

# Plant height and yield components of inbred isogenic and F<sub>1</sub> hybrid *Rht* dwarf wheats

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**Abstract.** Single and double-gene *Rht1*, *Rht2*, *Rht3*, *Rht1* + *Rht2* and *Rht3* + *Rht2* isogenic lines of wheat in four parental *rht* varieties were grown in drilled yield trials at four sites in 1989. The same lines were also grown in 1988 together with hybrid genotypes from CHA (chemical hybridising agent) F<sub>1</sub> production plots. In the inbred lines shorter than one metre, *Rht* alleles reduced total shoot biomass by shortening the straw; mass of straw per unit plant height was unaffected. Highest grain yield was obtained from plant heights between 70 and 100 cm. The *Rht* genotype achieving this stature varied according to parent varietal height. The hybrids grown allowed comparisons between intra- and inter-varietal crosses over a range of *Rht* genotypes. In F<sub>1</sub> hybrids positive heterosis was observed for plant height, grain yield and mean grain weight. Highest yields were obtained from inter-varietal hybrids carrying one, two or three doses of *Rht1* or *Rht2* or one dose of *Rht3*. An *Rht3/rht* hybrid showed resistance to premature  $\alpha$ -amylase production during grain ripening.

**Key words:**  $\alpha$ -amylase, chemical hybridising agent, heterosis, wheat.

## Introduction

The *Rht1* and *Rht2* semidwarfing genes are generally held to have been responsible for major increases in grain yields since their introduction into wheat breeding programmes around the world (GALE, YOUSSEFIAN 1985). The development of commercial varieties of hybrid wheat would undoubtedly lead to further major yield increases, given the 10% yield heterosis over highest parents often observed in elite F<sub>1</sub>s (BINGHAM 1986), however the large-scale introduction of hybrid wheats has been delayed by the lack of an efficient, commercially competitive hybridising system for this normally self-pollinating

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crop. Attempts to exploit cytoplasmic and genetic factors for male-sterility/restoration have not proved competitive and the attention of breeders has turned more recently to the use of chemical hybridising agents (CHAs) for F<sub>1</sub> seed production (CUBITT, CURTIS 1987).

In addition to polygenes for good general combining ability, the best parental lines for hybrid production will probably carry *Rht* alleles, but not necessarily the allelic combinations which are optimal for yield in the homozygous condition. Indeed the experience in maize suggests that some genotypes which perform poorly as inbreds may be among the best parents for F<sub>1</sub> hybrids. There is some evidence that wheats carrying the *Rht3* allele may fall into this category: although *Rht3* homozygotes often yield less than tall controls. An *Rht3/rht3* hybrid gave the highest overall yield in a previous investigation (GALE et al. 1989). This observation is perhaps the strongest evidence for overdominance of a single gene yet reported. An additional advantage of using *Rht3* may arise from the inhibition of  $\alpha$ -amylase synthesis in grains of *Rht3* genotypes. Since this inhibition is partially dominant, F<sub>2</sub> grains from an *Rht3/rht3* F<sub>1</sub> crop should have significantly reduced mean enzyme activity (GALE, MARSHALL 1975). High  $\alpha$ -amylase activity due to sprouting reduces the breadmaking quality of many wheat crops (DERERA 1990) and *Rht3* has been proposed as a source of resistance to such damage (FLINTHAM, GALE 1982).

A previous report described plant height and yield effects of *Rht1*, *Rht2* and *Rht3* in single-gene isogenic inbred lines and single-allele F<sub>1</sub> hybrids (GALE et al. 1989). These dwarfing alleles were shown to increase harvest index, grain yield, and number per ear relative to *rht* controls, except that yields of the most extreme dwarfs were depressed. Increased grain numbers in *Rht* ears combined with heterosis for mean grain size to generate the highest yields in inter-varietal dwarf hybrids. Subsequent trials reported here include the two-gene combinations: *Rht1* + *Rht2* and *Rht3* + *Rht2* as inbred isogenic lines and a more extensive array of F<sub>1</sub> hybrids. The effects of this comprehensive range of *Rht/rht* gene combinations on the performance of inbred and hybrid genotypes are presented, allowing prediction of optimal *Rht* genotypes for the expression of yield heterosis. In addition the effects of different *Rht/rht* combinations on premature production of  $\alpha$ -amylase in the variety Maris Huntsman are discussed.

