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SCREENING OF RUSSIAN POTATO CULTIVARS (*Solanum tuberosum* L.) WITH DNA MARKERS LINKED TO THE *R*-GENES CONFERRING EXTREME RESISTANCE TO POTATO VIRUS Y

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A b s t r a c t

Common potato *Solanum tuberosum* L. is infected by about 40 viruses, of which one of the most harmful is the potato virus Y (PVY). Crop losses of PVY susceptible cultivars can reach 80 %. At present, marker-assisted selection (MAS) using DNA markers linked to the *Ry* genes is widely used to create varieties highly resistant to PVY. MAS increases breeding efficiency and also allows one to assess the genetic protection or genetic vulnerability of the varieties' gene pool. A number of genes conferring different types of PVY resistance have been identified in potato, of which *Ry* genes, conferring extreme resistance (the absence of accumulation of viruses in infected plants regardless of the virus strain), are most often involved in breeding programs in different countries. The search for effective markers of target genes remains relevant due to MAS prospects. This paper is the first report on the use of STM0003 marker associated with Ry_{sto} gene for screening Russian potato varieties; another marker, Ry364, was previously used once on a small sample of Russian varieties. The objective of this work was to screen 178 domestic varieties with three markers, STM0003, Ry364, and RYSC3 linked to Ry_{sto}, Ry_{chc}, and Ry_{adg} genes which were introgressed into the breeding gene pool from wild species *S. stoloniferum*, *S. chacoense*, and from the Andean native varieties of *S. tuberosum* ssp. *andigenum*, respectively. As a result of the molecular screening, 39 (21.8 %) of 178 varieties were selected for which diagnostic fragments of at least one of the three markers were revealed, including 7.3 % varieties with STM0003 marker (Ry_{sto}), 11.7 % varieties with Ry364 (Ry_{chc}), and 4.5 % varieties with RYSC3 (Ry_{adg}) marker. The obtained results indicate a low level of genetic defense against PVY of the analyzed cultivars' subset among which 78.2 % varieties have none of the markers linked to the *Ry* genes. We compared molecular screening results with published PVY resistance/susceptibility data. The marker STM0003 linked to the Ry_{sto} gene had the highest diagnostic value, as almost all varieties with this marker are highly resistant (immune) to PVY, while the Ry364 and RYSC3 markers are not so efficient.

Keywords: potato, PVY, DNA markers, MAS, varieties

Potato plants are infected by about 40 viruses belonging to 13 families [1, 2]. Potato virus Y (PVY) of *Potyvirus* genus, *Potyviridae* family is one of the most harmful viruses affecting common potato (*Solanum tuberosum* L.) [1]. Representatives of 9 plant families can be PVY host plants in nature, and in experimental conditions — representatives of 31 plant families can be infected by PVY [3]. About 60 aphid species can be the natural vectors of this virus [4, 5]. Interac-

tions between numerous host plants and vectors as well as tolerance of many varieties (symptomless of infected plants) result in increase in viral load and lead to significant yield losses which can rich up to 80% in susceptible to PVY cultivars [1, 5-7, 8]. The cultivation of virus resistant varieties is the most efficient and environmentally safe method for plant protection; therefore, breeding of highly resistant to viral diseases varieties is of high priority.

A number of genes conferring different types of PVY resistance have been mapped in potato. The most studied resistance genes include the *Ny*-genes determining a strain-specific hypersensitive response (HR) of infected plants and the *Ry*-genes which prevent virus multiplication (no virus accumulation in infected plants regardless of virus strain — extreme resistance — ER) [8-12]. Therefore, potato cultivars with *Ry* genes are completely immune to PVY. The resistance of cultivars carrying *Ny* genes might be overcome by actively mutating virus [13, 14]; besides, hypersensitive response depends on temperature [15, 16] that is critical in the context of climate change.

Immunity to infection by PVY has been identified in accessions of many potato species [17], however the ER genes were introgressed into the breeding gene pool mainly from the three species: tightly linked genes Ry_{sto}/R_y-f_{sto} — from wild Mexican species *S. stoloniferum* [18-22]; Ry_{chc} — from Argentinean wild species *S. chacoense* [11, 23] and Ry_{adg} — from resistant to PVY Andean landraces of *S. tuberosum* ssp. *andigenum* [10, 19, 24]. Many varieties which are immune to PVY infection were developed based on involvement of *S. stoloniferum* accessions into the breeding programs of a number of Western European countries (Germany, Hungary, the Netherlands, Poland, Scotland) [18, 21, 22, 25]. The hybrids with *S. stoloniferum* were also actively used by Russian breeders [26-28]. Highly resistant to PVY accessions of *S. tuberosum* ssp. *andigenum* were most often used in the USA breeding programs [29, 30], in Spain [31] and Peru [32, 33]. Japanese breeders most frequently used PVY resistant accessions of *S. chacoense* to create immune potato varieties [11, 12, 34, 35]. The Russian breeding programs also actively used resistant samples of *S. chacoense* [26-28].

