IDENTIFICATION OF THE DIVERSITY OF CULTIVATED PLANTS AND THEIR WILD RELATIVES FOR SOLVING FUNDAMENTAL AND APPLIED PROBLEMS

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Genome-wide association study for identification of SNP markers associated with barley spike productivity (*Hordeum vulgare* L.)

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Background. Barley (*Hordeum vulgare* L.) is an important cereal crop with a wide range of uses. Barley yield is a complex indicator consisting of some yield structure components. Identification of molecular markers linked to spike morphology is of great importance for barley breeding improvement. The objective of this study was to search for significant markers and identify loci associated with barley spike traits through a genome-wide association study (GWAS).
Materials and methods. In 2021–2023, 199 accessions of spring barley of different breeding levels from the VIR collection were studied in the fields of Pushkin and Pavlovsk Laboratories of VIR. The set included 103 accessions of six-row and 96 accessions of two-row barley of various origin. Genotyping was conducted using the Barley 50K Illumina Infinium iSELECT chip. GWAS was performed in the R using the mixed linear model with a kinship matrix (MLM).
Results. A wide diversity of yield structure characters: spike length (SL), spikelet number per spike (SN), grain number per spike (GN), grain weight per spike (GW), and thousand-grain weight (TGW), was shown depending on spike row number and environmental impacts. As a result of GWAS, 129 markers associated with yield indicators were identified: 12 for SL, 73 for SN, 19 for GN, 9 for GW, and 16 for TGW. Significant markers were matched with genomic regions on all barley chromosomes. Some of them are associated with already known *Vrs* genes on the first five chromosomes. A protein–protein interaction analysis with k-means identified three functional clusters, including 19 SNPs linked to orthologous genes for spike development.
Conclusion. The identified markers, loci, and protein interactions are interesting for further studies of the spike architecture and quantitative traits contributing to barley yield.

Keywords: barley, GWAS, yield, spike characters, spike rows, SNP, *Vrs*, PPI

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ИДЕНТИФИКАЦИЯ ГЕНЕТИЧЕСКОГО РАЗНООБРАЗИЯ КУЛЬТУРНЫХ РАСТЕНИЙ И ИХ ДИКИХ РОДИЧЕЙ ДЛЯ РЕШЕНИЯ ФУНДАМЕНТАЛЬНЫХ И ПРИКЛАДНЫХ ПРОБЛЕМ

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Полногеномный анализ ассоциаций для идентификации SNP-маркеров, связанных с продуктивностью колоса ячменя (*Hordeum vulgare* L.)

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Актуальность. Ячмень (*Hordeum vulgare* L.) является важной зерновой культурой широкого использования. Урожайность ячменя – это комплексный признак, на который влияют основные элементы структуры урожая. Идентификация молекулярных маркеров, сцепленных с морфологией колоса, очень важна для селекционного улучшения ячменя. Целью исследования является выявление геномных локусов, ассоциированных с архитектурой колоса ячменя, с использованием полногеномного анализа ассоциаций (GWAS).

Материал и методы. Изучен набор из 199 образцов преимущественно голозерного ярового ячменя коллекции ВИР разного селекционного уровня, включая 103 образца шестирядного и 96 образцов двурядного ячменя разного происхождения. Фенотипирование по колосовым признакам выполнено в 2021–2023 гг. на экспериментальном поле научно-производственной базы «Пушкинские и Павловские лаборатории ВИР». Генотипирование проведено с использованием чипа Barley 50K Illumina Infinium iSELECT. GWAS выполнен в R с использованием смешанной линейной модели с учетом матрицы родства (MLM).

Результаты. Показано широкое разнообразие признаков структуры урожая: длина колоса (SL), число колосков в колосе (SN), число зерен в колосе (GN), масса зерна с колоса (GW), масса 1000 зерен (TGW) в зависимости от рядности колоса и влияния окружающей среды. В результате GWAS выявлены 129 маркеров для всех признаков, включая 12 для SL, 73 для SN, 19 для GN, 9 для GW, 16 для TGW. Выделенные значимые маркеры сопоставлены с геномными районами на всех хромосомах ячменя. Часть выделенных маркеров ассоциирована с уже известными генами *Vrs* на первых пяти хромосомах. Анализ белок-белковых взаимодействий выделил 3 функциональных кластера, включающие 19 SNP, сцепленных с генами-ортологами развития колоса.

Заключение. Выделенные маркеры, локусы и белковые взаимосвязи представляют интерес для дальнейшего изучения архитектуры колоса и количественных признаков, вносящих значительный вклад в урожайность ячменя.

Ключевые слова: ячмень, GWAS, урожайность, признаки колоса, рядность колоса, SNP, *Vrs*, PPI

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Introduction

Barley (*Hordeum vulgare* L.) is the fourth most widely cultivated cereal crop after wheat, rice, and maize (https://www.fao.org/statistics/en). It is used worldwide for feed, food and brewing purposes. In addition to its agricultural importance, barley serves as a model crop, and the data obtained on its genome are used for genetic research targeted at other representatives of the Triticeae L. tribe, such as wheat and rye (Rozanova, Khlestkina, 2020).

One of the main aims of barley breeding is the development of adaptable high-yielding cultivars. Barley yield is a complex character consisting of some yield structure components. The following indicators determine seed yield: spike length (SL), spikelet number per spike (SN), grain number per spike (GN), grain weight per spike (GW), and thousand-grain weight (TGW) (Trofimovskaya, 1972; Surin, 2011). To increase yield through selecting pairs for crossing and elite plants, it is necessary to set high requirements for quantitative indicators of yield and grain quality. Key components of the yield structure are formed at different stages of organogenesis during plant growth, and depend on the cultivar's biological characteristics and the weather conditions during the growing season (Trofimovskaya, 1972; Surin, 2011).

The spike architecture is one of the most important characteristics that directly affects the grains number in the spike and the yield per plant. It was precisely the change in the spike architecture that was the target of barley domestication. The inflorescence of barley is a spike: three single-flowered spikelets are arranged alternately at rachis nodes, including the central and two lateral spikelets. The cultivated species *H. vulgare* is divided into two forms based on the development of lateral spikelets and their fertility: six-row (*H. vulgare* L. subsp. *vulgare*) and two-row (*H. vulgare* L. subsp. *distichon* (L.) Koern.), which include groups of hulled and naked barleys (Trofimovskaya, 1972; Lukyanova et al., 1990). The six-row barley is characterized by all three fertile spikelets and normally developed grains, while in the two-row barley only one of the three spikelets is fertile. Therefore, the six-row barley has an advantage over the two-row barley in the number of spikelets and grains in the spike, but the grains of two-row barleys are significantly larger.

