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The relationship between the Rht_1 and Rht_2 dwarfing genes and grain weight in *Triticum aestivum* L. spring wheat *

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Summary. The study was carried out in the first year on samples of random F_5 lines, uniform in height and in heading date, of three crosses between semi dwarf spring wheat cultivars (*Triticum aestivum* L.), differing in grain weight and in their *Rht* gene. In the second year only the progenies of the early heading F_5 lines were studied. All the material was grown in the absence of lodging. The culm-length genotypes of the different lines were identified by test crosses and by a seedling GA response test. No differences in grain weight were found between the two semi dwarf genotypes (Rht_1Rht_1 rht_2rht_2 and rht_1rht_1 Rht_2Rht_2). The tall genotype (rht_1rht_1 rht_2rht_2) was significantly higher in grain weight than the two semi dwarf genotyes and the grain weight of these genotypes exceeded markedly the grain weight of the dwarf genotype (Rht_1Rht_1 Rht_2Rht_2). These genotypic effects were independent of differences in plant height, heading date or number of grains per spike.

Key words: Inheritance – Culm-length – GA insensitivity – Grain weight – Wheat

Introduction

Semi dwarf wheat (*Triticum aestivum* L.) cultivars are grown extensively in many parts of the world. The majority of these cultivars are derivatives of the Japanese cv. 'Norin 10' (Reitz and Salmon 1968). The semi dwarf stature of these cultivars is controlled by the Rht_1 and Rht_2 genes (Gale 1979). The following four homozygous height genotypes are obtained by the combination of these two *Rht* genes: the dwarf Rht_1Rht_1 Rht_2Rht_2; the two semi dwarfs Rht_1Rht_1 rht_2rht_2 and rht_1rht_1 Rht_2Rht_2; the tall rht_1rht_1 rht_2rht_2 (Allan and Pritchett 1980).

A positive relationship between the culm lengths of the height genotypes and their grain weights has been found in several studies (Allan and Pritchett 1980; Gale 1979; Gale et al. 1981; Heyne and Campbell 1971; Johnson et al. 1966; Joppa 1973; Reddi et al. 1969). However, none of these studies concerns *T. aestivum* spring wheat. Information concerning all the four genotypes is presented only by Allan and Pritchett (1980). Their results, as well as those of Heyne and Campbell (1971), may have been affected by lodging.

In the present investigation samples of random lines from hybrid populations segregating for both Rht_1 and Rht_2 have been studied. Thus, it is assumed, according to Gale (1979), that the background genetic effects have been nullified, enabling the analysis of the effects on grain weight associated with the height genotype per se.

Materials and methods

F_5 lines and their F_6 progenies of 'Mivhor' × 'Lakhish', 'Yafit' × 'Lakhish', and 'Mivhor' × 'B.L.24' were studied in 1981 and 1982, respectively. The parents in each cross are high yielding, semi dwarf spring cultivars, differing in grain weight and in their height genotype (Table 1). All of them, with the exception of the breeding line 'B.L.24', have been grown commercially in Israel. The height genotype of 'Mivhor' had been determined by M. D. Gale (personal communication 1980) and the other cultivars were classified according to the segregation of the progenies of their crosses with 'Mivhor'. Bulked F_2, F_3 and F_4 populations of the three crosses had been grown without any selection. The F_5 lines were progenies of a random sample of single F_4 plants from each cross.

336 F_5 lines of 'Mivhor' × 'B.L.24' and 348 lines of each of the two other crosses were grown in a fertile field, receiving supplementary irrigation at the Lakhish Regional Experiment Farm. About 120 plants of each line were grown in a 6 m-long

* This study is based on data obtained in the MSc Thesis work of the junior author

Table 1. Parentage, origin and characteristics of the parental wheat cultivars

Cultivar	Parentage	Origin	Grain wt	Dwarfing gene
'Lakhish'	('Yaktana' × 'Norin 10-Brevor') × ('Florence' × 'Aurore')	Bred by the late J. Ephrat, A.R.O., The Volcani Center, Bet Dagan	High	Rht_2
'B.L. 24'	'Bluebird' × ('Ciano-Chris' × 'Olesen')	Selected from CIMMYT material by Y. Atsmon, Hazera Seed Co.	High	Rht_2
'Mivhor'	'Penjamo' sib × 'Gabo 55'	Selected from CIMMYT material by Y. Atsmon, Hazera Seed Co.	Low	Rht_1
'Yafit'	('21931/Chapingo 53-Andes' × Gabo 56') × 'Andes 64'	Selected from CIMMYT material by Y. Atsmon, Hazera Seed Co.	Low	Rht_1

row, 60 cm between rows. The early, semi dwarf commercial cv. 'Miriam' was grown in every 20th row and served as a control. The field was kept free of weeds and no lodging occurred.

