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MINI REVIEW

Uneasy Unions: Quality Effects of Rye Chromatin Transfers to Wheat

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ABSTRACT

A number of genes of agronomic importance have been transferred from rye (Secale cereale L.) to its close relative, common bread wheat (Triticum aestivum L.). Largely through the production of interspecific chromosomal translocation and substitution lines, rye chromatin now resides within the genome of a large number of wheat breeding lines and cultivars. Rye chromosomal materials have been used to transfer resistance genes to fungal pathogens, especially rusts and powdery mildew, resistance to insect pests, and, in some cases, may enhance grain yield, grain yield stability, and grain protein content. Unfortunately, the transfer of some rye chromosomal materials has resulted in deleterious effects on grain processing quality. This report reviews the use of various wheat-rye chromosomal translocations and substitutions in wheat breeding programs, examines the nature of the observed quality defects, and speculates as to their causes and possible means by which the quality effects might be ameliorated.

Keywords: wheat, rye, chromosomal translocations, processing quality.

INTRODUCTION

Bread wheat (Triticum aestivum L., 2n = 6x = 42), an allohexaploid species, carries the genomes of three ancestral species. These three genomes, designated A, B and D, are each composed of seven pairs of chromosomes. Within each genome, chromosomes are numbered 1–7, with each number designating a homoeologous set. Members of each homoeologous set are similar both in structure and in gene organisation, and can compensate for each other in nullisomic-tetrasomic lines1. In addition, alien chromosomes derived from related species of the grass Tribe Triticeae also may substitute for wheat chromosomes2. A number of wild and domestic relatives of wheat in the Triticeae long have been recognised as valuable sources of genes for wheat improvement. While alien chromosomes from such species may substitute for wheat chromosomes after successful hybridisation, such chromosomes often will not pair and recombine with wheat chromosomes. However, wide hybridisation, when followed by radiation treatment or the induction of homoeologous recombination can result in the successful transfer of chromosomes arms, or even smaller chromatin segments, via the formation of wheat-alien translocation lines2. This process of rearranging wheat chromosomes via the incorporation of alien chromatin is known as chromosome engineering, and it has been a mainstay of wheat improvement programs for nearly 50 years.

Alien chromatin, while carrying beneficial genes, also may have negative impacts on wheat yield and performance. It is more desirable, therefore, to eliminate as much alien chromatin as possible, other than the gene(s) of interest. Homoeologous recombination most often involves the use of pb- mutants; in such backgrounds, some
rerecombination can occur between wheat and homoeologous alien chromosomes. Once stabilised in wheat genomes in the presence of PH1 (wild-type allele), chromatin from non-A, B or D genome chromosomes will not recombine with wheat chromosomes. Thus, an introduced fragment of alien chromatin will act as one completely linked block of genes, even if the amount of chromatin is large.

The majority of alien chromosome segments conferring disease and pest resistance to wheat have been derived from species of the genus Aegilops (recognised by some authorities as not being a distinct genus from Triticum), two species of perennial wheat-grasses, Thinopyrum elongatum (Host) Dewey and Elytrigia intermedia (Host) Nevski, and from rye (Secale cereale L.,). The development of triticale (×Triticosecale Wittmack) has facilitated the movement of chromatin from rye to wheat. Hexaploid (AABBDD) or octoploid (AABBDDRR) triticales may be crossed with bread wheats (AABBDD), with resulting F1 progeny generally displaying both female and male fertility. Subsequent backcrossing can lead to the substitution of whole rye chromosomes for wheat chromosomes, or, at times, spontaneous translocation of rye chromosome arms to wheat chromosomes.

Quality-related effects rarely have been encountered with transfers from non-rye sources. Transfers from rye, especially those involving rye chromosome 1R, often result in significant alterations of wheat processing quality. Desirable genes from rye are often linked to traits that alter the grain composition of the recipient wheat cultivars. This review will concentrate on the use of rye chromatin in wheat, describing both positive and negative effects. Rye chromosomal materials transferred to wheat will be discussed in order of their frequency and impact on wheat breeding programs.

CHROMOSOME ARM 1RS

Origin and distribution of 1RS translocations

Translocation of the short arm (1RS) of rye chromosome 1R to wheat is the most common means by which rye chromatin has been introduced to wheat. In its various forms (see below) 1RS confers to wheat resistance to a number of pests and pathogens, and may enhance grain yield. Unfortunately, 1RS also is known to have detrimental effects on grain processing quality. The decline in quality may be related to the presence of Sec-1, a complex locus conditioning the production of several rye secalin proteins.

1RS has been transferred to wheat in the form of 1AL.1RS, 1BL.1RS and 1DL.1RS wheat-rye chromosomal translocations, with the 1AL.1RS and 1BL.1RS translocations having the greatest impact in wheat breeding and production.

