


REVIEW

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# Resistance to biotic and abiotic stress in potato: the origin of the genes and corresponding molecular markers

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## Abstract

The integration of molecular markers in the realm of potato genetics has opened new avenues for accelerating genotype analysis and developing improved varieties. Many markers linked to important features have been discovered so far and are consistently distributed across 12 chromosomes ( $x = 12$ ) of potato. Notably, the genes allied to disease resistance stand out as significant and prevalent. Molecular markers associated with these genes have revolutionized selection processes, making them faster and more effective. Besides, advanced technologies such as kompetitive allele-specific PCR, high-resolution melting assay, SNP-array, genotyping by sequencing, and genome-wide association study, are emphasizing the use of those molecular markers with greater accuracy to detect *R* genes aligning with the phenotypes. This review discusses advances in potato breeding for resistance against common stresses, focusing on progress made through molecular marker-assisted selection.

**Keywords** Genotyping, *R* genes, Resistance source, SNP marker, *Solanum tuberosum*

## Background

Potato, *Solanum tuberosum* L, is an associate of the Solanaceae family and one of the world's top four widely grown crops. The appeal of potatoes lies in their nutritious content and high production rate per unit of time and area, making them particularly valuable in underdeveloped nations (Islam et al. 2022). Apart from being a staple food, potatoes are widely utilized in various industries for the production of a diverse range of products. Furthermore, its vast range of applications, including food, alcohol, starch-based products, and raw materials,

have made it quite popular in industrialized countries (Awasthi and Verma 2017). Owing to the vital importance of potato, it is imperative to enhance potato production. Its yield potential, on the other hand, is often reduced due to its high susceptibility to numerous disease invasions including various soil-borne pathogens and viruses (Awasthi and Verma 2017; Chakrabarti et al. 2022). Such infestations increase the use of fungicides or insecticides for disease management which reduces the grower's profit margins (Islam et al. 2018). In addition to biotic pressures, abiotic factors, such as drought, low temperature, and salinity, have caused challenges for producers during potato cultivation (Kikuchi et al. 2015). Therefore, both biotic and abiotic factors play major roles as stressors for potato cultivation. Subsequently, identifying molecular markers that are used to screen potatoes for resistance to these stresses, can be a remedy to overcome those stresses (Mangal et al. 2023).

However, among the various stresses, late blight (LB), caused by *Phytophthora infestans*, is one of the most

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prevalent and disruptive diseases that affect potato cultivation worldwide (Islam et al. 2022). In the severely affected potato field, LB can cause deprivation of yield by 70–100% (Islam et al. 2018). In order to lessen the impact of the disease, a significant amount of fungicides was applied, which resulted in increasing the cost of 6.7 billion USD using fungicides for growers (Seidl Johnson et al. 2015). Moreover, potato viruses, such as potato virus Y (PVY), potato leaf roll virus (PLRV), potato virus M (PVM), potato virus S (PVS), potato virus X (PVX), and potato virus A (PVA), are other disease-causing agents that have also a significant impact on yield. Hence, minimizing the risks in potato production by viruses is justifiably a crucial concern in the breeding of potatoes (Bhardwaj et al. 2019; Slater et al. 2020; Kumar et al. 2022). Furthermore, potato cyst nematodes (PCN) caused by *Globodera rostochiensis* and *Globodera pallida* (Price et al. 2021), and root-knot nematodes caused by *Meloidogyne* sp. (Khan et al. 2023), affect the growth rate and physiology of potatoes, respectively, resulting in weight loss. However, to reduce the disease impact of nematodes, farmers usually apply granular nematicides (Grabau and Noling 2019) which cost a lot of money.

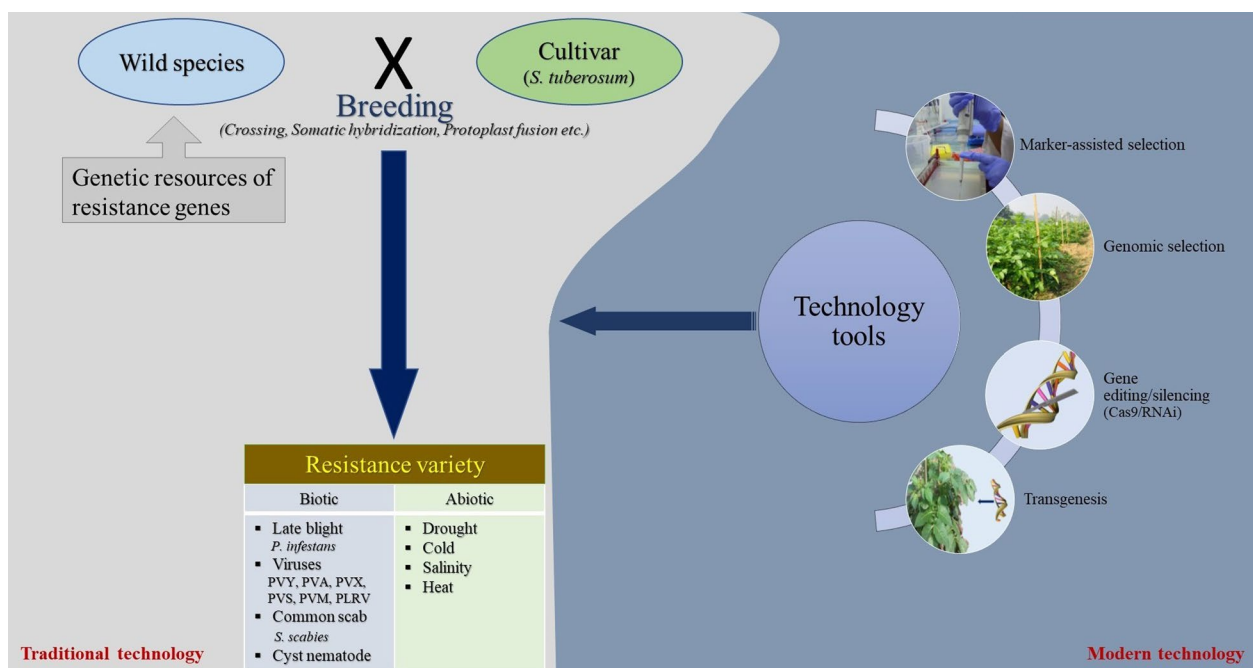
Like biotic stressors, potato is also more vulnerable to abiotic stressors than other plants. It is anticipated that, by the year 2050, the anticipated reduction in overall potato yield may potentially reach as high as 32% as a consequence of the influence of abiotic stress factors (Demirel 2023). Drought and salinity tolerance are said to be extremely low in potatoes (Kikuchi et al. 2015) due to their inability to acclimate to low temperatures and potato seedlings stop growing below 7 °C and experience chilling, frost, and death below −0.8 °C, −2 °C, and −3 °C, respectively (Yan et al. 2021). Besides, the rising temperatures and environmental pressures threaten the existence of wild potato relatives, which are crucial gene pools for breeding new potato varieties adapted to abiotic stress (Hussain 2016). In light of the aforementioned challenges, it is imperative for plant breeders to focus their efforts on developing crop varieties resistant to both biotic and abiotic stresses. The convergence of pathogens and climate change presents a dual challenge to crop cultivation, constraining yields through a combination of biotic and abiotic stresses (Haq et al. 2022).

