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Linkage mapping of genes for resistance to leaf, stem and stripe rusts and ω-secalins on the short arm of rye chromosome 1R

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Summary. The genes controlling resistance to three wheat rusts, viz., leaf rust (*Lr26*), stem rust (*Sr31*) and stripe or yellow rust (*Yr9*), and ω-secalins (*Sec1*), located on the short arm of rye chromosome 1R, were mapped with respect to each other and the centromere. Analysis of 214 seeds (or families derived from them) from test-crosses between a 1BL.1RS/1R heterozygote and 'Chinese Spring' ditelocentric 1BL showed no recombination between the genes for resistance to the three rusts, suggesting very tight linkage or perhaps a single complex locus conferring resistance to the three rusts. The rust resistance genes were located 5.4 ± 1.7 cM from the *Sec1* locus, which in turn was located 26.1 ± 4.3 cM from the centromere; the gene order being centromere – *Sec1* – *Lr26/Sr31/Yr9* – telomere. In a second test-cross, using a different 1BL.1RS translocation which had only stem rust resistance (*SrR*), the above gene order was confirmed despite a very large proportion of aneuploids (45.8%) among the progeny. Furthermore, a map distance of 16.0 ± 4.8 cM was estimated for *SrR* and the telomeric heterochromatin (C-band) on 1RS. These results suggest that a very small segment of 1RS chromatin is required to maintain resistance to all three wheat rusts. It should be possible but difficult to separate the rust resistance genes from the secalin gene(s), which are thought to contribute to dough stickiness of wheat-rye translocation lines carrying 1RS.

Key words: Rye – Secalins – Rust resistance – Stem rust – Leaf rust – Stripe/yellow rust – Linkage mapping

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Introduction

The short arm of chromosome 1R of cereal rye (*Secale cereale*) carries a number of genes of agronomic importance, and when transferred to wheat in the form of 1BL.1RS and 1AL.1RS translocations has resulted in some valuable new cultivars. For example, the highly successful 'Veery' lines developed at CIMMYT (Rajaram et al. 1983) were derived from cv 'Kavkaz', which carries chromosome arm 1RS from 'Petkus' rye as a 1BL.1RS translocation (Mettin et al. 1973; Zeller 1973). This rye arm carries genes conferring resistance to leaf, stem and stripe rusts and powdery mildew, described as *Lr26, Sr31, Yr9* and *Pm8*, respectively (McIntosh 1988), but the exact location and linkage relationships of these genes is not known. Another wheat, cv 'Amigo', possesses a 1AL.1RS translocation, and the rye arm in this line is thought to be responsible for the resistance of this cultivar to greenbug (*Schizaphis graminum*), powdery mildew and stem rust (Wood et al. 1974; Lowry et al. 1981; Zeller and Fuchs 1983). Due to their disease and pest resistance and high yielding potential, these translocation lines have been used widely in breeding programs around the world, and many cultivars have been released. However, in contrast to their desirable agronomic traits, wheats carrying these translocations generally produce a flour with serious quality defects (Zeller et al. 1982; Dhaliwal et al. 1987). In particular, doughs derived from them often show marked stickiness, reduced dough strength and intolerance to overmixing, and this has seriously limited their use in those countries where leavened bread is the main end-product of the flour.

Some other translocation lines involving 1RS of 'Imperial' rye have also been isolated, including a 1AL.1RS translocation in 'Chinese Spring' (CS) wheat background (Singh and Shepherd 1988b), a 1BL.1RS translocation in

'Gabo' wheat background (Koebner and Shepherd, 1986) and a 1DL.1RS translocation in 'CS' background (Shepherd 1973). These translocations confer resistance to all Australian strains of the stem rust pathogen, but are susceptible to leaf rust, stripe rust and powdery mildew. The last two have been transferred to several Australian wheat cultivars by backcrossing, and extensive yield and quality testing has revealed that while the 1BL.1RS lines are generally better than the 1DL.1RS lines, both have quality defects similar to those observed with the 1BL.1RS translocations derived from 'Petkus' rye (Shepherd and Singh 1984).

