The relationship between height and grain protein content in tetraploid wheat Triticum turgidum

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INTRODUCTION

The introduction of fertilizers for the improvement of wheat production was inevitably accompanied by increased plant height and consequently by lodging. The latter effect coupled with a decrease in the economic value of the straw has caused the reduction of plant height to be a major concern for plant breeders following the second World War.

Reduction of plant height can be accomplished either through the application of growth retardants, such as chlormequat, or by the predominant method, via the introduction of dwarfing genes. Two such genes (Rht1 and Rht2), originating from the Japanese variety Norin 10, had a great impact on wheat production worldwide : a large number of high yielding dwarf and semi-dwarf varieties carrying these genes were released, and in fact characterize the 'Green Revolution' (Law et al, 1978, Reitz and Salmon, 1968).

Unfortunately, modern lines derived from these varieties are relatively low in grain protein percentage (12% to 14%). Consequently it has become a major interest of wheat breeders to increase the grain protein content while maintaining a reduced plant height. However, many works reported a positive correlation between plant height and grain protein percentage (see literature review), implying that one of these parameters cannot be altered without affecting the other.

The purpose of this project was to study the relationship between plant height and grain protein content in durum wheat and, if established, to determine whether it reflects physiological and/or genetical factors.

LITERATURE REVIEW

Allan et al (1968) studied the genetic mechanism for culm length in a 5X5 parents diallel cross, between standard height and semi-dwarf hexaploid wheat selections and reported on two independent factors for semi-dwarfism. These two major genes carried by Norin10-Brevor14, later designated Rht1 and Rht2 (Gale and Law 1976), determine the dwarf habit, while the presence of just one of them gives rise to a semi-dwarf genotype. Although indicated by a capital letter, Rht1 and Rth2 are recessive (Gale and Law 1976). In addition to the two major genes, minor ones appear also to modify the expression of culm length (Allan et al 1968).

The height of Norin 10 derivatives was relatively unaffected by exogenous gibberrellic acid (GA) (Gale and Law 1976, Gale and Gregory 1977), while the internode lengths of tall genotypes was almost doubled . This character of Norin 10-Brevor 14 is controlled by the two partially dominant alleles, Gai1 and Gai2 (Gale and Law, 1976). A homozygous recessive plant would be sensitive to exogenous application of GA, whereas a plant carrying the two dominant alleles would be insensitive. However, a slight reaction could be obtained in plants carrying only one of the dominant alleles.

In crosses between tall and semi-dwarf lines (Rht1 or Rht2), no recombination was found between height and GA insensitivity i.e., neither tall genotypes having GA insensitivity nor any dwarf genotype with GA sensitivity were recorded. Gale and Law proposed that height stature could be a result from a pleiotropic effect of genes responsible for GA response, or that the dwarfing genes are closely linked to the Gai genes. At any rate, it is clear that Gai1 and Gai2 have the same chromosomal location as Rht1 and Rht2 (Gale and Law 1976).

The only work which reported on recombination between these two traits, contrary to the works stated above, is that of Hu and Konzak (1974). This is rather surprising in view of the fact that all the dwarf and semi-dwarf lines checked in the mentioned works of Gale and Law were insensitive to GA.

It has been found that genotypes carrying the Rht1 or Rht2 genes had a higher endogenous level of GA than the tall genotypes (Gale and Marshall 1973, Radley 1970).Their conclusion was that these Rht genes inhibited a step in the pathway of GA action , as opposed to blocking the biosynthesis of the hormone itself.

Studying the chromosomal location of the dwarfing genes in common wheat, *Triticum aestivum* (2n=42; genome AABBDD), the Rht1 gene has been allocated to chromosome 4A (Gale and Marshall 1976) and Rht2 to chromosome 4D (Gale et al 1975).

In semi-dwarf tetraploid wheat, *T.turgidum* (2n=28; genome AABB), only one of the two Norin 10 derived dwarfing genes is present- Rht1 on chromosome 4A.

Plant height can be reduced by growth retardants, such as clhoromequat (CCC). This well known height reducer of wheat (Clark and Fedack 1977, Humphries 1968, Johnson et al 1979, Pinthus 1968 and Tolbert 1960), is used commercially to prevent lodging. CCC is thought to be an antagonist of GA (Tolbert, 1960), probably inhibiting its biosynthesis (Adkins et al 1984 and Lang 1970). CCC may also have some influence on other agronomic traits such as stronger tillering (Humphries 1968, Tolbert 1960), and higher yield (Chrominski 1967), independantly of the reduced plant height.

Improvment in the nutritional value of wheat is quite limited by the low grain protein content of the cultivated varieties (Jonshon et al 1973). Yet, the wild tetraploid wheat (Triticum Turgidum var. dicoccoides) excells in a high grain protein content, and may be utilized as a source for increased grain protein content in cultivated wheat (Avivi 1978, 1979).The high level of pairing between chromosomes of T.dicoccoides and those of T.durum, and the high fertility of their F_1 hybrid facilitate this gene transfer. Using this approach Avivi (1978, 1979) crossed the Israeli variety 'Inbar' to T.dicocoides and selected progenies excelling in high protein percentage (18%-23%), and several agronomical traits like high yield, non-fragile spike and high kernel weight. The performance of the selected lines from these crosses under agricultural conditions was encouraging but severe lodging occurred (Avivi et al 1983). It came about that lines selected for high grain protein percentage were tall. Thus, a positive relation between height and grain protein content may be suspected.

Various studies deal with the height-protein relationship in wheat plants differing in their Rht genes (Deckard et al 1977, Gale 1979, Law and Payne 1983, Pepe and Heiner 1975 and Zittelli et al 1983). In most cases the Rht genes were associated with a reduction of 1% in grain protein (except in the work of Deckard et al (1977) who found an increase of 0.4% in the semi-dwarf lines compared with the tall ones). Yet, only Zittelli and coworkers (1983) mentioned a direct relation between Rht genes and protein content, while others attributed this decrease to a reduction in plant height (Gale 1979, Gale et al 1981, Law and Payne 1983, Pepe and Heiner 1975). The latter view is in agreement with workers who compared the protein percentage of plants differing in their height but not necessarily through the Rht genes, and found a positive correlation between the two traits (Corpus et al 1983, Kramer 1983, Loffler and Bush 1982, Loffler et al 1984).

It is assumed that most of the grain protein is derived from nitrogen accumulated in the stem before anthesis (Austin et al 1977, Desai and Bathia 1978, Herzog and Stamp 1983 and Kramer 1979, 1983). The stem appears to be a nitrogen reservoir (Kramer 1979, 1983). The nitrogen is accumulated in the stem as proteins until it is translocated to the grains in the form of amino acids (Austin et al 1977, Peterson 1965).

The increased yield of modern semi-dwarfs is thought to be primarily due to a change in the dry matter distribution in favor of the grains. This reflects a decrease in the relative amount of straw, and hence an increase in the harvest index (HI). Since the ratio of nitrogen storage to sink size is decreased in these lines, the protein concentration in the grains is expected to be diluted (Kramer 1979, 1983). A negative correlation between protein percentage in the grains and the HI is thus expected (Corpus et al 1983, Kramer 1979, 1983, Loffler and Bush 1982, Loffler et al 1985). In fact, in high yielding lines, having relatively little straw, the negative correlation between grain yield and protein percentage should be even more accentuated (Corpus et al 1983, Kibite and Evans 1984, Kramer 1979, 1983, Loffler and Bush 1982, Loffler et al 1985).

In addition to the size of the nitrogen reservoir, the extent to which this reservoir can be depleted also determines the protein level in the grains. The efficiency of this process, known as partitionning, is expressed as the Nitrogen Harvest Index (NHI) an index closely related to protein yield in the grains (Desai and Bathia 1978, Loffler and Bush 1982, Loffler et al 1985). Since NHI depends on both protein percentage and grain yield (see definitions in Materials and Methods) complex relations between these two traits may explain contradictory results between NHI and protein. Though NHI is directly related to HI (Austin et al 1977, Day et al 1985, Desai and Bathia 1978, Loffler and Bush 1982, Loffler et al 1985), it may not be correlated as it may be negatively correlated with height (Loffler et al, 1985) or with protein percent (Deckard et al 1977). However, positive correlation between NHI and protein percent has also been reported (Day et al, 1985).