## Material and Methods

### Genotypes

Six inbred isogenic lines (*rht*, *Rht1*, *Rht2*, *Rht3*, *Rht1* + *Rht2*, *Rht3* + *Rht2*) in each of the varieties Maris Huntsman (H), Maris Widgeon (W), Bersée (B)

and April Bearded (A) were grown in four replicates at four sites in 1989 and one site in 1988. F<sub>1</sub> hybrids from Nickersons Rothwell Plant Breeders CHA crosses between the inbred isogenics were included in the 1988 trial (the CHA used was azetidine-3-carboxylic acid). F<sub>1</sub> genotypes were as shown in Table 1, in the six genetic backgrounds H × H, W × W, B × B, (intra-varietal hybrids), H × W, H × B, B × W (inter-varietal hybrids).

**Table 1.** *Rht* genotypes of F<sub>1</sub> hybrids from CHA crosses

Pollen parent:	<i>rht1/rht1 rht2/rht2</i>	<i>Rht1/Rht1 rht2/rht2</i>	<i>rht1/rht1 Rht2/Rht2</i>
Female parents	F <sub>1</sub> hybrids		
<i>rht1/rht1 rht2/rht2</i>	<i>rht1/rht1 rht2/rht2</i>	<i>Rht1/rht1 rht2/rht2</i>	<i>rht1/rht1 Rht2/rht2</i>
<i>Rht1/Rht1 rht2/rht2</i>	<i>Rht1/rht1 rht2/rht2</i>	<i>Rht1/Rht1 rht2/rht2</i>	<i>Rht1/rht1 Rht2/rht2</i>
<i>rht1/rht1 Rht2/Rht2</i>	<i>rht1/rht1 Rht2/rht2</i>	<i>Rht1/rht1 Rht2/rht2</i>	<i>rht1/rht1 Rht2/Rht2</i>
<i>Rht1/Rht1 Rht2/Rht2</i>	<i>Rht1/rht1 Rht2/rht2</i>	<i>Rht1/Rht1 Rht2/rht2</i>	<i>Rht1/rht1 Rht2/Rht2</i>
<i>Rht3/Rht3 rht2/rht2</i>	<i>Rht3/rht1 rht2/rht2</i>	<i>Rht3/Rht1 rht2/rht2</i>	<i>Rht3/rht1 Rht2/rht2</i>

Low yields of F<sub>1</sub> grain in 1987 precluded inclusion of some genotypes in the 1988 trial, and where reciprocal hybrids were sown each was represented in only two replicates.

## Methods

All trials were drilled as continuous rows of 1.16 × 6 m<sup>2</sup> plots in four randomised blocks. Sub-blocks of genotypes were arranged to avoid shading and other competitive effects between tall and short plants. Plant height (mean cm from soil to tip of ear) was scored in each plot. Samples of twenty ripe tillers hand cut at ground level from plot centres were scored for harvest index, number of grains per ear and mean grain weight. Grain yield (Kg m<sup>-2</sup>) was measured on combine-harvested grain from plots trimmed back to 4 m length. α-Amylase activity in aqueous extracts of ripe, ungerminated grains from Maris Huntsman isogenic inbreds and intra-varietal hybrids was assayed against β-limit dextrin as described by FLINTHAM and GALE (1982).

## Results

### Effects of *Rht* dwarfism on total, grain, and non-grain yields in inbred isogenic lines

Variation in the relative yields of grain and non-grain tissues due to differences in plant height of different *Rht* combinations are shown in Figure 1.

