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Expression of late blight resistance gene markers in potato varieties and wild *Solanum* species

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ABSTRACT

DNA markers are increasingly used in potato breeding for resistance to late blight. Such markers are generally based on polymerase chain reaction amplification of sequences of resistance genes introduced into cultivated potato varieties from wild tuber-bearing *Solanum* species. However, if nonfunctional homologues of resistance genes are being revealed with DNA markers, there will be no association between plant resistance and the occurrence/absence of these markers. In order to increase the reliability of such DNA markers, it would be desirable to test the functionality of the genetic targets used to develop these markers. It makes sense to begin testing functionality by assessing the expression of these genetic targets, because the absence of expression will clearly indicate the absence of function, and this, in turn, will make it possible to immediately reject markers of inactive homologues of resistance (*R*) genes. The present study is dedicated to the examination of expression of 10 *R* genes: *R1*, *R2*, *Rpi-blb3*, *R3a*, *R3b*, *Rpi-blb1*, *Rpi-sto1*, *Rpi-blb2*, *Rpi-vnt1.3*, and *Rpi-chc1*, detected using 11 sequence-characterized amplified region markers of these genes in wild *Solanum* species and potato cultivars. As a result of this study, most markers were shown to be associated with expressed *R* genes, and these markers can be recommended for further use in marker-assisted selection for resistance to late blight. On the other hand, the revealed homologues of the *R3a* and *Rpi-blb2* genes seem to be inactive outside the species in which these genes were originally discovered, and the *Rpi-sto1* gene has both expressed and non-expressed variants.

1. INTRODUCTION

Potatoes are of particular importance in feeding humankind [1,2]. This plant is the third staple crop after rice and wheat. Unfortunately, potato is beset by a wide range of different diseases during all developmental stages. Among these diseases, late blight, caused by the oomycete *Phytophthora infestans* (Mont.) de Bary, is one of the most serious challenges in potato farming. The damage to the global potato industry resulting from late blight amounts to billions of euros per year [3]. vWhile synthetic crop protection chemicals continue to be important in the fight against late blight, many farmers in developing countries cannot afford to use them in potato growing by reason that synthetic agricultural chemicals are somewhat expensive. Additionally, fungicides are toxic to the environment and hazardous to human health, and consumers, especially in developed nations, demand environmentally friendly and safe food products. Therefore, the sustainable intensification of agriculture requires an increased use of genetic solutions instead of synthetic pesticides to protect potatoes against late blight. Such genetic solutions include potato varieties, which have been bred to be resistant to *P. infestans* infection through introgression of naturally occurring resistance genes (*R* genes/*Rpi* genes), which provide the plant with resistance against *P. infestans*. These genes had been originally discovered in the potato-related wild *Solanum* species, and some of them were later introduced into potato varieties. *R* genes belong to the large NB-LRR gene family. Some commercial potato cultivars gained their late blight resistance genes from the wild species *S. demissum*. In particular, the *R1*, *R2*, *R3a*, *R3b*, *R8*, and *R9a* genes in *S. demissum* were first characterized and then introduced into potato cultivars [4–9]. To track the introgression of resistance genes into potato cultivars, DNA markers based on polymerase chain reaction (PCR) amplification of the sequences of the corresponding *R* genes [the so-called sequence-characterized amplified region (SCAR) markers] are traditionally used. These markers are also used in potato breeding for resistance to late blight through marker-assisted selection (MAS).

However, 755 NB-LRR genes were recently found in the genome of the cultivated potato *S. tuberosum* [10]. Many of these genes are closely related homologues of *Rpi* genes that arose in ancestral species. In addition, using next-generation sequencing technologies, numerous homologues of the *R2* gene were discovered in the Mexican species *S. bulbocastanum*, *S. demissum*, *S. edinense*, *S. hjertingii*, and *S. schenckii* [11–13], and homologues of the *Rpi-blb1*/*Rpi-sto1* gene

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were found in the Mexican species *S. bulbocastanum*, *S. stoloniferum*, *S. papita*, and *S. polytrichon* [12,14–16]. Moreover, homologues of the *Rpi-vnt1* gene originally discovered in *S. venturii* were found in many South American species of the series *Tuberosa* [17–20]. At the same time, the functional activity of all these homologues remains unknown, and the identification of functionless homologues of *R* genes with the SCAR marker technique may cause a lack of correlation between the resistance and the occurrence of these markers. Therefore, to increase the reliability and predictivity of the SCAR markers used, it makes sense to verify the functionality of the target genes based on which these markers are designed. It is advisable to begin checking functionality by assessing the expression (transcription) of these genes because the absence of expression will clearly indicate the absence of function, and this, in turn, will make it possible to immediately reject markers of inactive homologues of *R* genes.

