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Quality and biochemical effects of a 1BL/1RS wheat-rye translocation in wheat

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Abstract Wheat (*Triticum aestivum* L.) breeders worldwide have used rye (*Secale cereale* L.) as a source of genes for agronomic improvement. The 1BL/1RS wheat-rye chromosomal translocation derived from the Russian cultivars 'Kavkaz' and 'Aurora' has been among the most common means of accessing useful rye genes. Unfortunately, deleterious wheat quality effects are often associated with the presence of 1RS. The identification of genetic backgrounds capable of alleviating the deleterious effects of 1RS is crucial for its continued exploitation. End-use quality parameters and flour protein composition, as measured by size-exclusion high-performance liquid chromatography (SE-HPLC) of 373 wheat lines, derived from seven 1BL/1RS breeding populations, were analyzed. In all populations, significant quality defects were detected in 1BL/1RS lines compared to non-1RS sister lines. The detrimental quality effects resulted from alteration of the ratio of flour protein composition, especially, decreased glutenin concentrations, and increased salt-water soluble protein concentrations. The end-use quality of 1BL/1RS lines, however, was highly dependent on genetic backgrounds. The potential exists for improvement in quality through crosses between 1RS lines with high glutenin, or low salt-water soluble protein concentrations, and non-1RS lines with strong dough properties.

Key words Wheat-rye translocations · 1BL/1RS · End-use quality · Flour protein composition · Size-exclusion high-performance liquids chromatography

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Introduction

Wheat (*Triticum aestivum*) – rye (*Secale cereale*) chromosomal translocations of the short arm of rye chromosome 1 (1RS) to the long arm of wheat group-1 chromosomes have been used in wheat breeding programs as sources of genes for cultivar improvement. Wheats possessing 1RS have been shown to possesss high yield potential and environmental stability (Moreno-Sevilla et al. 1991, 1992; Villareal et al. 1991). Thus, 1RS translocation lines have been widely used in modern wheat breeding programs. In 1988 about 50% of the CIMMYT advanced breeding lines carried 1RS (Villareal et al. 1991), and in the 21st International Winter Wheat Performance Nursery grown in 1989, 41.4% of the cultivars possessed 1RS translocations (Lukaszewski 1990).

In contrast to enhanced agronomic performance, most 1RS wheat lines have deleterious end-use quality properties, including low SDS-sedimentation volume, dough stickiness, and reduced dough strength (Zeller and Hsam 1984; Dhaliwal et al. 1988, 1990; Graybosch et al. 1990). However, considerable variation exists in end-use quality attributes of wheats possessing 1RS, and some 1RS lines display acceptable quality characteristics (Graybosch et al. 1990; Pena et al. 1990). Thus, identification of appropriate genetic backgrounds might improve the breadmaking quality of 1RS wheats.

Unreduced wheat flour proteins may be separated by size-exclusion high-performance liquid chromatography (SE-HPLC) into three major peaks on the basis of molecular-weight distributions: > 100 kDa, 25–100 kDa, < 25 kDa. These peaks are considered to represent protein components of mainly polymeric glutenins, monomeric gliadins, and albumins/globulins

(salt-water soluble proteins), respectively (Singh et al. 1990a), although the two smallest peaks do contain both salt-water soluble and insoluble components (Graybosch et al. 1993). Many researchers have reported that glutenin proteins positively influence dough development time and loaf volume, while higher proportions of albumins and globulins increased dough stickiness (Bietz 1986; Dhaliwal et al. 1988; Dachkevitch and Autran 1989; Lundh and MacRitchie 1989; Dhaliwal and MacRitchie 1990; Graybosch et al. 1990, 1993; Singh et al. 1990b; Primard et al. 1991). Gliadin proteins contribute to loaf volume potential and dough viscosity (Finney 1971). Increased salt-water soluble proteins and/or decreased glutenin proteins might contribute to poor end-use quality of 1RS wheats (Dhaliwal et al. 1988; Dhaliwal and MacRitchie 1990; Graybosch et al. 1990).

Most experiments dealing with the quality attributes of 1RS have been conducted in a limited number of genetic backgrounds. Numerous genetic backgrounds need to be examined before the precise causes of the detrimental effects of 1RS are known. More specifically, it is important to establish whether genetic backgrounds can be identified that are capable of alleviating the negative quality effects of 1RS. Determination of the unique biochemical attributes of such genetic backgrounds could suggest strategies useful in improving the quality of 1RS wheats. Additionally, assessment of native protein compostition from diverse genotypes on the basis of protein solubility and molecular-weight distributions may provide a more systematic approach to the improvement of the breadmaking quality of 1RS wheats.