Field evaluation and phenotypic screening in traditional breeding can span 10–15 years due to the need for multi-generational backcrossing (Tiwari et al. 2013). On the other hand, employing genotype analysis using a molecular marker to detect and select suitable species with desired traits has grown increasingly popular day by day (Caruana et al. 2019). This selection approach is known as marker-assisted selection (MAS). MAS uses a significantly cheap selection strategy per cultivar in

potato breeding compared to traditional phenotypic screening in the field (Slater et al. 2020). MAS identifies molecular markers, which corresponds to genes displaying the desired trait, from the genome of a particular species (Simko et al. 2013). It is also more reliable and precise since this method is independent of environmental conditions. Furthermore, the genetic map of potatoes is an integral part of the identification of molecular markers that are connected to the desired trait such as resistance to a certain disease (Caruana et al. 2019). Molecular markers can also be designed to identify quantitative trait loci (QTL), which are genetic loci responsible for controlling specific quantitative traits such as yield and tuber quality (Habe et al. 2019; Fenstermaker et al. 2023).

Hence, molecular markers can be used along with traditional breeding technology to pinpoint the exact genotype that expresses the desired attribute, such as disease resistance (Fig. 1). An informative marker has a strong relationship between the phenotypic trait and the gene and is close to the specific locus. Markers, such as simple sequence repeats (SSR), restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), sequence characterized amplified regions (SCAR), and cleaved amplified polymorphic sequence (CAPS), are the well-known molecular markers currently utilized in potato breeding (Kumar and Jorben et al. 2023). Furthermore, high-resolution melting analysis (HRM) is a relatively new technology that distinguishes amplicons of alleles with different haplotypes (one or more SNPs) (Nie et al. 2016; Meiyalaghan et al. 2018). HRM could detect homozygosity of morphological and genetic features in a single genetic map and identify resistant genes against numerous diseases (Nie et al. 2018).

However, it is critical to identify the exact disease-resistance gene using gene-specific markers. Several researches have been undertaken on different potato virus-resistant gene markers, including PVY (Bhardwaj et al. 2019; Slater et al. 2020), PLRV (Mihovilovich et al. 2014; Yermishin et al. 2016), and PVX (Fuentes et al. 2021; Liu et al. 2021). Additionally, a large number of researchers have generated LB-resistant potato varieties where the resistance genes' sources were taken mostly from potato wild-type varieties, *S. demissum* (6×), *S. berthaultii* (2×), and *S. stoloniferum* (4×) (Tiwari et al. 2013; Ramakrishnan et al. 2015). Such resistant genes against LB include *R1* (Ballvora et al. 2002; Khavkin et al. 2010; Rogozina et al. 2021), *R2* (Lokossou et al. 2009; Sokolova et al. 2014; Rogozina et al. 2021), *R3* (*a/b*) (El-Kharbotly et al. 1996; Tiwari et al. 2013; Rogozina et al. 2021), *Rpi-smira 1 & 2* (Jo et al. 2011; Tomczynska et al. 2014), *Rpi-bt1* (Oosumi et al. 2009; Ramakrishnan et al. 2015), *Rpi-blb1* (Naess et al. 2000; Tiwari et al. 2013), *Rpi-ber*



**Fig. 1** Harnessing the potato gene pools for enhanced resistance to biotic and abiotic stresses in new cultivars

(Park et al. 2009; Islam et al. 2018), and so on. Similarly, different resistant genes against potato cyst nematodes have also been reported including *H1* (Ellenby 1952; Asano et al. 2012; Chekushkina et al. 2020), *H2* (Strachan et al. 2019), *H3* (Bradshaw et al. 1998), *GroV1* (Jacobs et al. 1996), *Gro1* (Barone et al. 1990), and *Gpa2* (Asano et al. 2012).

This review focuses on addressing abiotic and biotic stress factors affecting potato cultivars. The main objective is to provide insights into resistance genes, their sources, and associated markers that can aid in identifying potato species resistant to common diseases and key abiotic factors. By doing so, it aims to expedite the cultivar selection process, enabling more efficient breeding programs and advancements in potato breeding.

## Molecular markers associated with biotic stress-resistant genes in potato

### Virus resistance genes and linked markers

Viral infections can be detrimental to crop production, resulting in reduced yields as the severity of the disease increases (Tiwari et al. 2022). There are approximately 50 viruses that can infect *Solanum* at various stages of growth and among them, six potato viruses are the most prominent due to their devastating yield impact (Kreuze et al. 2020). PVY is identified to be the deadliest virus for potatoes as it can decrease the yield from 30 to 80%. PLRV, the second most destructive disease, can reduce yield loss by up to 20 million tonnes per year (Kreuze

et al. 2020). On the other hand, the disease symptoms appear to increase in severity depending on certain combinations of viruses; such as the combinations between the PVY, PVS, PVX, PVM, and PVA (Kreuze et al. 2020).

As a result, constant efforts were carried out to introduce resistance genes into commercial potatoes to lessen the harm (Ramakrishnan et al. 2015). Virus-resistance genes have been found in a variety of wild potato species. Extreme resistance genes for PVY have been isolated from *S. Stoloniferum* (4X) or *S. tuberosum* ssp. *andigena* (2X) (Hamalainen et al. 1998; Ramakrishnan et al. 2015). R genes, *Ry<sub>adg</sub>* and *Ry<sub>stow</sub>* have been shown to exhibit resistance against PVY (Table 1), localized on chromosomes XI and XII (Fig. 2), are from *S. tuberosum* ssp. *andigena* (2X) and *S. stoloniferum* (4X), respectively (Ramakrishnan et al. 2015; Yermishin et al. 2016). Moreover, R genes, *Ny<sub>tblr</sub>* and *Ry<sub>chc</sub>* are located on chromosomes IV and IX, from *S. berthaultii* (2X) and *S. Chacoense* (2X), respectively (Table 2) (Park et al. 2005; Ramakrishnan et al. 2015). Hence, various molecular markers linked to such R genes have been developed to identify resistant potato varieties (Ramakrishnan et al. 2015). For instance, markers SC895 and TG506 are connected with *N*-genes, *Ny<sub>-1</sub>* and *Ny<sub>tblr</sub>*, known to exhibit hypersensitivity to the potato virus Y (Additional file 1: Table S1). On the other hand, markers RYSC3 (Sharma et al. 2014; Kneib et al. 2017; Bhardwaj et al. 2019; Slater et al. 2020), M45 (Kneib et al. 2017; Bhardwaj et al. 2019; Slater et al. 2020), ADG1, and ADG2 (Hamalainen et al. 1998) are

