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P. SOURDILLE[1], G. CHARMET[1], M. TROTTET[2], M. H. TIXIER[1], C. BOEUF[1], S. NÈGRE[1], D. BARLOY[2] and M. BERNARD[1]

[1] *INRA Station d'Amélioration des Plantes, Domaine de Crouël, 63039 Clermont-Ferrand CEDEX, France*
[2] *INRA Station d'Amélioration des Plantes. Domaine de la Motte, 35653 Le Rheu CEDEX, France*

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Identifying genotypes carrying the dwarfing genes *Rht-B1* and *Rht-D1* would be of great interest for wheat (*Triticum aestivum* L. em Thell) breeding. Two RFLP loci were found to be linked to those two genes, *Xpsr 144-4B* with *Rht-B1* on chromosome 4BS and *Xglk578-4D* with *Rht-D1* on chromosome 4DS, by genotyping two F_2 populations, Renan (*Rht-B1b*) × Camp-Rémy and Rendez-Vous (*Rht-D1b*) × Roazon. Utilisation of these markers in breeding schemes is discussed.

Michel Bernard, INRA Station d'Amélioration des Plantes, Domaine de Crouël, 63039 Clermont-Ferrand CEDEX, France

Reducing plant height in wheat is of great economical importance because it makes it possible to simultaneously increase lodging resistance, and thus stability of yield, and harvest index. Because many genetic factors which influence development, morphology or vigour will have effects on final plant height, this character involves most of the 21 chromosomes in wheat (SNAPE et al. 1977). Several genes have already been identified and "short" alleles have been designated *Rht* (for Reduced height) relative to their "tall" alleles *rht*. The Norin 10 dwarfing alleles *Rht1* and *Rht2* have been used extensively in the breeding schemes during the last 40 years due to the lack of consequences on yielding ability. In CIMMYT, BORLAUG (1968) made the first successful crosses between Norin 10-Brevor 14 and tall "daylength insensitive" wheats in 1955. The varieties Pitic 62 and Penjamo 62 were released to Mexican farmers in 1962. Since the registration in 1964 of the semi-dwarf variety 'Gaines' (VOGEL 1964), the proportion of varieties carrying dwarfing alleles is in constant increase and, at the present time, reaches more than 80% of the world registrations.

Dwarf wheat plants are classified into two groups following their reaction to the application of exogenous gibberellin (GA; REID 1986). The GA insensitive character of Norin 10 was first mentioned by ALLAN et al. (1959), and genes influencing this trait were named *Gai* (for GA insensitivity; MCINTOSH 1979). Genetic linkage analysis between *Rht1* and *Gai1* on one hand, and *Rht2* and *Gai2* on the other, made by GALE and MARSHALL (1975) and GALE and GREGORY (1977) showed absence of recombination. It was considered that the *Rht* and *Gai* genes were identical and that they conferred, by pleiotropic effects, both reduced height and gibberellin insensitivity (WORLAND et al. 1987). *Rht1* and *Rht2* act by reducing internode length without reducing spike morphology (ALLAN et al. 1968). Both are semi-dominant (GALE and YOUSSEFIAN 1985) and have similar effects on plant height (reduction of about 20 cm) even though *Rht2* seems to have a stronger effect than *Rht1* (ALLAN 1970; BÖRNER et al. 1993). Numerous alleles inducing different levels of dwarfism have already been identified for either *Rht1* by GALE et al. (1975; *Rht3*), WORLAND and PETROVIC (1988; *Rht1S*), WORLAND and SAYERS (1995; *Rht1(B.dw)*), or *Rht2* by BÖRNER and METTIN (1988; *Rht10*).

Combination of *Rht1* and *Rht2* in the same genotype generally produces a strong effect on plant height which, most of the time, induces a decrease of the agronomical value of the variety (ALLAN 1983). In addition, crosses between lines carrying different dwarfing genes generate a wide segregation for height which leads to the rejection of the majority of the plants only because they are too tall or too short. It would then be advisable to cross lines with the same dwarfing gene, especially for recurrent breeding. A large variation in height reduces the efficiency of breeding because of strong competition effects between tall and short plants resulting in difficulties in evaluating populations segregating for height. Unfortunately, the test using GA is unable to distinguish the lines carrying *Rht1* from those with *Rht2*. Test crosses with lines from a known genotype (*Rht1* or *Rht2*) must be done to identify the gene(s) of new lines.

