

Review

The Current Status and Prospects of Molecular Marker Applications in Head Cabbage (*Brassica oleracea* var. *capitata* L.): A Review

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Abstract

Modern head cabbage (*Brassica oleracea* var. *capitata* L.) breeding is based on the application of molecular markers through marker-assisted selection (MAS). In hybrid breeding, critical markers are deployed to assess cytoplasmic male sterility (CAPS and SSR for *orf138*), genic male sterility (KASP markers for *Ms-cd1*, InDel for *ms3*, and *BoCYP704B1*), fertility restoration (InDel marker for *Rfo*), combining ability and genetic diversity (using SSR and KASP marker sets), and to ensure F₁ hybrid seed genetic purity (RAPD and SSR markers sets). Disease resistance, a well-developed category due to frequent monogenic control, includes markers for major pathogens, including those for Fusarium wilt (for *Foc-Bo1* gene), black rot (race 1–7 specific SSR and InDel markers), clubroot (Kamogawa, Anno, and Yuki isolates), and downy mildew (*BoDMR2* InDel marker). Markers have also been identified for key agronomic and morphological traits, such as those governing petal color (InDel markers for *BoCCD4*), leaf waxiness (*BoGL1*, *BoGL-3*, *Cgl1*, *Cgl2*, *BoWax1*, and *BoCER2*), and leaf color (*ygl-1*, *BoMYB2*, *BoMYBL2-1*). The review also included markers for resistance to abiotically induced negative physiological processes, such as head splitting (QTL SPL-2-1, *BoI016058*), bolting (resistance loci-associated SSR marker), prolonged flowering time (*BoFLC1,2* genes), and high- and low-temperature tolerance (*BoTPPI-2*, *BoCSDP5*, *BoCCA1*). Despite these advancements, the review highlights that the marker repertoire for cabbage remains limited compared with other *Brassicaceae* species, particularly for complex polygenic traits. This synthesis is a valuable resource for breeders and researchers, facilitating the development of superior head cabbage cultivars and hybrids.

Keywords: cabbage; *B. oleracea* var. *capitata*; genetic marker; hybrid breeding; resistance; morphology



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1. Introduction

White cabbage (*Brassica oleracea* var. *capitata* L.) was originally domesticated in the Mediterranean region approximately 3000–4000 years ago [1,2]. Head cabbage initially spread across Europe and subsequently achieved global distribution. Currently, head cabbage ranks as the third most extensively cultivated crop within the *Brassicaceae* family, surpassed only by rapeseed and mustard [3]. The primary cultivation regions are concentrated in Asia—notably China, India, South Korea, and Vietnam—where it is predominantly used for pickling, and in Eastern Europe—including Russia, Ukraine, and Poland—alongside the United States where it is used for fermentation (e.g., sauerkraut).

or, particularly in the U.S., for use in fresh preparations such as coleslaw [4–7]. These geographical areas also serve as the leading regions for cabbage breeding research.

The traditional breeding of head cabbage relies on crossing parent lines with desirable traits, followed by multiple generations of selfing and selection to develop improved cultivars [8]. Pedigree breeding for pure line development and recurrent selection to increase the frequency of favorable alleles are common methods [9]. Pure lines often serve as parents for hybridization, where crossing genetically diverse lines produces F₁ hybrids exhibiting heterosis (hybrid vigor) [10]. Historically, parental diversity has been assessed primarily through morphological and biochemical differences. Although foundational, these classical methods face limitations such as long breeding cycles and difficulty in selecting complex, polygenic traits.

The establishment of trait-marker methodologies has enabled the use of molecular markers to overcome these constraints. To facilitate the selection of desirable genotypes, marker-assisted selection (MAS) utilizes molecular markers linked to target genes [11]. MAS is routinely applied to introgress major disease resistance genes against pathogens such as black rot, Fusarium wilt, and clubroot in cabbage. MAS also aids in improving polygenic traits; QTL mapping has identified markers for cabbage yield, quality, and abiotic stress tolerance, allowing for effective gene pyramiding [12]. Although MAS has enhanced selection efficiency, it has limitations, including the need for extensive marker validation and the potential for linkage drag. It is also less effective for traits controlled by many minor-effect QTLs.

The continued advancement of marker-based selection has led to genomic selection (GS), which uses genome-wide markers and statistical models to predict the breeding value of individuals for complex traits [13]. GS has shown promise in cabbage breeding for traits such as drought tolerance, accelerating the breeding cycle, and improving selection accuracy [14]. Gene editing, epigenetic breeding, and speed breeding methods can be used to supplement selection approaches. Gene editing techniques, such as knocking out susceptibility genes, such as *BraA.FR.a*, confer resistance to pathogens, such as *F. oxysporum* [15]. Complementary approaches include synthetic biology and metabolic pathways to design novel genetic circuits and epigenetic breeding to modulate stress responses through DNA methylation and histone modifications [16]. Speed breeding, which uses controlled environments to reduce generation times, synergistically accelerates these methods, enabling the rapid development of cultivars [17].

Contemporary breeding programs for cabbage are directed toward developing cultivars possessing traits that are universal across brassicas, such as disease resistance, head quality, and improved storability and characteristics specific to headed cabbage, including particular head morphologies and enhanced resistance to head splitting [18–20]. The high genetic similarity among *B. oleracea* subspecies indicates that many traits, including leaf color, disease resistance, and abiotic stress resistance, share a common genetic architecture controlled by orthologous genes [21]. This has led to the widespread use of a comparative genetics approach, where conserved genetic determinants are identified in one subspecies to map less-studied loci in another subspecies [22]. However, this strategy is not universally applicable because mapping certain loci requires a detailed understanding of subspecies-specific genetics. The MADS-box gene family, which governs the morphological diversity of *B. oleracea*, encompasses crops with hypertrophic inflorescences (e.g., cauliflower and broccoli) and those that form vegetative heads (e.g., head cabbage) [23,24]. These genes encode a large family of transcription factors that are master regulators of plant development, controlling the transition to flowering, floral meristem identity, and organ specification. The expansion and allelic diversity of key MADS-box genes, such as *APETALA1* (*AP1*) and *CAULIFLOWER* (*CAL*), are primarily responsible for the distinct phenotypes in

B. oleracea. The development of the edible curd in cauliflower and broccoli, characterized by proliferating and arrested inflorescence meristems, is strongly associated with specific mutations and allelic variations in these genes, as outlined in established genetic models. Domestication has been selected for these allelic variants, shaping the modern phenotypes. Expression analyses confirm the high activity of these genes in curd tissues, underscoring their central role. Therefore, understanding the diversity of MADS-box genes and genes similar to them is crucial for elucidating the evolution and domestication of different *B. oleracea* morphotypes and provides a foundational genetic context for marker-assisted breeding strategies aimed at improving complex architectural traits [25].

The control of trait inheritance, particularly for monogenic traits, alongside genetic screening is greatly facilitated by the widespread application of various genetic markers. These tools became firmly integrated into breeding practice following the advent of MAS and have been actively employed in cabbage breeding since the late 1990s [26,27]. Despite significant progress in cabbage genetics, marker-assisted selection remains the most widely adopted and practically accessible tool for plant breeders.

In Eastern European countries, where varieties predominate, breeding strategies primarily use markers associated with specific agronomically valuable traits [28]. Conversely, in production systems dominated by F₁ hybrids, this standard marker set is supplemented by specialized markers for hybrid breeding, such as those used to assess combining ability and the status of genes conferring cytoplasmic male sterility (CMS) [29,30].

The most extensive category of genetic markers in cabbage includes those associated with genes conferring resistance to infectious diseases and those utilized for assessing genetic diversity. In contrast, markers for traits such as bolting resistance or head shape uniformity—which are presumably polygenic in nature—are considerably less prevalent [26,31–33].

The number of genetic markers developed for cabbage is lower than that of other *Brassicaceae* species, such as Chinese cabbage (*Brassica rapa* subsp. *pekinensis*), a staple in the traditional cuisine of densely populated Asian nations [34]. Furthermore, the genetic underpinnings of certain cabbage traits have not yet been sufficiently elucidated, primarily due to the polyploid nature of its genome [35,36]. Therefore, the repertoire of head cabbage genetic markers remains relatively limited. Consequently, a comprehensive review of the existing molecular markers for head cabbage is a viable undertaking that meets the needs of cabbage breeders and scientific investigators alike.

2. Markers for Hybrid Breeding

2.1. Marker for Male Sterility Maintain

The use of markers linked to genes that maintain or restore pollen male sterility is a key feature of MAS in hybrid breeding [37] (Table 1). As in other dioecious plants, cabbage has two primary forms of male sterility: cytoplasmic (CMS) and genic (GMS), with the latter categorized as either dominant (DGMS) or recessive (RGMS).

Three main CMS types have been described: Ogura (Ogu), introgressed from radish (*Raphanus raphanistrum* subsp. *sativus* L.) [38], Polima (Pol), derived from rapeseed (*B. napus* L.) [39], and Nigra (Nig), originating from wild mustard (*B. nigra*) [40]. The Pol and Nig CMS systems have limited practical applications. The Nig type is associated with pleiotropic effects on plant development, whereas the Pol type exhibits incomplete pollen sterility. These types are rarely used in breeding programs for head cabbage. In contrast, the Ogu CMS type is highly employed; for instance, it was used to develop the widely used Ogu CMS R3 parent line [41,42]. To identify the CMS type in head cabbage cultivars, particularly older accessions, Zhang et al. [43] and Li et al. [44] developed polymerase chain reaction (PCR) markers that discriminate Ogu and Pol CMS types.

