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MOLECULAR-GENETIC EVIDENCE OF WHEAT-RYE CHROMOSOME SUBSTITUTION AND TRANSLOCATION IN WHEAT CULTIVARS AND INTROGRESSION STOCKS

With use of molecular-genetic and cytological analysis 1AL.1RS and 1BL.1RS translocations, (1B)1R wheat-rye chromosome substitution, as well as modified 1BL.1RS translocation with locus Sec1 replaced by wheat Gli-B1 locus, have been identified in new wheat cultivars, original introgression stocks and F_4 hybrid families. The translocations were suggested to support a resistance to leaf rust caused by the Lr genes, being not related to them, and to determine confident resistance to stem rust. The substitution stocks were susceptible to leaf and moderately susceptible or low resistant to stem rusts because of other than the wheat-rye chromosome translocation origination of the 1RS chromosome.

Key words: *Triticum aestivum*, *STS-markers, substitution, translocation.*

Introduction. The short arm of chromosome 1R of *S. cereale* carries a number of genes of agronomic importance, and when transferred to bread wheat in the form of 1BL.1RS or 1AL.1RS translocations has improved the adaptation of wheat plants and has resulted in valuable new cultivars. Derived from cv. Avrora a wheat-rye translocation 1BL.1RS, which carries chromosome arm 1RS from rye cv. Petkus, is the most widespread. This arm carries a gene cluster *Pm8/Yr9/Lr26/Sr31* conferring resistance to diseases [1]. Derived from cv. Amigo a 1AL.1RS translocation, which short arm originated from rye cv. Insave, is in the second place according its distribution among wheat cultivars, as reported in the rye gene map database (**http://www.rye-gene-map.de/ryeintrogression/**). The rye arm in this translocation determined the resistance to drought, greenbug (*Schizaphis graminum*) (gene *Gb2*), mite (*Aceria tosicheslla*) (*Cm3*), powdery mildew (*Pm17*), leaf and stem rust (*SrR*) [1]. Some other translocations (including a 1AL.1RS, a 1BL.1RS and a 1DL.1RS) involving 1RS from rye cv. Imperial have been isolated in Australia in

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different wheat backgrounds [2]. These translocations conferred resistance to all Australian strains of the stem rust pathogen, but were susceptible to leaf rust, stripe rust and powdery mildew. In Japan, cv. Salmon that has a translocation 1BL.1RS was obtained in the progeny of a hybrid between two strains of octoploid *Triticale*. The translocation is somewhat different from Avrora's one and carries a recognizably different allele at the *Sec1* locus [3]. The rye parent and breeding use of the Salmon's translocation are not considered in literature. Due to its increasing effect on wheat adaptability and productivity, numerous wheat cultivars and lines, carrying the 1RS as 1AL.1RS, 1BL.1RS or 1DL.1RS Robertsonian translocation, have been released worldwide [4].

The introduction of the translocations into Ukrainian bread wheat cultivars is a result following the utilization of the Avrora's and Amigo`s offspring in the hybridization programs. So, the translocated chromosomes 1BL.1RS (1RS from Petkus rye) and 1AL.1RS (1RS from Insave rye) have been identified in a number of cultivars developed in Ukraine [5]. In addition, a number of introgression stocks with high resistance to leaf and stem rust, high protein content and some morphological characters were developed as a result of wide crosses; and the 1BL.1RS translocation from Avrora had been identified among them [6]. Besides, within the stocks, chromosome 1R of rye cv. Voronezhskaya SHI substituted for chromosome 1B in a mixed cv. Hostianum 237/*T. durum* cv. Chernomor background. Recently we found that this rye chromosome does not confer resistance to leaf rust, carries a different allele at the *Sec1* locus, and moreover it has a new addition secalin locus 22.9 ± 3.1 cM distally from the *Sec1* in the 1RS arm [7].

