Bioscience Evidence 2025, Vol.15, No.6, 303-312
http://bioscipublisher.com/index.php/be

Case Study Open Access

Field Trials of Genetically Modified Potatoes Resistant to Late Blight

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Bioscience Evidence, 2025, Vol.15, No.6 doi: 10.5376/be.2025.15.0030
Received: 20 Oct., 2025
Accepted: 28 Nov., 2025
Published: 21 Dec., 2025

Preferred citation for this article:
Lv X.M., and Han Y.P., 2025, Field trials of genetically modified potatoes resistant to late blight, Bioscience Evidence, 15(6): 303-312 (doi: 10.5376/be.2025.15.0030)

Abstract Late blight of potato is caused by pathogenic oocytes Phytophthora infestans. Long-term reliance on fungicides for control not only incurs high costs but also brings environmental and health risks. To achieve long-lasting and stable resistance, this study analyzed the disease resistance performance of transgenic potatoes introduced with wild Solanaceous plant resistance genes (Rpi genes) under field conditions in different regions and over multiple years. Although materials carrying a single Rpi gene can delay the onset of the disease to a certain extent, their resistance is easily broken through by pathogenic bacteria. By achieving the superposition of multiple Rpi genes with different sources and complementary recognition effectors through genetic engineering, stable, broad-spectrum, and even complete resistance to late blight can be demonstrated under natural infection conditions, and no significant resistance attenuation has been observed in multi-season trials. The study also combined the molecular detection and field resistance performance of the Rpi gene in Chinese potato germplasm resources to conduct a risk assessment of transgenic disease-resistant potatoes from aspects such as pathogen evolution, ecological security and gene flow. The transgenic and cis-gene breeding strategies with multi-gene superposition provide an important technical path for the sustainable prevention and control of late blight in potatoes.

Keywords Potato (*Solanum tuberosum* L.); Late blight; Transgenic resistance; Rpi gene superposition; Field experiment

1 Introduction

The potato (*Solanum tuberosum* L.) is one of the most important food crops in the world and ranks third in global staple food crop consumption, only after rice and wheat. The sustainability and yield of potato production have long been seriously threatened by late blight. Late blight, caused by the oomycotic pathogen *Phytophthora infestans*, is a highly destructive disease that causes severe economic losses. It is estimated that the global annual cost due to reduced production and control measures exceeds €6 billion (Majeed et al., 2022). In regions such as sub-Saharan Africa, late blight causes 15%~30% yield loss each year and has a particularly severe impact on small-scale farmers. This disease can reproduce asexually and sexually and spread rapidly under suitable temperature and humidity conditions (Kieu et al., 2021). Although frequent spraying of fungicides can reduce losses, it also significantly increases production costs and brings environmental and health risks.

Although fungicides are effective in the short term, their long-term and excessive use will increase costs, cause environmental pollution, and promote the development of resistance in *P. infestans*. In some areas, fungicides used on potatoes account for 50% of the total pesticide usage. Due to the increasingly strict restrictions on pesticide use by regulations and consumers, there is an urgent need to find alternative methods (Resjö et al., 2025). Conventional breeding requires the introduction of resistance genes from wild related species into cultivated varieties. However, potatoes have genetic complexities such as tetraploid and high heterozygosity (Berindean et al., 2024).

To obtain persistent late blight resistance, researchers discovered and analyzed a large number of Rpi genes in many wild Solanum species, such as *S. demissum*, *S. bulbocastanum* and S. venturii (Rogozina et al., 2023). These genes encode NLR proteins, which can recognize the effector proteins of pathogens and activate plant immune responses (Wang et al., 2025; Zhao et al., 2025). Among them, representative Rpi genes include RPI-BLB1, RPI-BLB2, RPI-BLB3, RPI-Vnt1.1 and RB. Different genes can develop resistance to different strains of *P. infestans*. However, due to the rapid evolution of pathogenic bacteria, they may evade immune recognition through mutation or recombination (Rakosy-Tican et al., 2020). This study examines the field performance of transgenic potato materials resistant to late blight obtained by introducing and superimposing Rpi genes from wild Solanum species, including multi-year field trials, molecular identification of resistance gene integration, and environmental and economic impact assessment. By integrating the latest advancements in genetic engineering, discovery of resistance genes and field validation, this study aims to provide references for future breeding plans and policy formulation, and promote more sustainable strategies for the prevention and control of late blight in potatoes.