The total protein yield in the straw and grains of wheat plants the height of which had been reduced through treatment with CCC was found unaffected though a different distribution of the amino acids, compared to untreated plants, was detected (Clark and Fedack 1977, Grugzdev 1975, Linser et al 1965). However, according to Crominski (1977), CCC led to a decrease in protein percentage in grains, though it might have increased the soluble proteins in the leaves and stimulated the synthesis of RubPC-ase protein (Bode and Wild, 1984).

MATERIALS AND METHODS

1. F_2 experiments.

Plant material consisted of line 1124- an F_6 derivative of a cross between T.dicoccoides and T.durum cv. Inbar.
This tall line (rht rht) had been selected at the department of Plant Genetics at the Wiezmann Institute, for its high grain protein percentage (about 17%).
The cultivar Inbar originated from a cross between the two cultivars Jori and FG. It is semi-dwarf (Rht1 Rht1) and its grain protein percentage is about 12%.
Hazera-870

Line 1124 was crossed with H-870 and the F_2 generation of this cross was studied.

Two F_2 seed samples of the above cross were sown in the net-house of the Weizmann Institute in Rehovot on two different dates : the early 10.12.1983, and the late 29.2.1984. It was assumed that the late sown plants will produce shorter stems, and no height differences due to genotype will be expressed (Pinthus, 1983). This would allow to study the direct effect of the Rht1 gene on protein parameters independently of its effect on height.
At both sowings, the distance between plant rows was 30 cm. and the distance between plants within rows was 15 cm. Plants were sufficiently irrigated.

For each individual plant, the number of tillers and the following parameters of the main spike were determined : heading date, culm length, number of spikelets, grain yield, grain number, mean kernel weight, straw yield and HI. Straw nitrogen percentage and NHI were measured in a random sample from the two homozygous genotypes. Protein analysis in the early sowing was carried out on samples of 1 g. flour milled from main spike kernels using a Grain Quality Analyser (Neotec GQA 31). Semi micro-Kjeldahl procedure was used for the grain protein analysis of the late sowing, since the poor grain yield per plant from this sowing did not enable the Neotec analysis. Straw nitrogen percent was checked in all cases by the semi micro-Kjeldahl procedure.

The "GA seedling test" (Gale and Gregory 1977) was used to determine the Rht genotype of each F_2 plant. From each F_2 plant a sample of about 12 F_3-seedlings was sown in a 15 cm. long row in a germination tray filled with vermiculite and irrigated with 10 ppm GA (Berelex) solution. The distance between rows was 3 cm. The trays were kept in a growth chamber at 25 °C constant temperature and low light intensity (about 10 fc.). Fifteen days after sowing, at the emergence of the second leaf, the length of the coleoptile and of the first leaf sheath were measured. F_3 seedlings uniform for long or short coleoptiles and leaf sheaths indicated that their F_2 parent had been homozygous for rht1 or Rht1 respectively. F_3 seedlings segregating for these characters indicated that their F_2 parent had been heterozygous (Rht1 rht1). In the majority of cases the distinction between genotypes could be easily made, and only a few F_2 plants had to be discarded.

Remarks.

1) All given data is for the main spike only. This seems more accurate as number of tillers was greatly dependent upon rows : plants in outer rows had more tillers than plants in the inner rows.

2) Parents or F_1 of this cross were not grown together with the F_2 populations. The only information about the parental lines was obtained from plants sown at the early sowing date in a different part of the net-house. Mean height was 108.2 cm. for the tall parent (1124), and 85.7 cm. for the semi-dwarf variety (H-870). Mean protein percentage in grains was 17.5% and 14.9% respectively.

Definitions of parameters

Grain weight = grain yield/number of grains.

Harvest index (HI) = grain yield/(grain yield+total straw yield).

Spike protein yield = % protein in grains x grain yield/100.

Grain protein yield = %protein in grains x grain weight/100.

Nitrogen Harvest index (NHI) = % N in grains x grain yield/
(% N in grains x grain yield)+(% N in straw x straw yield).

2. CCC experiment.

The experiment was a bifactorial spilt-plot with 5 repliactes (blocks). The two factors were CCC treatment (with two levels:treated and control plants) in main plots and four genotypes (1243, 899, Inbar and H-870), in sub plots.

Sowing was on 11.12.1983, in the same net-house as the F_2 populations. Each sub plot consisted of one 1.5m. long row. Between rows distance was 20 cm. and within rows, plant-distance was 15 cm. Plants were sufficiently irrigated.

The CCC treatment consisted in sprays of CCC (24 g./l.), at the rate of 9.5 10 cm^3/m^2 The first spray was applied on 27.2.1984. When all plants had one developed internode, and the number of leaves varied from four to six. Since rainfall occurred immediately after this spray, another treatment was applied four days later.

Dissected embryonic apices exhibit at this time various stages of differentiation, from apex elongation (line 899) to flower differentiation (cv. H-870).

A third spray was applied on 15.02.1984. The phenological stages of the various lines, determined a week later were as follows: Inbar and 870 had three internodes, with six and seven leaves, respectively, and lines 1243 and 899 had two internodes, with six and five leaves respectively. At this time, all spikes were fully differentiated with the exception of line 899 which was at the flower differentiation stage.

Lines 1243 and 899 are two F_6 derivatives from crosses between *Triticum dicoccoides* and *T. durum* cv. Inbar. They both have a high kernel protein percent. 1243 is tall (rht rht) and 899 is semi-dwarf (Rht1 Rht1) The two above mentioned cultivars Inbar and H-870 are semi-dwarf (Rht1 Rht1).

Main spike heading date for each plot was recorded when half of the spikes had emerged from the upper leaf sheath in each replicate.
The same parameters as in the F_2 population were measured for a sample of about seven plants taken from each line in each replicate.
Grain protein percent for each replicate was analysed by Neotec.
Straw N content was determined by the semi micro-Kjeldahl procedure.

RESULTS

1. F_2 experiments.

The relationship between plant height and protein percentage was studied first in the entire populations of the early and late sowing. Each population was then divided into genetic height groups, corresponding to the 3 different Rht genotypes (Rht Rht, Rht rht and rht rht).

Division into genotypic height groups

Division into genotypic height groups was performed by the GA seedling test. Table 1 shows the mean ± S.E. and minimum and maximum values of coleoptiles and first leaf sheath lengths of the parents H-870 and 1124. The seeds from these lines originated from plants sown at the early sowing date.

Table 1 Coleoptile and first leaf sheath lengths (mm.) of GA treated, 15 days old seedings from H-870 and 1124.

Line	H-870			1124		
	Mean ± S.E.	Min.	Max.	Mean ± S.E.	Min.	Max.
Ceoloptile	39.6 ±1.6	35	47	76.0 ±1.9	70	80
First leave sheath	71.4 ±2.3	59	77	139.5 ±14	110	180

Tables 2 and 3 show the mean ± S.E. as well as the minimum and maximum values of coleoeptile and first leaf sheath lenghts of F_3 seedlings treated with GA.

Table 2 Coleoptile and first leaf sheath lengths (mm.) of GA treated, 15 days old F_3 seedings from the early sown F_2 plants (N=246).

Genotype	Rht Rht			rht rht		
	Mean ± S.E.	Min.	Max.	Mean ± S.E.	Min.	Max.
Ceoloptile	30.9 ±1.5	20	53	60.0 ±2.3	50	75
First leave sheath	66.4 ±2.7	45	80	152.3 ±4.7	130	180

The number of late sown F_2 plants checked by this test (Table 3) was much smaller (65) because of the insufficient number of F_3 seeds from many of the late sown F_2 plants. These plants had also smaller kernels than the early sown ones, and therefore, presumably, their F_3 seedlings were smaller than those of the early sown plants.

