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Genetic and physical mapping of sequence-specific amplified polymorphic (SSAP) markers on the 1RS chromosome arm of rye in a wheat background

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Abstract Three rye-specific repeated sequences, pSc10C, pSc20H and R173-1, were used to design sequence-specific anchored primers. These primers and 16 restriction site-specific adaptor primers were used in all possible combinations to establish sequence-specific amplified polymorphic (SSAP) markers for the 1RS chromosome arm of rye in a wheat background. Thirty 1RS-specific SSAP markers were detected in 19 primer combinations. Along with six markers localised previously on 1RS, 26 of the SSAP markers were mapped genetically in wheat genotypes carrying recombinant 1BL.1RS translocations. A clear decrease in recombination frequency from distal to proximal regions was observed. Wheat-rye addition lines for the 1R chromosome with different-sized deletions of the short arm were used to physically localise these markers. Physical mapping suggested an even distribution of the SSAP markers along the total length of the 1RS chromosome arm.

Keywords 1RS · Rye repeated sequences · SSAP · Genetic mapping · Physical mapping

Introduction

The short arm of rye (*Secale cereale* L.) chromosome 1R is the most frequently used alien chromatin in wheat (*Triticum aestivum* L.) breeding (Graybosch 2001). The 1BL.1RS translocation involves the 1RS arm of rye cv Petkus (Lein 1975). This chromosome arm carries resistance genes against different rust species and powdery mildew (*Lr26, Sr31, Yr9, Pm8*) (McIntosh 1988). Moreover, several studies have suggested that it enhances the yield potential of wheat in certain genetic backgrounds (Carver and Rayburn 1995; Moreno-Sevilla et al. 1995; Villareal et al. 1995, 1998). One major concern about this translocation is its single origin (Schlegel and Korzun 1997), with the consequence being the absence of any allelic variation on this chromosome arm. Because of this lack of variation, there is no possibility, for example, of replacing the resistance genes, which in the meantime have mostly been overcome by newly developed biotypes of the pests (Lutz et al. 1992).

Studies of 1RS in rye suggest that this chromosome arm harbours a wide range of genetic variability with valuable genes that could be utilised in wheat breeding (Shepherd 1973; Zeller and Fuchs 1983; Zeller and Hsam 1984; Porter et al. 1991; Porter and Friebe 1994; Marais et al. 1994). In previous work by the authors of this report, four octoploid triticale lines involving four different rye genotypes were crossed with 1BL.1RS wheat cultivars (Nagy et al. 2003). New genetic variation was introduced into the 1BL.1RS translocation through homologous recombinations between the 1RS of the translocation and that of the triticale, thereby demonstrating the possibility to widen the genetic base of 1RS in wheat by simple means.

Several molecular markers have been developed for the 1RS chromosome arm of diploid rye in the last decades (for review see Börner and Korzun 1998; as well as Hsam et al. 2000; Korzun et al. 2001; Ma et al. 2001; Masojc et al. 2001). Most of them are restriction fragment length polymorphism (RFLP) markers, along with a few A(amplified)FLP, isozyme, protein and randomly amplified polymorphic DNA (RAPD) markers and a single simple sequence repeat (SSR) marker. Cytological and genetic maps have revealed that the majority of these molecular markers are located in the distal region of the 1RS chromosome arm (Alonso-Blanco et al. 1994; Ma et al. 2001). Ma et al. (2001) concluded that no polymorphic

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marker is available between the centromere and the C-band designated as C1-1RS.

The insertion of transposable elements into a plant genome results in sequence divergences in homologous chromosome regions. This genetic variability has been exploited by a few recently developed marker systems (Waugh et al. 1997; Kalendar et al. 1999; Boyko et al. 2002), in which the flanking genomic regions around the retrotransposons are amplified. In the case of sequence-specific amplification polymorphism (SSAP), sequence-specific primers anchored to the end of a selected retroelement and a restriction-site-specific adaptor primer are combined (Waugh et al. 1997).

