Theor Appl Genet (2001) 103:346–352

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Transferability of wheat microsatellites to diploid Triticeae species carrying the A, B and D genomes

Received: 21 June 2000 / Accepted: 15 November 2000

Abstract Hexaploid wheat (*Triticum aestivum* L em Thell) is derived from a complex hybridization procedure involving three diploid species carrying the A, B and D genomes. In this study, we evaluated the ability of microsatellite sequences from *T. aestivum* to be revealed on different ancestral diploid species more or less closely related, i.e. to test for their transferability. Fifty five primer pairs, evenly distributed all over the genome, were investigated. Forty three of them mapped to single loci on the hexaploid wheat genetic map although only 20 (46%) gave single PCR products; the 23 others (54%) gave more than one band with either only one being polymorphic, the others remaining monomorphic, or with several co-segregating polymorphic bands. The other 12 detected two (9) or three (3) different loci. From the 20 primer pairs which gave one amplification product on hexaploid wheat, nine (45%) also amplified products on only one of the diploid species, and seven (35%) on more than one. Four microsatellites (20%) which mapped to chromosomes from the B genome of wheat, did not give any amplification signal on any of the diploid species. This suggests that some regions of the B genome have evolved more rapidly compared to the A or D genomes since the emergence of polyploidy, or else that the donor(s) of this B genome has(have) not yet been identified. Our results confirm that *Triticum monococcum* ssp. *urartu* and *Triticum tauschii* were the main donors of the A and D genomes respectively, and that *Aegilops speltoides* is related to the ancestor(s) of the wheat polyploid B genome.

Keywords Molecular markers · *T. monococcum* · *T. tauschii* · *Ae. speltoides* · Phylogeny · Polyploidy

Communicated by J.W. Snape

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Introduction

All previous studies concerning bread wheat (*Triticum aestivum* L. em Thell) phylogeny have shown difficulty in establishing unequivocal relationships between the elementary genomes constituting hexaploid wheat, and the genomes of the diploid ancestors, i.e. *Triticum monococcum* ssp. *urartu, Aegilops speltoides and Triticum tauschii* (Nishikawa and Furuta 1978; Kerby and Kuspira 1987; Dvorak and Zhang 1990; Breiman and Graur 1995; Le Corre and Bernard 1995; Dvorak et al. 1998). The present species are probably widely different from those that participated originally the construction of the wheat polyploid complex. Moreover, several studies have shown evidence for recurrent introgressive hybridization phenomena (Vardi 1973; Dvorak 1988), which have contributed to the structure of the elementary genomes characteristic of the polyploid species.

The recent development of molecular tools allows a more-precise approach to the structure and composition of the existing genomes in both diploid and polyploid species. This should enable the assessment of their phylogenetic relationships, and the establishment of the relevant evolutionary pathways. Molecular markers were first used to built genetic maps in order to tag agronomically important genes. The first molecular marker maps in wheat were constructed using RFLP markers (Chao et al. 1989; Devos and Gale 1993; Cadalen et al. 1997) but their level of polymorphism is rather limited, especially for the D genome. Therefore, due to the high polymorphism that they are able to detect, microsatellites [tandem repetitive DNA sequences with core sequences from 2–5 base pairs (Litt and Luty 1989)] have been recently developed in wheat (Ma et al. 1996; Bryan et al. 1997; Röder et al. 1998a, b). They are located all over the wheat genome (Röder et al. 1998a, b) and are thus well suited for mapping purposes (Röder et al. 1995; Ma et al. 1996), and for evolutionary studies (Schloetterer et al. 1991).

The number of microsatellite repeats is also supposed to evolve much faster, i.e. from 10^{-2} mutations per locus

per year for some human loci (Weber and Wong 1993) to 6.3×10^{-6} mutations per locus per year in *Drosophila* (Schug et al. 1997), than for other types of mutation (10^{-9} for nucleotide substitutions). Moreover, some data suggest that the length of the SSR regions evolves according to a stepwise mutation model (Estoup and Cornuet 1999). A genetic-distance index which takes into account the absolute difference in repeat number among the accessions would then be more powerful than classical indices usually based on the proportion of shared bands. However, this must be considered with caution since alleles can achieve the same size either by shortening a longer allele or increasing a shorter one.

