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Molecular mapping of gibberellin-responsive dwarfing genes in bread wheat

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Abstract Opportunities exist for replacing reduced height (*Rht*) genes *Rht-B1b* and *Rht-D1b* with alternative dwarfing genes for bread wheat improvement. In this study, the chromosomal locations of several height-reducing genes were determined by screening populations of recombinant inbred lines or doubled haploid lines varying for plant height with microsatellite markers. Linked markers were found for *Rht5* (on chromosome 3BS), *Rht12* (5AL) and *Rht13* (7BS), which accounted for most of the phenotypic variance in height in the respective populations. Large height differences between genotypes (up to 43 cm) indicated linkage to major height-reducing genes. *Rht4* was associated with molecular markers on chromosome 2BL, accounting for up to 30% of the variance in height. Confirming previous studies, *Rht8* was linked to markers on chromosome 2DS, whereas a population varying for *Rht9* revealed a region with a small but significant height effect on chromosome 5AL. The height-reducing effect of these dwarfing genes was repeatable across a range of environments. The molecular markers developed in this study will be useful for marker-assisted selection of alternative height-reducing genes, and to better understand the effects of different *Rht* genes on wheat growth and agronomic performance.

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Introduction

Dwarfing or reduced height (*Rht*) genes have been associated with large increases in the yield potential of cereals and have been a key component of the Green Revolution since they were introduced in wheat and rice breeding programs some 40–50 years ago (Evans 1993). Most current wheat varieties contain *Rht-B1b* (formerly *Rht1*) or *Rht-D1b* (formerly *Rht2*), which were transferred from the Japanese variety 'Norin10' into a wide range of CIMMYT germplasm before being taken up by other wheat breeding programs worldwide (Gale et al. 1985). These height-reducing genes are located on homoeologous chromosomes 4BS and 4DS and encode proteins involved in gibberellin (GA) signal transduction (Peng et al. 1999). By conferring insensitivity to GA, these genes have pleiotropic effects on plant growth, causing reductions in coleoptile length and seedling leaf area (Allan et al. 1962; Whan 1976; Rebetzke et al. 2001). Other dwarfing genes that do not confer GA insensitivity may therefore be more suitable in reducing final plant height without compromising early plant growth. The GA-responsive dwarfing genes *Rht8* and *Rht9* were introduced from the Japanese landrace Akagomugi into southern European varieties developed by the Italian wheat breeder N. Strampelli in the 1920s (Lorenzetti 2000). These dwarfing genes do not affect coleoptile length or seedling vigour (Rebetzke et al. 1999), and are being introduced into some Australian wheat varieties as replacements for the GA-insensitive dwarfing genes (Rebetzke and Richards 2000; Bonnett et al. 2001).

Other height-reducing genes have been reported by Konzak (1988), who listed 20 *Rht* genes in total including two additional GA-insensitive genes, *Rht3* (*Rht-B1c*) and *Rht10* (*Rht-D1c*) that are allelic *Rht-B1b*

and *Rht-D1b*, respectively. From the remaining *Rht* genes, Ellis et al. (2004) identified some genes that reduce adult plant height without affecting early growth. Further studies will examine the potential of these genes for use in wheat improvement.

The aim of this study was to map the most promising of these dwarfing genes and identify linked microsatellite markers that may be useful for the marker-assisted transfer of these genes in a breeding program. We generated segregating populations and used bulked segregant analysis (BSA) to identify chromosomal regions and molecular markers linked to *Rht4*, *Rht5* and *Rht13*. We also present new markers linked to *Rht8* and *Rht12* to add to previously published mapping information on these genes.

Materials and methods

Mapping population development

Seed of bread wheat (*Triticum aestivum* L.) obtained from the Australian Winter Cereals Collection (Tamworth, Australia) or breeders stocks, were used as sources of alternative dwarfing genes in a range of crosses (Table 1). Either doubled haploid lines or recombinant inbred lines (RILs), with at least six generations of self-pollination, were generated from these crosses.