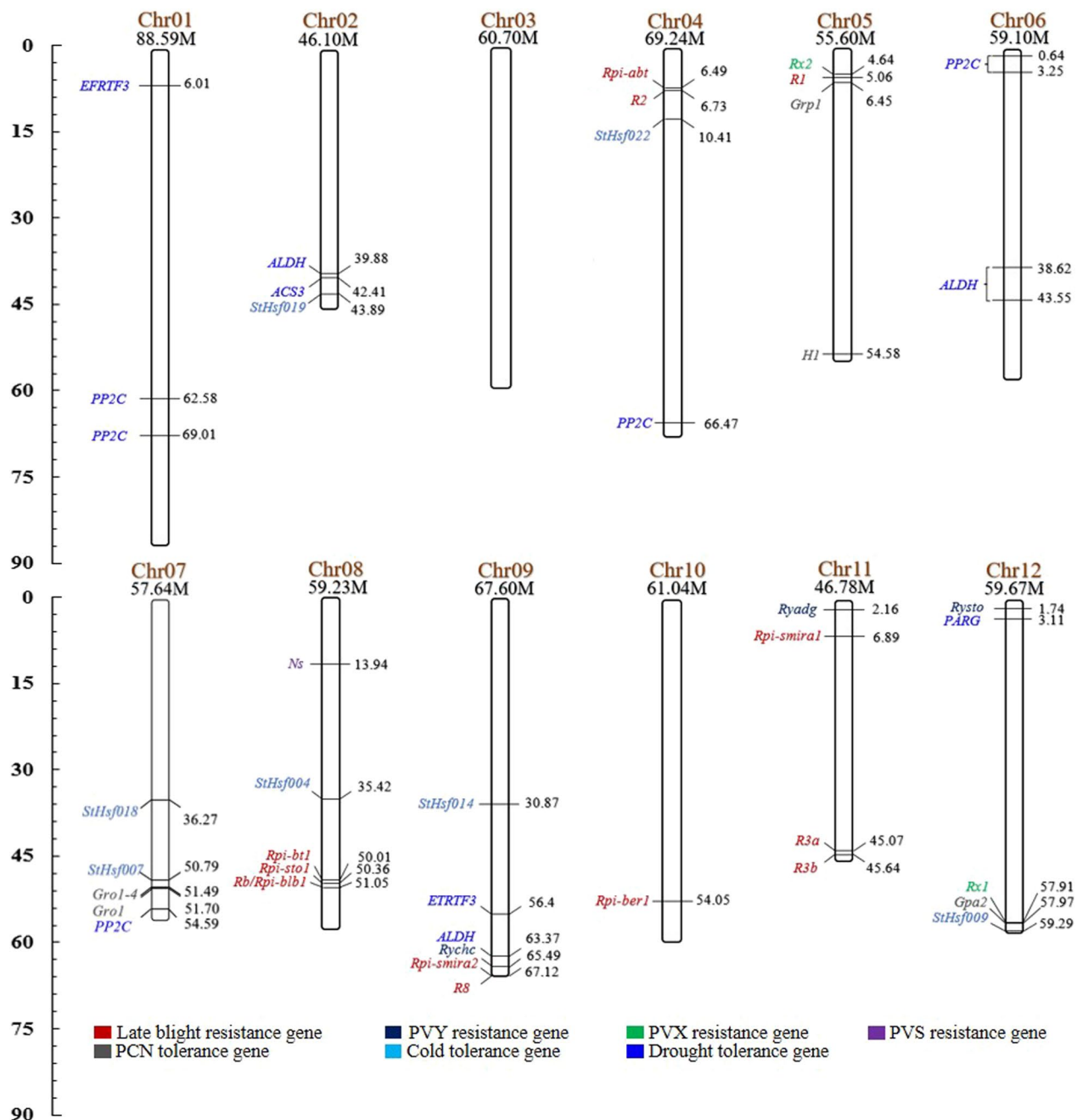
**Table 1** Association of markers with viruses, late blight, and potato cyst nematode resistance genes in potato

SL	Marker Type	Marker Name	Forward sequence	Reverse sequence	Gene	ER	References
1	SSR	STM 0003	GGAGAATCATAACAACCAG	AATTGTAACCTGTGTGTGTG	<i>Ry<sub>sto</sub></i>	PVY	Bhardwaj et al. (2019), Slater et al. (2020)
2	ESTS	Yes3-3A	TAACTCAAGCGGAATAACCC	AAATTCACCTGTTTACATGCTTCTTGTG	<i>Ry<sub>sto</sub></i>	PVY	Bhardwaj et al. (2019), Song and Schwarzfische, (2008)
3	ESTS	Yes3-3B	TAACTCAAGCGGAATAACCC	CATGAGATTGCCTTTGGTTA	<i>Ry<sub>sto</sub></i>	PVY	Song and Schwarzfische (2008)
4	SCAR	RYSC3	ATACACTCATCTAAATTTGATGG	AGGATATACGGCATCATTTTTCCGA	<i>Ry<sub>adg</sub></i>	PVY	Kneib et al. (2017), Sharma et al. (2014)
5	AFLP	M6	ACATGATATAAGTTGATATGGAGAAT	GTCCTTTGTCTTTTCTGCTATGTA	<i>Ry<sub>adg</sub></i>	PVY	Herrera et al. (2018)
6	AFLP	M45	GACTGCGTACATGCAGCT	GATGAGTCTGAGTAAGGA	<i>Ry<sub>adg</sub></i>	PVY	Kneib et al. (2017), Slater et al. (2020)
7	STS	RY186	TGGTAGGGATATTTCTTAGA	GCAAATCCTAGGTTATCAACTCA	<i>Ry<sub>chc</sub></i>	PVY	Biryukova et al. (2020), Rogozina et al. (2019)
8	SCAR	Ry364	CTATTATAAGTCTGGTACTAGGACG	GGCTATATGTTCAATGAATTCATGCTAA	<i>Ry<sub>chc</sub></i>	PVY	Klimenko et al. (2019)
9	PCR	5Rx1	TCAGGGCAAACCCTAACAC	ATCGGCCTAGAGTGACATCG	<i>Rx1</i>	PVX	Shaikhaldein et al. (2018)
10	PCR	PVX	ATCTTGGTTTGAATACATGG	CACAATATTGGAAGGATTC	<i>Rx1</i>	PVX	Mori et al. (2011)
11	PCR	106Rx2	GGAGAAATCCGCAATGTAAC	CTTGTCAAAGAAAGAAGGCCT	<i>Rx2</i>	PVX	Shaikhaldein et al. (2018)
12	RFLP	GP21	GGTTGGTGGCCTATTAGCATGTC	AGTGAGCCAGCATAGCATTACTTG	<i>Rx2</i>	PVX	De Jong et al. (1997)
13	CAPS	SC811	CGAACAAAATACGTAATGCATGGAATAA	GACCT ATATCAGTCCCTTCTAATCCACTAT	<i>Ns</i>	PVS	Flis et al. (2005)
14	SCAR	SCG17-321	ACGACCCGACACTCAAATTTGTACAAGAAA	GATGCCCCGACAGAGGAAG	<i>Ns</i>	PVS	Bhardwaj et al. (2019)
15	SCAR	N127	TAGAGAGCATTAAGAAGCTGC	TTTTGCCTACTCCCGGCATG	<i>PLRV1</i>	PLRV	Marczewski et al. (2004), Yermishin et al. (2016)
16	SSR	R1	CACTCGTGACATATCCTCACTA	CAACCCTGGCATGCCACG	<i>R1</i>	LB	Sokolova et al. (2014), Tiwari et al. (2013)
17	SSR	R2	ATGGCTGATGCCTTTCTATCATTTGC	TCACAACATATAATCCGCTTC	<i>R2</i>	LB	Kim et al. (2012)
18	SSR	SHa	ATCGTTGTCATGCTATGAGATGTT	CTTCAAGGTAGTGGGAGTATGCTT	<i>R3a</i>	LB	Huang et al. (2005)
19	SSR	R3b4	GTCGATGAATGCTATGTTTCTCGAGA	ACCAGTTTCTTGAATCCAGATTG	<i>R3b</i>	LB	Rietman (2011)
20	SCAR	CosA	CTCATCAAATCAGTTTGTATC	GAATGTTGAATCTTTTGTGAAGG	<i>R1</i>	LB	Bhardwaj et al. (2019), Sharma et al. (2014)
21	SSR	45/ XI	AGAGAGGTTGTTCCGATAGACC	TCGTTGTAGTTGTCATTCACAC	<i>Rpi-Smira1</i>	LB	Islam et al. (2022), Tomczynska et al. (2014)
22	SSR	184–81	CCACCGTATGCTCCGCCGTC	GTTCCACTTAGCCTTGCTTGCTCA	<i>Rpi-Smira2</i>	LB	Blatnik et al. (2022)
23	SCAR	N146	AAGCTCTTGCCTAGTGCTC	AGGCGGAACATGCCATG	<i>H1</i>	PCN	Asano et al. (2012)
24	SCAR	N195	TGGAAATGGCACCCACTA	CATCATGGTTTCACTTGTCAC	<i>H1</i>	PCN	Chekushkina et al. (2020)
25	SCAR	57R	TGCTGCCTCTCCGATTCT	GGTTCAGCAAAGCAAGGACGTG	<i>H1</i>	PCN	Finkers-Tomczak et al. (2009)
26	SCAR	Gro1-4	TCTTTGGAGATACTGATTCTCA	CGACCTAAAATGAAAAGCATCT	<i>Gro1-4</i>	PCN	Asano et al. (2012)
27	STS	Gpa2-2	GCACTTAGAGACTCATTCCA	ACAGATTGTTGGCAGCGAAA	<i>Gpa2</i>	PCN	Asano et al. (2012)

