Theor Appl Genet (2004) 109: 1105–1114
DOI 10.1007/s00122-004-1740-7

ORIGINAL PAPER

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A high-density microsatellite consensus map for bread wheat (*Triticum aestivum* L.)

Received: 4 March 2004 / Accepted: 25 May 2004 / Published online: 29 July 2004

Abstract A microsatellite consensus map was constructed by joining four independent genetic maps of bread wheat. Three of the maps were F_1-derived, doubled-haploid line populations and the fourth population was 'Synthetic' × 'Opata', an F_6-derived, recombinant-inbred line population. Microsatellite markers from different research groups including the Wheat Microsatellite Consortium, GWM, GDM, CFA, CFD, and BARC were used in the mapping. A sufficient number of common loci between genetic maps, ranging from 52 to 232 loci, were mapped on different populations to facilitate joining the maps. Four genetic maps were developed using MapMaker V3.0 and JoinMap V3.0. The software CMap, a comparative map viewer, was used to align the four maps and identify potential errors based on consensus. JoinMap V3.0 was used to calculate marker order and recombination distances based on the consensus of the four maps. A total of 1,235 microsatellite loci were mapped, covering 2,569 cM, giving an average interval distance of 2.2 cM. This consensus map represents the highest-density public microsatellite map of wheat and is accompanied by an allele database showing the parent allele sizes for every marker mapped. This enables users to predict allele sizes in new breeding populations and develop molecular breeding and genomics strategies.

Communicated by J. Snape

Electronic Supplementary Material Supplementary material is available for this article at http://dx.doi.org/10.1007/s00122-004-1740-7

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Introduction

The value of crop species genetic maps has steadily increased from when they were first introduced in the 1980s. Wheat molecular genetic maps first comprised RFLP markers (Chao et al. 1989; Devos et al. 1993; Devos and Gale 1997) and over time, PCR-based markers became the dominant marker type for genetic map construction, including RAPDs (Williams et al. 1990), AFLPs (Vos et al. 1995), and microsatellites (SSRs; Röder et al. 1998; Pestsova et al. 2000; Gupta et al. 2002). The primary reason to shift toward PCR-based markers and particularly SSR marker maps is the potential to use the maps in plant breeding (Gupta and Varshney 2000). Conventional plant breeding requires the analysis of thousands of plants in a short time period at low cost. Microsatellite markers and high-throughput capillary electrophoresis are good platforms upon which to implement marker-assisted selection (MAS) in breeding programs.

Molecular breeding is more effective if the molecular map is densely populated with markers. This provides molecular breeding strategies with more choice in the quality of markers and more probability of polymorphic markers in an important chromosome interval. The first microsatellite map in wheat possessed 279 microsatellites (Röder et al. 1998). This marker density is useful for QTL and gene mapping, but is limiting for the precise transfer of QTLs between different genetic backgrounds. Specifically, the limitation comes from the lack of polymorphic markers immediately flanking QTLs.

Wheat genomics research is increasing the use of genetic maps, particularly in map-based gene cloning efforts. Map-based cloning requires an accurate, fine genetic map to correctly position a gene of interest between close flanking markers (Peters et al. 2003).

Beginning with a robust, high-density map, the efforts to add more markers for fine mapping are greatly improved and narrows the number of possible BAC clones harbouring the gene.

Since single-wheat mapping populations vary in their level of polymorphism (typically 20–40%), there is a limitation in the number of markers that can be added to the map. The International Triticea Mapping Initiative (ITMI) population ('Synthetic'/'Opata') is one of the most polymorphic wheat mapping populations and has been extensively mapped with RFLP, AFLP, and SSR markers (Nelson et al. 1995; Röder et al. 1998) (http://wheat.pw.usda.gov). Although the current ITMI map has a high marker density, it is made up primarily of RFLP markers, which are not amenable to high-throughput molecular breeding strategies. In order to raise the density of microsatellite markers available on a wheat genetic map, a microsatellite consensus map could be constructed. This is done by mapping several common microsatellites on each chromosome in different mapping populations, such that this subset of markers anchors the chromosome maps from different populations. This approach derives a single genetic map constructed by the consensus of marker order and recombination distances.

In this study, four genetic maps were fused to derive a consensus map. The ITMI mapping population is one of the genetic maps, and thus the final consensus map is related to previous maps of this population. The final consensus map included 1,235 microsatellite markers, which is a significant improvement over single-population genetic maps and provides a new tool for wheat breeding and genomics research.

Materials and methods

Mapping populations

There were four mapping populations integrated into a single consensus map that are summarized in Table 1. The parents and number of lines mapped in the four mapping populations are 'Synthetic'/'Opata' [SO, 68 recombinant-inbred lines (RIL) lines], 'RL4452'/'AC Domain' (RD, 91 DH lines), 'Wuhan'/'Maringa' (WM, 93 DH lines), and 'Superb'/'BW278' (SB, 186 DH lines). The SO population was developed for ITMI with the purpose of having a shared mapping population among wheat scientists. The other three populations were developed at Agriculture and Agri-Food Canada to serve specific needs in trait analysis and QTL mapping. Additional *Triticum aestivum* accessions included 'Chinese Spring' (CS) and 21 nullisomic/tetrasomic (NT) lines of CS. The DNA of each accession and progeny line was extracted from leaf tissue of single plants using the DNeasy Plant DNA extraction kit (Qiagen, Mississauga, Ont., Canada).