2 Literature Review: Resistance Genes and Genetic Improvement Strategies

2.1 Major Rpi resistance genes and their sources

In the long-term search for potatoes' persistent resistance to late blight, researchers have discovered and utilized a variety of resistance (Rpi) genes, most of which are derived from wild Solanum plants. Among them, the more important genes include RB (also known as Rpi-blb1), Rpi-blb2, Rpi-vnt1.1 and Rpi-amr1. RB and Rpi-blb2 are from the Mexican wild species *Solanum bulbocastanum*, which has broad-spectrum resistance to *Phytophthora infestans*. Rpi-vnt1.1 is derived from the wild species *Solanum venturii* in South America and has shown strong resistance in both laboratory and field trials. The newer Rpi-amr1 and Rpi-amr3 were cloned from *Solanum americanum*. The main mechanism of action of these genes is to recognize the effector of pathogenic bacteria and then activate the immune response of plants. Through conventional breeding or biotechnological means, these genes have been successfully introduced into cultivated potato varieties (Witek et al., 2020).

2.2 Theoretical basis and advantages of polygene stacking

Due to the rapid variation and high genetic diversity of *P. infestans*, single resistance genes in commercial potato varieties are often broken through. Multi-gene stacking (pyramiding) is the combination of multiple Rpi genes that recognize effectors of different pathogenic bacteria into the same variety. Materials with stacked two or more Rpi genes have stronger resistance and are more stable than those with only a single gene (Wang et al., 2025). After the simultaneous introduction of RB, Rpi-blb2 and Rpi-vnt1.1 into some African highland potato varieties, complete disease resistance was demonstrated in the field for many consecutive years even without the use of fungicides. Multi-gene stacking can activate plant defense pathways more comprehensively and strongly (Zhao et al., 2025).

2.3 Comparison of transgenic, cisgenic and molecular marker-assisted selection (MAS) breeding

transgenic (transgenic) can introduce Rpi genes from unrelated species into potatoes, with the widest range of gene sources. However, this method often encounters problems such as strict supervision and low public acceptance. cisgenic genes only use genes from "hybridizable potato relatives" and are more likely to be recognized in terms of safety and consumer acceptance. Meanwhile, it still retains the advantages of genetic engineering, such as precise stacking of multiple R genes and short breeding cycle, etc. Marker-assisted selection (MAS) utilizes molecular markers closely linked to disease-resistant genes to accelerate the screening of resistant offspring in conventional breeding. MAS has a low cost and is relatively easy to be accepted. However, it is limited by the fact that donors and recipients must be genetically compatible, and it requires a long backcrossing and selection time (Meade et al., 2020; Beketova et al., 2021; Angmo et al., 2023).

2.4 Genetic diversity of late blight bacteria *Phytophthora infestans* and the challenges of resistance breeding

P. infestans have a large genetic diversity and strong adaptability, which is one of the biggest challenges faced by resistance breeding. Pathogenic bacteria can rapidly produce new pathogenic types, rendering many single Rpi genes (such as those from *S. demissum*) ineffective. Studies on pathogen populations from Africa, Europe and the Americas have shown that in some regions, the single clone type is dominant, but in some regions, the microbiota is very diverse (Rogozina et al., 2023).

The dynamic changes in pathogenic bacteria populations indicate that continuous monitoring, the constant discovery of resistance genes, and the integration of multiple resistance mechanisms in breeding are of great significance. Combining Rpi gene stacking with pathogen monitoring and integrated pest and disease management is an effective approach to addressing the evolving *P. infestans*.