ER Extreme Resistance, PVY potato virus Y, PVX potato virus X, PVA potato virus A, PVS potato virus S, PLRV potato leafroll virus, LB late blight, PCN potato cyst nematode

associated with the R gene *Ry<sub>adg</sub>*; GP122 (Valkonen et al. 2008; Lopez-Pardo et al. 2013), STO4 (Cernak et al. 2008), Yes3-3A (Song and Schwarzfischer 2008; Bhardwaj

et al. 2019), and Yes3-3B (Song and Schwarzfischer 2008) are linked with the R gene *Ry<sub>sto</sub>*; and markers RY186 (Kneib et al. 2017; Rogozina et al. 2019; Biryukova et al.



**Fig. 2** Mapping genomic locations of biotic and abiotic stress resistance genes in potato on the 12 chromosomes

2020), CT220 (Roupe Van der Voort et al. 2000), and TG506 (Park et al. 2005) are associated with the R gene *Ry<sub>chc</sub>* (Table 1 and Additional file 1). These R genes have been demonstrated to be extreme resistance to PVY.

Additionally, PVX resistance genes have been bred into *S. tuberosum* (4x) from *S. tuberosum* ssp. *andigena* (2x) mostly (Mori et al. 2011; Yermishin et al. 2016; Bhardwaj et al. 2019) and in some cases from *S. demissum* (6X)

(Marano et al. 2002). The majority of *N*- genes markers are CAPS markers, where the *Ny<sub>-1</sub>* and *Ny<sub>tbr</sub>* confer hypersensitivity towards PVY, whereas *Nb*-genes exhibit PVX resistance (De Jong et al. 1997; Szajko et al. 2014). In addition, the *Nc<sub>tbr</sub>* gene and a new putative gene *Nz<sub>tbr</sub>* were also reported to confer hypersensitive resistance against PVY (Table 2) (Chik-Ali 2014). Furthermore, resistance genes for PVS were also bred from *S.*



constituted in clusters of the *PLRV.1* (Table 1) and *PLRV.4* genes from chromosome XI, and *PLRV.2* and *PLRV.3* in chromosomes VI and V, respectively or the *Rladg* gene from chromosome V (Marczewski et al. 2004).

#### Late blight-resistant genes and linked markers

*P. infestans* causes rapid mutation against the plant's defense mechanism leading to the most destructive disease known as potato late blight (LB), so it has been the subject of ongoing and intense research for over a century (Ramakrishnan et al. 2015; Ivanov et al. 2021). To produce LB-resistant varieties, genes conferring resistance to LB were introduced from various wild potato varieties and cultivated species. As the LB-resistant genes are linked to *R* genes, a screening method utilizing *R* gene-associated markers was proposed to identify LB-resistant potato species (Ramakrishnan et al. 2015).

Resistant gene *R1* has been discovered in *S. demissum* (6×) (Ballvora et al. 2002; Bormann et al. 2004; Bhardwaj et al. 2019; Rogozina et al. 2021), *S. berthaultii* (2×), *S. hjertingii* (4×), *S. stoloniferum* (4×), and *S. pinnatisectum* (2×) (Sokolova et al. 2014) (Table 2). This *R1* gene can be detected with the markers CosA (Sharma et al. 2014; Bhardwaj et al. 2019), *R1* (Bhardwaj et al. 2019), *R1-1205* (Sokolova et al. 2014), *BA47f2* (Tiwari et al. 2013), *GP76* (Oberhagemann et al. 1999), *GP179* (Tiwari et al. 2013), and *GP 21* (De Jong et al. 1997; Tiwari et al. 2013) (Table 1 and Additional file 1: Table S1). The *R1* gene localized in chromosome V (Fig. 2) of *S. demissum* (6×) was even introgressed in the cultivated species *S. tuberosum* (Ballvora et al. 2002; Ramakrishnan et al. 2015; Rogozina et al. 2021). Apart from *R1*, several other significant *R* genes found in *S. demissum* (6×) are *R2*, *R3a*, and *R3b* (El-Kharbotly et al. 1996; Lokossou et al. 2009; Sokolova et al. 2014; Rogozina et al. 2021). Resistant gene *R2* can be targeted through SSR marker *R2* (Kim et al. 2012); *R3a* gene can be targeted by markers *R3* (Bhardwaj et al. 2019) and *R3a* (Sokolova et al. 2014); *R3b* gene can be identified through the marker *R3b* (Sokolova et al. 2014). Tiwari et al. (2013) also mentioned that *R3* genes (both *R3a* and *R3b*) residing on chromosome XI can be screened through *R3-1380* (Sokolova et al. 2014), *SHa* (Huang et al. 2005), and *R3b4* (Rietman 2011) markers. Other common sources for *R2*, *R3a*, and *R3b* genes can be *S. bulbocastanum* (2×), and *S. hougasii* (6×) (Table 2) (Sokolova et al. 2014; Sharma et al. 2014; Bhardwaj et al. 2019). Additionally, other LB-resistant *R* genes such as *Rpi-blb1* can be targeted either by SCAR markers like *Rb-1223* (Tiwari et al. 2013) and *RB-629/638* (Sokolova et al. 2014; Tiwari et al. 2013) or SSR markers such as *BLB1* (Chen et al. 2017) and *1521/518* (Additional file 1: Table S1) (Tan et al. 2010; Islam et al. 2022) found in *S. bulbocastanum* (2×), *S. hjertingii* (4×), *S. berthaultii* (2×),

and *S. stoloniferum* (4×) (Table 2) (Sokolova et al. 2014). Again, 45/XI can target the resistance gene *Rpi-Smira1*, located in the same region as the gene *R3* of Chromosome XI in *S. phureja* (2×) (Tomczynska et al. 2014; Islam et al. 2022). *Rpi-Smira2*, a different *Rpi* gene traced on chromosome IX (Fig. 2) was undergoing field trial (Jo et al. 2011; Tomczynska et al. 2014). The rest of the *Rpi* genes, *Rpi-bt1* and *Rpi-ber* (Table 1), were found scattered and constituting in different chromosomes such as chromosomes VIII and X (Fig. 2) (Tiwari et al. 2013; Ramakrishnan et al. 2015; Islam et al. 2022).