It has now been established that the development of a two-rowed spike, determined by the *Vrs* genes, is dominant in barley (Haaning et al., 2020). According to classical genetics and modern analysis methods, five main *Vrs* genes associated with complete or partial changes in the fertility of lateral spikelets in barley spikes have been identified: *Six-rowed spike1* (*Vrs1*), *Vrs2*, *Vrs3*, *Vrs4*, and *Intermedium-C* (*Int-c*)/*Vrs5* (Lundqvist, 2014). *Vrs1* (*HvHOX1*) encodes a basic helix -loop-helix (bHLH) transcriptional activator that inhibits the development of fertile lateral spikelets (Komatsuda et al., 2007). *Vrs2*, *Vrs4* (*HvRA2*) and *Vrs5*/*Int-c* (*HvTB1*) encode the transcription factors SHORT INTERNODES (SHI), LATERAL ORGAN BOUNDARY (LOB) and TEOSINTE BRANCHED1 (TB1), respectively (Ramsay et al., 2011; Koppolu et al., 2013; Youssef et al., 2017; Koppolu, Schnurbusch, 2019). *Vrs3* presumably encodes a putative Jumonji C-type H3K9me2/me3 demethylase, a regulator of chromatin state (Bull et al., 2017). Recessive mutant alleles of these genes show varying degrees of six-row spike expression and can cause the so-called intermediate phenotypes.

Understanding the genetic basis of the traits is an important part of potentially improving the yield and adaptability to different climatic conditions. Recently, the genome-wide association study (GWAS) has become an approach for revealing the molecular genetic basis of many important agronomic traits and properties that affect the plant's adaptability to abiotic and biotic stressors under various environmental conditions (Alqudah et al., 2020). GWAS is a modern bioinformatic method successfully used to identify the relationship between phenotypic variability and genetic polymorphism and to detect causal loci/genes. The method consists of statistical associations between each marker and the phenotypic expression of a trait within unrelated genotypes from a diverse collection (Huang, Han, 2014). The main goal of GWAS is to identify causal factors for a specific trait and determine the genetic architecture of the interesting trait. For successful determination of loci by GWAS, the studied accessions should be as heterogeneous as possible. Therefore, barley accessions to be tested were composed with due regard to both their diversity in origin and contrast in characteristics (morphological characters, ripeness groups, etc.).

GWAS has been used on barley since 2010 (Cockram et al., 2010), and the number of studies has increased significantly over the past 15 years. Using this approach, genomic regions associated with many barley traits have been discovered: various stages of plant development (Pasam et al., 2012; Alqudah et al., 2014); plant height (Pasam et al., 2012; Alqudah et al., 2014); leaf blade area (Alqudah et al., 2014); spike length, spike structure, and grain number per spike (Wang et al., 2012); thousand-grain weight (Pasam et al., 2012); root system development (Thabet et al., 2018); resistance to diseases and pests (Afanasenko et al., 2022); resistance to abiotic stress (Thabet et al., 2018). In addition, a large number of studies have been conducted on the biochemical composition of barley grains: the content and properties of starch (Pasam et al., 2012), protein (Pasam et al., 2012), β-glucans (Geng et al., 2021), anthocyanins (Cockram et al., 2010), etc. The obtained data are demanded in breeding programs for the development of adaptable high-yielding cultivars with high grain quality.

A review of the existing literature showed that the GWAS method is used to study sets of barley genotypes consisting of two-row (Faccini et al., 2021) or six-row (Belcher et al., 2015) cultivars, or both of them (Haaning et al., 2020; Rozanova et al., 2023). However, when investigating yield structure components, which include TGW, GW, and other indicators related to grain, it is necessary to understand how the loci that determine the row number will affect this trait. The next step after conducting GWAS is to validate the identified markers. Currently, only a few studies have been devoted to testing candidate markers on independent samples (Afanasenko et al., 2022; Rozanova et al., 2023).

The objective of this study was to search for significant markers and identify loci associated with barley spike traits using a genome-wide association study (GWAS).

Materials and methods

Plant material

The material for the study was 199 spring barley accessions from the VIR collection. The set included landraces, breeding lines, old and modern varieties, 96 accessions belong to two-row barley and 103 to six-row barley. In addition, the set was mainly represented by a group of naked barley (192) and 7 accessions of hulled barley of different ecological and geographical origins: 16 from the European part of Russia, 33 from Europe, 11 from the Asian part of Russia, 84 from Asia, 22 from Africa, 19 from North America, 12 from South America, and 2 accessions from Australia.

Field experiment and phenotyping

Barley accessions were planted at the optimal time in the fields of Pushkin and Pavlovsk Laboratories of VIR (59.710488; 30.427004) located in the northwest of the Non-Black-Earth Region of Russia. The accessions were sown manually on 1 m^2 plots. Observations and evaluation of accessions for important agronomic traits were conducted in accordance with the published guidelines (Loskutov et al., 2012).

Weather conditions during the growing seasons of 2021–2023 were variable and differed from the long-term means (Table 1). Differences in precipitation and air temperature during the growing season allowed us to evaluate accessions under contrasting conditions.

Table 1. **Weather conditions during the growing seasons in 2021–2023, Pushkin, Russia**
(http://www.pogodaiklimat.ru)

Таблица 1. **Метеорологическая характеристика периодов вегетации в 2021–2023 гг., Пушкин, Россия**
(http://www.pogodaiklimat.ru)

Month	Mean air temperatures, °C			Long-term mean air temperature, °C	Total precipitation amounts, mm			Long-term mean precipitation amount, mm
	2021	2022	2023		2021	2022	2023	
May	12.1	10.0	11.9	11.5	139.4	25.6	16.7	47.0
June	21.4	17.6	17.3	16.1	22.1	47.0	47.9	69.0
July	23.1	19.9	18.5	19.1	50.3	75.5	95.0	84.0
August	16.9	20.6	19.9	17.4	135.1	112.6	48.5	87.0

To study the main yield components, 10 plants from every accession were selected before harvesting. The following parameters were assessed: spike length (SL), spikelet number per spike (SN), grain number per spike (GN), grain weight per spike (GW), and thousand-grain weight (TGW). Statistical analysis for all characters was performed using the STATISTICA 10 software.

DNA extraction

DNA was extracted from 10 individual seedlings for each accession, pre-germinated in Petri dishes. The DNeasy Plant Mini Kit (Qiagen) was used according to the manufacturer's protocol. The concentration of the extracted DNA was controlled by a NanoDrop 2000 spectrophotometer (Thermo Scientific), as well as by electrophoresis in 1.5% agarose gel, and visualized by staining with ethidium bromide (EtBr) on a Bio-rad Gel DocTMXR gel documentation system.

Genotyping data

The accessions were genotyped using the Barley 50K Illumina Infinium iSELECT SNP chip (Bayer et al., 2017) for 44,040 markers (Traitgenetics GmbH, Gatersleben, Germany). To filter the markers, a minor allele frequency (MAF) threshold of ≤ 5% and a missing rate of > 5% were set. After filtering, 33,097 (75.2%) markers were retained for further analysis.

