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Heterosis, overdominance for grain yield, and alpha-amylase activity in F_1 hybrids between near-isogenic *Rht* dwarf and tall wheats

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SUMMARY

The *Rht-B1b*, *Rht-D1b* and *Rht-B1c* alleles for reduced height in wheat (the Norin 10 and Tom Thumb dwarfing genes previously known as *Rht1*, *Rht2* and *Rht3*) were exploited in combinations to generate a near-continuous range of plant heights, from 53 cm to 123 cm, amongst near-isogenic homozygotes and F_1 hybrids. Pleiotropic yield effects of *Rht* genes were measured in both homozygous (intravarietal) and heterozygous (intervarietal) genetic backgrounds. Heterosis due to overdominance of *Rht* genes was detected among intravarietal hybrids. The effects of heterozygosity at other genetic loci (mean dominance) were determined, independently of *Rht* effects, from comparisons between intravarietal and intervarietal F_1 hybrids.

Genotypes of intermediate plant heights gave maximum yields, in agreement with other trials of the homozygous lines, so that heterosis (hybrid exceeding best parent) for *Rht* yield effects was observed in crosses between tall and dwarf isogenic pairs. This heterosis combined additively with increased mean weight per grain in intervarietal crosses, generating the highest overall grain yields in hybrids with semi-dwarf stature in heterozygous genetic backgrounds. The *Rht-B1c* allele showed single-gene overdominance for grain yield, also the production of alpha-amylase in ripening grains of Maris Huntsman was effectively inhibited in the *Rht-B1a/c* intravarietal hybrid. The *Rht-B1c* allele thus offers advantages for both grain yield and grain quality in the heterozygous condition and should be considered as an alternative to the conventional semi-dwarfing genes *Rht-B1b* and *Rht-D1b* for F_1 varieties in environments conductive to preharvest sprouting.

INTRODUCTION

In a comprehensive review of progress in the development of hybrid wheat, Pickett (1993) has concluded that the levels of yield heterosis typically obtained are at best marginally sufficient to justify the extra expense of F_1 seed production. This conclusion rests in part on evidence that heterosis in hybrids is predominantly due to the bringing together in the F_1 of dispersed dominant genes (Law *et al.* 1978; Snape 1982) so that equivalent yields can also eventually be obtained by conventional inbreeding out of the same cross. When heterosis is 'fixable' in this fashion, the extra cost of F_1 seed production can be weighed against the extra time required to produce a pure-breeding variety. However, such comparisons are not valid for cases in which heterozygosity is an essential component of heterosis. This can arise when overdominance at a single locus is the major cause of heterosis, or when optimum heterosis is expressed at an intermediate phenotype associated with heterozygosity at a major locus for adaptation. The present study furnishes an example of this type of heterosis, which cannot be fixed in a pure-breeding inbred line.

Pleiotropic yield effects of *Rht* genes for reduced height and insensitivity to gibberellin in wheat are characterized by increases in harvest index and grain number associated with reduced total shoot yield and grain size, generating a net grain yield effect dependent on the balance between reductions and increases in the different components (reviewed in Gale & Youssefian (1985)). The optimum balance appears to be reached in plants of intermediate heights (Flintham *et al.* 1997). Previous reports have drawn contrasting conclusions concerning the merits of different *Rht* alleles in F_1 hybrids. Gale *et al.* (1987*a*, 1988) observed dominance for grain yield in intervarietal hybrids between tall and semi-dwarf near-isogenic lines, and dominance for mean grain weight was unaffected by the dwarfing alleles. Moreover the Tom Thumb allele displayed overdominance for yield in *Rht3/rht3* heterozygotes (Gale *et al.* 1987*a*, 1988; Zhao *et al.* 1993). On the other hand, Keyes & Sorrells (1989) and Ehdaie & Waines (1994) concluded that the dwarfing genes limited the expression of hybrid vigour. The plant heights of their tall controls were, however, short compared with the tall winter wheats described by Gale *et al.* (1987*a*, 1988).