However, the identification of flanking sequences is quite expensive and time consuming (Röder et al. 1998b). As has been previously reported for cattle and goat (Pépin et al. 1995), *Actinidia* species (Huang et al. 1998) or durum wheat (Korzun et al. 1999), it would be of interest to use primers developed for wheat on other related species, such as the putative wheat ancestors and other Triticeae, to assess the transferability of wheat microsatellites.

In this context, we used 55 microsatellite markers obtained from the bread wheat genome (Pläschke et al. 1995, 1996; Röder et al. 1995, 1998a, b) and giving at least one amplification product on this species. We have analysed their transferability to *T. monococcum* ssp. *urartu* (genome A), *T monococcum* ssp. *monococcum* (A), *T monococcum* ssp. *boeoticum* (A), *Ae. speltoides* (B), *Aegilops searsii* (S), *Triticum longissimum* (B), and *T. tauschii* (D). Our results allowed us to investigate simultaneously the genome specificity of wheat microsatellites, their transferability to a few diploid species, and wheat phylogeny.

Material and methods

Plant material and DNA extraction

Seven diploid species or sub-species, known to be potentially involved in the evolutionary process that gave rise to bread wheat, were employed (Table 1): *T. monococcum* ssp. *monococcum*, ssp. *boeoticum* and ssp. *urartu*, species carrying the A triticeae genome, *Ae. speltoides*, *Ae. searsii* and *T. longissimum* bearing the B (or S) genome, and *T. tauschii* (D genome). Two accessions for each species were used except one for *Ae. searsii*. A bread wheat variety (cv Courtot) was used as a control.

DNA from each plant was extracted from young freshly harvested leaves using a protocol involving potassium acetate, as described in Lu et al. 1994.

Microsatellite amplifications

The 55 primer pairs (Table 2) employed were developed by Röder et al. (1998a). They were chosen according to their map location in order to have at least one microsatellite on each chromosome arm. PCR reactions and the polyacrylamide-gel procedure were performed as described in Tixier et al. (1998). Microsatellites were visualised by the silver-staining method as detailed by Tixier et al. (1997). In order to ensure that non-amplification was not due to failed PCRs, most of the PCR amplifications were done twice.

According to Röder et al. (1998a), among these 55 primer pairs, 44 amplified sequences were mapped to a single locus, while the remaining 11 were mapped at either two (8) or three (3) loci. Results obtained in our laboratory (unpublished) showed that one (gwm111) among the 44 former sequences could be mapped at two distinct loci, both located on chromosome 7D. Thus, in the following study, we will consider that 43 primer pairs amplify sequences mapped at one locus, nine at two and three at three loci. This will result in 70 ($43+9\times2+3\times3$) microsatellite loci.

Statistical analysis

Amplification events were binarily encoded. Each time an amplification occurred the amplification product was coded 1, whereas a non-amplification was coded 0. *T. aestivum*, which is hexaploid, was separated into its three diploid genomes and coded TaeA, TaeB and TaeD. Thus, for example, a microsatellite located on the wheat map of the A genome will be scored 1 for TaeA and 0 for TaeB and TaeD. The patterns were summarised in a binary matrix, from which the Nei and Li (1979) distance was calculated, based on the proportion of shared amplifications. In our case, it was assumed that this distance is an indication of the mutation rate at each pair of primer sites. A dendrogram was built using the UPGMA method (Unweighted Pair Group Method with Arithmetic Mean, Sokal and Rholf 1995) assuming the mutation rate to be constant among species.