Genetic positions of the identified loci were specified using the Barleymap tool (https://barleymap.eead.csic.es/barleymap) (Cantalapiedra et al., 2015) on the POPseq_2017 and POPseq_2012 maps (Mascher et al., 2017). Physical positions were refined on the basis of the latest version of the MorexV3 reference genome (Mascher et al., 2021). Searching for genes and their amino acid sequences was done through open information platforms with the latest version of the barley genome (https://plants.ensembl.org/index.html) and the National Center for Biotechnology Information (https://www.ncbi.nlm.nih.gov).

Population structure analysis was made using the LEA package in the R (Frichot, François, 2015). The number of subpopulations (k) was estimated from 1 to 20. The optimal value of k was calculated with the minimum mean square error of the cross-entropy criterion.

Associating analysis

A genome-wide association analysis was performed in the R using the BGLR, rrBLUP, and qqman libraries (Hussain, 2018). To identify loci associated with a trait, a mixed linear model with the kinship matrix (MLM) was used. The results of the analysis were plotted on the Manhattan plots and QQ plots constructed using a script in the R (Hussain, 2018). To find the significance level of SNPs, the Bonferroni correction (Hommel, 1988) was applied, with the significance threshold (0.05) divided by the total number of markers studied (33,097), resulting in a significance level of 1.51×10^{-6}. On the Manhattan and QQ plots, the threshold value was determined as -log10 (threshold *p*-value) = 5.82. In addition, "suggestive" markers were selected, whose *p*-value was greater than 10^{-5} but did not exceed the threshold value.

Protein–protein interaction (PPI) network construction

To evaluate protein–protein interactions (PPI) associated with spike productivity the STRING gene/protein interaction search tool was used (http://www.string-db.org).

Results

Phenotyping

Weather conditions during the growing season were variable and had a significant impact on the traits. High temperatures and a lack of moisture in 2021 led to earlier heading and ripening of some accessions. The hydrothermal regime in 2022 and 2023 was more similar to the long-term mean. The most favorable year for barley growth and development was 2022, with the highest average values for the spikelet and grain numbers per spike, thousand-grain weight, and grain weight per spike. In the driest year, 2021, on the contrary, all indicators, except for spike length, showed minimum values. Such growth conditions made it possible to assess the contribution of the genotype and environment to the development of a trait. Phenotyping data (mean, minimum and maximum, standard error) of the studied indicators are presented in Figure 1 and Table 2.

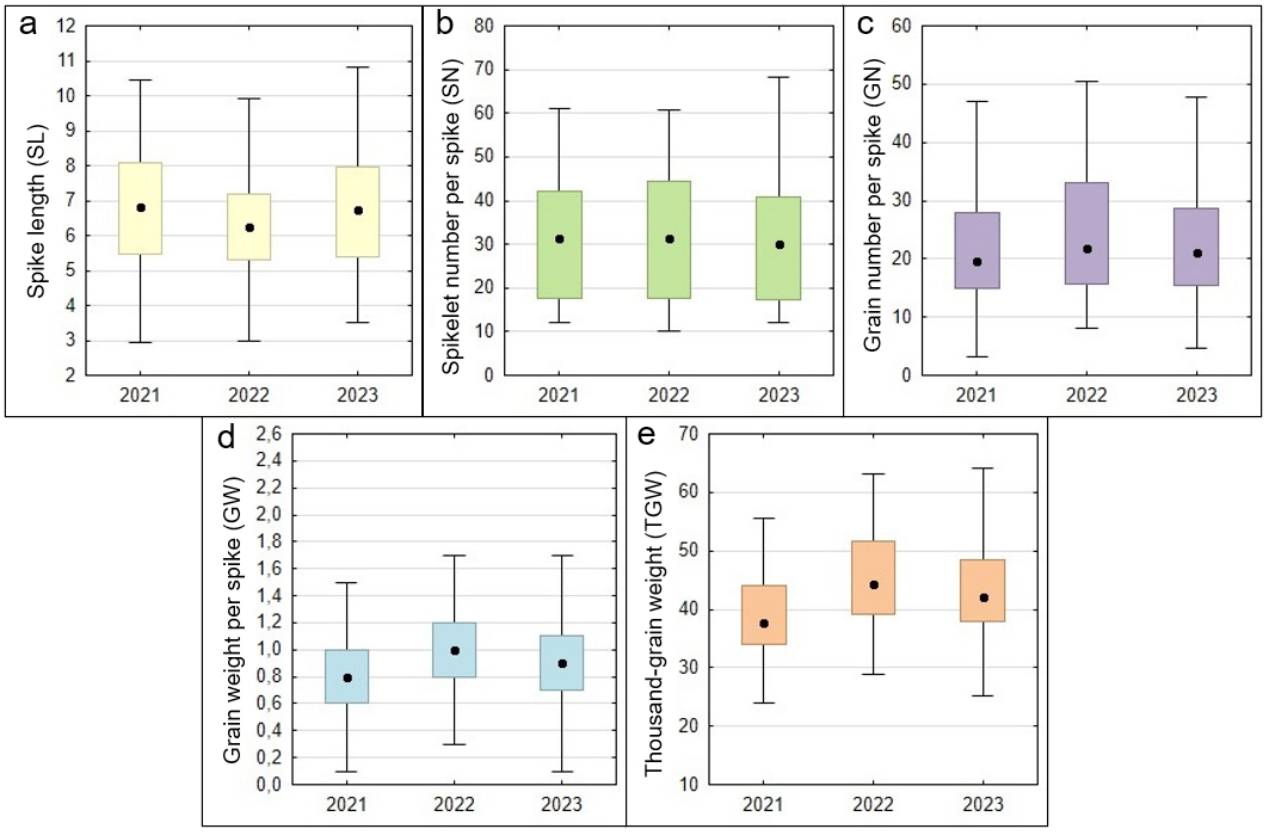

Fig. 1. **Distribution of phenotypic indicator values: (a) spike length (SL); (b) spikelet number per spike (SN); (c) grain number per spike (GN); (d) grain weight per spike (GW); (e) thousand-grain weight (TGW), in different years of the research**

Рис. 1. **Распределение значений фенотипических признаков: (a) длина колоса (SL); (b) число колосков в колосе (SN); (c) число зерен в колосе (GN); (d) масса зерна с колоса (GW); (e) масса тысячи зерен (TGW) в разные годы исследований**

Table 2. **Descriptive statistics of phenotypic characters in barley**

Таблица 2. **Варьирование фенотипических признаков ячменя**

Character	2021			2022			2023		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
SL	6.8 ± 0.1	2.9	10.5	6.2 ± 0.1	3.0	9.9	6. 7± 0.1	3.5	10.8
SN	30.4 ± 0.9	12.0	61.0	31.7 ± 1.0	10.0	60.7	31.1 ± 1.0	12.2	68.4
GN	22.1 ± 0.7	3.1	51.0	24.5 ± 0.7	8.0	50.4	23.3 ± 0.7	4.7	54.5
GM	0.8 ± 0.02	0.1	1.9	1.0 ± 0.03	0.3	2.4	0.9 ± 0.02	0.1	1.9
TGW	38.8 ± 0.5	24.0	55.6	45.6 ± 0.6	29.0	63.2	43.9 ± 0.6	20.4	65.9

The studied accessions included genotypes of various origin, with high variability in agronomic characters (for example, SL varied from 2.9 to 10.8; TGW from 20.7 to 63.2; see table 2). At the same time, the presence of approximately the same value range for each character in the accessions over three years helped to assess the contribution of the genetic component to the trait development.