#### Potato cyst nematode-resistant genes and linked markers

Potato cyst nematode (PCN) is a soil-borne disease caused by golden nematode which has long been recognized in Europe as a serious potato pest that reduces total potato yield. An efficient solution to produce PCN-free potatoes is to incorporate PCN-resistant genes in the cultivars. Numerous PCN-resistant genes have been identified with varying degrees of resistance, genes *Gro1.4*, *Gpa*, *Gpa4*, *Gpa5*, *Gpa6*, *Grp1*, *Gro1.2*, and *Gro1.3* were found with limited resistance to PCN, whereas *H1* (Ellenby 1952), *Gro1* (Barone et al. 1990), *GroVI*, and *Gpa2* (Asano et al. 2012) genes (Table 1) express strong resistance. Many of these genes are condensed in a precise location, including the QTL, consisting of *Grp1*, *Gpa3*, *Gpa5*, and *Gpa6*. *H1*, a heterozygous dominant gene obtained from *S. tuberosum* ssp. *andigena* (2×) located on chromosome V has been valuable commercially for decades for its resistant durability to the *Globodera rostochiensis* (Gartner et al. 2021). The CP113 marker, which was created during ultra-high-density genetic mapping of the *H1* locus (Bakker et al. 2004), was found to be one of the most closely linked markers to the *H1* gene, while other markers such as *GP22*, *GP265*, *GP270*, *GP78*, and *GP188*, which are close in distance to CP113, were also linked to the *H1* locus (Gebhardt et al. 2006). Besides, the markers, *239E4left*, *CT51* (Bakker et al. 2004), *N146*, *N195* (Asano et al. 2012), were also found to be linked with the PCN extreme resistance gene *H1* (Table 1 and Additional file 1: Table S1). Again, *Gro1* was the first highly dominant *G. rostochiensis* resistant gene, located on Chromosomes VII and IX (Fig. 2), and was mapped with RFLP markers (Barone et al. 1990; Barone et al. 2004). Moreover, the *H2* nematode resistance gene was mapped to chromosome V's distal end in tetraploid potato (Strachan et al. 2019).

#### Other potato disease-resistant genes and linked markers

Markers can help to screen for many other potato diseases, such as potato warts, potato blackleg, potato scab, and potato wilt. The PCR-based marker *N125*, which is designed to target the resistance gene *Sen1* (*S.*

*endobioticum* pathotype 1), located at a position on chromosome XI similar to *Ryadg* genes, can be used to screen for potato wart resistance (Gebhardt et al. 2006). While the AFLP markers can be used to test resistance against potato blackleg disease through the blackleg disease-resistant gene *Eca*, mapped to all 12 potato chromosomes (Zimnoch-Guzowska et al. 2000). Moreover, researchers have successfully identified a few genes conferring resistance to *Streptomyces*, the causative agent for the common scab. Some resistant genes were reported to have been isolated from chromosome XI of the *S. chacoense* (2×) (Kaiser et al. 2020). Previously, a study conducted by Flores et al. reported having accomplished to design of Stx1a and Stx1b markers for *txtA* and *txtB* genes mapped from *S. acidiscabies* (Flores-González et al. 2008). Furthermore, 4 PCR-based primer pairs, namely ScabI and ScabII, TurgI and TurgII, AurI and AurII, pA and pH' have been developed for genes that confer resistance to *S. turgidiscabies* and *S. scabies* in potato species *S. tuberosum* (Lehtonen et al. 2004). The resistance genes *qBWR-2*, *qBWR-3*, and *qBWR-4*, which protect potatoes from bacterial wilt (BW) caused by *Ralstonia solanacearum*, were found in potato chromosomes III, VII, and X, respectively (Habe et al. 2019). To find the BW-resistant genes in potatoes, researchers used a variety of markers, including RAPD, SSR, and AFLP. SSR marker STM0032 on chromosome XII and three RAPD markers, OPG05<sub>940</sub>, OPR11<sub>800</sub>, and OPO13<sub>770</sub>, were discovered to be tightly connected to the bacterial wilt-resistant gene in potatoes (Patil et al. 2012). Additionally, the suppression subtractive hybridization and microarray techniques were applied by Li et al. (2010) to identify genes that confer resistance to *R. solanacearum* in potato and *STA51*, *STC84*, and *STD62*, as well as *STSN2* (STM21), had been identified as significant resistance genes to BW. Besides, expression of the genes *snakin1* and *snakin2* genes in potato were also found to boost BW resistance (Li et al. 2010). Alternatively, over-expression of these two genes *Snakin-1* and *Snakin-2* encoded the proteins Gibberellin Stimulated-Like 1 (Jacobs et al. 2022) and Gibberellin Stimulated-Like 2 (Mohan et al. 2014), respectively, in transgenic potato, were also conferred resistance to blackleg disease caused by *Pectobacterium atrosepticum*. In addition, early blight, caused by *Alternaria solani*, is also one of the major diseases in potato worldwide, and up to 54% yield loss occurs without fungicide application (Abuley et al. 2018; Xue et al. 2022). The early blight resistance in potato is highly heritable, with high broad sense and narrow sense heritability. Two wild potato species, *S. berthaultii* and *S. commersonii* subsp. *malmeanum*, exhibits promising resistance against early blight (Wolters et al. 2021). Genetic mapping-identified QTLs on chromosomes V and VII contribute to early

blight resistance, providing potential markers for breeding resistant varieties (Xue et al. 2022). Although earlier studies had limitations such as small population sizes and incomplete linkage maps, the development of high-density SNP marker linkage maps has made QTL mapping more convenient in potato research (Odilbekov et al. 2020). Further research is needed to determine more accurate genetic basis resistance to early blight.

In addition to the aforementioned diseases, the potato confronts a spectrum of other significant maladies that exert substantial economic and agricultural impact. These afflictions include pink rot (*Phytophthora erythroseptica*), pythium leak (*Pythium ultimum*), dry rot (*Fusarium oxysporum*), soft rot (*Dickeya dianthicola*, *Pectobacterium* spp.), silver scurf (*Helminthosporium solani*), and black dot (*Colletotrichum coccodes*). These phytopathogens manifest their detrimental influence predominantly during the storage phase of potatoes. Hence, Osusky et al. (2004) found that MsrA3, a modified form of the naturally occurring antimicrobial cationic peptide temporin A, when expressed in potato plants, conveys strong resistance to late blight and pink rot. On the other hand, Thompson et al. (2007) reported that a potato clone derived from *S. berthaultii* and *S. etuberosum* exhibited resistance to *P. erythroseptica* and *P. ultimum*. Besides, the inheritance of dry rot resistance was investigated by Sobkowiak et al. (2022) in two diploid potato hybrid populations, leading to the identification of multiple QTLs on chromosomes II, VII, IX, and XII, including the first mapping of loci affecting tuber dry rot resistance in the potato genome. However, the dry rot resistance genes might derived from the wild-type potato *S. chacoense*, *S. microdontum*, and *S. gourlayi* as they were shown extreme resistance to dry rot (Sobkowiak et al. 2022). Moreover, consistent QTLs for soft rot resistance from wild potato *S. microdontum* were spotted in chromosomes I, III, and V, responsible for resistance to *Dickeya dianthicola* (Fenstermaker et al. 2023). Henceforth, increasing more extensive research activities on those diseases will help in understanding the molecular underpinnings of resistance mechanisms against these diverse pathogens which is pivotal for the development of improved potato cultivars with enhanced storage durability.