Unfortunately, in contrast to their desirable agronomic traits, wheats carrying these translocations generally produce a flour with low quality. Doughs derived from them show marked stickiness, reduced dough strength and intolerance to overmixing, and this seriously limited their use in Ukraine where leavened bread is the main end-product of the flour [8]. Recently a program was started to reduce the amount of rye chromatin in 1BL.1RS translocation by induction of homoeologous pairing between 1RS and 1BS chromosomes, with the aim of separating the quality defects from the stem rust resistance gene *Sr31* [9]. Similar attempts are now being made to introduce the recombined rye arm of Pavon MA1 line into Odessa`s cvs [10] to separate the sticky dough problem from the disease resistance and high yield associated with the 1BL.1RS translocation derived from rye cv. Petkus.

Various methods have been employed to detect the wheat-rye translocations, however the abundance of DNA markers in cereal genomes provided a powerful tool to detect or verify the presence of rye chromatin in wheat backgrounds [11]. The aim of the work was to detect the (1B)1R wheat-rye chromosome substitution, 1AL.1RS and 1BL.1RS translocation in Ukrainian cultivars, introgression stocks and hybrid families with PCR markers.

Material and methods. A sets of 30 winter bread wheat cvs, 10 original primary introgression stocks (2*n*=42) and 13 F_4 hybrid families have been in-

vestigated. The cvs were of different pedigree and mainly of Ukrainian breeding. Among them Odesskaya 267 (Od.267), Kuyal`nik and Pavon as a negative control for 1AL.1RS and 1BL.1RS translocations, Amigo as a positive control for 1AL.1RS translocation and Avrora as a positive control for 1BL.1RS translocation, were included in this study.

The majority of the introgression stocks (F_∞) were developed from a cross: triticale (8x) cv. AD825/*T. durum* Desf. cv. Chernomor and following spontaneous hybridization of the F_3 hybrids with the collection sib-strain H74_90–245 or H74_90–258, or without it. Triticale AD825 is a primary amphidiploid (*T. aestivum* L. cv. Hostianum 237/*S. cereale* L. cv. Voronezhskaya SHI) [12]. The strains H74_90–245 and H74_90–258 were derived in Dobroudja Agricultural Institute (General Toshevo, Bulgaria) from the step cross: Dr. Savov`s synthetic (*T. timopheevii* Zhuk./*Ae. tauschii* Coss.)/Tom Pouce Blanc//Avrora/3/Rusalka and received from Dr. Ivan Panayotov.

The stocks CWXs and CWXr were derived from a cross between the primary introgression stocks H273_97, having a (1B)1R chromosome substitution, and H242_97–2, carrying a 1BL.1RS translocation [Kozub, unpublished].

The F_4 hybrid families were obtained from a cross Kuyal`nik/Pavon MA1 and provided by Dr. A. I. Rybalka [10]. The line Pavon MA1, having a modified 1BL.1RS translocation, was created by Dr. A. J. Lukaszewski [13] and kindly supplied to Dr. Rybalka for exclusive exploiting (Rybalka 2005, personal communication).

The material was evaluated to contain a field resistance to leaf and stem rusts and was investigated by PCR-analysis with microsatellite markers. The F_1 hybrids between some of the introgression stocks or the F_4 families and corresponding bread wheat tester (Od.267 or Kuyal`nik, respectively) were studied cytologically with routine acetocarmine methods. Plant pathological evaluations were carried out by the plant infection intensity in field (at the adult plant stage) with use of a unified international scale based on modified Cobb scale [14]. Were ‘VR’, ‘R’ and ‘MR’ characterized high, simple and moderate resistance, and ‘VS’, ‘S’ and ‘MS’ — respectively, susceptibility. The leaf and stem rust resistance were scored both at natural epiphytotic conditions and under an artificial infection pressure. Herewith, population mixtures of the most aggressive local races of both diseases were used.

