

Enhancing the resistance of triticale by using genes from wheat and rye

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Abstract. At present two separate nomenclature systems exist for wheat and rye. This paper provides a proposed common catalogue of wheat, rye and triticale resistance gene symbols. More than 130 postulated wheat resistance genes are listed. Over 39 rye and 6 triticale resistance (R) genes have been identified and named. Genes responsible for reaction to powdery mildew and to leaf, stem and yellow rusts are the best-represented group of resistance genes. From the common catalogue it can be concluded that there exists a potential for further transfer of rye resistance genes to wheat and triticale. Many molecular markers can be applied for marker-assisted gene transfer, but the expression of the R genes in the new genetic background of triticale remains to be investigated.

Key words: homoeologous genes, pathogen resistance genes, rye, triticale, wheat.

Introduction

The Catalogue of Gene Symbols for Wheat has been compiled for over 30 years; after each Wheat Genetic Symposium it is updated on GrainGenes websites, such as <http://wheat.pw.usda.gov/ggpages/wgc/98/> (McIntosh et al. 2003). Over 130 postulated resistance genes are included there, with established rules of assigning them names and symbols. Information on rye and triticale genes and resistance genes in particular, is less abundant. A catalogue of genes identified in rye and their linkage map were elaborated by Schlegel and Melz (1996). That catalogue includes 31 disease and pest resistance genes. Korzun et al. (2001) mapped five rye (*Secale cereale*) resistance genes.

The available information on wheat and rye resistance genes and on their genetic markers may be very useful for triticale breeding. Primary triticale combines genomes A and B of wheat

and R of rye, along with vulnerability to pathogens characteristic for these species. The occurrence of selected pathogens and symbols of resistance genes are summarised in Table 1. For triticale breeding, rye diseases such as ergot (*Claviceps purpurea*) and scald (*Rhynchosporium secalis*) should be added as important diseases.

Wheat resistance genes and a list of accessions having them, along with rye genes used for wheat breeding, are described in the Catalogue of Gene Symbols for Wheat and respective updates published on-line (McIntosh et al. 2003). A number of resistance genes have been transferred to common wheat *Triticum aestivum* from wild relatives (Table 2). All those genes were subsequently included into the wheat catalogue and can be exploited for triticale breeding. At present, rye has a separate nomenclature, with gene symbols overlapping those of wheat. The 1BL.1RS translocation derived from 'Petkus' rye, having four R genes *Pm8*, *Lr26*, *Yr9* and *Sr31*, has been exploited in wheat

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Table 1. Symbols of identified resistance/tolerance (R) genes against 15 fungal pathogens, 1 bacterial pathogen, 3 viruses and 7 pests in wheat and its relatives (Cunfer 1993, Zamorski et al. 1994, Schlegel, Melz 1996, Arseniuk, Czembor 1999, Scharen 1999, Barbieri et al. 2000, Wiese et al. 2000, Korzun et al. 2001, McIntosh et al. 2003)

Gene symbols			Pathogen name (disease symptom)	Wheat	
Wheat	Rye	Triticale		Loci	QTL
<i>Lr</i>	–	<i>Lr</i>	<i>Puccinia recondita</i> f. sp. <i>tritici</i> (brown rust, leaf rust)	51 (+5)	8
–	<i>Lr</i>	–	<i>Puccinia recondita</i> f. sp. <i>recondita</i>		
<i>Sr</i>	<i>Sr</i>	<i>Sr</i>	<i>Puccinia graminis</i> (black rust; black stem rust; stem rust)	44 (+5)	
<i>Yr</i>	<i>Yr</i>	<i>Yr</i>	<i>Puccinia striiformis</i> (stripe rust, yellow rust)	32 (+24)	2
<i>Pm</i>	<i>Pm</i>	<i>Pm</i>	<i>Blumeria (Erysiphe) graminis</i> powdery mildew)	29 (+6)	20
<i>Crr</i>			<i>Cochliobolus sativus</i> (cochliobolus root rot)	1	
<i>Fhs</i>	<i>Fr</i>	<i>Fhs</i>	<i>Fusarium graminearum</i> (Fusarium head scab)	2	
<i>Stb</i>	+	+	<i>Mycosphaerella graminicola</i> (<i>Septoria tritici</i> blotch) = <i>Septoria tritici</i>	8	
–	+	–	<i>Septoria secalis</i>		
<i>Snb</i>	+	+	<i>Phaeosphaeria nodorum</i> (<i>Septoria nodorum</i> blotch) = <i>Stagonospora nodorum</i>	6	
+	–	+	<i>Stagonospora avenae</i> f. sp. <i>triticea</i>		
<i>Pch</i>	+	+	<i>Tapesia yallundae</i> = <i>Pseudocercospora herpotrichoides</i> (eyespot, strawbreaker footrot)	4	
<i>tsn, Tsc</i>	+	+	<i>Pyrenophora tritici-repentis</i> (tan spot, yellow leaf spot)	1, 1	
<i>Bt</i>	–		<i>Tilletia caries</i> , <i>T. foetida</i> , <i>T. controversa</i> (bunt, dwarf smut, stinking smut)	10	
<i>Kb</i>	<i>Cbt</i>	<i>Kb</i>	<i>Tilletia indica</i> (kernal bunt)	6	2
<i>Ut</i>	–	–	<i>Ustilago tritici</i> (loose smut)	4	
–	+	+	<i>Urocystis occulta</i> (stalk smut)		
–	+	+	<i>Cephalosporium gramineum</i> (<i>Cephalosporium</i> stripe)		
–	+	+	<i>Claviceps purpurea</i> (ergot)		
–	+	+	<i>Rhynchosporium secalis</i> (scald)		
–	–	+	<i>Typhula incarnata</i> (speckled snow mold)		
<i>Bls</i>	<i>Xct</i>	<i>Bls</i>	<i>Xanthomonas campestris</i> pv. <i>undulosa</i> (bacterial leaf streak)	5	
<i>Bdv</i>	<i>Byd</i>	<i>Bdv</i>	Barley Yellow Dwarf Virus	2	
<i>Wsm</i>	<i>Wsm</i>	<i>Wsm</i>	Wheat Streak Mosaic Virus	1	
<i>Cmc</i>			<i>Eriophyes tulipae</i> (<i>Aceria tulipae</i>) (wheat curl mite)	4	
<i>H</i>	<i>H (Hfr)</i>	<i>H</i>	<i>Mayetiola</i> (<i>Phytophaga</i>) <i>destructor</i> (Hessian fly)	30	
<i>Dn</i>	<i>Dnr</i> (<i>Gbr</i>)	<i>Dn</i>	<i>Diuraphis noxia</i> (Russian aphid)	10	
<i>Gb</i>			<i>Schizaphis (Toxoptera) graminum</i> (greenbug)	6	
<i>Rkn</i>	+	+	<i>Meloidogyne</i> spp. (root knot)	1	
<i>Cre</i>	<i>Cnr</i> (<i>Cre</i>)	<i>Cre</i>	<i>Heterodera avenae</i> (cereal cyst nematode)	8	
<i>Sm</i>			<i>Sitodiplosis mosellana</i> (orange blossom wheat midge, wheat midge)	1	

