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L. L. Qi · S. L. Wang · P. D. Chen · D. J. Liu
B. Friebe · B. S. Gill

Molecular cytogenetic analysis of *Leymus racemosus* chromosomes added to wheat

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Abstract Five disomic, two double-disomic, and two ditelosomic addition lines and one disomic substitution line derived from the crosses of *Triticum aestivum* (2n = 6x = 42, AABBDD) × *Leymus racemosus* (2n = 4x = 28, JJNN) were identified by C-banding analysis. The homoeology of the added *Leymus* chromosomes was determined by RFLP analysis. Four of five disomic addition lines belonged to group 2, 5, 6 and 7 chromosomes of *L. racemosus*; these were designated as 2Lr#1(NAU516), 5Lr#1(NAU504, NAU514), 6Lr#1 (NAU512), and 7Lr#1(NAU501). Two additional chromosomes, 1Lr#1 and 3Lr#1, were present in double-disomic addition lines 1Lr#1 + 5Lr#1 (NAU525) and 3Lr#1 + 7Lr#1(NAU524), respectively. In the disomic substitution line wheat chromosome 2B was replaced by *L. racemosus* chromosome 2Lr#1 (NAU551). Two telocentric chromosomes, 2Lr#2S (NAU509) and 7Lr#1S (NAU511), were isolated as ditelosomic addition lines. The study presented here provides the first evidence of homoeology of the added *L. racemosus* chromosomes with wheat chromosomes using DNA markers. Our data provide the basis for further directed chromosome engineering aimed at producing compensating wheat-*L. racemosus* translocation lines.

Key words *Triticum aestivum* · *Leymus racemosus* · Chromosome addition lines · C-banding · RLFP analysis · Homoeology

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L. L. Qi · S. L. Wang · P. D. Chen · D. J. Liu
Department of Agronomy, Nangjing Agricultural University, Nangjing, 210095, P.R. China

B. Friebe · B. S. Gill (✉)
Department of Plant Pathology, Kansas State University, Throckmorton Hall, Manhattan, KS 66506-5502, USA

Introduction

The genus *Leymus* consists of about 30 species, all previously belonging to the genus *Elymus*. *Leymus* species are long-lived perennials with drought and salt tolerance, disease resistance, and a high number of seeds per spike (Dewey 1984). Attempts were made in the early 1940s to incorporate useful genes from *Leymus* into wheat. Some *Leymus* species were successfully crossed with wheat (Petrova 1960; Mujeeb-Kazi and Rodriguez 1980; 1981; Majeeb-Kazi et al. 1983; Comeau et al. 1985; Plourde et al. 1989 a, b, 1992). Evaluations of barley yellow dwarf virus resistance (BYDV) in the BC_3 and BC_2F_2 derivatives of *T. aestivum* × *L. multicaulis* and the F_1 of *T. aestivum* × *L. angustus* indicated that *Leymus* species may have potential in improving the BYDV resistance of bread-wheat (Plourde et al.1989, 1992).

Leymus racemosus (syn. *Elymus giganteus*) is a tetraploid species (2n = 4x = 28, genomically JJNN) distributed throughout central Asia. The first *T. aestivum* (AABBDD) × *L. racemosus* (JJNN) hybrid (ABDJN) was reported in 1981 (Mujeeb-Kazi and Rodriguez 1981). *L. racemosus* was later found to be a potential resource of resistance to wheat scab (Mujeeb-Kazi et al. 1983), but addition or substitution lines were not developed. In 1984, a program was initiated in China aimed at introducing the genes for scab resistant from *L. racemosus* into common wheat. The cytology of the F_1 hybrid of *T. aestivum*/*L. racemosus* and its BC_1 and BC_2 derivatives had been reported previously (Wang et al. 1986, 1991), and seven disomic addition lines and two ditelosomic addition lines were developed from BC_2F_2–BC_2F_5 and screened for scab resistance. (Chen et al. 1993, 1995; Ren et al. 1996; Sun et al. 1997a, b) One disomic addition line and one double disomic addition-substitution line were developed using anther culture (Lu et al. 1995).

