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Genetic analysis of the dwarfing gene (*Rht8*) in wheat. Part I. Molecular mapping of *Rht8* on the short arm of chromosome 2D of bread wheat (*Triticum aestivum* L.)

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Abstract Two sets of single chromosome recombinant lines comparing 2D chromosomes from the wheat varieties 'Ciano 67' and 'Mara' with the common 2D chromosome of 'Cappelle-Desprez' in a 'Cappelle-Desprez' background were used to detect a diagnostic wheat microsatellite marker for the dwarfing gene *Rht8*. The genetic linkage maps place the wheat microsatellite marker WMS 261 0.6 cM distal to *Rht8* on the short arm of chromosome 2D. By PCR analysis the WMS 261 alleles of 'Mara', 'Cappelle-Desprez' and 'Ciano 67' could be distinguished by different fragment sizes of 192 bp, 174 bp and 165 bp, respectively. A screen of over 100 international varieties of wheat showed that the three allelic variants were all widespread. It also demonstrated that a limited number of varieties carried novel WMS 261 variants of over 200 bp. Following classification of the individual recombinant lines for allelic variants at the WMS 261 locus it was possible to attribute a 7- to 8-cm reduction in plant height with the WMS 261-192-bp allele compared to the WMS 261-174-bp allele in the set of recombinant lines comparing 2D chromosomes of 'Mara' and 'Cappelle-Desprez'. A height reduction of around 3 cm was detected between the WMS 261-174-bp allele and the WMS 261-165-bp allele in the recombinant lines comparing 2D chromosomes of 'Cappelle-Desprez' and 'Ciano 67'.

Key words Microsatellites · Marker assisted breeding · Dwarfing gene (*Rht8*) · Wheat

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Introduction

In recent years, much effort has been directed towards the construction of genetic linkage maps in the *Gramineae* species which constitute important staple crops of mankind. Among those, hexaploid wheat has received much attention (Chao et el. 1989; Liu and Tsunewaki 1991; Devos et al. 1992, 1993; Nelson et al. 1995; Van Deynze et al. 1995). However, most of the published molecular maps of wheat include only a few mutant loci and agronomically important genes. The mapping of such genes using DNA markers was demonstrated for the leaf rust resistance locus *Lr1* on chromosome 5D (Feuillet et al. 1995), the dwarfing gene (*Rht12*) on chromosome 5A (Korzun et al. 1997a), the aluminum tolerance locus on chromosome 4D (Luo and Dvorak 1996) and the loci for vernalisation (*Vrn1*) and frost resistance (*Fr1*) genes on chromosome 5A (Galiba et al. 1995).

The use of dwarfing genes to reduce height and improve yield has been one of the main strategies in breeding modern high-yielding hexaploid bread wheat varieties. The semi-dwarfing genes *Rht1* and *Rht2*, derived from the variety 'Norin 10', have influenced major advances in varietal performance (Gale and Youssefian 1984). However, these genes are not universally beneficial, and in Mediterranean countries they can reduce rather than promote improvement in plant performance. In these countries, a second source of semi-dwarfism, from the variety 'Akakomugi', has been favoured (Worland and Law 1986). Unlike the 'Norin 10' dwarfing genes, dwarfing genes from 'Akakomugi', including *Rht8*, do not confer insensitivity to exogenous gibberellic acid and are not easily identified in segregating populations, thereby making genetic studies of these genes and their effects on plant height and agronomic characters difficult.

In order to identify a gene corresponding to a specific dwarfing genotype, it is important to have it marked by

molecular markers and located on the genetic map. The use of restriction fragment length polymorphism (RFLP) and isozyme markers for this purpose has been inefficient because of a low level of allelic variation among cultivated varieties (Chao et al. 1989; Kam-Morgan et al. 1989). Microsatellites represent abundant highly polymorphic probes evenly distributed over the genome. Therefore, they are highly suitable as genetic markers in wheat for mapping agronomically important genes (Korzun et al. 1997a), detecting genetic diversity (Plaschke et al. 1995) and testing the correctness of genetic stocks (Korzun et al. 1997b). They can assist in the utilisation of such stocks for the detection of genes of agronomic importance in breeding programmes and provide readily detectable markers for these genes and facilitate their handling in segregating breeding populations.

The present paper describes the genetic map location of the dwarfing gene *Rht8* on chromosome 2D in relation to microsatellite and RFLP markers and provides additional information on its alleles in diverse wheat varieties.

