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# Genetic, agronomic and quality comparisons of two 1AL.1RS. wheat-rye chromosomal translocations

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With 2 figures and 4 tables

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#### **Abstract**

The 1AL.1RS wheat-rye chromosomal translocation originally found in 'Amigo' wheat possesses resistance genes for stem rust, powdery mildew and greenbug biotypes B and C, but also has a negative effect on wheat processing quality. Recently, a second 1AL.1RS translocation carrying Gb6, a gene conferring resistance to greenbug biotypes B, C, E, G and I, was identified in the wheat germplasm line 'GRS1201'. Protein analytical methods, and the DNA polymerase chain reaction were used to identify markers capable of differentiating the 1RS chromosome arms derived from 'Amigo' and 'GRS1201'. The secalin proteins encoded by genes on 1RS chromosome arms differed in 'Amigo' and 'GRS1201'. A 70 kDa secalin was found in the 'Amigo' 1AL.1RS, but did not occur in the 'GRS1201' 1AL.1RS. Polymorphisms detected by PCR primers derived from a family of moderately repetitive rye DNA sequences also differentiated the two translocations. When 'GRS1201' was mated with a non-1RS wheat no recombinants between 1RS markers were observed. In crosses between 1RS and non-1RS parents, both DNA markers and secalins would be useful as selectable markers for 1RS-derived greenbug resistance. Recombination between 1RS markers did occur when 1RS from 'Amigo' and 1RS from 'GRS1201' were combined, but in such intermatings, the molecular markers described herein could still be used to develop a population enriched in lines carrying Gb6. No differences in grain yield or grain and flour quality characteristics were observed when lines carrying 1RS from 'Amigo' were compared with lines with 1RS from 'GRS1201'. Hence, differences in secalin composition did not result in differential quality effects. When compared with sister lines with 1AL.1AS derived from the wheat cultivar 'Redland', lines with 'GRS1201' had equal grain yield, but produced flours with significantly shorter mix times, weaker doughs, and lower sodium dodecyl sulphate sedimentation vol-

**Key words:** Secale cereale — Triticum aestivum — agronomic and quality effects — chromosomal translocation — greenbug resistance — markers — rye — wheat

Translocations of rye, Secale cereale L., chromatin into the wheat, Triticum aestivum L., genome have been used in wheat breeding programmes to introduce genes of agronomic importance. The 1BL.1RS translocation derived from the Russian cultivar 'Kavkaz', possesses resistance genes for major wheat diseases such as stem, stripe and leaf rusts, and powdery mildew (Mettin et al. 1973, Zeller 1973), while the 1AL.1RS translocation, derived from 'Amigo', carries genes for stem rust, powdery mildew, and greenbug resistance (Zeller and Hsam 1984). The 'Amigo'-derived 1AL.1RS translocation has been more successful in the Great Plains of North America than in

other parts of the world. 1AL.1RS cultivars, including 'TAM107', 'TAM200', 'TAM202' and 'Century' have been registered from several US wheat breeding programmes, and occupy significant production acres, especially in the semi-arid western edges of hard winter wheat cultivation.

Recently, 'GRS1201', a wheat germplasm line with resistance to greenbug biotypes B, C, E and G, was developed by Porter et al. (1991). The greenbug resistance allele in 'GRS1201' was designated Gb6. Porter et al. (1994), using C-banding, found 'GRS1201' to carry a 1AL.1RS wheat-rye translocation and described it as being cytologically indistinguishable from the 'Amigo' 1AL.1RS. 'GRS1201' differs significantly from 'Amigo'-derived 1AL.1RS lines in terms of greenbug biotypespecific resistance, even though both were derived from 'Insave' rye. 'Amigo'-derived 1AL.1RS lines carry Gb2 and are resistant to greenbug biotypes B and C, but susceptible to biotypes E and G (Porter et al. 1991). Since rye is crosspollinated and genetic heterogeneity within cultivars and accessions is extensive, such differences among 1AL.1RS lines are likely. Markers capable of differentiating these translocations would be quite useful since the identification of greenbug race resistance can be difficult.

