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# A genetic linkage map of durum wheat

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**Abstract** A genetic linkage map of tetraploid wheat [*Triticum turgidum* (L.) Thell.] was constructed using segregation data from a population of 65 recombinant inbred lines (RILs) derived from a cross between the durum wheat cultivar Messapia and accession MG4343 of *T. turgidum* (L.) Thell. ssp *dicoccoides* (Korn.) Thell. A total of 259 loci were analysed, including 244 restriction fragment length polymorphisms (RFLPs), one PCR (polymerase chain reaction) marker (a sequence coding for a LMW (low-molecular-weight) glutenin subunit gene located at the *Glu-B3* locus), seven biochemical (six seed-storage protein loci and one isozyme locus) and seven morphological markers. A total of 213 loci were mapped at a LOD $\geq 3$ on all 14 chromosomes of the A and B genomes. The total length of the map is 1352 cM and the average distance between adjacent markers is 6.3 cM. Forty six loci could not be mapped at a LOD $\geq 3$. A fraction (18.6%) of the markers deviated significantly from the expected Mendelian ratios; clusters of loci showing distorted segregation were found on chromosomes 1B, 3AL, 4AL, 6AL and 7AL. The durum wheat map was compared with the published maps of bread wheat using several common RFLP markers and general features are discussed. The markers detected the known structural rearrangements involving chromosomes 4A, 5A and 7B as well as the translocation between 2B-6B, but not the deletion on 2BS. This map provides a useful tool for analysing and breeding economically important quantitative traits and for marker-assisted selection, as well as for studies of genome organisation in small grain cereal species.

**Key words** Durum wheat · Mapping · Linkage map · RFLP · Morphological markers

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## Introduction

Durum wheat [*Triticum turgidum* (L.) Thell. convar. *durum* (Desf.) MK.] is a tetraploid species ($2^n = 28$, genomes AABB) widely cultivated in the Mediterranean Basin, and also in Canada, U.S.A., Argentina and India. With about 21.0 million hectares under cultivation (about 8% of the total wheat cultivated area), durum wheat ranks eighth among all cereals. Except for the small amount used in manufacturing couscous and local bread in some Mediterranean countries, its only significant finished product is represented by alimentary pasta. Annual grain yield is estimated around 27.5 million tonnes, with wide variation due to drought stress, diseases and pests. High-yielding cultivars endowed with drought tolerance and disease resistance, in addition to high commercial and technological value, are therefore highly desirable.

Genetic research on important agronomic and quality traits in this crop has lagged far behind other cereals and, at the present time, detailed genetic information is urgently required as a basis for more-sound breeding programmes. The construction of a genetic map may be particularly helpful for the efficient exploration of plant genetic potential. Molecular linkage maps of many plant species have been obtained recently and utilised in quantitative trait analysis, gene tagging, genome organisation and evolutionary studies, as well as in improved selection activities (see reviews by Paterson

et al. 1991; Whitkus et al. 1994). Restriction fragment length polymorphism (RFLP) markers, first proposed by Botstein et al. (1980), have been extensively used to construct genetic maps in many cultivated species (see Phillips and Vasil 1994).

Bread wheat, *Triticum aestivum* (L.) Thell., has received much attention and several RFLP-based maps either for groups of homoeologous chromosomes (Chao et al. 1989; Devos et al. 1992, 1993; Kota et al. 1993; Xie et al. 1993; Hohmann et al. 1994; Delaney et al. 1995a, b; Mickelson-Young et al. 1995; Nelson et al. 1995 a, b, c; Van Deynze et al. 1995; Gill et al. 1996; Jia et al. 1996; Marino et al. 1996) or for all the chromosome groups (Liu and Tsunewaki 1991; Anderson et al. 1992; Gale et al. 1995) have been reported.

Molecular markers have already been utilised in wheat for identifying a series of QTLs, including resistance to pre-harvest sprouting (Anderson et al. 1993), resistance to Hessian fly (Ma et al. 1993), resistance to powdery mildew (Ma et al. 1994), seed protein content (Blanco et al. 1996) and kernel hardness (Sourdille et al. 1996). In durum wheat the only genetic map so far reported concerns the group-6 chromosomes (Chen et al. 1994).

