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Stem Rust Resistance in 1BL.1RS and 2RL.2BS Double Wheat-Rye Translocation Lines

Mahbubjon RAHMATOV[1], Larisa GARKAVA-GUSTAVSSON[1], Ruth WANYERA[2], Brian STEFFENSON[3], Matthew ROUSE[4] and Eva JOHANSSON[1]

[1]Department of Plant Breeding, Swedish University of Agricultural Sciences, Alnarp, Sweden; [2]Food Crops Research Center, Kenyan Agricultural and Livestock Research Organization (KALRO), Njoro, Kenya; [3]Department of Plant Pathology, University of Minnesota, St. Paul, USA; [4]Cereal Disease Laboratory, United States Department of Agriculture – Agricultural Research Service, St. Paul, USA

Abstract

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The wheat stem rust pathogen, *Puccinia graminis* f.sp. *tritici*, is a significant and devastating disease of wheat crops worldwide. Wheat has many wild relatives in which to source new resistance genes, including the cereal crop of rye in the tertiary genepool. The aim of this study was to assess the reaction of 1BL.1RS and 2RL.2BS double wheat-rye translocation lines to virulent stem rust races from Africa and North America. BC_1F_3 and BC_1F_4 populations from a cross between the line KR99-139 (a double wheat-rye translocation line with 1BL.1RS and 2RL.2BS) and the bread wheat cultivar Topper were used in the study. Several of the populations homozygous for 1BL.1RS and heterozygous for 2RL.2BS showed resistance and low severity adult plant resistance (20RMR-50MSS) to the African stem rust race TTKSK in the field. None of the tested populations with varying chromosome combinations showed seedling resistance to any of the tested stem rust races. Thus, these resistant populations likely carry gene/s effective at the adult plant stage since all stage resistance genes with major effect appear to be absent based on the seedling assays. Resistant lines combined three chromosomes (1RS, 2RS and 2BS) which make their direct use in breeding more complicated. Mapping studies followed by potential transfer of genes between 2R and 2B will make the identified minor genes more useful in wheat breeding.

Keywords: backcrossing; durable resistance; minor genes; *Puccinia graminis* f.sp. *tritici*

Wheat-rye and other alien introgressions are useful in wheat breeding programs to diversify the sources of resistance against various pathogen and pest populations worldwide (Friebe *et al*. 1996; Merker & Lantai 1997). The most well-known and widely used rye chromosome for wheat improvement is 1R translocated as 1RS into the wheat genome, i.e. as 1AL.1RS, 1BL.1RS and 1DL.1RS (Merker 1982; Gupta & Shepherd 1993; Rabinovich 1998). The 1BL.1RS and 2RL.2BS translocations have been extensively used as alien sources of resistance genes in wheat breeding worldwide (Rabinovich 1998). The 1BL.1RS translocation was first derived from the rye cultivar Petkus and carries a number of race-specific resistance genes against stem rust (*Sr31*), yellow rust (*Yr9*), leaf rust (*Lr26*) and powdery mildew (*Pm8*) (Zeller 1973; Friebe *et al*. 1996). The chromosome 2R translocation carries several resistance genes against Hessian fly, tan spot, powdery mildew, leaf rust and stem rust (Hatchett *et al.* 1993; Hysing *et al*. 2007).

Stem rust is one of the most devastating diseases of cereal crops on a global scale (Kurt & Szabo 2005) and is best controlled through the use of host

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resistance. The stem rust resistance gene *Sr31* derived from rye has been widely used in wheat cultivars around the world. Although this gene provided stable resistance for over 40 years in wide deployment, it was overcome by the emergence of a new virulent race of *P. graminis* f.sp. *tritici* (race TTKSK, isolate Ug99) originating in Uganda in 1998 (Singh *et al*. 2008). Race TTKSK is unique in that it possesses novel virulence to *Sr31* and other broadly deployed resistance genes making wheat cultivars vulnerable to stem rust epidemics in many production areas of the world (Pretorius *et al*. 2000; Jin *et al*. 2007). More than eight variants in the "Ug99" lineage of stem rust races have been reported (http://rusttracker.cimmyt.org/), and they are spreading across eastern and southern Africa as well as the Middle East. It is likely that these races will continue to spread to other regions in the ensuing years (Singh *et al*. 2011). Because of the frequent emergence of new stem rust races, the identification and exploitation of novel sources of resistance genes is an important priority for wheat breeding.

