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Cytogenetical studies in wheat XVI. Chromosome location of a new gene for resistance to leaf rust in a Japanese wheat-rye translocation line *

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Summary

A leaf rust resistant wheat-rye translocation stock, ST-1, introduced from Japan, comprised distinct morphological types. One type possessed a T1BL·1RS chromosome with genes *Lr26, Yr9* and *Sr31*. A second type carried a new gene, *Lr45*, located in a large segment of rye chromosome translocated to wheat chromosome 2A. Its structure was identified as T2AS-2RS·2RL. Despite the homoeology of the 2A and 2R chromosomes and the high level of compensation provided by the translocation, *Lr45* was not normally inherited and is probably associated with agronomic deficiencies that will prevent its exploitation in agriculture.

Introduction

Future breeding of wheat with resistance to diseases such as leaf or brown rust, caused by *Puccinia recondita* f. sp. *tritici*, will depend on the availability of resistance sources likely to be different from those in current use. Because current resistance provides no assurance that resistance, even if claimed to be durable, will be effective in the future, it is essential that alternative sources be available. Relatively few resistance genes in common wheat derived from sources other than hexaploid or tetraploid wheat have been exploited in crop production.

Cereal rye, *Secale cereale*, is one of the species commonly used as donors of disease and pest resistance to wheat. Among the many transfers from rye only two have been widely exploited. In both cases the short arm of chromosome 1R is involved. In certain European wheats and their derivatives, a 1RS rye arm in a T1BL·1RS chromosome carries genes for resistance to leaf rust (*Lr26*), stem rust (*Sr31*), stripe rust (*Yr9*) and possibly powdery mildew (*Pm8*) (Mettin et al., 1973; Zeller, 1973; Heun & Friebe, 1990). In the other case a group of U.S.A. wheats carry a T1AL·1RS chromosome bearing genes on the 1RS arm for resistance to greenbug (*Schizaphis graminum*) (*Gb2*), powdery mildew (*Pm17*) and stem rust (unknown gene) (Zeller & Fuchs, 1983; Friebe et al., 1994c).

Other wheat-rye translocation derivatives have not been successfully exploited either because detrimental agronomic effects associated with the alien chromatin outweigh the advantages of the disease resistance attributes for which they were selected, or insufficient agronomic tests have been conducted for adequate assessment. These derivatives include WRT238, a T3AS-3RS with *Sr27* (Acosta, 1962; G.F. Marais, personal communication; B. Friebe, unpublished), Transec, a T4BS·4BL-5RL translocation with *Lr25* and *Pm7* (Driscoll & Anderson, 1967; Driscoll & Bielig, 1968; Heun & Friebe, 1990; Friebe et al., 1994c), a T6BS·6RL derivative with *Pm20* (Friebe et al., 1994a), and several lines with resistance to hessian fly, including Hamlet, a T2BS·2RL derivative with *H21* (Friebe et al., 1990; Sears et al., 1992), and T6BS·6BL-6RL, T4BS·4BL-6RL and Ti4AS·4AL-6RL-4AL (Ti = intercalary translocation) chromo-

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somes with *H25* (Friebe et al., 1991a; Mukai et al., 1993).

Mukade et al. (1970) reported the production of wheat-rye transfers with leaf rust resistance by spontaneous and X-irradiation-induced translocations. This paper reports a cytogenetic analysis of the line ST-1 selected in that study.

Materials and methods

Three wheat lines with leaf rust resistance derived from cereal rye cultivar Petkus were kindly provided to one of the authors (McIntosh) by Dr. K. Mukade in 1975, together with the wheat parents, Norin 40 and Aobakomugi. The derivatives included the putative spontaneous translocation stock ST-1 (Mukade et al., 1970), a monosomic addition line (2n = 43) and a disomic addition line (2n = 44). Preliminary studies showed that the monosomic addition line segregated for seedling resistance to leaf rust with the added chromosome being responsible for resistance and the other two lines were homozygous resistant with the expected chromosome numbers.