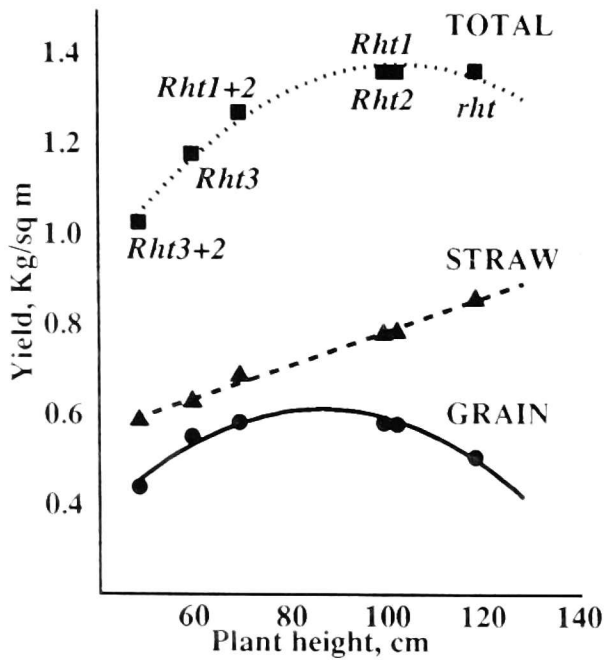


Figure 1. Total (stem + leaf + ear) yield, non-grain (straw + chaff) yield, and grain yield, versus mean plant height in inbred isogenic lines carrying different *Rht* and *rht* genes

Note: Yields are means over 4 varietal backgrounds  $\times$  5 sites  $\times$  4 replicate blocks per point. Fitted quadratic curves and linear regressions shown:

$$\text{Total} = 0.0237(\text{Height}) - 0.000116(\text{Height})^2 + 0.17$$

$$\text{Straw} = 0.0037(\text{Height}) + 0.41$$

$$\text{Grain} = 0.0191(\text{Height}) - 0.000111(\text{Height})^2 - 0.211$$

The ranking of different *Rht* combinations for plant height was consistent over the different trials and varietal backgrounds, i.e.,

$$Rht3 + Rht2 < Rht3 < Rht1 + Rht2 < Rht1 = Rht2 < rht .$$

The *Rht* alleles showed no effect on straw yield per unit plant height: reduction in plant height led to a linear decrease in the non-grain yield. The relationship between total shoot yield and plant height was not linear but more closely fitted a quadratic response, reaching a maximum at around 100 cm

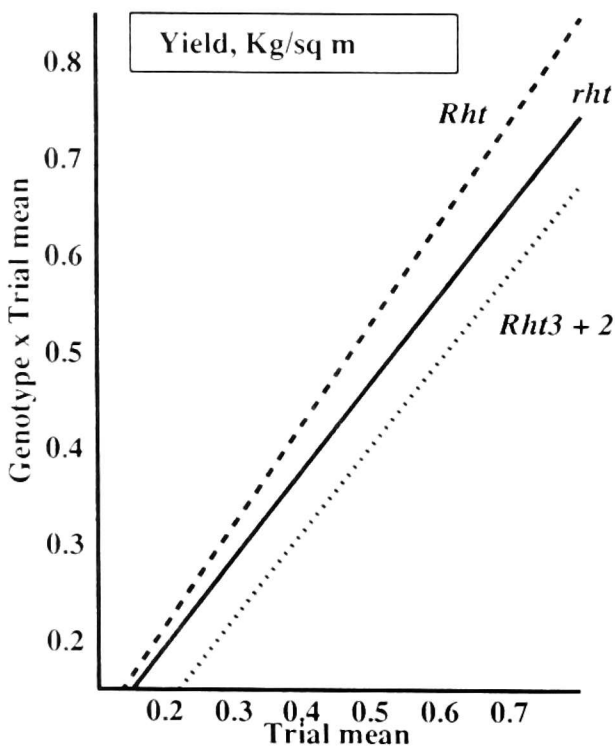


Figure 2. Genotype  $\times$  environment interaction for grain yields of inbred isogenic lines carrying different *Rht* and *rht* genes

Note: Regression lines are shown for *Rht/rht*  $\times$  site means over 4 varietal backgrounds  $\times$  4 replicates, versus overall site means for 5 different trials. Site means were 0.20, 0.35, 0.63, 0.75, and 0.76  $\text{Kg m}^{-2}$ , respectively. A pooled *Rht* regression is shown for genotypes *Rht1*, *Rht2*, *Rht1 + Rht2*, and *Rht3*, in the absence of significant differences between their separate regressions.