The results of an analysis of a population of 65 RI lines derived from a *durum* x *dicoccoides* cross are presented in this paper, together with a genetic linkage map containing 198 RFLPs, one PCR marker (a sequence coding for a LMW glutenin subunit gene located at the *Glu-B3* locus), seven biochemical (six seed-storage protein loci and one isozyme locus) and seven morphological markers.

## Materials and methods

### Genetic material

The material utilised was a set of 65 recombinant inbred lines developed at the Institute of Plant Breeding, University of Bari, Bari, Italy, from a cross between the durum wheat cv Messapia and *T. turgidum* (L.) Thell. ssp *dicoccoides* (Korn.) Thell. accession MG4343 by advancing random individual $F_2$ plants to the $F_7$ generation by single-seed descent. After the last selfing, every line was bulk-harvested to provide seed for field experiments and DNA extraction.

Nulli-tetrasomic (Sears 1966) and di-telosomic (Sears and Sears 1978) lines were used to assign polymorphic DNA fragments to specific chromosome arms and to determine the approximate position of centromeres. The designations of 4A and 4B chromosomes used were those agreed upon at the 7th International Wheat Genetics Symposium held in 1988 at Cambridge, UK (Anonymous 1988).

### DNA probes and RFLP analysis

Genomic and cDNA clones used as probes were from: Institute of Plant Breeding, University of Bari, Bari, Italy (MGB and UBP clones, Figliuolo et al. 1991); Department of Agrobiology and Agrochemistry, University of Tuscia, Viterbo, Italy, (UTV clones, D'Ovidio et al. 1994); Kansas State University, Manhattan, Kansas, USA (KSU clones, Gill et al. 1991); John Innes Institute, Norwich, UK (PSR and PSB clones, Chao et al. 1989); and Cornell University, Ithaca, NY, USA (BCD, CDO and WG clones, Heun et al. 1991). A total of 238 single- or low-copy RFLP clones were analysed by hybridisation with parental DNAs, and the 168 detecting one or more polymorphisms were subsequently analysed for segregation among the RIL population. A mixture of digoxigenin-labelled heterologous probes of the 18S (pPD5) and 25S (pPD4) coding regions of poplar rDNA (D'Ovidio et al. 1991) was used to detect the ribosomal genes *Nor-B1* and *Nor-B2*.

Durum wheat DNA was prepared from fresh or frozen leaf tissues according to Sharp et al. (1988) and analysed as described in Davis et al. (1989). The most appropriate restriction enzyme for analysing each DNA clone was identified by probing individual DNA clones against blots containing parental DNA digested with 3–5 different restriction enzymes (*Bam*HI, *Eco*RI, *Eco*RV, *Hin*dIII and *Pst*I). Cloned inserts were labelled either by preliminary PCR amplification (Saiki et al. 1988), followed by random primed labelling with $^{32}P$ (Feinberg and Vogelstein 1984), or directly by PCR amplification with DIG11-dUTP (D'Ovidio et al. 1994).

### PCR markers

A pair of PCR primers which amplify a sequence coding for a LMW-glutenin subunit gene located at the *Glu-B3* locus (D'Ovidio 1993) were used to analyse the segregation of the RI lines.

### Seed storage proteins and isozyme markers

Polymorphisms for the isozyme aromatic alcohol dehydrogenase (*Aadh-A1*) and for gliadin and LMW- and HMW-glutenin components of grain storage proteins were identified in the RIL population. Analyses of *Aadh-A1* was performed as described by Jaaska (1978). Total seed-protein extraction and sodium dodecyl sulphate polyacrylamide-gel electrophoresis (SDS-PAGE) in 10% gels were carried out according to Payne et al. (1981). Monomeric prolamins were extracted from crushed single half-grains with 1.5 M dimethylformamide at a 1 : 5 w/v ratio; after centrifugation (15 min at 10000 g) the clear supernatant was used for electrophoretic separation, as described by Lafiandra and Kasarda (1985).