1. DNA markers of *Ry*-genes conferring extreme resistance to PVY which were most frequently used in molecular screening

Gene (chromosome)	Marker	References
Ry_{sto} (12)	STM0003 (SSR)	[20[a], 31, 36, 38, 43-45]
	YES3-3A (SCAR), YES3-3B (SCAR)	[22[a], 46-49]
	YES3-3A (SCAR)	[39, 42, 50-56]
	YES3-3B (SCAR)	[57, 58]
Ry-f_{sto} (12)	GP81, GP122, GP204, GP269 (все CAPS)	[21[a], 43]
	GP122-718 (CAPS)	[21[a], 36, 44, 48, 53, 59, 60]
	GP122-614 (CAPS)	[36[a]]
	GP122-564 (CAPS)	[36, 37, 61-63]
	GP122-406 (CAPS)	[36[a], 39, 42, 44, 64-67]
Ry_{adg} (11)	RYSC3 (SCAR)	[30, 31, 38, 40, 42, 44, 45, 48-58, 62, 64-66, 68[a]-77]
Ry_{chc} (9)	Ry186 (SCAR)	[12, 40, 51, 54-56, 78, 79]
	38−530 (RAPD)	[11[a], 34, 35, 51, 52, 80]
	Ry364 (SCAR)	[12[a], 42]

N o t e. SSR — simple sequence repeat, SCAR — sequence-characterized amplified region, CAPS — cleaved amplified polymorphic sequence, RAPD — random amplification of polymorphic DNA; letter ([a]) indicates the references to studies. in which corresponding DNA markers were developed.

The marker-assisted selection (MAS) with the use of DNA markers linked to the *Ry*-genes (intragenic markers have not yet been developed) increases breeding efficiency and is commonly used now to create immune to PVY potato varieties [31, 34-36]. Furthermore, the application of DNA markers associated with Ry_{sto}/Ry-f_{sto} [22, 37-39], Ry_{adg} [38, 40], Ry_{chc} [11, 40] genes can provide the data about diversity, genetic protection from viral diseases and genetic vulnerability to viruses of the breeding gene pool [11, 22, 37-40]. The list of the DNA markers of

Ry genes most commonly used in MAS is shown in Table 1. Note that the distances between the certain *Ry* gene and different markers of this gene can vary significantly. For instance, the RAPD marker 38-530 linked to the gene Ry_{chc} (recombination frequency is 16.3%) has been reported as efficient marker for MAS [11], and SCAR markers Ry364 and Ry186 developed later flank Ry_{chc} at a distance of 0.085 and 0.203 cM [12, 41].

DNA markers of *Ry* gene have a different diagnostic value. For instance, Witek et al. [61] detected three CAPS markers of the $Ry\text{-}f_{sto}$ gene (GP122-718, GP122-614, GP122-564) in all 24 Polish varieties which are immune to PVY, whereas 31 susceptible cultivars had negative MAS results. However, German researchers who analyzed the segregating population of androgenic dihaploids from immune to PVY variety Assia (having in pedigree *S. stoloniferum*) failed to detect linkage between the resistance gene and the marker GP122-718; relative linkage (34.9 cM) was shown only for one marker of the GP series — GP81 [20]. Cernák et al. [43] indicated high diagnostic value of the SSR marker STM0003 (linkage 2.95 cM with Ry_{sto}), whereas all markers of the GP series [21] did not segregate in the mapping population analyzed in this study. It may be assumed that Cernák at al. [43] analyzed recombinant genotypes and their progeny, in which GP markers were linked with recessive allele of Ry_{sto} gene.

The search for efficient markers of the target *Ry* genes remains relevant due to prospects of marker-assisted selection.