## Molecular markers associated with abiotic stress tolerance genes in potato

### Drought tolerance genes and linked markers

A deficit in the water supply may adversely affect various developmental stages of potatoes, especially limiting their growth, reproduction, tuber quality, tuber size, and yield (Anithakumari et al. 2011). Numerous genes involved in carbohydrate metabolism, cellular



communication, protein synthesis, ATP metabolism, and cell signaling are upregulated or downregulated when exposed to water stress (Ambrosone et al. 2011). The expressions of such genes have been evaluated within potato tissues under drought conditions and adequate water conditions (Obidiegwu et al. 1999). Using SNP markers revealed 23 QTLs related to drought tolerance phenotypes (Anithakumari et al. 2011). Moreover, five specific genes, *ACS3*, *ALDH*, *ETRTEF3*, *PARG*, and *PP2C*, encoding 1-aminocyclopropane-1-carboxylate synthase 3, aldehyde dehydrogenase, ethylene-responsive transcription factor, poly (ADP-ribose) glycohydrolase, and protein phosphatase 2C, respectively, have been reported being present in drought-sensitive cultivars. These *ACS3*, *ALDH*, *ETRTEF3*, *PARG*, and *PP2C* genes were discovered on potato chromosomes I, II, IV, X, and XII using SSR markers HRO\_ACS3\_1, HRO\_ALDH\_H, HRO\_ETRTF\_5a\_D, HRO\_PARGH\_1A\_B, and HRO\_PP2C\_1\_B, respectively (Table 3) (Ghislain et al. 2009; Schumacher et al. 2021). Furthermore, the positions of these genes associated with drought resistance are not fixed to one specific allele rather the locations vary in alleles among different potato varieties, making them ideal candidates for MAS as well as genetic diversity analysis (Malosetti et al. 2007). Moreover, the presence of an extra allele in drought-sensitive cultivars suggests that the selection of cultivars against these alleles will facilitate the selection of drought-tolerant varieties (Schumacher et al. 2021).

### Cold tolerance genes and linked markers

The potato is a highland crop that grows in cold regions, yet frost damage in cold climates is also a significant issue in potato production. Cold stress stunts potato growth and development, resulting in lower yields (Tu et al. 2021). Even though there are some wild potato species with cold tolerance characteristics yet a commercial cultivar with such characteristics is yet to be found. In terms of cold tolerance, *S. commersonii* (2×/3×) showed supreme tolerance against cold and was potent to resist frost and achieved tuber hardening in a temperature range from 2 to 12°C. Furthermore, *S. acaule* (4×) showed remarkable resistance to cold stress whereas *S. tuberosum* (4×), *S. verrucosum* (2×/3×/4×), and *S. stoloniferum* (4×) showed the most sensitivity to cold stress (Kikuchi et al. 2015; Ramakrishnan et al. 2015). Besides, it was reported that *S. tuberosum* hybrids had been made with *S. brevidens* and *S. commersonii* (2×/3×) to get a cold stress-resistant breed (Orczyk et al. 2003). Tu et al. (2021) conducted a study on the hybridization of *S. malmeanum* (2×/3×), a wild species known for its strong freezing tolerance, with the freeze-sensitive commercial cultivar *S. tuberosum*, with the goal of creating improved varieties that are more tolerant to freezing. And after hybridization via protoplast fusion, the somatic hybrids were screened with eight SSR primers, S215, *ssr\_165426*, *ssr\_165497*, *ssr\_165552*, *ssr\_165648*, *ssr\_165659*, S165, and *ssr\_166097*. On the other hand, some heat shock transcription factors (HSTF), *StHsf004*, *StHsf007*, *StHsf009*, *StHsf014*, *StHsf018*, *StHsf019*, and *StHsf022* genes were found with potentiality against cold

**Table 3** Correlation of SSR markers with drought and cold tolerance in potato

S/N	Marker type	Marker name	Gene name*	Tolerance	References
1	SSR	HRO_ACS3_1	<i>ACS3</i>	Drought	Ghislain et al. (2009), Malosetti et al. (2007), Schumacher et al. (2021)
2	SSR	HRO_ALDH_H	<i>ALDH</i>	Drought	Ghislain et al. (2009), Malosetti et al. (2007), Schumacher et al. (2021)
3	SSR	HRO_ETRTF_5a_D	<i>ETRTEF3</i>	Drought	Ghislain et al. (2009), Malosetti et al. (2007), Schumacher et al. (2021)
4	SSR	HRO_PARGH_1A_B	<i>PARG</i>	Drought	Ghislain et al. (2009), Malosetti et al. (2007), Schumacher et al. (2021)
5	SSR	<i>HRO_PP2C_1_B</i>	<i>PP2C</i>	Drought	Ghislain et al. (2009), Malosetti et al. (2007), Schumacher et al. (2021)
-	-	-	<i>Hsp90-2</i>	Drought	Ambrosone et al. (2011)
-	-	-	<i>rgga</i>	Drought	Ambrosone et al. (2011)
-	-	-	<i>susy</i>	Drought	Schafleitner et al. (2007)
6	SSR	S215	-	Cold	Tu et al. (2021)
7	SSR	S165	-	Cold	Tu et al. (2021)
8	SSR	STHSF004_F_R	<i>StHsf004</i>	Cold	Tang et al. (2016)
9	SSR	STHSF007_F_R	<i>StHsf007</i>	Cold	Tang et al. (2016)
10	SSR	STHSF009_F_R	<i>StHsf009</i>	Cold	Tang et al. (2016)
11	SSR	STHSF014_F_R	<i>StHsf014</i>	Cold	Tang et al. (2016)
12	SSR	STHSF018_F_R	<i>StHsf018</i>	Cold	Tang et al. (2016)
13	SSR	STHSF019_F_R	<i>StHsf019</i>	Cold	Tang et al. (2016)
14	SSR	STHSF022_F_R	<i>StHsf022</i>	Cold	Tang et al. (2016)

stress (Table 3 and Fig. 2). Previously, the roles of *HSTFs* were confirmed for cold stress via RT-qPCR using specific markers named by their corresponding gene names (Tang et al. 2016).

