

Molecular-genetic marking of *Brassica* L. species for resistance against various pathogens: achievements and prospects

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Cruciferous plants belonging to the genus *Brassica* of the Cabbage family (Brassicaceae) are cultivated as vegetables, oilseeds and forage crops; they occupy one of the first places in Russia in the gross yield of vegetables. The yield of cabbage crops is adversely affected by various pathogens, including bacterial, viral and fungal infections. The diseases such as black rot of cabbage (caused by the bacterium *Xanthomonas campestris* pv. *campestris*), downy mildew (caused by *Hyaloperonospora parasitica*), Turnip Mosaic Virus (TuMV) are not included in the list of quarantine diseases in the territory of the Russian Federation and Eurasian Economic Union (EAEU), but they can affect a part of the sown area and lead to significant (up to 100 %) crop losses. The development of cultivars resistant to these pathogens is an important trend in *Brassica* crop breeding in addition to existing methods of agrotechnical and chemical protection. The development of molecular marker techniques and marker-assisted selection (MAS) methods makes it possible to significantly increase the efficiency of breeding resistant cabbage cultivars. The review contains information on the currently known genes and quantitative trait loci (QTLs) associated with resistance to black rot, downy mildew, and TuMV. Molecular mapping data for resistance genes of *Brassica* species are shown. The molecular markers (RFLP, AFLP, SSR, EST, SNP, InDel, SLAF and others) closely linked to the resistance loci and SCAR-, STS- and dCAPS-markers derived from them for molecular screening are listed. The use of the markers reviewed to assess the *Brassica* accessions and lines can help the researchers in finding sources and donors of pathogen resistance of cabbage crops.

Key words: *Brassica*; resistance; *Xanthomonas campestris*; *Hyaloperonospora parasitica*; TuMV; MAS; QTL.

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Достижения и перспективы молекулярно-генетического маркирования устойчивости к некоторым патогенам у видов рода *Brassica* L.

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Крестоцветные растения, относящиеся к роду *Brassica* семейства Капустные (Brassicaceae), возделываются как овощные, масличные и кормовые культуры. В Российской Федерации они занимают одно из первых мест по валовому сбору овощей. На урожайность капустных культур негативно влияют различные патогены, в том числе бактериальные, вирусные и грибные инфекции. Такие заболевания, как сосудистый бактериоз (возбудитель *Xanthomonas campestris* pv. *campestris*), ложная мучнистая роса, или пероноспороз (*Hyaloperonospora parasitica*), вирус мозаики турнепса (Turnip Mosaic Virus – TuMV), хотя и не входят в список карантинных болезней на территории Российской Федерации и Евразийского экономического союза (ЕАЭС), но могут поражать часть посевных площадей и приводить к значительным (вплоть до 100 %) потерям товарной продукции. Создание устойчивых к этим патогенам сортов является важным направлением в селекции культур *Brassica*, дополняющим существующие методы агротехнической и химической защиты. Развитие методов молекулярного маркирования и маркер-вспомогательной селекции (MAS) позволяет намного повысить эффективность отбора устойчивых генотипов. В обзоре рассмотрены актуальные сведения об известных генах и локусах количественных признаков (QTL), ассоциированных с устойчивостью к сосудистому бактериозу, пероноспорозу капусты и вирусу TuMV. Приведены данные о локализации генов устойчивости на молекулярных картах геномов видов рода *Brassica* (*B. rapa*, *B. oleracea*, *B. napus*, *B. carinata*), разработанных с использованием разных типов молекулярных маркеров (RFLP, AFLP, SSR, EST, SNP, InDel, SLAF и др.). Систематизирована информация

о молекулярных маркерах, тесно сцепленных с локусами устойчивости, часть из которых конвертирована в SCAR-, STS- и dCAPS-маркеры для молекулярного скрининга, пригодные для непосредственного применения в практической селекции. Использование приведенных данных для оценки образцов культур рода *Brassica* может помочь исследователям в поиске источников и доноров генетической устойчивости к рассматриваемым заболеваниям выращиваемых капустных культур.

Ключевые слова: *Brassica*; resistance; *Xanthomonas campestris*; *Hyaloperonospora parasitica*; TuMV; MAS; QTL.

Introduction

Meeting the people's ever growing demand for food, feed and industrial plant products in the world and in the Russian Federation requires a considerable increase of crop yield and expansion of crop areas. One of the main ways to increase yields is searching for methods that could minimize losses from diseases caused by various pathogens. Biological and chemical plant protection techniques (fungicides and bactericides) are costly, often show unstable results in disease control, and in time induce tolerance in their objects. Besides, chemical means of disease control are extremely detrimental to the environment. The most effective and economically justified tool to resist causative organisms is the use of genetically resistant cultivars or genotypes with such morphological and physiological features that preclude infection.