The dates of heading (emergence of the peduncle from the flag-leaf sheath) of the first plant and of the last plant in each line were recorded. Lines in which the period between the heading of these plants exceeded 12 days, as well as lines within which culm length differed by more than 20 cm, were discarded. From each of the remaining 342 lines a sample of 10 main-shoot spikes was threshed for the determination of mean grain weight.

The classification of the lines into tall, semi dwarf and dwarf lines was done by means of a seedling GA response test (Gale and Gregory 1977). From each line, 10–15 seedlings were grown during the summer in the Laboratory at 25 °C, in trays filled with vermiculite and irrigated with a 10 ppm GA_3 solution. Their coleoptiles and first-leaf sheaths were measured and compared with those of the semi dwarf parental cultivars and the tall cvs 'FA 8193' and 'Alfa' and the dwarf cv. 'Barkaee', which were included in this test. The test enabled distinct classification of all the lines because of the small within-line variations and the absence of overlapping between the three groups.

From each cross 15–30 randomly selected F_5 lines, which appeared in the field to be semi dwarfs (70–110 cm), were test-crossed with the semi dwarf cv. 'Pitic 62', which carries the Rht_2 gene (Gale et al. 1981). Five spikes of each such line were sampled and with their bulked pollen two emasculated spikes of cv. 'Pitic 62' were pollinated. From each test cross 50 F_2 seeds were sown in a seedling GA response test similar to that described above. When the lengths of the coleoptile and the first-leaf sheath varied within a range similar to that of 'Pitic 62' the line was assumed to be of the same height genotype, namely rht_1rht_1 Rht_2Rht_2. F_2 populations in which these parameters varied within a range 3–5 times greater than in the former ones indicated that their parental F_5 line belonged to the Rht_1Rht_1 rht_2rht_2 genotype. Since no intermediate cases were observed the distinction between the two semi dwarf genotypes was clear-cut.

The test of the F_6 progenies of the F_5 lines was carried out at Rehovot in two replicated nursery plots consisting of single 80 cm-long rows, 25 cm apart, 15 plants per row. In this test only the progenies of the 'early' F_5 lines, which had not been more than nine days later than cv. 'Miriam', were included. The plots were adequately fertilized and irrigated and no lodging or leaf-diseases occurred. Grain weight was determined on the bulked yield of 10 main-shoot spikes from each plot.

Results and discussion

Comparison of the two semi dwarf genotypes

The mean grain weights in a random sample from each cross of F_5 semi dwarf lines and their F_6 progenies, of which the height genotypes had been identified by means of test crosses, are presented in Table 2. No significant differences were found between the two genotypes in any of the three crosses. Allan (1971) similarly found no consistent differences in grain weight between near-isogenic lines of semi dwarf winter wheat differing in the height genotype.

The similarity in grain weight between the two semi dwarf genotypes found in the present study indicates that the differences in grain weight between the parental cultivars, in each cross, are controlled by factors which are independent of the *Rht* genes since in each of the three crosses the heavy grained parental cultivar carried the Rht_2 gene and the light grained parent carried the Rht_1 gene (Table 1).

Assuming that the similarity in grain weight between the two semi dwarf genotypes, found for the random samples of lines of the three crosses, is valid for all the semi dwarf lines of these crosses, the data for all these lines, in each cross, were combined in the following analyses.

Height group × earliness interaction

An extremely high variability in heading date was observed for the F_5 lines of all the three crosses. The mean heading date of the earliest lines was 5 days earlier than that observed for cv. 'Miriam' (12 March 81), whereas the latest lines headed 37 days later than cv. 'Miriam'. In accord with local agricultural concepts, all the lines which were more than nine days later than cv. 'Miriam' were considered 'late' and all the other lines were considered 'early'.