breeding, as it provides resistance to leaf rust, stem rust, yellow rust, and powdery mildew (Metten et al. 1973, Zeller 1973, Heun and Friebe 1990). A group of US wheats carries the translocation from 'Insave F.A.' rye, with *Gb2*, *Pm17* and *Sr31* genes (Friebe et al. 1996). As a result of the transfer of resistance genes from rye to wheat, a high number of new wheat cultivars appeared in Europe, Asia and America (Lukaszewski 1990, 1993). Other examples of transfer of rye chromatin into wheat are coupled with detrimental

effects and comprise *Sr27*, *Lr25*, *Pm7*, *Pm20*, *Lr45*, *H21* and *H25* resistance genes, as reviewed by McIntosh et al. (1995). Genes located on rye chromosomes may be present in triticale cultivars and accessions. This suggests the need for establishing a uniform wheat-based nomenclature of gene symbols for wheat, rye and triticale.

Triticale is affected by the same diseases as its parental species but is still less susceptible. However, the expansion of its cultivation leads to a better adaptation of the pathogen to the crop

Table 2. Resistance genes from wild relatives transferred to wheat (McIntosh et al. 2003)

Wheat relative	Genome ¹	Resistance genes
<i>Aegilops comosa</i>	M	<i>Yr8</i>
<i>Aegilops longissima</i>	S ^l	<i>Pm13</i>
<i>Aegilops speltoides</i>	S	<i>Lr28, Lr35, Lr36, Lr47, Lr51, Sr32, Sr39, Pm12, Gb5</i>
<i>Aegilops tauschii</i> syn. <i>Aegilops squarrosa</i> syn. <i>Triticum tauschii</i>	D	<i>Lr20, Lr21, Lr22a, Lr32, Lr39, Lr41, Lr42, Lr43, Sr33, Sr45, Yr28, Pm2, Pm19, Stb5, Snb3, Cmc1, Cmc4, H13, H26, Dn3, Rkn, Cre3, Cre4,</i>
<i>Aegilops triuncialis</i>	UC	<i>H30, Cre7</i>
<i>Aegilops umbellulata</i>	U	<i>Lr9</i>
<i>Aegilops peregrina</i> syn. <i>Aegilops variabilis</i>	SU	<i>Rkn-mn1</i>
<i>Aegilops ventricosa</i>	DN	<i>Lr37, Sr38, Yr17, Pch1, H27, Cre2, Cre5, Cre6,</i>
<i>Agropyron elongatum</i>	P	<i>Lr19, Lr24, Lr29, Sr24, Sr25, Sr26, Sr43, Cmc2</i>
<i>Agropyron intermedium</i>	P	<i>Lr38, Sr44, Bdv2, Wsm1</i>
<i>Haynaldia villosa</i>	V	<i>Yr26, Pm21,</i>
<i>Secale cereale</i>	R	<i>Lr25, Lr26, Lr45, Sr27, Sr31, Yr9, Pm7, Pm8/Pm17, Pm20, Cmc3, H21, H25, Dn7, Gb2, Gb6, Cre8</i>
<i>Triticum araraticum</i>	AG	<i>Sr40</i>
<i>Triticum carthlicum</i>	AB	<i>Pm4b</i>
<i>Triticum dicoccoides</i>	AB	<i>Yr15, YrH52, Pm16, Pm30, Pm31,</i>
<i>Triticum dicoccum</i>	AB	<i>Pm5</i>
<i>Triticum monococcum</i>	A	<i>Lr50, Sr21, Sr22, Sr35, Pm25,</i>
<i>Triticum spelta</i>	ABD	<i>Lr44, Yr5, Yr10, Pm1d</i>
<i>Triticum timopheevi</i>	AG	<i>Sr36, Sr37, Pm6, Pm27, SnbTM</i>
<i>Triticum turgidum</i>	AB	<i>Pm26</i>
<i>Triticum sphaerococcum</i>	ABD	<i>Pm5c</i>

¹ genome constitution according to Graingenes <http://www.ksu.edu/wgrc/Taxonomy/taxintro.html>

(Schinkel 2002). Therefore, breeding of resistant cultivars is of growing importance. This paper provides a common catalogue of wheat, rye and triticale gene symbols. It will be profitable to use this extended catalogue to avoid confusions in triticale breeding. Resistance genes *Pm*, *Lr*, *Sr*, *Yr*, *Pch1*, *Pch2* and others in three species may be included in this catalogue, with numbers related to given genes and their alleles.

R genes of wheat, rye, and triticale

An on-line database of cereal rust resistance genes with chromosomal locations and alleles can be found on the website: http://www.cdl.umn.edu/res_gene/res_gene.html. According to Chelkowski and Stepień (2001), the following genes of resistance to leaf rust have been identified in Polish wheat cultivars: *Lr1*, *Lr3*, *Lr11*, *Lr13*, *Lr14*, *Lr16* and *Lr26*. Those genes, when present as single genes, do not prevent infection of wheat cultivars. Virulences to *Lr9*, *Lr19* and *Lr24* have not been detected in Poland so far. All those genes

have been introduced into wheat A and B genomes from relatives and thus can be transferred into triticale. Other European countries use additionally *Lr20*, *Lr10*, *Lr37* and *Lr17* in commercial cultivars. Johnson (2000) suggests that combining *Lr34* and *Lr46* might be a useful strategy. Molecular markers for those genes have already been identified (Faris et al. 1999, William et al. 2003).

