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Marker breeding of white cabbage

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Abstract. Modern accelerated development of agricultural production actualizes the development of new technologies aimed at more economical and environmentally friendly production of high-quality products with specified quality and properties. In this regard, the method of molecular markers, which significantly increases the efficiency of breeding, is gaining wide popularity and demand. The technology of marker-assisted selection accelerates selection of the required characteristics of plants at early stages of their development until their manifestation in the adult state, increasing its efficiency regardless of the environment influence. This technology is widely applied to a huge range of crops, including white cabbage. This crop is cultivated over significant areas worldwide and is important due to its high demand and health benefits. Although a significant number of new varieties and hybrids of white cabbage with individual characteristics have been developed by breeders to date, the demand for increasing its yield is becoming increasingly high. Therefore, interest in molecular marker-assisted breeding is increasing and manipulation of agronomic and economically important traits of promising lines is becoming relevant. The lack of generalizations of material in this area is essential. Therefore, the aim of this work was to review the current state of the issue, to identify the main and most demanded directions of research in the field of marker technology in application to white cabbage and to draw attention to this currently relevant topic. Accordingly, we conducted a search and systematic review of available modern specialized literature and relevant recent scientific data over the last two decades on marker-mediated breeding of white cabbage. In the study, markers of biotic and abiotic stress as well as quality of white cabbage were analyzed. As

the collected information on markers shows, scientific research in these areas is prioritized but poorly covered in the literature. A very small proportion of promising KASP markers was observed, as well as insufficient research on the different ripeness groups of white cabbage varieties. The systematization of the available knowledge with emphasis on problem areas undertaken in this review may be important and useful for breeders and producers for their practical application in practice.

Keywords: molecular markers, *Brassica oleracea* L. convar. *capitata* L. *Alef. var. capitata* L. f. *alba* DC, genetic improvement, marker-assisted selection

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Introduction

A typical cross-pollinated cruciferous plant and an important vegetable crop, white cabbage (*Brassica oleracea* L. var. *capitata* L. *f. alba* DC) is one of the most cultivated and popular vegetables in the world [1] and has great economic importance as a valuable source of biologically active, healthy substances [2].

With the continuing growth of the population, reducing cultivated lands and intensification of agriculture, demand for increasing cabbage yield is becoming increasingly high. The production of white cabbage is negatively affected by both environmental factors and viral, bacterial and fungal pathogens that cause various diseases. Plant breeding continues to have a great influence on improvement of agricultural crops, including white cabbage and its yield. One of the approaches to offsetting the negative impact of various factors is the search for and use in breeding of the host plant Brassica's own resistance genes [3]. The discovery of such genes associated with various stresses and their mapping, as well as the development of markers, transcriptome analysis and knowledge in the field of regulation of physiological and biosynthetic mechanisms have ensured significant progress in white cabbage breeding [4]. A special contribution to breeding is made by the presence of the reference genome of white cabbage [5].

In genetics and plant breeding, genotyping and molecular selection with the detection of appropriate markers are increasingly used, i. e. a method in which the selection process is carried out on the basis of a marker, and not the trait. The use of molecular markers increases the probability of detecting the presence of a genotype combining advantageous alleles in a population [6—8]. Molecular or genetic DNA markers are nucleic acid sequences located near the target genes of

the desired traits. They are used to characterize the genome architecture and study gene polymorphisms [9], with the goal of increasing white cabbage yield and quality [10]. Selection using DNA markers can help in finding sources and donors of genetic resistance to diseases or stressful conditions of cabbage cultivation [11, 12]. The use of these methods allows us to significantly speed up the selection process and reduce the costs. The advantages of DNA marker selection include a rare dependence on environmental conditions, as well as the fact that it can be carried out at early stages of development in many variants, testing several traits simultaneously in one sample [11, 13]. There is a significant pool of different types of molecular genetic markers that permit to assess genetic diversity of DNA. This is the basis for all subsequent theoretical and applied research [14]. Selection based on specific markers associated with economically valuable traits ensures direct genotypic selection and efficient use of genes for growing new varieties of white cabbage with new useful properties [15]. Simple sequence repeats (SSR), insertion-deletion markers (InDel) and kompetitive allele-specific PCR (KASP) are used as molecular markers. Single nucleotide polymorphisms, SNP markers, have many advantages: high prevalence in the genome, low mutation rate, dimorphism, high stability and the possibility of automated analysis with high throughput. KASP assays provide flexibility in terms of the number of SNPs used for genotyping. The accuracy of KASP assays is high and the cost is low. The cost of one SNP decreases with their number. This feature gives an advantage to KASP analysis over other SNP genotyping [16].

