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Production of a new wheat line possessing the 1BL.1RS wheat-rye translocation derived from Korean rye cultivar Paldanghomil

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Abstract The 1BL.1RS translocations between wheat (*Triticum aestivum* L.) and rye (*Secale cereale* L.) are widely used in bread wheat breeding programs, but all modern wheat cultivars with the 1BL.1RS have shown genetic vulnerability due to one rye source – a German cultivar, Petkus. We have developed, a new 1BL.1RS wheat-rye translocation line from the backcross of the F_1 hybrid of wheat cv. Olmil and rye cv. Paldanghomil, both cultivars from Korea. The GISH technique was applied to identify the presence of rye chromatin in 467 BC_1F_6 lines selected from 77 BC_1F_5 lines. Only one line, Yw62–11, showed wheat-rye translocated chromosomes, with a somatic chromosome number of 2n=42. C-banding patterns revealed that the translocated chromosome was 1BL.1RS, showing prominent bands in the terminal and sub-terminal regions of the short arm as well as in the centromeric region and terminal region of the long arm. This new 1BL.1RS translocation line formed 21 bivalents like common wheat at meiotic metaphase I, thereby showing complete homology.

Keywords *Triticum aestivum* · *Secale cereale* · 1BL.1RS translocation · Genomic in situ hybridization · C-banding

Introduction

Rye (*Secale cereale* L.) has great potential for increasing the genetic variability and germplasm resources of cultivated hexaploid wheat (*Triticum aestivum* L.). The rye chromosome arm 1RS, in particular, has been widely used in wheat breeding programs worldwide (Lukaszewski 1990; Villareal et al. 1994). Globally, numerous wheat cultivars carrying the 1BL.1RS wheat-rye translocation have been released (Rabinovich 1998), and these currently occupy over five million hectares of cultivated area (Villareal et al. 1998).

According to Rabinovich (1998), only four sources of 1RS were the progenitors of hundreds of commercial wheat cultivars grown currently in different countries. Two were developed in Germany by G. Riebesel and G. Kattermann in the 1920s–1930s, one in Japan in the 1960s and one in the USA in the 1970s. The two German lines are clearly the main source of 1RS in most contemporary wheat varieties that carry 1BL.1RS, although some authors believed that there is only one German source (Lein 1975; Moonen and Zeven 1984) due to the lack of information on pedigrees. The rye source of the two German translocation lines was cv. Petkus (2×). A Japanese wheat cultivar Salmon with 1BL.1RS was bred from an octaploid triticale (Tsunewaki 1964), but only one line was developed using cv. Salmon in the USA. The two German lines and a Japan cultivar are composed of the 1BL.1RS translocated chromosomes, while a wheat cultivar, Amigo, the source of 1RS in USA, carries the 1AL.1RS translocation (Zeller and Fuchs 1983). The rye source of cv. Amigo is an Argentine cultivar, Insave (2×) (Sebesta et al. 1994).

The widespread utilization of the 1BL.1RS translocation is partially due to the fact that the 1RS segment carries the resistant genes *Lr26* to leaf rust (*Puccinia recondita* f.sp. *tritici*), *Sr31* to stem rust (*Puccinia graminis* f.sp. *tritici*), *Yr9* to stripe rust (*Puccinia striiformis* f.sp. *tritici*) and *Pm8* to powdery mildew (*Erysiphe graminis* f.sp. *tritici*) (Singh et al. 1990; McIntosh et al. 1993) and genetic factors for wide adaptation and stress tolerance (Rajaram et al. 1983; Villareal et al. 1994). The 1BL.1RS translocation lines also exhibit higher grain yield (Carver and Rayburn 1994; Moreno-Sevilla et al. 1995; Villareal et al. 1998). In addition, the presence of the 1BL.1RS translocation has enhanced haploid produc-

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tion and green-plant regeneration from anther culture (Henry et al. 1993).

Despite the positive effects of the translocation, the 1BL.1RS translocation was disqualified from breeding programs developing high-quality bread wheat because it has detrimental effects on bread making quality (Dhaliwal et al. 1987; Graybosch et al. 1993; Fenn et al. 1994). Resistance to *Pm8 and Lr26* derived from 1RS has broken down in Europe (Zeller and Hsam 1983; Lutz et al. 1992). Villareal et al. (1998) believe that genetic vulnerability caused principally by wide cultivation of the 1BL.1RS cultivars, is the consequence of a narrow genetic base contributed by the 1RS chromosome arm from cv. Petkus rye in all wheats.