Table 3 Coleoptile and first leaf sheath lengths (mm.) of GA treated, 15 days old F_3 seedings from the late sown F_2 plants (N=65).

Genotype	Rht Rht			rht rht		
	Mean ± S.E.	Min.	Max.	Mean ± S.E.	Min.	Max.
Ceoloptile	30.3 ±1.2	25	35	34.4 ±1.6	30	40
First leave sheath	50.0 ±2.4	32	60	66.8 ±1.2	62	70

The observed and expected values of the different genotypes in each of the two F_2 populations is presented in table 4.

Table 4 Observed and expected frequencies of the three different F_2 genotypes in the early and late sowing.

Sowing	Genotype	Observed	Expected	
Early	rht rht	49	61.5	$X^2 = 6.1$
	rht Rht	142	123	
	Rht Rht	55	61.5	
Late	rht rht	8	16.25	$X^2 = 5.9$
	rht Rht	40	32.50	
	Rht Rht	17	16.25	

The critical value $X^2.95.$ with two degrees of freedom equals 5.99. Consequently, the observed frequencies deviated somewhat more than expected by chance from the Mendelian single gene segregation 1:2:1 (Rht Rht:Rht rht:rht rht). This deviation may be due to an overestimate of the frequency of segregating F_3 lines based on the occurrence of individual retarded seedlings.

Height distributions

The frequency distribution of culm length in each of the three genotypic height groups and in the whole early sown population are presented in Fig.1. It is obvious that the extremely short and the extremely tall plants belonged entirely to the homozygous Rht1 Rht1 and rht1 rht1 genotypes, respectively. In the remaining groups, with 65-120 cm. culm lenght, plants belonging to two or three genotypes were represented.

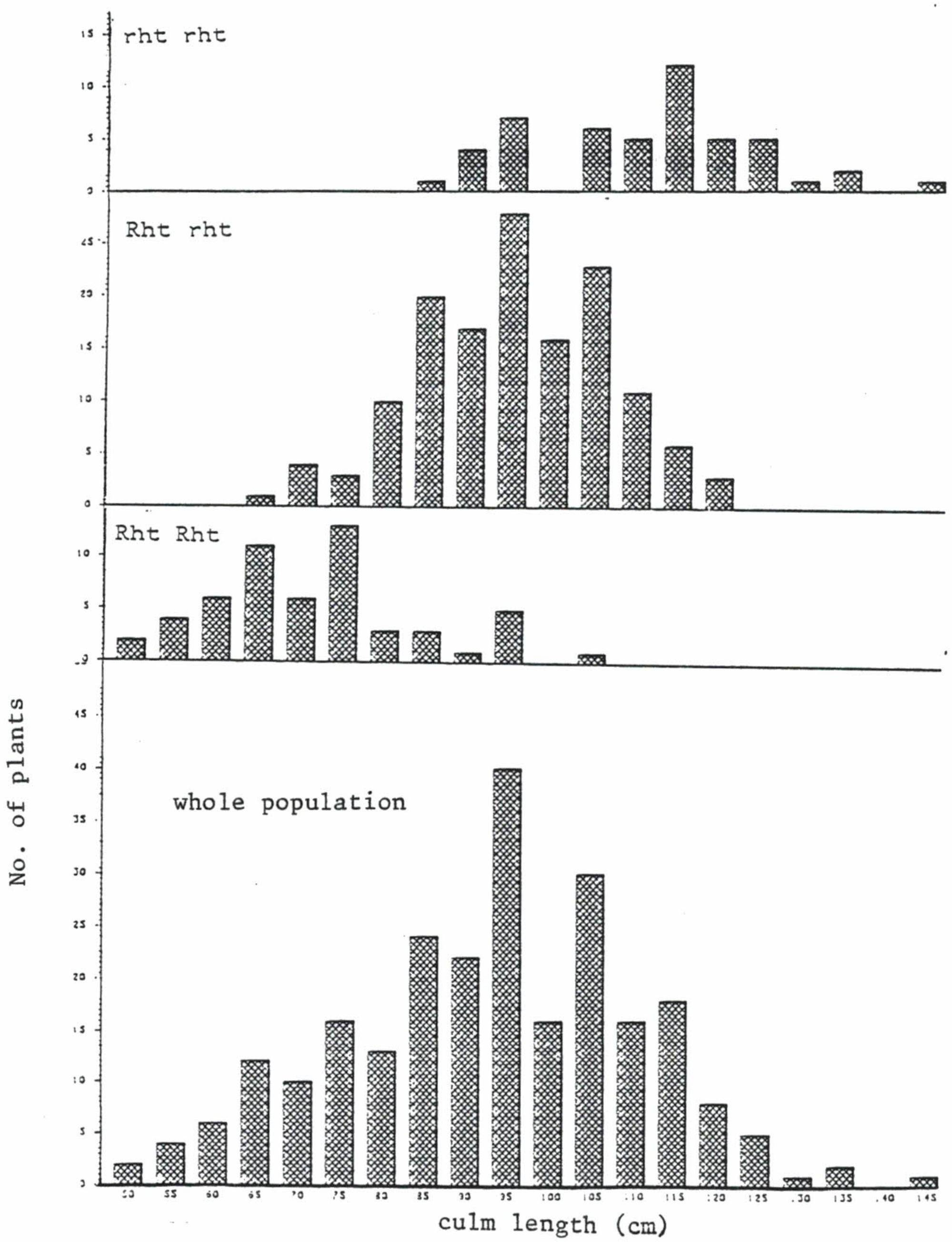

Fig. 1. Culm length distribution in the whole early sown F_2 population and in each genotypic height group.

The corresponding frequencies for the late sown F_2 population are presented in Fig.2. In this population, culm length was much shorter than in the earlier sown population, and its variation was smaller. The three different genotypes did not differ markedly in the range of their culm lenght.

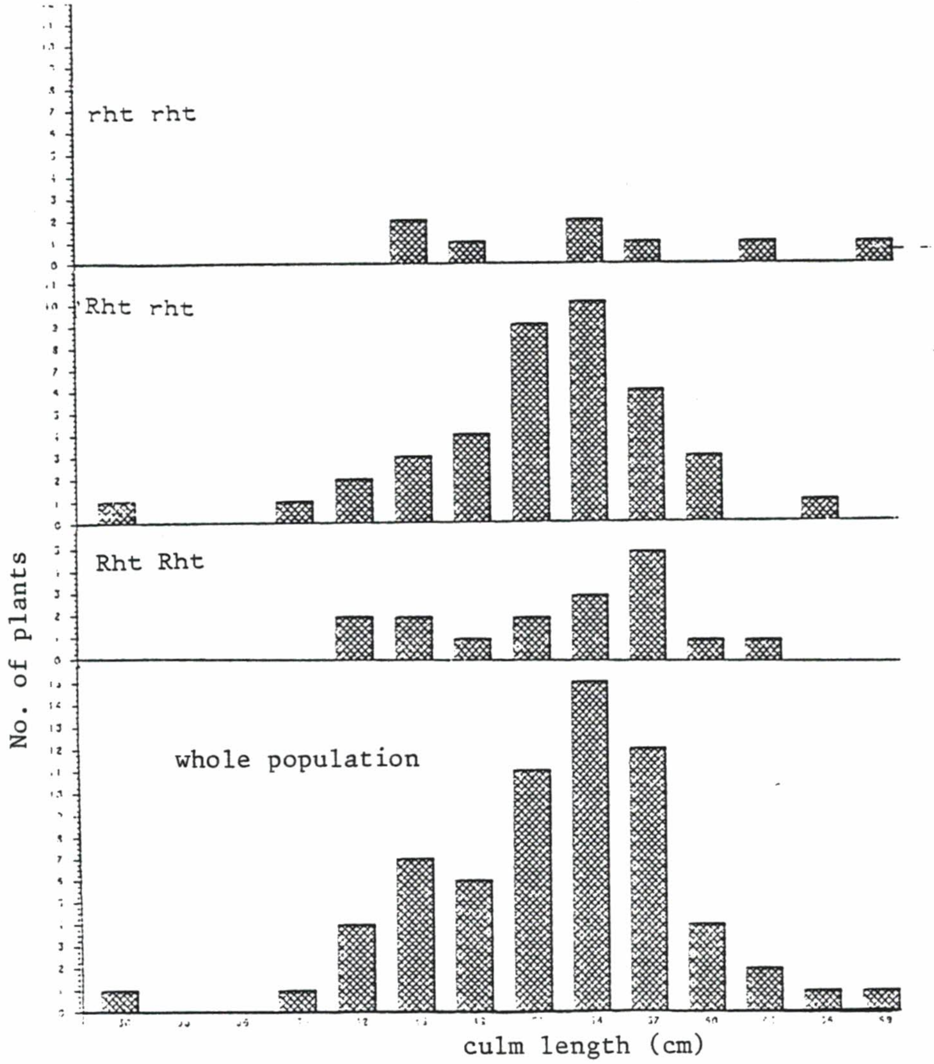

Fig. 2. Culm length distribution in the whole late sown F_2 population and in each genotypic height group.