Population structure analysis

Genotyping data were used to analyze the population structure. The lowest k-value on the 'plateau' recording the true value of subpopulations was taken into account. Five subpopulations/clusters (k = 5) were identified in this study (Fig. 2).

In the subsequent analysis of the population structure, the range of k-values k = 4–6 was used, as shown in Figure 3. The population structure analysis revealed the presence of admixtures of all SNPs in other clusters, indicating the complex structure of the barley accessions' pedigrees. The genotypes included in the selected clusters were analyzed according to their origin, spike row type, and breeding level.

The studied genotypes were divided into 5 clusters (k = 5). The first cluster included 57 accessions of mainly six-row naked barley from Japan, China, Mongolia, Afghan-

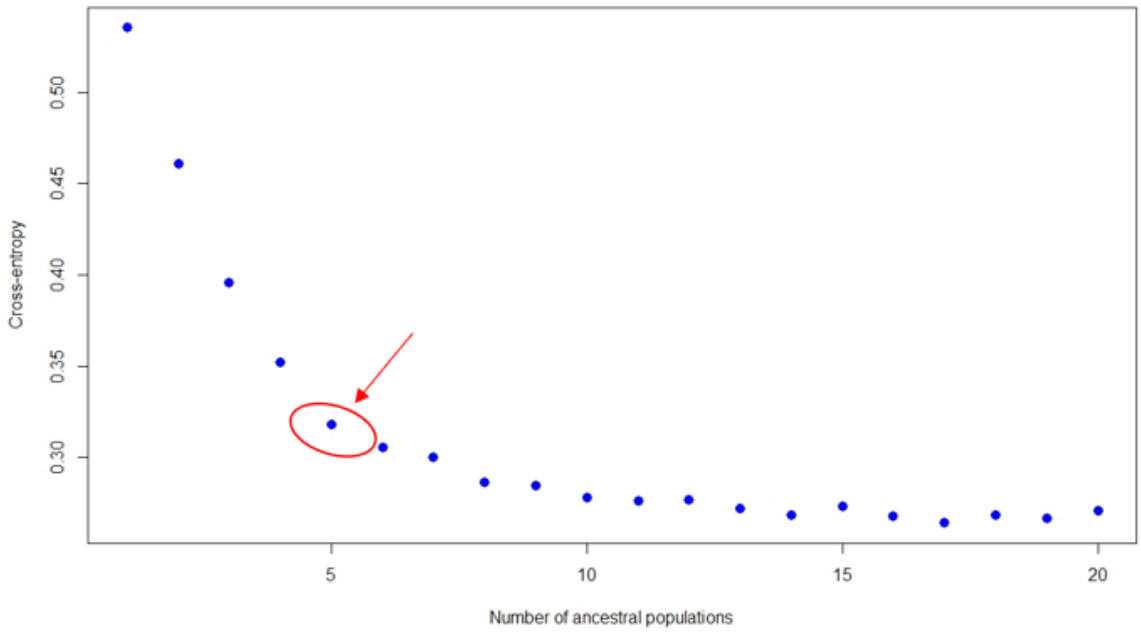

Fig. 2. **The plot showing the optimal number of subpopulations in the studied set of barleys**

Рис. 2. **График определения оптимального количества субпопуляций в изучаемой выборке ячменя**