The Ogu CMS type is controlled by the orf138 mitochondrial gene. Zhang et al. developed two CAPS markers, m92-143 MseI and m1-346 MseI, based on polymorphisms in MseI restriction sites between the Ogu CMS source lines Ogura CMSHY and CMSR₃ [45]. The same study reported that the SSR marker mtSSR2 can also be used to distinguish Ogu CMS using conventional PCR.

The fertility restorer gene *Rfo* has been identified for the widely used Ogu CMS. Because this gene is native to *R. sativus*, it has been introgressed into the genomes of *B. oleracea* via interspecific hybridization coupled with embryo rescue or genetic engineering [46,47]. Yu et al. developed a universal InDel marker for *B. oleracea*, BnRFO-AS2F/BnRFO-NEW-R, based on a multiple sequence alignment of the radish *Rfo* gene with homologous sequences in *B. oleracea* var. *capitata* and *B. rapa* [48]. This marker was subsequently used to track the introgression of the *Rfo* gene from rapeseed into Chinese kale, demonstrating 100% selection accuracy [49].

The dominant genic male sterility (DGMS) trait in cabbage is primarily controlled by the *Ms-cd1* gene (Bol035718, candidate gene). This gene was first identified in a spontaneous mutant of the spring cabbage line 79-399 in 1979 [50]. Currently, DGMS systems utilizing *Ms-cd1* are extensively employed in hybrid cabbage breeding [51]. Fang et al. proposed an efficient method for generating homozygous *Ms-cd1* lines, which involves the in vitro propagation of sterile, homozygous male plants (*Ms-cd1*/*Ms-cd1*) followed by natural pollination with a sister inbred line. Several molecular markers for *Ms-cd1* selection have been developed. One of the earliest markers was the RAPD marker OT11₉₀₀, which was located 7.8 cM from the gene [52]. This marker was later converted into more user-friendly ERPAR and SCAR markers [53]. Subsequently, the same research group developed a set of three AFLP markers (semi-dominant TC/CCT1; dominant AAT/CTG1 and ACC/CGT1) and three SCAR markers (semi-dominant S_{AAG/CCC1}; dominant S_{TC/CCT1} and S_{T11900}), mapping at distances of 13 cM, 14 cM, 20 cM, and 16 cM, 13 cM, 7.8 cM from *Ms-cd1*, respectively. These markers enabled the distinction between dominant homozygotes (*MsMs*), heterozygotes (*Msms*), and recessive homozygotes (*msms*) in a BC₃ population [54].

Further marker development reaches the co-dominant SSR marker, BoE332 (3.6 cM from *Ms-cd1*), reported by Chen et al. BoE332 showed 100% accuracy in field trials for pre-screening 56 test-cross populations. However, due to incomplete linkage, plants classified as sterile using this marker may be heterozygotes [55]. More recently, Han et al. developed two universal KASP markers, K6 and K13, based on SNP alleles within the *Ms/ms* locus for use across *Brassica oleracea* subspecies. The K6 marker demonstrated 100% selection accuracy, whereas K13 showed 72.2% accuracy and was ineffective in five DGMS lines of broccoli, kohlrabi, and Chinese kale (though it performed reliably in head cabbage). The K6 marker is also suitable for genotyping self-pollinated heterozygous plant progeny [56].

In contrast to DGMS, the genetic basis of recessive genic male sterility (RGMS) is less characterized. Among candidate genes, *ms3* (candidate gene *BoTPD1*) has been associated with a molecular marker. *BoTPD1* homologs are known to regulate anther cell fate determination during reproductive development. *BoTPD1* is highly transcribed in various tissues except roots, with the highest expression levels observed in anthers and floral buds. An intronic 182 bp insertion identified in 51S of *ms3*, disrupting the conserved motif at the 5' splicing site of the third intron. This disruption is predicted to result in a truncated transcript. Han et al. developed the InDel marker ms3-dec based on this 182 bp *ms3* gene insertion. This marker demonstrated 100% accuracy when genotyping 80 plants from a cross between the sterile line 51S and 130 cabbage inbred lines [57].

Ji et al. identified another RGMS gene, *BoCYP704B1*, in the 83121A spontaneous male-sterile mutant. The *BoCYP704B1* mutant allele harbor an LTR retrotransposon insertion that reduces gene transcriptional activity and disrupts sporopollenin and exine formation. Ji et al.

developed two molecular markers, RTMS-1 and RTMS-2, to function as a single genotyping system using the sequence polymorphism between the sterile mutant 83121A and its fertile maintainer line 83121B. Validation of the RTMS-1 marker on a testcross population of 526 individuals (derived from 83121A and 83121B) revealed a distinct size polymorphism. Amplification in male-fertile (MF) plants yielded a fragment of approximately 1.5 kb, while in male-sterile (MS) plants, the presence of the retrotransposon resulted in a larger ~7.0 kb fragment. However, RTMS-1 could not discriminate between homozygous and heterozygous male-fertile plants, a limitation attributable to PCR amplification bias. The dominant marker RTMS-2 was used to overcome this. RTMS-2 was detected in all testcross individuals but was absent in all wild-type lines when tested on 86 wild-type cabbage lines lacking the RGMS locus and 179 individuals from the testcross population, confirming that it specifically targets the mutant allele [58].

2.2. Evaluation of Combining Ability, Population Genetic Diversity and Phylogenetic Relationships

Two principal hypotheses account for heterosis: the dominance and overdominance hypotheses [59,60]. Although both provide partial explanations, the genetic basis and origin of heterosis remain complex and not fully elucidated. Generally, heterosis is more prominent in hybrids derived from genetically distant parents than in those from closely related parents. Classification of parental lines into heterotic groups based on genetic relationships is a standard practice. Inbred lines within the same heterotic group share three fundamental traits: high combining ability, close genetic relatedness, and similarity in major agronomic traits. The standard methodology for developing F₁ hybrids with maximum heterosis involves crossing parents from different heterotic groups [30,61].

Heterotic group classification is frequently applied in head cabbage breeding when crossing different cabbage cultivation groups or ecotypes (spring, autumn, and winter types). These groups typically exhibit distinct morphological differences, making genetic screening a valuable tool for planning heterotic hybrid combinations [62].

Dedicated marker sets are employed to evaluate genetic relatedness for individual cultivars and populations [63–66]. These same marker resources also facilitate phylogenetic studies within *Brassicaceae* [67–70]. The technical specifications and development approaches for population genetic marker sets align completely with those for fingerprinting sets. The crucial distinction lies in their legal frameworks, as fingerprinting sets for variety identification require standardization through national and international organizations [70–72]. Notwithstanding this legal aspect, numerous studies have recommended the simultaneous application of marker sets in genetic diversity assessment, combining ability evaluation, and fingerprinting [73–77].

A more fundamental differentiation in set development concerns the scale and composition of plant materials. For crosspollinate head cabbage, studies on genetic diversity and combining ability may use populations from limited parental combinations [78]. In contrast, fingerprinting must distinguish not only intravarietal variation—arising from genetic heterogeneity or environmental adaptation—but also substantial inter-cultivar differences [30,62,79]. Consequently, fingerprinting set development typically involves significantly more cultivars than other applications [74–76].

Cabbage screening sets primarily comprise SSR and SNP markers developed specifically for head cabbage or broadly applicable across *Brassica oleracea* subspecies. Universal systems include RAPD panels (62, 100 and 89 markers) developed by Margale et al. using 1100 accessions from France representing 24 cauliflower, 3 head cabbage, 21 Savoy cabbage, and 48 kale populations [80]. Notably, fingerprints generated with these sets showed clear concordance with morphological and phenological differentiation according to geographic origin.

Louarn et al. established another universal set of 11 SSR markers based on genome assemblies from 12 broccoli, 10 Brussels sprouts, 21 cabbage, 6 savoy cabbage, and 10 cauliflower accessions [67]. By amplifying up to 47 fragments, this set generated distinct fingerprints for all 59 accessions, with differentiation exceeding 50% allele state variation for most markers. Fingerprints were consistently clustered by botanical variety, although diversity levels remained comparable across varieties.

El-Esawi et al. developed a comparable 12-SSR set using 25 accessions: 2 fodder kale, 2 Brussels sprouts, 3 kale, 3 cauliflower, and 15 Irish head cabbage [81]. The head cabbage panel included common (2 units), cattle (4 units), and spring (5 units) cabbage types. The set amplified 45 fragments (50–276 bp, 2–5 bands per marker), successfully distinguishing *B. oleracea* via 4 species-specific amplicons from 3 markers. No subgroup-specific fragments were identified for the head cabbage types. Overall head cabbage differentiation used 8 SSR markers (heterozygosity 0.693), with minimal variation among subgroups—the ‘Roscommon’ cultivar (Cabbage group) showed the lowest differentiation (6 markers, heterozygosity 0.533).