Plants possess efficient mechanisms that enable them to avoid infections or produce protective responses, thus making them resistant to a pathogen's attack. Barriers against infection may be set up by anatomic and morphological features (plant habit, leaf pubescence, waxy bloom, arrangement and structure of stomata, or structure of internal tissues), biochemical factors (for example, phytoncides, phenolic compounds, or glucosinolates), and some specific proteins (PR proteins, plant defensins, thionines, etc.) (Dyakova, 2017). The most effective protection, however, is provided by genetic resistance to pathogens. According to H.H. Flor's popular 'gene-for-gene' hypothesis (Flor, 1971), resistance occurs when a resistance (*R*) gene in the plant recognizes a corresponding specific avirulence (*Avr*) gene in the pathogen (McDowell, Simon, 2006).

There are 37 species within the genus *Brassica* L. Six of them are cultivated species of vital economic significance; they are combined in the classical 'triangle of U' (Nagaharu, 1935), which includes 3 diploid species: *B. rapa* L. (AA, *n* = 10), *B. nigra* L. (BB, *n* = 8), and *B. oleracea* L. (CC, *n* = 9) as well as 3 amphidiploid ones: *B. juncea* Czern. (AABB, *n* = 18), *B. carinata* A. Braun (BBCC, *n* = 17), and *B. napus* L. (AACC, *n* = 19). Diverse forms of these species are cultivated as vegetable, forage, oil and ornamental crops. It has been observed that "in the course of their evolution, diploid *Brassica* spp. developed independently, therefore their genomes underwent various qualitative and quantitative changes, leading to accumulation and combination of preferable alleles in their genes, which ensured their survival in the process of natural selection and shaped their economically useful traits in the process of artificial selection" (Fadina, 2014, p. 24). Broad genetic diversity within and between different crops of the genus *Brassica* and species of other genera in the family Brassicaceae secures a rich resource of resistance genes against major pathogens (Walsh, Jenner, 2002; Neik et al., 2017).

The main diseases that inflict mass damage upon the *Brassica* crops in Russia are: (1) bacterial diseases, such as black rot or vascular bacteriosis (caused by *Xanthomonas campestris* pv. *campestris*, *X. campestris* pv. *raphani*, and *X. arboricola*) and slimy bacteriosis (caused by *Erwinia carotovora* subsp. *carotovora* (Jones) Berqey); (2) fungal diseases, such as club-root disease of crucifers (caused by *Plasmodiophora brassicae* Woron.), dark spot (caused by *Alternaria brassicae*, *A. brassicicola* and other *Alternaria* spp.), downy mildew (caused by *Hyaloperonospora parasitica*), powdery mildew (caused by *Erysiphe cruciferarum*), and blackleg disease (caused by *Leptosphaeria maculans* and *L. biglobosa*); and (3) viral infections, such as turnip mosaic virus (TuMV), cauliflower mosaic virus (CaMV), and turnip yellows virus (TuYV). It should be mentioned that none of the above-mentioned diseases is included in the Common List of Plant Quarantine Objects of the Eurasian Economic Union of February 2018, but they are capable of damaging up to 100 % of crop areas under crucifers.

In this review, we are discussing three important pathogens of crucifers, causing a destructive effect on *Brassica* crops cultivated in Russia: vascular bacteriosis or black rot, downy mildew, and turnip mosaic virus. We have chosen the most harmful diseases among bacterial, fungal and viral infections, against which biochemical control methods do not bring about stable positive results, but there are molecular marker systems developed for relevant resistance genes.

Black rot (vascular bacteriosis)

Black rot is a disease of cruciferous crops caused most frequently by the gram-negative bacterium *Xanthomonas campestris* pv. *campestris* (Pam). Dowson (hereinafter referred to as *Xcc*). Cabbage may also be affected by other *Xanthomonas* species and pathovars (Ignatov, 2014), differing mostly in the symptoms of infection and the set of susceptible host plants. This disease is one of the most harmful for crucifers in the world. All cultivated *Brassica* crops are subject to black rot: turnip, radish, rapeseed, swede, and numerous cruciferous weeds. Within the species *B. rapa*, the disease is most dangerous for both root turnips and leafy forms, including Chinese cabbage (*B. rapa* ssp. *pekinensis*) (Artemyeva et al., 2018).

The pathogen is disseminated by seeds and in recent years have been inducing epiphytotic in all areas where cruciferous crops are grown, inflicting losses on the harvested plant produce from 10 to 100 % (Ignatov, 2014). A number of chemicals have been recommended to protect crops from black rot (Lazarev et al., 2017), but they are not always as effective as expected.

Table 1. Characterization of molecular gene markers and QTL associated with resistance to black rot in *Brassica* spp.