In wheat breeding programs, C-banding and genomic in situ hybridization (GISH) are powerful techniques for chromosome identification (Friebe and Larter 1988; Xu et al. 1994) and the detection of alien chromosomes and chromosome segments in hexaploid wheat cultivars (Heslop-Harrison et al. 1990; Mukai and Gill 1991; Schwarzacher et al. 1992). Alien chromatins can be easily visualized by GISH, not only in high-quality metaphase spreads but also within interphase nuclei. Therefore, GISH is the most efficient and accurate method to detect the breakpoint and estimate the amount of alien chromatin of the translocated chromosomes.

Here we report on the production of a new 1BL.1RS translocation line from the backcross of the F_1 hybrid between wheat cultivar Olmil and rye cultivar Paldanghomil.

Materials and methods

Plant material

Wheat×rye F_1 hybrids were produced by crossing soft red winter wheat cv. Olmil (hexaploid, 2n=AABBDD=42) and winter rye cv. Paldanghomil (diploid, 2n=RR=14). Wheat cv. Olmil was developed at the National Yeongnam Agricultural Experiment Station in Korea (Park et al. 1977); rye cv. Paldanghomil was bred at the National Crop Experiment Station in Korea (Hwang et al. 1985). The wheat×rye F_1 hybrids were backcrossed using cv. Olmil as the male parent. After one backcross, subsequent generations were progressed by selfing. The BC_1F_3 seeds obtained from BC_1F_2 plants were planted in bulk, and individual plants selected in the BC_1F_3 and BC_1F_4 generations were grown as lines in the BC_1F_4 and BC_1F_5 generations, respectively. Rate of seed set was obtained from each of the plants in the BC_1F_3 generation and from ten plants per line in BC_1F_4 and BC_1F_5. The selection in the BC_1F_4 and BC_1F_5 generations was based on relatively good grain shape, high seed set and wheat-like plant type.

To detect the presence of rye chromatin in BC_1 derivatives of *T. aestivum* cv. Olmil×*S. cereale* cv. Paldanghomil, we carried out GISH analysis on seeds of the 467 BC_1F_6 lines selected in the BC_1F_5 generation. The seeds in which rye chromatin was detected were grown for meiotic analysis in the greenhouse.

Chromosome preparation

Root tips 2–3 cm in length were excised and placed in ice water for 24 h, then fixed in acetic acid:ethanol (1:3) for 2 days. The root cap was removed with a razor blade, and a small piece of root meristem was squashed under a cover slip in 45% acetic acid. Slide preparations were frozen on dry ice or liquid nitrogen, and the cover slips were removed by a razor blade. Slides with an acceptable number of cells in somatic metaphase were selected under phase contrast microscope. The slides were dried overnight at room temperature, then stored at –20°C for immediate use.

For GISH analysis of meiotic stages, spikes were first fixed in Carnoy's fixative (6:3:1, ethanol:chloroform:acetic acid) for 48 h, and then stored in 70% ethanol at 4°C until use. The pollen mother cells were squeezed from the anthers in 45% acetic acid, stained and squashed in 1% aceto-carmine. The slides were screened and photographed using a phase-contrast microscope, following which the slides were frozen in liquid nitrogen and the coverslips removed. The slides were destained in 45% acetic acid for 5 min, air-dried and stored at –20°C until GISH analysis.

Probe labeling

Total genomic DNA of *S. cereale* cv. Paldanghomil was prepared from young growing leaves according to Dellaporta et al. (1983). The isolated DNA was mechanically sheared to 10- to 20-kb fragments and then labeled with biotin-14-dATP by nick translation (Gibco BRL). Unincorporated nucleotides were separated from the labeled DNA using repeated ethanol precipitation.

