# South American species *Solanum alandiae* Card. and *S. okadae* Hawkes et Hjerting as potential sources of genes for potato late blight resistance

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## Южноамериканские виды *Solanum alandiae* Card. и *S. okadae* Hawkes et Hjerting как потенциальные источники генов устойчивости к фитофторозу картофеля

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For several decades, wild species of *Solanum* L. section *Petota* Dumort. have been involved in potato cultivar breeding for robust resistance to pests and diseases. Potato late blight (LB) is caused by oomycete *Phytophthora infestans* (Mont.) de Bary, and the genes for race-specific resistance to *P. infestans* (*Rpi* genes) have been introgressed into cultivated potatoes by remote crosses and trans- or cisgenesis, first from *S. demissum* Buk. and, more recently, from other wild species, such as *S. bulbocastanum* Dun., *S. stoloniferum* Schlechtd. et Bché, and *S. venturii* Hawkes et Hjerting (according to the nomenclature by Hawkes, 1990). Most wild species already involved in breeding for LB resistance came from North and Central Americas: series *Bulbocastana* (Rydb.) Hawkes, *Demissa* Buk. and *Longipedicellata* Buk., and some *Rpi* genes of these species have been already characterized in much detail. *Rpi* genes of South American species, including the series *Tuberosa* (Rydb.) Hawkes, have not been sufficiently investigated. Among the latter, this study focuses on the *Rpi* genes of *S. alandiae* Card. and *S. okadae* Hawkes et Hjerting. Four accessions of *S. alandiae*, one accession of *S. okadae* and 11 clones of interspecific potato hybrids comprising *S. alandiae* germplasm from the VIR collection were PCR-screened using specific SCAR (Sequence Characterized Amplified Region) markers for eight *Rpi* genes. SCAR amplicons of five *Rpi* genes registered in this study were validated by comparing their sequences with those of prototype genes deposited in the NCBI Genbank. Among the structural homologues of *Rpi* genes found in *S. alandiae* and *S. okadae*, of special interest are homologues of CC-NB-LRR resistance genes with broad specificity towards *P. infestans* races, in particular *R2=Rpi-blb3*, *R8*, *R9a*, *Rpi-vnt1* and *Rpi-blb2* (94□99, 94□99, 86□89, 92□98 and 91% identity with the prototype genes, respectively). Our data may help to better understand the process of *Rpi* gene divergence along with the evolution of tuber-bearing *Solanum* species, particularly in the series *Tuberosa*.

**Key words**: tuber-bearing *Solanum* species, *Phytophthora infestans,* CC-NB-LRR genes, structural homologues, SCAR markers.

Дикорастущие виды *Solanum* L. секция *Petota* Dumort., сначала *S. demissum* Buk., а позже *S. bulbocastanum* Dun., *S. stoloniferum* Schlechtd. et Bché, *S. venturii* Hawkes et Hjerting (здесь и далее по системе Hawkes, 1990) и другие – служат источниками генов устойчивости к *Phytophthora infestans* (Mont.) de Bary (genes for resistance to *P. infestans*, *Rpi*-гены) в селекции картофеля на устойчивость к фитофторозу методами отдаленной гибридизации и трансили цисгеноза. В отличие от *Rpi*-генов, детально охарактеризованных у видов *Solanum* из Северной и Центральной Америки, прежде всего серий *Bulbocastana* (Rydb.) Hawkes, *Demissa* Buk. и *Longipedicellata* Buk., *Rpi*-гены южноамериканских видов, включая серию *Tuberosa* (Rydb.) Hawkes, изучены очень слабо. К числу последних относятся *S. alandiae* Card. и *S. okadae* Hawkes et Hjerting. Четыре образца *S. alandiae,* образец *S. okadae* и 11 клонов межвидовых гибридов *S. alandiae* с культурным картофелем из коллекции ВИР исследовали методом ПЦР с помощью специфичных SCAR-маркеров (Sequence Characterized Amplified Region) восьми *Rpi*-генов. Последовательности SCAR-маркеров пяти обнаруженных *Rpi*-генов валидировали, сравнивая их с генами-прототипами из Генбанка NCBI. Среди структурных гомологов *Rpi*-генов, найденных у *S. alandiae* и *S. okadae*, особый интерес представляют гомологи *Rpi*-генов с широкой расовой специфичностью: *R2=Rpi-blb3*, *R8*, *R9a*, *Rpi-vnt1* и *Rpi-blb2* (соответственно 94–99, 94–99, 86–89, 92–98 и 91% сходства с генами-прототипами). Полученные данные будут способствовать лучшему пониманию дивергенции *Rpi*-генов в процессе эволюции клубненосных видов *Solanum*, особенно в серии *Tuberosa*.

**Ключевые слова**: клубнеобразующие виды *Solanum*, *Phytophthora infestans,* CC-NB-LRR гены, структурные гомологи, SCAR-маркеры.

## Introduction

Late blight (LB) caused by oomycete *Phytophthora infestans* (Mont.) de Bary is among the major obstacles on the road to sustainable potato production. To limit this disease, breeders deploy the technologies of remote crosses and trans- and cisgenesis to transfer the genes of resistance to *P. infestans* (*Rpi* genes) from wild *Solanum* species into susceptible potato cultivars, which are demanded by the market. However, due to rapid genome evolution and migration of new strains, severe outbreaks of the pathogen have been relentlessly overcoming plant defense barriers built up by breeders and negating, literally within a few days, their many years of effort (Cooke et al., 2012; Fry, 2016). By combining (pyramiding) several *Rpi* genes in one potato plant, breeders provide for robust and durable resistance of new cultivars to a broad range of *P. infestans* pathotypes. Therefore, it is an urgent task of plant biologists to constantly seek for new sources of resistance, predominantly in wild *Solanum* genotypes, which have not been as yet introduced into potato breeding, and expand the scope of *Rpi* genes thoroughly characterized and documented with molecular methods (Vossen et al., 2014; Bethke et al., 2019).