High alpha-amylase activity is a serious grain quality defect of many high-yielding wheats, and Maris Huntsman has been implicated as a source of this genetic susceptibility in UK breeding programmes. In previous studies, the *Rht3* gene has been shown to reduce alpha-amylase production in a dwarf isogenic line of Maris Huntsman and in the *Rht3/rht3* hybrid (Gale *et al.* 1987*b*, 1988). The present study was undertaken in order to confirm and expand previous results, using a more comprehensive range of homozygous and hybrid genotypes, including double and triple combinations of dwarfing genes.

The Norin 10 and Tom Thumb 'gibberellin insensitive' dwarfing alleles in wheat, formerly referred to as *Rht1*, *Rht2* and *Rht3*, and the 'tall' *rht* alleles conferring sensitivity to the hormone, have been assigned new symbols to conform with the recommended rules for gene symbols in wheat (Law 1989; Börner *et al.* 1996). Under the new nomenclature, alleles at the locus on the short arm of chromosome 4B are designated as follows: *Rht-B1a* (formerly *rht1* = *rht3*), *Rht-B1b* and *Rht-B1c* (formerly *Rht1* and *Rht3* respectively). Alleles at the homoeologous locus on 4DS are designated *Rht-D1a* and *Rht-D1b* (formerly *rht2*, *Rht2*). These allelic relationships allow gene dosage effects to be assessed in comparisons between gibberellin sensitive controls and isogenic lines carrying one, two, three, or four copies of different *Rht* dwarfing genes.

GENOTYPES

Genetic backgrounds are denoted by the prefix *BB*, *WW* or *HH*, indicating homozygous inbred lines (or intravarietal F_1 hybrids) derived from the cultivars Bersée, Maris Widgeon, or Maris Huntsman respectively. Prefixes *BW*, *WH* or *HB* indicate intervarietal F_1 hybrids, from crosses between the different genetic backgrounds (these cross combinations are not distinguished from their reciprocals *WB*, *HW*, *BH*, see below). Homozygous inbreds carrying *Rht-B1a*, *Rht-D1a* (talls), *Rht-B1b*, *Rht-D1a* or *Rht-B1a*, *Rht-D1b* (single-gene semidwarfs), *Rht-B1b*, *Rht-D1b* (two-gene dwarfs) or *Rht-B1c*, *Rht-D1a* (single-gene dwarfs) in each varietal background were used as female parents in each of nine F_1 hybrid grain production blocks. The pollen parent for each block was either an *Rht-B1a*, *Rht-D1a*, an *Rht-B1b*, *Rht-D1a*, or an *Rht-B1a*, *Rht-D1b* inbred, in each varietal background. Combining reciprocal crosses, and equivalent doses of *Rht* alleles, 11 different F_1 *Rht* genotypes were produced in each of three intravarietal (homozygous) and three intervarietal (heterozygous) genetic backgrounds. Two additional *Rht* homozygotes (*Rht-B1c*, *Rht-D1a* and *Rht-B1b*, *Rht-D1b*) were only available as inbred lines.

The 11 *Rht* hybrids in each of the six genetic backgrounds were included in a yield trial, together with the inbred lines. F_1 seed was not available from crosses onto the Maris Widgeon *Rht-B1b*, *Rht-D1b* parent and scores for the two missing F_1 hybrids *WW Rht-B1b/b*, *Rht-D1a/b* and *WW Rht-B1a/b*, *Rht-D1b/b* were estimated by combining the effect of the *WW* background, averaged over *Rht* genotypes of similar plant height, with the effects of the relevant *Rht* genotype averaged over the other intra- and intervarietal backgrounds.

METHODS

Kilogram quantities of each F_1 hybrid were produced in 1987 using the Shell gametocide Azetidine-3-carboxylic acid to induce male sterility in female parent plots surrounded by untreated pollen parents. The yield trial was sown from a seven-row drill in October 1987 at River Farm, Cambridge, as continuous strips of plots in four randomized blocks. Altogether, the trial comprised 316 experiments plots (each 6 m long × 1·16 m wide), separated from the surrounding commercial milling wheat crop by double guard plots. Sub-blocks of tall, semidwarf and dwarf genotypes were arranged in order to avoid shading and other competitive effects between tall and short stands, based on plant height data from preliminary trials. Seed was pretreated with Baytan systemic fungicide and sown at a rate of 15 g m^{-2}. The trial was given the same fertilizer and fungicide treatments as the surrounding commercial crop and no growth regulators were applied.

