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Molecular markers linked to genes affecting plant height in wheat using a doubled-haploid population

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Abstract Plant height in wheat (*Triticum aestivum* L. em Thell) is known to be under polygenic control. Crosses involving genes *Rht-B1* and *Rht-D1*, located on chromosomes 4BS and 4DS, respectively, have shown that these genes have major effects. Two RFLP loci were found to be linked to these two genes (*Xfba1-4B* with *Rht-B1* and *Xfba211-4D* with *Rht-D1*) by genotyping a population of F_1-derived doubled-haploid lines ['Courtot' (*Rht-B1b* + *Rht-D1b*) × 'Chinese Spring']. Using a well-covered molecular marker map, we detected three additional regions and one interaction influencing plant height. These regions, located on chromosome arms 4BS (near the locus *Xglk556-4B*), 7AL (near the locus *Xglk478-7A*) and 7BL (near the locus *XksuD2-7B*) explained between 5% and 20% of the variability for this trait in this cross. The influence of 2 loci from chromosome 4B (*Xfba1-4B* and *Xglk556-4B*) suggests that there could be a duplication of *Rht-B1* on this chromosome originating from Cv 'Courtot'. Moreover, an interaction effect between loci from chromosome arms 1AS (near the locus *Xfba393-1A*) and 1BL (near the locus *Xcdo1188-1B*) was comparable to or even higher than those of the *Rht-B1b* and *Rht-D1b* alleles. A model including the main effects of the loci from chromosomes 4B and 4D (*Xfba1-4B*, *Xglk556-4B* and *Xfba211-4D*) and the interaction effect between *Xfba393-1A* and *Xcdo1188-1B* is proposed, which explains about 50% of the variation in plant height. The present results are discussed in relation to those obtained using nullisomic or substitution lines.

Key words Plant height · Molecular markers · QTL · Wheat · Doubled-haploid lines

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Introduction

Plant breeders have paid considerable attention to final plant height in order to achieve the best compromise between an adequate lodging resistance and acceptable yield levels. A reduction in plant height is usually obtained by introducing specific dwarfing genes into the genotype. The *Rht-B1b* and *Rht-D1b* alleles (according to the new nomenclature; Börner et al. 1996), previously known as the 'Norin 10-Brevor14' *Rht1* and *Rht2* dwarfing alleles, respectively, have been the most widely used of the dwarfing genes in plant breeding schemes for the last 50 years (for a review, see Gale and Youssefian 1985). Two corresponding genes were located on the short arms of chromosomes 4B and 4D (McVittie et al. 1978), and molecular markers have recently been found to be associated to them (Sourdille et al. 1997).

Nevertheless, other studies indicate that different regions of the genome are also involved in the variation of plant height. Sears (1954), working with aneuploid lines of 'Chinese Spring', observed that nullisomy for most of the 21 chromosomes generated height reduction. Nullisomic lines of the homoeologous groups 1, 2 and 4 were the most effective in reducing plant height. Kuspira and Unrau (1957), who studied three sets of substitution lines of 'Chinese Spring' as recipient with chromosomes from vars 'Thatcher', 'Hope' and 'Timstein' as donors, found that 8 of the 21 wheat chromosome carried genes associated with height. Only chromosome 7B from 'Thatcher' increased

'Chinese Spring' height, while the chromosomes from homoeologous group 4 were most often involved in reducing it. Using the complete set of single chromosome substitution lines of 'Capelle-Desprez' into 'Chinese Spring', Snape et al. (1977) revealed that 17 of the 21 chromosomes displayed genetic variation for plant height. In addition they showed that epistatic effects could be an important component of the variation.

Since the beginning of the 1990s, molecular marker linkage maps of wheat have brought a new tool to enhance the genetic studies of complex agronomic traits. However, owing to the poor level of polymorphism in wheat (Chao et al. 1989) molecular marker maps have been derived from 'interspecific-type crosses', such as crosses between cultivars and synthetic wheats (Gale et al. 1995; Van Deynze et al. 1995; Nelson et al. 1995a,b,c; Marino et al. 1996) or a cross between 'Chinese Spring' and *Triticum spelta* (Liu and Tsunewaki 1991). The dissection of agronomic traits will require working within an intraspecific context in order to use informative markers for marker-assisted selection. Thus, we developed an intervarietal molecular map in wheat using a doubled-haploid (DH) population obtained from a cross between cvs 'Chinese Spring' and 'Courtot' (Cadalen et al. 1997).

The purpose of the study presented here was to use this map to find regions of the genome showing significant associations with plant height. In order to verify the stability of the QTLs detected, we collected height data over several years.