All presently characterized *Rpi* genes belong to the CC-NB-LRR type: their protein products comprise coiled-coil, nucleotide-binding and leucine-rich region domains (Hein et al., 2009; Jupe et al., 2012; Rodewald, Trognitz, 2013). The mechanisms of immediate molecular interactions between the products of *P. infestans* avirulence genes and the products of *Solanum Rpi* genes, that is, effector recognition by receptor kinase, have been sufficiently researched only in few cases, such as Avr3a – R3a interaction. However, such lack of information on the *Rpi* genes does not hinder the genetic studies aimed at mining *Solanum* collections for new *Rpi* genes and introducing these genes into breeding for durable LB resistance. Following the marker-assisted mapping and cloning of *Rpi* genes, recent years have seen a considerable progress in this direction. New methodologies, such as effectoromics, allele profiling and diagnostic resistance gene enrichment sequencing (dRenSeq), tremendously facilitated the search for new *Rpi* genes and new alleles of *Rpi* genes already characterized in other species of *Solanum* L. within the section *Petota* Dumort (Vossen et al., 2014; van Weymers et al., 2016; Chen et al., 2018; Jiang et al., 2018; Armstrong et al., 2019). Currently some of these genes have been introgressed into commercial potato cultivars (Haesaert et al., 2015).

The potato genetic collection maintained at the N.I. Vavilov Institute of Plant Genetic Resources (VIR) in St. Petersburg is a major source of prospective *Rpi* genes. These genes can be found in the collection accessions of wild potatoes (Zoteyeva, 2012) and in the multiparental interspecific hybrids comprising numerous *Rpi* genes of broad race specificity toward *P. infestans*. It is most significant that such hybrids could keep *Rpi* genes already lost from the collections of wild species (Fadina et al., 2017; Rogozina et al., 2018).

Most *Rpi* genes already characterized in sufficient detail and employed by breeders (Hein et al., 2009; Rodewald, Trognitz, 2013; Vossen et al., 2014; Aguilera-Galvez et al., 2018; Rogozina et al., 2018) come from wild *Petota* species growing in North and Central America: series *Bulbocastana* (Rydb.) Hawkes, *Demissa* Buk. and *Longipedicellata* Buk. South America hosts three fourth of unique *Petota* species (Spooner et al., 2014); nevertheless, most of these species are *terra incognita* as far as *Rpi* genes are concerned, with the best known exception of the *Rpi-vnt1* gene from *S. venturii* Hawkes et Hjerting. This fully applies to two species from the series *Tuberosa*, *S. alandiae* Card. (accepted by Spooner et al., 2014, as *S. brevicaule* Bitter) and *S. okadae* Hawkes et Hjerting. We screened these species with specific SCAR (Sequence Characterized Amplified Region) markers of eight *Rpi* genes and found several structural homologues of *Rpi* genes with broad specificity toward *P. infestans* races: *R2 / Rpi-blb3*, *R8*, *R9*, *Rpi-vnt1* and *Rpi-blb2*. Some data presented below have been reported at the XVII EuroBlight Workshop (Muratova [Fadina] et al., 2019).

## Materials and methods

Plant material from the VIR potato genetic collection included the lines isolated from *S. alandiae* accessions k-18473, k-20408 and k-21240. The *S. okadae* line was isolated from the accession k-25397 derived from *P. infestans* resistant accession CGN 18279, which was kindly provided by Roel Hoekstra (Wageningen University & Research, Wageningen [WUR]). In addition, our study included potato interspecific hybrids containing *S. alandiae* germplasm and several potato cultivars and hybrids employed as references in LB assessments and as positive and negative controls in the marker analysis. These hybrids and cultivars are maintained in the collection of the All-Russian Research Institute of Phytopathology, Moscow Province, Russia (http://www.vniif.ru).

Resistance of wild species to *P. infestans* was evaluated in the laboratory tests with detached leaves according to Fadina et al. (2017) using a highly virulent and aggressive isolate of *P. infestans* 161 (races 1.2.3.4.5.6.7.8.9.10.11, mating type A1) collected in Moscow Province (the collection of the Institute of Phytopathology), and cv. 'Santé' as a reference. The LB resistance of potato hybrids and cultivars was assessed in the field trials at the Institute of Phytopathology and VIR under natural infestation by registering the area under the disease progress curve (AUDPC) against several cultivars used as references. All experimental data for LB resistance were converted to 1–9-point scores.

Plant DNA samples were PCR-screened for eight *Rpi* genes: *R1, R2/Rpi-blb3, R3a, R3b, R8, Rpi-blb1 = Rpi-sto1, Rpi-blb2* and *Rpi-vnt1* (Fadina et al., 2017). Specific SCAR markers are based on the sequences of *Rpi* prototype genes, that is, the genes extensively characterized by their structure and function. The markers were validated against *Solanum* genotypes comprising the functional alleles of the corresponding genes. Methods for DNA isolation, PCR primers (Fig. 1; Table 1) and protocols for PCR analysis, cloning and sequencing of DNA fragments as well as bioinformatic procedures were described previously (Fadina et al., 2017; Muratova [Fadina] et al., 2019). SCAR amplicons were verified by comparing their sequences to those of prototype genes deposited in the NCBI Genbank.