Thus, the aim of this work was to determine the potential functional activity of late blight resistance genes being revealed with formerly applied SCAR markers in cultivated potato varieties and wild *Solanum* species. To this end, we estimated the expression of the targets of these markers to subsequently use only those markers in the breeding process, which mark the genes being expressed.

2. MATERIALS AND METHODS

2.1. Overall Experimental Design

The preliminary determination of the functional activity of *R* genes detected using SCAR markers was carried out by qualitatively determining the presence of transcripts of these genes. To this end, total DNA and total RNA were isolated from the studied plant samples. The total RNA samples were then converted into cDNA in a reverse transcription reaction with random primers. Further, the total DNA samples were screened for 11 SCAR markers, and for those samples in which certain markers were detected, the cDNAs obtained from these samples were analyzed with the same markers. So we could know whether these markers were expressed or not.

2.2. Plant Material

In this study, we examined plants of nine potato varieties ÒBryanskij krasnyj,Ó ÒGolubizna,Ó ÒZhukovskij rannij,Ó ÒCaprice,Ó ÒLugovskoj,Ó ÒSvitanok kievskij,Ó ÒSudarynya,Ó ÒAlouette,Ó and ÒDesireeÓ as well as plants of two complex interspecific potato hybrids 2359-13 and 2372-60. These varieties and hybrids are supported by the Russian Potato Research Centre. In addition, we used plants of nine accessions of tuber-bearing *Solanum* species deposited in the N.I. Vavilov Institute of Plant Genetic Resources. These were *S. avilesii* 20884, *S. bulbocastanum* 243508, *S. bulbocastanum* 243512, *S. demissum* PI161176, *S. microdontum* k25390, *S. okadae* 25394, *S. polytrichon* 24463, *S. stoloniferum* 24263, and *S. stoloniferum* 24976. Accordingly, the working collection consisted of 20 samples in total.

2.3. DNA Extraction

Genomic DNA was extracted from the true leaves of young plants with the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the supplier's instructions. Then, individual DNA samples from eight plants of each accession were blended into one combined sample.

Table 1. The SCAR markers used in the study.

Prototype gene	NCBI accession number (if any)	Marker name	Product size, bp	Primer sequences	Annealing temp., °C	References
R1	AF447489	R1-1206	1206	F-cactcgtgacatatcctcacta	61	[21–26]
				R-gtagtacctatcttatttctgcaagaat		
R2	FJ536325	R2-686	686	F-gctcctgatacgatccatg	54	[22,27,28]
	FJ536325	R2-1137	1137	R-acggcttcttgaatgaa	60	
				F-aagatcaagtggtaaaggctgatg		
				R-atctttctagctaaagatcacg		
Rpi-blb3	FJ536346	Rpi-blb3	305	F-agctttttgagtgtgtaattgg	63,5	[5,29]
				R-gtaactacggactcgaggg		
R3a	AY849382	R3a-1380	1380	F-tccgacatgtattgatctccctg	64	[21–24,26,30]
				R-agccacttcagcttcttacagtagg		
R3b	JF900492	R3b-378	378	F-gtcgatgaatgctatgtttctcgaga	64	[26,27,30]
				R-accagtttcttgcaattccagattg		
Rpi-blb1	AY336128	Blb1-821	821	F-aacctgtatggcagtggcatg	62	[14,25,29,31,32]
				R-gtcagaaaagggcactcgtg		
Rpi-sto1	EU884421	Rpi-sto1	890	F-accaaggccacaagattctc	65	[25,28,32,33]
				R-cctgcggttcggttaataca		
Rpi-blb2	DQ122125	Blb2-953	953	F-attgctggartcattgctgg	55	[14,29,31,34]
				R-agcacgagttcccctaatgc		
Rpi-vnt1.3	FJ423046	Rpi-vnt1.3	612	F-ccttcctcatcctcacatttag	58	[17,35]
				R-gcatgccaactattgaaacaac		
Rpi-chc1	-	Rpi-chc1-572	572	F -ctatttgacttccctcgaattct	60	[36]
				R- cttctaacaatggacaatcacgt		