The use of rye with novel disease resistances will broaden the genetic diversity in wheat breeding programs. A wheat-rye double translocation line with 1BL.1RS and 2RL.2BS was developed and found to carry promising resistance genes e.g. against powdery mildew (Merker & Forsstrom 2000; Forsstrom & Merker 2001). The objective of this study was to characterize these wheat-rye translocations for their possible resistance against the widely virulent African race TTKSK as well as others from North America.

MATERIAL AND METHODS

Plant materials. BC_1F_3 and BC_1F_4 populations from a cross between KR99-139, a double wheat-rye translocation line with 1BL.1RS and 2RL.2BS, and the German bread wheat cultivar Topper were evaluated for stem rust resistance. KR99-139 and Topper were initially crossed and the resulting F_1s were then backcrossed to both parents to subsequently generate the BC_1F_1 populations. BC_1F_1 populations were divided into four possible homozygous and heterozygous groups based on Simple Sequence Repeat (SSR) genotyping. Additionally, selections were made based on coleoptile colours and C-banding analyses in order to obtain BC_1F_2 and BC_1F_3 populations with various combinations of homozygosity and heterozygosity of the two rye translocations 1BL.1RS and 2RL.2BS originating from KR99-139 (Rahmatov 2012). The BC_1F_3 populations were thereafter selfed to obtain BC_1F_4 populations and both populations were used for stem rust evaluations in the present study.

Adult plant stem rust resistance. Evaluations for adult plant resistance (APR) were performed on the BC_1F_3 and BC_1F_4 populations (plus parents) in 2010 and 2011, respectively, at the Kenyan Agricultural and Livestock Research Organization (KALRO) in Njoro, Kenya. Since the materials were winter types, they were vernalized for about 7–8 weeks before transplanting in the field. To establish uniform disease development on plants, the stem rust nursery was surrounded by a planting of susceptible cultivars, which became heavily infected and spread rust urediniospores onto the test entries. To establish the initial rust infections, stems of the susceptible cultivars were needle injected with an aqueous solution of fresh urediniospores and later by direct inoculation of foliage at the boot stage with urediniospores suspended in a light mineral oil (Soltrol 170, Chevron Phillips Chemical Company LP, Woodlands, USA) (Bhavani *et al*. 2011). The percentage of stem and leaf sheath foliage infected by stem rust (0-100% basis) was assessed visually based on the modified Cobb scale (Peterson *et al*. 1948). In addition to disease severity, the infection types (size and type of uredinia) observed on host genotypes were also scored where R – resistant, MR – moderately resistant, MS – moderately susceptible and S – susceptible (Roelfs *et al*. 1992). Some translocation lines exhibited a wider range of infection responses and were therefore classified into the broader groups of resistant to moderately resistant (R–MR), moderately resistant to moderately susceptible (MR–MS) and moderately susceptible to susceptible (MS–S).

Seedling stem rust resistance. Seedling stem rust resistance tests were conducted at the University of Minnesota and United States Department of Agriculture – Agricultural Research Service Cereal Disease Laboratory in St. Paul, Minnesota USA in 2012. The African stem rust races TTKSK (Ug99), TTKST, TTTSK, TRTTF, and North American races TPMKC, TTTTF, QTHJC and RKQQC (Rouse *et al*. 2011) were used for evaluation of BC_1F_4 wheat-rye translocation lines (Table 1). For the inoculations, urediniospores were taken from –80°C storage, heat shocked at 40–45°C for 10 min, and placed in a rehydration chamber (80% humidity over potassium hydroxide solution) for about 4 h (Rowell 1984). Thereafter, the urediniospores were suspended in Soltrol oil and used for inoculation of 8-day-old