## Results and discussion

Several accessions of *S. alandiae* were reported to manifest considerable resistance to *P. infestans* (Perez et al., 2001; Bhardwaj et al., 2018; Zoteyeva, 2019); however, the *Rpi* genes in *S. alandiae* have not been researched extensively. By screening *S. alandiae* accessions and *S. alandiae* hybrids with potato cultivars we found the structural homologues of several *Rpi* genes of broad specificity toward *P. in-*

**Table 1.** SCAR markers of *Solanum Rpi* genes (according to Muratova [Fadina] et al., 2019, modified)

**Таблица 1.** SCAR-маркеры *Rpi*-генов *Solanum* spp. (по Muratova [Fadina] et al., 2019, с изменениями)

| Gene | Prototype gene* | Marker and its size, bp | Position on the prototype genes, bp | Primer sequences | Anneal. temp., °C | Reference |
|---|---|---|---|---|---|---|
| *R1* | AF447489 | R1-1205 | 5126-6331 | F-cactcgtgacatatcctcacta<br>R-gtagtacctatcttatttctgcaagaat | 61 | Sokolova et al., 2011 |
| *R2/Rpi-blb3* | FJ536325 | R2-686 | 1370-2055 | F-gctcctgatacgatccatg<br>R-acggcttcttgaatgaa | 54 | Kim et al., 2012 |
| *R3a* | AY849382 | R3a-1380 | 1677-3056 | F-gtagtacctatcttatttctgcaagaat<br>R-agccacttcagcttcttacagtagg | 64 | Sokolova et al., 2011 |
| *R3b* | JF900492 | R3b-378 | 94818-95195 | F-gtcgatgaatgctatgtttctcgaga<br>R-accagtttcttgcaattccagattg’ | 64 | Rietman et al., 2012 |
| *Rpi-blb1 = Rpi-sto1* | AY336128 | Rpi-blb1-820 | 2304-3124 | F-aacctgtatggcagtggcatg<br>R-gtcagaaaagggcactcgtg | 62 | Wang et al., 2008 |
| | EU884421 | Rpi-sto1-890 | 241–1130 | F-accaaggccacaagattctc<br>R-cctgcggttcggttaataca | 65 | Haesaert et al., 2015 |
| *Rpi-blb2* | DQ122125 | Rpi-blb2-976 | 3226-4202 | F-ggactgggtaacgacaatcc<br>R-atttatggctgcagaggacc | 55 | Van der Vossen et al., 2005 |
| *Rpi-vnt1* | FJ423046 | Rpi-vnt1.3-612 | 89-701 | F-ccttcctcatcctcacatttag<br>R-gcatgccaactattgaaacaac | 58 | Pel, 2010 |
| *R8* | KU53015 | R8-1276 | 73694-74970 | F-aacaagagatgaattaagtcggtagc<br>R-gctgtaggtgcaatgttgaagga | 62.5 | Modified after Vossen et al., 2016 |

* Accession numbers in the NCBI Genbank (https://www.ncbi.nlm.nih.gov/)
* Номера последовательностей в Генбанке NCBI (https://www.ncbi.nlm.nih.gov/)

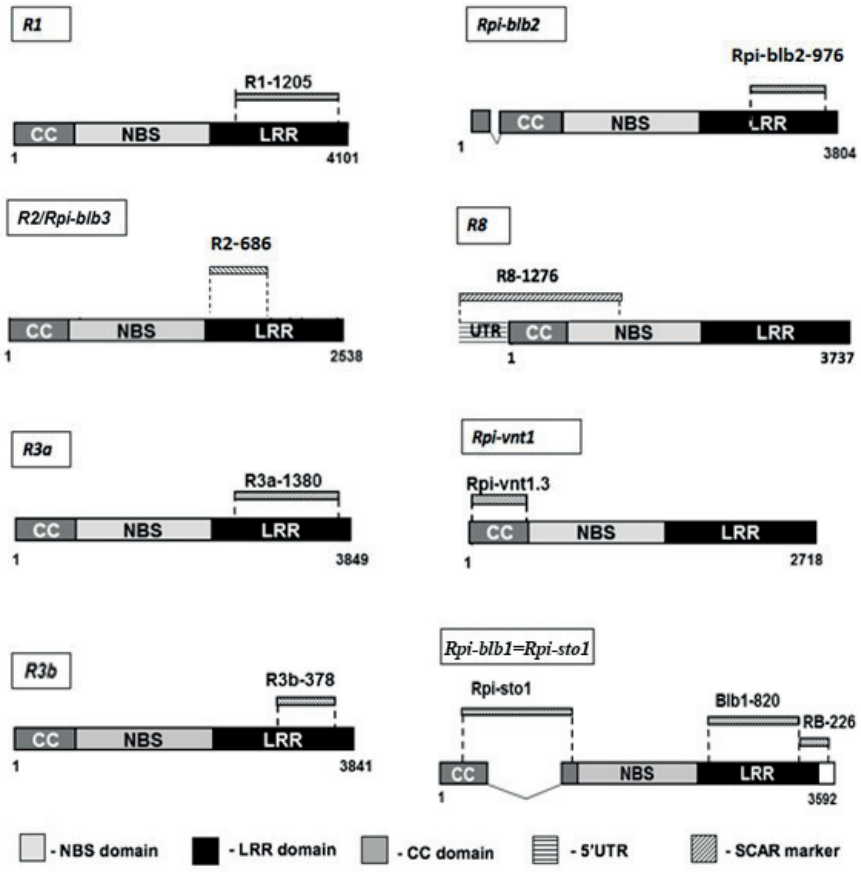


**Fig. 1.** SCAR markers of the *Rpi* genes are schematically positioned against the CC-NB-LRR domains (according to Muratova [Fadina] et al., 2019, modified)

**Рис. 1.** Схема положения SCAR-маркеров в последовательностях CC-NB-LRR доменов *Rpi*-генов (по Muratova [Fadina] et al., 2019, с изменениями)

*festans* races (Table 2, Table 3). Comparison of marker sequences to those of the prototype genes showed that the *S. alandiae* genome comprised the structural homologues of *R2/Rpi-blb3*, *R8*, *R9a*, *Rpi-vnt1* and *Rpi-blb2* (with 94–99, 94–99, 86–89, 92–98 and 91% identity with the prototype genes, respectively). The marker of the *R1* gene, found only in potato cultivars and their hybrids, was apparently derived from that of *S. demissum*. The markers of the *R3b* and *Rpi-blb1 = Rpi-sto1* genes were not found in the analyzed genotypes.