Since 1989, dense RFLP linkage maps of the hexaploid wheat *Triticum aestivum* L. em. Thell. have been developed from interspecific crosses for the homoeologous groups 1 (VAN DEYNZE et al. 1995), 2 (DEVOS et al. 1993; NELSON et al. 1995a), 3 (DEVOS et al. 1992; NELSON et al. 1995b), 4 and 5 (XIE et al. 1993; DEVOS et al. 1995; NELSON et al. 1995c), 6 (JIA et al. 1996; MARINO et al. 1996) and 7 (CHAO et al. 1989; NELSON et al. 1995c) and from an intervarietal cross (CADALEN et al. 1997). These maps would be useful to identify markers linked to *Rht1* and to *Rht2* for an accurate selection of the plants having these dwarf alleles. Previous studies indicate that these two genes are carried on the short arms of the homoeologous group 4. Using telocentric mapping, it was shown that *Rht1* is located at 13 map units from the centromere on chromosome 4BS while *Rht2* falls 15 map units from the centromere on the chromosome 4DS (MCVITTIE et al. 1978).

The aim of this study was to look for markers linked to these two genes, using segregation in two F_2 populations. We have thus focused our study on chromosomes 4B and 4D. In the present study, we will use the conventional and newly proposed nomenclature of the GA insensitive *Rht* alleles in wheat (BÖRNER et al. 1996) i.e., *Rht-B1a* and *Rht-D1a* (formerly *rht1* and *rht2*) and *Rht-B1b* and *Rht-D1b* (formerly *Rht1* and *Rht2*).

MATERIAL AND METHODS

Plant material

Two F_2 populations were elaborated at the INRA Plant Breeding Station at Rennes. The first one, of 116 plants, was from the cross between the cultivars Renan (*Rht-B1b*) and Camp-Rémy, and height was ranging between 58 and 105 cm. The second one, of 115 individuals, was produced from the cross between the cultivars Rendez-Vous (*Rht-D1b*) and Roazon, and height was ranging between 61 and 127 cm.

Plant height evaluation

Plant height of F_2 plants and of the four parents (Renan, Camp-Rémy, Rendez-Vous, Roazon) was scored under field conditions at INRA Station at Rennes in 1995. The genotype at the loci *XRht-B1* and *XRht-D1* was determined in the greenhouse in 1996 on F_3 seedlings, using a method derived from that of GALE and GREGORY (1977). Two replications of 20 seeds were sown in wet sand in seed trays and placed into controlled environments to ensure even germination and to avoid etiolation. The seeds were then irrigated once a day with a solution containing 5 mg/l of GA_3. Measurements were taken 12–15 days after sowing, and plantlets were divided into two groups. Those homozygous for *Rht-B1b* or *Rht-D1b* ("short" alleles) present short sheaths and first leaves, while those heterozygous (*Rht-B1a*/*Rht-B1b* or *Rht-D1a*/*Rht-D1b*) or homozygous for *Rht-B1a* or *Rht-D1a* ("tall" alleles) have long sheaths and first leaves twice as long as short plants.

Molecular markers and RFLP analysis

The probes used in this study are given in Table 1. The techniques for DNA extraction, digestion, electrophoresis, blotting, and hybridization were described by CADALEN et al. (1997). The protocol using non-radioactive probes was detailed in LU et al. (1994) and SOURDILLE et al. (1996).

One microsatellite (GWM165; PLASCHKE et al. 1996) was also mapped on these populations. PCR reactions were carried out in a final volume of 50 µl in a Perkin-Elmer 9600 thermocycler. The reaction buffer contained 100 ng of template DNA, 0.2 mM of each deoxynucleotide, 1.5 mM $MgCl_2$, 500 nM of each primer, and 1 unit of Taq-DNA-polymerase (Boehringer). Thirty-five cycles with 1 min at 96°C, 1 min at 60°C (in some cases 57°C), and 2 min at 72°C were realised, followed by a final elongation step of 10 min at 72°C. Polyacrylamide (6 %) denaturing gels (0.4 mm thick) were prepared with 1X TBE buffer (90 mM Tris, 90 mM boric acid, 2 mM EDTA, pH 8.2) and cast between glass plates, one previously treated with Sigmacote (Sigma) and the other with Silane A-174 (Sigma). From each sample, 1.6 µl were loaded together with 0.8 µl of loading buffer (10 mM NaOH, 0.05 % bromophenol blue, 0.05 % xylen cyanol, in 95 % deionized formamide) after a 5 min denaturation in boiling water. Samples were then run for 2 h at 2000 V, 36 mA and 61 W. DNA was revealed by a silver staining method derived from the protocol of BASSAM et al. (1991). The gel was first fixed for 20 min in 10 % acetic acid, rinsed three times with water and stained in a solution containing 0.1 % silver nitrate and 0.05 % formaldehyde for 30 min. After a quick rinse (not exceeding 10 s) microsatellites were revealed by adding the developer (3 % sodium carbonate, 0.05 %