Materials and methods

Plant material and field trials

A population of 275 DH lines was produced by anther culture from F_1 hybrids issued from the cross between the French semidwarf cultivar 'Courtot' (Ct: *Rht-B1b* and *Rht-D1b*) and 'Chinese Spring' (CS). This population has already been described by Félix et al. (1996) and Cadalen et al. (1997). A sample of 106 DH lines was used in the present study. The DH plant height was scored in the greenhouse in 1993 (hereafter denoted 93GH) and in the field in 1993 (spring sowing; one replication), 1994 and 1995 (autumn sowing; two replications each year) on individual plants. An average value was calculated for each genotype. The field trials included a three-row nursery plot (1.5 m) in 1993 (93FT) and two nursery plots (1 row and 3 rows) in 1994 (94R1 and 94R3, respectively) and 1995 (95R1 and 95R3) for each of the 106 genotypes. Sub-blocks of tall, semidwarf and dwarf genotypes were arranged in order to limit competition effects between short and tall stands based on plant height data from greenhouse observations. Nets were placed on the taller genotypes to prevent lodging. In each trial, the height of the parents Ct and CS was evaluated.

Molecular markers and RFLP analysis

The probes used in this study as well as the techniques for DNA extraction, digestion, electrophoresis, blotting and hybridization have been described by Cadalen et al. (1997). The protocol using non-radioactive probes was detailed in Lu et al. (1994) and Sourdille et al. (1996). Some microsatellite sequences (Devos et al. 1995; Röder et al. 1995; Plaschke et al. 1995, 1996) were also mapped on this population. Polymerase chain reaction (PCR) protocols and the silver-staining method for their detection are described in Sourdille et al. (1997).

Mapping and linkage analysis

The intervarietal molecular marker map (named CtCS map) has been described by Cadalen et al. (1997). The associations between molecular markers and plant height (quantitative trait loci, QTLs) were evaluated by one-way analysis of variance (ANOVA) and mutiple-factor ANOVA using the general linear model (GLM) SAS^R procedure (SAS Institute 1991). Interaction effects between all the loci were computed with Splus software (Becker et al. 1992) using a three-way ANOVA model (45,000 combinations tested). Significance thresholds were set at $\alpha = 0.01$ for one-way ANOVA and mutiple-factor ANOVA, and at $\alpha = 0.0005$ for interaction effects.

Results

Trait analysis

The two parents of the DH population, 'Courtot' (Ct: *Rht-B1b* + *Rht-D1b*) and 'Chinese Spring' (CS), were very different, and height ranged between 55 and 75 cm (average of 64 cm at Clermont-Ferrand) for Ct and between 110 and 133 cm (average of 122 cm at Clermont-Ferrand) for CS. The magnitude of variation between the highest and the shortest lines of the population was between 85 and 128 cm. The difference in height between Ct and CS is supposed to be mostly due to the presence of the dwarfing alleles *Rht-B1b* and *Rht-D1b* in Ct. Despite the fact that we found a high heritability for this trait on this population ($h^2 = 0.8$; Cadalen 1996) the shape of the distributions (Fig. 1) did not produce the three expected classes for the segregation of the 2 major alleles *Rht-B1b* and *Rht-D1b*. This result strengthened the hypothesis that factors other than these 2 alleles were involved in the trait variation.

The normality of the distributions was tested using the Pearson's chi-square test of fitness (Dagnelie 1975: data not shown). The distributions in plant height were found not to differ significantly from normality at $\alpha = 0.01$ for the data collected in 1993 (93GH and 93FT; Fig. 1a and b, respectively) and in 1994 (94R1 and 94R3; Fig. 1c and d). This was not the case for the 1995 data (95R1 and 95R3; Fig. 1e and f). The absence of normality was expected as the consequence of the presence of the 2 major alleles, *Rht-B1b* and *Rht-D1b*, leading to a multimodal distribution.

