

***Solanum alandiae* as a potential source of late blight resistance genes**

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SUMMARY

The Bolivian species *S. alandiae* is among the insufficiently researched representatives of *Solanum* series Tuberosa. Accessions of *S. alandiae* and its hybrids with potato varieties were screened with specific SCAR markers of genes for resistance to *Phytophthora infestans* (*Rpi* genes). SCAR amplicons derived from *S. alandiae* genome included the structural homologues of several *Rpi* genes of broad specificity, such as *R2=Rpi-blb3* (94-98% identity), *R8* (98% identity), *R9/Rpi-vnt1* (95% identity) and *Rpi-blb2* (99% identity). *R9/Rpi-vnt1* homologues in *S. alandiae* and other South American potato species merit special interest in the context of evolution in *Solanum* series Tuberosa.

KEYWORDS

Phytophthora infestans, *Solanum alandiae*, *Solanum okadae*, late blight, resistance genes, *R2*, *R8*, *R9*, *Rpi-blb2*, *Rpi-vnt1*, SCAR markers

INTRODUCTION

To contain potato late blight (LB), the introgression breeding depends on continual search, identification, and deployment of new genes for resistance to *Phytophthora infestans* (*Rpgenes*). When these genes are of broad specificity to pathogen races and in particular, when they come from the sources that have not been as yet widely exploited by breeders, such genes are not rapidly overcome by the *P. infestans* strains currently dominating the commercial potato plantations and in this way promise durable LB resistance. Many wild relatives and landraces of potato from South America are a prospective lode to mine for these genes (Bethke *et al.*, 2019; Gaiero *et al.*, 2018; Li *et al.*, 2018; Machida-Hirano, 2015; Vossen *et al.*, 2014). Among them, the Bolivian species *S. alandiae* Cárdenas (EBN 2x), a member of *S. brevicaulis* Bitter complex (Spooner *et al.*, 2014), is among the insufficiently researched wild species of *Solanum* L. series Tuberosa Rydb. Wild. Some accessions of *S. alandiae* were reported to manifest considerable resistance to *P. infestans* (Bhardwaj *et al.*, 2018; Perez *et al.*, 1999/2000; Zoteyeva *et al.*, 2012); however, the *Rpi* genes of *S. alandiae* have been studied but sporadically (Srivastava

et al., 2018). Here we report on a pilot study of the *Rpi* genes in *S. alandiae* and its hybrids with cultivated potatoes from the VIR collection. Plant resistance to *P. infestans* was assessed in the laboratory and field experiments, and the resistant individuals have been maintained as the clonal collections. Plants were screened for structural homologues of the *Rpi* genes using PCR analysis of the plant genome with highly specific sequence characterized amplified region (SCAR) markers, and the identity of amplicons was recognized by comparative phylogenetic analysis of their sequences.

MATERIALS AND METHODS

Plant material and assessment of LB resistance

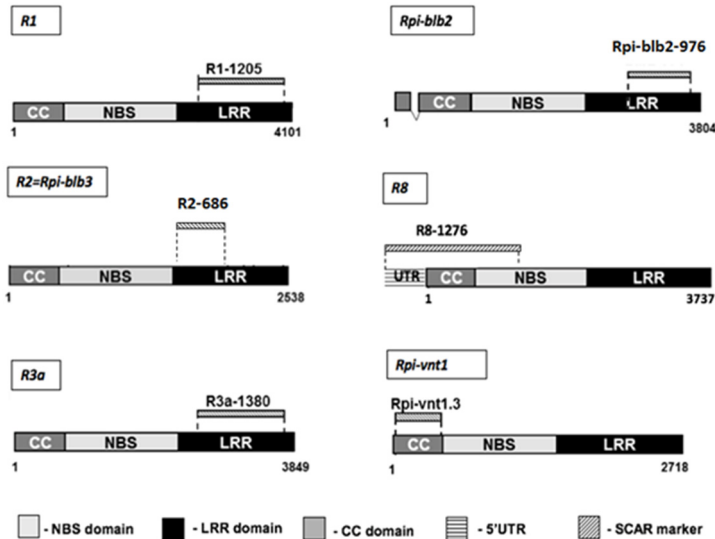
Several accessions of *S. alandiae* and its hybrids with potato varieties together with wild species and potato varieties that served as positive and negative controls in PCR screening for *Rpi* gene homologues with SCAR markers of these genes come from the clonal collections maintained in VIR and the Institute of Phytopathology (Fadina *et al.*, 2017). The accession of *S. okadae* K-25397 was introduced from the accession CGN 18279 (CGN Potato Collection, the Netherlands) kindly provided by Roel Hoekstra (Wageningen University, the Netherlands). Resistance of this accession to *P. infestans* was reported to depend on the *Rpi-vnt1-2* gene (Foster *et al.*, 2009). Resistance of wild species to *P. infestans* was assessed in the laboratory test with detached leaves according to the Eucablight protocol (www.euroblight.net/) using a highly virulent and aggressive isolate of *P. infestans* N161 (races 1.2.3.4.5.6.7.8.9.10.11, mating type A1) collected in the Moscow region (the collection of the Institute of Phytopathology) and var. Santé as a standard. LB resistance of potato hybrids and varieties was assessed in the field trials at the Institute of Phytopathology (Bol'shiye Vyazemy, Moscow region, Russia) under conditions of natural infestation by registering the area under the disease progress curve (AUDPC) against several varieties used as standards. The experimental data for LB resistance were transformed to 1-9-point scores.

