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ASSOCIATIONS BETWEEN ALLELIC DIFFERENCES OF THE FIFTH GROUP CHROMOSOME LOCI AND A COMPLEX OF AGRONOMICALLY VALUABLE TRAITS IN COMMON WHEAT (*TRITICUM AESTIVUM* L.)

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Aim. Characterization of recombinant inbred wheat lines by agronomically relevant traits and detection of associations between their expression level and allelic differences of microsatellite loci of the fifth group chromosomes. **Methods.** Phenological observations, morphometric indicators, and elements of crop structure. Statistical analysis of the obtained data was carried out in Microsoft Excel. The significance of the difference between samples was assessed by Fisher's F test. A difference of $p < 0.05$ was considered statistically significant for all indicators. **Results.** The polymorphism of the parental genotypes and the population of 47 recombinant-inbred lines (RILs) F_7 from the crossing of the winter wheat varieties Luzanivka odeska and Odeska chervonokolosa over three years (2016–2018) in conditions of the Southern Steppe (Odesa) was evaluated according to eight characteristics: duration of a period prior to heading, plant height, productive tillering, grain number per spike, grain weight per spike, thousand-grain weight, productive tiller number per unit area and grain yield. The comparison of the data of line evaluation by agronomic traits against the data of microsatellite analysis of lines by 14 microsatellite loci of the fifth group chromosomes demonstrated the associations between several loci and grain yield and between two loci and plant height. **Conclusions.** The changes in grain yield in the most unfavorable year, 2018, were associated with allelic differences of lines at locus *Xbarc319-5A*, and in the most favorable year, 2017, – with another locus of chromosome 5A, *Xbarc330-5A*. In both cases, the lines that had an allele from Odeska chervonokolosa were characterized by a significantly higher level of grain yield compared to the lines that had an allele from the Luzanivka odeska variety. There are at least two QTLs on 5B chromosome, associated with winter wheat grain yield in favorable growing years. The first of them is located in the region of locus *Xbarc88-5B*, and the second – in the region of loci *Xwmc415-5B*, *Xgpw3191-5B,* and *Xcfd7-5B*. Based on the alleles of the specified microsatellite loci, which are linked QTLs of grain yield, it is possible to select genotypes at the early stages of selection that will give a higher yield in years with favorable conditions for growing wheat.

Key words: common wheat (*Triticum aestivum* L.), recombinant-inbred lines, gene, allele, microsatellite loci, QTL.

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INTRODUCTION

Common wheat (*Triticum aestivum* L.) is one of the most relevant crops, grown nowadays. It provides 20 % calories and about 23 % protein, consumed by the global population (Breiman, Graur, 1995; FAOSTAT 2017). Rapidly growing demand for food products and fodder requires a considerable increase in the yield of all the main crops (Grainger, 2010). By the end of this century, the global population is expected to be 10,9 billion, which will lead to a considerably higher consumption of wheat (Enghiad et al, 2017). In addition, droughts, diseases, and widespread pests aggravate the concerns about insufficient wheat cultivation (Yue et al., 2019). Nonetheless, the suspension in the increase of wheat yield was registered in all the main regions of wheat production in the world, including Europe, the USA, Asia, and Australia (Brisson et al, 2010; Ray et al, 2012).

Wheat yield continues to increase over time due to selection, but current growth rates will be insufficient to meet the future needs of the growing population (Ray et al, 2013). To meet future demand, one should accelerate selection in terms of increasing the grain yield. In general, the final grain yield of wheat and cereals is a result of the growth and development of plants; thus, a large number of genes affect grain yield either directly or indirectly (Quarrie et al, 2006; Brinton, Uauy, 2019). Grain yield can be divided into several components: thousand-grain weight, grain number per spike, grain weight per spike, and number of productive tillers per area unit (Brinton, Uauy, 2019; Cao et al, 2020). High grain yield results from maintaining a fine balance between the critical components of yield in specific conditions. Traditional selection of wheat is mainly based on phenotype selection. Genotypes are evaluated for grain yield in different media for several years to enlarge the perspective for the elaboration of a new, more productive cultivar. Due to negative correlations between the yield components, simple selection for the improvement of specific components is inefficient (Wang et al, 2018; Zhang et al, 2018). QTL mapping plays a relevant role in enhancing the grain yield, suggesting an alternative approach to improving the traditional selection using molecular markers, closely linked to the yield component traits.

In the recent decade, there have been considerable studies of wheat, aimed at the determination of quantitative trait loci (QTL) of grain yield and its components, spread on almost all the chromosomes of wheat (Zanke et al, 2015; Quraishi et al, 2017; Guan et al, 2018; Guan et al, 2019; Yan et al, 2019). Most QTL, related to the yield, can impact one or several components of yield (Juliana et al, 2019; Li et al, 2019; Yang et al, 2020). For instance, Voss-Fels et al (2019) developed a genetic map of high resolution and found a reliable QTL for the number of spikes per spikelet (NSS) on the long arm of 7AL chromosome. Guan et al (2020) identified a cluster of QTL for thousand-grain weight (TGW) on 4B chromosome, and demonstrated in their further study that gene *Rht-B1* was the most reliable candidate gene with pleiotropic effect on the size of a kernel and thousand-grain weight. Liu et al (2020) suggested that *TaFT-D1* can be a candidate gene for two QTLs, one of which is related to TGW (QTkw.cas-7D.2), and the other – to grain weight (Qkw.cas-7D.1). The study of Isham et al (2021) found four genomic regions on chromosomes 4A, 6A, 7B, and 7D, each of them having several closely linked QTL (QTL clusters), associated with two-three components of yield. Cluster 7D QTL was linked to grain yield, number of fertile spikes per spikelet, thousand-grain weight, and heading date.

