

The Tom Thumb dwarfing gene *Rht3* in wheat

2. Effects on height, yield and grain quality

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Received March 16, 1983

Communicated by R. Riley

Summary. The effects of the 'Tom Thumb' *Rht3* dwarfing gene in wheat on plant height, yield components and grain quality in field trials of random inbred lines from two 'Minister Dwarf' (*Rht3*) \times *rht3* crosses are described. Limited genetic increases in *Rht3* plant height, up to 70 cm, were achieved by incorporating genes from the extremely tall variety 'April Bearded'. Amongst lines from the higher yielding cross, the dwarfing gene did not reduce grain yield but was associated with an increase in grain number of over 25%. Although *Rht3* reduced grain protein content by up to 0.8%, breadmaking quality, as measured by SDS sedimentation values and baking tests, was not affected. A controlled environment experiment with near-isogenic *Rht3* and *rht3* lines indicated that reduced grain size in the dwarfs is a competitive response to the increase in fertility rather than a primary effect of the dwarfing gene.

Key words: Wheat – Dwarfism – Yield – Quality

Introduction

The discovery that the 'Tom Thumb' dwarfing gene, *Rht3* inhibited the release of the enzyme α -amylase in germinating grains (Gale and Marshall 1973) has led to a re-evaluation of the gene's potential in commercial varieties. The use of wheat grists containing high levels of the enzyme, usually caused by preharvest sprouting, results in deleterious effects both in commercial bread (Chamberlain et al. 1981) and noodle making (Moss 1980) processes. *Rht3* could thus provide a simple genetic means of reducing this source of damage to wheat quality.

The feasibility of this approach has been tested first by characterising the extent to which *Rht3* could

provide adequate protection against preharvest sprouting damage in the field and second by assessing whether the gene has any other significant pleiotropic effects that might affect its suitability for incorporation in commercial varieties.

The gene has been shown to reduce levels of α -amylase in field trials both in years of exceptionally high and very low observed preharvest sprouting damage (Flintham and Gale 1982). This reduction of about 80% should be adequate to provide protection in most years and in most genetic backgrounds.

This paper reports the effects of *Rht3* on plant height, the possibility of modifying the extreme dwarfism conferred by the 'Tom Thumb' allele, and the pleiotropic effects of the gene on yield components and other components of breadmaking quality besides α -amylase content of the grain.

Genotypes

Random inbred lines

Random F_2 plants from the crosses 'Minister Dwarf' (MD, *Rht3*) \times 'April Bearded' (AB) and MD \times 'Cappelle-Desprez' (CAP) were classified retrospectively as homozygous *Rht3*, homozygous *rht3*, or *Rht3/rht3* by testing seedling sensitivity to gibberellic acid as described by Gale et al. (1975). Outcrossing was prevented up to F_3 while F_4 and F_5 generations were produced by self-pollination under field conditions.

Near isogenic lines

Lines homozygous for *Rht3* and *rht3*, in a genetic background expected to be 15/16ths that of AB (except for loci linked to *Rht3*), were produced by backcrossing and MD \times AB F_1 three times onto the tall parent while retaining the dwarfing gene by selecting for gibberellin insensitive seedlings at each generation. *Rht3* and *rht3* homozygous lines were derived by selfing third backcross plants (Fig. 1).