Table 1 Different accessions of the diploid lines used in the analysis. For genetic-distance analysis, *T. aestivum* was separated into its three elementary genomes and coded TaeA, TaeB and TaeD

Species	Accessions	Chromosome number	Genome	Codes	Abbreviations
Triticum monococcum ssp urartu	77 097	2n=2*x*=14	AA	1	Tu77097
	77 098	2n=2*x*=14	AA	2	Tu77098
Triticum monococcum ssp monococcum	81 051	2n=2*x*=14	AA	3	Tm81051
	81 187	2n=2*x*=14	AA	4	Tm81187
Triticum monococcum ssp boeticum	68 181	2n=2*x*=14	AA	5	Tb68181
	94 114	2n=2*x*=14	AA	6	Tb94114
Aegilops speltoides	37	2n=2*x*=14	BB	7	As37
	38	2n=2*x*=14	BB	8	As38
Aegilops searsii	4	2n=2*x*=14	BB	9	Asear4
Triticum longissima	1	2n=2*x*=14	BB	10	Tlong1
	3	2n=2*x*=14	BB	11	Tlong3
Triticum tauschii	15	2n=2*x*=14	DD	12	Tt15
	42	2n=2*x*=14	DD	13	Tt42
Triticum aestivum	cv Courtot	2n=6*x*=42	AABBDD	14	Taes

Table 2 List of the 55 primer pairs used for microsatellite detection in the diploid species. Loci indicate the chromosomes where the microsatellites were mapped according to Röder et al. (1998b)

Primers	Loci	Primers	Loci	Primers	Loci
WMS2	Xgwm2–3A	WMS111	Xgwm111.1–7D	WMS297	Xgwm297–7B
	Xgwm2–3D		Xgwm111.2–7D		
WMS3	Xgwm3–3D	WMS113	Xgwm113–4B	WMS349	Xgwm349–2D
WMS4	Xgwm4–4A	WMS120	Xgwm120–2B	WMS369	Xgwm369–3A
WMS5	Xgwm5–3A	WMS131	Xgwm131–1B	WMS383	Xgwm383–3D
			Xgwm131–3B		
WMS11	Xgwm11–1B	WMS135	Xgwm135–1A	WMS400	Xgwm400–7B
WMS18	Xgwm18–1B	WMS154	Xgwm154–5A	WMS427	Xgwm427–6A
WMS43	Xgwm43–7B	WMS155	Xgwm155–3A	WMS428	Xgwm428–7D
WMS44	Xgwm44–7D	WMS159	Xgwm159–5B	WMS437	Xgwm437–7D
WMS46	Xgwm46–7B	WMS160	Xgwm160–4A	WMS458	Xgwm458–1D
WMS47	Xgwm47.1–2A	WMS165	Xgwm165–4A	WMS495	Xgwm495–4B
	Xgwm47.2–2A		Xgwm165–4B		
	Xgwm47–2B		Xgwm165–4D		
WMS52	Xgwm52–3D	WMS174	Xgwm174–5D	WMS515	Xgwm515–2A
					Xgwm515–2D
WMS55	Xgwm55.1–2B	WMS190	Xgwm190–5D	WMS537	Xgwm537–7B
	Xgwm55.2–2B				
	Xgwm55–6D				
WMS67	Xgwm67–5B	WMS192	Xgwm192–5D	WMS539	Xgwm539–2D
WMS68	Xgwm68–5B	WMS194	Xgwm194–4D	WMS570	Xgwm570–6A
	Xgwm68–7B				
WMS82	Xgwm82–3D	WMS205	Xgwm205–5A	WMS573	Xgwm573–7A
			Xgwm205–5D		Xgwm573–7B
WMS88	Xgwm88–6B	WMS261	Xgwm261–2D	WMS577	Xgwm577–7B
WMS95	Xgwm95–2A	WMS271	Xgwm271–5D	WMS608	Xgwm608–2D
					Xgwm608–4D
WMS102	Xgwm102–2D	WMS274	Xgwm274–1B	WMS610	Xgwm610–4A
			Xgwm274–7B		
				WMS661	Xgwm661–5D

Table 3 Results of amplification using the 55 primer pairs on the diploid species according to the number of loci (NL), the number of PCR products (NPP: >1=more than one) and the map location (Map) on the three different genomes (A, B or D). NM is the number of primer pairs for each case. A, B, D, AB, AD, BD, ABD and TA are the numbers of primers amplifying on the genomes A, B, D, A and B, A and D, B and D, A and B and D, and *T. aestivum* only, respectively