All lines were analyzed by using DNA-markers. DNA was isolated from leaf material of adult plants and seedlings according to standard CTAB-methods [15]. Rye microsatellites: *Xrems1303*, *SR1R003*, a secalin-specific STS-marker — ω-*sec*-P3+ω-*sec*-P4, wheat microsatellites: *Xgwm18* (1BS), *Xgwm550* (1BS), *Xgwm140* (1BL), *Xgwm153* (1BL), *Xbarc263* (1AS), *Xgwm357* (1AL), *Taglut* (1AS) and allele-specific molecular markers: *GliB1.b* and *GliB1.d* have been applied for the PCR-analysis. The PCR products were analyzed with using standard electrophoresis procedure in 2 % agarose gel. The fragment sizes were calculated by comparison with molecular weight marker — pUC19/MspI. Detailed characteristics of the

markers and molecular procedure used is described at methodical recommendations [16].

1RS chromosome presence was detected with the rye microsatellites and the secalin-specific STS-marker. Substitution or translocation was identified by the absence of 1A or 1B chromosome corresponding arm via application of the wheat microsatellites. The (1B)1R chromosome substitution and 1BL.1RS translocation presence in some introgression stocks was confirmed cytologically for meiotic configurations at metaphase I (MI) in pollen mother cells (PMCs) of the F_1 hybrids.

Results and discussion. The presence of 1RS chromosome was detected in the cvs, introgression stocks and the F_4 hybrid families studied when specific products with the markers: *Xrems1303*, *SR1R003*, ω-*sec-P3* + ω-*sec-P4* had been found. The absence of PCR products with the markers *Xbarc263* (1AS) or *Xgwm550* (1BS) evidenced the substitution of corresponded wheat chromosome arm 1AS or 1BS by the short arm of rye chromosome 1R and allowed to differentiate wheat cultivars with 1AL.1RS and 1BL.1RS translocations (Table 1). Thus, several cvs carry the arm 1RS from Insave rye as a 1AL.1RS translocation, and the others have a 1BL.1RS translocation. Two bread wheat cultivars without the translocations and negative controls for both translocations also were presented.

Within the introgression stocks the microsatellite markers *Xgwm18* (1BS), *Xgwm550* (1BS), as well as *Xgwm140* (1BL) and *Xgwm153* (1BL) have been applied for the identification and differentiation of 1B chromosome translocation or substitution. The detection of PCR-products of the *Taglut* (1AS) and *Xgwm357* (1AL) markers, irrespective of the polymorphism, proved the presence of intact 1A chromosome in the investigated introgression stocks.

The amplification products with the markers *Xgwm140* and *Xgwm153* were not detected for the stocks H273_97, H274_97 and H269_97–5, but were obtained within the stocks E200_97–1, E200_97–2, H242_97–1, H242_97–2, CWXs and CWXr, as well (Table 2). Thus, the stocks H273_97, H274_97 and H269_97–5 carry a (1B)1R substitution, and all the others carry a 1BL.1RS translocation chromosome. As for E217_97, the translocation 1BL.1RS heterozygosis was revealed in this stock at the previous investigation [6]. So that, an individual selection of a plant with a big spike was carried out in the E217_97. Evidently, the plant without the translocation was chosen and, correspondently, the stock E217_97 without the translocation has been derived (table 2).

Meiotic observations revealed the presence of 19 closed bivalents (the maximum) plus an open bivalent and 2 univalents ($19^{II}_{C}+1^{II}_{O}+2^{I}$) at meiotic MI in the F_1 of H273_97/Od.267 and H274_97/Od.267 hybrids (Fig. 1 a), and $20^{II}_{C}+1^{II}_{O}$ (Fig. 1 b) as the highest chromosome association in the test crosses Od.267/translocation stocks, supporting the molecular-genetic evidence. There were only one PMC (0.3 %) with $20^{II}_{C}+2^{I}$ as the highest meiotic association (Fig. 1 c) and complete absence of pairing between 1R and 1B

