Late blight resistance genes in potato breeding

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Abstract

Main conclusion Using late blight resistance genes targeting conservative effectors of Phytophthora infestans and the constructing gene pyramids may lead to durable, broad-spectrum resistance, which could be accelerated through genetic engineering.

Abstract Potato (Solanum tuberosum L.) is one of the most important food crops worldwide. In 2020, potato production was estimated to be more than 359 million tons according to the Food and Agriculture Organization (FAO). Potato is affected by many pathogens, among which Phytophthora infestans, causing late blight, is of the most economic importance. Crop protection against late blight requires intensive use of fungicides, which has an impact on the environment and humans. Therefore, new potato cultivars have been bred using resistance genes against P. infestans (Rpi genes) that originate from wild relatives of potato. Such programmes were initiated 100 years ago, but the process is complex and long. The development of genetic engineering techniques has enabled the direct transfer of resistance genes from potato wild species to cultivars and easier pyramiding of multiple Rpi genes, which potentially increases the durability and spectrum of potato resistance to rapidly evolving P. infestans strains. In this review, we summarize the current knowledge concerning Rpi genes. We also discuss the use of Rpi genes in breeding as well as their detection in existing potato cultivars. Last, we review new sources of Rpi genes and new methods used to identify them and discuss interactions between P. infestans and host.

Keywords Cultivar · Effector · Genetic engineering · Phytophthora infestans · Solanum tuberosum · Wild crop relatives

Introduction

Potato (Solanum tuberosum L.) plants are cultivated worldwide; the largest areas can be found in Asia and Europe and potato production is systematically increasing in Africa (Haverkort and Struik 2015). Late blight is the most economically important potato disease. Costs associated with crop loss and chemical control of late blight were estimated to be more than € 9 billion per year (Haverkort et al. 2016). Late blight is caused by Phytophthora infestans (Mont.) de Bary, an oomycete within the kingdom Stramenopiles, which also infects tomato (Solanum lycopersicum L.) plants. This pathogen can infect stems, berries, leaves and tubers, which leads to complete crop loss. In the nineteenth century, P. infestans caused severe destruction of potato crops in Europe, especially in Ireland, where potatoes were the staple food (Kamoun et al. 2015). Intensive research on potato late blight has led to the discovery of dominant resistance genes against P. infestans (Rpi genes) in potato wild species. Research was initiated to introduce the Rpi genes from Solanum demissum into potato cultivars (Black et al. 1953; Malcolmson and Black 1966). Potato cultivars carrying resistance genes derived from S. demissum, including Pentland Ace (R3), Pentland Dell (R1, R2 and R3) and Epoka (R4), have been registered and cultivated on a large scale in Europe (Malcolmson 1969; Rudkiewicz 1985). However, Rpi genes introduced from S. demissum were quickly overcome by new virulent P. infestans strains (Jo et al. 2014). Rpi gene introgression from wild relatives of the potato into commercial cultivars through crossing is time-consuming, especially in the case of species separated from potato with crossing barriers such as different endosperm balance numbers (EBNs). For example, the introgression of a single Rpi...
gene (Rpi-blb2) from the wild species Solanum bulbocastanum to potato cultivars Bionica and Toluca necessitated more than 45 years (Haverkort et al. 2016). Compared with conventional breeding, genetic engineering techniques such as cisgenesis facilitate a faster introduction of Rpi genes into commercial cultivars (Ghislain et al. 2019). However, to avoid a rapid overcoming of resistance in newly engineered cultivars, introducing not one but several Rpi genes at a time has been proposed (Haverkort et al. 2016).

In this review, we summarize the knowledge concerning Rpi genes. We discuss the use of Rpi genes in traditional and genetic modification-based breeding as well as their detection in existing potato cultivars. We present new sources of Rpi genes and new methods used to identify them and discuss the interactions between P. infestans and the host.

Sources of Rpi genes

Hawkes’s taxonomy originally distinguished 232 potato wild species (Hawkes 1990). However, recent morphological and molecular studies have reduced the number of potato wild species to 107 (Spooner et al. 2016). These wild species grow in America from the southwestern United States to central Argentina and Chile (Hijmans and Spooner 2001). The highest number of species (93) occurs in Peru, 43 of which can be described as rare. Another country where species richness is particularly high is Mexico, which has 36 potato wild species (Hijmans and Spooner 2001).

Wild relatives of the potato are unique sources of genetic variation. They are characterized as being highly resistant to various diseases, including late blight, and they have been used in breeding programmes for more than 100 years (Machida-Hirano 2015). To date, more than 70 Rpi genes have been identified and mapped in 32 Solanum species (Table 1). Most of the Rpi genes have been derived from tuber-bearing species (25): Mexican (9 species), Bolivian (6), Peruvian (4), Argentine (3), Paraguayan (1), USA (1) and one species found generally in the Andes. Novel Rpi genes were found also in S. tuberosum subspecies andigena and in Hungarian cultivar Sárpó Mira. Six Rpi genes were identified in four non-tuber-bearing species and five from the tomato wild species S. pimpinellifolium. Single resistance genes were identified in 15 potato wild species. Frequently, multiple functional Rpi genes have been found within a single species, e.g., S. demissum (14 Rpi genes), S. bulbocastanum (5), S. berthaultii (5), S. stoloniferum (4), S. edinense (4), S. venturii (4), S. hjertingii (3), S. chacoense (3), S. huancabambense (2), S. pinnatisectum (2) S. schenckii (2) and S. tarijense (2). The Rpi genes were mapped in clusters onto potato chromosomes I, IV, V, VI, VII, VIII, IX, X, and XI. For example, on chromosome IV, a total of 13 Rpi genes from seven potato wild species were found. Several Rpi genes have not yet been mapped, including the following: Rpi-pta2 from S. stoloniferum; R401 and R40A from S. demissum; Rpi-ber1.2, Rpi-ber1.3, and Rpi-ber1.4 from S. berthaultii; Rpi-tar1.3 from S. tarijense, Rpi-nrs1 from S. neorossii and putative novel Rpi genes from S. jamesii and S. tuberosum subsp. andigena (Table 1).

Recently, using advanced techniques, new Rpi genes have been identified. Through genetic linkage analysis and colinearity analysis, a new dominant resistance gene, Rpi2, from the Mexican diploid wild species S. pinnatisectum was mapped onto potato chromosome VII (Yang et al. 2017). The Rpi2 locus is different from the previously reported resistance locus Rpi1, which is on the same chromosome. Rpi2 provides broad-spectrum resistance against various P. infestans isolates, including those that overcome resistance conferred by R9. Resistance gene enrichment sequencing (RenSeq) was used to finely map onto chromosome X, the Rpi-rz1 gene from S. ruiz-cebalsii, which confers high and broad-spectrum resistance to 500 diverse Polish P. infestans isolates, (Jupe et al. 2013; Brylińska et al. 2015). Two complementary enrichment strategies that target resistance genes (RenSeq) and single/low-copy number genes (GenSeq, generic-mapping enrichment sequencing) independently positioned the broad-spectrum resistance gene Rpi-ver1 from the Mexican wild species S. verrucosum on potato chromosome IX (Chen et al. 2018). Diploid wild potato, S. jamesii (JAML-4) is completely resistant to the super virulent P. infestans isolate 2013–18–306, which can overcome the resistance conferred by the genes R1, R2, R3a, R3b, R4, R5, R6, R7, R8, R9, R10, and R11 (Zheng et al. 2020). Diagnostic RenSeq (dRenSeq) analysis demonstrated JAML-4 harbors R3a. However, transgenic Désirée plants containing R3a are susceptible to the isolate 2013–18–306. The authors speculated that resistance in JAML-4 was provided by uncharacterized novel resistance gene(s), Rpi-amr3 from S. americanum was identified and cloned via RenSeq and single-molecule real-time (SMRT) sequencing (SMRT RenSeq) (Witek et al. 2016). Bulked segregant analysis coupled with RenSeq mapped Rpi-amr3 on chromosome IV of the potato reference genome of a doubled monoploid clone of S. tuberosum group Phureja DM1–3 516 R44 (DM). Transgenic diploid potato carrying Rpi-amr3 showed resistance against three P. infestans isolates. Another new Rpi gene from S. americanum Rpi-amr1, was positionally cloned and mapped onto the short arm of chromosome XI (Witek et al. 2021). Using association genomics and long-read RenSeq, the authors identified three allele-specific proteins, which showed 100% identity to Rpi-amr1 protein, from two S. americanum assessments and one S. nodiflorum assessment. Eight additional Rpi-amr1 allele-specific proteins, sharing 90% homology to Rpi-amr1 proteins, were identified from six accesses of S. americanum and two accesses of S. nigrescens and they all conferred late blight resistance.
Table 1 Resistance genes against *Phytophthora infestans* (*Rpi* genes) in *Solanum* species