In at least some genetic backgrounds, 1BL.1RS translocations appear to increase grain yield and environmental stability for yield (Lukaszewski 1990, Villareal et al. 1991, Moreno-Sevilla et al. 1995). Espitia-Rangel et al. (1998a) found no difference in grain yield in 1AL.1RS ('Amigo'-derived) and 1AL.1AS sister lines selected from the heterogeneous cultivar 'Nekota', although the 1AL.1RS lines had significantly heavier seeds in stressful environments. 1AL.1RS ('Amigo'-derived) lines had higher flour protein content but lower mixograph times and tolerances, than their 1AL.1AS sibs. The objectives of this study were to distinguish the 'GRS1201' 1AL.1RS translocation from the 'Amigo' 1AL.1RS translocation using either DNA oligonucleotide primers and the polymerase chain reaction (PCR) and/or analysis of prolamines (seed storage proteins soluble in 70% ethanol), to determine whether such markers would be useful in the selection of new breeding lines with desired greenbug resistance alleles, and to determine whether any grain yield or quality effects could be attributed to the presence of the 'GRS1201'-derived 1AL.1RS translocation.

# **Materials and Methods**

The following parental lines were used: 'Redland', a non-1RS greenbug susceptible hard red winter wheat cultivar, 'TAM202', a hard red winter

wheat carrying the 'Amigo' 1AL.1RS translocation, and 'GRS1201'. Each of the 1RS wheats was crossed to 'Redland', and 'GRS1201' and 'TAM202' were intermated. Crosses were made in the greenhouse in the spring of 1992;  $F_1$  seed was fall-sown in Yuma, AZ, USA, in 1992. In 1993,  $F_2$  populations were grown in the greenhouse at Lincoln, NE, USA.  $F_3$  seed was harvested from each  $F_2$  plant separately.

A 10-mg sample was removed from the brush end of 10 randomly selected  $F_3$  seeds from each  $F_2$  plant. Samples were pooled for analysis. Prolamines were extracted with 70% ethanol, separated on 11% sodium dodecyl sulphate (SDS)–polyacrylamide gels and silver-stained (Graybosch and Morris 1990). Rye prolamines (secalins) were identified by comparison with known 1RS wheats and through immunoblot analysis using a secalin-specific monoclonal antibody (Graybosch et al. 1993).

Total genomic DNA was isolated from individual F2 plants (Saghai-Maroof et al. 1984). Oligonucleotide primers were synthesized by the Oligonucleotide Synthesis Laboratory, Centre for Biotechnology, University of Nebraska. Primers PawS5 (5'-AACGAGGGGTTC-GAGGCC-3') and PawS6 (5'-GAGTGTCAAACCCAACGA-3') (Rogowsky et al. 1992) were derived from the R173 family of ryespecific repeated DNA sequences (Guidet et al. 1991). Polymerase chain reaction (PCR) was carried out in a 15-μl volume containing 50-60 ng genomic DNA, 2 µl of each primer (2 µM), 2 µl of each deoxyribonucleotide (Pharmacia, Piscataway, NJ, USA) (1.25 mM) mix, 0.5 units Taq DNA polymerase (Promega, Madison, WI, USA), and  $3 \mu l 5 \times buffer (250 \text{ mM Tris-HCl}, pH 8.5, 7.5 \text{ mM MgCl}_2, 100 \text{ mM KCl},$ 2.5 mg/ml bovine serum albumin (BSA), 7.5% (w/v) Ficoll 400 (Pharnacia), 0.05% xylene cyanole). A Corbett Research (Sydney, Australia) AB Technology thermal cycler was used. Conditions were: two cycles of 2 min at 94°C for denaturation, 10 s at 45°C for annealing, and 70 s at 72°C for DNA synthesis, followed by 38 cycles of 10 s at 92°C, 7 s at 55°C, and 70 s at 72°C, and then finally incubation at 72°C for 5 min. PCR products were separated on 11% polyacrylamide gels. After electrophoresis, gels were stained in ethidium bromide solution (0.5  $\mu$ g/1 ml 0.5 × TBE) for 30-40 min and then destained in distilled water for

Rows of 25–32  $F_3$  seed, plus resistant and susceptible check rows, were planted in flats. The flats were watered and placed in a growth chamber under a photoperiod of 13 h of light at 22°C and 11 h of dark at 18°C. When plants reached a height of approximately 1 cm, flats were infested so that each plant received  $\approx 10-20$  greenbugs. Seven days after infestation, the plants were clipped to a height of 10-13 cm and rated when susceptible control plants were damaged enough to distinguish them easily from resistant control plants (13–14 days after infestation). Susceptible plants were chlorotic and stunted. Resistance to biotype C was used to verify presence of Gb2 in the cross 'Redland'/'TAM202'. In the 'Redland'/'GRS1201' and 'GRS1201'/ 'TAM202', crosses, biotype G was used to verify the presence of Gb6. For genetic analysis, both homogeneous resistant and segregating rows were scored as 'resistant'.