Seedling emergence and tiller density (number per $0·5 \times 1·16$ m^2 quadrat in plot centres) and plant height (cm from soil to tips of ears) were scored in the field. Prior to harvest twenty ripe fertile tillers from inside rows of each plot were cut at ground level, dried, and threshed to determine grain number per ear and mean weight (mg per grain). Ripe plots were trimmed back to measured lengths ($4·2 \pm 0·3$ m) and individually combine-harvested for grain yield (g m^{-2}). Alpha-amylase activities in ripe ungerminated grains of Maris Huntsman genotypes were assayed against β-limit dextrin as described by Flintham & Gale (1982).

The experiment was analysed as a randomized block design with three main variance components: replicate blocks, differences between genotypes over blocks, and (genotype × block) interaction as error estimate. Variances due to factors with non-significant effects (reciprocal crosses, homozygotes from F_1 production plots versus inbreds) were combined with the error variance. Carry-over effects from the gametocide were tested for in nine paired comparisons between parental inbreds and reconstituted homozygotes of equivalent genotypes. Twelve paired comparisons between reciprocal or quasi-reciprocal intervarietal hybrids of similar nuclear genotype, but of different maternal variety, provided a test for differences due to cytoplasmic effects.

Sources of heterosis were partitioned between genetic background effects, effects due to *Rht* alleles, and (background × *Rht*) fixed effects. Mean dominance of genetic background was measured in orthogonal comparisons between the means of intravarietal and intervarietal groups at each level of *Rht* dosage. Heterosis due to *Rht* effects, equivalent to overdominance of single genes, was estimated from intravarietal comparisons between *Rht* heterozygotes and the best parental inbred in the same genetic background.

RESULTS

Gametocide and maternal effects

In comparison between inbred lines and intravarietal hybrids of the same *Rht* genotypes, reconstituted homozygotes' seedling emergence was reduced by 30% compared to the corresponding inbred lines. This effect was highly significant in eight out of nine comparisons and was attributed to disease and sprouting observed in F_1 hybrid seeds. Despite this reduced emergence, no significant gametocide effects on F_1 tiller numbers, plot yields or yield components were detected. Evidently the thinner stands were able to compensate for low plant density by increased tillering during spring growth; there was no indication of any carry-over effects from the gametocide. No significant differences were detected between yield components of hybrids from reciprocal or quasi-reciprocal crosses, indicating the absence of cytoplasmic or other maternal differences between the three parental cultivars.

Plant height

The different *Rht* combinations exhibited a wide range of plant heights. Within genetic backgrounds, genotypes fell into *Rht* dosage groups of equal plant height as listed in Table 1*a*. The genes *Rht-B1b* and *Rht-D1b* were equivalent in their effects on height and other characters; substitution of one or more copies of one allele by the appropriate number of copies of the homoeoallele had no significant effect on phenotype. Genotypes with the same number of *Rht-B1b* and/or *Rht-D1b* alleles in each genetic background are therefore pooled within a dosage group. Similarly, a single copy of the *Rht-B1c* allele conferred a height phenotype equivalent to three-copy combinations of *Rht-B1b* with *Rht-D1b* and these genotypes are pooled in Table 1.

There were significant differences between the effects of particular *Rht* alleles in different genetic backgrounds (Table 1*a*). Differences between varieties reflected background genetic effects evident amongst the tall controls and the ranking of plant height ($BB > WW > HH$) was maintained over different *Rht* genotypes. The difference between inter- and intravarietals (dashed and solid lines in Fig. 1*a*) reflects mean dominance over mid-parent. Net dominance of background genes for increased plant height was consistent and positive over *Rht* groups.