Repetitive sequences are a major constituent of the rye genome (Flavell et al. 1974). The repeated sequence family R173 is highly specific to rye and is distributed in several thousands of copies in diploid rye in a dispersed manner throughout all seven chromosomes with the exception of the centromeric regions, as detected by in situ hybridisation (Guidet et al. 1991). The longest member of this family, R173-1 (5,808 bp), is bordered by long terminal repeat (LTR) sequences, which is a major component of LTR-retrotransposons. However, it shows no further structural homology to any type of retrotransposon (Rogowsky et al. 1992). Recently, Ko et al. (2002) described two new repeated sequences in rye, pSc10C and pSc20H, dispersed in a high copy number over all seven chromosomes. PSc10C was localised mainly in proximal regions but not at the centromeres, while sequence pSc20H was evenly distributed along the whole length of the chromosomes except for the telomeric regions. Like the R173 elements, these two sequences are also specific to rye chromosomes, showing very little hybridisation sites with wheat (Ko et al. 2002).

In the present investigation, three rye-specific repetitive elements: R173-1, pSc10C and pSc20H, were used to generate SSAP markers for 1RS in the 1BL.1RS chromosome. Based on the physical distribution of these sequences along the rye chromosomes, we expected DNA fragments to arise from both proximal and distal regions of the 1RS chromosome arm. Polymorphism was sought by comparing the 1BL.1RS translocation to four primary octoploid triticale lines developed earlier (Nagy et al. 2003). SSAP markers were mapped genetically in a mapping population established between a 1BL.1RS wheat and one of the four octoploid triticales. Physical mapping was carried out using disomic 1R wheat-rye addition lines with different-sized deletions of the short arm.

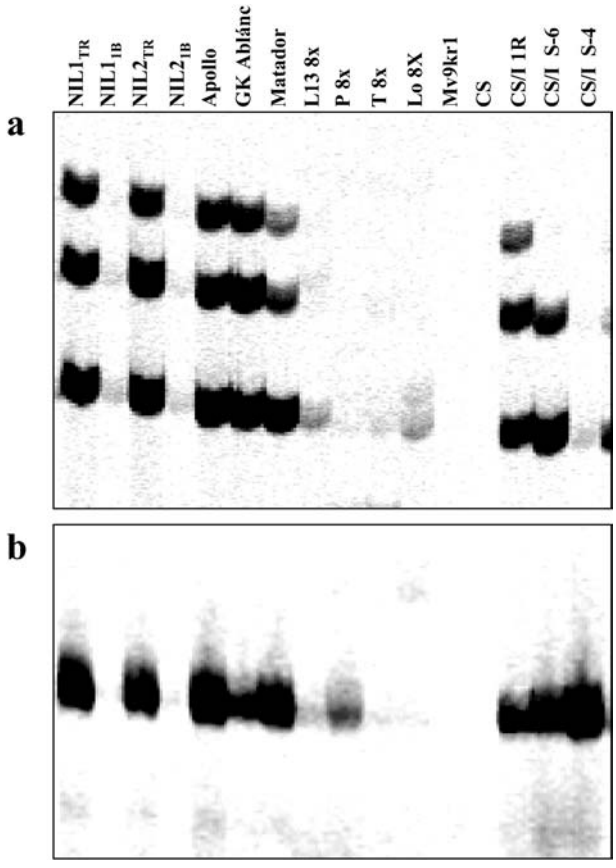

Fig. 1 Electrophoretic pattern of four SSAP markers as revealed in the 'tester set': **a** S17D-12a, b, c (from *bottom* to *top*), **b** S10-16b. Two pairs of near-isogenic wheat lines (NIL1 and NIL2) differing pair-wise in the presence ($NIL1_{TR}$, $NIL2_{TR}$) or absence ($NIL1_{1B}$, $NIL2_{1B}$) of the 1BL.1RS translocation were used to ascertain the localisation of 1RS-specific bands in a wheat background. Apollo, GK Ablánc and Matador are 1BL.1RS cultivars. Four octoploid triticale lines including rye L13, Petroneller, Tschermak and Lovászpatonai were used to establish polymorphism to the 1BL.1RS translocation. CS/I addition lines for the chromosome 1R were used to localise the markers physically. The line CS/I 1R carried the complete 1R chromosome, while lines CS/I S-6 and CS/I S-4 included terminal deletions on 1RS. Wheat line Mv9kr1 and wheat cultivar Chinese Spring represented the wheat background of the octoploid triticale lines and that of wheat-rye addition lines, respectively