Giemsa C-banding and *in situ* hybridization techniques are useful in detecting alien chromatin in a wheat background (Jiang and Gill 1994; Friebe et al. 1996, for review). The homoeologous relationships between alien and wheat chromosomes are determined by the use of isozymes and morphological and molecular markers, especially restriction fragment length polymorphisms (RFLPs) (Gale and Miller 1987; Miller and Reader 1987; Forster et al. 1987; Sharp et al. 1989; Chen et. al. 1994; Hart 1996). This paper combines evidence from C-banding analysis and RFLP markers to determine the homoeology of seven chromosomes and two telocentrics of *L. racemosus* present in the wheat-*L. racemosus* addition lines.

Materials and methods

Plant materials

Twenty-three lines from C.S. × *L. racemosus* BC_2–BC_4 derivatives were chosen on the basis of chromosome number, plant morphology, and meiotic chromosome pairing and C-banding analyses. Some lines were backcrossed with other wheat cutivars in order to facilitate their use in wheat breeding. Five accessions of *L. racemosus* (TA12094, TA12095, TA12096, TA12097, and TA12098) were provided by the Wheat Genetic Resource Center, Kansas State University, U.S.A.

Cytogenetic analysis

The C-banding technique described by B. S. Gill et al. (1991) was used for chromosome identification.

Molecular analysis

Clones of seven wheat homoeologous groups were selected based on previously published aneuploid and linkage data from *Triticeae* species. The RFLP probes used were: BCD, barley cDNA; CDO, oat cDNA; WG, wheat genomic DNA; PSR, wheat cDNA or genomic DNA. All probes were generously supplied by Dr. M. E. Sorrells, Cornell University, USA, and Dr. M. D. Gale, Cambridge Laboratory, Norwich, UK.

DNA extraction, restriction digestion, Southern blotting, probe labelling and hybridization were according to K. S. Gill et al. (1991) with minor modifications. Samples of 2–4 g of leaf tissue were ground to a fine powder with liquid nitrogen and incubated in 1.5 × CTAB buffer in a waterbath at 60°C for 3 h. For the Southern blot experiments 15 μg of each genomic DNA was digested, electrophoresed through a 0.8% agarose gel and blotted onto a MSI (Micro Separations, Westboro, USA.) nylon membrane. After hybridization, the filters were washed in 2 × SSPE and 0.5% SDS at 65°C for 30 min.

Results

C-banding and RFLP variation in *Leymus racemosus*

Four accessions of *L. racemosus* were analyzed by C-banding. A high level of polymorphism for C-band size and position was found between and within accessions. Most of the chromosomes were observed to have terminal bands in one or both arms. Figure 1 shows the C-banding pattern of the accession TA12097. The 14 chromosome pairs are designated alphabetically at random with letters from A to N because the genome affinity and homoeologous relationships of these chromosomes are unknown.

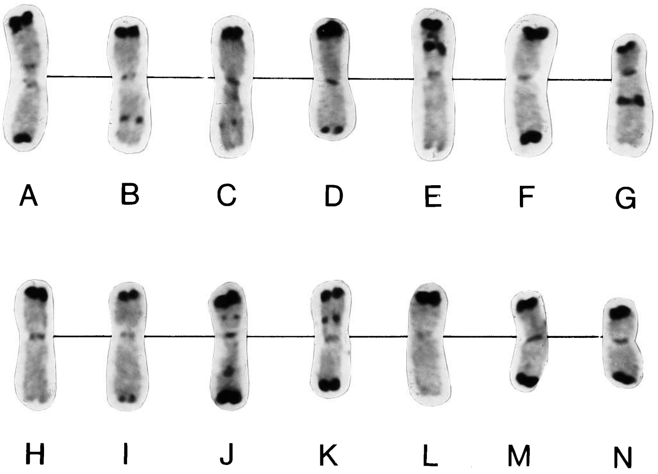


Fig. 1 C-banded karyotype of *L. racemosus* accession TA12097

DNA from the *L. racemosus* accessions and plants derived from C.S. × *L. racemosus* BC_2–BC_4 were digested separately with the restriction enzymes *Eco*RI and *Eco*RV. Each of 41 probes, chosen from each of the seven wheat homoeologous groups, was hybridized individually to Southern blots. Most probes hybridized to more than 3 fragments on chromosomes of *L. racemosus* (range: 1–11 fragments). High polymorphism between C.S. and *L. racemosus* was found, and few of the RFLP bands in *L. racemosus* were similar to those in C.S. The polymorphism for size and number of DNA fragments was also detected among *L. racemosus* accessions. When a unique DNA fragment was detected in wheat-*L. racemosus* additions, in most cases the DNA fragment was common in all of the *L. racemosus* accessions tested.

