programmes. The genotypes were, therefore, likely to have been genetically similar, thus reducing the number of possibly advantageous gene combinations within the population. The experiments described in this paper were carried out to test the hypothesis that, in wheat, heterosis is greater in hybrids obtained from crosses between parental varieties with contrasting genetic backgrounds than in those obtained from crosses between parents with similar backgrounds. Hybrids have been tested, together with their parents, from selected crosses made between a combination of 'old' and 'modern' varieties with contrasting phenotypes which are likely to be genetically dissimilar. In this paper the physiological and agronomic relationships between these hybrids and their parents are described and the expression of potence in relation to the genetic diversity of the parents analysed.

MATERIALS AND METHODS

Plant material

Four varieties were chosen as male parents. Two modern varieties, Bert and Motto (introduced in 1979 and 1984 respectively), were chosen for their suitability as pollen donors. The 'older' varieties, Squareheads Master and Partridge, were also selected for their suitability as pollen donors as well as for their phenotypes, which contrasted with those of the two 'modern' varieties. They are very tall, late maturing genotypes derived from old landraces (the first records of varieties with these names were in 1830 and 1907 respectively). All four varieties were used to pollinate six modern semi-dwarf wheats; Brock, Riband, Hornet, Rendezvous, Haven (all containing the height reducing gene *Rht2*), Sleijpner; and a taller isogenic line of Huntsman (both containing the height reducing gene *Rht1*). Under favourable growing conditions these genes reduce plant height by *c*. 20% with a corresponding increase in grain yield (Gale & Youssefian 1985). These 'modern' varieties, used as female parents, were shorter and higher yielding than the male parents, none of which contained either *Rht* gene (Table 2).

The F_1 seed used in these trials was harvested from seed production plots in 1986, as described by Morgan *et al*. (1989). Seed of the parents and the control varieties, Norman, Avalon, Aquila and Galahad, was produced in the same year.

Experimental design and layout

Trials were carried out in 1986/87 and 1987/88; subsequently these will be referred to by their year of harvest, i.e. 1987 and 1988. The trials in both years were grown on a fertile, clay loam at Trumpington,

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Table 2. *Yields, yield components, biomass, harvest index, height and date of ear emergence of the four male parents, the mean of the F_1 hybrids derived from them and the mean of the female parents averaged for 1987 and 1988*

	Motto[1]	F_1[2]	Bert[1]	F_1[2]	Partridge[1]	F_1[2]	Squareheads Master[1]	F_1[2]	Female mean[3]	S.E. ♂[4]	S.E. F_1[5]	S.E. ♀[6]
Grain yield (g/m²)*	593	731	666	729	524	713	394	65·7	697	32·3	12·1	16·2
Mean grain weight (mg)*	49·2	50·4	45·8	49·1	41·8	46·8	37·9	46·1	46·3	1·08	0·37	0·56
Grain number/ear	33·0	39·8	34·7	37·7	36·5	39·8	28·3	40·7	39·3	2·50	0·83	1·28
Number of ears/m²	395	379	447	415	389	39·9	393	382	399	33·5	11·5	17·0
Biomass (g/m²)*	1518	1664	1551	1613	1568	1742	1418	1673	1496	101·4	37·0	51·0
Harvest index	0·39	43·9	0·43	45·3	0·34	41·9	0·28	40·1	0·46	0·013	0·005	0·007
Height (cm)	86	88	87	88	126	107	131	113	75·9	2·88	1·09	1·55
Date of ear emergence (June)	5·3	9·3	7·4	7·1	11·9	9·7	12·1	8·9	7·7	0·93	0·33	0·47

* 0% moisture; [1]Based on 6 replicates; [2]Based on 7 means (6 replicates); [3]Based on 28 means (6 replicates); [4]4 degrees of freedom; [5]40 degrees of freedom; [6]166 degrees of freedom.

Cambridge. Both trials were of a double split-plot design. There were four main plots corresponding to the four male parents. Each main plot consisted of seven plots comprising two subplots; one of a female parent and the second of the hybrid derived from the cross between it and the male parent used to produce the hybrids within that main plot. There was also an eighth subplot comprising one of the four control varieties and the male parent used to make the hybrids sown in that main plot.