Materials and methods

Parental varieties

'Cappelle-Desprez', a standard-height French variety widely grown throughout western Europe during the 1960s and 1970s is a photoperiod-sensitive (*ppd1*, *ppd2*, *ppd3*) and vernalisation-sensitive (*vrn1*, *vrn2*, *vrn3*) winter wheat. 'Mara', a semi-dwarf Italian wheat carrying the 'Akakomugi' dwarfing genes *Rht8*, *Rht9* and *Ppd1* on chromosomes 2D, 7BS and 2D, respectively, is a photoperiod-insensitive (*Ppd1*, *ppd2*, *ppd3*) and vernalisation-insensitive (*vrn1*, *Vrn2*, *vrn3*) spring wheat. 'Ciano 67', a semi-dwarf CIMMYT variety carrying the giberellic acid (GA)-insensitive dwarfing gene *Rht D1b* (*Rht2*) on chromosome 4D, is a photoperiod-insensitive (*Ppd1*, *ppd2*, *ppd3*) and vernalisation insensitive (*Vrn1*, *vrn2*, *vrn3*) spring wheat.

International varieties

Seeds from selected international varieties, including important *Rht8* parental varieties and derivatives, were obtained from John Innes Centre and IPK genebank collections.

Single-chromosome recombinant lines

To map *Rht8* against other genes segregating on chromosome 2D and to study the pleiotropic effects of *Rht8* without interference from the other genes, we developed separate single-chromosome recombinant lines for the 2D chromosome of 'Ciano 67' and of 'Mara' in an otherwise uniform 'Cappelle-Desprez' varietal background. The recombinant lines were developed using techniques described by Law (1966) in which initially the 2D chromosomes of 'Mara' or 'Ciano 67' were substituted into a 'Cappelle-Desprez' background by backcrossing to the existing 'Cappelle-Desprez' monosomic stock for chromosome 2D (Law and Worland 1973). Substitution lines were then crossed to the recipient variety 'Cappelle-Desprez'. The resulting F_1 was further crossed onto the 2D monosomic of 'Cappelle-Desprez', and 41-chromosome progeny extracted from the hybrid progeny. Each 41-chromosome plant was then selfed again for extraction of disomic lines carrying different 2D chromosomes with homozygous recombination events in an otherwise homozygous 'Cappelle-Desprez' background. Approximately 100 disomic recombinant lines were established for each of the progenies.

Analysis of target trait

The two sets of chromosome 2D recombinant lines were grown in replicated field experiments to measure plant height and other agronomic characters. Details of the analysis of the lines recombining chromosomes 2D of 'Mara' and 'Cappelle-Desprez' are found in Worland and Law (1986). This analysis enabled the classification of 88 recombinant lines with respect to the presence or absence of *Rht8*, *Ppd1* and *Yr16*. Analysis of the lines with recombinant chromosomes 2D of 'Ciano 67' and 'Cappelle-Desprez' is described by Worland et al. (1998) and enabled classification of the lines for *Ppd1*, *Yr16* and a number of RFLP markers but failed to classify the material for height differences such as would be expected if 'Ciano 67' carried *Rht8*. The complete set of 93 duplicated recombinant lines was grown in a replicated field trial at the Morley Research Centre after sowing in autumn 1993. A subset of 40 lines was grown for further trials at the same site during the following 2 years. In 1993, trial lines were grown in five replicated blocks being represented in each block as a row of 11 seeds spaced 10 cm apart within rows and with 30-cm spacing between rows. Each line was scored for ear emergence time, plant height, average yield per plant and, from two tillers that were removed prior to harvest, for spike length, spikelet number, 1000 grain weight, ear yield, grains per ear and grains per spikelet. In the 1994 and 1995 sowings, each line was grown in 5 replicates as a drilled 1.0×6.0-m plot that was cut back to 1.0×4.5-m prior to harvest. For each plot, flowering time, plant height and combined plot yield were measured. Prior to harvest, two ears were removed from each plot to determine the yield components.

Microsatellite analysis

For the mapping of *Rht8*, microsatellite markers were chosen based on their location on the short arm of chromosome 2D of the ITMI mapping population (Röder et al. in preparation). The development of the microsatellite markers was described in Röder et al. (1995) and Plaschke et al. (1996). The information about the microsatellites is presented in Table 1.