Microsatellite primer sequences

There are several sources of wheat microsatellite primer sequences available in the public domain and these are listed in Table 2. The Wheat Microsatellite Consortium (WMC) was a private effort coordinated by Dr. P. Isaac (IDnagenetics, Norwich, UK) and included 38 members. The majority of the WMC primer sequences were made publicly available in January 2004; the remainder of the WMC markers become available in January 2006. There was a small subset of WMC markers not available to the public and excluded from the accompanying database, but they are included in the final consensus map. The BARC markers (Song et al. 2002) were developed for the US Wheat and Barley Scab Initiative to map and characterize genes for fusarium resistance. The CFA and CFD markers were kindly provided by Dr. P. Sourdille (INRA). The GWM and GDM markers are taken from the publication by Röder et al. (1998) and Pestsova et al. (2000), respectively. Microsatellite primers were synthesized by the National Research Council (Dr. D. Tessier, Montreal, Que., Canada) and were diluted to 1–10 pmol/μl, depending on the detection method to be used.

Chinese spring NT analysis

The WMC markers were amplified in the CS/NT series in order to assign specific alleles to chromosomes prior to genetic mapping. The PCR conditions were: 24 ng DNA, 1.5 mM $MgCl_2$, 50 mM KCl, 0.8 mM dNTPs, 2 pmol γ-[^{33}P]-dATP-labelled forward primer, 2 pmol reverse primer, and 0.5 U *Taq* DNA polymerase (Promega, Madison, Wis., USA). Thermal cycling included: 94°C, 2 min; 30 cycles of 95°C, 1 min (0.5°C/s to 61/51°C); 61/51°C, 50 s (0.5°C/s to 73°C); 73°C, 1 min; 1 cycle 73°C, 5 min. PCR products were separated by electrophoresis in 0.4 mm × 50 cM, 4% polyacrylamide (1× TBE) gels, and followed by autoradiography.

Table 1 Summary of four mapping populations used to construct the microsatellite consensus map of *Triticum aestivum*

Mapping parents	Population type[a]	Number of lines	Trait segregation[b]
'Synthetic'/'Opata'	F_6 RIL	68	Various
'RL4452'/'AC Domain'	DH	91	Quality/agronomy/disease
'Wuhan'/'Maringa'	DH	91	FHB
'Superb'/'BW278'	DH	186	Yield/FHB

[a] *RIL* Recombinant-inbred lines, *DH* F_1-derived doubled haploid lines
[b] Represents the primary traits segregating in the population

Table 2 Summary of publicly available wheat microsatellites used in this study

Microsatellite developer	Microsatellite code	Quantity available	Public source
WMC[a]	WMC	423	http://wheat.pw.usda.gov
Marion Röder (IPK)	GWM	279	Röder et al. (1998)
Marion Röder (IPK)	GDM	55	Pestsova et al. (2000)
Perry Cregan (USDA)	BARC	166	http://www.scabusa.org
Pierre Sourdille (INRA)	CFA	55	http://wheat.pw.usda.gov
Pierre Sourdille (INRA)	CFD	130	http://wheat.pw.usda.gov
Total		1,108	

[a]Wheat Microsatellite Consortium

Segregation data collection

Segregation data for part of the SO map and all of the WM map were collected using γ-[^{33}P]-dATP end-labelled primers and PCR as described above. Segregation data for the remainder of the SO map and all of the RD and SB maps were collected using M13 tailing and fluorescent capillary electrophoresis on an ABI3100 genotyper (Applied Biosystems, Foster City, Calif., USA). M13 tailing required adding the M13 sequence (CACGACGTTGTAAAACGAC) to the 5′ end of the forward primer during primer synthesis (Schuelke 2000). The PCR conditions were: 24 ng DNA; 1.5 mM $MgCl_2$; 50 mM KCl; 0.8 mM dNTPs; 2 pmol reverse primer; 0.2 pmol forward primer; 1.8 pmol M13 primer (CACGACGTTGTAAAACGAC) fluorescently labelled with 6-FAM, VIC, NED, or PET (Applied Biosystems); and 0.5 U *Taq* DNA polymerase (Promega). Thermal cycling included: 94°C, 2 min; 30 cycles of 95°C, 1 min (0.5°C/s to 61/51°C); 61/51°C, 50 s (0.5°C/s to 73°C); 73°C, 1 min; and 1 cycle 73°C, 5 min. The internal molecular weight standard for the ABI3100 was Genescan 500-LIZ (Applied Biosystems). Data collected by fluorescent capillary electrophoresis were first converted to a gel-like image, using Genographer (available at http://hordeum.oscs.montana.edu/genographer).

The microsatellite allele sizes from the mapping parents were measured on the ABI3100 and recorded without the 19-bp M13 tail, in a database accompanying the consensus map (available at http://wheat.pw.usda.gov).