Materials and methods

Plant materials

Three-hundred and seventy-three lines, derived from seven 1BL/1RS breeding populations, were planted in unreplicated single-row plots at the University of Nebraska Agronomy Farm, Lincoln, Nebraska, in the fall of 1989 and 1990. Seven cultivars, 'Redland', 'Siouxland', Abilene, 'Plainsman V', 'Lancota', 'TAM-200', and 'Karl', were included as controls. Siouxland carries a 1BL/1RS wheat-rye translocation derived from 'Kavkaz', while TAM-200 possesses a 1AL/1RS translocation from 'Amigo'. The remaining control lines were non-1RS hexaploid wheats. Controls were planted randomly, with one control line per every 15 rows. At least one parent of each population carried a wheat-rye translocation (Table 1). The non-1BL/1RS parents used to develop breeding populations had diverse bread making quality and were obtained from regional breeding and germplasm enhancement programs.

End-use quality analysis

After harvest, 35-g seed samples were tempered to 15% moisture for 18 h and milled on a Brabender Quadraplex laboratory mill. Flour protein (FP) was determined from 1 g of sample (0% moisture) by the Kjeldahl procedure using a conversion factor of 5.7 of the total nitrogen to percent protein. Mixograph characteristics were evaluated with 10 g (14% moisture) of flour and 60% added water using a National Manufacturing Mixograph (AACC 1983). Mixograph mixing time (MT) was recorded as time, in min, to peak-dough development. Mixograph tolerance (MTO) was measured as the width of the Mixograph curve at 2 min past peak time. Sodium dodecyl sulfate sedimentation (SDSS) was performed using 2 g (14% moisture) of flour with a modified AACC (1983) method, 56-61A, and the sedimentation volume was recorded after 20 min. Flour samples from each year were analyzed independently.

Identification of wheat-rye translocation lines

Sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) with silver staining was used (Graybosch and Morris 1990; Lookhart et al. 1991). Seventy percent ethanol-soluble proteins were separated to detect 1RS lines. Two groups of rye secalins, omega secalins and gamma secalins, produced by genes on 1RS, were readily detected in SDS-PAGE separations. Unreduced ethanol-soluble proteins from single seeds were used to determine questionable identifications.

Protein extraction and SE-HPLC

Flour protein fractions were analyzed by SE-HPLC (Singh et al. 1990a, b; Graybosch et al. 1993). SE-HPLC was performed using a BioRad HPLC system with a Waters 10 micron Protein-Pak 300 SW silica column. Protein samples were eluted in 0.5% SDS in 0.05 M sodium phosphate elution buffer (pH 6.9) filtered through 0.2-μm membranes. Error variance from both column and protein settling time was measured by a control sample which was analyzed at the beginning and end of each sample run. Absorbance was measured at 210 nm. Five protein fractions, described by Graybosch et al. (1993), were analyzed. The fractions were: (1) glutenin-polymeric protein of Mol Wt > 100 kDa; (2) gliadin-monomeric, salt-water insoluble proteins of Mol Wt 25–100 kDa; (3) low-molecular-weight insoluble protein or salt-water insoluble monomers of Mol Wt < 25 kDa; (4) salt-water soluble (SWS) proteins of Mol Wt 25–100 kDa, and (5) salt-water soluble (SWS) proteins < 25 kDA. The percent area of each peak was used to determine protein concentration based on molecular-weight distribution and solubility as a percent of the total extracted protein.

To estimate the percentage of flour protein extracted via sonication, dilutions of a standard protein (bovine serum albumin, Sigma)

Table 1 Pedigrees of each population

Populations	No. of lines	Pedigrees
Population 1	67	Siouxland[a]/Plainsman V
Population 2	35	Siouxland[a]/Sumner
Population 3	36	New 66.1.8/Siouxland[a]
Population 4	45	OK81322[a]/4 /Atlas 66/Cmn/2/Nebr. Restorer/3/Aurora[a]
Population 5	32	NE7060/Siouxland[a]
Population 6	33	Aurora[a]/NE701154/3/NE7060/2/Rannaya 12/Bezostaya 4/4/*Agrotriticum* × *T. aestivum*
Population 7	35	Lindon/NE7060/2/NE80413[a]

[a] = 1BL/1RS line

were applied to the SE-HPLC column. A standard curve for the prediction of μg protein was developed. The average percent extraction was calculated from a subset of 96 samples by dividing protien content, as estimated from the SE-HPLC standard curve, by flour protein content, as measured by the Kjedahl procedure.