This is the first report on the structural homologue of the *Rpi-vnt1* gene in *S. alandiae*. *S. okadae* amplicons sequenced in this study were 97–98% identical to the *Rpi-vnt1.3* homologue from the *S. alandiae* genome (Table 3). The *Rpi-vnt1.2* allele was reported in the accession CGN 18279 (Pel, 2010), corresponding to *S. okadae* k-25397; however, Pel and his associates (Pel, 2010) presumed that this accession belonged to the species *S. venturii*.

The structural homologues of the *Rpi-vnt1* gene from *S. alandiae* and *S. okadae* differed from the prototype gene

**Table 2. Presence or absence of the SCAR markers *Rpi* genes in accessions of *Solanum okadae*, *S. alandiae* and in *S. alandiae* hybrids with potato cultivars (according to Muratova [Fadina] et al., 2019, modified)**

**Table 2. Наличие / отсутствие SCAR-маркеров *Rpi*-генов у образцов *Solanum okadae*, *S. alandiae* и гибридов *S. alandiae* с сортами картофеля (по Muratova [Fadina] et al., 2019, с изменениями)**

| Genotype | VIR accession number and pedigree* | R1-1250 | R2-686 | R3a-1380 | Rpi-blb2-976 | R8-1259 | Rpi-vnt1.3-612 | Resistance to *P. infestans*, points |
|---|---|---|---|---|---|---|---|---|
| *S. alandiae* | k-21240 D17-329 | 0 | 0 | 0 | 1 | 1 | 0 | 5 |
| *S. alandiae* | k-18473-1 | 0 | 1 | 0 | 1 | 1 | 1 | nd |
| *S. alandiae* | k-19443 | 0 | 0 | 0 | 1 | 0 | 0 | 5 |
| *S. alandiae* | k-20408 | 0 | 0 | 0 | 1 | 1 | 0 | 3 |
| *S okadae* | k-25397-1 | 0 | 1 | 0 | 1 | 1 | 1 | nd |
| cv. Atzimba P1 | nd | 0 | 0 | 0 | 1 | 1 | 0 | 5 |
| 39-1-2005 | Atzimba × *S. alandiae* | 0 | 0 | 0 | 0 | 1 | 1 | 6 |
| cv. Elizaveta P2 | acl, adg, dms, phu, sto, vrn | 1 | 0 | 1 | 0 | 0 | 0 | 4 |
| cv. Svitanok Kievskij P2 | dms | 0 | 1 | 1 | 0 | 1 | 0 | 5 |
| 24-1 | Atzimba × *S. alandiae* | 0 | 0 | 0 | 1 | 1 | 1 | 6 |
| 24-2 | | 0 | 1 | 0 | 1 | 0 | 1 | 6 |
| 117-1 | | 0 | 0 | 0 | 1 | 0 | 1 | 5 |
| 117-2 | | 0 | 0 | 0 | 1 | 1 | 1 | 5 |
| 25-1-2007 | 24-1 × Elizaveta | 1 | 0 | 0 | 1 | 0 | 0 | 5 |
| 25-2-2007 | | 1 | 0 | 0 | 1 | 0 | 1 | 4 |
| 134-6-2006 | 24-2 × Svitanok Kievskij | 0 | 0 | 1 | 0 | 1 | 1 | 5 |
| 134-2-2006 | | 0 | 0 | 0 | 0 | 1 | 1 | 6 |
| 135-1-2006 | Svitanok Kievskij × 24-2 | 1 | 1 | 1 | 0 | 0 | 1 | 5 |
| 135-2-2006 | | 1 | 1 | 1 | 0 | 0 | 0 | 4 |
| cv. Alouette | | 0 | 0 | 1 | 0 | nd | 1 | 8 |

* acl, *S. acaule* Bitt.; adg, *S. tuberosum* subsp. *andigena* Hawkes; aln, *S. alandiae* Cárd.; dms, *S. demissum* Lindl.; phu, *S. phureja* Juz. et Buk.; sto, *S. stoloniferum* Schlechtd. et Bché; vrn, *S. vernei* Bitt. et Wittm.; nd, no data.

* acl, *S. acaule* Bitt.; adg, *S. tuberosum* subsp. *andigena* Hawkes; aln, *S. alandiae* Cárd.; dms, *S. demissum* Lindl.; phu, *S. phureja* Juz. et Buk.; sto, *S. stoloniferum* Schlechtd. et Bché; vrn, *S. vernei* Bitt. et Wittm.; nd, нет данных.