Materials and methods

Plant material

Four octoploid triticale lines were synthesised between a Hungarian winter wheat line, Mv9kr1, showing high fertility in interspecific crosses (Molnár-Láng et al. 1996), and four rye genotypes differing from each other with respect to their ω-secalin banding patterns. Rye cultivars Petroneller and Tschermak from Austria, Lovászpatonai from Hungary and inbred line L13 from the University of Hohenheim, Germany, were used as the male parents. The primary triticales were developed in the Agricultural Research Institute of the Hungarian Academy of Sciences, Martonvásár. The triticale line including the rye Tschermak was crossed with a Hungarian 1BL.1RS wheat cultivar, GK Ablánc. F_1 plants were backcrossed with the translocated wheat cultivar to eliminate the redundant rye chromosomes. Genetic mapping was carried out on 80 BC_1F_2 plants. This mapping population is designated below as MP_T.

A group of 16 different genotypes ('tester set') was screened to characterise SSAP bands (Fig. 1). Two pairs of near-isogenic lines differing pair-wise in the presence or absence of the 1BL.1RS translocation (Lelley et al., unpublished) were used to determine which bands were located on 1RS in a wheat background. Three additional 1BL.1RS wheat cultivars, Apollo from Austria, and Matador and GK Ablánc from Hungary, were used to confirm the localisation of the selected bands. The four newly developed octoploid triticale lines were included to reveal polymorphism as

Table 1 Primers anchored to rye-specific repetitive elements and used in the development of SSAP markers

Primer	Template	Accession no.	Location (bp)	Sequence[a]
S10	pSc10C	AF305942	956–974	*CCTGCTGATGGGTTCTA*CA
S20	pSc20H	AF305943	58–76	*ATTCTTGGCAAAAGAGGC*G
S17D	R173-1	X64100	5449–5467	*GTGGGACTCTCTTTGGA*TG
S17U	R173-1	X64100	245–263	*CTGTCACCTTGGTCTCG*GG

[a] Preselective amplification was carried out with the 17-mer sequences typed in italics. Whole primer sequences were used for selective amplification

Table 2 1RS-specific SSAP markers[a] developed using four different anchored primers in combination with *Eco*RI adaptor primers plus two selective nucleotides

Preselective	Selective	S10	S20	S17D	S17U
*Eco*ad + A	*Eco*ad + AA	S10-1			S17U-1
	*Eco*ad + AT		S20-2a,-b		
	*Eco*ad + AC			S17D-3a,-b,-c	
	*Eco*ad + AG			S17D-4	
*Eco*ad + T	*Eco*ad + TA		S20-5		
	*Eco*ad + TT	S10-6			
	*Eco*ad + TC			S17D-7a,-b,-c	
	*Eco*ad + TG				
*Eco*ad + C	*Eco*ad + CA		S20-9	S17D-9	S17U-9
	*Eco*ad + CT		S20-10	S17D-10a,-b	
	*Eco*ad + CC	S10-11			
	*Eco*ad + CG			S17D-12a,-b,-c	
*Eco*ad + G	*Eco*ad + GA		S20-13		
	*Eco*ad + GT			S17D-14a,-b,-c	
	*Eco*ad + GC				
	*Eco*ad + GG	S10-16a,-b	S20-16		