Statistical analysis

All HPLC data and flour quality data were analyzed using SAS programs and procedures (SAS User's Guide 1985). In the analyses of variance (ANOVA), years (YEAR) and lines (LINE) were considered as random effects, and population (POPN) and classes (RS) classified as fixed effects. Years (YEAR) were used as a replication term due to the lack of replication of lines within years. The mean square of the YEAR*LINE (POPN) interaction from the analysis of variance was used as the error term to compute contrasts between classes (1BL/1RS lines and non-1BL/1RS lines), and between classes within populations. Heterogeneous lines (90 lines) were not analyzed due to biased sample size among classes within populations. Check cultivars were analyzed separately. Mean responses, averaged over years, were used to calculate genotypic correlations (Pearson correlations coefficients), as a means of relating SE-HPLC fractions to flour quality variables.

In order to estimate the average genetic effect of 1BL/1RS on quality, individual line responses were adjusted by population mean, and adjusted values were plotted as frequency distributions. Values were adjusted by the following equation:

adjusted value = observed value − (population mean − grand mean).

Results

Variation in flour quality characteristics

Check cultivars and years differed significantly for flour protein concentration (FP), SDS sedimentation volume (SDSS), Mixograph mixing time (MT), and Mixograph tolerance (MTO) (data not shown). However, variation among plots of each check cultivar within each harvest year was nonsignificant, indicating that field conditions were reasonably uniform. Flour quality of check varieties is given (Table 2) for comparisons with the experimental lines used in this study.

Populations and lines within populations differed significantly for FP, SDSS, MT, and MTO (Table 3). In most populations, genotypic classes (1BL/1RS vs non-

Table 2 Flour quality characteristics of check varieties

Cultivars	Observations per year	FP[a] (%)		SDSS[a] (cc)		MT[a] (min)		MTO[a] (mm)	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Redland	5	12.25	0.38	36.40	2.43	5.03	1.06	18.50	3.15
Siouxland	5	13.20	0.89	28.87	2.84	3.55	0.79	12.55	2.77
Abilene	6	13.09	1.56	38.58	3.99	3.75	0.56	19.00	2.37
Plainsman V	5	16.07	0.56	39.41	1.75	4.22	0.43	27.87	4.34
Lancota	5	14.70	1.14	39.16	2.94	2.98	0.48	21.80	4.32
TAM 107	5	12.05	1.22	35.22	3.07	4.25	0.82	16.00	2.21
Karl	5	14.11	0.29	38.91	2.68	3.96	0.52	19.22	2.39

[a] FP = flour protein concentration; SDSS = SDS sedimentation volume; MT = Mixograph mixing time; MTO = Mixograph tolerance

Table 3 Mean squares from analysis of variance of breadmaking quality characteristics of wheat genotypes from seven populations

Source of variance	*df*[a]	FP[a] (%)	SDSS[a] (cc)	MT[a] (min)	MTO[a] (mm)
Year	1	20.29**	106.09**	38.70**	35.43**
Popn[b]	6	32.18**	1349.66**	34.68**	1093.00**
Year*popn	6	5.19	87.90**	2.78**	231.41**
Line (popn)	276	1.77**	29.77**	0.955**	29.44**
Contrasts: 1RS vs non-1RS					
Popn 1	1	1.55	931.62**	41.38**	1917.13**
Popn 2	1	9.57**	1009.81**	8.02**	744.86**
Popn 3	1	5.09**	819.33**	6.30**	490.17**
Popn 4	1	11.70**	65.94**	0.00	1.56
Popn 5	1	3.58**	117.99**	0.38**	78.77**
Popn 6	1	8.42**	64.73**	1.54**	106.40**
Popn 7	1	0.01	399.46**	0.01	160.95**
Error	274	0.64	5.92	0.16	6.38

** = significant at $P = 0.01$; * = significant at $P = 0.05$
[a] *df* = degrees of freedom; FP = flour protein concentration; SDSS = SDS sedimentation volume; MT = Mixograph mixing time; MTO = Mixograph tolerance
[b] Popn = population

1RS) differed significantly for flour quality parameters (Table 3). Within 1RS classes, significant differences were frequently observed for protein content and SDS sedimentation volumes, while mean squares for Mixograph tolerance (MTO) were significant only in population 1.