GISH and C-banding

Before hybridization, the slides were incubated in RNase A and pepsin, then fixed with formaldehyde according to the method of Schwarzacher et al. (1994). In situ hybridization and probe detection followed the method of Islam-Faridi and Mujeeb-Kazi (1995). After probe detection, the slides were counterstained with 20 µl propidium iodide (1 µl/ml) in Vectashield (Vector Laboratories); a glass cover slip was put in place, and the slide preparations were kept at 4°C for 1 day. Slides were examined under a Zeiss Axioplan fluorescence microscope with filter 23 or filter 09. Photographs were taken on a Kodak MAX 400 color print film. The C-banding technique was applied for chromosome identification of the plants carrying wheat-rye chromosomal translocations according to the method described by Gill et al. (1991).

Results

Production of backcross derivatives of the wheat×rye hybrid

The backcross derivatives of the F_1 hybrid of *T. aestivum* cv. Olmil and *S. cereale* cv. Paldanghomil are produced as shown in Fig. 1. Only one BC_1F_1 seed was obtained from backcrossing the F_1 hybrid of *T. aestivum* cv. Olmil and *S. cereale* cv. Paldanghomil using Olmil as the male parent. The BC_1F_1 plant by self pollination produced only five BC_1F_2 seeds, and in next generation five BC_1F_2 plants produced 119 BC_1F_3 seeds. The data on seed set in the BC_1F_3, BC_1F_4 and BC_1F_5 generations are shown in Table 1. In the BC_1F_3 generation, 27 of the 119 plants were inviable or sterile, while the 92 plants that displayed fertility showed a seed set that ranged extensively from only 1% to above 80%. Most of BC_1F_4 lines had a seed set ranging from 60% to 80%, but three lines were sterile. All 77 lines planted in BC_1F_5 generation were fertile, and the seed set was higher than 60%.

Table 1 Distribution of lines according to seed-setting percentage in each generation of backcross derivatives of *Triticum aestivum* cv. Olmil×*S. cereale* cv. Paldanghomil

Generation	Number of line	Number of lines according to seed-setting percentage					
		0%	1–20%	21–40%	41–60%	61–80%	Above 80%
BC_1F_3	119 (100%)	27 (22.7)	11 (9.2)	20 (16.8)	30 (25.2)	25 (21.0)	6 (5.1)
BC_1F_4	92 (100%)	3 (3.3)	0 (0)	0 (0)	6 (6.5)	69 (75.0)	14 (15.2)
BC_1F_5	77 (100%)	0 (0)	0 (0)	0 (0)	0 (0)	37 (48.1)	40 (51.9)

[a] Percentages are given in parenthesis

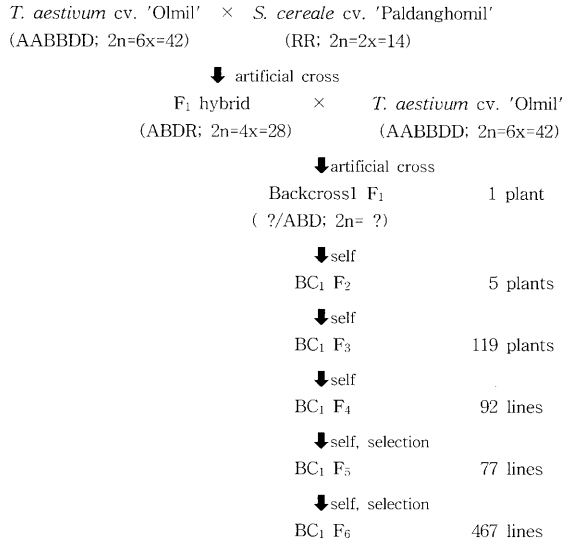

Fig. 1 Diagram showing the production of backcross derivatives of *T. aestivum* cv. Olmil×*S. cereale* cv. Paldanghomil

Identification of a new 1BL.1RS translocation

Upon GISH analysis, the root-tip preparations in which rye chromatin was present were distinguishable by yellow-green fluorescing domains at interphase and metaphase. Among the 467 BC_1F_6 lines selected from 77 BC_1F_5 lines, rye chromatin was identified in 32 lines; the existence of the rye chromatin was abortive with one or two chromosome arms (data not shown). Only one line, Yw62–11, contained a wheat-rye translocation chromosome. Sister lines of Yw62–11 derived from Yw62 had a rye chromosome arm or did not contain rye chromatin at all.