QTL/ resistance gene	Chromosome/linkage group	Marker	Marker type	Reference
<i>B. oleracea</i> L.				
<i>Xcc Resistant gene</i>	–	C-111000	RAPD	Kaur et al., 2009
QTL-1	C02	BoCL5989 s BoCL5545 s	dot-blot-SNP	Kifuji et al., 2013
<i>XccBo (Reiho)1</i>	C05	BoGMS1330	SSR	Tonu et al., 2013
	C02	BoCL6200s	SNP	
	C02	BoCL5584		
	C05	BoCL5860		
	C05	BoCL1135		
<i>XccBo (Reiho)2</i>	C08	BoGMS0971	SSR	
	C08	OL12D05		
<i>XccBo (GC)1</i>	C09	CB10459	SSR	
	C05	pW114	CAPS	
	C05	pW164		
	C09	pX117		
	C09	pW143		
	C03	pW188		
<i>Xca1bo</i>	III	RAPD04	RAPD	Saha et al., 2016
		ISSR11	ISSR	
<i>BRQTL-C1_1</i>	C01	BnGMS301	dCAPS	Lee et al., 2015
<i>BRQTL-C1_2</i>	C01	BoESSR089	SSR	
<i>BRQTL-C3</i>	C03	B041F06-2	SSR	
<i>RQTL-C6</i>	C06	OI10-G06	SSR	
–	C03	BoESSR291	SSR	Afrin et al., 2018a
–	C01	BoESSR726	SSR	
–	C01	BnGMS301	SSR	
–	C08	BoGMS0971	SSR	
–	C06	OI10G06	SSR	
–				
<i>B. rapa</i> L.				
<i>R4</i>	–	WE22 WE49	RAPD	Ignatov et al., 2000
<i>XccR1d-1, XccR1i-1</i>	A06	E11M50_280b E12M48_171r	AFLP	Soengas et al., 2007
		<i>XccR4d-1, XccR4i-1</i>		
<i>XccR4i-2</i>	A02	E11M59_178r	AFLP	
<i>XccR4i-3</i>	A09	E12M48_1330b	AFLP	
QTL	A03	BRMS-043	SSR	Artemyeva et al., 2016, 2018
	A03	BRMS-050		
	A09	BRMS-051		
	A06	SSR-089		
	A03	Na12E02		
<i>B. carinata</i> L.				
<i>Xca1bc</i>	B07	At1g70610 At1g71865 Na14-G02	ILP	Sharma et al., 2016
			SSR	

Initially five races of the pathogen were identified; afterwards their number grew to eleven (Cruz et al., 2017). *Xcc* races 1 and 4 are considered the most harmful among them. In Russia, before 2012, the most widespread were races 1, 3 and 4, but later, for white cabbage and rapeseed, races 5 and 6 became quite threatening (Lazarev et al., 2017). Resistance to different *Xcc* races is supposed to be controlled by different *R*-genes and QTL. Sources of resistance to major harmful *Xcc* races (1 and 4) are mainly associated with the A and B genomes (*B. rapa* and *B. nigra*) and rarely occur in the C genome (*B. oleracea*) (Taylor et al., 2002; Vicente, Holub, 2013). At the same time, forms resistant to less pathogenic races 2, 3 and 6 are frequent enough (Soengas et al., 2007).

***B. oleracea* (C genome).** There are few sources of genetic resistance to the most pathogenic *Xcc* races (1 and 4) in *B. oleracea*. Nevertheless, research efforts to identify and map *R*-genes and QTL for *B. oleracea* are quite intensive. Molecular maps of this crop's genome have been developed independently by several groups of researchers (Kaur et al., 2009; Kifuji et al., 2013; Tonu et al., 2013; Lee et al., 2015; Saha et al., 2016; Iglesias-Bernabe et al., 2019) using different types of markers (RAPD, SSR, ISSR, dCAPS or SNP). Genes and QTL of resistance to most pathogenic races 1 and 4 were found on different chromosomes/linkage groups (Table 1). For example, Lee et al. (2015) mapped altogether 14 QTL associated with resistance to *Xcc* on eight chromosomes out of nine in *B. oleracea*, and four of them represented the main loci affecting resistance in plants. Thus, the control of this trait in *B. oleracea* is polygenic by nature. For a number of resistance genes and QTL, molecular markers, securely linked with them and associated with resistance, were identified (see Table 1). Afrin et al. (2018a) tested some of those markers (9 SSR and 1 InDel) on 27 inbred cabbage lines resistant to different races of the pathogen. Comparing the results of molecular screening and phytopathology tests helped to select five markers capable of distinguishing resistant forms from susceptible ones. It is noteworthy that those markers were also distributed among different chromosomes: BnGMS301 and BoESSR726 were localized on C01, BoESSR291 on C03, OI10G06 on C06, and BoGMS0971 on C08 (Afrin et al., 2018a).

