

The Fifth International Scientific Conference PlantGen2019

Identification of QTLs for resistance to leaf and stem rusts in bread wheat (*Triticum aestivum* L.) using a mapping population of 'Pamyati Azieva × Paragon'

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Leaf rust (LR) and stem rust (SR) are harmful fungal diseases of bread wheat (*Triticum aestivum* L.). The purpose of this study was to identify QTLs for resistance to LR and SR that are effective in two wheat-growing regions of Kazakhstan. To accomplish this task, a population of recombinant inbred lines (RILs) of 'Pamyati Azieva × Paragon' was grown in the northern and southeastern parts of Kazakhstan, phenotyped for LR/SR severities, and analyzed for key yield components. The study revealed a negative correlation between disease severity and plant productivity in both areas. The mapping population was genotyped using a 20,000 Illumina SNP array. A total of 4595 polymorphic SNP markers were further selected for linkage analysis after filtering based on missing data percentage and segregation distortion. Windows QTL Cartographer was applied to identify QTLs associated with LR and SR resistances in the RIL mapping population studied. Two QTLs for LR resistance and eight for SR resistance were found in the north, and the genetic positions of eight of them have matched the positions of the known *Lr* and *Sr* genes, while two QTLs for SR were novel. In the southeast, eight QTLs for LR and one for SR were identified in total. The study is an initial step of the genetic mapping of LR and SR resistance loci of bread wheat in Kazakhstan. Field trials in two areas of the country and the genotyping of the selected mapping population have allowed identification of key QTLs that will be effective in regional breeding projects for better bread wheat productivity.

Key words: bread wheat; linkage mapping; recombinant inbred lines; qualitative trait loci; leaf rust; stem rust.

For citation: Genievskaya Y., Fedorenko Y., Sarbayev A., Amalova A., Abugalieva S., Griffiths S., Turuspekov Y. Identification of QTLs for resistance to leaf and stem rusts in bread wheat (*Triticum aestivum* L.) using a mapping population of 'Pamyati Azieva × Paragon'. Vavilovskii Zhurnal Genetiki i Seleksii = Vavilov Journal of Genetics and Breeding. 2019; 23(7):887-895. DOI 10.18699/VJ19.563

Идентификация локусов количественных признаков устойчивости к листовой и стеблевой ржавчинам мягкой пшеницы (*Triticum aestivum* L.) с использованием картирующей популяции Памяти Азиева × Парагон

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Листовая и стеблевая ржавчины являются вредоносными грибными болезнями мягкой пшеницы (*Triticum aestivum* L.). Целью данного исследования была идентификация локусов количественных признаков (ЛКП), связанных с устойчивостью к болезням, в двух регионах возделывания пшеницы в Казахстане. Для этого картирующая популяция Памяти Азиева × Парагон, состоящая из 98 рекомбинантно-инбредных линий и выращиваемая на севере и юго-востоке Казахстана, была фенотипирована по степени поражения листовой и стеблевой ржавчиной и проанализирована по ключевым компонентам урожайности. Выявлена отрицательная корреляция между степенью поражения болезнью и продуктивностью растений в обоих регионах. Картирующая популяция была генотипирована с использованием ДНК микрочипа Illumina на 20000 маркеров ОНП (однонуклеотидный полиморфизм). Для дальнейшего анализа отобрано 4595 полиморфных маркеров ОНП. Для идентификации

ЛКП, связанных с устойчивостью картирующей популяции к листовой и стеблевой ржавчинам, использовалась программа Windows QTL Cartographer v2.5. В северном регионе были обнаружены два ЛКП устойчивости к листовой ржавчине и восемь ЛКП – к стеблевой. Локализации восьми из них совпали с позициями известных генов *Lr* и *Sr*. Два ЛКП для стеблевой ржавчины были обозначены как новые. Для юго-восточного региона обнаружено восемь ЛКП, ассоциированных с устойчивостью к листовой ржавчине, и один – к стеблевой. Настоящее исследование является первым шагом в генетическом картировании локусов устойчивости к листовой и стеблевой ржавчинам мягкой пшеницы в Казахстане. Полевые исследования в двух регионах страны и генотипирование выбранной картирующей популяции позволили выявить ключевые ЛКП, которые будут эффективны в региональных селекционных проектах, направленных на улучшение продуктивности мягкой пшеницы. Ключевые слова: мягкая пшеница; картирование; рекомбинантно-инбредные линии; локусы количественных признаков; листовая ржавчина; стеблевая ржавчина.

Introduction

Wheat is one of the most important cereal crops in the World and Kazakhstan (<http://www.fao.org>). In Kazakhstan wheat is grown on about 13 million hectares annually. The country produces up to 20–25 million tons of bread wheat per year, and exports up to 5–7 million tons of the grain (<http://stat.gov.kz>). However, an annual infection of bread wheat by fungal diseases is causing a serious yield reduction (Koyshybaev et al., 2017).