This design was used in order to maximize the accuracy of the estimate of the effects of heterosis in the F_1 hybrid compared with the best yielding parent (from previous data this was expected to be the female parent). There were three replications in each year. In both trials, seed was treated with fungicide and was drilled in mid-October at a sowing density of 230 seeds/m², allowing for the heavier seed of the hybrids (mean = 54·8 mg) compared with that of the parents and controls (mean = 48·4 mg). Subplots were *c.* 4 m long and contained seven rows 17 cm apart.

The trials were treated with proprietary agro-chemicals to control pests and diseases at the rates and timing recommended by the manufacturers. In 1987 all plots were sprayed with the growth regulator, cycocel. The 'old' parents and all the hybrid plots derived from them were very tall and therefore susceptible to lodging. Consequently they were supported by coarse nylon netting (14 × 14 cm mesh) tied to iron stakes placed in the corners of each plot. Nitrogen was applied at the rate of 170 kg/ha.

Sampling and harvesting

The average plant height to the base of the ear was measured in each plot at maturity. Plots were sampled for yield components as follows. The number of fertile ears in two 30 cm-wide transects across each plot were counted and the results expressed as the number of ears/m². Immediately before harvest, all the plants in a 10 cm-wide transect across each plot were pulled up with their roots. The roots of these plants were cut off at the crown and the ears cut off, counted and threshed. The weights of grain and straw (including chaff) were determined after drying at 80 °C for 48 h. From these weights the harvest index of the sample was calculated as the ratio of grain : grain + straw. Mean grain weight was determined by weighing a sample of 200 grains taken from the dried harvest index samples. The number of grains/ear was calculated by dividing the weight of grain in the harvest index samples by the number of ears in the sample, and dividing the weight of grain/ear by the mean grain weight. Grain yield was obtained by combine harvesting the remainder of the plot, determining the moisture content from a subsample, adjusting the yield to 0% moisture and adding in the weight of dry grain in the harvest index sample. The lengths of all plots were measured and the area of each plot calculated assuming a plot width of 1·5 m (Austin & Blackwell 1980). This plot width corrects the measured yield for edge effects. Yields were expressed as g/m². Biomass was calculated by dividing the grain yield by the harvest index. All yields and mean grain weights were expressed at 0% moisture.

RESULTS

In both years the plots of the two 'old' varieties, Squareheads Master and Partridge, and the hybrids derived from them, were significantly taller than the plots of the two 'modern' varieties Motto and Bert, the hybrids derived from them, the female parents and the control varieties. In 1987, when the plots had been sprayed with cycocel, the average height of all the hybrids was 36% less than in 1988 (Table 1). The active component of this growth regulator is chlormequat chloride, which mimics the effect of the *Rht2* gene in reducing stem elongation (and also, perhaps, increasing the number of grains per ear although no effects were observed in these trials) by inhibiting the biosynthesis of gibberellins (Lenton *et al.* 1987). The reduction in height was, therefore, greatest in the tallest plots (i.e. genotypes without the *Rht2* or with the *Rht1* gene) and least in the shortest plots (genotypes with *Rht2*), thus the reduction was only *c.* 10% for the female parents. For each trial the effect of the differences in height between adjacent plots on grain yield, biomass and yield components was analysed by using the difference between the height of a plot and the mean of the height of the two neighbouring plots on its long axis as a covariate in the analysis of covariance. The regression coefficient of the covariate was not significant for any variate in 1987, showing that tall plots did not significantly reduce yield, or affect the other characters, in adjacent shorter plots. In 1988, however, the regression coefficient was significant for grain yield, biomass and mean grain weight, showing that these characters were affected by the height of neighbouring plots. The data obtained in 1988 were, therefore, adjusted for mean plot height differences and the adjusted values were used for all subsequent calculations.

The mean grain yield of the hybrids in 1988 was *c.* 38% greater than in 1987 (Table 1). The greater number of ears/m² (+26%) in 1988 was the main reason for this increase, although mean grain weight (+8%) and the number of grains/ear (+5%) also contributed to it. There was, however, no genotype × year interaction for grain yield or yield components and consequently, to simplify the presentation of the results, the data from both years have been combined and the means are presented. Despite the application of cycocel in 1987, genotype × year interaction for height among the F_1 hybrids was very small compared with the main effects (year and genotype) and did not alter genotype ranking. Data from each year were therefore combined as above to simplify the presentation of the results. However, because of the effect of the growth regulator, mean values of height will underestimate heterosis.