Specific marker systems have been developed for the interspecific screening of *B. oleracea* subspecies and *B. napus*. Leroy et al. established one such set containing four ISSR markers using previously described *B. oleracea* types (one cultivar per type, excluding cauliflower) and one turnip cultivar. Of the 136 generated bands, 84 provided phylogenetic information, 25 fragments were conserved across all *Brassica* accessions and 27 fragments represented unique sequences [68].

Flannery et al. designed a set of nine SSR markers for chloroplast genome analysis across five *Brassicaceae* species (41 accessions), including head cabbage, with eight markers showing polymorphism. The number of amplified alleles per chloroplast locus varied between 5 and 11. These markers enable maternal lineage tracing, organelle haplotype characterization, and hybrid introgression detection. However, the lower mutation rate of chloroplast DNA compared with nuclear DNA results in reduced interspecific variation. Applying this set, Flannery et al. detected 28 haplotypes that distinguished 22 of 41 accessions, with no haplotype shared across species boundaries [69].

The development of universal marker systems peaked in the 2000s before the widespread use of NGS. Although largely replaced by customized sets, these universal tools are still useful for examining *Brassicaceae* phylogenetic relationships [81–83] and identifying interspecific introgression [84,85].

Contemporary research emphasizes specialized head cabbage sets, representing the focus of most recent publications. The first customized marker set for cabbage contained 24 RAPD primers selected by Koutita et al. through screening four Greek populations (18 plants each). Populations showed an average genetic similarity of 40%. The Jaccard similarity coefficients revealed 6–7 distinct clusters, with genetic grouping patterns matching morphological differentiation [63]. Faltusová et al. employed 30 AFLP primer combinations, yielding 1084 fragments, including 364 polymorphic fragments across 20 cabbage accessions. Accessions were separated into two primary clusters with geographic-based subgroups. Ten primer pairs uniquely identified all accessions and were deemed the most informative [86]. For genebank conservation planning, van Hintum et al. implemented a 100 AFLP marker system that produced 103 polymorphic bands. Genetic changes during standard regeneration matched the variation between closely related accessions. These alterations mainly stemmed from significant allele frequency shifts in limited fragments, whereas most fragments maintained stability. This study proposed that accessions showing comparable differentiation levels could be safely merged considering generational drift [87].

Shapturenko et al. introduced 15 EST-SSR markers directly associated with expressed sequences. Evaluation across 26 cultivars and inbred lines identified Bo20TR, BoDCTD4,

BoPC34, BoPLD1, BoCalc, and BoPC15 as the most polymorphic. Genotyping separated the collection into two clear groups sharing genetic kinship and typically geographic origin [88]. Li et al. implemented 20 SSR markers to categorize 63 winter cabbage inbred lines into seven heterotic groups incorporating genetic data and head morphology. Seventeen markers produced polymorphic bands (2–6 bands per primer, mean 2.8), generating 47 polymorphic bands across all lines [62]. Li et al. constructed a 442-KASP marker panel based on whole-genome resequencing of 50 inbred lines, classifying 244 ecotypically diverse lines into 18 haplogroups [89].

Addressing the significant heterogeneity of cabbage, some investigators adopt integrated methodologies. Saxena et al. concurrently applied 17 RAPD and 27 SSR markers to examine genetic diversity among seven *Xanthomonas campestris* pv. *campestris*-resistant cultivars. The combined system produced 157 bands (135 polymorphic), with Jaccard coefficients ranging from 0.21 to 0.77 (RAPD), 0.42–0.82 (SSR), and 0.43–0.89 (combined) [90].

Palmé et al. deployed an extensive 500-SNP array originally designed for *B. napus* to evaluate inter- and intra-cultivar diversity among 10 accessions, supplemented by 11 morphological traits. While cultivars demonstrated clear genetic separation, morphological distinctions remained limited. Although labor-intensive, the complete 500-marker system offers high resolution for extensive collections, including closely related accessions. For smaller-scale studies, 50 randomly selected markers provide comparable informativeness, whereas 100 markers better replicate full-set results. A minimal 10-marker set showed restricted utility but supported basic population structure analysis [91].

2.3. Markers for Genetic Purity Testing of F_1 Hybrid Seeds

A major obstacle in heterotic hybrid seed production is the occurrence of false hybrids. These arise when mechanisms such as sporophytic self-incompatibility and cytoplasmic male sterility break down under environmental influences, resulting in uncontrolled outcrossing [92]. The conventional method for confirming the genetic purity of seeds is the grow-out test (GOT) [93,94], which can be added with screening data obtained from specialized molecular marker sets [93,95,96].

One of the initial marker sets for seed purity testing, developed by Crockett et al., consisted of 36 RAPD markers. This set yielded 241 scorable amplification products, 54 (22%) of which were polymorphic. From this array, the authors selected two markers that were identified as the most suitable for assessing seed purity [97]. Latter Liu et al. proposed the use of a marker combination—two RAPD (NAURP2068 and NAURP2079), two ISSR (NAUISR1034 and NAUISR1062) and one SSR (NAUSSR1011)—that generated specific markers for both parental lines simultaneously in the hybrid. Screening of 228 F_1 hybrids with this combination identified 16 false hybrids, a finding that was consistent with the GOT results [98].

Employing a multi-marker approach, Ye et al. validated a total of 325 SSR, RAPD, ISSR, and SRAP markers, ultimately selecting a set of 7 markers (comprising three SSR, two SRAP, and two ISSRs) suitable for purity assessment. When this set was applied to 216 F_1 plants, the results from the molecular screening and GOT differed by a single plant, which was identified by the morphological evaluation [99]. Kawamura et al. developed a panel of 31 SSR markers and derived a core set of 17 markers spaced at large intervals across the genome. Evaluation of this core set on 35 F_1 plants showed that, on average, six SSR markers were sufficient to reliably distinguish between parental alleles [100].

2.4. Fingerprinting Markers Sets

For a new variety to be commercially released, it must fulfill the distinctness, uniformity, and stability (DUS) requirements to ensure differentiation from existing cultivars.

While the mandatory DUS testing protocol relies predominantly on morphological characterization, supplemented at times by isozyme and molecular marker analysis, international regulatory frameworks now authorize the implementation of genetic markers for the purposes of variety identification and seed certification [71,72]. Molecular profiling offers reduced labor requirements compared to conventional DUS evaluation, and unlike certain DUS traits with low heritability and high environmental sensitivity, properly validated marker systems maintain generational stability. Consequently, fingerprinting markers differ fundamentally from other molecular markers not only through their application in the final breeding stages but also through the essential requirement for neutrality—they must remain unlinked to agronomic traits to prevent varietal profile distortion during cultivation.

Early cabbage fingerprinting used 18 RAPD markers developed based on 16 Brazilian commercial cultivars. This system generated 195 amplification bands, with 105 polymorphic fragments (54%) ranging from 100 to 2500 bp and 90 monomorphic bands conserved across cultivars [101]. Technological advances enabled the development of a 50-KASP marker set by Li et al. using 59 cabbage inbred lines, achieving similarity coefficients from 0.43 (21-marker divergence) to 0.98 (single-marker difference) in varietal discrimination [102]. Jo J. et al. established parallel systems containing 24 and 10 SNP markers (conventional PCR-based) selected through genome-wide association analysis of 96 commercial cultivars. Both sets originated from an expanded 87-SNP panel suitable for fingerprinting development, with all systems capable of resolving 17 essential DUS traits [103].

Table 1. Markers for head cabbage hybrid breeding.

Target Trait	Gene	GenBank Gene ID	Chr	Gene Product	Marker Type	Marker(s) Name(s)	Marker Reference
Ogu and Pol CMS types identification	orf138 (Ogu CMS) orf222 (Pol CMS)	GQ464371.1 DQ872162.1	mitochondrial	Ogu CMS protein Pol CMS protein	PCR	PCR markers	[43,44]
Ogu CMS	<i>orf138</i>	GQ464371.1	mitochondrial	Ogu CMS protein	CAPS	m92-143 MseI, m1-346 MseI	[45]
					SSR	mtSSR2	[45]
Fertility restoration	<i>Rfo</i>	FJ455099.1	C09	restorer-of-fertility protein	InDel	BnRFO-AS2F/BnRFO-NEW-R	[49]
					RAPD	OT11900	[52]
					ERPAR, SCAR	Converted from OT11900	[53,54]
DGMS	<i>Ms-cd1</i>	OR523690.1	C07	MS-cd1 protein	AFLP	TC/CCT1, AAT/CTG1, ACC/CGT1	[54]
					SCAR	^S _{AAG/CCCL} , ^S _{TC/CCT1} , ^S _{T11900}	[54]
					SSR	BoE332	[55]
					KASP	K6, K13	[56]
RGMS	<i>ms3 (BoTPD1)</i>	XM_013729780.1	C05	TPD1 protein homolog 1	InDel	ms3-dec	[57]
RGMS	<i>BoCYP704B1</i>	KX980030.1	C06	CYP704B1 protein	InDel	RTMS-1, RTMS-2	[58]
Genetic diversity and phylogenetics (universal for <i>B. oleracea</i>)	-	-	-	-	RAPD	Panels of 62, 89 and 100 markers	[80]
					SSR	Set of 11 SSR markers	[67]
					SSR	Set of 12 SSR markers	[81]
Interspecific phylogenetics (<i>B. oleracea</i> vs. <i>B. napus</i>)	-	-	-	-	ISSR	Set of 4 ISSR markers	[68]

Table 1. Cont.