Recently a program was carried out to reduce the amount of rye chromatin in these translocations by induction of homoeologous pairing (allosyndesis) between 1RS and short arms of group 1 wheat chromosomes, with the aim of separating the quality defects from the stem rust resistance gene (Koebner and Shepherd 1986, 1988). Similar attempts are now being made to recombine the rye arm in the 'Veery' lines to separate the sticky dough problem from the disease resistance and high yield associated with this particular 1BL.1RS translocation derived from 'Petkus' rye (Shepherd, unpublished). However, both of these programs have been impeded by the lack of information on the linkage relationships between these genes and the other gene markers located on 1RS. In particular, we need to ascertain whether the several disease resistance genes occur in a tightly linked cluster or are dispersed along the entire chromosome arm. Also, it is important to know the degree of linkage between these genes and the *Sec1* locus since the presence of secalins is postulated to be one of the main causes of the quality defects in wheats with these translocations (Dhaliwal et al. 1987). Although *Sec1* has been mapped with respect to the *Pgd-2, Sec3 (Glu-R1), Gpi-R1* and *Nor-R1* genes located on chromosome 1R (Shewry et al. 1984; Lawrence and Appels 1986), its linkage relationship with the rust resistance genes is not known.

Lawrence (1969) substituted chromosome 1R of 'King II' rye for wheat chromosome 1B in a mixed 'CS/Holdfast' background. Recently we found that this rye chromosome does not confer resistance to any of the rust diseases and moreover it carries a recognizably different allele at the *Sec1* locus. Thus, it was possible to carry out mapping studies with these genes using a translocation mapping method developed earlier for mapping genes for high-molecular-weight (HMW) glutelin subunits on the long arm of 1R (Singh and Shepherd 1984). In the present paper we report the results of these mapping experiments and provide data on the linkage relationships between genes controlling ω-secalins and resistance to leaf, stem and stripe rusts of wheat, and their map position with respect to the centromere and telomeric heterochromatin on 1RS.

Materials and methods

1. Genetic stocks

Two different wheat-rye translocation lines involving 1RS from (i) 'Petkus' rye (Egret/Kavkaz 1BL.1RS) and (ii) 'Imperial' rye (Gabo 1BL.1RS, Koebner and Shepherd 1986) were used as one parent, and a wheat-rye substitution line with 1R from 'King II' rye (CS/Holdfast 1R(1B), Lawrence 1969) was used as the other parent to produce two kinds of F_1 heterozygotes. Test-cross seeds were produced using CS ditelocentric (Dt) lines 1BL or 1BS (Sears and Sears 1978) as the third parent. All of these stocks are maintained at the Waite Agricultural Research Institute.

2. Crossing scheme

The translocation mapping procedure used was similar to that described earlier by Singh and Shepherd (1984) to map genes on rye chromosome arm 1RL. Two test-cross populations were produced using the crossing scheme shown in Fig. 1.

3. Electrophoresis

Endosperm halves of individual test-cross seeds were analyzed for secalins and HMW glutelin subunits by sodium dodecyl sulphate-polyacrylamide gel electrophoresis (SDS-PAGE) as described earlier (Singh and Shepherd 1985), except that the separating gel contained 10% acrylamide with 2% cross-linker (bisacrylamide to acrylamide ratio). To improve the resolution of the secalin bands, proteins were extracted from the crushed endosperm halves of the test-cross seeds with an ethanol (60%, v/v)-sucrose (20%, w/v) mixture at 25°C (Singh and Shepherd 1988 b) without the addition of a reducing agent. Subsequently, the endosperm residue was treated with SDS-PAGE sample buffer containing 4% SDS and 2% 2-mercaptoethanol to extract the HMW glutelin subunits.

4. Rust testing

The relationship between *Lr26, Sr31* and *Yr9* was determined by disease tests on the progeny (test-cross F_2) of individual plants from test-cross 1. Separate plantings of 16–20 seedlings derived from each test-cross plant were inoculated with avirulent cultures of the respective pathogens from the University of Sydney culture collection, viz., *Puccinia recondita* f.sp. *tritici*, culture 76694 (strain 104-2,3,6(7)), *P. graminis* f.sp. *tritici*, culture 74-L1 (34-1,2,3,4,5,6,7) and *P. striiformis* f.sp. *tritici*, culture 831917 (strain 108 E141 A+). Seedlings within lines were scored either resistant or susceptible. In a few instances where the results for two pathogens appeared to differ, the tests were repeated in order to sample an increased number of plants. In some cases, families were grown to maturity and the progeny tested.