The Yw62–11 line was still segregating for the translocated chromosome in the BC_1F_6 generation. Out of 37 seeds of the Yw62–11 line analyzed, 12 seeds contained one wheat-rye translocated chromosome (Fig. 2A), 14 seeds had two translocated chromosomes (Fig. 2B) and the remainder only contained wheat chromosomes. The chromosome number of the Yw62–11 line was 2n=42, and the translocation breakpoint was at the centromere.

C-banding patterns showed that the Yw62–11 line had complete wheat genomes consisting of the A, B and

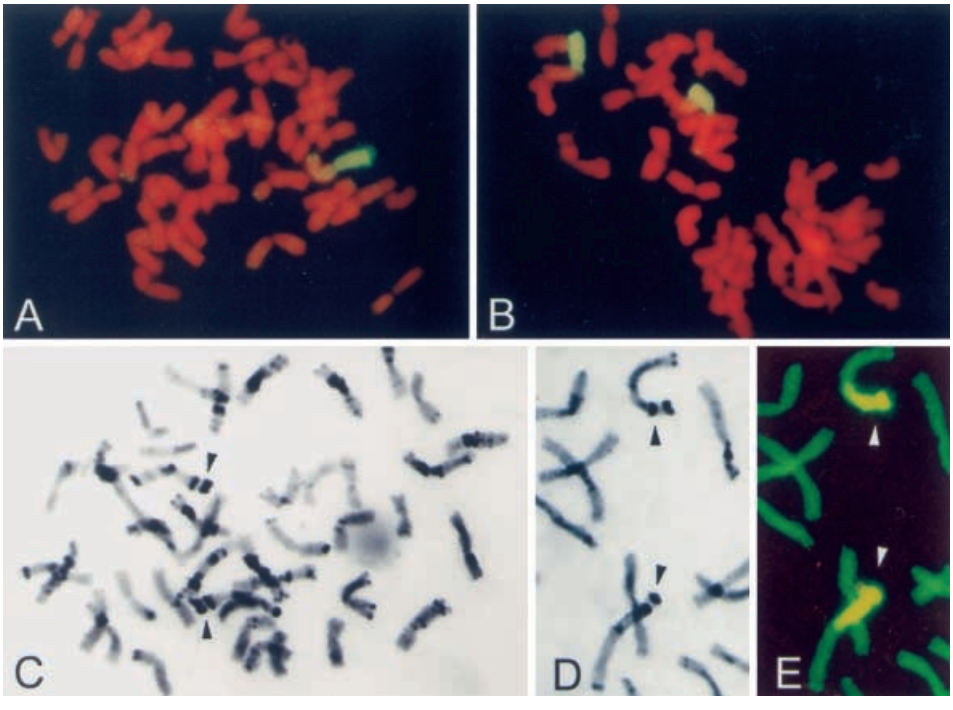

Fig. 2A–E Genomic in situ hybridization and C-banding of a wheat-rye chromosomal translocation line detected in BC_1F_6 generation of *T. aestivum* cv. Olmil×*S. cereale* cv. Paldanghomil. **A** GISH of the plant including one translocated chromosome; **B, C** GISH (**B**) and C-banding (**C**) of the plant, including two translocated chromosomes; **D, E** comparison of wheat-rye translocated chromosome by C-banding (**D**) and GISH (**E**) in the same cell of the translocation plant. *Yellow-green* signals after GISH indicate rye chromatin. The *arrowheads* indicate wheat-rye translocated chromosomes

