JOURNAL OF AGROBIOTECHNOLOGY 2023, VOL 14(2):28-43
e-ISSN: 2180-1983
http://dx.doi.org/10.37231/jab.2023.14.2.333
https://journal.unisza.edu.my/agrobiotechnology/index.php/agrobiotechnology/index

Validated Molecular Marker for Downy Mildew Disease Resistance Breeding of Sunflower: A Short Review

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Received: 05/05/2023, Accepted: 07/08/2023, Available Online: 15/08/2023

ABSTRACT

The oomycete pathogen *Plasmopara halstedii* responsible for sunflower downy mildew (DM), that is a significant and important disease that greatly affects the economy. As of now, there is no non-race-specific resistance for this disease and breeders are depended on race-specific resistance to control DM disease. On the other hand, using conventional breeding procedure introgression of the DM resistance genes is a long-term task due to the highly virulent and aggressive nature of the *P. halstedii* pathogen. Molecular markers that can be applied at the seedling stage, offers rapid response for selection with higher precision as well as a lower cost. There are currently 36 downy mildew resistance genes (R genes), designated as Pl (Pl1-Pl36, Plhra, and PlArg, in sunflowers, each with a unique linkage group (LGs). The availability of DM resistance genomic data of sunflower, related to Single Nucleotide Polymorphisms (SNP) based markers with mine allelic diversity maximize the opportunity of utilizing Marker assisted selection (MAS) techniques for downy mildew resistance breeding. This review highlights the available genetic marker and their utilization at MAS techniques for enhancing downy mildew disease resistant breeding program of sunflowers.

Keywords: Sunflower, downy mildew disease, *Plasmopara halstedii* , marker assisted selection (MAS)

INTRODUCTION

Sunflower is one of the dominant oil crops successfully addressed up to 12% of the global vegetable oils and 10% of the total edible oil (FAOSTAT, 2018). It is representing the second significant crop after maize (Gerald *et al.,* 2017) based on hybrid breeding whereas ranks fourth among the oil producing crops such as palm, soybean and canola (Rauf *et al.,* 2017). The sunflower, *Helianthus annuus* L., is an annual, monoecious, dicotyledonous plant that is a member of the Asteraceae family (Nabipour *et al.,* 2021), having chromosome number 2n =34 (Darvishzadeh *et al.,* 2010), with an estimated 3000 Mbp genome size (Kolkman *et al.,* 2007). The diversity of

the sunflower germplase is due to its large genome size, which even larger than Arabidopsis (125 Mbp), Rice (430 Mbp), Sorghum (750Mbp), Tomato (950 Mbp) or even Soybean (1100 Mbp) (Rashid *et al.,* 2011). Sunflower oil has multiple uses in both food and non-food industries (biofuel, lubricants, surfactants, polymer synthesis). Standard sunflower oil is naturally rich in polyunsaturated linoleic acid that makes up about 70% of the total sunflower oil content and the second most abundant is monounsaturated oleic acid contributing with 20% (Cvejić *et al.,* 2014a). High-oleic acid content of sunflower oil derived its higher demand on the market due to its heart-healthy properties (Dimitrijević *et al.,* 2017).

Similar to other crops, sunflower production is often hindered by many factors, including biotic (e.g., diseases, pests, birds, etc.) and abiotic stresses (e.g., drought, waterlogging, and high and low temperature). More than 30 phytopathogenic microorganisms, mostly fungi, can be found in sunflower, which, depending on the climate, can significantly lower yield and product quality (Regina, 2014). According to Hussain *et al.* (2018) diseases are responsible for an average annual loss of 12% of the world production of sunflower, this being the most limiting factor for crop production in most regions. The practice of resistance against disease in crops is widely acknowledged and considered as most efficient and environmentally responsible method of reducing disease infestation. To be successful in breeding for disease resistance, the sunflower breeder must be thoroughly acquainted with general principles of resistance breeding with trait specific varietal improvement process. Exploitation of available plant genetic resources regarding tolerance gene and incorporate in the targeted genotypes is the basic of disease resistance varietal development process. Generally, trait incorporation is a laborious task, required to do backcross breeding handling a large population. Due to linkage effect of gene probability the unwanted gene transfer hampers the total effort. Using specific molecular markers helps confirm the presence of targeted traits at an early stage provide additional benefits of handling limited populations. In this dynamic era specific area-based knowledge of the recent progress help for the better tuning of anyone's work. There for the aim of this task is to know the progress of MAS based selection for DM resistance breeding of sunflower.