1 – presence of the marker, 0 – absence of the marker

1 – наличие маркера, 0 – отсутствие маркера

**Table 3. Similarity levels (% identity) of nucleotide sequences in sequenced fragments of *Solanum alandiae* and *S. okadae* genomes as compared with the homologous regions of known *Rpi* genes**

**Таблица 3. Уровень сходства (в %) нуклеотидных последовательностей секвенированных фрагментов геномов *Solanum alandiae* и *S. okadae* с гомологичными районами известных *Rpi*-генов**

| | *R2*<br>*S. demissum*<br>FJ536325** | *Rpi-blb3*<br>*S. bulbocastanum*<br>FJ536346 | *R2/Rpi-blb3*<br>*S. okadae** | | |
|---|---|---|---|---|---|
| *R2/Rpi-blb3* homologue from *S. alandiae** | 94 | 97 | 98-99 | | |
| | *Rpi-blb2*<br>*S. bulbocastanum*<br>DQ122125 | *Mi-1.2*<br>*S. lycopersicum*<br>AF091048 | | | |
| *Rpi-blb2* homologue from *S. alandiae** | 91 | 86 | | | |
| | *R9a*** | *Rpi-vnt1.1*<br>*S. venturii*<br>FJ423044 | *Rpi-vnt1.2*<br>*S. venturii*<br>FJ423045 | *Rpi-vnt1.3*<br>*S. venturii*<br>FJ423046 | *Rpi-vnt1*<br>*S. okadae*<br>k-25397* |
| *Rpi-vnt1.3* homologue from *S. alandiae** | 86-89 | 92-93 | 92-93 | 92-93 | 97-98 |
| * | *R8*<br>*S. demissum*<br>KU530153 | *Sw5-b*<br>*S. lycopersicum*<br>AY007366 | *R8*<br>*S. okadae**<br>k-25397 | | |
| *R8* homologue from *S. alandiae** | 99 | 85 | 94 | | |

* Cloned in our laboratory; ** compared to the sequence published by Armstrong et al. (2019) as Appendix S1 (https://onlinelibrary.wiley.com/doi/full/10.1111/pbi.12997).

* Клонированы в нашей лаборатории; **в сравнении с последовательностью, опубликованной Armstrong et al. (2019) в Приложении S1 (https://onlinelibrary.wiley.com/doi/full/10.1111/pbi.12997).

** Accession numbers in the NCBI Genbank (https://www.ncbi.nlm.nih.gov/) are indicated

** Указаны номера образцов в Генбанке NCBI Genbank (https://www.ncbi.nlm.nih.gov/)

*Rpi-vnt1.1* of *S. venturii* (FJ423044) by several single nucleotide polymorphisms (SNPs) and one three-nucleotide insertion. *Rpi-vnt1* clones from *S. alandiae* (accession k-18473) revealed two diverse variants of sequences with 90% identity: the sequence *Rpi-vnt1 S. alandiae 2* comprised a 24-nucleotide deletion, which was also characteristic of the *Rpi-vnt1.1* sequences in *S. okadae,* the prototype gene from *S. venturii* (FJ423044) and the marker Rpi-vnt1.3-612 (MH297492) cloned from cv. Alouette (Fig. 2). One of the SNPs in *Rpi-vnt1* from *S. alandiae 1* resulted in a stop codon and, as a consequence, a shortened protein (Fig. 3), which was 83% identical to Rpi-vnt1-like amino acid sequence from *S. okadae* (ADB85624) and only by 77% to the corresponding sequence from *S. venturii* (ACJ66596). The amino acid sequences were identical to the corresponding Rpi-vnt1 sequence (ACJ66596) encoded by the functionally active *Rpi-vnt1.3* allele of *S. venturii* (FJ423046). Thus, we can assume that at least some regions of *Rpi-vnt1* in *S. alandiae* and *S. okadae* are translatable. In addition, *S. alandiae* comprised sequences resembling the *Rpi-vnt*-like, which were different from the functional gene *Rpi-vnt1*.

The presence of the Rpi-vnt1.3-612 marker in *S. alandiae* and potato hybrids was significantly related to elevated LB resistance (the Spearman's correlation coefficient 0.54 at 5% confidence level).

The Rpi-vnt1.3-612 sequences cloned from cv. Atzimba × *S. alandiae* hybrids resembled the functional gene *R9a/Rpi-edn2* (Jo et al., 2015), rather than *Rpi-vnt1.* Their amino acid sequences differed from those of prototype genes by several single amino acid substitutions and a characteristic KGA insertion (Fig. 3). The identity of *Rpi-vnt1* from the South American species *S. alandiae* and *S. okadae* to its close homologue *R9a* from North American species *S. demissum* (Aguilera-Galvez et al., 2018; Armstrong et al., 2019) was below 90% (Table 3).

The presence of the functional *Rpi-vnt1.1* gene in resistant *S. okadae* accessions and their resistant progeny was later confirmed by dRenSeq and corroborated by *Avr-vnt1* recognition in transient expression assays (van Weymers et al., 2016). In addition to *S. venturii*, M. A. Pel (2010) cloned *Rpi-vnt1* homologues sharing 80 to 97% identity with the prototype gene from 13 wild South American species belonging to the series *Tuberosa*; the gene was represented by three alleles of monophyletic origin, with *Rpi-vnt1.1* and *Rpi-vnt1.3* alleles apparently evolved from *Rpi-vnt1.2*. We compared these sequences to *Rpi-vnt1* homologues from