Height phenotyping

The populations were grown at several locations in the Eastern Australian wheat belt (Table 1). Diseases and weeds were controlled, and nutrition was adequate for yield in those environments. The plots were irrigated at the Ginnindera (Canberra) and Griffith experimental stations.

The lines were grown as 2-m-long rows or plots (5 m long and five rows wide, with 18 cm between rows). Heights were measured at maturity in the middle row, at three positions along each plot.

Molecular mapping

For extracting DNA, seeds or leaves were freeze-dried in deep-well microtiter plates (Integrated Sciences). The samples were ground by adding 5-mm stainless steel beads to the wells and shaking the plates in a vibration mill (Qiagen, Hilden, Germany) for 4 min at a frequency of 29 s^{-1}. The ground material was incubated for 1 h at 65°C with 600 µl of 0.1 *M* Tris-HCl (pH 8.0), ethylenediaminetetraacetic acid (pH 8.0) and 1.25% SDS. Three hundred microlitres of 6 *M* ammonium acetate were added to the samples, which were then incubated for 15 min at 4°C and centrifuged (30 min at 1,610 *g*). The supernatants were then precipitated (360 µl isopropanol, 5 min room temperature, 30 min centrifugation at 1,610 *g*). The pellets washed with 70% ethanol, briefly air-dried and dissolved in 300 µl distilled water overnight. The plates were then centrifuged (1,610 *g*) and 250 µl of the extracts transferred to a fresh plate.

The PCR conditions were as follows (20 µl total volume): 1X Hotstar Buffer, 1 µl template DNA, 4 nmole dNTPs, 10 pmole each forward and reverse primers and 1 U Hotstar *Taq* polymerase (Qiagen). Amplification was carried out on a thermal cycler running the following program: 5 min at 94°C; seven cycles (30 s at 94°C; 30 s at 65°C; 1 min, 20 s at 72°C) with a 1°C drop in annealing temperature at each cycle; 30

Table 1 Reduced height (*Rht*) gene mapping populations and field-testing environments. *DH* Doubled haploid, *RIL* recombinant inbred line

Population	Type	Parents	Accession no.[a]/reference	*Rht* genotype	Height Data		
					Trial Location[b]	Year	Scale
Vigour 18 × Burt *ert*	DH	Vigour 18	Richards and Lukacs (2002)	Tall	GES	2002	Rows
		Burt *ert* 937	AUS15997	*Rht4*	GES	2003	Rows
Vigour 18 × Marfed M	RIL	Vigour 18	Richards and Lukacs (2002)	Tall	Gundi	2002	Plots
		Marfed M mutant	AUS13741	*Rht5*			
Chuan Mai 18 × Mara	RIL	Chuan Mai 18	AUS24482	*Rht8*	Moom	1999	Plots
		Mara	AUS10472	*Rht8, 9*	Moom	2000	Plots
					Moom	2001	Plots
					Condo	2001	Plots
					Gundi	2001	Plots
Vigour 18 × Mercia 12	RIL	Vigour 18	Richards and Lukacs (2002)	Tall	Gundi	2002	Rows
		Mercia 12		*Rht12*	GES	2003	Rows
Chuan Mai 18 × Magnif M	RIL	Chuan Mai 18	AUS24482	*Rht8*	Gundi	2002	Rows
		Magnif 41 *ert*1	AUS17520	*Rht13*	GES	2003	Plots
					Griffith	2004	Plots

[a]The accession number of the parental lines from the Australian Winter Cereal Collection (Tamworth, Australia)

[b]*GES* Ginnindera experimental station, Canberra, ACT; *Gundi* Gundibinjal, Stockingbingal, NSW; *Moom* Moombooldool, NSW; *Condo* Condobolin, NSW

cycles of 15 s at 94°C, 15 s at 58°C and 50 s at 72°C. The PCR products were separated on 2% agarose gels and visualised after ethidium bromide staining using standard procedures (Sambrook et al. 1989).

In the case of marker WMC410, the PCR primers were labeled with 6-carboxyfluorescein, and the PCR products were separated on an ABI3700 capillary sequencer and their sizes measured using Genescan and Genotyper fragment analysis software (Applied Biosystems, Foster City, Calif., USA).