Distribution of the trait for the DH population (Fig. 1) indicated the presence of transgressive lines. Thus, the dispersal of other regions of the genome between the parents may influence this character. In addition, the presence in the population of individuals

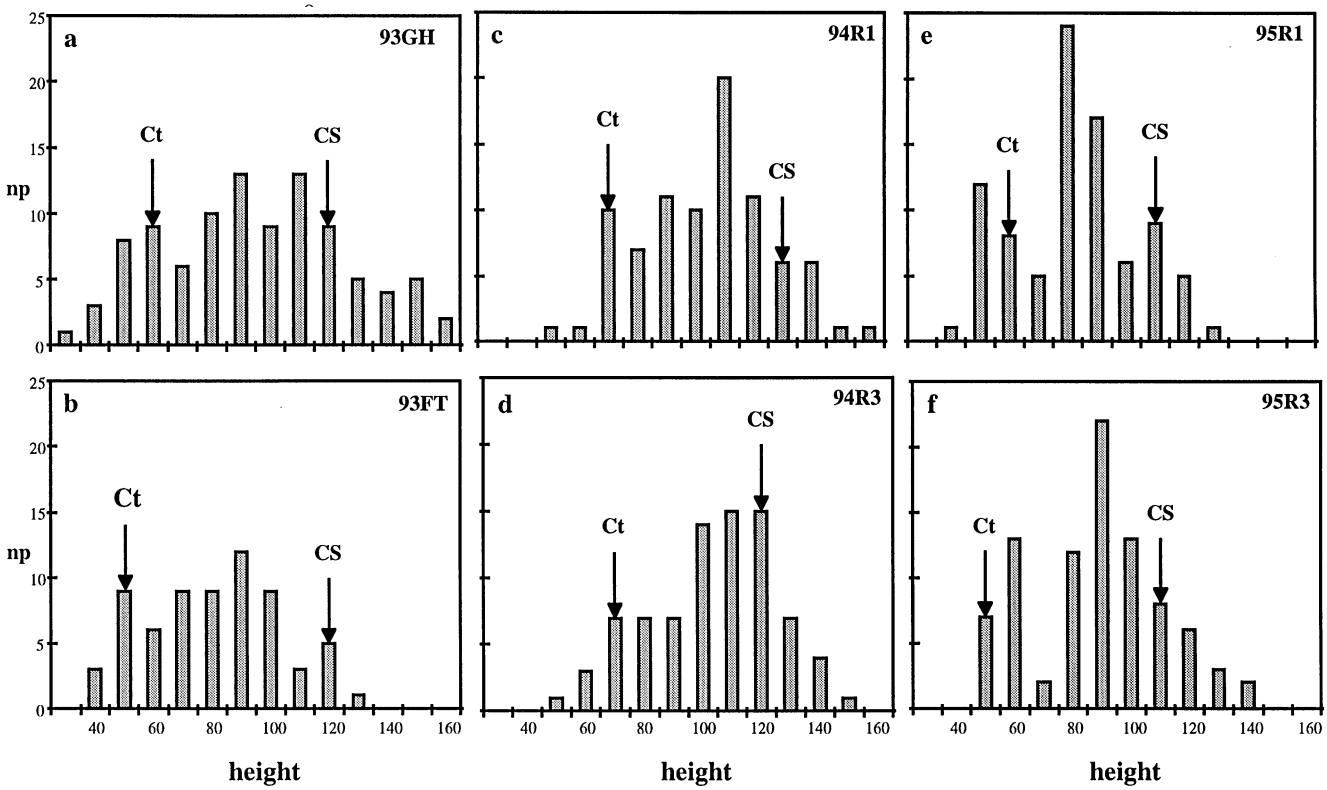

Fig. 1a–f Distribution of plant height values for the different field experiments. **a** 1993 greenhouse (93GH), **b** 1993 field trial (93FT), **c** 1994 1-row nursery plots (94R1), **d** 1994 3-row nursery plots (94R3), **e** 1995 1-row nursery plots (95R1), **f** 1995 3-row nursery plots (95R3)

with a stature shorter than that of the parent carrying the two dwarfing alleles *Rht-B1b* and *Rht-D1b* (Ct) suggested that positive alleles for plant height reduction could be found in the tallest parent.

One-way ANOVA

Table 1 summarizes the most significant markers of chromosomes 4B and 4D associated with a reduction in plant height. This analysis revealed the importance of locus *Xglk556-4B* on the short arm of chromosome 4B. This marker explained between 13% and 21% of the variation of the trait with an additive effect ranging between 8 and 11 cm. This effect was similar to those already described in the literature for *Rht-B1* (Allan 1970; Börner et al. 1993). Unfortunately, and although it was assigned to chromosome 4BS, it was not possible to link *Xglk556-4B* with certainty to the markers located on the long arm of this chromosome ($\theta = 0.38$; Fig. 2).

The locus *Xfba211-4D* was also significantly linked with plant height. It explained between 8% and 17% of the variation depending on the experiment, with an additive effect ranging between 7 and 9 cm. This effect was smaller than those expected for *Rht-D1* (10 cm) and than the one of *Xglk556-4B*. This locus remained unlinked to any other marker, although it was assigned to chromosome 4D (Cadalen 1996). In addition, it was also located on the same chromosome in a F_2 population (Sourdille et al. 1997). It was likely that the effect detected was due to the gene *Rht-D1*.