### Morphological markers

Genetic polymorphism was analyzed in terms of seven morphological markers, including black glumes (*Bg*), red glumes (*Rg1*), hairy glumes (*Hg*), response to gibberellic acid (*Gai1*), purple anther (*Pan2*), red coleoptile (*Rc1*) and purple culm (*Pc1*) (see catalogue by McIntosh et al. 1994, 1995).

### Data analysis and linkage mapping

The significance of deviations of observed allelic frequencies of the marker loci from the expected ratio (1 : 1) were tested by chi-square. Linkage analysis and map construction were performed by using the MAPMAKER/EXP software (Lander et al. 1987). In this program, a two-point/group command was used for establishing possible linkage groups with a minimum LOD score of 3.0 and a recombination fraction of 0.37. The most likely order of markers in each group was determined by using "order", "compare", "build", "place" and "ripple" commands. Order information from previously published maps (Gale et al. 1995; Nelson et al. 1995 a, b, c) was also considered in some regions.

Recombination frequencies were converted into map distances by the Kosambi mapping function (Kosambi 1944). Markers detected with MGB, UBP and UTV probes, and their associated linkage groups, were assigned to wheat chromosomes and chromosome arms by hybridisation of probes to Chinese Spring (CS) nulli-tetrasomic and di-telosomic blots; markers detected with PSR, KSU, CDO, BCD, WG probes were assigned according to the above-cited maps.

## Results and discussion

### Parental polymorphism survey and marker segregation

Out of 238 clones, 168 (70.1%) detected one or more RFLPs between the cv Messapia and the var. *dicoccoides* accession MG4343 for at least one of the 3–5 restriction enzymes used. The overall level of polymorphism between the two parents was equal to 54.1%. RFLP frequencies were considerably higher than those detected in derivatives of wide crosses involving hexaploid wheat (Chao et al. 1989; Liu and Tsunewaki 1991; Devos et al. 1992; Nelson et al. 1995 a), but almost identical to those observed in the *durum-dicoccoides* recombinant substitution lines (Chen et al. 1994).

RFLP loci detected in clones by specific hybridisation signals, classified as single- or low-copy and for which a RFLP variant was detected, were mapped. Restriction enzyme/probe combinations detecting variation between the parental lines were used for segregation analysis of the RILs. Analyses of the restriction fragment patterns produced with the 168 probes provided information on 244 loci, with an average of 1.4 RFLP loci per probe. Most RFLPs and other loci (81.4%) showed Mendelian segregation (1 : 1) in the RIL population, whereas 24 (9.3%) showed significant ($P < 0.05$) and 24 (9.3%) highly significant ($P < 0.01$) deviations from the expected ratio (* and ** in Fig. 1). These deviations are higher than those reported in previous wheat mapping studies (Liu and Tsunewaki 1991; Devos et al. 1993; Nelson et al. 1995 a). Most loci showing distorted segregation were clustered on chromosome 1B (from *Xbcd98* to *Xpsr162*); other clusters of 3–4 markers were present in 3AL, 4AL, 6AL and 7AL. Distortion favoured Messapia for the loci on 4AL and 7AS, and *dicoccoides* for the loci on 1B, 3AL and 7BL. A satisfactory order could not be found for eight distorted markers, which were therefore discarded.

Molecular markers showing distorted segregation have been observed in linkage maps derived from intra- and inter-specific hybrids in potato (Gebhart et al. 1989), maize (Gardiner et al. 1993), rice (Causse et al. 1994), common bean (Vallejos et al. 1992), and barley (Heun et al. 1991). Chromosomal rearrangements (Tanksley 1984; Faure et al. 1993), alleles inducing gametic or zygotic selection (Nakagarha 1986), and parental reproductive differences (Foolad et al. 1995) have been indicated as possible causes of deviation. The analysis of additional populations from other crosses displaying segregation distortion would provide further indications on specific causes of deviation, such as the presence of lethal genes or evolutionary chromosomal rearrangements.

### Linkage map of durum wheat

Two-point linkage analysis of the 259 loci resulted in 29 linkage groups containing 235 loci. Twenty five groups comprising 213 loci were assigned to individual chromosomes of durum wheat (Fig. 1) by nulli-tetrasomic and di-telosomic analysis and by comparison of common markers with previously published maps for bread wheat (Gale et al. 1995; Nelson et al. 1995 a, b, c). Eight chromosome maps consist of more than one linkage subgroup (Fig. 1), even when analysed at a LOD value below 3.0. These subgroups contain loci mapping at chromosome ends, and most likely will be joined when additional loci are identified.