Marker association with height

BSA was used to map each dwarfing gene to a specific chromosome arm. Two bulks, each consisting of eight to ten RILs or doubled haploid (DH) lines of short or tall phenotype, were tested with the parents of each population using a subset of 627 microsatellite markers chosen for their PCR quality, high polymorphism and good coverage of the genome. Microsatellite markers were sourced from the Wheat Microsatellite Consortium (Röder et al. 1998), the John Innes Centre (http://www.jic.bbsrc.ac.uk), Trait Genetics (http://www.traitgenetics.de) and Beltsville Agricultural Research Centre (http://www.scabusa.org), as well as markers internally developed by Syngenta. Microsatellite markers were used to associate genomic regions with plant height in each of the mapping populations. First, the MAPMAKER program was used to establish the most likely microsatellite marker order along each chromosome (Lincoln et al. 1993). Association with height and the percentage of height variation accounted for by each molecular marker was determined using Student's *t*-test in the Generalised Linear Models procedure in SAS (SAS 1990). For the Chuan Mai 18 × Magnif M population segregating for *Rht8* and *Rht13*, both main and interaction effects were fitted for the two chromosomal regions identified in the study. Details of those markers accounting for the largest portion of the phenotypic variance in height are given in Table 2.

Results

Height distribution of *Rht* mapping populations

Populations of RILs or DH lines varying for different *Rht* genes were grown under field conditions and plant heights measured at maturity. Representative height distributions of each population are presented in Fig. 1. In populations varying for *Rht5* and *Rht12*, large differences in height resulted in bi-modal distributions, allowing the classification of most lines into short and tall categories (Fig. 1b, d). This suggests that height in these populations is largely determined by a single gene of major effect. The height distribution in the Vigour 18 × Mercia 12 population was skewed towards the tall class deviating significantly from the expected 1:1 ratio of tall to short lines. The bias against short lines is probably due to linkage of *Rht12* to the main vernalisation gene *Vrn1* on chromosome 5AL (Korzun et al. 1997). Plants were not vernalised during cycles of single seed descent, causing a selection against the chromosome 5AL from the winter wheat Mercia 12 carrying *vrn1*.

The Vigour 18 × Burt *ert* (*Rht4*) population had distinguishable height classes but with a substantial overlap between the tall and short groups (Fig. 1a). The Chuan Mai 18 × Magnif M population, which varies for both *Rht8* and *Rht13* ranged in height from 35–135 cm, with short (median height 55 cm) and tall (100 cm) groups distinguishable in the population (Fig. 1e).

Table 2 Microsatellite markers used in this study

Marker	Primers sequence 5′–3′	Chromosomal location			Polymorphism[a]	
		Chromosome atm	ITMI (cM)[b]	Del. bin[c]	Variety	Fragment size (bp)
WMC317	TGCTAGCAATGCTCCGGGTAAC TCACGAAACCTTTTCCTCCTCC	2BL	250.9	2BL6-0.89–1.00	Vigour 18 Burt *ert*	150 170
BARC102	GGAGAGGACCTGCTAAAATCGAAGACA GCGTTTACGGATCAGTGTTGGAGA	3BS	26.9	3BS8-0.78–1.00	Vigour 18 Marfed M	165 200
WMC503	GCAATAGTTCCCGCAAGAAAAG ATCAACTACCTCCAGATCCCGT	2DS	46.4	2DS5-0.47–1.00	Chuan Mai 18 Magnif M	275 240
BARC151	TGAGGAAAATGTCTCTATAGCATCC CGCATAAACACCTTCGCTCTTCCACTC	5AL	–	5AL10-0.57–0.78	Chuan Mai 18 Mara	230 220
WMC410	GGACTTGAAAAGGAAGCTTGTGA CATGGATGGCATGCAGTGT	5AL	–	5AL23-0.87–1.00	Vigour 18 Mercia 12	112 114
WMS577	ATGGCATAATTTGGTGAAATTG TGTTTCAAGCCCAACTTCTATT	7BL	270.6	7BL7-0.63–0.78	Chuan Mai 18 Magnif M	120 130