Eight other loci were also significantly associated with plant height (Table 2). They were assigned as follows: *Xfba347-3D* and *Xfba213-3D* on chromosome 3DL, *Xwg1026-5A* on chromosome 5AL, *Xglk510-5B* on chromosome 5BL, *Xfbb250-6B* on chromosome 6BL, *Xglk547-6D* on chromosome 6DS, *Xglk478-7A* on chromosome 7AL and *XksuD2-7B* on chromosome 7BL. The first locus mentioned (*Xfba347-3D*) remained unlinked to the rest of chromosome 3D and was not mapped (Cadalen et al. 1997). Markers *Xfba347-3D* and *Xfba213-3D* could detect the same locus since they were both assigned to the same chromosome arm.

The effects of these markers were lower than those of the loci closer to the *Rht* genes (between 7% and 20% of the variation), but they did reach 20% in some cases (*XksuD2-7B*: 93FT). Some loci were only detected in one experiment (*Xwg1026-5A*, *Xglk510-5B*, *Xfbb250-6B*). This may be explained either by genotype-by-environment interactions or by statistical artefacts (false positive). The effect of locus *Xglk547-6D* on 6DS seemed to be due to an environmental effect since it was only revealed in 1995 (Table 2: 95R1 and 95R3). On the other hand, 2 others (*Xglk478-7A* on 7AL and *XksuD2-7B* on 7BL) were identified in most of the experimental

Table 1 Markers of chromosomes 4B and 4D associated with plant height at a significance threshold $\alpha = 0.01$. Only the most significant locus of each chromosome arm concerned is indicated

Marker	Chromosome arm	Field experiments[a]	*F* value	*P*	*df*	$R^{2\,b}$	+ allele[c]	Add[d]
Xfba211-4D	4DL	93GH	9.12	0.0033	94	0.088	CS	9.24
		93FT	ns	ns	ns	ns	ns	ns
		94R3	8.59	0.0044	78	0.099	CS	7.09
		94R1	7.57	0.0073	81	0.085	CS	6.62
		95R3	17.08	0.0001	85	0.167	CS	9.15
		95R1	16.48	0.0001	85	0.162	CS	8.29
Xglk556-4B	4BS	93GH	14.71	0.0002	95	0.134	CS	11.28
		93FT	17.13	0.0001	64	0.211	CS	10.56
		94R3	17.51	0.0001	80	0.179	CS	9.40
		94R1	19.59	0.0001	83	0.191	CS	9.76
		95R3	15.25	0.0002	87	0.149	CS	8.52
		95R1	16.81	0.0001	87	0.162	CS	8.17

[a] 93GH = 1993 greenhouse, 93FT = 1993 field trial, 94R3 = 1994 3-row nursery plots, 94R1 = 1994 1-row nursery plots, 95R3 = 1995 3-row nursery plots, 95R1 = 1995 1-row nursery plots
[b] R^2 = Coefficient of determination of the locus with the main effect
[c] Origin of alleles increasing plant height
[d] Additive effect of the locus