The fifth group chromosomes bear a number of genes and loci of quantitative traits that condition the type and tempo of wheat development, have a considerable impact on the level of adaptivity of plants to the winter-fall and spring-summer period as well as other agronomically valuable traits of wheat. In our previous studies, the RIL Luzanivka odeska/Odeska chervonokolosa were analyzed by a number of the fifth group chromosome loci; we detected microsatellite loci, associated with frost resistance of common winter wheat (Galaeva et al, 2013; Galaeva et al, 2014) and the variation of stomatographic features (Lamari et al, 2017; Lamari et al, 2018).

The aim of this work was to characterize recombinant-inbred lines by agronomically relevant traits and detect associations between their expression level and allelic differences of microsatellite loci of the fifth group chromosomes.

MATERIALS AND METHODS

The material of the study was found in two paternal varieties and 47 recombinant-inbred lines Luzanivka odeska/Odeska chervonokolosa, which were created in the Department of General and Molecular Genetics of the Selection and Genetics Institute, the National Center of Seed and Cultivar Investigation. In our previous studies (Galaeva et al, 2013; Galaeva et al, 2014; Lamari et al, 2018), we identified the genotypes of RIL and paternal varieties by a number of microsatellite loci of the fifth group chromosomes, and these data of genotyping were used in this study. RIL and paternal varieties are polymorphic in terms of alleles (in terms of the length of amplification fragments) of 14 microsatellite loci of the fifth group chromosomes. The number of homozygous RIL with a specific allele by a particular locus from Luzanivka odeska variety varied from 21 (*Xwmc75*) to 27 (*Xgwm182*), and those from Odeska chervonokolosa – from 20 (*Xbarc322*) to 26 (*Xwmc75*), which is sufficient for the evaluation of associations between microsatellite loci and economically valuable traits. By loci *Xbarc322* and *Xbarc 117,* two lines for each were found heterozygous.

To find the connection between different alleles of microsatellite loci and the manifestation of some economically valuable traits, the seeds of the parental varieties and 47 lines were sown in autumn (on October 8, 10, and 20 in 2015, 2016, 2017) estimated as 500 similar grains per one sq.m. The registration area of the plot was three sq.m. The experiment had three repeats. During vegetation, we registered the heading date visually, if 75 % of plants with spikelets were present in the plot, and then transformed it into the duration of the period prior to heading (DPH) and counted the number of productive tillers per area unit (NPT). While harvesting, the grain yield (GY) of the land plot was determined. After harvesting, 45 selected plants of each genotype (15 plants per one repeat) were evaluated for the plant height (PH), productive tillering (PT), grain number per spike (GNS), grain weight per spike (GWS), and thousand-grain weight (TGW). All the abovementioned indices were compared against the data of the PCR-analysis of the lines by microsatellite loci of the fifth group chromosomes, by which the differences between parental varieties were found, and RIL F_7 of Luzanivka odeska/Odeska chervonokolosa were identified.

The meteorological conditions during the period of the study covered the entire spectrum of possible unfavorable environmental factors, common for the Steppe of Ukraine. It ensured the objective evaluation of the initial material regarding the average adaptation to these conditions and allowed for the differentiation of RIL of winter wheat by the complex of economically valuable traits depending on the year of the study and the presence of specific alleles of microsatellite loci.

The statistical processing of the obtained data was conducted by common methods of variation statistics and one-factor analysis of variance (ANOVA) using the Microsoft Excel package (2007). While comparing two samplings, Fisher's F test was used to evaluate the significance of the "genotype" factor for the variation of traits under consideration. The presence of links between loci of specific chromosomes was assessed based on the threshold value for the reliability ratio of the logarithm of odds (LOD-score). LOD was calculated using the Join Map program (version 4.1) (free access at https://kyazma.nl/index.php/JoinMap).

RESULTS

The characterization of recombinant-inbred lines Luzanivka odeska/Odeska chervonokolosa by a complex of agronomically valuable traits. During the years of the study, there were different weather conditions, which led to considerable differences in the mean indices of grain yield and its components in the recombinant-inbred lines. The most favorable year for wheat growing was 2017, and the least favorable – 2018, which was mainly reflected in the indices of grain yield and plant height.

Recombinant-inbred lines Luzanivka odeska/Odeska chervonokolosa had considerable differences in many traits (**Table 1**). In most years of the study and by most traits, the determined genetic diversity exceeded that between parental lines. The exception was found only by the trait of "duration of a period prior to heading" in 2018 and 2017 and "grain number per spike" in 2016. In the first two cases, the minimal, and in the third – the maximal value for the RIL population equaled that of one parental line.

The variation degree by the duration of a period prior to heading was from 4 to 6 days in different years, while for parental lines, it was 1 to 3 days. In 2016 and 2017, with the early start of spring vegetation, the DPH (counting from May 1) was almost the same for the population of RIL on average, amounting to 8.2 and 8.1 days, respectively. A long and cold spring of 2018 promoted later heading, on Day 17.4. At the same time, later heading and the subsequent drought in 2018 caused a decrease in the PH, GNS, and GWS, and, thus, grain yield as compared to those in other years of the study. The difference in the PH between the lines with the minimal and maximal values of the trait in the population was 54–82 cm – from 40–58 to 94–137 cm in different years. The grain number per spike in the population was from 25.6 to 43.4, with the variation – from 16–34 to 39–59. The grain weight per spike in specific lines varied from 0.53–0.83 g to 1.33–1.97 g, and the thousand-grain weight – from 19–28 to 37–41 g. The number of productive tillers varied from 294–344 to 539–584 per sq.m.(the difference of 195–274 per sq.m.). The grain yield of more productive lines was 0.57–0.67 kg/sq.m. and exceeded that of less productive lines by 0.27–0.37 kg/sq.m. Thus, the obtained results demonstrated a wide polymorphism of the population of lines by the studied traits which provides for the comparative analysis of the groups of lines-carriers of alternative alleles of specific microsatellite loci.