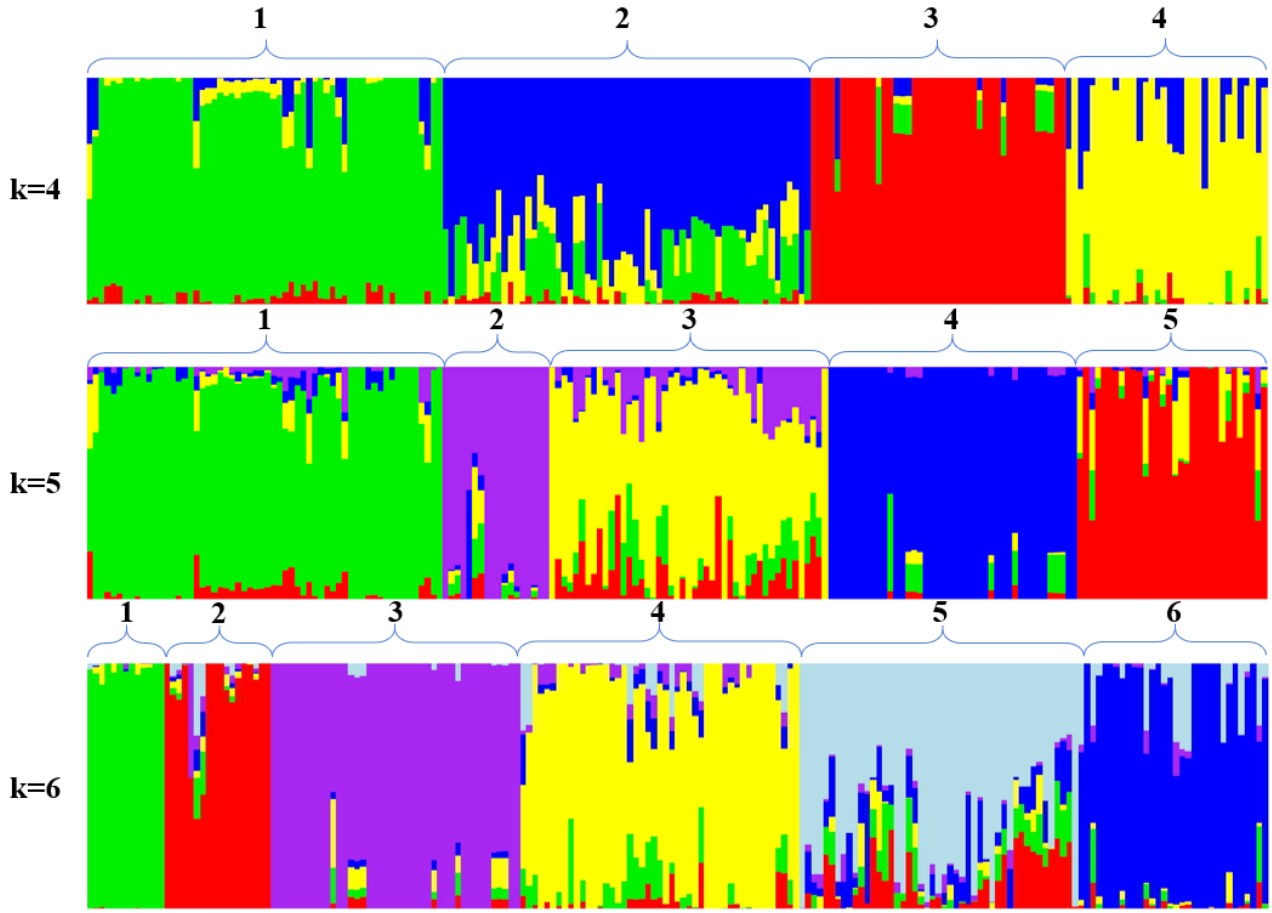

Fig. 3. **Population structure of 199 barley genotypes. Clusters with different subpopulation values (k = 4, k = 5, and k = 6) are highlighted with different colors and numbers**

Рис. 3. **Популяционная структура 199 генотипов ячменя. Различными цветами и цифрами выделены кластеры при разных значениях субпопуляций (k = 4, k = 5, k = 6)**

istan, and Tajikistan, and a few representatives from other countries. This cluster corresponds to the East Asian and Central Asian centers of cultivated barley diversity.

The second cluster included 18 predominantly six-row old cultivars from the European part of Russia, and a few accessions from Central Europe (Austria, Germany, France, and Poland).

The third cluster incorporated 47 modern cultivars and breeding lines of various geographic origin. This cluster is characterized by the largest number of admixtures (genotypes from other clusters), thus indicating their complex pedigrees in breeding.

The fourth cluster united 43 genotypes, mainly two-row naked landraces from Turkey, Iran, Tajikistan, Uzbekistan, Turkmenistan, Georgia, India and the Caucasus regions of Russia (North Ossetia, and Dagestan). This cluster corresponds to the Near Eastern center, with elements of the Central Asian one. In addition, the fourth cluster is characterized by the lowest amount of admixtures, i.e., other genotypes.

The fifth cluster included 34 accessions, mainly local forms from Ethiopia, and selected lines and cultivars developed with the use of genetic material from that country. It corresponds to the Ethiopian diversity center. This cluster is represented by rare botanical varieties: var. *duplinigrum* Koern., var. *nigrinudum* Vav., var. *duplialbum* Koern., and var. *nudimelanocrithum* Giess., which confirms the concentration of unique forms in Ethiopia and their specificity in a number of breeding characteristics.

Differences in the division of the studied genotypes at different subpopulation values showed that at k = 4, four clusters were distinguished, including the first, fourth and fifth clusters at k = 5 and combining the second and third clusters into one. If we consider six clusters (k = 6), the only difference will be that two groups will be distinguished from the first cluster, the first of which includes only Japanese cultivars, and the second all the others.

Association analysis

The association analysis identified 129 markers on all seven barley chromosomes (Electronic Supplementary Materials, Table[1]; Electronic Supplementary Materials, Figure[2]) associated with the analyzed characters.

For spike length, 12 significant markers were identified on chromosome 4H at locus 25.92–26.35 cM (see Electronic Supplementary Materials, Figure, a), which was evident throughout the three years of the study.

The largest number of significant markers was found for spikelet number per spike. Seventy-three significant markers were found on all seven barley chromosomes (see Electronic Supplementary Materials, Figure, b). Three genomic regions on chromosome 1H (10.38 cM, 59.42 cM, 130.81 cM), six genomic regions on chromosome 2H (5.52 cM, 12.11 cM, 38.1 cM; 59.21 cM, 79.89–80.59 cM, 92.71 cM), two genomic regions on chromosome 3H (59–60 cM, 151–153.27 cM), three genomic regions on chromosome 4H (3.54 cM, 24.07 cM, 115.23 cM), 2 genomic regions on chromosome 5H (17.64 cM, 47.72 cM), 2 genomic regions on chromosome 6H (24.58 cM, 63–68 cM, 121.68 cM), and 5 genomic regions on chromosome 7H (43.84 cM, 70.54 cM, 76.29–77.62 cM, 85.98 cM, 104.82 cM) were identified.

For grain number per spike, GWAS identified 19 significant markers on all chromosomes, except 4H (see Electronic Supplementary Materials, Figure, c). Two loci on chromosome 1H (59.42 cM, 130.81 cM), two loci on chromosome 2H (38.1 cM, 92.71 cM), 3 loci on chromosome 3H: (59.42–60 cM, 142.63 cM, 151–153.27 cM), 2 loci on chromosome 5H (17.64 cM, 47.72 cM), and 2 loci on chromosome 6H (63.46–68 cM, 121.68 cM) were spotted.

For thousand-grain weight, 16 significant markers were identified on chromosomes 1H, 2H, 4H, 5H, and 6H (see Electronic Supplementary Materials, Figure, d). Only two genomic regions were repeated over three years on chromosome 5H at position 17.64 cM and on chromosome 4H at position 115.23 cM.

For grain weight per spike, 9 markers were found on chromosomes 2H, 3H, and 6H (see Electronic Supplementary Materials, Figure, e), which were combined into 3 genomic regions on chromosomes: 2H at position 149.15 cM, 3H at position 25.5 cM, and 6H at position 63.5 cM.

Protein–protein interaction (PPI) network construction

For functional interpretation of the loci identified by GWAS, an analysis of protein–protein interactions and products of corresponding genes located in those loci was conducted using the STRING database (http://www.string-db.org). The STRING database contains an assessment of the reliability of protein interactions, i.e., it takes into account the results of experiments, literature analysis, databases, co-expression, proximity, co-occurrence, and gene fusion. The area of protein–protein interactions in STRING is "functional association". Proteins are considered related when there is evidence indicating an evolutionary, specific functional interaction between them. Proteins can operate together to achieve a common goal in a metabolic or signaling pathway, can regulate each other through intermediaries, or can jointly contribute to the overall cellular structure.

To gain a deeper understanding of the spike productivity mechanisms and reduce the number of markers entering further validation, an *in silico* analysis of significant SNPs identified by GWAS was performed. When evaluating the functional and regulatory interactions between the products of the genes in which the detected SNPs were located, no interaction data were available for barley. Therefore, for the selected significant markers, orthologous genes in the *Arabidopsis thaliana* (L.) Heynh. genome were identified.