Our objective was to screen a large subset of domestic potato cultivars using three markers, STM0003, Ry364, RYSC3 linked with the $Ry_{sto}/Ry\text{-}f_{sto}$, Ry_{chc}, Ry_{adg} genes correspondingly, which confer extreme resistance to potato virus Y. The STM0003 marker was involved in molecular screening of Russian varieties for the first time, and the Ry364 marker had been previously used once in molecular screening of a small set of domestic varieties [42].

Techniques. The subset included 178 domestic potato cultivars (138 were bred in Russia, 22 — in Republic of Belarus, 11 — in Ukraine, and 4 — in other adjacent countries) from collection of N.I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR). The cultivars were qualified as resistant or susceptible to PVY based on data from scientific publications and catalogues of potato varieties bred in Russia and in Republic of Belarus [27, 81-84].

DNA was extracted from frozen leaves by a modified CTAB extraction method [85]. Trueness to type of varieties grown in the VIR' field gene bank was previously verified based on plant morphological characters.

Polymerase chain reaction (PCR) mixture (20 μl) contained 10 ng DNA, 1× reaction buffer (Dialat Ltd, Russia), 2,5 mM $MgCl_2$, 0.6 mM of each dNTP, 0.2 rM of each (forward/reverse) primer and Taq DNA-polymerase (1 U) (Dialat Ltd, Russia). PCR was conducted using Mastercycler® Nexus Gradient thermal cycler (Eppendorf, Germany). For RYSC3 and Ry364 primers PCR conditions were followed to the literature [12, 68] and were modified by the use of the touchdown option for the microsatellite marker STM0003 as following: 3 min 15 s at 94 °C; 45 s at 94 °C, 1 min 30 s at 54 °C with a 0.5 °C gradual reduce in each next cycle, 1 min at 72 °C (8 cycles); 45 s at 94 °C, 45 s at 50 °C, 1 min at 72 °C (30 cycles); final elongation for 5 min at 72 °C. The reactions were performed at least three times for each sample.

The highly PVY resistant cultivars with the diagnostic markers of the $Ry_{sto}/Ry\text{-}f_{sto}$, Ry_{adg}, Ry_{chc} genes were used as positive controls: cv. Ania for STM0003 [36], cv. Saikai 35 for Ry364 [12], cv. Effect for RYSC3 [64]; deionized water was used as negative control.

Amplicons were separated in 2% agarose gel with ethidium bromide for UV visualization (Gel Doc XR+ gel documentation system, Bio-Rad, USA). Size of the

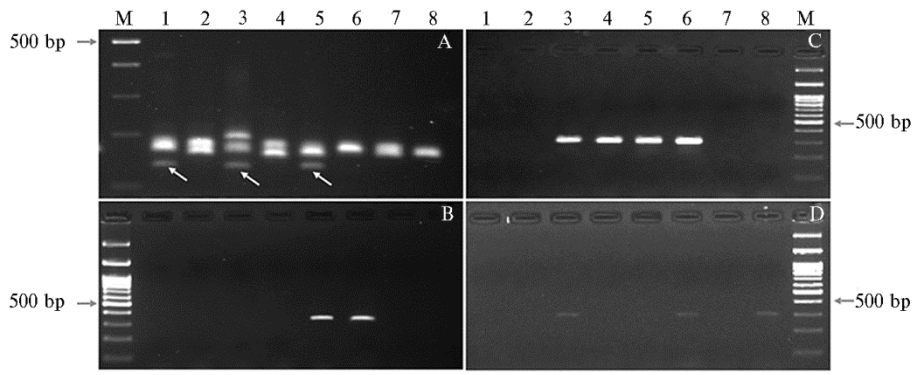
fragments was determined with the molecular weight marker 100 bp + 1500 + 3000, SibEnzim, Russia.

The *t*-test (Student's *t*-test) was used for statistical analysis with a significance level at p 0.05.

Results. The PCR screening of *Ry*-genes was performed with known from literature primers (table 2).

2. Markers of PVY resistance genes *Ry* used in screening of Russian potato cultivars

Gene	Marker	Primer sequence (5′→3′)	Tm, °C	Diagnostic fragment	References
Ry_{sto}	STM0003	F: GGAGAATCATAACAACCAG			
		R: AATTGTAACTCTGTGTGTGTG	50	111 bps	[20], [86]
Ry_{adg}	RYSC3	3.3.3s: ATACACTCATCTAAATTTGATGG			
		ADG23R: AGGATATACGGCATCATTTTTCCGA	60	321 bps	[68]
Ry_{chc}	Ry364	RY364-14: CTATTATAAGTCTGGTACTAGGACG			
		RY364-19: GGCTATATGTTCAATGAATTCATGCTAA	55	298 bps	[12], [41]



Screening of Russian potato (*Solanum tuberosum* L.) varieties using markers of PVY resistance genes: A — STM0003 (Ry_{sto}), B — RYSC3 (Ry_{adg}), C — Ry364 (Ry_{chc}); D — example of weak amplification of diagnostic fragments of Ry364 marker in three cultivars. M — molecular marker 100 bp + 1500 + 3000 (SIbEnzym, Russia).