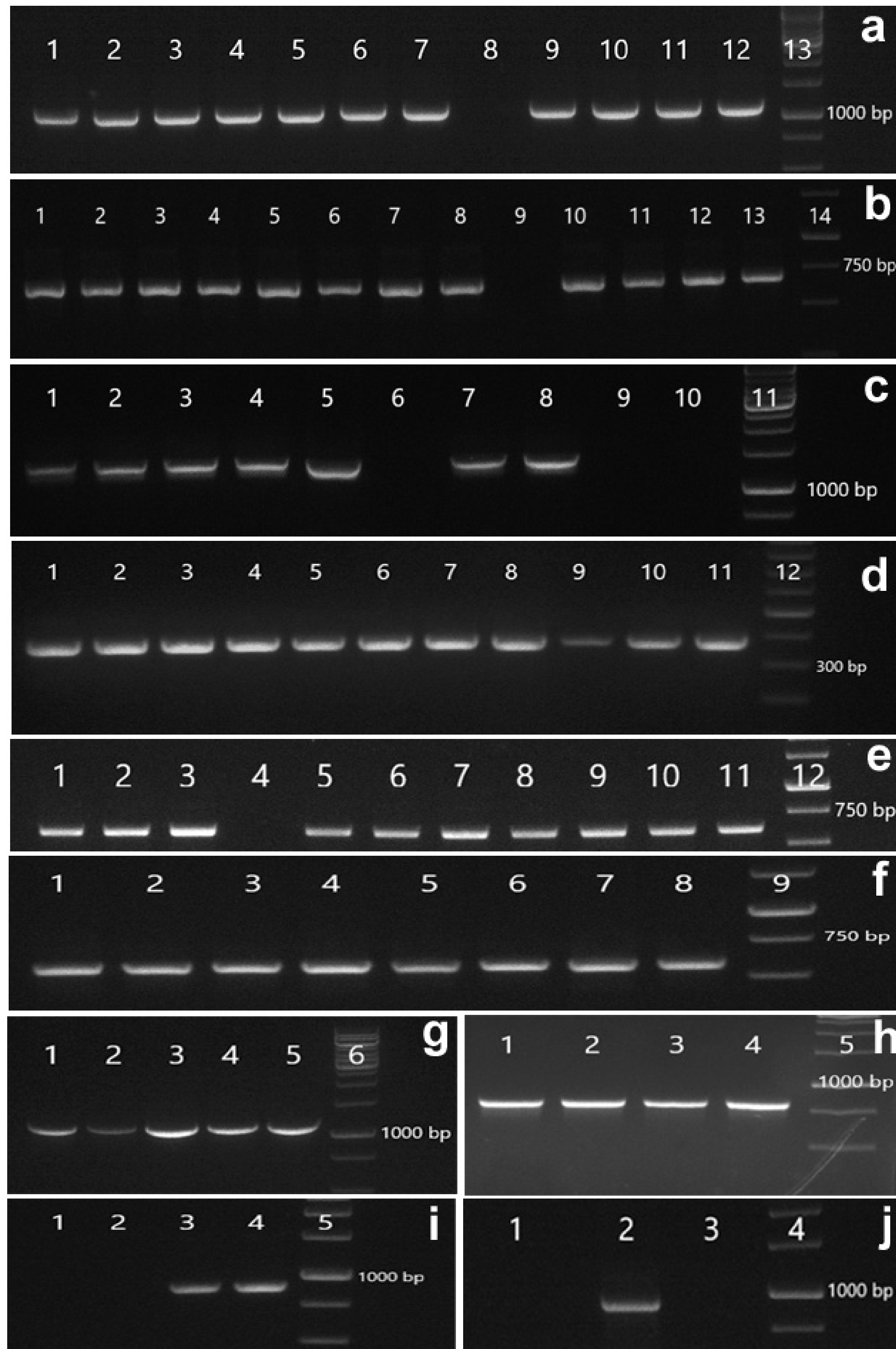

Figure 1. Results of PCR amplification of cDNA of potato varieties and wild *Solanum* species with primers of late blight resistance gene markers.* **(a) R2-1137:** 1- 2359-13, 2- Sudarynya, 3- Svitanok kievskij, 4- 2372-60, 5- Lugovskoj, 6- Brjanskij krasnyj, 7- *S. demissum* PI 161176, 8- *S. stoloniferum* 24263, 9- *S. bulbocastanum* 243512, 10- *S. polytrichon* 24463, 11- *S. bulbocastanum* 243508, 12- *S. stoloniferum* 24976, 13- Gene Ruler 1 Kb DNA Ladder; (**b) R2-686**: 1- 2359-13, 2- Sudarynya, 3- Svitanok kievskij, 4- 2372-60, 5- Lugovskoj, 6- Brjanskij krasnyj, 7- *S. demissum* PI 161176, 8- *S. stoloniferum* 24263, 9- *S. microdontum* 25390, 10- *S. bulbocastanum* 243512, 11- *S. polytrichon* 24463, 12- *S. bulbocastanum* 243508, 13- *S. stoloniferum* 24976, 14- Gene Ruler 1 Kb DNA Ladder; (**c) R3a-1380**: 1- 2359-13, 2- Caprice, 3- Sudarynya, 4- Svitanok kievskij, 5- Alouette, 6- Zhukovskij rannij, 7- 2372-60, 8- Brjanskij krasnyj, 9- *S. bulbocastanum* 243512, 10- *S. polytrichon* 24463, 11- Gene Ruler 1 Kb DNA Ladder; (**d) R3b-378**: 1- 2359-13, 2- Caprice, 3- Sudarynya, 4- Svitanok kievskij, 5- Alouette, 6- Zhukovskij rannij, 7- Golubizna, 8- 2372-60, 9- Brjanskij krasnyj, 10- *S. demissum* PI 161176, 11- *S. stoloniferum* 24263, 12- Gene Ruler 100 bp Plus DNA Ladder; (**e) Rpi-vnt1.3**: 1- Svitanok kievskij, 2- Alouette, 3- Zhukovskij rannij, 4- Lugovskoj, 5- Brjanskij krasnyj, 6- *S. demissum* PI 161176, 7- *S. stoloniferum* 