### High throughput genotyping technologies for potato disease resistance genes detection

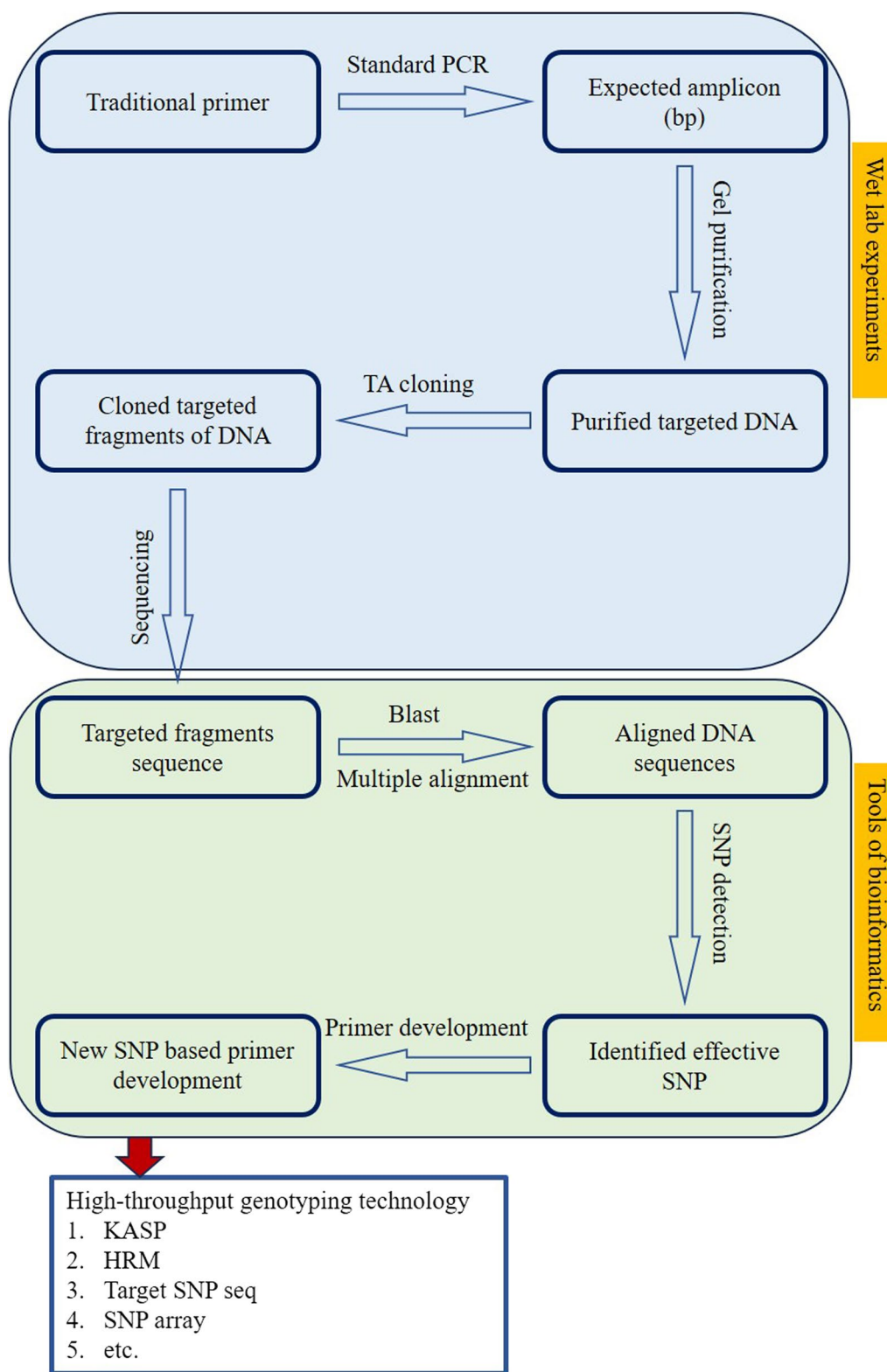
Further research on technological advancements, and high throughput technologies are being practiced for unlocking the full potential of molecular markers in developing improved disease-resistant potato (Fig. 3). High throughput genotyping technologies such as genotyping by sequencing (GBS) was applied to discover dense markers for detecting disease resistance and other important traits in potato and a significant number of SNP markers were identified and filtered to create a high-quality subset (Caruana et al. 2019). In addition, high throughput melting (HRM) assay was employed to detect *HI*-linked resistance to potato cyst nematode. The HRM assay utilized the markers TG689 and 57R-1P for this purpose (Meiyalaghan et al. 2018). In another study by Nie et al. (2018), the markers 5Rx1 and 106Rx2 were utilized in HRM to identify the PVX resistance genes *Rx1* and *Rx2*, respectively. Nie et al. (2016) employed the YES3-3A marker in an HRM assay to precisely locate the PVY resistance gene *Rysto* in potato (Table 4). However, another high throughput genotyping technology, namely kompetitive allele-specific PCR (KASP), is a rapidly emerging high throughput genotyping technology, particularly popular for single nucleotide polymorphism (SNP) based analyses. It is a homogeneous and fluorescence-based genotyping variant of the PCR method. In the realm of potato genotyping, numerous studies have already reported the successful application of KASP. For instance, Sood et al. (2022), Kante et al. (2021), and Caruana et al. (2021) have utilized KASP to confirm the presence of resistance genes *Ry<sub>adg</sub>* and *Ry<sub>sto</sub>* against potato virus Y, employing the marker M6 and YES3-3A, respectively (Table 4). Additionally, KASP has proven valuable in identifying various late blight resistance genes, including *Rpi<sub>-cap1</sub>* (Ram et al. 2018), *R2* (Meade et al. 2020), *Rpi<sub>-blb3</sub>* (Karki et al. 2021), *R8* (Sood et al. 2022), and *RB/Rpi<sub>-blb1</sub>* (Sorensen et al. 2023), across different late blight-resistant genotypes. Furthermore, KASP technology has been effectively employed to detect potato cyst nematode resistance genes *H1*, using the marker 57R (Meade et al. 2020) and *H2*, through the markers CPRISNP 01–11 (Sood et al. 2022). Indeed, the SNP array is another powerful SNP-based genotyping technology that has been effectively utilized in potato genotyping, particularly in the detection of resistance genotypes. Prodhomme et al. (2020) employed the SNP array to identify specific markers, namely hs-SNP, STM1002-24, and St1004-96,

associated with the potato wart disease resistance genes *Sen1* (Prodhomme et al. 2020), *Rse-Ivb*, and *Rse-VIa* (Obidiegwu et al. 2015), respectively. Moreover, the SNP array has also been instrumental in detecting the marker MG-64-17, which is associated with the PVY resistance gene *Ry<sub>chc</sub>* (Table 4), as demonstrated by Li et al. (2022). Nonetheless, genome-wide association studies (GWAS) have been conducted to identify the genomic regions associated with resistance in potato such as GWAS was employed to locate genetic markers linked to resistance against late blight (Prakash et al. 2020; Wang et al. 2020) and potato common scab (Yuan et al. 2020).

On the other hand, the current understanding of genotyping technologies for detecting abiotic stress tolerance genes in potato is relatively limited. However, Anithakumari et al. (2011) made significant strides in this field by identifying several SNP-based markers associated with drought stress in potatoes. Notably, they observed that the gene markers PotSNPs (PotSNP838, PotSNP67) were co-located with the root-to-shoot ratio QTL, suggesting a potential link between these markers and improved drought tolerance in potatoes. Since plants with an increased root-to-shoot ratio are reliable indicators of drought adaptation. Besides, researchers demonstrated proactive efforts in a separate study by transferring the *AtDREB1A* gene from *Arabidopsis thaliana* to tetraploid potatoes. This gene was found to function as a transcriptional factor, imparting enhanced protection against various abiotic stresses, particularly drought and salt (Watanabe et al. 2011). These findings underscore the potential of genetic engineering to enhance abiotic stress tolerance in potato crops. Moving forward, addressing the challenges in this area will necessitate a more comprehensive exploration of potato genetic resources with altered functions related to abiotic stress tolerance, particularly those sourced from wild potato species. Fundamental research efforts should focus on elucidating the molecular mechanisms and physiological functions of these tolerances, which will inform the development of effective germplasm enhancement strategies using genetic resources. Moreover, parallel efforts should be directed towards harnessing exotic genes to augment the potato's capacity to withstand extreme abiotic stresses. Such scientific endeavors hold great promise for the advancement of resilient potato varieties, better equipped to thrive under challenging environmental conditions.