Primer sequence; chromosomal location as determined by previous studies

[a]Polymorphism in the parental lines used in this study

[b]*ITMI* International Triticeae Mapping Initiative position on the 'Opata' × 'Synthetic' consensus map (Röder et al. 1998)

[c]*Del. bin.* position on 'Chinese Spring' deletion bins (http://www.graingenes.org)

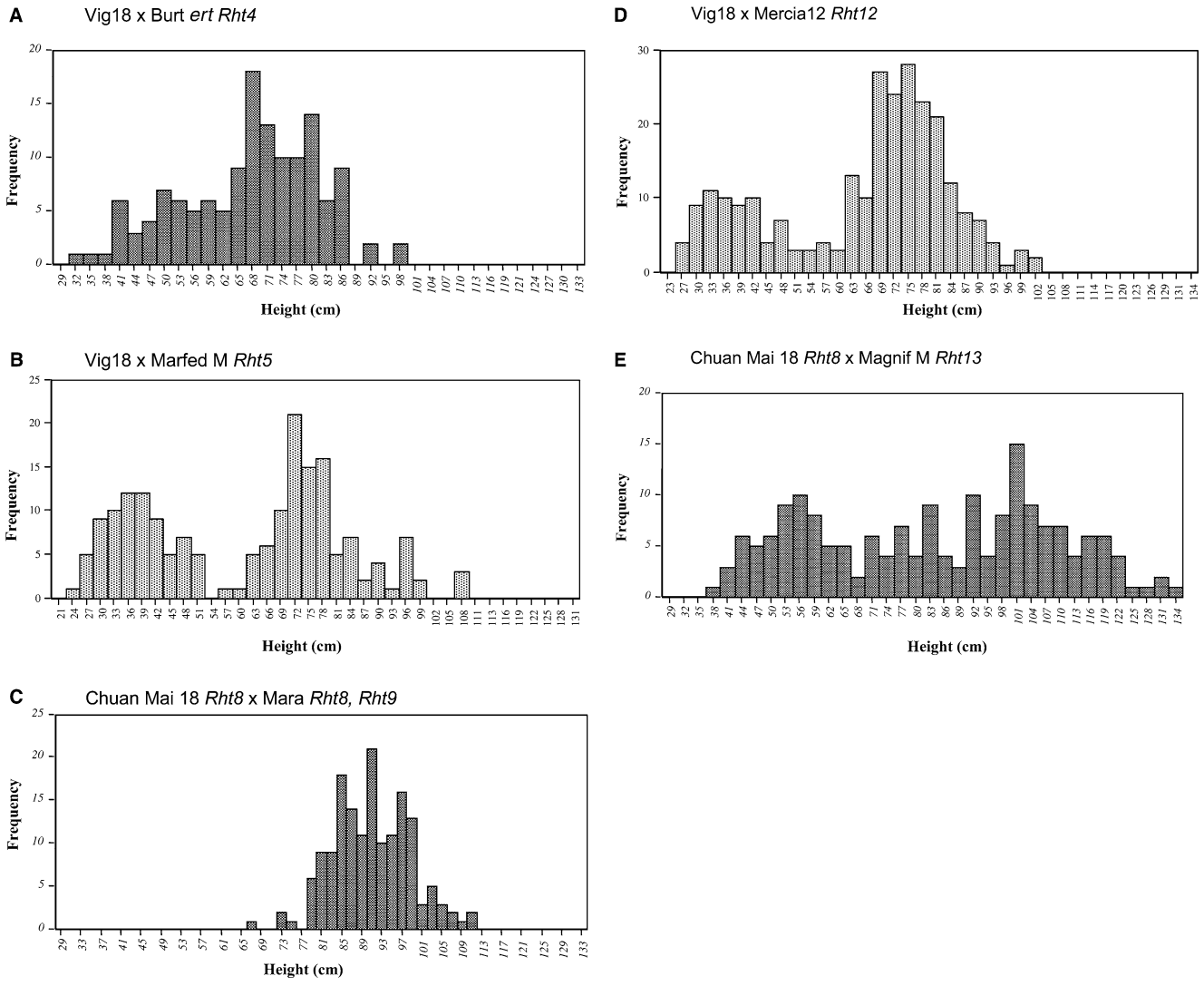

Fig. 1 Height distributions of populations varying for reduced height (*Rht*) genes. **a** Vigour 18 × Burt *ert* (*Rht4*), GES 2003; **b** Vigour 18 × Marfed M (*Rht5*), GES 2003. **c** Chuan Mai 18 (*Rht8*) × Mara (*Rht8*, *Rht9*), Gundi 2001; **d** Vigour 18 × Mercia 12 (*Rht12*), GES2003; **e** Chuan Mai 18 (*Rht8*) × Magnif M (*Rht13*), GES 2003

Plant heights in the Chuan Mai 18 (*Rht8*) × Mara (*Rht8 Rht9*) population were normally distributed (Fig. 1c), with a narrow height range of 80–100 cm.

Chromosomal location and microsatellite markers associated with *Rht* genes

In each population, DNA samples of 16–20 of the tallest and shortest lines were pooled and screened with microsatellite markers of known map location. Linked markers were used on whole segregating populations and marker genotypes were correlated with plant height, as outlined below (Table 3). The markers used in this study had previously been mapped (http://www.graingenes.org), enabling us to infer the chromosomal location of the *Rht* genes, as summarised in Fig. 2).

Rht4

Several microsatellite markers on chromosome 2BL were significantly ($P < 0.05$) associated with height in the Vigour 18 × Burt *ert* (*Rht4*) population. The highest proportion of phenotypic variation was explained by marker WMC317, which amplified a 170-bp band in Burt *ert* (*Rht4*) and a 150-bp band in the Vigour 18 parent (Table 2). Genotypes