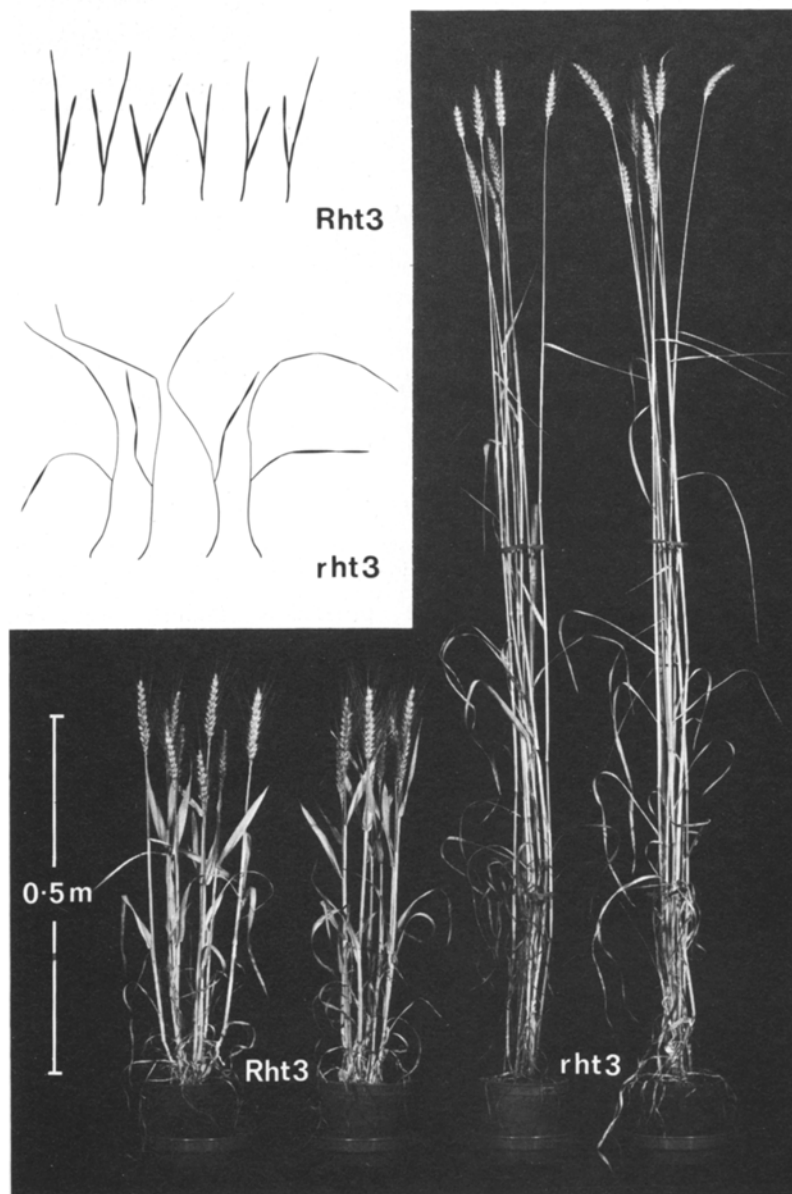


Fig. 1. Mature plants and GA₃-treated seedlings of *Rht3* and *rht3* near-isogenic lines. *Note:* The GA responsive (*rht3*) and insensitive (*Rht3*) seedling phenotypes are shown (inset). Growth conditions 3 weeks treatment with 10 ppm GA₃ at 18 °C

The experiments

Single-row trials

Three trials were autumn sown at 10 cm spacing within rows and 30 cm between rows. Basic fertilizer (40 kg N ha⁻¹) was applied each spring. All plants were scored at maturity for height from soil level to the tip of the tallest ear (excluding awns).

Twenty-three homozygous dwarf and 23 homozygous tall random lines from the MD×AB cross were each represented in F₃ by single rows of 11 plants in two randomised blocks and in F₄ by five random family rows in separate dwarf and tall sub-blocks. Parents were included in duplicate in each trial.

Thirty-three *Rht3* and 33 *rht3* random F₄ lines from MD×CAP were grown in separate dwarf and tall stands in two randomised blocks. In each block tallest tillers of five mature plants per line were scored for yield components and

bulk grain samples per line were assessed for total nitrogen content (Starr and Smith 1978) and wholemeal sodium dodecyl sulphate (SDS) sedimentation value (Axford et al. 1979).

Drilled MD×CAP F₅ plots

Eight *Rht3* and eight *rht3* random F₅ lines plus duplicates of parents were sown in plots at 400 grains m⁻² in three randomised blocks. Individual plots of 2.5 m×1 m (seven drills) were arranged in dwarf and tall sub-blocks separated and surrounded by *Rht3* guards. Fertilizer was applied as above and *rht3* plots were supported against lodging using 5 cm² plastic mesh.

At harvest, ends and outside drills of each plot were discarded and sheaves were cut from the central 0.833 m² to within 2 cm of soil level. Each plot sheaf was scored for harvest index, grain yield, mean grain size (from 500 grains)

and number of grains (yield/grain size). A 1.5 kg grain sample (14.5% moisture) from each line was ground and refined on a Buhler mill. The flours were scored for nitrogen content and sedimentation value. Loaves made by a small-scale Chorleywood process (Chamberlain et al. 1962) were scored for displacement volume.