Monosomic analysis. ST-1 was crossed to the Chinese Spring set of monosomic lines. When the monosomic F_1 hybrids were grown in a rust-infected nursery it was noted that they were morphologically variable and also differed in response to stem rust. Resistant hybrids had compact spikes whereas susceptible hybrids had lax spikes. Closer examination of ST-1 revealed three plant types, two with compact spikes, and stem rust resistance but differing in the degree of awning, and one with lax spikes and stem rust susceptible. Cytological studies and tests with stem rust and leaf rust revealed that the first two types comprised a substitution of chromosome 1B with an entire 1R chromosome (awned spikes), and a T1BL·1RS translocation line (non-awned). Because the lines were derived from Petkus rye and were susceptible with a *P. recondita tritici* pathotype that was virulent for *Lr26* it was assumed that the T1BL·1RS source duplicated similar materials available from Europe. The stem rust susceptible component was clearly different and subsequent work was directed to it.

When the Norin 40 parent of ST-1 and the other lines were grown in the rust nursery it was resistant to stem rust but susceptible to leaf rust. It has been shown to possess a unique gene for resistance to stem rust (R.A. McIntosh, unpublished).

Further crosses of the stem rust susceptible component of ST-1 were made to the Chinese Spring monosomics in order to complete the series (Table 1). The lines used at Kansas State University comprised various backcross derivatives of the stem rust susceptible ST-1 selection, viz. 95606 (ST-1/4*XL23), 10321 (ST-1/6*Condor), 22627 (ST-1/6*Teal) and RL6144 (Thatcher*6/ST-1).

Leaf rust tests. F_2 and F_3 seedling populations derived from monosomic F_1 plants were tested with *P. recondita tritici* pathotypes 26-1,3 (PBI Cobbitty, Culture 67028) and/or pt 104-2,3,6,(7) (76694). The same gene was involved in resistance to both cultures.

Cytogenetic analyses. For chromosome identification the C-banding protocol of Gill et al. (1991) was followed. For genomic *in situ* hybridization (GISH), total genomic DNA of *S. cereale* was labeled with biotin-11-dUTP (uridine 5'-triphosphate) by nick translocation following the manufacturer's instruction (Enzo Diagnostics, Farmingdale, New York). Sheared wheat genomic DNA was added in excess (150–200 : 1) to the hybridization solution to block cross hybridization of the probe to the wheat chromosomes. Signal detection with horseradish peroxidase-conjugated streptavidin and diaminobenzidine tetrahydrochloride was as described by Rayburn & Gill (1985). For fluorescence *in situ* hybridization (FISH) analysis, FITC-conjugated avidin (Boehringer, Mannheim) was used for detecting the biotin-labeled rye probe.

Chromosome measurements were taken on 10 wheat-rye translocation chromosomes of the ST-1 derivatives after banding and GISH to determine the position of translocation breakpoint. These were calculated as fractions of total chromosome arm length from the centromere (FL). For ST-1 a compensation index (CI) was calculated from the length of the missing wheat segment as a percentage of the corresponding wheat chromosome arm divided by the length of the transferred rye segment as a percentage of the corresponding rye arm (Friebe et al., 1994a). Photographs were taken with a Zeiss photomicroscope III using Kodak Imagelink HQ microfilm 1461 for C-banded chromosomes and with an Olympus BH-2 photomicroscope using Kodak technical Pan film 2415 and Ektachrome 20 after GISH.

Table 1. Segregation of responses to leaf rust in F_2 populations from F_1 monosomics from crosses of the Chinese Spring monosomics and ST-1 selection

Chromosome	Resistant	Susceptible	Ratio Res : Sus
1A	79	24	3.29
2A	66 (+ 65)[1]	17 (+ 15)[1]	3.88
3A	44	17	2.59
4A	28	11	2.55
5A	59	30	1.97
6A	29	14	2.07
7A	32	15	2.13
1B	37	15	2.47
2B	32	17	1.89
3B	34	11	3.09
4B	63	32	1.97
5B	37	24	1.54
6B	77	40	1.93
7B	104	49	2.12
1D	74	25	2.96
2D	25	21	1.19
3D	43	13	3.30
4D	32	23	1.39
5D	29	18	1.61
6D	31	13	2.38
7D	64	35	1.83
Total Exc 2A[2]	953	447	2.13

[1] Data from Table 2.
[2] $\chi^2_{3:1} = 35.8$; $P < 0.01$.