Across all populations, mean values of FP in 1BL/1RS lines were significantly, though only slightly, higher than those in non-1BL/1RS lines, while 1BL/1RS lines had lower mean values for SDSS volumes, MT and MTO (Table 4). Similar results were observed within all populations, except for population 4. No differences in mean MT and MTO were detected between genotypic classes in this population, which had a low quality genetic background characterized by the lowest mean MTO for non-1RS lines. The mean SDSS volume of 1BL/1RS lines in five of the six populations was higher than that of the 1BL/1RS check variety, Siouxland (28.9 cc), while mean MTO values of 1BL/1RS lines exceeded Siouxland (12.6 mm) only in population 1.

Distribution of flour quality parameters across populations

The distribution of FP among both 1BL/1RS lines and non-1RS lines was nearly identical when adjusted by population mean (Fig. 1). The distribution in SDS sedimentation volume among lines (Fig. 2) revealed 5% of the 1BL/1RS lines as having SDSS values of 35 cc or greater; 35 cc is considered a minimally acceptable value for inclusion in a breeding program. Fifty-four percent of the non-1RS lines exceeded the SDSS values of 35 cc. Among check cultivars, only Siouxland failed to exceed 35 cc. SDS sedimentation volume, adjusted by overall population mean, showed a 27% reduction in 1BL/1RS lines compared with that of non-1RS lines (mode of 30 for 1BL/1RS vs mode of 36 for non-1RS lines).

In 1BL/1RS lines, the distribution observed in Mixograph mixing time was narrower than that among non-1RS lines (Fig. 3). Many 1BL/1RS and non-1RS lines displayed acceptable values (>3.5 min). Modal Mixograph mixing time, adjusted by population mean (Fig. 3), was 14% lower in 1BL/1RS lines (3 min) than that in non-1RS lines (3.8 min). The distribution of observed Mixograph tolerance (Fig. 4) revealed only 10% of 1BL/1RS lines as possessing values above a minimally acceptable value of 15 mm; among check cultivars, again only Siouxland did not exceed the minimally acceptable value. A 25% reduction in mean Mixo-

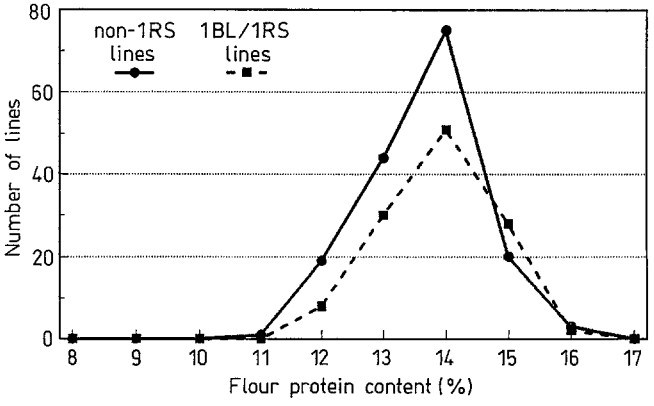

Fig. 1 Flour protein contents of 1BL/1RS and non-1RS lines, adjusted by population means

Table 4 Means and ranges for flour quality parameters of 1BL/1RS and non-1BL/1RS (non-1RS) lines from seven breeding populations

Pop	Class[a]	No.[b]	FP[b] (%)		SDSS[b] (cc)		MT[b] (min)		MTO[b] (mm)	
			Means[c]	Ranges	Means[c]	Ranges	Means[c]	Ranges	Means[c]	Ranges
All	1RS	120	14.1^A	10.4–16.4	29.7^B	19.8–39.4	3.1^B	1.8–4.9	11.2^B	5.0–26.5
	Non	163	13.9^B	10.9–16.4	35.1^A	17.9–43.6	3.8^A	2.3–7.6	16.5^A	7.5–29.5
1	1RS	20	14.8^A	13.1–16.4	33.5^B	26.4–39.4	3.6^B	2.4–4.8	13.9^B	5.0–26.5
	Non	47	14.5^A	13.1–15.8	39.3^A	33.3–43.6	4.9^A	3.2–7.6	22.3^A	11.0–29.5
2	1RS	15	14.3^A	13.1–15.3	31.6^B	27.6–33.9	2.9^B	2.3–3.6	11.1^B	7.5–16.5
	Non	20	13.5^B	11.6–15.2	39.3^A	35.6–41.5	3.6^A	3.0–4.4	17.7^A	12.0–21.0
3	1RS	22	14.7^A	12.7–16.1	27.4^B	20.9–34.6	2.4^B	1.8–3.2	8.9^B	6.0–14.5
	Non	14	14.2^B	12.5–16.4	34.4^A	28.5–39.4	3.1^A	2.3–4.0	14.6^A	7.5–23.0
4	1RS	18	12.5^B	10.4–14.6	29.2^B	24.0–34.1	3.1^A	2.4–4.5	11.5^A	8.5–15.0
	Non	27	13.3^A	11.4–16.1	30.9^A	25.1–40.1	3.1^A	2.5–4.8	11.7^A	7.5–17.0
5	1RS	16	14.4^A	11.7–16.0	28.9^B	23.4–33.4	3.1^B	2.0–4.1	11.3^B	9.0–13.5
	Non	16	13.9^B	12.7–14.8	31.6^A	25.4–35.3	3.3^A	2.8–3.7	13.5^A	10.5–17.5
6	1RS	15	14.3^A	13.4–15.6	25.6^B	19.8–30.3	3.2^B	2.4–4.9	9.5^B	7.0–14.0
	Non	18	13.6^B	10.9–15.0	27.6^A	17.9–33.4	3.5^A	2.4–4.7	12.1^A	9.5–21.5
7	1RS	14	13.4^A	10.8–15.1	32.1^B	28.5–39.4	3.4^A	2.9–4.0	12.3^B	9.0–14.5
	Non	21	13.4^A	11.6–15.6	36.9^A	29.9–42.1	3.4^A	2.9–4.1	15.4^A	11.0–19.0