The first 1AL.1RS translocation was found in the wheat germplasm line ‘Amigo’, and was derived from ‘Insave’ rye via the octoploid triticale ‘Gaucho’. X-ray treatment was used to induce the translocation. The Amigo translocation carries genes for resistance to powdery mildew (Erysiphe graminis DC.) and green bug (Schizaphis graminum Rond.) and provides tolerance to the wheat curl mite (Eriophyes tulipae Keiffer), the vector of wheat streak mosaic virus (WSMV). The Amigo translocation also apparently carries a gene for stem rust (Puccinia graminis Pers.) resistance, but the precise allelic series is not known. A second 1AL.1RS translocation was released in the germplasm line GRS12015. The GRS translocation also confers resistance to green bug, but the resistance allele (Gb6) differs from that (Gb2) found on 1AL.1RS of Amigo. The GRS and Amigo translocations also may be differentiated by secalin pattern as determined by sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) and through use of DNA markers. The GRS translocation can be traced to the same rye source (Insave) as the Amigo translocation, but, based on the traits noted above, it clearly differs in its genetic composition. Insave rye must have been polymorphic for genes present on 1RS, and two independent translocations were produced. Rye is an open-pollinated crop, and such heterogeneity is to be expected.

At least two, and perhaps three, independent origins of 1BL.1RS translocations are known. Two 1BL.1RS translocations can be traced to 1R(1B) substitution lines independently produced by two breeding programs in Germany. Subsequent crossing to wheat led to the production of 1BL.1RS translocations. The substitution line ‘Zorba’, developed in Weihenstephan, gave rise to a number of 1BL.1RS translocation lines in the former West Germany. A second 1R(1B) substitution line, ‘Salzmünder Bartwiesen’, produced in Salzmünde, gave rise to a number of 1BL.1RS translocation lines in Eastern European breeding programs.

‘Kavkaz’, a 1BL.1RS derivative of Salzmünder Bartwiesen produced in Krasnodar, Russia, was distributed by various channels to wheat breeding
programs throughout the world. The Kavkaz 1BL.1RS translocation probably has had more worldwide impact on wheat breeding and production than any other piece of alien chromatin.

The two 1BL.1RS translocations originating in Germany may have a common ancestry. Molecular markers, and responses to stem and leaf rust races of the two translocations are identical. The Salzmünde translocation reportedly was derived from ‘Petkus’ rye, while the Weihenstephan translocation can be traced to crosses with triticale. However, it also has been reported that seed of Salzmünde Bartwiezen was distributed to wheat breeding programs throughout Germany. Whatever their origin, these two 1BL.1RS translocations are nearly identical in the phenotypes they confer to wheat. Both condition resistance to stem, leaf and stripe rusts, and each carries a gene for resistance to powdery mildew. The powdery mildew resistance gene is suppressed, however, in some wheat backgrounds.

In Japan, a third 1BL.1RS translocation was produced in the wheat ‘Salmon’. Salmon was derived from crosses between two octaploid triticales. This translocation conditions resistance to the wheat curl mite, but does not confer resistance to mechanical inoculation of WSMV. Unlike the European 1BL.1RS translocations, the Salmon translocation apparently has not been widely used in wheat improvement programs. Salmon did contribute to the development of KS80H4200, a wheat germplasm line released by Kansas State University (U.S.A.). KS80H4200 is resistant to the wheat curl mite. At least in the U.S.A., neither Salmon nor KS80H4200 have contributed to further cultivar development. A search of the USDA-GRIN database for contributions to pedigrees of registered wheats revealed no contribution for either line. Based on molecular markers, the Salmon translocation is distinct from the German sources.

A 1DL.1RS translocation was produced in Australia, incorporating 1RS from ‘Imperial’ rye. This translocation also carries a gene for resistance to stem rust, but it is not known whether the resistance allele differs from that found in Kavkaz 1BL.1RS translocations. To date, no rust race has been found that will differentiate the two alleles. Isolines of the cultivars ‘Gabo’ and ‘Warigal’ carrying 1DL.1RS have been developed, but the translocation apparently has not been released in any cultivars to date.

In addition to the disease and pest resistance genes, 1RS translocations, especially Kavkaz 1BL.1RS, have further beneficial effects. Kavkaz 1BL.1RS has been shown to increase grain protein content, and to increase grain yield, at least in some genetic backgrounds and in some environments. Both the Kavkaz and Salmon 1BL.1RS translocations can be used to generate haploid seedlings, when combined with the cytoplasts of certain species of Aegilops. Haploid induction is useful as a means of increasing the rate at which lines reach homozygosity in wheat breeding programs. Genes on 1RS translocations enhance embryo and callus growth in tissue culture, and improve regeneration of microspore derived haploid embryos. It may be no accident that ‘BobWhite’, long a favourite cultivar in tissue culture and wheat transformation experiments, carries 1BL.1RS.