Genetic map construction

The CS/NT analysis showed the likely physical location of the WMC markers, and this information was used to anchor the chromosomes of the SO map. GWM marker segregation data produced by Röder et al. (1998) for the SO map are available at http://wheat.pw.usda.gov, and this information was also used to anchor the linkage groups of the SO map to chromosomes. The individual lines of the SO population mapped in this study were the same as those mapped by Röder et al. (1998). Table 4 shows which populations were used to map each of the marker collections. Each of the four genetic maps was constructed separately using MapMaker V3.0 (Lander et al. 1987; Lincoln et al. 1993), with an LOD threshold of 2.5 and maximum recombination fraction of 0.35. The 'TRY' and 'RIPPLE' commands were used to add markers to framework maps and check the final marker order. Recombination distances were determined using the Kosambi mapping function (Kosambi 1944).

Consensus map construction

JoinMap, version 3.0 (Biometris, Wageningen, The Netherlands, http://www.joinmap.nl), was used to construct the wheat microsatellite consensus map. First, JoinMap was used to calculate the individual genetic map distances and marker orders using the raw segregation data and Kosambi mapping function (Kosambi 1944), and then, was used to calculate the consensus map. Second, the comparative mapping program CMap (http://www.gmod.org/cmap), developed by Lincoln Stein, was used to align the four genetic maps with the consensus map for a visual inspection of the maker order. Third, an alignment of the individual Mapmaker- and JoinMap-derived maps was made for each chromosome using CMap. The CMap comparisons were used to identify errors in the individual genetic maps based on consensus. These errors typically included incorrect marker orders over short 10-cM intervals or localized inversions of linkage blocks flanked by gaps in the maps. The individual genetic map segregation data were checked for errors, and the final version of each genetic map was constructed with JoinMap. Finally, the marker order and recombination distance displayed in the consensus map was based on the corrected individual maps as calculated by JoinMap.

Results

The consensus map covered 2,569 cM, included 1,235 microsatellite markers, and did not contain linkage gaps. There were several large linkage distances, notably on the A genome, and these linkages were also observed in the individual genetic maps (Fig. 1). Included on the map are several ESTs mapped via a PCR that interrogates a single nucleotide polymorphism (SNP) between two mapping parents. The ESTs are indicated by Genebank accession number-nucleotide position of the SNP (Somers et al. 2003b). Further, several genes for disease resistance, storage proteins, and plant height are indicated since these loci segregated as Mendelian factors in at least one population. The microsatellite markers are colour coded

by source to facilitate identification of a specific marker by name. There are characteristic clusters of microsatellites near the centromere of each chromosome. A shaded zone on each chromosome indicates the approximate position of the centromere based on comparative mapping to both physical and genetic maps of RFLP and microsatellite markers available at GrainGenes (http://wheat.pw.usda.gov). In a separate study, approximately 250 WMC and GWM microsatellites from the consensus map were physically mapped into chromosome bins, using the disomic deletion stocks of CS (Endo and Gill 1996; data not shown). This facilitated an improved ordering of markers around the centromere and helped with correct positioning of the centromere (Fig. 1).

The density of markers on the map ranged from 1.2 cM/marker on 4B to 4.1 cM/marker on 6A, with an average density of 2.2 cM/marker. There was variation in marker density on the basis of homoeologous group, ranging from 1.6 cM/marker for group 3 to 2.6 cM/marker for group 5 chromosomes. The A-, B-, and D-genome chromosomes had genetic lengths of 944, 851, and 778 cM, with marker densities of 2.6, 1.7, and 2.1 cM/marker, respectively. The length of the chromosomes ranged from 59 cM (4B) to 184 cM (5A) (Table 3).