Table 1. *DNA probes and microsatellites used in this study*

Probes	References
GLK335	LIU and TSUNEWAKI (1991)
GLK556	LIU and TSUNEWAKI (1991)
GLK578	LIU and TSUNEWAKI (1991)
GWM165	PLASCHKE et al. (1996)
PSR144	GALE et al. (1995)
FBA41	QUETIER (personal gift)
FBA177	QUETIER (personal gift)
FBA211	QUETIER (personal gift)
FBB58	QUETIER (personal gift)

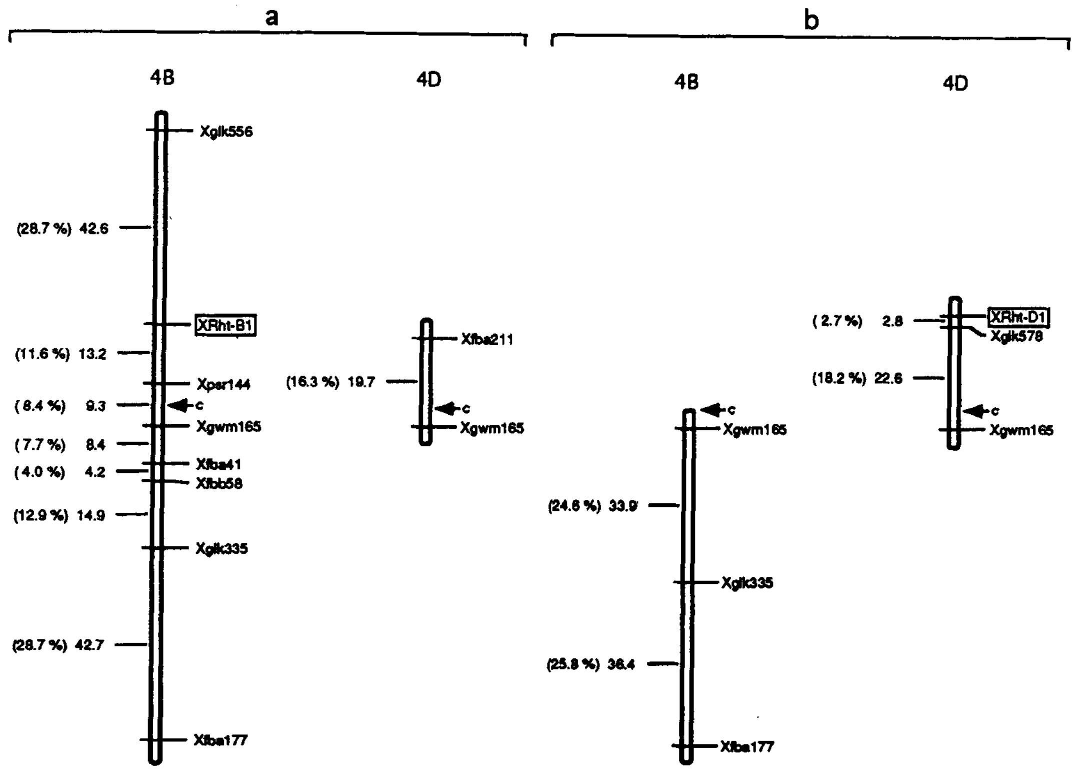

Fig. 1. Maps of wheat chromosomes 4B and 4D obtained from the F_2 populations Renan × Camp-Rémy (a) and Rendez-Vous × Roazon (b). Markers are in LOD 3.0 order. Distances on the left of the chromosome are in cM according to KOSAMBI (1944) and numbers in brackets indicate recombination values. Approximate position of the centromere (c) is indicated with an arrow.

formaldehyde, 2 mg/l sodium thiosulfate). Image development was conducted at a maximum temperature of 12°C during 3 to 10 min. The reaction was stopped by addition of acetic acid (10 %), and the gel was rinsed in water and dried at room temperature.