[a] Class: 1RS = 1BL/1RS wheat -rye translocation line; non = non-translocation line

[b] No. = number of lines; FP = flour protein content; SDSS = SDS sedimentation volume; MT = Mixograph mixing time, MTO = Mixograph tolerance; within each population

[c] Two or more means followed by the same letter (*A* or *B*) were not significantly different at $P = 0.05$

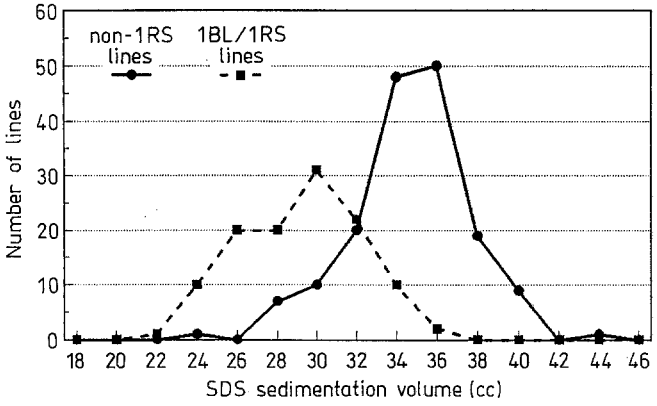

Fig. 2 SDS sedimentation volumes of 1BL/1RS and non-1RS lines, adjusted by population means

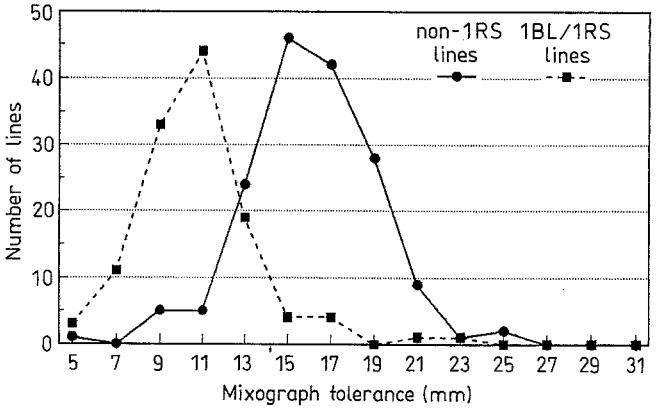

Fig. 4 Mixograph tolerances of 1BL/1RS and non-1RS lines, adjusted by population mean

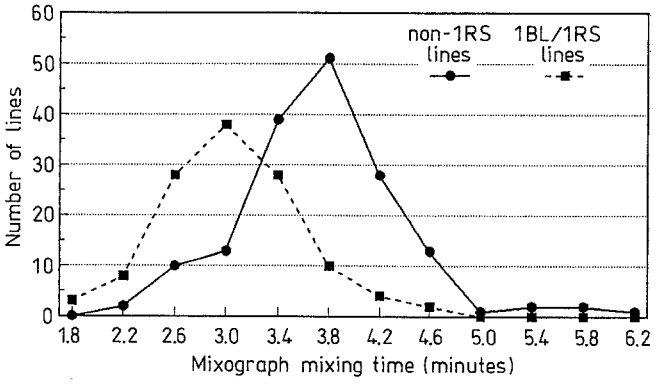

Fig. 3 Mixograph times of 1BL/1RS and non-1RS lines, adjusted by population means

graph tolerance (mode of 11 for 1BL/1RS lines vs mode of 16 for non-1RS lines) was associated with the presence of 1BL/1RS. Only 5% of 1BL/1RS lines equalled or exceeded the mean MTO value (16.5 mm) of non-1BL/1RS lines.