Regression slopes and standard errors (s.e.) for the different *Rht*, *rht* genotypes were as follows:

Genotype	Slope	s.e.
<i>rht</i>	0.913	0.022
<i>Rht1</i>	1.018	0.022
<i>Rht2</i>	1.058	0.031
<i>Rht1 + Rht2</i>	1.085	0.022
<i>Rht3</i>	1.027	0.028
<i>Rht3 + Rht2</i>	0.898	0.061

plant height. The difference between total shoot and straw yields represents the net yield of grain and followed a second quadratic, with a maximum between 70 and 100 cm plant height. Yields of *Rht* genotypes were greater than or equal to *rht* controls until plant height was reduced below approximately 60 cm. The *Rht* genes appear to modulate grain yield by decreasing the amount of assimilates partitioned into the straw, in addition to their effects on total shoot biomass. The net grain yield effect of a particular *Rht* combination thus depends upon the balance between a reduction in total yield and an increase in harvest index.

#### **Genotype × environment interaction for grain yield**

Yields of *Rht3* + *Rht2*, *rht*, and other grouped *Rht* inbred lines in each of 5 sites, meaned over four varietal backgrounds, are shown plotted against the overall site mean yields in Figure 2. Comparisons between the regression slopes show that most of the *Rht* genotypes responded better than *rht* controls to improvements in the site as measured by grain yield. The exception was the extreme *Rht3* + *Rht2* group which consistently failed to equal *rht* yields.

#### ***Rht* × variety interaction for grain yield**

The effects of different *Rht* combinations on yield varied somewhat in the four different varieties, although ranking of genotypes for plant height was consistent over backgrounds (Figure 3). A different quadratic response in grain yield to increasing plant height was obtained in each variety but all gave maximum yields when height was in the range 70 to 100 cm, which may be optimum for West European conditions. Different *Rht* genotypes achieved this optimum in different backgrounds; for example, highest yield in the shortest varietal background (Maris Huntsman) came from the *Rht1* line, but in the tallest background (April Bearded) *Rht3* and *Rht1* + *Rht2* lines outyielded the others. Thus, the choice of dwarfing source can vary according to other genotypic factors: only a mild *Rht* effect is needed in varieties carrying multiple minor dwarfing genes in their genetic backgrounds, but inherently taller genotypes achieve highest yields with stronger *Rht* combinations.

#### ***Rht* and heterotic effects on plant height and yield components in F<sub>1</sub> hybrids**

No significant differences were observed between homozygous intra-varietal hybrids and inbreds of equivalent genotypes, nor between reciprocal crosses. There was thus no evidence of carry-over CHA or maternal effects on the characters examined.