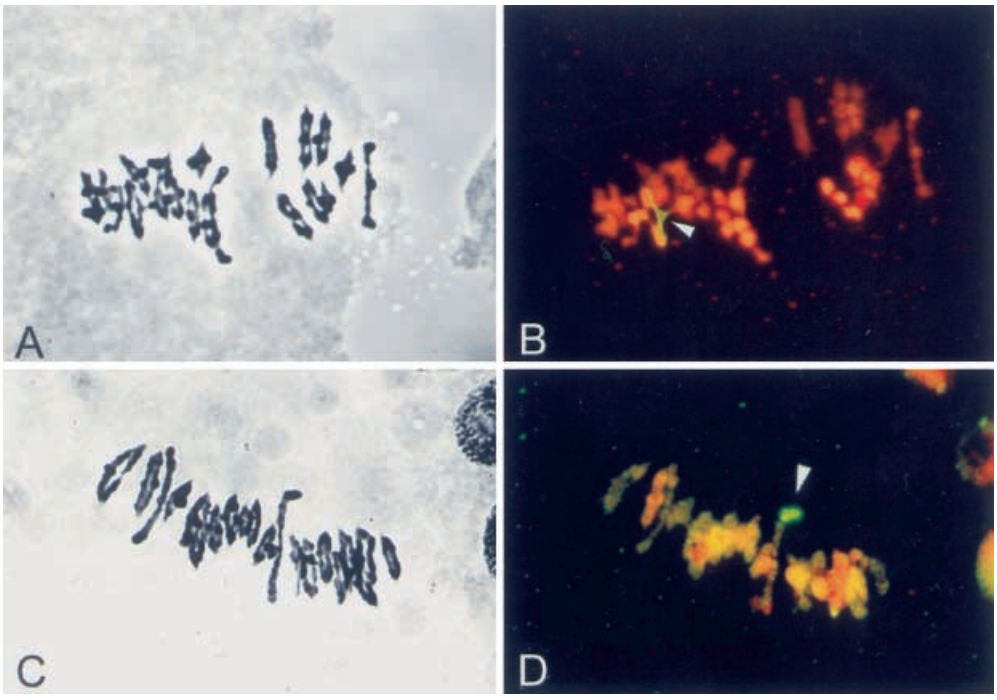

Fig. 3A–D Aceto-carmine staining and genomic in situ hybridization at meiosis of a new wheat line carrying the 1BL.1RS translocation in the BC_1F_6 generation of *T. aestivum* cv. Olmil×*S. cereale* cv. Paldanghomil. Metaphase I of the cells with two translocated chromosomes (**A, B**) and one translocated chromosome (**C, D**) showing 21 bivalents. The *arrowheads* indicate wheat-rye translocated chromosomes

D genomes except for the introgressed rye chromatin (Fig. 2C). Sequential C-banding and GISH confirmed that the translocated chromosome was 1BL.1RS, with the translocation resulting from the centric fusion between the short arm of rye chromosome 1R (1RS) and the long arm of wheat chromosome 1B (1BL) (Fig. 2D, E). The short arm of the wheat-rye translocated chromosome showed the distinctive C-banding patterns of rye 1RS, which have strong bands in the terminal and subterminal regions, and the centromere and terminal regions of the long arm also exhibited strong bands. A faint interstitial band was present in the long arm of the translocated wheat 1B chromosome. These C-banding patterns were identical with those of the 1BL.1RS chromosome in several wheat cultivars reported by Villareal et al. (1994).

Meiotic studies of the new 1BL.1RS translocation line

Meiotic analysis was carried out to examine the genome stability of the Yw62–11 line carrying the wheat-rye translocation. A wheat plant with two translocated chromosomes showed a regular meiotic configuration, similar to that of common wheat, producing 21 bivalents at metaphase I (Fig. 3A). The chromosomal pairing between two translocated chromosomes was clearly identifiable by GISH (Fig. 3B).

In a plant with one translocation, the chromosomal pairing was also a normal meiotic configuration (Fig. 3C). GISH analysis showed that the pairing between one wheat chromosome and one translocated chromosome occurred (Fig. 3D), and the mode of this pairing was observed with rod bivalents in most of the pollen mother cells.

Discussion

Only one backcross (BC_1) plant was produced from the backcross of *T. aestivum* cv. Olmil×*S. cereale* cv. Paldanghomil using wheat cv. Olmil as the male parent. At fertilization, the egg cell of the wheat-rye F_1 hybrid would consist of the mixed genome of wheat and rye as a result of abnormal meiosis, while the pollen of the wheat cultivar would consist of a normal haploid genome (n=3x=21). Hence, the one BC_1F_1 plant produced would be composed of a complete set of the wheat genome and a partial mixed genome of wheat and rye. Low homology between chromosomes in the BC_1F_1 plant resulted in partial fertility and low seed set in the BC_1F_2, BC_1F_3 and BC_1F_4 generations. The percentage of seed set in the backcross derivatives of *T. aestivum* cv. Olmil×*S. cereale* cv. Paldanghomil improved with each subsequent generation (Table 1). In the BC_1F_5 generation, all of the plants investigated were fertile, and 40 out of 77 lines showed above 80% seed set. This indicates that chromosome homology in this generation was considerably high.