Xcc resistance genes have also been identified through a search in the genome of *B. oleracea* for sequences containing characteristic domains (LRR, NBS, TIR, etc.). For example, Afrin et al. (2018b) sought NBS-containing sequences in the Gene Expression Omnibus (GEO) database and studied their expression in various plant tissues (leaves, roots, xylems and stems) of *Xcc*-resistant and *Xcc*-susceptible lines. As a result, they selected 7 loci whose expression was associated with resistance for the line SCNU-C-4118, and two more loci for the line SCNU-C-3273. A comparison between the sequences of those loci in resistant and susceptible forms disclosed several InDels and SNP variants which may be used in the development of markers for molecular screening (Afrin et al., 2018b).

***B. rapa* (A genome).** Studying resistance to race 4 in the *B. rapa* line G011 with RAPD analysis resulted in identifying the marker WE22₉₈₀ associated with resistance to *Xcc*. The marker was present in 100 % of resistant dihaploid lines and genotypes of F₂, but was also found in 18 % of susceptible dihaploids. The gene of resistance to *Xcc* (race 4) in *B. rapa* was observed at a distance of approximately 3 cM

from the QTL responsible for clubroot resistance (Ignatov et al., 2000).

Soengas et al. (2007) employed AFLP and SSR analyses to study a splitting population of F₂ hybrids from crossing the *Xcc*-resistant line B162 with the susceptible Ro-18. As a result, they developed a molecular map of the *B. rapa* genome, which included ten linkage groups with the total coverage of 664 cM. A cluster containing two main QTL associated with resistance to races 1 and 4 was found on chromosome A06, while linkage groups A02 and A09 carried additional QTL controlling resistance to race 4.

Microsatellite analysis of two mapping populations of the doubled haploid *B. rapa* lines (DH30 and DH38) made it possible to make a map full of SSR markers (Artemyeva et al., 2016) and isolate several markers associated with *Xcc* resistance (see Table 1). Later, the loci linked with resistance to different races in the line DH30 were mapped to linkage groups A01, A03 and A07, and in the line DH38 to groups A03, A06 and A08 (Artemyeva et al., 2018).

***B. carinata* (BC genome).** Using mapping populations of F₂ hybrids obtained from the resistant line NPC-9 and the susceptible line NPC-17, a bulked segregant analysis was carried out with 41 polymorphic markers (ILP and SSR) (Sharma et al., 2016). Only three of them (ILP-At1g70610, ILP-At1g71865 and SSR-Na14-G02) were able to generate polymorphic fragments between resistant and susceptible lines. The resistant locus *Xca1bc* was mapped at a distance of 30.1 cM from the microsatellite marker Na14-G02, which had earlier been found on chromosome B07. On this basis, the authors concluded that the *Xca1bc* locus was also situated on chromosome B07.

Thus, plenty of black rot resistance gene markers have been developed on the *B. oleracea* crops, which provides a possibility to screen collections in search of new donors. For the species *B. rapa* and *B. carinata*, the information on mapped genes and resistance QTL is still limited by now. Further research efforts are needed in this field.

Downy mildew

Downy mildew is a destructive disease caused by the oomycete *Peronospora brassicae* Gaum. from the family Peronosporaceae. Initially, on the basis of morphological descriptions and cross-inoculation tests, 52 *Peronospora* spp. were identified in crucifers; however, following the results of more recent studies, all downy mildew causative agents in *Brassica* crops were grouped into the single aggregate species *Peronospora parasitica* (Pers. ex Fr.) Fr. The modern classification implies that the name *P. parasitica* should be reclassified and enter the genus *Hyaloperonospora*. The taxonomically correct name for this causative agent in *Brassica* spp. is *Hyaloperonospora brassicae* (Goker et al., 2009). Under favorable conditions, *H. brassicae* can infect up to 50–60 % of cabbage seeds and reduce the harvest by 16–20 % (Saharan et al., 2017).

By now, different research teams have identified 5 genes and 4 QTL responsible for the resistance of cruciferous crops to *H. brassicae*, which will be discussed below.

***B. oleracea* (C genome).** Downy mildew resistance in cauliflower was shown to be controlled by a dominant allele of the gene called *Ppa3* (Mahajan et al., 1995). The *Ppa3* gene was later mapped using a splitting population of backcrosses

Table 2. Characterization of molecular gene markers and QTL associated with resistance to downy mildew in *Brassica* spp.