There is no uniform nomenclature system of *Lr* genes in rye. According to Solodukhina (1994, 2002), rye resistance to leaf rust is controlled by the genes: *Lr4(=Pd)* in 'Sanim', 'Chernigovskaya RPd', 'Baltiiskaya RPd', and 'I125/79'; *Lr5(=Pd1)* in 'Immunaya 1' and 'Malysh 72-2'; and *Lr6(=Pd3)* in 'Chulpan 3' and 'Immunaya 4'. Roux et al. (2000) selected 17 potential sources for leaf rust resistance in rye among more than 530 gene bank accessions. In segregating F₂ and BC₁ families, five dominant major resistance genes were identified. Those genes have preliminarily been designated as *Lr-a*, *Lr-b*, *Lr-c* ('Yaroslavna 3'), *Lr-g*, and *Lr-h*, respectively. They are effective both at the seedling and at the adult plant stages. By means of genetic

Table 3. Catalogue of wheat, rye and triticale resistance genes based on the catalogue of gene symbols for wheat (McIntosh et al. 2003). Genes with available DNA markers are marked with asterisks

Wheat		Source	Rye		Chromosomal location
1	2		3	4	
<i>Pm1a-e*</i>	<i>T. aestivum</i> (+ <i>Lr20</i> , <i>Sr15</i>) <i>T. spelta</i>				7AL
<i>Pm2*</i>	<i>Aegilops squarrosa</i>				5DS
<i>Pm3a-f*</i>	<i>T. aestivum</i>				1AS
<i>Pm4a*</i>	<i>T. dicoccum</i>				2AL
<i>Pm4b</i>	<i>T. carthlicum</i>				
<i>Pm5*</i>	<i>T. aestivum</i>				7BL
<i>Pm6*</i>	<i>T. timopheevii</i>				2B
<i>Pm7</i>	<i>Secale cereale</i>		<i>Pm2</i> ; <i>Pm8</i>		T4BS.4BL-2RL
<i>Pm8*/Pm17*</i>	<i>Secale cereale</i> Petkus		<i>Pm1</i> ; <i>Pm</i>		1BL.1RS (Yr9, Lr26, Sr31)
<i>Pm9</i>	<i>T. aestivum</i>				7AL
<i>Pm10</i>	<i>T. aestivum</i>				1D
<i>Pm11</i>	<i>T. aestivum</i>				6BS
<i>Pm12*</i>	<i>Aegilops speltoides</i>				6B = 6BS-6SS.6Sl
<i>Pm13*</i>	<i>Aegilops longissima</i>				3B = T3BL.3BS-3S ¹ #1S
<i>Pm14</i>	<i>T. aestivum</i>				6B
<i>Pm15</i>	<i>T. aestivum</i>				7DS
<i>Pm16</i>	<i>T. dicoccoides</i>				4A
<i>Pm19</i>	<i>Aegilops squarrosa</i>				7D
<i>Pm20</i>	<i>Secale cereale</i> Prolific		<i>Pm5</i> ; <i>Pm?</i>		T6BS.6R#2L
<i>Pm21*</i>	<i>Haynaldia villosa</i>				6AS = T6AL.6VS
<i>Pm22</i>	<i>T. aestivum</i>				1D
<i>Pm23</i>	<i>T. aestivum</i>				5A
<i>Pm24*</i>	<i>T. aestivum</i>				6D
<i>Pm25*</i>	<i>T. monococcum</i>				1A
<i>Pm26*</i>	<i>T. turgidum</i> var. <i>dicoccoides</i>				2BS
<i>Pm27*</i>	<i>T. timopheevii</i>				6B
<i>Pm28</i>	<i>T. aestivum</i>				1B
<i>Pm29*</i>	<i>T. aestivum</i>				
<i>Pm30*</i>	<i>T. dicoccoides</i>				5BS
<i>Pm31*</i>	<i>T. dicoccoides</i>				
	<i>Secale cereale</i>		<i>Pm3</i>		3RS
	<i>Secale cereale</i>		<i>Pm4</i>		5RL
	<i>Secale cereale</i>		<i>Pm6</i>		4R
	<i>Secale cereale</i>		<i>Pm7</i>		1R
<i>Lr1*</i>	<i>T. aestivum</i>				5DL
<i>Lr2a-c</i>	<i>T. aestivum</i>				2DS
<i>Lr3 complex*</i>	<i>T. aestivum</i>				6BL
<i>Lr4 – Lr8</i>	<i>T. aestivum</i>				
<i>Lr9*</i>	<i>Aegilops umbellulata</i>				6BL = T6BS.6BL-6U#1L
<i>Lr10*</i>	<i>T. aestivum</i>				1AS
<i>Lr11</i>	<i>T. aestivum</i>				2A
<i>Lr12</i>	<i>T. aestivum</i>				4B
<i>Lr13*</i>	<i>T. aestivum</i> Maris Huntsman				2BS
<i>Lr14a-b</i>	<i>T. aestivum</i>				7BL
<i>Lr15</i>	<i>T. aestivum</i>				2DS
<i>Lr16+Sr23</i>	<i>T. aestivum</i>				2BS
<i>Lr17a-b</i>	<i>T. aestivum</i>				2AS
<i>Lr18*</i>	<i>T. aestivum</i>				5BL
<i>Lr19*+Sr25</i>	<i>Agropyron elongatum</i>				7DL = T7DS.7DL-7Ae#1L 7AL = T7A-7Ae#1
<i>Lr20 + Pm1*+Sr15</i>	<i>T. aestivum</i>				7AL
<i>Lr21*</i>	<i>T. tauschii</i>				1DS