SCAR markers for Rpi genes

The sequences of primers for SCAR markers recognizing the *Rpi* genes were compiled from several publications (Table 1). Primers for *R8* were further modified in our laboratory. The positions of the markers as related to gene sequences are presented at Figure 1. Primers were verified using potato genotypes reported to comprise the corresponding functional *Rpi* genes.

Table 1. SCAR markers of *Rpi* genes

Gene	Prototype gene	Marker and its size, bp	Position on the prototype genes, bp		Annealing temp., °C	Reference
<i>R1</i>	AF447489	R1-1205	5126-6331	F-cactcgtgacatatcctcacta R-gtagtacctatcttattctgcaagaat	61	Sokolova <i>et al.</i> , 2011
<i>R2=Rpi-blb3</i>	FJ536325	R2-686	4215-5357	F-gtctcctgatacgcattcatg R-acggcttcttgaatgaa	54	Kim <i>et al.</i> , 2012
<i>R3a</i>	AY849382	R3a-1380	1677-3056	F-gtagtacctatcttattctgcaagaat R-agccacttcagcttctacagtagg	64	Sokolova <i>et al.</i> , 2011
<i>Rpi-blb2</i>	DQ122125	Rpi-blb2-976	3226-4202	F-ggactgggtaacgacaatcc R-attatggctgcagaggacc	55	Van der Vossen <i>et al.</i> , 2005
<i>Rpi-vnt1.3</i>	FJ423046	Rpi-vnt1.3-612	89-701	F-ccttctcatcctcacatttag R-gcatgcccaactattgaaacaac	58	Foster <i>et al.</i> , 2009; Pel., 2010
<i>R8</i>	KU53015	R8-1276	73694-74970	F-aacaagagatgaattaagtcggtagc R-gctgtagtgcaatgtgaagga	62.5	Modified after Vossen <i>et al.</i> , 2016

**Figure 1.** SCAR markers of the *Rpi* genes

RESULTS AND DISCUSSION

We screened 29 potato genotypes: six clones of *S. alandiae* K-21240 (K-21240 D17-329, K-21240-1 - K-21240-5), five clones of *S. alandiae* K-18473 (K-18473-1-K-18473-5), *S. alandiae* K-20408, *S. alandiae* K-19443, three clones of *S. okadae* K-25397 (K-25397-1 - K-25397-3), three parental varieties Atzimba, Elizaveta, Svitanok kievskiy and ten clones of interspecific hybrids (Table 2).

The *R1* and *R3a* genes were absent from *S. alandiae*, and the amplicons of both these genes in the hybrids are apparently derived from a *S. demissum* progenitor. We cloned and sequenced amplicons for the gene markers R2-686, Rpi-blb2-976, R8-1276 and Rpi-vnt1.3-612 derived from *S. alandiae* and *S. okadae* as a positive control (Table 2). Below we discuss only the sequences that are highly identical to the prototype genes and their orthologues with established *Rpi* function (Table 3).