These (*Rht* × background) interactions were not significant when plant height was expressed as a percentage of the tall control genotype in the same genetic background. Thus, in each genetic background the presence of a single copy of either *Rht-B1b* or *Rht-D1b* reduced plant height by about 6% relative to tall controls. Corresponding height reductions in other *Rht* dosage groups were 16% (genotypes carrying two *b* alleles), 32% (three *b* alleles, or one *c* allele), 39% (one *b* allele plus one *c* allele), 45% (four *b* alleles), and 49% (two *c* alleles).

Grain yield

Variation in grain yield showed effects due to *Rht* dosage, different genetic backgrounds, *Rht* × background interaction, dominance and overdominance (Table 1*b* and Fig. 1*b*). The yield advantage of semi-dwarfs confirms results from other trials of the inbred lines, arising from the optimum balance between increased harvest index and reduced total shoot yield at intermediate plant heights (Flintham *et al.* 1997). *Rht* × background interaction for grain yield followed the pattern expected from the general height/yield relationship: inherently taller varieties tolerate stronger *Rht* effects than shorter varieties. In the case of Maris Huntsman, the tall control was of near-optimal height and no significant yield increase was achieved by adding *Rht* dwarfing alleles.

The association between intermediate plant height and maximum grain yield resulted in overdominance for yield in the case of *Rht-B1c*. The dwarf *BB Rht-B1c*, *Rht-D1a* inbred line outyielded the tall control, but the *BB Rht-B1a/c*, *rht-D1a/a* hybrid yielded more than either parent as a consequence of its closer proximity to optimum plant height (Table 1*b*). *Rht-B1c* also exhibited overdominance for yield in the *WW* background, and there were indications of overdominance of smaller magnitude with *Rht-B1b* or *Rht-D1b* in some backgrounds. It is noted that the yields of the *Rht-B1a/c*, *Rht-D1a/a* hybrids were generally lower yielding than genotypes carrying three *b* alleles, in the same *Rht* dosage group. This effect may be an artefact, since it breaks the otherwise general trend in yield with decreasing height and was not observed in the data for yield per ear (not shown).

Dominance for yield effects in the genetic back-

Table 1. *Plant heights and yield components of* Rht *isolines and hybrids in different homozygous (intravarietal) and heterozygous (intervarietal) genetic backgrounds*

	(*a*) Plant height (cm)						(*b*) Grain yield (g m^{-2})					
	Intravarietal genotypes			Intervarietal genotypes			Intravarietal genotypes			Intervarietal genotypes		
Rht dosage group	*BB*	*WW*	*HH*	*BW*	*WH*	*HB*	*BB*	*WW*	*HH*	*BW*	*WH*	*HB*
Tall controls (no dwarfing alleles)												
B1a/b, *D1a/a*	123·7	122·3	106·2 (±2·5)	122·0	123·0	122·0 (±3·6)	771	732	915 (±37)	831	904	835 (±52)
Genotypes carrying a single *b* allele												
B1a/b, *D1a/a*	112·8	113·6	103·5	118·1	116·4	111·5	941	883	933	900	930	929
B1a/a, *D1a/b*	117·5	113·4	102·1	120·5	113·9	109·5	889	907	939	906	970	955
Mean	115·1	113·5	102·8 (±2·5)	119·3	115·1	110·5 (±2·5)	915	895	936 (±37)	903	950	942 (±37)
Genotypes carrying two *b* alleles												
B1b/b, *D1a/a*	105·7	99·4	86·2	105·5	102·4	97·5	907	829	948	934	931	881
B1a/a, *D1b/b*	109·4	95·1	89·1	103·0	99·5	107·0	891	852	929	935	967	899
B1a/b, *D1a/b*	111·4	101·0	86·8	103·2	98·8	106·5	889	888	853	954	953	830
Mean	108·8	98·5	87·4 (±1·6)	103·9	100·2	103·7 (±2·1)	895	856	910 (±23)	929	940	893 (±30)
Genotypes carrying three *b* alleles, or one *c* allele												
B1b/b, *D1a/b*	78·5	78·5*	76·0	83·0	78·1	78·2	937	886*	936	936	943	959
B1a/b, *D1b/b*	89·5	84·1*	76·0	82·3	81·5	83·8	965	876*	887	932	972	1031
B1a/c, *D1a/a*	89·4	83·9	74·3	87·5	85·3	84·9	877	803	767	819	883	881
Mean	85·8	82·2*	75·4 (±2·1)	84·3	81·6	82·3 (±2·1)	926	855*	863 (±30)	895	933	957 (±30)
Genotypes carrying one *b* allele plus one *c* allele												
B1b/c, *D1a/a*	74·9	74·5	66·0	77·3	74·2	69·6	906	809	805	897	812	827
B1a/c, *D1a/b*	75·8	72·6	67·0	78·4	73·5	78·1	890	777	823	874	839	776
Mean	75·3	73·6	66·5 (±2·5)	77·9	73·8	73·9 (±2·5)	898	793	814 (±37)	885	826	802 (±37)
Genotypes carrying four *b* alleles												
B1b/b, *D1b/b*	73·0	62·6	57·3 (±3·6)	—	—	—	830	749	948 (±52)	—	—	—
Genotypes carrying two *c* alleles												
B1c/c, *D1a/a*	63·9	62·5	53·0 (±3·6)	—	—	—	830	762	861 (±52)	—	—	—