The 213 markers are distributed on all 14 chromosomes, covering a total of 1352 cM. The average distance between marker pairs is 6.3 cM, with some gaps wider then 20 cM on linkage groups 2A, 5B and 7A. Additional markers assayed to fill these gaps failed to detect RFLPs for the two parents.

Marker distribution along the linkage groups was far from uniform, with clusters of tightly linked loci and regions with low density. Several chromosomes (notably 1B, 2A, 2B, 3A, 6A, 7A and 7B) had marker clusters in the centromeric regions of the genetic maps, a feature that has been observed in most wheat mapping studies (Chao et al. 1989; Gale et al. 1995; Nelson et al. 1995 a, b, c) and attributed to reduced recombination in the proximal region of chromosome arms.

Two clones hybridised to multiple fragments from the same chromosome and nine to fragments in non-homoeologous chromosomes (these fragments are located in chromosome regions not involved in translocations), possibly as a result of intra- and inter-chromosome duplications and/or restriction sites within the target sequence in the clone. Overall, co-linearity between chromosomes within a homoeologous group was conserved, as shown by several DNA probes hybridising to orthologous loci on the two chromosomes of a homoeologous group. The marker order generally agreed with the already published bread-wheat genetic maps. However, alternative orders were detected at a few regions within a ten-fold probability of being as likely as the orders presented.

Homoeologies within groups 4, 5 and 7 seem to be affected by several rearrangements in chromosomes 4A, 5A and 7B. The presence of linkage subgroups at these chromosome ends, however, does not exclude other evolutionary events. The structure of chromosomes 4A, 5A and 7B of bread wheat has been explained by a translocation of a short terminal segment between chromosome arms 4AL and 5AL, possibly at the