QTL/ resistance gene	Chromosome/linkage group	Marker	Marker type	Reference
<i>B. oleracea</i> L.				
QTL	–	UBC359620 OPM16750	SCAR	Giovannelli et al., 2002
<i>Pp523</i>	C08	OPK17980 OPR15920 OPJ19550 AT.CTA_133/134	RAPD	Farinhó et al., 2004
<i>Pp523</i>	C08	SCJ19443 SCR15920 SCAFB1216	SCAR	Farinhó et al., 2007
<i>Pp523</i>	C08	CB10139 CB10028	SSR	Carlier et al., 2012
<i>Ppa3</i>	–	OPC141189 OPE141881 ISSR-231103	RAPD ISSR	Singh et al., 2012
<i>B. rapa</i> L.				
<i>BraDM</i>	A08	K14-1030 OI12-G04	RAPD SSR	Yu et al., 2009
<i>BraDM</i>	A08	SCK14-825 kbrb006c05-2 kbrb058m10-1	SCAR SSR	Yu et al., 2011
<i>BrDW</i>	A08	Brb062-Indel230 Brb094-Dral787 Brb094-AatII666 Brb043-Bg1II715 Brh019-SNP137	Indel CAPS SNP	Li et al., 2011
<i>BrRPHP1</i>	A01	OPA08650 BrPEK15B	RAPD SCAR	Kim et al., 2011
<i>sBrDM</i>	A08	A08-028 A08-018	SNP	Yu et al., 2016
QTL	A01	A0124655323	SLAF	Zhi et al., 2016

from the resistant line BR-2. The gene was localized between the flanking RAPD markers OPC14₁₁₈₉ and OPE14₁₈₈₁, not far (26.4 cM) from the marker ISSR-23₁₁₀₃ (Singh et al., 2012).

Another team of researchers, while studying a splitting population of doubled haploids and F₂ hybrids obtained from the line USVL089 of *B. oleracea* (Italica Group), identified one more dominant locus of resistance to downy mildew (Farnham et al., 2002). RAPD analysis of the same population revealed two markers (UBC359₆₂₀ and OPM16₇₅₀) linked with

the resistance locus (Giovannelli et al., 2002). To ensure more stable results, RAPD sequences were converted into SCAR markers (Table 2).

One more research team identified the dominantly inherited *Pp523* gene in the resistant broccoli accession OL87125 (Farinhó et al., 2007). The gene was mapped in a population of F₂ hybrids using AFLP, RAPD, ISSR and SSR markers with the LG.3 linkage group. Bulk analysis (19 resistant and 17 susceptible genotypes per each accession) was em-

ployed to isolate the markers OPK17₉₈₀, OPJ19₅₅₀, OPR15₉₂₀ and AT.CTA_133/134 flanking the *Pp523* gene. The markers OPJ.19₅₅₀ and OPR.15₉₂₀ were sequenced and converted into SCAR and CAPS markers (see Table 2).

On the basis of the OPJ19₅₅₀ and OPR15₉₂₀ marker sequences linked with *Pp523*, probes (BoT01 and BoCig) were developed for screening genomic libraries of *B. oleracea*, with isolation of sites containing sequences complementary to the probes. DNA fragments in the isolated BAC clones were shown to be located in three different parts of the genome of *B. oleracea*: 83 clones were mapped to chromosome C08 near *Pp523*, 33 clones also to chromosome C08 at a distance of 60 cM from the resistance gene, and 63 more to chromosome C05 (Carlier et al., 2011). The presence of such triplication supports the hypothesis concerning the existence of *Brassica*'s hexaploid ancestor some 14–24 million years ago and the formation of the *B. oleracea* genome by rearrangements and translocations (Carlier et al., 2011).

The authors later supplemented the obtained map for *B. oleracea* by adding 44 SSR markers with a known localization on chromosomes of the C genome. It enabled them to correlate the earlier identified nine linkage groups with nine chromosomes in the *B. oleracea* genome. As a result, the *Pp523* gene was localized in chromosome C08 and correlated with two SSR markers – CB10139 and CB10028 (Carlier et al., 2012).

***B. rapa* (A genome).** Yu et al. (2009) isolated and mapped the main locus (QTL) of downy mildew resistance in Chinese cabbage (*B. rapa* ssp. *pekinensis*) plants in the sprouting stage, and it was named *BraDM*. Using the molecular map developed by Zhang et al. (2008) and supplemented in their work with new SSR, SCAR, STS, SRAP and isoenzyme markers, the authors localized the QTL *BraDM* on chromosome A08 of the *B. rapa* genome. *BraDM* was shown to be located within a site of 2.9 cM, which was flanked by isoenzyme and RAPD markers, PGM (phosphoglucumutase) and K14-1030, respectively. Besides, the SSR marker O112G04 was found to be linked to *BraDM* at a distance of 4.36 cM (Yu et al., 2009).

K14-1030 was later sequenced and remapped as a SCAR marker – SCK14-825 (Yu et al., 2011). In addition, using K14-1030 as a probe, Li et al. (2011) isolated from the library the BAC clone KBrB058M10, which was in association with the resistance QTL. On the basis of the obtained information, markers for MAS were developed: the InDel marker Brb062-InDel₂₃₀, CAPS markers Brb094-DraI₇₈₇, Brb094-AatII₆₆₆ and Brb043-BglIII₇₁₅, and SNP marker Brh019-SNP₁₃₇. All markers, except Brh019-SNP₁₃₇, had sufficiently high correlation with resistance (69.7–74.2 %) (Li et al., 2011).

