EFFECTS OF HEIGHT REDUCING GENES ON YIELD IN BREAD WHEAT: OVERSEAS AND NEW ZEALAND RESULTS

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ABSTRACT

The effects of the Norin 10 semidwarfing genes *Rht1* and *Rht2* on grain yield have been studied in a number of overseas countries using specially developed lines. In most studies 1 gene dose semidwarf lines (genotypes *Rht1Rht1rht2rht2* or *rht1rht1Rht2Rht2*) produced the highest yields, but 2 gene dose lines (*Rht1Rht1Rht2Rht2*) yielded well in certain situations and 0 gene dose tall lines (*rht1rht1rht2rht2*) were best in an Israeli study. Within the 1 gene dose class *Rht1* lines outyielded *Rht2* lines in three studies, while the reverse was true in a fourth study. Environment and genetic background modify the effect of *Rht* genes.

Semidwarf cultivars carrying either *Rht1* or *Rht2* have been released in New Zealand, yet little is known about the comparative yields and adaptation of *Rht* genotypes in this country. We report on a comparison of 1 gene dose lines (*rht1rht1Rht2Rht2*) with shorter 2 gene dose lines (*Rht1Rht1Rht2Rht2*) in the Manawatu. The 1 and 2 gene dose lines were extracted from populations maintained as heterozygous for *Rht1* to the F_6 generation. In both years of the study the 1 gene dose lines outyielded the 2 gene dose lines. Spikelet fertility was enhanced by the 2 gene dose but grain size was reduced. The implications of these results for wheat breeding are considered.

Additional Key Words: Rht genes, semidwarf, GA insensitivity, yield components

INTRODUCTION

Over the past 20 years major yield increases have been achieved worldwide through the introduction of the semidwarfing genes *Rht1* and *Rht2*, from the Japanese cultivar Norin 10, into wheat breeding programmes. These genes were originally introduced to reduce lodging under high fertility conditions but are now known to increase yields even in the absence of lodging. Height reduction by Norin 10 genes is associated with a lack of shoot growth response to the hormone gibberellic acid. The first semidwarf cultivar released in New Zealand was Karamu which substantially outyielded local standards in the 1970s. The semidwarf habit in most cultivars is controlled by only a single gene, either *Rht1* or *Rht2*. Semidwarf cultivars carrying both *Rht1* or *Rht2* are uncommon (see survey by Gale *et al.*, 1982).

When the two *Rht* genes are combined, as can happen when two semidwarf cultivars are crossed, four homozygous height genotypes are possible; viz. the 2 gene dose dwarf *Rht1Rht1Rht2Rht2*, the 1 gene dose semidwarfs *Rht1Rht1rht2rht2* and *rht2rht2Rht1Rht1*, and the 0 gene dose tall *rht1rht1rht2rht2*. In the quest for higher yields, 1 gene dose cultivars have been released in New Zealand. Ten of the 16 recently released and recommended cultivars listed in Table 1 are 1 gene dose semidwarfs. The remaining six recent releases are 0 gene dose lines ("talls") while 2 gene dose cultivars are not yet represented in New Zealand. With the predominance of 1 gene dose semidwarf releases it is timely to ask if this class is best for all of our wheat growing areas. Overseas research reviewed later in this paper suggests that there may be New Zealand environments where either 2 or 0 gene dose lines will outperform 1 gene dose semidwarfs. At the moment very little information is available to breeders on the comparative adaptation and yielding abilities of *Rht* genotypes in this country. This study compared grain yields of closely related 1 gene dose lines (*Rht2*) and 2 gene dose lines (*Rht1* and *Rht2*) in a North Island environment.

TABLE 1: Classification of cultivars recently released in New Zealand for Norin 10 semidwarfing genes.

Semidwarfing gene dose			
0		1	
		Rht1	
Konini	1981	Karamu	1972*
Abele	1983	Hotspur	1985
Crossbow	1983		
Kotare	1984	**Rht2**	
Weka	1984	Rongotea	1979
Pegasus	1985	Oroua	1979
		Tiritea	1981
		Bounty	1982
		Otane	1984
		Rht?†	
		Advantage	1982
		Newbury	1985
		Wembley	1985

*Year of release.
†Identity of *Rht* gene yet to be determined.