1	2	3	4
Lr22a	<i>Aegilops squarrosa</i> var. <i>strongulata</i>		2DS
Lr22b	<i>T. aestivum</i> Thatcher		
Lr23*	<i>T. aestivum</i>		2BS
Lr24*	<i>Agropyron elongatum</i>		1BL = T1BL.1BS-3Ae#1L
Lr25*+Pm7	<i>Secale cereale</i> Rosen	Lr2?	T4BS.4BL-2R#1L
Lr26*+Yr9+Sr31 +Pm8	<i>Secale cereale</i> Petkus	Lr1	T1BL.1RS
Lr27*+Sr2	<i>T. aestivum</i>		3BS
Lr28*	<i>Aegilops speltoides</i>		4AL = T4AS.4AL-7S#2S
Lr29*	<i>Agropyron elongatum</i>		7DS = T7DL-7Ae#1S
Lr30	<i>T. aestivum</i>		4AL
Lr31*	<i>T. aestivum</i>		4BL
Lr32*	<i>T. tauschii</i>		3DS
Lr33	<i>T. aestivum</i>		1BL
Lr34*+Yr18+Bdv1	<i>T. aestivum</i>		7DS
Lr35*	<i>Aegilops speltoides</i>		2B
Lr36	<i>Aegilops speltoides</i>		6BS
Lr37*+Yr17+Sr38	<i>Aegilops ventricosa</i>		2AS
Lr38	<i>Agropyron intermedium</i>		1DL = T1DS.1DL-7Ai#2L 2AL = 2AS.2AL-7Ai#2L 3DS = 3DL.3DS-7Ai#2L 5AS = 5AL.5AS-7Ai#2L 6DL = 6DS.6DL-7Ai#2L
Lr39*	<i>T. tauschii</i>		2DS
Lr40	<i>T. aestivum</i>		
Lr41	<i>T. tauschii</i>		1D
Lr42	<i>T. tauschii</i>		1D
Lr43	<i>T. tauschii</i>		7DS
Lr44	<i>T. spelta</i>		1B
Lr45	<i>Secale cereale</i>	Lr2?	T2AS-2R#3S.2R#3L
Lr46+Yr29*	<i>T. aestivum</i>		1B
Lr47*	<i>Aegilops speltoides</i>		7AS = Ti7AS-7S#1S-7AS.7AL
Lr48	<i>T. aestivum</i>		4BL
Lr49	<i>T. aestivum</i>		2AS
Lr50*	<i>T. monococcum</i>		2BL
Lr51*	<i>Aegilops speltoides</i>		1BL
	<i>Secale cereale</i>	Lr3	3R
	<i>Secale cereale</i>	Lr-a	6RL
	<i>Secale cereale</i>	Lr-b	
	<i>Secale cereale</i>	Lr-c	1RS
	<i>Secale cereale</i>	Lr-g	1RL
	<i>Secale cereale</i>	Lr-h	
	× <i>Triticosecale</i>	LrSatu	
Sr2*	<i>T. aestivum</i>		3BS
Sr3/Sr4	<i>T. aestivum</i>		
Sr5	<i>T. aestivum</i>		6DS
Sr6	<i>T. aestivum</i>		2DS
Sr7a-b	<i>T. aestivum</i>		4AL
Sr8a-b	<i>T. aestivum</i>		6AS
Sr9a-g/Sr1	<i>T. aestivum</i>		2BL
Sr10	<i>T. aestivum</i>		2B
Sr11	<i>T. aestivum</i>		6BL
Sr12	<i>T. aestivum</i>		3BS
Sr13	<i>T. aestivum</i>		6AL
Sr14	<i>T. aestivum</i>		1BL
Sr15+Pm1+Lr20*	<i>T. aestivum</i>		7AL
Sr16	<i>T. aestivum</i>		2BL
Sr17	<i>T. aestivum</i>		7BL

1	2	3	4
<i>Sr18</i>	<i>T. aestivum</i>		1D
<i>Sr19</i>	<i>T. aestivum</i>		2BS
<i>Sr20</i>	<i>T. aestivum</i>		2B
<i>Sr21</i>	<i>T. monococcum</i>		2AL
<i>Sr22*</i>	<i>T. monococcum</i>		7AL
<i>Sr23+Lr16</i>	<i>T. aestivum</i>		2BS
<i>Sr24+Lr24</i>	<i>Agropyron elongatum</i>		3DL = T3DS.3DL-3Ae#1L
<i>Sr25</i>	<i>Agropyron elongatum</i>		7DL = T7DS.7DL-7Ae#1L
<i>Sr26*</i>	<i>Agropyron elongatum</i>		6AL = T6AS.6AL-6Ae#1L
<i>Sr27</i>	<i>Secale cereale</i> Imperial	<i>Sr2</i>	T3BL.3R#1S
<i>Sr28</i>	<i>T. aestivum</i>		2BL
<i>Sr29</i>	<i>T. aestivum</i>		6DL
<i>Sr30</i>	<i>T. aestivum</i>		5DL
<i>Sr31*</i>	<i>Secale cereale</i> Petkus	<i>Sr1; Sr+</i>	T1BL.1RS
<i>Sr32</i>	<i>Aegilops speltiodes</i>		2A = T2AL.2S#1L.2S#1S 2B = T2BL-2S#1S 2D = T2DL-2S#1L.2S#1S
<i>Sr33*</i>	<i>Aegilops squarrosa</i>		1DS
<i>Sr34</i>	<i>Aegilops comosa</i>		2A = T2AS-2M#1L.2M#1S 2D = T2DS-2M#1L.2M#1S
<i>Sr35</i>	<i>T. monococcum</i>		3AL
<i>Sr36</i>	<i>T. timopheevii</i>		2BS
<i>Sr37</i>	<i>T. timopheevii</i>		4BL
<i>Sr38+Lr37+Yr17</i>	<i>Aegilops ventricosa</i>		
<i>Sr39+Lr35</i>	<i>Aegilops speltoides</i>		2B
<i>Sr40</i>	<i>T. araraticum</i>		2BS = T2BL/2G#2S
<i>Sr41</i>	<i>T. aestivum</i>		4D
<i>Sr42</i>	<i>T. aestivum</i>		6DS
<i>Sr43</i>	<i>Agropyron elongatum</i>		7DL = T7DL-7Ae#2L.7Ae#2S
<i>Sr44</i>	<i>Agropyron intermedium</i>		T7DS-7Ai#1L.7Ai#S
<i>Sr45</i>	<i>T. tauschii</i>		1DS
	× <i>Triticosecale</i>	<i>SrNin; SrBj; SrVent</i>	2R
<i>Sr27</i>	× <i>Triticosecale</i>	<i>SrSatu; SrLa1</i>	3R
	× <i>Triticosecale</i>	<i>SrLa2</i>	
<i>Yr1</i>	<i>T. aestivum</i>		2AL
<i>Yr2</i>	<i>T. aestivum</i>		7B
<i>Yr3a-c</i>	<i>T. aestivum</i>		1B
<i>Yr4a-b</i>	<i>T. aestivum</i>		6B
<i>Yr5*</i>	<i>T. spelta album</i>		2BL
<i>Yr6</i>	<i>T. aestivum</i>		7BS
<i>Yr7</i>	<i>T. aestivum</i>		2BL
<i>Yr8</i>	<i>Aegilops comosa</i>		2D = T2DS-2M#1L.2M#1S
<i>Yr9*</i>	<i>Secale cereale</i>	<i>Yr1</i>	1RS.1BL
<i>Yr10*</i>	<i>T. spelta</i>		1BS
<i>Yr11</i>	<i>T. aestivum</i>		
<i>Yr12</i>	<i>T. aestivum</i>		
<i>Yr13</i>	<i>T. aestivum</i>		
<i>Yr14</i>	<i>T. aestivum</i>		
<i>Yr15*</i>	<i>T. dicoccoides</i>		1BS
<i>Yr16</i>	<i>T. aestivum</i>		2D
<i>Yr17*+Lr37+Sr38</i>	<i>Aegilops ventricosa</i>		2AS
<i>Yr18*</i>	<i>T. aestivum</i>		7DS
<i>Yr19</i>	<i>T. aestivum</i>		5B
<i>Yr20</i>	<i>T. aestivum</i>		6D
<i>Yr21</i>	<i>T. aestivum</i>		1B