Controlled environment experiment

Seedlings of the near-isogenic *Rht3* and *rht3* lines were grown for eight weeks at 3°C in 8 h days, then transferred to 18 h days at 15°C with 150 W m⁻² light, 10°C at night. Two controlled environment cabinets were used, one for each genotype. Eighty plants in each cabinet were spaced 16 cm apart in a 10×8 plant grid. Eight random plants from the centre of each cabinet were allocated to each of the following four treatments, designed to vary the number of grains per plant:

1. control;
2. removal of florets three days after anthesis to leave all tillers with only basal and second florets of twelve central spikelets per ear;
3. removal, at emergence, of all tillers after the first to emerge, leaving two shoots per plant;
4. a combination of the degrading and detillering treatments to leave all treated plants with a maximum of 48 grains per plant.

Yield, grain size and grain number was scored for each plant. Individual grain weights were measured for all grains on the two tallest shoots and mean nitrogen contents were measured in grains from the basal and second florets of the central spikelets of the same spikes.

Results

Potential for increasing Rht3 plant height

In the homozygous condition, *Rht3* reduces plant height to about half of that of comparable *rht3* lines, (Fig. 1). The *Rht3* groups from both crosses were examined for evidence of genes capable of ‘promoting’ plant height to an agriculturally more acceptable level in the presence of the dwarfing gene.

Table 1 shows that some variation is available in both crosses and that the height-promoting effects derived from the taller parent (AB) are the more effective. In both crosses *Rht3* was associated with reduced variation in plant height. The F₃/F₄ regressions (Fig. 2) demonstrate that these effects are highly heritable, however, the tallest of these lines bred true at only just above 70 cm.

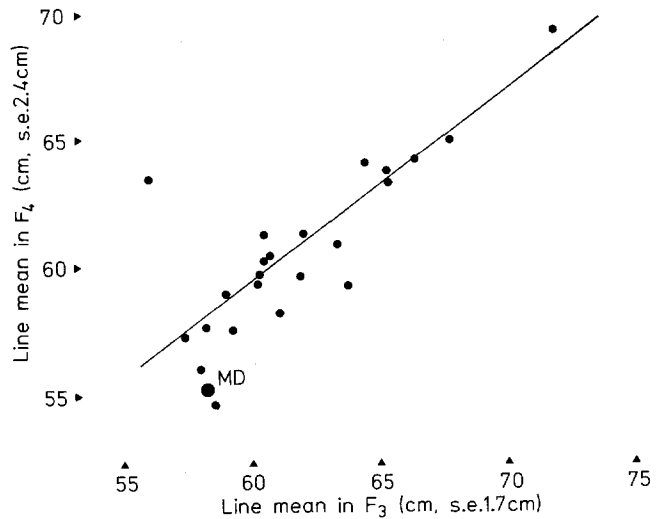


Fig. 2. Heritable variation for plant height amongst random *Rht3* lines from ‘Minister Dwarf’ (MD) × ‘April Bearded’. Note: Coefficient of correlation of line means $r_{F_3/F_4} = 0.792$ ($P < 0.001$)

A further incentive to increasing *Rht3* plant height is provided by the positive height-yield relationships found among semi-dwarf random lines by Gale and Law (1977) and Gale (1979). A similar analysis of tallest tiller yields of the higher yielding MD×CAP F₄s (Fig. 3) shows that the same association pertains among the *Rht3* lines.

Effects of Rht3 on yield components and grain quality

Yield components. The parental, random *Rht3* and random *rht3* means for grain yield and its components in F₄ spaced-plant and F₅ drilled field trials from the MD×CAP cross are given in Tables 2 and 3.

The presence of the dwarfing gene had no adverse effects on grain yield per tallest tiller in the spaced plants or per unit area in drilled plots in either the random lines or the parents.

Dwarf lines showed consistently high fertility and reduced grain size in both trials. In tallest tillers of

Table 1. Variation in plant height in homozygous dwarf and tall random lines derived from two *Rht3* × *rht3* crosses

		Parents		Random lines		
			<i>n</i>	Mean	Range	Variance ^a
MD × AB (F ₃)	<i>Rht3</i>	58.2 ± 0.8	23	61.3	55.7 – 71.9	275
	<i>rht3</i>	153.5 ± 0.8	23	129.5	112.2 – 141.2	1709
MD × CAP (F ₄)	<i>Rht3</i>	60.6 ± 0.7	33	58.7	51.5 – 66.2	117
	<i>rht3</i>	106.6 ± 0.9	33	108.2	94.2 – 124.7	660