Table 1

Results of PCR-analysis of the winter bread wheat cultivars studied

Cultivar	Trans-location	Presence of amplification products of the marker loci [a]			
		Xrems1303 (1RS)	ω-*secalin-P3/P4* (1RS)	*Xgwm550* (1BS)	*Xbarc263* (1AS)
Amigo (control)	1AL.1RS	+	+	+	–
Rastavitsa	1AL.1RS	+	+	+	–
Vikhovanka	1AL.1RS	+	+	+	–
Zolotokolosa	1AL.1RS	+	+	+	–
Vesnyanka	1AL.1RS	+	+	+	–
Columbia	1AL.1RS	+	+	+	–
Smuglyanka	1AL.1RS	+	+	+	–
Etude	1AL.1RS	+	+	+	–
Knyaginya Ol`ga	1AL.1RS	+	+	+	–
Avrora (control)	1BL.1RS	+	+	–	+
Bilosnizhka	1BL.1RS	+	+	–	+
Veselka	1BL.1RS	+	+	–	+
Krizhinka	1BL.1RS	+	+	–	+
Libid`	1BL.1RS	+	+	–	+
Mirich	1BL.1RS	+	+	–	+
Mirleben	1BL.1RS	+	+	–	+
Mironivs`ka 33	1BL.1RS	+	+	–	+
Mironivs`ka 61	1BL.1RS	+	+	–	+
Mironivs`ka 65	1BL.1RS	+	+	–	+
Pobeda-50	1BL.1RS	+	+	–	+
Favoritka	1BL.1RS	+	+	–	+
Kharkivs`ka 96	1BL.1RS	+	+	–	+
Elegia	1BL.1RS	+	+	–	+
Shchedrist` od.	1BL.1RS	+	+	–	+
Pavon MA1	1BL.1RS	+	–	–	+
Antonivka	–	–	–	+	+
Bezostaya 1	–	–	–	+	+
Od.267 (control)	–	–	–	+	+
Kuyal`nik (control)	–	–	–	+	+
Pavon (control)	–	–	–	+	+

[a] + primer amplification product presence (irrespective of the polymorphism), — primer product absence.

chromosomes in all 322 PMCs studied in the test crosses Od.267/substitution stocks. On the contrary, a quite regular meiosis (21^{II}_{C} the highest association) in the F_1 plants (Fig. 1 d) and a high level of pairing were observed in the Od.267/E217_97 test cross.

Thereby, the original primary introgression stocks studied have (1B)1R wheat-rye chromosome substitution or 1BL.1RS translocation. That was determined with PCR-markers (Table 2) and confirmed cytologically (Fig. 1). The translocation was contributed by the collection sib-strain H74_90–245 or H74_90–258 and originated from cv. Avrora. Therefore, the rye 1RS

Table 2

Results of plant pathological evaluations and PCR-analysis of the introgression stocks

Introgression stock[a]	Resistance to		*Xrems 1303* (1RS)	SR1R 003 (1RS)	ω-*seca-lin-P3/P4* (1RS)	*Xgwm 18* (1BS)	*Xgwm550* (1BS)	*Xgwm140* (1BL)	*Xgwm 153* (1BL)	*Tag-lut* (1AS)	*Xgwm357* (1AL)
	Leaf rust	Stem rust									
E200_97–1	MS-R	VR	+[b]	+	+	–	–	+	+	+	+
E200_97–2	VR(S)	VR	+	+	+	–	–	+	+	+	+
E217_97	VS-S	VS	–	–	–	+	+	+	+	+	+
H242_97–1	R-VR	VR	+	+	+	–	–	+	+	+	+
H242_97–2	R-VR	VR	+	+	+	–	–	+	+	+	+
H273_97	VS-MS	MS	+	+	+	–	–	–	–	+	+
H274_97	S-MS	MS	+	+	+	–	–	–	–	+	+
H269_97–5	S-MS	MS	+	+	+	–	–	–	–	+	+
CWXs	S	MR	+	+	+	–	–	+	+	+	+
CWXr	MR	MR	+	+	+	–	–	+	+	+	+

[a] H — Hostianum, E — Erythrospermum; [b] + primer amplification product presence (irrespective of the polymorphism), — primer amplification product absence.