3 Case Study One: Multi-Seasonal Field Trials of Rpi-amr1 / Rpi-amr3 Potatoes in Sweden (2018-2020)

3.1 Research background and objectives

Late blight of potato, caused by oomycetes *Phytophthora infestans*, has long been a major threat to global potato production, causing severe economic losses and making production highly dependent on fungicides. With the increasing environmental and policy pressure to reduce chemical input, more sustainable disease management methods are becoming increasingly important. One effective direction is to introduce the resistance genes (Rpi genes) from wild potatoes into cultivated varieties.

Solanum americanum is a wild species closely related to the common weed S. nigrum, and it has strong and broad-spectrum resistance to *P. infestans*. Researchers have cloned two genes, Rpi-amr1 and Rpi-amr3, from *S. americanum* and demonstrated good resistance in both laboratory and early field trials. However, the stability of these genes under multi-year and natural disease conditions still needs further verification (Lin et al., 2022).

3.2 Resistance performance under natural infection conditions

The field trial site was in southern Sweden, where the climate was suitable for the outbreak of late blight and the genetic diversity of the pathogen population was very high. During three consecutive growing seasons, transgenic Maris Piper carrying Rpi-amr1 and Rpi-amr3 was planted together with susceptible control varieties. No fungicides were sprayed throughout the entire test period to truly test the ability of the resistance gene. Researchers monitored the disease development throughout the season and collected *P. infestans* samples for genotype analysis (Resjö et al., 2025).

The test results show that the materials carrying Rpi-amr1 and Rpi-amr3 exhibit strong resistance to late blight. Although there were occasional mild symptoms, the onset of the disease was significantly delayed, and the condition was much milder than that of the susceptible control group, which was completely infected shortly after the onset of the disease. More importantly, this resistance remained stable for three years, even when the weather conditions were different and even new genotypes with greater infectivity emerged (such as EU_41_A2). The emergence of these new genotypes did not increase the disease degree of transgenic materials (Lin et al., 2022).

3.3 Comparison with susceptible materials and single-gene materials

All the susceptible controls were infected within a few weeks after the onset of the disease, the leaves completely rotted, and the yield was severely reduced. The Rpi-amr1 and Rpi-amr3 materials are almost unaffected throughout the season, and at the most severe times, only a few lesions appear at the end of the season. This distinct difference indicates that the genes derived from *S. americanum* can provide a very strong protective effect. Compared with single-gene materials, the advantages of combining multiple R genes are also more obvious. A single Rpi gene usually only provides partial resistance or the resistance lasts for a relatively short period of time. When Rpi-amr1 and Rpi-amr3 are stacked (gene stacking), the resistance is stronger and more stable.

3.4 Key finding: genes derived from *S. americanum* provide stable and strong resistance

Rpi-amr1 and Rpi-amr3 can provide stable and strong resistance under natural infection conditions. Even in the face of a diverse population of *P. infestans* with new genotypes emerging year by year, they can effectively control the disease. The performance remained stable for three consecutive years. Although minor lesions occurred occasionally, they did not affect the health and yield of the plants (Lin et al., 2022). These prove that *S. americanum* is an important genetic resource for resisting late blight and is worthy of further in-depth exploration and utilization. At the same time, the importance of gene superposition was once again emphasized. Even a broad-spectrum gene like Rpi-amr3 performs better when combined with other R genes.

4 Case Study II: Field Trial of Transgenic Potatoes Resistant to Late Blight with Multiple Gene Superpositions

4.1 Gene superposition strategy (e.g. Rpi-vnt1.1 + Rpi-blb3 + Rpi-chc1)

In the past, commercial potato varieties often contained only a single resistance gene (R gene), but this resistance usually only lasted for a very short time because pathogenic bacteria would quickly adapt and break through this defense. To address such issues, researchers began to superimpose multiple R genes that recognize effectors of different pathogenic bacteria onto the same potato variety. Multi-gene superposition can make resistance broader and more persistent because pathogenic bacteria must simultaneously break through multiple recognition systems to cause disease, which greatly increases the difficulty of breaking through resistance.

