Theor. Appl. Genet. 59, 33-37 (1981)

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Identification of a 4A/7R and a 7B/4R Wheat-rye Chromosome Translocation

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Summary. By producing chromosome substitutions with 'Imperial rye' chromosomes 4R (C) and 7R (D) in the wheat cultivar 'Chinese Spring' two spontaneous translocation lines were obtained. One involves segments of wheat chromosome 4A and rye chromosome 7R, the other involves portions of wheat chromosome 7B and rye chromosome 4R

Key words: Wheat – Rye – Gene transfer – Translocations – Homoeologous genes

Introduction

Homoeologous chromosome pairing in wheat and related species has been employed to transfer genes to *Triticum aestivum* L. (2n = 6x = 42) from several of its relatives, including *Aegilops* and *Agropyron*. However, hybrids involving wheat and *Secale cereale* L. (2n = 14) exhibit a very low level of homoeologous pairing both in the presence of chromosome 5B (Riley 1960; Lacadena 1967; Lelley 1976; Mettin et al. 1976; Dvořák 1977; Schlegel and Weryszko 1979; Driscoll et al. 1979; Lelley and Larter 1980) and even in its absence (Riley 1960; Bielig and Driscoll 1970a, b; Driscoll et al. 1979; Lelley and Larter 1980). Nakaijma and Zennyozi (1966) and Joshi and Singh (1979), on the contrary, reported F_1 hybrids between several wheat and rye strains showing high chromosome pairing ranging from 6.1 to 9.3 mean chiasmata per cell. Very little pairing can be observed in crosses between wheat and rye with the 5B-effect suppressed by the *Aegilops speltoides* genome (Riley and Kimber 1966) or by using an induced mutant, in which the *Ph*-gene, the chromosome 5B suppressor of homoeologous pairing, is deleted (Sears 1977; Dhaliwal et al. 1977; Darvey 1979). Thus, so far the most effective procedure to incorporate genes from rye into wheat is the establishment of chromosome substitution and translocation lines. The majority of the seven rye chromosomes are able to compensate for the absence of corresponding homoeologous wheat chromosomes (Gupta 1971; Koller and Zeller 1976). Also several wheat-rye chromosome translocation lines are known.

Translocations involving rye chromosome arm 1RS and wheat chromosome segments of homoeologous group 1 (long arms) were reported by Mettin et al. (1973), Zeller (1973), and Shepherd (1973). The transferred rye segments appear to condition mildew and rust resistance (Zeller 1973; Bartoš et al. 1973), resistance to the wheat curl mite, the vector of the wheat streak mosaic virus (Martin et al. 1976), certain prolamin bands (Shepherd 1973), and a gene for the polypeptide thionin (Sánchez-Monge et al. 1979). Another translocation includes segments of 2AL and 2RL (Sears 1972) and reveals a significant increase in kernel protein content (Jagannath and Bhatia 1972; May and Appels 1978). Using a double monosomic substitution, 2B/2R, May and Appels (1980) selected a line in which the short arm of wheat chromosome 2B had been replaced by the short arm of rye chromosome 2R and another line in which the long arm of 2B had been substituted by the long arm of 2R. A 4A/2R translocation 'Transec' confers resistance to powdery mildew and leaf rust (Driscoll and Jensen 1964; Driscoll 1968) in wheat. Acosta (1961) produced a 3A/3R wheat-rye chromosome translocation (analyzed by Barber et al. 1968) which contains a gene from rye conditioning stem rust resistance (Stewart et al. 1968; Luig and Watson 1976). The long arm of rye chromosome 5R carrying the hairy neck gene was successfully translocated to wheat chromosome 4A (Driscoll and Sears 1965), 5BS (Sears 1967), 6BL (Sears 1973), 5DL (Muramatsu 1968), and 6D (Sears 1967), respectively. Finally a segment of 6RL that carries a gene for the restoration of pollen fertility in *Triticum timopheevii* cytoplasm has been translocated to wheat chromosome 6BS (Tuleen, pers. communication). The

0040-5752/81/0059/0033/$ 1.00

present report deals with the identification of two new translocation lines involving segments of rye chromosomes 4R and 7R.