[a] Marker designation consists of the name of the original repeated sequence, whether upstream (U) or downstream (D), followed by the number of primer combination in sequence (1–16) and by a letter of the alphabet (in a sequence)

compared to the 1BL.1RS translocation. Physical localisation of the markers was carried out using 1RS deletion lines. These deletions were produced by Friebe et al. (2000) in the 1R chromosome of the Chinese Spring (CS)/Imperial (I) addition line. Two deletion lines together with the complete 1R addition line were kindly provided by Dr. B. Friebe (Kansas State University, USA). Deletion line S-6 has lost the satellite and the NOR region of 1RS, while deletion line S-4 has retained approximately one-fifth of the short arm. The three regions, which can be physically differentiated, are considered in this paper to be *terminal* (the distal part of the chromosome from the S-6 deletion), *intercalary* (between breakpoints S-6 and S-4) and *proximal* (the remaining 1RS chromatin in S-4). The wheat line Mv9kr1 and the cultivar Chinese Spring represented the genetic background for the triticale lines and addition lines, respectively, in the 'tester set'.

Sequence-specific amplified polymorphism

Genomic DNA was isolated from plants of the 'tester set' and of MP_T using the Wizard Genomic DNA Purification kit (Promega Madison, Wis.) according to the instructions of the manufacturer. Genomic DNA was restricted with *Eco*RI and ligated with the *Eco*RI adaptor (5′-CTCGTAGACTGCGTACC-3′; 5′-CTGACG-CATGGTTAA-3′). Adaptor-specific primers were combined with a total of six primers anchored to both ends of each of the three rye-specific repetitive elements pSc10C, pSc20H and R173-1, oriented outwards. Repeated sequence specific primers were designed using the program PRIMER 3 (Whitehead Institute for Biomedical Research, Cambridge, Mass.). Two primers designed to the 5′ end of pSc10C and 3′ end of pSc20H produced very few rye-specific bands in the translocation lines, therefore, they were omitted from further investigations. The remaining four primers are listed in Table 1. Since the LTR sequences of R173-1 on both ends are identical, theoretically, fragments inwards of the repeated element could be expected. However, as the R173-1 sequence contains no *Eco*RI restriction sites, amplifications could only occur outwards of this element on both ends. Two consecutive PCRs were performed. The preselective amplification was carried out using the 17-bp anchored primers (in italics in Table 1) in combination with *Eco*RI adaptor primers (*Eco*ad) (5′-GACTGCGTACCAATTC-3′) plus one selective nucleotide (Table 2). PCR was carried out in a Primus 96 Plus thermocycler (MWG AG Biotech, Germany). The total 10-μl volume of reaction mixture contained 3 μl diluted template DNA, 0.13 μM of each primer, 100 μM dNTPs, 1× PCR buffer and 0.4 U Biotherm *Taq* polymerase (both from Genecraft, Germany). Touch-down PCR was applied using the following conditions: 2 min at 95 °C; 21 cycles of 30 s at 94 °C, 30 s at 64 °C (–0.7 °C per cycle); 1 min and 20 s at 72 °C; 18 cycles of 30 s at 94 °C, 30 s at 50 °C, 1 min and 20 s at 72 °C. The final elongation step was done at 72 °C for 5 min. The preselective amplification product was diluted 21 times with distilled water. Selective anchored primers (total sequences in Table 1) were labelled at the 5′ end with either IRDye 700 or IRDye 800 fluorescent dye (MWG AG Biotech). Selective amplification was carried out using the preselected PCR product as a template. The labelled primers were combined in all 64 possible combinations with *Eco*ad primers extended with two selective nucleotides (Table 2). The 10-μl mixture included 2 μl template DNA, 0.08 μM of labelled and 0.3 μM of unlabelled primer, 67.5 μM dNTPs, 1× PCR buffer and 0.35 U Biotherm *Taq* polymerase (both from Genecraft). The PCR conditions were as described above, except that the annealing temperatures were increased by 4 °C. After PCR, the samples were diluted with 11 volumes of loading buffer (95% formamide, 25 mM EDTA, pH 8, 0.05% acid fuchsin), heat-denatured and directly cooled on ice. The samples were loaded on 5% Long Ranger sequencing gel (BMA, USA) in a LI-COR DNA Sequencer, Long Readir 4200 (LI-COR Biosciences, Lincoln, Neb.). The electrophoresis was carried out in 1× TBE at a constant power of 40 W.