NL	NPP	Map	NM	A	B	D	AB	AD	BD	ABD	TA
1	1	A	4	4							
		B	7		3						4
		D	9			3		3	3		
	>1	A	8	1				1		6	
		B	7		2		2			3	
		D	8				2		1	5	
2		B	3							3	
		D	2							2	
		AB	1							1	
		AD	3					1		2	
3		AB	1		1						
		BD	1							1	
		ABD	1							1	

Results

Among the 43 primer pairs mapped to a single locus, only 20 (46%) gave a single amplification product on the hexaploid wheat cultivar Courtot. Four mapped to the A genome, seven to the B genome and nine to the D genome (Table 3). Concerning the transferability of these 20 primer pairs on the diploid species, all those mapped on the A genome amplified only on the diploid species carrying the A genome (*T. monococcum* ssp. *monococcum*, *T. monococcum* ssp. *boeoticum* and *T. monococcum* ssp. *urartu*: gwm155 Fig. 1a), either on *T. monococcum* ssp. *urartu* alone, or on all species bearing the A genome. On the other hand, only three among the nine mapped on the D genome (33%) amplified only on the diploid species carrying the D genome (*T. tauschii*); the six remaining amplifying either on the lines carrying the A genome (3: *T. monococcum* ssp. *monococcum*, *T. monococcum* ssp. *boeoticum* and *T. monococcum* ssp. *urartu*) or on those carrying the B genome (3: *Ae. speltoides*, *Ae. searsii* and *T. longissimum*, gwm539, Fig. 1b). Considering the seven loci mapped on the B genome, three amplified only on lines carrying the B genome (*Ae. speltoides*, *Ae. searsii* and *T. longissimum*), the four others amplifying only on *T. aestivum* (gwm577, Fig. 1c). This result suggests that the flanking sequences have remained stable (no mutation) since the occurrence of polyploidisation in wheat. This is related to the results