| Rpi gene | Species | Chromosome | Origin | References |
|----------|---------|------------|--------|------------|
| *Rpi-avl1* | *S. avilesii* | XI | Bolivia | Verzaux (2010) |
| *Rpi-ber1; Rpi-ber2* | *S. berthaultii* | X | | Park et al. (2009) |
| *Rpi-ber1.2; Rpi-ber1.3; Rpi-ber1.4* | NA | | | Monino-Lopez et al. (2021) |
| *Rpi-blh1 (RB)* | *S. bulbocastanum* | VIII | Mexico | Naess et al. (2000) |
| *Rpi-blh2* | VI | | Van der Vossen et al. (2005) |
| *Rpi-blh3* | IV | | Park et al. (2005a); Lokossou et al. (2009) |
| *Rpi-bt1* | VII | | Oosumi et al. (2009) |
| *Rpi-chc1.1; Rpi-chc1.2; Rpi-chc2* | *S. chacoense* | X | Paraguay | Monino-Lopez et al. (2021); Haverkort et al. (2016) |
| *Rpi-cap1* | *S. capsiciibaccatum* | XI | Bolivia | Verzaux et al. (2012) |
| *Rpi-quat1* | *S. circarefolium ssp. quinse* | XI | | |
| *R1* | *S. demissum* | V | Mexico | Ballvora et al. (2002); Lokossou et al. (2009); Dunan et al. (2011) |
| *R2; Rpi-dmfl* | | | | |
| *R3a; R3b* | XI | | El-Kharbotly et al. (1996); Huang et al. (2004) |
| *R4*; *R4MA* | NA | | Van Poppel (2010) |
| *R5* | XI | | Huang (2005) |
| *R6; R7* | XI | | El-Kharbotly et al. (1996); Huang (2005) |
| *R8 (Rpi-Smira2)*; *R9a (Rpi-edn2)* | IX | | Jo et al. (2011); Vossen et al. 2016; Jo et al. 2015; Keijzer et al. (2021) |
| *R10; R11* | | | Bradshaw et al. (2006) |
| *Rpi-edn1.1; Rpi-edn1.2* | *S. edinense* | IV | | Champouret (2010) |
| *Rpi-edn2 (R9a)* | IX | | Verzaux (2010); Keijzer et al. (2021) |
| *Rpi-edn3* | XI | | Verzaux (2010); |
| *Rpi-hjt1.1; Rpi-hjt1.2; Rpi-hjt1.3* | *S. hjertingii* | IV | | Champouret (2010) |
| *Rpi-hcb1.1; Rpi-hcb1.2* | *S. huancabambense* | IX | Peru | Aguilera-Galvez et al. (2020) |
| *Novel Rpi gene(s)* | *S. jamesii* | NA | USA | Zheng et al. (2020) |
| *Rpi-mch1* | *S. michoacanum* | VII | Mexico | Śliwka et al. (2012b) |
| *Rpi-mcd1* | *S. microdontum* | IV | Argentina | Sandbrink et al. (2000) |
| *Rpi-mcq1 (Rpi-moc1)* | *S. mochiquense* | IX | Peru | Smilde et al. (2005) |
| *Rpi-nrs1* | *S. neorossii* | IX | Argentina | Jones et al. (2009) |
| *Rpi-pcs* | *S. paucissectum* | XI | Peru | Villamon et al. (2005) |
| *Rpi-phu1 (Rpi-vnt1.1)* | *S. phureja* | IX | Andes | Śliwka et al. (2006); Foster et al. (2009) |
| *Rpi1; Rpi2* | *S. pinnatisectum* | VII | Mexico | Kuhl et al. (2001); Yang et al. (2017) |
| *Rpi-pur1* | *S. piarae* | XI | Peru | Rietman (2011) |
| *Rpi-rec* | *S. ruiz-cellosii (S. brevicaule)* | X | Bolivia | Śliwka et al. (2012a) |
| *Rpi-snk1.1; Rpi-snk1.2* | *S. schenckii* | IV | Mexico | Champouret (2010) |
| *Rpi-sto1*; *Rpi-pta1* | *S. stolomiferum* | VIII | | Vleeshouwers et al. (2008); Wang et al. (2008) |
| *Rpi-sto2* | | XI | | Champouret (2010) |
| *Rpi-pta2* | NA | | Vleeshouwers et al. (2008); Wang et al. (2008) |
| *Rpi-tar1* | *S. tarjense* | X | Bolivia | Haverkort et al. (2016) |
| *Rpi-tar1.3* | NA | | Monino-Lopez et al. (2021) |
| *Rpi-Smira1* | *S. tuberosum cv. Sárpo Mira* | XI | Hungary | Rietman et al. (2012); Tomczyńska et al. 2014; Vossen et al. 2016 |
| *Rpi-Smira2 (R8)* | | IX | | |
to *P. infestans* isolate 88069 in transient assays. One homologue, Rpi-amr1-3409 from *S. nigrescens*, was mapped onto chromosome I based on the potato DM reference genome, suggesting that a fragment of DNA from the end of the short arm of chromosome XI in other resistant accessions was translocated to the end of the long arm of chromosome I in *S. nigrescens*. Moreover, the authors identified Rpi-amr1 homologues in hexaploid *S. nigrum* accessions, providing resistance to the *P. infestans* isolate 88069. Previous studies indicated that *S. nigrum* is a non-host to *P. infestans* and *S. americanum* may be the diploid ancestor of hexaploid *S. nigrum* (Colon et al. 1992; Poczai and Hyvönen 2010). The Rpi-amr1 homologues, which confer late blight resistance in *S. nigrum*, were most likely inherited from *S. americanum* (Witek et al. 2021). Rpi-amr1 confers broad-spectrum late blight resistance in cultivated potato. Stably transformed transgenic potato cultivar Maris Piper plants carrying Rpi-amr1, resist 19 *P. infestans* isolates tested, including those overcoming Rpi-vnt1, Rpi-blb1 and Rpi-blb2. In potato wild species *S. chacoense*, two resistance genes, Rpi-chc1.1 and Rpi-chc1.2 have been identified (Monino-Lopez et al. 2021). An allele-mining strategy allowed the identification of Rpi-chc1.1 orthologue in *S. chacoense*, *S. berthaultii* and *S. tarijense* accessions resistant to late blight. For many years, researchers have continued to search for new Rpi genes among wild potato. The largest collections of potato germplasm are available in International Potato Center (CIP) in Peru, the USDA Potato Genebank in Wisconsin, USA, and IPK Gatersleben Genebank in Germany (Karki et al. 2021b). An analysis of resistance to *P. infestans* carried out over a period of more than 20 years has shown that among 34 potato wild relatives there are accessions characterized by a high level of resistance, but the genes underlying this resistance are still unknown (Pérez et al. 1999; Zoteyeva et al. 2012; Khiutti et al. 2015; Bachmann-Pfaebe et al. 2019; Zoteyeva 2020; Karki et al. 2021b). A list of such potato wild relatives is shown in Table 2. These species are native to Mexico, Argentina, Bolivia, Peru, Ecuador and Chile. Research using aggressive *P. infestans* isolates, showed that these species can contribute to development of new durable resistant cultivars. It is worth noting that species having 2EBN and 4EBN (Table 2) can cross with cultivated potato and can be used in potato breeding programs (Karki et al. 2021b). On the other hand, species with 1EBN cannot be crossed with cultivated potato and require application of other methods for the Rpi gene introgression. Recently, 189 potato genotypes, from 20 wild species and cultivated *Solanum tuberosum* from Andigenum and Chilotanum groups, were screened for their resistance against *P. infestans* (Duan et al. 2021). Ten genotypes from five wild species originating in Mexico showed a broad-spectrum resistance to all four *P. infestans* used, suggesting that each of these genotypes contains Rpi gene(s) other than R1-R11. They belong to *S. bulbocastanum* (3 genotypes), *S. cardiophyllum* (4), *S. jamesii* (1), *S. brachycarpum* (1) and *S. trifidum* (1). The other 127 genotypes displayed isolate-specific resistance.

**Table 1 (continued)**

| Rpi gene | Species | Chromosome | Origin | References |
|----------|---------|------------|--------|------------|
| Novel Rpi gene(s) | *S. tuberosum* subsp. andigena | NA | South America | Duan et al. (2020) |
| Rpi-vnt1,1 (Rpi-phu1); Rpi-vnt1,2; Rpi-vnt1,3* | *S. venturii* | IX | Argentina | Foster et al. (2009); Śliwka et al. (2006) |
| Rpi-vnt2 | | | | |
| Rpi-ver1 | *S. verrucosum* | IX | Mexico | Chen et al. (2018) |
| Non-tuber-bearing *Solanum* species | | | | |
| Rpi-amr1,3* | *S. americanum* | IV | Mexico | Witek et al. (2016) |
| Rpi-amr1-2273* | | XI | NA | Witek et al. (2021) |
| Rpi-amr1-3409* | *S. nigrescens* | I | NA | |
| Rpi-dlc1 | *S. dulcamara* | IX | Mexico | Golas et al. (2010) |
| Rpi-dlc2 | | X | | Golas et al. (2013) |
| Rpi-crp1 | *S. caripense* | IX | Andes | Naitandwe (2007) |
| Wild tomato relatives | | | | |
| Ph-1 | *S. pimpinellifolium* | VII | Peru; Ecuador | Bonde and Murphy (1952) |
| Ph-2 | | X | | Gallegly and Marvel (1955) |
| Ph-3 | | IX | | Chunwongse et al. (2002) |
| Ph-5.1 | | I | | Merk and Foolad (2012) |
| Ph-5.2 | | X | | |