In total, 58 of the 71 proteins were found by the Search Tool for the Retrieval of Interacting Genes/Proteins within the STRING database (Fig. 4). The protein–protein interaction (PPI) analysis with k-means clustering identified three functional clusters containing two or more proteins closely related to each other. Based on the results of component (Gene Ontology) enrichment, the main direction in the interaction of the identified factors was determined as the intracellular anatomical structure. The greatest interaction (0.726) was found between VPS15 and RID3. At the same time, the role of VPS15 is presumably required for pollen development and germination, probably via the modulation of phosphatidylinositol 3-phosphate (PI3P) formation and vacuolar organization. RID3 is involved in meristem development. It acts as a negative regulator of the CUC-STM pathway in the formation of the shoot apical meristem (SAM).

[1] Приложение представлено в онлайн-формате. Электронная версия статьи: (https://doi.org/10.30901/2227-8834-2025-4-182-194) / See Electronic Supplementary Materials in the online version of this article: (https://doi.org/10.30901/2227-8834-2025-4-182-194).
[2] Приложение представлено в онлайн-формате. Электронная версия статьи: https://doi.org/10.30901/2227-8834-2025-4-182-194 / See Electronic Supplementary Materials in the online version of this article: https://doi.org/110.30901/2227-8834-2025-4-182-194

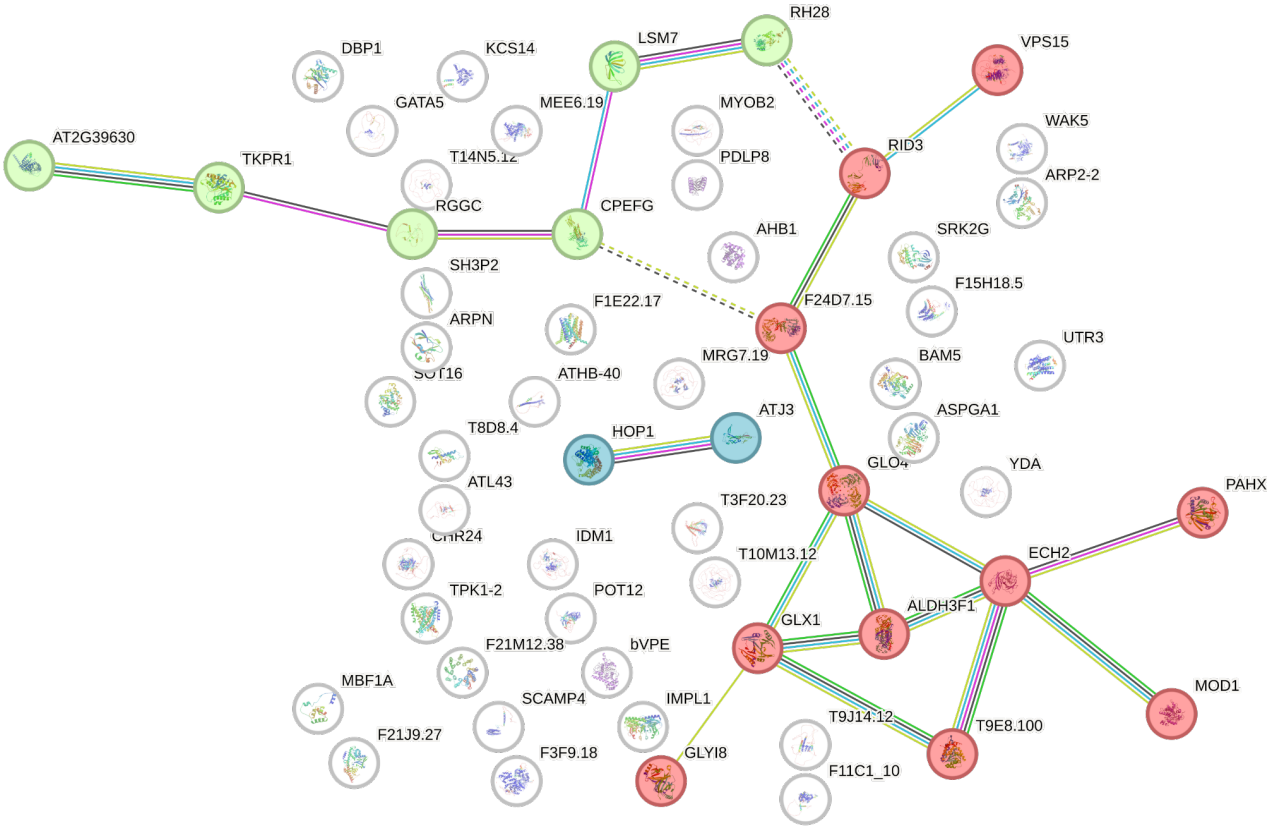

Fig. 4. Protein–protein interaction (PPI) network with k-means clustering for the identified selected barley orthologous genes for spike characters.
The network and clustering were obtained via the API access to the STRING database (https://string-db.org) and based on the *Arabidopsis thaliana* protein database. Each colored group represents a separate protein cluster. Colored lines represent various types of evidence supporting protein–protein interactions: curated databases (light blue), experimental data (purple), gene neighborhood (green), gene co-occurrence (blue), text mining (yellow), co-expression (black), and protein homology (lavender)

Рис. 4. Сеть белок-белковых взаимодействий (PPI) с кластеризацией методом k-средних для выделенных генов-ортологов ячменя по колосовым признакам. Сеть и кластеризация получены через API-доступ к базе данных STRING (https://string-db.org) и выполнены на основе базы данных белков *Arabidopsis thaliana*. Каждая цветная группа представляет собой отдельный белковый кластер. Линии представляют различные типы белок-белковых взаимодействий: проверенные базы данных (голубой), экспериментальные данные (фиолетовый), соседство генов (зеленый), совместное проявление генов (синий), анализ текста (желтый), коэкспрессия (черный) и гомология белков (лавандовый)

Thus, SNPs linked to barley orthologous genes from the identified clusters were selected (Table 3). Based on the obtained results, 19 SNPs associated with barley spike characters may be proposed as promising markers. The selected markers can be considered in further works to establish close relationships between quantitative traits associated with the row number type and contribution to barley yield.

Discussion

The barley germplasm collection held by the N.I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR) is the main source of new material for breeding programs aimed at developing competitive cultivars in Russia. The collection contains over 18,000 accessions of diverse origin and preserves rare genetic material collected in the early 20th century. The current study analyzed a set of 199 spring barley accessions from the VIR collection, which included 192 naked barley accessions of varying breeding levels, from local landraces to modern cultivars. The barley germplasm from the VIR collection, including naked barley accessions, had not previously been analyzed in similar studies. The valuable genetic material of the collection, studied using modern methods of genetics and bioinformatics, can provide new information about quantitative plant characters, new loci and genes associated with productivity and other valuable traits.