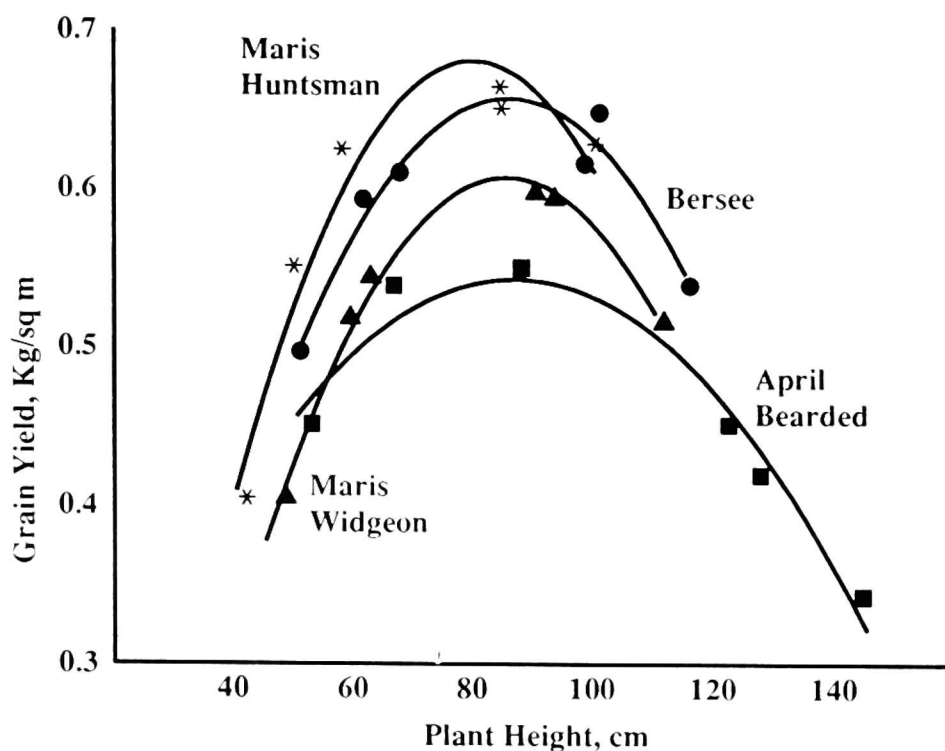


Figure 3. Grain yield versus plant height in inbred isogenic lines carrying different *Rht* or *rht* genes in different varietal backgrounds

Note: Significant differences were found between coefficients of the separate quadratic regressions shown for Maris Huntsman (stars), Maris Widgeon (triangles), Bersée (circles) and April Bearded (squares). In all four varieties the ranking of *Rht* genotypes with respect to plant height was as shown in Fig. 1. Points are *Rht* or *rht* genotype  $\times$  variety means over 5 sites  $\times$  4 replicate blocks.

The genetic backgrounds  $H \times H$ ,  $W \times W$ ,  $B \times B$  (intra-varietal),  $H \times W$ ,  $H \times B$  and  $B \times W$  (inter-varietal) were each represented by an *rht* line and ten different *Rht* genotypes (Table 1). For analyses of plant height and yield components it was found that *Rht/rht* genotypes could be conveniently divided into 5 groups in decreasing order of plant height as follows:

- i) *rht1/rht1 rht2/rht2*
- ii) *Rht1/rht1 rht2/rht2; rht1/rht1 Rht2/rht2*
- iii) *Rht1/Rht1 rht2/rht2; Rht1/rht1 Rht2/rht2; rht1/rht1 Rht2/Rht2*
- iv) *Rht1/Rht1 Rht2/rht2; Rht1/rht1 Rht2/Rht2; Rht3/rht1 rht2/rht2*
- v) *Rht3/Rht1 rht2/rht2; Rht3/rht1 Rht2/rht2.*

Each of these groups was represented equally in the 3 intra-varietal and the 3 inter-varietal backgrounds (Figure 4). No consistent differences were detected between different *Rht* combinations within (*Rht*  $\times$  background) groups. Comparisons between intra- and inter-varietal hybrids allowed estimation of mean heterosis at each level of *Rht* dosage as:

Mean heterosis = Mean of inter-varietals – Mean of intra-varietals.

This difference is equivalent to mean heterosis over mid-parents.

The obvious dosage effects of different *Rht* alleles on mean plant heights of intra- and inter-varietal hybrids (Figure 4a) show that different combinations of *Rht* genes can be exploited to generate near-continuous variation in height of F<sub>1</sub> hybrids, without relying on favourable combinations of minor polygenes. The stature of hybrids can thus be optimised by choosing parents carrying appropriate *Rht* alleles. Plant height of inter-varietal hybrids was increased by an average 3.9% heterosis over mid-parents, although this effect was less marked in group iv), with one dose of *Rht3* or three of (*Rht1* or *Rht2* ).

Heterosis was not evident for harvest index but increasing severity of *Rht* dwarfism led to improved harvest index, up to a maximum of 48% in the extreme dwarf *Rht* groups iv) and v) (Figure 4b).