A, B, C: 1 — Korona, 2 — Babushka, 3 —Olimp, 4 — Sintez, 5 — Resurs, 6 — Severyanin, 7 — Avrora, 8 —Veselovskiy 2-4.

D: 1 — Aksamit, 2 —Moskvoretskiy, 3 — Skarb, 4 — Effect, 5 — Golubizna, 6 — Temp, 7 — Barin, 8 — Kristall.

Results of molecular screening revealed diagnostic fragments of at least one of the three markers in 39 (21.9%) of 178 cultivars (Fig., Table 3). We detected diagnostic fragments of the $Ry364_{298}$ marker of Ry_{chc} gene in 21 (11.8%) cultivars, of the $STM0003_{111}$ marker of Ry_{sto} — in 13 (7.3%) cultivars, and of the $RYSC_{321}$ marker of Ry_{adg} gene — in 8 (4.5%) cultivars. Three cultivars (Bryanskiy ranniy, Buket, Zhivitsa) had the two markers, Ry364 and RYSC3, simultaneously. The overwhelming majority of the analyzed cultivars (78.0%) didn't have any of the markers of *Ry* genes (see table 3). According to the Student's *t*-test, differences in the frequency of cultivars with markers to different *Ry*-genes were not significant with the exception of two groups with the Ry364 (Ry_{chc}) and RYSC3 (Ry_{adg}) markers, where frequency of cultivars with the Ry364 marker was significantly higher ($p < 0.05$).

Among 39 cultivars in which at least one of the three markers of *Ry*-genes was detected (see Table 3), for 18 cultivars (Bryanskiy ranniy, Bryanskiy krasny, Vektar, Golubizna, Zhivitsa, Kolobok, Korona, Loshitskiy, Meteor, Moskvoretskiy, Nakra, Olimp, Pogarskiy, Rezerv, Resurs, Sokolskiy, Effect, Yubiley Zhukova) a high and very high resistance to PVY has been reported, and 6 cultivars (Barin, Zolskiy, Ilinskiy, Kristall, Skarb, Temp) were described as moderately resistant [26, 27, 81-84]. We have not found any available information

about phenotypic resistance to PVY for the remaining 15 cultivars. In sum, almost all tested cultivars with STM0003 marker of Ry_{sto} gene were highly resistant (immune) to PVY, whereas some cultivars with the Ry364 and RYSC3 markers were moderately resistant.

3. Molecular screening of 178 potato (*Solanum tuberosum* L.) Russian cultivars using three markers of PVY resistance genes