GWAS and PPI data were used to map the identified loci onto the barley chromosomes and then compared with the known locations of the *Vrs* and *Nud* genes (Fig. 5).

The *Vrs1* gene (*HvHOX1*, HORVU.MOREX.r3.2HG0184740) is a key gene in controlling the fertility of lateral spikelets (Komatsuda et al., 2007). It has a physical location of 570,802,392–570,803,252 bp on chromosome 2H, and is located in the interval 79.89–80.59 cM (https://plants.ensembl.org/index.html). A total of 19 markers were found in this interval. The largest number of SNPs was identified for the SN indicator (18), and one marker (BOPA2_12_30897) was located inside the *Vrs1* gene. The most common markers in this genomic region significant during the three years of research were: JHI-Hv50k-2016-107351, JHI-Hv50k-2016-

Table 3. **Significant barley markers of spike characters and associated proteins identified by the gene interaction analysis via the STRING database**

Таблица 3. **Значимые маркеры ячменя по колосовым признакам и связанные с ними белки, выделенные с помощью анализа взаимодействия продуктов генов через базу данных STRING**

Marker	Chromosome	Physical position, bp	Barley gene ID	*Arabidopsis* gene ID	Protein name
First cluster					
JHI-Hv50k-2016-107664	2	570497279	123430587	817390	GLYI8 (Lactoylglutathione lyase)
JHI-Hv50k-2016-107988	2	572436828	123427382	829782	ALDH3F1 (Aldehyde dehydrogenase family 3 member F1-like)
JHI-Hv50k-2016-86874	2	97903463	123425301	820630	GLO4 (Peroxisomal (S)-2-hydroxy-acid oxidase GLO4-like)
JHI-Hv50k-2016-231066	4	16052716	123447407	814677	PAHX (Phytanoyl- CoA dioxygenase 1)
JHI-Hv50k-2016-324502	5	508498490	123451775	843947	ECH2 (Enoyl-CoA hydratase 2, peroxisomal)
JHI-Hv50k-2016-377672	6	17106768	123401149	842670	F24D7.15 (GMP synthase (Glutamine-hydrolyzing)
JHI-Hv50k-2016-423251	6	540636728	123405962	829059	VPS15 (Serine/threonine-protein kinase VPS15)
JHI-Hv50k-2016-489205	7	496072694	123407481	826967	T9E8.100 (3-hydroxyisobutyryl-CoA hydrolase-like protein 3, mitochondrial)
JHI-Hv50k-2016-489164	7	496428714	123407454	815152	MOD1 (Enoyl-[acyl-carrier-protein] reductase [NADH] 1, chloroplastic)
JHI-Hv50k-2016-489103	7	497110185	123407128	837731	GLX1 (Lactoylglutathione lyase)
JHI-Hv50k-2016-489359	7	497912876	123409101	824079	RID3 (Protein ROOT INITIATION DEFECTIVE 3)
Second cluster					
JHI-Hv50k-2016-56722	1	512898113	123452521	834767	RGGC (RGG repeats nuclear RNA binding protein A-like)
JHI-Hv50k-2016-107450	2	570235145	123427368	842573	CPEFG (Elongation factor G-2, chloroplastic)
SCRI_RS_150232	5	521852577	123452121	827364	RH28 (DEAD-box ATP-dependent RNA helicase 28)
JHI-Hv50k-2016-351825	5	563500362	123453046	818546	AT2G39630 (Dolichyl-phosphate beta-glucosyltransferase)
JHI-Hv50k-2016-362931	5	579992296	123395121	829695	TKPR1 (Phenylacetaldehyde reductase-like)
JHI-Hv50k-2016-489337	7	497788000	123410023	814913	LSM7 (Sm-like protein LSM7)
Third cluster					
JHI-Hv50k-2016-107461	2	570231148	123427367	837781	HOP1 (Hsp70-Hsp90 organizing protein-like)
JHI-Hv50k-2016-343289	5	542796018	123452599	823531	ATJ3 (Dnaj protein homolog)

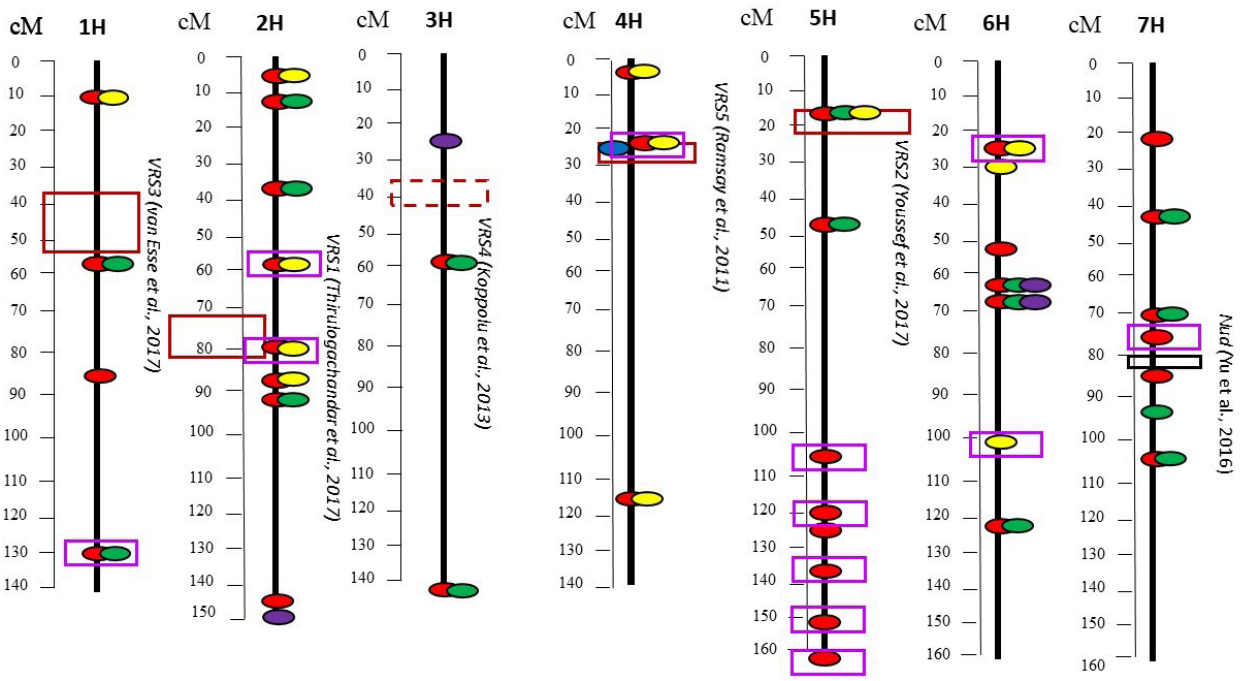

Fig. 5. The most promising genomic regions on barley chromosomes associated with spike characters.
Red rectangles indicate the location of the *Vrs* genes, black rectangles indicate the location of the *Nud* gene according to published data. Characters are marked with different colors: blue for SL, red for SN, green for GN, yellow for GW, and purple for TWG. Purple rectangles indicate significant markers identified by analyzing gene product interactions via the STRING database