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Table 1. Virulence profile of the isolates which was performed for seedling resistance test (Rouse *et al.* 2011)

Race	Isolate	Origin	Avirulence profile	Virulence profile
TPMKC	74MN1409	USA	6 9a 17 24 30 31 38	5 7b 8a 9a 9d 9e 9g 10 11 21 36 Tmp McN
TTTTF	01MN84A-1-2	USA	6 24 31	5 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McN
QTHJC	75ND717C	USA	7b 9a 9e 9g 24 30 31 36 Tmp	5 6 8a 9b 9d 10 11 17 21 38 McN
RKQQC	99KS76A-1	USA	9e 10 11 17 24 30 31 38 Tmp	5 6 7b 8a 9a 9b 9d 9g 21 McN
TTKST	06KEN19v3	Kenya	17 36 Tmp	5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 24 30 31 38 McN
TRTTF	06YEM34-1	Yemen	8a 21 24 31	5 6 7b 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McN
TTKSK	04KEN156/04	Kenya	24 36 Tmp	5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 30 31 38 McN
TTTSK	07KEN24-4	Kenya	24 Tmp	5 6 7b 8a 9a 9b 9d 9e 9g 10 11 21 30 31 36 38 McN

seedlings (5 plants for each line) with the first leaves fully expanded. The inoculated materials were incubated in a dew chamber for 14 h at 18°C in darkness and then illuminated with fluorescent light for an additional 3–4 h before being transferred to a greenhouse at 18 ± 2°C with a photoperiod of 16 h. At 14 days post-inoculation (Jin *et al.* 2007), the stem rust infection types of seedlings were scored on 0 to 4 scale as described by Stakman *et al.* (1962).

RESULTS

Evaluation of APR in translocation lines. APR evaluations were performed on BC_1F_3, each with a defined combination of homo/heterozygous 1RS.1BL and 2RL.2BS, and BC_1F_4 (selfed from BC_1F_3) populations (Table 2). In both years of the field trials, high levels of stem rust (race TTKSK+Sr24) were present in the nursery at KALRO allowing for the easy separation of materials with known resistance and susceptibility. The two parents of Topper and KR99-139 both showed susceptible disease responses in 2010, with the former exhibiting a higher severity (30S) than the latter (10S). The parents of the cross showed slightly different disease responses (Topper MSS and KR99-139 R) in 2011 as compared to 2010. With respect to the BC_1F_3 populations screened in 2010, 18 exhibited susceptible infection responses (S), 8 exhibited moderately susceptible to susceptible infection responses (MS–S) and 2 exhibited resistant infection responses (R). The two resistant populations had the chromosomal combination of 1RS++ and 2RL+–. In addition to the infection response assessment, these resistant populations also exhibited lower disease severities (range of 20 R–MR to 50 MS–S) compared to other populations (20 S to 60 S). With respect to the BC_1F_4 populations screened in 2011, 14 exhibited susceptible infection responses (S), 8 exhibited moderately susceptible to susceptible infection responses (MS–S), 3 exhibited moderately susceptible infection responses (MS), 1 exhibited moderately resistant-moderately susceptible infection responses (MR–MS) and 2 exhibited moderately resistant infection responses (MR). The agreement between BC_1F_3 and BC_1F_4 populations with respect to the disease phenotypes was generally quite close. The two populations showing resistance in 2010 exhibited moderately resistant reactions in 2011. Moreover, the populations exhibiting susceptible reactions with the chromosomal combination of 1RS++ and 2RL+– in 2010 showed less susceptible reactions (MS–S to MR–MS) in 2011. With respect to the disease severity assessments, populations with 1RS++ and 2RL+– showed higher disease severity in