Variation in SE-HPLC fractions

From the subset of 96 samples, an average extraction rate of 94.7% (SD = 4.3%) was estimated via sonication. Mean squares from ANOVA of SE-HPLC fractions are presented in Table 5. With the exception of the glutenin fraction, significant differences in SE-HPLC fractions were not observed among populations. Within all seven populations, concentrations of glutenin were significantly different between 1BL/1RS and non-1RS lines. In six populations, gliadin concentrations did not differ among genotypic classes. Differences in the remaining protein fractions were population dependent. Significant variation among lines within classes and populations was also dependent upon the population (Table 6). Differences for glutenin content were observed among 1BL/1RS lines from four populations, differences for SWS proteins of MW 25–100 kDa were observed among 1BL/1RS lines from six of seven populations.

Means of flour protein components, as measured by SE-HPLC, are listed in Table 7. Consistent differences

Table 5 Mean squares from analysis of variance of protein molecular-weight distributions within seven 1BL/1RS populations

Source of variance	*df*	Glutenin	Gliadin	Low-molecular-weight insoluble protein	SWS protein (25–100 kDa)	SWS protein (< 25 kDa)
Year	1	90.84**	28.79	3.54	121.25*	4.01
Popn	6	226.32*	757.67	18.70	546.95	70.20
Year*Popn	6	52.38	431.68**	25.16**	192.95**	25.98**
Line (vs Popn)	269	58.52**	33.17**	3.04*	90.04**	3.98**
Contrasts: 1RS vs non-1RS						
Popn 1	1	2133.84**	55.42	0.21	942.33**	57.72**
Popn 2	1	3403.08**	69.83	43.88**	4016.14**	98.87**
Popn 3	1	2064.01**	42.81	23.74**	2502.22**	46.57**
Popn 4	1	100.59**	527.48**	6.42	949.31**	22.27**
Popn 5	1	535.69**	8.72	22.85**	842.57**	3.42
Popn 6	1	1311.63**	47.83	17.06**	2105.97**	1.88
Popn 7	1	1175.52**	41.06	12.01**	1529.72**	25.48**
Error	268	5.04	20.37	2.48	21.30	2.50

** = significant at $P = 0.01$, * = significant at $P = 0.05$

Table 6 Flour protein composition, as measured by SE-HPLC of lines from seven 1BL/1RS wheat populations. Two or more percentage values followed by the same letter (A or B) were not significantly different at $P = 0.05$

Pop	Class[a]	No.[b]	Glutenin (%)	Gliadin (%)	Low-molecular-weight insoluble protein (%)	SWS protein (25–100 kDa) (%)	SWS protein (< 25 kDa) (%)
All	1RS	120	33.2^B	32.9^B	9.4^B	17.4^A	7.1^A
	Non	163	41.6^A	35.0^A	10.2^A	7.6^B	5.7^B
1	1RS	20	32.0^B	39.6^A	9.6^A	12.8^A	5.9^A
	Non	47	40.8^A	38.2^A	9.5^A	7.1^B	4.4^B
2	1RS	15	31.0^B	30.2^A	9.3^B	21.6^A	7.8^A
	Non	20	45.4^A	33.1^A	10.9^A	5.3^B	5.3^B
3	1RS	22	31.2^B	33.9^A	8.8^B	18.8^A	7.1^A
	Non	14	42.6^A	35.5^A	10.0^A	6.4^B	5.5^B
4	1RS	18	39.0^B	28.8^B	9.8^A	15.0^A	7.4^A
	Non	27	41.2^A	33.6^A	10.3^A	8.5^B	6.4^B
5	1RS	16	33.0^B	33.2^A	9.4^B	17.8^A	6.7^A
	Non	16	38.1^A	33.9^A	10.6^A	10.6^B	6.2^A
6	1RS	15	33.4^B	29.2^A	8.7^B	21.8^A	7.8^A
	Non	18	41.4^A	30.9^A	9.7^A	10.5^B	7.5^A
7	1RS	14	33.7^B	33.6^A	10.0^B	15.5^A	7.2^A
	Non	21	42.1^A	35.1^A	10.9^A	6.0^B	6.0^B