REVIEW OF OVERSEAS STUDIES

In comparing the yield performance of *Rht* genotypes the confounding effects of differences in genetic background must be avoided and this has required the development of special lines for trial work. Two approaches have been used overseas to remove genetic background effects. The first has been to develop lines that are isogenic for the *Rht* genes in a locally adapted cultivar background. The second approach has been to develop groups of random lines from hybrid populations segregating for *Rht1* and *Rht2*. Background genetic effects are assumed to be nullified in this case (Gale, 1979).

Gene dose effects have been studied in four countries. In most instances 1 gene dose semidwarf lines have outyielded 0 gene dose tall and 2 gene dose dwarf lines. Gale (1979) and Gale and Youssefian (1983) in England and O'Brien and Pugsley (1981) in Australia compared 0 and 1 gene dose random lines and showed an 8-20% yield advantage for the 1 gene dose class. Using isogenic lines in Washington State, Allan and Pritchett (1980) obtained relative yields of 100, 116, and 109 for the 0, 1 and 2 gene dose classes respectively. Allan (1983), also in Washington State, used isogenic lines to study gene dose effects in six parental backgrounds at six sites over two years. When averaged over all populations and tests the relative yields of the gene dose classes in this study were similar to those of Allan and Pritchett (1980). However, in Allan's (1983) study there were very significant gene dose x environment interactions. At sites with high yield potential and lodging, the 1 and 2 gene dose classes had large and similar yield advantages over the 0 gene dose class while, at sites with low yield potential, no such advantage existed. Further, under low rainfall/shallow soil conditions Allan found that the 2 gene dose lines outyielded the 1 gene dose lines. Gene dose x parental background interactions were also evident in Allan's (1983) study. The 1 gene dose enhanced yield relative to 0 gene dose in both short and tall backgrounds while the 2 gene dose was beneficial only in tall backgrounds.

In Israel, Pinthus and Levy (1984) obtained rather different gene dose effects from those of Allan (1983). Using random lines, Pinthus and Levy found that 0 gene dose lines were the highest yielding class. Relative yields were 100, 88 and 64 for the 0, 1 and 2 gene dose classes respectively. While the results of Pinthus and Levy (1984) are in apparent conflict with those of Allan (1983), it is necessary to take into account differences between the two studies in environment and genetic material used. There were other experimental differences as Allan used four row plots and measured whole plot yields while Pinthus and Levy used single row plots and measured yields on 10 main-shoot spikes per plot.

Four studies have compared *Rht1* lines with *Rht2* lines within the 1 gene dose class. Gale and Youssefian (1983) in England, Pinthus and Levy (1984) in Israel and Allan (1970) in Washington found that *Rht1* lines outyielded *Rht2* lines by 4-15%. In the Burt cultivar background, Allan (1970) found that *Rht1* was better adapted to dry conditions than *Rht2* as in a dry year the yield advantage for *Rht1* lines was 15% while in a wetter year it was only 6%. Interestingly, the yield ranking of the two genotypes was reversed in other work in Washington by Allan and Pritchett (1980) which involved a different genetic background and a different season. In the Omar cultivar background (taller than Burt) *Rht2* lines outyielded *Rht1* lines by 12%.

From the overseas results it can be concluded that the *Rht* gene dose classes can be ranked 1 >2 >0 for yield potential and that within the 1 gene dose semidwarf class, *Rht1* is superior to *Rht2* in yield enhancement. However, it is clear that environment and genetic background can modify these rankings.

MATERIALS AND METHODS

Production of 1 and 2 gene dose lines

All lines were derived from a cross of the two modern semidwarf lines 61,05 (=RAVEN/1966 ISWRN430) and TRIPLE DIRK/2*KARAMU. The sources of *Rht1* and *Rht2* were Karamu and 1966 ISWRN430 respectively. From an F_2 population of plants segregating for height, 75 individuals from the middle of the height range were extracted to obtain 75 F_3 populations. At F_3, 31 populations segregating for height were chosen and from each several midheight plants were selected to obtain replicate lines at F_4. This policy of only taking midheight plants from populations segregating for height was continued at F_4 and F_5. At F_6 four families (traceable to four F_2 plants), each with 3-6 F_5-derived selections, were chosen but now a pair of "short" and "tall" plants were extracted and midheight segregates discarded. This provided 18 pairs of lines in which the "tall" (1 gene) and "short" (2 gene) lines could be used to compare the agronomic effect of the difference in height against a common genetic backgroung.