DOWNY MILDEW DISEASE OF SUNFLOWER

Leaf chlorosis, dwarf seedlings with white sporulation on beneath of the leaves, downy mildew of sunflowers is known as a seedling disease (Fig. A) that can cause up to a 100% yield loss under favourable conditions and vary from year to year based on environmental factors (Maryam, 2017; Robert *et al.*, 2012; Molinero-Ruiz *et al.*, 2003)). Due to its high capacity to acquire unique virulence and its widespread distribution, downy mildew continues to pose the biggest threat to the production of sunflowers.

Origin, spreading and global distribution of Sunflower Downy Mildew (SDM) disease

In 1946, firstly the SDM pathogen was recognized in sunflower fields of former Yugoslavia (in Croatia and Serbia). Then it quickly spread other Eastern European countries such as Romania, Bulgaria, Hungary, Russia and considered as a first route of spreading the disease. On the others, a second wave of this diseases was declared when it was founded at Uruguay, Brazil and Paraguay which was considered as outbreaks from Chile (Otmar, 2019). According to Viranyi (2018), there have been no reports of DM infections in Oceania, while the number of reports is maximum in Europe (26 countries), followed by Asia (13), Africa (8), South America (5), and North America (3). Oospore-contaminated seeds are almost certainly exchanged, which results in the long-distance dispersal of SDM. These imported seeds were either used by breeders to increase their genetic pool for breeding or by farmers to increase yields with new cultivars. Therefore, it is hardly surprising that SDM introductions in the context of worldwide marketplaces are no longer one-off events but rather frequent processes.