^a Variances are the between line, within *Rht* genotype mean squares

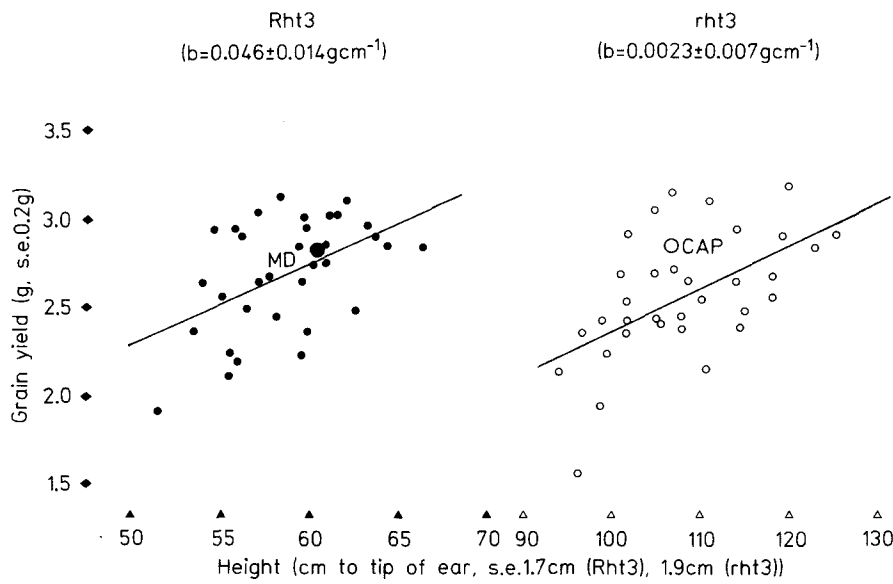


Fig. 3. Association of tallest-tiller grain yield and height amongst *Rht3* and *rht3* random F_4 lines from 'Minister Dwarf' (*MD*) \times 'Cappelle-Desprez' (*CAP*). Note: The *rht3* (o) height scale has been compressed such that σ_{rht3} compares with σ_{Rht3}