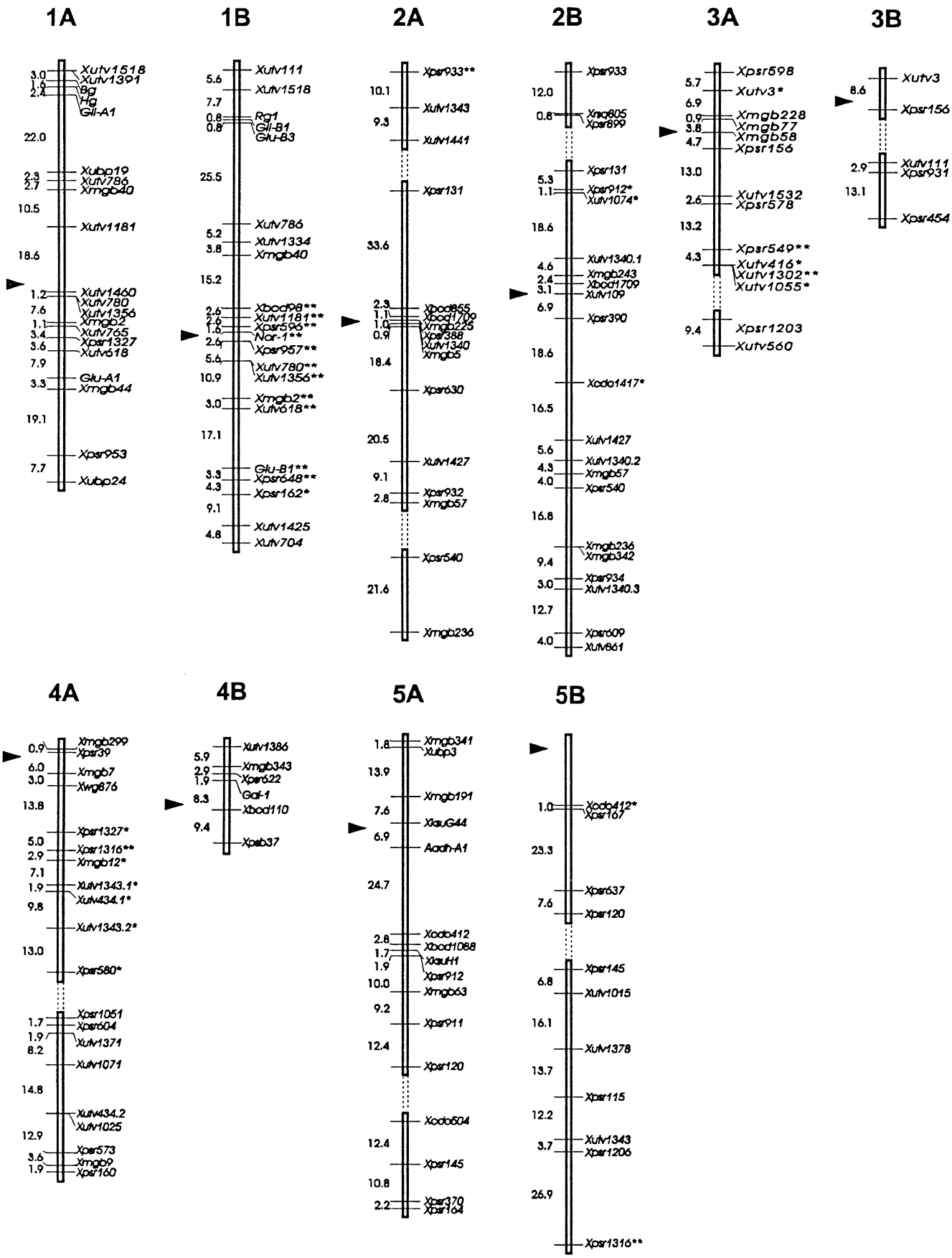


**Fig. 1** See page 725 for legend

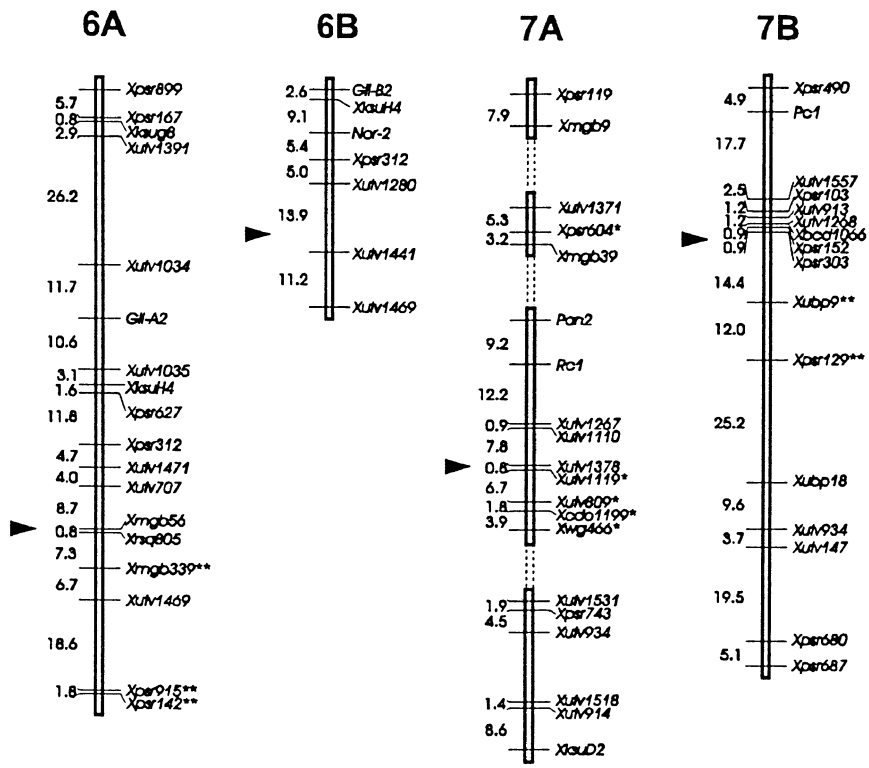


**Fig. 1** Linkage map of durum wheat. Individual linkage subgroups of a chromosome (joined by ::::::) are arranged in their most likely order by null-itetra- and di-telosomic analysis and by comparison with previously published maps. The approximate locations of the centromeres are indicated by an *arrow* ( > ). Short arms are at the top. Markers preceded by an *X* are DNA markers and those *without an X* indicate genes controlling morphological traits, isozymes or proteins that were assayed within the population. Map distances (cM) and marker names are shown on the left and right sides of each chromosome, respectively. Markers showing significant deviations from the expected segregation ratios at the 0.05 and 0.01 levels are indicated with * and **, respectively