The establishment of seedlings was, on average, 18% less for the hybrids than for the parental lines although both were within normal stand densities and were not considered to have affected yield.

Significant variation was found among both male and female parents for most of the characters studied. The largest variation, however, was observed among and between the two 'modern' and the two 'old' male parents and attention has therefore been focused on the effective contribution to hybrid advantage by the four male parents. A summary of the measurements on the male parents is given in Table 2.

There was no interaction between years for variation in yield, yield components or associated characters among the female parents and the results are presented as the means for both years (Table 3). Additionally, because the female parents were

Table 3. *Yields and yield components, biomass, harvest index, height and date of ear emergence for the female parents averaged for 1987 and 1988*

	Brock	Riband	Hornet	Sleijpner	Rendezvous	Haven	Huntsman *Rht1*	S.E. (22 D.F.)
Grain yield (g/m²)*	675	731	720	712	683	714	647	16·2
Mean grain weight (mg)*	40·5	46·2	51·5	43·2	46·4	47·9	48·4	0·56
Grain number/ear	35·3	45·1	42·7	43·0	35·8	36·9	36·6	1·28
Number of ears/m²	487	372	339	397	429	401	370	17·0
Biomass (g/m²)*	1468	1505	1575	1451	1480	1542	1449	51·0
Harvest index	0·46	0·49	0·45	0·49	0·46	0·46	0·44	0·007
Height (cm)	71·6	75·5	77·5	72·3	78·6	75	80·9	1·55
Ear emergence (June)	4·2	7·2	8·9	10·2	9·1	8·5	5·6	0·47

* Values adjusted using covariate analysis with the difference between a plot and the mean height of its neighbouring plots as covariate in 1988.