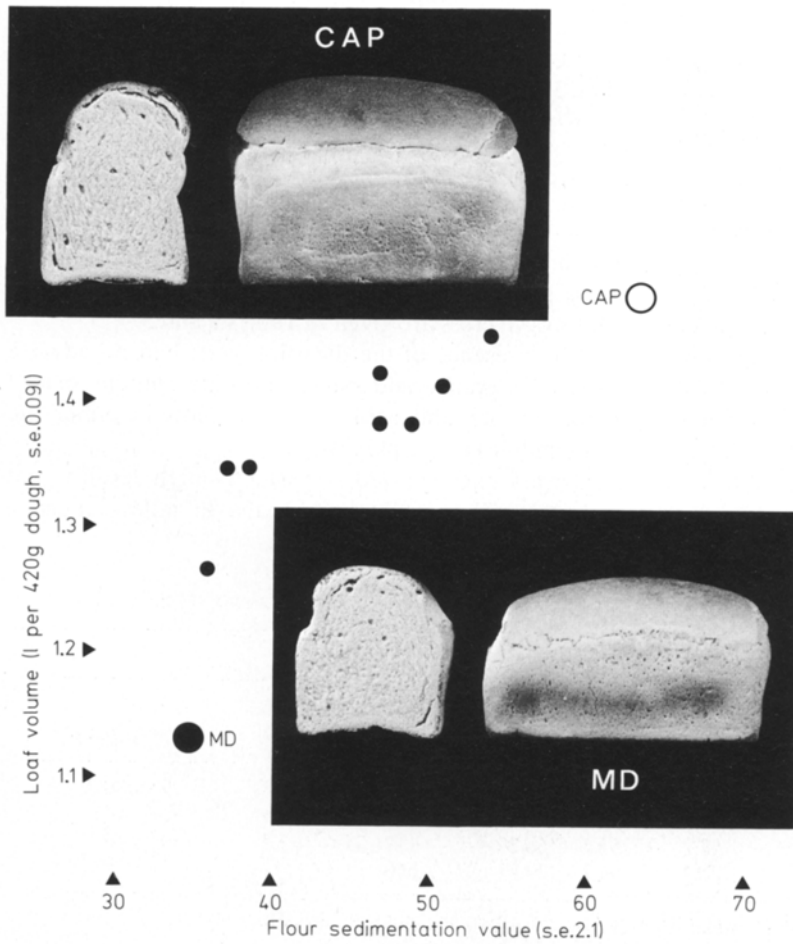


Fig. 4. Baking quality in 'Minister Dwarf' (*MD*) and 'Cappelle-Desprez' (*CAP*) and F_5 *Rht3* lines from *MD* \times *CAP* as measured by loaf volume and SDS sedimentation value. Note: Sedimentation values (line means over 3 blocks) are taken as an index of gluten quality, coefficient of correlation with loaf volumes $r = 0.834$, ***

Table 2. Tallest tiller yield components in F₄ *Rht3* and *rht3* random lines from 'Minister Dwarf' × 'Cappelle-Desprez'

	Parents		F ₄ lines		
	MD	CAP	<i>Rht3</i>	<i>rht3</i>	sed (p)
Ear yield (g)	2.97	2.71	2.68	2.54	0.17 (NS)
Spikelet no.	22.0	19.8	21.3	20.0	0.2***
Grains per ear	76.2	48.8	70.0	49.1	1.3***
Mean grain wt (mg)	39.0	55.6	38.1	51.4	1.2***

The standard errors (sed) and levels of significance relate to the difference between 33 *Rht3* and 33 *rht3* lines. NS not significant; *** $P < 0.001$

Table 3. Drilled plot yield components in F₅ *Rht3* and *rht3* random lines from 'Minister Dwarf' × 'Cappelle-Desprez'

	Parents		F ₅ lines		
	MD	CAP	<i>Rht3</i>	<i>rht3</i>	sed
Harvest index (%)	47.9	39.2	45.0	39.0	0.7***
Grain yield (Kg m ⁻²)	0.94	0.88	0.84	0.87	0.02 (NS)
Thousand-grain wt (g)	38.2	52.7	38.2	49.8	0.4***
Grain no. (m ⁻² × 10 ⁻³)	24.6	16.7	22.1	17.4	0.7***

Sed's and levels of significance relate to the differences between eight *Rht3* and eight *rht3* lines. Significance levels as in Table 2

Table 4. Grain nitrogen content and wholemeal sedimentation values in random F₄ lines from 'Minister Dwarf' × 'Cappelle-Desprez'

	Parents		F ₄ lines		
	MD	CAP	<i>Rht3</i>	<i>rht3</i>	sed
Nitrogen content (%)	2.24	2.47	2.29	2.43	0.03***
Sedimentation value	51.5	60.8	61.3	58.0	1.7 (NS)

*** Standard errors as for Table 2

Table 5. Plant yields and yield components in dwarf and tall near-isogenic lines at surgically controlled levels of grain fertility

Genotype treatment	<i>Rht3</i>			<i>rht3</i>		
	Grain yield g plant ⁻¹	Mean grain size (mg)	No. of grains plant ⁻¹	Grain yield g plant ⁻¹	Mean grain size (mg)	No. of grains plant ⁻¹
1. Control	10.9 ± 1.1	33.9 ± 1.4	322 ± 31	10.2 ± 1.0	37.0 ± 1.6	275 ± 28
2. Degraded	8.9 ± 0.8	43.6 ± 1.5	205 ± 16	7.7 ± 0.9	47.3 ± 1.8	163 ± 14
3. Detillered	6.9 ± 0.5	39.6 ± 1.4	174 ± 11	6.2 ± 0.6	42.7 ± 1.4	145 ± 9
4. Combined 2+3	2.4 ± 0.1	57.7 ± 1.3	42 ± 2	2.5 ± 0.1	54.5 ± 2.2	45 ± 2

For details of treatments and genotypes see text. All values (± 95% confidence limits) are means of 8 plants

spaced plants the fertility of dwarf ears was 43% higher than in tall but was compensated by a 26% reduction in grain size. The increase in grain number was almost entirely due to increased fertility per spikelet. Qualitatively similar disturbances in *Rht3* yield components were found in the drilled trial, dwarf lines producing 27% more, but 23% smaller, grains than the comparable tall.

Grain quality. The role of *Rht3* in protecting grain quality in wheat exposed to pre-harvest rainfall has been discussed previously (Flintham and Gale 1982). In unsprouted harvests, grain protein content and quality are among the most important components of breadmaking quality. If effective use is to be made of *Rht3* resistance to sprouting damage the dwarfing gene must be compatible with these other aspects of breadmaking quality.