Characterization and homoeology of addition and substitution lines

All of the *L. racemosus* chromosomes were found to differ in C-banding patterns from those of wheat. Five disomic, two double-disomic, and two telosomic addition lines and one disomic substitution line were identified by their characteristic C-banding patterns (Fig. 2 and Table 1). Those addition or substitution lines showing unique DNA fragments from *Leymus* accessions and not present in C.S. or other wheat cultivars were assigned to their homoeologous groups. The

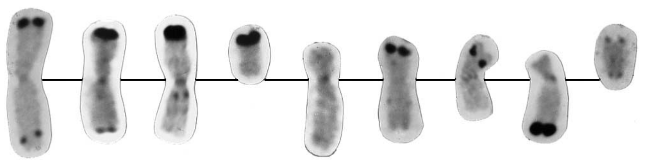


Fig. 2 C-banding patterns of the *L. racemosus* chromosomes and telosomes added to wheat

chromosomes in the addition series were designated from 1Lr # 1 to 7Lr # 1 according to their homoeology with wheat. The results are summarized in Table 2. The C-banding patterns and RFLP results of the alien chromosomes in the wheat-*Leymus* hybrids are as follows.

Disomic addition line 2Lr # 1, substitution line 2Lr # 1, and ditelosomic addition line 2Lr # 2S

Lines 96-1022 and 96-1022-5-1 had the same *L. racemosus* chromosome pair either added to the chromosome complement of wheat or substituting wheat chromosome 2B. The *L. racemosus* chromosome is submetacentric and has a telomeric C-band in the short arm and a subtelomeric C-band in the long arm.

Line 96-1016 was identified as a ditelosomic addition line. The telocentric chromosomes had faint bands in the telomeric, mid-arm, and the centromeric regions (Fig. 2).

Six group 2 probes showed polymorphic bands in lines 96-1022, 96-1022-5-1, and 96-1016 (Table 1). Common polymorphic bands were detected in lines 96-1022 and 96-1022-5-1. In addition, a missing band, previously mapped on chromosome 2B of C.S., was detected by the probe BCD240 in line 96-1022-5-1, indicating that the *L. racemosus* chromosome replaced chromosome 2B of wheat (Fig. 3). The short arm probe PSR666 detected a polymorphic band in line 96-1016, but not in lines 96-1022 and 96-1022-5-1. Different polymorphic bands were detected by the short-arm probe BCD433 in the three lines described above. The results indicate that the chromosomes present in 96-1022, 96-1022-5-1, and 96-1016 belong to homoeologous group 2 but involve different genomes of *L. racemosus*. The *L. racemosus* chromosomes present in 96-1022 (NAU516) and 96-1022-5-1(NAU551) are designated as 2Lr # 1 and that in line 96-1016 (NAU509) is designated as 2Lr # 2S.

Disomic addition line 5Lr # 1 and double-disomic addition line 1Lr # 1 + 5Lr # 1

Lines 96-1014 and 96-1020 were identified as disomic addition lines and designated as NAU504 and NAU514, respectively. The *L. racemosus* chromosome in these lines are acrocentric and are lacking diagnostic C-bands.

Line 96-1028 (NAU525) was identified as a double-disomic addition line, with 2n = 46 and two alien chromosomes pairs. One of the *L. racemosus* chromosomes was found to be identical to the added *L. racemosus* chromosome pair in lines NAU504 and NAU514, and the other chromosome is acrocentric, with a diagnostic C-band close to the telomere in the short arm.

The most complex polymorphic patterns were detected by group 5 clones. The short arm clones hybridized to fragments on both chromosomes in lines 96-1014, 96-1020, 96-1028, 96-1012, and 96-1021 (Table 2.). The polymorphic band detected by the long-arm probes appeared only in 96-1014, 96-1020, and 96-1028. When two specific probes, PSR115 and PSR164, that detect the 4/5 translocation in *Triticeae* were hybridized to the alien addition lines, no 4/5 translocation was detected. These data show that the *L. racemosus* chromosome in lines 96-1014 and 96-1020 belongs to homoeologous group 5; it was consequently designated 5Lr # 1.