PCR phenotypes were scored directly on  $F_2$  plants; pooled results from  $F_3$  progeny were used to infer  $F_2$  genotypes for prolamines and for greenbug resistance. In populations derived from crosses with the non-1RS cultivar 'Redland', cosegregation of secalin and/or PCR products with greenbug resistance was used to define 1RS-specific markers. Marker segregation and transmission of 1RS through gametes was compared with expected frequencies by  $\chi^2$ -square analysis (Steele and Torrie 1980). When appropriate, recombination frequencies were calculated through the use of maximum likelihood equations (Allard 1956).

From each of the 'GRS1201'-derived populations, two sub-populations were derived for grain yield and quality testing. From the 'Redland'/'GRS1201' population, six F<sub>2</sub>-derived lines of each class, 1AL.1RS and 1AL.1AS, were selected at random. From the 'GRS1201'/'TAM202' population, six F<sub>2</sub>-derived lines of each parental 1AL.1RS genotype were selected on the basis of secalin, PCR and greenbug resistance phenotypes. F<sub>3</sub> seed of all lines was planted at Yuma in the autumn of 1994; the F<sub>4</sub> generation was seeded at Lincoln in 1995. At the 1996 harvest, 20 seeds per line were tested by sodium

dodecyl sulphate–polyacrylamide gel electrophoresis (SDS–PAGE) for prolamine patterns, to ensure uniformity. In the autumn of 1996,  $F_5$  lines were seeded, along with the parental lines 'Redland', 'GRS1201' and 'TAM202', in a three-replication randomized complete block design at three locations, McCook and Sidney, NE, USA, and Vernon, TX, USA. Four-row, 3-m plots were used.

Grain yield was measured as kg/ha. For quality analyses, a 500-g sample from each replication was combined to form one 1.5 kg sample per entry per location. A 300-seed sample from each was analysed with a SKCS 4100 Single Kernel Classification System (Perten Instruments, Reno, NV, USA) to determine kernel weight and kernel hardness. Kernel hardness was expressed in arbitrary hardness units. Grain was tempered to 15% grain moisture content, and milled to flour on a Quadrumat Sr. experimental mill (Brabender, Hackensack, NJ, USA). Grain and flour protein concentrations (14% moisture basis) were measured by near-infrared reflectance (NIR), as per AACC (1983) Method (39-70A). A mixograph (National Manufacturing, Lincoln, NE, USA) was used to measure dough strength, using a 10-g flour sample (AACC 1983, Method 54-40). Mixograph time was recorded as time, in minutes, to peak dough resistance. Mixograph tolerance, or resistance to overmixing, was measured as the width of the mixogram at 2 min past peak time. SDS sedimentation volumes of flour samples were determined using a 2-g modification of AACC (1983) Method 56-61A. Pup loaves were baked as per Finney (1984). The bread formulation was 100 g flour, 6 g sucrose, 3 g shortening (Vream, Bunge Foods, Bradley, IL, USA), 1.5 g NaCl, 1.0 g dry active yeast (Fleischmann, Fenton, MO, USA) and 0.005 g ascorbic acid. Loaf volume (ml) was measured by rapeseed displacement, bake absorption (%) was recorded as the amount of water necessary to reach peak dough development and loaf grain was rated on a 0-6 scale, with 0 indicating unsatisfactory and 6 being outstanding.

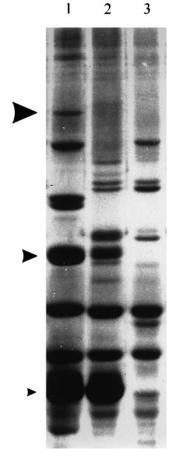
Analysis of variance with appropriate error terms was used to partition error to main effects. Means were compared by calculations of least significant differences (LSD). SAS (1985) software and procedures were used for all computations.

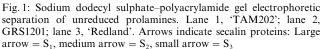
## Results

Numerous polymorphisms were observed among prolamines of the parental lines (Fig. 1) but only those found to cosegregate with greenbug resistance will be discussed. Both 'TAM202' and 'GRS1201' produced secalins herein designated  $S_2$  and  $S_3$ ; these proteins are generally described as  $\gamma$ -secalins ( $S_2$ ) and  $40~\rm kDa~\gamma$ -secalins ( $S_3$ ) and are assumed to arise from the Sec-1 locus on 1RS (Shewry et al. 1985). 'TAM202' displayed an additional 70 kDa secalin ( $S_1$ ) not observed in 'GRS1201'. Secalins of similar molecular mass to  $S_1$ , identified as higher  $M_r$  forms of  $\omega$ -secalins, have been described by Carrillo et al. (1992) as arising from the Sec-4 (also termed Gli-R3) locus, also found on 1RS.  $S_1$ ,  $S_2$  and  $S_3$  were absent in 'Redland', and all reacted with the antisecalin monoclonal antibody (not shown).