The goal of the research was to identify, evaluate and summarize the results of studies on available molecular markers, and to clarify the main directions of development of marker selection of white cabbage for its improvement.

Markers of cabbage quality and abiotic stress

Low temperatures significantly affect plant growth and development, reducing crop productivity [17—21]. Low temperature tolerance or cold stress in plants is considered to occur under chilling (< 20 °C) and freezing (< 0 °C) [22]. Winter survival is an important trait in Brassica, especially in cabbage grown in northern climates, which is also affected by genetic variations for other cold-regulated traits such as frost tolerance, vernalization, ripening time, and leaf characteristics [23].

Based on the characterized allelic variations in *CSDPs* gene, a molecular marker was developed to detect low temperature tolerance in cabbage (*Brassica oleracea* var. *capitata*) [24]. Plant *CSDPs* have additional glycine-rich regions interspersed with CCHC zinc fingers (ZCCHC) in the C-terminal portion [25]. The function of these CCHC domains in cold tolerance is not yet clear. Cold-tolerant inbred lines contained a variant type *BoCSDP5v*, which encodes an additional CCHC zinc finger domain at the C-terminus and is associated with cold tolerance. Allelic variation in the *BoCSDP5* gene produces different proteins with different numbers of CCHC zinc finger domains. A cold tolerance marker generated from polymorphism between

BoCSDP5 and *BoCSDP5v* was validated on accessions used in the previous validation of the *B. oleracea* CIRCADIAN CLOCK ASSOCIATED 1 (*BoCCA1*) marker. For reliable identification of cold-tolerant cabbage, it is necessary to use two markers simultaneously (*BoCCA1*; *BoCSDP5v*) [24].

Cabbage is a flowering plant sensitive to vernalization. *BoFLC2* is an important transcription factor that allows cabbage plants to remain in the vegetative phase in response to cold. It was first shown in the study by Li et al. [26] that *BoFLC2E* and *BoFLC2L*, cloned from extremely early and extremely late flowering cabbage, respectively, exhibited 215 bp indel in intron I, three non-synonymous SNPs, and 3 bp indel in exon II [26]. *BoFLC2L* is associated with late flowering, which was confirmed using the indel-FLC2 marker. The 215 bp deletion in intron I of *BoFLC2*, without causing alternative splicing, slows down its suppressive activity (*BoFLC2L* silencing) due to feedback with the essential genes of the PHD-PRC2 complex, which leads to decrease in their transcription level and ultimately to late flowering of cabbage. Among the genetic variations of *BoFLC2*, the 215 bp deletion in intron I was the main cause of flowering delay. This study not only provides an effective molecular marker-based breeding strategy for identifying resistant and breeding improved cabbage varieties, but also opens the way to studying the mechanisms of flowering time in plants sensitive to vernalization [26].

Another research group discovered a polymorphic gene *BoFLC1.C9* (*Bo9gl73400*), proposed as a molecular marker [27]. A 67 bp insertion in the second intron of this gene *BoFLC1.C9* in an early flowering line caused a distinct mutation, disrupted the function of the gene and showed lower expression, causing early flowering. This «indel» confirmed by the insertion-based marker F7R7 allows characterization of different flowering times in cabbage lines. The variability in flowering time in this case reaches 83 % for F2 individuals and 80 % for commercial lines. The F7R7 marker is useful in breeding for selection of cabbage varieties with different flowering times before cultivation [23].

In higher plants, cuticular wax deposited on the surface of epidermal cells plays an important role in resistance to biotic and abiotic stresses [28]. To protect against ultraviolet radiation, phytopathogens and insects [29, 30], plants secrete wax on cuticle surface, which affects the reduction of extrastomatal evaporation and prevents contaminants from reaching the plant surface [31, 32]. Cuticular waxes also have other functions: they affect the morphological development and pigmentation of leaves and fruits, reduce fruit cracking, etc. [33, 34]. Some genes associated with the biosynthesis of cuticular wax have been identified in many cruciferous crops, including *Brassica oleracea* [35]. However, the molecular mechanism regulating the biosynthesis and secretion of cuticular wax in cruciferous crops and *B. oleracea* remains poorly understood.