Besides, the additional SSR markers kbrb058m10-1 and kbrb006c05-2 flanking the target resistance gene were developed. Interval mapping showed that SCK14-825, kbrb058m10-1 and kbrb006c05-2 had high LOD values (23.2, 19.5 and 15.5) (Yu et al., 2011).

The same population as for mapping the main QTL *BraDM* was used to isolate six additional QTL affecting downy mildew resistance: 4 major (sBrDM8, yBrDM8, rBrDM8 and hBrDM8) and 2 minor (rBrDM6 и hBrDM4) loci (Yu et al., 2016). The locus sBrDM8 responsible for seedling resistance was mapped to chromosome A08 and appeared identical to *BraDM*. The loci yBrDM8, rBrDM8 and hBrDM8 controlled

resistance at the young plant, rosette and heading stages; they were also mapped to chromosome A08 in the *BraDM* region. The authors arrived at the conclusion that all those loci could aggregately represent a new dominant gene, *BraDM8*.

A dominant downy mildew resistance gene, *BrRHP1*, was also identified by Kim et al. (2011) in Chinese cabbage (*B. rapa* ssp. *pekinensis*). Using bulked analysis of mapping populations, this gene was localized in the A01 linkage group close to the RAPD marker OPA08₆₅₀. After sequencing a 650 bp DNA fragment generated by the primer OPA08, the SCAR markers BrPERK15A and BrPERK15B were developed. Of these, BrPERK15B revealed polymorphism between resistant and susceptible parental lines. Besides, six SSR markers were developed for identification of the *BrRHP1* gene (Kim et al., 2011).

One more locus of downy mildew resistance was found on chromosome A01 using GWAS analysis, when 960 polymorphic SLAF markers were employed to study 202 inbred lines. The new locus, named SLAFMarker A0124655323, was reliably linked with resistance. Comparing sequences of the locus SLAFMarker A0124655323 in resistant and susceptible lines helped to isolate SNP variants and develop KASP markers for their identification. Their linkage with resistance was higher than 80 % (Zhi et al., 2016). Thus, the main genes controlling resistance to downy mildew in both *B. rapa* and *B. oleracea* concentrated in linkage group 8, and additionally, for *B. rapa* alone, in group 1. For all identified genes, effective molecular markers (SCAR and CAPS) were developed for screening. For *B. carinata*, as far as we know, no downy mildew resistance genes were identified or mapped.

Turnip mosaic virus (TuMV)

TuMV was for the first time described in 1921 in the United States on *B. rapa* plants, and later, in 1935, in the UK on *B. oleracea* (Walsh, Jenner, 2002). Presently, TuMV incidence is registered in all regions of the world. This virus can afflict all crucifers; it is dispersed by polyphagous aphids, by seeds, and via infected plant material. The TuMV incidence in the open field is rated second after cucumber mosaic virus (Gibbs et al., 2015).

TuMV is one of over 100 species in the genus *Potyvirus*; it emerged from a lineage of monocotyledon-infecting potyviruses about 1000 years ago. Potyvirus virions contain a single copy of the genome, a single-stranded RNA molecule of about 10,000 nucleotides (Gibbs et al., 2015). A rich diversity of pathotypes has been found within the virus, and the most widespread among them are pathotypes 1, 3 and 4 (Jenner et al., 2002).

Hypersensitive resistance to viruses in *Brassica* crops is mainly characterized by monogenic dominant inheritance (Fraser, 1992). Extreme and other types of resistance are controlled by both dominant and recessive genes, the share of the latter being unusually large (up to 40 %) (Walsh, Jenner, 2002). The resistance controlled through a combined effect of recessive and dominant genes was described for Chinese cabbage (Rusholme et al., 2007). Below is the information on the identified (described) loci and genes of resistance and on the markers associated with them for different *Brassica* spp.

***B. oleracea* (C genome).** Screening of *B. oleracea* cultivated types failed to identify any sources of resistance (Walsh, Jenner, 2002).

***B. napus* (AC genome).** The dominant *TuRB01* gene was the first to be mapped in *Brassica*; it conveys extreme resistance to some isolates of TuMV pathotype 1 (Walsh et al., 1999). The work was done on a mapping population of dihaploid lines (DH) employing RFLP markers. The *TuRB01* gene was localized on chromosome N6 of the A genome, near the pO120b cluster. The location of *TuRB01* in linkage group 6 within the A genome of *B. napus* indicates that *B. rapa* may possibly be the source of this gene. The second locus, *TuRB02*, which seems likely to quantitatively control the level of susceptibility to the CHN1 isolate, was identified in linkage group N14 of the C genome (Walsh et al., 1999).