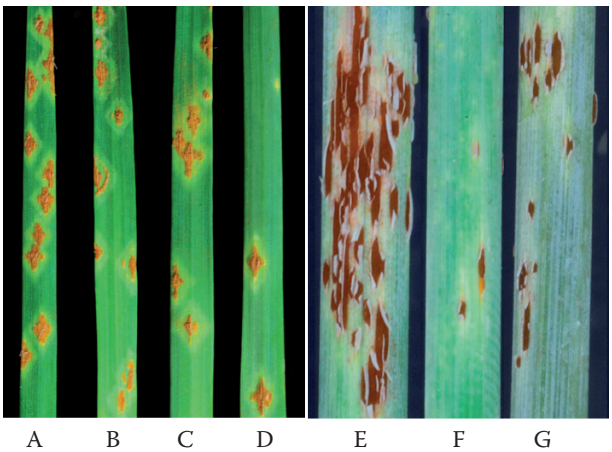

Figure 1. Seedling stem rust response to *Puccinia graminis* f.sp. *tritici* race TTKSK of A – Topper, B – KR99-139, C – BC_1F_4 #45, D – BC_1F_4 #63 and adult stem rust responses to TTKSK of E – Topper, F – KR99-139, and G – BC_1F_4 #45; all lines were highly susceptible to all applied races at the seedling stage (A–D) while KR99-139 (F) and BC_1F_4 #45 (G) showed slow rusting compared to Topper (E)

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Table 2. Adult plant and seedling resistances of BC_1F_3 and BC_1F_4 wheat-rye translocation lines and their parents

Family No.	Chromosomal combination	Adult plant resistace		Average severity	Seedling resistance 2012							
		2010	2011		TTKSK	TTTSK	TTKST	TRTTF	TPMKC	TTTTF	QTHJC	TRTTF
1	Topper	30S	40MSS	35	4	4	4	4	4	4	4	3+
2	KR99-139	10S	5R	7.5	3+	3+	3+	4	4	4	4	3+
30	1RS++; 2RL++	30S	40MS	35	4	4	4	4	4	4	4	4
34	1RS++; 2RL++	40S	30S	35	4	4	4	3+	4	4	4	4
65	1RS++; 2RL++	20S	40MSS	30	3+	4	4	4	3+	4	4	4
81	1RS++; 2RL++	30MSS	40S	35	4	4	4	4	4	4	4	4
93	1RS++; 2RL++	50MSS	20S	35	3+	4	4	4	4	4	4	4
7	1RS++; 2RL+–	20S	40MSS	30	4	4	3+	3+	4	4	4	4
37	1RS++; 2RL+–	30S	20RMR	25	4	4	3+	3+	4	4	4	4
45	1RS++; 2RL+–	5R	20MRMS	12.5	3+	3+	3+	3+	4	4	4	4
51	1RS++; 2RL+–	30S	50MSS	40	4	4	3+	3+	4	4	4	4
63	1RS++; 2RL+–	10R	40MR	20	4	4	4	3+	4	4	4	4
1	1RS+–; 2RL++	30S	20MS	25	3+	4	4	4	4	3+	4	4
19	1RS+–; 2RL++	50MSS	50S	50	4	3+	4	4	4	4	4	4
58	1RS+–; 2RL++	50MSS	30S	40	3+	4	4	4	3+	4	4	3+
79	1RS+–; 2RL++	40S	40S	40	3+	4	4	4	4	4	4	4
94	1RS+–; 2RL++	50S	60MSS	50	4	4	4	4	4	4	4	4
6	1RS+–; 2RL+–	50MSS	60S	55	4	3+	4	4	4	3+	4	4
27	1RS+–; 2RL+–	30S	50S	40	3+	4	4	4	4	4	3+	4
56	1RS+–; 2RL+–	30S	60S	45	4	4	4	4	4	4	4	4
73	1RS+–; 2RL+-	40S	60S	50	4	4	4	4	4	4	4	3+
88	1RS+–; 2RL+–	20MSS	50MSS	35	3+	4	4	3+	4	4	4	4
10	1RS––; 2RL+–	40S	60S	30	4	4	4	4	4	4	4	4
28	1RS––; 2RL+–	40S	50MSS	45	4	4	4	4	4	4	4	4
29	1RS––; 2RL+–	20S	30MS	25	3+	4	4	4	4	4	4	4
30	1RS––; 2RL+–	5S	20MSS	12.5	3	4	4	4	4	4	4	4
45	1RS––; 2RL+–	60MSS	60S	60	4	4	4	4	4	4	4	4
93	1RS––; 2RL+–	40S	60S	50	4	4	4	4	4	4	4	4
95	1RS––; 2RL+–	20S	30MSS	25	3+	4	4	4	4	4	4	4
98	1RS––; 2RL+–	50MSS	60S	55	4	4	4	4	4	4	4	4