Table 1. *continued*

	(*c*) Grains per ear						(*d*) Weight per grain (mg)					
	Intravarietal genotypes			Intervarietal genotypes			Intravarietal genotypes			Intervarietal genotypes		
Rht dosage group	*BB*	*WW*	*HH*	*BW*	*WH*	*HB*	*BB*	*WW*	*HH*	*BW*	*WH*	*HB*
Tall controls (no dwarfing alleles)												
B1a/a, *D1a/a*	39·8	33·8	42·8 (±4·1)	37·3	37·8	48·0 (±5·8)	43·1	55·9	56·8 (±2·6)	50·9	61·0	56·6 (±3·7)
Genotypes carrying a single *b* allele												
B1a/b, *D1a/a*	54·2	39·2	52·7	48·4	47·2	48·3	46·5	50·2	55·8	53·3	57·6	53·5
B1a/a, *D1a/b*	49·6	45·5	55·0	45·1	43·4	48·6	45·3	50·1	56·0	50·8	56·5	58·2
Mean	51·9	42·3	53·8 (±4·1)	46·8	45·3	48·5 (±4·1)	45·9	50·1	55·9 (±2·6)	52·0	57·0	55·8 (±3·7)
Genotypes carrying two *b* alleles												
B1b/b, *D1a/a*	51·8	41·2	50·2	49·6	47·8	51·2	44·3	46·3	48·8	47·8	53·9	52·3
B1a/a, *D1b/b*	52·7	40·2	50·3	43·2	48·1	44·4	41·6	47·9	48·7	43·8	56·8	55·3
B1a/b, *D1a/b*	42·5	42·5	56·1	42·2	49·6	45·9	54·0	46·5	46·8	48·0	53·8	52·7
Mean	49·0	41·3	52·2 (±3·4)	45·0	48·5	47·2 (±3·4)	46·6	46·9	48·1 (±1·7)	46·5	54·8	53·4 (±2·2)
Genotypes carrying three *b* alleles, or one *c* allele												
B1b/b, *D1a/b*	55·8	43·9*	64·5	48·4	58·8	48·8	39·7	45·2*	51·8	44·4	49·1	46·1
B1a/b, *D1b/b*	59·3	42·5*	57·3	49·4	51·8	56·2	45·7	47·3*	50·1	46·6	47·4	48·3
B1a/c, *B1a/a*	54·4	40·5	55·9	51·2	55·6	51·0	44·4	50·2	46·1	45·8	50·5	56·3
Mean	56·5	45·0*	59·2 (±3·4)	49·7	55·4	52·0 (±3·4)	43·2	47·6*	49·3 (±2·2)	45·6	49·0	50·2 (±2·2)
Genotypes carrying one *b* allele plus one *c* allele												
B1b/c, *D1a/a*	64·4	48·4	61·4	47·8	44·9	53·6	41·9	44·0	48·5	47·2	50·2	44·8
B1a/c, *D1a/b*	59·1	46·4	57·8	49·6	48·4	55·0	45·8	40·6	46·3	46·3	51·7	48·1
Mean	61·7	47·4	59·6 (±4·1)	48·7	46·7	54·3 (±4·1)	43·9	42·3	47·4 (±2·6)	46·7	50·9	46·4 (±2·6)
Genotypes carrying four *b* alleles												
B1b/b, *D1b/b*	58·5	47·6	40·0 (±5·8)	—	—	—	35·0	36·0	48·3 (±3·7)	—	—	—
Genotypes carrying two *c* alleles												
B1c/c, *D1a/a*	49·3	48·8	41·2 (±5·8)	—	—	—	39·6	44·8	49·1 (±3·7)	—	—	—