1	2	3	4
Yr22	<i>T. aestivum</i>		4D
Yr23	<i>T. aestivum</i>		6D
Yr24	<i>T. aestivum</i>		1BS
Yr25	<i>T. aestivum</i>		1D
Yr26*	<i>Haynaldia villosa</i>		6AS (6AL.6VS)
Yr27+Lr13	<i>T. aestivum</i>		2BS
Yr28*	<i>T. tauschii</i>		4DS
Yr29+Lr46	<i>T. aestivum</i>		1BL
Yr30+Sr2+Lr27	<i>T. aestivum</i>		3BS
Yr31	<i>T. aestivum</i>		2BS
Yr32	<i>T. aestivum</i>		2BS
YrH52*+Yr15	<i>T. dicoccoides</i>		1BS
	<i>Secale cereale</i>	Yr2	2RL
	<i>Secale cereale</i>	Yr3	6R
	<i>Secale cereale</i>	YrBl	6R
Bdv1+Lr34+Yr18	<i>T. aestivum</i>		7DS
Bdv2*	<i>Agropyron intermedium</i>		7DL= T7DS.7DL-7Ai#1L 1B = T1BS-7A#1S.7Ai#1L
	<i>Secale cereale</i>	Byd1	1R
	<i>Secale cereale</i>	Byd2	2R
Crr	<i>T. aestivum</i>		5BL
Dn1*/Dn2*	<i>T. aestivum</i>		7DL
Dn3	<i>T. tauschii</i>		D
Dn4*	<i>T. aestivum</i>		1DL
Dn5*	<i>T. aestivum</i>		7DL
Dn6*	<i>T. aestivum</i>		
Dn7	<i>Secale cereale</i>	Dnr	1BL.1RS
Dn8*	<i>T. aestivum</i>		7DS
Dn9*	<i>T. aestivum</i>		1DL
Dnx*	<i>T. aestivum</i>		7DS
	<i>Secale cereale</i>	Dnr1	1RL
	<i>Secale cereale</i>	Dnr2	3RS
	<i>Secale cereale</i>	Dnr3; Dn	4R
	<i>Secale cereale</i>	Dnr4	7R
QFhs.ndsu.2A	<i>T. aestivum</i>		2AL
QFhs.ndsu.3AS	<i>T. turgidum</i> var. <i>dicoccoides</i>		3AS
Cre1*	<i>T. aestivum</i>		2B
Cre2	<i>Aegilops ventricosa</i>		
Cre3	<i>T. tauschii</i>		2DL
Cre4	<i>T. tauschii</i>		2D
Cre5	<i>Aegilops ventricosa</i>		2AS = 2A-2Nv-6Nv.
Cre6	<i>Aegilops ventricosa</i>		5Nv
Cre7	<i>Aegilops triuncialis</i>		
Cre8*	<i>Secale cereale</i>	CreR; Cre8	6RL
H1	<i>T. aestivum</i>		
H2	<i>T. aestivum</i>		
H3*	<i>T. aestivum</i>		5A
H4	<i>T. aestivum</i>		
H5*	<i>T. aestivum</i>		1AS
H6*	<i>T. aestivum</i>		5A
H7=H8	<i>T. aestivum</i>		5D
H9*	<i>T. aestivum</i>		5A
H10*	<i>T. aestivum</i>		5A
H11*	<i>T. aestivum</i>		1A
H12*	<i>T. aestivum</i>		5A
H13*	<i>T. tauschii</i>		6DL
H14*	<i>T. aestivum</i>		5A