Genetic engineering is faster and more effective, that is, directly introducing multiple R genes from wild potato varieties into superior varieties. The researchers introduced Rpi-vnt1.1 from *Solanum venturii*, Rpi-blb3 from *S. bulbocastanum*, and Rpi-chc1 from *S. chacoense* into the highly susceptible variety Desiree together. Obtain a transgenic line capable of expressing three genes. Researchers will use specific molecular markers and effector detection methods to confirm whether each gene is functioning properly. These materials superimposed with multiple R genes will enter field trials to detect their performance in real disease environments.

4.2 Resistance evaluation under different pathogenic bacterial populations

The key to evaluating the effectiveness of multi-R gene superposition lies in whether they can maintain resistance in different regions and different types of *P. infestans* populations. Relevant field trials were carried out in multiple regions, including areas with high genetic diversity and the presence of dominant pathogenic clones. In these experiments, transgenic potato materials carrying two or three R genes showed stable resistance to a variety of *P. infestans* isolates, including those highly virulent strains capable of breaking through the defense of a single R gene (Ghislain et al., 2018; Byarugaba et al., 2021) (Figure 1).

In field trials conducted in the Netherlands, Belgium and sub-Saharan Africa, the materials superimposed with Rpi-vnt1.1, Rpi-blb3 and Rpi-sto1 demonstrated strong resistance in multiple seasons and at various locations. These materials not only have a wide range of resistance but also are more durable. Even when facing local pathogenic bacteria with the ability to break through single-gene, no "resistance failure" has occurred.

Figure 1 Confined field trial 60 days after planting during the second season (Oct 14, 2015-Jan 20, 2016) with a close-up on nontransgenic ‘Victoria’ plant heavily infected by *Phytophthora infestans* (Adopted from Ghislain et al., 2018)

4.3 ‘Complete resistance’ was observed under field conditions

The transgenic material carrying three R genes did not show any lesions or symptoms throughout the entire growth period. In multi-seasonal field trials in Uganda, transgenic materials (containing RB, Rpi-blb2, and

Rpi-vnt1.1) from the varieties Desiree and Victoria demonstrated complete resistance for three consecutive seasons. The control non-transgenic varieties were quickly destroyed by late blight, further demonstrating the obvious advantages of the gene superposition strategy.

Similar manifestations were also observed in field trials in Europe. Materials containing three R genes were not infected by late blight until the end of their growth period, even when diverse and highly virulent pathogen strains were produced locally. Meanwhile, the agronomic traits and yields of these materials are comparable to those of the original varieties, indicating that superimposing multiple R genes does not affect plant growth or yield. More importantly, in years of field trials, the pathogenic bacteria have shown no obvious signs of adaptation or breakthrough of superimposed resistance.

5 Case Study III: Rpi Gene Detection and Field Resistance Analysis of 255 Chinese Potato Germplasm Materials

5.1 Molecular detection of broad-spectrum Rpi genes (R8, RB, RPI-BLB2)

Broad-spectrum late blight resistance genes (Rpi genes) such as R8, RB (RPI-BLB1), and RPI-BLB2 are becoming increasingly important in modern potato breeding, especially in countries like China where late blight has long threatened food security. To detect these genes in a large amount of germplasm materials, breeding research generally employs molecular marker techniques specifically targeting genes, such as SCAR markers and PCR detection methods, which can help researchers quickly screen whether hundreds of materials carry key Rpi genes. It is much faster than the traditional method of judging resistance based on field performance (Islam et al., 2024) (Figure 2).

In the research of potato resources in China, these molecular detection techniques have been used to systematically investigate whether R8, RB and Rpi-blb2 exist in germplasm materials. Some cultivated varieties and breeding materials in China carry one or more broad-spectrum Rpi genes, and some even coexist with other Rpi genes. The detection of R8 is often achieved through long-fragment PCR or effector protein-based detection methods. RB and Rpi-blb2 are usually detected by specific primers, and sometimes their functions are verified by using the corresponding Avr effector proteins.