The marker for the *R2* gene was found in *S. okadae* accession K-25397, in *S. alandiae* accession K-18473 (94% identical to the *R2* prototype gene from *S. demissum* and 97% identical to *Rpi-blb3* from *S. bulbocastanum*, DQ122125) and in Atzimba x *S. alandiae* hybrid. The accession of *S. alandiae* K-21240, which was used in the latter cross, was not saved for analysis; nevertheless, we presume that in the hybrid 24-2 (Atzimba x *S. alandiae*), the marker R2-686 arrived from *S. alandiae*. In the hybrid 24-2 x Svitanok kievskiy, both *S. alandiae* and *S. demissum* could be the sources of this marker. The *R2* cluster in the Mexican *Solanum* species on chromosome IV has been described in detail (Destafanis *et al.*, 2015; Lokossou *et al.*, 2009). Our data on *R2* structural homologues in *S. alandiae* and *S. okadae* complement previously reported evidence on *R2=Rpi-blb3* homologues on chromosome IV in another South American species, *S. microdontum* (Lokossou, 2010; Lokossou *et al.*, 2009).

Table 2. SCAR markers of the *Rpi* genes in *S. okadae*, *S. alandiae* and its hybrids with cultivated potatoes (1/0 – presence/absence)

Genotype	VIR accession, clone and pedigree*	R1-1250	R2-686	R3a-1380	Rpi-blb2-976	R8-1259	Rpi-vnt1.3-612	Resistance to <i>P. infestans</i> , points
<i>S. alandiae</i>	K-21240 D17-329	0	0	0	1	1	0	5
<i>S. alandiae</i>	K-21240-1	0	0	0	1	1	0	n. d.
<i>S. alandiae</i>	K-21240-2	0	0	0	1	0	0	n. d.
<i>S. alandiae</i>	K-21240-3	0	0	0	1	1	0	n. d.
<i>S. alandiae</i>	K-21240-4	0	0	0	1	1	0	n. d.
<i>S. alandiae</i>	K-18473-1	0	1	0	1	1	1	n. d.
<i>S. alandiae</i>	K-18473-2	0	1	0	1	0	1	n. d.
<i>S. alandiae</i>	K-18473-3	0	1	0	1	1	1	n. d.
<i>S. alandiae</i>	K-18473-4	0	1	0	1	0	1	n. d.
<i>S. alandiae</i>	K-18473-5	0	1	0	1	1	1	n. d.
<i>S. alandiae</i>	K-19443	0	0	0	1	0	0	5
<i>S. alandiae</i>	K-20408	0	0	0	1	1	0	3
<i>S. okadae</i>	K-25397-1	0	1	0	1	1	1	n. d.
<i>S. okadae</i>	K-25397-2	0	1	0	1	1	1	n. d.
<i>S. okadae</i>	K-25397-3	0	1	0	1	1	1	n. d.
Atzimba P1	n. d.	0	0	0	1	1	0	5
Elizaveta P2	acl, adg, dms, phu, sto, vrn	1	0	1	0	0	0	4
Svitanok kievskiyi P2	dms (Victoria Augusta, Adretta)	0	1	1	0	1	0	5
24-1		0	0	0	1	1	1	6
24-2		0	1	0	1	0	1	6
117-1	Atzimba x <i>S. alandiae</i>	0	0	0	1	0	0	5
117-2		0	0	0	1	1	1	n. d.
25-1-2007	24-1 x	1	0	0	1	0	0	5
25-2-2007	Elizaveta	1	0	0	1	0	1	4
134-6-2006		0	0	1	0	1	1	5
134-2-2006	24-2 x	0	0	0	0	1	1	6
135-1-2006	Svitanok	1	1	1	0	0	1	5
135-2-2006	kievskiyi	1	1	1	0	0	0	4

*acl – *S. acaule* Bitter, adg – *S. andigenum* Juz. & Bukasov, aln – *S. alandiae* Cárdenas, dms – *S. demissum* Lindl., phu – *S. phureja* Juz. & Bukasov, sto – *S. stoloniferum* Schltdl., vrn – *S. vernei* Bitter & Wittm.

The marker of the *R8* gene was found in all accessions of *S. okadae* and in most individuals of *S. alandiae* and Atzimba x *S. alandiae* hybrids. In *S. alandiae*, all cloned markers are 98-99% similar to the *R8* prototype gene from *S. demissum* (KU530153). Four cloned sequences of *R8*-1259 marker from potato hybrid 24-1 are 94% similar to the prototype gene and *R8*-1259 marker from *S. alandiae*.