Correlations

The different agronomic traits studied at both sowings ranged widely among the plants. The range of these parameters (± S.E.) are presented in table 5.

Table 5 Range (± S.E.) of several traits of the main culm of the F_2 population at the early and late sowings.

	Sowing					
	Early			Late		
Character	Min.	Max.	±S.E.	Min.	Max.	±S.E.
Culm height (cm.)	49	145	±1.05	31	69	±0.81
Straw yield (mg.)	668	5771	±53	749	2921	±55
Grain protein %	9.2	20.6	±0.10	11.4	23.9	±0.32
Spike protein yield (mg.)	91.3	603	±6.3	68.0	399	±9.2
Grain protein yield (mg.)	4.7	16.9	±0.11	1.7	14.7	±0.29
HI	0.12	0.61	±0.004	0.26	0.55	±0.004
NHI	0.83	0.97	±0.004	0.83	0.95	±0.008
Grain yield (mg.)	317	4573	±42	472	2065	±45
Mean grain weight (mg.)	43.5	98.1	±0.47	9.8	69.8	±1.2
Days from sowing to heading	89	112	±0.28	60	86	±0.71

The coefficient of correlation between different traits in the early and the late sowing are given in tables 6 and 7, respectively. In the early sowing, it can be noted that height was positively correlated with all the yield and protein components, with the exception of HI and NHI. In the late sowing, non-significant correlation was found between height and protein percentage. Height was positively correlated with yield components, and negatively with HI and NHI. In both sowings, straw yield (which included stem, leaves, and bracts), was closely correlated with height.

Table 6 Coefficients of correlation between several traits of the main culm in the early sown F_2 population.

	Straw yield	Grain protein %	Spike protein yield	Grain protein yield	HI	NHI	Grain yield	Mean grain weight	Days from sowing to heading
Height	$.73^{**}$	$.22^{**}$	$.43^{**}$	$.28^{**}$	$-.32^{**}$	0	$.37^{**}$	$.17^{**}$	$-.28^{**}$
Straw yield		$.14^{*}$	$.64^{**}$	$.27^{**}$	$-.32^{**}$	.15	$.65^{**}$	$.22^{**}$	$-.15^{*}$
Grain prot.%			$.35^{**}$	$.78^{**}$	$-.21^{*}$	.02	.02	$.23^{**}$	-.03
Spike prot.yi.				$.44^{**}$	$.32^{**}$	$.44^{**}$	$.92^{**}$	$.34^{**}$	-.13
Gr.Prot. yield					$.15^{*}$	.05	$.78^{**}$	$.78^{**}$	-.03
HI						$.80^{**}$	$.52^{**}$	-.04	.02
NHI							$.42^{**}$	.05	0
Grain yield								$.18^{**}$	-.01
Mean gr.wt.									-.02

*:p<.05; **:p<.01

Table 7 Coefficients of correlation between several traits of the main culm in the late sown F_2 population.

	Straw yield	Grain protein %	Spike protein yield	Grain protein yield	HI	NHI	Grain yield	Mean grain weight	Days from sowing to heading
Height	.53**	.11	.54*	.22	-.17-	-.18	.60**	.29**	-.27
Straw yield		.16	.67*	.13	-.30*	-.02	.55**	.07	-.21
Grain prot.%			.46*	.69*	-.19	.30	.02	.20	.12
Spike prot.yi.				.65*	.35	.11	.54**	.55**	-.16
Gr. Prot. yield					.33*	.38	.37*	.64**	.01
HI						.58	.59**	-.63	-.17
NHI							.09	.39	.31
Grain yield								.60**	-.31
Mean gr.wt.									.02

*:p<.05; **:p<.01

Since in the early sowing, height variation was wide within each genotypic height group (Fig.1), dividing the population into height groups, excluded the effects of the Rht genes. Analysing the relations between height and grain protein within each genotypic groups enabled to isolate possible effects of the height *per se*, when height variation was due to minor genes or environment. Coefficients of correlation between height and protein within each genotypic group are presented in tables 8 a, b and c.

Table 8 Coefficients of correlation between several traits of the main culm within each of the genotypic groups, rht rht (a), Rht rht (b) and Rht Rht (c) of the early sown F_2 population.

a	Straw yield	Grain protein %	Spike protein yield	Grain protein yield	HI	NHI	Grain yield	Mean grain weight	Days from sowing to heading
Height	.72**	-.12	.35*	.07	-.28*	.17	.35*	.18	-.08
Straw yield		.14	.69**	.08	-.05	.38	.70**	.22**	.06
Grain prot.%			.21	.76**	-.01	-.30	-.12	.33*	.08
Spike prot.yi.				.31*	.63**	.66*	.94**	.31*	.06
Gr.Prot. yield					0	-.17	.07	.86**	0
HI						.90**	.65**	.07	.11
NHI							.66*	.03	.17
Grain yield								.23	.09
Mean gr.wt.									-.05

b	Straw yield	Grain protein %	Spike protein yield	Grain protein yield	HI	Grain yield	Mean grain weight	Days from sowing to heading
Height	.66**	.14	.29**	.25**	-.17*	.32**	.25**	-.20*
Straw yield		.06	.54**	.20*	-.25**	.55*	.25**	-.11
Grain prot.%			.30**	.79**	-.22*	-.12	.23**	-.03
Spike prot.yi.				.40**	.47**	.90**	.33*	-.14
Gr.Prot. yield					-.12	.08	.78**	.01
HI						.64**	-.04	-.05
Grain yield							.18*	-.14
Mean gr.wt.								-.01

C	Straw yield	Grain protein %	Spike protein yield	Grain protein yield	HI	NHI	Grain yield	Mean grain weight	Days from sowing to heading
Height	.49**	.12	.35*	.26	-.28*	.02	.27	.14	-.09
Straw yield		.07	.57**	.28*	-.33*	-.63*	.64**	.41**	0
Grain prot.%			.43**	.80**	0	.33	.08	.19	.03
Spike prot.yi.				.55**	.36**	.43	.92**	.41**	-.04
Gr.Prot. yield					-.05	.30	.28*	.74**	.08
HI						.85**	.45**	.08	-.23
NHI							.37	.07	-.26
Grain yield								.44**	-.13
Mean gr.wt.									.06

*:p<.05; **:p<.01

In none of the groups was the correlation between height and protein percentage significant. Positive correlations were found in all groups between protein yield and height. This fact could be related to the positive correlation found between height and grain yield (Table 8).

For the late sown F_2 population, (Table 9), correlation coefficient between height and protein percentage was not significant. Significant correlations coefficient between height and protein yield were found in the heterozygous and homozygous Rht1 Rht1 genotypes.