Target Trait	Gene	GenBank Gene ID	Chr	Gene Product	Marker Type	Marker(s) Name(s)	Marker Reference
Genetic diversity	-	-	-	-	RAPD	Set of 24 RAPD markers	[63]
					RAPD, SSR	Combined set of 17 RAPD and 27 SSR	[90]
					AFLP	Set of 10 AFLP markers	[86]
					AFLP	Set of 100 AFLP markers	[87]
					EST-SSR	Set of 15 EST-SSR markers	[88]
					SNP	Array of 500 SNP markers	[91]
Heterotic haplogrouping	-	-	-	-	SSR	Set of 20 SSR markers	[62]
					KASP	Panel of 442 KASP markers	[89]
					cpSSR	Set of 9 SSR markers	[69]
F ₁ hybrid seed genetic purity testing	-	-	-	-	RAPD	Set of 36 RAPD markers	[97]
					RAPD, ISSR, SSR	Combination of 2 RAPD, 2 ISSR and 1 SSR markers	[98]
					SSR, SRAP, ISSR	Combination of 2 SSR, 2 SRAP and 2 ISSR markers	[99]
					SSR	Set of 17 SSR markers	[100]
					RAPD	Set of 18 RAPD markers	[101]
Fingerprinting	-	-	-	-	KASP	Set of 50 KASP markers	[102]
					SNP	Sets of 10 and 24 SNP markers	[103]

3. Markers for Morphological Traits

3.1. Petal Color

Cabbage petal color ranges from white to, most commonly, yellow [104]. This variation has a dominant–recessive inheritance pattern, where the white phenotype is dominant over the yellow phenotype. The petal coloration is governed by the carotenoid content in the floral petals. Carotenoid biosynthesis and degradation is regulated by multiple genes, with the *cpc-1* locus (candidate gene *BoCCD4*) making the primary contribution to this trait in cabbage [104,105]. The *cpc-1* locus encodes carotenoid cleavage dioxygenase 4, an enzyme involved in carotenoid degradation that negatively regulates carotenoid content. Through the genotyping of a germplasm collection, Han F. et al. identified an InDel marker M4131 that shows polymorphism between plants with different flower colors and is applicable for MAS (Table 2). Subsequent work by the same research group revealed a polymorphism in the Bol035718D771 InDel marker among genotypes with varying flower colors and established that white petal color exhibited dominance over yellow [106].

Overall, the development of molecular markers for morphological traits used as marker traits in hybrid breeding remains limited. Conventional breeding practices use parents with contrasting phenotypes, producing heterozygous offspring with intermediate characteristics that eliminate the necessity for genetic screening [107]. Implementation of marker-assisted selection for these traits may only be justified in contexts requiring accelerated breeding, enabling pre-flowering screening of hybrid plants and early elimination of undesirable genotypes [108].

3.2. Cabbage Waxiness

Important morphological traits in cabbage include those without direct consumer value but which mitigate the impact of adverse environmental factors or help maintain the head's marketable quality [20]. A key trait in this category is the epicuticular wax

coating (glaucousness). These cuticular waxes, comprising a complex mixture of lipid compounds, form a hydrophobic layer on the aerial surfaces of plants [109]. This coating serves multiple protective functions: it reduces ultraviolet radiation penetration, acts as a primary barrier against pathogens and insects, minimizes non-stomatal water loss, and provides physical protection [110,111]. Furthermore, cuticular waxes influence various physiological processes, including the prevention of head cracking and affect the development and pigmentation of leaves and the head itself. They also play a role in fertility by influencing pollen development [112].

In the last decade, a specific breeding objective has been the development of brilliant green cabbage, which exhibits lustrous, wax-free green leaves [113–115]. Genetic analyses of glossy (wax-deficient) cabbage mutants indicate that this trait is typically monogenic, with different mutants harboring distinct recessive alleles. For example, in the glossy mutant 10Q-974gl, Liu et al. identified the *BoGL1* gene (candidate genes *Bol018503* and *Bol018504*) mapped to the end of chromosome C08. Screening with 100 SSR markers revealed nine that were polymorphic between the contrasting parents. Among these, the marker SSR08–76 (C08SSR76) was the closest to *BoGL1*, at a genetic distance of 0.2 cM, making it a potential tool for the marker-assisted selection of waxiness [114].

Prior to this work, Liu et al. mapped the *Cgl1* gene from the glossy mutant 10Q-961 to a 188.7 kb region at the terminus of chromosome C08. They identified *Bol018504* as the most probable candidate for *Cgl1*, a homolog of the *Arabidopsis CER1* gene involved in wax biosynthesis [116]. A characteristic 2722 bp InDel in the mutant allele enabled the development of an InDel marker, ISP1, which produces an ~3300 bp amplicon in the 10Q-961 mutant compared with a 600 bp fragment in wild-type plants. Additionally, the SSR marker LTSSR740, located 3.17 cM from *Cgl1*, was identified and shown to be polymorphic between the glossy and waxy lines [117]. Subsequently, Ji et al. discovered a separate 252 bp InDel that distinguished the mutant and wild-type *Cgl1* alleles. This discovery led to the development of the InDel marker DX-1, which demonstrated 100% accuracy when validated on a BC₁P₂ population of 424 plants. Upon electrophoresis, DX-1 yielded two bands (0.70 kb and 0.95 kb) in waxy (wild-type) individuals and a single band (0.95 kb) in glossy (mutant) individuals [118].

Further work by Dong et al. on the mutant CGL-3 led to the identification of the *BoGL-3* locus, with *Bol018504* again proposed as the candidate gene. However, no sequence variations in *Bol018504* were found between the CGL-3 mutant and the wild type (WT). The researchers developed a PCR marker, C08-98, located at 0.2 cM from *Bol018504*, which successfully genotyped 1088 F₂ plants from a CGL-3 × WT cross [113].

Another gene conferring the glossy phenotype, *Cgl2*, was identified by Liu et al. in the mutant LD10GL. This gene was mapped to a 170 kb region on chromosome C01, with *Bol013612* identified as the candidate gene. *Bol013612* is homologous to the *Arabidopsis CER4* gene, which encodes a fatty acyl-coenzyme A reductase essential for wax biosynthesis. Fine mapping placed *Cgl2* between the polymorphic markers C01SSR147 and C01SSR150 at genetic distances of 0.2 and 0.1 cM, respectively [119].

In a subsequent study, Liu et al. mapped the *BoWax1* gene from the mutant HUAYOU2, with *Bol013612* also emerging as the likely candidate. Two flanking SSR markers, C01gSSR148 and C01gSSR150, positioned 0.2 cM from *BoWax1*, exhibited polymorphism in a segregating F₂ population of 808 plants [120]. Ji et al. characterized another key gene, *BoCER2* (candidate gene *Bol1g039030*), a homolog of *Arabidopsis CER2* and rice *OsCER2*. A single nucleotide polymorphism (SNP) at position 1452 bp (A in the mutant allele wdtl28 vs. G in the WT) differentiates the alleles. This SNP was used to develop a KASP marker, CER2-KASP-1. The utility of this marker for breeding was validated on 200 wax-deficient F₂ individuals and 150 diverse glaucous cabbage lines [121].

3.3. Leaf Color

Leaf color serves as a marker trait for evaluating hybrid purity at the seedling stage [122,123] or functions as a commercial trait determining the nutritional value and consumer appeal [124,125]. This complex trait is governed by genes regulating the biosynthesis of chlorophyll, anthocyanins, and carotenoids [126,127]. Hybrid breeding uses two leaf color variants as marker traits: yellow-green (mutant) and green (wild type). The leaf phenotype is determined by the functionality of the nuclear gene *ygl-1*, which is hypothesized to participate in chlorophyll synthesis [128,129]. Plants homozygous for the recessive mutant *ygl-1* allele display a yellow-green leaf color. Liu et al., who identified the *ygl-1* gene, mapped it to chromosome C01, flanked by the InDel markers ID2 and M8. These markers were developed from the polymorphic InDel marker BCYM516 that differentiated the two trait variants. While BCYM516 requires optimization for routine application, it remains the sole reported marker for this trait [129].

In 2024, Zhang et al. identified the *BoYgl-2* locus (with *Bo3g001140* as the candidate gene) in the cabbage mutant 4036Y. This mutant exhibits significantly reduced chlorophyll content and abnormal chloroplast development during the early leaf stages. *BoYgl-2* encodes a novel nuclear-targeted P-type PPR protein that is absent in the 4036Y line. The mutant carries a 162 kb deletion at this locus, which the authors identified as the causal mutation underlying the observed phenotype. Furthermore, the DEL163 marker, designed to target an InDel outside the 162 kb deletion region, produced a specific amplification fragment unique to the 4036Y mutant, demonstrating its utility for marker-assisted selection [130].

Purple leaf color is increasingly preferred over conventional green as a commercial trait. Anthocyanin accumulation responsible for purple pigmentation is regulated by *BoMYB1*, *BoMYB2*, *BoDFR1*, *BoMYBL2-1*, and *BoMYBL2-2* [131]. Zhu et al. discovered one of cabbage's initial anthocyanin synthesis genes, *BoMYB2* (*BoPur*), and established its crucial role in trait determination. Homozygous *BoMYB2* plants exhibit extreme phenotypes: dark purple leaves in dominant homozygotes versus green leaves in recessive homozygotes. Heterozygotes show light purple heads with intense anthocyanin pigmentation in the leaf veins. The researchers also developed BoC06ID22, an InDel marker that effectively distinguished genotypes in an F₂ population of 83 plants [132].