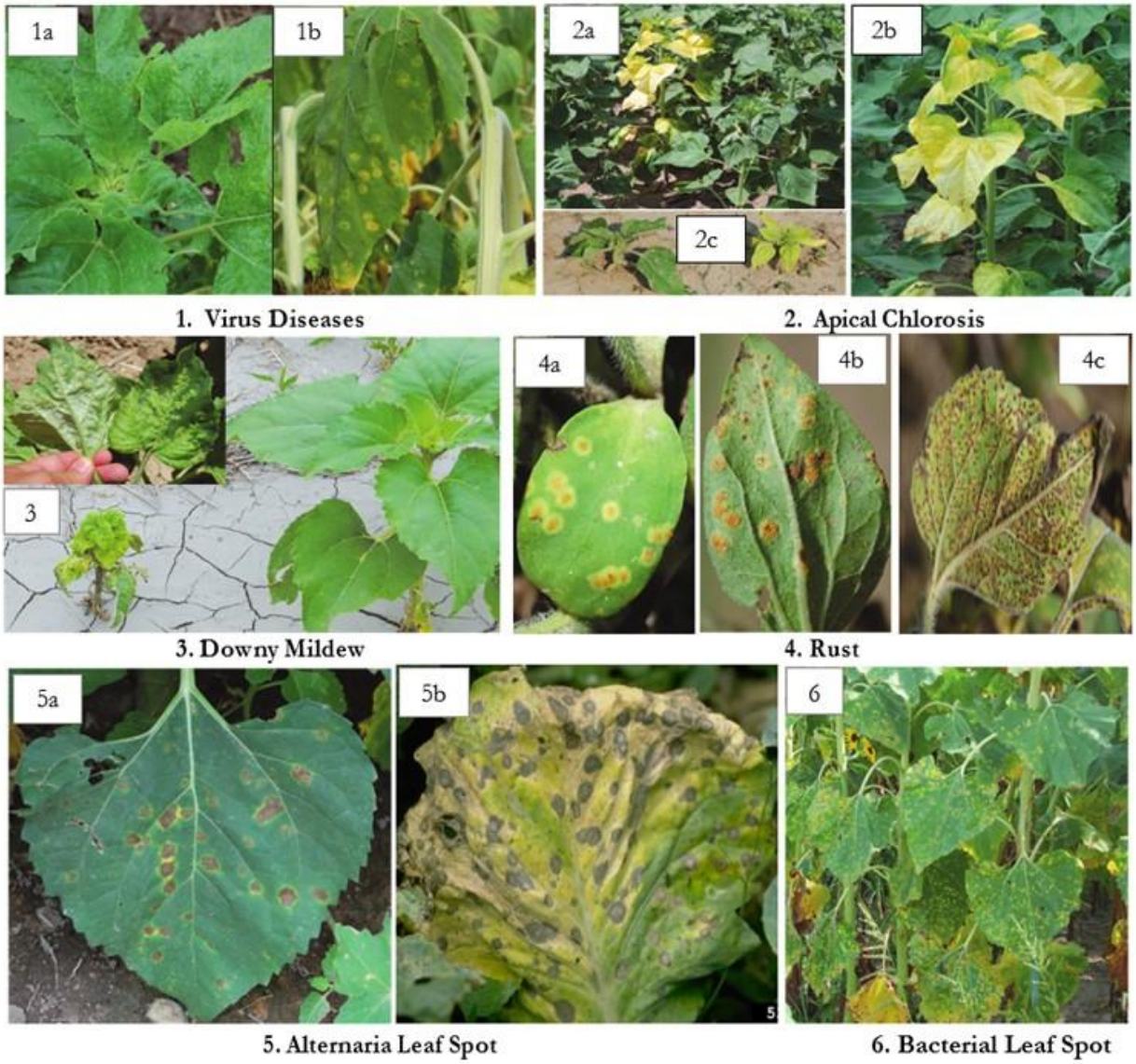

Fig. A (1-6). Sunflower disease profiles (extracted from Robert *et al.*, 2012)

UTILIZATION OF MOLECULAR MARKER

Given the context of current trends of population growth with climate change, traits relating to yield stability and sustainability should be a major focus of breeding. The fundamental basis of plant breeding is the selection of specific plants with desirable traits. In the commonly used breeding method, selecting desirable plants begins in early generations. For traits of higher heritability or dominant trait it is considerable, whereas for recessive trait need to wait until/unless homogeneity of the population take place which obtained from later generation that increased the expense of research. Use of molecular Marker based selection strategy is an effective tool for overcome this problem considering that the selected markers closely linked to underlying genes or chromosome (Song *et al.*, 2023; Hasan *et al.*, 2021; Nadeem *et al.*, 2017; Xu & Crouch, 2008).

Environmental factors and management practices have no influence on the regulation of molecular or DNA markers, which are not visible during the plant's developmental phases (Hasan *et al.*, 2021). As more molecular markers and genetic maps have been available, MAS has become possible for traits controlled by considerable quality as well as for quantitative trait loci (QTLs). The usefulness of a particular molecular marker

depends on its capacity to identify nucleotide polymorphisms that allow segregation between different molecular marker alleles (Nadeem *et al*., 2017). It can be used for monitoring the presence or absence of these genes in breeding populations and can be combined with conventional breeding approaches to increase the efficiency of the program (Salgotra & Stewart, 2020). Marker assisted selection (MAS) breeding has been used to effectively integrate major genes or quantitative trait loci with large effect into widely grown varieties (Fig. 1).