24263, 8- *S. microdontum* 25390, 9- *S. bulbocastanum* 243512, 10- *S. polytrichon* 24463, 11- *S. okadae* 25394, 12- Gene Ruler 1 Kb DNA Ladder; (**f) Rpi-chc1-572**: 1- 2359-13, 2- Caprice, 3- Sudarynya, 4- 2372-60, 5- Lugovskoj, 6- Brjanskij krasnyj, 7- Desiree, 8- *S. avilesii* 20884, 9- Gene Ruler 1 Kb DNA Ladder; (**g) R1-1206**: 1- 2359-13, 2- Svitanok kievskij, 3- Zhukovskij rannij, 4- 2372-60, 5- *S. demissum* PI 161176, 6- Gene Ruler 1 Kb DNA Ladder; (**h) Blb1-821**: 1- Sudarynya, 2- *S. bulbocastanum* 243512, 3- S. *bulbocastanum* 243508, 4- *S. stoloniferum* 24976, 5- Gene Ruler 1 Kb DNA Ladder; (**i) Rpi-sto1**: 1- Sudarynya, 2- *S. bulbocastanum* 243512, 3- *S. bulbocastanum* 243508, 4- *S. stoloniferum* 24976, 5- Gene Ruler 1 Kb DNA Ladder; (**j) Blb2 -953**: 1- *S. stoloniferum* 24263, 2- *S. bulbocastanum* 243512, 3- *S. stoloniferum* 24976, 4- Gene Ruler 1 Kb DNA Ladder.
*Results are presented only for samples that were positive in genomic DNA analysis with the corresponding SCAR markers (see Table 2).

2.4. RNA Extraction

Total RNA was extracted from the true leaves of young plants with the ExtractRNA reagent (Evrogen, Russia) according to the supplier's instructions. Then, individual RNA samples from eight plants of each accession were blended into one combined sample.

2.5. cDNA Synthesis

cDNA preparations were obtained from total RNA samples using Mint reverse transcriptase (Evrogen, Russia) and random primers following the supplier's instructions.