The three most common wheat fungal pathogens in the world are *Puccinia triticina* Erikss. (leaf rust), *Puccinia graminis* Pers. f. sp. *tritici* Erikss. & Henn. (stem rust), and *Puccinia striiformis* Westend. f. sp. *tritici* Eriks. (stripe or yellow rust) (Bushnell, Roelfs, 1984). *P. recondita* is now recognized as one of the most dangerous pathogens in wheat production worldwide, causing significant yield losses over the large geographical areas (Bolton et al., 2008). The infection with any rust fungus results in decreased numbers of kernels per spike and lower kernel weights due to the parasitic consumption of host nutrients, which leads to apparent yield losses and poor quality of the grains (Afzal et al., 2008).

In Kazakhstan, leaf rust (LR) and stem rust (SR) together cause the most severe yield losses in bread wheat (Rsaliev et al., 2005). When the epidemic develops at the early stage, and the infection persists until wheat is fully ripe, the yield loss increases up to 40–60 % (Koyshybaev, 2010). It happens because of the favorable climate conditions for the spreading of *P. recondita* in the fields, especially in south and south-east of Kazakhstan, where the high temperature and water deficiency stimulate the expansion of spores (Koyshybaev, 2010). As for the SR, the constantly widening areal of aggressive stem rust race Ug99 creates a threat to the food security of the entire planet (Singh et al., 2011; Bhardwaj et al., 2014), including Kazakhstan (Shamanin et al., 2010; Rsaliev, 2011). With epiphytotic SR development, the yield losses of spring wheat can potentially reach 40–50 % (Koyshybaev, 2010; Soko et al., 2018).

One of the most effective ways to protect wheat from LR and SR is the development of resistant cultivars with high yield potential (Ellis et al., 2014). In the last 100 years, approximately 80 LR resistance genes designated from *Lr1* to *Lr78*, *Lrac104*, and *Lrac124*, have been identified and described in common wheat, durum wheat and diploid wheat species (McIntosh et al., 1998, 2007, 2017). In the last 10 years in Kazakhstan, there were active research works on the identification of genes, which are effective against LR, screening of wheat cultivars for the presence of resistance gene (Kokhmetova et al., 2009; Akhmetova et al., 2015) and investigation

on population of *P. recondita* in the country and neighboring territories (Agabaeva, Rsaliev, 2013; Gulytaeva et al., 2018).

As for the SR, to date, nearly 60 *Sr* genes have been identified in wheat and its wild relatives (McIntosh et al., 2017). Almost all of the wheat cultivars approved for use on the territory of Kazakhstan demonstrate poor resistance to SR pathogens (Koyshybaev et al., 2017). For this reason, the analysis of SR and methods of its prevention in Kazakhstan are an important issue and require comprehensive genetic and breeding studies. Several experiments were conducted to search SR resistance sources in wheat germplasm of Kazakhstan (Rsaliev, 2011; Kokhmetova, Atishova, 2012). However, no efforts were done to identify effective genes and quantitative trait loci (QTL) based on genetic mapping approach. Genetic mapping is an effective tool for the identification of QTLs that are responsible for natural phenotypic variations in complex traits, such as resistance to rust diseases (Goutam et al., 2015; Xu et al., 2017). During the past two decades, linkage mapping has been commonly used in various plant species, numerous wheat dense genetic maps were developed (Yang et al., 2017), and a large number of QTL have been cloned or tagged (Price, 2006).

The purpose of this study was the identification of QTL for LR and SR resistance by using 98 recombinant inbred lines (RILs) of 'Pamyati Azieva × Paragon' mapping population (MP). As these lines were tested in environmental conditions of North and South-East Kazakhstan, it was expected that important insights of the genetic control for two types of rust disease resistance in bread wheat will be revealed. This work is a continuation of our recent studies of bread wheat undertaken in our research organization (Turuspekov et al., 2017a, b).

Materials and methods

'Pamyati Azieva × Paragon' mapping population. The MP comprising of 98 F_8 RILs was assembled via crossing between two spring wheat cultivars – 'Pamyati Azieva' (PA) and 'Paragon' (P). These two cultivars were chosen because of their different genetic background and differences in morphological traits. The first parental cultivar is Russian medium-early spring wheat cultivar 'Pamyati Azieva' recommended for the Western Siberian region (<https://reestr.gossort.com>), approved for commercial cultivation in the North Kazakhstan (<http://www.goscomsort.kz/index.php/ru>), and susceptible to LR and SR. The second parental cultivar was a modern UK elite spring wheat cultivar 'Paragon' that was used as a key parent for Wheat Genetic Improvement Programme (<http://www.wgin.org.uk>) resources but poorly studied for the resistance to LR and SR. The MP, as well as the genetic

map, was developed within ADAPTAWHEAT project in greenhouse conditions by using facilities of the John Innes Centre (Norwich, UK) during 2011–2015 (<https://www.jic.ac.uk/adaptawheat>).