### Summary and conclusions

Even in tetraploid plants such as potatoes, molecular markers help to transport valuable genes and allow for the selection of superior genotypes. Potato disease resistance molecular markers have revolutionized the field of



**Fig. 3** A schematic for high-throughput genotyping in potato breeding using conventional primers connected to genes for disease resistance

**Table 4** High-throughput genotyping technologies for the detection of potato disease resistance genes

Sl no	Genotyping technology	Gene	Marker	Resistance/Tolerance	References
1	HRM	<i>Rx1</i>	5Rx1	PVX	Nie et al. (2018)
		<i>Rx2</i>	106Rx2		
		<i>Ry<sub>sto</sub></i>	YES3-3A	PVY	Nie et al. (2016)
		<i>H1</i>	TG689	PCN	Meiyalaghan et al. (2018)
2	KASP	<i>Ry<sub>adg</sub></i>	M6	PVY	Caruana et al. (2021), Kante et al. (2021), Sood et al. (2022)
			M45		Caruana et al. (2021)
			RYSC3		Caruana et al. (2021)
			YES3-3A		Sood et al. (2022)
		<i>Ry<sub>sto</sub></i>	YES3-3A		Sood et al. (2022)
		<i>H1</i>	57R	PCN	Meade et al. (2020)
		<i>H2</i>	CPRISNP 01–11		Sood et al. (2022)
		<i>R2</i>	R2	LB	Meade et al. (2020)
		<i>Rpi-blb1</i>	RB		Sorensen et al. (2023)
		<i>R8</i>	-		Sood et al. (2022)
3	SNP array	<i>Ry<sub>chc</sub></i>	M50	PVY	Li et al. (2022)
			<i>Sen1</i>	Hs-SNP	Wart
		<i>Sen1-4/Rse-IVb</i>	STM1002-24		Obidiegwu et al. (2015)
		<i>Rse-VIa</i>	St1004-96		
		<i>SFwrec</i>	PotSNP838	Drought	Anithakumari et al. (2011)
		<i>phtrec</i>	PotSNP67		
4	GWS	<i>R2</i>	R2	LB	Prakash et al. (2020)

HRM high resolution melting, KASP kompetitive allele specific PCR (KASP), SNP single nucleotide polymorphism, GWS genome wide sequence, PVY potato virus Y, PVX potato virus X, LB late blight, PCN potato cyst nematode

agriculture by offering advanced tools for breeding and potato improvement programs. However, resistance genes for late blight (*R1*, *R2*, *R3a*, *R3b*, and *Rpi*-genes), PVY (*Ry<sub>adg</sub>*, *Ry<sub>sto</sub>*, and *Ry<sub>chc</sub>*), PLRV (*PLRV1*), PVX (*Rx1* and *Rx2*), PVS (*Ns*), and PCN (*H1*, *H2*, *Gpa2*, *Gor1-4*, and *Gpr1*) are available in potato and these *R* genes linked molecular markers are widely used in potato breeding for the genetic gain against those destructive diseases (Asano et al. 2012; Yermishin et al. 2016; Kneib et al. 2017; Bhardwaj et al. 2019; Klimenko et al. 2019; Chekushkina et al. 2020; Slater et al. 2020).

The benefits of molecular markers for enhancing potato disease resistance are multifaceted. They offer remarkable speed and precision in the breeding process, allowing for the early identification of disease-resistant plants. For instance, Sharma et al. (2014) successfully employed molecular markers to identify elite germplasm with resistance to late blight (*R1*, *R2*, and *R3a*), potato virus Y (*Ry<sub>adg</sub>* and *Ry<sub>sto</sub>*), and potato cyst nematode (*H1* and *Gor1-4*). Besides, marker-assisted selection (MAS) facilitates the introduction of resistance genes into elite cultivars without compromising desirable traits, while

simultaneously decreasing breeding costs and time requirements, as reported by Bhardwaj et al. (2019) for resistance to potato viruses (PVY, PVS, PVX, and PLRV). Moreover, molecular markers enable the pyramiding of multiple resistance genes, as demonstrated by Mori et al. (2011) in their development of a multiplex PCR to spot resistance genes for late blight, PVX, PVY, and PCN. Similarly, another multiplex PCR protocol was developed by Rogozina et al. (2019) to identify potato genotypes for breeding *R* genes resistance to PVY (*Ry<sub>sto</sub>*, *Ry<sub>chc</sub>*), PVX (*Rx*), PCN (*H1* and *Gor1-4*), and potato wart (*Sen1*) disease. This broadens genetic diversity and bolsters resistance against various diseases. They also aid in the conservation of genetic diversity by preserving rare and unique disease-resistant genes in wild relatives, ensuring the long-term sustainability of potato production in the face of evolving disease pressures.

However, potato breeding for disease resistance using molecular markers faces significant challenges in practical implementation. The diverse and complex nature of potato diseases, combined with the indirect link between molecular markers and resistance genes, leads

to potential false results. Moreover, the tetraploid nature of potatoes makes it difficult to identify and track genes, which further affects the accuracy of marker-based breeding. Addressing the challenges, several advanced genotyping technologies have already been established such as genotyping by sequencing (GBS), high-resolution melting (HRM), competitive allele-specific PCR (KASP), SNP array, genome-wide association studies (GWAS), and so on. Those technologies offer several advantages for potato breeding in terms of disease resistance. They are (a) highly precise, reducing errors, and enhancing the accuracy of genetic variation detection; (b) more sensitive in identifying disease-associated genetic variations; (c) possess superior resolution, enabling the detection of subtle genetic variations linked to resistance genes; (d) high-throughput, allowing for the simultaneous identification of multiple resistance genes; (e) capable of detecting numerous single nucleotide polymorphisms (SNPs) across the genome, facilitating a comprehensive analysis of genetic diversity and the discovery of new resistance genes; (f) cost-effective and efficient, facilitating the selection of disease-resistant potato varieties. Moreover, the unlabeled probe HRM assay has the capability to detect allele dosage, which can be considered an additional advantage of advanced genotyping technologies (Meiyalaghan et al. 2019).

Finally, it might be concluded that based on the molecular markers' researchers can perform high-throughput technology like SNP-dependent technologies, KASP, HRM, target SNP-seq as well as develop new technologies to identify more efficient and specific resistance gene locus for genotyping the potato breeding population against different biotic and abiotic stresses.

#### Abbreviations

ACS3	1-Aminocyclopropane-1-carboxylate synthase 3
AFLP	Amplified fragment length polymorphism
ALDH	Aldehyde dehydrogenase
BW	Bacterial wilt
CAPS	Cleaved amplified polymorphic sequence
ETR1F3	Ethylene-responsive transcription factor
GBS	Genotyping by sequencing
GWAS	Genome-wide association study
HRM	High-resolution melting
KASP	Kompetative allele-specific PCR
LB	Late blight
MAS	Marker-assisted selection
PARG	Poly (ADP-ribose) glycohydrolase
PCN	Potato cyst nematode
PCR	Polymerase chain reaction
PLRV	Potato leaf roll virus
PP2C	Protein phosphatase 2C
PVA	Potato virus A
PVM	Potato virus M
PVX	Potato virus X
PVY	Potato virus Y
QTL	Quantitative trait loci
RAPD	Random amplified polymorphic DNA

RFLP	Restriction fragment length polymorphism
SCAR	Sequence characterized amplified regions
SNP	Single nucleotide polymorphism
SSR	Simple sequence repeats
StHsf	Heat shock transcription factor

#### Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42483-023-00222-9>.

**Additional file 1. Table S1:** Markers linked to biotic stress resistance genes in potato.

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#### Author contributions

S.I. collected the gene information from online portals such as NCBI or Ensemble Plants, wrote the original draft, and helped in final editing, L.J. performed to review and corrections, M.A.R. performed the literature collection and helped with the writing of the original draft, X.F. performed literature review, B.S. performed review, final editing, and corrections, B.N. performed conceptualization, final review, and editing, corrections.

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#### Availability of data and materials

Raw sequence data of the resistance genes are available in the NCBI (<https://www.ncbi.nlm.nih.gov/>) portal and the chromosomal location of the resistance genes is retrieved from Spud (<http://spudbuga.edu/>). Besides the information markers linked to R genes are listed in the supplementary documents attached to this manuscript as Additional file 1.

#### Declarations

##### Ethics approval and consent to participate

Not applicable.

##### Consent for publication

Not applicable.

##### Competing interests

The authors declare that they have no known competing interests that could have appeared to influence the work reported in this paper.

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