Рис. 5. Наиболее перспективные геномные районы на хромосомах ячменя, связанные с колосовыми признаками.
Красными прямоугольниками показана локализация генов *Vrs,* черным прямоугольником – ген *Nud* по литературным данным. Разным цветом отмечены признаки: SL – синий, SN – красный, GN – зеленый, GW – желтый, TWG – фиолетовый. Фиолетовыми прямоугольниками отмечены значимые маркеры, выделенные с помощью анализа взаимодействия продуктов генов через базу данных STRING

07401, JHI-Hv50k-2016-107461, JHI-Hv50k-2016-107664, BOPA2_12_30897, JHI-Hv50k-2016-107729, SCRI_RS_196853, JHI-Hv50k-2016-107751, JHI-Hv50k-2016-107804, JHI-Hv50k-2016-107988, JHI-Hv50k-2016-108011, JHI-Hv50k-2016-108035, and JHI-Hv50k-2016-108079.

The *Vrs2* gene (NCBI: KX601696 to KX601720) is located on the 5H chromosome in the 19.0 cM interval; it encodes a homologue of the *Arabidopsis SHORT INTERNODES* gene, whose loss of function is associated with hormonal imbalance between auxin and cytokinin along the spike (Youssef et al., 2017). As a result of GWAS on the 5H barley chromosome, two repetitive genomic regions were found: 17.64 cM (JHI-Hv50k-2016-280992), and 47.42 cM (JHI-Hv50k-2016-302298). In addition, seven loci only for SN were identified on this chromosome.

The *Vrs3* gene encodes a putative Jumonji C (JMJC) type H3K9me2/me3 demethylase, whose loss of function is associated with increased fertility of lateral spikelets. It has been shown that *Vrs3* stimulates the expression of all other *Vrs* genes throughout spikelet development, and that the *Vrs3* function modulates networks related to sugar and hormone metabolism as well as stress signaling (Bull et al., 2017). *Vrs3* is located on chromosome 1H in the interval 376,489,422–380,295,554 bp (Bull et al., 2017); according to G. M. van Esse and colleagues (2017), the gene was identified in the interval 35.69 cM to 52.55 cM. In the present study, no markers were found in this region. Three genomic regions on chromosome 1H were identified for two characters at once: 10.38 cM (JHI-Hv50k-2016-8553), 59.42 cM (JHI-Hv50k-2016-34218), and 130.81 cM (JHI-Hv50k-2016-56722).

The *Vrs4* (HvRA2) locus is located on chromosome 3H and controls spike row number through *Vrs1* (*HvHox1*). Furthermore, *Vrs4* may also regulate transcripts of SISTER OF RAMOSA3 (*HvSRA*), a putative trehalose-6-phosphate phosphatase involved in trehalose-6-phosphate homeostasis, which is implicated in the spikelet determination control. *Vrs4* is thought to be located on the short arm of chromosome 3H in the interval 37.17–41.68 cM (Koppolu et al., 2013; Koppolu and Schnurbusch, 2019). However, in our study, no significant markers at this locus were found. For the SN and GN traits, two repetitive genomic regions of 59–60 cM (JHI-Hv50k-2016-186829, JHI-Hv50k-2016-187013) and 151–153.27 cM (JHI-Hv50k-2016-224200) were identified for SN and GN traits.

The *INT-C* gene (*Vrs5*, *HvTB1*, HORVU4Hr1G007040) is located on chromosome 4H and encodes a class II TCP transcription factor, whose homologues in maize, rice, wheat, and *Arabidopsis* suppress shoot bud growth, promoting apical dominance. The *INT-C* gene modifies lateral spikelet fertility in barley and can influence the phenotypic effect of *Vrs1*. The gene is presumably located in the genomic region of 26.19 cM (Ramsay et al., 2011). In the present study, we identified 12 significant markers associated with SL, located within the genomic region of 25.92–26.35 cM, which is comparable to

the localization of the *Vrs5* gene. In addition, another significant marker was located within the 24.07 cM locus (JHI-Hv50k-2016-230796), which was identified for SN and TWG together.

This study also identified genomic regions on chromosomes 6H and 7H, which were not associated with the known *Vrs* genes. Three genomic regions on chromosome 6H are promising: 24.58 cM (JHI-Hv50k-2016-377584), JHI-Hv50k-2016-377672), 63.46 cM (SCRI_RS_152841, JHI-Hv50k-2016-409100), and 121.68 cM (JHI-Hv50k-2016-432785); they were identified in different years of research and simultaneously for several spike characters. Three promising genomic regions, repeated over three years on chromosome 7H, were identified: 43.84 cM (JHI-Hv50k-2016-462405), 70.54 cM (JHI-Hv50k-2016-485943), and 104.82 cM (JHI-Hv50k-2016-498295). In addition, a genomic region of 76.29–76.98 cM was identified, which included 12 SNPs associated with SN.

Significant markers revealed by the PPI cluster analysis are plotted on barley chromosomes (see Fig. 5). It is shown that some of the markers are located in two loci associated with *Vrs* genes: on chromosome 2H in the interval 79.89–80.59 cM, and on chromosome 4H in the interval 25.92–26.35 cM. The remaining markers are distributed in genomic regions not associated with the genes for the row number (*Vrs*). The selected markers and loci are interesting for further studies of the spike architecture and quantitative traits contributing to yield.

Conclusion

The study of 199 spring barley accessions in 2021–2023 employed plant characters associated with yield: spike length, spikelet number per spike, grain number per spike, grain weight per spike, and thousand-grain weight. These indicators manifested wide variability, depending on the number of rows in a spike and the influence of the environment.

A genome-wide association study helped to locate markers, genomic regions, and protein interactions associated with important yield structure components. Using GWAS, 129 markers were identified for all characters: 12 for SL, 73 for SN, 19 for GN, 9 for GW, and 16 for TGW, located in genomic regions on all barley chromosomes.

Some of the identified markers were associated with the already known *Vrs* genes on the first five chromosomes. Other identified markers and individual genomic regions may prove promising for further studies of the spike architecture and quantitative traits contributing to yield.

Studying barley accessions of different breeding levels emphasizes the importance of preserving intact the gene pool of VIR's barley collection as a source of valuable genetic diversity for breeding and genetic research. The obtained data can be used to continue fundamental research into the mechanisms shaping yield-related quantitative traits. The theoretical findings can be helpful for the designing of DNA markers specifically for trait-targeted breeding.

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