Evaluation of the MP for variation in agronomic traits, and LR/SR severity in South-East and North Kazakhstan. Field evaluations of the MP were conducted in North Kazakhstan agricultural experimental station (North Kazakhstan region) and Kazakh Research Institute of Agriculture and Plant Industry (South-East Kazakhstan, Almaty region). Ninety-eight RILs, the parental cultivars ('Pamyati Azieva' and 'Paragon'), and standard check cultivars ('Astana' and 'Omskaya 35' in the North, and 'Kazakhstanskaya 4' and 'Kazakhstanskaya rannespelaya' in the South-East) were evaluated in 2018 under field conditions for resistance to LR and SR, as well as for key adaptation traits and yield components. The population was planted at each site in randomized triplicated experiments. Plants were grown in 15 cm distance between rows and 5 cm distance between plants within a row. Each row contained 25 plants. In the field conditions the MP was tested using 11 traits, including HT (heading time), MT (seed maturation time), PH (plant height), PL (peduncle length), SL (spike length), NPS (number of productive spikes per plant), NKS (number of kernels per spike), WKS (weight of kernels per spike), TKW (thousand kernels weight), WKP (weight of kernels per plant), YSM (yield per square meter).

Evaluation of rusts resistance in both locations was conducted in two randomized replicates with a natural source of infection. LR and SR resistance was evaluated on two growth stages – phase of grain formation on 75 of Zadoks scale and at the beginning of grain ripening on 83 of Zadoks scale (Zadoks et al., 1974). Averaged values for both diseases in two regions were calculated. Field infection response of the test materials was assessed visually. In both regions assessment of resistance/susceptibility levels was performed using the scale of Stakman (Stakman et al., 1962) for SR, the scale of Mains and Jackson (Mains, Jackson, 1926) for LR. The severity of rust infection on leaf and stem surfaces was assessed using the modified Cobb scale (Peterson et al., 1948; Roelfs et al., 1992). To meet the data format required for association analysis, the conventional scale was converted to the 0–9 linear disease scale described by Zhang and co-authors (Zhang et al., 2011). Pearson correlation analysis between agronomic traits and

SR/LR severity was performed using the R statistical platform (<https://www.r-project.org>).

Linkage mapping and QTL analysis. Genomic DNA for 98 RILs and their parental cultivars was extracted from seedlings using the cetyltrimethyl ammonium bromide (CTAB) method (Doyle J.J., Doyle J.L., 1990) and genotyped with the Illumina's iSelect 20K SNP array at the TraitGenetics Company (TraitGenetics GmbH, Gatersleben, Germany). MapChart v2.32 software was used to draw the genetic map (Voorrips, 2002). Each repetition experiments and their average results for studied traits in each environment were used for QTL analysis. For analysis of QTL, the Windows QTL Cartographer v2.5 software (<http://statgen.ncsu.edu/qtlcart/WQTLCart.htm>) with composite interval mapping (CIM) method at a logarithm of the odds (LOD) for the threshold of 3.0 was used.

Results

Phenotypic variations of resistance to stem and leaf rusts in two environmental conditions. Generally, mean values of SR and LR severity of two parental cultivars and 98 RILs in two regions demonstrated non-equal distribution with deviations towards resistance in the North and susceptibility in the South-East for both diseases (Fig. 1). Out of 98 RILs, fourteen lines were recognized as fully resistant to SR (1 point), 67 lines as moderate resistant on the level of 2–3 points, and only one line was determined as susceptible with 8 points of infection severity (see Fig. 1, a). In the South-East area, the severity of SR infection at the stage of grain ripening is higher and less diverse than in the North. SR scores of RILs at the adult plant stage were not normally distributed and were strongly skewed towards susceptibility. Here, 89 lines were affected by stem rust on the level of 8 points, with no lines identified as resistant (see Fig. 1, a).

As per the LR resistance, parents and lines of the MP grown in North Kazakhstan had demonstrated clear evidence of infection at the phase of grain ripening. The majority of RILs (81 lines) was identified as moderately resistant with the severity level on 2–3 points. The remaining six lines were resistant, and 11 lines had shown intermediate (4–5 points) level of infection (see Fig. 1, b). In the region of South-East Kazakhstan, as in the case of stem rust, the severity of leaf rust infection was significantly higher than in the northern part of the country.