Polymorphic bands also were detected by group 1 clones in line 96-1028. Although the long-arm probe BCD386 also detected a polymorphic band in lines 96-1014 and 96-1020 similar to that of 96-1028, no polymorphic bands were detected by the short-arm probes in 96-1014 and 96-1020. These data suggest that the second *L. racemosus* chromosome of 96-1028 is homoeologous to group 1; it was therefore designated 1Lr # 1.

Disomic addition line 6Lr # 1

Line 96-1019 was identified as a disomic addition and designated as NAU512. The added *L. racemosus* chromosome was observed to be nearly metacentric with a terminal C-band in the short-arm and a faint terminal C-band in the long arm. The five group 6 clones hybridized to the fragments in NAU512 only, showing that the *L. racemosus* chromosome in this line belongs to homoeologous group 6 of wheat. This chromosome was designated 6Lr # 1.

Disomic addition line 7Lr # 1, ditelosomic addition line 7Lr # 1S, and double-disomic addition line 3Lr # 1 + 7Lr # 1

The *L. racemosus* chromosome in line 96-1011 (NAU501) is also nearly metacentric with a telomeric band in the short arm. In addition, a faint band is located near the centromere of the long arm.

A telocentric chromosome was found in line 96-1018 (NAU511). The C-banding pattern and RFLP analysis

Table 1 Homoeology of the *L. racemosus* chromosomes added to common wheat[a] identified by RFLP markers[a]

Probes	Group	96-1011 (44)	96-1012 (44)	96-1014 (44)	96-1016 (44tt)	96-1018 (44tt)	96-1019 (44)	96-1020 (44)	96-1021 (44)	96-1022 (44)	96-1022-5-1 (42)	96-1027 (46)	96-1028 (46)
PSR596	1 S	–[b]	–	–	–	–	–	–	–	–	–	–	+
BCD371	1 S	–	–	–	–	–	–	–	–	–	–	–	+
BCD1434	1 S	–	–	–	–	–	–	–	–	–	–	–	+
CDO580	1 S	–	–	–	–	–	–	–	–	–	–	–	+
PSR544	1 L	–	–	–	–	–	–	–	–	–	–	–	–
PSR164	1 L	–	–	–	–	–	–	–	–	–	–	–	–
BCD386	1 L	–	–	+	–	–	–	+	–	–	–	–	+
PSR126	2 S	–	–	–	–	–	–	–	–	–	–	–	–
PSR666	2 S	–	–	–	+	–	–	–	–	–	–	–	–
BCD433	2 S	–	–	–	+	–	–	–	–	+	+	–	–
PSR388	2 L	–	–	–	–	–	–	–	–	+	**	–	–
BCD240	2 L	–	–	–	–	–	–	–	–	+	+	–	–
PSR926	3 S	–	–	–	–	–	–	–	–	–	–	+	–
CDO480	3 S	–	–	–	–	–	–	–	–	–	–	–	–
PSR578	3 L	–	–	–	–	–	–	–	–	–	–	+	–
BCD589	3 L	–	–	–	–	–	–	–	–	–	–	+	–
PSR584	4 S	–	–	–	–	–	–	–	–	–	–	–	–
BCD734	4 L	–	–	–	–	–	–	–	–	–	–	–	–
BCD327	4 L	–	–	–	–	–	–	–	–	–	–	–	–
PSR104	4 L	–	–	–	–	–	–	–	–	–	–	–	–
PSR164	4 L	–	–	–	–	–	–	–	–	–	–	–	–
PSR628	5 S	–	+	+	–	–	–	+	+	–	–	–	+
PSR929	5 S	–	+	+	–	–	–	+	+	–	–	–	+
CDO1335	5 S	–	+	+	–	–	–	+	+	–	–	–	+
PSR360	5 L	–	–	+	–	–	–	+	–	–	–	–	+
PSR370	5 L	–	–	+	–	–	–	+	–	–	–	–	+
PSR911	5 L	–	–	–	–	–	–	–	–	–	–	–	–
BCD1088	5 L	–	–	–	–	–	–	–	–	–	–	–	–
PSR115	5 L	–	–	+	–	–	–	+	–	–	–	–	+
PSR113	6 S	–	–	–	–	–	+	–	–	–	–	–	–
PSR167	6 S	–	–	–	–	–	+	–	–	–	–	–	–
BCD21	6 S	–	–	–	–	–	+	–	–	–	–	–	–
PSR142	6 L	–	–	–	–	–	+	–	–	–	–	–	–
CDO497	6 L	–	–	–	–	–	–	–	–	–	–	–	–
WG286	6 L	–	–	–	–	–	+	–	–	–	–	–	–
PSR103	7 S	–	–	–	–	–	–	–	–	–	–	–	–
BCD385	7 S	+	+	–	–	+	–	–	**	–	–	+	–
CDO786	7 S	–	–	–	–	–	–	–	–	–	–	–	–
PSR311	7 L	+	–	–	–	–	–	–	–	–	–	+	+
PSR547	7 L	+	–	–	–	–	–	–	–	–	–	+	+
WG466	7 L	+	–	–	–	–	–	–	–	–	–	+	–