Later the same chromosome N6 of the A genome was used to map with AFLP and SSR markers the *TuRB03* gene whose dominant allele ensures resistance to the CDN1 isolate (pathotype 4) and some isolates of pathotype 3 (Hughes et al., 2003). One AFLP and two SSR markers tightly linked with the *TuRB03* gene were offered for its screening (Table 3).

Other single dominant genes, *TuRB04* and *TuRB05*, were found in the differential rapeseed line 165 (Jenner et al., 2002). The *TuRB04* gene controls extreme resistance to some TuMV isolates, while *TuRB05* is responsible for a hypersensitive or necrotic response (HR), which restrains systemic dissemination of the virus. Interaction between *TuRB04* and *TuRB05* ensures extreme resistance (possibly, immunity) of *B. napus* plants to the TuMV isolates of pathotypes 1 and 3.

***B. rapa* (A genome).** Analyzing a splitting population of B1S1 backcrosses – descendants of the resistant RLR22 line – with the use of RFLP and SSR markers resulted in identification and mapping of two genes jointly controlling resistance to pathotypes 4 (CDN1 isolate) and 3 (CZE1 isolate). The *retr01* gene, with its recessive expression, is located on chromosome A04 and linked with the pN202e1 marker. The second gene, dominant *ConTR01*, was mapped to chromosome A08 between the markers pO85e1 and pO85e2. The *retr01* gene is the first registered example of a recessive resistance gene mapped in *Brassica* plants (Rusholme et al., 2007).

Chinese researchers (Zhang et al., 2008) identified two more QTL, *Tu1* and *Tu2*, associated with TuMV resistance at the seedling stage. The *Tu1* locus was mapped between the RAPD marker A04-850 and AFLP marker CA_TG270 in linkage group LG5, and *Tu2* in group LG10. Two additional QTL, linked with TuMV resistance in adult plants under field conditions, were localized in groups LG3 and LG4, respectively. Flanking markers for these loci are presented in Table 3.

For bok choy (*B. rapa* ssp. *chinensis*), TuMV resistance genes were mapped by Xinhua et al. (2009, 2011). After 180 genotypes of the F₂ population from the resistant line Q048 had been evaluated, the bulk analysis of resistant and susceptible backcrosses (10 genotypes in each bulked sample) was performed using AFLP markers (36 polymorphic pairs of primers earlier selected from 240). Monogenic control of resistance was shown, and the dominant *TuRBCH01* gene was mapped to linkage group R6 between the markers EaccMctt3 (7.8 cM) and EatcMcacl (20.3 cM) (Xinhua et al., 2009). Afterwards, the map was saturated with AFLP and SSR markers, with a total coverage of 1123 cM and an average interval between markers of 5.43 cM. The *TuRBCH01* gene was associated with linkage group R06 flanked by the AFLP markers E36M62-3 and E44M48-1 (Xinhua et al., 2011).

One more recessive resistance gene, *retr02*, was isolated by Qian et al. (2013) in the F₂ population obtained from the TuMV (pathotype C4) resistant line BP8407. At the initial stage, the authors conducted a bulked segregant analysis using SSR markers. Parent forms, F₁ hybrids, and two bulked samples were examined, involving 10 resistant and 10 susceptible F₂ genotypes in each sample. The SSR marker BC84, localized in scaffold000048, was associated with resistance to TuMV-C4. To make gene localization more precise, 145 InDel markers were developed and tested. As a result, 4 polymorphic ones were selected and put to use in the individual screening of 239 F₂ representatives. The *retr02* gene was mapped between the markers BrID10694 (scaffold000060) and BrID101309 (scaffold000104) on chromosome A04. In scaffold000104, the authors identified by BLAST analysis the *Bra035393* sequence, homologous to the sequence AT5G35620 in *Arabidopsis* (recessive resistance gene *lsp*). After the *Bra035393* locus had been sequenced in 52 resistance and 13 susceptible genotypes, the authors identified SNP variants associated with resistance (in exon 3, homozygous resistance forms all had A at position 455 bp, susceptible homozygotes had G at this position, and heterozygotes had A and G) (Qian et al., 2013).

Later, a single-nucleotide insertion (G) was detected at the exon/intron boundary in resistant forms; it was found to be responsible for missplicing and non-functional protein formation (Li et al., 2016). To identify this insertion, dCAPS and KASP markers were developed, which makes the use of MAS methods applicable in the selection of resistant forms, homozygous in the recessive allele of the *retr02* gene.