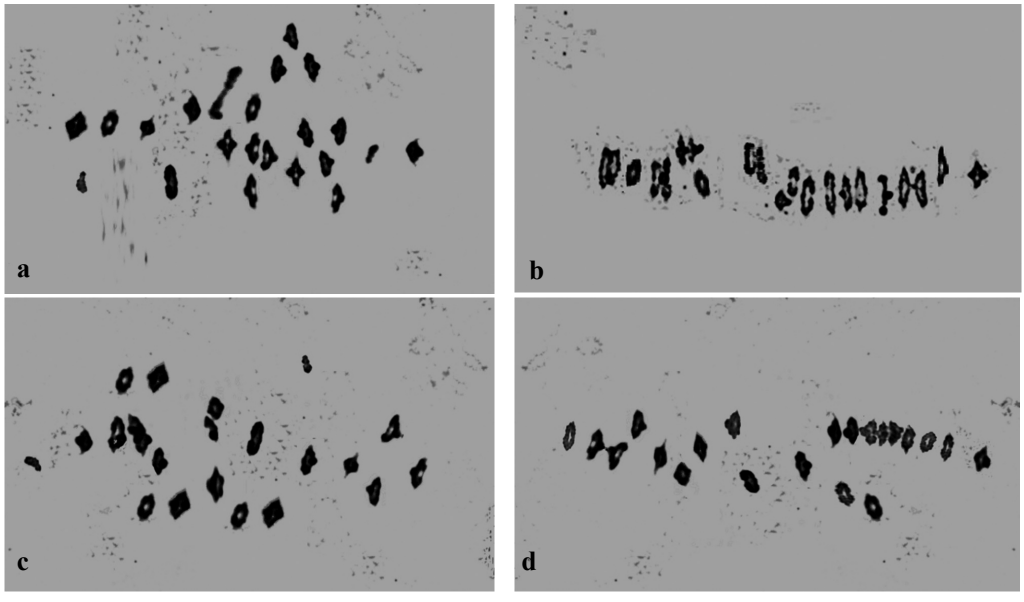

Fig. 1. The highest chromosome associations at meiotic MI of F1 hybrids derives in test-crosses (590×): a) H274_97/Od.267–$19^{II}_{C}+1^{II}_{O}+2^{I}$; b) Od.267/H242_97–2–$20^{II}_{C}+1^{II}_{O}$; c) H273_97/Od.267–$20^{II}_{C}+2^{I}$; d) Od.267/E217_97–$21^{II}_{C}$

chromosome originated from Petkus rye. The intact rye chromosome 1R for the substitution was contributed by triticale (8x) cv. AD825 and, therefore, originated from rye cv. Voronezhskaya SHI.

Depending on the rye chromosome arm pedigree the stocks were considerably different for resistance to leaf and stem rusts (Table 2). The stocks E200_97–1, E200_97–2, H242_97–1 and H242_97–2, carrying 1BL.1RS translocation from cv. Avrora, had a high resistance to both diseases with a preference of E200_97–2 under E200_97–1. However, the stock E200_97–2, that has been confirming the rust resistance for years, segregated susceptible plants in 2013 and has been subjected to individual selection. E217_97 was susceptible. The substitution stocks, carrying 1R chromosome from rye Voronezhskaya SHI, were moderately defeated by stem rust (MS) and did not have any leaf rust resistance (S-MS). The introgression stocks CWXs and CWXr were isolated from the same cross H273_97/H242_97–2 [Kozub, unpublished] as, respectively, susceptible and resistant (MR) to leaf rust. Both sib-stocks contain a long arm of 1B chromosome and a short arm of 1R chromosome (Table 2), so, carrying an original 1BL.1RS recombinant translocation. The stocks are susceptible to powdery mildew [Kozub 2014, personal communication] and were moderately resistant to stem rust in weak infectious background of 2014.