Mean mid-parent heterosis for grain yield per square meter was 3.5%, but varied according to *Rht* genotype (Figure 4c). Maximum heterosis was realised among inter-varietal hybrids in *Rht* group iv). These hybrids also gave maximum yields, equivalent to those of the taller groups ii) and iii). Yield was substantially reduced in the tallest (group i) and shortest (group v) genotypes.

In comparisons between individual *Rht* × variety/inter-variety means the effects of heterozygosity for *Rht* genes can be separated from those of heterozygosity for genetic background. Background heterosis over high-parent is estimated as the difference between a single inter-varietal hybrid and the better of the two corresponding intra-varietals at the same *Rht* level. This estimate is not necessarily the same as a direct comparison between the actual parental inbreds used to produce a cross, e.g., the hybrid H × B *Rht1/rht1 rht2/rht2* can be produced either from H *Rht1* × B *rht* or from H *rht* × B *Rht1* and the direct estimate of heterosis, hybrid versus the true parents, is confounded with *Rht* and *Rht* × variety effects.

Out of 15 comparisons (3 inter-varietal combinations × 5 *Rht* levels) inter-varietals showed yield heterosis over best "parental" intra-varietals in 8 cases, and heterosis over mid-parent in 11 cases.

No heterosis was observed for the number of grains per ear, although this character varied markedly due to additive effects of *Rht* alleles (Figure 4d). This increased grain number is a commonly observed effect of the *Rht* genes (GALE, YOUSSEFIAN 1985).

The most marked and consistent component of heterosis for yield was a 7.4% increase in mean grain weight of inter-varietal hybrids relative to their intra-varietal equivalents (Figure 4e). This differential was maintained over all *Rht* genotypes and high-parent heterosis was present in eight out of fifteen comparisons. No hybrids were significantly lower than mid-parent. This effect was in opposition to the reducing effects of *Rht* alleles on the same character.