[a] Class:1RS = 1BL/1RS wheat-rye translocation line, Non = non-translocation line
[b] No. = number of lines

between 1BL/1RS and non-1BL/1RS lines over populations were found in two protein fractions: glutenin and SWS proteins of MolWt 25–100 kDa. In all seven populations, the mean glutenin concentrations of 1BL/1RS lines was significantly lower than that of non-1BL/1RS lines, and the mean concentrations of SWS protein of MolWt 25–100 kDa were significantly higher for 1BL/1RS lines than for non-1RS lines. In six populations, however, no differences between classes were detected in gliadin concentrations. The mean SWS protein < 25 kDa concentrations of 1BL/1RS lines exceeded (in five populations) or equalled (in two populations) that of non-1BL/1RS, while the mean low-molecular-weight insoluble protein content of 1BL/1RS lines equalled (in two populations) or was less than that of non-1BL/1RS lines.

Distribution in SE-HPLC fractions

The distribution in glutenin concentration among lines is presented in Fig. 5 a. Among both 1BL/1RS and non-

Table 7 Significant correlations[a] between flour protein compositions and flour quality characteristics for 1BL/1RS and lines in seven wheat populations segregating for 1BL/1RS

Fraction	FP	SDSS	MT	MTO
1BL/1RS lines				
Glutenin	−0.62**	–	0.26**	0.33**
Gliadin	0.55**	0.31**	–	–
Low-molecular-weight insoluble protein	−0.25**	0.35**	0.33**	0.40**
SWS protein (25–100 kDa)	–	−0.36**	–	−0.36**
SWS protein (< 25 kDa)	−0.33**	−0.42**	–	−0.29**
Flour protein		–	−0.33**	–
Non-1RS lines				
Glutenin	−0.21**	0.26**	–	0.21**
Gliadin	0.65**	0.55**	0.40**	0.52**
Low-molecular-weight insoluble protein	−0.28**	–	–	–
SWS protein (< 25–100 kDa)	−0.18*	−0.50**	−0.28**	−0.39**
SWS protein (< 25 kDa)	−0.48**	−0.67**	−0.49**	−0.61**
Flour protein		0.41**	0.21**	0.41**

[a] Only statistically significant ($P < 0.05$) correlation coefficients are given with * = $P < 0.05$, ** = $P < 0.01$

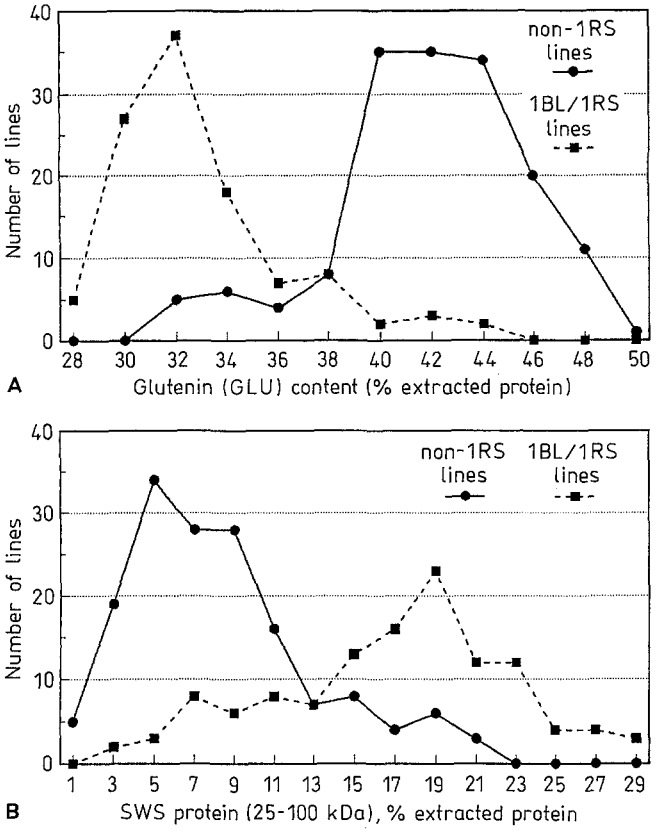

Fig. 5A, B Flour protein composition of 1BL/1RS and non-1RS lines. **A** Glutenin (GLU) contents of non-1RS and 1BL/1RS lines. **B** Salt-water soluble proteins, 25–100 kDa of non-1RS and 1BL/1RS lines

1RS lines, a relatively narrow distribution in glutenin concentration was observed. 1BL/1RS lines with glutenin concentrations that fell within the range of non-1RS lines were observed, although at a low frequency. SWS protein of MolWt 25–100 kDa illustrated an opposite trend compared with glutenin (Fig. 5 b). This fraction was significantly higher among 1BL/1RS than non-1RS lines. Again, only a minority of 1BL/1RS lines displayed concentrations of SWS protein of MolWt 25–100 kDa within the range observed for non-1RS lines.