Numerous genes related to wax biosynthesis have been characterized in glossy green mutants of cabbage. The glossy trait is controlled by a single recessive gene *Cgl1* located at the end of chromosome C08 [36]. Several new markers closely related to the target gene have been developed according to the reference sequence of the cabbage genome. Based on the insertion (2722 bp), a molecular marker ISP1

was developed that could distinguish the glossy mutant 10Q-961 from other cabbage species [35]. Probably, the gene *Bol018504* with insertion in the first intron (homolog of *Arabidopsis thaliana* CER1 [35]) is *Cgl1*. Accordingly, PLN02869 domain controlling the fatty aldehyde decarbonylase activity was missing in the *Bol018504* gene of the glossy mutant 10Q-961, resulting in the glossy cabbage mutant. This study may facilitate the development of new cabbage cultivars exhibiting the glossy green phenotype.

A large number of genetic analyses have shown that most wax deficiency mutations in cabbage are controlled by a single, relatively conserved recessive gene [35, 37, 38] in cruciferous plants. A candidate gene, *Bol026949*, controlling the glossy green trait was identified on chromosome 5 [28]. It belongs to the Agenet/Tudor family of domain proteins, whose members are thought to be involved in chromatin remodeling and RNA transcription. Sequence analysis revealed that a single nucleotide polymorphism mutation (C→G) in the second exon of *Bol026949* results in a premature stop codon formation, which may lead to premature termination of its protein translation at 98—1030gl. *Bol026949* may participate in cuticular wax production by regulating transcript levels of genes involved in post-translational cellular process and phytohormone signaling. According to the authors' suggestion, *Bol026949* may participate in cuticular wax production by modulating transcript levels of some key post-translational regulators of the phytohormone signaling pathway rather than by directly affecting the expression of genes involved in cuticular wax biosynthesis [28].

Liu et al. reported dominant inheritance of *BoGL1* gene controlling the glossy green trait in a wax-deficient mutant of cabbage [39]. The dominant glossy mutation results in cuticular wax deficiency in the CGL-3 mutant of cabbage [40]. Identification of candidate genes for the glossy green trait in model plants showed that the candidate genes responsible for wax deficiency are predominantly some critical genes involved in wax biosynthesis, transport and regulation [41].

Head splitting resistance (HSR) of cabbage is an important trait closely related to both quality and overall yield. This trait has complex genetic mechanisms, and its genetic control remains unclear. An attempt was made to analyze the inheritance and detect quantitative trait loci (QTL) for HSR using mixed inheritance analysis of major genes and polygenes and QTL mapping with simple sequence repeat (SSR) and insertion-deletion (InDel) markers [42]. The results of QTL mapping and classical genetic analysis were consistent. The identified nine QTL (Chr. C3, C4, C7 and C9) explained 39.4 to 59.1 % of the phenotypic variations. Three major QTL (Hsr 3.2, 4.2, 9.2) demonstrated a relatively greater effect than the others [42]. Another six QTL loci on chromosomes 2, 4, 6 are responsible for resistance to head splitting in cabbage. In this case, markers BRPGM0676 and BRMS137 showed a strong association with cabbage HSR, and conservatism was noted in the QTL SPL-2—1 region. The obtained QTL are useful for molecular marker-assisted selection of resistant plants at the seedling stage [43]. This characteristic allows determining the efficiency of genotypes in terms of ripening rate and yield [44].

Biotic stress markers

Various pathogens, such as Fusarium wilt, black rot, Sclerotinia stem rot, black leg, white rust, downy mildew, white leaf spot, turnip mosaic virus, etc., can infect *Brassica* crops [3, 45]. Developing cultivars resistant to major bacterial, fungal, viral, and other parasitic diseases is considered to be the most viable and environmentally sustainable approach to disease control [44]. Identifying and cultivating disease-resistant cultivars can provide a highly effective and environmentally friendly way to control plant pathogens without the need for chemical treatment [46]. The presence of resistance genes in plants, particularly *Brassica* cultivars, provides protection against pathogens [47, 48]. In this case, proteins [49, 52, 53] encoded by resistance genes with a nucleotide-binding site and enriched in leucine repeats [49—51] play an important role in protecting cabbage. This makes it possible to develop a DNA marker of disease resistance [3, 54, 55]. Based on three susceptibility alleles of *B. oleracea* (focbo1—1,2,3), sets of DNA markers have been developed [1, 56]. In *B. oleracea*, only one major CR locus (Rcr7) and about 50 QTL associated with clubroot disease caused by *Plasmodiophora brassicae* have been detected [54, 57], including twenty-three QTL detected using the single nucleotide polymorphism (SNP) microarray method [58]. The resistance gene *Rcr7* is probably located on chromosome 7 (LG 7) in two cabbage cultivars Tekila and Kilaherb [57]. The presence of several CR loci in cabbage indicates that clubroot resistance in *B. oleracea* is controlled polygenically, confirming the complex genetic organization of the trait, when one locus is not enough for this [59]. Comparison of the detected QTL is currently impossible due to the lack of common molecular markers [54] and the use of different sources of clubroot and the pathogen [60].