The *Rht* genotype of the "short" line and the "tall' line from all 18 pair selections was determined using the method of Gale and Gregory (1977). All lines (at F_8) were crossed with the following testers of known *Rht* genotype: Karamu (*Rht1*), Pataka (*Rht2*) and Raven (*rht1*). Seedling gibberellin insensitivity tests were then performed on the F_2 progenies of the test crosses. All "tall" lines were confirmed as 1 gene dose semidwarfs *rht1rht1Rht2Rht2* and all "short" lines were confirmed as 2 gene dose dwarfs *Rht1Rht1Rht2Rht2*. Therefore, from F_2 to F_5 the progenitors of the 18 pair selections were heterozygous for *Rht1* and homozygous for *Rht2*.

Field trials

The 1 and 2 gene dose lines were compared in yield trials conducted in 1978/79 (lines at F_7) and 1982/83 (lines at F_9) at the DSIR research farm "Aorangi" near Palmerston North. The soil type was Kairanga fine sandy loam (USDA classification: Typic Haplaquept, coarse loamy mixed mesic). Trial areas were cultivated out of four-year-old ryegrass/clover pasture in the three months prior to sowing. No fertilisers or irrigation were applied. Monthly summaries of meteorological data collected within 500 m of the trials are presented in Table 2.

TABLE 2: Weather for 1978/79 and 1982/83.

Month	Rainfall (mm)		Maximum daily temperature (C)		Minimum daily temperature (C)		Daily windrun (km)	
	1978/79	1982/83	1978/79	1982/83	1978/79	1982/83	1978/79	1982/83
September	75.4	54.1	15.8	14.7	5.8	5.1	264	264
October	84.3	140.4	16.1	14.8	5.7	6.8	290	431
November	70.2	47.8	18.7	18.2	8.5	11.4	390	582
December	74.6	148.4	21.0	18.5	10.6	9.6	356	405
January	35.8	43.8	22.3	19.5	12.9	11.2	391	523
February	52.3	30.4	22.0	21.4	11.5	10.7	344	339

Plots were three rows, each 5 m long, spaced 30 cm apart, with 15 cm between rows. Split plot designs were used in both years. In 1978/79 the 18 selections were the main plots and the 1 and 2 gene doses the subplots, with three replications. Buffer plots of the short semidwarf cv. Karamu were placed between the experimental plots to minimize any deleterious neighbour effects of "tall" lines on "short" lines. In 1982/83 the 1 and 2 gene doses were main plots and the selections subplots, with four replications. This design reduced neighbour effects at the expense of precision when comparing the gene dose classes.

The 1978/79 trial was sown on 19 September and the 1982/83 trial on 6 September. Approximately 1000 seeds were sown per plot. Ear emergence occurred on 7 December in 1978/79 and on 30 November in 1982/83 in all lines (± 3 days). Plots were harvested in late February in both years using a Hege 125B small plot header. Plant height was measured at four places in each plot prior to harvest. Grain yields are quoted on the basis of 12% moisture. Analyses of variance were performed on height and yield data from each year.

In 1982/83 yield component analyses were performed on the 1 and 2 gene dose lines from all replicates of six pair selections and from one replicate of the other 12 pair selections. Subsamples for analyses consisted of plants pulled from a 2 m length of the central row of plots (area 2 m x 0.15 m) and were threshed using an Almaco plant thresher.

The trials were kept free of weeds and disease. In 1982 stripe rust was controlled using Bayleton fungicide.

RESULTS AND DISCUSSION

The 2 gene dose lines were 26-35 cm shorter in stature than their respective 1 gene dose counterparts. Mean plant heights for the gene dose classes are presented in Table 3. All 2 gene dose lines were dwarf in stature as the plant height range in this class was 53-64 cm and 51-59 cm in 1978/79 and 1982/83 respectively. The 1 gene dose line had typical semidwarf plant heights of 87-98 cm in 1978/79 and 77-87 cm in 1982/83.

The 2 gene dose line was lower yielding than the 1 gene dose line in all 18 pair selections in both years. Differences between pair selections and selection x gene dose interactions were either not statistically significant or were only just significant (P = 0.05), so that yield data are presented as gene dose class means in Table 3. The yield reduction caused by the second *Rht* gene was consistent at about 14% in both years even though overall trial yields differed considerably between years. Our results agree with those obtained by Allan and Pritchett (1980) and Allan (1983) in Washington State and by Pinthus and Levy (1984) in Israel for the 1 vs. 2 gene dose comparison. Therefore the introduction of a second *Rht* gene has had a yield reducing effect in a variety of genetic backgrounds and environments and in trial lines produced by different genetic methods. To date, only Allan has shown a yield advantage for the 2 gene dose over the 1 gene dose and then only in a rather specific environment (low rainfall and shallow soil). Genetically, our study is closer to the work of Pinthus and Levy (1984) than to Allan's work as we crossed modern high yielding semidwarf lines as did Pinthus and Levy. Allan (1983) by comparison made extensive backcrosses to older, lower yielding tall cultivars.