Mapping and linkage analysis

The maps obtained from the F_2 populations were constructed using Mapmaker/exp version 3.06 (LANDER et al. 1987). The linkage groups were established by calculating recombination frequencies with the following conditions: thresholds for LOD = 3 and $\theta = 0.35$. Association between molecular markers and plant height (QTLs) was evaluated by the "marker regression" method (KEARSEY and HYNE 1994) computed with Splus software (BECKER et al. 1992).

RESULTS

The averages of plant height of the cultivars Renan (Re), Rendez-Vous (RV), Camp-Rémy (CR) and Roazon (Rz) scored at the Plant Breeding Station at Rennes were 91, 80, 93, and 92 cm respectively. The parents of the F_2 populations (Re × CR and RV × Rz) were not highly contrasted in height.

Mapping of Rht-B1 and Rht-D1

The GA_3 test allowed identification of the genotype for each F_2 plant in both populations (Re × CR and RV × Rz). The two genes have been considered as genetic markers and their localisation on the maps is given in Fig. 1a and 1b. Assignation of the linkage groups to the chromosomes 4B and 4D was realised using a microsatellite (GWM165) which gave homoeologous loci on each of the three chromosomes of the group 4 (PLASCHKE et al. 1996). The loci on chromosomes 4B and 4D were both polymorphic for both F_2 populations. The *Rht-B1* gene was located between *Xpsr144-4B* and *Xglk556-4B*. Nevertheless, the linkage was not very strong since the gene was 13 cM distal to the former and 43 cM distal to the latter (Fig. 1a). On the other hand, the gene *Rht-D1* was very close to *Xglk578-4D* (3 cM), but we did not find a more distal marker beyond this gene. The level of polymorphism detected between the two parents of this cross was low (RV and Rz: 18 % of polymorphic probes). This, combined with the poor polymorphism generally detected on the D genome (CHAO et al. 1989; CADALEN et al. 1997) can explain our result.

The marker regression method conducted on the data from the Re × CR F_2 population detected the