In one of the studies, several cultivars carrying resistance to two recently emerged pathotypes of *P. brassicae*, F3—14 (3A) and F-359—13, were identified [61]. Association analysis using SNP QTL markers allowed us to identify genomic QTL regions associated with resistance to *P. brassicae* [61]. The QTL markers identified in this study can be used in molecular breeding of *Brassica* crops for resistance to this pathogen. In most QTL regions, only a limited number of SNP markers have been identified, and fine mapping is still required to identify additional markers in these genomic regions [61].

Cabbage Fusarium wilt (CFW) resistance genes have been isolated from *Brassica* vegetables and are used in marker-assisted breeding programs in cabbage [62]. The pathogen is *Fusarium oxysporum* f. sp. *conglutinans*. [63] and Lv et al. [64, 65] developed two InDel markers for the CFW resistance gene [64]. The genotypes can be easily identified by polyacrylamide gel electrophoresis [66]. One dominant candidate gene, the R gene *Bol037156* for *FOC1* in cabbage, confers resistance to the fungal pathogen in *B. oleracea* with a toll-interleukin-1 receptor nucleotide binding site-like leucine-rich repeat (TIR-NBS-LRR) [65]. In contrast, two types of InDel (1 bp insertion and 10 bp deletion) were found among the susceptible lines, each causing a frameshift and a termination mutation in the cDNA sequences. To improve resistance to CFW by marker-assisted selection (MAS), DNA markers associated with the disease resistance allele were successfully used, which contributed to the elucidation of the molecular mechanisms regulating this trait and accelerated the breeding of new cabbage varieties

resistant to the disease [54]. Improvement of elite lines was achieved by transferring CFW into plants. This procedure involves the combined use of microspore culture, complete genomic background analysis and the selection of a marker specific for CFW resistance [62]. To ensure resistance of cabbage to Fusarium wilt, a number of molecular markers have been developed and successfully applied in cabbage breeding, such as the SSR marker Frg13 [62, 64], the *Rfo* marker BnRFO [67, 68]. The CFW-specific marker Frg13 can be useful for accurate and rapid identification of this trait in cabbage material and in developing an effective method for improving elite cabbage lines.

Breeders are trying to develop lines that are resistant to different diseases at the same time, using DNA markers, which will overcome the problem of simultaneous infection with several pathogens. An association was found between the allele of resistance to Fusarium wilt and tuber rot based on DNA markers, and lines resistant to both diseases were developed [1].

The Fusarium wilt resistance gene (*FocBr1*, Chr.A03) is located in the region of CR genes (*CRa*/*CRb*, *Rcr1*, *Crr3* and *CRk*) [54]. Recombination of the two genes [69] allows accumulation of alleles resistant to Fusarium wilt and tuber rot. *FocBo1* of *B. oleracea* (Chr. C06) is located near the tuber rot QTL, but is weakly linked to it [59, 63, 70, 71]. Linkage between dissimilar resistance loci may allow inheritance of resistance genes to both Fusarium wilt and tuber rot, which may lead to the creation of varieties resistant to both diseases [72].

Pathogen *Xanthomonas campestris* pv. *campestris* (Xcc) causes a disease of *Brassica* vegetables called black rot [73, 74]. Although little is known about the NBS-encoding R genes in cabbage cultivars, the exon-intron structure and sequence variants (SNPs and indels) in these NBS-encoding genes in resistant and susceptible cabbage lines to Xcc infection have been previously reported [75]. Nine NBS-encoding R genes that may be involved in resistance to black rot disease in cabbage were identified based on the gene expression profiles in resistant and susceptible lines. These candidate genes provide an important resource for the functional characterization and genetic improvement of black rot resistance in cabbage [75]. Thus, the molecular marker InDel BR6-InDel was developed to assess the relationship between the *Bol031422* variations and those associated with resistance to races Xcc 6 and 7. The candidate gene R *Bol031422* on chromosome C08 consisted of one exon with a 3 bp insertion/deletion (InDels), a 292 bp polymorphism (insertion in the exon of the resistant line in relation to the susceptible line) and several single nucleotide polymorphisms (SNPs). This developed marker can be used by breeders to create cabbage varieties resistant to black rot races Xcc 6 and 7 [74].