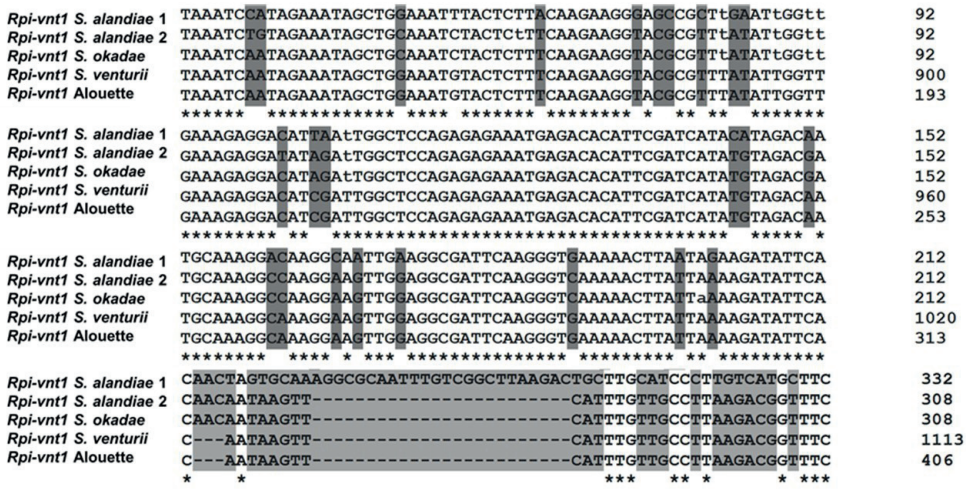


**Fig. 2. Multiple alignment of nucleotide sequences of the fragments of *Rpi-vnt1* structural homologues from *Solanum alandiae* and *S. okadae*, and a region of the functional *Rpi-vnt1* gene.**
*Rpi-vnt1 S. alandiae 1* and *Rpi-vnt1 S. alandiae 2*, marker Rpi-vnt1.3-612 cloned from *S. alandiae* k-18473; *Rpi-vnt1 S. okadae*, marker Rpi-vnt1.3-612 cloned from *S. okadae* k-25397; *Rpi-vnt1 S. venturii*, the prototype gene *Rpi-vnt1.1* (FJ423044); *Rpi-vnt1* Alouette, marker Rpi-vnt1.3-612 cloned from cv. Alouette (MH297492). Identical nucleotides are indicated by asterisks. Regions of diversity are highlighted in grey

**Рис. 2. Множественное выравнивание нуклеотидных последовательностей фрагментов структурных гомологов генов *Rpi-vnt1 Solanum alandiae* и *S. okadae*, а также участка функционального *Rpi-vnt1*-гена.**
*Rpi-vnt1 S. alandiae 1* и *Rpi-vnt1 S. alandiae 2* – полиморфные варианты 1 и 2 маркера *Rpi-vnt1.3-612*, клонированного из *S. alandiae* к-18473; *Rpi-vnt1 S. okadae*, маркер *Rpi-vnt1.3-612*, клонированный из *S. okadae* к-25397; *Rpi-vnt1 S. venturii*, ген-прототип *Rpi-vnt1.1* (FJ423044); *Rpi-vnt1* Alouette, маркер Rpi-vnt1.3-612, клонированный из сорта Alouette (MH297492). Идентичные нуклеотиды обозначены звездочками. Области различия выделены серой заливкой


**Fig. 3. Multiple alignment of the Rpi-vnt1 protein sequences from interspecific Atzimba × *S. alandiae* hybrids (24-1, 24-2, 117-1, 117-2 and 39-1-2005) and cv. Alouette against those encoded by known functional genes.**
RPI-EDN2 corresponds to *Rpi-edn2* from *S. edinense* (US Patent 2014/0041072 A1), Rpi-vnt1.1, Rpi-vnt1.2 and Rpi-vnt1.3 are fragments of the corresponding *S. venturii* proteins ACJ66594, ACJ66595 and ACJ66596, RPP13-like is *S. tuberosum* disease resistance protein RPP13-like XP_015170549. Regions of diversity are highlighted in grey; KGA are amino acid residues characteristic of Rpi-vnt-like and RPI-EDN2

**Рис. 3. Множественное выравнивание участков последовательностей белков Rpi-vnt1 из межвидовых гибридов Atzimba × *S. alandiae* (24-1, 24-2, 117-1, 117-2 и 39-1-2005), сорта Alouette и соответствующих последовательностей белков, кодируемых известными функциональными генами.**
RPI-EDN2 соответствует *Rpi-edn2* из *S. edinense* (US Patent 2014/0041072 A1), Rpi-vnt1.1, Rpi-vnt1.2 и Rpi-vnt1.3 – фрагменты соответствующих белков *S. venturii* ACJ66594, ACJ66595 и ACJ66596; RPP13-like – белок RPP13-like гена устойчивости *S. tuberosum* к болезням XP_015170549. Области различия выделены серой заливкой; KGA – аминокислотные остатки, характерные для белков Rpi-vnt-like и RPI-EDN2

*S. alandiae* and *S. okadae* characterized in this study. To eliminate polymorphisms due to synonymic substitutions, we aligned amino acid sequences corresponding to the Rpi-vnt1.3-612 marker found in *S. alandiae* and *S. okadae* with the sequences corresponding to Rpi-vnt1 proteins in other South American species (Fig. 4).

These South American species comprise an insertion absent in other sequences, including *S. okadae* GU338334, and a deletion shared with *S. bukasovii* GU338315 and *S. microdontum* GU338312. It is of special significance that we failed to discern the marker Rpi-vnt1.3-612 in *S. verrucosum* Schltdl. accessions k-24995, k-24991, k-23760, k-24313, k-23015, k-23760, and PI195171, the only *Tuberosa* species in North and Central Americas (Spooner et al., 2014). The absence of *Rpi-vnt1* in *S. verrucosum* was also reported using dRenSeq technology (Chen et al., 2018).