Polymerase chain reactions (PCR) were performed in a volume of 25 µl in a Perkin-Elmer thermocycler. The reaction mixture contained 250 n*M* of each primer, 0.2 m*M* of each deoxynucleotide, 1.5 m*M* $MgCl_2$, 1 U *Taq* polymerase and 50–100 ng template DNA. The 45 cycles were performed with 1 min at 94°C, 1 min at either 50°, 55° or 60°C (depending on the individual microsatellite marker), 2 min at 72°C and a final extension step of 10 min at 72°C. From each PCR amplification 1.0–1.5 µl was mixed with 3.0 µl loading buffer (deionized formamide including 5 mg/ml dextran blue) and, after denaturation for 1 min at 94°C, loaded and separated on an automated laser fluorescence (A.L.F.) sequencer (Pharmacia) with fragments of known sizes as standards in each lane. To accomplish this, we prepared denaturing gels (0.35 mm thick) with 6% SequaGel™ XR (Biozym) using the short gel cassettes and $1 \times$ mol TBE as running buffer. Running conditions were 600 V, 50 mA and 50 W with 2 mW laser power and a sampling interval of 0.84 s. The gels were re-used four to five times. Fragment sizes were calculated using the computer programme FRAGMENT MANAGER Version 1.2 (Pharmacia) and compared to internal size standards.

For variety analysis, DNA was extracted from one to five grains according to the procedure described by Plaschke et al. 1995.

Table 1 Primer sequences, MS sequence compositions, fragment sizes and annealing temperature for microsatellite markers

Markers	Primers sequences (5′ → 3′)	MS composition (in CS)	Fragments size in CS (in bp)	Annealing temperature (°C)
WMS 102	TCTCCCATCCAACGCCTC TGTTGGTGGCTTGACTATTG	(GT)15	143	60
WMS261	CTCCCTGTACGCCTAAGGC CTCGCGCTACTAGCCATTG	(CT)21	192	55
WMS296[a]	AATTCAACCTACCAATCTCTG GCCTAATAAACTGAAAACGAG	(CT)28	149	55
WMS484	ACATCGCTCTTCACAAACCC AGTTCCGGTCATGGCTAGG	(CT)29	145	55

[a] Additional locus on 2AS

RFLP analysis

The RFLP probes used in the investigation consisted of both cDNAs and genomic DNA from various wheat libraries (Devos et al. 1993). DNA was extracted from 5- to 6-week-old seedlings according to McCouch et al. (1988) and cut with the restriction enzymes *Hin*dIII, *Dra*I, *Eco*RI and *Eco*RV. Southern blots, probe labelling and filter hybridisation followed the method described by Devos et al. (1992). The only modification was the addition of 1/10 volume 3 *M* NaOH for denaturation of the probe.

Mapping of *Rht8* on chromosome 2DS

Recombination frequencies were calculated using MAPMAKER (Lander et al. 1987) and converted to centiMorgans (cM) using the Kosambi mapping function.

Results and discussion

Microsatellite analysis

Microsatellite analysis of the parental varieties indicates that the 3 varieties carry different allelic variants at the WMS 261 locus. 'Cappelle-Desprez' carries an allele with 174 bp, 'Ciano 67' with 165 bp and 'Mara' with 192 bp.

Analysis of the recombinant lines developed between 2D chromosomes of 'Mara' and 'Cappelle-Desprez' indicated a 1 : 1 segregation for WMS 261, with 53 lines carrying the WMS 261-192-bp allele and 43 lines carrying the WMS 261-174-bp allele. When this analysis was compared to previous classifications of the lines for the *Rht8* gene, a single recombinant was detected between the two loci, indicating very tight linkage. Thus, the wheat microsatellite WMS 261 can be used as a diagnostic marker for *Rht8*. The location of WMS 261 and *Rht8* in relation to a number of RFLP and microsatellite loci is shown in Fig 1.

The recombinant lines for chromosome 2D between 'Ciano 67' and 'Cappelle-Desprez' segregated with 46 lines carrying the WMS 261-l65-bp allele characteristic of 'Ciano 67' and 47 lines carrying the WMS 261-174-bp allele characteristic of 'Cappelle-Desprez'. A comparison of the chromosome 2D maps developed from the two sets of single-chromosome recombinant lines showed a consistency in the order of loci showing polymorphism in both mapping populations (*Xgwm 296*, *Xgwm 261* and *Xgwm 484*). There are several sites where polymorphism differs between 'Ciano 67' or 'Mara' 2D loci and the common 'Cappelle-Desprez' 2D loci. This is of interest since both 2D chromosomes of 'Ciano 67' and 'Mara' are ancestrally derived from a cross made by the Italian breeder Strampelli between the Japanese variety 'Akakomugui' and a hybrid between the Dutch variety 'Wilhelmina' and the Italian landrace 'Riete'. Both the 'Ciano 67' and 'Mara' 2D chromosomes carry a common *Ppd1* allele derived from 'Akakomugi'. 'Mara' was selected two generations after the original Strampelli cross and 'Ciano 67' four generations after that cross.