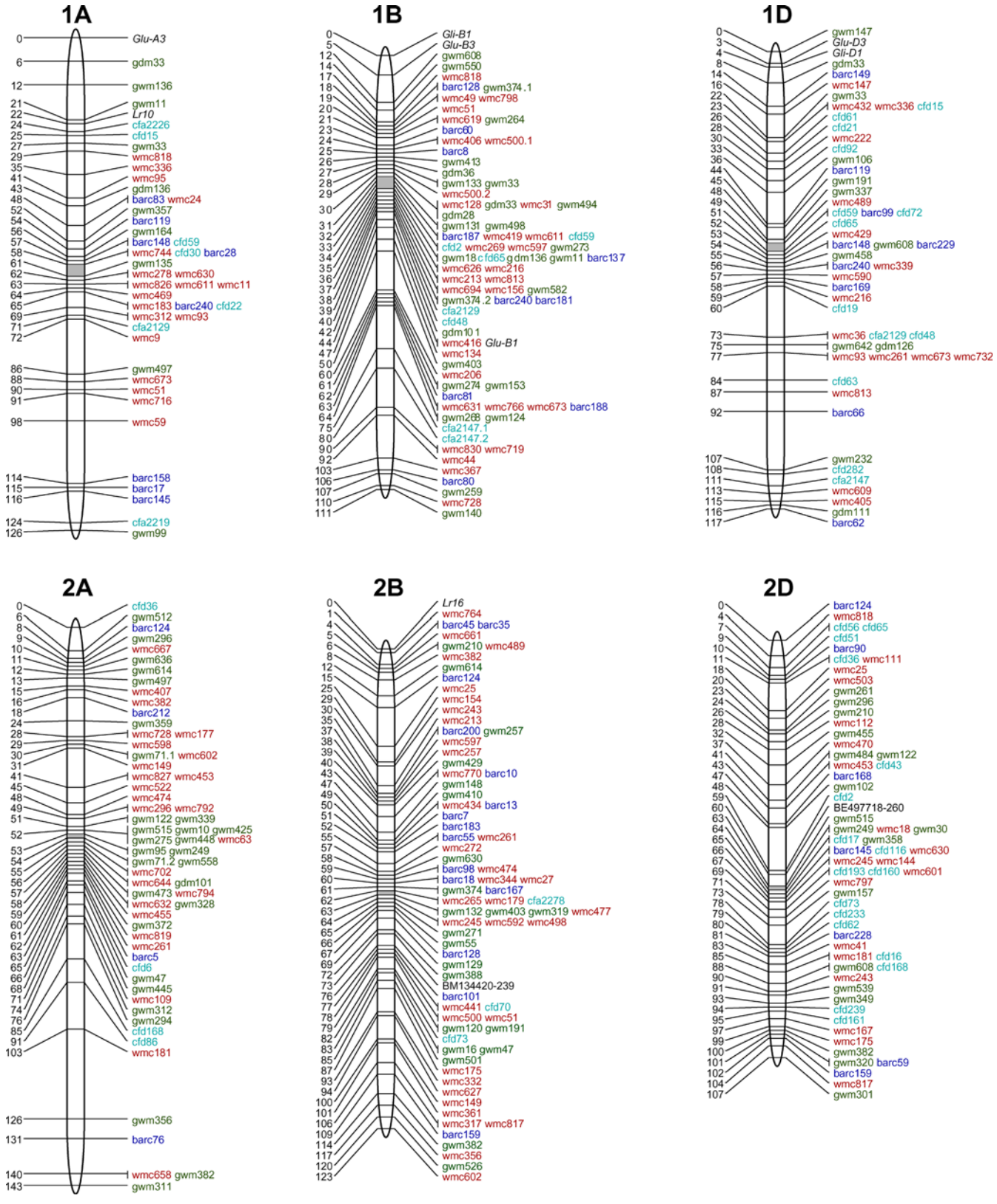
The program CMap was used to summarize the number of markers mapping to homoeologous positions in the genome. There were 16, 17, 12, 6, 13, 10, and 3 markers mapping to more than one homoeologue in the group 1 through 7 chromosomes, respectively. There were 143 markers mapping to at least two non-homoeologous (paralogous) positions in the genome. The proportion of BARC, CFA/CFD, GWM, and WMC markers amplifying paralogous loci ranged from 14.2% to 18.6%. The proportion of GDM markers amplifying paralogous loci was 9.5% (Fig. 1).

The eight mapping parents are included in a database that records the allele size, excluding the M13 tail, for each parent for each mapped marker. The M13-tailing method described would add 19 bp to each allele size. A comparison was made among the four populations with respect to the differences in parent allele size across all the mapped loci. Genetically, wide crosses such as SO and RD with >40% polymorphism had greater differences in parent allele size compared to genetically narrow crosses such as SB and WM with <40% polymorphism. Over all populations, WMC markers had the greatest parent allele-size differences (12.2 bp) compared to BARC markers with the lowest parent allele-size difference (9.0 bp). Allele pairs differing by 4 bp or less between mapping parents occurred on average at 38% of the mapped loci, with a tendency of genetically narrow crosses (SB and WM) to have a larger fraction of parent allele pairs at 4 bp or less (Table 4). The GWM and CFA/CFD markers had the largest fraction of markers, with parent allele pairs of 4 bp or less. There were 402 microsatellite loci mapped to at least two of the four mapping populations. An allele pair of 4 bp or less between parents from different crosses was observed for 245 (61%) of the 402 microsatellite loci.

Fig. 1 A microsatellite consensus map of bread wheat (*Triticum aestivum*) derived from four independent genetic maps using JoinMap, version 3.0, and CMap. Functional genes and phenotypic loci are identified in *italics*. ESTs (*black*) are identified by Genebank accession number, followed by the position of a SNP within the EST. The remainder of the loci are microsatellite markers and are colour coded by microsatellite source (*red* Wheat Microsatellite Consortium, *green* GWM/GDM, *cyan* CFA/CFD-cyan, *blue* BARC). Loci that cosegregated are grouped beside a vertical line *on the right side of the chromosome*. Microsatellites amplifying two mapped loci on a single chromosome have the suffix ".1," or ".2". *Numbers on the left* show the distance in centiMorgans from the *top of each chromosome*. (The allele database is available at http://wheat.pw.usda.gov.) The accompanying database of microsatellite alleles from 1,235 loci includes the locus name (microsatellite), the chromosome, primer sequences, followed by the size of the allele (in base pairs) amplified from 'Opata', 'Synthetic', 'AC Domain', 'RL4452', 'BW252', 'BW278', 'Wuhan', and 'Maringa'. *Null* indicates the marker was not codominant and only one allele was identified. Alleles listed in more than one pair of parents indicate the marker was mapped in more than one cross. All allele sizes are shown as they were amplified using the untailed primers

Table 3 The distribution and density of microsatellite markers across the 21 wheat chromosomes of the consensus map