Note: * Estimate, see text. 95% confidence limits for Group means in each background are given in parentheses. Eight replicates for tall, *Rht-B1b*, and *Rht-D1b* homozygotes; four replicates for others.

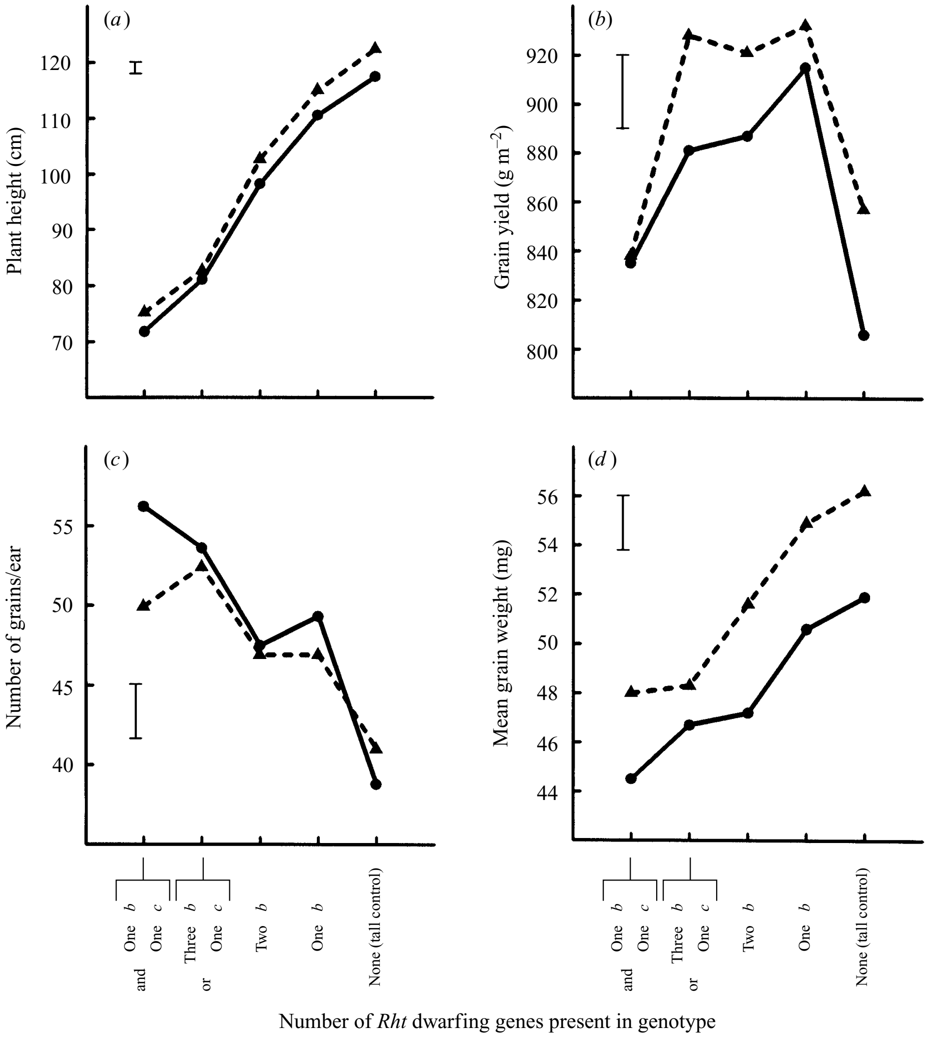

Fig. 1. Effects of *Rht* dwarfing genes and background genetic heterozygosity on (*a*) plant height (cm), (*b*) grain yield (g m^{-2}), (*c*) number of grains per ear and (*d*) mean grain weight (mg). For plant height, grain yield, number of grains per ear and mean grain weight, L.S.D.$_{(P<0\cdot05)}$ is denoted by a vertical bar. Means for each *Rht* dosage group (Table 1) are shown over intervarietal (heterozygous, ▲) or intravarietal (homozygous, ●) genetic backgrounds.

ground was also evident, as positive mean deviations of intervarietals over mid-parents (Fig. 1*b*). The yield advantages of intervarietal hybrids were maintained as *Rht* dosage was increased up to three *b* alleles, but were eroded (as was yield itself) in the more extreme dwarfs.

Grain number per ear and mean grain weight

Genotypic factors had no significant effects on number of tillers per unit area, nor were tiller counts correlated with yield. Genotypic variation in grain yield per unit area was therefore attributed to differences for the yield components grain number per ear and mean grain weight.

Rht dwarfs yielded significantly higher numbers of grains per ear than tall controls (Table 1*c*, Fig. 1*c*), although some of the more extreme dwarfs showed smaller increases and maximum grain numbers were often obtained from plants of intermediate height. Overdominance of the *Rht-B1c* effect on grain number was statistically significant in the *HH* background and a smaller but non-significant effect was observed in the *BB* background. Heterosis was also evident in