at this locus were significantly ($P < 0.01$) associated with height differences in two environments (Table 3). When grown in Canberra in 2003 (GES 2003), lines with the 170-bp allele were on average 15.1 cm shorter than lines with the 150-bp allele, accounting for 30% of the total phenotypic variance in height for the population.

Rht5

Several markers on chromosome 3BS were associated with height differences in selected lines from the Vigour 18 × Marfed M (*Rht5*) population. Differences in the BARC102 genotype (165-bp product in Vigour 18 and

Table 3 Marker association with height

Gene	Marker	Chromosome	Population	Environment	Genotype	*n*	Mean height (cm)	Additive effect (cm)	Phenotypic variance explained (%)
Rht4	WMC317	2BL	Vigour 18 (A) × Burt *ert* (B)	GES 2002	A	60	72.8	5.6**	17
					B	52	61.2		
				GES 2003	A	77	75.1	7.7**	30
					B	57	60.0		
Rht5	BARC102	3BS	Vigour 18 (A) × Marfed M 1(B)	Gundi 2002	A	109	74.8	15.1**	48
					B	73	44.5		
Rht8	WMC503	2DS	Chuan Mai 18 (A) × Magnif M (B)	Gundi 2002	A	59	75.2	−10.0**	18
					B	63	97.0		
				GES 2003	A	46	53.9	−6.3**	14
					B	45	66.5		
				Griffith 2004	A	63	79.5	−10.1**	18
					B	60	99.7		
Rht9	BARC151	5AL	Chuan Mai 18 (A) × Mara (B)	Moom 1999	A	56	80	3.3*	8
					B	63	73		
				Moom 2000	A	61	72.4	3.4**	18
					B	60	65.6		
				Moom 2001	A	71	77.5	3.0*	9
					B	52	71.4		
				Condo 2001	A	71	63.7	2.3**	23
					B	52	59		
				Gundi 2001	A	84	97.3	2.8**	12
					B	70	91.8		
Rht12	WMC410	5AL	Vigour 18 (A) × Mercia 12 (B)	Gundi 2002	A	112	77.4	18.1**	76
					B	45	41.1		
				GES 2003	A	111	91.2	21.6**	65
					B	32	48.0		
Rht13	WMS577	7BS	Chuan Mai 18 (A) × Magnif M (B)	Gundi 2002	A	82	98.9	14.6**	35
					B	81	69.6		
				GES 2003	A	63	69.0	8.8**	25
					B	67	51.4		
				Griffith 2004	A	82	101.7	15.1**	40
					B	82	71.4		