Haplotype grouping	Gene/marker		
	Ry_{sto}/ STM0003	Ry_{adg}/ RYSC3	Ry_{chc}/ Ry364
Group I, *n* = 13 (7.3 %)			
Ilinskiy; highly resistant and extremely resistant cultivars: Bryanskiy krasny, Vektar belorusskiy, Kolobok, Korona, Meteor, Moskvoretskiy, Nakra, Olimp, Pogarskiy, Resurs, Sokolskiy, Yubiley Zhukova	1	0	0
Group II, *n* = 3 (1.7 %)			
Buket; highly resistant and extremely resistant cultivars: Bryanskiy ranniy, Zhivitsa	0	1	1
Group III, *n* = 18 (10.1 %)			
Imandra, Krasnaya gorka, Lider, Maugli, Oktyabrenok, Primorskiy (= Pri-12), Rassvet, Severyanin, Sineva, Sintez, Khibinskiy ranniy, Bezhitskiy[a], Bronnickiy[a], Kristall[a], Skarb[a], Temp[a]; highly resistant and extremely resistant cultivars: Rezerv, Loshitskiy*	0	0	1
Group IV, *n* = 5 (2.8 %)			
Barin, Zolskiy, Yubileyny Osetii; highly resistant and extremely resistant cultivars: Golubizna, Effekt	0	1	0
Group V, *n* = 139 (78.1 %)			
Avrora, Aksamit, Alena, Alisa, Alpinist, Ametist, Amur, Antoshka, Arlekin, Arkhideya, Babushka, Baron, Belukha, Bolvinskiy, Bolshevik, Borodyanskiy rozovy, Bravo, Brat-2, Bryanskaya novinka, Varmas, Varsna, Veselovskiy 2-4, Viza, Virazh, Volzhskiy, Vympel, Vyatka, Gart, Gorizont, Gornouralskiy, Goryanka, Granat, Gubernator, Divo, Dontsovskiy, Zhavoronok, Zhukovskiy ranniy, Zagadka, Zarevo, Zauralskiy, Zvezdochka, Zdabytak, Iskra, Kabardinskiy, Kalinka, Kamenskiy, Kameraz, Katyusha (bred in Ukraine), Kemerovskiy, Kemerovchanin, Kolpashevskiy, Komsomolets 20, Korenevskiy, Kormilets, Krasavitsa, Krasnaya zarya, Krasnaya roza, Krasnoufimskiy, Krepysh, Kustarevskiy, Ladozhskiy, Lazar, Lazurit, Laymdota, Lekar, Lorkh, Lugovskoy, Lybid, Lyuks, Mats, Matushka, Murmanskiy, Musinskiy, Nadezhda, Nalchikskiy, Naroch, Nart 1, Narymka, Nauka, Nezabudka, Nesterovskiy, Ognivo, Parus, Pobeda, Prestizh, Pribrezhny, Prigozhiy 2, Priekulskiy ranniy, Priobskiy, Prolisok, Rapsodiya, Romashka, Rosinka (Rasinka), Rossiyanka, Rumyanka, Rusalka, Rusich, Ryabinushka, Samba, Saprykinskiy, Sarovskiy, Svenskiy, Svetlyachok, Sentyabr, Solnyshko, Start, Tango, Teshcha, Tomich, Ukrainskiy rozovy, Uspekh, Utenok, Fermer, Filatovskiy, Fioletovy, Fokinskiy, Chaya, Shaman, Shurminskiy 2, Energiya, Yupiter, Yavar; highly resistant and extremely resistant cultivars: Garant, Bryanskiy delikates, Bryanskiy nadezhny, Druzhny, Zhigulevskiy, Kortni, Kuznechanka, Lasunak, Lyubava, Manifest, Nikulinskiy, Odissey, Prizer, Skoroplodny, Smena, Falenskiy, Chayka	0	0	0
The number (%) of varieties with a diagnostic fragment of marker	13 (7.3 %)	8 (4.5 %)	21 (11.8 %)

Note. "1" — presence and "0" — absence of the diagnostic fragment.
Letter ([a]) marks cultivars with unstable amplification of Ry364 diagnostic fragments.

Among 139 cultivars for which we have not identified none of the three markers of the three *Ry* genes, clear and consistent data about PVY resistance were found only for 43 varieties. Thus, high PVY resistance was reported for 17 cultivars (Bryanskiy delikates, Bryanskiy nadezhny, Garant, Druzhny, Zhigulevskiy, Kortni, Kuznechanka, Lasunak, Lyubava, Manifest, Nikulinskiy, Odissey, Prizer, Skoroplodny, Smena, Falenskiy, Chayka) and moderate and low PVY resistance was reported for 21 cultivars [26, 27, 81, 82, 84, 87]. For the rest 101 cultivars we have not found such information.

Unfortunately, most cited above sources did not provide data on whether the detected type of PVY resistance was due to the absence of virus accumulation in infected plants (ER), or to the hypersensitive response (HR), field resistance or to the resistance to virus vectors. It is also not specified, which methods were used to evaluate resistance (field tests under natural viral load

during wide spread of diseases or artificial inoculation, i.e. mechanical inoculation or grafting). Therefore, the available information is not enough for exact matching of the results of molecular screening with data on PVY resistance characters phenotyping.