The mean grain weight of the 'early' lines, in all three crosses, was significantly higher than that of the

Table 2. Mean grain weights of Rht_1- and Rht_2 semi dwarf lines of three wheat crosses (statistical analysis see below)

Cross	Generation	Height genotype			
		Rht_1Rht_1	rht_2rht_2	rht_1rht_1	Rht_2Rht_2
		No. of lines	Grain wt (mg)	No. of lines	Grain wt (mg)
'Mivhor' × 'Lakhish'	F_5	6	40.5	8	40.6
	F_6	3	43.6	6	43.1
'Yafit' × 'Lakhish'	F_5	10	43.5	11	39.0
	F_6	8	46.7	6	46.0
'Mivhor' × 'B.L. 24'	F_5	12	37.8	14	37.5
	F_6	8	41.4	8	37.3

Statistical analysis

Source of variation	F_5 (1981)			F_6 (1982)		
	df	Mean square	*P* (F)	df	Mean square	*P* (F)
Genotype	1	33	0.28	1	25	0.46
Cross	2	85		2	177	
Genotype × cross	2	33	0.32	2	15	0.71
Error	55	28		33	45	

Table 3. Analysis of variance for the effects of height groups, earliness and cross on grain weight, heading date and number of grains per main-shoot spike of F_5 lines of three wheat crosses

Source of variation	df	Mean squares		
		Grain wt	Heading date	Grains per spike
Height group	2	910**	2	19
Earliness ('early' vs 'late')	1	758**	5,524**	60
Cross	2	43	254**	1,238**
Height group × earliness	2	115*	48	107
Height group × cross	4	31	16	55
Earlines × cross	2	36	237	1
Height group × earliness × cross	4	36	13	79
Error	324	30	22	55

*, ** Significant $P < 0.05$ and $P < 0.001$, respectively

'late' lines. This was presumably due to the higher temperature prevailing during the grain filling period of the 'late' lines which may shorten the duration of grain filling and thus reduce grain weight (Pinthus and Sar-Shalom 1978; Wiegand and Cuellar 1981).

A significant height group × earliness interaction effect on grain weight was obtained (Table 3). Because of this interaction and because of the vulnerability of late developing grains to the adverse effects of high temperature the following analysis was restricted to the early lines.

Grain weight of early F_5 lines and their F_6 progenies in the different height groups

In all the three crosses, in F_5 as well as in F_6, the grain weight of the tall lines was higher than that of the semi dwarf lines which, in turn, was higher than that of the dwarf lines (Table 4). These differences among the three height groups were highly significant and were not significantly affected by any interaction (Table 5).

The difference in grain weight between the semi dwarf and the dwarf lines was conspicuously greater

Table 4. Height and grain weight of tall, semi dwarf and dwarf 'early' F_5 lines and their F_6 progenies in three wheat crosses

Cross	Generation	Tall					Semi dwarf					Dwarf				
		No. of lines	Culm length (cm)	Grain wt (mg)			No. of lines	Culm length (cm)	Grain wt (mg)			No. of lines	Culm length (cm)	Grain wt (mg)		
			Range of line means	Mean	SE	Range		Range of line means	Mean	SE	Range		Range of line means	Mean	SE	Range
'Mivhor' × 'Lakhish'	F_5	21	105 – 140	45.0	0.97	35.8 – 52.8	15	85 – 110	44.3	1.29	33.1 – 50.9	7	55 – 65	32.5	1.64	28.2 – 41.5
	F_6	21	98 – 129	43.4	0.90	33.8 – 51.1	15	78 – 111	42.1	0.92	36.8 – 46.9	7	51 – 61	32.6	1.71	27.7 – 39.0
'Yafit' × 'Lakhish'	F_5	12	105 – 140	44.9	1.09	39.6 – 50.0	39	75 – 110	41.2	0.68	31.5 – 49.8	13	60 – 70	32.6	1.32	25.8 – 43.0
	F_6	12	107 – 137	48.7	1.87	37.5 – 58.3	39	70 – 117	46.1	0.89	35.3 – 62.9	13	49 – 67	37.6	1.29	28.6 – 43.9
'Mivhor' × 'B.L. 24'	F_5	38	100 – 135	45.0	0.98	34.4 – 60.3	30	70 – 110	38.8	0.70	29.8 – 46.2	20	50 – 65	31.9	1.31	21.9 – 31.9
	F_6	38	90 – 132	43.6	1.05	33.4 – 59.9	30	71 – 114	39.7	1.12	30.1 – 51.9	20	42 – 65	35.2	1.58	20.6 – 47.4
Height group means				44.7	0.57				42.0	0.52				33.9	0.75	

than the difference between the tall and the semi dwarf lines (Table 4). This apparently synergistic effect of the two *Rht* genes on the reduction of grain weight is not evident in the data presented by Allan and Pritchett (1980).