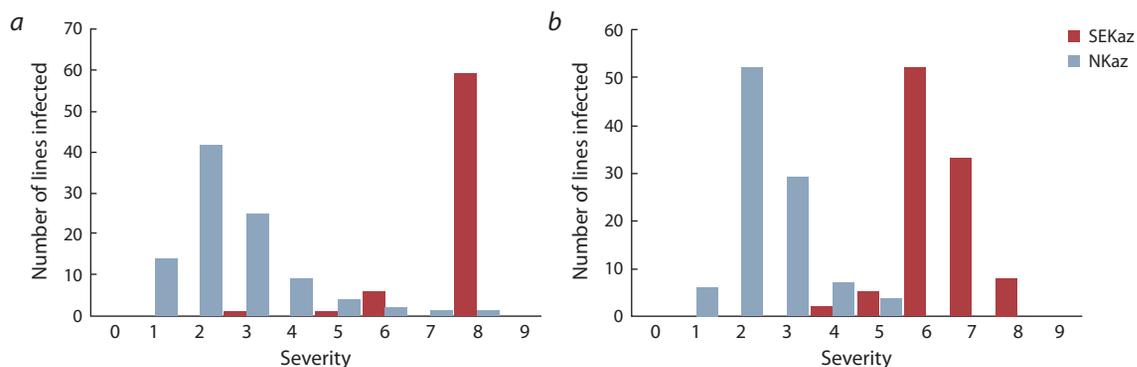


Fig. 1. Phenotypic variations of recombinant inbred lines for stem (a) and leaf rust (b) severity in two environments. The severity of infections was determined based on the 9-point scale. SEKaz – South-East Kazakhstan, NKaz – North Kazakhstan.

Coefficients of pairwise Pearson correlations (*r*) between the leaf and stem rusts infections severities and adaptation/yield-related traits in RILs population grown in North Kazakhstan

Parameter	SR (grain formation)	SR (grain ripening)	SR (average)	LR (average)
HT	-0.254*	-0.072	-0.059	0.129
MT	-0.295**	-0.191	-0.211*	-0.054
PH	-0.061	-0.219*	-0.214*	-0.123
PL	-0.047	-0.037	-0.042	-0.085
NPS	0.159	-0.113	-0.060	-0.215*
SL	0.208*	0.098	0.124	0.019
NFS	-0.180	-0.113	-0.155	-0.094
NKS	-0.148	-0.117	-0.151	-0.237*
WKS	0.053	-0.144	-0.141	-0.295**
WKP	0.010	-0.214*	-0.230*	-0.168
TKW	0.031	-0.168	-0.198	-0.059

Notes: SR, stem rust severity; LR, leaf rust severity; HT, heading time; MT, maturation time; PH, plant height; PL, peduncle length; NPS, number of productive spikes per plant; SL, spike length; NFS, number of fertile spikelets per spike; NKS, number of kernels per spike; WKS, weight of kernels per spike; WKP, weight of kernels per plant; TKW, thousand kernels weight.

* Significance level at $p < 0.05$; ** significance level at $p < 0.01$.

Correlation analysis for resistance to LR/SR and agronomic traits. North Kazakhstan is the biggest wheat-growing area in Kazakhstan that gives around 85 % of bread wheat grain annually (<http://stat.gov.kz>). Therefore, a separate evaluation of the relationship between yield components and rust indexes was performed (see the Table).

The severity of LR and SR infections measured on two growth stages and averaged values revealed generally negative influence on all key adaptation and yield-related traits. In North Kazakhstan, the averaged level of SR infections was negatively correlated with three important traits – MT, PH, and WKP. At the same time, the level of SR infections measured during the phase of grain formation demonstrated a negative correlation with HT, MT, while measures at the beginning of grain ripening were negatively correlated with PH and WKP. LR severity made a significant negative impact on NPS, NKS, and WKS.

Genetic linkage map of the studied RILs population. A total of 4595 polymorphic SNP markers from 21 chromosomes were used in the current study. All SNPs showed a good fit to 1:1 segregation in the RILs mapping population ($p > 0.001$ in Chi-squared test). The distribution of markers among genomes was the following: A genome – 1939 SNPs, B genome – 2099 SNPs, and D genome – 557 SNPs. The lengths of genetic maps for individual chromosomes ranged from 218.9 cM (chromosome 3B) to 16.9 cM (chromosome 4D). Chromosome 2B was identified as the densest with 563 SNPs per 150.6 cM (average spacing 0.27 cM), while chromosome 5D demonstrated the least markers density with the average 2.65 cM between neighboring SNPs.

QTL analysis of resistance to LR and SR. Information about QTL identified in this research work is summarized in Supplementary 1¹. Ten putative QTL for LR resistance were identified in seven different chromosomes (Fig. 2, Supple-

mentary 1). The majority of QTL was revealed in South-East Kazakhstan, where the severity of LR was on a maximum level. Four of QTL for LR resistance were located on 3B chromosome on short distances from each other. One QTL is observed on 3A chromosome while remaining five QTL were on chromosomes 1B, 1D, 2A, 2B and 4B.