A dominant resistance gene, *TuRB01b*, that confers immunity to the virus isolate UK 1 (pathotype 1 of TuMV) was identified in the Chinese cabbage cultivar Tropical Delight. The *TuRB01b* locus was mapped using RFLP techniques on chromosome A06 that was flanked by RFLP markers pN101e1 and pW137e1 (Lydiat et al., 2014). Comparative mapping confirmed that chromosome A06 of *B. rapa* was equivalent to chromosome 6 of the *B. napus* genome and that the map position of *TuRB01b* is similar to that of *TuRB01* or *TuRB03* in *B. napus* (Walsh et al., 1999; Lydiat et al., 2014). Hence, an assumption was made that *TuRB01*, *TuRB01b* and *TuRB03* represent the same cluster of resistance genes and may even be allelic (Lydiat et al., 2014).

On the shorter arm of the same chromosome (A06), in the region flanked by SSR markers H132A24-s1 and KS10960, one more gene of resistance to TuMV (isolate C4), *TuRB07*, was localized while studying the resistant *B. rapa* line VC1 (Jin et al., 2014). Comparing it with the reference genome of cv. 'Chiifu' revealed that *TuRB07* was associated with the *Bra018863* gene of the CC-NBS-LRR class.

Thus, TuMV resistance in *B. napus* was under monogenic control mainly by isolate- or pathotype-specific dominant genes (Walsh et al., 1999; Jenner et al., 2002; Hughes et al., 2003). Contrariwise, *B. rapa* demonstrated multigenic control of resistance (additionally to the monogenic one) with broad-spectrum effect, and genes in that case often had recessive inheritance (Rusholme et al., 2007; Qian et al., 2013). Prevailing monogenic resistance in *B. napus* may be explained by possible emergence of this species from one of infrequent interspecific crosses between *B. rapa* and *B. oleracea*. Since

Table 3. Characterization of markers associated with resistance to turnip mosaic virus in *Brassica* spp.

QTL/ resistance gene	Chromosome/linkage group	Marker	Marker type	Reference
<i>B. napus</i> L.				
<i>TuRB01</i>	N6	pO120b	RFLP	Walsh et al., 1999
<i>TuRB02</i>	N14	pW133a	RFLP	
	N14	pR113bNM		
<i>TuRB03</i>	N6	sNRB93	SSR	Hughes et al., 2003
	N6	sS1949		
	N6	EtcMcac1	AFLP	
<i>retr01</i>	R4	pN202e1	RFLP	Rusholme et al., 2007
<i>ConTR01</i>	R8	pO82e2	RFLP	Rusholme et al., 2007
		pO85e1		
<i>B. rapa</i> L.				
<i>Tu1</i>	LG5	A04-850	RAPD	Zhang et al., 2008
		CA_TG270	AFLP	
		E31M48470		
		STS3-e32m50-447-320	STS	
		STS1-e31m48-437		
<i>TuRBCH01</i>	R6	E36M62-3	AFLP	Xinxua et al., 2011
	R6	E44M48-1		
	R6	EatcMcac1		
	R6	EaccMctt3		
<i>retr02</i>	A04	BrID10694	InDel	Qian et al., 2013
		BrID101309		
		BC84	SSR	
<i>TuRB01b</i>	A06	pN101e1	RFLP	Lydiate et al., 2014
		pW137e1		
<i>TuRBCS01</i>	A04	BrID10723	InDel	Li et al., 2014
		SAAS_mBr4055_194	SSR	
<i>TuRB07</i>	A06	H132A24-s1	SSR	Jin et al., 2014
	A06	KS10960		
<i>retr02</i>	A04	CAPS-BsII	CAPS	Li et al., 2016
		KASP_retr02	KASP	
		CA_TG270	AFLP	
		E31M48470		
		STS3-e32m50-447-320	STS	
		STS1-e31m48-437		

B. oleracea failed to manifest extreme forms of resistance, *B. napus* could inherit from *B. rapa* only single resistance genes (Walsh, Jenner, 2002).

Conclusion

The pathogens discussed in this review seriously affect the yield of cultivated *Brassica* crops. Growing resistant cultivars is an effective way of infection control. In the past two decades, application of molecular genetic methods enabled researchers to identify and map resistance genes in cruciferous crops, understand principles of their functioning, and develop molecular markers for their identification.

The size of available information on marker-aided identification of the genes controlling resistance to pathogens is not the same for different *Brassica* spp. In the cases of *B. napus* and *B. carinata*, resistance genes have been mapped only for individual pathogens (TuMV and black rot, respectively). Genes of resistance to black rot and downy mildew are studied well enough for *B. oleraceae*, and to all three pathogens for *B. rapa*. In view of this, there is a need to go on with research efforts aimed at identification of new resistance-controlling genes and QTL and development of new markers to expand the applicability of MAS methods and introduce them into *Brassica* crop breeding practice.

On the whole, however, the number of markers developed to search for genes responsible for various types of resistance and efficient for molecular screening is sufficiently large, as far as the discussed *Brassica* spp. are concerned. Their introduction into breeding practice could accelerate the selection of resistant genotypes manifold and ensure pyramiding genes for resistance.

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