Chromosome	No. of markers	Genetic length	Marker density (cM/marker)
1A	44	126	2.9
1B	75	111	1.5
1D	51	117	2.3
2A	62	143	2.3
2B	76	123	1.6
2D	61	107	1.8
3A	49	116	2.4
3B	88	148	1.7
3D	57	79	1.4
4A	53	88	1.7
4B	49	59	1.2
4D	34	91	2.6
5A	62	184	3.0
5B	77	173	2.2
5D	76	120	1.5
6A	38	156	4.1
6B	50	82	1.6
6D	35	110	3.1
7A	62	131	2.1
7B	68	151	2.2
7D	69	154	2.2
A genome	369	944	2.6
B genome	483	847	1.7
D genome	383	778	2.1
Group 1	170	354	2.0
Group 2	198	373	1.9
Group 3	194	343	1.6
Group 4	136	238	2.3
Group 5	215	477	2.6
Group 6	123	348	2.3
Group 7	199	436	2.2



Discussion

The microsatellite consensus map is a good estimation of the marker position from four genetic maps, assembled by consensus onto a single linkage map. This current consensus map shows the position of microsatellites at a density that makes the map useful in plant breeding and physical mapping (Fig. 1; Table 3). Consensus maps have

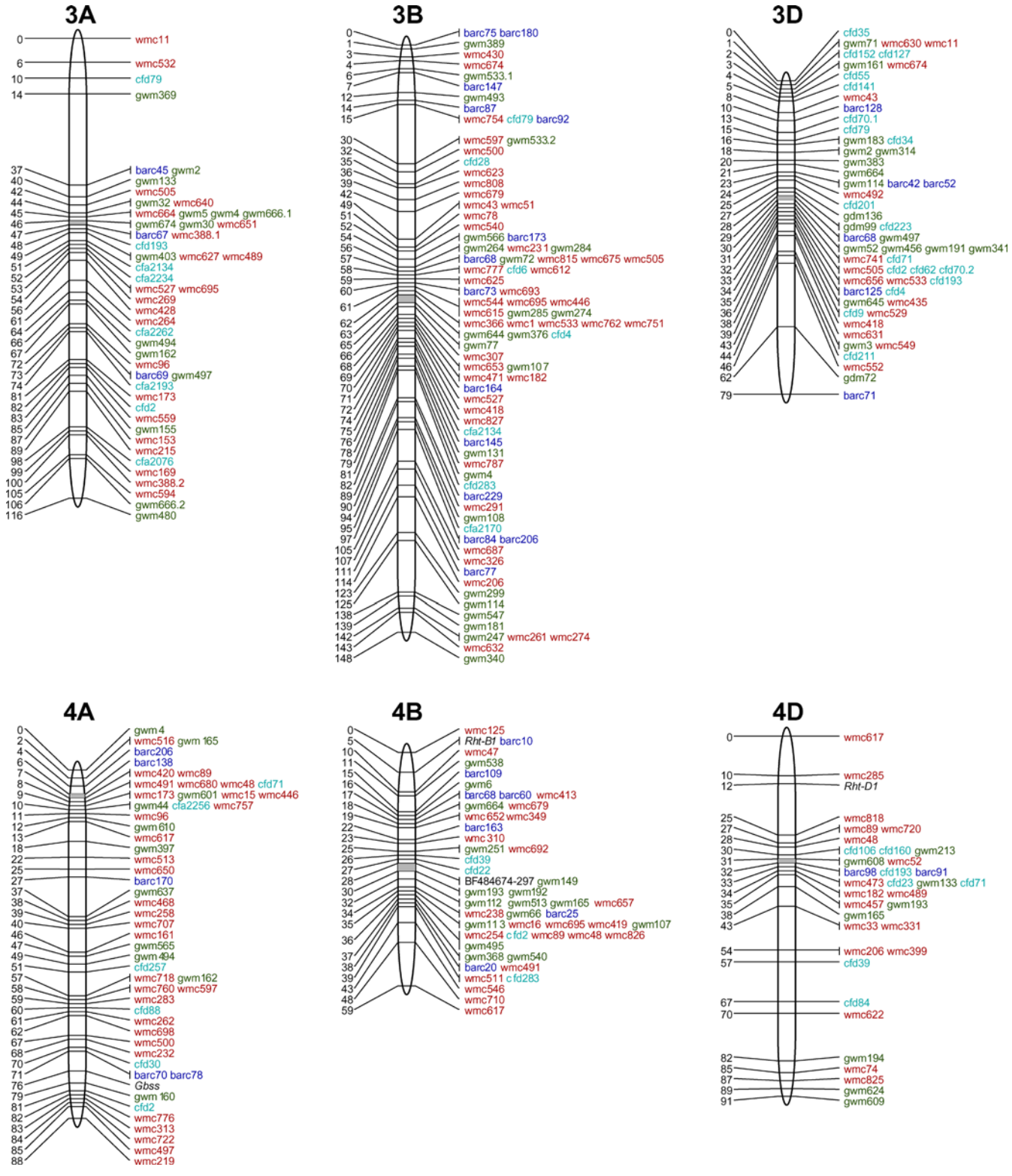


Fig. 1 (continued)

been produced before for beans and cowpeas (Kelly et al. 2003), barley (Thiel et al. 2003; Karakousis et al. 2004), and wheat (Gale et al. 1995; Appels 2003) based on RFLP and microsatellite markers. The present map represents the highest density public microsatellite map of wheat.