The markers with the most significant association with height are listed, as well as the average height of the lines in each genotypic class, and the percentage of the total phenotypic variance in height accounted for by the marker

Significance levels: $*P < 0.05$; $**P < 0.01$

200-bp product in Marfed M) accounted for approximately 30 cm of height difference and over 60% of the phenotypic variance in height. Most of the lines in the Vigour 18 × Marfed M population could be readily classified as tall (*rht5*) or short (*Rht5*). We could therefore estimate the linkage *Rht5* and locus *Xbarc102* (chromosome 3BS) with a genetic distance of approximately 10 cM.

Rht8

BSA of the Chuan Mai 18 (*Rht8*) × Magnif M1 (*Rht13*) population revealed two regions associated with height reduction. One of these was associated with the tightly linked markers WMC503 and WMS261 (these markers failed to recombine in this population). The locus *Xwms261* was previously mapped to chromosome 2DS and linked to *Rht8* (Korzun et al. 1998). Depending on the environment, there was a 6- to 10-cm height reduction associated with the WMS261 and WMC503 genotypes, accounting for up to 18% of the phenotypic variance in height.

Rht9

The RIL population Chuan Mai 18 (*Rht8*) × Mara (*Rht8Rht9*), is fixed for *Rht8* but varies for *Rht9*. The microsatellite marker BARC151, which maps to chromosome 5AL was associated with a small height difference. Lines that amplified the Mara allele (220 bp) were on average 5–7 cm shorter than lines with the 230-bp allele from Chuan Mai 18. These genotypic differences were significant ($P < 0.01$) over five environments (Table 3).