Table 9 Coefficients of correlation between several traits of the main culm within each of the genotypic groups, rht rht (a), Rht rht (b) and Rht Rht (c) of the late sown F_2 population.

a	Straw yield	Grain protein %	Spike protein yield	Grain protein yield	HI	NHI	Grain yield	Mean grain weight	Days from sowing to heading
Height	.93**	-.06	.45	-.21	-.38	-.70	.65	-.39	-.57
Straw yield		-.10	.52	-.18	-.24	-.65	.78*	-.29	-.62
Grain prot.%			.62	.93**	.47	.26	.21	.76*	-.05
Spike prot.yi.				.65	.60	-.18	.88**	.57	-.69
Gr.Prot. yield					.66	.22	.24	.94**	-.16
HI						.42	.41	.79*	-.04
NHI							-.35	.24	.33
Grain yield								.21	-.79*
Mean gr.wt.									-.24

b	Straw yield	Grain protein %	Spike protein yield	Grain protein yield	HI	Grain yield	Mean grain weight	Days from sowing to heading
Height	.44**	.10	.57**	.35*	.29	.65**	.40**	-.30
Straw yield		.32*	.77**	.36*	-.35*	.71**	.21	-.02
Grain prot.%			.55**	.60**	-.38*	.07	-.01	.11
Spike prot.yi.				.73**	.11	.86**	.48**	.09
Gr.Prot. yield					.20	.50*	.79**	.14
HI						.40*	.54*	-.11
Grain yield							.61**	-.08
Mean gr.wt.								.02

c	Straw yield	Grain protein %	Spike protein yield	Grain protein yield	HI	NHI	Grain yield	Mean grain weight	Days from sowing to heading
Height	.47*	.31	.57*	.32	-.04	.51	.44	.04	-.12
Straw yield		.16	.75**	.19	-.23	.31	.76**	.16	-.15
Grain prot.%			.40	.77**	-.30	.31	.07	-.16	.13
Spike prot.yi.				.61*	.39	.75*	.88**	.43	-.03
Gr.Prot. yield					.22	.71*	.29	.50	.03
HI						.79**	.55*	.64*	.09
NHI							.72*	.77**	.23
Grain yield								.58*	-.11
Mean gr.wt.									-.15

*:p<.05; **:p<.01

Effects of the Rht genes

A one way analysis of variance as well as a Duncan multiple range test were performed in both populations in order to determine the effects of the Rht genes on several plant characters (Tables 10 and 11). In the early sown F_2 population (Table 10), there was a significant effect of the Rht1 genes on culm length, and the mean values of this trait could be ranked by genotype : rht1 rht1>Rht1 rht1>Rht1 Rht1. This pattern was found for most of the parameters, although differences between genotypes were not always significant. The Rht1 gene had a decreasing effect on all protein and yield components, except on grain weight. Straw nitrogen percentage as well as NHI, was similar in both homozygous genotypes.

In the late sown F_2 population (Table 9), the three Rht genotypes did not differ in their culm height. We can therefore assume that differences among genotypes in other characters are solely due to the influence of the Rht1 gene, not mediated through the effect of height. The Rht1 Rht1 genotype had significantly lower spike and grain protein yield, as well as lower grain weight than the rht rht group. In this genotype, grain protein percentage and grain yield were also reduced, though not significantly.

Table 10 Effects of Rht genes on several characters of the main culm in the early sown F_2 population. Values of a given character designated by different letters differ at the 5% significance level. (Mean ± S.E.).

Character	rht rht	Rht rht	Rht Rht
Culm height (cm)	111.4^{a} ±1.9	95.4^{b} ±0.95	72.0^{c} ±1.67
Straw yield (mg)	3886^{a} ±127	3295^{b} ±62	2587^{c} ±98
Protein % in grains	14.8^{a} ±0.21	14.3^{a} ±0.14	13.6^{b} ±0.22
Spike protein yield (mg)	376.50^{a} ±17.0	341.00^{b} ±7.9	287.00^{c} ±12.1
Grain protein yield (mg)	10.4^{a} ±0.27	10.0^{a} ±0.27	9.3^{b} ±0.23
% N in straw*	0.16^{a} ±0.008	-	0.18^{a} ±0.008
Straw N yield (mg)*	6.10^{a} ±0.44	-	4.40^{b} ±0.45
Harvest Index	0.39^{c} ±0.008	0.41^{b} ±0.005	0.44^{a} ±0.009
NHI*	0.91^{a} ±0.005	-	0.91^{a} ±0.008
Grain yield (mg)	2499^{a} ±112	2344^{a} ±55	2054^{b} ±85
Grain weight (mg)	69.9^{a} ±1.77	69.9^{a} ±0.67	67.9^{a} ±1.07
No. of grains	35.9^{a} ±1.53	33.8^{a} ±0.80	30.2^{b} ±1.14
No. of spikelets	15.2^{a} ±0.21	14.6^{a} ±0.21	13.9^{b} ±0.21
Days from sowing to heading	97.9^{b} ±0.60	99.2^{b} ±0.39	101.2^{a} ±0.72

* Mean of 15 plants of each genotype.

Table 11 Effects of Rht genes on several characters of the main culm in the late sown F_2 population. Values of a given character designated by different letters differ at the 5% significance level. (Mean ± S.E.).

Character	rht rht	Rht rht	Rht Rht
Culm height (cm)	54.1^{a} ±3.0	51.8^{a} ±1.00	52.5^{a} ±1.54
Straw yield (mg)	1718^{a} ±219	1652^{a} ±71	1687^{a} ±83
Protein % in grains	18.2^{a} ±1.14	16.19^{a} ±0.43	17.0^{a} ±0.45
Spike protein yield (mg)	246.6^{a} ±32.1	227.0^{ab} ±11.6	180.4^{b} ±11.0
Grain protein yield (mg)	10.38^{a} ±1.08	7.87^{b} ±0.34	6.68^{b} ±0.24
% N in straw*	0.24^{a} ±0.054	-	0.21^{a} ±0.012
Straw N yield (mg)*	4.45^{a} ±1.32	-	3.54^{b} ±0.24
Harvest Index	0.44^{a} ±0.017	0.44^{a} ±0.009	0.38^{a} ±0.011
NHI*	0.91^{a} ±0.017	-	0.89^{a} ±0.009
Grain yield (mg)	1343^{a} ±157	1311^{a} ±55	1076^{a} ±63
Grain weight (mg)	56.0^{a} ±3.00	46.0^{b} ±1.52	40.0^{b} ±0.96
No. of grains	24.2^{a} ±3.23	29.1^{a} ±0.80	25.1^{a} ±1.37
No. of spikelets	12.6^{a} ±0.80	12.3^{a} ±0.27	11.6^{b} ±0.31
Days from sowing to heading	73.3^{a} ±2.96	69.1^{a} ±0.77	70.3^{a} ±1.23

* Mean of 8 rht rht plants, and 14 Rht Rht plants.

Protein percentage distributions

The distribution of grain protein percentage in the early and late sowing are presented in Figs.3 and 4 respectively. A wide range was found for this traits in the entire populations.

Distribution of grain protein percentage within each homozygous genotype in the two sowings are shown in Figs. 5, 6, 7 and 8. Variation for grain protein percentage was observed within the different genotypes (Figs.5, 6, 7 and 8). In the early sowing, Figs. 5 and 6 show clearly that the rht1 rht1 genotype had higher grain protein percentage than the Rht1 Rht1 genotype : minimum and maximum values of the first were 1% higher than those of the later. In the late sowing, it can be remarked (Figs 7 and 8) that the rht1 rht1 genotype had higher maximum grain protein percentage than the Rht1 Rht1 genotype.