Material and Methods

Two translocation lines, T8 and T22 were recovered in the progeny of 42-chromosome hybrids 'Chinese Spring' (CS) monosomic 4A X CS/'Imperial' addition line 7R (D), and CS monotelocentric 7BL X CS/'Imperial' addition line 4R (C), resp. Strain T8 was analyzed cytologically by crossing it to CS ditelo-β-monotelo-α-4A, CS ditelo-4Aα, CS/'Imperial' addition lines 7R (21"+1"), 7RS (21"+t"), and 7RL (21"+t"). T22 was crossed with CS double ditelo-7B, CS ditelocentrics 7BS and 7DS and CS/'Imperial' addition line 4RS (21"+t"). Anthers from the plants studied were fixed in acetic-alcohol and stained by the Feulgen procedure.

Results

Cytology of Translocation Line T8

From the cross T8 X CS ditelo-β-monotelo-α-4A and its reciprocal, two types of offspring were obtained: those

Table 1. Chromosome pairing in F_1 hybrids of translocation line T8 with various 'Chinese Spring' aneuploids and 'Chinese Spring'/'Imperial' addition lines

F_1 hybrids	No. of plants	21" + t'	20" + 1" '	20" + t2" '	20" + t1" + t'	20" + t' + t' + 1'	20" + t' + 2'	20" + t' + 1'	20" + t1"	Other
T8 X DT4Aα 2n = 41 + t	5	–	–	–	–	–	–	82	109	–
T8 X DβMTα4A 2n = 41 + t + t	2	–	–	–	41	8	–	–	–	–
DβMTα4A X T8 2n = 41 + t + t	1	–	–	–	28	2	–	–	–	–
DβMTα4A X T8 2n = 41 + t	5	–	–	–	–	–	–	46	–	5[a]
Add. 7R X T8 2n = 43	2	–	16	–	–	–	–	–	–	1[b]
Add. 7RS X T8 2n = 42 + tS	4	–	–	70	21	–	2	–	–	–
Add. 7RL X T8 2n = 42 + tL	3	92	–	–	–	–	22	–	–	2[c]

[a] 19" + t' + 3'
[b] 21" + 1'
[c] 19" + t' + 4'

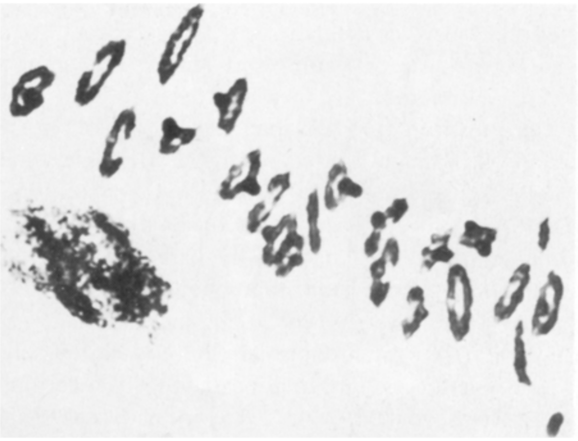

Fig. 1.

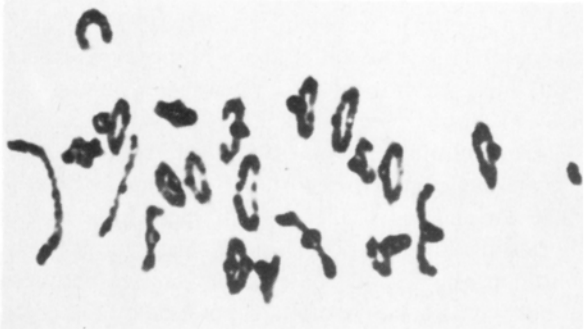

Fig. 2.