Song et al. subsequently confirmed the significant role of *BoMYBL2-1* in anthocyanin accumulation. For allele differentiation, they designed three InDel marker pairs: (1) *BoMYBL2-1w* amplifying the coding sequence, (2) *BoMYBL2-1v* detecting the promoter-substituted variant, and (3) *BoMYBL2-1sub* targeting the replacement sequence of the entire gene. Each marker identifies the corresponding alleles in the purple cabbage. *BoMYBL2-1sub* demonstrated superior performance with distinct band sizes: 190 bp in green and approximately 2075 bp in purple cabbage. The remaining markers amplified both common bands in purple/white cabbages and unique bands in specific purple-headed cultivars [131]. Molecular marker development for leaf color remains limited due to its visually detectable nature and inherent role as a phenotypic marker. In hybrid breeding, leaf color trails petal color as a marker trait.

Table 2. Markers for head cabbage morphological traits.

Target Trait	Gene	GenBank Gene ID	Chr	Gene Product	Marker Type	Marker(s) Name(s)	Marker Reference
Petal color	<i>BoCCD4</i>	MK599258.1	C03	carotenoid cleavage dioxygenase 4	InDel	Bol035718D771	[105]
					InDel	M4131	[106]
Glossy/wax leaf	<i>BoGL1</i>	HQ162471.1	C08	R2-R3 MYB transcription factor	SSR	SSRC08-76 (C08SSR76)	[114]

Table 2. Cont.

Target Trait	Gene	GenBank Gene ID	Chr	Gene Product	Marker Type	Marker(s) Name(s)	Marker Reference
Glossy/wax leaf	<i>Cgl1</i>	-	C08	CER1 like protein	InDel	ISP1	[117]
					InDel	DX-1	[118]
					SSR	LTSSR740	[117]
Glossy/wax leaf	<i>BoGL-3</i>	-	C08	CER1 like protein	PCR	C08-98	[113]
Glossy/wax leaf	<i>Cgl2</i>	-	C01	CER4 like protein	SSR	C01SSR147, C01SSR150	[119]
Glossy/wax leaf	<i>BoWax1</i>	-	C01	-	SSR	C01gSSR148, C01gSSR150	[120]
Glossy/wax leaf	<i>BoCER2</i>	-	C01	CER2 like protein	KASP	CER2-KASP-1	[121]
Yellow-green leaf color	<i>ygl-1</i>	-	C01	-	InDel	BCYM516	[129]
Purple leaf color	<i>BoMYBL2-1</i>	-	C03	P-type PPR protein	InDel	BoMYBL2-1w, BoMYBL2-1v, BoMYBL2-1sub	[130]
Purple leaf color	<i>BoMYB2 (BoPur)</i>	-	C02, C06	MYBL2 like protein	InDel	BoC06ID22	[131]

4. Markers for Resistance to Abiotic Factors

4.1. Resistance to Head Splitting

Head splitting, or cracking, is a significant preharvest physiological disorder in cabbage. Its occurrence is primarily triggered by environmental conditions such as pre-harvest rainfall, sudden rises in soil moisture, pronounced diurnal variations in humidity and temperature, and light exposure [133]. This disorder is highly detrimental, negatively impacting crop yield, marketable appearance, quality, and postharvest storability [134]. Head splitting resistance (HSR) is considered to be controlled by multiple genes whose effects are primarily additive with partial dominance [135,136]. The current understanding of the genetic basis of this resistance is confined to quantitative trait loci (QTLs), with the reported number varying among different studies [137].

In an early study, Pang et al. mapped six QTLs for head splitting resistance using an F₂ population of 188 individuals from a cross between inbred lines 747 and 748. Two QTLs, SPL-2-1 (chromosome C02) and SPL-4-1 (C04), were stably identified over two growing seasons, accounting for 6.05–6.16% and 4.93–5.46% of the phenotypic variance, respectively. Four other QTL were detected in a single season: SPL-2-2 on chromosome C02, SPL-6-1, SPL-6-2 and SPL-6-3, all on chromosome C06. For the major-effect QTL SPL-2-1, the authors identified two tightly linked SSR markers, BRMS137 and BRPGM0676, which showed clear segregation when tested on 40 resistant and 40 susceptible plants [137] (Table 3).

In a double haploid (DH) population, Su et al. identified nine HSR QTLs, three of which were characterized as major (Hsr3.2 on C3, Hsr4.2 on C4, and Hsr9.2 on C9) [138]. Using bulked segregant analysis (BSA), Pang et al. detected six HSR-associated QTLs, identifying two major QTLs (SPL-2-1 and SPL-4-1). Within the major QTL SPL-2-1, they identified the SSR markers BRPGM0676 and BRMS137, which showed complete co-segregation with the resistance trait in 80 randomly selected plants from the segregating F₂ and F_{2:3} populations, achieving 100% accuracy [137].

A more recent study by Zhu et al. analyzed an F₂ population from a cross between a susceptible (G274) and a resistant (G279) parent, pinpointing a QTL on chromosome 3 (45.8–51.4 Mb). Among the 47 genes in this interval, *Bol016058* was nominated as the prime candidate gene. It exhibits high leaf expression and is a homolog of *Arabidopsis PRP4*, which encodes a structural cell wall protein abundant in aerial organs. Based on a 45 bp insertion in *Bol016058*, they developed an InDel marker that discriminates between resistant (*Bol016058IN1 allele*) and susceptible (*Bol016058 allele*) genotypes. The marker demonstrated 100% accuracy when validated on 45 cabbage inbred lines with field-confirmed resistance phenotypes [139].

4.2. Bolting Resistance and Flowering Time

Premature bolting in commercially grown cabbage adversely affects harvest scheduling, reduces yield, and compromises head quality. Although often limited to sporadic plants within a field, its prevalence can rise substantially under environmental conditions that promote early flowering, such as long-term low temperatures, long-day conditions, abiotic stresses end, etc., [140,141].

The genetic mechanisms underlying bolting resistance in head cabbage are less elucidated compared with other *B. oleracea* vegetables [141]. Currently, only one SSR marker, BolSSR040196, has been associated with a bolting resistance locus, mapped to chromosome C05 at a distance of 10.69 cM. This marker harbors a CT repeat motif, exhibiting 9 repeats in bolting-susceptible lines and 11 repeats in resistant lines. An analogous locus for bolting resistance on chromosome C05 has been identified in *B. juncea* [142,143]. Validation of BolSSR040196 on a panel of 34 cabbage accessions showed an accuracy of 82.35%, correctly classifying the phenotype in 28 varieties [144].

Flowering time is a key trait that influences the development of many other characteristics in cabbage. This trait is of interest primarily for two reasons. First, seed production directly determines both seed yield and the duration of the vegetative growth period [145,146]. Second, early and reduced flowering is viewed as a strategy to shorten the growth cycle, avoid cold seasons, and mitigate associated bolting issues, making it valuable for commercial cultivation [147,148].

The regulation of flowering genes in cabbage is mediated by five *FLC* genes (Flowering Locus C) named *BoFLC1*, *BoFLC2*, *BoFLC3*, *BoFLC4*, and *BoFLC5*. Among these, *BoFLC2* is a key regulator responding to low temperature during vernalization. To differentiate the alleles of this gene, Li et al. developed an InDel marker, indel-FLC2 [149]. The marker distinguishes alleles based on a 215 bp insertion in the first intron of the early-flowering allele *BoFLC2E* present in early-flowering homozygous plants (flowering at 201–203 days after planting) but absent in the late-flowering allele *BoFLC2L* (flowering at 207–209 days after planting). It has been proposed that in response to cold, the 215 bp deletion in intron I of *BoFLC2* delays its silencing through feedback regulation of core genes in the PHD-PRC2 complex, leading to delayed flowering.

A comparable InDel marker targeting *BoFLC1* was developed by Abuyusuf et al. Named F7R7, this marker detects a 67 bp insertion in intron 2 of *BoFLC1*, which contributes to the variation in flowering time by accelerating *BoFLC1* down-regulation during vernalization. The 67 bp insertion is characteristic of the early-flowering allele. In the study by Abuyusuf et al., lines homozygous for the early-flowering allele flowered on average between 140–150 days after sowing, while late-flowering lines flowered in ≥ 190 days. Heterozygous F_1 genotypes flowered within 160–175 days. When tested on 20 commercial lines, marker F7R7 demonstrated 80% accuracy [150].

4.3. Tolerance to Prolonged High and Low Temperatures

Plant growth and development in *B. oleracea* are negatively impacted by both high temperature (HT) and low temperature (LT) compared to 20 °C [151,152]. Heat shock proteins (Hsps) and their encoding genes are the primary contributors to heat stress response [153]. In cabbage, marker development for these genes has been slow, and evaluating the expression levels of Hsp genes and specific transcription factors under temperature stress is one of the limited approaches for selecting HT-tolerant plants [154,155].