Adult plant resistance was evaluated through the use of severity (0–100% basis) following the modified Cobb Scale (Peterson *et al.* 1948), and the host response to infection is determined based on pustule type and size (Roelfs *et al.* 1992); by the use of pustule type and size plants were classified into: R – resistant; RMR – resistant to moderately resistant; MR – moderately resistant; MRMS – moderately resistant to moderately susceptible; MS – moderately susceptible; MSS – moderately susceptible to susceptible; S – susceptible; seedling resistance was determined based on infection types using a 0 to 4 scale (Stakman *et al.* 1962); the scale was: 0; – immune to very resistant, 1 – resistant, 2 – moderately resistant, 3 – moderately susceptible, 3+ –susceptible, 4 – very susceptible

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2011 as compared to 2010. However, these populations still showed relatively lower values as compared to the rest of the evaluated population types.

Seedling resistance tests. All of the populations and parents exhibited susceptible infection types of 3+ to 4 in response to the African and North American races. Thus, this germplasm lacks any major effect seedling resistance genes (Table 2; Figure 1).

DISCUSSION

Based on the susceptibility of the populations and parents to African and North American stem rust races, it was clearly evident that no major seedling resistance gene was present in the germplasm. Thus, the resistance observed in the field to African stem rust in Kenya was due to APR. This APR was conferred in BC_1F_3 populations with a chromosomal combination of homozygosity for 1RS and heterozygosity for 2RL. Moreover, rust severity was generally lower in the BC_1F_3 populations with the chromosomal constitution of 1RS++ and 2RL+– as compared to the other populations.

The fact that resistance (APR) was found only in populations with the chromosomal combination of 1RS++ and 2RL+– and also the lowest disease severity was found in these populations, indicates that several minor effects (i.e. Quantitative Trait Locus) are responsible for the resistance and at least three chromosomes 1RS, 2RL and 2BL. Previous studies have shown the importance of minor genes, and also the importance of additive and epistatic actions among genes for APR of stem rust in bread wheat (Rouse *et al*. 2014). In fact, most studies so far have reported complex additive and epistatic interactions for APR against races in the Ug99 lineage (Singh *et al*. 2013, 2014), and a large proportion of the resistance has been derived from the wheat cultivar Thatcher and its *Sr12* gene combined with complementary epistasis genes (Rouse *et al*. 2014). In the present study, three chromosomes had to be combined in order to attain resistance, thereby indicating additive or epistatic effects among genes for the resistance. In durum wheat, the proportion of accessions carrying resistance against TTKSK and other races in the Ug99 lineage is higher than in bread wheat (Singh *et al*. 2011). Furthermore, a number of resistance QTLs effective against race TTKSK has been identified in durum wheat (Haile *et al*. 2012). Through composite interval mapping in durum wheat, several QTLs were identified on different chromosomes, suggesting that APR is oligogenic and with a potential presence of previously unidentified minor resistance genes (Haile *et al*. 2012).

