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UPDATES ON MOLECULAR MARKERS LINKED TO POTATO VIRUS Y (PVY) RESISTANCE GENES IN POTATO

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ABSTRACT: Potato is the leading non-grain food product in the world and stands third important food crop after wheat and rice. It is a future crop for ensuring food security in the developing world but it is affected by several biotic and abiotic factors which reduce the total yield. Among the biotic stresses, PVY is also the worldwide problem in potato causing serious damage. PVY^{O}, $PVY^{N,}$ and PVY^{C} are the main strains of PVY causing losses to potato cultivation. The complex strains of the PVY are responsible for different foliar and tuber symptoms in potato. The recombination between different strains creates new harmful strains (PVY^{NTN}, $PVY^{N:O}$, PVY^{N-Wi}) which from the last many years becomes a serious problem. Two types of resistance genes (HR and ER) are mapped on different potato species for PVY strains. Extreme resistance genes are reported in *S. tuberosum gp. andigenum* (Ry_{adg}), *S. stoloniferum* (Ry_{sto} and Ry_{fsto}) and *S. chacoense* (Ry_{chc}). Likewise, hypersensitive response (HR) genes are found in *S. tuberosum* (Ny_{tbr}, *Ny-1*, and *Ny-2*), *S. sparsipilum* (Nc_{spl}), and Sarpo Mira (*Ny-Smira*). Ry_{adg} and *Ny-2* genes were reported on chromosome no XI, Ry_{sto} and Ry_{fsto} on chromosome no XII, Ny_{tbr} and Nc_{spl} chromosome no IV, and Ry_{chc}, *Ny-1*, and *Ny-Smira* on chromosome no IX. Till now various molecular markers (AFLP, SCAR, RAPD, STS, CAPS, and RGL) linked to different PVY resistance genes are reported in various populations. Marker-based selection in the breeding programme can hasten the breeding process and reduce dependency on taking up chemical or other management practices.

KEYWORDS: Potato virus Y (PVY), extreme resistance (ER), Hypersensitive resistance (HR)

INTRODUCTION

Potato is the leading non-grain food product in the world and stands third important food crop after wheat and rice (Spooner & Hetterscheid, 2016) and a future crop for ensuring food security in the developing world (Tiwari et al., 2020). The area under potato worldwide is 19.2 Mha with a 376.8 MT annual production (Tiwari et al., 2021). More than 50 viruses affect potato production worldwide (Lal et al., 2021) but out of all, six viruses Potato leaf roll virus (PLRV), Potato virus Y (PVY), potato virus X (PVX), potato virus A (PVA), potato virus S (PVS), and potato virus M (PVM), is the most important viruses in terms of distribution and their effect on yields (Ahmadvand et al., 2012).

PVY problem in potato is worldwide and it is mainly transmitted through aphids in a non-persistent manner. It was reported to affect more than 9 families including 14 genera of the Solanaceae, such as potato, pepper, tomato, brinjal, tomato. PVY is a type member of the genus Potyvirus, family Potyviridae. The virus has a positive-sense single-stranded linear RNA genome responsible for coding for a large polyprotein. The yield losses by PVY in potato varies between 30 to 80% (Ahmadvand et al., 2012) depending upon the genotype. Globally, it's a common problem in most potato-producing areas especially in seed potato production because of the strict tolerance limit for certification. The virus is transmitted to the next generation through its vegetative mode of propagation from infected material. Under field conditions, it