Rye chromatin was identified in 467 BC_1F_6 lines by GISH analysis. The GISH technique was highly satisfactory for identifying the presence of rye chromatin both at metaphase and interphase. Among 467 BC_1F_6 lines analyzed, only one line (Yw62–11) was identified as having the translocated chromosome with the centric fusion of wheat and rye chromosome. King et al. (1994) studied homoeologous chromosome pairing in wheat×rye hybrids by GISH analysis and confirmed the potential of wheat-rye recombination by their chromosome pairing at meiosis. If this is the case, the translocation of Yw62-11 was also likely to have generated from homoeologous

pairing between the wheat and rye chromosome. However, gene introgression by homoeologous recombination in early generations is very difficult (Chen et al. 1992). The frequency of the translocation between the wheat and rye chromosomes will increase when continuously maintained in subsequent generations. In segregating wheat-rye lines, therefore, it is necessary for selection in early generations to maintain plants carrying the rye chromatin because successive selections and the maintenance of plants with rye chromatin will increase the chance of the rye chromatin being introgressed into wheat. The segregations of the Yw62 line in the BC_1F_5 generation and of the Yw62–11 line in the BC_1F_6 generation indicate that the translocation is generated by homoeologous recombination in the pollen or egg mother cell of the BC_1F_4 plant with the rye chromosome or chromosomal segment.

The translocated chromosome detected in the Yw62–11 line was identified on the basis of C-banding patterns. C-banding analysis on 1BL.1RS translocation lines originating from rye cv. Petkus have shown that the translocated chromosome is characterized by prominent banding sites on terminal and subterminal sites of the short arm, at the centromere region and at the terminal end of the long arm; there are also fainter interstitial banded sites on the long arm (Villareal et al. 1994; Muzeeb-kazi et al. 1996). In our study, the C-banding pattering of the newly observed translocated chromosome of the Yw62–11 line were identical with those of the 1BL.1RS chromosome reported by those authors. On the basis of this result, we conclude that the short arm of the wheat-rye translocation chromosome is part of cv. Paldanghomil rye chromosome 1R and the long arm is that of cv. Olmil wheat chromosome 1B.

The genome stability of the Yw62–11 line in the BC_1F_6 generation was observed at meiotic metaphase I (Fig. 3). The plants with two translocated chromosomes in the BC_1F_6 generation showed that the meiotic associations were 21 bivalents. The bivalent pairing between two translocated chromosomes was strict. Chromosome pairing associations of plants with one translocation also showed 21 bivalents. At that time, the translocated chromosome was observed with a bivalent, though the pattern of the pairing was always a rod because the region of the rye 1RS and wheat 1BS did not pair. The results indicate that the genome stability of the Yw62–11 line was accomplished in the wheat-rye translocated chromosome as well as in all wheat chromosomes. This strict pairing implies that the genome of this line will be stable in subsequent generations and that this line can be directly used for wheat improvement.

The new 1BL.1RS wheat-rye translocation line has not yet been examined for agricultural traits. The powdery mildew resistance gene (*Pm17*) in cv. Amigo wheat, which is on a 1AL.1RS translocation derived from rye cv. Insave, is different from *Pm8* located on the 1RS chromosome segment of 1BL.1RS cultivars derived from rye cv. Petkus (Heun et al. 1990). Graybosch et al. (1993) found that the 1AL.1RS translocation is also less detrimental to bread making quality than the 1BL.1RS translocation. These facts suggest that the 1RS derived from cv. Paldanghomil may possess new genes for resistance to some pathogens and for a reduction of negative effects on bread quality in wheat, as well as increased genetic variability of 1RS in cultivated wheat. Before it can be widely used in wheat breeding programs, this new translocation line will be investigated for several agronomic traits, including disease resistance, insect resistance, salt and drought tolerance and yield.

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