The Kavkaz 1BL.1RS and Amigo 1AL.1RS translocations most frequently appear in wheat cultivar improvement programs. To date, approximately 300 cultivars and germplasm lines carrying 1BL.1RS have been released, and most were released since 1970. 1BL.1RS cultivars are worldwide in their distribution, with the notable exception that none have been released in Australia. In contrast, 1AL.1RS translocations are present only in wheats released in the U.S.A. Based on their continued presence in elite germplasm, 1RS translocations will probably continue to be deployed in newly released cultivars. The frequency of 1RS translocations in U.S. hard and soft winter wheat breeding programs has been assessed by screening breeding lines entered in the USDA-ARS coordinated Regional Performance Nurseries. These five trials (Uniform Western Hard Winter Wheat Regional Performance Nurseries, and the Southern, Northern and Western Plains Hard Winter Wheat Regional Performance Nurseries) include experimental lines being considered for cultivar release from breeding programs primarily located east of the North American Continental Divide. In 1989, the first year a survey was conducted, the frequency of 1BL.1RS and 1AL.1RS was 7.8%, respectively. The survey was initiated in 1993, and has been conducted each year since. Throughout the 1990s, the total frequency of 1RS in these trials has ranged from 20–30%; there has been a slight decline in the frequency of 1AL.1RS lines, but 1BL.1RS frequencies have remained essentially constant (Table I). As many of the lines entered
in these trials eventually are released as cultivars, and all of the lines are used as parents in cultivar improvement programs, 1RS translocations likely will continue to have an impact on wheat production systems.

Several possible factors may explain the widespread occurrence of 1RS translocations in wheat improvement programs and cultivars. One possibility is meiotic drive; that is, 1RS may be transferred to progeny at a higher than expected frequency. As 1RS enhances embryo growth from microspore-derived calli, it is tempting to speculate that a similar effect could occur in pollen, and 1RS-containing pollen might reach the ovule more often than non-1RS pollen in F1 plants. However, studies on the inheritance of 1RS in crosses13,19,25 have suggested that when departures from expected frequencies are observed, there is a deficiency, rather than an excess, of 1RS.

Selection for disease resistance is the most likely cause for the widespread distribution of 1RS. Even though resistance to stripe and leaf rusts broke down after 20 years ago25, and the green bug resistance gene found on the Amigo 1AL.1RS translocation also has been overcome12, stem rust and powdery mildew resistance genes are still effective. As most disease resistance selection is based on phenotypic responses, 1RS can unconsciously be perpetuated in breeding programs.

Stem rust is more prevalent in drier regions of wheat cultivation (e.g., the northern Great Plains of North America), while powdery mildew is prevalent in more mesic zones such as eastern North America and Western Europe. Selection for resistance to these two pathogens in two vastly different wheat gene pools may have contributed to the worldwide distribution of 1BL.1RS. In this regard, however, it is puzzling that the Amigo 1AL.1RS translocation has not moved into breeding programs outside of North America, especially as it does carry a gene for resistance to powdery mildew.

Enhanced grain yield associated with the presence of 1RS in some genetic backgrounds and environments23,25 has also, no doubt, contributed to its widespread distribution. This effect, however, is not always observed33,35. Perhaps more important is the fact that, by this stage in its history, 1RS just happens to be present in a large number of lines that wheat breeders would consider ‘good’ parents in crossing programs. Just as in thoroughbred breeding, good parents beget good progeny, and 1RS is maintained via accidental inheritance, as a consequence of selection for disease resistance traits, by conditioning higher grain yield or stability for grain yield, or by a combination of the above.

Identification of 1RS translocations in wheat

There apparently are as many procedures for the identification of 1RS as there are scientists studying 1RS. The presence of specific disease resistance alleles may be used to infer the presence of a given translocation. For example, a line possessing Pm17 may be assumed to carry Amigo 1AL.1RS, or a line possessing La26, Sc31, Th9, or Pm8, no doubt carries Kavkaz 1BL.1RS3. Such identifications require specialised knowledge of pathogen races, and detailed testing. Alternative, and more widely used methods include cytogenetic observations, especially after G-banding of chromosomes3,34,35,36, DNA-based approaches37,41 using either labelled rye DNA as probes in Southern hybridisations or rye-specific DNA sequences as primers for polymerase chain reactions, isozyme analysis35, near infrared reflectance spectroscopy (NIR)3, or various methods based on the detection of rye grain storage proteins, also known as secalins.

1RS contains the Se-1 locus, a complex locus encoding two types of rye storage proteins, α-secalins and γ-secalins37. Estimates of the Mrs of α-secalins range from 40 000 to 51 000, while the Mrs of the 1RS-encoded γ-secalins range from 36 000 to 40 000.44,45. When 1RS is present, loci

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**Table I** Frequency of 1RS wheats in USDA-ARS Southern Soft Red, Eastern Soft Red, Southern Hard, Northern Hard and Western Plains Hard Winter Wheat Regional Performance Trials

<table>
<thead>
<tr>
<th>Year</th>
<th>Total no. lines</th>
<th>% 1AL.1RS</th>
<th>% 1BL.1RS</th>
<th>% non-1RS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>140</td>
<td>5.7</td>
<td>7.8</td>
<td>86.5</td>
</tr>
<tr>
<td>1993</td>
<td>106</td>
<td>16.0</td>
<td>15.1</td>
<td>68.9</td>
</tr>
<tr>
<td>1994</td>
<td>170</td>
<td>12.9</td>
<td>14.0</td>
<td>73.1</td>
</tr>
<tr>
<td>1995</td>
<td>171</td>
<td>12.9</td>
<td>14.0</td>
<td>73.1</td>
</tr>
<tr>
<td>1996</td>
<td>142</td>
<td>12.7</td>
<td>13.3</td>
<td>74.0</td>
</tr>
<tr>
<td>1997</td>
<td>172</td>
<td>7.6</td>
<td>18.0</td>
<td>74.4</td>
</tr>
<tr>
<td>1998</td>
<td>166</td>
<td>6.0</td>
<td>16.9</td>
<td>77.1</td>
</tr>
<tr>
<td>1999</td>
<td>175</td>
<td>8.0</td>
<td>14.2</td>
<td>77.8</td>
</tr>
<tr>
<td>2000</td>
<td>183</td>
<td>6.6</td>
<td>13.3</td>
<td>79.1</td>
</tr>
<tr>
<td>mean</td>
<td>161</td>
<td>10.3</td>
<td>14.7</td>
<td>75.0</td>
</tr>
</tbody>
</table>