The four maps underpinning the current wheat consensus map were all constructed at an LOD >2.5 with 52 to 232 loci in common between the genetic maps. Given the population sizes of 68 (SO) to186 (SB) progeny, there could be some disagreement in the order of closely linked

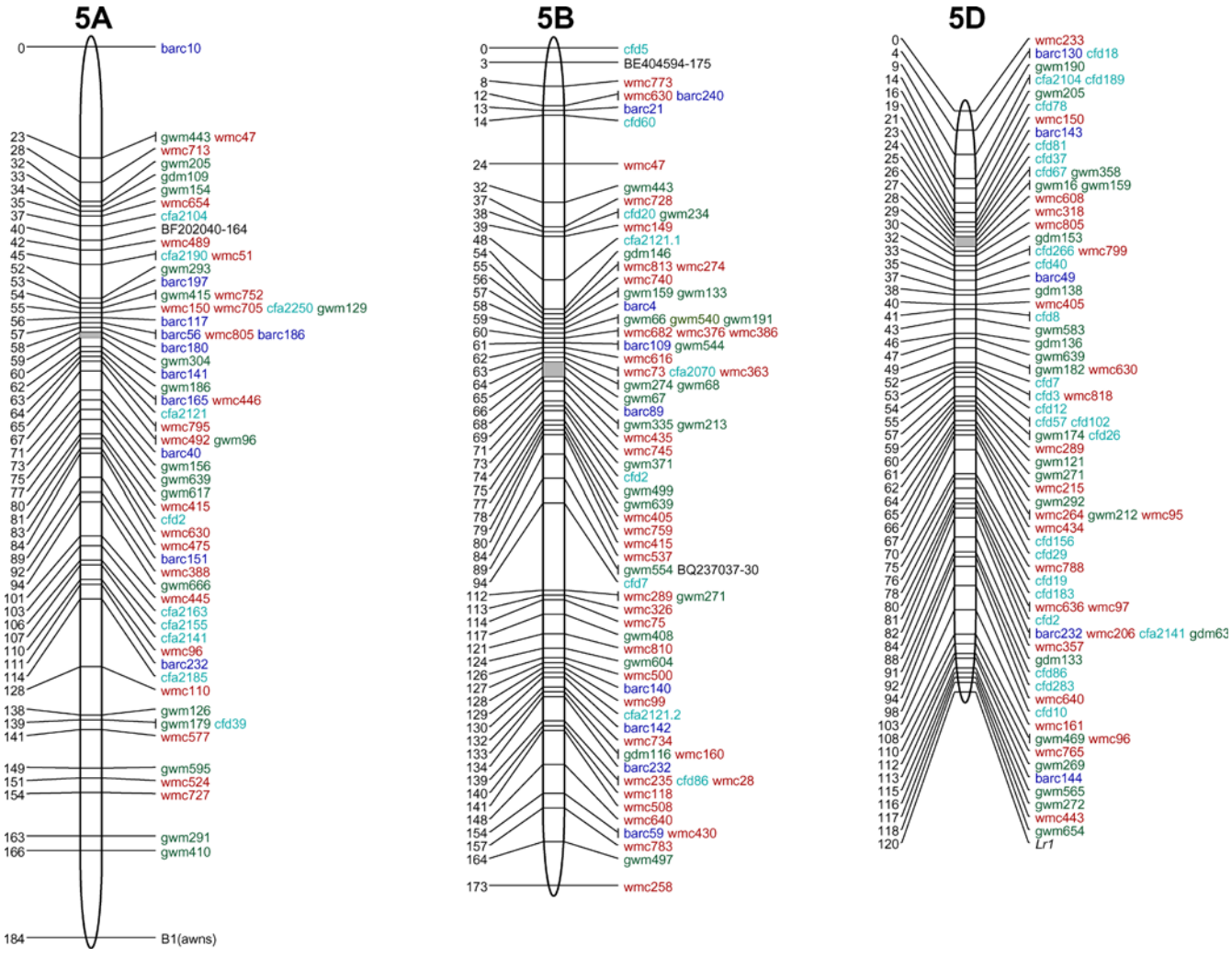


Fig. 1 (continued)

markers between the maps within some chromosome intervals. In smaller populations, the chance that informative recombinant progeny lines are present in the population to accurately position markers is lower than in larger populations. The disagreements in marker order of closely linked markers between genetic maps and derivation of the most correct marker order can be facilitated by construction of the consensus map. Users of the microsatellite consensus map must consider that the marker order is conditioned by the populations used and the position of crossovers along chromosomes within the progeny lines. The exact fine marker order may differ slightly in other populations, and users should be prepared to establish the order for closely linked markers in their mapping and breeding populations.