2.6. SCAR Markers and PCR Conditions

We examined the presence/absence of expression of 10 *R* genes: *R1*, *R2*, *Rpi-blb3*, *R3a*, *R3b*, *Rpi-blb1*, *Rpi-sto1*, *Rpi-blb2*, *Rpi-vnt1.3*, and *Rpi-chc1*, detected using 11 SCAR markers of these genes: R1-1206, R2-1137, R2-686, Rpi-blb3, R3a-1380, R3b-378, Blb1-821, Rpi-sto1, Blb2-953, Rpi-vnt1.3, and Rpi-chc1-572 in wild *Solanum* species and cultivated potato varieties. These markers used to be applied in MAS for breeding resistant to late blight potatoes. Primer sequences for PCR amplification of these markers as well as their annealing temperatures and product size are listed in Table 1. PCR conditions for each of these markers were previously described in the relevant publications (see Table 1), and we used these cycling conditions without changes. The reaction mixture was prepared in a volume of 25 µl; 50 ng of genomic DNA/cDNA was added to each reaction mixture. The thermocycler GeneAmp PCR System 2700 (Applied Biosystems, Inc., USA) was used for PCR amplification. Electrophoresis of PCR products was performed in 1% agarose gel in the presence of ethidium bromide (0.5 µg/ml) in 1X Tris-acetate-EDTA buffer followed by visualization under UV light.

Table 2. Results of analysis of the expression of potato late blight resistance genes.

Expression of potato late blight resistance gene markers

	R genes										
	R1	*R2*		*Rpi-blb3*	*R3a*	*R3b*	*Rpi-blb1*	*Rpi-sto1*	*Rpi-blb 2*	*Rpi-vnt1.3*	*Rpi-chc1*
	SCAR markers										
Cutivars	R1-1206	R2-1137	R2-686	Rpi-blb3	R3a-1380	R3b-378	Blb1-821	Rpi-sto1	Blb2 -953	Rpi-vnt1.3	Rpi-chc1-572
2359-13	1	1	1	1	1	1	0	0	0	0	1
Caprice	0	0	0	0	1	1	0	0	0	0	1
Sudarynya	0	1	1	0	1	1	1	1	0	0	1
Svitanok kievskij	1	1	1	1	1	1	0	0	0	1	0
Alouette	0	0	0	0	1	1	0	0	0	1	0
Zhukovskij rannij	1	0	0	0	1	1	0	0	0	1	0
Golubizna	0	0	0	0	0	1	0	0	0	0	0
2372-60	1	1	1	1	1	1	0	0	0	0	1
Lugovskoj	0	1	1	1	0	0	0	0	0	1	1
Bryanskij krasnyj	0	1	1	1	1	1	0	0	0	1	1
Desiree	0	0	0	0	0	0	0	0	0	0	1
Wild species											
S. demissum PI 161176	1	1	1	1	0	1	0	0	0	1	0
S. stoloniferum 24263	0	1	1	1	0	1	0	0	1	1	0
S. microdontum k 25390	0	0	1	0	0	0	0	0	0	1	0
S. bulbocastanum 243512	0	1	1	1	1	0	1	1	1	1	0
S. polytrichon 24463	0	1	1	0	1	0	0	0	0	1	0
S. okadae 25394	0	0	0	0	0	0	0	0	0	1	0
S. avilesii 20884	0	0	0	0	0	0	0	0	0	0	1
S. bulbocastanum 243508	0	1	1	1	0	0	1	1	0	0	0
S. stoloniferum 24976	0	1	1	1	0	0	1	1	1	0	0

1 - a maker is present. **0** - a marker is absent. **Yellow** - an expressed marker. **Red** - an unexpressed marker.

3. RESULTS

We screened 20 samples of the working collection with 11 SCAR markers of 10 *R* genes. The results of this screening are presented in Figure 1 and Table 2. In this table, the occurrence or absence of a marker in a sample is indicated as 1 or 0, respectively, while markers of expressed genes are shown on a yellow ground color, and markers of genes for which we were unable to detect expression are shown on a red ground color.

The target genes of markers R1-1206, R2-1137, R2-686, R3b-378, Blb1-821, Rpi-vnt1.3, and Rpi-chc1-572 were expressed in almost all analyzed samples (Table 2). On the other hand, the *Rpi-blb3* gene, detected with the Rpi-blb3 marker, was not expressed in any of the samples in which this marker was present.

The *R3a* gene marker, named R3a-1380, was found in eight potato varieties, and in all of these samples, with the exception of the variety ÒZhukovskij rannij,Ó this gene was expressed. In wild species, this marker was found only in two accessions: *S. bulbocastanum* 243512 and *S. polytrichon* 24463, but we failed to find the expression of *R3a* gene homologues in these samples.