Five 1RS-specific markers, IAG95, GPI, 5S, SCM9 and Sec-1, together with a barley (*Hordeum vulgare* L.) SSR marker (Bmac0213) that was found to have a locus on 1RS (Nagy et al. 2003) were mapped genetically in MP_T in a previous work by the authors (Nagy et al. 2003). SSAP markers were mapped genetically along with these six markers using the computer programme MAPMAKER v. 3.0 (Lander et al. 1987). The segregation data were processed as if they originated from an F_2 intercross population. The Kosambi function was used to convert recombination values to genetic distances. Default linkage criteria were applied (LOD 3.0 and 50 cM maximum distance).

Results

Each primer combination produced a multi-banding SSAP profile. Primer combinations (Table 2) which generated at least one polymorphic, 1RS-specific band were included in the evaluation, while the others were omitted. A total of 163 SSAP bands were obtained in 19 primer combinations, with an average of 8.6 (4–15). Most of the bands (118; 72%) occurred only in genotypes which contained rye chromatin in the 'tester set', i.e. in the translocation, the octoploid triticale and the CS/I addition lines (Fig. 1). These bands were considered to be rye-specific. Of the 118 rye-specific bands, 60 occurred in the 1BL.1RS translocation genotypes, indicating that they have a locus on 1RS. The remaining 58 bands occurred in the octoploid triticale lines but not in the translocation lines, demonstrating that they were located in rye, but on chromosomes other than 1RS. The bands detected in both translocation and triticale lines may have more than one amplification site including that on 1RS. On the other hand, polymorphism between the 1BL.1RS translocation and triticale lines can only be observed when no other amplification site is present elsewhere in the rye genome for this band. Of the 60 fragments from the 1BL.1RS translocation, 30 were absent in at least one of the four octoploid triticale lines (Tables 2, 3). This polymorphism was scored and evaluated during genetic mapping. The triticale line Mv9kr1 × Lovászpatonai gave the lowest number of polymorphic bands (21 bands; 35%), while Mv9kr1 × Tschermak gave the most (26 bands; 43%), relative to the translocation wheat genotypes. On average, 38% of the 1BL.1RS-specific bands were polymorphic in a pair-wise comparison between the translocation and the triticale lines.

Nine markers could not be localised physically to the CS/I deletion-addition lines because they had a null allele

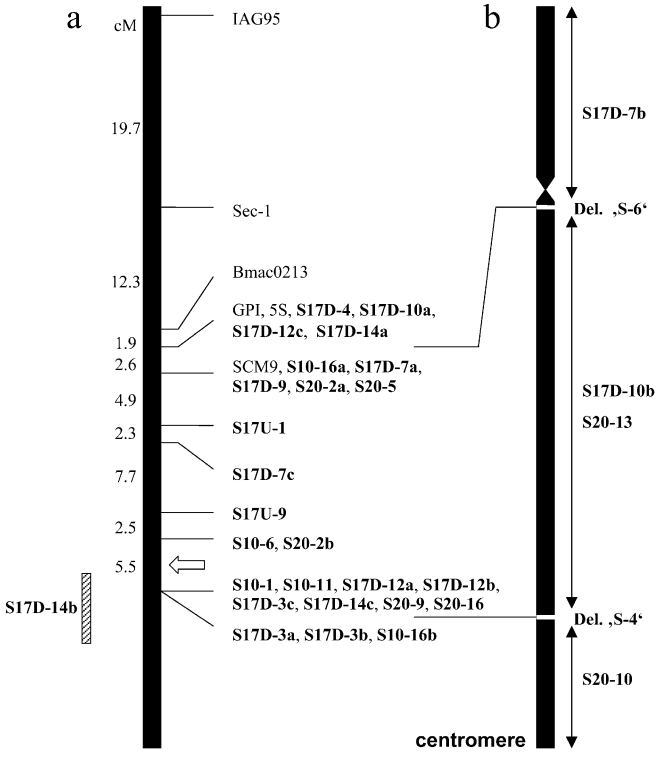

Fig. 2 Genetic (**a**) and physical (**b**) map of 30 SSAP markers (*bold*) along with six markers mapped previously on the 1RS chromosome arm. The *empty arrow* shows the site of the most proximal recombination breakpoint. The marker S17D-14b belonged to the most proximal group of markers on the genetic map, but its position relative to the deletion breakpoint in line S-4 could not be determined. Markers displayed *right* of the physical map could be localised physically but not genetically, because they were not polymorphic between the parents of MP_T