Of the two parents, CAP has considerably better baking potential and gluten quality than MD, however Table 4 shows that, in the F₄ spaced plants, gluten quality, as measured by the SDS sedimentation value, was not reduced in the *Rht3* lines relative to the tall. This apparent independence of breadmaking quality from the dwarfing gene was confirmed in the flour samples from the drilled F₅ trial where the sedimentation values and loaf volumes of *Rht3* lines, which were positively related as expected, spanned the parental difference (Fig. 4). *Rht3* thus appears not to affect the potential for high gluten and baking quality.

Although *Rht3* did not affect the quality of grain gluten, total grain nitrogen contents were consistently reduced in dwarf random lines. In the F₄'s this reduction amounted to a loss of 0.8% protein by weight. In white flours from the F₅ trial the equivalent reduction was 0.4%.

The basis of reduced size and nitrogen content of Rht3 grains

In all of the experiments described above, *Rht3*, while showing a neutral effect on total grain yields, was

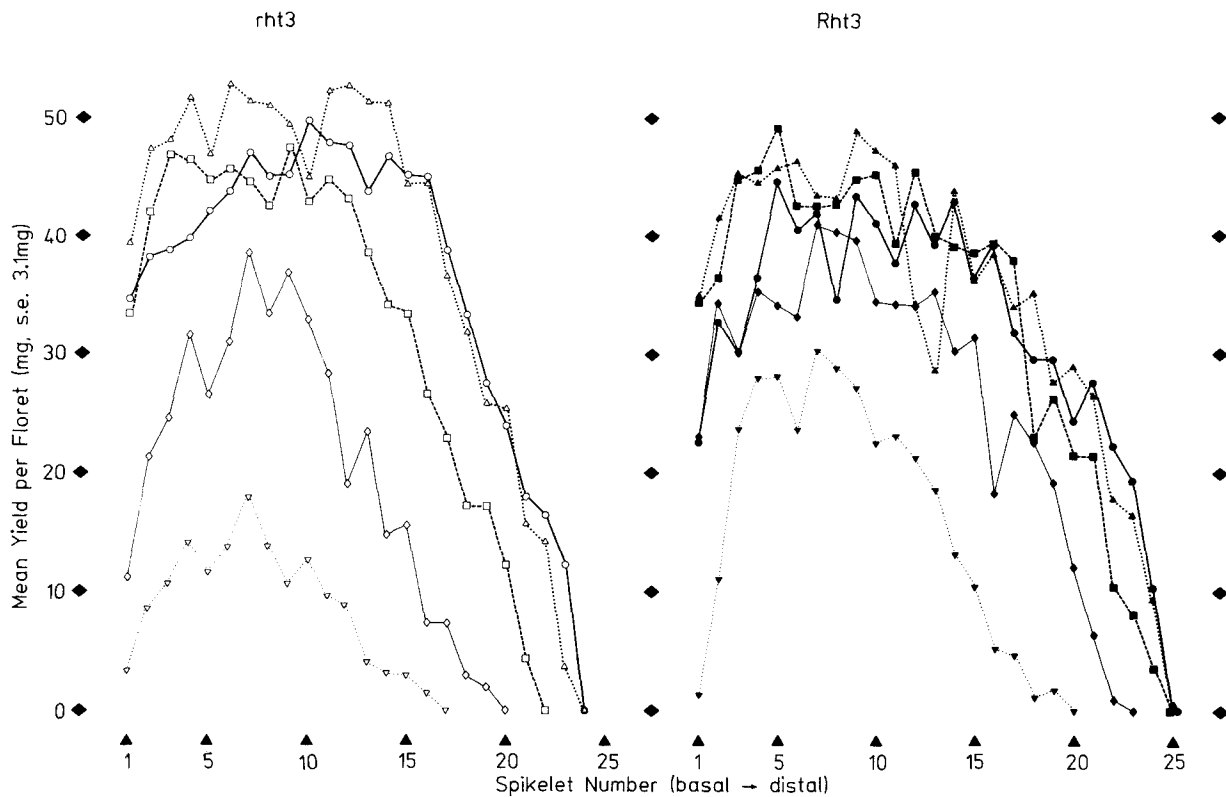


Fig. 5. Individual grain yields in ears of near-isogenic *rht3* and *Rht3* lines. Note: Mean floret yields were obtained from 16 ears per genotype for basal (○, ●), second (△, ▲), third (◇, ◆), fourth (□, ♦) and higher order florets (▽, ▼)

consistently associated with increased grain number to grain weight ratio. Also grain nitrogen contents, and hence nitrogen yields, are consistently decreased in lines carrying *Rht3*. To investigate possible competitive effects of increased fertility on grain size and nitrogen content, surgical treatments were applied to tall and dwarf near-isogenic lines to artificially reduce the fertility differences between them.