Progress in marker development has so far been achieved only for a gene outside the Hsp group—*BoTPPI-2*. Song et al. identified an HT-resistant *BoTPPI-2* allele carrying an LTR retrotransposon insertion that leads to aberrant transcription. This structural difference allowed Song H. et al. to develop a PCR marker consisting of two primer sets for identifying

thermotolerant plants (primers BoTPPI-2-RF/-RR) and thermosensitive plants (primers BoTPPI-2-SF/-SR). The marker was tested on 116 plants from an F₂ population segregating for thermotolerance and showed 80% accuracy [156].

Tolerance to the opposite abiotic stress—prolonged low temperatures (LT)—is of greater importance for cabbage seed production in regions with severe winters. LT influences freezing tolerance, vernalization-responsive flowering time, and leaf characteristics beyond direct negative effects [157]. For commercial production, LT tolerance may be relevant in areas experiencing unseasonal spring frosts or consistently cold summers. As a negative abiotic factor, cold stress in plants occurs during chilling (<20 °C) and freezing (<0 °C) temperatures [158]. The main damaging effects of freezing are acute cellular dehydration and severe cell membrane damage [159].

As in many plants, the response to LT in cabbage is controlled by Cold Shock Domain Proteins (CSDPs) and their corresponding genes [160]. For one such gene—BoCSDP5—Song et al. developed PCR markers. The marker system comprises three primers: one universal forward primer and two reverse primers. To distinguish homozygous and heterozygous genotypes, the F1/R1 primer pair produced two different band sizes, whereas the F1/R2 primer pair amplified DNA exclusively from LT-tolerant genotypes. The genotypic difference in tolerance is based on LT-tolerant inbred lines containing a variant form of *BoCSDP5* (designated *BoCSDP5v*), which encodes an extra CCHC zinc-finger domain at the C-terminus. Allelic variation in the *BoCSDP5* gene does not affect gene expression levels but produces different proteins with varying numbers of CCHC zinc-finger domains [161].

Similar work was conducted by Song et al. with the *BoCCA1* gene (*CIRCADIAN CLOCK ASSOCIATED 1*), which is also involved in LT resistance mechanisms by upregulating C-repeat binding factor (CBF) pathway genes. Song H. et al. developed three PCR markers to distinguish the two *BoCCA1* alleles (tolerant and susceptible): two based on SNPs (*BoCCA1*-1/2 (2262) and *BoCCA1*-1/2 (2346/2352)) and one InDel marker (*BoCCA1*-F/R). The InDel marker *BoCCA1*-F/R uses one universal forward primer binding to the third exon of *BoCCA1* and two allele-specific reverse primers targeting the sixth (*BoCCA1*-1R1) and fifth (*BoCCA1*-2R1) exons. In LT-resistant varieties, the primer pairs *BoCCA1*-F/*BoCCA1*-1R1 and *BoCCA1*-F/*BoCCA1*-2R1 amplified ~1 kbp and ~800 bp fragments, respectively. The authors recommend using this *BoCCA1*-F/R marker together with the aforementioned *BoCSDP5* marker because they are convenient and demonstrate high concordance (matching patterns for 25 of 26 resistant lines and 17 of 18 susceptible lines). The SNP-based markers target the eighth exon, which contains three SNPs: C/G at nucleotide 2262, T/C at 2346, and C/A at 2352. The allele differentiation method is analogous to the InDel marker, although the SNP markers provide higher precision [162].

Table 3. Markers for resistance to abiotic factors.

Target Trait	Gene/Loci/QTL	GenBank Gene ID	Chr	Gene Product	Marker Type	Marker(s) Name(s)	Marker Reference
Head splitting resistance	QTL SPL-2-1	-	C02	-	SSR	BRMS137, BRPGM0676	[137]
	<i>BoI016058</i>	-	C03	PRP4 like protein	InDel	-	[139]
Bolting resistance	-	-	C05	-	SSR	BolSSR040196	[144]
Flowering time	<i>BoFLC2</i>	NC_027750.1	C02	MADS-box flowering time protein	InDel	indel-FLC2	[149]
Flowering time	<i>BoFLC1</i>	EF158122.1	C02	MADS-box flowering time protein	InDel	F7R7	[150]
High temperature tolerance	<i>BoTPPI-2</i>	MN477455.1	C09	trehalose-phosphate phosphatase 1-2	PCR	Primer set for thermotolerant plants: BoTPPI-2-RF/BoTPPI-2-RR Primer set for thermosensitive plants: BoTPPI-2-SF/BoTPPI-2-SR	[156]

Table 3. Cont.

Target Trait	Gene/Loci/QTL	GenBank Gene ID	Chr	Gene Product	Marker Type	Marker(s) Name(s)	Marker Reference
Low temperature tolerance	<i>BoCSDP5</i>	MT741953.1	C01	HCT09 cold shock domain protein 5	PCR	A three-primer system: universal forward (F1), R1, R2	[161]
Low temperature tolerance, <i>BoCCA1</i>	<i>BoCCA1</i>	KY695111.1	C04	circadian clock associated 1 protein	InDel	A three-primer system: universal forward (BoCCA1-F), BoCCA1-1R1, BoCCA1-2R1	[162]
					SNP	BoCCA1-1/2 (2262), BoCCA1-1/2 (2346/2352)	[162]

5. Markers for Disease Resistance

Molecular markers for disease resistance constitute one of the most well-established categories in the breeding of head cabbage (Table 4). This extensive development is driven by two primary factors: the frequent monogenic basis of resistance, often explained by the gene-for-gene hypothesis, and the significant economic impact of diseases capable of causing yield losses exceeding 50% [163].

5.1. *Fusarium* Wilt Resistance

Cabbage *Fusarium* wilt (CFW), caused by the soil-borne fungus *Fusarium oxysporum* f. sp. *conglutinans*, is a major economic concern due to substantial yield losses [164,165]. The pathogen's ability to persist in soil for decades renders it particularly damaging. Two pathogenic races of *F. oxysporum* have been identified: Race 1, which has a global distribution, and Race 2, which has only been reported in the United States and Russia [166].

Genetic control of resistance differs among races. Resistance to Race 2 (A resistance) is polygenic, whereas resistance to the more common Race 1 (B resistance) is conferred by a single dominant allele of the *Foc-Bo1* gene [167–169]. The initial sources of this resistance were developed in the United States in the early 20th century [170,171]. The first molecular marker for *Foc-Bo1* was the SSR marker KBrS003O1N10, which was developed by Pu et al., who identified the gene itself. This marker was located 1.2 cM from *Foc-Bo1* but did not achieve full accuracy, prompting the recommendation to use it in conjunction with the SNP/InDel marker BSA8 (4.6 cM away, flanking the opposite side) for reliable genotyping. The same study also identified a QTL on chromosome C04 associated with resistance to wilt [169]. Subsequently, a simpler system using the single SCAR marker S46M48199 (2.78 cM from *Foc-Bo1*) was proposed by Jiang Ming J. M. et al., showing 81–83% accuracy in segregating populations [172]. Later, Lv et al. developed codominant InDel markers A1 (0.6 cM) and M10 (1.2 cM). Marker A1 demonstrated high accuracy (96%) in an F₂ population and 82% accuracy across diverse inbred lines [173].

Fine mapping by Lv et al. localized the *Foc-Bo1* locus to a 382 kb region on chromosome C06, with *Bol037156* (encoding a TIR-NBS-LRR protein) identified as the prime candidate gene [173]. This team also developed the SSR marker Frg13, mapped 75 kb from the gene, which showed 97.2% selection accuracy. This marker was successfully applied in marker-assisted backcrossing to create the resistant line YR01-20, which retains 99.8% of the genetic background of the susceptible elite line 01-20 [174]. The markers A1 and M10 have been similarly used to develop wilt-resistant double haploid lines [175].

Dubina et al. conducted a comparative study to evaluate four markers (A1, M10, Frg13, and Ol10-D01) on cabbage. Only M10 and the novel marker Ol10-D01 reliably discriminated resistant and susceptible plants in a segregating F₂ population. Ol10-D01 was noted for its close linkage to *Foc-Bo1* and its co-segregation with the resistance trait in a Mendelian 1:2:1 ratio, making it a highly practical tool for selection [176]. In 2017, Kawamura et al. developed a codominant PCR-RFLP marker, Fusa6m, for the *FocBo1* gene,

which was validated on 35 F₁ plants, including a subset of seven that were also assessed via direct pathogen inoculation. Kawamura et al. further demonstrated the utility of marker-assisted selection in cabbage by applying the Fusa6m marker, in conjunction with markers for seed purity assessment and S haplotype identification, to evaluate multiple agronomic traits [100]. A subsequent study by Sato et al. (2019) involved sequencing the *Foc-Bo1* locus across 19 *B. oleracea* accessions (15 head cabbage) from Japan, revealing a sequence variation that defined two resistant (*FocBo1*) and six susceptible (*focbo1*) alleles [177]. The dominant *FocBo1a* allele was specific to cabbage, whereas *FocBo1b* was identified in the “Shaster” broccoli cultivar. The susceptible recessive alleles in cabbage were designated as *focbo1-1a*, *focbo1-1b*, *focbo1-1c*, *focbo1-1d*, *focbo1-2*, and *focbo1-3*.