Figs. 1 and 2. Metaphase I in PMC's of F_1 hybrids: (1) 'Chinese Spring' di-β-monotelo-α-4A X translocation line T8 (4Aα/7RS) showing 20"+t1"+t'; (2) Translocation line T22 (7BL/4RL) X 'Chinse Spring' ditelocentric 7BS with 20"+t'+1'

Table 2. Chromosome pairing in F_1 hybrids of translocation line T22 with various 'Chinese Spring' aneuploids and 'Chinese Spring'/'Imperial' addition line 4RL

F_1 hybrids	No. of plants	$21'' + t'$	$20'' + t2'''$	$20'' + t' + 1'$	$20'' + t' + 2'$	$20'' + t' + t1''$	$20'' + t1''$	$19'' + 2' + t2'''$	$19'' + t' + 2' + t1''$	$19'' + t' + 3'$	$18'' + 1'''' + t1''$
T22 X DDT7B 2n = 41 + t + t	5	–	–	–	–	81	–	–	5	–	–
T̄22 X DT 7BS 2n = 41 + t	6	–	–	144	–	–	–	–	–	16	–
T22 X DT 7DS 2n = 41 + t	3[a]	–	–	2	–	–	25	–	–	–	14[a]
T22 X Add. 4RL 2n = 42 + tL	7	5	31	–	2	–	–	15	–	–	–

[a] One T22 plant presumably possesses a wheat-wheat chromosomal translocation

with both telocentrics and those with only telo-4Aβ (Table 1). The former showed maximum pairing of $20'' + t'' + t'$ (Fig. 1), while the latter had a maximum of $20''+t'+1'$. In the cross T8 X CS ditelo-4Aα, however, mainly $20'' + t1''$ occured, though $20''+t'+1'$ was nearly as frequent (Table 1). These chromosome configurations indicate that a rye segment replaces most or all of the β-arm of 4A.

In hybrids of T8 with addition line 7R, chromosome configurations of $20''+1'''$ usually occurred. When only the 7RS telocentric was present it mainly formed a monotelosomic trivalent which also included 4A and the translocated chromosome, whereas 7RL, when present, never paired (Table 1). This leads to the conclusion that T8 is a translocation consisting of the complete α-arm of wheat chromosome 4A or a part of it and the entire 7RS arm or a segment of it. The translocation line shows good fertility.

Cytology of Translocation Line T22

In the F_1 plants from the cross CS ditelocentric 7DS x T22, the telosome mainly formed a heteromorphic bivalent (Table 2). Crosses of double ditelocentric 7B with T22 showed most commonly $20''+t1''+t'$, while no pairing of telo-7BS occurred in the F_1 hybrid between ditelocentric 7BS and T22 (Fig. 2). These results indicate that the translocated chromosome includes either an intact 7BL arm or a substantial portion of it.

In the cross between the ditelocentric addition line 4RL and T22, a monotelocentric trivalent involving the translocated chromosome, the complete chromosome 7B and telo-4RL most frequently was formed (Table 2). From this it is concluded that translocation T22 consists of at least part of wheat arm 7BL and rye arm 4RL. The line is vigorous (Fig. 3) and exhibits a fertility of approximately 80%.

Discussion

Several methods have been developed for the transfer of alien variation from related species into common wheat: i) induction of homoeologous chromosome pairing, ii) use of ionizing radiation and iii) exploitation of the tendency of univalent chromosomes to misdivide and form an interchanged chromosome having one entire arm from each of the two parental univalents. It appears that the translocation lines described in this paper resulted through union of newly formed telocentric chromosomes. With a univalent 4A and a univalent 7R present in the cross between CS monosomic-4A and the disomic addition line CS/'Imperial' 7R, two telocentrics were presumably formed in the same daughter nucleus after simultaneous misdivision and united to give rise to the 4Aα/7RS translocation T8 that was recovered in the progeny of the F_1 hybrid.