With test-cross 2, the embryos of the test-cross seeds were germinated and the seedlings subsequently inoculated at the Waite Institute with stem rust strain 343-1,2,3,4,5,6 to determine their rust reactions. The rust reactions of euploid test-cross plants were verified by progeny testing.

5. Cytology

To determine the extent of pairing between the homologous 1RS arms from different sources, pollen mother cells (PMCs) from the F_1 heterozygotes were analyzed. PMCs were taken from anthers of the same F_1 plants that were used to produce the test-cross seeds, and were analyzed at both metaphase I and diakinesis to estimate the frequency of desynapsis (precocious terminalization of chiasmata). Individual anthers at the required stage of meiosis were fixed in 3 parts absolute ethanol: 1 part

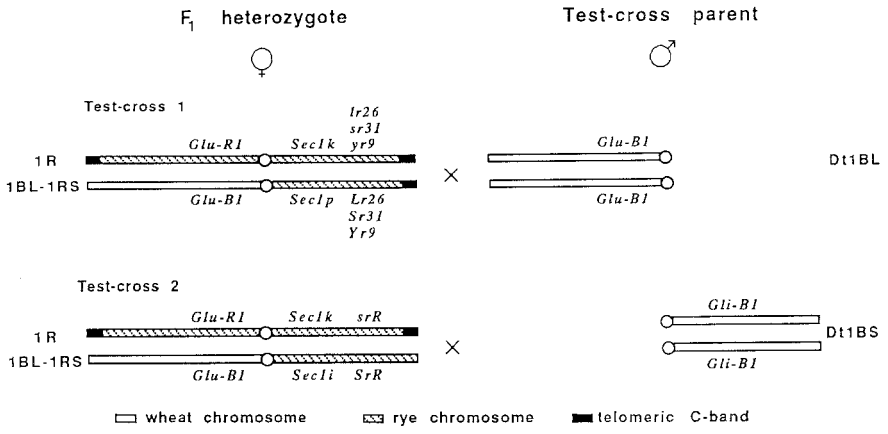

Fig. 1. Crossing procedures for mapping genes controlling resistance to leaf (*Lr26*), stem (*Sr31*, *SrR*) and stripe (*Yr9*) rusts and ω-secalins (*Sec1*) on the short arm of rye chromosome 1R, with respect to centromere and telomeric heterochromatin (C-band). *Test-cross 1*: [CS/Holdfast 1R(1B) × Egret/Kavkaz 1BL.1RS] × CS DT 1BL. *Test-cross 2*: [CS/Holdfast 1R(1B) × Gabo 1BL.1RS] × CS Dt 1BS; CS = 'Chinese Spring'

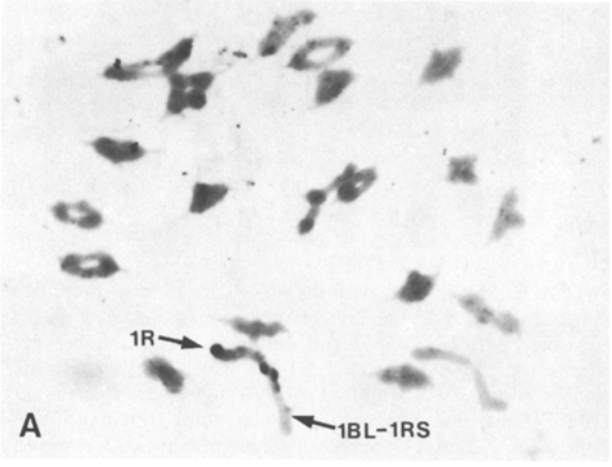

Fig. 2 A, B. C-banded squash preparations of pollen mother cells at metaphase I from the F_1 heterozygote ['Chinese Spring'/ Holdfast 1R(1B) × Egret/Kavkaz 1BL.1RS] used to map genes on chromosome arm 1RS. **A** Cell showing a 1R/1BL.1RS bivalent; **B** cell showing 1R and 1BL.1RS univalents

glacial acetic acid for 30 min to 2 h before making squash preparations and staining with a C-banding procedure modified from Vosa and Marchi (1972).