As in the field grown experiments *Rht3* had no effect on overall plant yield either in the intact plants or at the lower yield levels induced in the surgically treated plants. Table 5 shows that the *Rht3* plants had higher grain numbers and lower mean grain weights in the three treatments (1, 2 and 3) in which grains per ear or tiller numbers were not both artificially controlled.

The difference in grain numbers in untreated ears was, as in the field trials, due mainly to increased fertility within *Rht3* spikelets. Figure 5 shows an analysis of individual grain weights from plants in treatment 3, which had two intact ears each.

Two differences between the genotypes are clear. Firstly, although individual floret yields decline distally within spikelets generally, this decline is significantly reduced in the *Rht3* ears, resulting in a narrower range of grain sizes within spikelets. This effect is similar to that described by Radley and Thorne (1981), in a

varietal comparison involving *Rht2*. The second genotypic difference concerns the decline in floret yields from the highest-yielding spikelets in the middle of the ear to the smallest, most distal and lowest yielding terminal spikelet. The *Rht3* ears show a more gradual yield decline in this distal portion of the spike and have on average one more fertile spikelet than the *rht3* ears.

The relatively high contributions of small grains from distal florets to *Rht3* yields may be partly responsible for the overall reduction in mean grain size, however, the size of grains in the basal higher yielding florets is also reduced.

The relationship between grain size in the highest-yielding florets and grain number per plant is shown in Fig. 6. The consistent, and linear, increase in size with decreasing grain number, irrespective of whether the fertility is reduced by genotype (*rht3* vs *Rht3*) or artificially (treatment differences), indicates that competition between florets for a limited supply of assimilates is an adequate explanation of reduced grain sizes in the dwarfs. Certainly when the fertility of both genotypes is reduced to a constant level (treatment 4) *Rht3* grains grow as large as equivalent *rht3* grains.

The relationship between grain number and nitrogen contents shown in Fig. 6 is similar in that the genotype difference in grain protein level is removed in

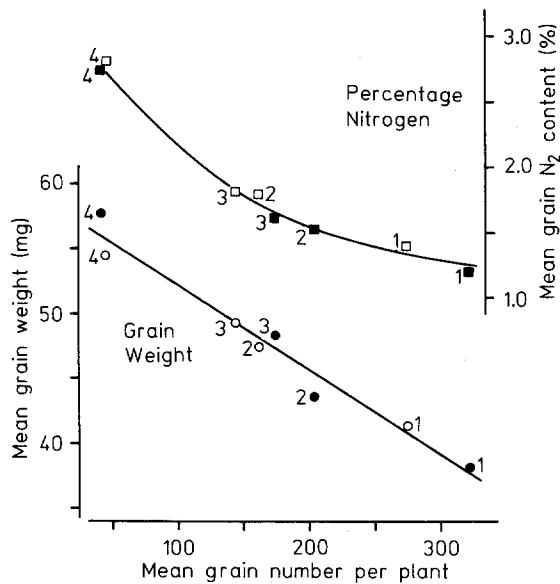


Fig. 6. Effects of detillering and degrading treatments on grain number, size and nitrogen content in *Rht3* and *rht3* near-isogenic lines. *Note:* The degrading and detillering treatments (2,4) are described fully in the text. Grain weights are means of basal and second florets in spikelets 5 to 16 on main shoots and first tillers of *Rht3* (●, ■) and *rht3* (○, □) plants

treatment 4. In all other treatments *Rht3* reduced percent nitrogen content. Since total grain yields were unaffected by genotype, this represents a direct effect of *Rht3* on protein yield per plant.