NA, not available

*Rpi* genes described as providing durable resistance against late blight in literature
Table 2  New sources of late blight resistance in Solanum species, where the underlying genes have not been described

| Species               | Accession | Endosperm Balance Number | Origin   | # Tested plants | # Resistant plants | P. infestans isolate/clonal lineage | Resistance | Score   | References                  |
|-----------------------|-----------|--------------------------|----------|----------------|-------------------|------------------------------------|------------|---------|-----------------------------|
| S. albornozii         | 561636    | 2                        | Ecuador  | 5              | 1                 | US-23                              | 7–9        |         | Karki et al. (2021b)        |
| S. agrimonifolium     | 545748    | 2                        | Mexico   | 5              | 3                 | US-23                              | 7–9        |         |                             |
| S. acaule             | 30040     | 2                        | Bolivia  | NA             | NA                | NA                                 | 7          |         | Bachmann-Pfabe et al. (2019) |
|                       | 30044     | 2                        | NA       | NA             | NA                | NA                                 | 2.7        |         |                             |
|                       | 30052     | 2                        | NA       | NA             | NA                | NA                                 | 5.9        |         |                             |
| S. albicans           | NA        | 4                        | Ecuador  | NA             | NA                | US-23                              | 8.3        |         | Khiutti et al. (2015)       |
| S. antipovichii       | Buk 59b   | NA                       | Mexico   | NA             | NA                | MP-324                             | 6.8        |         | Zoteyeva et al. (2012)      |
| S. chomatophilum      | 275202    | 2                        | Peru     | 5              | 5                 | US-23                              | 7–9        |         | Karki et al. (2021b)        |
| S. ehrenbergii        | 184762    | 1                        | Mexico   | 5              | 1                 | US-23                              | 7–9        |         |                             |
|                       | 255519    | 2                        | Mexico   | 5              | 2                 | US-23; NL13316                      | 7–9        |         |                             |
| S. fendleri           | CIP 761921| 2                        | Mexico   | 48             | 6                 | PCO002                             | NA         |         | Pérez et al. (1999)         |
|                       | CIP 761923| 45                       | NA       | NA             | NA                | PCO002                             | NA         |         |                             |
|                       | CIP 761926| 48                       | NA       | NA             | NA                | PCO002                             | NA         |         |                             |
| S. gourlayi           | NA        | 4                        | Argentina| 45*            | 3                 | NA                                 | 6–9        |         | Zoteyeva (2020)              |
| S. guerreroense       | PI 473088 | 4                        | Mexico   | NA             | NA                | MP322                              | 8.0        |         | Zoteyeva et al. (2012)      |
| S. hougasii           | CIP 761902| 4                        | Mexico   | 48             | 12                | PCO002                             | NA         |         | Pérez et al. (1999)         |
|                       | CIP 761899| 48                       | NA       | 11             | PCO002             | NA                                 | NA         |         |                             |
| S. hypacararhnum      | 473477    | 1                        | Peru     | 5              | 5                 | US-23                              | 7–9        |         | Karki et al. (2021b)        |
| S. inmote             | NA        | 4                        | Peru     | NA             | NA                | US-23                              | 8.4        |         | Khiutti et al. (2015)       |
| S. iopetalum          | CIP 761928| 4                        | Mexico   | 48             | 0                 | PCO002                             | NA         |         | Pérez et al. (1999)         |
|                       | CIP 761923| 48                       | NA       | PCO002         | NA                | PCO002                             | NA         |         |                             |
|                       | CIP 761926| 48                       | 16       | PCO002         | NA                | PCO002                             | NA         |         |                             |
| S. kurzianum          | NA        | 2                        | Argentina| 82*            | 1                 | NA                                 | 6–9        |         | Zoteyeva (2020)              |
| S. lesteri            | NA        | 1                        | Mexico   | NA             | NA                | US-23                              | 8.6        |         | Khiutti et al. (2015)       |
| S. megistacrolobum    | 35387     | 2                        | Bolivia  | NA             | NA                | NA                                 | 8.0        |         | Bachmann-Pfabe et al. (2019) |
| S. morelliforme       | 275222    | NA                       | Mexico   | 5              | 3                 | US-23; NL13316                      | 7–9        |         | Karki et al. (2021b)        |
|                       | 545774    | 5                        | 2        | US-23; NL13316 | 7–9                |                                    |            |         |                             |
| S. neoantipovichii    | NA        | NA                       | Mexico   | 20             | NA                | NA                                 | 6.5        |         | Zoteyeva et al. (2012)      |
| S. neocardensasi      | 498129    | NA                       | Bolivia  | 5              | 2                 | US-23; NL13316                      | 7–9        |         | Karki et al. (2021b)        |
| S. oplocense          | NA        | NA                       | Bolivia  | 32*            | 2                 | NA                                 | 6–9        |         | Zoteyeva (2020)              |
| S. oxyacarpum         | NA        | 2                        | Mexico   | 2              | 2                 | NA                                 | 6–9        |         |                             |
| S. palustre           | 473401    | 1                        | Chile    | 5              | 1                 | US-23                              | 7–9        |         | Karki et al. (2021b)        |
|                       | 558169    | 5                        | 5        | US-23          | 7–9                |                                    |            |         |                             |
| S. papita Rydb        | Japa, W 273| 2                        | Mexico   | 18             | NA                | NA                                 | 5.8        |         | Zoteyeva et al. (2012)      |
| S. papita             | PI 251740 | 18                       | NA       | NA             | NA                | NA                                 | 6.4        |         |                             |
|                       | PI 251741 | 12                       | NA       | NA             | NA                | NA                                 | 6.8        |         |                             |
|                       | PI 283105 | 9                        | NA       | NA             | NA                | 6                                  |            |         |                             |
| S. polytrichon        | GLKS 62.102.6.3| 2              | Mexico   | 30             | NA                | NA                                 | 4.6        |         |                             |
| Rydb                  |           |                          |          |                |                   |                                    |            |         |                             |
| S. polytrichon        | Germany, plt. 102| 22           | NA       | NA             | NA                | 5.9                                |            |         |                             |
|                       | PI 255545 | 6                        | NA       | NA             | NA                | 7.5                                |            |         |                             |
| S. raphanifolium      | NA        | 2                        | Peru     | 6*             | 1                 | NA                                 | 6–9        |         | Zoteyeva (2020)              |
| S. sparsipillum       | NA        | 2                        | NA       | 39*            | 10                | NA                                 | 6–9        |         |                             |
| S. spagazzinii        | NA        | 2                        | Argentina| 58*            | 7                 | NA                                 | 6–9        |         |                             |
Structure of Rpi genes and their distribution in the potato genome

Most of the plant resistance (R) genes are members of a large gene family that encodes nucleotide-binding site and leucine-rich repeat (NB-LRR; NLR) domain-containing proteins (Lozano et al. 2015). On the basis of the structure of NLR proteins, two main groups can be distinguished. The first is the so-called TIR-NB-LRRs (TNLs) with N-terminal domain homologous to the Drosophila Toll domain and human interleukin-1 receptor. The second group is non-TIR-NB-LRRs known as CNLs, which contains coiled coil (CC) structure or leucine zipper (LZ) motif in N-terminal region (Ballvora et al. 2002; Sekhwal et al. 2015).

Genome sequencing revealed that the diploid potato clone RH89-039-15 (S. tuberosum ssp. tuberosum) contains 738 partial or full-length NLR sequences (Bakker et al. 2011). In the potato reference genome DM, 438 out of 40,000 identified genes contain the characteristic NB-LRR domain (Jupe et al. 2012). The use of RenSeq led to an increase in the number of identified NLR in the DM reference genome from 438 to 755 (Jupe et al. 2013). All twelve potato chromosomes contain genes belonging to the CNL and TNL groups, except for chromosomes III and X, on which genes from the TNL group are not found. The majority of NLR genes were found on chromosomes IV (57) and XI (54). The fewest number of NLR genes (3) was found on chromosome III. Moreover, the greatest number of NLR gene clusters is on chromosome IV. There are 4.7 times more CNL genes than TNL genes in the analyzed potato genome (Jupe et al. 2012).

Recently, using Illumina HiSeq 2000 technology, 585 NBS domains, including 11 not previously described, were analyzed in 96 potato genomes (Prakash et al. 2020).

To date, nearly 50 Rpi genes that are from Solanum species have been cloned. Most of the cloned genes belong to the CNL family, but several NLR genes remain unclassified (Table 3). The size and structure of different Rpi genes, as well as of different alleles of the same Rpi gene, are diverse. Examples of the longest Rpi genes include Rpi-amr1-2307 (7277 bp) from S. americanum and Rpi-blb2 from S. bulbocastanum (4858 bp) belonging to the CC-NB-LRR class, and R1 from S. demissum (4102 bp) which is part of LZ-NB-LRR group. The shortest genes include R2 family members, e.g., R2 from S. demissum (2538 bp), Rpi-edn1.1 from S. edinense (2544 bp), Rpi-hjt1.1, Rpi-hjt1.2 and Rpi-hjt1.3 from S. hjertingii (2544 bp). These genes are located on chromosome IV and are members of the LZ-NB-LRR group. Most of the Rpi genes are intron-free. Variation in the size and structure of Rpi gene alleles is well described for Rpi-amr1. The size of the identified alleles of this gene ranged from 2768 to 7277 bp and the number of introns range from one to four (Table 3). The listed homologues of the Rpi-amr1 gene have been identified in different species and in different accessions. Molecular cloning of the Rpi genes facilitates studies at the molecular level of the control of resistance to potato late blight (Ballvora et al. 2002). The cloned genes can be used in genetic engineering to develop late blight resistant cultivars.