The marker *Rpi-vnt1.3-612* was found in *S. okadae* and in *S. alandiae* K-18473; it was absent from Atzimba and three other accessions of *S. alandiae* and present in most Atzimba x *S. alandiae* hybrids. The sequences of the marker for *Rpi-vnt1* gene from hybrids are 84-89% similar to the *Rpi-vnt1-3* gene, whereas the markers from *S. alandiae* and *S. okadae* were 92-93% identical to this gene. Mining for *Rpi-vnt1* alleles across *Solanum* section Petota showed that the three functional alleles were confined within *S. venturii*, whereas only two accessions of the closely related species *S. weberbaueri* Bitter and *S. mochiquense* Ochoa carried *Rpi-vnt1.1* (Pel, 2010). Three orthologues of *Rpi-vnt1* from *S. venturii* and *S. alandiae* are 87-89% identical to the 3307-5925-bp stretch in *R9a* sequence (Armstrong *et al.*, 2019); whereas the region of *Rpi-vnt1.3* in *S. alandiae* spanning 809-1374 bp in the sequence FJ423044 is 99% identical to the corresponding fragment of *R9a*. Comparison of the *Rpi-vnt1* structural homologues from *S. alandiae* with the already reported *Rpi* homologues from other South American species (Pel, 2010; van Weymers *et al.*, 2016) showed 90-94% identity; in particular, the sequences of *Rpi-vnt1* from *S. alandiae* resemble those in *S. okadae* (GU338334) and *S. raphanifolium* (GU338338) with 94% identity. While the *R9* gene is characteristic of the Mexican species *S. demissum*, no *Rpi-vnt1* homologues have been reported to this day in the Central American species.

Table 3. Structural homologues of the *Rpi* genes from *S. alandiae* as compared to the prototype *Rpi* genes and their already identified orthologues/homologues, % identity

Prototype	<i>R2=Rpi-blb3</i> <i>S. bulbocasta-num</i> DQ122125	<i>R2=Rpi-blb3</i> <i>S. demissum</i> FJ536325	<i>R2/Rpi-hjt1</i> <i>S. hjertingii</i> GU563971	<i>R2/Rpi-edn1</i> <i>S. edinense</i> GU563963	<i>R2/Rpi-blb3</i> <i>S. okadae*</i>	<i>R2-like</i> <i>S. bulbocasta-num</i> FJ536331	<i>R2/Rpi-snk1</i> <i>S. schenckii</i> GU563975	<i>R2-like</i> <i>S. demissum</i> FJ536331
<i>R2/Rpi-blb3</i> from <i>S. alandiae</i>	97	94	97	97	98-99	92	97	94
Prototype	<i>Rpi-blb2</i> <i>S. bulbocasta-num</i> DQ122125	<i>Mi-1.2</i> <i>S. lycopersicum</i> AF091048						
<i>Rpi-blb2</i> from <i>S. alandiae</i>	91	86						
Prototype	<i>R9a</i> (Armstrong <i>et al.</i> , 2019)	<i>Rpi-vnt1.1</i> <i>S. venturii</i> FJ423044	<i>Rpi-vnt1.2</i> <i>S. venturii</i> FJ423045	<i>Rpi-vnt1.3</i> <i>S. venturii</i> FJ423046	<i>Rpi-vnt1-like</i> <i>S. okadae</i> GU338336	<i>Rpi-vnt1</i> <i>S. okadae</i> K-25397	<i>Rpi-vnt1-like</i> <i>S. microdontum</i> GU338312	
<i>Rpi-vnt1.3</i> from <i>S. alandiae</i>	86-89	92-93	92-93	92-93	88-89	97-98	90-91	
Prototype	<i>R8</i> <i>S. demissum</i> KU530153	<i>R8</i> <i>S. okadae</i> K-25397	<i>Sw5-b</i> <i>S. lycopersicum</i> AY007366					
<i>R8</i> from <i>S. alandiae</i>	99	94	85					