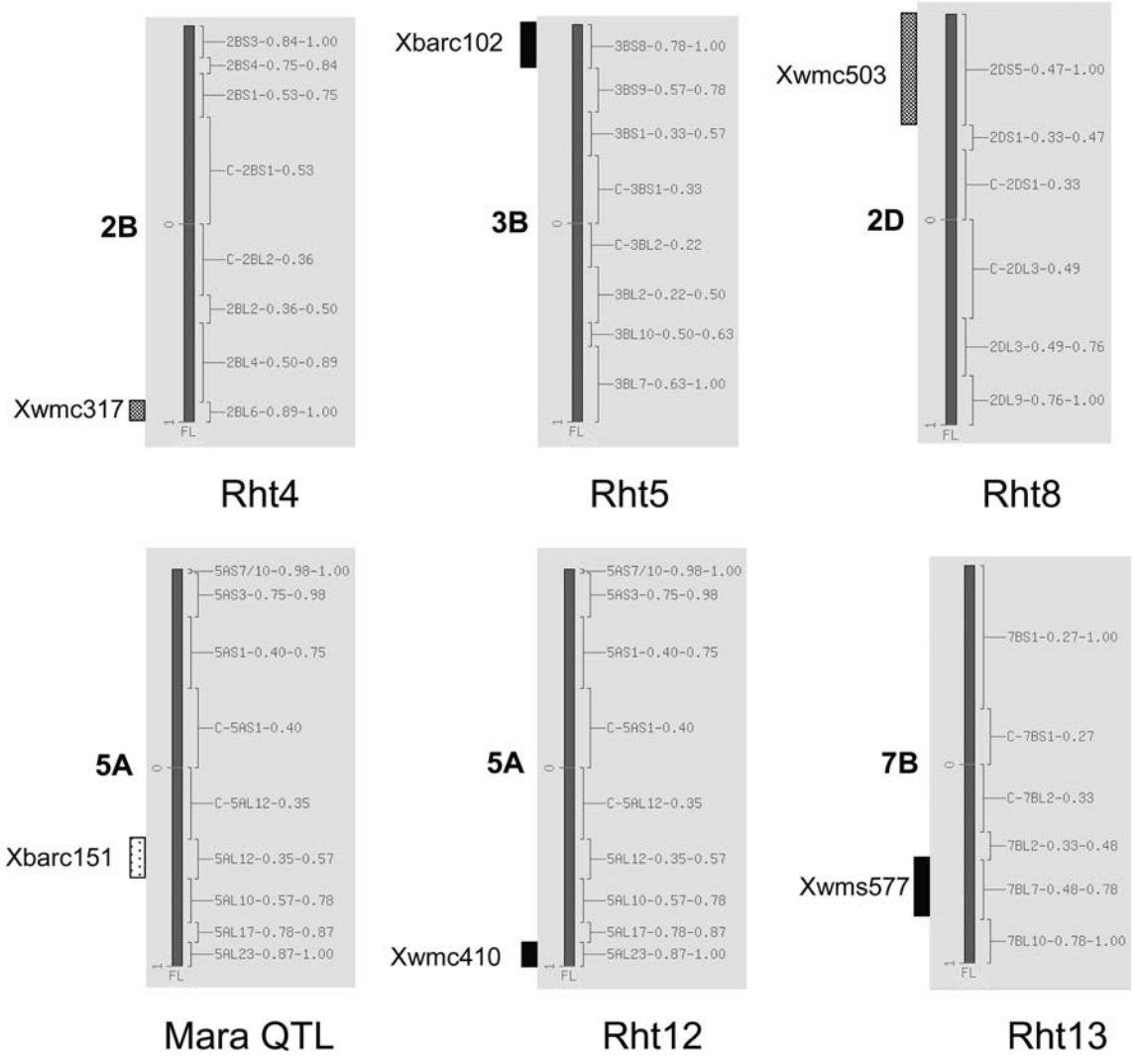

Fig. 2 Chromosomal location of dwarfing genes in wheat. The markers are indicated in relation to their respective 'Chinese Spring' deletion (http://www.graingenes.org/). The *shaded bars* summarise the association of the marker with height: *solid bars* over 10 cm, additive effect on height; *shaded bars* 5–10 cm, additive effect on height; *open bar* < 5 cm, additive effect on height

Rht12

Height variation in the Vigour 18 × Mercia 12 (*Rht12*) population was associated with markers on chromosome 5AL, the region which previously was reported to contain *Rht12* (Korzun et al. 1997). Because most of the Vigour 18 × Mercia 12 lines could be classified as tall or short, we were able to map *Rht12* to a single locus that was tightly linked to microsatellite marker WMC410. This marker accounted for up to 43.2 cm in height difference between genotypes and up to 76% of the height variance of the population.

Rht13

In addition to the region on chromosome 2DS, a second region associated with height was identified in the Chuan Mai 18 × Magnif M population. Several markers from chromosome 7BL showed a strong association with height in three environments (Table 3). Polymorphism generated by marker WMS577 accounted for up to 30.2 cm between genotypes, 40% of the phenotypic variance in the population. There were no interactions between the markers on 7BL and 2DS ($P > 0.05$), indicating that the two regions have additive effects on plant height.

Discussion

Genes reducing plant height are required to prevent lodging and to increase harvest index and yield. Height can also be limited by the environment, and in such conditions a strong genetic limitation on height may not be required. In a study of dwarf and tall near-isogenic lines of wheat, Singh et al. (2001) reported that *Rht-B1b* and *Rht-D1b* conferred a yield advantage in favourable environments, but that they had no or even negative effects in lower yielding, semi-arid conditions. Conversely, in long-season, irrigated environments, the

height reduction associated with *Rht-B1b* and *Rht-D1b* may not be sufficient: excessive height and severe lodging can occur in varieties containing these dwarfing genes (Stapper and Fischer 1990) and a stronger genetic limitation to adult plant height may be necessary. It would therefore be useful for breeders to have a range of dwarfing genes at their disposal, to use the appropriate height reduction for the target environment (Richards 1992). Studies by Rebetzke et al. (1999) and Rebetzke and Richards (2000) have demonstrated the benefits of reducing adult height without compromising on coleoptile length and vigour. Several *Rht* genes have no pleiotropic effects on GA responsiveness, coleoptile length or seedling leaf growth (Ellis et al. 2004). In this study, we generated populations varying for the presence of these GA-responsive *Rht* genes (*Rht4*, *Rht5*, *Rht8*, *Rht9*, *Rht12* and *Rht13*) and identified chromosomal regions and microsatellite markers associated with height reduction.