Plant R genes encode proteins that directly or indirectly detect effector proteins introduced by pathogens (Sekhwal et al. 2015). This leads to the activation of effector-triggered immunity (ETI) and results in reactive oxygen species (ROS) production, callose deposition, and programmed cell death through the hypersensitive response (HR) (Turnbull et al. 2019). The mechanism of potato Rpi gene activation by P. infestans effectors is poorly understood. Studies conducted on Arabidopsis thaliana show that the conformation of NLR
Table 3  Sequenced resistance genes against Phytophthora infestans (Rpi genes)

| Rpi gene         | Class of NB-LRR protein | Accession/patent number | CDS (bp) | Number of introns | References                |
|------------------|--------------------------|--------------------------|----------|-------------------|---------------------------|
| R1               | LZ                       | AF447489.1               | 4102     | 2                 | Ballvora et al. (2002)    |
| R2               | LZ                       | FI536325.1               | 2538     | 0                 | Lokossou et al. (2009)    |
| R3a              | CC                       | AY849382.1               | 3849     | 0                 | Huang et al. (2005)       |
| R3b              | CC                       | JP900492.1               | 3582     | 0                 | Li et al. (2011)          |
| R8               | CC                       | KU530153.1               | 3738     | 0                 | Vossen et al. (2016)      |
| R9a              | CC                       | NA                       | 2593     | NA                | Jo (2013)                 |
| Rpi-albp         | LZ                       | FI536324.1               | 2538     | 0                 | Lokossou et al. (2009)    |
| Rpi-amr1-1032    | CC                       | MW345287.1               | 5120     | 4                 | Witek et al. (2021)       |
| Rpi-amr1-1101    | CC                       | MW345288.1               | 5126     | 4                 |                           |
| Rpi-amr1-1123    | CC                       | MW345289.1               | 5128     | 4                 |                           |
| Rpi-amr1-2271a   | CC                       | MW345290.1               | 2768     | 1                 |                           |
| Rpi-amr1-2272    | CC                       | MW345291.1               | 5056     | 4                 |                           |
| Rpi-amr1-2273    | CC                       | MW345286.1               | 4810     | 3                 |                           |
| Rpi-amr1-2300    | CC                       | MW345292.1               | 5125     | 4                 |                           |
| Rpi-amr1-2307    | CC                       | MW345293.1               | 7277     | 4                 |                           |
| Rpi-amr1-3408    | CC                       | MW345294.1               | 3749     | 3                 |                           |
| Rpi-amr1-3409    | CC                       | MW345295.1               | 5130     | 4                 |                           |
| Rpi-amr3         | CC                       | KT373889.1               | 2664     | 0                 | Witek et al. (2016)       |
| Rpi-ber1.1,94-2031| CC                     | MW410790.1               | 3909     | 0                 | Monino-Lopez et al. (2021)|
| Rpi-ber1.2,493-7a| CC                     | MW410793.1               | 3912     | 0                 |                           |
| Rpi-ber1.3       | CC                       | MW410798.1               | 3912     | 0                 |                           |
| Rpi-ber1.4       | CC                       | MW410802.1               | 3898     | 0                 |                           |
| Rpi-blb1         | CC                       | AY426259.1               | 3592     | 1                 | Van der Vossen et al. (2003)|
| Rpi-blb2         | CC                       | DQ122125.1               | 4858     | 2                 | Van der Vossen et al. (2005)|
| Rpi-blb3         | LZ                       | FJ536346.1               | 2544     | 0                 | Lokossou et al. (2009)    |
| Rpi-bt           | NA                       | FJ188415.1               | 3379     | 1                 | Oosumi et al. (2009)      |
| Rpi-chc1.1       | CC                       | MW383255.1               | 3909     | 0                 | Monino-Lopez et al. (2021)|
| Rpi-chc1.2a      | CC                       | MW410797.1               | 3912     | 0                 |                           |
| Rpi-edn1.1       | LZ                       | GU563963.1               | 2544     | 0                 | Champouret (2010)         |
| Rpi-edn1.2       | NA                       | NA                       | NA       | NA                |                           |
| Rpi-edn2         | CC                       | US20140041072A1          | 2593     | NA                | De Vetten et al. (2014)   |
| Rpi-hcb1.1       | CC                       | NA                       | NA       | NA                | Aguilera-Galvez et al. (2020)|
| Rpi-hcb1.2       | CC                       | NA                       | NA       | NA                |                           |
| Rpi-hj1.1        | LZ                       | GU563971.1               | 2544     | 0                 | Champouret (2010)         |
| Rpi-hj1.2        | LZ                       | GU563972.1               | 2544     | 0                 |                           |
| Rpi-hj1.3        | LZ                       | GU563973.1               | 2544     | 0                 |                           |
| Rpi-mcd1         | NA                       | NA                       | NA       | NA                | Lokossou (2010)           |
| Rpi-mcq1         | CC                       | WO2009013468A2           | NA       | NA                | Jones et al. (2009)       |
| Rpi-nrs1         | CC                       | WO2009013468A2           | NA       | NA                |                           |
| Rpi-pta1         | NA                       | EU884422.1               | 3592     | 1                 | Vleeshouwers et al. (2008)|
| Rpi-snk1.1       | LZ                       | GU563975.1               | 2544     | 0                 | Champouret (2010)         |
| Rpi-snk1.2       | LZ                       | GU563976.1               | 2535     | 0                 |                           |
| Rpi-sto1         | NA                       | EU884421.1               | 3592     | 1                 | Vleeshouwers et al. (2008)|
| Rpi-sto2         | CC                       | NA                       | NA       | NA                | Champouret (2010)         |
| Rpi-tar1.1,852-5 | CC                       | MW390807.1               | 3912     | 0                 | Monino-Lopez et al. (2021)|
| Rpi-tar1.3       | CC                       | MW410799.1               | 3912     | 0                 |                           |
| Rpi-vnt1.1       | CC                       | FJ423044.1               | 2676     | 0                 | Foster et al. (2009)      |
| Rpi-vnt1.2       | CC                       | FJ423045.1               | 2718     | 0                 |                           |
| Rpi-vnt1.3       | CC                       | FJ423046.1               | 2718     | 0                 |                           |
| Ph-3             | CC                       | KJ569333.1               | 2556     | 0                 | Zhang et al. (2014)       |

*aNon-functional/susceptible homolog

bp, base pairs; CDS, coding sequence; LZ, leucine zipper motif; CC, coiled coil motif; NA, not available
proteins may influence their function. The *A. thaliana* NLR protein *Peronospora parasitica* 1 protein (RPP1), which recognizes the ATR1 effector from *Peronospora parasitica*, remains in an inactive form in the absence of an effector in the cell environment. Binding of the effector to the LRR domain leads to oligomerization and activation of the RPP1 protein (Schreiber et al. 2016). Another *A. thaliana* NLR protein, ZAR1, in an inactive form, forms a multicomponent complex with resistance-related kinase 1 (RKS1) (Wang et al. 2019). Inactive ZAR1-RKS1 complex is activated by the effector AvrAC from *Xanthomonas campestris*. AvrAC uridylates the PBL2 kinase to produce PBL2UMP. Interactions between PBL2UMP and the inactive ZAR1-RKS1 complex then lead to conformational changes and the formation of the active pentameric ZAR1 resistosome (ZAR1-RKS1-PBL2UMP). The active resistosome has a funnel-shaped structure required for AvrAC-induced ZAR1 plasma membrane association, cell death, and resistance to *X. campestris*. Nonetheless, how widespread these models are and whether the mechanism of action is the same in potato are unknown (Wang et al. 2019). Activation of Rpi genes may also depend on external factors. Rpi-vnt1.1 requires light to confer resistance against *P. infestans*. In the dark, plants produce shortened chloroplast protein glycylate 3-kinase (GLYK), which does not bind Avrvt1 and that results in a lack of activation of the Rpi-vnt1.1 protein (Gao et al. 2020).

**Arms race**

The host immune response against pathogen invasion can be summarized by the zig-zag model, which involves two steps. The first step relates to the detection of the conserved pathogen-associated molecular pattern (PAMP) which triggers PAMP-triggered immunity (PTI). To avoid PTI, the pathogen secretes effector proteins into the host cells to disrupt the immune response. Effectors are detected by the host's NLRs, leading to activate more robust and faster response termed ETI, which represents the second level of activation the host immune response. Interactions between R genes and effectors represent host–pathogen molecular co-evolution when effectors evolve to evade detection and R proteins evolve to establish or retain detection (Hein et al. 2009; Naveed et al. 2020).