Table 4 Comparison of allele size differences among mapping parents and microsatellite sources. *SE* Standard error

Marker source	Population[a] Allele pair difference (bp)				Marker source (average ± SD)	Markers ≤4 bp (%)
	SO	RD	SB	WM		
WMC	13.9	16.1	10.1	8.7	12.2±3.4	36
BARC	11.8	6.3	8.8	ND[b]	9.0±2.8	34
CFA/CFD	14.2	ND	8.8	ND	11.5±3.8	40
GDM	11.2	10.6	7.7	10.6	10.0±1.6	27
GWM	14.3	5.8	11.8	11.8	10.9±3.6	41
Population (average ±SD)	12.9 ±13.9	13.3 ±27.1	9.1 ±11.2	9.4 ±10.9	11.2±2.2	38
Markers ≤4 bp (%)	31	42	46	44	38	

[a] *SO* 'Synthetic'/'Opata', *RD* 'RL4452'/'AC Domain', *SB* 'Superb'/'BW278', *WM* 'Wuhan'/'Maringa'
[b] *ND* No data available

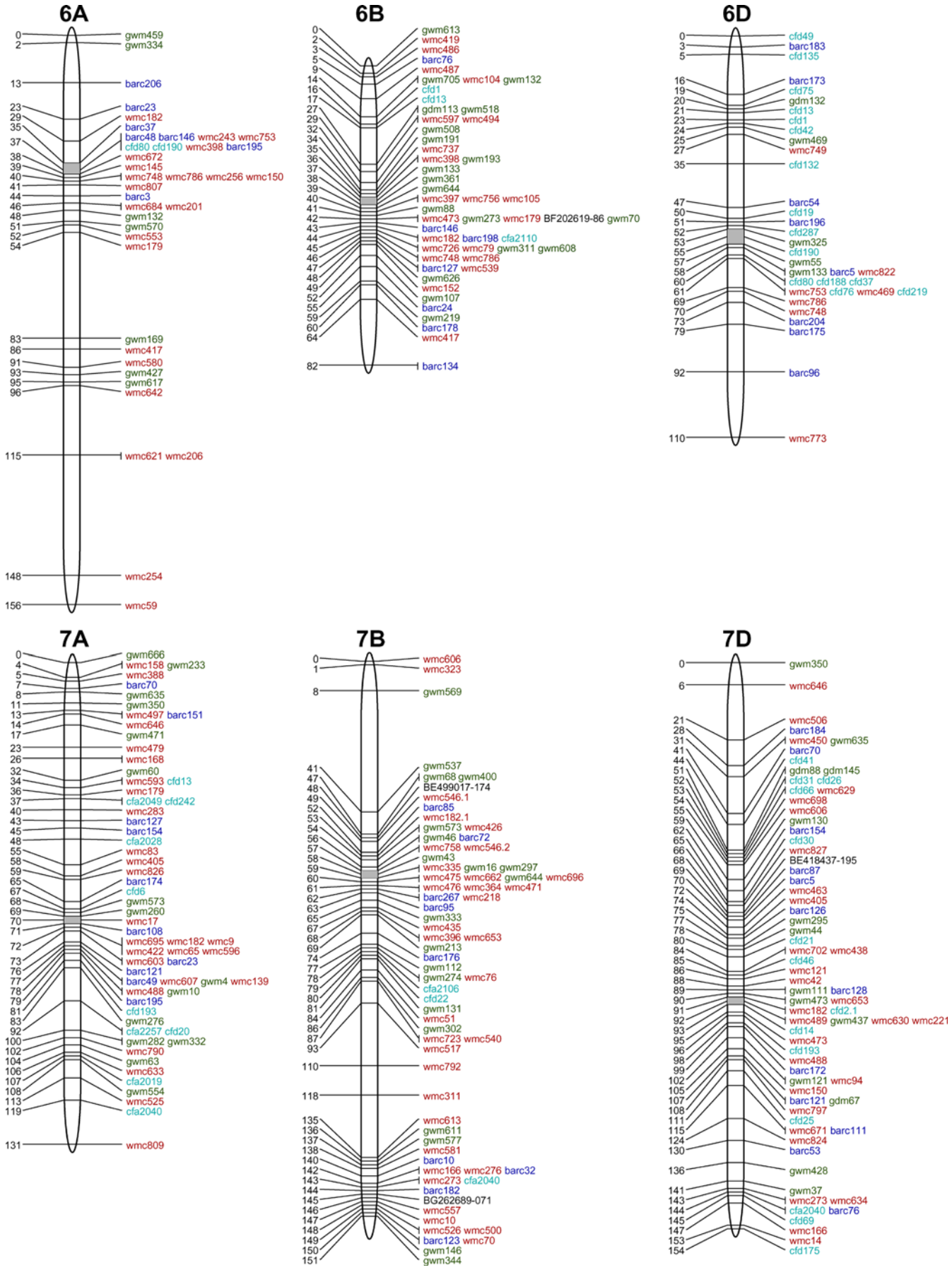


Fig. 1 (continued)

The length of the consensus map (2,569 cM) was larger than the four individual genetic maps, which had lengths of 2,332 cM (SO), 2,211 cM (RD), 2,166 cM (WM), and 1,836 cM (SB). The SO map is based on an F_6-derived RIL population, while the other three maps are all F_1-derived DH populations. The SO map should be longer in length due to the increased number of meioses and opportunity for recombination. The SB map consisted of just 20 chromosomes and was a genetically narrow cross; thus, it is the shortest of the four maps.