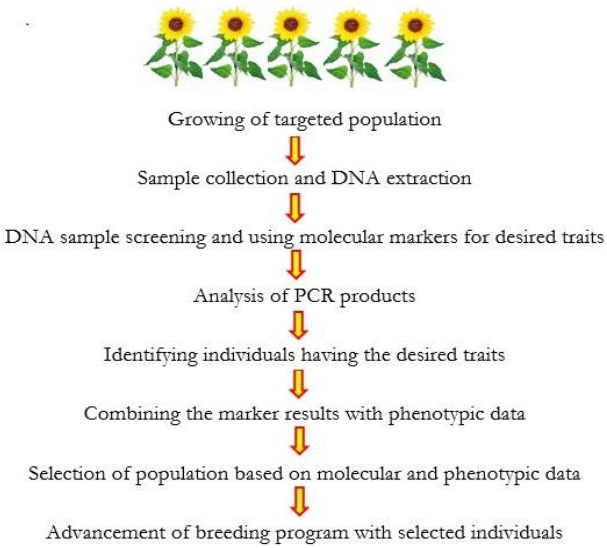

Fig 1. Basic procedure for use of molecular marker in breeding program

Use of molecular marker against Diseases tolerant of Sunflower Breeding Program

Molecular markers are crucial for understanding genome organization and provide important advantages in the means of development of new lines (Hvarleva *et al*., 2009) and determination of differentiation between initial germplasm (Santalla *et al*., 1998). The development of molecular markers in sunflower is at an advanced level and different types of markers have been developed for marker-assisted selection (MAS) over the years. There are numerous different molecular markers available which can be used in sunflower breeding. Pérez-Vich and Berry (2010) described three different generations of markers in sunflower research: firstly, anonymous deoxyribonucleic acid (DNA) markers like RFLP (Restriction Fragment Length Polymorphism), RAPD (Random Amplified Polymorphic DNA), AFLP (Amplified Fragment Length Polymorphism) and genomic SSR (Simple Sequence Repeat) markers were developed (Al-Chaarani *et al*., 2002; Berry *et al*., 1995; Gentzbittel *et al*., 1995; Lawson *et al*., 1998; Lu *et al*., 2000; Quagliaro *et al*., 2001; Tang *et al*., 2002). Usage of several molecular markers combined with numerous linkage maps makes it possible to develop a hybrid line that provides required properties (Knapp *et al*., 2001). There are several linkage maps available to use for marker assisted selection programmes. Researchers completed the first linkage map of sunflower in 2002 (Tang *et al*., 2002) and this was improved by another research group in 2003 through usage of new recombinant inbred lines population with SSR markers (Yu *et al*., 2003). Another research group accomplished the genetic mapping of the fertility restoration gene by using SSR and TRAP (Targeted Region Amplified Polymorphism) markers (Yue *et al*., 2010). Molecular markers related to different downy mildew resistance genes have been identified by bulk segregant analysis methods (Michelmore *et al*., 1991). Mapping studies completed by RFLP and RAPD markers for identification of Pl1 (Mouzeyar *et al*., 1995), STS (Sequence Tagged Site) markers for identification of Pl5/Pl8 cluster (Radwan *et al*., 2004), and SSR markers for identification of Pl6 and Pl13 locus. The Pl13 could be a useful source of resistance to the four major races of downy mildew and can be successfully transferred to different genetic backgrounds (Gulya *et al*., 2010). The identified markers closely linked to downy mildew resistance are expected to greatly enhance the efficiency of breeding using MAS (Mulpuri *et al*., 2009). Another study showed that Plarg loci provide resistance all known *Plasmopara halstedii* races (Mouzeyar *et al*., 1995).