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is transmitted naturally by several species of aphids i.e., more than 50 species with varying efficiency (Ragsdale et al., 2001). The common symptoms are yellowing of leaflets, mottling, vein necrosis, plant dwarfing, leaf-dropping, lower quality tubers, and under heavy infection premature plant death (Slater et al., 2020). Potyvirus is known for their tendency to evolve more rapidly through recombination's which might be to gain the selective advantage in a specific host/ in a given environment (Gibbs et al., 2017a)and it almost certainly originated in the Andes, where its hosts were domesticated. We have inferred the phylogeny of the published genomic sequences of 240 PVY isolates collected since 1938 worldwide, but not the Andes. All fall into five groupings, which mostly, but not exclusively, correspond with groupings already devised using biological and taxonomic data. Only 42 percent of the sequences are not recombinant, and all these fall into one or other of three phylogroups; the previously named C (common. The strains of PVY are distinguished based on their reactions toward a series of resistance genes present in potato. If a strain is eliciting hypersensitive (HR) response in genotypes of potato carrying the Ny gene, like 'Desiree' and 'Maris Bard' it was named as PVY^{O}. On the other hand, if the genotype, such as 'King Edward' carrying the *Nc* gene elicits HR response, the strain was as PVY^{C}. The strains not eliciting HR responses toward these two genes (*Ny* and *Nc*) in potato genotypes were named PVY^{N} (Jones 1990; Singh et al., 2008; Valkonen et al., 1997).

Till now various PVY strains (PVY^{O}, PVY^{N}, PVY^{NTN}, $PVY^{N\text{-}Wi}$, PVY^{C}, PVY^{Z}, PVY^{E}) are recognized which causes heavy losses to potato cultivation (Lacomme *et al*., 2017; Singh *et al*., 2008). The PVY^{O} and PVY^{C} strains were distinguished by their reactions with the potato Ny and Nc hypersensitivity genes (Gibbs *et al*., 2017b). The ordinary strain PVY^{O} is most prevalent in the majority of the potato growing areas. The symptoms and severity of PVY^{O} vary with potato cultivars, but generally, it causes mosaic, leaf necrosis followed by the leaf drop. The recombinant strains of PVY i.e., PVY^{NTN}, $PVY^{N\text{-}Wi}$ an $PVY^{N:O}$ induces characteristic veinal necrosis in tobacco, and therefore they are called necrotic strains. These strains are often associated with tuber syndromes i.e., potato tuber necrotic disease (PTNRD) in susceptible cultivars of potato (Beczner *et al*., 1984; Glais *et al*., 2002) and canoe-shaped cracks (Benedict *et al*., 2015) and hence pose a real threat for potato production. Since potato crop is mainly propagated through tuber so chances of virus spread across generations is more through infected tubers. Host resistance is the ultimate solution of this virus so many resistance genes are reported in wild and cultivated species. So the development of resistant variety by incorporating these resistance genes in a breeding programme is the most effective way to control this virus (Ana C. Fulladolsa *et al*., 2015). The utilization of wild species in potato breeding programme have already an intricate history due to their large secondary gene pool (Sood *et al*., 2021).

Mapping of resistance genes in potato species

Various extreme resistance (ER) and hypersensitive response (HR) genes are mapped for PVY resistance in potato. Hypersensitive response genes are effective against a single strain of PVY, related to cell death, and prevent the spreading of virus-cell to cell and extreme resistance genes are effective of all strains of PVY with strong suppression. Extreme resistance genes are reported in *S. tuberosum sp. Andigenum* (Ry_{adg}) (Dalla Rizza et al., 2006a; Kasai et al., 2000)based on nucleotide differences within

resistance gene-like fragments isolated from a potato plant carrying the Ry adg gene, which confers extreme resistance to potato Y potyvirus (PVY, *S. stoloniferum* (Ry_{sto} and Ry_{fsto}) (I. Cernák et al., 2008; Song & Schwarzfischer, 2008) and *S. chacoense* (Rychc) (Hosaka *et al*., 2001; Sato *et al*., 2006). Likewise hypersensitive response (HR) genes are found in *S. tuberosum* (Nytbr, Ny-1 and Ny-2) (Celebi-Toprak *et al*., 2002; K Szajko *et al*., 2008; Katarzyna Szajko *et al*., 2014), *S. sparsipilum* (Ncspl) (Moury *et al*., 2011) and Sarpo Mira (Ny-Smira) (Tomczyńska *et al*., 2014). Ryadg and Ny-2 genes were reported on chromosome no XI (Katarzyna Szajko *et al*., 2014), Rysto and Ryfsto on chromosome no XII (Flis *et al*., 2005; Milbourne *et al*., 1998), Nytbr and Ncspl chromosome no IV (Celebi-Toprak *et al*., 2002; Moury *et al*., 2011) Rychc, Ny-1 and Ny-Smira on chromosome no IX (Hosaka *et al*., 2001; Tomczyńska *et al*., 2014). These genes are used in the various breeding programme at the global level according to the prevalence of different PVY strains.