TABLE 3: Mean plant heights and yields of 1 and 2 semidwarfing gene dose lines in 1978/79 and 1982/83.

Parameter	Year	Semidwarfing gene dose 1	Semidwarfing gene dose 2	LSD (5%)
Plant height (cm)	1978/79	93.6	58.3	13.4
	1982/83	82.1	55.6	9.5
Yield (g/plot)	1978/79	2478	2145	74
	1982/83	1606	1365	193

Plant height and yield in all lines were lower in 1982/83 than 1978/79 (Table 3) and this is probably a reflection of the cool, windy conditions prevailing in 1982/83 (Table 2; 1978/79 data were similar to the 17 year mean). The 1982/83 growing conditions reduced plant height in the 1 gene dose lines more than in the 2 gene dose lines. In November 1982 a six-day windstorm in the two weeks prior to ear emergence may have been a significant factor in the lower yield level in 1982/83. Wheat is known to be very susceptible to wind damage in the 1-2 weeks prior to ear emergence (Armbrust, 1984).

Consistent gene dose effects on yield components were recorded in all pair selections in 1982/83 and gene dose class means are presented in Table 4. Differences between

TABLE 4: Yield component means for 1 and 2 semidwarfing gene dose lines in 1982/83.

Component	Semidwarfing gene dose 1	Semidwarfing gene dose 2	LSD (5%)
Ears/m^2	561	524	n.s.
Spikelets/ear	15.2	15.6	n.s.
Grains/spikelet	1.56	1.69	0.10
Grain weight (mg)	44.1	39.7	0.69
Grain yield ex. thresher (g/m^2)	582	551	n.s.
Grain yield ex. 2.4 mm sieve (g/m^2)	494	419	60
Biomass (g/m^2)	1341	1161	139
Nongrain yield (g/m^2)	759	611	95
Harvest index	0.43	0.48	0.02

the 1 and 2 gene dose classes in ear numbers and spikelet numbers per ear were not significant. However, the second *Rht* gene caused a significant increase of 7% in spikelet fertility (grains per spikelet) and a significant decrease of 10% in grain weight. Other studies have shown larger gene dose effects than these. In comparing 1 and 2 gene doses, Allan and Pritchett (1980) and Pinthus and Levy (1983) found grain weight decreases of 17% and 19% respectively in 2 gene dose lines. In comparing 0 and 1 gene dose lines, Gale (1978) and Gale and Youssefian (1983) found that on average a single *Rht* gene increased spikelet fertility by 20% and decreased grain weight by 14%, which translated into yield increases. In our study the gene dose effect on grain weight predominated and grain size was decreased as well. Grain size effects were noted when subsample grains were passed over a 2.4 mm sieve during yield component analysis. Losses of small grains through the sieve were higher from 2 gene dose subsamples than from 1 gene dose subsamples. The sieving step amplified the difference in yield between the 1 and 2 gene dose classes, as can be seen by comparing subsample yields ex. thresher and ex. 2.4 mm sieve in Table 4.

Biomass production was significantly reduced by the 2 gene dose (Table 4), as was nongrain yield (straw and chaff). The second *Rht* gene reduced nongrain yield more than grain yield so that harvest index was significantly higher in 2 gene dose lines than in 1 gene dose lines.

The consistent yield advantage for the 1 gene dose lines over the 2 gene dose lines in two contrasting years has implications for wheat breeding in the Manawatu spring wheat region. The results suggest that cultivars carrying two *Rht* genes are unlikely to have a significant role in this region. Hence the use of only 1 gene dose in breeding semidwarf cultivars for Manawatu would seem justified. It is emphasised that our study used a limited range of genetic material and that further work is needed before final conclusions can be drawn. There is a need to study the effects of *Rht* genes on yield in other regions of New Zealand using genetically diverse materials. All four *Rht* genotypes could be usefully compared and we are currently developing lines for this purpose.

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