Table 2. Association of leaf rust reaction and somatic chromosome number in pooled F_2 progenies from monosomic F_1 plants of the cross between Chinese Spring Mono-2A and ST-1

2n =	Resistant (X- to X)[1]	Intermediate (X+ to X++)	Susceptible (3 + 4)	Total
42	10	6	–	16
41	8	37	4	49
40	–	–	8	8
Subtotal	18	43	12	73
Others				
$41 + t^l + t^s$	1			1
$40 + t^l$		2	1	3
$40 + t^s$			1	1
$40 + 2t^l$			1	1
$41 + t^l$		1		1
Total	19	46	15	80

[1] Infection types on a scale of 0 to 4 with X indicating mesothetic response and -, + indicating relative degrees of sporulation.

Results

Monosomic analysis of the stem rust susceptible selection of ST-1. The F_2 segregations of leaf rust response for progenies of monosomic F_1 plants are given in Table 1. The data were obtained in a series of different experiments and were not produced with a common *P. recondita* culture (see Materials and methods). By 1992 all chromosomes had been assayed, except for 2A and 1D. Field observations of ST-1 derived material in 1992 led to the prediction that the chromosome bearing the resistance gene was 2A (see below).

It is clear from the data that resistance was not inherited normally for a single gene; there was a consistent excess of susceptible relative to resistant segregates. Excluding the result for chromosome 2A, the ratio of pooled resistant : susceptible seedlings was 2.13 : 1 (χ^2 contingency table = 19.86; $P_{19 d.f.} > 0.3$). Because of failure to locate the resistance gene when the majority of chromosomes had been assayed, random F_2 plants from 18 segregating populations were progeny tested. The pooled F_2 genotypic segregation was 51 homozygous resistant: 151 segregating: 100 homozygous susceptible, confirming the reduced gametic transmission of the resistant allele ($\chi^2_{1:2:1} = 73.2$; $P < 0.01$). However, the F_2 plants were previously classified, so the data were not independent of the F_2 results. Because F_2 plants with resistant, intermediate and susceptible responses were identified, the F_3 results confirmed that the resistance gene was incompletely dominant and that resistant and susceptible individuals were usually correctly phenotyped.

The most deviant F_2 segregation for the monosomic populations was 2A. In this case, eight of the susceptible segregates showed phenotypes consistent with nullisomy for chromosome 2A whereas the other nine were more normal in appearance. These plants may have been secondary aneuploids or outcrosses because the F_1 plants were not bagged to enforce self-pollination.

In a separate experiment, progenies of two monosomic 2A hybrids were subjected to somatic chromosome counts and to seedling leaf rust tests. The results are summarized in Table 2. In this experiment, infection types for individual seedlings were recorded and plants were grouped into three response groups assuming incomplete dominance of resistance. The most resistant plants tended to have 2n = 42, plants with intermediate responses were predominantly 2n = 41 and all 8 plants scored as 2n = 40 were susceptible. These results demonstrated a high probability that