[a] Of the 24 lines tested showing RFLP bands 12 are listed in this Table. Somatic chromosome numbers are given in brackets

[b] +, Polymorphic band; –, no polymorphic band; **, no data

Table 2 The constitution and molecular markers of the wheat-*L. racemosus* addition, substitution and telosomic lines

Pedigree	Constitution	Mapped markers
Disomic additions (2n =44)		
96-1022	DA2Lr#1 (NAU516 = TA7643)	BCD433-2S, PSR388-2L, BCD240-2L
96-1014	DA5Lr#1 (NAU504 = TA7646-1)	BCD386-1L, PSR628-5S, PSR929-5S, BCD1335-5S, PSR360-5L, PSR370-5L, PSR115-5L
96-1020	DA5Lr#1 (NAU514 = TA7646-2)	
96-1019	DA6Lr#1 (NAU512 = TA7647)	PSR113-6S, PSR167-6S, BCD21-6S, PSR142-6L, CDO497-6L, WG286-6L
96-1011	DA7Lr#1 (NAU501 = TA7648)	BCD385-7S, PSR311-7L, PSR547-7L, WG466-7L
96-1012	DA?Lr#1 (NAU502 = TA7652-1)	PSR628-5S, PSR929-5S, BCD1335-5S
96-1021	DA?Lr#1 (NAU515 = TA7652-2)	
Ditelosomic additions (44tt)		
96-1016	Dt2Lr#2S (NAU509 = TA7645)	PSR666-2S, BCD433-2S
96-1018	Dt7Lr#1S (NAU511 = TA7649)	BCD385-7S
Disomic substitution (2n =42)		
96-1022-5-1	DS2Lr#1(2B) (NAU551 = TA7644)	BCD433-2S, BCD240-2L
Double disomic additions (2n =46)		
96-1028	dDA1Lr#1 +5Lr#1(NAU525 = TA7650)	PSR596-1S, BCD371-1S, BCD1434-1S, CDO580-1S, BCD386-1L, PSR628-5S, PSR929-5S, BCD1335-5S, PSR360-5L, PSR370-5L, PSR115-5L, PSR311-7L, PSR547-7L
96-1027	dDA3Lr#1 +7Lr#1(NAU524 = TA7651)	PSR926-3S, PSR578-3L, BCD589-3L, BCD385-7S, PSR311-7L, PSR547-7L, WG466-7L