In the matter of the *Rpi-blb2* gene, the marker of this gene named Blb2-953 was not detected in potato varieties, but this marker was present in three accessions of wild species: *S. bulbocastanum* 243512, *S. stoloniferum* 24263, and *S. stoloniferum* 24976. However, expression of the *Rpi-blb2* gene was observed only in the *S. bulbocastanum* sample. Both *S. stoloniferum* samples had no expression of this gene.

We found the *Rpi-sto1* gene marker only in the variety ÒSudarynya,Ó while expression of the *Rpi-sto1* gene was absent in this cultivar. In wild species, this marker was found in three accessions: *S. bulbocastanum* 243512, *S. bulbocastanum* 243508, and *S. stoloniferum* 24976. The *Rpi-sto1* gene predictably was expressed in *S. stoloniferum*. Speaking of *S. bulbocastanum*, a homologue of this gene was expressed in *S. bulbocastanum* 243508 only, and its expression was absent in *S. bulbocastanum* 243512.

4. DISCUSSION

Marker-assisted selection for resistance to late blight is increasingly being applied in potato farming. Recently, many *R* gene markers have been developed based on the sequences of these genes. However, because these genes have structural homologues that do not have functional activity, the used markers may detect such homologues, leading to false-positive results when assessing the association of markers with resistance. For example, a homologue of the *Rpi-vnt1* gene was found in the late blight-susceptible variety ÒBintje.Ó The authors of the abovementioned research attribute the lack of association between the presence of the *Rpi-vnt1* gene and resistance to late blight to the identification of nonfunctional homologues of this gene [37]. In addition, another study [26] showed the absence of a correlation between the levels of resistance to late blight and the number of *R* gene markers in potato varieties, which, in our opinion, is also due to the fact that the used markers revealed, among other ones, nonfunctional homologues of *R* genes. In our study, we showed that of the 11 *R* gene markers analyzed, the markers R1-1206, R2-1137, R2-686, R3b-378, Blb1-821, Rpi-vnt1.3, and Rpi-chc1-572 were expressed in almost all analyzed samples, making these markers good candidates for their further use in MAS for resistance to late blight.

Speaking about the lack of expression of the Rpi-blb3 marker, it should be noted that the Rpi-blb3 marker was originally designed for mapping and cloning the *Rpi-blb3* gene [5], and we may conclude that the Rpi-blb3 marker is not suitable for use in breeding process because this marker amplifies an unexpressed target.

Based on the data obtained for the R3a-1380 marker, it can be assumed that outside of *S. demissum*, the species in which the *R3a* gene was originally found, homologues of this gene are not expressed and do not have functional activity. Similarly, we can conclude that the *Rpi-blb2* gene is not active outside of *S. bulbocastanum* and the gene from *S. bulbocastanum* only should be introgressed into potato varieties, but not its homologues from other species. Our data also indicate that the genome of *S. bulbocastanum* contains both expressed homologues of the *Rpi-sto1* gene and unexpressed variants of this gene.

5. CONCLUSIONS

Thus, we analyzed the expression of 10 potato late blight resistance genes that we detected in potato varieties and wild *Solanum* species using 11 SCAR markers. Our data show that the markers R1-1206, R2-1137, R2-686, R3b-378, Blb1-821, Rpi-vnt1.3, and Rpi-chc1-572 are associated with expressed *R* genes, and these markers can be recommended for further use in marker-assisted selection for resistance to late blight. Meanwhile, the homologues of the *R3a* and *Rpi-blb2* genes that we identify using the SCAR markers are apparently inactive outside the species in which these genes were originally discovered—*S. demissum* and *S. bulbocastanum*, respectively, and the *Rpi-sto1* gene has both expressed and non-expressed variants.

6. CONFLICTS OF THE INTEREST

The authors declare that they have no financial or any other competing interests.

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8. AUTHOR CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agree to be accountable for all aspects of the work. All the authors are eligible to be an author as per the International Committee of Medical Journal Editors (ICMJE) requirements/guidelines.

9. ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

10. DATA AVAILABILITY

All the data is available with the authors and shall be provided upon request.

11. PUBLISHER'S NOTE

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12. USE OF ARTIFICIAL INTELLIGENCE (AI)-ASSISTED TECHNOLOGY

The authors declares that they have not used artificial intelligence (AI)-tools for writing and editing of the manuscript, and no images were manipulated using AI.

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