The link between 5A chromosome loci and grain yield and its components. Among the loci of 5A chromosome, studied by us, some loci were associated with yield in specific years (**Table 2**).

For instance, no significant link between 5A chromosome loci and grain yield and its components was found in 2016. Only locus *Xbarc 117-5A* was associated with productive tillering, and higher indices were

Table 1. The main statistical indices of economically valuable traits of the population of RIL F_7 Luzanivka odeska/Odeska chervonokolosa

Feature	Year	n	$\bar{x} \pm S\bar{x}$*	*min*	*max*	σ	CV, %
DPH, days	2016	47	8.1 ± 0.16	5	10	1.07	13.13
	2017	47	8.2 ± 0.10	7	10	0.66	8.07
	2018	47	17.4 ± 0.16	16	20	1.11	6.35
PH, cm	2016	47	101 ± 2.8	55	137	19.12	18.80
	2017	47	102 ± 2.3	58	128	15.57	15.32
	2018	47	61 ± 1.7	40	94	11.72	19.37
PT, it.	2016	47	1.9 ± 0.03	1.0	2.3	0.24	12.78
	2017	47	1.6 ± 0.04	1.2	2.4	0.27	16.29
	2018	47	1.0 ± 0.01	1.0	1.2	0.06	5.30
GNS, it.	2016	47	33.9 ± 0.65	26	47	4.46	13.15
	2017	47	43.4 ± 0.90	34	59	6.16	14.21
	2018	47	25.6 ± 0.77	16	39	5.28	20.68
GWS, g	2016	47	1.05 ± 0.018	0.79	1.41	0.13	12.26
	2017	47	1.44 ± 0.038	0.83	1.97	0.26	18.21
	2018	47	0.86 ± 0.027	0.53	1.33	0.19	21.81
TGW, g	2016	47	34.1 ± 0.42	28	41	2.90	8.50
	2017	47	34.0 ± 0.53	25	40	3.65	10.76
	2018	47	29.2 ± 0.72	19	37	4.93	16.90
NPT, it./ sq.m.	2016	47	433 ± 7.0	344	539	47.85	11.03
	2017	47	450 ± 6.9	294	568	47.28	10.50
	2018	47	443 ± 8.6	325	584	59.16	13.34
GY, kg/sq.m.	2016	47	0.45 ± 0.010	0.27	0.57	0.073	16.36
	2017	47	0.56 ± 0.010	0.40	0.67	0.071	12.69
	2018	47	0.43 ± 0.009	0.24	0.61	0.065	15.13

Note: $\bar{x} \pm S\bar{x}$ – mean value of the index ± standard error, n – number of lines, *min* – the minimal value of the index, *max* – the maximal value of the index, σ – standard error, CV – coefficient of variation; DPH – duration of a period prior to heading (counting from the date of May 1), days; PH – plant height, cm; PT – productive tillering, items; GNS – grain number per spike, items; GWS – grain weight per spike, g; TGW – thousand-grain weight, g; NPT – number of productive tillers, items/sq.m.; GY – grain yield, kg/sq.m.

notable for lines with the allele of 230 bp from Odeska chervonokolosa.

Significant allelic differences in terms of grain yield were noted in 2018, unfavorable for winter wheat growing, by locus *Xbarc 319-5A,* and in 2017, a favorable year, by locus *Xbarc 330-5A*. In both cases, due to unreliable increases in GWS, TGW, and NPT, the lines with alleles of 206 bp and 106 bp in their genotype, which descend from Odeska chervonokolosa, were characterized by much higher grain yield than those with alleles of 218 bp and 104 bp from Luzanivka odeska. No link between other loci of 5A chromosome and the investigated economically valuable traits was found in all three years of the study.

The link between 5D chromosome loci and grain yield and its components. Recombinant-inbred lines Luzanivka odeska/Odeska chervonokolosa were analyzed by 5D chromosome loci: *Xcfd8-5D*, *Xgwm182-5D, Xbarc322-5D*, which demonstrated polymorphism between parental varieties; we compared the data of microsatellite analysis to the complex of economically valuable traits (**Table 3**).

However, no significant link between the mentioned loci and economically valuable traits was found in all three

Table 2. The mean values of economically valuable traits for the groups of RIL Luzanivka odeska/Odeska chervonokolosa – carriers of different alleles of 5A chromosome loci