Sato et al. developed a panel of the following four markers to facilitate the genotyping of these alleles: (i) CAPS marker #1 (*EcoRI*), which is specific for differentiating the *FocBo1* and *focbo1-1* alleles. Digestion yields a 1042 bp fragment in resistant (*FocBo1*) plants and 668- and 375 bp fragments in susceptible (*focbo1-1*) plants. This marker does not distinguish *FocBo1* from other recessive alleles; (ii) InDel marker #2 targets a 10 bp InDel in exon 5 to discriminate between *FocBo1* and *focbo1-2*. It employs two primer sets: one (SATSU-F/SATSU-R) amplifies an 865 bp product from *FocBo1*, while the other (#2-2F1/#2-2R1) amplifies a 1365 bp product from *focbo1-2*; (iii) dCAPS marker #3 (*EcoRI*) is capable of distinguishing *FocBo1*, *focbo1-2*, and *focbo1-3*. Digestion produces a 689 bp fragment for *FocBo1*, a 450 bp fragment for *focbo1-2*, and 660 bp and 240 bp fragments for *focbo1-3*. (iv) A universal CAPS marker was developed for practical breeding applications. This marker differentiates resistant alleles (*FocBo1a*, *FocBo1b*) from susceptible alleles (*focbo1-1*, *focbo1-2*, and *focbo1-3*). It exploits an SNP in intron 3 that creates an *EcoRV* site in resistant alleles, generating 265 and 810 bp bands upon digestion. Susceptible alleles yield an undigested product of 1075 bp. Validation of 78 commercial cabbage cultivars confirmed 100% genotyping accuracy for all markers [177].

5.2. Black Rot Resistance

Black rot, caused by the bacterium *Xanthomonas campestris* pv. *campestris* (*Xcc*), represents another economically significant disease in cabbage cultivation, causing yield losses of up to 50% [163,178]. Primary disease dissemination occurs through infected seeds, with secondary transmission via contaminated transplants, infested soil, crop residues, and alternative weed hosts [179,180]. The pathogen demonstrates soil persistence independent of host plants, surviving for approximately 40 days in winter and 20 days in summer conditions [181,182].

The current classification systems recognize 11 pathogenic races of *Xcc* affecting *Brassicaceae* species [178,183–185]. Cabbage shows predominant susceptibility to widely distributed races 1 and 4, with limited susceptibility to geographically restricted races 2 (spread in India), 3 (in Japan), 5 (in South Asia), and 8 (in Brazil) [178,185,186].

Genetic resistance to races 1 and 4 is governed by introgressed loci from *B. rapa* and *B. nigra* sources within the A and B subgenomes, respectively [187,188]. The C subgenome of *B. oleracea* contributes minimal resistance determinants [178]. Following the single-gene resistance model, Dohroo et al. developed the RAPD marker C-11₁₀₀₀, mapping 3.1 cM from a putative resistance gene and amplifying a 1000 bp fragment in resistant genotypes [189]. Validation using 200 F₂ plants demonstrated concordance between phenotypic resistance and marker profile, except for seven recombinant individuals. The specific race used in this study remained unspecified.

Contemporary genetic studies have identified approximately 12 QTLs and 9 candidate genes associated with resistance to black rot [190–194]. These discoveries leveraged comprehensive genetic maps developed during 2011–2014 using SNP and SSR mark-

ers [195,196]. Afrin et al. selected five SSR markers incorporating cabbage QTL positions and the cauliflower Xca1bo locus using comparative genomics approaches. The markers' efficacy varied across different races. Specifically, marker OI10G06 achieved 83.3% accuracy in identifying resistance to race 1, whereas both BoESSR291 and OI10G06 discriminated resistant cabbage lines against race 2 with 73.9% accuracy. For race 3, BnGMS301 showed 81.5% accuracy. Marker BnGMS301 also demonstrated the highest accuracy for race 4 (79.2%) and exhibited exceptional performance against race 5 (91.3%). Marker applicability proved race-specific, with BoGMS0971 ineffective against race 1 and BnGMS301 unsuitable for race 2. The markers' accuracy was evaluated by inoculating plants from 27 cabbage inbred lines with the corresponding races of black rot [192].

In parallel studies, Makukha et al. identified two polymorphic SSR markers (OI10-C01 and OI11-H06) differentiating near-isogenic resistant and susceptible lines. OI10-C01 demonstrated superior diagnostic utility with distinct fragment size differentiation (198 bp vs. 272 bp), while OI11-H06 showed minimal fragment length variation (217 bp vs. 222 bp) [197].

Gene-specific marker development by Hong et al. yielded BR6-InDel, targeting candidate gene *Bol031422* associated with races 6 and 7 resistance. This codominant marker detects a 292 bp insertion polymorphism, generating 724- and 1013 bp fragments in resistant and susceptible genotypes, respectively. Validation across 186 F₂ individuals and 27 inbred lines confirmed 83.9% for race 6 and 69.0% for race 7 [198].

5.3. Clubroot Resistance

Clubroot is a destructive disease of cruciferous crops caused by the soil-borne, obligate biotroph *Plasmodiophora brassicae* [199]. While all *Brassicaceae* species are potential hosts, cultivated varieties exhibit particular susceptibility [200]. The pathogen persists in soil for many years through long-lived resting spores, which are disseminated via water and infected plant debris [199].

The inability to axenically culture *P. brassicae* presents a major classification challenge, leading to the identification of distinct pathotypes specific to different countries and regions [201]. This pathotype diversity complicates the genetic analysis of resistance. Although approximately 20 quantitative trait loci (QTLs) for resistance have been reported, many confer isolate-specific or variety-specific resistance [202–204]. Typically, only one or two major-effect QTLs account for a substantial portion of phenotypic variance [205].

Early efforts to map resistance loci involved screening segregating populations using large sets of RFLP, RAPD, and SCAR markers. For instance, Nomura et al. converted several such markers into a panel of 10 dominant SCAR and two codominant CAPS markers (CB74c and CA63), which were linked to resistance against three *P. brassicae* isolates (Kamogawa, Anno, and Yuki) and showed clear segregation with the resistance phenotype [206].

Because clubroot resistance genetics in *B. napus* and *B. rapa* were better characterized, we used markers from these species to identify homologous loci in head cabbage. This comparative genomics approach enabled Nagaoka et al. to identify five QTLs, comprising one major locus, pb-Bo(Anju)1 (explaining 47% of phenotypic variance), and four minor QTLs (pb-Bo(Anju)2 to 5). The SSR marker KBrH059L13R was developed to discriminate the major QTL between the resistant “Anju” allele and the susceptible “Green Comet” broccoli allele [205]. Subsequent work by Tomita et al. identified marker CB10026, which is linked to both *B. rapa* resistance gene and the minor QTL PbBo (Anju)2 in cabbage, and marker CB10065, which is linked to the minor QTL PbBo (GC) [202]. Kawamura et al. screened 35 F₁ hybrids using a combination of these markers and found that only two accessions, “YCR Rinen” and “Fruit cabbage,” which possessed the resistant allele at the major QTL PbBo(Anju)1 and three minor QTLs (PbBo(Anju)2–4), exhibited complete resistance [100].

Clubroot resistance loci specific to headed cabbage have been reported. In a 2025 study, Shi et al. applied bulk segregant analysis to a BC₁ cabbage mapping population, identifying the *Bol.CR7.1* locus. Two candidate genes, *Bol.TNL.2* and *Bol.TNL.3*, were identified within this locus, with *Bol.TNL.2* contributing most significantly to the resistance phenotype. Functional validation demonstrated that the overexpression of the resistant *Bol.TNL.2* allele (*Bol.TNL.2W*) in Arabidopsis and rapeseed significantly reduced the disease index after *P. brassicae* inoculation compared to wild-type controls. In contrast, overexpression of the susceptible *Bol.TNL.2* allele (*Bol.TNL.2Z*) or either allele of *Bol.TNL.3* (resistant *Bol.TNL.3W* and susceptible *Bol.TNL.3Z*) resulted in symptoms similar to wild-type plants. It is assumed that *Bol.TNL.2* confers resistance by modulating pathways involved in reactive oxygen species, cell wall metabolism and modification, and secondary metabolite synthesis. Furthermore, Shi Y. et al. identified clubroot resistance-associated marker *Bol.CR7.1_InDel*, which is applicable for marker-assisted selection in breeding programs [207].

To expand the limited number of known clubroot (CR) resistance loci in headed cabbage, researchers are identifying loci from other *B. oleracea* species for potential introgression. In 2024, Zhang et al. used QTL-seq and linkage analysis on an F_{2:3} population from a cross between a CR-resistant wild cabbage accession B2013 (*Brassica macrocarpa* Guss.) and a susceptible broccoli accession 90,196 to identify the *BolC.Pb9.1* QTL for CR resistance. Expression analysis of wild cabbage plants after *P. brassicae* infection identified the resistance gene *Bol044004* within this QTL. The gene, named *BoUGT76C2* by the authors, encodes a cytokine N-glycosyltransferase. Zhang et al. created transgenic lines overexpressing *BoUGT76C2* in susceptible broccoli background 90,196 via *Agrobacterium*-mediated transformation using a set of eight markers to track the transgene. Artificial inoculation of three transgenic lines revealed significantly higher CR resistance, with disease indices of approximately 20–28 (disease index), compared to the wild-type control (disease index >90). The authors conclude that this strategy can be used to develop CR-resistant lines in cultivated *B. oleracea* crops, including headed cabbage [208].