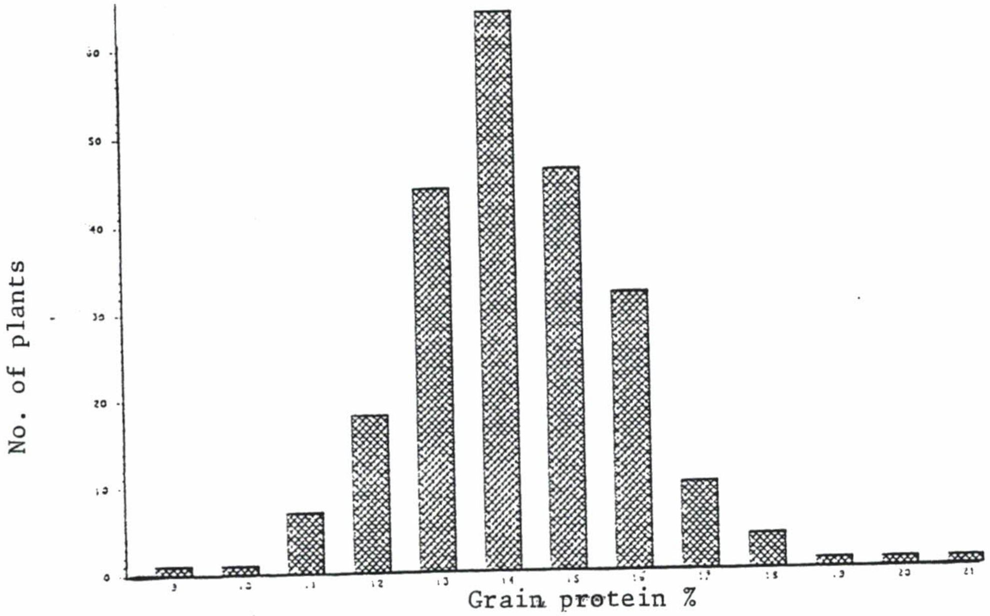

Fig. 3. Distribution of grain protein percentage in the early sown F_2 population.

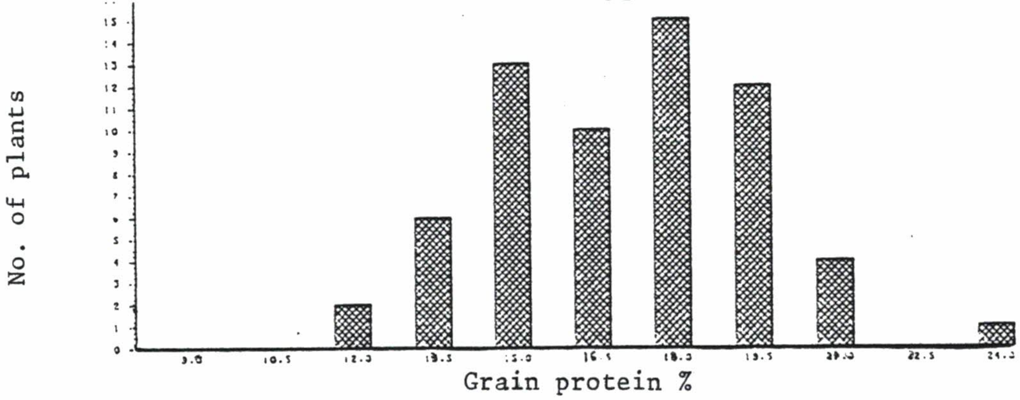

Fig. 4. Distribution of grain protein percentage in the late sown F_2 population.

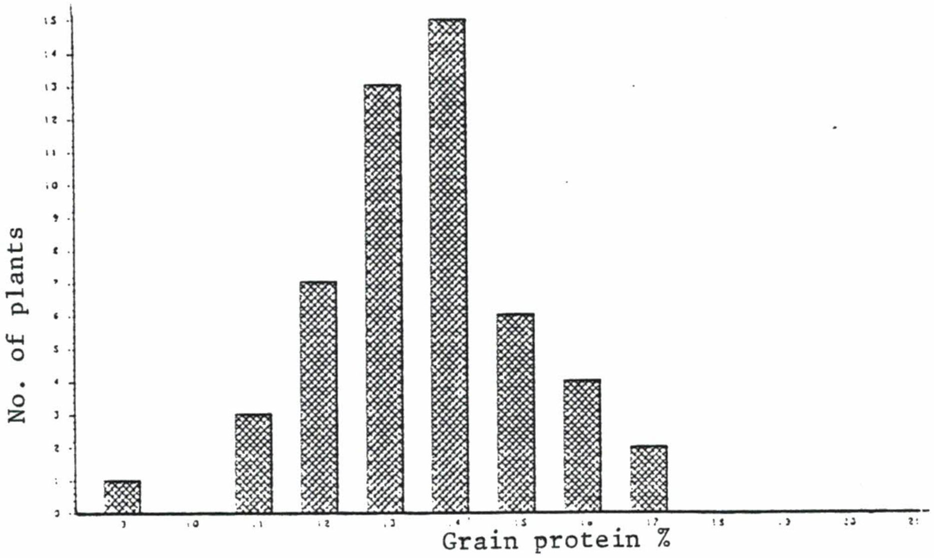

Fig. 5. Distribution of grain protein percentage of the Rht Rht genotype in the early sown F_2 population.

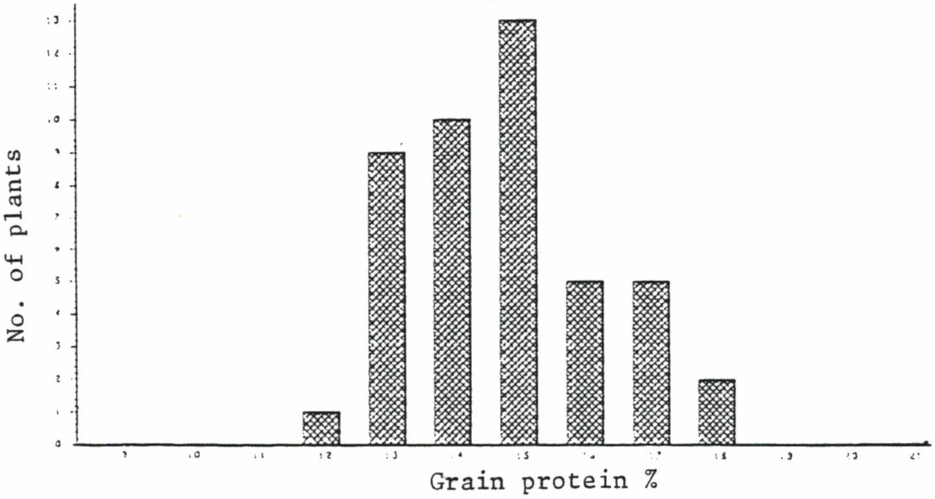

Fig. 6. Distribution of grain protein percentage of the rht rht genotype in the early sown F_2 population.

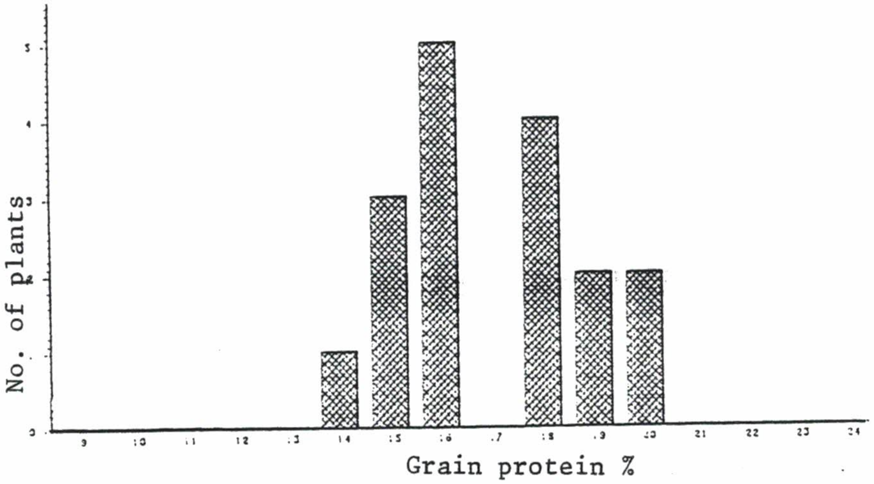

Fig. 7. Distribution of grain protein percentage of the Rht Rht genotype in the late sown F_2 population.