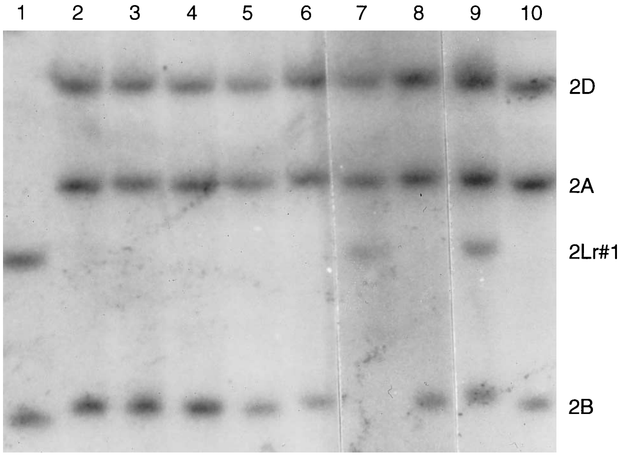


Fig. 3 Hybridization of homoeologous group 2 probe BCD240 to *Eco*RI-digested genomic DNA of the donor accessions and C.S. × *L. racemosus* BC_2–BC_4 derivatives. *L. racemosus* accession TA12097 (*lane 1*), 'Chinese Spring' (*lane 2*), disomic substitution 2Lr#1 NAU551 (*lane 7*), disomic addition 2Lr#1 NAU516 (*lane 9*).

showed that the telocentric chromosome was derived from the short arm of the chromosome present in line 96-1011.

Line 96-1027 was identified as a double-disomic addition. C-banding analysis revealed the presence of a pair of *L. racemosus* chromosomes. The *L. racemosus* chromosome is submetacentric, with a telomeric C-band in the short arm and a faint interstitial C-band at the middle of the long arm. The other alien chromosome pair in this line was identical to the *L. racemosus* chromosomes in line 96-1011.

Most of the group 7 probes used detected loci on the chromosomes present in 96-1011 and 96-1027. In addition, the short-arm probe BCD385 also detected a locus on the chromosome in line 96-1018. C-banding data were in agreement with the DNA hybridization results. The telocentric chromosome in 96-1018 was identical to the short arm of the chromosome in 96-1011. The chromosomes in 96-1011 and 96-1018 were designated as 7Lr#1 and 7Lr#1S, respectively. A further complication was that the probe BCD385, as well as PSR311 and PSR547, detected loci on the alien chromosome in line 96-1012 and chromosome 1Lr#1 in the line 96-1028, indicating that these chromosomes also contain some group 7 genetic material (Table 1).

Three of four group 3 probes hybridized to alien fragments in line 96-1027 designated as NAU524. No similar polymorphic bands were detected by these probes in line 96-1011. Three clones clearly hybridized to fragments of a chromosome different than 7Lr#1 in line 96-1011 (Fig. 4). Thus, the other chromosome in NAU524 was assigned to homoeologous group 3 and named 3Lr#1.

Disomic addition with unknown homoeology

Lines 96-1012 and 96-1021 were identified as disomic addition lines and designated as NAU 502 and NAU515, respectively. The *L. racemosus* chromosome in NAU502 and NAU515 is acrocentric with the telomeric band on the long arm. One *L. racemosus* chromosome with similar morphology and C-banding pattern was observed in the accession TA12096 (Fig. 5).