Table 3 Polymorphism detected by 1RS-specific SSAP markers in four different octoploid triticale lines as compared to wheat genotypes with the 1BL.1RS translocation

Sequence	Marker	Polymorphism[a]
pSc10C	S10-1	L13, Lo, P, T
	S10-6	L13, P, T
	S10-11	L13, Lo, P, T
	S10-16a[b]	T
	S10-16b	P, T
pSc20H	S20-2a[b]	L13, Lo, P, T
	S20-2b	L13, Lo, P, T
	S20-5[b]	L13, Lo, P, T
	S20-9	L13, Lo, P, T
	S20-10	L13, P
	S20-13	L13
	S20-16	L13, Lo, P, T
R173-1	S17D-3a	Lo, P, T
	S17D-3b	L13, Lo, P, T
	S17D-3c	L13, Lo, P, T
	S17D-4[b]	Lo, P, T
	S17D-7a	L13, P, T
	S17D-7b	P
	S17D-7c[b]	T
	S17D-9	L13, Lo, P, T
	S17D-10a[b]	L13, Lo, P, T
	S17D-10b	Lo, P
	S17D-12a	L13, Lo, P, T
	S17D-12b	L13, Lo, P, T
	S17D-12c	L13, Lo, P, T
	S17D-14a	P, T
	S17D-14b[b]	L13, Lo, P, T
	S17D-14c	L13, Lo, P, T
	S17U-1[b]	L13, Lo, P, T
	S17U-9[b]	L13, Lo, P, T

[a] Triticale lines are designated according to the rye genotypes they include: 'L13' (L13), 'Lovászpatonai' (Lo), 'Petroneller' (P), 'Tschermak' (T)

[b] These markers did not give any fragments in CS/I addition line 1R

in the 1R chromosome of cv. rye Imperial (Table 3). However, the physical location of eight of these markers could be unambiguously established based on linkage data. The ninth marker, S17D-14b, belonged to the most proximal group in the genetic map. However, as the S-4 deletion breakpoint divides this group into two subgroups in the physical map (Fig. 2), the position of this marker remains unclear.

Six of the markers (IAG95, Sec-1, Bmac0213, GPI, 5S, SCM9) have already been mapped on 1RS in MP_T (Nagy et al. 2003). In this study, their physical position was determined using 1RS deletions. Five of them were placed on the satellite or the NOR-region because they disappeared in the S-6 deletion line. The marker SCM9 was present in deletion line S-6 (Fig. 2). The SSAP markers developed in this work showed an even physical distribution over the whole length of the 1RS arm. Four markers were located in the proximal region, and five in the distal region. Twenty markers were distributed along the intercalary chromosome region between the two deletion breakpoints. Marker S17D-14b was located to either the proximal or in the intercalary region (Fig. 2), as described above. Markers anchored to sequences pSc10C and pSc20H were concentrated in the proximal and intercalary chromosome regions, whereas markers from R173-1 covered the whole chromosome arm (Table 2, Fig. 2).

Of the 30 SSAP markers, 26 were polymorphic between the 1BL.1RS translocation and the octoploid triticale (developed using the rye 'Tschermak') (Table 3). They were mapped genetically in MP_T along with the six previously mapped markers (Nagy et al. 2003) (Fig. 2). Of the 26 markers, 12 were localised between the most proximal recombination breakpoint and the centromere (Fig. 2a).

Four of the thirty markers, S20-10, S20-13, S17D-7b and S17D-10b, were not polymorphic between the 1BL.1RS translocation genotypes and the Mv9kr1 × Tschermak octoploid triticale, so they could not be mapped genetically. Their physical locations are shown in Fig. 2b.