Relationships between quality parameters and SE-HPLC fractions

Based on quality and biochemical characteristics, 1BL/1RS and non-1RS genotypes essentially formed two distinct groups. Genetic correlations were calculated separately for each genotypic class, in order to ascertain possible relationships between biochemical variation and flour quality.

Among 1BL/1RS lines (Table 7), glutenin was significantly correlated with MT and MTO. Gliadin concentrations were positively correlated only with SDSS volume, while low-molecular-weight insoluble protein was positively correlated with SDSS, MT, and MTO. Conversely, salt-water soluble fractions (SWS proteins, both fractions) were negatively associated with SDSS and MTO values.

Among non-1RS lines (Table 7), the amount of gliadin showed high positive correlations with all quality parameters. Both salt-water soluble fractions and low-molecular-weight insoluble protein were negatively correlated with all quality characteristics. Relatively low correlations between quality parameters and glutenin were observed among non-1RS lines, no doubt due to the narrow range in values observed for this fraction.

Discussion

The end-use quality and protein composition of 1BL/1RS lines was shown to be dependent on genetic background, as observed in previous studies (Graybosch et al. 1990; Pena et al. 1990). Compared within common genetic backgrounds, mean SDS sedimentation volume and Mixograph tolerance of 1RS lines was lower in six of seven populations. The populations in which no significant differences were observed between 1BL/1RS and non-1RS lines were characterized by comparatively low flour protein concentration and low quality values even for non-1RS lines. In populations 1 and 7, descended from the strong gluten parents Plainsman V and NE 80413, respectively, mean flour quality (SDSS, MTO) of 1RS lines equalled or exceeded the mean quality of the 1BL/1RS check variety, Siouxland. In most populations, 1RS lines (about 5% of the total sampled) with 'acceptable' quality (SDSS > 35 cc, MT > 3.5 min, and MTO > 15 mm) were observed; among non-1RS lines, approximately 50% were considered to have acceptable quality. Significant differences among 1RS lines for both SDS sedimentation volumes and Mixograph tolerance were observed in nearly all populations and indicate that enhancement of quality through traditional breeding and selection will be difficult, though possible.

Flour protein composition, as measured by molecular weight and solubility through SE-HPLC, showed variation among populations, and among 1RS and non-1RS sister lines within populations. The polymeric glutenin proteins are considered to be the most important component for dough elasticity and strength. Gliadin proteins are assumed to contribute to gluten viscosity or plasticity (Miflin et al. 1983). Glutenin concentration of 1RS lines was lower than that of non-1RS sister lines, and salt-water soluble proteins were increased in 1RS lines in all populations; in 1RS lines, the SWS protein fraction (MolWt 25–100 kDa) consists of albumins + globulins, omega secalins, and a portion of the gamma secalins (Graybosch et al. 1993). The percentage of gliadin in non-1RS lines did not differ from the percentage of gliadin in 1RS lines (which includes the salt-water insoluble gamma secalins), except in population 4. Differences observed in the remaining protein fractions also varied according to populations.

These results confirm, as previously observed (Dhaliwal et al. 1988; Lundh and MacRitchie 1989; Dhaliwal and MacRitchie 1990; Graybosch et al. 1990, 1993), that deleterious quality effects of 1BL/1RS lines arise from increased levels of salt-water soluble proteins, and decreased glutinin concentrations, resulting from the addition of rye secalin genes on 1RS, and the loss of low-molecular-weight glutenin genes located on the short arm of group-1 chromosomes. Both protein quality and quantity are important for end-use quality. In this study, flour quality characteristics were related to variations in protein solubilty, as previously reported (Dhaliwal et al. 1988; Lundh and MacRitchie 1989; Dhaliwal and MacRitchie 1990; Graybosch et al. 1990), as well as to variations in protein molecular-weight distributions, as observed earlier (Dachkevitch and Autran 1989; Singh et al. 1990 b; Graybosch et al. 1993).

In conclusion, while 1RS has a substantial negative effect on quality, the end-use quality of 1BL/1RS lines was highly dependent on genetic background. The potential exists for improvement in quality through breeding by combining 1RS lines with parents possessing high glutenin and gliadin, or low salt-water soluble protein, and non-1RS lines with strong gluten type. The detrimental quality effects of 1BL/1RS lines result from changing the appropriate ratio of flour protein compositions, especially decreased glutenin concentrations and increased salt-water soluble concentrations.

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