The embryo halves of seeds from test-cross 2 [Gabo 1BL.1RS × CS/Holdfast 1R(1B)] × CS Dt1BS were germinated to determine the number of large heterochromatic dots (rye telomeres) in the interphase nuclei of root-tip cells using the C-banding procedure of Koebner and Shepherd (1985). Since both arms of 1R from 'King II' rye have prominent telomeric heterochromatin (Fig. 2B and Singh and Shepherd 1984) and 'Imperial' 1RS has none, the joint segregation pattern of these dots with the other markers in the test-cross progeny provided information on their mutual linkage relationships.

Results and discussion

1. *Cytological analysis of F_1 heterozygotes*

Chromosome 1R of 'King II' rye [in CS/Holdfast 1R(1B)] and the 1RS arm of 'Petkus' rye (in Egret/ Kavkaz 1BL.1RS translocation) were easily distinguished from the wheat chromosomes by the presence of prominent telomeric C-bands on each of the rye chromosome arms in test-cross 1 (Figs. 1 and 2). Although the 1BL.1RS chromosome in test-cross 2 was not easily distinguished because of the absence of a major C-band on 1RS from 'Imperial' rye, the frequency of its pairing with the readily identifiable 1R from 'King II' rye could be determined. There was an almost sixfold difference in the degree of metaphase I pairing shown by 1R of 'King II' rye with the 1BL.1RS of 'Petkus' origin as compared with the 1BL.1RS of 'Imperial' origin (Table 1). The increased pairing with 'Petkus' 1RS may be due to homozygosity for the telomeric heterochromatin (C-band) in this cross (test-cross 1) as compared to its heterozygosity in test-cross 2 (Benavente and Orellana 1989). The frequency of pairing between the rye chromosomes was higher at diakinesis in both the crosses, indicating that a significant level of desynapsis was occurring. However, the level of desynapsis in test-cross 2 was much higher than in test-cross 1. As expected, the rye chromosome arms 1RS and 1RL did not pair with any of the wheat chromosomes.

The effect of metaphase univalents and the resultant aneuploidy in test-cross populations on the estimates of map distance has been discussed in detail elsewhere

Table 1. Frequency of pairing in PMCs at diakinesis and metaphase I between complete chromosome 1R, derived from 'King II' rye, and homologous 1RS arms present in two different 1BL.1RS translocations

F_1 heterozygote	Meiotic stage	No. of PMCs	No. with 1R paired	% pairing
CS/Holdfast 1R (1B) × Egret/Kavkaz 1BL.1RS[a]	Diakinesis	22	20	90.9
	Metaphase I	251	163	64.2
CS/Holdfast 1R (1B) × Gabo 1BL.1RS[b]	Diakinesis	98	67	68.4
	Metaphase I	381	39	10.2

PMCs, Pollen mother cells
[a] 1RS from 'Petkus' rye
[b] 1RS from 'Imperial' rye

(Singh and Shepherd 1984, 1988 a). Based on these earlier studies we conclude that the level of pairing in test-cross 1 was sufficient to provide accurate estimates of map distances, provided that the aneuploids could be distinguished and eliminated from the analysis. Although the low level of metaphase I pairing in test-cross 2 (10.2%) almost certainly resulted in underestimation of map distances, the gene order could still be determined from this cross.

2. Gene mapping

Test-cross 1. Due to the lack of pairing between wheat and rye chromosomes the genes located on the long arms of 1R and 1B (e.g., *Glu-R1* and *Glu-B1*, coding for HMW glutelin subunits, Fig. 1) acted as markers for the centromeres. Thus, it was possible to estimate the map distances of *Sec1, Lr26, Yr9* and *Sr31* genes from the centromere. The HMW subunits (Glu-R1 and Glu-B1) and the ω-secalins (Sec1p and Sec1k) were easily distinguished in the parents (Fig. 3 A, B, tracks a, b). Similarly, the *Lr26, Yr9* and *Sr31* genes on 'Petkus' 1RS provided clear-cut resistance to the respective pathogens, whereas plants carrying 1RS from 'King II' were fully susceptible and were assumed to have the recessive alleles *lr26*, *yr9* and *sr31*. Since the test-cross parent CS Dt1BL lacked all of the rye genes, the segregation of all the genes under study could be reliably determined in the test-cross progeny. However, due to overlapping bands, the presence or absence of ω-secalin Sec1p could not be ascertained in those test-cross progeny possessing Sec1k protein. In such instances the Sec1 phenotype was determined by progeny testing. The inheritance of the *Glu-B1* gene through the female gamete was determined on the basis of a much increased staining intensity of the Glu-B1 band (3 doses vs, 1 dose) because the test-cross parent (CS Dt1BL) always contributed one dose of *Glu-B1*. Howev-