PCR using primers PawS5 and PawS6 revealed several distinct polymorphic bands among 'GRS1201', 'TAM202' and 'Redland' (Fig. 2), the most reproducible of which occurred in the region between 220 and 350 bp. Only bands in this region were used as markers in genetic analyses. Both 'GRS1201' and 'TAM202' produced several PCR products in this region not found in 'Redland'. A unique PCR product of 320 bp was found in 'TAM202', but was missing in 'GRS1201' (Fig. 2); the remaining PCR products were identical in the two sources of 1RS. Both lines produced a 220-bp fragment not found in 'Redland'. For simplicity, only the 220 and 320 bp products were used in the genetic analyses.

To verify 1RS as the origin of the PCR markers, cosegregation of the 220 and 320 bp PCR products, secalin proteins and greenbug resistance was examined in progeny of the crosses with Redland. In both crosses (Table 1) the PCR products





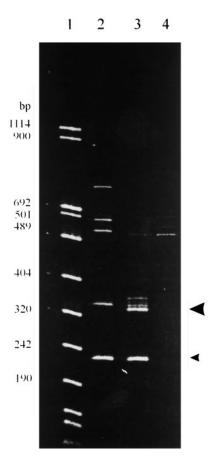


Fig. 2: Polyacrylamide gel separations of polymerase chain reaction products. Lane 1, markers; lane 2, GRS1201; lane 3, 'TAM202'; lane 4, 'Redland'. Arrows indicate 320 bp (large arrow) and 220 bp (small arrow) fragments used in genetic analyses.

showed 100% cosegregation with both secalin proteins and greenbug resistance, confirming the 1RS origin of the PCR markers. No susceptible lines were found to carry secalins or these specific PCR products in either cross and no recombination between secalins and either PCR marker was observed. A  $\chi^2$ -square analysis revealed a significant departure from the expected 3:1 ratio of 1RS:1AS markers in the 'Redland'/'GRS1201' cross, with a deficiency of 1RS progeny. This deficiency was not observed in the 'Redland'/'TAM202' population

The population derived from 'GRS1201'/'TAM202' was used to determine whether these markers could differentiate lines with Gb2 from those with Gb6 in crosses between two 1AL.1RS parents. Plants were scored for the presence of the 'Amigo'-derived markers S<sub>1</sub> and the 320 bp PCR fragment and for the presence of the 'GRS1201'-derived Gb6. S1 and the 320 bp PCR fragment were the only two protein and DNA markers found to differentiate the two translocations. Significant departures from a 9:3:3:1 segregation ratio were observed for each of the three pairs (Table 2), confirming that the markers and Gb6 arise from linked loci on 1RS. Recombinants between the loci giving rise to S<sub>1</sub> and the 320 bp PCR fragment were identified but only one line lacking both markers, and still carrying Gb6, was detected. A recombination frequency of  $12.3 \pm 4.5$  was calculated for the marker pair  $S_1$  and the 320 bp PCR fragment. The rate of recombination was too low to provide an accurate assessment of linkage between the markers and the Gb6 locus. When ratios of  $S_1$ , the 320 bp PCR fragment and Gb6 were independently compared with the expected 3:1 segregation (data not shown) no significant departures were detected by  $\chi^2$  analysis. Hence, there was no preferential transmission of either the 'Amigo' 1AL.1RS or the 'GRS1201' 1AL.1RS in this cross.

In the 'Redland'/'GRS1201' population, no significant differences in grain yield, seed weight or kernel hardness were observed when lines carrying the 'GRS1201'-derived 1AL.1RS translocation were compared with non-1RS sibs (Table 3). Significant effects on flour quality were detected (Table 4), with mixograph peak times, mixograph tolerances, bake mix times and SDS sedimentation volumes being lower in the 1AL.1RS lines. In the 'GRS1201'/'TAM202' population, no differential effects on any measured traits were detected (Tables 3 and 4).