In addition to *Rpi-vnt1* genes, SCAR marker analysis of *S. alandiae* and *S. okadae* revealed structural homologues of *R2/Rpi-blb3*, *Rpi-blb2* and *R8* characteristic of North and Central American species (Table 3). The *S. alandiae* fragment was 91% homologous to *Rpi-blb2* in *S. bulbocastanum* (DQ122125) and differed from the prototype by several SNPs and deletions (Fig. 5). The *S. alandiae* and *S. okadae* fragments were both 99% identical to *R8* from *S. demissum* (KU530153) and differed in several SNPs and one nucleotide deletion. The *R8* homologue from hybrid 24-1 (Atzimba × *S. alandiae* k-21240) completely matched the R8-1276 sequence from *S. alandiae* k-20408 (Fig. 6). *R8* homologues from *S. alandiae* and *S. okadae* differed by three deletions from the corresponding fragment of *Sw5b* (Fig. 6), which was only 83% identical to *R8* in *S. demissum* (Jiang et al., 2018).

*R2* homologues from *S. alandiae* and *S. okadae* were 94–97% identical to the prototype gene from *S. demissum* (FJ536325) and its orthologue *Rpi-blb3* from *S. bulbocastanum* (FJ536346). Notably, the latter, together with *R2* homologues from *S. alandiae* and *S. okadae*, differed from the *R2* of *S. demissum* by several SNPs and a six-nucleotide insertion (Fig. 7).


**Fig. 4. Multiple alignment of nucleotide sequences of the fragments of *Rpi-vnt1* structural homologues from *Solanum alandiae* and *S. okadae*, and regions of the known *Rpi-vnt1* genes from South American species of *Tuberosa* series (Pel, 2010).**

*S. alandiae* and *S. okadae**, the Rpi-vnt1.3-612 marker cloned in this study from the *S. alandiae* accession k-18473 and the *S. okadae* accession k-25397. All other sequences are from the NCBI Genebank: *S. bukasovii* Juz. GU338315, *S. microdontum* Bitt. GU338312, *S. stenotomum* Juz. & Buk. GU338323, *S. sucrense* Hawkes GU338339, *S. raphanifolium* Cárd. & Hawkes GU338338, *S. orophilum* Corr. GU338320, *S. medians* Bitt. GU338344, *S. neorossii* Hawkes & Hjert. GU338331, *S. oplocense* Hawkes GU338317, *S. okadae* GU338334, and *S. tarijense* Hawkes U338326.

For other notations see Fig. 2

**Рис. 4. Множественное выравнивание нуклеотидных последовательностей фрагментов структурных гомологов генов *Rpi-vnt1 Solanum alandiae* и *S. okadae*, а также участков гена *Rpi-vnt1* из южноамериканских видов серии *Tuberosa* (Pel, 2010).**

*S. alandiae* и *S. okadae** – маркер Rpi-vnt1.3-612, клонированный в этом исследовании из образца к-18473 *S. alandiae* и образца к-25397*S. okadae*. Все другие последовательности – из Генбанка NCBI: *S. bukasovii* Juz. GU338315, *S. microdontum* Bitt. GU338312, *S. stenotomum* Juz. & Buk. GU338323, *S. sucrense* Hawkes GU338339, *S. raphanifolium* Card. & Hawkes GU338338, *S. orophilum* Corr. GU338320, *S. medians* Bitt. GU338344, *S. neorossii* Hawkes & Hjert. GU338331, *S. oplocense* Hawkes GU338317, *S. okadae* GU338334 и *S. tarijense* Hawkes GU338326. Остальные обозначения как на рис. 2


**Fig. 5.** **Structural homology between the cloned marker fragment Rpi-blb2-976 from *Solanum alandiae* accession k-19443, the *Rpi-blb2* gene from *S. bulbocastanum* (DQ122125), and its analogue *Mi-1* from *S. lycopersicum* L. (AF091048).**
For other notations see Fig. 2

**Рис. 5.** **Сравнение нуклеотидных последовательностей клонированного маркерного фрагмента Rpi-blb2-976 из образца к-19443 *Solanum alandiae*, последовательностей гена *Rpi-blb2* из *S. bulbocastanum* (DQ122125) и его аналога *Mi-1* из *S. lycopersicum* L. (AF091048).**
Другие обозначения как на рис. 2


**Fig. 6.** **Structural homology between the cloned marker fragment R8-1276 from *Solanum alandiae* accession k-20408, hybrid 24-1 comprising *S. alandiae* germplasm, and the prototype gene *R8* from *S. demissum* (KU530153); *Sw5b*, *R8* analogue from *S. lycopersicum* (AY007366).**
For other notations see Fig. 2

**Рис. 6.** **Сравнение нуклеотидных последовательностей клонированного маркерного фрагмента R8-1276 из образца к-20408 *Solanum alandiae*, гибрида 24-1, содержащего генетический материал *S. alandiae*, и гена-прототипа *R8* из *S. demissum* (KU530153); *Sw5b* - аналог *R8* из *S. lycopersicum* (AY007366).**
Другие обозначения как на рис. 2

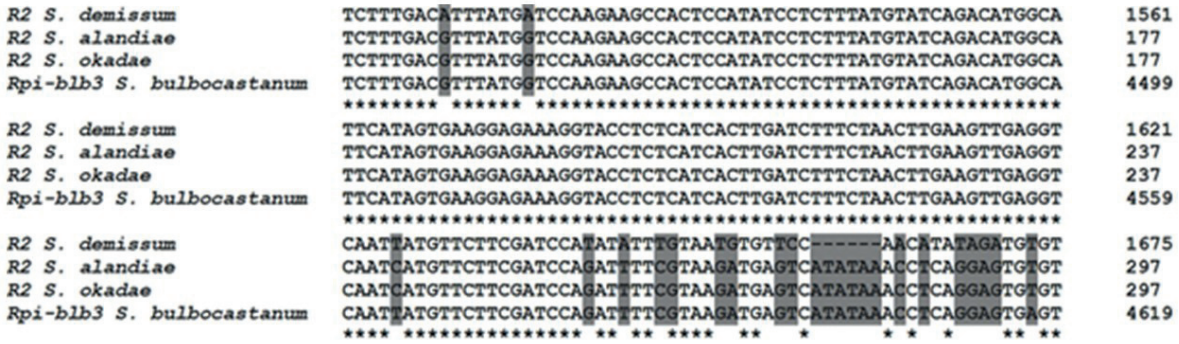


**Fig. 7. Structural homology between the cloned marker fragment R2-686 from *Solanum alandiae* accession k-18437 and *S. okadae* accession k-25397, the prototype gene *R2* from *S. demissum* (FJ536325), and its orthologue *Rpi-blb3* from *S. bulbocastanum* (FJ536346).**