Analysis of over 100 additional wheat varieties showed the three WMS 261 allelic variants detected in 'Cappelle-Desprez', 'Ciano 67' and 'Mara' are widespread in international wheat varieties with the WMS 261-174-bp WMS 261-165-bp and WMS 261-192-bp alleles being detected in 25, 28 and 58 varieties, respectively. In addition to the three common alleles, 6 varieties carried novel fragments at the WMS 261 locus with fragments of 201 bp ('Pliska'), 202 bp ('Courtot'), 210 bp ('Chino', 'Klein Esterelo', 'Klein 157') and 215 bp ('Klein 49'). The distribution of the WMS 261 alleles in worldwide breeding programmes and the possible adapative significance of this distribution will be discussed in a separate publication (Worland et al. 1998).

Genetic map location of the *Rht8* gene in relation to microsatellite and RFLP markers

The dwarfing gene *Rht8* was mapped onto the short arm of chromosome 2D of wheat against four microsatellite and three RFLP markers. Whereas only three of nine RFLP markers in this analysis were polymorphic, four of five microsatellite markers were informative in the cross 'Cappelle × Cappelle (Mara 2D)'. All mapped

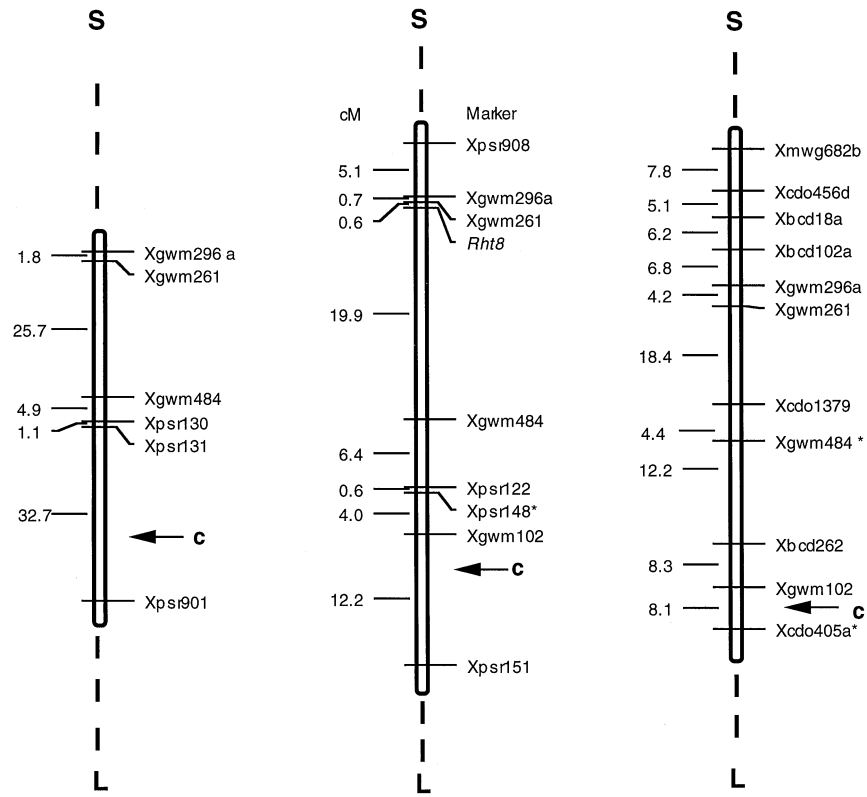

Fig. 1 Map location of the dwarfing gene *Rht8* on 'Cappelle × Cappelle(Mara 2D)' mapping population (*middle*) in relation to the molecular map of the short arm of chromosome 2D produced from cross 'Cappelle × Cappelle (Ciano 2D)' (*left*) and 'Opata × Synthetic' map (*right*). Markers with LOD < 2.0 are placed at their most likely location and indicated by asterisks. *C* Centromere, *S* and *L* indicate short and long arms, respectively

microsatellites appeared evenly distributed throughout chromosome 2D.

Interesting, the microsatellite WMS 296 is present at a second locus on chromosome 2A (Röder et al. in preparation) and may be suitable for mapping of the homoeologous dwarfing gene *Rht7* (Worland et al. 1980) on the short arm of chromosome 2A of wheat.