Among all identified QTL for LR, the *QLR.IPBB-3B.1* located on the 3B chromosome was detected in the South-East region during the peak of infection. It had demonstrated the highest 7.8 LOD score among the others and explained 27 % of the phenotypic variances. Other QTL demonstrated LOD score in the range from 3.3 up to 6.0 and phenotypic variances from 11 to 20 %.

Nine tentative QTL for SR were detected in this study (Fig. 3, see Supplementary 1). All of them are distributed among six chromosomes, where 3B chromosome contained three QTL, 6B chromosome – two QTL while remaining QTL were spread in chromosomes 1A, 2B, 2D, and 4A. The majority of QTL for SR resistance was identified in the North region, while there was only one QTL identified in the South-East. The highest LOD score was observed for two QTL – *QSR.IPBB-2D* and *QSR.IPBB-6B.1* – on chromosomes 2D and 6B, and explained 22 and 20 % of the stem rust resistance variances, respectively.

Discussion

Identified QTL for LR resistance and their comparison to previously LR mapping studies. The literature survey suggests that LR pathotypes of infections, as well as the sources of infection and wheat genes that are effective against them, are different in two regions. For example, in South-East Kazakhstan, seven *Lr* genes were reported to be highly effective (0R, 1–5 MR) – *Lr9*, *Lr12*, *Lr13*, *Lr18*, *Lr19*, *Lr24*, and *Lr37* (Koyshybaev, 2018). In the North, the difference in *Lr* genes effectiveness was observed even between two sites. For Akmola site, there were nine genes with good effective-

¹ Supplementary Materials 1 and 2 are available in the online version of the paper: <http://www.bionet.nsc.ru/vogis/download/pict-2019-23/appx20.pdf>