The GDM and CFD markers (which are D genome-specific markers) provided an improved marker density on the D genome relative to the maps of Röder et al. (1998) and Pestsova et al. (2000) (Fig. 1). Further, 9.5% of the GDM markers amplified paralogous loci on the consensus map compared to 14.2–18.8% of the markers from the other sources. This is consistent with the expectation that microsatellites derived from a diploid progenitor species will be more genome specific, although it is unexplained as to why 18.8% of the CFD markers amplified paralogous loci on the consensus map. There were 863 microsatellite markers used to amplify and map 1,235 microsatellite loci, which indicated the vast majority of the microsatellite primer pairs amplified only one polymorphic allele pair from the parents.

The primary use of the consensus map is in molecular mapping of traits and plant breeding. The precise marker order over short chromosome intervals (<10 cM) may not be that important to make plant selections. The marker order between 10 cM bins along the chromosome is more important in order to detect recombination events in gametes and make proper plant selections. The consensus map provided a large number of markers along the length of the chromosome that can be used to genotype individuals for detecting recombinants, fixing loci, restoring a recurrent genetic background, or assembling complex genotypes in complex crosses (Gupta et al. 1999; Huang et al. 2003).

The microsatellite consensus map is employed in the AAFC wheat breeding and genomics programs to assemble complex genotypes including pyramiding of up to eight separate loci. In addition, the consensus map is routinely used to perform bulked segregant analysis (Michelmore et al. 1991; McCartney et al. 2003), QTL mapping (Somers et al. 2003a), and genome scanning. Backcross populations are examined to select individuals with the highest restoration of an elite genetic background. In one representative experiment, 80 individuals from a BC_1F_1 population were genotyped, with 70 markers distributed across the genome. Plants were selected with >70% fixation of the recurrent parent alleles (data not shown). These activities are possible because of the high density of the genetic map, the quality of microsatellite markers, and accurate description of microsatellite alleles.

The marker density on the consensus map can provide a better choice of markers for specific breeding populations to ensure adequate polymorphic marker coverage in regions of interest. Further, the marker density on the consensus map is likely sufficient to perform association mapping and possibly linkage disequilibrium (LD) studies on germplasm collections. There were a sufficient number of markers distributed over the genome, which amplified single loci only or low complexity profiles that are well suited for association mapping and LD studies (Fig. 1; Table 3). These types of markers would avoid the confusion of scoring alleles amplified from parologous or homoeologous loci, which is a concern in a polyploid species such as wheat.

A database of allele sizes is provided at http://wheat.pw.usda.gov so users can consider the approximate size of DNA fragments in their breeding parents and populations and how best to use the map to develop molecular breeding strategies. This present study provided insight into the variation in allele size between mapping parents, which may be extended to other parents and breeding populations. A parent allele difference of 4 bp was chosen as a reference point since this is approximately the limit of resolution of microsatellite alleles on agarose gels, but which can be resolved on polyacrylamide gels or by capillary electrophoresis. The data showed a substantial proportion of the microsatellites (38%) have parent allele-pair differences of 4 bp or less. Thus high-resolution polyacrylamide or capillary electrophoresis is essential to make use of the large collection of markers and the consensus map. The allele pairs among all eight mapping parents had a size difference averaging 11.2 bp. Further, when allele size was compared across mapping populations, 61% of the markers had at least one allele pair differing by 4 bp or less (Table 4). This indicated that the consensus map and associated allele database can be used in concert to select markers distributed over the genome and to predict the approximate allele sizes in unknown breeding populations mapping to the expected chromosome region.

The allele database directs the user toward the expected PCR-fragment size to be detected by electrophoresis. Many of the microsatellite primer pairs amplified complex, multilocus profiles, and the allele size become important information in order to know which fragment maps to which locus. Although the M13-tailing technique was used for most of the genotyping underpinning the consensus map, the allele database reports the allele size as it would appear using a conventional silver-staining or radioisotope-detection platform. The M13-tailing method is very cost effective in that primers are not directly labelled with fluors, but rather are tailed with 19 additional nucleotides (Schuelke 2000). In this way, any primer pair can be fluorescently labelled with any dye colour. This can be important when trying to match more robust microsatellites with weaker fluors in complex pooling strategies.

In summary, the microsatellite consensus map brings together large collections of publicly available microsatellites onto a single genetic map derived by joining four independent genetic maps. There are still hundreds of microsatellite markers in the public domain that could be added to the present consensus map. Future prospects include adding more microsatellite and SNP-based markers to the consensus map, a thorough alignment to

the physical map of wheat, as well as implementation of the map in haplotype diversity studies of bread wheat.

Acknowledgements The authors wish to thank all the members of the WMC for assisting with marker development, Dr. P. Sourdille (INRA) for providing the CFA and CFD sequences, and Dr. P. Cregan for providing the BARC sequences. We are also grateful to Drs. G. Fedak, F. Townley-Smith, and G. Humphreys for providing the mapping populations. Many people worked to provide segregation data including Janice Cuthbert, Curt McCartney, Mira Popovic, Zlatko Popovic, Monika Eng, Yanfen Zheng, Leslie Bezte, Brent McCallum, Gavin Humphreys, Odean Lukow, Nancy Ames (AAFC), and Laurie Bertrand (Agrogene). This is contribution no. 1882 from the Agriculture and Agri-Food Canada Cereal Research Centre.

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