Molecular markers linked to different resistance genes

Till now various molecular markers linked to different PVY resistance genes are reported in different populations. Kasai et al. 2000 reported SCAR marker (RYSC3) linked to Ry_{adg} gene, likewise AFLP (TG 508, M45) marker (Dalla Rizza et al., 2006a; Hämäläinen et al., 1997), CAPS (ADG2) marker (Sorri et al., 1999), RGL (ADG1 and ADG2) marker (Hämäläinen et al., 1998) were also reported linked to this gene which are mentioned in table no 1. SSR (STM0003), AFLP (M35, M45), STS (YES3-3A and YES3-3B), SCAR ($SCAR_{ysto4}$), and CAPS (GP122) markers were reported by various workers which linked to extreme resistance gene Ry_{sto} in different potato populations (Brigneti et al., 1997; István Cernák et al., 2008; Dalla Rizza et al., 2006a; Heldák et al., 2007; Milbourne et al., 1998; Song et al., 2005; Song & Schwarzfischer, 2008). One CAPS (GP122) and ISSR marker (UBC857) linked to Ry_{fsto} gene were reported by Flis *et al*. 2005; Witek *et al*. 2006. Celebi-Toprak *et al*. 2002 reported RFLP marker (TG506) was linked to hypersensitive response Ny_{tbr} gene. For Ry_{chc} gene Hosaka *et al*. 2001 reported RAPD marker (38-530) linked to this gene. Szajko *et al*. 2008, 2014 reported SCAR (SC895) and CAPS marker (S1d11) linked to *Ny-1* gene and one CAPS marker (B11.6) linked to *Ny-2* gene. Tomczyńska *et al*. 2014 reported STS marker (Ry186) linked to *Ny-Smira* gene.

Use of linked markers in the breeding programme

Slater *et al*. 2020 screened Australian parental collection for PVY resistance gene *Ryadg* or *Rysto* with the help of STM0003, M45, and RYSC3 linked marker. These markers differentiate all the parental cultivars for PYV resistance and they concluded that these markers can be used in marker-assisted selection (MAS) for the breeding programme. Whitworth et al. 2009 evaluate *S. tuberosum ssp. Andigena* derived accessions for multiple PVY strains (PVY^{NTN}, $PVY^{N:O}$, PVY^{O}, PVY^{N}) with the help of ADG2, RYSC3 and RYSC4 linked markers. The presence of the marker was also in close agreement with potato virus Y (PVY) resistance in the cultivars/ clones. This study is helpful for breeders for the development of variety which will show durable resistance to PVY and pyramiding of divergent resistance genes. Dalla Rizza et al. 2006beye depth, shape screened potato germplasms for extreme resistance to PVY with the help of two molecular markers (RYSC3 and M45) and out of total germplasm 44% of accessions shown extreme resistance genes. Ottoman et al. 2009 evaluate segregating population of potato for Ry_{adg}