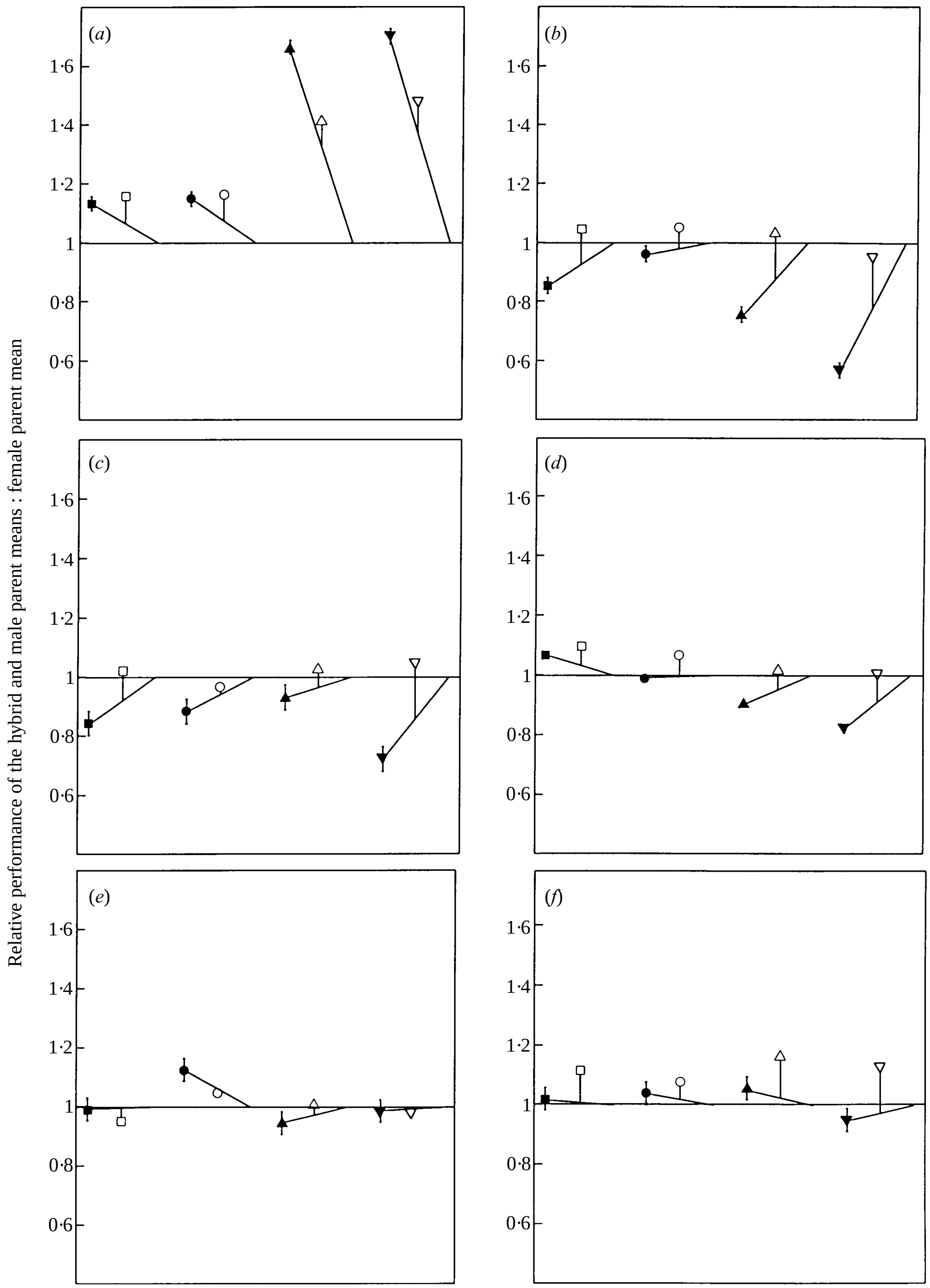

Fig. 1. Relative performance (averaged over 2 years) of the mean of the seven F_1 hybrids (open symbols) derived from each male parent (closed symbols); Motto (□, ■), Bert (○, ●), Partridge (△, ▲) and Squareheads Master (▽, ▼) with respect to the combined mean of the female parents (normalized to 1) for: (*a*) height; (*b*) grain yield; (*c*) grains/ear; (*d*) mean grain weight; (*e*) ears/m^2 and (*f*) biomass. Bars indicate twice the S.E. for the male parents; S.E.s for the F_1 hybrids and female parents were within the size of the symbol.

Table 4. *Heterosis (expressed as the percentage by which the F_1 hybrid exceeded the better parent) for mean grain yield, yield components, biomass and height for the mean of the hybrids derived from each of the four male parents*

	'Modern'		'Old'		
	Motto	Bert	Partridge	Squareheads Master	S.E. (40 D.F.)
Grain yield (g/m^2)	+4·3	+4·8	+3·0	none	1·28
Mean grain weight (mg)	+9·5	+6·7	+1·3	none	0·96
Grain number/ear	+1·8	none	+2·0	+4·3	3·07
Number of ears/m^2	−3·8	none	none	−2·5	1·65
Biomass (g/m^2)	+9·5	+3·5	+10·6	+12·2	1·83
Height (cm)	+2·3	+1·0	none	none	0·86

represented equally within each of the main plots, and because there was no observed interaction between the female and the male parents, the mean of all the female parents within the trial has been used as the basis of comparison with the hybrids. This maximizes the precision of the estimates of hybrid advantage and heterosis. Thus, to estimate heterosis, the means of the seven F_1 hybrids derived from each male parent were compared with the combined mean of all the female parents.

Parents

The female parents were characterized by high harvest indices, resulting from both high grain and low straw yield. In contrast, the two 'old' male parents, Squareheads Master and Partridge, had considerably longer straw, lower grain yields and correspondingly lower harvest indices. Both 'modern' male parents had slightly longer straw than the female parents. Of the two 'modern' male parents Motto was similar in yield to the lower yielding female parents, while Bert was similar to the mean of the female parents. Partridge and Squareheads Master were lower yielding than the average of the 'modern' male parents by 17 and 38% respectively. Mean grain weights of the 'old' male parents were less than those of the 'modern' male parents which were, in turn, similar to those of the female parents. The female parents had more grains/ear than any of the male parents with the exception of Partridge; Squareheads Master had markedly fewer grains/ear than any of the other parents. The female parents showed large variations in number of ears/m^2, with Brock having the highest number and Hornet the lowest. The mean number of ears/m^2 in the male parents was similar to the mean of the female parents, although Bert had 14% more than the other male parents. In contrast to its grain yield, Partridge had the highest biomass of any of the parents and Squareheads Master, although it had the lowest grain yield (44% of the mean of the female parents), had a biomass only 8% less than that of the female parents. Both ear emergence and maturity in the 'older' varieties was 5–6 days later than in most of the 'modern' varieties.