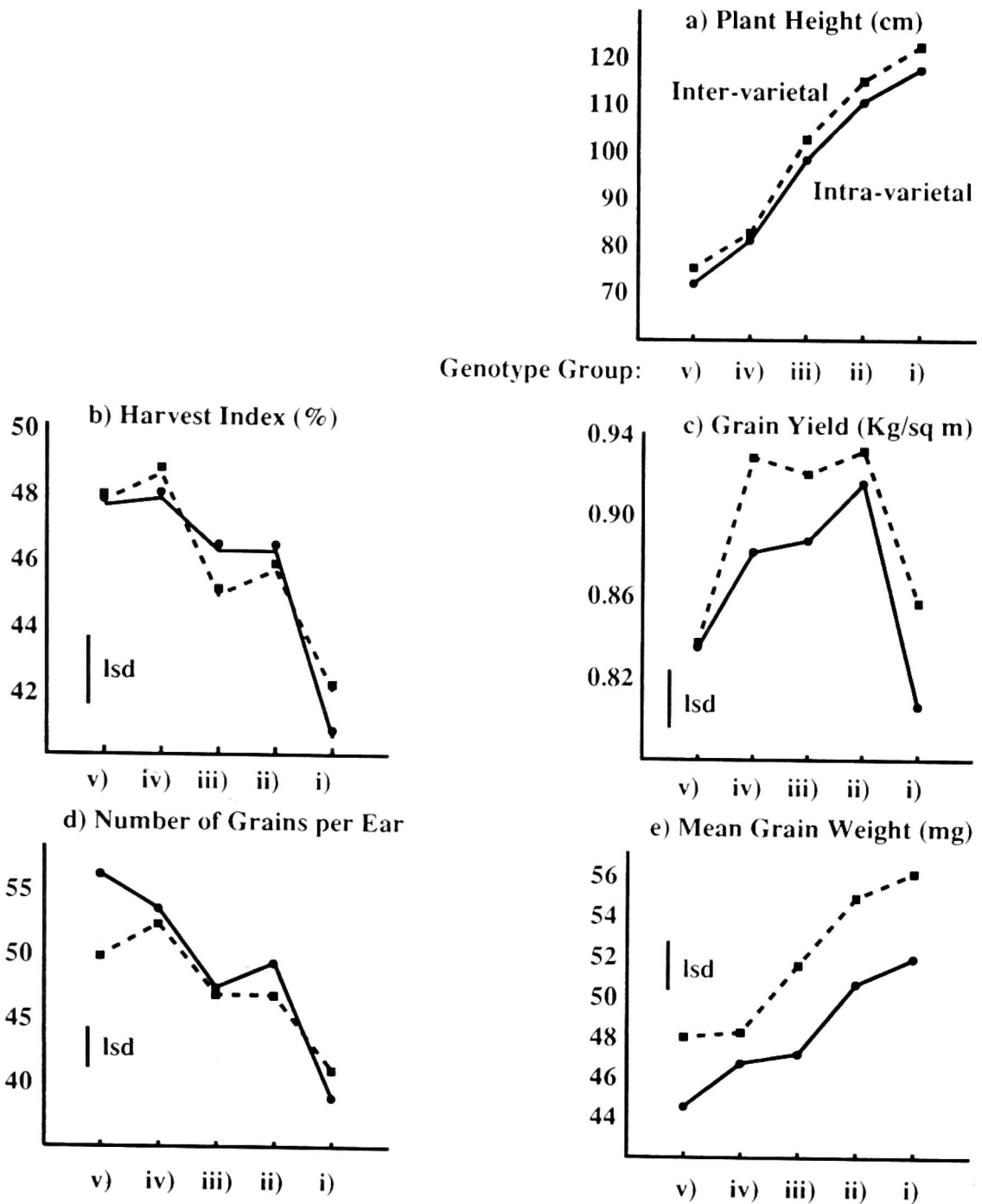


Figure 4. Plant heights and yield components of intra-varietal and inter-varietal F<sub>1</sub> hybrids carrying different combinations of *Rht/rht* alleles

Note: *Rht/rht* genotypes in groups i) to v) are described in the text. Dashed lines show means of inter-varietal hybrids, solid lines show means of intra-varietal hybrids with equivalent *Rht* dosage. Vertical bars denote least significant differences for yield components, all height differences were significant.

However, the reduction in grain weight due to adding a single *Rht* allele was easily overcome by hybrid heterosis.

In summary, the *Rht1*, *Rht2* and *Rht3* dwarfing alleles show mainly additive genetic effects on plant height, with (*Rht1*) = (*Rht2*), and (*Rht3*) = 3 × (*Rht1*). The resulting decreases in plant height are associated with proportional increases in harvest index and in the number of grains per ear. Grain size (mean weight) is inversely related to grain number, so that the overall result on grain



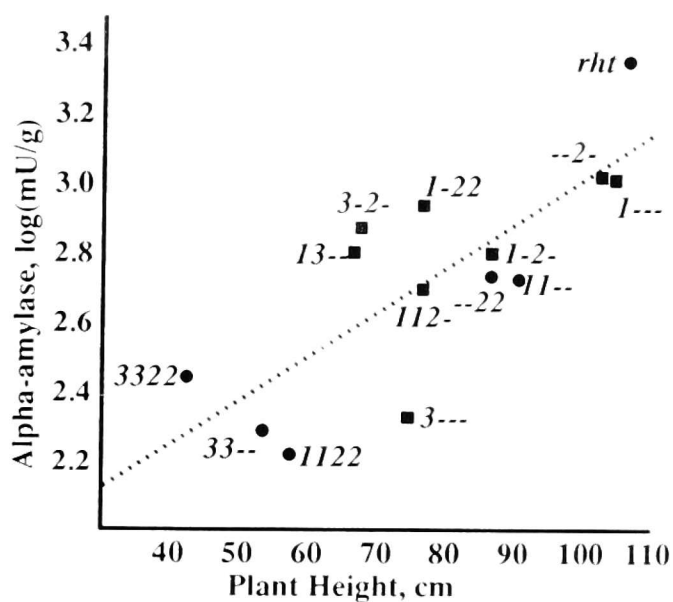
yield depends on the balance between the increase in grain number and the decrease in grain size. The main component of yield heterosis in F<sub>1</sub> hybrids is a marked increase in grain size, which can be combined with *Rht*-induced high grain number to generate maximum yield.