During the pathogenesis of *P. infestans*, a key step is the formation of haustorium in potato tissue through which the pathogen secretes effectors. These proteins manipulate and alter the host's immune response to promote infection. Genes encoding pathogen effectors that induce R gene response are defined as avirulence (Avr) genes (Qutob et al. 2006). Cytoplasmic effectors secreted by *P. infestans* can be divided into two classes, CRN (crinkling, necrosis) and RxLR effectors. The effectors of RxLR type possess arginine-any amino acid residue-leucine–arginine motifs in N-terminal region. All known *P. infestans* effectors, which are recognized by the products of corresponding potato *Rpi* genes, belong to the RxLR class (Martynov and Chizhik 2020). The RxLR effectors contain the highly conserved N-terminal RxLR motif involved in the translocation of *P. infestans* effector proteins into plant cells, and the heterogeneous C-terminal region that can be recognized by plant *R* gene products (Dou et al. 2008).

The function of the *P. infestans* effector in the infection process has been defined for only a few examples. Avr2, by interacting with members of the BR11-suppressor 1-like family proteins (BSL1, BSL2 and BSL3) from potato, inhibits the activity of the oomycete effector 1 (INF1); as a result, programmed cell death does not occur (Turnbull et al. 2019). Avr3 inactivates the host ubiquitin E3 ligase CMPG1, leading to programmed cell death inhibition (Bos et al. 2010). The effector Avr3a-like, by stabilizing host cinnamyl alcohol dehydrogenase 7 (CAD7), limits the activation of defense mechanisms, such as callose deposition, the ROS burst and WRKY33 expression (Li et al. 2019).

In the genome of *P. infestans*, 563 effector genes with the RxLR motif have been identified (Haas et al. 2009). For 15 of them, the respective potato *Rpi* genes have been identified (Table 4). According to the gene-for-gene concept, specific pathogen effectors activate corresponding host plant *R* proteins (Flor 1971). However, some effectors can be recognized by products of multiple *Rpi* genes, or vice versa, a specific *Rpi* gene product can detect multiple effectors from the same or different Phytophthora pathogens. The Avr2 effector can be recognized by not only R2 protein from *S. demissum* but also by Rpi-blb3 from *S. bulbocastanum*, Rpi-mcq1 from *S. mochiquense*, Rpi-hcb1.1 and Rpi-hcb1.2 from *S. huanacambense* (Aguilera-Galvez et al. 2018, 2020). The *Rpi* genes encoding these proteins are located on different chromosomes, R2 and Rpi-blb3 on chromosome IV, Rpi-mcq1, Rpi-hcb1.1 and Rpi-hcb1.2 on chromosome IX (Table 1). *Rpi-amr1* from *S. americanum* recognizes the effector Avramr1 from *P. infestans* but also the Avramr1 homologues from *Phytophthora parasitica* and *Phytophthora cactorum* (Witek et al. 2021). Likewise, recognition of Avramr3 by *Rpi-amr3* from *S. americanum* activates resistance against not only *P. infestans* but also against other economically important Phytophthora pathogens, including *P. parasitica* and *Phytophthora palmivora* (Lin et al. 2021). The authors suggest that *Rpi-amr1* and *Rpi-amr3* provide non-host type resistance to multiple Phytophthora pathogens in *S. americanum* (Lin et al. 2021; Witek et al. 2021). In some cases, different alleles from the same *Rpi* gene can recognize different effectors which belong to the same RxLR family (Monino-Lopez et al. 2021). Protein products of *Rpi- chc1.1* and *Rpi- chc1.2* which are allelic variants recognize two different effectors within the same effector class Avr chc1.1 and
Avrhc1.2, respectively. The LRR domain is involved in the recognition of cognate effector and changes in its structure may lead to the loss of the ability to recognize the effector or to shift the recognition ability from one effector to another. The exchange of the LRR domain in the chimeric receptors changed the recognition spectrum of the Avrchc1.1 to Avrchc1.2 (Monino-Lopez et al. 2021).

To date, several mechanisms have been identified that allow effectors to avoid recognition by corresponding host R proteins. The products of such unrecognized alleles act as virulence factors. *P. infestans* virulence can arise in multiple ways (Huang et al. 2019). The simplest one involves point mutations, e.g., the *P. infestans* effector Avr3a. In tested *P. infestans* populations, two alleles of Avr3a differing at the protein level by only two amino acids can be distinguished. Avr3aKL activates the potato resistance gene R3a, leading to a HR, while Avr3aEM is not recognized by the product of the R3a gene, leading to infection (Armstrong et al. 2005). Isolates with truncated Avr4 protein resulting from a frameshift generated by two single deletions are not detected by the product of the R4 gene in potato. Functional analysis shows that two single deletions do not affect the elicitor activity of the Avr4 protein (Van Poppel et al. 2008). *P. infestans* isolates that possess the Avr1 homologue Avr1-like (A-L) do not induce a resistance response in R1 potato. The sequence of the Avr1-like (A-L) effector is in 82% identical to that of the Avr1 protein but is truncated by the T region at the C-terminal end of Avr1 (Du et al. 2018). Due to changes in expression regulation, the Avrvnt1 effector is not detected by Rpi-vnt1 plants (Stefaniczyk et al. 2017; Pais et al. 2018). Expression of Avrchc1.2 effector is rapidly downregulated in the first hours after inoculation with *P. infestans* isolates, which explains why the presence of Rpi-chc1.2 in the potato plants does not provide resistance to late blight (Monino-Lopez et al. 2021). The Rpi-blb1 protein recognizes ipiO (Avrblb1) effectors from classes I and II, resulting in a HR. Effectors from class III, i.e., ipiO4, are not recognized by the Rpi-blb1 protein and inhibit HR caused by classes I and II of the effector (Champouret 2010). Potentially, the effectors that are essential for infection could not be mutated without a fitness cost and loss of pathogenicity. R proteins recognizing such essential effectors would likely provide broad-spectrum and durable resistance. *P. infestans* Avr3a, especially virulent allele Avr3aEM, may be an example of an essential effector since this gene is conserved among diverse *P. infestans* strains and is highly expressed at the early stage of infection (Yin et al. 2017). Further searching and functional characterization of conserved effectors and corresponding Rpi genes may inform strategies for obtaining durable late blight resistance.

The adaptation of potato to the continuous evolution of the pathogen is through the diversification of *R* genes by recombination, gene conversion, duplication and/or selection (Jupe et al. 2012). While some of the *S. demissum* Rpi genes were found to be race-specific and rapidly became ineffective, the following genes have been described as providing a broad-spectrum of resistance against *P. infestans*: Rpi-blb1, Rpi-blb2 and Rpi-blb3 from *S. bulbocastanum*; R8 and R9 from *S. demissum* and Rpi-vnt1.1 from *S. venturii* (Vleeshouwers et al. 2011; Vossen et al. 2016). However, these genes have not yet been widely introduced into potato cultivars, in part because of crossing barriers. This continuous co-evolution of pathogen effectors and plant *R* genes

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**Table 4** *Phytophthora infestans* genes encoding RxLR effectors and corresponding resistance genes (Rpi genes) in host plants

| *P. infestans* effectors | Corresponding Rpi gene(s) | References |
|--------------------------|--------------------------|------------|
| Avr1                     | R1                       | Van der Lee et al. (2001) |
| Avr2                     | R2; Rpi-mcq1; Rpi-hbl3; Rpi-hcb1.1; Rpi-hcb1.2 | Aguilera-Galvez et al. (2018); Aguilera-Galvez et al. (2020) |
| Avr3a                    | R3a                      | Armstrong et al. (2005) |
| Avr3b                    | R3b                      | Rietman et al. (2012) |
| Avr4                     | R4                       | Van Poppel et al. (2008) |
| Avr8                     | R8                       | Vossen et al. (2016) |
| Avrbllb1(ipiO)           | Rpi-blb1                 | Song et al. (2003) |
| Avrbllb2                 | Rpi-blb2                 | Van der Vossen et al. (2005) |
| Avrvnt1                  | Rpi-vnt1.1               | Pais et al. (2018) |
| AvrsMir1                 | Rpi-Smira1               | Rietman et al. (2012) |
| AvrsMir2                 | Rpi-Smira2               | |
| Avrhccl.1                | Rpi-chc1.1: Rpi-ber1.1   | Monino-Lopez et al. (2021) |
| Avrhccl.2                | Rpi-chc1.2: Rpi-ber1.2   | |
| Avrarmr1                 | Rpi-armr1               | Witek et al. (2021) |
| Avrarmr3                 | Rpi-armr3               | Lin et al. (2021) |
represents a so-called arms race between plants and pathogens (Khavkin 2015).

**Rpi genes in potato cultivars and breeding lines**

Breeding potato cultivars with resistance genes against *P. infestans* gives opportunities to limit the use of fungicides (Haverkort et al. 2016). However, breeders often do not know what *R* genes are present in existing potato cultivars and which of them are effective against local *P. infestans* populations. Some potato cultivars show moderate or high levels of resistance to late blight, but the basis of their resistance remains unknown. Various methods, including PCR, effectomics, transcriptomics, single nucleotide polymorphism (SNP) array genotyping or dRenSeq, have been used to determine which *Rpi* genes are present in potato cultivars (Table 5). Frequently, a combination of more than one method was used.