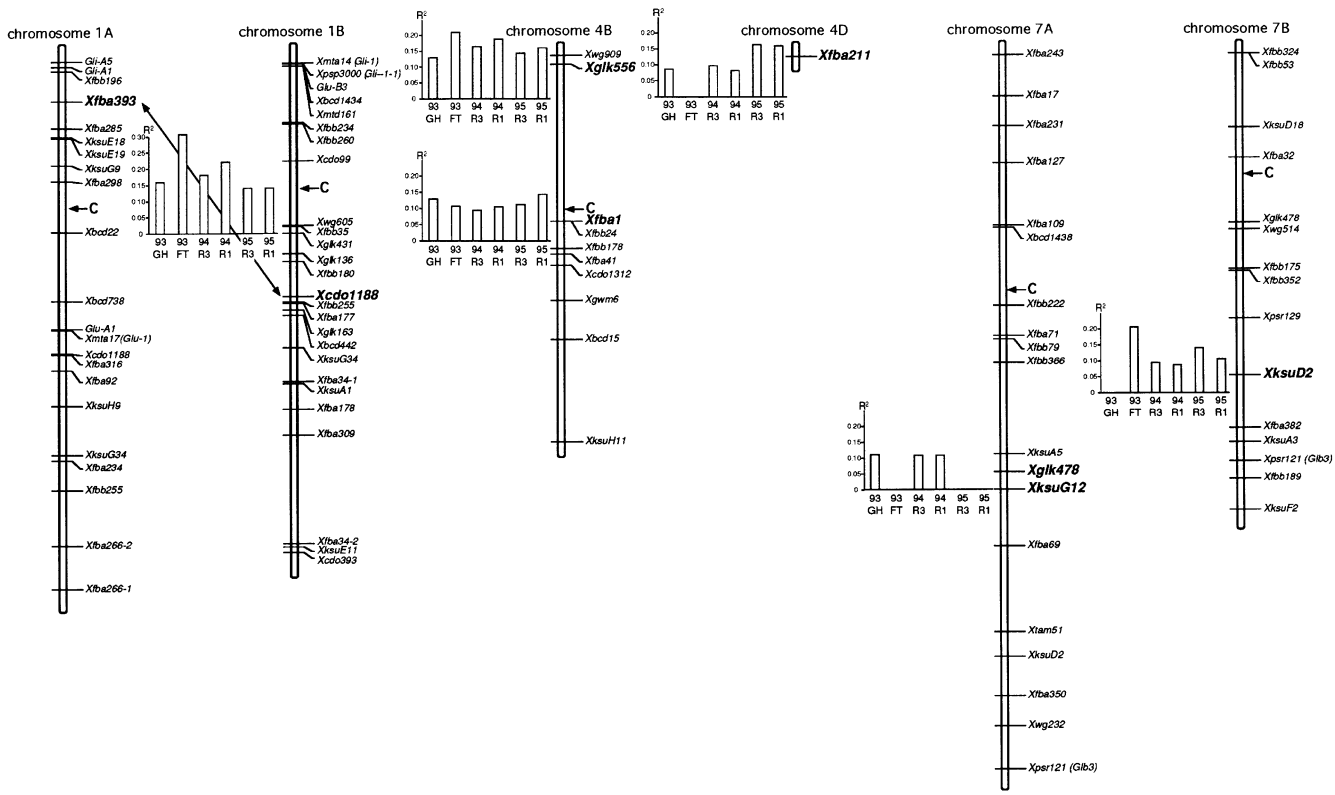

Fig. 2 Main regions of the genome involved in plant height variation detected with the DH population CtCS

conditions (greenhouse: 93GH, or field: 93FT, 94R1, 94R3, 95R1, 95R3).

The alleles from CS at loci *Xglk556-4B* and *Xfba211-4D* increased height (Table 1), which was also consistent with the presence of the *Rht-B1b* and *Rht-D1b* alleles in cv 'Courtot'. On the other hand, the allele from CS at locus *Xglk478-7A* decreased height (Table 2), which is contrary to the effect of locus *XksuD2-7B* which increased it. This may explain the occurrence of transgressive lines in the CtCS population.

Table 2 Markers associated with plant height at a significance threshold $\alpha = 0.01$. Only the most significant locus of each chromosome arm is indicated. Markers from chromosomes 4B and 4D carrying the *Rht-B1b* and *Rht-D1b* alleles are omitted. Abbreviations are the same as in Table 1. Markers in bold characters are consistent across most of the experiments

Experiments	Markers	Chromosome arm	*F* value	*P*	*df*	R^2	+ allele	Add
93GH	*Xfbb250-6B*	6BL	7.53	0.0073	95	0.073	CS	8.48
	Xglk478-7A	**7AL**	**11.66**	**0.0010**	**90**	**0.115**	**Ct**	**10.37**
93FT	*Xfba347-3D*	3DL	10.66	0.0018	62	0.147	Ct	9.22
	XksuD2-7B	**7BL**	**16.54**	**0.0001**	**64**	**0.205**	**CS**	**10.43**
94R3	*Xwg1026-5A*	5AL	9.55	0.0028	80	0.107	CS	7.24
	Xglk510-5B	5BL	7.19	0.0089	79	0.083	CS	6.44
	Xglk478-7A	**7AL**	**10.33**	**0.0019**	**75**	**0.121**	**Ct**	**7.79**
	XksuD2-7B	**7BL**	**8.17**	**0.0055**	**78**	**0.095**	**CS**	**6.82**
94R1	***Xglk478-7A***	**7AL**	**10.77**	**0.0015**	**78**	**0.121**	**Ct**	**7.86**
	XksuD2-7B	**7BL**	**7.69**	**0.0069**	**81**	**0.087**	**CS**	**6.56**
95R3	*Xfba213-3D*	3DL	8.32	0.0050	82	0.092	CS	6.67
	Xglk547-6D	6DS	7.61	0.0071	85	0.082	Ct	6.22
	XksuD2-7B	**7BL**	**14.03**	**0.0003**	**85**	**0.142**	**CS**	**8.21**
95R1	*Xfba213-3D*	3DL	9.73	0.0025	82	0.106	CS	− 6.60
	Xglk547-6D	6DS	8.59	0.0043	85	0.091	Ct	6.22
	XksuD2-7B	**7BL**	**10.03**	**0.0021**	**85**	**0.106**	**CS**	**6.53**