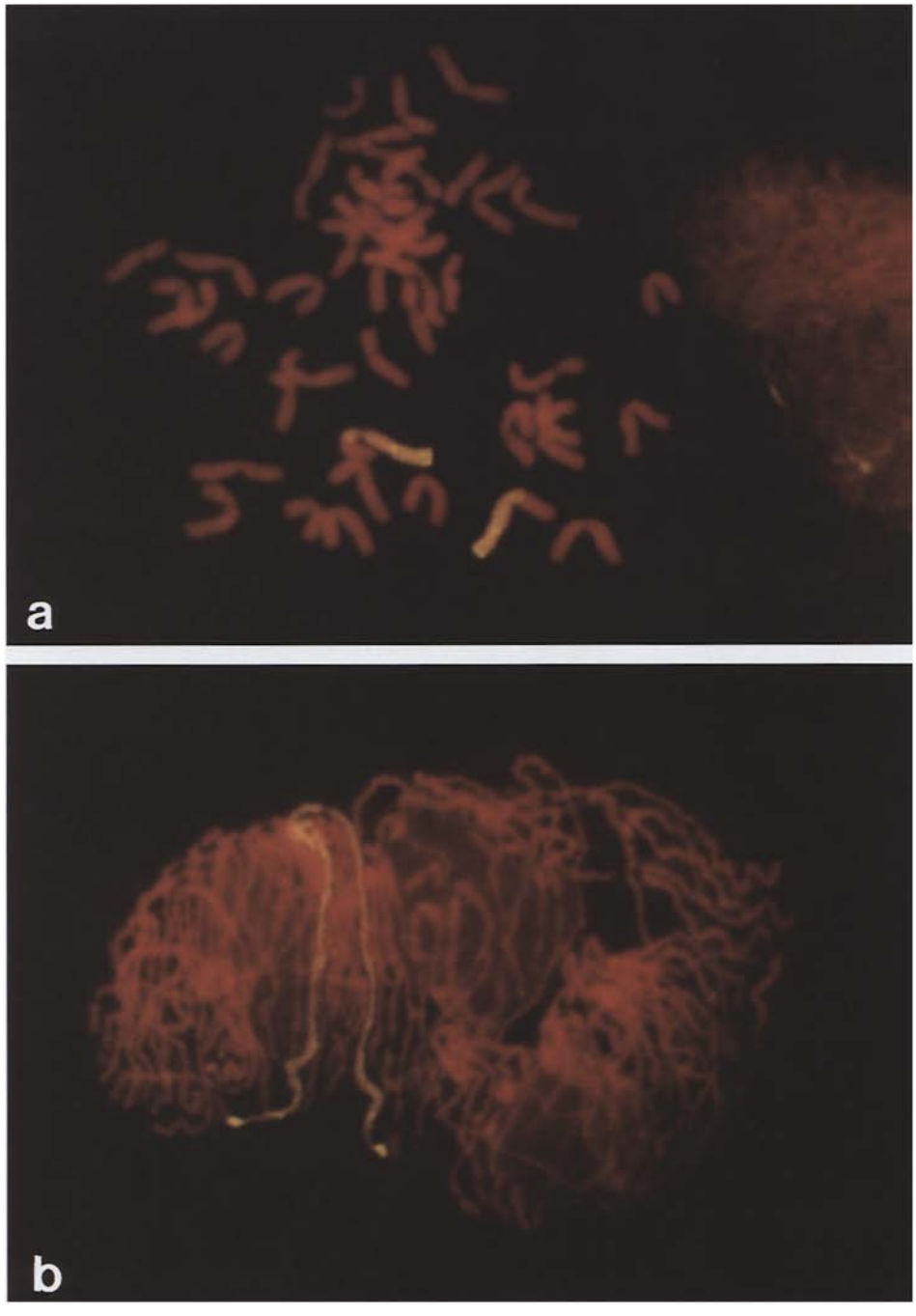

Fig. 1. (*a.*) Fluorescence *in situ* hybridization (FISH) of an entire mitotic metaphase cell of an ST-1 derivative. The rye chromosome segment is clearly distinguished from the wheat segment. Note the darkly staining telomeric region of chromosome 2R. (*b.*) A FISH image of a mitotic prophase cell of the same plant showing the rye chromosome segment, again with the more intensely staining telomeric regions.

the resistance gene was present in chromosome 2A. A number of plants possessed telosomic chromosomes that were of distinct types, long and short. In addition, a similar frequency of isochromosomes that would not be detected by the Feulgen staining method, can also be assumed. Such misdivision products and their somatic loss following chromosome counting as well as outcrossing of the original F_1 plants could contribute to

the discrepant results in Table 2, especially the 4 susceptible seedlings scored as 2n = 41. When the rust response results were presented in the same form as in Table 1 (in parenthesis, Table 1) the frequencies of resistant and susceptible seedlings were very similar to those obtained earlier.

Anthocyanin pigmentation of glumes and anthers. While the cytogenetic studies were in progress, the stem rust susceptible selections of ST-1 were used as a source of leaf rust resistance in an Australian germplasm enhancement program. All backcross derivatives were characterized by a distinct purple pigmentation of glumes and anthers following extrusion and pollen shedding. In 1991 ST-1 derived material was grown next to some Chinese Spring-Imperial rye 2R-derived chromosome addition lines from Dr. E.R. Sears. The latter lines showed similar, but less obvious purple colouring to the ST-1 derived material. A postulation was made that a 2R-derived gene in ST-1 was located in chromosome 2A, one of two chromosomes untested at that time. A similar form of glume pigmentation occurs in the wheat cultivar Hamlet (R.G. Sears, personal communication) which possesses a T2BS·2RL (Friebe et al., 1990).