**S. okadae* - *Rpi-vnt1.3-612* cloned from the accession K-25397 in this study

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S. alandiae -----AAAAAAGAAATTAAGAAAAAGAGATGGCTGAATTCCTC 42 CCGTGAATTCACAATCCACAATAGTTCACCTTTGGCTTAAGACGGTTCTTTTGGC 341
S. okadae** TCCTCACATTTAGAAAA-----AGAAATTAAGAAAAAGAGATGGCTGAATTCCTC 98 CCTGA-ATTCACAATCCACAATAGTTCATTTGGCTTAAGACGGTTCTTTTGGC 396
S. bukasovii TCCTCACATTTAGAAAAAGAAATTTAA-GGAAATTAAGAGAGATGGCTGAATTCCTC 177 CCAAAATTCACAATCC-----ATAATTTTCATTTGGCTTAAGACGGTTCTTTTGGC 473
S. microdontum TCCTCACATTTAGAAAAAGAAATTTAAAGGAAATTAAGAGAGATGGCTGAATTCCTC 157 CCAAAATTCACAATCC-----ATAAGTTCATTTGGCTTAAGACGGTTCTTTTGGC 453
S. stenotomum TCCTCACATTTAGAAAAAGAAATTT-----AAGGAAAAAGAGAGATGGCTGAATTCCTC 173 CCAAAATTCACAATCC-----ATAATTTTCATTTGGCTTAAGACGGTTCTTTTGGC 469
S. sucrense -----ATGGCTGAATTCCTC 16 CCAAAATTCACAATCC-----ATAATTTTCATTTGGCTTAAGACGGTTCTTTTGGC 312
S. raphanifolium -----ATGGCTGAATTCCTC 16 CCAAAATTCACAATCC-----ATAATTTTCATTTGGCTTAAGACGGTTCTTTTGGC 312
S. orophilum TCCTCACATTTAGAAAAAGAAATTT-----AAGGAAAAAGAGATGGCTGAATTCCTC 174 CCAAAATTCACAATCC-----ATAATTTTCATTTGGCTTAAGACGGTTCTTTTGGC 470
S. medians -----ATGGCTGAATTCCTC 16 CCAAAATTCACAATCC-----ATAATTTTCATTTGGCTTAAGACGGTTCTTTTGGC 312
S. neorossi -----ATGGCTGAATTCCTC 16 CCAAAATTCACAATCC-----ATAATTTTCATTTGGCTTAAGACGGTTCTTTTGGC 313
S. oplocense TCCTCACATTTAGAAAAAGAAATTT-----AAGGAAAAAGAGATGGCTGAATTCCTC 173 CCAAAATTCACAATCC-----ATAATTTTCATTTGGCTTAAGACGGTTCTTTTGGC 469
S. okadae -----ATGGCTGAATTCCTC 16 CCAAAATTCACAATCC-----ATAATTTTCATTTGGCTTAAGACGGTTCTTTTGGC 312
S. tarijense GCCTCACATTTAGAAAAAGAAATTTAAAGGAAATTAAGAGAGATGGCTGAATTCCTC 157 CCAAAATTCACAATCC-----ATAAGTTCATTTGGCTTAAGACGGTTCTTTTGGC 453
*****
S. alandiae AGGCAACTTACAAATACAGATACAAGTAAAC---AATGATGATGATTGCATCCATTG 45 GACCGGAGAAGATTGTTCCCTCATGCTGATGAAACAGAGGTC---ATCGGTCTGGAAGAT 515
S. okadae** AGGCAACTTACAAATACAGATACAAGTAAAC---AATGATGATGATTGCATCCATTG 51 GACCGGAGAAGATTGTTCCCTCATGCTGATGAA-----545
S. bukasovii AGGCAACTTACAGATACAAGTAAAC---ATAATGATGATTGCATCCATTG 58 GACCGGAGAAGATTGTTCCCTCATGCTGATGAAACAGAGGTC---ATCGGTCTGGAAGAT 646
S. microdontum AGGCAACTTACAAATACAGATACAAGTAAAC---ATAATGATGATTGCATCCATTG 57 GACCGGAGAAGATTGTTCCCTCATGCTGATGAAACAGAGGTC---ATCGGTCTGGAAGAT 627
S. stenotomum AGGCAACTTACAAATACAGATACAAGTAAAC---ATAATGATGATTGCATCCATTG 59 AACAGAGAAGATTATCCCTCATGCTGATGAAACAGAGGTC---ATCGGTCTGGAAGAT 646
S. sucrense AGGCAACTTACAAATACAGATACAAGTAAAC---ATAATGATGATTGCATCCATTG 43 AACAGAGAAGATTATCCCTCATGCTGATGAAACAGAGGTC---ATCGGTCTGGAAGAT 489
S. raphanifolium AGGCAACTTACAAATACAGATACAAGTAAAC---ATAATGATGATTGCATCCATTG 43 AACAGAGAAGATTATCCCTCATGCTGATGAAACAGAGGTC---ATCGGTCTGGAAGAT 489
S. orophilum AGGCAACTTACAAATACAGATACAAGTAAAC---ATAATGATGATTGCATCCATTG 59 AACAGAGAAGATTATCCCTCATGCTGATGAAACAGAAATGTCATCGTTTGGATGAT 650
S. medians AGGCAACTTACAAATACAGATACAAGTAAAC---ATAATGATGATTGCATCCATTG 43 AACAGAGAAGATTATCCCTCATGCTGATGAAACAGAGGTC---ATCGGTCTGGAAGAT 489
S. neorossi AGGCAACTTACAAATACAGATACAAGTAAAC---ATAATGATGATTGCATCCATTG 43 AACAGAGAAGATTATCCCTCATGCTGATGAAACAGAGGTC---ATCGGTCTGGAAGAT 490
S. oplocense AGGCAACTTACAAATACAGATACAAGTAAAC---ATAATGATGATTGCATCCATTG 58 AACAGAGAAGATTATCCCTCATGCTGATGAAACAGAGGTC---ATCGGTCTGGAAGAT 646
S. okadae AGGCAACTTACAAATACAGATACAAGTAAAC---ATAATGATGATTGCATCCATTG 43 AACAGAGAAGATTATCCCTCATGCTGATGAAACAGAGGTC---ATCGGTCTGGAAGAT 489
S. tarijense AGGCAACTTACAAATACAGATACAAGTAAAC---ATAATGATGATTGCATCCATTG 57 GACCGGAGAAGATTGTTCCCTCATGCTGATGAAACAGAGGTC---ATCGGTCTGGAAGAT 627
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Figure 2. The structural homologues of the *Rpi-vnt1* gene from of *S. alandiae* and *S. okadae* as compared to already published sequences of *Rpi-vnt1* genes from several South American species (Pel, 2010) and R9a (Armstrong et al., 2019)