1 From Lukaszewski30.
encoding wheat low-molecular-weight (LMW) glutenin subunits and gliadins are lost from the particular short arm (1AS, 1BS, or 1DS) of the chromosome involved in the translocation. The presence of the rye secalins, coupled with the loss of wheat LMW glutenin and gliadin proteins, has led to a number of procedures to identify 1RS based on grain storage protein composition. In addition, the γ-secalins are more water-soluble than γ-gliadins and most wheat gliadins; this has facilitated the development of storage protein-based methods of 1RS identification. Procedures include the detection of the presence of secalin or absence of wheat proteins in seed or flour protein extracts via acid- or SDS-PAGE, high-performance liquid chromatography (HPLC), capillary electrophoresis, and various immunological approaches. The latter include both the use of monoclonal antibodies against wheat proteins whose absence indicates the presence of 1BL.1RS, or the use of anti-secalin monoclonal antibodies to directly detect 1RS gene products.

Speculation as to the ‘best’ approach to identify 1RS is somewhat fruitless. The ‘best’ approach is dependent upon the expertise and goals of the individual research group. Secalin detection systems for 1RS identification do have some distinct advantages over disease resistance, cytogenetic observations or DNA-based procedures. Secalins are easily extracted from grain or flour with single solvent treatments, using either aqueous ethanol ranging from 30–70%, 0.04 M NaCl, or even water. In addition, secalins may be detected in flour samples, where no chromosomes and precious little DNA will be found. Many end-users of wheat products, especially bakers, only deal with flour samples, but may still wish to screen samples to determine whether they were derived from 1RS wheats.

Cytogenetic observations can unambiguously determine the nature of the 1RS translocation present. DNA approaches also can identify the origin of the 1RS segment. The Amigo 1AL.1RS translocation and the Kavkaz 1BS.1RS translocations may be differentiated by isozyme analysis, a combination of anti-secalin and anti-gliadin monoclonal antibodies, or by SDS-PAGE separation of grain or flour proteins to detect differences in secalin patterns. In addition, coupled with knowledge of pedigrees, any procedure that can detect 1RS-encoded secalins may be used to identify the precise translocations in breeding programs. Caution may need to be exercised in the future, however, with respect to the use of methods, other than cytogenetic, to distinguish the various 1RS translocations. Green bug resistance alleles, DNA markers, and secalin patterns may differentiate the GRS 1AL.1RS translocation from the Amigo 1AL.1RS translocation. However, the two will recombine in intermatings, giving rise to new allelic combinations on 1RS. The secalin pattern of GRS 1AL.1RS does not differ than that of Kavkaz.

Use of secalin proteins alone could therefore give erroneous results. In addition, the Kavkaz 1RS segment has been moved, via centric misdivision, to form a new 1BL.1RS translocation, and the Amigo 1RS has been used to create a new 1BL.1RS translocation. In the future, it might be necessary to identify both the 1RS arm in question, and its chromosomal location, if a precise identification is required.

All that glitters is not gold—quality effects of 1RS in wheat

It has long been recognised that the introduction of 1RS to wheat has not been without negative effects, particularly with regard to end-use quality. Once introduced to wheat, 1RS segments are inherited as one non-recombined block of genes; thus, any beneficial genes are perpetually linked to any deleterious ones. In addition, introduction of 1RS requires the loss of the short arm of at least one wheat chromosome pair, with a concomitant loss of some potentially important wheat genes.

Severe quality problems most often are recognised when 1BL.1RS is present in hard wheat backgrounds. The most typical defects, generally determined from small-scale or ‘breeder’ level tests, include low specific loaf volumes (loaf volume per unit flour protein), the production of ‘sticky’ doughs, a lack of tolerance of doughs to overmixing, and low SDS sedimentation volumes. In addition, when dough strength is measured in a Mixograph, there is a pronounced lack of correlation between time to peak dough resistance, and tolerance to overmixing (measured as width of the mixogram at a defined time, perhaps 2 or 3 min, after peak resistance). The term ‘dough unmixing’ was coined to describe this effect. When tested with commercial-scale equipment, problems with dough handling and dough stickiness also were noted.
Quality effects of 1DL.1RS translocations are similar to those of 1BL.1RS\textsuperscript{65}, but the commercial impact of such translocations has been negligible. 1AL.1RS translocations also diminish quality, but the effect is not as severe as that observed with 1BL.1RS\textsuperscript{52,63}. Relative to non-1RS sister lines, mixing strength and SDS sedimentation volumes are reduced in 1AL.1RS lines, but the effects are not as great as in 1BL.1RS wheats. Elevated flour protein contents were reported when 1AL.1KS lines were compared to non-1RS sibs\textsuperscript{65}. Certain 1AL.1KS cultivars, especially TAM-107, have been long criticised by the American milling and baking industry for poor commercial performance. TAM-107 does suffer from poor internal appearance of baked loaves, but it is not known whether this effect is attributable to the presence of 1RS. TAM-107 also differs more from conventional wheats in large scale testing than in small-scale tests. A collection of 48 samples per cultivar were independently assayed in a small-scale test bake laboratory at the University of Nebraska, and in a large-scale quality control lab at the American Institute of Baking in Manhattan, Kansas. Data (Table II) revealed that while TAM-107 differed little from a set of typical U.S. hard red winter wheats in small-scale tests, mean mixing times of TAM-107 in the larger scale quality control tests were significantly lower than those of all other cultivars. Thus, while quality defects are not always detected with testing methods used in wheat improvement programs, there may still be an impact at the commercial level.