diploid level; whereas, at the tetraploid level, the distal portion of 5AL translocated to 4AL was exchanged with a terminal segment from 7BS, followed, or preceded, by paracentric and pericentric inversions of 4A (Naranjio et al. 1987; Liu et al. 1992; Devos et al. 1995; Nelson et al. 1995 c). These rearrangements were present in the analysed RIL population. Therefore linkage group 4A consists of a short segment of the original 4AL arm (*Xmgb299* and *Xpsr39* markers), a small segment of the original 4AS (*Xmgb7* and *Xwg876*), a large segment of 5AL (from locus *Xpsr1316* to locus *Xpsr580*), and a large segment (not linked at a LOD threshold of 3.0) of 7BS (from locus *Xpsr604* to locus *Xpsr160*) also carrying a very short segment of the original 4AL, including the locus *Xpsr1051*. Only a short segment of the original 4AL (including the locus *Xpsr164*) mapped at the distal end of 5AL (tightly linked to the locus *Xpsr370-5A*), confirming the translocation 4AL-5AL. No segment from the original 5AL translocated to 4AL was detected on chromosome 7BS.

Another ancestral rearrangement, resulting in the transfer of a chromosome segment from the extreme end of 6BS to 2BS and the deletion of a short segment from 2BS, has been described in hexaploid wheat (Devos et al. 1993; Nelson et al. 1995 b). The present results confirm the exchange event 6BS-2BS at the tetraploid level, mapping the markers *Xpsr899* and *Xrsq805* (having orthologous loci on group 6S) on 2BS, tightly linked to *Xpsr933*, which has orthologous loci on 2S. Devos et al. (1993), using five different probes, including PSR933, detected orthologous loci on 2AS and 2DS but not on 2BS, which had probably undergone deletion of its distal end. The deletion at the hexaploid level was further confirmed by Nelson et al. (1995 a). The mapping of *Xpsr933* on 2BS in the present analysis indicates that the deletion may have occurred at the hexaploid level or else in the limited number of tetraploid wheats that gave rise to hexaploids.

## Mapping of the genes coding for biochemical and morphological traits

Seven biochemical loci, one PCR marker (sequence coding for a LMW glutenin subunit gene located at the *Glu-B3* locus) and seven morphological markers, which showed polymorphism in the parent material, were analysed and mapped. RI segregation for these characters showed a good fit to a 1:1 ratio, indicating that each of them is controlled by a single gene; only the $\gamma$-gliadin gene *Gli-B1* showed distorted segregation in favour of the *dicoccoides* allele. Durum wheat cv Messapia and *dicoccoides* accession MG4343 differed at four analysed components of the complex gliadin loci *Gli-1* and *Gli-2* on the short arm of group-1 and -6 chromosomes, at the HMW glutenin loci *Glu-A1* and *Glu-B1* on the long arm of group-1 chromosomes (Blanco and De Giovanni 1994), and at the *Glu-B3* locus on 1BS. Segregation at *Glu-B3* was analysed by PCR amplification with primers (D'Ovidio 1993) for

a specific LMW glutenin subunit gene located at the *Glu-B3* locus. Messapia had no protein encoded at *Glu-A1* and contains HMW glutenin subunits 6 + 8 at *Glu-B1*; MG4343 had two new alleles coding for HMW glutenin subunits 1* (*Glu-A1*) and 7* + 22* (*Glu-B1*), not reported in the Payne and Lawrence (1983) catalogue. The positions of the seven loci on the present map are in good agreement with the mapping data reported by Payne et al. (1982, 1986), Singh and Shepherd (1988 a, b), and Jia et al. (1996). The *Glu-B3* locus for the LMW glutenins was mapped at 0.8 cM from *Gli-B1*.