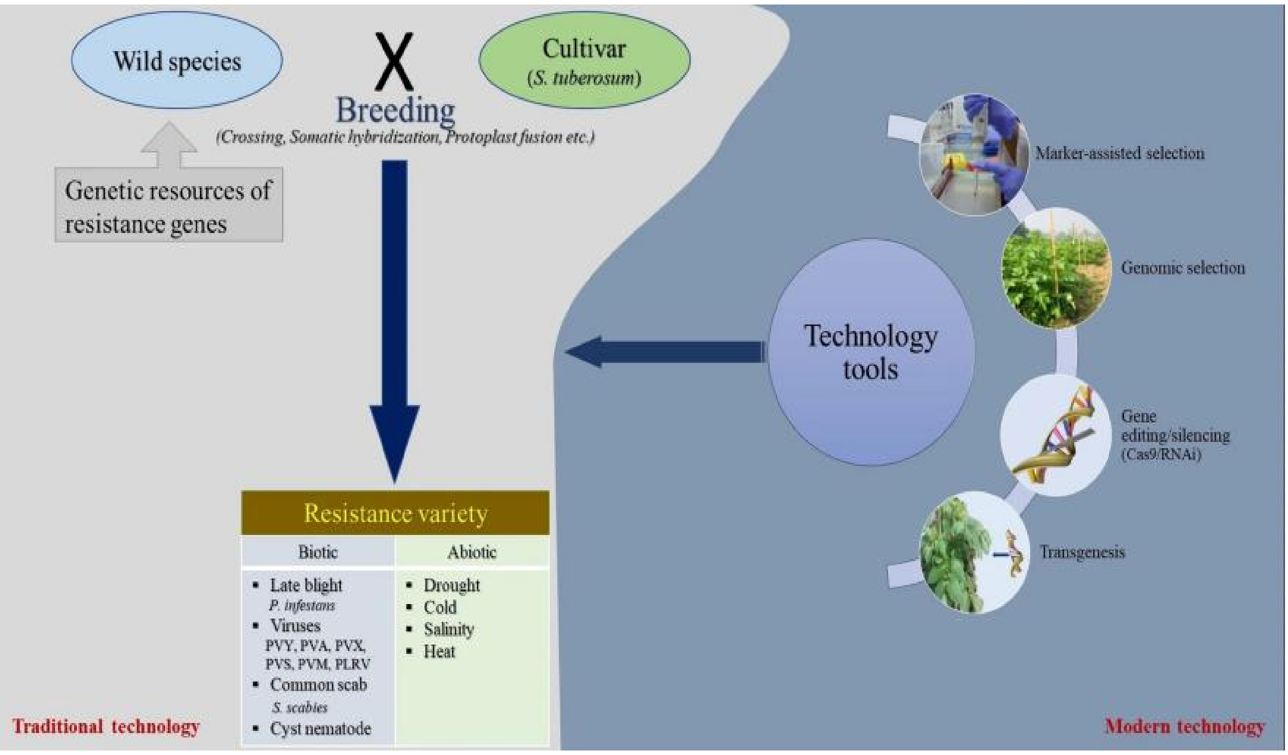

Figure 2 Harnessing the potato gene pools for enhanced resistance to biotic and abiotic stresses in new cultivars (Adopted from Islam et al., 2024)

5.2 Correspondence between molecular markers and field resistance

In Rpi gene breeding, one thing that researchers are very concerned about is whether the genes detected by molecular markers can really show disease resistance in the field. Although molecular markers can rapidly screen resistant materials, whether genes play a role in the field is also influenced by factors such as the genetic background of the material itself, gene expression levels, and differences in pathogen populations.