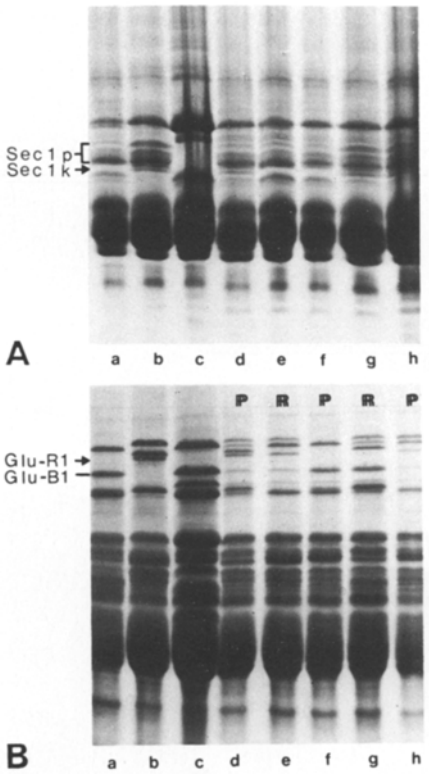

Fig. 3 A, B. SDS-PAGE patterns of seed protein extracts from the parental (*a*, *b*, *c*) and five of the test-cross progeny used to map the *Sec1*, *Lr26*, *Sr31* and *Yr9* genes. **A** Unreduced prolamins (ethanol-sucrose extracts): *a* Egret/Kavkaz 1BL.1RS translocation, *b* CS/Holdfast 1R(1B) substitution, *c* CS DT 1BL, *d–h* test cross progeny; **B** reduced total proteins from the same seeds used in **A**. *P* parental, *R* recombinant with respect to the Glu-1 and Sec1 classifications. CS = 'Chinese Spring'

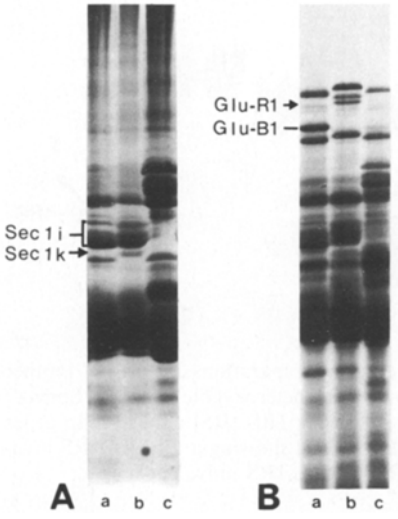

Fig. 4 A, B. SDS-PAGE patterns of seed protein extracts from the parental lines (*a*, *b*, *c*) used to produce test-cross progeny for mapping *Sec1* and *SrR* genes with respect to the centromere, a telomeric C-band and each other. **A** Unreduced prolamins (ethanol-sucrose extracts): *a* 'Gabo' 1BL.1RS translocation, *b* CS/Holdfast 1R(1B) substitution, *c* CS Dt 1BS; **B** reduced total proteins from the same seeds in **A**. CS = 'Chinese Spring'

Table 2. Protein and rust resistance phenotypes and their frequencies in the test-cross progeny used to map *Sec1*, *Lr26*, *Sr31* and *Yr9* genes

Progeny class	Protein phenotypes		Reaction to rusts[a]	No. of progeny	Recombination p (%)[b]	Map distance (cM)
	Glu-1	Sec1				
Parentals						
	B1i	p	R	60		
	R1k	k	S	60		
Recombinants						
c.o. region 1[c]						
	B1i	k	S	18		
	R1k	p	R	20	24.0[c]	26.1±4.3[c]
c.o. region 2[d]						
	B1i	p	S	4		
	R1k	k	R	3	5.4[d]	5.4±1.7[d]
d.c.o.[cd]						
	B1i	k	R	2		
	R1k	p	S	0		
Aneuploids (22%)						
	–	–	S	9		
	–	–	?	2		
	B1i+R1k	p	R	5		
	–	p	R	16		
	–	k	S	7		
	B1i	–	S	2		
	R1k	–	S	2		
	B1i	p+k	R	1		
	B1i+R1k	k	R	1		
	B1i+R1k	k	S	1		
	B1i+R1k	–	R	1		
Total				214		