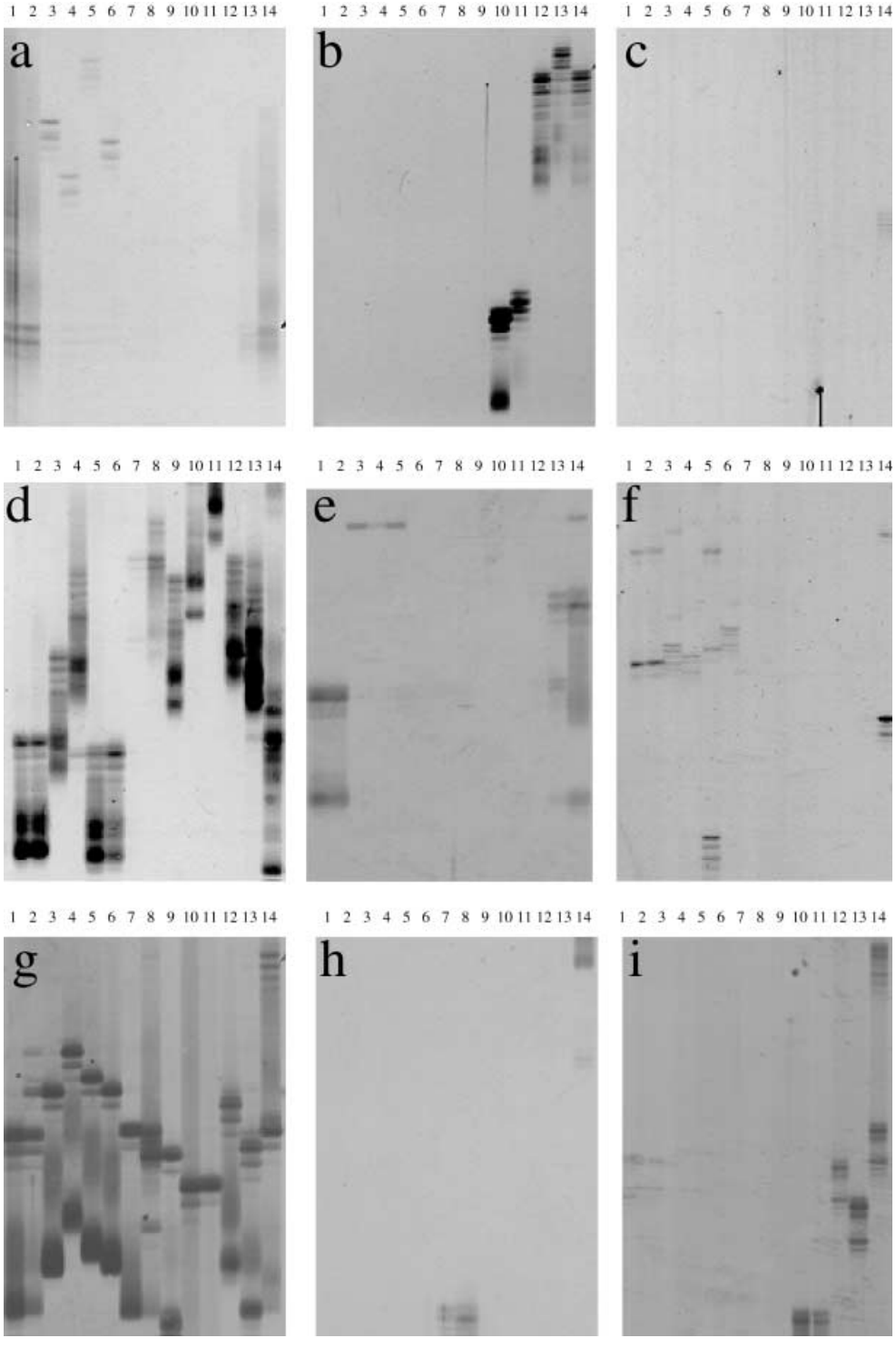

Fig. 1a–i Amplification results of nine microsatellites on different accessions of *T. monococcum* ssp. *urartu* (*lanes 1 and 2*), *T. monococcum* ssp. *monococcum* (*lanes 3 and 4*), *T. monococcum* ssp. *boeoticum* (*lanes 5 and 6*), *Ae. speltoides* (*lanes 7 and 8*), *Ae. searsii* (*lane 9*), *T. longissima* (*lanes 10 and 11*), *T. tauschii* (*lanes 12 and 13*) and *T aestivum* cultivar Courtot (*lane 14*). **a** gwm155, **b** gwm539, **c** gwm577, **d** gwm192, **e** gwm95, **f** gwm427, **g** gwm205, **h** gwm47, **i** gwm111

obtained by Wei and Wang (1995) who described that approximately 30% of RAPD amplified fragments were genome-specific among diploid perennial species in the Triticeae.

The other 23 gave one polymorphic and mapped locus (eight on A, seven on B and eight on D; Table 3), and also at least one additional band which was either monomorphic or which was co-segregating with the former. Among these 23 primer pairs, 14 (61%) amplified on all the lines (gwm192, Fig. 1d) while six gave an amplification product on only two among the three groups of species (either A+B, A+D or B+D: gwm88, Fig. 1e), the three remaining were specific to lines carrying the same genome as the one where they were mapped (one on A, the other two on B: gwm427, Fig. 1f).

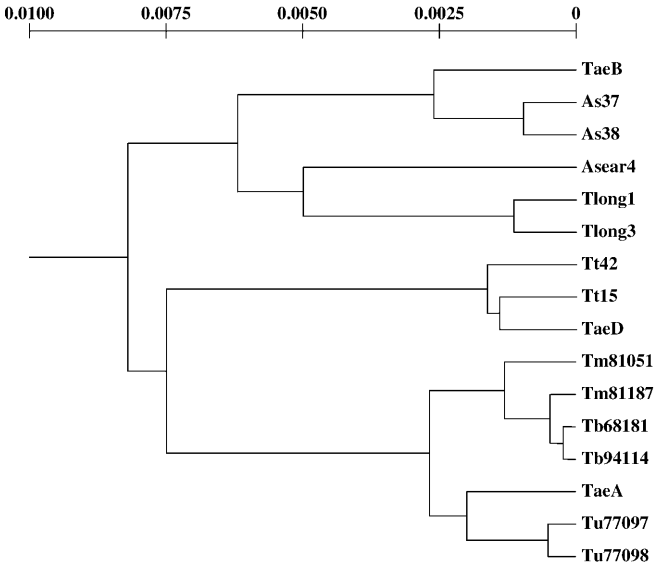

Fig. 2 Dendrogram obtained using a matrix elaborated from the occurrence of amplification products. The distance used is that from Nei and Li (1979). Codes of the lines are those detailed in Table 1