Year	Alleles	n	DPH, days	PH, cm	PT, it.	GNS, it.	GWS, d	TGW, g	NPT, it./sq.m.	GY, kg/sq.m.
					Xbarc 117					
2016	224 [1]	23	8.1	101	1.8	33	1.04	34.5	423	0.445
	230 [2]	22	8.1	102	2.0	35	1.07	33.9	440	0.460
	F_{est} [3]	F_{est} [3]	0.01	0.03	6.74*	0.82	0.32	0.50	1.45	0.44
2017	224 [1]	23	8.1	103	1.7	43	1.44	34.3	437	0.571
	230 [2]	22	8.2	100	1.6	44	1.44	33.8	464	0.547
	F_{est}	F_{est}	0.18	0.50	2.35	0.01	0.06	0.20	3.80	1.23
2018	224 [1]	23	17.3	61	1.0	26	0.88	28.7	443	0.426
	230 [2]	22	17.4	61	1.0	25	0.85	29.7	438	0.436
	F_{est}	F_{est}	0.002	0.02	0.47	0.34	0.26	0.51	0.08	0.23
					Xbarc 330					
2016	104 [1]	24	8.2	104	1.8	33	1.02	34.5	443	0.432
	106 [2]	23	8.1	99	1.9	35	1.09	33.8	424	0.472
	F_{est}	F_{est}	0.23	0.69	2.10	2.78	3.70	0.67	1.99	3.64
2017	104 [1]	24	8.3	105	1.62	42	1.43	33.4	440	0.533
	106 [2]	23	8.1	99	1.65	44	1.45	34.5	461	0.585
	F_{est}	F_{est}	1.66	1.74	0.14	1.32	0.09	1.21	2.39	7.06*
2018	104 [1]	24	17.4	62	1.0	26	0.87	29.0	434	0.417
	106 [2]	23	17.4	59	1.0	25	0.85	29.4	453	0.442
	F_{est}	F_{est}	0.001	0.47	0.14	0.29	0.13	0.10	1.28	1.81
					Xgwm156					
2016	311 [1]	26	8.4	101	1.8	33	1.02	34.0	428	0.435
	290 [2]	21	7.9	103	1.9	35	1.09	34.2	440	0.471
	F_{est}	F_{est}	2.31	0.09	2.42	2.37	4.00	0.05	0.71	2.91
2017	311 [1]	26	8.3	102	1.65	43	1.41	33.8	444	0.559
	290 [2]	21	8.1	101	1.62	44	1.48	34.1	458	0.558
	F_{est}	F_{est}	0.66	0.06	0.14	0.27	0.85	0.10	0.94	0.002
2018	311 [1]	26	17.6	60	1.0	26	0.85	28.6	452	0.420
	290 [2]	21	17.3	61	1.0	25	0.87	29.9	433	0.440
	F_{est}	F_{est}	1.07	0.07	1.33	0.04	0.11	0.84	1.16	1.14
					Xbarc 319					
2016	218 [1]	22	8.2	98	1.9	34	1.05	33.9	437	0.449
	206 [2]	25	8.1	106	1.9	34	1.05	34.4	430	0.454
	F_{est}	F_{est}	0.12	1.72	0.37	0.004	0.003	0.32	0.22	0.04
2017	218 [1]	22	8.2	100	1.65	43	1.40	33.5	451	0.560
	206 [2]	25	8.2	104	1.61	44	1.48	34.5	449	0.556
	F_{est}	F_{est}	0.03	0.82	0.33	0.08	0.97	0.80	0.02	0.03
2018	218 [1]	22	17.5	59	1.0	26	0.87	28.3	437	0.405
	206 [2]	25	17.4	62	1.0	25	0.84	30.2	450	0.456
	F_{est}	F_{est}	0.19	0.75	0.09	0.74	0.29	1.66	0.58	8.57 *

Note. [1] – allele from Luzanivka odeska, [2] – allele from Odeska chervonokolosa, [3] F – Fisher's F test, * – $F_{est}>F_{0.05;}$ DPH – duration of a period prior to heading (counting from May 1), PH – plant height, PT – productive tillering, GNS – grain number per spike, GWS – grain weight per spike, TGW – thousand-grain weight, NPT – number of productive tillers, GY – grain yield.

Table 3. The mean values of economically valuable traits for the groups of RIL Luzanivka odeska/Odeska chervonokolosa – carriers of different alleles of 5D chromosome loci

Year	Alleles	n	DPH, days	PH, cm	PT, it.	GNS, it.	GWS, d	TGW, g	NPT, it./sq.m.	GY, kg/sq.m.
Xcfd8										
2016	160[1]	23	8.0	99	1.8	34	1.05	33.9	431	0.451
	162[2]	24	8.3	104	1.9	34	1.06	34.3	436	0.451
	F_{est}[3]	F_{est}[3]	0.43	0.68	2.57	0.001	0.11	0.11	0.14	0.0004
2017	160[1]	23	8.1	101	1.62	41	1.37	33.9	445	0.552
	162[2]	24	8.3	102	1.65	46	1.50	34.0	456	0.565
	F_{est}	F_{est}	1.66	0.02	0.20	7.55 *	3.24	3.24	0.61	0.39
2018	160[1]	23	17.3	60	1.0	27	0.90	28.0	435	0.427
	162[2]	24	17.6	61	1.0	24	0.81	30.3	451	0.431
	F_{est}	F_{est}	0.53	0.0003	0.52	3.70	3.17	3.17	0.83	0.03
Xgwm182										
2016	165[1]	27	8.2	99	1.9	34	1.05	34.1	431	0.452
	162[2]	20	8.1	105	1.9	34	1.06	34.2	437	0.450
	F_{est}	F_{est}	0.01	1.25	0.11	0.17	0.23	0.02	0.17	0.01
2017	165[1]	27	8.1	100	1.64	42	1.42	34.1	448	0.554
	162[2]	20	8.3	103	1.63	45	1.46	33.8	454	0.564
	F_{est}	F_{est}	0.36	0.44	0.03	1.55	0.33	0.08	0.19	0.23
2018	165[1]	27	17.2	61	1.0	26	0.88	29.0	449	0.439
	162[2]	20	17.7	60	1.0	24	0.83	29.3	435	0.415
	F_{est}	F_{est}	2.53	0.01	1.25	1.70	0.73	0.03	0.63	1.61
Xbarc322										
2016	224[1]	25	8.0	103	1.9	35	1.06	33.8	429	0.461
	230[2]	20	8.3	98	1.8	34	1.05	34.2	438	0.444
	F_{est}	F_{est}	1.23	0.82	0.41	0.63	0.15	0.21	0.36	0.52
2017	224[1]	25	8.1	103	1.61	44	1.47	34.2	445	0.564
	230[2]	20	8.3	100	1.66	43	1.39	33.6	457	0.551
	F_{est}	F_{est}	0.57	0.52	0.35	0.19	1.11	0.24	0.72	0.38
2018	224[1]	25	17.5	60	1.0	25	0.83	28.3	446	0.432
	230[2]	20	17.6	60	1.0	26	0.90	30.0	440	0.424
	F_{est}	F_{est}	0.005	0.001	0.33	0.75	1.60	1.48	0.10	0.17

Note. [1] – allele from Luzanivka odeska, [2] – allele from Odeska chervonokolosa, [3] F – Fisher's F test, * – $F_{est} > F_{0.05}$; DPH – duration of a period prior to heading (counting from May 1), PH – plant height, PT – productive tillering, GNS – grain number per spike, GWS – grain weight per spike, TGW – thousand-grain weight, NPT – number of productive tillers, GY – grain yield.

years of the study. Only in 2017, we observed considerable differences by grain number per spike in the lines-carriers of alternative alleles of locus *Xcfd8-5D*. Higher indices were noted for lines with the allele of 162 bp from Odeska chervonokolosa (46 grain per spike), but it did not lead to a considerable increase in the grain yield.