## Discussion

In the mating of 'GRS1201' and the non-1RS wheat 'Redland', the lack of recombination between rye-derived markers and greenbug resistance genes was not unexpected, since rye chromatin does not recombine with wheat unless a *ph* mutant is present (Koebner and Shepherd 1986). In crosses between 1RS and non-1RS wheats, and in the absence of *ph*–, 1RS is inherited as a non-recombined block of genes. Thus, in such matings, secalin proteins or rye-specific PCR markers identified

Table 1: Progeny data for secalin proteins, PCR markers, and response to greenbugs in two F<sub>2</sub> populations derived from crosses of Redland (non-1RS) and 1AL.1RS wheats

Pedigree	Secalins	Phenotype PCR products <sup>1</sup>	Greenbug assay <sup>2</sup>	No.	$\chi^2(3:1)$	P
'Redland'/GRS1201	+	+	R	29	7.71	0.009
,	_	_	S	21		
'Redland'/'TAM202'	+	+	R	35	0.67	0.312
,	_	_	S	15		

<sup>&</sup>lt;sup>1</sup> 220 bp PCR product in the 'Redland'/GRS1201 mating; 220 + 320 bp products in 'Redland'/TAM202'.

Table 2: Segregation analysis of polymorphic 1RS loci in progeny derived from cross 'GRS1201'/ 'TAM202'

Markers	Number	of progeny wit	th respective pl	henotype <sup>1</sup>	$\chi^2 (9:3:3:1)$	P
Secalin/Gb6	$S_1 + /GBR$		$S_1 - /GBR$	$S_1-/GBS$		
	39	27	28	1	19.72	0.0002
PCR <sup>2</sup> /Gb6	320 + /GBR	320 + /GBS	320 - /GBR	320 - /GBS		
	40	28	27	1	19.06	0.0002
Secalin/PCR	$S_1 + /320 +$	$S_1 + /320 -$	$S_1 - /320 -$	$S_1 - /320 -$		
	60	6	8	22	54.53	0.0001

<sup>&</sup>lt;sup>1</sup>Phenotypes:  $S_1 + = S_1$  secalin present,  $S_1 - = S_1$  secalin absent, GBR = resistant to greenbug biotype G; GBS = susceptible to greenbug biotype G, 320 + = 320 bp PCR product present, 320 - = 320 bp PCR product absent

Table 3: Grain yield and kernel characteristics of parental genotypes and progeny lines derived from matings of 'Redland'/'GRS1201' and 'GRS1201'/TAM202' from three Nebraska locations

	Grain	yield (kg/ha)	Kernel	weight (mg)	Kernel h	ardness (units)	Grain	protein (%)
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Parental lines								
'Redland'	3850		28.9		52.0		11.9	
'TAM202'	3805		30.5		66.0		12.4	
GRS1201	2344		35.7		62.3		13.4	
'Redland'/GRS1201 G1AL.1RS lines <sup>1</sup>	3105	2878-3230	31.3	27.2–33.4	61.7	54.0-66.0	12.7	12.32–13.2
Non-1RS lines GRS1201/'TAM202'	3456	3029–3984	30.9	27.8–33.2	57.2	52.0-62.0	12.6	12.2–13.1
G1AL.1RS lines	3319	3009-3701	32.9	29.7-35.0	62.6	60.3-65.7	13.0	12.6-14.0
AIAL.1RS lines <sup>2</sup>	3216	2731–3642	32.8	31.8–35.4	62.1	55.7–68.0	13.0	12.3–13.5

<sup>&</sup>lt;sup>1</sup>G1AL.1RS designates 1AL.1RS chromosome derived from 'GRS1201'.

in this study would serve as effective means to track *Gb2* or *GB6*. Similarly, the reduced transmission of 1RS in the 'Redland'/'GRS1201' cross confirms previous observations. Koebner and Shepherd (1986) also reported reduced frequency of transmission of 1RS through pollen in some cases, but the phenomenon evidently is not universal, since 1RS was transmitted at an expected frequency in the 'Redland'/'TAM202' mating

In the mating of 'GRS1201'/'TAM202' a very low frequency of recombination between markers and Gb6 was detected. Twenty-two progeny lacking both  $S_1$  and the 320 bp PCR product were identified (Table 2); of these, only one (4.5%) was susceptible to biotype G. At present, simultaneous selection against both the 'Amigo'-derived  $S_1$  and 320 bp markers in matings between lines carrying these two 1AL.1RS translocations will result in populations enriched in lines carrying

*Gb6*. No dominant markers unique to the 'GRS1201'-derived translocation were identified. Future work directed at the identification of such markers would be useful in designing systems to track *Gb6* in matings with lines carrying 'Amigo'-derived 1AL.1RS.