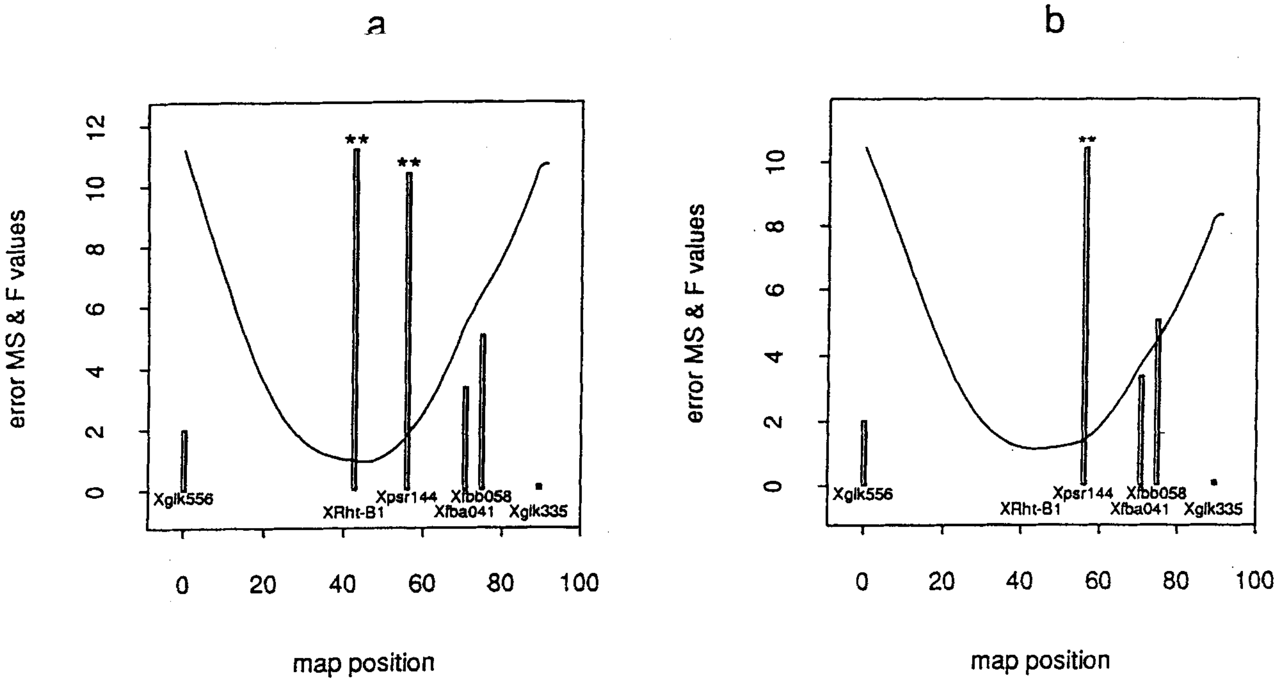

Fig. 2 a and b. Detection of loci associated with plant height on the F_2 population Renan × Camp-Rémy using the regression method (KEARSEY and HYNE 1994). Only partial maps (around 90 cM long) are given. Positions of the anchor markers are given in cM along the abscissa according to KOSAMBI (1944). The long arm of each chromosome is toward the right of the graphics and the short arm toward the left. The origin (0) indicates the first marker of the short arm. The graphs represent the *F* tests for each marker (vertical bars). The curve indicates the changes in residual mean square for various putative QTL positions as defined by KEARSEY and HYNE (1994).
(**a**) all markers, (**b**) when omitting *XRht-B1* from the analysis.

same QTL (Fig. 2) with or without including the *Xrht-B1* locus in the analysis. This QTL was located at the same position in both cases. This locus explained only 9 % of the variability for plant height on this population and the locus *Xglk556-4B* was not found to be significantly associated with this trait (*F* probability 0.15). The positive allele (increasing plant height) came from CR, which was consistent with the fact that Re carried the *Rht-B1b* allele. The additive value was 5.4 cm while the dominance effect was only 0.4 cm. This result was not expected since *Rht-B1* was described as semi-dominant (GALE and YOUSSEFIAN 1985).

DISCUSSION

Molecular markers linked to dwarfing genes would allow more rational breeding schemes concerning plant height. In this study, we have found two loci (*Xpsr144-4B* and *Xglk578-4D*) associated with two such genes (*Rht-B1* and *Rht-D1*, respectively). In the case of *Rht-B1*, information from the two loci flanking the gene (*Xpsr144-4B* and *Xglk556-4B*) should be necessary for integration of these molecular markers in a breeding scheme. The gene *Rht-D1* was not framed between two markers. It is located on the D genome (chromosome 4D), which was often 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 found only few markers on this chromosome.

It was unexpected to find so weak additive and dominance values (5.4 cm and 0.4 cm, respectively) on the Re × CR F_2 population. Perhaps, they are due to epistatic effects between *Rht-B1* and other regions on the genome, which reduce the effect of *Rht-B1*.

Two loci found to be associated with these genes were revealed by a unique microsatellite (GWM165). Microsatellites have several advantages versus RFLP markers: (1) the level of polymorphism detected is much higher (e.g., PIC values for the three loci for this microsatellite on the A, B, and D genomes, respectively: 0.42, 0.81, 0.42) than the level of polymorphism of RFLP (mean of PIC value 0.3); (2) each locus is genome-specific and, in our case, previous chromosome assignment done on aneuploid lines (PLASCHKE et al. 1996) allowed each linkage group to be attributed to a chromosome.

Our results should be validated on a core collection of genotypes with the probes PSR144 and GLK578. We will probably be confronted with the lack of polymorphism detected by RFLP probes in wheat. For example, the probe PSR144 reveals very few polymorphisms and is thus difficult to use in a breeding scheme (J SNAPE, personal communication). Microsatellites could be a way to solve this problem.

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REFERENCES

Allan RE, (1970). Differentiating between two Norin 10/ Brevor 14 semidwarf genes in a common genetic background. Seiken Zihô 22: 83–90.