As was mentioned above, two of the three markers, Ry364 (Ry_{chc} gene) and STM0003 (Ry_{sto} gene), were used in molecular screening of all 178 cultivars for the first time. However, for a number of cultivars the information about potential presence/absence of these genes had been obtained earlier, though with the use of other markers, i.e. RAPD marker 38-530 (Ry_{chc} gene) [11], as well as SCAR marker YES3-3A [22] and CAPS marker GP122-406/EcoRV [21] for the Ry_{sto}/Ry-f_{sto} genes. For these cultivars we can compare the result of molecular screening performed with different markers of the same gene. For instance, we identified diagnostic fragment 111 bps of the STM0003 marker of Ry_{sto} gene in 13 cultivars (see Table 3) in which we had earlier detected another marker of this gene — YES3-3A [39, 51], as well as the GP122-406 [39, 64] and GP122-564 markers [37] of Ry-f_{sto} gene closely linked with Ry_{sto}. Therefore, the results obtained with all three markers (STM0003, YES3-3A and GP122) of the *Ry*-genes introgressed from *S. stoloniferum* completely matched for these 13 domestic cultivars. Ten of these 13 cultivars (Bryanskiy krasny, Vektar, Kolobok, Korona, Moskvoretskiy, Nakra, Pogarskiy, Resurs, Sokolskiy, Yubiley Zhukova) have interspecific hybrids with *S. stoloniferum* in their pedigree [17, 28, 88, 89]. The diagnostic fragment of the $RYSC3_{321}$ marker is rare: it was found in 8 out of 178 screened cultivars (see Table 3, Fig.). It has to be pointed out that presence of the SCAR marker RYSC3 of the Ry_{adg} gene was reported earlier for four cultivars — Effect [64], Bryanskiy ranniy and Golubizna [51], and Zhivitsa [49]. Furthermore, it was also mentioned that $RYSC3_{321}$ marker is not present in cultivars Oktyabrenok [58] and Resurs [72]. However, there are only a few data about negative MAS results with this marker which were obtained for small subsets [42, 58, 72].

It has to be pointed out that the RYSC3 marker of the Ry_{adg} gene was identified in several immune to PVY cultivars (e.g. Bryanskiy ranniy, Golubizna, Effect), which have in their pedigrees hybrids with *S. stoloniferum* (as the *Ry* gene donors) [26]. However, the markers of Ry_{sto}/Ry-f_{sto} genes expected in these cultivars were not identified. In this connection we would like to emphasize the following. RYSC3 marker is considered as specific for Ry_{adg} gene which was mapped on chromosome 11. However, initially there was a report about mapping of the Ry_{sto} gene on the same chromosome [90]. Later, an opinion about wrong mapping of the Ry_{sto} gene on chromosome 11 was accepted. The other researchers [68] identified PVY resistance gene located on chromosome 11 as Ry_{adg}. This was due to the absence of co-segregation of the markers of Ry_{sto} gene with the RYSC3 marker [36]; as well as to the fact that in resistant potato cultivars RYSC3 marker and M45 marker described by Brigneti et al. [90] were always identified together [70]. It seems, however, quite likely that the one ortholog of *Ry* gene conferring extreme resistance to PVY and linked with the RYSC3 marker is located on chromosome 11 both in *S. stoloniferum* and in *S. tuberosum* ssp. *andigenum*. Indeed, we earlier detected RYSC3 marker in 5 out of 8 (62.5%) accessions of *S. stoloniferum* and only in 2 out of 95 (2.1%) accessions of *S. tuberosum* ssp. *andigenum* from the VIR potato collection [65].

Based on the literature data, interspecific hybrids with *S. chacoense* were involved in breeding of a number of Russian cultivars: Alena, Alisa, Borodyanskiy rozovy, Bryanskiy delikates, Bryanskiy krasny, Bryanskiy nadezhny, Goryanka, Krepysh, Lugovskoy, Meteor, Nakra, Nikulinskiy, Pobeda, Saprykinskiy, Sentyabr, Utenok [28, 88, 89]. However, in our study we did not detect the Ry364 marker in these cultivars. It must be pointed out that in four highly re-

sistant cultivars, Bryanskiy delikates, Bryanskiy nadezhny, Meteor, and Nikulinskiy, another marker of Ry_{chc} gene — RAPD marker 38-530 — was detected earlier [51]. At the same time, *S. chacoense* was specified in pedigree of only the two cultivars — Bezhitskiy and Bronnickiy [89], out of 21 those had the $Ry364_{298}$ diagnostic fragment of the Ry_{chc} gene. Hence it cannot be ruled out that in the initial interspecific hybrids with *S. chacoense* involved in breeding of mentioned above PVY resistant domestic varieties there were recombination events in the region between Ry_{chc} gene and the Ry364 marker. Intragenic markers required for selection of genotypes with functional allele of Ry_{chc} gene have not been developed yet.