The strongest height effects were found in populations varying for *Rht5* (3BS), *Rht12* (5AL) and *Rht13* (7BS), with single markers accounting for 30- to 40-cm height differences and up to 70% of the phenotypic variance in height. The height effect of markers identified for *Rht4* (2BL) and *Rht8* (2DS) were intermediate, accounting for up to 15.4- and 20-cm height difference, or 30% and 36% of the variance in height of the populations, respectively. Height data obtained from different years and sites indicates the influence of the different GA-responsive *Rht* genes on height reduction is repeatable across a broad range of environments. Therefore, selection of these genes for reducing plant height is likely to be useful in breeding wheats across a range of environments.

The *Rht* genes in this study were mapped to different chromosomes, indicating that they are neither allelic nor homoeoallelic, confirming the early studies of Konzak (1988). The chromosomal location of *Rht12* and *Rht8* was determined in previous studies. Korzun et al. (1997) mapped *Rht12* to the distal end of chromosome 5AL, approximately 2.6 cM from locus *Xwms291*. We identified an additional marker that is tightly linked to *Rht12* that may be useful in backgrounds where WMS291 is not polymorphic. The *Rht8* gene was associated with markers WMC503 and WMS261 on chromosome 2DS, WMS261 was previously linked to *Rht8* (Korzun et al. 1998). The association of these two markers with height variation was comparable in our population, providing additional marker choice for backgrounds where WMS261 is not polymorphic.

The Chuan Mai 18 × Mara population, which is expected to vary for *Rht9*, revealed a location on chromosome 5AL with a small effect on height (4.6- to 6.8-cm difference between genotypes). This height-reducing QTL from Mara (Fig. 2) was significant ($P < 0.05$) over five environments. This observations differ from the previously determined chromosomal location for *Rht9*. Using single chromosome substitution lines of Mara into the tall wheat 'Capelle Desprez', Gale et al. (1982) found significant height-reducting effects with chromosomes 2D (ascribed to *Rht8*) and 7B (ascribed to *Rht9*) from Mara. We identified no QTL for height on chromosome 7B in our study. The reason for this difference is not known; it may be due to environmental effects on the expression of height-reducing genes, or complexities in the interpretation of chromosome substitutions.

Molecular markers associated with agronomic traits provide breeders with rapid, cost-effective and non-destructive screening tools that are independent of the environment. This paper reports chromosomal locations for *Rht4*, *Rht5* and *Rht13* and describes linked markers that will help breeders to select for dwarfing genes appropriate for particular environments, as possible replacements for *RhtB1b* and *RhtD1b*. Spielmeyer et al. (2001) discussed the successful use of marker-assisted selection for the replacement of *Rht-B1b* and *Rht-D1b* with *Rht8*. These markers will also help researchers to further evaluate dwarfing genes by assessing the impact of chromosomal regions on plant characteristics. Determining the map locations also allows candidate genes to be identified that may be responsible for the height-reducing phenotype. The rapidly growing map information on wheat ESTs, in time, may suggest potential candidate for the different *Rht* genes. Possible candidates for dwarfing genes are mutations in genes involved in the biosynthesis of GA growth hormones. Using a set of aneuploid lines, Spielmeyer et al. (2004) determined the chromosomal location of GA biosynthesis genes in wheat and barley. Several biosynthesis genes are present on chromosome 2BL, and a GA 3-oxidase gene is located on chromosome 3BS. Further work will determine whether the correlation of these chromosomal locations with *Rht4* and *Rht5* is meaningful or incidental.

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