S. alandiae – *Rpi-vnt1.3-612* cloned from the accession K-18473 in this study, **S. okadae* – *Rpi-vnt1.3-612* cloned from the *S. okadae* Hawkes & Hjert. accession K-25397 in this study, *S. bukasovii* Juz. GU338315, *S. stenotomum* Bitter GU338312, *S. stenotomum* Juz. & Bukasov GU338323, *S. sucrense* Hawkes GU338339, *S. raphanifolium* Cárdenas & Hawkes GU338338, *S. orophilum* Correll GU338320, *S. medians* Bitter GU338344, *S. neorossi* Hawkes & Hjert. GU338331, *S. oplocense* Hawkes GU338317, *S. okadae* GU338334, *S. tarijense* Hawkes GU338326

CONCLUSION

Genomes of *S. okadae*, *S. alandiae* and interspecific hybrids comprising genetic material from *S. alandiae* contain the structural homologues of genes *R2*, *Rpi-blb2*, *R8* and *R9* well known to provide the broad specific resistance to *P. infestans*. The homologues of *R2=Rpi-blb3* were 94-99% identical to the prototype genes in *S. bulbocastanum* and *S. demissum* and their orthologues in several other Mexican species, such as *S. edinense*, *S. schenckii* and *S. hjertjingii*. Among South American potatoes, the closest homologues to these structures is the sequence from *S. microdontum*, which is evolutionarily and functionally different from *S. demissum* *R2* (Lokossou, 2010; Lokossou et al., 2009; Vossen et al., 2014).

The *Rpi-vnt1* gene is apparently restricted to the South American species of *Solanum* series Tuberosa. The structural homologues of this gene in *S. alandiae* are 92-97% identical to the already known sequences from several species from Argentina, Bolivia and Peru. The evaluation of the breeding potential of the reported structural homologues must wait until we will clone the full-size sequences of the presumed genes and assess their function as the *Rpi* genes.

ACKNOWLEDGMENTS

The authors thank the Center for Collective Use of Equipment “Biotechnology” at the Institute of Agricultural Biotechnology for sequencing *Solanum* genome fragments. The study was supported by the Russian Foundation for Basic Research (project 18-016-00138a) and the State Tasks 0574-2019-0001 (Institute of Agricultural Biotechnology), 0662-2019-0004 (N.I. Vavilov Institute of Plant Genetic Resources).

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