Flours from 1BL.1RS wheats often have been described as producing 'sticky' doughs; the term rarely is applied to 1AL.1RS wheats. Some reports on the topic\textsuperscript{66,67} considered the effect to be associated with over-mixing, and suggested a common cause to both dough stickiness and lack of tolerance to overmixing. Others\textsuperscript{67} presented evidence that dough stickiness could be measured at peak dough resistance, and that it was not necessarily an effect of overmixing. Complicating the matter is the observation that factors such as sprout damage, which have no relationship to the presence/absence of 1RS, also may cause dough stickiness\textsuperscript{66}.

Investigations as to the origin of the quality defects associated with 1RS have concentrated on changes in flour protein and carbohydrate.

### Table II  Small-scale and large-scale results of TAM-107 (1AL.1RS) relative to non-1RS hard winter wheat cultivars

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>flour protein (0% mb)</th>
<th>bake absorption (%)</th>
<th>bake mix time (min)</th>
<th>loaf volume (mL)</th>
<th>loaf grain score (0–10)</th>
<th>Mixograph peak time (min)</th>
<th>Mixograph tolerance (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abilene</td>
<td>13.5</td>
<td>60.6</td>
<td>5.7</td>
<td>932</td>
<td>7</td>
<td>3.7</td>
<td>17.8</td>
</tr>
<tr>
<td>Arapahoe</td>
<td>13.2</td>
<td>60.7</td>
<td>6.9</td>
<td>848</td>
<td>6</td>
<td>4.9</td>
<td>16.5</td>
</tr>
<tr>
<td>Gimirron</td>
<td>13.6</td>
<td>60.2</td>
<td>7.0</td>
<td>926</td>
<td>8</td>
<td>4.5</td>
<td>20.6</td>
</tr>
<tr>
<td>Karl</td>
<td>14.5</td>
<td>60.5</td>
<td>6.5</td>
<td>987</td>
<td>6</td>
<td>4.2</td>
<td>20.4</td>
</tr>
<tr>
<td>Scout 66</td>
<td>13.7</td>
<td>61.1</td>
<td>4.6</td>
<td>867</td>
<td>6</td>
<td>3.1</td>
<td>18.4</td>
</tr>
<tr>
<td>TAM-107</td>
<td>13.3</td>
<td>61.4</td>
<td>5.4</td>
<td>876</td>
<td>6</td>
<td>3.7</td>
<td>17.1</td>
</tr>
<tr>
<td>ls.d. (0.05)</td>
<td>0.60</td>
<td>0.50</td>
<td>0.50</td>
<td>22</td>
<td>1</td>
<td>0.5</td>
<td>0.90</td>
</tr>
</tbody>
</table>