### Inhibition by *Rht* alleles of premature $\alpha$ -amylase synthesis in ripening grains of Maris Huntsman

Enzyme contents in hand-cleaned, ungerminated grains from Maris Huntsman inbreds and intra-varietal F<sub>1</sub> hybrids are shown in Figure 5. Premature production of  $\alpha$ -amylase during ripening is an important defect of grain quality in this variety and many other high-yielding wheats.

Figure 5.  $\alpha$ -amylase activity in ripe ungerminated grains plotted against plant height for Maris Huntsman isogenic inbreds and intra-varietal F<sub>1</sub> hybrids

Note: Homozygotes (circles) and heterozygotes (squares) carried the *rht* (-) and *Rht* (numbers) alleles indicated next to each point. Points are means over 4 replicate blocks, and the dotted line shows the regression of enzyme activity onto plant height (from FLINTHAM 1990).



Increasing severity of dwarfism was correlated with progressive reductions in enzyme activity, although the only genotypes with low enough activity for breadmaking were the extreme dwarf inbreds and the *Rht3* × *rht* F<sub>1</sub>. The latter genotype was the only one in which adequately low  $\alpha$ -amylase activity was combined with agronomically practical plant height (stands shorter than about 70 cm can be difficult to combine and, on the basis of results above, are unlikely to give satisfactory yields of grain). *Rht3* is thus the allele of choice for controlling  $\alpha$ -amylase levels in high-yielding hybrid wheats.

## Conclusions

Although CHA hybrids have not been adopted on a large scale, F<sub>1</sub> wheats may yet have an important contribution to make in maintaining high yields in

the face of reduced inputs. The stable performance expected of heterozygotes might be an additional advantage, as would the ability to accumulate multiple dominant disease resistance alleles, and the inhibition of  $\alpha$ -amylase production by *Rht3*. With *Rht* genes common in almost all breeding programmes the  $F_1$  breeder can by careful management maximise the benefits available from different alleles. The yield advantages of *Rht* wheats are likely to be most marked in high-yielding environments and the *Rht1* and *Rht2* alleles will undoubtedly continue to make important contributions to grain supplies.

The choice of dwarfing allele for breeding high-yielding wheats depends on the genetic background in which it is to be exploited. Over sites examined in this study *Rht* alleles generally improved yields relative to *rht* controls, except in the more extreme dwarfs. Yield advantages of *Rht* dwarfs were a consequence of reduced partitioning of assimilate into stem growth, allowing a greater proportion of total biomass to be recovered in the grains. Prior to anthesis this resulted in the development of a greater number of competent florets per ear, resulting in increased number of grains (given satisfactory grain set).

Highest yields of grain are achieved when adequate assimilate is available to fill these extra grains, as in heterotic  $F_1$  hybrids. *Rht3*  $\times$  *rht* inter-varietal hybrids were among the highest-yielding genotypes. An added advantage of *Rht3* as a source of dwarfism could arise from its exceptionally marked inhibition of preharvest damage to breadmaking quality. The *Rht3* allele has reduced preharvest accumulation of  $\alpha$ -amylase in trials carried out over several years including several where severe damage was otherwise widespread. This study indicated that the inhibition of enzyme production was at least partially dominant, providing effective resistance in  $F_1$  *Rht3/rht* hybrids.

The overdominance observed for yield of *Rht3/rht* heterozygotes results from partial dominance for the dwarfing effect, coupled with the general curvilinear relationship between plant height and grain yield shown in Figures 1 and 3. Since plants of intermediate heights give highest yields, the semidwarf  $F_1$  from crossing between extreme *Rht3* dwarf and tall *rht* genotypes can be expected to outyield either parent.

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