Multiple factor analysis

The effect of the gene located close to *Xglk556-4B* was strong since it was detected with markers located on the long arm of chromosome 4B (Cadalen 1996). A three-way analysis of variance was performed to detect any possible effects of markers on plant height that were hidden due to the presence of the major loci. This was accomplished by including *Xglk556-4B* and *Xfba211-4D* in the model and looking for QTLs in the residuals. Results are given in Table 3. An additional locus on chromosome 4BL (*Xfba1-4B*) was found to be highly significant and consistent across all the experiments. *Xfba1-4B* explained between 9% and 14% of the variability of the trait with an additive effect ranging between 7 and 11 cm, which was similar to the effect of *Xglk556-4B*. Because *Xfba1-4B* was located close to the centromere (Fig. 2) it was likely that this locus, rather than *Xglk556-4B*, detected the effect of *Rht-B1*.

The two regions of chromosomes 7AL and 7BL previously detected in the one-way ANOVA were again detected. The *XksuG12-7A* locus on chromosome 7AL was found to be the most significantly associated with plant height rather than *Xglk478-7A*. These 2 loci were strongly linked (6% recombination) and the QTL was probably located between them. Additional loci were found, but they were not consistent across the experiments.

Interaction effects

Interaction effects between loci were analysed to test for allelic associations on plant height. Table 4 summarizes the results of the analysis. None involves a locus with a significant individual effect. A significant interaction at $\alpha = 0.0005$ was observed between a set of loci located on chromosome arm 1AS and another group situated on chromosome arm 1BL. The most significant interaction appeared between loci *Xfba393-1A* and *Xcdo1188-1B* in four of the six experiments. In the other two, interaction was found between the latter and *XGliA1*, a neighbouring locus of *Xfba393-1A* (7% recombination). The magnitude of these interactive effects varied depending on the experiment. However, these effects were comparable (e.g. 94R1 or 94R3: Table 4) and sometimes higher (e.g. 93FT: Table 4) than those of markers *Xglk556-4B* and *Xfba211-4D* (between 8% and 21%: Table 1). In each case, positive effects (increasing plant height) appeared in coupling phase when both alleles came from the same parent (CS or Ct), while the combination of alleles coming from different parents (repulsion) was associated with a decrease in plant height.

Other interactions were detected at $\alpha = 0.001$ (data not shown) but they were specific to one year or one replication, and the percentage of variability explained by each of these regions was weak. This suggests that those interactions were caused by environmental effects or were due to artefacts.

General model

Figure 2 summarizes the most important regions of the genome detected in this study that influence plant height. To find the best model explaining plant height by marker genotypes, we used the STEPWISE procedure from GLM (SAS Institute 1991). The different

Table 3 Markers associated with plant height at a significance threshold $\alpha = 0.01$ after substraction of the effects of the loci *Xglk556-4B* and *Xfba211-4D*. Only the most significant locus of each chromosome arm is indicated. Abbreviations are the same as in Table 1. Markers in bold characters are consistent across most of the experiments