Association of pleiotropic effects with the WMS 261/*Rht8* locus

Previous analysis of the 'Cappelle-Desprez/Mara' chromosome 2D recombinant lines indicated that the *Rht8* dwarfing gene significantly reduced plant height by approximately 7–8 cm in England and Yugoslavia (Worland et al. 1988). The reduction in plant height was achieved predominantly without pleiotropic effects on other agronomic characters except for a slight increase in spikelet fertility. Since only 1 of 89 recombinant lines showed recombination between the *Rht8* and the WMS 261 loci, a re-analysis of the results for the WMS 261 alleles would not significantly alter the results previously obtained for *Rht8*.

Genetic analysis of the 2D recombinant lines developed between 'Ciano 67' and 'Cappelle-Desprez' 2D chromosomes failed to classify the lines into two classes for a height-reducing gene, even though the 'Ciano 67' 2D chromosome carries the same *Ppd1* that has been linked to *Rht8* in the ancestral varieties 'Akakomugi' and 'Mara' (Worland et al. 1997). By classifying the recombinant lines for allelic variation at the WMS 261 locus we can now use previously obtained agronomic data from the 1993, 1994 and 1995 trials to investigate whether any pleiotropic effects linked to the WMS 261 locus can be detected for height, ear emergence, yield and various additional components of yield. The results of the ANOVA analysis (Table 2) show that in each of the three seasons, lines carrying the WMS 261-165-bp allelic variant were significantly taller (probability < 0.05) than lines carrying the WMS 261-174-bp allele. This could indicate that there are allelic differences at the tightly linked *Rht8* locus and that the WMS 261-165-bp allele marks an allele at the *Rht8* locus that increases height over the normal tall allele present in 'Cappelle Desprez'. It is therefore suggested that the height difference between the *Rht8* allele of 'Mara' and the height-promoting allele of 'Ciano 67' is in the range of 10–11 cm assuming a difference of 7–8 cm between the *Rht8* alleles linked to WMS 261-192 bp and WMS 261-174 bp and a 3-cm difference between alleles linked to WMS 261-174-bp and WMS 261-165-bp. No significant differences were detected between the WMS 261-165-bp and WMS 261-174-bp alleles for ear emergence, spike length, spikelet number, plot yield, ear yield, 1000 grain weight, number of grains/ear or number of grain/spikelet. On the other hand, it is possible that another, presently unknown, gene tightly linked to

Table 2 Comparison of the effects of wheat microsatellite alleles WMS 261-165 bp ('Ciano 67') to WMS 261-174 bp ('Cappelle-Desprez') observed for a range of agronomic characters, on single chromosome recombinant lines developed in 'Cappelle-Desprez' background. Trials grown at Morley, UK from sowings in autumn 1993, 1994 and 1995

	1993/4	1994/5	1995/6
Ear emergence (days)	− 0.09	− 0.12	− 0.08
Height (cm)	+ 2.52*	+ 3.78*	+ 2.46*
Spike length (cm)	+ 0.45	+ 0.41	—
Spikelet number	− 0.15	+ 0.18	+ 0.04
1000 grain weight (gm)	+ 0.32	+ 0.36	+ 0.66
Ear yield	+ 0.06	+ 0.25	− 0.09
Plot yield	+ 3.3[a]	+ 41.5[b]	+ 43.5[b]
Grain/ear	− 1.67	− 0.25	− 2.04
Grain/spikelet	− 0.06	− 0.19	− 0.10

* Probability = 0.05–0.01
[a] Data from single plants
[b] Data from 1.0 × 4.5-m plots

Rht8 is also affecting plant height in 'Mara'. This could be investigated by generating more recombinants around *Rht8* and using more markers for this region.

Conclusions

Genetic analysis of two sets of single-chromosome recombinant lines indicated very tight linkage between the *Rht8* dwarfing gene locus and wheat microsatellite WMS 261. Linkage is such that the microsatellite could be used as a diagnostic marker for the dwarfing gene which, until now, has been difficult to detect in breeding populations and to study in genetic analysis.

The WMS 261 locus appears to be highly polymorphic with three main allelic variants characteristic, respectively, of 'Ciano 67' (165 bp), 'Cappelle-Desprez' (174 bp) and 'Mara' (192 bp). A number of additional novel allelic variants with more than 200 bp were detected in a varietal screen. Interestingly, in precise genetic stocks significant differences in plant height could be associated with three main WMS 261 allelic variants suggesting these could possibly be reflected in different allelic variants at the *Rht8* locus, where the 165-bp allele of 'Ciano 67' appears to promote height even more than the 'tall' allele present in 'Cappelle-Desprez'. It is possible that the novel allelic variants of WMS 261 of over 200 bp might be linked to additional allelic variants at the *Rht8* locus that can be used in breeding programmes.

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