Allan RE, (1983). Yield performance of lines isogenic for semidwarf genes doses in several wheat populations. In: Proc. 6th Int. Wheat Genet. Symp. (ed. S Sakamoto) Kyoto, Japan, p. 265–270.

Allan RE, Vogel OA and Craddock JC, (1959). Comparative response to gibberellic acid of dwarf, semi-dwarf, and standard short and tall winter wheat varieties. Agron. J. 51: 737–740.

Allan RE, Vogel OA and Peterson CJ, (1968). Inheritance and differentiation of semidwarf culm length of wheat. Crop Sci. 8: 701–704.

Bassam BJ, Caetano-Anolles G and Gresshoff PM, (1991). Fast and sensitive silver staining of DNA in polyacrylamide gels. Anal. Biochem. 196: 80–83.

Becker RA, Chambers JM and Wilks AR, (1992). The new S language: A Programming Environment for Data Analysis and Graphics. Wadsworth and Brooks. Cole Advanced Books and Software. Pacific Grove, California.

Borlaug NE, (1968). Wheat breeding and its impact on world food supply. In: Proc. 3rd Int. Wheat Genet. Symp. (eds KW Finlay and KW Shepherd) Australian Acad. Sci. Canberra, Australia, p. 1–36.

Börner A and Mettin D, (1988). The genetic control of gibberellic acid insensitivity of the wheat variety Ai-Bian. In: Proc. 7th Int. Wheat Genet. Symp. (eds TE Miller and RMD Koebner) Cambridge, UK, p. 489–492.

Börner A, Worland AJ, Plaschke J, Schumann E and Law CN, (1993). Pleiotropic effects of genes for reduced height (Rht) and day-length insensitivity (Ppd) on yield and its components for wheat grown in middle Europe. Plant Breed. 111: 204–216.

Börner A, Plaschke J, Korzun V and Worland AJ, (1996). The relationships between the dwarfing genes of wheat and rye. Euphytica 89: 69–75.

Cadalen T, Boeuf C, Bernard S and Bernard M, (1997). An intevarietal molecular marker map in Triticum aestivum L. em. Thell. and comparison with a map from a wide cross. Theor. Appl. Genet. 94: 367–377.

Chao S, Sharp PJ, Worland AJ, Warham EJ, Koebner RMD and Gale MD, (1989). RFLP-based genetic maps of wheat homoeologous group 7 chromosomes. Theor. Appl. Genet. 78: 495–504.

Devos KM, Atkinson MD, Chinoy CN, Liu CJ and Gale MD, (1992). RFLP-based genetic map of the homoeologous group 3 chromosomes of wheat and rye. Theor. Appl. Genet. 83: 931–939.

Devos KM, Millan T and Gale MD, (1993). Comparative RFLP maps of the homoeologous group 2 chromosomes of wheat, rye and barley. Theor. Appl. Genet. 85: 784–792.

Devos KM, Dubcovsky J, Dvorak J, Chinoy CN and Gale MD, (1995). Structural evolution of wheat chromosomes 4A, 5A, 7B and its impact on recombination. Theor. Appl. Genet. 91: 282–288.

Gale MD and Gregory RS, (1977). A rapid method for early generation selection of dwarf genotypes in wheat. Euphytica 26: 733–739.

Gale MD and Marshall GA, (1975). The nature and genetic control of gibberellic insensitivity in dwarf wheat grain. Heredity 35: 55–65.

Gale MD and Youssefian S, (1985). Dwarfing genes in wheat. In: Progress in Plant Breeding I (ed. GE Russel) Butterworth and Co, London, U.K., p. 1–35.

Gale MD, Law CN, Marshall GA and Worland AJ, (1975). The genetic control of gibberellic acid insensitivity and coleoptile length in 'dwarf' wheat. Heredity 34: 393–399.

Jia J, Devos KM, Chao S, Miller TE, Reader SM and Gale MD, (1996). RFLP-based maps of the homoeologous group 6 chromosomes of wheat and their application in the tagging of Pm12, a powdery mildew resistance gene transferred from Aegilops speltoides to wheat. Theor. Appl. Genet. 92: 559–565.

Kam-Morgan LNW, Gill BS and Muthukrishnan S, (1989). DNA restriction fragment length polymorphisms: a strategy for genetic mapping of D genome of wheat. Genome 32: 724–732.