Experiments	Markers	Chromosome arm	*F* value	*P*	*df*	R^2	+ allele	Add
93GH	***Xfba1-4B***	**4BL**	**18.71**	**0.0000**	**89**	**0.133**	**CS**	**11.60**
	XksuG12-7A	**7AL**	**8.80**	**0.0038**	**92**	**0.067**	**Ct**	**9.68**
93FT	***Xfba1-4B***	**4BL**	**10.29**	**0.0021**	**60**	**0.106**	**CS**	**7.49**
	XksuD2-7B	**7BL**	**13.53**	**0.0005**	**62**	**0.128**	**CS**	**10.43**
94R3	***Xfba1-4B***	**4BL**	**11.49**	**0.0011**	**74**	**0.094**	**CS**	**7.72**
	Xwg1026-5A	**5AL**	**9.26**	**0.0032**	**76**	**0.076**	**CS**	**7.17**
	XksuG12-7A	**7AL**	**8.43**	**0.0048**	**76**	**0.070**	**Ct**	**7.57**
	XksuD2-7B	**7BL**	**8.27**	**0.0053**	**74**	**0.068**	**CS**	**7.25**
94R1	***Xfba1-4B***	**4BL**	**13.34**	**0.0005**	**76**	**0.103**	**CS**	**7.85**
	XksuG12-7A	**7AL**	**10.77**	**0.0030**	**79**	**0.073**	**Ct**	**7.74**
	XksuD2-7B	**7BL**	**7.22**	**0.0088**	**77**	**0.057**	**CS**	**7.05**
95R3	***Xfba1-4B***	**4BL**	**16.49**	**0.0001**	**81**	**0.110**	**CS**	**6.93**
	XksuD2-7B	**7BL**	**12.74**	**0.0006**	**81**	**0.085**	**CS**	**8.46**
	Xpsr103-7D	7DS	7.71	0.0068	80	0.058	CS	5.64
95R1	*Xglk538-3B*	3BS	9.69	0.0025	82	0.068	Ct	4.40
	Xfba1-4B	**4BL**	**22.39**	**0.0000**	**81**	**0.140**	**CS**	**7.28**
	Xfbb95-6A	6AL	7.01	0.0097	82	0.052	CS	3.66
	XksuD2-7B	**7BL**	**7.31**	**0.0084**	**81**	**0.052**	**CS**	**6.51**

Table 4 Markers from chromosomes 1AS (Marker 1A) and 1BL (Marker 1B) showing significant interactions with plant height at $\alpha = 0.0005$. Only the most significant interaction is considered. Abbreviations for field experiments are the same as in Table 1

Field experiment	Marker 1A	Marker 1B	P × 1000[a]	R^2int.[b]	R^2tot.[c]	Interaction effects	
						Coupling[d]	Repulsion
93GH	*Xfba393-1A*	*Xcdo1188-1B*	0.035	0.173	0.188	+ 13.39	− 13.39
93FT	*Xfba393-1A*	*Xcdo1188-1B*	0.001	0.322	0.336	+ 13.41	− 13.41
94R3	*Xfba393-1A*	*Xcdo1188-1B*	0.089	0.184	0.185	+ 9.86	− 9.86
94R1	*Xfba393-1A*	*Xcdo1188-1B*	0.011	0.224	0.224	+ 10.96	− 10.96
95R3	*XGliA1-1A*	*Xcdo1188-1B*	0.476	0.142	0.147	+ 8.53	− 8.53
95R1	*XGliA1-1A*	*Xcdo1188-1B*	0.484	0.124	0.144	+ 7.86	− 7.86

[a] *F* probability × 1000
[b] Coefficient of determination explained by the interaction between marker 1 and marker 2
[c] Total coefficient of determination explained by the individual effect of markers 1 and 2 and the interaction effect between markers 1 and 2
[d] Coupling means that interactive alleles come from the same parent and repulsion that they come from different parents

Table 5 Coefficient of determination (R^2) explained by the model including the main effects for loci *Xglk556-4B*, *Xfba211-4D* and *Xfba1-4B* and the interaction between loci *Xfba393-1A* and *Xcdo1188-1B*. Abbreviations for field experiments are the same as in Table 1

Field experiment	*df*	R^2	PR[a] (cm)	OR[a] (cm)
93GH	80	0.451	59–135	37–165
93FT	57	0.525	54–111	40–133
94R3	68	0.502	79–138	58–151
94R1	67	0.528	79–136	59–161
95R3	71	0.480	55–112	50–140
95R1	71	0.526	60–118	45–130

[a] PR is the range predicted by the model among the population while OR is the range observed (in cm)

R^2 values as well as the ranges of variation explained by the model are indicated in Table 5. This model includes main effects for loci *Xglk556-4B*, *Xfba211-4D* and *Xfba1-4B* and the interaction between loci *Xfba393-1A* and *Xcdo1188-1B*. Loci from chromosomes 7A and 7B were omitted to prevent the model from being overfitted. This model accounted for 45.1% to 52.8% of the total phenotypic variation for plant height.

Discussion

Wheat breeders have mostly used the dwarfing alleles *Rht-B1b* and *Rht-D1b* to decrease plant height in wheat.

In this study, we were able to find 2 loci (*Xfba1-4B* and *Xfba211-4D*) associated with these two genes (*Rht-B1* and *Rht-D1,* respectively). *Rht-D1* was associated with only 1 marker. It is located on the D genome (chromosome 4D) which has often been mentioned to be less polymorphic than the A and B genomes (Chao et al. 1989; Kam-Morgan et al. 1989; Liu and Tsunewaki 1991; Cadalen et al. 1997). This may explain the fact that we only found a few markers on this chromosome.