13 F_4 hybrid families from a cross Kuyal`nik/Pavon MA1 were studied by using PCR-analysis [10]. Among them 6 families had a Dr. Lukaszewski modified 1BL.1RS translocation [13] with wheat locus *Gli-B1* and without rye locus *Sec1* and one more was heterogeneous. 4 (6.6 % of 61 studied) F_4 hybrid plants were found to have a recombination because of pairing between short arms of modified 1BL.1RS translocation and intact wheat chromosome 1B. Of them 3 recombinants carried the modified wheat-rye translocation with allele *Gli-B1b* (is preferred for a high flour quality) from cv. Kuyal`nik instead of Pavon MA1's *Gli-B1d* allele (determined a low flour quality).

Cytological observations, generally, supported the heterogeneity of the hybrid families. 4 of 8 evidently studied plants from 4 resistant to leaf rust families had $20^{II}_{C}+1^{II}_{O}$ as the highest chromosome association and probably were heterozygous for the translocation. The rest plants had 21^{II}_{C} and were homozygous. However, no PMC (of 253 studied) with 21^{II}_{C} as the highest meiotic association proving the pairing between modified 1RS and 1BS chromosomes were observed at MI of the F_1 hybrid plants Kuyal`nik/Pavon MA1, as well as of 730 PMCs at MI of the F_4 plants heterozygous for the translocation.

The F_4 recombinant plants were isolated and F_5 families from them together with parental forms were verified for resistance to rusts. In 2013, descendants of the recombinant plant 3–4_13 without the rye translocation (*Xrems1303* amplification product absence) were susceptible to leaf rust, but segregated plants moderately resistant to stem rust. The other recombinants carried the modified translocation (*Xrems1303* amplification product presence), as well as the allele *Gli-B1b* from cv. Kuyal`nik, and their progenies were moderately resistant to leaf rust, but defeated by stem rust (Table 3). However, in the progeny of the plant 8–2_13 a resistant to stem rust segregant was also found. As a result, the plants with reactions 'MS' or 'MR' to leaf and 'MR' or 'R' to stem rust were isolated respectively in progenies of recombi-

nants 3–4_13 or 8–2_13, and 2 recombinant stocks with different level of resistance to both diseases were derived in 2014.

Table 3

Results of plant pathological evaluations and PCR-analysis of progenies of the F_4 recombinant plants isolated

Line or F_5 family	Resistance to		*Xrems1303* (1RS)	*Xgwm18* (1BS)	*Xgwm 550* (1BS)	*GliB1.b* (1BS)	*GliB1.d* (1BS)
	Leaf rust	Stem rust					
Kuyal`nik	VS-S	VS-S	–[b]	+	+	+	–
Pavon MA1	R	MR	+	–	–	–	+
3–4_13	S(MS)-MS[a]	S;MR-MR	–	+	+	–	+
8–2_13	MR	MS(R)-R	+	–	–	+	–
8–3_13	MR	VS	+	–	+	+	–
10–3_13	MR	VS	+	–	–	+	–

[a] S(MS) — majority of plants had 'S' reaction and single plants had 'MS' reaction, S;MR — segregation; [b] + primer amplification product presence, — primer amplification product absence.

Generally, the gene *Sr31* was determined to be effective in South Ukraine [17], and the 1BL.1RS translocation from cv. Avrora was the source of the resistance of the studied cultivars, introgression stocks and hybrid families to stem rust. Unfortunately, the gene *Lr26* was determined to be ineffective [18], but usually the lines with the translocation confirmed any level of leaf rust resistance. Therefore, the presence of the 1BL.1RS translocation is thought to be a factor supporting other genes for the resistance. Due to their agronomic advantages, the translocations with 1RS are more widespread in wheat cultivars from Forest-Steppe zone of Ukraine, but not from South. In South Ukraine, the 1RS chromosome has not been used in wheat breeding, because of traditional for PBGI — NCSCI storage protein composition selection for the high technological quality [19]. However, a program for the wheat-rye translocation involvement in wheat breeding for disease resistance has been started at the end of last century [20], and the cvs Vikhovanka, Knyaginya Ol`ga and Zhitnitsa (with 1AL.1RS translocation, leaf and stem rust resistance and middle quality) and Schedrist` (with 1BL.1RS translocation and low quality) have been developed [21]. Because leaf-disease resistance of rye chromosome 1RS had been overcome by new mildew and leaf rust races, breeders may select only for stem rust resistance in order to use the translocations in breeding programs. This is of great advantage, since cytological, biochemical of molecular-genetic methods is not needed for the successful introduction of the desired segment of rye chromosome 1R into bread wheat.