Often, materials marked with R8, RB or Rpi-blb2 do exhibit strong resistance in the field, especially when these genes are present alone or multiple genes are superimposed. Some materials, although Rpi gene markers have been detected, show unstable or only partial resistance in the field. This may be due to incomplete function of the genes, silencing, or attack by pathogenic bacteria with breakthrough capabilities. On the contrary, there are also some materials that have not been found to have these genes in molecular testing, but still show strong resistance in the field. This may be due to the presence of resistance genes that have not yet been discovered, or they belong to quantitative resistance.

6 Case Comparisons and Comprehensive Analyses

6.1 Differences between single-gene resistance and multi-gene superimposed resistance

Single-gene resistance is usually achieved by transferring an R gene from a wild species into cultivated varieties. This approach generally provides relatively strong but narrow-range resistance. Pathogenic bacteria *Phytophthora infestans* (late blight pathogen) evolve rapidly and often break through this resistance by generating new pathogenic subspecies, rendering the previously effective single R gene ineffective (Rakosy-Tican et al., 2020).

gene pyramiding is the process of introducing two or more R genes that recognize different pathogenic effectors together. Potatoes carrying the three superimposed R genes of RB, Rpi-blb2, and Rpi-vnt1.1 all showed complete resistance under different regions and different pathogen pressures, and showed no disease symptoms in multi-season trials (Bubolz et al., 2022). The superposition of multiple genes not only expands the resistance range but also activates more defensive-related genes (Zhao et al., 2025).

6.2 Comparison of the stability of transgenic resistance and traditional breeding resistance

Traditional disease-resistant breeding relies on hybridization to introduce the R gene into varieties, but is limited by the low genetic diversity of cultivated potatoes and the rapid evolution of pathogens (Duan et al., 2021; Rogozina et al., 2023). Many disease-resistant varieties obtained through traditional breeding lose their resistance very quickly as stronger pathogenic bacteria subspecies emerge, and the breeding process needs to be repeated repeatedly. Transgenic technology can precisely superimpose multiple R genes from different sources together, without being limited by hybridization incompatibility, etc., and can rapidly breed varieties with broad-spectrum and persistent resistance. Transgenic potatoes with multiple gene superpositions maintained stable complete resistance under multi-year and multi-site conditions regardless of how high the disease stress was (Bubolz et al., 2022).

6.3 Key factors affecting field resistance performance

In areas with high disease stress, transgenic potatoes carrying the superimposed R gene can still maintain complete disease resistance, while susceptible control varieties are quickly infected (Byarugaba et al., 2021). The genetic diversity of the local *P. infestans* population can affect the effectiveness of resistance. If a region is dominated by a single clonal pathogen and carries a specific effector, the corresponding R gene resistance can be maintained for a relatively long time. However, in regions where there are many types of pathogens and multiple highly virulent subspecies, single-gene resistance is more likely to fail (Rogozina et al., 2023).

Environmental factors such as temperature, humidity and rainfall can affect the occurrence of diseases and their resistance performance. Multi-site trials have shown that different environments can lead to fluctuations in disease pressure and yield performance. However, the resistance superimposed with the R gene was stable in different ecological regions such as the African Highlands and Northern Europe.

7 Risk assessment of Genetically Modified potatoes resistant to Late blight

7.1 Pathogen evolution risk and resistance persistence

A core concern in promoting genetically modified (GM) potatoes with late blight resistance is the possible evolution of the pathogen *Phytophthora infestans* (late blight pathogen). With the advancement of genetic engineering technology, researchers can "stack" multiple R genes from wild potatoes, which can recognize the key effectors of pathogens. Because pathogenic bacteria must simultaneously break through multiple defense mechanisms, the probability of this situation occurring in natural populations is extremely low (Berindean et al., 2024).

Transgenic potatoes carrying two to three superimposed R genes exhibited complete or near-complete resistance in multiple seasons and different environments, and showed no signs of resistance failure even under conditions of high disease stress. However, the evolutionary ability of late blight bacteria remains a potential risk, especially in areas with high diversity of pathogenic bacteria or inadequate resistance management strategies.