The aromatic-alcohol-dehydrogenase enzymes are controlled by two sets of orthologous loci (*Aadh-1* and *Aadh-2*) on the long arm of group-5 (Jaska 1978) and group-6 chromosomes (Schmidt and Seliger 1982; Hart 1987). The gene encoding the polymorphic isozyme in the RI population (*Aadh-A1*) was mapped near the centromere (within 5 cM) on 5AL.

The genes *Gai1* and *Gai3* on 4BS and *Gai2* on 4DS, controlling gibberellic-acid insensitivity, have been described by several studies, indicating either their pleiotropic effect or else a tight association with the reduced-plant-height genes *Rht1*, *Rht3* and *Rht2*, respectively (see review by Gale and Law 1976). *Gai1* has been mapped within 20 cM of the centromere on 4BS.

Red glume colour is controlled by *Rg1* on 1B (Unrau 1950), *Rg2* on 1D (Rowland and Kerber 1974), and a putative third gene associated with hairy glume on 1A (Schmalz 1958). *Rg1* was mapped closely linked to *Gli-B1*, on chromosome arm 1BS. A single factor for black glume colour, *Bg*, has been reported in diploid, tetraploid and hexaploid wheat (Sikka et al. 1961), and is located on 1A (McIntosh et al. 1995). *Bg* was mapped on chromosome arm 1AS, tightly linked to *Hg* (1.6 cM) and *Gli-A1* (4 cM).

A single gene controlling hairy glumes (*Hg*) was described at all levels of ploidy and located on 1AS (Sears 1954; McIntosh and Bennett 1978) linked with *Bg* (black glumes) (Sikka et al. 1961). *Hg* was mapped on 1AS closely linked to *Bg* (1.6 cM) and *Gli-A1* (2.4 cM) in the present analysis.

Three genes controlling red coleoptile (*Rc1*, *Rc2* and *Rc3*) were firstly reported on chromosomes 7A (Sears 1954), 7B (Kuspira and Unrau 1958) and 7D (Jha 1964) by aneuploid analysis. The *Rc1* and *Rc3* loci have successively been placed 10–16 cM from the centromere (Rowland and Kerber 1974; Nelson et al. 1995 c). The gene *Rc1* contributed by the *dicoccoides* parent was mapped on the 7AS chromosome arm at 21 cM from the centromere in the present population.

The *Pc1* gene was mapped 23 cM from the centromere on 7BS. It is one of the two genes for purple culm (*Pc1* and *Pc2*) located on chromosome arms 7BS (Kuspira and Unrau 1960; Law 1966) and 7DS (Maystrenko 1992), but not yet mapped. A gene which controls the anther pigmentation in *dicoccoides*, *Pan2*, was mapped at 30 cM from the centromere in 7AS. It seems different from the single dominant gene for purple anthers (*Pan1*) described by Maystrenko (1992) as present in 7DS.

## Conclusion

A genetic linkage map for durum wheat has been constructed on the basis of the segregation of 198 RFLPs, one PCR marker, seven biochemical markers and seven morphological markers. The total distance covered is 1352 cM with an average of 6.3 cM between loci.

The development of a genetic linkage map is a first step toward the detection of factors controlling the expression of economically important traits. Much of the effort in constructing the durum wheat map was directed towards the identification of polymorphic markers. The linkage information developed in this map may also be used directly, because the mapped population, which was derived from an interspecific cross, shows variation for a large number of traits, such as height, heading-time, powdery mildew resistance, seed-protein content, sedimentation value and yield components. The homozygosity of recombinant inbreds is particularly useful for QTL mapping. Such lines constitute a permanent segregating population that can be used indefinitely and evaluated over space and time, permitting the reduction of experimental error to the extent necessary for detecting small genetic differences (Mather and Jinks 1977). Finer dissection of quantitative agronomic characters may result in a more precise mapping of QTLs and determination of the effects of each factor independently. The identification of markers linked with genes controlling economically important traits may be used for marker-aided selection in breeding programs, which would allow a more accurate and efficient selection of superior genotypes and a reduction of time and space during the early breeding steps.

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