While significant differences in quality were detected when means of 1RS and non-1RS sister lines were compared, individual lines carrying 1AL.1RS did display values for all quality traits that would fall within acceptable limits for USA hard wheat breeding programmes. Similar yield and quality effects were observed when the 'Amigo'-derived 1AL.1RS was compared with 1AL.1AS (Espitia-Rangel et al. 1998a, b). The lack of any yield or quality differences between sister lines carrying either 1AL.1RS translocation suggests breeders wishing to employ the broader spectrum of greenbug resistance genes found on 'GRS1201'-derived 1AL.1RS translocation may do

<sup>&</sup>lt;sup>2</sup> Greenbug assay: S = susceptible, R = resistant; resistant includes both homozygous and heterozygous lines. Greenbug biotype G was used in population derived from 'GRS1201'; biotype C was used in population derived from 'TAM202'.

 $<sup>^{2}</sup>$  PCR = chromosomal site from which 320 bp PCR product arises: not an accepted gene symbol.

<sup>&</sup>lt;sup>2</sup>A1AL.1RS designates 1AL.1RS chromosome derived from 'Amigo' through 'TAM202'.

Table 4: Flour quality characteristics of parental genotypes and progeny lines derived from matings of Redland/GRS1201 and GRS1201/TAM202 from three Nebraska locations

	Frot Mean	Flour protein (%) .n Range	Mixo peak ti Mean	Mixograph beak time (min) Mean Range	Mixo toleran Mean	Mixograph tolerance (mm) ean Range	absor Mean	Bake absorption (%) Mean Range	Bal time Mean	Bake mix time (min) Mean Range		Loaf grain (0–6) Mean Range	Loaf ( Mean	Loaf volume (ml) Mean Range	sedime: Mean	SDS sedimentation (ml) Mean Range
Parental lines	,				•		,				;		9			
'Redland'	10.5		5.2		13.0		65.5				6.1		882		38.5	
'TAM202'	10.9		5.1		12.1		64.7				5.5		938		39.7	
GRS1201	12.3		3.0		9.4		64.7				3.3		942		35.3	
'Redland'/GRS1201																
G1AL.1RS lines <sup>1</sup>	11.5	11.1–11.9	3.9	3.2-4.6	11.3	9.1 - 13.0	65.4	65.0-66.1	4.4	3.5-5.3	3.6	3.1-4.2	927	902–952	38.8	36.7–42.5
Non-1RS lines GRS1201/'TAM202'	11.3	11.0–11.7	4.83	4.1–4.5	12.83	11.2–14.6	9:59	65.1–66.2	$6.0^{3}$	5.1–7.3	3.9	3.7–4.1	895	845–940	41.8*	40.5–43.5
G1AL.1RS lines	11.6	11.2–12.6	3.9	3.2-4.3	10.6	8.9 - 11.4	66.5	65.9–67.1	4.3	3.5-5.0	3.1	2.0-3.8	696	923-998	39.9	38.3-41.0
A1AL.1RS lines <sup>2</sup>	11.6	10.8 - 12.2	4.5	3.9-5.2	10.7	9.9–11.4	66.3	65.3-66.6	8.4	4.0-6.3	2.7	2.0-4.0	918	878-950	46.5	27.0–39.7

<sup>1</sup> G1AL.1RS designates 1AL.1RS chromosome derived from GRS1201.
<sup>2</sup> A1AL.1RS designates 1AL.1RS chromosome derived from 'Amigo' through 'TAM202' Denotes significantly higher mean within the 'Redland'/GRS1201' population.

so in the knowledge that the effects will be similar to those conditioned by the 'Amigo'-derived translocation. Despite the differences in secalins found arising from these two translocations, no differential flour quality effects were observed. Merely changing the secalin composition may not be a useful approach to improving 1AL.1RS quality.

If grain yield is not elevated in the presence of 1AL.1RS, the question arises as to whether wheat breeders should not eliminate it by selection, especially when potential quality problems may arise. However, Espitia-Rangel et al. (1998a) did find the 'Amigo'-derived 1AL.1RS translocation to result in significantly higher seed weights under conditions of stress. Hence, there may be an effect on the stability of agronomic performance associated with 1AL.1RS. In addition, genes for resistance to greenbug and powdery mildew and tolerance to the wheat curl mite, the vector of wheat streak mosaic virus, still make 1AL.1RS an attractive addition to hard wheat breeding programmes.

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