According to Melz et al. (1992) genes *An1* (Anthocyanin) and *An3* (purple seeds) are located in chromosome 2R but the relationship of the phenotype observed here to *An1* is not known.

C-banding and in situ *hybridization.* GISH analysis showed that the ST-1 derived lines were either homozygous (10321, 22627, RL6144) or segregating (95606) for a wheat-rye translocation chromosome (Fig. 1a). The labeling pattern of this chromosome indicated that the complete long arm and the proximal 39% of the short arm were derived from rye (Table 3). The telomere of the long arm showed a strong hybridization signal compared to the rest of the translocated rye chromatin. This stronger signal was detected in metaphase chromosomes as well as all other nuclear stages (Fig. 1a, b).

C-banding analysis revealed that lines 10321, 22627 and RL6144 were lacking wheat chromosome 2A and were homozygous for a wheat-rye translocation chromosome, whereas line 95605 showed segregation for the translocation chromosome and 2A of wheat. The translocated chromosome has proximal, telomeric and a subtelomeric C-bands in the long arm (Fig. 2). This pattern is diagnostic for rye chromosome 2R. The intense hybridization signal at the telomere of the long arm corresponds to the telomeric C-band and reflects the presence of highly repetitive DNA sequences in this region. The short arm of the translocation chromosome has only a subtelomeric C-band similar in size and position to a C-band of wheat chromosome 2A (Fig. 2). Combining the GISH and C-banding patterns identifies the translocation chromosome as T2AS-2RS·2RL.

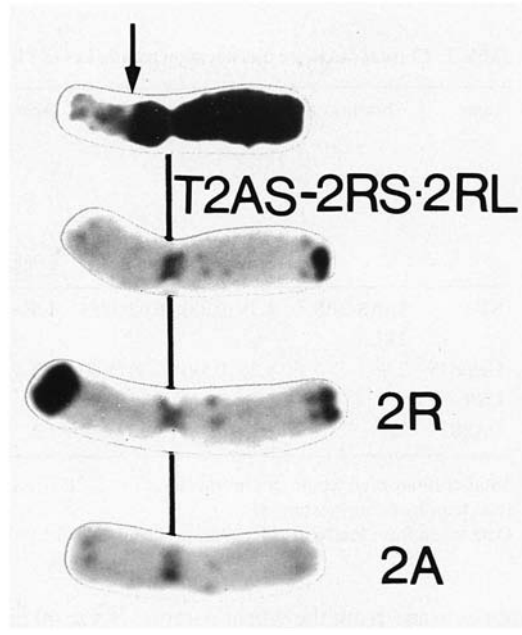

Fig. 2. C-banding of chromosomes 2A (bottom), 2R and T2AS-2RS·2RL. The genomic *in situ* hybridization (GISH) of the translocation chromosome is shown at the top with the breakpoint arrowed.

The relative arm lengths of the translocation chromosome in ST-1 backcross derivatives are compared with those of chromosomes 2A and 2R in Table 3. The Compensation Index of 1.06 for the translocation chromosome indicated a close relationship between the deleted wheat chromatin and the rye chromatin with which it was replaced.

Discussion

The line originally introduced to Australia as ST-1, and possibly mixed at the time of introduction, consisted of three morphological sublines shown to comprise a 1R(1B) substitution component, a T1BL·1RS component and a line with a T2AS-2RS·2RL chromosome. The latter line was selected for further study because it appeared to possess a unique gene for leaf rust resistance and was morphologically distinct from the other

Table 3. Chromosome and translocation parameters in ST-1 derivatives

Line	Chromosome	Arm length (SD)		Arm ratio	Fraction Length of of trans-location breakpoint	Rye segment (% of the corresponding rye arm)	Missing wheat segment (% of the corresponding wheat arm)	Compensation index
		μm						
		Short	Long	Long/short		μm	μm	
ST-1	T2AS-2RS 2RL	4.39 (0.33)	6.02 (0.54)	1.4	0.39	1.71 (35%)	1.58 (37%)	1.06
Heine IV CS/I	2A[1]	4.26 (0.59)	5.36 (1.00)	1.3				
DA2R	2R[2]	4.87 (0.53)	5.90 (0.49)	1.2				

Total chromosome length of chromosome T2AS-2RS·2RL, 2A and 2R correspond to 96%, 85%, and 104%, respectively, of the total length of chromosome 3B.
Data taken from Friebe et al. (1992)[1] and Mukai et al. (1992)[2].

components and from the wheat parents, Norin 40 and Aobakomugi.