Sunflower is susceptible to many yield-limiting diseases, which are largely caused by pathogens that have coevolved with sunflower for thousands of years (Harveson *et al*., 2016). More than 90 sunflower diseases caused by 30 different pathogens have been reported worldwide (Table 1). Among them diseases caused by different fungi present the most serious problem. Broomrape; the parasitic angiosperm, is in the second place, viruses and bacteria in third and fourth. The most common diseases of sunflower are caused by fungi and oomycetes these include rust (*Puccinia helianthi* Schwein.), downy mildew (*Plasmopara halstedii* Farl.) Berl. & de Toni), Verticillium wilt (*Verticillium dahliae* Kleb.), Sclerotinia stalk and head rot (*Sclerotinia sclerotiorum* Lib.) de Bary), Phoma black stem (*Phoma macdonaldii* Boerema), *Rhizopus* head rot (*Rhizopus* spp.), Charcoal rot (*Macrophomina phaseolina* Tassi Goid) and Phomopsis stem canker (*Diaporthe* spp.).

Table 1. List of the most common sunflower diseases with their causal organism (Škorić, 2012)

Disease	Pathogen
Downy mildew	*Plasmopara halstedii*
Broomrape	*Orobanche cumana*
White rot	*Sclerotinia sclerotiorum*
Stem canker	*Diaporthe helianthi*
Alternaria blight	*Alternaria helianthi, A. helianthinficiens*
Rust	*Puccinia helianthi*
Phoma black stem	*Phoma macdonaldii*
Virus	*Sunflower chlorotic mottle virus*
Verticillium wilt	*Verticillium dahliae*
Charcoal rot	*Macrophomina phaseolina*
White blister rust	*Albugo tragopogonis*
Fusarium wilt	*Fusarium* spp.
Rhizopus head rot	*Rhizopus* spp.

Sunflower breeders have achieved significant results in finding genes for resistance or high tolerance to certain diseases in wild species and incorporating them into cultivated sunflower genotypes possessing high combining ability. This provides the opportunity to utilize and practices most convenient and economic marker-based selection techniques for varietal improvement of sunflower against major diseases.

Resistant genes and their utilization for Downy mildew resistance breeding through MAS

Traditional plant breeding mostly entails choosing superior individuals based on phenotype utilization that was time-consuming, expensive, and unreliable some extent due to genotype-environment interactions. Molecular markers are highly treasured in plant genetics that have played a prominent and versatile role in breeding for cultivar improvement (Veluru *et al.,* 2020). The advancement of molecular methods in plant breeding has significantly broadened the identification of various R-genes. The recognition of specific pathogen effectors by the products of specialized host genes, called R-genes, is necessary for the induction of plant defence signalling. R-genes convey resistance against the pathogen by producing R proteins (Knepper *et al.,* 2010). The identification of molecular markers tightly linked to R-genes allows indirect selection which reduces reliance on laborious and time-consuming screening procedures considered as a powerful and reliable tool in crop improvement (Hasan *et al*., 2021). Generally, but not always, host R-genes are dominant; however, there are a few examples of recessive R-genes as well. Once the nature and pattern of inheritance of the R-gene are known, next step is to find or identify tightly linked marker(s) that can be used for indirect selection in MAS. Resistance (*R*) against downy mildew in sunflower is, in most cases, governed by a single dominant gene (designated as *Pl*), although some partial and quantitative resistance have also been reported. To date, a total of 36 *Pl* genes, Pl_1–Pl_{35}, and Pl_{Arg} have been reported from the DM resistance pool in cultivated sunflower and its wild relatives (Table 2).