The link between 5B chromosome loci and grain yield and its components. The comparative analysis for the presence of specific alleles by seven loci of chromosome 5B in the genotype of RIL Luzanivka odeska/Odeska chervonokolosa and for the determination of economically valuable traits demonstrated a significant impact of genetic differences by specific microsatellite loci on some economically valuable traits. Among 5B chromosome loci, we detected four loci, namely, *Xbarc88-5B*, *Xwmc415-5B*, *Xgpw3191-5B,* and *Xcfd7-5B*, whose allelic differences were associated with the changes in grain yield (**Table 4**). For instance, under

Table 4. The mean values of economically valuable traits for the groups of RIL Luzanivka odeska/Odeska chervonokolosa – carriers of different alleles of 5B chromosome loci

Year	Alleles	n	DPH, days	PH, cm	PT, it.	GNS, it.	GWS, d	TGW, g	NPT, it./sq.m.	GY, kg/sq.m.
Xbarc88										
2016	84 [1]	27	8.1	107	1.9	33	1.07	34.7	445	0.447
	80 [2]	20	8.3	95	1.8	35	1.03	33.3	418	0.457
	F_{est} [4]	F_{est} [4]	0.31	4.91*	3.07	0.99	0.71	2.68	3.90	0.18
2017	84 [1]	27	8.1	105	1.67	45	1.51	34.7	456	0.579
	80 [2]	20	8.2	96	1.61	42	1.34	33.0	441	0.532
	F_{est}	F_{est}	0.38	4.31*	0.49	2.50	4.56*	2.68	1.17	6.07*
2018	84 [1]	27	17.5	63	1.0	25	0.87	30.4	443	0.419
	80 [2]	20	17.3	57	1.0	26	0.84	27.5	445	0.442
	F_{est}	F_{est}	0.42	3.59	0.05	0.01	0.32	4.30 *	0.01	1.37
Xbarc4										
2016	180 [1]	27	8.1	105	1.9	33	1.06	34.6	442	0.445
	158 [2]	20	8.3	97	1.8	35	1.04	33.5	423	0.460
	F_{est}	F_{est}	0.31	1.93	1.40	1.50	1.50	1.52	1.83	0.52
2017	180 [1]	27	8.2	104	1.66	44	1.48	34.6	459	0.574
	158 [2]	20	8.2	99	1.60	43	1.38	33.1	439	0.536
	F_{est}	F_{est}	0.09	1.36	0.53	0.52	0.52	1.73	2.07	3.51
2018	180 [1]	27	17.5	62	1.0	26	0.89	30.2	439	0.421
	158 [2]	20	17.4	58	1.0	25	0.83	28.0	448	0.440
	F_{est}	F_{est}	0.20	1.86	0.06	0.26	0.26	2.64	0.28	1.02
Xbarc89										
2016	130 [1]	26	8.0	104	1.9	33	1.06	34.6	449	0.458
	124 [2]	21	8.3	99	1.8	35	1.04	33.6	415	0.444
	F_{est}	F_{est}	0.77	0.82	0.31	1.34	0.18	1.54	6.23*	0.40
2017	130 [1]	26	8.1	103	1.66	45	1.49	34.5	457	0.573
	124 [2]	21	8.3	100	1.60	42	1.37	33.3	442	0.539
	F_{est}	F_{est}	0.65	0.50	0.58	3.55	2.79	1.11	1.31	2.76
2018	130 [1]	26	17.5	62	1.0	26	0.88	30.5	446	0.426
	124 [2]	21	17.4	58	1.0	25	0.82	27.6	440	0.433
	F_{est}	F_{est}	0.02	1.17	0.07	0.20	1.32	4.28 *	0.13	0.13
Xwmc415										
2016	174 [1]	22	8.0	100	1.9	34	1.07	34.3	441	0.466
	172 [2]	25	8.3	103	1.9	34	1.04	34.0	427	0.439
	F_{est} [3]	F_{est} [3]	0.50	0.20	0.25	0.26	0.60	0.07	0.98	1.64
2017	130 [1]	22	8.1	100	1.69	45	1.46	33.7	455	0.592
	124 [2]	25	8.3	103	1.58	42	1.42	34.2	446	0.528
	F_{est}	F_{est}	0.80	0.50	2.00	2.01	0.37	0.21	0.44	11.97*
2018	130 [1]	22	17.6	60	1.0	25	0.87	30.0	453	0.421
	124 [2]	25	17.3	61	1.0	26	0.84	28.5	435	0.436
	F_{est}	F_{est}	0.77	0.16	0.16	0.02	0.27	1.11	1.17	0.59
Xgpw319										
2016	178 [1]	22	8.1	100	1.9	34	1.07	34.3	437	0.469
	236 [2]	25	8.2	104	1.9	34	1.04	34.0	430	0.434
	F_{est}	F_{est}	0.23	0.49	0.38	0.09	0.91	0.09	0.24	2.78