Mukade et al. (1970) reported the production of translocation lines by two methods, namely X-irradiation and spontaneous translocation. The line derived by the latter method was, in fact, designated ST-1. This line was also a direct derivative of Norin 40 wheat. We conclude that the component identified above as a T1BL·1RS chromosome is the line originally designated ST-1.

Mukade et al. (1970) also reported evidence of an undefined translocation from the irradiation experiment. This line had been crossed with Aobakomugi and was therefore likely to be morphologically different from the line based on Norin 40. We conclude that the component with T2AS-2RS·2RL was derived from the irradiaton experiment and that two different rye chromosomes with resistance to leaf rust must have been derived from Petkus rye.

The gene present in the T2AS-2RS·2RL chromosome appears to be a new gene for wheat. It is therefore designated *Lr45*. It confers resistance to almost all of the *P. recondita tritici* cultures with which it has been tested. P.L. Dyck (personal communication) observed that a line with *Lr45* was susceptible to a culture that was also virulent for *Lr25* which was derived from cereal rye. *Lr25* is presumed to be located in a non-compensating T4BS·4BL-5RL chromosome (Heun & Friebe, 1990; Friebe et al., 1994c) rather than a T4BS-2R chromosome as implied by Driscoll & Anderson (1967) on the basis of genetic compensation of the putative source rye telosome for chromosome 2BL of wheat. The fact that *Lr45* and *Lr25* are located in segments from different rye chromosomes makes it highly unlikely that they can be the same gene. Inheritance studies indicated that *Lr45* was transmitted to progeny at less than the normal rate. This is not unusual, even for well compensated translocation chromosomes (Koebner & Shepherd, 1986; McIntosh, unpublished).

Although the postulation that *Lr45* was located in chromosome 2A was made prior to C-banding and GISH determinations, it is clear that these techniques would have achieved the same result much more quickly. Additionally, they provided accurate positioning of the translocation breakpoint in 2AS and permitted calculation of a Compensation Index (Friebe et al., 1994b) of 1.06. When homoeologous chromosomes are involved, a CI value approaching unity indicates that the missing wheat chromatin should be compensated by an equivalent segment from rye, provided the related chromosomes have conserved synteny.

The location of *Lr45* within the rye segment is unknown. Although telocentric chromosomes tentatively described as long and short were identified among F_2 individuals used for monosomic analysis (Table 2), the leaf rust infection type data gave ambivalent results. Provided seed can be recovered from plants with telocentric chromosomes, chromosome analysis and rust reactions of the progenies should permit identification of the chromosome arm bearing *Lr45*. With this information it may be possible to design a strategy to reduce the size of the rye segment by induced homoeologous pairing.

Devos et al. (1993) showed that the cereal rye genome had accumulated a complex series of translocation differences relative to wheat. They further sug-

gested that as a consequence, these effectively chimeric chromosomes relative to wheat were greatly reduced in ability to undergo recombination with wheat chromosomes even in the absence of inhibitors of chromosome pairing, and that when exchanges did occur between homoeologous rye and wheat chromosomes, they were likely to show poor compensation. They noted the close genetic co-linearity of chromosome 1R and group 1 wheat chromosomes in relation to their obviously successful compensation abilities. Their rye map also showed a largely conserved 2R chromosome relative to group 2 chromosomes of wheat with only the distal portion of 2RS being involved in a translocation. This information is consistent with the relatively normal appearance of ST-1 and various backcross-derived lines with the T2AS-2RS·2RL chromosome. However, derivatives were not retained when provided as enhanced germplasm to Australian wheat breeders. The large size of the rye segment presumably introduces sufficient non-wheat characteristics to prevent exploitation of this translocation as a source of leaf rust resistance in wheat.

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