1	2	3	4
<i>H15</i>	<i>T. aestivum</i>		5A
<i>H16*</i>	<i>T. aestivum</i>		5A
<i>H17*</i>	<i>T. aestivum</i>		5A
<i>H18</i>	<i>T. aestivum</i>		
<i>H19+H16</i>	<i>T. aestivum</i>		
<i>H20</i>	<i>T. aestivum</i>		2B
<i>H21*</i>	<i>Secale cereale</i>	<i>H1</i>	2BS.2R#2L
<i>H22</i>	<i>T. aestivum</i>		1D
<i>H23*</i>	<i>T. aestivum</i>		6DL
<i>H24*</i>	<i>T. aestivum</i>		6DL
<i>H25</i>	<i>Secale cereale</i>	<i>H2</i>	T6BS.6BL-6R#1L; T4BS.4BL-6R#1L; Ti4AS.4AL.-6R#1L-4AL.
<i>H26</i>	<i>T. tauschii</i>		4D
<i>H27</i>	<i>Aegilops ventricosa</i>		4Mv
<i>H28</i>	<i>T. aestivum</i>		5A
<i>H29</i>	<i>T. aestivum</i>		5A
<i>H30</i>	<i>Aegilops triuncialis</i>		
<i>H31*</i>	<i>T. aestivum</i>		5BS
<i>Rkn</i>	<i>Aegilops squarrosa</i>		
<i>Rkn-mn1*</i>	<i>Aegilops variabilis</i>		
<i>Stb1-4</i>	<i>T. aestivum</i>		
<i>Snb1</i>	<i>T. aestivum</i>		3AL
<i>Snb2</i>	<i>T. aestivum</i>		2AL
<i>Snb3</i>	<i>T. tauschii</i>		5DL
<i>SnbTM*</i>	<i>T. timopheevii</i>		3AL
<i>Stb5*</i>	<i>T. tauschii</i>		7DS
<i>Stb6</i>	<i>T. aestivum</i>		3AS
<i>Stb7*</i>	<i>T. aestivum</i>		4AL
<i>Stb8*</i>	<i>T. aestivum</i>		7BL
<i>Pch1*</i>	<i>Aegilops ventricosa</i>		7A
<i>Pch2*</i>	<i>T. aestivum</i>		7AL
<i>Pch3</i>			4V
<i>PchDV*</i>			4VL
<i>Tsn1*</i>	<i>T. aestivum</i>		5BL
<i>Tsc1*</i>	<i>T. aestivum</i>		1AS
<i>Gb1</i>	<i>T. aestivum</i>		
<i>Gb2</i>	<i>Secale cereale</i>	<i>Gbr</i>	T1AL.1R#2S
<i>Gb3*</i>	<i>T. aestivum</i>		7D
<i>Gb4</i>	<i>T. aestivum</i>		
<i>Gb5</i>	<i>Aegilops speltoides</i>		7AL = Ti7AS.7AL-7S#1L-7AL
<i>Gb6</i>	<i>Secale cereale</i> Insave	<i>Gbr</i>	T1AL.1R#2S
<i>Bt1</i>	<i>T. aestivum</i>		2B
<i>Bt2</i>	<i>T. aestivum</i>		
<i>Bt3</i>	<i>T. aestivum</i>		
<i>Bt4</i>	<i>T. aestivum</i>		1B
<i>Bt5</i>	<i>T. aestivum</i>		1B
<i>Bt6</i>	<i>T. aestivum</i>		1B
<i>Bt7</i>	<i>T. aestivum</i>		2D
<i>Bt8</i>	<i>T. aestivum</i>		
<i>Bt9</i>	<i>T. aestivum</i>		
<i>Bt10*</i>	<i>T. aestivum</i>		
<i>Kb1-6</i>	<i>T. aestivum</i>		
	<i>Secale cereale</i>	<i>Ctb1</i>	6R
	<i>Secale cereale</i>	<i>Ctb2</i>	4R
	<i>Secale cereale</i>	<i>Kb?</i>	7R
<i>Ut1-4</i>	<i>T. aestivum</i>		
<i>Ut-x*</i>	<i>T. aestivum</i>		2BL

1	2	3	4
<i>Cmc1</i>	<i>Aegilops squarrosa</i>		
<i>Cmc2</i>	<i>Agropyron elongatum</i>		6A = T6AS.6Ae#2S 5B = T5BL.6Ae#2S 6D = T6DL.6Ae#2S
<i>Cmc3</i>	<i>Secale cereale</i>		1AL.1RS
<i>Cmc4</i>	<i>Aegilops tauschii</i>		6DS
<i>Wsm1*</i>	<i>Agropyron intermedium</i>		4A = T4AL.4Ai#2S 4D = T4DL.4Ai#2S
	<i>Secale cereale</i>	<i>Wsm</i>	1RS
<i>Bls1-5</i>	<i>T. aestivum</i>		
<i>Rlnn1*</i>	<i>T. aestivum</i>		
<i>Sm1*</i>	<i>T. aestivum</i>		
<i>wssmv</i>	<i>T. aestivum</i>		

and molecular analysis, four of them were mapped on chromosomes 1R (3 *Lr* genes) and 6R (1 *Lr* gene) (Roux et al. 2002). Recently, Wehling et al. (2003) used the symbols *Pr1* and *Pr2* instead of *Lr-a* and *Lr-b* for rye genes.

Grzesik and Strzembicka (1999) evaluated the inheritance of the resistance to leaf rust in triticale crosses of 'Presto', 'Vero', and 'Ugo' with 'Almo' and 'Tornado' as susceptible varieties. At the seedling stage, the resistance to isolate 65a/95 was controlled by 1-2 genes and at the adult plant stage, resistance was determined by 1-3 genes. According to Singh and McIntosh (1990), approximately 50% of lines in the 17th International Triticale Screening Nursery possessed *SrSatu* and *LrSatu*. Both genes occurred more frequently among complete than among substituted triticale lines.

Adhikari and McIntosh (1998) studied 9 triticale cultivars and lines to determine the presence and identity of stem rust resistance genes. Resistance to stem rust is an important trait of triticale cultivars in Australia. Segregation in seedling tests showed the presence of some new genes: *SrLa1* and *SrLa2* in 'Lasko'; *SrBj* and *SrJ* in 'Bejon'; *SrVen* in 'Currency'; *SrBj* in 'Abacus'; and 'RM4' and *SrNin* in 'Tahara', 'Maiden', and 'Madonna'. *SrNin* and *SrBj* were located in chromosome 2R. The gene *SrLa1* behaved as a third allele at or near the *Sr27/SrSatu* locus in chromosome 3R. The work demonstrated that chromosomes 2R and 3R are important bearers of genes for stem rust resistance in hexaploid triticale. Johnson (2000) lists the following genes carrying durable resistance to wheat breeding: *Sr2* derived from 'Emmer' wheat via 'Hope', which can be followed in the breeding process assisted by the pseudo black chaff character (Hare and McIntosh 1979); *Sr26* derived from

Agropyron elongatum, associated with yield reduction; and *Sr31* from 'Petkus' rye.