The resistance (APR) against the race TTKSK+Sr24 reported in the present study may be of particular interest because it originates from a completely different genepool than those previously reported. For example the Thatcher cultivar is not found in the genetic background of the evaluated wheat material, and thus novel genes may be present. However, the fact that the heterozygotic combination of 2RL and 2BL is needed for resistance complicates the usefulness of the genes in a breeding program. This complication is clearly shown in the present investigation as well; selfing of the BC_1F_3 populations resulted in only 50% of the 1RS++, 2RL+– populations still being 2RL+– and the remaining 50% being half 2RL++ and 2RL––, respectively. Thus, as could be expected from such a segregation pattern, the resistance decreased in the 1RS++, 2RL+– populations. A further complication in using the results for practical breeding purposes is that only two out of five populations with this chromosomal combination exhibited APR, indicating the importance of combining all of the relevant genes in order to confer resistance. When using chromosomes originating from both wheat and rye, there is always a risk of losing small, but important parts of the chromosomes while creating the translocations (Lukaszewski 2008).

To conclude, the present study has clearly shown the presence of APR resistance against African stem rust races in the evaluated 1BL.1RS, 2RL.2BS double rye translocation lines. The basis of this resistance is likely due to several minor genes located on chromosomes 1RS, 2RL and 2BL, and also most likely to additional genes on other chromosomes that were not detected. The resistance reaction seems to be based on genes with additive or epistatic interactions. In order to clarify the background for the resistance, further studies are needed, including mapping studies of recombinant inbred lines (Rouse *et al*. 2014) or similar methods.

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References

Bhavani S., Singh R.P., Argillier O., Huerta-Espino J., Singh S., Njau P. (2011): Mapping durable adult plant stem rust resistance to the race Ug99 group in six CIMMYT wheats to Ug99 group of races. In: Proc. Borlaug Global Rust Initiative 2011 Technical Workshop, June 13–16, 2011, St. Paul: 43–53.

Forsstrom P.O., Merker A. (2001): Sources of wheat powdery mildew resistance from wheat-rye and wheat-leymus hybrids. Hereditas, 134: 115–119.

Friebe B., Jiang J., Raupp W.J., McIntosh R.A., Gill B.S. (1996): Characterization of wheat-alien translocations conferring resistance to diseases and pests: Current status. Euphytica, 91: 59–87.

Gupta R.B., Shepherd K.W. (1993): Production of multiple wheat-rye 1RS translocation stocks and genetic analysis of LMW subunits of glutenin and gliadins in wheat using these stocks. Theoretical and Applied Genetics, 85: 719–728.

Haile J.K., Nachit M.M., Hammer K., Badebo A., Röder M.S. (2012): QTL mapping of resistance to race Ug99 of *Puccinia graminis* f.sp. *tritici* in durum wheat (*Triticum durum* Desf.). Molecular Breeding, 30: 1479–1493.

Hatchett J.H., Sears R.G., Cox T.S. (1993): Inheritance of resistance to Hessian fly in rye and in wheat-rye translocation lines. Crop Science, 33: 730–734.

Hysing S.C., Hsam S.L.K., Singh R.P., Huerta-Espino J., Boyd L.A., Koebner R.M.D., Cambron S., Johnson J.W., Bland D.E., Liljeroth E., Merker A. (2007): Agronomic performance and multiple disease resistance in T2BS·2RL wheat-rye translocation lines. Crop Science, 47: 254–260.

Jin Y., Singh R.P., Ward R.W., Wanyera R., Kinyua M., Njau P., Fetch T., Pretorius Z.A., Yahyaoui A. (2007): Characterization of seedling infection types and adult plant infection responses of monogenic *Sr* gene lines to race TTKS of *Puccinia graminis* f.sp. *tritici*. Plant Disease, 91: 1096–1099.

Kurt J.L., Szabo L.J. (2005): Stem rust of small grains and grasses caused by *Puccinia graminis*. Molecular Plant Pathology, 6: 99–111.

Lukaszewski A.J. (2008): Unexpected behavior of an inverted rye chromosome arm in wheat. Chromosoma, 117: 569–578.

Merker A. (1982): 'Veery' a CIMMYT spring wheat with the 1B/1R chromosome translocation. Cereal Research Communications, 10: 105–106.

Merker A., Lantai K. (1997): Hybrids between wheats and perennial *Leymus* and *Thinopyrum* species. Acta Agriculturae Scandinavica, Section B – Soil & Plant Science, 47: 48–51.