Discussion

Sequence-specific amplification polymorphism has been demonstrated to be a potent marker system in several plant species (Waugh et al. 1997; Ellis et al. 1998; Gribbon et al. 1999; Yu and Wise 2000; Melayah et al. 2001; Berenyi et al. 2002). The technique described in the present communication differs from those of previous studies in that various kinds of rye repeated sequences were used, instead of retrotransposons, to anchor the sequence-specific primers. The level of sequence and structural homology of these elements to known retrotransposons is fairly low (Rogowsky et al. 1992; Ko et al. 2002). However, their dispersed genomic organisation suggests that they may have been reproduced and propagated in the rye genome in a similar way to retrotransposons. If this is true, comparable genetic variability can be expected in the genomic regions flanking the site of insertion, which can be revealed using SSAP.

The high proportion of rye-specific bands (72%) detected in a wheat background confirms the results obtained by in situ hybridisation (Guidet et al. 1991; Ko et al. 2002). Guidet et al. (1991) found that while about 1,000 copies of the repeated sequence R173 occurred on each rye chromosome, only 20 copies were present in the entire wheat genome.

More than half of the bands originating from rye had an amplification site on the conventional translocated 1RS arm. Assuming a near-random distribution of the bands over all seven rye chromosomes, the frequency of rye-specific bands on 1RS seems to be much higher than expected. This is probably due to the fact that primer combinations producing no polymorphic 1RS-specific bands were omitted from the evaluation. Moreover, bands which occurred in both the 1BL.1RS wheat genotypes and the triticale lines but not in wheat without rye chromatin may have further loci in rye in addition to that on 1RS. On average, 38% of the rye-specific bands amplified on 1BL.1RS were polymorphic between the translocation and one of the four octoploid triticale lines involved in the 'tester set'. This reflects a higher level of polymorphism in rye as compared to that reported in other SSAP studies made in barley and *Avena* species (Waugh et al. 1997; Yu and Wise 2000) but, as mentioned before, the results may be biased by the discriminating selection of SSAP profiles for evaluation.

The physical distribution of the sequences pSc10C, pSc20H and R173-1 revealed by anchored SSAP markers was in good agreement with results obtained using in situ hybridisation (Guidet et al. 1990; Ko et al. 2002). Markers from pSc10C and pSc20H were confined to the proximal and intercalary chromosome regions, whereas those from R173-1 were dispersed along the whole chromosome arm.

Twenty-six newly generated SSAP markers along with six further 1RS-specific markers were mapped genetically in wheat genotypes carrying recombinant 1BL.1RS translocations. Eighteen of the genetically mapped SSAP markers were localised physically to the intercalary region of 1RS. The most proximally recombined markers are S10-6 and S20-2b (Fig. 2a). From these two markers, at a distance of 5.5 cM towards the centromere, a further 11 SSAP markers were found that showed polymorphism with respect to the octoploid triticale with the rye Tschermak but no recombination in our mapping population. Three of these eleven SSAP markers were localised physically to the proximal region of 1RS. This finding is in good agreement with the results of Lukaszewski (1992), who found that recombination decreased towards the centromere on 1RS. On the other hand, the polymorphism of our SSAP markers facilitated the search of recombination events even in close proximity to the centromere in an appropriately sized mapping population.

The physical location of the marker SCM9 to the intercalary region together with its tight linkage to the marker loci in the terminal region allows for a positioning of this marker to the distal end of this chromosome region. This is in good agreement with recent results of Korzun et al. (2001) and Ma et al. (2001).

A wide range of genetic variability may be harboured in the 1RS arm of different rye genotypes (Shepherd 1973; Zeller and Fuchs 1983; Zeller and Hsam 1984; Porter et al. 1991; Porter and Friebe 1994; Marais et al. 1994). This variation could be of great value for wheat breeding. The easy introduction of new 1RS chromatin into the 1BL.1RS translocation by homologous recombination was demonstrated in this work. SSAP markers were generated and mapped using recombinant translocated chromosomes. In future, these markers can be tested for polymorphism in diploid rye and used for broadening the genetic variation of the 1BL.1RS translocation.

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