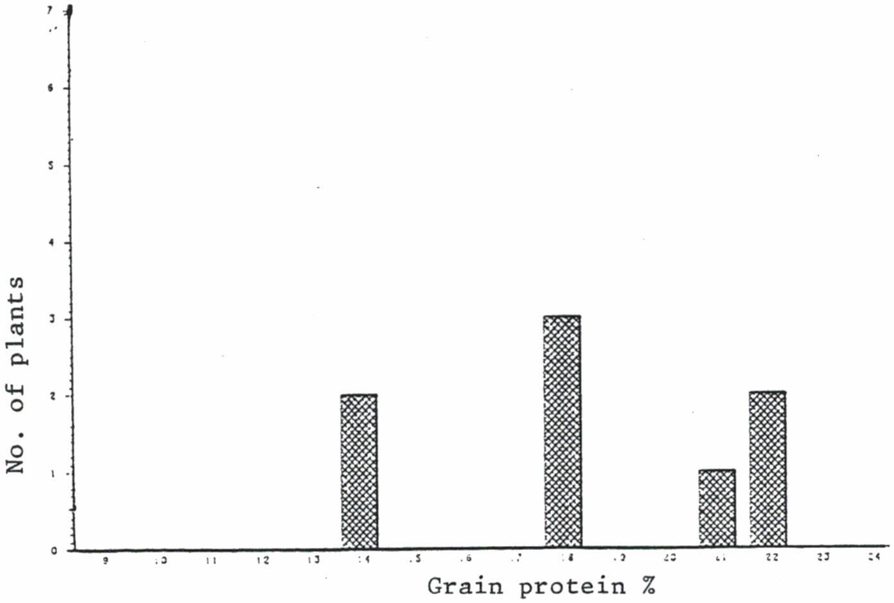

Fig. 8. Distribution of grain protein percentage of the rht rht genotype in the late sown F_2 population.

2. CCC Experiment

CCC affected the plants in different ways (pictures 1, 2 and table 12).

Picture 1:Effect of CCC on line 1243 60 days after sowing; treated plants are on the left side

Picture 2:Effect of CCC on line 899 60 days after sowing; treated plants are on the left side.

Table 12 Effects of CCC on different main culm characters and and tillering of two wheat varieties and of two lines.

Character	Treatment	Varieties		Lines		
		Inbar	870	1243	899	S.E.@
Height (cm.)	control	61.7	65.5	104.9	65.5	1.95
	CCC	54.0*	55.4*	78.6*	61.3	
Straw yield (mg.)	control	3659	2795	4406	2403	71.2
	CCC	3061	2031	3513*	2932	
Grain protein %	control	14.9	13.4	20.7	22.4	0.86
	CCC	12.6	13.7	19.5	19.5	
Spike protein yield (mg.)	control	635	389	423	174	48.6
	CCC	471	424	418	224	
Grain protein yield (mg.)	control	10.1	7.7	10.4	9.4	0.94
	CCC	8.1	7.7	9.5	7.5	
N % in straw	control	0.17	0.21	0.19	0.35	0.02
	CCC	0.15	0.23	0.18	0.26	
Straw N yield (mg.)	control	6.3	5.9	8.1	8.5	0.78
	CCC	4.8	4.7	6.7	7.5	
HI	control	0.54	0.51	0.32	0.27	0.02
	CCC	0.55	0.60*	0.38	0.30	
NHI	control	0.95	0.92	0.90	0.79	0.01
	CCC	0.94	0.94	0.91	0.84	
Grain yield (mg.)	control	4264	2894	2037	912	160
	CCC	3738	3063	2162	1251	
Mean grain weight (mg.)	control	67.8	57.2	50.4	47.7	2.34
	CCC	64.6	55.7	49.2	41.3	
No. grains	control	62.9	50.5	40.4	19.8	2.46
	CCC	57.9	55.0	44.0	30.3	
No. tillers/plant	control	1.74	2.13	1.94	3.45	0.35
	CCC	2.11	2.67	2.62	4.27	
Days from sowing to heading	control	76	81	66	105	2.23
	CCC	80	85	68	112	

* significant at the 5% level.
@ Square root of MSE/5. (MSE = (3(MSE2)+MSE1)/4).

In all cases, except for line 899, height was reduced significantly by the CCC treatment. Straw yield was also reduced by the treatment. CCC increased HI in each of the tested genotype, though this increase was found to be significant only for H-870. Grain protein percentage was reduced in treated plants in Inbar, 1243 and 899, but never significantly. CCC influenced differently yield and yield components of the four genotypes, as it reduced grain yield in Inbar, increased it in 899, while that of 1243 and H-870 were almost not affected. The effect of CCC on protein yield was according to its effect on grain yield. Grain weight was hardly affected by CCC. The differences in grain protein yield between treated and control plants were concomitant with differences in grain protein percentage.

Straw nitrogen yield followed the variations of straw yield. NHI was not affected by the CCC treatment.

DISCUSSION

In the present experiments the relation between plant height and grain protein has been studied genetically and physiologically. The genetical aspect was examined in an F_2 segregating population sown on two dates. The late sowing enabled the comparison between different Rht genotypes having similar height. This approach had never been adopted before to examine the relationship between the Rht genotypes and grain protein. The early sowing provided some information about the physiological aspect of this relationship, i.e, the influence of height, which was further studied in the CCC experiment. In the study of the F_2 population, it was assumed that the background genetic effects was nullified (Gale, 1979), enabling the analysis of the Rht genotypes per se. The protein analysis of F_3 seeds represented the F_2 variation; since in wheat the grain protein percentage is mainly determined by the mother plant (Millet et al 1984).

A decrease in grain protein percent of 1.2% in the Rht1 Rht1 genotype compared to the rht1 rht1 was found in both sowings of the F_2 population (Tables 10 and 11). This may indicate a direct decreasing effect of the Rht gene on grain protein. However, it should be noted in the early sowing that the different Rht genotypes differed significantly in their height. Therefore, the effect of the Rht1 gene on grain protein could have been mediated through their effect on plant height, and the reduction in height could account for the decrease in grain protein percent recorded in the semi-dwarfs (Rht1 Rht1). It was therefore critical to differentiate between the direct gene effect and the physiological influence via height. In this population, the effect of height was studied by dividing the population into the different genetic height groups; relationship between height and protein was then checked within each group. In this way, the effects of the Rht1 gene were nullified, but large variation in height -due to minor genes and environment was still maintained. Correlation coefficient between height and grain protein percentage within each group was low and non-significant (Table 8), indicating that height was not involved in affecting grain protein percentage.

Physiological involvement of height in the determination of grain protein was studied predominantly in the CCC experiment, where the same genotypes had different heights. CCC reduced plant height significantly in three out of the four genotypes, (Inbar, 870 and 1243), while in the fourth (899), no significant effect could be detected. In three genotypes (Inbar, 1243 and 899) CCC had a decreasing effect on grain protein percent, while in the fourth (870), no difference for this trait was observed. However, the reduction in grain protein percentage does not seem to be proportional to the decrease in height. It is therefore more likely that the decrease in grain protein percentage found in CCC treated plants was due to a direct effect of CCC, rather than as a consequence of height reduction.

Information on the effect of CCC on grain protein content is scarce. Crominsky (1977) found a decrease in grain protein percentage of plants treated with CCC. Clark and Fedack (1977), Grugzdev (1975), and Linser et al (1965) found a different distribution of amino acids in CCC treated plants, but did not report any change in total grain protein percentage. In an experiment carried out in pots on during the year of the current work (M. Zaccai, unpublished data), CCC did not affect grain protein percentage of any of the four genotypes studied in the present work. Lack of influence of CCC on protein percentage in a field experiment was also found by Millet ,1985 (personal communication)

Thus, both the analysis of the early sown F_2 population and the CCC experiment demonstrated that in the studied plant material plant height did not play any considerable role in the determination of protein percentage. It seems therefore plausible to assume that the decrease in protein percentage recorded in the Rht1 Rht1 genotype was due to a direct gene effect. The hypothesis of a direct gene effect is strongly supported by the results of the late sowing. In this sowing, where plant height was reduced, and the height differences between genotypes (rht1 rht1, Rht1 rht1 , Rht1 Rht1) were obliterated, the direct effect of the Rht1 gene on grain protein could be estimated. Therefore, the decrease in grain protein percentage found in the Rht1 Rht1 genotypic group could not be attributed to height, but to a direct effect of the Rht1 gene.