End of Table 4

Year	Alleles	n	DPH, days	PH, cm	PT, it.	GNS, it.	GWS, d	TGW, g	NPT, it./sq.m.	GY, kg/sq.m.
2017	178 [1]	22	8.1	100	1.70	44	1.45	33.4	452	0.586
	236 [2]	25	8.3	104	1.57	43	1.43	34.5	448	0.531
	F_{est}	F_{est}	0.29	0.70	2.98	0.96	0.06	1.17	0.08	8.06*
2018	178 [1]	22	17.6	60	1.0	25	0.87	29.8	453	0.420
	236 [2]	25	17.3	61	1.0	26	0.84	28.6	434	0.438
	F_{est}	F_{est}	0.45	0.31	0.02	0.04	0.21	0.60	1.19	0.90
Xcfd7										
2016	194 [1]	27	7.8	98	1.9	35	1.09	33.6	442	0.479
	null [2, 3]	20	8.6	107	1.8	33	1.01	34.8	423	0.414
	F_{est}	F_{est}	7.00*	2.82	1.72	3.37	5.01	1.94	1.74	11.03 *
2017	194 [1]	27	8.0	97	1.70	46	1.45	33.1	445	0.580
	null [2, 3]	20	8.4	108	1.54	40	1.42	35.0	458	0.528
	F_{est}	F_{est}	4.03	5.39 *	4.58 *	9.50 *	0.19	3.27	0.93	7.09 *
2018	194 [1]	27	17.4	58	1.0	25	0.84	28.8	452	0.418
	null [2, 3]	20	17.5	65	1.1	27	0.88	29.7	431	0.444
	F_{est}	F_{est}	0.24	4.33 *	1.05	1.17	0.55	0.39	1.48	1.80
Xwmc75										
2016	210 [1]	21	7.9	100	1.9	34	1.07	34.0	443	0.474
	190 [2]	26	8.3	103	1.8	34	1.04	34.2	426	0.432
	F_{est}	F_{est}	1.76	0.16	0.90	0.09	0.98	0.09	1.53	3.83
2017	210 [1]	21	8.2	99	1.70	46	1.46	33.3	458	0.564
	190 [2]	26	8.2	104	1.58	42	1.42	34.4	444	0.553
	F_{est}	F_{est}	0.01	1.52	2.88	4.97*	0.32	1.04	1.01	0.26
2018	210 [1]	21	17.6	60	1.0	26	0.88	29.0	458	0.419
	190 [2]	26	17.3	61	1.0	25	0.84	29.3	432	0.437
	F_{est}	F_{est}	0.67	0.07	0.94	0.01	0.60	0.06	2.20	0.91

Note. [1] – allele from Luzanivka odeska, [2] – allele from Odeska chervonokolosa, [3] null – absent fragment of amplification (null-allele), [4] F – Fisher's F test, * – $F_{est} > F_{0.05}$; DPH – duration of a period prior to heading (counting from May 1), PH – plant height, PT – productive tillering, GNS – grain number per spike, GWS – grain weight per spike, TGW – thousand-grain weight, NPT – number of productive tillers, GY – grain yield.

conditions favorable for the growth and development of wheat in 2017, the lines with the allele of 174 bp and 178 bp by loci *Xwmc415-5B* and *Xgpw3191-5B,* respectively, which originate in Luzanivka Odeska, were notable for a much higher grain yield due to an insignificant increase in all the components (PT, GNS, GWS, TGW, and NPT). A similar regularity was noted for locus *Xbarc88-5B*. The lines with the allele of 84 bp of this locus, which also originated from Luzanivka odeska, were characterized by considerably higher indices of grain yield.

Yet contrary to two previous loci, the lines with the allele of 84 bp were notable for a considerably higher GWS along with an insignificant increase in PT, GNS, TGW, and NPT which in total resulted in a reliable increase in grain yield. A significant connection between allelic differences by locus *Xbarc88-5B* in 2016 and 2017 was also related to the plant height. In both cases, the lines, carriers of allele of 84 bp from Luzanivka odeska, were 12 and 9 cm higher, respectively. Under conditions of 2018, the difference in the height of plants between lines-carriers of alternative alleles of this locus was insignificant, but the ratio of the groups of lines was similar to that in other years of the study. At the same time, in 2018, which was unfavorable for winter wheat growing, we found allelic associations between locus *Xbarc88-5B* and a thousand-grain weight. The larger kernel was notable for the lines, carriers of the allele of 84 bp from Luzanivka odeska. Similar tendencies regarding TGW were noted in more favorable 2016 and 2017.

The highest number of associations between allelic differences and a number of economic traits were registered by locus *Xcfd7-5B*, especially in 2016 and 2017, which were more favorable for wheat growing. In both years, the lines with the allele of 194 bp, which originated from Luzanivka odeska, formed a much higher, by 0.65 and 0.52 kg/sq.m., grain yield as compared to the carriers of a null-allele, which originated from Odeska chervonokolosa. In both years, the lines with the allele of 194 bp were characterized by reliably higher indices of productive tillering, grain number, and grain weight per spike (only in 2016) against the background of an insignificant increase in the number of productive tillers, which resulted in a considerable increase in grain yield of these lines. It should be noted that by grain yield, the ranks of the groups of lines-carriers of alternative alleles of locus *Xcfd7-5B* in unfavorable 2018 changed to the opposite as compared to the first two years of the study, and the differences between the groups of lines were insignificant. In conditions of 2016, we found an association between allelic differences in locus *Xcfd7-5B* and the duration of a period prior to heading. A shorter period till heading (7.8 days) was notable for the lines with the allele of 194 bp from Luzanivka odeska. A significant connection between allelic differences by locus *Xcfd7-5B* in all three years of the study was related to the plant height. In all the years, the lines, carriers of null-allele Odeska chervonokolosa, had higher plants. At the same time, in 2016 and 2017, higher yield was remarkable for genotypes with lower stalks, and in 2018 – for plants with high stalks.