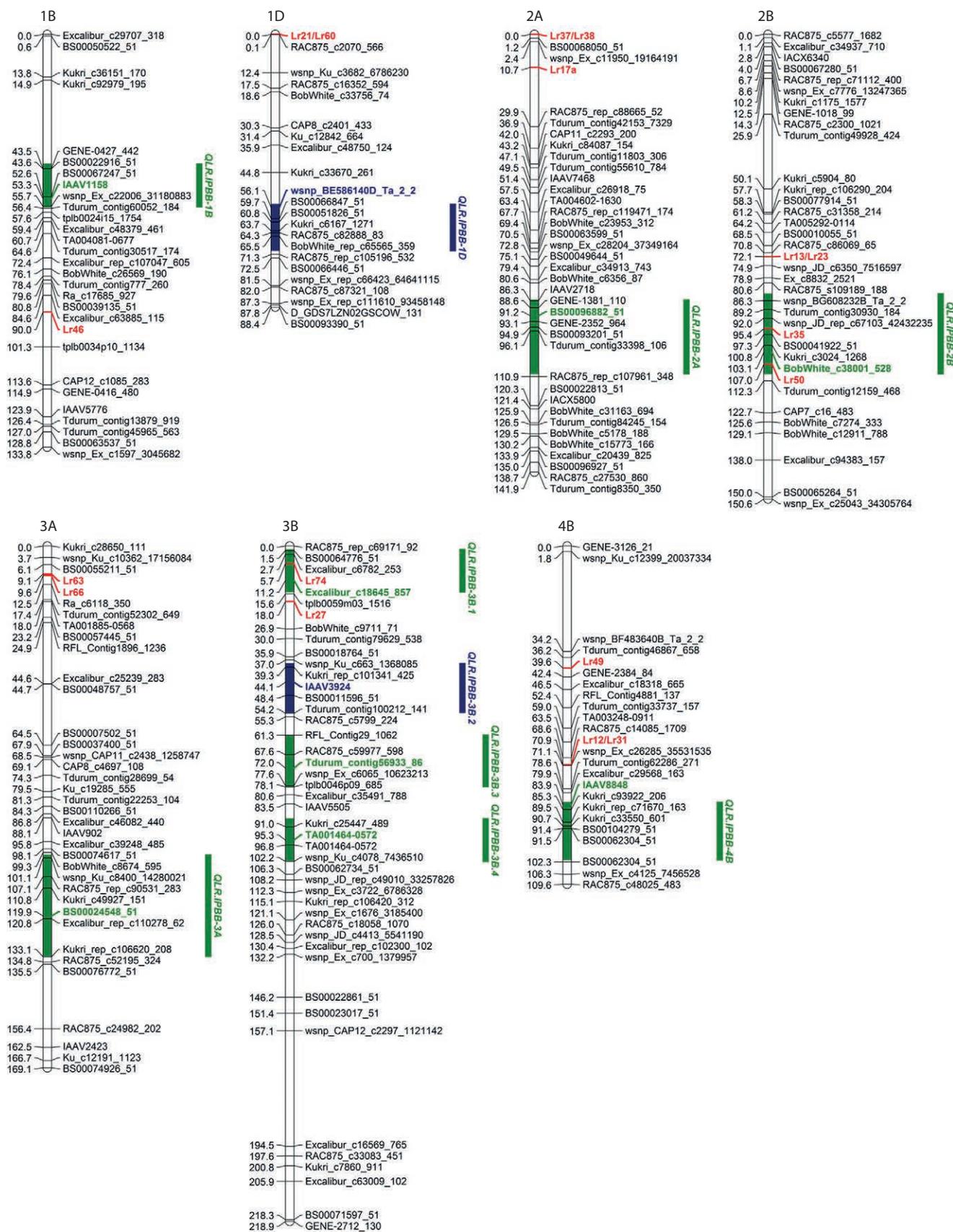


Fig. 2. Genetic map with QTL for leaf rust (LR) resistance detected using mapping population ‘Pamyati Azieva×Paragon’ and previously mapped *Lr* genes.

In each case, the genomic region containing the QTL is indicated by the vertical bar on the right and followed by the name of the QTL. SNP markers are indicated on the right, and their genetic positions (cM) are shown on the left. Peak marker for each QTL is highlighted in bold.

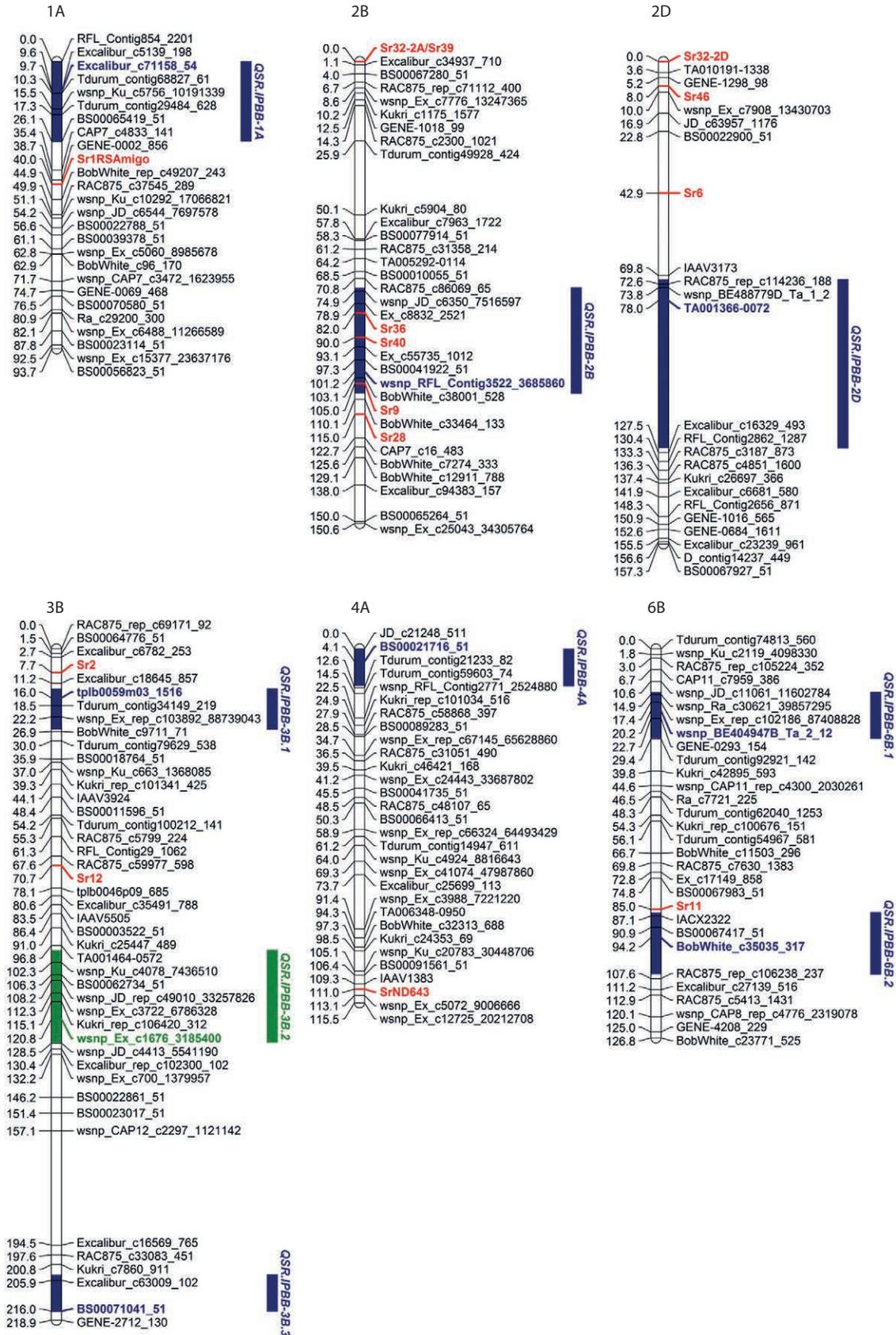


Fig. 3. QTL for stem rust (SR) resistance identified in mapping population 'Pamyati Azieva x Paragon' and previously mapped Sr genes.