Merker A., Forsstrom P.O. (2000): Isolation of mildew resistant wheat-rye translocation lines from a double substitution line. Euphytica, 115: 167–172.

Peterson R.F., Campbell A.B., Hannah A.E. (1948): A diagrammatic scale for estimating rust severity on leaves and stems of cereals. Canadian Journal of Research, Section C, 26: 496–500.

Pretorius Z.A., Singh R.P., Wagoire W.W., Payne T.S. (2000): Detection of virulence to wheat stem rust resistance gene *Sr31* in *Puccinia graminis* f.sp. *tritici* in Uganda. Plant Disease, 84: 203.

Rabinovich S.V. (1998): Importance of wheat-rye translocations for breeding modern varieties of *Triticum aestivum* L. Euphytica, 100: 323–340.

Rahmatov M. (2012): Isolation and evaluation of different wheat-rye translocation lines obtained from a disease resistant double translocation line with 1BL.1RS and 2RL.2BS. [Master Thesis.] Alnarp, Swedish University of Agricultural Sciences.

Roelfs A.P., Singh R.P., Saari E.E. (1992): Rust Diseases of Wheat: Concepts and Methods of Disease Management. Mexico, D.F., CIMMYT.

Rouse M.N., Wanyera R., Njau P., Jin Y. (2011): Sources of resistance to stem rust race Ug99 in spring wheat germplasm. Plant Disease, 95: 762–766.

Rouse M.N., Talbert L.E., Singh D., Jamie D., Sherman J.D. (2014): Complementary epistasis involving *Sr12* explains adult plant resistance to stem rust in Thatcher wheat (*Triticum aestivum* L.). Theoretical and Applied Genetics, 127: 1549–1559.

Rowell J.B. (1984): Controlled infection by *Puccinia graminis* f.sp. *tritici* under artificial conditions. In: Bushnell W.R., Roelfs A.P. (eds): The Cereal Rusts, Volume 1. Orlando, Academic Press: 291–332.

Singh R.P., Hodson D.P., Huerta-Espino J., Yue J., Njau P., Wanyera R., Herrera-Foessel S., Ward R.W. (2008): Will stem rust destroy the world's wheat crop? Advanced Agronomy, 98: 271–309.

Singh R.P., Hodson D.P., Huerta-Espino J., Yue J., Bhavani S., Njau P., Herrera-Foessel S., Singh P.K., Singh S., Govindan V. (2011): The emergence of Ug99 races of the stem rust fungus is a threat to world wheat production. Annual Review of Phytopathology, 49: 465–482.

Singh A., Knox R.E., DePauw R.M., Singh A.K., Cuthbert R.D., Campbell H.L., Singh D., Bhavani S., Fetch T., Clarke F. (2013): Identification and mapping in spring wheat of genetic factors controlling stem rust resistance and the study of their epistatic interactions across multiple environments. Theoretical and Applied Genetics, 126: 1951–1964.

Singh R., Herrera-Foessel S., Huerta-Espino J., Singh S., Bhavani S., Lan C., Basnet B. (2014): Progress towards

doi: 10.17221/80/2015-CJGPB

genetics and breeding for minor genes based resistance to Ug99 and other rusts in CIMMYT high-yielding spring wheat. Journal of Integrative Agriculture, 13: 255–261.

Stakman E.C., Steward D.M., Loegering W.Q. (1962): Identification of Physiologic Races of *Puccinia graminis* var. *tritici*. Saint Paul, USDA, Agricultural Research Service: E-617.

Zeller F.J. (1973): 1B/1R wheat-rye chromosome substitutions and translocations. In: Proc. 4th Int. Wheat Genetics Symposium, Aug 6–11, 1973, Columbia: 209–221.

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Corresponding author:

Mahbubjon Rahmatov, MSc., Swedish University of Agricultural Sciences, Department of Plant Breeding, Box 101, SE-230 53, Alnarp, Sweden; e-mail: mahbubjon@gmail.com