To summarize, the obtained results allow us to draw the following conclusions. In our study, the STM0003 marker associated with Ry_{sto} gene has the highest diagnostic value. Almost all cultivars with this marker are highly resistant (immune) to potato virus Y (PVY), whereas Ry364 and RYSC3 markers turned out be not so effective. The results of MAS indicate a low genetic protection against PVY in the studied subset of domestic cultivars of which 78.2% had none of the markers of *Ry*-genes.

REFERENCES

1. Valkonen J.P.T. Viruses: economical losses and biotechnological potential. In: *Potato biology and biotechnology, advances and perspectives*. Elsevier, Oxford, 2007: 619-633 (doi: 10.1016/B978-044451018-1/50070-1).
2. Lacomme C., Jacquot E. General characteristics of Potato virus Y (PVY) and its impact on potato production: an overview. In: *Potato virus Y: biodiversity, pathogenicity, epidemiology and management*. C. Lacomme, L. Glais, D. Bellstedt, B. Dupuis, A. Karasev, E. Jacquot (eds.). Springer, Cham, 2017: 1-19 (doi: 10.1007/978-3-319-58860-5_1).
3. Edwardson J.R., Christie R.G. *Potyviruses*. In: *Florida Agricultural Experiment Station Monograph Series 18-II — viruses infecting pepper and other Solanaceous crops*. University of Florida, Gainesville, 1997.
4. Al-Mrabeh A., Anderson E., Torrance L., Evans A., Fenton B. *A literature review of insecticide and mineral oil use in preventing the spread of nonpersistent viruses in potato crops*. Potato council, Agriculture and Horticulture Development Board, Stoneleigh Park, United Kingdom, 2010.
5. Lacomme C., Pickup J., Fox A., Glais L., Dupuis B., Steinger T., Rolot J.-L., Valkonen J.P.T., Kruger K., Nie X., Modic S., Mehle N., Ravnikar M., Hullé M. Transmission and epidemiology of Potato virus Y. In: *Potato virus Y: biodiversity, pathogenicity, epidemiology and management*. C. Lacomme, L. Glais, D. Bellstedt, B. Dupuis, A. Karasev, E. Jacquot (eds.). Springer, Cham, 2017: 141-176 (doi: 10.1007/978-3-319-58860-5_6).
6. Gray S., De Boer S., Lorenzen J., Karasev A., Whitworth J., Nolte P., Singh R., Boucher A., Xu H.M. Potato virus Y: an evolving concern for potato crops in the United States and Canada. *Plant Disease*, 2010, 94: 1384-1397 (doi: 10.1094/pdis-02-10-0124).
7. Solomon-Blackburn R.M., Barker H. A review of host major-gene resistance to Potato viruses X, Y, A and V in potato: genes, genetics and mapped locations. *Heredity,* 2001, 86: 8-16 (doi: 10.1046/j.1365-2540.2001.00798.x).
8. Solomon-Blackburn R.M., Barker H. Breeding virus resistant potatoes (*Solanum tuberosum*): a review of traditional and molecular approaches. *Heredity*, 2001, 86(1): 17-35 (doi: 10.1046/j.1365-2540.2001.00799.x).
9. Ross H. Inheritance of extreme resistance to virus Y in *Solanum stoloniferum* and its hybrids with *Solanum tuberosum*. *Proc. of 3rd Conf. on potato virus diseases*. Veenman, Lisse-Wageningen, 1958: 204-211.
10. Muňoz F.J., Plaisted R.L., Thurston H.D. Resistance to potato virus Y in *Solanum tuberosum* ssp. *andigena*. *American Journal of Potato Research*, 1975, 52(4): 107-115 (doi: 10.1007/BF02852043).
11. Hosaka K., Hosaka Y., Mori M., Maida T., Matsunaga H. Detection of a simplex RAPD marker linked to resistance to potato virus Y in a tetraploid potato. *American Journal of Potato Research*, 2001, 78(3): 191-196 (doi: 10.1007/bf02883544).
12. Mori K., Mukojima N., Nakao T., Tamiya S., Sakamoto Y., Sohbaru N., Hayashi K., Watanuki H., Nara K., Yamazaki K., Ishii T., Hosaka K. Germplasm release: Saikai 35, a male and female fertile breeding line carrying *Solanum Phureja*-derived cytoplasm and potato cyst nematode resistance (H1) and potato virus y resistance (Ry_{chc}) Genes. *American Journal of Potato Research*, 2012, 89(1): 63-72 (doi: 10.1007/s12230-011-9221-4).
13. Valkonen J.P.T. Elucidation of virus-host interactions to enhance resistance breeding for control