Analysis of 600 potato cultivars from Europe, Asia, and South America by PCR using gene-specific primers, allowed to detect *R1* in 135 potato genotypes (Gebhardt et al. 2004). Using gene-specific markers, it was possible to confirm the presence of the *R1* and *R2-like* genes in the Polish cultivar Bzura showing a high level of field resistance (Plach et al. 2015). The Mastenbroek potato late blight differential set is a group of 11 potato genotypes (MaR1-MaR11) expected to contain 11 individual *S. demissum* *Rpi* genes (Mastenbroek 1952). However, studies using *Rpi* gene-specific markers and agroinfiltration assay showed that differential plants harbor more than one *Rpi* gene. MaR8 and MaR9 plants, which have a broad-spectrum resistance in both the field and the greenhouse, contain four (*R3a, R3b, R4, R8*) and seven (*R1, Rpi-abpt, R3a, R3b, R4, R8, R9*) *Rpi* genes, respectively (Kim et al. 2012; Zhu et al. 2015). *R1* was additionally found in MaR5 and MaR6 genotypes. These findings are consistent with those of Trognitz and Trognitz (2007), who found *R1* in the *R5, R6* and *R9* plants also within the Scottish Black’s differential set. The *Rpi-vnt1* gene from *S. venturii* and *Rpi-phal* from *S. phureja* were mapped to the same region on the potato chromosome IX and the nucleotide sequences of both genes are identical (Śliwka et al. 2006; Foster et al. 2009). The *Rpi-vnt1.1* confers resistance to a wide range of *P. infestans* strains, except isolates EC1 and EC3626 from Ecuador (Foster et al. 2009; Witek et al. 2021). The presence of the *Rpi-vnt1.1* gene has been confirmed in Dutch cultivar Alouette and in Polish cultivar Gardena using the PCR marker *phu1_2069* (Stefańczyk et al. 2020). The *Rpi-vnt1.1* have been also found in six other cultivars (Table 5). It is worth underlining that PCR markers designed on the basis of gene sequence may display low specificity. Detection of the *Rpi-vnt1* gene in late blight susceptible cultivars, including Bintje and Early Rose, is most likely due to use of non-specific markers and the detection of non-functional homologues (Rogozina et al. 2021). Detection of the presence *Rpi* genes in potato cultivar with the use of PCR markers requires additional methods confirming resistance to *P. infestans*, as it is prone to false-positive results.

Another strategy is the effectomics approach, where effectors are functionally tested in potato germplasms for their response to cognate *R* gene using agroinfiltration assay (Domazakis et al. 2017). More than 200 predicted *RxLR* effectors selected from *P. infestans* genome sequence were used in an agroinfiltration test, which allowed to detect five effective *Rpi* genes (*R3a, R3b, R4, Rpi-Smira1, Rpi-Smira2*) in the Sárpo Mira cultivar characterized by a high level of field resistance (Rietman et al. 2012). Four of them were pyramided qualitative *Rpi* genes. The remaining one, *Rpi-Smira2*, provides a quantitative field resistance, and its presence in potato cultivar can only be detected in field tests. *R8* with nucleotide sequence identical to that of *Rpi-Smira2* can be found also in the resistant potato cultivars Jacqueline Lee, Missaukee, PB-06 and S-60, by long-range PCR (Vossen et al. 2016). Agroinfiltration with ten *P. infestans* effectors revealed that *Avr4* and *Avr8* effector induce HR in potato cultivar Qingshu9, *Avrvt1.1* induces *HR* in Longshu7, *Avr3aEM* effector (i.e., virulent allele of *Avr3a*) induces *HR* in cultivars Qingshu9 and Longshu7 (Elmahal et al. 2020). Screening with over 50 different *P. infestans* *RxLR* effectors has shown a specific response to *Avr2*, which confirms that *SW93-1015* contains a functional homologue of the *R2* gene. Out of *R2* gene homologues cloned from *SW93-1015*, one encoded a protein identical to Rpi-abpt. Transgenic potato cultivar Désirée with this gene was resistant to *P. infestans* (Lenman et al. 2016).

Analysis of the transcriptome of the Chinese cultivar Cooperation 88 (C88), which has been characterized as displaying durable late blight resistant for 20 years, revealed the presence of multiple *Rpi* genes (Hao et al. 2018). This cultivar is highly resistant to two super virulent *P. infestans* strains, IPO 428–2 and XA-4. Within 5 days of inoculation with XA-4, a change in the expression of *Rpi* genes was noted. These genes can be classified as *R1, R2, R3a, Rpi-blb1, Rpi-blb2* and *Rpi-vnt1* homologues (Hao et al. 2018).

SNP array genotyping can also be used to detect the *R* genes in the cultivated potato (Karki et al. 2021a). F1 population containing 79 progeny clones derived from crossing Payette Russet with A0012–5 was screened for resistance to the US-23 genotype of *P. infestans* in detached leaf assay. Linkage mapping using markers from the potato SNP array confirmed the presence of a single resistant gene on the short arm of chromosome IV of cultivar Payette Russet, in the same locus as that for *R2, Rpi-abpt*, and *Rpi-blb3*. Using the primers for *Rpi-blb3*, a PCR product of the expected size (~2500 bp) was obtained and sequenced. The *Rpi* gene allele
| Year of registration | Cultivar       | Rpi gene                   | Methods of detection                  | References                                      |
|----------------------|---------------|----------------------------|---------------------------------------|------------------------------------------------|
| Europe               |               |                            |                                       |                                                 |
| 2014                 | Alouette      | Rpi-vnt1.3; R3a; R3b       | dRenSeq                               | Armstrong et al. (2019)                         |
| 1925                 | Alpha<sup>a</sup> | R8                         | PCR markers; DLA; field trials; pedigree | Rogozina et al. (2021)                         |
| NA                   | Avora         | R8/Rpi-bb1; Rpi-sto1       | PCR markers; sequencing               | Antonova et al. (2018)                         |
| 1910                 | Bińtje<sup>a</sup> | Rpi-vnt1.3                 | PCR markers; DLA; field trials; pedigree | Rogozina et al. (2021)                         |
| 2004                 | Biogold       | Rpi-abpt                   | NA                                    | Park et al. (2005b)                            |
| 2008                 | Bionica       | Rpi-bb2; Rpi-abpt; R3a; R3b| dRenSeq; pedigree                     | Havekort et al. (2009); Armstrong et al. (2019)|
| 1983                 | Bzura         | R1; R2-like                | PCR markers; field trials; DLA; sequencing; pedigree | Gebhardt et al. (2004); Plich et al. (2015) |
| 1973                 | Cara          | R1; R3a; R3b               | dRenSeq                               | Armstrong et al. (2019)                         |
| 1941                 | Craigs Snow White | R1                         |                                       |                                                 |
| 1961                 | Dorita        | R3b                        | PCR markers; DLA; field trials; pedigree | Brown-Donovan et al. (2021)                     |
| 1892                 | Eersteling<sup>a</sup> | R8                         | PCR markers; DLA; field trials; pedigree | Rogozina et al. (2021)                         |
| 1999                 | Innovator     | R1; R2-like; R3a; R3b      | dRenSeq                               | Armstrong et al. (2019)                         |
| 1908                 | Jbel          | R1; R2; R8; Rpi-bb2; Rpi-vnt1.3 | PCR markers; DLA; field trials; pedigree | Rogozina et al. (2021)                         |
| NA                   | Nayada        | R1; R2; Rpi-bb3; R8; Rpi-bb2 |                                       |                                                 |
| NA                   | Negr<sup>a</sup> | R2                         |                                       |                                                 |
| NA                   | Ognivo        | R8/Rpi-bb1; Rpi-sto1       | PCR markers; sequencing               | Antonova et al. (2018)                         |
| 1952                 | Pentland Ace<sup>a</sup> | R3a; R3b                   | dRenSeq                               | Armstrong et al. (2019)                         |
| 1961                 | Pentland Dell | R1; R3a; R3b; Rpi-abpt     |                                       |                                                 |
| 1994                 | Picasso       | R1; R3a; R3b               |                                       |                                                 |
| 1976                 | Pirola        | Rpi-phu1                   | PCR markers; DLA; field trials; pedigree | Brown-Donovan et al. (2021)                     |
| NA                   | Priekul'skij rannij | R8; Rpi-bb1               |                                       | Rogozina et al. (2021)                         |
| 1926                 | Robijn        | R2                         |                                       |                                                 |
| NA                   | Särpo Axona   | R3a; R3b; Rpi-vnt1.3       |                                       |                                                 |
| 2003                 | Särpo Mira    | R3a; R3b; R4; Rpi-Smir1; Rpi-Smir2 | Effectoromics; DLA | Rietman et al. (2012)                         |
| 1968                 | Spunta        | R1                         | dRenSeq                               | Armstrong et al. (2019)                         |
| 1991                 | Stirling      | R1; R3b                    | PCR markers; DLA; field trials; pedigree | Brown-Donovan et al. (2021)                     |
| NA                   | Svitanok kievskij | R2; Rpi-bb3; R3a; R3b; R8; Rpi-bb1 |                                       | Rogozina et al. (2021)                         |
| 2006                 | Toluca        | Rpi-bb2                    | dRenSeq; pedigree                     | Havekort et al. (2009); Armstrong et al. (2019)|
| 1988                 | Torridon      | R1; R3b                    | PCR markers; DLA; field trials; pedigree | Brown-Donovan et al. (2021)                     |
| North America        |               |                            |                                       |                                                 |
| 1970                 | Abnaki<sup>a</sup> | R1                         | PCR markers; DLA; field trials; pedigree | Brown-Donovan et al. (2021)                     |
| NA                   | Atzimba       | R8; Rpi-bb1; Rpi-bb2       |                                       | Rogozina et al. (2021)                         |
| 1867                 | Early Rose<sup>a</sup> | Rpi-bb2; Rpi-vnt1.3       |                                       |                                                 |
| 1999                 | Jacqueline Lee | R8                         | Long-range PCR; sequencing            | Vossen et al. (2016)                           |
| 2009                 | Missaukee     | R8                         |                                       |                                                 |
from Payette Russet is identical to the \textit{Rpi-abpt} sequence except for a synonymous C to T substitution at position 87 (Karki et al. 2021a).