Conclusion

The main objective of cabbage breeding is to create competitive new and improve existing varieties with increased, stable productivity, rapid maturation, uniformity and improved consumer quality (taste, appearance, adequate size, shape and density

of heads, high nutrient content and a certain chemical composition, storage ability). At the same time, quality traits are of relatively high importance in white cabbage breeding, which should also include the development of biotically and abiotically resistant varieties/hybrids in changing climatic conditions.

A review of the published literature on markers of economically valuable traits showed that most of the studies are devoted to resistance to pathogens, morphological indicators and head splitting. It is especially important to highlight the great importance of breeding new lines and varieties that are resistant to different diseases at the same time, which will not only overcome the problem of multiple infections, but will also help reduce the impact of pesticide residues on food products and the environment. The literature contains numerous studies of genes involved in cold adaptation of white cabbage, which is associated with its wide distribution in various climatic zones. Associations of molecular markers with the feature of the time of transition to flowering have also been identified. At the same time, the share of markers for genetic identification of cabbage varieties of different maturity groups turned out to be very insignificant, although selection for the presence of variations in early, middle and late cabbage varieties for maximum use of the available vegetation period and sowing areas is in great demand. Therefore, the creation of varieties, hybrids and lines resistant to biotic and abiotic stresses, rich in nutraceuticals, with the potential to obtain a stable yield uniform in maturity and features is a priority goal of cabbage breeding. It should be considered that obtaining cabbage with increased productivity, nutritional value and improved quality from the point of view of consumer demand is a serious task for breeders.

Among the variety of markers used in the selection of white cabbage identified in the literature, there was only a relatively insignificant presence of KASP markers, which have high potential and have recently become increasingly important due to their rapidity and cost-effectiveness. Therefore, it is extremely important to fully utilize the capabilities of modern biotechnological methods for improving the genetic traits of white cabbage, among which the use of molecular markers is a useful resource for increasing the efficiency of selection. This opens opportunities for accelerating breeding practice using markers in background selection. This approach will facilitate the creation of completely new high-yielding varieties, characterized by increased and complex resistance to diseases and unfavorable cultivation factors, capable of ripening large heads of cabbage with excellent consumer and technological quality. We expect that efforts will also be made to breed new varieties of cabbage not only for their culinary properties or better adaptability to growing and management conditions, but also for therapeutic purposes. New tasks in cabbage breeding will encourage the integration of the latest innovations in biology and genetics to improve the yield.

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Маркерная селекция капусты белокочанной

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Аннотация. Современное ускоренное развитие сельскохозяйственного производства актуализирует развитие новых технологий, направленных на более экономичное и экологичное получение высококачественной продукции с заданным качеством и свойствами. Приобретает популярность и востребованность метод молекулярных маркеров, значительно повышающий эффективность селекции. Технология маркерной селекции дает возможность ускорить отбор требуемых характеристик растений на ранних стадиях их развития до момента их проявления во взрослом состоянии, повышая эффективность отбора вне зависимости от влияния окружающей среды. Эта технология применяется к широкому спектру сельскохозяйственных культур, включая капусту белокочанную, возделываемую на значительных площадях во всем мире в связи с высокой востребованностью и пользой для здоровья. Несмотря на то, что селекционерами создано значительное число новых сортов и гибридов капусты белокочанной с индивидуальными особенностями, спрос на увеличение ее урожайности с единицы площади становится все более высоким. Возрастает интерес к молекулярной маркерной селекции и становятся актуальными манипулирования агрономическими и экономически важными признаками перспективных линий, но отсутствует обобщение полученного исследовательского материала. Проведен поиск доступной современной специализированной литературы и актуальных научных данных за последнее двадцатилетие и выполнен систематический обзор современного состояния, выявлены главные и наиболее востребованные направления исследований в области маркерной технологии — маркеропосредованной селекции капусты белокочанной. Проанализированы маркеры биотического и абиотического стресса, а также качества капусты белокочанной. Подтверждена приоритетность направления исследований и слабая освещенность в литературе. Отмечена очень малая доля перспективных KASP маркеров, а также недостаточная изученность различных групп

спелости сортов капусты белокочанной. Предпринятая систематизация имеющихся знаний с акцентом на проблемные направления может быть полезна для селекционеров и производственников.

Ключевые слова: молекулярные маркеры, *Brassica oleracea L*. convar. *capitata* L. Alef. var. *capitata* L. f. *alba* DC, генетическое улучшение, маркеропосредованная селекция

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