### Table II  Large-scale tests

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>bake absorption (%)</th>
<th>bake mix time (min)</th>
<th>bake tolerance (0–6)</th>
<th>loaf volume (mL)</th>
<th>loaf grain (0–10)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abilene</td>
<td>57.8</td>
<td>11.5</td>
<td>3</td>
<td>2744</td>
<td>7</td>
</tr>
<tr>
<td>Arapahoe</td>
<td>54.6</td>
<td>11.1</td>
<td>3</td>
<td>2551</td>
<td>6</td>
</tr>
<tr>
<td>Gimirron</td>
<td>57.6</td>
<td>16.4</td>
<td>4</td>
<td>2685</td>
<td>7</td>
</tr>
<tr>
<td>Karl</td>
<td>58.8</td>
<td>20.9</td>
<td>4</td>
<td>2799</td>
<td>7</td>
</tr>
<tr>
<td>Scout 66</td>
<td>58.9</td>
<td>13.2</td>
<td>3</td>
<td>2638</td>
<td>6</td>
</tr>
<tr>
<td>TAM-107</td>
<td>60.8</td>
<td>7.1</td>
<td>2</td>
<td>2804</td>
<td>5</td>
</tr>
<tr>
<td>ls.d. (0.05)</td>
<td>1.5</td>
<td>3.1</td>
<td>0.4</td>
<td>72</td>
<td>1</td>
</tr>
</tbody>
</table>
composition. The secalin proteins arising from Sec-1 locus on 1RS are monomeric proteins, while LMW glutenin subunits arising from Gli-3 loci, lost with the short arms of group 1 wheat chromosomes, can form intermolecular disulphide bonds, and can participate in the formation of the glutenin protein matrix, the primary determinant of dough strength. Numerous reports have shown changes in protein composition associated with 1RS. In all studies, there was a measurable decrease in the amount of polymeric glutenin protein, and an increase in the amount of water-soluble proteins. The loss of glutenin is a consistent feature of 1RS wheats; the identification of 1RS via NIR appears not to be a direct measure of secalin proteins, but to be based on the detection of diminished glutenin content. The α-secalins are more abundant in the water-soluble fraction. In addition, the loss of glutenin protein is not as great in 1AL.1RS wheats, coinciding with a less drastic reduction in dough strength. Also, lines carrying both 1AL.1RS and 1BL.1RS in homozygous condition, showed a marked reduction in dough strength over lines with 1BL.1RS alone, and exhibited both an increased loss of glutenin content and an enhanced elevation in the amount of water-soluble proteins. It is not possible to determine whether the loss of glutenin or the increased water-soluble proteins is the primary cause of diminished quality, as the effects are always exhibited together. The loss of glutenin protein leads to a reduction in the amount of insoluble gel protein, and the insoluble gel protein removed from 1RS wheats breaks down faster under mixing. Interchange experiments, on the other hand, suggested that dough stickiness was due to the water-soluble fraction. In addition, the α-secalins are extremely water soluble, and replace more hydrophobic gliadin proteins, also arising from genes on the short arms of group 1 wheat chromosomes. Gliadins, while not forming part of the glutenin matrix, do contribute to quality factors, especially water absorption and loaf volumes. It is very likely that the loss of glutenin, and gain of more water-soluble proteins, work in concert to reduce wheat processing quality.

The role of carbohydrates in the reduction of 1RS wheat quality also has been addressed. Rye flour is known to contain significant levels of pentosans, so there has been some thought that these might be elevated in 1RS lines. However, several investigations failed to detect elevated pentosans in 1RS wheats. Unpublished findings in the author’s laboratory have found higher pentosans in TAM-107, a 1AL.1RS wheat, but the same effect was observed in several other hard wheats derived from the southern Great Plains of the U.S., and all did not carry 1AL.1RS. Thus, it is not known whether the elevated pentosans of TAM-107 are due to 1RS, or to some other factor in the genetic background. The elevated pentosans of TAM-107 may be the cause of the consistently higher bake water absorptions observed with this cultivar (Table II). Finally, a substance causing sticky doughs was purified from the 1BL.1RS cultivar ‘Siouxland’. This substance was reported to be a ferulic acid moiety attached to a carbohydrate chain. No studies with isogenic lines or sister lines were reported, and the compound apparently has been purified from only one 1RS wheat. Hence, it remains to be determined whether this compound indeed is related to dough stickiness of other 1RS wheats.

Little is known of the effects of 1AL.1RS on soft wheat quality. In contrast to the situation in hard wheats, the presence of 1BL.1RS in soft wheats has not been considered to be overly detrimental to processing quality. Some effects, however, have been observed. Dough stickiness of the Australian cultivar ‘Egret’ differed little from that of a backcross derivative carrying 1BL.1RS. Samples of 1BL.1RS and non-1RS sister lines, examined in two soft red winter wheat backgrounds, showed reduced flour yield and an increase in alkaline water retention capacity, which may be detrimental to soft wheat baking quality. With the same materials, no significant effect of 1BL.1RS on soft wheat grain yield was detected. In a recent study, Farinograph mixing tolerances, cake volumes and cake texture of 1BL.1RS soft wheats did not differ from non-1RS controls; however, 1BL.1RS displayed lower flour yields, increased Farinograph water absorption and lower cookie spreads.

The effects of 1BL.1RS on soft wheat quality, then, appear to be dependent upon the trait in question. Traits related to water absorption seem to be negatively affected, perhaps due to the increase in hydrophilic secalin proteins, and the decrease in hydrophobic glutenin proteins. As most soft wheat products do not require a strong gluten, or high protein, negative effects might not be observed. There is anecdotal evidence in the U.S., however, that suggests 1BL.1RS has a negative effect on soft wheat products such as crackers, in which some gluten strength is desired. Reduced
flour yields associated with 1BL.1RS in soft wheats have not been reported in hard wheats, although 1AL.1RS wheats derived from the heterogenous hard red winter cultivar ‘Nekota’ had reduced flour yields relative to non-1RS sibs. The origin of this effect is unknown.

**Strategies to improve the quality of 1RS wheats**

Several strategies have been or could be used to alleviate the deleterious quality effects associated with 1RS. In the U.S., several cultivars, including ‘Rawhide’, ‘Nekota’ and ‘Niobrara’, all from Nebraska, have been released with either 1AL.1RS or 1BL.1RS present in a heterogeneous condition. In such lines the disease resistance traits may still be partially exploited, and the deleterious effects of 1RS are somewhat masked by the presence of non-1RS sibs within any cultivated field. Similarly, deployment of 1RS in hybrid wheats, with one parent being a non-1RS line, can be used to mask the negative effects. Recent economically based decisions in the private sector, however, have cast doubt on the future of hybrid wheats in North America.