[a] No recombination was observed between the genes controlling resistance to leaf, stem and stripe rusts
[b] Based on euploid progeny
[c] Between centromere and *Sec1*
[d] Between *Sec1* and the *Lr26/Sr31/Yr9* complex

er, the scoring of this marker was made easier because usually the *Glu*-B1 and *Glu-R1* genes were inherited as alternatives (Fig. 3 B; d-h). The homoeoalleles *Glu-R1* and *Glu-B1* and the allele pairs *Sec1p/Sec1k, Lr26/lr26* (including *Sr31/sr31* and *Yr9/yr9*) each segregated in the expected 1:1 ratio (all $\chi^2 < 0.027$, $P \geq 0.80$). Analysis of their joint segregation revealed an unbroken linkage between the three rust resistance genes, a tight linkage between *Sec1* and the rust resistance genes, and a loose linkage between the centromere and *Sec1* (Table 2). The gene order was: centromere – *Sec1* – *Lr26/Yr9/Sr31* – telomere. The centromere – *Sec1* map distance (26.1 cM, Table 2) is in agreement with the value of 32.1 cM deduced for this interval from earlier studies (Singh and Shepherd 1984; Lawrence and Appels 1986). Since no recombination was detected between the genes conferring resistance to the three rust used, these genes are either very tightly linked (the upper limit of recombination, using Hanson's (1959) formula at the 95% confidence limit, was 1.8%), or they are part of a single complex locus conferring resistance to all three rusts.

The practical significance of this finding is that only a very small segment of rye chromosome needs to be introduced into wheat in order to transfer resistance to these three rust pathogens. The small map distance between secalins and the rust resistance genes (5.4 cM) indicates that it should be possible, but perhaps difficult, to add the rye rust resistance to wheat without the adjacent gene(s) for secalins by inducing allosyndesis and recombination between wheat and rye chromosomes (Koebner and Shepherd 1985, 1986).

Test cross 2. The purpose of this cross was to map the position of the stem rust resistance gene *SrR* on chromosome arm 1RS from 'Imperial' rye with respect to the centromere, ω-secalins and telomeric heterochromatin (C-band). With the rust strains used in this study, plants carrying 'Imperial' rye 1RS (e.g. Gabo 1BL.1RS) exhibited resistance to stem rust, but were susceptible to leaf and stripe rusts. Furthermore, 'Imperial' 1RS does not show any prominent telomeric C-band (Koebner and Shepherd 1986). Thus the F_1 heterozygote used in test-cross 2 was

Table 3. Protein and rust resistance phenotypes and their frequencies in the test-cross progeny used to map *Sec1* and *SrR* genes with respect to the centromere and a telomeric C-band

Progeny class	Protein phenotypes		Reaction to stem rust	No. of telomeric dots (i/k)[a]	No. of progeny	Recombination (%)[b]	Map distance (cM)
	Glu-1	Sec1					
Parentals							
	B1i	i	R	0 (i)	28		
	R1k	k	S	2 (k)	21		
Recombinants							
c.o. region 1[c]							
	B1i	k	S	1 (k)	4		
	R1k	i	R	1 (i)	4	11.3[c]	11.5±4.0[c]
c.o. region 2[d]							
	B1i	i	S	1 (k)	1		
	R1k	k	R	1 (i)	2	7.0[d]	7.0±3.1[d]
c.o. region 3[e]							
	B1i	i	R	1 (k)	7		
	R1k	k	S	1 (i)	2	15.5[e]	16.0±4.8[e]
d.c.o.[d,e]							
	B1i	i	S	0 (i)	1		
	R1k	k	R	2 (k)	1		
Aneuploids (45.8%, not tested for rust reaction)							
	–	–			23		
	B1i+R1k	i or i+k			11		
	B1i+R1k	–			1		
	B1i	i+k (progeny tested)			1		
	B1i	–			3		
	R1k	–			10		
	–	i or i+k			3		
	–	k			8		
Total					131		