Available evidence from zymogram phenotypes shows that the segment of rye chromosome 7R which is involved in translocation T8 (4Aα/7RS) is homoeologous to wheat

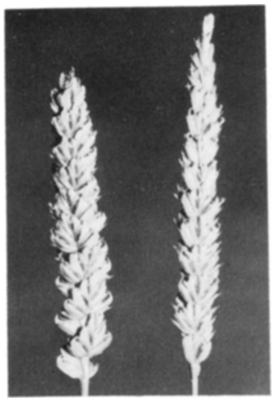

Fig. 3. Spikes of (left) normal wheat 'Chinese Spring' and (right) homozygous translocation line T22 (7BL/4RL)

chromosome arms 4Aβ, 4BS, and 4DL (Hart 1978). Using the disomic wheat-rye addition 7R and the ditelosomic addition lines for each arm of rye chromosome 7R. Hart (1973, 1978; Tang and Hart 1975) located a gene for the isozyme 'acid phosphatase' (ACPH) in the short arm of rye chromosome 7R. The translocation line T8 also expresses the 'Imperial' rye ACPH gene (Hart 1978). In 'Chinese Spring', structural genes for ACPH were found in the wheat chromosome arms 4Aβ, 4BS, and 4DL.

Translocation T22 most likely also arose by union of telocentrics, after misdivision of wheat univalent 7B and rye univalent 4R in the F_1 of the cross between monotelocentric 7BL and CS/'Imperial' addition line 4R. In the translocation, a segment or the entire 7BS wheat chromosome arm was replaced by a segment or the entire rye chromosome arm 4RL. Koller and Zeller (1976) demonstrated that the long arm of rye chromosome 4R is able to compensate for the loss of homoeologous chromosomes of wheat group 7.

Plants of translocation T22 (7BL/4RL) are characterized by red coleoptiles conditioned by a gene for anthocyanin production in the long arm of rye chromosome 4R. Loci for anthocyanin production (red coleoptiles) were also found in the short arms of wheat chromosomes 7B (Law 1966) and 7D (Rowland and Kerber 1974; Sutka 1977). This finding provides evidence of homoeologous genes in the long arm of rye chromosome 4R and the group 7 wheat chromosomes 7BS and 7DS.

The knowledge of homoeologous relationships between wheat and rye chromosomes enables the selection of chromosome translocation lines which arise as the result of the union of telocentrics after univalent misdivision in a double monosomic substitution (one wheat, one rye univalent). Since even in the absence of the 5B-effect in wheat, little or no pairing takes place between wheat and rye chromosomes, to date, incorporation of genetic material from rye into the wheat genome can only be done by the production of substitution lines or by the induction of translocation lines through ionizing irradiation or by union of telocentrics. Although union of misdivided telosomes can occur between homoeologous and non-homoeologous chromosomes (Muramatsu 1968; Sears 1972, 1973; Shepherd 1973), exchange of homoeologous chromosome arms should have less deleterious effects and appear to be more desirable.

The availability of wheat-rye translocation lines and the chromosomal localization of valuable rye genes by means of trisomic lines and gene mapping enables the transfer of rye genes into wheat through homologous crossingover in F_1 hybrids followed by recurrent backcrossing to the translocation line.

In crosses wheat and wheat-rye chromosome addition lines with *Secale cereale* L., *Secale montanum* Guss. and other wild *Secale* species Lelley (1976; Lelley and Larter 1980) and Schlegel and Weryszko (1979) found several alleles in rye that effect homoeologous pairing between wheat chromosomes and wheat and rye chromosomes. It is reasonable to assume that in rye mutants can be found and maintained which permit pairing and gene transfer between wheat and rye chromosomes in appropriate hybrids.

It should also be noted that homoeologous pairing may occur between *Aegilpos squarrosa*, the donor of the wheat D-genome, and rye (Melnyk and Unrau 1959). If recombinants can be recovered after backcrossing to *Aegilops*, gene transfer from rye into wheat by means of synthetic hexaploid amphiploids should also be feasable.

Acknowledgement

'Chinese Spring'/'Imperial' wheat-rye chromosome addition lines and aneuploid Chinese Spring material was kindly supplied by Dr. E.R. Sears, University of Missouri, Columbia (USA)

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Received July 30, 1980
Communicated by R. Riley

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