Table 2. Originating species of the designated downy mildew resistance genes of Sunflower (Guojia, 2019)

Gene	Linkage group	Source	Origin of *Pl* genes	Reference
Pl_1	8	AD66, RHA 265/RHA 266, HA 60	*Helianthus annuus*	Vrânceanu *et al.,* 1970; Gedil *et al.,* 2001
Pl_2	8	HA 61, RHA 274	*Helianthus annuus*	Zimmer and Kinman 1972; Vear, 1997
Pl_3	-	HA 61	*Helianthus annuus*	Vear and Leclercq 1971
Pl_4	-	HIR34	*Helianthus tuberosus*	Vear 1974; Vear *et al.,* 2008
Pl_5	13	RF-S11-5566-74-10, Novinka and Progress	*Helianthus tuberosus*	Miller and Gulya 1987; Bert *et al.,* 2001
Pl_6	8	HA 335, HA 336	*Helianthus annuus*	Miller and Gulya 1991; Roeckel-Drevet *et al.,* 1996
Pl_7	8	HA 337, HA 338, HA 339,	*Helianthus praecox*	Miller and Gulya 1991; Slabaugh *et al.,* 2003
Pl_8	13	RHA 340	*Helianthus argophyllus*	Miller and Gulya 1991; Radwan, 2003
Pl_9	-	RHA 274	-	Gulya *et al.,*1991
Pl_{10}	-	RHA 274, RHA 325	-	Gulya *et al.,* 1991
Pl_{Arg}	1	ARG-1575	*Helianthus argophyllus*	Seiler 1991; Dußle *et al.,* 2004
Pl_{11}	-	AMES 3235, PI 497250, RHA 274, PI 497938, DM-2	-	Rahim *et al.,* 2002
Pl_{12}	-	AMES 3235, PI 497250, RHA 274, PI 497938, DM-2	-	Rahim *et al.,* 2002
Pl_{13}	1	HA-R5	*Helianthus annuus*	Gulya, 1985; Mulpuri *et al.,* 2009
Pl_{14}	1	29004, HA-R4	Unknown wild sunflower species	Bachlava *et al.,* 2011
Pl_{15}	8	RNID	-	Romano *et al.,* 2010
Pl_{16}	1	HA-R4	Unknown wild sunflower species	Gulya, 1985; Liu *et al.,* 2012
Pl_{17}	4	PI 468435, HA 458	*Helianthus annuus*	Hulke *et al.,* 2010; Qi *et al.,* 2015
Pl_{18}	2	PI 494573, HA-DM1	*Helianthus argophyllus*	Qi *et al.,* 2016
Pl_{19}	4	PI 435414, HA-DM5	*Helianthus annuus*	Zhang *et al.,* 2017
Pl_{20}	8	PI 494578, HA-DM7	*Helianthus argophyllus*	Ma *et al.,* 2017
Pl_{21}	13	RHA 274	*Helianthus annuus*	Vincourt *et al.,* 2012
Pl_{22}	13	PMI3	*Helianthus tuberosus*	Pecrix *et al.,* 2018a
Pl_{23}	1	HIS33, INTER35	*Helianthus resinosus*	
Pl_{24}	1	HAS62	*Helianthus annuus*	
Pl_{25}	1	HAS40	*Helianthus annuus*	
Pl_{26}	2	HAS103	*Helianthus annuus*	Pecrix *et al.,*2018b
Pl_{27}	4	HIS32	*Helianthus tomentosus*	
Pl_{28}	4	HIS36	*Helianthus tomentosus*	
Pl_{29}	4	HAS85	*Helianthus annuus*	

Pl$_{30}$	11	HAS6	-	
Pl$_{31}$	13	HAS42	*Helianthus annuus*	
Pl$_{32}$	13	HAS54	*Helianthus annuus*	
Pl$_{33}$	4	TX16R	*Helianthus annuus*	Jan and Gulya 2006; Liu *et al.,* 2019
Pl$_{34}$	13	PI 413157, RHA 428	*Helianthus annuus*	Miller *et al.,* 2002; Talukder *et al.,* 2019
Pl$_{35}$	1	PI 494576, HA-DM6	*Helianthus argophyllus*	Qi *et al.,* 2019