The 12 other primer pairs that were mapped at more than one locus also gave at least two different bands. Most of them (83%) amplified on all the lines (gwm205, Fig. 1g). Only one was specific to the B genome despite the fact that it was previously mapped at three different loci (gwm47, Fig. 1h) distributed on the A (two) and B (one) genomes. This may be explained by the fact that this primer pair frequently gave null alleles (no amplification; Röder et al. 1998b). The other two amplified on either lines carrying A or B genomes or those with B or D genomes (gwm111, Fig. 1i).

Phylogenetic relationships between all the species were studied using a binary matrix elaborated from scoring the occurrence of amplification products. On the dendrogram (Fig. 2), we distinguished the three groups of diploid species representing the three genomes. The two accessions tested for each species were always grouped together. *T. aestivum* was divided into its three diploid genomes (TaeA, TaeB and TaeD), each being related to the corresponding diploid species group. TaeA was closer to *T. monococcum* ssp. *urartu*, than to *T. monococcum* ssp. *monococcum* or to *T. monococcum* ssp. *boeoticum*. Likewise, TaeB was closer to *Ae. speltoides* than to *Ae. searsii* or to *T. longissima*, and TaeD was directly related to *T. tauschii*. The lines carrying the A genome seemed to be closer to those with the D genome rather than to those with the B genome. Thiellement et al. (1989) and Monte et al. (1993) had earlier found that the B group was closer to the D group.

Discussion

Microsatellites are a powerful tool for species distinction or phylogenetic relationship evaluations. Considering the microsatellite loci mapped on the B genome, it was noteworthy that half of them were specific to the B genome of *T. aestivum*, i.e. that no amplification occurred in any of the other species carrying a B genome. Three different hypotheses can be proposed to account for this:

(1) The true donor species of these microsatellites was not present among the species we had chosen in this study. Therefore, it should be advisable to test them on a much larger number of accessions of the *Sitopsis* section (being the best candidate to be at the origin of the B genome) of *Aegilops*, in order to discover other possible donors.
(2) These microsatellites appeared and evolved in the context of the polyploid species some 10,000 years ago, as they do not exist in any of the diploids. However, it would be surprising that such "neo-sequences" were not found in the other two genomes (A and D). This could mean that selection pressures were particularly high for this genome to acquire a particular status, probably towards a higher differentiation from the original diploid(s) and from the other ancestors. Thus, we can expect that the microsatellites developed from a B diploid species would be poorly transferable to the wheat B genome. This is currently being checked in our laboratory.
(3) The B genome of wheat could have a polyphyletic origin as suggested by Vardi (1973) or it could have undergone a genetic bottleneck and diverged from diploid B-genome donor (Talbert et al. 1998, Blake et al. 1999). However, through analyses of the homologous chromosome pairing at metaphase in hybrids between *T. aestivum* and *Ae. speltoides*, Maestra and Naranjo (1998) stated that no apparent rearrangements occurred in the evolution of *A. speltoides* relative to wheat. This indicates that, during the constitution and evolution of *T. aestivum*, there were only microarrangements located mostly in repeated DNA. A more extensive study would allow us to determine the DNA regions which were brought by donors different from *Ae. speltoides*, as described by Nishikawa and Furuta (1978).

Considering primer pairs giving several amplification products, but with only one polymorphism mapped to a single locus, PCR products were mainly observed on at least two of the ancestral diploids (83%) and more generally on all the species (58%). There were two different cases:

(1) the primer pair gave several bands but only one was polymorphic in wheat. This suggests that the other monomorphic bands were located elsewhere on the genome and, more probably, at homoeologous positions. This hypothesis was supported by amplification on Chinese Spring aneuploid lines (data not shown).
(2) the primer pair gave several polymorphic bands which always co-segregated. These microsatellites are those remaining specific to the genome where they

were mapped. This may be due to a tandem duplication of one of the flanking sequences. This hypothesis could be verified by picking up the bands on the gel and sequencing them.