Conclusion. The use of molecular-genetic and cytological analysis permit to identify the 1AL.1RS and 1BL.1RS translocation, 1B-1R wheat-rye chromosome substitution, particularly modified 1BL.1RS translocation with locus

Sec1 replaced by wheat *Gli-B1* locus, in the original introgression stocks, cultivars and F_4 hybrid families. The 1AL.1RS translocation was contributed by the collection cultivars, derived from wheat cv. Amigo and originated from rye cv. Insave. The 1BL.1RS translocation, including the modified 1BL.1RS translocation, contributed by cv. Avrora and originated from Petkus rye. All these translocations were suggested to support a resistance to leaf rust caused by the other Lr genes and to determine confident resistance to stem rust. The intact rye chromosome 1R for the substitution was contributed by triticale (8x) cv. AD825 and originated from rye cv. Voronezhskaya SHI. The substitution stocks were susceptible to leaf and moderately susceptible or low resistant to stem rusts because of another origination of the 1R chromosome.

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МОЛЕКУЛЯРНО-ГЕНЕТИЧНЕ ВИЗНАЧЕННЯ ПШЕНИЧНО-ЖИТНІХ ХРОМОСОМНИХ ЗАМІЩЕНЬ І ТРАНСЛОКАЦІЙ У СОРТІВ І ІНТРОГРЕСИВНИХ ЛІНІЙ ПШЕНИЦІ

1AL.1RS і 1BL.1RS транслокації, (1B)1R пшенично-житнє заміщення, а також модифікована 1BL.1RS транслокація з локусом *Sec1*, заміщеним локусом *Gli-B1* пшениці, ідентифіковані за допомогою молекулярно-генетичного і цитологічного аналізу у нових сортах пшениці, оригінальних інтрогресивних лініях і гібридних сім'ях F_4. Досліджені транслокації, очевидно, підсилюють стійкість до бурої іржі, спричинену *Lr* генами, які не мають до них стосунку, і визначають певну стійкість до стеблової іржі. Заміщені лінії були сприйнятливі до листової і помірно сприйнятливі або слабко стійкі до стеблової іржі завдяки відмінному від пшенично-житніх транслокацій походженню хромосоми 1RS.

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МОЛЕКУЛЯРНО-ГЕНЕТИЧЕСКОЕ ОПРЕДЕЛЕНИЕ ПШЕНИЧНО-РЖАНЫХ ХРОМОСОМНЫХ ЗАМЕЩЕНИЙ И ТРАНСЛОКАЦИЙ В СОРТАХ И ИНТРОГРЕССИВНЫХ ЛИНИЯХ ПШЕНИЦЫ

1AL.1RS и 1BL.1RS транслокации, (1B)1R пшенично-ржаное замещение, а также модифицированная 1BL.1RS транслокация с локусом *Sec1*, замещенным локусом *Gli-B1* пшеницы, идентифицированы с помощью молекулярно-генетического и цитологического анализа в новых сортах пшеницы, оригинальных интрогрессивных линиях и гибридных семьях F_4. Изученные транслокации усиливают устойчивость к бурой ржавчине, вызванную *Lr* генами, не имеющими к ним отношения, и определяют надежную устойчивость к стеблевой ржавчине. Замещенные линии были восприимчивы к листовой и умеренно восприимчивы или слабо устойчивы к стеблевой ржавчине из-за отличного от пшенично-ржаных транслокаций происхождения хромосомы 1RS.