The overlapping, among the three height groups, of the ranges of the mean grain weights is attributed to the effects of the above mentioned factors controlling grain weight independently of the *Rht* genes. In the cross 'Yafit'×'Lakhish' the grain weight of the highest ranking semi dwarf line exceeded that of the heaviest tall line (Table 4). The significance of this case is somewhat doubtful because of the small number of tall lines tested from this cross. However, if it were due to a recombination of the *Rht* gene and a linked factor controlling grain weight this would weaken the hypothesis of pleiotropic effects of the *Rht* genes on grain weight.

The similar grain weight of the two semi dwarf genotypes seems to indicate that if the Rht_1 and Rht_2 dwarfing genes, derived from 'Norin 10', have any pleiotropic effect on grain weight this effect should be similar for both of them. Furthermore, if these *Rht* genes are closely linked with any genes controlling grain weight the latter genes must be of similar effect, which is plausible considering that the location of the Rht_1 and Rht_2 genes is on homoeologous chromosomes, 4A and 4D respectively, probably at homoeologous loci (Gale 1979). However, this does not exclude the possibility that in certain cultivars the rht_1 and rht_2 genes have different pleiotropic effects on grain weight, or are closely linked to genes with different effects on grain weight. In progenies of crosses between such cultivars and dwarf genotypes, differences in grain weight between the two semi dwarf genotypes would be expected. Indeed, in isogenic lines of 'Omar'//'Suwon 92'/6* 'Omar' the semi dwarf lines with the genotype rht_1rht_1 Rht_2Rht_2 had distinctly heavier grains than the

Table 5. Analysis of the effects of height group, cross and generation (F_5 in 1981 vs F_6 in 1982) on in grain weight of 'early' wheat lines

Source of variation	df	Mean square	*P* (F)
Height group	2	2,781	<0.0001
Cross	2	243	<0.01
Height group × cross	4	69	0.198
Error A	186	45	
Generation	1	149	<0.01
Generation × cross	2	183	<0.001
Height group × generation	2	33	0.112
Height group × generation × cross	4	13	0.480
Error B	186	15	

lines with the Rht_1Rht_1 rht_2rht_2 genotype (Allan and Pritchett 1980).

The possibility of indirect effects of the height genotype on grain weight

A range of 14 days was observed for the heading dates of the 'early' lines tested in this study. However, heading date was not affected by height group (Table 3). Therefore, the differences in grain weight among these groups could not be due to differences in the grain filling period following different heading dates.

Mean grain weight may be reduced by an increase in the number of grains per spike (Pinthus and Millet 1978). In the present study the number of grains per spike of the F_5 lines was not affected by height group (Table 3). In the progenies of the early F_5 lines, of all three crosses, the number of grains per spike was highest in the tall lines, followed by the semi dwarf lines, and lowest in the dwarf lines. Consequently, if there was any effect of grain number on grain weight it only could have moderated the effects of height group on grain weight rather than having induced them.

A positive phenotypic relationship between height and grain weight may be attributed to physiological factors associated with culm length e.g. the photosynthetic active area of the upper stem internodes. An analysis of grain weight of genotypically tall and genotypically semi dwarf lines with similar culm length, involving 39 lines in the F_5 generation and 50 lines in the F_6 generation, is presented in Table 6. Considerable genotypic effects on grain weight were obtained. These were statistically significant in the F_5 generation ($P<0.05$) and almost so ($P<0.10$) in the F_6 generation. The mean grain weight of the genotypically tall lines was 45.8 mg in F_5 and 44.8 mg in F_6. In spite of the similarity in height it exceeded that of the genotypically semi dwarf lines which was 40.9 mg in F_5 and 40.4 mg in F_6. No semi dwarf and dwarf lines with similar culm length were available for a parallel analysis (Table 4). The existing comparison between the tall and the semi dwarf lines, however, indicates the independence of the effects of the height genotype on grain weight from its effects on culm length. A previous single case of an association between grain weight and the height genotype, in spite of phenotypic similarity in culm length, has been observed by Pinthus (1983).

It is concluded that the different mean grain weights of the three height groups, found in this study, were entirely due to their respective *Rht* genotypes.

Table 6. Analysis of the difference in grain weight between genotypically tall and genotypically semi dwarf wheat lines with similar culm length

Source of variation	df	F_5 generation		F_6 generation	
		Mean square	*P* (F)	Mean square	*P* (F)
Genotype	1	140	0.04	114	0.09
Cross	2	43		48	
Genotype × cross	2	6	0.83	38	0.27
Error	33	33		38	

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