Significant associations were found between specific traits and other loci. For instance, in conditions of 2016 and 2018, we found a reliable association between allelic differences in locus *Xbarc89-5B* and the number of productive tillers and thousand-grain weight, respectively. In 2017, allelic differences by locus *Xwmc75-5B* were closely related to the changes in GNS. Higher indices for all three traits were notable for the lines-carriers of alleles of the corresponding loci of 130 bp and 210 bp from Luzanivka odeska.

DISCUSSION

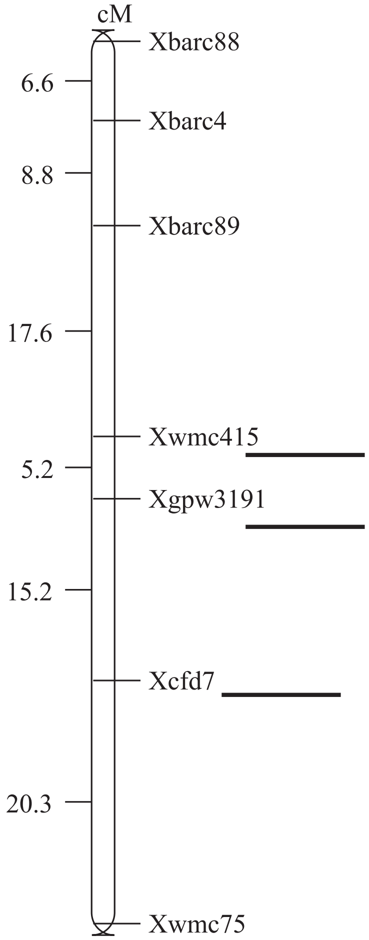
Two loci that demonstrated an association with grain yield were identified on 5A chromosome: locus *Xbarc 330-5A* was associated with the changes in grain yield in favorable 2017, and locus *Xbarc 319-5A* – in unfavorable 2018. In both cases, the lines with alleles of 106 bp and 206 bp from Odeska chervonokolosa, had higher yield. Loci *Xbarc 330-5A* and *Xbarc 319-5A* are on 5A chromosome at a considerable distance from each other (29.9 cM). Chromosome 5A may have two regions with QTL, which affect grain yield. QTL linked to locus *Xbarc 330-5A* may be associated with the yield components, and QTL linked to locus *Xbarc 319-5A* may affect both the yield and resistance to abiotic stress factors.

It is known that 5A chromosome has gene Q, which provides for unobstructed grain threshing (Xie et al, 2018). In addition, gene Q has a pleiotropic impact on many other traits, including heading time, plant height, fragility, length, and compactibility of a spike. Some publications stated that on 5A chromosome, there are QTLs, affecting spike length (Ji et al, 2021). The studies demonstrated (Zhai et al, 2016) that QTLs of the spike length and compactibility of spikes are in the area of localization of microsatellite locus *Xgwm639-5A*. Locus *Xbarc 330-5A*, associated with grain yield in our study, is closely linked to locus *Xgwm639-5A*; the distance between them is 2.7 cM. It can be assumed that on 5A chromosome in the area of localization of loci *Xbarc 330-5A* and *Xgwm639-5A,* there is QTL, affecting not only the spike length but also grain yield.

No definite association between 5D chromosome loci and grain yield and its components was found in our study. To the best of our knowledge, the main QTLs for GY or TGW on 5D chromosome have not been reported yet. The study of Mohler et al., 2016 found QTL of the length, width, and area of a kernel on 5D chromosome, but the found QTL did not affect the differences in GY and TGW. It may be assumed that no genes, consistently affecting grain yield, are located on 5D chromosome. At the same time, 5D chromosome carries several valuable genes, including frost resistance genes *Fr* (Snape et al, 2001). In our previous study, we demonstrated that locus *Xgwm182-5D* was associated with frost resistance of winter wheat (Galaeva et al, 2013). Thus, the selection by this locus will ensure the selection of frost-resistant genotypes without a decrease in their yield because there is a known negative correlation between the yield and frost resistance of winter wheat.

It is noteworthy that in terms of all loci of 5B chromosome, higher indices of yield were notable for the lines with alleles from Luzanivka odeska, though the latter variety itself is known for lower yield as compared to Odeska chervonokolosa.

It should be noted that some of the abovementioned loci are at a considerable distance from one another (**Figure**). Locus *Xbarc88-5B* is in the most proxi-



Molecular genetic map of 5B chromosome. MC-loci, which demonstrated an association to grain yield of RIL Luzanivka odeska/Odeska chervonokolosa are underlined (https://kyazma.nl/index.php/JoinMap)

mal position. The distance from it to the nearest locus *Xwmc415-5B*, also associated to grain yield, is 33 cM, according to our data. Loci *Xwmc415-5B* and *Xgpw3191-5B* are linked, the distance between them is 5.2 cM. Locus *Xcfd7-5B* is in a distal position, at a distance of 15.2 cM from locus *Xgpw3191-5B*.

It may be assumed that there are at least two QTLs on chromosome 5B, associated with winter wheat yield in favorable growing years. The first of them is located in the region of the *Xbarc88-5B*, i.e., on the short arm of 5B chromosome, and the second QTL is on the long arm of the mentioned chromosome, in the area of localization for *Xwmc415-5B*, *Xgpw3191-5B,* and *Xcfd7-5B*.