In each case, the genomic region containing the QTL is indicated by the vertical bar on the right and followed by the name of the QTL. SNPs are indicated on the right, and their genetic positions (cM) are shown on the left. Peak marker for each QTL is highlighted in bold.

ness – *Lr9*, *Lr12*, *Lr13*, *Lr19*, *Lr23*, *Lr24*, *Lr28*, *Lr33*, and *Lr35*, while for North Kazakhstan site only three genes were highly effective – *Lr9*, *Lr28*, and *Lr36* (Koyshybaev, 2018). Here, ten QTL for LR were identified for two studied regions, and there were no matchings between them. Differences in QTL identification in North and South-East regions agreed with the data on differences in the composition of the pathogen populations between these regions (Koyshybaev, 2018). All comparison information concerning candidate genes and previously mentioned resistance QTL in the literature is presented in Supplementary 2.

One of two QTL identified in the North (*QLR.IPBB-1D*) is located in the long arm of 1D chromosome. The 1D chromosome has four *Lr* genes (see Supplementary 2) positioned on the far distances from the *QLR.IPBB-1D*. The second association found in the North region was *QLR.IPBB-3B.2*. The locus was within the interval of 38.0–54.0 cM on the 3B chromosome, near the locus *QLR.IPBB-3B.3*, which was identified in the South-East study. The *QLR.IPBB-3B.2* was distantly located from both *Lr27* and *Lr74* genes (see Fig. 2, Supplementary 2), but in close proximity to QTL described earlier (Gao et al., 2016; Zhang et al., 2017). Interestingly, none of *Lr* genes or QTL on chromosomes 1D and 3B had been described as effective in Kazakhstan before.

Field assessment of LR resistance in South-East allowed revealing eight QTL in six different chromosomes (see Supplementary 2). These QTL can be formally separated into two groups: the first group has QTL overlapping with previously identified and well described *Lr* genes, and the second group has QTL identified in this study. The first group is presented by two QTL on 2B and 3B chromosomes. On 2B chromosome, the *QLR.IPBB-2B* has similar positions with *Lr35* and *Lr50* (see Supplementary 2). Also, Gao and colleagues (Gao et al., 2016) and Zhang with co-authors (Zhang et al., 2017) identified similar QTL for LR in this part of the genome. The *Lr35* was previously described as highly effective in East, West, and North Kazakhstan regions (Koyshybaev, 2018). The second QTL *QLR.IPBB-3B.1* is positioned in the interval 1.1–15.0 cM of 3B chromosome, where it possibly overlaps with *Lr74* located approximately 4.9 cM away from *xgwm533* at 10.6 cM (Quarrie et al., 2005). Also, *Lr27* is another previously reported gene located in this region (see Supplementary 2). Notably, *QLR.IPBB-3B.1* was the most significant QTL for LR identified in this study with the highest R² and additive effect.

The remaining six QTL for LR belong to the second group of putatively new genetic factors for studied environments. The first QTL from this group is *QLR.IPBB-1B* that located on the 1B chromosome. There are two QTL for LR described by Kumar and colleagues (Kumar et al., 2013) and Gao with co-authors (Gao et al., 2016) that were positioned in the same vicinity as the *QLR.IPBB-1B*. The *QLR.IPBB-2A* was the only identified association on 2A chromosomes in this study, and it was mapped in the interval 86.0–110.1 cM. The interval of the *QLR.IPBB-2A* is near to genetic positions of QTL for LR resistance that were described in previous studies (Kumar et al., 2013; Gao et al., 2016). The *QLR.IPBB-3A* was located in the interval 100.0–133.1 cM, and it is coinciding with the position of QTL for LR resistance described by Chu with colleagues (Chu et al., 2009). On the 3B chromosome, two

QTL for LR were identified in this group of study in South-East region. These are *QLR.IPBB-3B.3* and *QLR.IPBB-3B.4* positioned in 61.2–78.1 and 88.2–102.3 cM intervals, respectively. It appears that QTL for LR in these regions were previously identified (Kumar et al., 2013; Muhammad et al., 2018). Finally, the *QLR.IPBB-4B* was located in the interval 82.9–101.8 cM, which is overlapping with the position of QTL for LR resistance described by Gao and co-authors (Gao et al., 2016).