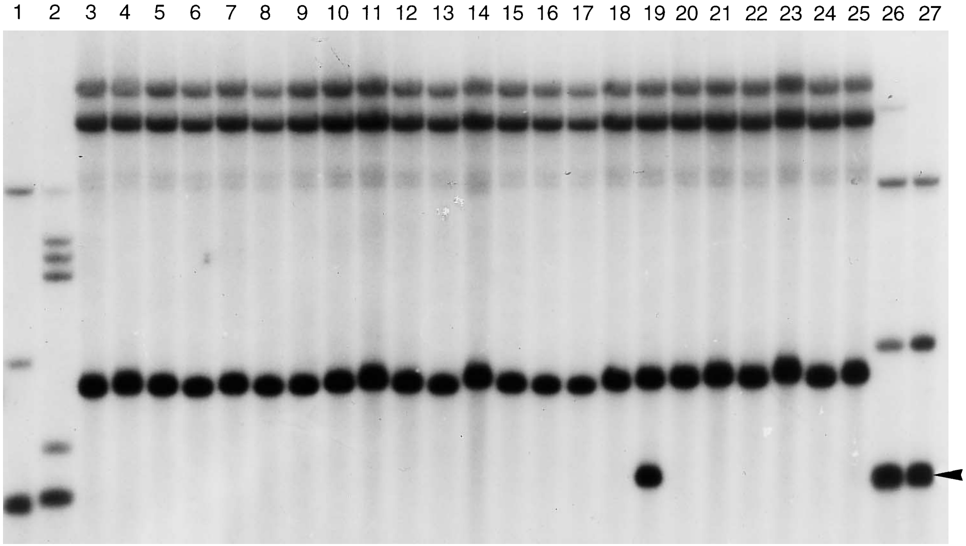


Fig. 4 Hybridization of homoeologous group 3 probe BCD589 to *Eco*RV-digested genomic DAN of the donor accessions and C.S. × *L. racemosus* BC_2–BC_4 derivatives. *L. racemosus* accessions TA12094, TA12095, TA12096, and TA12098 (*lanes 1*, *2*, *26*, and *27*), wheat cutivar 'Yangmei5' (*lane 3*), 'Chinese Spring' (*lane 4*), double- disomic addition 3Lr#1 +7Lr#1 NAU524 (*lane 19*). *Arrow* shows a polymorphic band

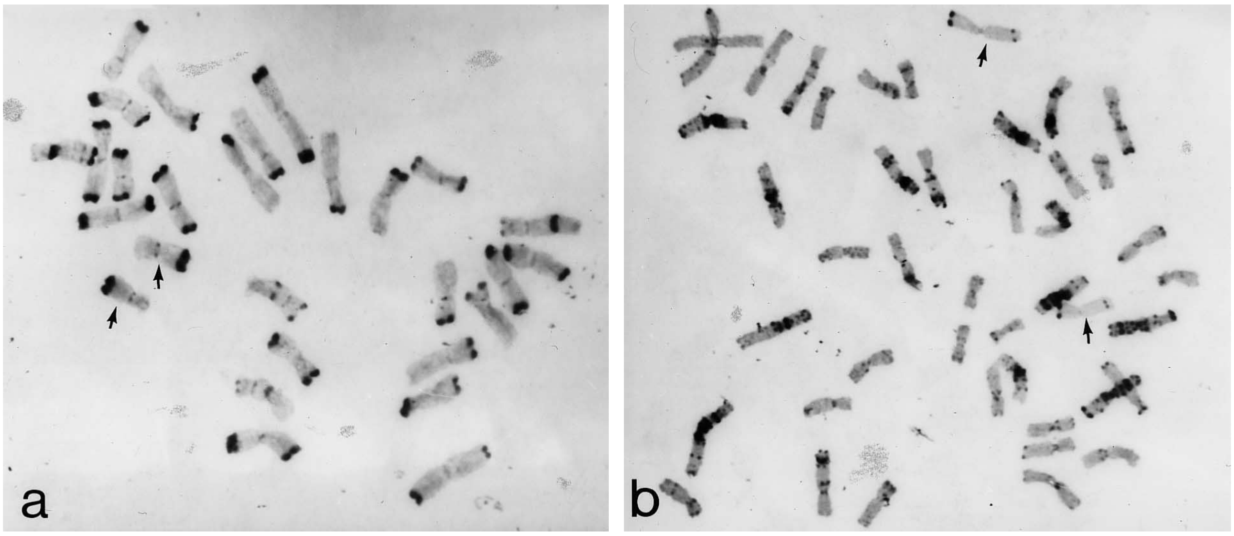
The short-arm probes of group 5 detected all of the polymorphic bands in NAU502 and NAU515 to be similar to those in 96-1014 and 96-1020, indicating that the short-arm of the chromosome is homologous with that of the chromosome in lines 96-1014 and 96-1020. However, none of 41 probes detected polymorphism for the long arms, and their homoeology is not known.

C-banding and RFLP analyses of the remaining 12, putative wheat-*L. racemosus* introgression lines did not reveal any evidence of *L. racemosus* chromatin. In addition, Southern blotting of five group 4 probes indicated that none of the alien chromosomes of the present addition series involved group 4 (Table 1).

Fig. 5a, b C-banded mitotic metaphase chromosomes. **a** *L. racemosus* accession TA12096; *arrows* show chromosomes similar to Lr#1 in Fig. 2. **b** Disomic addition line NAU516 (96–1022); *arrows* show chromosomes 2Lr#1

Discussion

C-banding analysis detected a large amount of polymorphism within and between different accessions of *L. racemosus*, which is typical for cross-pollinated species. The original *L. racemosus* accession was not available for the present analysis. Therefore, because of the large amount of polymorphism the *L. racemosus* chromosomes present in the set of chromosome addition lines can not be directly related to the corresponding chromosomes in the donor species. Some chromosomes, such as Lr#1 in Fig. 2, were observed in accession TA12096 (Fig. 5). Chromosome 5Lr#1



could not be identified in any of the accessions, indicating that this chromosome probably is rearranged. Furthermore, RFLP analysis provides a particularly efficient tool by which to assign addition lines to homoeologous groups. In alien chromosome substitution lines, the probes not only allowed the detection of the alien chromosome but also permitted the identification of the absent wheat chromosome.