Susceptibility of triticale cultivars to yellow rust has been observed in Mexico. Screening of a triticale collection for resistance to yellow rust revealed that 80% of advanced lines were susceptible. A higher percentage of resistance lines was identified in winter × spring crosses (31%) and older breeding lines (41%) (Hede et al. 2002).

Wheat resistance genes to powdery mildew, along with molecular markers, were reviewed by Chen and Chełkowski (1999) and Hsam and Zeller (2002). In the last two decades the following varieties were used as sources of disease resistance genes for wheat breeding: 'Normandie' (*Pm1 + Pm2 + Pm9 + Lr20 + Sr15*); 'Maris Huntsman' and 'Norman' (*Pm2 + Pm6, Lr13*); 'Demoisot' (*Lr3*); 'VPM1' and 'Randezvous' (*Lr37 + Yr17 + Sr38 + Pm2 + Pm4b + Pm6*); 'Soissons' (*Lr14a*); 'Etoile de Choisy' (*Lr16 + Sr23*); 'Kavkaz' and 'Aurora' (*Pm8, Lr26, Sr31, Yr9*). The suppressor for the powdery mildew (*Erysiphe graminis*) resistance of allelic *Pm8* and *Pm17* genes is located on chromosome 7D (Zeller and Hsam 1996), thus it will not be active in triticale. Eight *Pm* genes were found in rye (Schlegel and Melz 1996).

Reaction of wheat and triticale cultivars to inoculation with different isolates of *Septoria nodorum* was determined mainly by genotype (Arseniuk and Czembor 1999). Arseniuk et al. (1994) found no completely resistant germplasm to SNB in a pool of over 300 triticale, wheat and rye germplasms. Sowa et al. (1999) found continuous variation for expression of gene action for resistance to *S. nodorum* in winter triticale. The most resistant cultivars (RAH121 and RAH108)

showed some level of additive gene action for increased resistance.

Triticale is rather sensitive to snow mould (*Typhula*). Attempts are being undertaken to transfer resistance genes from landraces of wheat into triticale. Five varieties from that breeding programme have so far been submitted for registration: 'Gaetan' and 'Formulin' in France, and 'Brio', 'Meridal', and 'Tridel' in Switzerland (Fossati et al. 1996).

Nkongolo et al. (1992) found that resistance to the Russian wheat aphid (RWA), *Diuraphis noxia* (Mordvilko), in three winter triticale cultivars is controlled by a single dominant gene. The lack of segregation for susceptibility in F₂ progenies from the resistant × resistant crosses indicates a high probability that the resistance genes in those lines are at a common locus.

Gene transfer to triticale

Exploitation of rye genes for wheat breeding connected with the loss of resistance conferred by genes *Yr9* and *Lr26*, suggests a need for pyramiding new genes for durable resistance in triticale. However, in some cases pyramiding of resistance genes is not justified. Porter et al. (2000) suggest that in case of wheat *Gb* genes, pyramiding may not be effective due to dilution of effects. According to Johnson (2000) recognition of resistance as durable does not guarantee its future performance, particularly after genetic re-assortment in the breeding process. This suggests that selection of durable resistance gene and economic stimulation prior to introduction or pyramiding genes may not guarantee success of the resultant cultivar.

Well-characterized wheat varieties seem to be the best source for transfer of new resistance genes to triticale. However, improving the performance and genetic variability of the triticale gene pool can be accomplished also by: deriving of new primary triticales; triticale × rye crosses; and crosses between hexaploid and tetraploid triticales (Skovmand et al. 1984). Those crosses can lead to deriving forms where some chromosomes from the R genome are replaced by chromosomes from the D genome. Chromosomes 2D and 6D appear to be selectively propagated by breeders in populations segregating for R- and D-genome chromosomes (Gustafson et al. 1989) as in case of hexaploid triticale 'Bronco 90' with 2D(2R) chromosome substitution (Taketa et al. 1997). Production of substitution and translocation triticale enables transfer of resistance genes not

only from A and B wheat genomes but also from the D genome.

D-genome species, such as *Aegilops tauschii* and *Ae. ventricosa*, are less accessible but highly valuable gene sources. 23 and 8 resistance genes respectively, have been transferred from *Ae. tauschii* and *Ae. ventricosa* to common wheat varieties (Table 2). Bernard and Bernard (1987) exploited those species for creating new forms of 4x, 6x and 8x primary triticale. Genetic material from the D genome can be introduced into hexaploid triticale mainly by hybridization between 6x triticale and common wheat. However, other approaches can be considered, e.g. hybridization between 8x triticale and 4x triticale, and synthesis of amphiploid plants associating species bearing D and R genomes (Bernard and Bernard 1987).

As a rule, segments of alien chromosomes carrying valuable resistance genes are introduced in blocks located in distal parts of chromosomes (Lukaszewski 1995). These examples of introgression are quite easy to detect, as molecular markers tag translocations in fact and span an extensive region of DNA. Genes located in the proximal, non-recombining regions of chromosomes may be completely linked. Such linkages can be difficult to break. Premeiotic applications of weak colchicine solutions can be applied to move recombination in favour of the proximal regions (Lukaszewski 1995). A 5-azacytidine (5-AC) treatment was reported to increase recombination between human chromosomes (Kokalj-Vokac et al. 1993). Treatment of triticale seedlings with 5-AC enhanced the percentage of nuclei with R chromosomes intermixed with wheat chromosomes from 25% to 60%. 5-AC treated plants showed occasionally the presence of multiple terminal, intercalary, centromeric and sub-centromeric translocations between wheat and rye chromosomes, which were not detected in water-germinated plants (Castilho et al. 1999). This suggests that chemical agents can be used to increase the recombination rate and induce small/interstitial translocations with the gene of interest – with reduced detrimental effects.