7.2 Ecological risk: impact on non-target organisms and soil microorganisms

The environmental safety assessment of genetically modified late blight resistant potatoes mainly focuses on whether they will affect non-target organisms, including beneficial insects, other pests and soil microbial communities. Multiple trials and biosafety assessments have shown that Introducing disease-resistant genes (such as the RB gene from *Solanum bulbocastanum*) does not affect non-target pests (such as Alternaria) Adverse effects are caused by solani, leaf miners, potato borer, aphids, mites, etc. Or beneficial soil microorganisms (such as nitrogen-fixing bacteria, phosphorus-solubilizing bacteria, soil fungi) (Ambarwati et al., 2022).

There was no significant difference in the quantity and diversity of soil bacteria and fungi between GM potato and non-GM varieties. These results were verified in multiple locations and multiple years (Krause et al., 2020). The use of fungicides has a more significant impact on certain soil microbial indicators than genetic modification itself, but this effect is not unique to GM varieties.

7.3 Gene mobility and biosecurity issues

The genes of genetically modified potatoes do not transfer at a distance of more than 10 meters, and agricultural measures such as crop rotation, isolated planting, and mechanical cleaning further reduce the risk (Forbes et al., 2023). Through fine molecual-level analysis of transgenic events, it can be ensured that only the target genes are transferred in, and there will be no accidental insertions such as vector skeleton fragments (Zarka et al., 2021).

8 Future Prospects and Breeding Strategies

Searching for new resistance genes (R genes) remains a core task, and many wild Solanum plants provide rich genetic diversity for gene sources. Nowadays, effectoromics technology and genome-wide association analysis (GWAS) have greatly accelerated the discovery of resistance genes and quantitative resistance loci (QRLs). GWAS has identified resistance hotspots on chromosome 11 and screened out excellent materials that can be used for backcrossing breeding, helping to broaden the genetic basis of disease-resistant breeding.

Unlike traditional genetic modification, gene editing can achieve precise alterations, such as knocking out susceptibility genes (S genes) or repairing unfavorable mutations, and it does not require the introduction of exogenous DNA. Editing S genes such as StDMR6-1 and StCHL1 can endow potatoes with strong resistance without affecting plant growth and yield. Therefore, it is very suitable for breeding. Editing metabolic pathway genes such as StCCoAOMT can also enhance resistance by strengthening the cell wall or increasing the accumulation of defense metabolites. RNA interference (RNAi) and host-induced gene silencing (HIGS) have further enriched the means of controlling *Phytophthora infestans*, providing more options for disease-resistant breeding.

A large number of field trials have shown that potatoes carrying two or more R genes simultaneously exhibit broad-spectrum and persistent resistance, maintaining good performance even when the local *P. infestans* population is complex and variable. The advantage of modular stacking lies in that breeders can combine different

R genes based on local pathogenic bacteria conditions and update them when new genes emerge or pathogenic bacteria change in the future. Cisgenesis and label-free transformation techniques enable more precise gene stacking, allowing genes from hybrids to be transferred into cultivated varieties without introducing exogenous DNA and selective markers. Data from the DuRPh project show that by dynamically stacking and rationally arranging the usage time and spatial layout of the R gene, the use of fungicides can be reduced by more than 80%.

Transgenic and cis-gene methods can rapidly introduce the R gene of wild relatives into cultivated varieties, bypassing the problems of long breeding cycle and complex process in traditional breeding. MAS technology can help breeders directly locate resistance genes or QRLs. Gene editing provides further optimization means, which can directly modify the R gene or S gene, or repair specific alleles that affect resistance and agronomic traits. Somatic cell hybridization and protoplast fusion have also been used to combine broad-spectrum R genes with specific R genes, enabling varieties to resist multiple diseases simultaneously without yield loss. Genomic selection (GS), using whole-genome prediction models, can capture additive and dominant effects at multiple genomic loci and also improve selection efficiency in tetraploid potatoes.

Acknowledgments

Sincerely thanks the reviewers for their constructive criticisms and suggestions during the review process.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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