Due to the limited number of effective resistance genes within the primary cabbage gene pool, strategies have focused on introgressing genes from related species. For example, Zhu et al. successfully transferred a 3.42 Mb segment from *B. rapa* containing the resistance genes *CRa*, *CRb*, and *CRc* (conferring resistance to pathotype 4) into cabbage, followed by in vitro regeneration and fertility restoration. The Introgression tracked using *B. rapa*-derived markers: SC2930 and KBrH129J18 for *CRa*, ZM91 for *CRb*, and *cnu_m090a* for *Pb8.1* [209].

As demonstrated by Fang et al., interspecific hybridization in Brassicaceae represents a strategy for generating diverse breeding material with varying sizes of introgressions. In their study, Fang et al. developed monosomic alien addition lines (MAALs) in radish, characterized by a broad spectrum of improved traits. This approach establishes a framework for using interspecific hybridization to transfer large introgressions, such as those conferring disease resistance loci in cabbage [210].

5.4. Downy Mildew Resistance

Downy mildew is the fourth most common major disease in cabbage, followed by clubroot, Fusarium wilt, and black rot. This disease is caused by the invasion of *Hyaloperonospora parasitica*, an obligate biotrophic oomycete that threatens cabbage's entire life cycle. In recent years, it has become increasingly prevalent across the world's cabbage-growing areas, leading to serious losses in global yield [211].

Unlike broccoli and cauliflower, only one resistance gene, *BoDMR2*, has been identified in head cabbage on chromosome C07 [212]. Wu et al., who discovered this gene, developed an InDel marker, I1-3, based on a 3 bp insertion in the coding region of the susceptible

BoDMR2 allele. Subsequently, this marker was used to analyze resistant and susceptible plant pools and sister line materials. Marker I1-3 amplified a 92 bp fragment in susceptible lines and an 89 bp fragment in resistant lines. The marker demonstrated 100% accuracy in a test of 148 inbred lines.

Markers targeting unannotated downy mildew resistance loci are also known. For example, Gutierrez et al. developed a set of 14 KASP markers to target a resistance locus and its surrounding regions on chromosome C02. KASP markers 3 and 12 showed a maximum accuracy of 100% when tested on 468 lines and are recommended for use in MAS [213].

Table 4. Markers for disease resistance.

Target Trait	Gene/Loci/QTL	GenBank Gene ID	Chr	Gene Product	Marker Type	Marker(s) Name(s)	Marker Reference
Black rot resistance (Race unspecified)	-	-	-	-	RAPD	C-11 ₁₀₀₀	[189]
Fusarium wilt race 1 resistance	<i>Foc-Bo1</i>	AB981182.1	C07	FocBo1 protein	PCR-RFLP	Fusa6m	[100]
					SCAR	S46M48199	[172]
					SSR	KBrS003O1N10	[169]
					SNP/InDel	BSA8	[169]
					InDel	A1, M10	[173]
					SSR	Frg13	[174]
					SSR	O110-D01	[176]
					CAPS	CAPS #1 (<i>EcoRI</i>)	[177]
					InDel	InDel #2	[177]
					dCAPS	dCAPS #3 (<i>EcoRI</i>)	[177]
Black rot race 1 resistance	-	-	C06	-	SSR	O110G06	[196]
Black rot race 2 resistance	-	-	C06, C03	-	SSR	BoESSR291, O110G06	[196]
Black rot race 3, 4 and 5 resistance	-	-	C01	-	SSR	BnGMS301	[196]
Black rot resistance (General)	-	-	-	-	SSR	O110-C01, O111-H06	[197]
Black rot races 6 and 7 resistance	-	-	C08	-	InDel	BR6-InDel	[198]
Clubroot isolates Kamogawa, Anno and Yuki resistance	QTL1, QTL2, QTL3	-	C01, C02, C03	-	SCAR, CAPS	Panel of 10 SCAR and 2 CAPS markers	[206]
Clubroot resistance	pb-Bo(Anju)1 QTL	-	C02	-	SSR	KBrH059L13R	[205]
Clubroot resistance	PbBo(Anju)2 QTL	-	C02	-	SSR	CB10026	[202]
Clubroot resistance	PbBo(GC)1 QTL	-	C05	-	SSR	CB10065	[202]
Clubroot pathotype 4 resistance (introgressed from <i>B. rapa</i>)	<i>CRA</i> , <i>CRb</i>	AB751517.1	A03 (in <i>B. rapa</i>)	putative disease resistance protein	SCAR, SSR, CAPS	SC2930, KBrH129J18 (for <i>CRA</i>), ZM91 (for <i>CRb</i>), cnu_m090a (for <i>Pb8.1</i>)	[209]
Downy mildew resistance	<i>BoDMR2</i>	-	C07	theoretical leucine-rich repeat domain protei	InDel	I1-3	[212]
Downy mildew resistance	Resistance locus	-	C02	-	KASP	KASP marker №3 and №12	[213]

6. Conclusions

The integration of molecular markers has become an indispensable tool in the breeding of modern head cabbage. This review demonstrates significant progress in this field, detailing a wide array of markers developed for diverse applications.

The most established and routinely applied markers are those for hybrid breeding and disease resistance. In hybrid breeding, PCR-based markers are widely used to identify the Ogura CMS type and the fertility restorer gene *Rfo*. KASP markers (e.g., K6 for *Ms-cd1*) and InDel markers (e.g., ms3-dec for *ms3*) are becoming the tools of choice for genic male sterility due to their high accuracy and throughput. Furthermore, SSR and KASP marker sets are routinely employed for assessing genetic diversity, classifying heterotic groups, and ensuring the genetic purity of F₁ hybrid seeds, which is critical for commercial production.

For disease resistance, marker-assisted selection is heavily reliant on traits with monogenic inheritance. A suite of markers targeting the *Foc-Bo1* gene, including CAPS, InDel (e.g., A1, M10), and PCR-RFLP (*Fusa6m*) markers, are commonly applied for Fusarium wilt resistance. SSR markers linked to specific QTLs or resistance genes are frequently used for black rot and clubroot resistance, although their application can be pathotype-specific. The development of KASP markers for downy mildew resistance represents a move toward more modern, high-throughput screening for this emerging disease.

For morphological traits, the application of markers is more targeted. InDel markers for glossy waxlessness (e.g., DX-1 for *Cgl1*) and specific leaf colors (e.g., BoMYBL2-1sub for purple leaves) are valuable for improving the appearance of cultivars. Although abiotic resistance QTLs for complex traits, such as head splitting and bolting resistance, have been identified, their application in breeding is still emerging, with linked SSR markers (e.g., BRMS137 for head splitting) serving as initial tools for selection.

A clear technological shift is evident from early techniques, such as RAPD and AFLP, toward more robust, co-dominant, and high-throughput marker systems. SSR markers remain a versatile and widely used workhorse for diversity studies and preliminary trait mapping. However, KASP and SNP markers are increasingly favored for their precision, scalability, and automation compatibility, especially for large-scale fingerprinting and pyramiding multiple genes.

However, despite these advancements, the repertoire of molecular markers for cabbage remains limited compared with other *Brassicaceae* crops, such as rapeseed (*Brassica napus*) or Chinese cabbage (*Brassica rapa* subsp. *pekinensis*), which is popular in Asian countries. This is attributed to both the polyploid nature of its genome, which complicates genetic analysis, and the insufficient elucidation of the genetic foundations of many important agronomic traits, particularly those with a polygenic nature, such as resistance to head splitting and bolting. Allele mining is a strategy for addressing the limited understanding of the genetics underlying complex traits in cabbage, distinguished by its reliance on bioinformatic tools. This approach has been successfully employed to identify novel genetic determinants of Fusarium wilt resistance in heading cabbage (*Brassica oleracea* var. *capitata*) [214]. An alternative method involves integrating MAS with genomic selection to overcome these constraints. This combined strategy utilizes established markers to predict phenotypic changes across diverse environmental conditions [13]. The framework of genomic selection, which is based on the application of mathematical models, is also applicable for discovering new genetic determinants of traits, including those with a polygenic architecture. The development of molecular markers for head cabbage is more advanced than that for most other subspecies (e.g., kohlrabi and Brussels sprouts), many of which are cultivated only as regional crops.

The pace of cabbage breeding can also be accelerated by integrating molecular markers with advanced technologies, such as genetic engineering [215] and speed breeding [216].

Combining genetic markers with biochemical markers that directly assay gene products further enhances selection accuracy [217]. Digitalization is also pivotal, enabling the integrated analysis of genotyping and digital phenotyping data for comprehensive multi-trait selection [218].

Therefore, while existing markers already contribute substantially to accelerating the breeding process, future research should focus on the in-depth genetic dissection of quantitative traits, the development of new, more efficient markers, such as KASP and SNP markers based on whole-genome sequencing, and the expansion of the marker toolkit to cover a broader spectrum of valuable characteristics. This comprehensive synthesis serves as a foundation for further research and the practical application of MAS in developing new cabbage cultivars and hybrids.

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Abbreviations

The following abbreviations are used in this manuscript:

MAS	Marker-assisted selection
CMS	Cytoplasmic male sterility
GMS	Genic male sterility
DGMS	Dominant genic male sterility
RGMS	Recessive genic male sterility

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