Possibility of marker-assisted selection on resistance in triticale breeding

Conventional triticale breeding is time-consuming and takes 8-12 years. Biotechnology proposes new tools in order to speed up the release of new

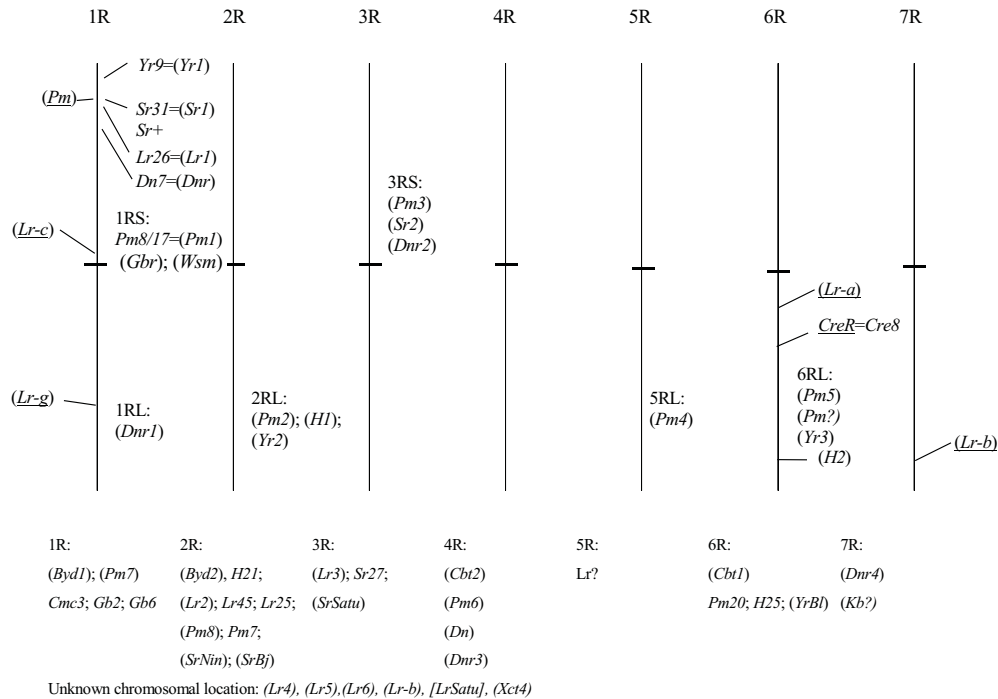


Figure 1. Schematic presentation of rye resistance genes on chromosomes of *Secale cereale* according to Schlegel and Melz (1996), Korzun et al. (2001), and Wehling et al. (2003). Symbols for rye gene nomenclature are given in brackets.

cultivars by improving selection strategies (Bauer and Korzun 2002). Currently, a website devoted to marker-assisted selection of wheat (<http://maswheat.ucdavis.edu/protocols/protocols.htm>), includes protocols for genes of resistance to fungal diseases (*Lr21*, *Lr25*, *Lr29*, *Lr37*, *Lr39*, *Lr47*, *Lr50*, *Sr38*, *Sr39*, *Yr5*, *Yr15*, *Yr17* and to FHB), viruses (*Wsm1*, *Bdv2*, to the wheat spindle streak mosaic bymovirus), and insects (*H9*, *H13*, to Hessian fly, and *Dn2* and *Dn4*, to Russian wheat aphid). However the best source of available molecular and morphological markers remains the Catalogue of Gene Symbols for Wheat (McIntosh et al. 2003). Rye resistance genes were partly characterized within that catalogue to the extent required for wheat breeding. For 1RS, the rust resistance genes were located 5.4 ± 1.7 cM from the *Sec1* locus, which in turn was located 26.1 ± 4.3 cM from the centromere, the gene order being: centromere–*Sec1*–*Lr26*/*Sr31*/*Yr9*–telomere (Singh et al. 1990).

PCR-based markers, tightly linked to the rust resistance genes in ‘Imperial’ and ‘Petkus’ rye, have been developed. They can be used in marker-assisted breeding. Three non-cross-hybridizing Resistance Gene Analogue markers, one of them derived from the *Mla* gene family, have been mapped within the same region of 1RS (Mago et al. 2002). Baranova et al. (2001) found linkage between genes controlling resistance

to brown rust and isozyme loci *Est 6/9* and *Est2*, located on rye chromosome 5R. Yong (2001) performed an AFLP analysis in order to identify 2RL-specific markers in a wheat-rye translocation line (2BS/2RL) developed for resistance to biotype L of Hessian fly. He developed an STS primer for diagnostics of 2RL (SJ07), applicable in wheat, rye and triticale. Triticale has been scarcely studied with molecular markers. A co-dominant marker amplified by the primer OP-M09 was found on chromosome 4R and explained 55% of the variation observed for resistance to Russian wheat aphid (RWA, *Diuraphis noxia*) in PI 386156 triticale (Fritz et al. 1999).

Genetic maps of rye have been published and a number of resistance genes have been localised. Korzun et al. (2001) presented a genetic map of rye, combining 139 RFLP, 19 isozyme and protein, 13 microsatellite, and 10 gene loci. Five resistance genes were mapped: *CreR* (= *Cre8*) and *Lr-a* in 6RL, *Lr-c* and *Lr-g* in 1R, and *Pm* in 1RS. Abundance of rye DNA markers makes it possible to trace the presence of given arms and chromosomes in triticale. The genetic map of 73 DH lines derived from F_1 : ‘Torte’ \times ‘Presto’ triticale has been produced with Random Amplified Polymorphic DNA (RAPD), Random Amplified Microsatellite Polymorphism (RAMP), Amplification Fragments Length Polymorphism (AFLP)

and Simple Sequence Repeats (SSR) markers (Gonzalez et al. 2002). Map and catalogue of rye genes were published by Schlegel and Melz (1996) and Korzun et al. (2001). The distribution of 40 R gene markers over rye chromosomes including 11 mapped markers is presented in Figure 1. Additionally, 10 markers were used in wheat breeding and have no rye nomenclature.

Conclusions

At present two separate nomenclature systems exist for wheat and rye (Table 3, Figure 1). We suggest one catalogue of resistance gene symbols for wheat, rye, and triticale, which can be very useful for genetic and breeding purposes. From the common catalogue, it can be concluded that there exists a potential of further transfer of rye resistance genes to wheat and triticale.

Genes responsible for reaction to powdery mildew and to leaf, stem and yellow rusts are the best-represented group of resistance genes. Many molecular markers can be applied for marker-assisted gene transfer, but the expression of R genes in the new genetic background of triticale remains to be investigated.

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