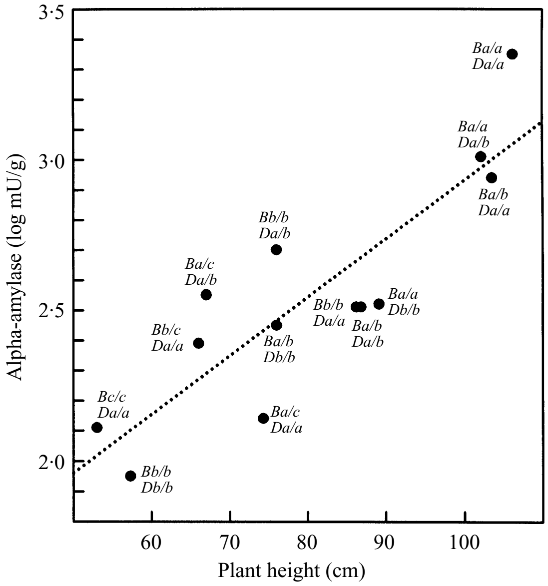

Fig. 2. Grain alpha-amylase activity versus plant height in Maris Huntsman *Rht* isolines and intravarietal hybrids. *Rht* genotypes (●) are labelled as in Table 1. L.S.D.$_{(p<0·05)}$ is $\pm 5·05$ cm for plant height, $\pm 0·72$ log (mU) for enzyme activity. Correlation coefficient $r = 0·869$, $P < 0·001$.

the *WH Rht-B1a/c*, *Rht-D1a/a* hybrid, regardless of which parent was used as the source of the *Rht-B1c* allele. Background heterozygosity had no significant effect on grain number except in extreme dwarfs, which as intervarietal hybrids set fewer grains than intravarietals. The reason for the latter difference is not clear, but may be related to the decline in grain number seen in the even more extreme homozygotes (*Rht-B1b/b*, *Rht-D1b/b* and *Rht-B1c/c*, *Rht-D1a/a* inbreds).

Mean grain weight was positively correlated with plant height (Fig. 1*a*, *d*). Across different genetic backgrounds, mean grain size within *Rht* groups followed the ranking seen in the tall controls: the differences between parents were maintained independently of *Rht* effects. There was marked and consistent mean dominance of background genes for high grain weight which was maintained in opposition to the reducing effects of the dwarfing genes.

Highest overall yields were thus obtained from semi–dwarf intervarietal hybrids as a result of the combination of increased grain number due to *Rht* effects with background genetic dominance for increased grain size.