A new tool used for genetic mapping, searching, and testing the functionality of resistance genes in cultivars and breeding lines is dRenSeq (Armstrong et al. 2019). dRenSeq has been used to identify and validate all currently known NLRs effective against potato virus X, the potato cyst nematode \textit{Globodera pallida} and \textit{P. infestans}. Screening by dRenSeq for the presence of 22 functional \textit{Rpi} genes in 11 potato cultivars and one late blight differential line 2573 led to the identification of one to seven \textit{Rpi} genes in each tested genotype (Table 5). Single \textit{Rpi} genes were found in cultivars Craig’s Snow White, Spunta and Toluca. Seven \textit{Rpi} genes, i.e., \textit{R1}, \textit{R1}^{\text{T4109}}, \textit{R3a}, \textit{R3b}^{G1069G311}, \textit{R8}, \textit{R9a}, and \textit{Rpi-abpt}^{T86}, have been identified in the differential line 2573 (Armstrong et al. 2019).

### Genetic improvement for durable \textit{P. infestans} resistance

The introgression of \textit{Rpi} genes into susceptible potato cultivars is limited by long breeding cycles and the high level of heterozygosity across the potato genome (Jo et al. 2014). An attempt to introgress the \textit{Rpi} genes from \textit{S. bulbocastanum} began in 1959. In the first step, a cross was made between \textit{S. bulbocastanum} (B, 2x) bearing \textit{Rpi-blb2} and \textit{S. acaule} (A, 4x) to obtain an AB (3x) plants, which after polyploidisation to the hexaploid level, was crossed with \textit{S. phureja} (P, 2x) resulting in ABP (4x) material. Successive rounds of bridge crosses between ABP (4x) and \textit{S. tuberosum}, led to produce ABPT plants which, after three backcrossing to \textit{S. tuberosum}, eventually led to registration in 2006 and 2008 of two \textit{P. infestans} resistant cultivars Toluca and Bionica (Haverkort et al. 2016). Another example of the introduction of \textit{Rpi} genes into the potato gene pool is the 11-year-long project Bioimpuls, which resulted in the development of true seed population with single or multiple \textit{Rpi} genes against late blight through classical breeding (Keijzer et al. 2021). In this project, three groups of sources of resistance to \textit{P. infestans} were distinguished. The first group includes cultivars and advanced breeding clones containing the \textit{R8}, \textit{Rpi-cap1}, \textit{Rpi-chl1}, \textit{Rpi-vnt1} and \textit{Rpi-blb2} genes that is ready for the commercial crossing. The second group includes breeding clones with \textit{R9} and \textit{Rpi-edn2} genes which require one or two rounds of backcrossing. The third group is potato wild species that have not been used so far, including \textit{S. brachycarpum}, \textit{S. bukasovii}, \textit{S. iopetalum}, \textit{S. multiinterruptum}, and \textit{S. sucrense}. This group needs two or three additional rounds of backcrossing to be used for commercial crosses (Keijzer et al. 2021).

Different approaches have been developed to overcome crossing barriers and to shorten the time for introducing

| Year of registration | Cultivar | \textit{Rpi} gene | Methods of detection | References |
|----------------------|----------|------------------|----------------------|------------|
| 2015                 | Payette Russet | \textit{R2} | SNP array genotyping; DLA; KASP markers | Karki et al. (2021a) |
| 1950                 | Pungo     | \textit{R1}    | PCR markers; DLA; field trials; pedigree | Brown-Donovan et al. (2021) |
| NA                   | Saginaw Chipper | \textit{R2} |                        |            |
| 1980                 | Tollocon  | \textit{R3b}   |                        |            |
| 2006                 | Yukon Gem |          |                        |            |
| Asia                 | Cooperation 88 (C88) | \textit{R1}; \textit{R2}; \textit{R3a}; \textit{Rpi-blb1}; \textit{Rpi-blb2}; \textit{Rpi-vnt1} | RNA-seq; DLA | Hao et al. (2018) |
| NA                   | Longshu 7 | \textit{R3a}; \textit{Rpi-vnt1.1} | PCR markers; agroinfiltration assay; pedigree | Elnahal et al. (2020) |
| NA                   | PB-06    | \textit{R8}    | Long-range PCR; sequencing | Vossen et al. (2016) |
| NA                   | Qingshu 9 | \textit{R3a}; \textit{R4}; \textit{R8} | PCR markers; agroinfiltration assay; pedigree | Elnahal et al. (2020) |
| 1961                 | Rishiri   | \textit{R1}    | Pedigree | Akino et al. (2014) |
| NA                   | S-60     | \textit{R8}    | Long-range PCR; sequencing | Vossen et al. (2016) |
| 1976                 | Toyoshiro | \textit{R1}    | Pedigree | Akino et al. (2014) |
| 1958                 | Yoraku   | \textit{R4}    |                        |            |

*PCR marker detected, but the cultivar is described in literature as susceptible to late blight

| Year of registration | Cultivar | \textit{Rpi} gene | Methods of detection | References |
|----------------------|----------|------------------|----------------------|------------|
| 1958                 | Yoraku   | \textit{R4}    |                        |            |

\textit{dRenSeq}, diagnostic resistance gene enrichment sequencing; DLA, detached leaf assay; SNP, single-nucleotide polymorphism; NA, not available
Rpi genes into susceptible cultivars, including the use of somatic hybrids, hybrid breeding and genetic engineering. To transfer late blight resistance from S. michoacanum to the gene pool of cultivated potato, somatic hybridization and backcrossing (BC) have been used (Smyda et al. 2013; Smyda-Dajmund et al. 2017). The genetic composition of the obtained somatic hybrids was analyzed using diversity array technology (DArT) (Smyda-Dajmund et al. 2016). Using somatic hybridization, crossing and backcrossing, four Rpi genes (Rpi-blb1, Rpi-blb3, R3a, R3b) were introduced into cultivated potato (Rakosy-Tican et al. 2020). The presence of these genes in the back-crossed progeny (BC1 and BC2) was confirmed via gene-specific markers. In addition, the functionality of Rpi-blb1, Rpi-blb3, R3a and R3b was confirmed via agroinfiltration with the corresponding Avr effectors (Avrblb1, Avr2, Avr3a, Avr3b).

Another method to facilitate transfer of resistance to late blight to potato cultivar is hybrid breeding. This method enables obtaining plants with single or pyramided Rpi genes without disrupting the genetic composition of the parental breeding lines that have good agronomic performance. Su et al. (2020) described the introgression of Rpi genes into homozygous diploid potato. First, four different Rpi genes, which were derived from S. avilesii, S. tarijense, S. venturii and S. chacoense, were introduced in three highly homozygous (e.g., with homozygosity scores as 88%, 88% and 79%) diploid potato breeding lines via marker-assisted introgression. After two backcrosses supported with marker selection and one selfing, parents with the homozygous resistance allele were produced and were used for crossing. The two backcrossing steps ensured the removal of most of the genome of the donor wild species parent, and the selfing step helped to remove any remaining unwanted introgressions. The hybrids were made by crossing two homologous parents, each having a different Rpi gene. Finally, hybrids with single Rpi gene (Rpi-avv1, Rpi-tar1, Rpi-vnt1.1, Rpi-chc1.1) and hybrids with combination of two Rpi genes (Rpi-avv1 and Rpi-chc1, Rpi-avv1 and Rpi-tar1, Rpi-avv1 and Rpi-vnt1.1, Rpi-tar1 and Rpi-vnt1.1, Rpi-vnt1.1 and Rpi-chc1) were obtained. The hybrids were tested for resistance to P. infestans in three separate field trials. The hybrids with two resistance genes were more resistant compared to the ones with the respective single Rpi gene. Hybrid breeding with the use of existing elite material and marker-assisted introgression allows obtaining resistant plants in a relatively short time (Su et al. 2020).