[a] 1RS telomere from 'Imperial' (i) or 'King II' (k) rye
[b] Based on euploid progeny
[c] Between centromere and *Sec1*
[d] Between *Sec1* and *SrR*
[e] Between *SrR* and telomeric C-band

heterozygous for this cytological C-band marker, which was easily identified as two prominent dots representing telomeres of the chromosome 1R from 'King II' rye, in the interphase nuclei of root tip cells (Koebner and Shepherd 1985). A single cross-over between the 1RS telomere and its centromere could be detected because the recombinant progeny would have only one prominent dot in their interphase nuclei (either the long or short arm telomere of 1R from 'King II'), whereas parental types would have either two (both long and short arm telomeres of 1R) or nil (1BL of wheat and 1RS of 'Imperial' rye) dots. CS Dt1BS was chosen as the test-cross parent because it would not interfere with the scoring of segregating Glu-R1, Glu-B1, Sec1i and Sec1k protein bands (Fig. 4A, B; tracks a–c) among the test-cross progeny. Furthermore, CS Dt1BS was susceptible to stem rust and did not carry a major C-band on its chromosomes, thus allowing easy scoring for these markers also.

The value of the data obtained from this cross was limited because of the high frequency of univalents at both diakinesis and metaphase I in the F_1 (Table 1) and the consequent very high frequency of aneuploids in the test-cross progeny (Table 3). Although the reduced pairing between the rye arms in this experiment still allowed the gene order to be deduced, it was expected to result in reduced recombination frequencies and hence lower map distances. For example, the recombination frequency across the whole 1RS arm from centromere to telomere was only 28.2% (Table 3) compared to the value of around 50% expected across the complete arm. Furthermore, the map distance between the centromere and the *Sec1* locus was less than half of that observed in test-cross 1 (11.5 cM vs.26.1 cM, Tables 2,3) where the level of pairing at diakinesis was close to normal (91%, Table 1). In contrast, the *Sec1* – *SrR* map distance (7.0 cM) was slightly higher than the estimated 5.0 cM for the *Sec1* – *Lr26/Sr31/Yr9* interval in test-cross 1. However, we do

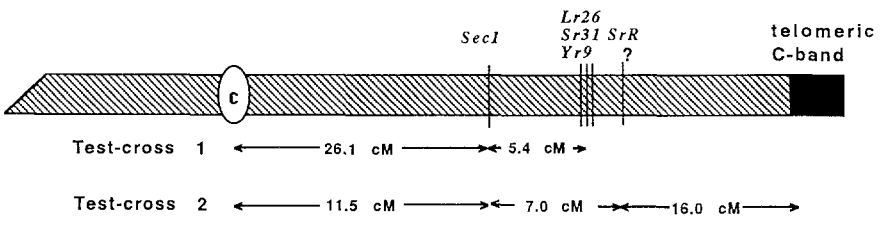

Fig. 5. Linkage map of rye chromosome arm 1RS showing the location of genes controlling rust resistance and secalins. The smaller centromere-*Sec1* map distance in test-cross 2 is thought to be due to reduced chromosome pairing at meiosis. It is not known whether *SrR* is an allele of the *Sr31* gene

not know whether this is due to *SrR* being another locus at a more distal location, or due to the effect of genetic background differences between the two crosses influencing the localization of chiasmata in this region. The possible allelism of *Sr31* and *SrR* genes is currently being investigated in other crosses involving the 'Petkus' and 'Imperial' rye derived translocations carrying these different genes. Test-cross 2 also allowed linkage mapping of the genes with respect to the 1RS telomere, due to heterozygosity of F_1 plants for the telomeric C-bands. The observed recombination frequency between *SrR* and the telomeric C-band was 15.5%, but again this probably represents an underestimate due to the reduced meiotic pairing in this cross.

Lawrence and Appels (1986) found very little recombination between the centromere and the *Nor-R1* locus, an interval representing about two-thirds of the 1RS chromosome arm. But they observed 22.5% recombination between the *Nor-R1* and the more distal *Sec1* locus. A further 16.9% recombination (probably an underestimate) was observed between *Sec1* and the 1RS telomere in the present study, indicating that the frequency of chiasmata in this relatively short satellite region of 1RS is very high. A diagrammatic summary of the linkage mapping results from the present study is shown in Fig. 5. The rust resistance genes mapped distally to the *Sec1* locus and therefore must be located in the satellite region of 1RS.

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