Discussion

Although *Rht3* has been available to breeders for many years (Dalrymple 1978) the gene has generally been considered to have too severe an effect on plant height for use in commercial varieties. Modern harvesting techniques require a crop at least 70 cm tall for maximum yield return with minimum danger to machinery. Hence, although a few *Rht3* wheats have been produced, e.g. 'Tordo' and 'Topo' (CIMMYT 1968) this dwarfing gene has been neglected by breeders in favour of the less potent semi-dwarfing genes derived from 'Norin 10', *Rht1* (allelic with *Rht3* on chromosome 4A, Gale and Marshall 1976) and *Rht2* (carried at a homoeologous locus on chromosome 4D, McVittie et al. 1978).

The close genetic and physiological relationship of *Rht3* with the successful 'Norin 10' semi-dwarfing genes suggest that the 'Tom Thumb' gene could also be used as a basis for stiff straw and high yield in commercial breadwheats. Although the 'Tom Thumb' gene does cause excessive dwarfism, plant height can be increased while retaining *Rht3* by introducing height-promoting

genes at other loci. The tallest *Rht3* line obtained in these experiments, from a cross with the long-stawed variety 'April Bearded', was only 70 cm tall under near ideal growing conditions, however, the gene(s) responsible were easily fixed in the homozygous condition at F₃. Further genetic increases in *Rht3* plant height might be obtained by introducing either more additive, height promoting genes from other tall varieties, but the observed reductions in variation for height in *Rht3* populations suggest that such genes will be less potent in the dwarfs than in standard wheats.

The incentive for this reappraisal of 'Tom Thumb' wheats is the reduction in α -amylase levels produced during preharvest sprouting (Flintham and Gale 1982). This pleiotropic effect of *Rht3* would be sufficient to significantly reduce this recurrent cause of damage to large proportions of bread and noodle wheat crops (Derera 1980). Examination of other grain quality components revealed that the gene causes a small reduction in grain nitrogen level, similar to that reported for *Rht2* by Gale (1979). Apart from this deleterious effect, *Rht3* was found to be otherwise fully compatible with good gluten and breadmaking quality.

In both spaced-plant and drilled conditions *Rht3* had no adverse effects on grain yield, although overall biomass was reduced in dwarf plots. The yields from *Rht3* stands characteristically had higher grain number to grain size ratios than comparable tall stands. The increase in grain number is qualitatively similar to but more extreme than effects reported for *Rht2* (Gale 1979) and for *Rht1*, *Rht2* and *Rht3* in other experiments (Gale 1982).

Analysis of the effects of *Rht3* on the distribution of yield within ears indicates that increased grain number is a primary effect of the gene achieved via increased grain set in distal florets within spikelets. This suggests that the dwarfing gene reduces the dominance of the high-yielding basal florets during ear and grain development. Other indications that the GA-insensitive *Rht* genes interfere with apical dominance include the demonstration that wheats carrying these genes respond to GA application by increasing tiller production, as opposed to the reverse response characteristic of conventional tall varieties (Gale and Marshall 1975). Evidence for modified auxin responses in *Rht* dwarfs has been described by Romanova and Priluk (1975) in intact plants and by Flintham (1981) in excised coleoptiles. It seems likely that hormonal abnormalities in *Rht1* 2 and 3 genotypes extend beyond the GA response differences.

The increased grain set within *Rht3* spikelets was found to be responsible for the reduced grain size, both by increasing the proportion of small grains from distal florets and via competitive reduction in the size of the larger grains from basal florets. There was no evidence

for a direct effect of the gene on grain growth potential when fertility differences were artificially removed. The same experiment showed that *Rht3* does not directly affect the capacity of the grain to store nitrogen. Therefore the reduction in grain protein content is probably due to a reduction in nitrogen supply. Reduced protein yield may be a result of reduced biomass in dwarf stands providing a smaller source of nitrogen for grain-filling.

In conclusion, the results discussed here and by Flintham and Gale (1982) show that the 'Tom Thumb' gene could be incorporated usefully in future wheat varieties, particularly where pre-harvest sprouting tolerance is a major breeding objective. The problem of increasing *Rht3* plant height to an agriculturally acceptable level remains to be solved, however in the genetic backgrounds used here no significant adverse effects, apart from a one per cent reduction in protein content, were found on grain yield or quality.

Acknowledgements. We would like to acknowledge Geraldine Marshall for making available several of the genotypes used in the study, Carol Starr for carrying out the protein determinations and John Blackman for assistance with other grain quality tests. The senior author is indebted to the Home Grown Cereals Authority for support during the tenure of his post-graduate research fellowship.

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