It is quite clear that the magnitude of the effect of 1RS on quality varies with genetic background, that significant differences exist among 1RS lines within populations, and that populations derived from at least one strong gluten parent have the best chances of producing 1RS wheats with acceptable dough strength. By judicious selection of parents in crosses with 1RS wheats, the effects can be diminished. In some backgrounds, 1RS lines with mixing tolerance nearly equal to that of non-1RS sibs may be obtained. The experimental line N95L11881, a homogeneous 1BL.1RS line with the pedigree Siouxland/2*N86L177, demonstrated tolerance to overmixing equal to that of N95L11880, a non-1RS sister line. Mixing tolerance of N95L11881 was not as great as its strong gluten parent, N86L177, but it was far superior to that of Siouxland, the 1BL.1RS parent (Fig. 1). Careful selection of parents is necessary, however, to obtain lines with this degree of mixing tolerance.

Selection of parents requires more than merely placing 1RS in a genetic background with optimal combinations of high-molecular-weight (HMW) glutenin subunits. Lines with optimal HMW glutenin subunits and 1RS will still exhibit quality defects, especially relative to non-1RS sister lines. However, as diminished glutenin content is symptomatic of 1RS lines, strategies that could increase glutenin content might alleviate the quality problems. Even though only LMW glutenin subunits are lost when 1RS is present, the glutenin matrix is a massive polymer composed of both HMW and LMW subunits. If increasing either HMW or LMW glutenin subunit content can increase the size and amount of this complex, then 1RS quality might improve. Introducing Glu-A1 alleles from certain accessions of *T. dicoccoides* could increase the number of active HMW glutenin subunits. The HMW glutenin encoding loci are compound loci, composed of two tightly linked genes, one encoding an ‘x’ subunit, the second producing a ‘y’ subunit. In nearly all bread wheats, the y-encoding gene on chromosome 1A is inactive; however, in some *T. dicoccoides* samples, both Glu-A1 x and y subunits are produced. Similarly, at least two wheat lines, 1AA36 and ‘Red River 68’, carry duplications at the Glu-B1 locus that result in an over-production of HMW glutenin subunit 1Bx7.

Chromosome engineering also can be employed to improve 1RS quality. By use of ph- mutants, recombination between 1RS and 1DS produced secondary recombinant chromosomes in which the amount of rye chromatin was reduced. One line, designated 82-180, carried a chromosome containing the portion of 1RS carrying Sec-1 and a stem rust resistance gene, but also had the terminal region of 1DS on which Glu-D1 (and most likely the closely linked Glu-D3 locus as well) resides. Dough strength of 82-180, as measured by an Extensigraph, was markedly greater than that of the 1DL.1RS parental line. Additional chromosome engineering of 1RS has been conducted. The 1RS arm from Kawkaz 1BL.1RS has been used to create a new 1AL.1RS translocation. This could allow continued exploitation of useful genes from this 1RS source, but, as 1AL.1RS appears to be a better vehicle for the deployment of rye chromatin, the quality effects might not be as severe. Chromosome rearrangement of 1RL also might be useful. The region of 1DL encoding HMW glutenin subunits 1Dx5 + 1Dy10, the most beneficial in terms of effects on dough strength and processing quality, has been transferred to chromosome 1R, and used to replace the region surrounding the Sec-3 locus. Introgression of this chromosome into wheat could result in 1RS lines possessing double doses of these highly beneficial glutenin subunits. Recently, novel 1RS arms were produced in which the portion en-
coding Sec-1 was removed by homoeologous recombination, leaving the disease resistance genes intact. The use of such materials may herald the end of 1RS-related quality problems.

Genetic engineering also may contribute to improved 1RS quality. Antisense RNA approaches could be used to reduce secalin production; however, the Sec-1 locus is rather complex, and it has been estimated that at least 10–30 copies of the α-secalin structural gene are present. Thus, it might be difficult to “knock-out” all the RNA arising from Sec-1 to reduce secalin concentration. Also, elimination of secalin alone may not solve the problem. If the reduction of secalin were accompanied by an increase in gluten protein synthesis, then one would expect an improvement in dough strength. However, the loss of HMW glutenin genes via spontaneous mutation does not result in compensation by other gluten proteins; rather, there is an increase in non-gluten water-soluble proteins. Thus elimination of secalins should perhaps be accompanied by an increase in gluten protein content.

Figure 1. Mixograms of parental lines. (a) Siouxland (1BL.1RS), (b) N86L177 (non-1RS), and two progeny lines, (c) N95L11880 (non-1RS) and (d) N95L11881 (1BL.1RS).

Genetic engineering has successfully introduced additional copies of HMW glutenin subunit encoding genes. In one case, such experiments led to an increase in the amount of HMW glutenin subunit 1Dy10, with a concomitant increase in dough strength. The recipient cultivar, BobWhite, carries 1BL.1RS; thereby this experiment demonstrates that addition of HMW glutenin genes to translocation lines via transformation can improve quality. Similar experiments to replace lost LMW glutenins and gliadins might restore 1RS quality to wild-type levels.