Mid-parent advantage of F_1 hybrids

Figure 1 shows the relative performance, averaged over 2 years, for each of the male parents and the mean of the seven F_1 hybrids derived from them with respect to the combined mean of the female parents which have been normalized to unity. There was an increase in the expression of all the characters compared with the mean of the parents (mid-parent advantage) except for number of ears/m^2, which was less than the mid-parent value. The hybrids derived from Squareheads Master showed the greatest mid-parent advantage for all the characters measured except number of ears/m^2. There was no consistent trend among the hybrids derived from the other male parents.

Heterosis of F_1 hybrids

There was no clear and consistent trend when comparing heterosis for the different characters between hybrids derived from the 'old' or 'modern' male parents (Table 4). Heterosis for grain yield was, however, greatest in those F_1 hybrids derived from the 'modern' male parents. In the F_1 hybrids derived from Motto, Bert and Partridge, the most important of the yield components determining heterosis for yield was mean grain weight and there was no heterosis for the number of grains/ear within these groups. Squareheads Master, in contrast, showed no heterosis for mean grain weight but did show heterosis for grains/ear. It is interesting to note that in Motto, the 'modern' parent with the greatest heterosis for mean grain weight, there was negative heterosis for number of ears/m^2. Although the 'modern' parents had greater heterosis for grain yield they had lower heterosis for biomass than those derived from the 'old' male parents. The greater heterosis for biomass was due to the large increase in straw weight in these groups, although this was not reflected in the length of straw (height).

DISCUSSION

In Fig. 2, the mean mid-parent advantage of the hybrids for grain yield and associated characters, expressed as a fraction of the mid-parent mean, is plotted against the difference between the parents. The horizontal line shows the level at which there is no mid-parent advantage (i.e. mid-parent advantage = 1). The interpretation of these data depends on the number of alleles involved in determining the character and the degree of dominance which they exhibit. Where only a single gene is involved, hybrids falling above this line exhibit the result of the dominance of the allele derived from the 'better' parent. Hybrids which fall below this line, however, result either from the dominance of the alleles in the 'less good' parent or in the negative directional dominance of the allele in the 'better' parent. Where more than one allele is involved, especially likely in the case of grain yield, the phenotype of the hybrid is the result of the mean dominance of all the alleles, which may show positive or negative directional dominance (ambidirectional dominance). Similar increases in a character among the hybrids may result from differing combinations of alleles; thus for instance, the increase in grain yield in Motto was the result of an increase in the number of grains/ear and mean grain weight with a reduction in the number of ears/m², while that in Partridge showed an increase in all yield components. The more a hybrid lies above the line (i.e. the greater its mid-parent advantage) the greater the mean effect of the dominant alleles from the parents. Figure 2 shows that the mean effect of the alleles of genes for the yield components, number of grains/ear and mean grain weight, is to confer a positive increase in these characters, while the alleles of the genes for number of ears/m² act negatively to reduce the number of ears.

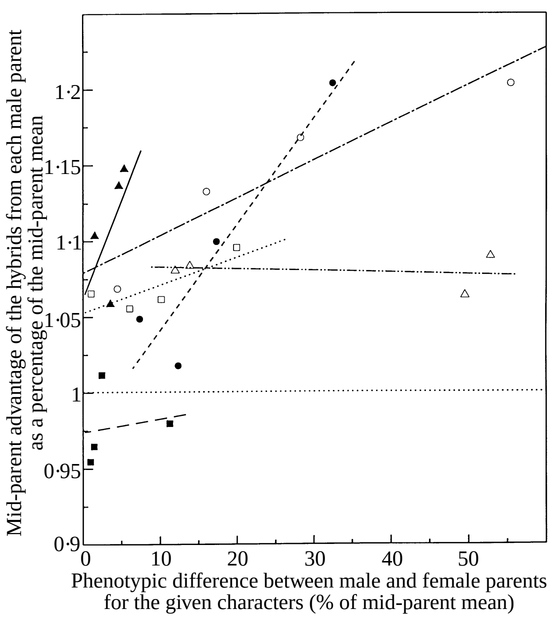

Fig. 2. Mid-parent advantage for the mean of seven F_1 wheat hybrids derived from each male parent plotted against the phenotypic difference between the parents (expressed as a percentage of the mid-parent value) for grain yield, –·○·– (+0·940); mean grain weight, ······□······ (+0·814); number of grains/ear, ---●--- (+0·939); number of ears/m², – –■– – (+0·179); biomass, —▲— (+0·540); height, –··–△··–·· (−0·221). Figures in parentheses are correlation coefficients (D.F. = 2).