As all identified genetic factors associated with the resistance to LR in this study were genetically positioned with associations identified in recent GWAS for LR resistance (Gao et al., 2016; Muhammad et al., 2018), it is strong indications that QTL identified in this study may play an important role in local breeding projects.

Identified QTL for SR resistance and their comparison to previously SR mapping studies. Unlike in LR study, where the majority of QTL for SR were found based on the data from South-East, in SR study almost all QTL (8 out of 9) were identified in the North region. The only SR resistant locus from the South-East was *QSR.IPBB-3B.2* in the interval 98.3–128.3 cM on the 3B chromosome, and it was significantly far from *Sr* genes mapped in this linkage group (see Supplementary 2). Other QTL for SR resistance can also be formally divided into two groups, likewise in LR study. The first group of marker-trait associations includes four QTL. The *QSR.IPBB-1A* was located in the interval 0–26.0 cM at a relatively short distance from the *Sr1RS^{Amigo}* mapped at 40.0 cM (Yu et al., 2014), and two QTL described in other studies (Yu et al., 2012; Bajgain et al., 2016). The next QTL *QSR.IPBB-2B* lies in the interval 73.8–108.2 cM and overlaps with three mapped *Sr* genes (*Sr9*, *Sr36*, and *Sr40*) and adjoins *Sr28* (see Fig. 3), as well as several QTL for SR from literature (Yu et al., 2012; Bajgain et al., 2015; Edae et al., 2018). Two of these genes – *Sr9* and *Sr36* – were distinguished as effective against the Western Siberian population of SR (Shamanin et al., 2011). On the 3B chromosome, there are three identified QTL for SR, but only *QSR.IPBB-3B.1* was positioned in the vicinity of previously mapped gene *Sr2*, and QTL for SR resistance described by Elbasyoni with co-authors (Elbasyoni et al., 2017). Notably, the *Sr2* is the most important disease resistance gene to be deployed in modern plant breeding and provided partial resistance for many years over large areas and under high and prolonged disease pressure in the field (Ellis et al., 2014). Finally, the *QSR.IPBB-6B.2* was positioned just in 2.1 cM from *Sr11* (see Supplementary 2).

The second group of QTL for SR resistance included associations that previously were not mentioned in Kazakhstan. This group was comprised of five QTL located on chromosomes 2D, 3B, 4A, and 6B. The region 71.1–126.0 cM of chromosome 2D, which is associated with the *QSR.IPBB-2D*, has not been mentioned in connection with previous QTL for SR mapping studies. The *QSR.IPBB-2D* demonstrated the highest impact on the SR resistance in this study, explaining 22 % of the variation. Also, on the 3B chromosome, there is *QSR.IPBB-3B.3*, which is another presumably novel QTL for SR resistance in Kazakhstan. The *QSR.IPBB-4A* on the 4A chromosome resembles two SR-associated loci described in previous studies (see Supplementary 2) (Basnet et al., 2015), but it has no candidate *Sr* genes nearby. The remaining QTL

QSR.IPBB-6B.1 was located in the short arm of the 6B chromosome. It seems that the position of the *QSR.IPBB-6B.1* is matching the position of QTL for SR resistance that was previously described by Yu with co-authors (Yu et al., 2012).

Conclusion

The constructed RILs MP 'Pamyati Azieva × Paragon' was very efficient in the identification of QTL for LR and SR resistance in bread wheat. The MP consisted of 98 RILs and analyzed by using 4595 polymorphic SNP markers densely populated all 21 wheat chromosomes. Field trials output suggested a negative correlation between LR and SR severity and key yield components in the North and South-East regions of Kazakhstan. The CIM method allowed the identification of ten QTL for LR and nine QTL SR resistance associated with resistance to these two rust diseases. The comparative analysis of the findings in this study and reports from previously published data suggested that the majority of identified QTL were well described in existed literature, confirming the robustness of obtained results. Nevertheless, two QTL for SR identified in the North region of the country were never described before, and they are presumably novel genetic factors. Overall, identified QTL both for LR and SR resistances in newly developed MP 'Pamyati Azieva × Paragon' can be efficiently used in local breeding projects for higher yield in bread wheat.

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Acknowledgements. This work was done in the framework of the project "Development of new DNA markers associated with the resistance of bread wheat to the most dangerous fungal diseases in Kazakhstan" in Program "Development of the innovative systems for increasing the resistance of wheat varieties to especially dangerous diseases in the Republic of Kazakhstan" BR06249329 supported by the Ministry of Agriculture of the Republic of Kazakhstan.

Conflict of interest. The authors declare no conflict of interest.

Received August 21, 2019. Revised September 23, 2019. Accepted September 23, 2019.