Direct effect of the Rht genes on protein level may also be explained either by linkage between the dwarfing genes and genes affecting protein content (Zittelli et al 1983), or by pleiotropy. Linkage may be detected by the presence of recombinants. However, no distinct recombinants were found in this study, as maximum and minimum values of grain protein percentage of the rht1 rht1 genotype were higher or at least equal to those of the Rht1 Rht1 genotype (see

Figs.5 and 7). Larger populations should be examined for recombinants, especially if such linkage is close.

Rht1 may perhaps affect grain protein via its effect on GA sensitivity. GA is known to be involved with some enzyme activity (Stoddart 1971), and it could therefore be hypothesized that the activity of enzymes involved with protein accumulation in the grains may be altered by GA insensitivity of plants carrying Rht genes. For example, Gale and Marshall (1975) reported that alpha-amylase levels were specially low in mature grains of plants carrying the Rht3 dwarfing gene; they associated this fact to GA insensitivity of the alleurone layer of these grains. However, this kind of insensitivity was not found in plants carrying the Norin 10 derived dwarfing genes (Gale and Marshall, 1973, 1975).

Significant decrease in the activity of alpha-amylase in the seeds borne on plants treated with CCC was also observed by Salmon et al (1981). Both Rht1 and Rht2 genes and CCC alter the plant balance of GA. Involvement of this hormone with grain protein would account for the direct effect -not mediated trough height- of the Rht genes and CCC on this trait.

Pleiotropy associated with the Rht -Norin 10 derived- genes was previously demonstrated. Pinthus and Levy (1983), reported that Rht1 and Rht2 have a direct decreasing effect on grain weight. The Rht2 gene was also found to increase grain number per ear (Gale 1979). Gale and Youssefian (1983) observed that Rht1 increased grain number per ear and number of tillers per plant. The assumption that the Rht genes affect a number of agronomic traits by pleiotropy seems more plausible than a linkage between these genes and other genes controlling agronomic traits.

In almost all cases mentioned in the literature where a decreasing effect of the Rht genes on grain protein was reported, this effect was attributed to the smaller nitrogen source of the (semi-)dwarf lines (smaller stems) which could not provide high enough amounts of N to the grains (Gale 1979, Law and Payne 1983, Pepe and Heiner 1979). This particular source-sink relationship was more accentuated in high yielding dwarf and semi-dwarf lines, where simultaneously the N source was reduced while the sink size was increased, leading to a negative correlation between grain yield and grain protein percentage (Corpus et al 1983, Kibite and Evans 1984, Kramer 1979, 1983, Loffler and Bush 1982, Pepe and Heiner 1975). In the present study, the Rht1 gene had a decreasing effect on yield -in agreement with the findings of Pinthus and Levy, 1983- as well as on grain protein percentage. In the early sown F_2 population, Rht1 reduced N source, by decreasing the height, but also diminished the sink size, by decreasing grain yield. This could explain the lack of negative correlation between grain protein percentage and grain yield. Grain and spike protein yield followed the variations in grain weight and grain yield, and were reduced in the Rht1 Rht1 genotype.

Neither CCC nor the Rht1 gene affected N percentage in straw, or NHI, indicating that the partitioning of N was independent of these factors. The relatively low NHI value of line 899 should be attributed to the late and poor development of this line.
The number of days from sowing to heading were apparently not involved

with grain protein percentage. In the early F_2 population, no correlation was found between these two traits.

In the early sowing, the grain protein percentage mean was very close to the low parent (H-870). This may indicate a certain dominance of genes for low protein of the cultivated variety (Millet et al 1984).

Breeding implications

When breeding for higher grain protein percentage in semi-dwarf plants, the decreasing effect of the Rht1 gene on this trait should be taken in consideration. Breeding in lines carrying Norin 10 derived dwarfing genes may be a complex task because of the several pleiotropic effects of these genes on important agronomical traits. However, the possibility of increasing grain protein percentage in such lines by crossing them with high protein plants should not be excluded, as Rht1 gene reduced grain protein percentage only by 1%. Other dwarfing genes (Gale and Youssefian, 1985) which do not affect grain protein could be also introduced in breeding programs.

Selection for grain protein percentage in early generations of crosses between semi-dwarf and tall plants may lead to the elimination of genotypes homozygous for Rht. In the case of such crosses, selection should be made primarily for semi-dwarfism and in the following generations for high grain protein percentage, among plants homozygous for Rht. However, large populations should be available, in order to obtain sufficient amount of semi-dwarf plants.

ABSTRACT

The relationship between plant height and grain protein content was studied in an F_2 population of a cross between a high protein line and a semi-dwarf cultivar, segregating for the dwarfing gene Rht1 and for grain protein percentage. Samples of this population were sown at the normal sowing time and at a late sowing date at which height was reduced and no differences in height between genotypes were observed; enabling the elucidation of the direct relationship between the Rht1 gene and grain protein excluding its effect via culm height. At both sowing dates, grains of the plants homozygous for the dwarfing allele Rht1 had about 1% less protein than grains of plants homozygous for rht1. Additional information about the effects of the Rht1 gene and CCC on yield and on protein content in the straw and the grains is presented. In another experiment, CCC-treated and untreated high protein tetraploid lines and *durum* varieties were tested in order to determine the effect of height on grain protein content in identical genotypes. In this experiment, plant height was not related with grain protein percentage.

The nature of the effect of Rht1 on grain protein percentage as well as implications of this effect on breeding for high protein wheat are discussed.

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הקשר בין גובה הצמח ותכולת חלבון הגרגר בחיטה טטרפלאואידית מהמין Triticum turgidum

הקשר בין גובה הצמח ותכולת חלבון הגרגר נחקר באכלוסיות F2 צאצאי הכלאה בין קו גבה-קומה ועתיר חלבון לזן של חיטה קשה נושאת הגן לננסיות Rht1. אוכלוסיה זו נזרעה במועד הזריעה המקובל וכן במועד מאוחר יותר. הזריעה המאוחרת גרמה להנמכת קומת הצמחים באופן שנמנעו הבדלי גובה בין הגנוטיפים השונים. התאפשרה איפא הערכה של השפעת הגן Rht1 על חלבון בגרגר, שלא דרך השפעתו על גובה הצמח.

בשני מועדי הזריעה נמצא שבגנוטיפים הומוזיגוטיים לגן הננסיות Rht1 היה בממוצע כ-1% פחות חלבון בגרגרים מאשר בהומוזיגוטיים גבוהי-קומה (rht1 rht1).

השפעת ריסוס בחומר מננס(CCC) על תכולת החלבון ועל קומת הצמחים נבחנה בניסוי אחר בשתי שושלות עתירות חלבון ובשני זנים.

לא נמצא קשר עקבי בין הנמכת הצמחים ע"י ה-CCC לבין הפחתת אחוז החלבון בגרגריהם.

אופי הקשר שבין האלל Rht1 לבין אחוז החלבון בגרגר וההשלכות שיש לכך על טיפוח חיטה עתירת חלבון נדונים, כ"כ מובא מידע על השפעות של הגן Rht1 והחומר המננס CCC על יבול ותכולת חלבון בקש ובגרגירים.

מ. פלדמן

הקשר בין גובה הצמח ותכולת חלבון הגרגר בחיטה טטרפלואידית

Triticum turgidum

עבודת גמר מוגשת לפקולטה לחקלאות

של האוניברסיטה העברית בירושלים לשם קבלת התואר

"מוסמך למדעי החקלאות"

מאת

מישל זכאי

הדר תשמ"ו

פברואר 1986