Most (93%) of the microsatellites derived from bread wheat were usable on the corresponding ancestral diploid species. This transferability was far higher than that observed from wheat to other triticeae species (rye, barley; unpublished results) or between homoeologous genomes. This observation indicates that microsatellite loci were more subject to a rapid evolution than the coding sequences. Similar observations were already reported for transferring microsatellites between *Bos taurus* (cattle), *Capra hircus* (goat) and related species (Pépin et al. 1995) where the transferability was about 40%.

There was also a difference in transferability depending on the mapping position of the locus. It was clear that the microsatellites from the A and D wheat genomes always amplified on the A and D diploid genomes, and sometimes beyond. This suggests that microsatellites developed from these diploid species should be usable in wheat, which is currently being verified in our laboratory (unpublished data).

Finally, because of the rather low level of transferability of microsatellites between homoeologous genomes, they would probably be excellent markers to follow introgressions from other species (e.g. rye, *Ae. ventricosa*) to wheat, owing to their great specificity. However, it would be necessary to develop a set of microsatellites for each donor species. This approach should probably be accompanied by classical procedures, using highly transferable RFLP (cDNA) and in situ hybridization with species-specific probes or total DNA from the donor, in order to target the acceptor region.

Acknowledgements The authors thank colleagues for critical comments on the manuscript. All the experiments comply with the current laws of the country in which the experiments were performed.

References

Blake NK, Lehfeldt BR, Lavin M, Talbert LE (1999) Phylogenetic reconstruction based on low-copy DNA sequence data in an allopolyploid : the B genome of wheat. Genome 42:351–360

Breiman A, Graur D (1995) Wheat evolution. Israël J Plant Sci 42:85–98

Bryan GJ, Collins AJ, Stephenson P, Orry A, Smith JB, Gale MD (1997) Isolation and characterisation of microsatellites from hexaploid bread wheat. Theor Appl Genet 94:557–563

Cadalen T, Boeuf C, Bernard S, Bernard M (1997) An intervarietal molecular 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, Gale M (1989) RFLP-based genetic map of wheat homoeologous group-7 chromosomes. Theor Appl Genet 78:495–504

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

Dvorak J (1988) Cytogenetical and molecular inferences about the evolution of wheat. In: Miller TE, Koebner RMD (eds) Proc 7th Int Wheat Genet Symp, Cambridge, UK, pp 187–192

Dvorak J, Zhang HB (1990) Variation in repeated nucleotide sequences sheds light on the phylogeny of the wheat B and G genomes. Proc Natl Acad Sci USA 87:9640–9644

Dvorak J, Luo MC, Yang ZL, Zhang HB (1998) The structure of the *Aegilops tauschii* genepool and the evolution of hexaploid wheat. Theor Appl Genet 97:657–670

Estoup A, Cornuet JM (1999) Microsatellite evolution: inferences from population data. In: Goldstein DB, Schlotterer C (eds) Microsatellites – evolution and applications. Oxford University Press, Oxford, pp 49–65

Huang WG, Ciapriani G, Morgante M, Testolin R (1998) Microsatellite DNA in *Actinidia chinensis*: isolation, characterisation and homology in related species. Theor Appl Genet 97:1269–1278

Kerby K, Kuspira J (1987) The phylogeny of the polyploid wheats *Triticum aestivum* (bread wheat) and *Triticum turgidum* (macaroni wheat). Genome 29:722–737

Korzun V, Röder MS, Wendehake K, Pasqualone A, Lotti C, Ganal MW, Blanco A (1999) Integration of dinucleotide microsatellites from hexaploid bread wheat into a genetic linkage map of durum wheat. Theor Appl Genet 98:1202–1207

Le Corre V, Bernard M (1995) Assessment of the type and degree of restriction fragment length polymorphism (RFLP) in diploid species of the genus *Triticum*. Theor Appl Genet 90: 1063–1067