Kearsey MJ and Hyne V, (1994). QTL analysis: a simple "marker-regression approach". Theor. Appl. Genet. 89: 698–702.

Kosambi DD, (1944). The estimation of map distances from recombination values. Ann. Eugen. 12: 172–175.

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE and Newburg I, (1987). Mapmaker: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1: 174–181.

Liu Y and Tsunewaki K, (1991). Restriction fragment length polymorphism (RFLP) in wheat. II-Linkage maps of the RFLP sites in common wheat. Jpn. J. Genet. 66: 617–633.

Lu YH, Merlino M, Isaac PG, Staccy J, Bernard M and Leroy P, (1994). A comparative analysis between [^{32}P] and digoxygenin-labelled single-copy probes for RFLP detection in wheat. Agronomie 14: 33–39.

Marino CL, Nelson, JC, Lu YH, Sorrells ME, Leroy P, Lopes CR and Hart GE, (1996). RFLP-based linkage maps of the homoeologous group 6 chromosomes of hexaploid wheat (Triticum aestivum L. em. Thell). Genome 39: 359–366.

McIntosh RA, (1979). Catalog of gene symbols for wheat. In: Proc. 4th Int. Wheat Genet. Symp. (ed. S Ramanujam) New Delhi, India, p. 1299–1309.

McVittie JA, Gale MD, Marshall GA and Westcott B, (1978). The intra-chromosomal mapping of the Norin 10 and Tom Thumb dwarfing genes. Heredity 40: 67–70.

Nelson JC, Van Deynze AE, Autrique E, Sorrells ME, Lu YH, Merlino M, Atkinson M and Leroy P, (1995a). Molecular mapping in bread wheat. Homoeologous group 2. Genome 38: 516–524.

Nelson JC, Van Deynze AE, Autrique E, Sorrells ME, Lu YH, Negre S, Bernard M and Leroy P, (1995b). Molecular mapping in bread wheat. Homoeologous group 3. Genome 38: 525–533.

Nelson JC, Van Deynze AE, Sorrells ME, Lu YH, Atkinson M, Bernard M, Leroy P, Faris J and Anderson JA, (1995c). Molecular mapping of wheat: major genes and rearrangements in homoeologous groups 4, 5 and 7. Genetics 141: 721–731.

Plaschke J, Börner A, Wendehake K, Ganal MW and Röder MS, (1996). The use of aneuploids for the chromosomal assignment of microsatellite loci. Euphytica 89: 33–40.

Reid JB, (1986). Gibberellin mutants. In: Plant Gene Research: A Genetic Approach to Plant Biochemistry (eds AD Blonstein and PJ King) Springer-Verlag, Wien, New York, p. 1–34.

Snape JW, Law CN and Worland AJ, (1977). Whole chromosome analysis of height in wheat. Heredity 38: 25–36.

Sourdille P, Perretant MR, Charmet G, Leroy P, Gautier MF, Joudrier P, Nelson JC, Sorrels ME and Bernard M, (1996). Linkage between RFLP markers and genes affecting kernel hardness in wheat. Theor. Appl. Genet. 93: 580–586.

Van Deynze AE, Dubcovsky J, Gill KS, Nelson JC, Sorrells ME, Dvorak, J, Gill BS, Lagudah ES, McCouch SR and Appels R, (1995). Molecular genetic maps for group 1 chromosomes of Triticeae species and their relation to chromosomes in rice and oat. Genome 38: 45–59.

Vogel OA, (1964). Registration of Gaines wheat. Crop Sci. 4: 116–117.

Worland AJ and Petrovic S, (1988). The gibberellic acid insensitive dwarfing gene from the wheat variety Saitama 27. Euphytica 38: 55–63.

Worland AJ and Sayers EJ, (1995). Rht1 (B.dw) an alternative allelic variant for breeding semi-dwarf wheat varieties. Plant Breed. 114: 397–400.

Worland AJ, Gale MD and Law CN, (1987). Wheat genetics. In: Wheat Breeding; its Scientific Basis (ed. FGH Lupton) Chapman and Hall, New York, p. 129–171.

Xie DX, Devos KM, Moore G and Gale MD, (1993). RFLP-based genetic maps of the homoeologous group 5 chromosomes of bread wheat (Triticum aestivum L.). Theor. Appl. Genet. 87: 70–74.