These genes were found in different accessions, and *Pl* alleles are dominant. *Pl*$_1$ and *Pl*$_2$ are the most common genes, which are present in almost all breeding specimens of sunflower (*Kucherenko et al.,* 2022). However, continuous use of specific resistance material in the breeding programe reduce the virulent and make ineffective by the rapid genetic breakdown due to the coevolution between the pathogen and sunflower host (Viranyi *et al.,* 2015). Research finding from Gulya *et al.* (2010) and Ahmed *et al.* (2012) confirmed that *Pl*6 and *Pl*7 have already been ineffective against new races of *P. halstedii,* this was because of their rapid utilization in breeding program. On the others research down by Gilley *et al.* (2016) summarized that only the *Pl*$_{arg}$, *Pl*$_{15}$, *Pl*$_{17}$, *Pl*$_{18}$, and *Pl*$_{33}$ genes remained effectively resistant against a total of 185 *P. halstedii* isolates collected from North Dakota, South Dakota and Nebraska sunflower production regions in the United States when a total of twelve known DM R genes were tested, including *Pl*$_1$, *Pl*$_2$, *Pl*$_5$, *Pl*$_6$, *Pl*$_{13}$, *Pl*$_{15}$–*Pl*$_{18}$, *Pl*$_{21}$, *Pl*$_{33}$, and *Pl*arg. Recently, four additional novel DM R genes, *Pl*$_{27}$–*Pl*$_{29}$ and *Pl*$_{33}$, were identified in proximity to *Pl*$_{17}$ and *Pl*$_{19}$ on chromosome 4 by Pecrix (2018a and 2018b) and Liu (2019) which was highly effective toward the most predominant and virulent races of *P. halstedii* and have not been widely used for commercial sunflower production. The broad-spectrum DM resistance and similar position of these R genes make it infeasible to select individuals harboring respective R gene based on phenotyping.

Table 3. List of validated SSR and SNP markers for confirming downy mildew resistance gene of Sunflower

Gene	(Chromosome locations)	Markers	Original mapping population	References
Simple-sequence repeats (SSR)				
Pl$_1$	(LG8)	SCT06 (950 b)	RHA 279	Qi *et al.* (2011)
Pl$_2$	(LG9)	ORS-333	MC 29	Qi *et al.* (2011)
Pl$_2$	(LG9)	SFW-00211 and SFW-01272	117 F2 individual HA-89 MC 29	Qi *et al.* (2015)
Pl$_4$	(LG13)	ORS-316	HA-R3	Qi *et al.* (2011)
Pl$_{4u}$	(LG13)	ORS-799	Suncross 53	Qi *et al.* (2011)
Pl$_{4u}$	(LG13)	ORS-45	Suncross 53	Qi *et al.* (2011)
Pl$_5$	(LG2)	ORS-316	HA-R2	Qi *et al.* (2011)
Pl$_5$	(LG2)	ORS-630	HA-R2	Qi *et al.* (2011)
Pl$_6$	LG8	ORS328	RHA-419 × I3BC2 (VK585 × VK195)	Alekseevna *et al.* (2021)
Pl$_8$	LG8	ORS781	RHA-419 × I3BC2 (VK585 × VK195)	Alekseevna *et al.* (2021)
Pl$_{11}$	(LG13)	ORS-728 and ORS-45	Rf ANN-1742	Qi *et al.* (2012)
Pl$_{12}$	(LG11)	CRT-275 and ZVG-53	RHA 464	Talukder *et al.* (2014)
Pl$_{13a}$ and *Pl*$_{13b}$	(LG13)	ORS-316	HA-R6 and RHA 397	Qi *et al.* (2011)
*Pl*15	(LG8)	SFW01920, SFW00128,	HA-R8	Ma *et al.* (2018)