Litt M, Luty JA (1989) A hypervariable microsatellite revealed by in vitro amplification of dinucleotide repeats within the cardiac muscle actin gene. Am J Genet 44:397–401

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

Ma ZQ, Röder M, Sorrells ME (1996) Frequencies and sequence characteristics of di-, tri-, and tetra-nucleotide microsatellites in wheat. Genome 39:123–130

Maestra B, Naranjo T (1998) Homologous relationship of *Aegilops speltoides* chromosomes to bread wheat. Theor Appl Genet 97:181–186

Monte JV, McIntyre CL, Gustafson JP (1993) Analysis of phylogenetic relationships in the Triticeae tribe using RFLPs. Theor Appl Genet 86:649–655

Nei M, Li WH (1979) Mathematical model for studying genetic variation in terms of restriction endonucleases. Proc Natl Acad Sci USA 76:5269–5273

Nishikawa K, Furuta Y (1978) DNA content of nucleus and individual chromosomes and its evolutionary significance. Proc 5th Int Wheat Genet Symp, pp 133–138

Pépin L, Amigues Y, Lépingle A, Berthier JL, Bensaid A, Vaiman D (1995) Sequence conservation of microsatellites between *Bos taurus* (cattle), *Capra hircus* (goat) and related species. Examples of use in parentage testing and phylogeny analysis. Heredity 74:53–61

Plaschke J, Ganal MW, Röder MS (1995) Detection of genetic diversity in closely related bread wheats using microsatellite markers. Theor Appl Genet 91:1001–1007

Plaschke J, Börner A, Wendehake K, Ganal M, Röder M (1996) The use of aneuploids for the chromosomal assignment of microsatellite loci. Euphytica 89:33–44

Röder MS, Plaschke J, König SU, Börner A, Sorells ME, Tanksley SD, Ganal MW (1995) Abundance, variability and chromosomal location of microsatellites in wheat. Mol Gen Genet 246:327–333

Röder MS, Korsun V, Gill BS, Ganal MW (1998a) The physical mapping of microsatellite markers in wheat. Genome 41: 278–283

Röder MS, Korsun V, Wendehake K, Plaschke J, Tixier MH, Leroy P, Ganal MW (1998b) A microsatellite map of the wheat genome. Genetics 149:2007–2023

Schlöterer C, Amos B, Tautz D (1991) Conservation of polymorphic simple sequence loci in cetacean species. Nature 354: 63–65

Schug MD, Mackay TF, Aquadro CF (1997) Low mutation rates of microsatellite loci in *Drosophila melanogaster*. Nature Genet 15:99–102

Sokal RR, Rholf FJ (1995) Biometry, 3rd edn. WH Freeman, New York

Talbert LE, Smith LY, Blake NK (1998) More than one origin of hexaploid wheat is indicated by sequence comparison of low-copy DNA. Genome 41:402–407

Thiellement H, Seguin M, Bahrman N, Zivy M (1989) Homoeology and phylogeny of the A, S and D genomes of the Triticinae. J Mol Evol 29:89–94

Tixier MH, Sourdille P, Röder M, Leroy P, Bernard M (1997) Detection of wheat microsatellites using a non-radioactive silver-nitrate staining method. J Genet Breed 51:175–177

Tixier MH, Sourdille P, Charmet G, Gay G, Jaby C, Cadalen T, Bernard S, Nicolas P, Bernard M (1998) Detection of QTL for crossability in wheat using a doubled-haploid population. Theor Appl Genet 97:1076–1082

Vardi A (1973) Introgression between different ploidy levels in the wheat group. In: Sears ER, Sears LMS (eds) Proc 4th Int Wheat Genet Symp Missouri, Columbia, USA, University Missouri Press, pp 131–141

Weber JL, Wong C (1993) Mutation of human short tandem repeats. Hum Mol Genet 2:1123–1128

Wei JZ, Wang RRC (1995) Genome- and species-specific markers and genome relationships of diploid perennial species in the Triticeae based on RAPD analyses. Genome 38:1230–1236