Locus *Xglk556-4B* located on 4BS was also found to be linked to plant height in Ct × CS. This locus was mapped in the same region in a F_2 population ('Renan × Camp-Rémy'; Sourdille et al. 1997). It was found to be strongly associated with plant height in the Ct × CS population, whereas this was not the case in Re × CR, indicating that plant height in the CtCS cross would be mostly controlled by two different genes located on chromosome 4B. This may suggest that there could be a duplication of *Rht-B1* on chromosome 4B from Ct or that there is a second gene with an effect similar to the one of *Rht-B1*. This would explain why we found two different genes on this chromosome in our study, while it is generally admitted that there is only one.

Other regions of the genome were also involved in the expression of this trait. Locus *XksuD2-7B* on chromosome 7BL explained a high percentage of variability for this trait (between 8% and 20% depending on the year). Law (1967) revealed a linkage between a factor involved in plant height variation and the resistance gene *Pm5* located on this chromosome arm. Gale et al. (1995) showed a strong linkage between *XksuD2-7B* and *Pm5* (about 1 cM). The QTL observed in the present study could be the same as that previously detected by Law. Another locus on chromosome arm 7AL (*Xglk478-7A*) was significantly involved in plant height in our study. Hyne et al. (1994) also revealed a significant linkage with plant height in the interval between the loci *Xpsr117-7B* and *Xpsr150-7B*. These 2 loci flanked locus *Xglk478*-7B on the CtCS map (Cadalen et al. 1997). This suggests that the QTL we detected on chromosome arm 7AL, close to the locus *Xglk478-7A*, could be homoeologous to the one pointed out by Hyne et al. (1994), which fell just on the locus *Xglk478-7B*. In addition, genes conferring gibberellic acid insensitivity have been identified in rye (Börner and Melz 1988; Börner 1990). These genes are located on chromosome arm 7RL of rye (Melz et al. 1992) and could thus be homoeologous to one or both of those found on chromosome arms 7AL and 7BL in our study.

A significant interaction appeared between two groups of markers located on chromosome arms 1AS and 1BL, especially between the loci *Xfba393-1A* and *Xcdo1188-1B*. The effect of these two chromosomes on plant height has been described by Sears (1954) using nullisomic lines of 'Chinese Spring' (CS). Our study indicated that a combination of alleles issued from the same parent (Ct or CS) induced an increase in plant height. This suggests that in Sears's study, interaction effects between the 2 CS alleles involved were broken in nullisomic lines. Consequently, a decrease in height was observed. Our results underline the fact that studies using aneuploid lines reveal not only gene effects per se but also interaction effects.

Our experiments revealed only 5 main loci (*Xfba1-4B*, *Xfba211-4D* linked to the *Rht* genes, *Xglk556-4B*, *Xglk478-7A*, *XksuD2-7B*) and one interaction (*Xfba393-1A* Xcdo1188-1B*) to be associated to plant height. They were located on seven different chromosome arms (1AS, 1BL, 4BS, 4BL, 4DS, 7AL, 7BL) while at least 17 among the 21 chromosomes have been described as influencing this trait (Sears 1954; Kuspira and Unrau 1957; Snape et al. 1977). One possibility is that some of the genes involved in the wheat plant height pathway do not show any allelic variation between the two parents (Ct and CS). Consequently, no correlation can be pointed out in these regions. Furthermore, the coverage of the genome is not complete in the CtCS map, particularly in the D genome (Cadalen et al. 1997). There could be associations with D-genome-specific markers which show no polymorphism between the two parental lines, or some of the markers, not yet mapped, would have been able to indicate a correlation with plant height. It is also possible that the effect of some genes could be too weak to be detected within a population of 106 DH plants.

Alleles increasing height can be found in the shortest line (Ct), whereas some decreasing it issue from the tallest (CS). This result is in accordance with the presence of transgressive lines (shorter than Ct or higher than CS) in the CtCS population. Although *Rht* genes have long been known to be important for plant height, we show that they do not explain all the variation for this trait. Modifying factors increase the variation in height explained by the two *Rht* genes from about 30% to more than 50%. Our study confirms that plant height is under polygenic control, even though this character is mostly influenced by the two dwarfing genes, *Rht-B1* and *Rht-D1*. We were able to characterize more precisely some of the regions associated with this trait. Our results should now be validated in a multilocal trial and on a collection of different genotypes.

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