Gene	(Chromosome locations)	Markers	Original mapping population	References
		SFW05824 NSA_008457		
Pl18	(LG2)	CRT214 and ORS203	HA 89 and *H. argophyllus*	Qi *et al.* (2016)
Pl19	LG4	ORS963 and HT298	BC1F2:3 families derived CMS CONFSCLB1 and PI 435414	Zhang *et al.* (2017)
Pl_{33}	LG4	ORS644, ORS963, SFW04901 and SFW04052	TX16R	Liu *et. al.* (2018)
Pl_{har6}	(LG13)	ZVG-61 and ORS-581	HAR6	Bulos *et al.* (2013)
Pl_{arg}	(LG13)	ORS662, ORS509, ORS-316, NSA-001392, NSA-002798, linked to genes R4, R12, and PlA	HA-R3, HA-R2, HA-R8, RHA-397	Qi and Ma (2020), Alekseevna *et al.* (2021)
Single nucleotide polymorphisms (SNP)				
Pl8	LG13	SFW01497 and SFW06597	RHA 340/RHA 464	Qi *et al.* (2017)
Pl_{33}	LG4	NSA_006089 and NSA_008496	TX16R	Liu *et al.* (2018)
Pl_{36}	LG13	SFW05743	803–1	Qi *et al.* (2022)
PlArg	LG1	NSA_007595 and NSA_001835	RHA 340/RHA 464	Qi *et al.* (2017)
Pl20	(LG) 8	SFW02745, SFW09076, S8_11272025, and S8_11272046	BC2F2 progenies (HA 89 and PI 49457)	Ma *et al.* (2017)
Pl18	LG2	SFW03013and SFW03060	(NMS) HA 89 × H. argophyllus accession PI 494573	Ma *et al.* (2020)
Pl20	(LG) 8	SFW01920 and S8_100385559	(NMS) HA 89 × H. argophyllus accession PI 494573	
Pl35	LG1	NSA_006938, NSA_005423, NSA_009758, and NSA_000630,	BC2F3 CONFSCLB1/PI 494576	

Diagnostic molecular markers would provide a timely and accurate selection tool for sunflower breeding programs. DNA-based markers have become important components of crop improvement; their importance has already been highlighted in enhancing global food production by improving the efficiency of conventional breeding programs (Kasha K. J 1999). DNA markers having tight linkage with the gene of interest (in this case, the R-gene), which is an important requirement for MAS in plant breeding (Ribaut *et. al.,* 1998).

CONCLUSION

Sunflower diseases are more difficult to control than many others due to the challenges of chemical application, the patterns of plant growth, which can make it difficult or impossible for machinery to enter the field, and in some cases, the need for aerial fungicide application. Therefore, many causes should not benefit from preventative measures for disease management. Hereditary resistance to diseases is highly favored, because it does not directly increase the production costs. Molecular breeding is the most advanced technology in this scientific era and the use of marker - assisted breeding is an example of how plant breeders achieving this objective of trait-specific crop improvement program. In principle, MAS is able to increase the precision of breeding where the breeder can select on a single plant basis for a trait (or trait combination), which may be neither appropriate or not by conventional phenotypic selection. However, the high cost of MAS will consider as a major obstacle and that can be potentially reduced considerably by using new marker technology like SNP. To dates more than 36 different race-specific DM resistance genes (*R* genes) in sunflower, denoted as *Pl* genes with a few quantitative trait loci (QTL) associated with DM non-race-specific resistance were identified and validated through MAS techniques. This type of distinct information obtained from the current study will be very useful resources for breeding of DM resistance in sunflower.

ACKNOWLEDGMENTS

The author(s) sincerely acknowledges to Bangladesh Institute of Nuclear Agriculture (BINA) and Universiti Malaysia Sabah (UMS) for the guidance and support for the preparation of this review manuscript and initiatives to publish.

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How to cite this paper:

M. S. H. Bhuiyan, M. A. Malek, Nazmul Alam Khana, Majharul Islam, Md. Hasan Sofiur Rahman & Md. Amirul Alam (2023). Validated Molecular Marker for Down Mildew Disease Resistance Breeding of Sunflower: A review. Journal of Agrobiotechnology, *14*(2), 28-43.