Grain alpha-amylase activity

The grain samples from Maris Huntsman intravarietal hybrids and inbred lines showed no visible evidence of germination, but enzyme activity in the tall control line was high and typical for this variety. Alpha-amylase activity was reduced among the genotypes carrying dwarfing genes, the reductions on a logarithmic scale being proportional to the severity of dwarfism (Fig. 2). Similar effects have been observed in several other field trials of the inbred lines, not reported here. In the case of *Rht-B1c*, low enzyme activity might be attributed to genetic insensitivity of the aleurone to gibberellic acid (Gale & Marshall 1975; Flintham & Gale 1982). However, aleurone insensitivity cannot account for low enzyme activities in the other dwarf genotypes, since distal half-grains from homozygous lines carrying *Rht-B1b*, or *Rht-D1b*, or both alleles, produce as much enzyme as the tall control line when challenged with gibberellic acid (data not shown). There is no obvious reason why reduced plant height should be expected to have a direct effect on enzyme production in ripening grains, however this might be linked to the correlated reduction in grain size. Evidence is beginning to emerge that large grain size may predispose some wheat varieties to pre-harvest alpha-amylase production (Evers *et al.* 1995) and the correlation between alpha-amylase activity and mean grain weight in the present data set was similar to that between enzyme activity and plant height.

DISCUSSION

In comparisons between near-isogenic lines carrying different *Rht* alleles, differences between lines are assumed to be due to *Rht* effects. The possibility of effects due to other genes in tight linkage with the *Rht* loci in the isolines cannot be discounted, however the yield effects described above can be predicted from an apparently general relationship between plant height and grain yield (Flintham *et al.* 1997). Yield differences between the *Rht* genotypes in this study are therefore attributed to pleiotropic effects of dwarfism rather than to linkage.

The availability of the three different *Rht* dwarfing alleles discussed enables the hybrid wheat breeder to vary F_1 stature in a near-continuous manner, using alleles at just two loci of major effect. Data from other trials of inbred lines and from the present study indicate that grain yield will be highest when plant height is intermediate between the tall *Rht-B1a*, *Rht-D1a* and the extreme dwarf phenotypes. In F_1 hybrids, this optimum intermediate height can be achieved simply by using a major dwarfing gene in heterozygous condition. This can result in single gene overdominance for grain yield, when the tall and dwarf inbreds used to produce the F_1 are respectively taller and shorter than optimum, as in the case of the *Rht-B1c* allele in the Bersée and Maris Widgeon backgrounds. This type of overdominance is not to be expected in wheats such as Maris Huntsman, which are already near optimum height.

Interactions between genetic background and individual *Rht* effects arise from differences in background plant height, such that inherently taller backgrounds require stronger *Rht* effects to achieve optimum plant height than do shorter backgrounds. One option, open only to the hybrid breeder, would be to use the stronger *Rht-B1c* allele in heterozygous condition to achieve semidwarf plant stature and to use the genetic background to accumulate genes for increased plant vigour, applying the 'tall dwarf' model proposed by Law *et al.* (1978).

A further advantage of using *Rht-B1c* would be the inhibition of pre-harvest alpha-amylase production in genetic backgrounds predisposed to this failing. This effect, observed in *Rht-B1a/c* isogenic hybrids of both Maris Huntsman (this study) and of the Australian variety Spica (Mrva & Mares 1996), is a particular advantage of using the Tom Thumb allele. As noted by Mrva & Mares (1996), homozygosity for either the *Rht-B1b* or for the *Rht-D1b* alleles does not provide effective general control of enzyme production, since many commercial wheat varieties of these genotypes are notoriously susceptible to this problem. *Rht-B1a/c* hybris can also be expected to have some resistance to germinative increases in alpha-amylase during pre-harvest sprouting (Gale & Marshall 1975; Flintham & Gale 1982). *Rht-B1c* thus confers a combination of useful pleiotropic effects on grain yield and quality not found with the more conventional *Rht-B1b* and *rht-D1b* Norin 10 alleles.

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