In addition, loci *Xbarc88-5B* and *Xcfd7-5B* are associated with plant height. A considerable shortening in plant height by 9–12 cm was related to the allele of locus *Xbarc88-5B*, which originated from Odeska chervonokolosa. It should be noted that by locus *Xcfd7-5B,* higher plants were observed in the lines with the allele from Odeska chervonokolosa, though this variety is remarkable for a smaller height as compared to Luzanivka odeska. The manipulation of such a trait as the height of wheat plants is rather important in modern selection. It is believed that the wide application of short-stalk plants of common wheat in agriculture is a key to the success of all the programs of wheat selection in the course of the "green revolution" which conditions a total increase in the yield (Peng et al, 1999; Hedden, 2003), mostly related to the resistance of plants from new varieties to lodging. This increase in wheat resistance to lodging due to its short stalk is mainly impacted by *Rht* genes (reduced height) that control the manifestation of a "plant height" trait. In common wheat, there are 25 main known genes of short stalk *Rht* (*Rht1-Rht25*) (McIntosh et al, 2017; Mo et al, 2018; Agarwal et al, 2020), yet none of the known genes is located on 5B chromosome. Therefore, it can be assumed that there are two new genes of 5B chromosome, which impact the "plant height" trait to some degree, one of them is located on the short arm in the area of localization of locus *Xbarc88-5B*, and the other – on the long arm in the area of locus *Xcfd7-5B*.

Based on the alleles of the specified microsatellite loci, which are associated with the yield and height of plants, it is possible to select genotypes at the early stages of selection that will give a higher yield in years with favorable conditions for growing wheat. However, in unfavorable years, the mentioned loci will not be efficient, thus, the elaboration of a more improved system of DNA markers requires thorough molecular-genetic and field studies in different years and different regions of Ukraine. Under unfavorable conditions, a relevant role in preserving stable yield may be played, for instance, by drought-resistance genes in the years with considerable droughts, genes of frost and winter resistance in the years with severe winters, or genes of resistance to some biotic stress factors in years with epiphytoties of the disease agents. Therefore, it is a complex approach with the application of molecular markers that will allow selectionists to choose productive and stable genotypes in the early stages of the selection.

CONCLUSIONS

Recombinant-inbred lines Luzanivka odeska/Odeska chervonokolosa were analyzed in terms of a complex of agronomically relevant traits, including grain yield, duration of a period prior to heading, plant height, productive tillering, grain number per spike, grain weight per spike, thousand-grain weight, and number of productive tillers for three years (2016–2018) which differed considerably in their hydrometeorological conditions.

The comparison of the data of line evaluation by agronomic traits with the data of microsatellite analysis of lines by loci of the fifth group chromosomes demonstrated the associations between a number of loci and grain yield, and the association between two loci and plant height.

The changes in yield in the most unfavorable year, 2018, were associated with allelic differences of lines by locus *Xbarc319-5A*, and in the most favorable year, 2017, – with another locus of chromosome 5A *Xbarc330-5A*. In both cases, the lines that had an allele from the Odeska chervonokolosa were characterized by a significantly higher level of grain yield as compared to the lines that had an allele from the Luzanivka odeska variety.

There are at least two QTLs on chromosome 5B, associated with winter wheat grain yield in favorable growing years. The first of them is located in the region of locus *Xbarc88-5B*, and the second – in the region of loci *Xwmc415-5B*, *Xgpw3191-5B,* and *Xcfd7-5B*. Based on the alleles of the specified microsatellite loci, which are linked QTLs of grain yield, it is possible to select genotypes at the early stages of selection that will give a higher yield in years with favorable conditions for growing wheat.

Adherence to ethical principles. All the experimental results, presented in this article, were obtained without the use of any animals.

Conflict of interests. The authors declare the absence of any conflicts of interests.

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Асоціації алельних відмінностей локусів п’ятої групи хромосом з комплексом агрономічно цінних ознак пшениці м’якої (*Triticum aestivum* L.)

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Мета. Характеристика рекомбінантно-інбредних ліній пшениці за агрономічно важливими ознаками та виявлення асоціацій їх рівня прояву з алельними відмінностями мікросателітних локусів хромосом п’ятої групи. **Методи.** Фенологічні спостереження, морфометричні показники та елементи структури врожаю. Статистичний аналіз отриманих даних проводився в Microsoft Excel. Значущість різниці між зразками була оцінена за критерієм F Фішера. Різниця $p < 0{,}05$ вважалася статистично достовірною для всіх показників. **Результати.** Оцінено поліморфізм батьківських генотипів та популяції з 47 рекомбінантно-інбредних ліній F_7 від схрещування сортів озимої пшениці Лузанівка одеська і Одеська червоноколоса на протязі трьох (2016–2018) років в умовах Південного Степу (м. Одеса) за восьми ознаками: тривалість періоду до колосіння, висота рослини, продуктивне кущіння, кількість зерна з колоса, маса зерна колоса, маса 1000 зерен, кількість продуктивних пагонів і урожайність зерна. Зіставлення даних оцінювання ліній за агрономічними ознаками з даними мікросателітного аналізу ліній за 14 мікросателітними локусами п’ятої групи хромосом, дало змогу виявити асоціації ряду локусів з урожайністю зерна та двох локусів – з висотою рослин. **Висновки.** Зміни урожайності зерна у найбільш несприятливому 2018 році асоціювались з алельними відмінностями ліній за локусом *Xbarc 319-5A*, а у найбільш сприятливому 2017 році – з іншим локусом хромосоми 5A *Xbarc 330-5A*. В обох випадках лінії, що мали алель від сорту Одеська червоноколоса, характеризувались істотно вищою урожайністю зерна порівняно з лініями, що мали алель від сорту Лузанівка одеська. На хромосомі 5B є щонайменше два QTL, які асоціюються з урожайністю зерна озимої пшениці в сприятливі для вирощування роки. Перший з них знаходиться в області локалізації локусу *Xbarc88-5B*, а другий в області локусів *Xwmc415-5B, Xgpw3191-5B* та *Xcfd7-5B*. За алелями зазначених мікросателітних локусів, що є зчепленими QTL урожайністю зерна, можна добирати на ранніх етапах селекції генотипи, які будуть давати вищу урожайність у роки зі сприятливими для вирощування пшениці умовами.

Ключеві слова: пшениця м’яка (*Triticum aestivum* L.), рекомбінантно-інбредні лінії, ген, алель, мікросателітні локуси, QTL.

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