C-banding and RFLP analysis detected polymorphism in the wheat background of most of the addition and substitution lines, indicating that not only 'Chinese Spring' but also other wheat cultivars were used in the production of those lines. In addition, C-banding analysis revealed the presence of a deleted chromosome 5B missing about the distal 30% of its long arm in lines 96-1011, 96-1018, 96-1020, and 96-1028. Furthermore, line 96-1020 is homozygous for a translocation chromosome involving wheat chromosome arm 2AL and an unidentified chromosome arm.

In the present study the results of the RFLP analysis were consistent with those of C-banding. Lines sharing a common alien chromosome also have identical RFLP patterns. In addition to C-banding polymorphism, the unique DNA fragments contributed by alien accessions could be observed in wheat-alien addition lines. The data in Table 1 provide the first evidence of homoeology of alien chromosome in wheat-*L. racemosus* addition lines using DNA markers.

With the exception of group 4, chromosome homoeologies were revealed by RFLP probing of the addition series, where at least four clones were used to detect the polymorphism in each homoeologous group. Line NAU551 was identified as a disomic substitution line by RFLP analysis, in which the band located on chromosome 2B of C.S. was missing and wheat chromosome 2B was replaced by *L. racemosus* chromosome 2Lr#1. RFLP analysis also indicated that both chromosomes 2Lr#1 and 2Lr#2S belong to the homoeologous group 2 but involve different genomes of *L. racemosus*. It is worth mentioning that the short-arm probes of group 5 hybridized to fragments both on chromosomes Lr#1 and chromosome 5Lr#1, indicating that the short-arm of chromosome Lr#1 is homologous with that of chromosome 5Lr#1. However, the long arms of the two chromosomes are different for both C-banding and RFLP patterns. Two long-arm clones of group 7 also hybridized to fragments on nonhomoeologous chromosomes 7Lr#1 and 1Lr#1 (Table 2) and may represent interchromosome duplication.

Chromosome pairing and molecular marker analyses have revealed the presence of a reciprocal translocation involving chromosomes 4AL, 5AL, and 7BS (Naranjo et al. 1987, 1990; Liu et al. 1992; Devos et al. 1995). Similar chromosomal rearrangments were also detected in cultivated rye, *Secale cereale* L. (Liu et al. 1992; Devos et al. 1993), and some closely related wild species have the 4/5 and 4/7 translocation (King et al. 1994). *L. racemosus* has been assigned the genome symbols JJNN, where the JJ donor was derived from *Thinopyrum bessarabicum* (Savul & Rayss) Love, and the NN genome was contributed by *Psathyrostachys juncea* (Fisch.) Nevski (Dewey 1984). King et al. (1994) reported that *T. bessarabicum* has a reciprocal translocation involving the chromosomes of group 4 and 5. However no 4/5 translocation was detected in the addition lines in this study. The probe PSR115, previously mapped on 4AL, 5BL and 5DL of C.S., gave a polymorphic band which appeared only in DA5Lr#1 and dDA1Lr#1 +5Lr#1. The probe PSR164, previously mapped on 4BL, 4DL, and 5AL of C.S., did not show any polymorphic band in DA5Lr#1 and dDA1Lr#1 + 5Lr#1.

The likelihood of a successful gene transfer depends on the degree of relatedness between the alien and the wheat chromosomes. The assignment of homoeology of the added *L. racemosus* chromosomes offers the possibility for inducing substitutions or translocations by homoeologous pairing. The availability of alien substitution or translocation permits preselection of the specific homoeologous chromosome segment to be replaced by the alien segment. Because the substitution or translocation involves homoeologous wheat and alien chromosomes, the transfer will genetically compensate for the missing wheat chromosome or segment. This aspect of the work is now in progress.

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