An alternative approach involves genetic engineering, which significantly shortens the long time to introgress resistance genes through breeding cycle for tetraploid potato plants (Van Esse et al. 2020). One such method is cisgenesis, i.e., the introduction of genetic material from the same species or from a crossable species (Hou et al. 2014). Transformed potato cultivars obtained by genetic engineering are shown in Table 6. Single Rpi genes have been introduced into several potato cultivars. Rpi-vnt1.1 or Rpi-sto1 have been introduced separately into the cultivars Atlantic, Bintje and Pota9 (Jo et al. 2014). The obtained transgenic plants were evaluated for late blight resistance in detached leaf assay and agroinfiltration assay using five P. infestans isolates. Transgenic Atlantic, Bintje and Pota9 with Rpi-sto1 were resistant to all tested isolate except pic99189. Transgenic Atlantic and Bintje with Rpi-vnt1.1 gene were resistant to all tested isolate except EC1 (Jo et al. 2014). Rpi-vnt1.1 and Rpi-mcq1 have been transformed separately into the cultivar Désirée and tested in field experiment (Jones et al. 2014). All transgenic plants with the Rpi-mcq1 gene were susceptible to late blight. Transformed Désirée plants with the Rpi-vnt1.1 gene remain fully resistant to P. infestans or have reduced disease severity compared to susceptible controls (Jones et al. 2014). In another study, whole-plant resistance assays were carried out in the confined biosafety greenhouse to evaluate the late blight resistance of the Désirée plants transformed with Rpi-vnt1 (Roman et al. 2017). Unexpectedly, 5 out of 52 transgenic events showed resistance to two Peruvian P. infestans isolates belonging to the EC-1 lineage. As reported previously, a different isolate of the EC-1 lineage (isolate EC1 from Ecuador, the only one tested from the lineage), in which the cognate effector gene Avrvnt1 was not expressed, was able to break the resistance conditioned by the Rpi-vnt1 gene in transformed Désirée plants based on a detached leaf assay (Foster et al. 2009; Pel et al. 2009. The authors inferred the EC-1 isolates used in Peru may differ in virulence within the EC-1 lineage (Roman et al. 2017).

The resistance provided by a single Rpi gene can be quickly overcome by an adapted P. infestans strain. A promising breeding approach involves pyramiding several different Rpi genes in one potato cultivar. In 2006, a Durable Resistance in potato against Phytophthora (DuRPh) project has been initiated at Wageningen University and aimed at developing durable resistance in existing potato cultivars by pyramiding Rpi genes via cisgenesis (Haverkort et al. 2009, 2016). Transgenic Désirée potato plants with two Rpi genes (Rpi-blb3:sto1, Rpi-vnt1:ch1 or Rpi-vnt1:sto1) and with three Rpi genes (Rpi-blb3:vnt1:sto1) have been produced. These plants have not been infected by P. infestans during the two-year field tests (Haverkort et al. 2016). Transgenic potato cultivar Désirée with three Rpi genes (Rpi-blb3, Rpi-vnt1.1 and Rpi-sto1) was obtained also by Haesaert et al. (2015). Plants with these genes showed complete resistance to late blight during two-year field trials in Belgium and the Netherlands (Haesaert et al. 2015). In another study, successful stacking of RB and Rpi-blb2 from S. bulbocastanum and Rpi-vnt1.1 from S. venturii in the susceptible potato cultivars Désirée and Victoria resulted in complete resistance to late blight (Ghislain et al. 2019). Compared with
those with a single \textit{Rpi} gene (\textit{RB}, \textit{Rpi-blb2} or \textit{Rpi-vnt1.1}), transgenic plants with three \textit{Rpi} genes showed a significantly higher level of resistance. In three-year field trials involving transgenic plants in southwestern Uganda, no isolate of \textit{P. infestans} that could overcome the resistance provided by the three \textit{Rpi} genes was found (Ghislain et al. 2019). The same three \textit{Rpi} genes, \textit{RB}, \textit{Rpi-blb2} and \textit{Rpi-vnt1.1}, were stacked in two popular Kenyan potato cultivars Tigoni and Shangi (Webi et al. 2019).

The level of resistance to late blight in transgenic plants not only is dependent on the recognition spectrum and activity of \textit{Rpi} gene(s), but also can depend on the genetic background of the recipient genotype (Shandil et al. 2017). Potato F1 progenies, obtained from crossing transgenic cultivar Katahdin carrying an \textit{RB} gene with non-transgenic susceptible cultivar Kufri Bahar or resistant cultivar Kufri Jyoti, were screened for resistance to late blight by whole plants assay. The cultivar Kufri Jyoti is late blight resistant, with resistance inherited from \textit{S. demissum} containing three \textit{Rpi} genes (\textit{R3}, \textit{R4}, \textit{R7}). A high level of resistance was observed in the 85.2\% of progeny plants from the cross with resistant cultivar Kufri Jyoti, while only 36.4\% of progeny were resistant in a cross with the susceptible one. A few F1 genotypes with the \textit{RB} transgene were highly resistant to late blight, while others were completely susceptible, despite having the \textit{RB} transgene. The authors explain that by the effects of diversity in genetic background of parental cultivars including the genes involved in signal transduction cascade and encoding pathogenesis-related proteins (Shandil et al. 2017).

Gene editing techniques are an alternative approach to introducing \textit{Rpi} genes into potato cultivar by conventional methods or by genetic engineering. Gene editing can be used to repair non-functional alleles of \textit{Rpi} genes. In the study by Van Doorn (2020), a non-functional allele of the \textit{Rpi-chc1} was used from two, susceptible to late blight, cultivars

| \textit{Rpi} gene(s) | Transformed cultivar | Assessment of resistance | References |
|---------------------|----------------------|--------------------------|------------|
|                     |                      | Laboratory assay         | Field trials |
| \textit{Rpi-vnt1.1} | Atlantic             | R                        | NA         | Jo et al. (2014) |
|                     | Bintje               | R                        | NA         | |
|                     | Potae9               | R                        | NA         | |
| \textit{Rpi-sto1}   | Atlantic             | R                        | NA         | |
|                     | Bintje               | R                        | NA         | |
|                     | Potae9               | R                        | NA         | |
| \textit{Rpi-nt1.1}  | Désirée              | NA                       | R          | Jones et al. (2014) |
| \textit{Rpi-mcq1}   | Désirée              | NA                       | S          | |
| \textit{Rpi-blb2}   | Désirée              | R                        | NA         | Orbegozo et al. (2016) |
| \textit{Rpi-sto1}   | Désirée              | R                        | R          | Haesaert et al. (2015) |
| \textit{Rpi-vnt1.1} | Désirée              | R                        | R          | |
| \textit{Rpi-blb3; Rpi-vnt1; Rpi-sto1} | Désirée              | R                        | R          | Haverkort et al. (2016) |
| \textit{Rpi-blb3; Rpi-sto1} | Désirée              | NA                       | R          | |
| \textit{Rpi-vnt1; Rpi-chc1} | Désirée              | NA                       | R          | |
| \textit{Rpi-vnt1; Rpi-sto1} | Désirée              | NA                       | R          | |
| \textit{Rpi-blb3; Rpi-vnt1; Rpi-sto1} | Désirée              | NA                       | R          | |
| \textit{Rpi-vnt1.1} | Désirée              | R                        | NA         | Roman et al. (2017) |
| \textit{RB; Rpi-blb2; Rpi-vnt1.1} | Désirée              | NA                       | R          | Ghislain et al. (2019) |
|                     | Victoria             | NA                       | R          | |
| \textit{RB; Rpi-blb2; Rpi-vnt1.1} | Tigoni               | R                        | NA         | Webi et al. (2019) |
|                     | Shangi               | R                        | NA         | |
| \textit{Rpi-ber1.1_94-2031} | Désirée              | R                        | NA         | Monino-Lopez et al. (2021) |
| \textit{Rpi-tar1.1_852-5} | Désirée              | NA                       | R          | |
| \textit{Rpi-chc1.1} | Désirée              | R                        | NA         | |
| \textit{Rpi-amr1-2272} | Maris Piper          | R                        | NA         | Witek et al. (2021) |
| \textit{Rpi-amr1-2273} | Maris Piper          | R                        | NA         | |

R, resistant; S, susceptible; NA, not available

Table 6 Resistance genes against \textit{Phytophthora infestans} (\textit{Rpi} genes) transferred to potato cultivars by genetic engineering
Colombia and Altus. A chimeric receptor was created with exchanges in the LRR domain between the susceptible allele of the Rpi-chc1 gene and the functional Rpi-chc1.1 and Rpi-chc1.2 alleles from S. chacoense. This resulted in the restoration of the recognition of P. infestans effectors Avr-chc1.1 and Avr-chc1.2, which was associated with resistance to late blight (Van Doorn 2020).

Currently, transgenic potato is not available on the European market. In 2003, the transgenic potato cultivar Fortuna carrying Rpi-blb1 and Rpi-blb2 from S. bulbocastanum, which was produced by a German company BASF, was not approved for introduction in Europe (Storck et al. 2012). The American company Simplot developed Innate technology, which is used to improve known potato cultivars through genetic engineering. The second-generation Innate transgenic potato lines containing Rpi- vnt1.1 are resistant to P. infestans (Richael 2021).

In conclusion, searching for new Rpi genes among potato wild relatives and then applying these genes in potato cultivars represents an alternative to the use of fungicides for late blight control. Due to rapid evolution of new virulent isolates of P. infestans, potato breeding for durable late blight resistance is challenging. The use of Rpi genes recognizing conservative, essential effectors of P. infestans and the construction of Rpi gene pyramids may help to achieve durable, broad-spectrum late blight resistance, which could be accelerated through genetic engineering.

Author contribution statement PP performed the literature analysis and wrote the manuscript. JS and ZY reviewed and corrected the manuscript. All authors contributed to the conception and design of the review.

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Availability of data and material Not applicable.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no competing interests.

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