For other notations see Fig. 2

**Рис. 7. Сравнение нуклеотидных последовательностей клонированного маркерного фрагмента R2-686, из образцов к-18437 *Solanum alandiae* и к-25397 *S. okadae*, гена-прототипа *R2* из *S. demissum* (FJ536325) и его ортолога *Rpi-blb3* из *S. bulbocastanum* (FJ536346).**

Другие обозначения как на рис. 2

## Conclusion

The comparative SCAR marker analysis of *S. alandiae* and *S. okadae* accessions in the VIR collection discovered several structural homologues of already known *Rpi* genes. When analyzing these data, two caveats are appropriate. First, we dealt with rather short DNA fragments, which never covered more than one third of the complete gene sequence. Secondly, even when these fragments were translatable, the proof of functionality of *Rpi* homologues in *S. alandiae* and *S. okadae* must await further studies by independent methods. Our data match the evidence that the *Rpi-vnt1* gene is specific to South American species of series *Tuberosa* (Pel, 2010) and is absent in Mexican *S. verrucosum* (Chen et al., 2018), despite the fact that the latter species is often grouped with South American *Tuberosa* germplasm (Hardigan et al., 2015). Other *Rpi* homologues found in *S. alandiae* and *S. okadae* resemble the *R2*, *R8*, *R9* and *Rpi-blb2* genes of Mexican species *S. demissum* and *S. bulbocastanum.* An *Rpi-mcd1* gene orthologous to *R2* but distinct in its chromosomal localization was reported in South American species *S. microdontum* (Hein et al., 2009; Rodewald, Trognitz, 2013; Vossen et al., 2014; van Weymers et al., 2016; Aguilera-Galvez et al., 2018); however, the sequence of *Rpi-mcd1* has not yet been published. South American homologues of *Rpi* genes reported here for the first time are notably distinct from their Mexican prototypes. Among the *Rpi* homologues found in *S. alandiae* and *S. okadae*, especially promising for potato breeders are those resembling the genes of broad specificity toward *P. infestans* races, such as *R2 / Rpi-blb3*, *R8*, *R9*, *Rpi-vnt1* and *Rpi-blb2*. In this context, it seems proper to mention our evidence that the presence of an *Rpi-vnt1* marker significantly correlated with superior LB resistance.

Our search for new sources of *Rpi* genes among wild *Solanum* species takes us to two entwined issues of evolutionary genomics of the tuber-bearing *Solanum*: genome and species evolution in the section *Petota* and the origin of *Rpi* genes associated with the evolution of *P. infestans* – potato interactions often resulting in LB outbursts. In this context, the genes for defense against pests and diseases in *S. alandiae* and *S. okadae* are especially interesting as regards the evolution of the tuber-bearing *Solanum*. J. G. Hawkes (1990) emphasized close relations of these two species with *S. microdontum* and resemblance of *S. okadae* to the Argentinian endemic *S. venturii*. The areas of distribution of the two latter species are located in neighboring highlands of Bolivia and northwestern Argentina. *S. alandiae* is a Bolivian endemic from the bordering Departments of Cochabamba, Santa Cruz and Chuquisaca, with its plants growing in contrasting climates of cold and hot dry grasslands and warm and wet territories (Fuentes, 2014). The area of *S. okadae* is disjunct. In Bolivia, it is an endangered species, with few tiny islands in the Departments of Cochabamba and La Paz. Here, its natural habitat is alpine wet meadows and forests, where plants are affected by LB (Coca Morante, Castillo Plata, 2007). The Argentinian part of the *S. okadae* area of distribution is in the Provinces of Jujuy and Salta. On the basis of molecular evidence, the Argentinian *S. okadae* accessions have been recently identified as *S. venturii* (PBI *Solanum* Project, 2020). These data presume independent evolution of *S. alandiae* and *S. okadae / S. venturii*.

All presently characterized *Rpi* genes belong to the CC-NB-LRR structures, with their evolution widely researched in tuber-bearing *Solanum* species (Hein et al., 2009; Pel, 2010; Jupe et al., 2012; Rodewald, Trognitz, 2013; Aguilera-Galvez et al., 2018). These species are primarily found in the Mexican and Andean centers of *Petota* diversity (Spooner et al., 2014; Hardigan et al., 2017), where they successfully cohabit with local *P. infestans* races (Grünwald, Flier, 2005; Fry, 2016). Many aspects of *Petota* evolution and *Rpi* gene geography are hotly debated (Vossen et al., 2014; Spooner et al., 2014; Hardigan et al., 2015; Hardigan et al., 2017), and our data may supplement the research into divergence of *Rpi* genes as related to the evolution of *Solanum* species, emergence of tuber-bearing forms and their distribution between two Americas. An impressive illustration of the latter issue is the presumably reciprocal segregation of the *Rpi-blb1* and *Rpi-vnt1* genes between the Mexican and Andean species, respectively.

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