CHROMOSOME ARM 1RL

Several cultivars carrying whole 1R chromosomal substitutions have been released, especially from European breeding programs. Such lines carry chromosome arm 1RL, in addition to 1RS. 1RL does not appear to carry any genes of direct agronomic importance in wheat. It does, however, carry the Sec-3 locus; Sec-3 encodes HMW
scalins, proteins homologous to HMW glutenins. While wheat-rye chromosomal translocations involving 1RL have been reported, no direct observations of the quality effects of HMW scalins, independent of the 1RS-encoded scalins, have been reported. When purified HMW scalins were reoxidised and incorporated into wheat gluten, a significant reduction was observed in both dough and gluten strength. The effect was attributed to lower surface hydrophobicities, and it was predicted that the expression of HMW scalins in wheat would have negative effects on quality. This was confirmed when 1B(1R) substitution lines were compared to 1BL 1RS sister lines. The addition of 1RL resulted in further reductions in dough strength parameters relative to 1RS alone. In addition, 1R(1B) lines had softer kernels than 1BL 1RS lines, but it was not determined whether this was due to an undescribed gene directly effecting grain hardness, or if it was due to some secondary effect of HMW scalins. A rearranged 1RL chromosome incorporating the portion of 1DL containing Glu-D1 has been developed; this chromosome could be used to increase the dosage of genes encoding the beneficial HMW subunits 1Dx5 1Dy10. Otherwise, the lack of any beneficial genes, and the apparent negative impact on quality, suggest 1RL should be avoided in breeding programs.

CHROMOSOME 2R

Both 2RL and 2RS have been introduced to wheat, primarily in the form 2BS 2RL and 2BL 2RS chromosomal translocations. 2RL carries genes for resistance to powdery mildew, leaf rust, and Hessian fly (Mayetiola destructor Say), and confers tolerance to barley yellow dwarf virus. Germplasm lines carrying 2RL have been released. One 2RL line was given the name ‘Hamlet’, an unfortunate choice as there also is a European cultivar with the same name that carries 1BL 1RS. 2RL does not carry any known genes encoding grain storage proteins. PCR markers have been developed that allow the identification of 2RL in wheat genetic backgrounds. Lines carrying 2RL had reduced grain test weights, flour yields and grain hardness relative to non-translocation sister lines. The effects, however, were modest, and there were no apparent effects on breadmaking properties. Hence, 2RL may prove quite useful to wheat breeding programs in the future.

2RS carries Sec-2, a locus encoding 75 k γ-scalins. Wheat lines carrying 2RS may be identified either by SDS-PAGE or via monoclonal antibodies specific to the 75 k γ-scalins. 2RS also reportedly carries genes that elevate grain protein in wheat; however, 2RS also appears to reduce grain yield, so it is not known whether the elevated protein is due to any active genes for the trait, or if it is a secondary consequence of reduced grain yield. In triticale, the 75 k γ-scalins will form polymers with HMW scalins; however, the observed polymers were of lower molecular weight than typical wheat glutenin polymers. Such a situation in wheat could result in diminished dough strength, although lines carrying 2RS were found to have higher extensigraph resistances than non-2RS sister lines. 2RS lines also had significantly higher protein content, so, at this time, it is not known whether the observed changes in Extensigraph resistance arise from some effect of the 75 k γ-scalins, or are merely a consequence of higher flour protein contents.

CHROMOSOMES 3R-7R

Chromosomes 3R, 4R, 5R, 6R and 7R carry genes of potential benefit to wheat breeding programs, and several translocations involving these chromosomes have been produced. Genes for resistance to powdery mildew are found on chromosomes 5R and 6R, genes for enhanced tolerance to high soil aluminium are found on chromosomes 3R, 4R, 6R and 7R. 6R carries a gene for resistance to cereal cyst nematode (Heterodera avenae Woll). Chromosome 5RL can enhance copper efficiency in wheat. Several rye chromosomes were found to be involved in triticale tolerance to the Russian wheat aphid (Diuraphis noxia Mordvilko), and further study confirmed the presence of a single dominant gene on chromosome 4R. No reports of quality effects of these chromosome arms are known.

CONCLUSIONS

Various rye chromosomes have been found to carry genes of verified or possible agronomic importance in wheat. Chromosome arms 1RS and 2RL are most notable in this regard. Quality problems are most acute with chromosome arms (1RS, 1RL) that encode rye grain storage proteins.
These effects arise as a consequence of biochemical features of the secalin, or are due to the loss of glutenin and gliadin encoding genes from the replaced wheat chromosome arms. 1RS translocations, in their original Kavkaz and Amigo packages, will continue to impact breeding programs for many years to come. These translocations are widespread in the elite wheat gene pools of many countries. Hence, crosses with 1RS parents will continue, and phenotypic selection for disease resistance and grain yield will result in continued deployment of this beneficial, though at times, annoying, chromosome arm. Careful selection of parents for crosses with known 1RS lines, coupled with rigorous selection for end-use quality, can diminish the negative impact of 1RS on wheat quality. In addition, the tools of chromosome engineering or genetic engineering can now be used to improve the quality of 1RS lines. Concerted efforts by geneticists and breeders are needed to deploy new forms of 1RS, to couple 1RS with new genes introduced via novel and conventional means, and to move these traits to elite genetic backgrounds. Through such efforts, a plant species many consider to be a roadside weed can continue to contribute to the improvement of its biological cousin.

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