In Fig. 2, the slope of the regression line for a character shows the effect of the difference in phenotype between the parents for a character on the F_1 hybrids, a reflection of their genetic difference. Where the slope is positive it shows that greater genetic diversity between the parents increases the positive expression of the character. This is not, however, observed for the height response in the F_1 hybrids, where the mid-parent advantage is unaffected by the large difference in heights between the parents. This suggests that the alleles for height found in the 'old' male parents are recessive or show ambidirectional dominance.

For many of the traits measured in these trials, the F_1 hybrids outperformed the better parent thus displaying 'true' heterosis (Table 4). Of the yield components, the number of grains/ear and mean grain weight showed heterosis above (positive) that of the 'better' parent while, in contrast, the number of ears/m² showed either no or negative heterosis below that of the 'less good' parent. These results are similar to those reported for drilled trials of F_1 hybrids by Morgan *et al.* (1989). These results are, however, in contrast to experiments with spaced plants (Walton 1971) where the hybrids showed strong positive heterosis for number of tillers/m². This may have been due in part to the poorer germination of the hybrids in the present trials which led to fewer plants/m² than the parents and hence fewer tillers/m². Alternatively, increased competition between plants sown at high density may have inhibited the expression of the genes for high tillering. The product of these yield components determines grain yield and so, where the mean of the heterosis for these characters is positive, there will be also be positive heterosis for yield. Squareheads Master had the greatest mid-parent advantage for grain yield, number of grains/ear, mean grain weight (positive) and number of ears/m² (negative) but only had the greatest heterosis for number of grains/ear. This probably arose from the greater difference between the parents in crosses involving Squareheads Master where even the combination of favourable dominant alleles from both parents could not increase the F_1 hybrid yield above that of the female parent because of the presence of less beneficial, or negatively acting, alleles already present in Squareheads Master. Keyes & Sorrells (1989) have suggested that the presence of *Rht1* and *Rht2* genes have a pleiotropic effect on yield which reduces mid-parent advantage in hybrids despite giving greater yields in the homozygous parents. They found that the decrease in hybrid yield advantage was greatest where there were more copies of these genes. Because all of the female parents, except Sleijpner, in our trials contained *Rht* genes, this effect may explain why the mean of the hybrids did not show greater mid-parent advantage for yield despite the large genetic difference between the parents. This idea is supported by the greater mid-parent advantage for yield obtained in hybrids derived from Sleijpner than from the other female parents (data not given) and suggests that hybrid advantage may be greater from male crossed with female lines which do not contain *Rht* genes.

These results show that, when grown in closely spaced plots, mid-parent advantage was more likely to occur and to be greatest where the parents came from different genetic backgrounds. Heterosis, on the other hand, defined as the increase in a character above its 'better' parent, was only evident where the genetic background, and hence phenotypes, of the parents were similar, because of deleterious genes arising from the 'less good' parent. As has been suggested above, and by Morgan *et al.* (1989), wheat varieties from current UK breeding programmes are likely to be homozygous for many of the alleles conferring high yield. Under these conditions, heterosis will only occur if suitable dominant alleles conferring yield advantage can be introduced from other sources. In these trials the 'older' parents either did not contain such useful alleles or they were not expressed. Alternatively these parents may have contained deleterious alleles at different loci. Useful alleles may be present in material in wheat breeding programmes elsewhere or from landraces of wheat, though they may occur with other alleles with undesirable effects such as unsuitable photoperiod response or no winter hardiness. F_1 hybrids, showing heterosis for yield, may only retain their superiority over their parents for a limited time because the advantageous alleles from the parents can be fixed within a homozygous breeding line. Heterosis, however, may be a useful indicator in predicting the breeding value of potential parents within a wheat breeding programme.

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