Table 1: Molecular marker linked to different PVY resistance genes

Gene	Species	Resistance response (HR/ER)	Chromosome location	Linked marker	Type of marker	Reference
Ry_{adg}	*S. tuberosum sp. Andigenum*	ER	XI	RYSC3	SCAR	Kasai et al., 2000
				TG508	AFLP	Hämäläinen et al., 1997
				ADG2	CAPS (*BbvI*)	Sorri et al., 1999
				ADG1	RGL	Hämäläinen et al., 1998
				ADG2	RGL	Hämäläinen et al., 1998
				M45	AFLP	Dalla Rizza et al., 2006a
Ry_{sto}	*S. stoloniferum*	ER	XII	STM0003	SSR	Milbourne et al., 1998; Song et al., 2005
				M35	AFLP	Brigneti et al., 1997
				M45	AFLP	Dalla Rizza et al., 2006a
				YES3-3A	STS	Song & Schwarzfischer, 2008
				YES3-3B	STS	Song & Schwarzfischer, 2008
				SCARysto4	SCAR	István Cernák et al., 2008
				GP122	CAPS (*Eco*RV)	Heldák et al., 2007
Ry_{fsto}	*S. stoloniferum*	ER	XII	GP 122	CAPS (*Eco*RV)	Flis et al., 2005
				UBC857	ISSR	Flis et al., 2005
				GP122	CAPS (*Eco*RV)	Witek et al., 2006
Ny_{tbr}	*S. tuberosum*	HR	IV	TG506	RFLP	Celebi-Toprak et al., 2002
Ry_{chc}	*S. chacoense*	ER	IX	38-530	RAPD	Hosaka et al., 2001; Sato et al., 2006
Ny-1	*S. tuberosum*	HR	IX	$SC895_{1139}$	SCAR	K Szajko et al., 2008
				S1d11	CAPS (*Mn/I*)	Katarzyna Szajko et al., 2014
Ny-2		HR	XI	$B11.6_{1600}$	CAPS (*Eco*RI)	Katarzyna Szajko et al., 2014
Nc_{spl}	*S. sparsipilum*	HR	IV			Moury et al., 2011
Ny-Smira	Sarpo Mira	HR	IX	Ry186	STS	Tomczyńska et al., 2014

gene, artificially inoculated with PVY^{O} strain via two molecular markers (RYSC3 and ADG2) and their results showed close agreement with ELISA assay. So the use of molecular markers can be an alternative tool to ELISA for the detection of PVY strain. Valkonen et al. 2008 Solanum stoloniferum, carries a dominant gene, Ry_{sto}, which confers extreme resistance (ER used two molecular markers (GP122 and STM00003) for the detection of Ry_{sto} gene in F_1 diploid populations which were derived from *S. stoloniferum* accession and these markers detected those populations which expressed ER to PVY. Likewise, Fulladolsa et al. 2015 used YES3-3B and RYSC3 markers linked to genes Ry_{sto} and Ry_{adg} respectively in their breeding population. Bhardwaj et al. 2015 screened 119 genotypes of potato for Ry_{sto} and Ry_{adg} gene via STM0003 and RYSC3 marker respectively and concluded that RYSC3 was the better marker for diagnostic of PVY resistance. A similar type of study was done by Sharma et al. 2014; Kneib et al. 2017; Bhardwaj et al. 2019; Fulladolsa et al. 2019; Byarugaba et al. 2021late blight, viruses and nematodes are

the most devastating. Varieties resistant to individual stress have been deployed but the production remained limited because of other biotic stresses affecting the crop. Potato cultivars having multiple disease resistance are urgently required to boost production. Resistance to late blight is both qualitative and quantitative while extreme resistance to PVY can be imparted by the single dominant genes Ryadg and Rysto. Likewise resistance to potato cyst nematode is mainly imparted by the single dominant H1 and Gro1-4 genes. All these genes have been mapped and tightly linked molecular markers are available to perform marker-assisted selection (MAS in different breeding populations for detection of PVY resistance via various linked molecular markers. Elison et al. 2020 used three linked markers (RYSC3, YES3-3B, and RY186) for simultaneous detection of three independent genes (Ry_{adg}, $Ry_{sto,}$ and Ry_{chc}) in multiplex PCR and concluded that this assay allows higher throughput and simplicity in developing varieties with multiple Ry genes.

CONCLUSION

It is now clear that different recombinant strains of PVY virus are emerging which can cause severe damage in the future. So, screening of more wild species for mapping of other resistance genes and used them in a breeding programme is the need of the hour. Using wild species where resistance genes were already mapped in a regular breeding programme is in the infancy stage. If they are not crossable to cultivated species breeder should them by either manipulating their ploidy level or by protoplast fusion techniques. The use of molecular markers linked to resistance genes will reduce time or cost compared to conventional phenotypic screening. Potato has a large secondary gene pool as compared to other crops so a new source of resistance should search in other wild species to broaden our experimental gene pool.

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