of virus diseases in potato. *Breeding Science,* 2015, 65(1): 69-76 (doi: 10.1270/jsbbs.65.69).
14. Davie K., Holmes R., Pickup J., Lacomme C. Dynamics of PVY strains in field grown potato: Impact of strain competition and ability to overcome host resistance mechanisms. *Virus Research*, 2017, 241: 95-104 (doi: 10.1016/j.virusres.2017.06.012).
15. Valkonen J.P.T. Novel resistance to four potyviruses in tuber bearing potato species and temperature — sensitive expression of hypersensitive resistance to potato virus Y. *Annals of Applied Biology*, 1997, 130: 91-104 (doi: 10.1111/j.1744-7348.1997.tb05785.x).
16. Szajko K., Chrzanowska M., Witek K., Strzelczyk-Żyta D., Zagyrska H., Gebhardt C., Henning J., Marczewski W. The novel gene *Ny*-1 on potato chromosome IX confers hypersensitive resistance to Potato virus Y and is an alternative to *Ry* genes in potato breeding for PVY resistance. *Theoretical and Applied Genetics*, 2008, 116(2): 297-303 (doi: 10.1007/s00122-007-0667-1).
17. Valkonen J.P.T., Gebhardt C., Zimnoch-Guzowska E., Watanabe K.N. Resistance to Potato virus Y in potato. In: *Potato virus Y: biodiversity, pathogenicity, epidemiology and management*. C. Lacomme, L. Glais, D. Bellstedt, B. Dupuis, A. Karasev, E. Jacquot (eds.). Springer, Cham, 2017: 207-241 (doi: 10.1007/978-3-319-58860-5_8).
18. Cockerham G. Potato breeding for virus resistance. *Annals of Applied Biology*, 1943, 30: 105-108.
19. Ross H. Potato breeding — problems and perspectives. In: *Fortschritte der Pflanzenzüchtung*, *13*. Verlag Paul Parey, Berlin & Hamburg, 1986.
20. Song Y.-S., Hepting L., Schweizer G., Hartl L., Wenzel G., Schwarzfischer A. Mapping of extreme resistance to PVY (Ry_{sto}) on chromosome XII using anther-culture-derived primary dihaploid potato lines. *Theoretical and Applied Genetics*, 2005, 111(5): 879-887 (doi: 10.1007/s00122-005-0010-7).
21. Flis B., Hennig J., Strzelczyk-Żyta D., Gebhardt C., Marczewski W. The Ry-f_{sto} gene from *Solanum stoloniferum* for extreme resistant to *Potato virus Y* maps to potato chromosome XII and is diagnosed by PCR marker $GP122_{718}$ in PVY resistant cultivars. *Molecular Breeding*, 2005, 15: 95-101 (doi: 10.1007/s11032-004-2736-3).
22. Song Y.-S., Schwarzfischer A. Development of STS markers for selection of extreme resistance (Ry_{sto}) to PVY and maternal pedigree analysis of extremely resistant cultivars. *American Journal of Potato Research*, 2008, 85(2): 159-170 (doi: 10.1007/s12230-008-9012-8).
23. Asama K., Ito H., Murakami N., Itoh T. New potato variety "Konafubuki". *The Bulletin of Hokkaido Prefectural Agricultural Experiment Stations*, 1982, 48: 75-84.
24. Valkonen J.P.T., Slack S.A., Plaisted R.L., Watanabe K. Extreme resistance is epistatic to hypersensitive resistance to potato virus Y in a *Solanum tuberosum* ssp. *andigena*-derived potato genotype. *Plant Disease*, 1994, 78: 1177-1180.
25. Bradshaw J.E. Potato breeding at the Scottish Plant Breeding Station and the Scottish Crop Research Institute: 1920-2008. *Potato Research*, 2009, 52: 141-172 (doi: 10.1007/s11540-009-9126-5).
26. Yashina I.M., Sklyarova N.P., Simakov E.A. *Trudy po prikladnoi botanike, genetike i selektsii*, 2007, 163: 118-135 (in Russ.).
27. Yashina I.M. *Znachenie sorta v sovremennykh tekhnologiyakh proizvodstva kartofelya*. Available https://refdb.ru/look/1153053-pall.html. Accessed 17.10.2019 (in Russ.).
28. Simakov E.A., Yashina I.M. *Materialy konferentsii «Mirovye geneticheskie resursy kartofelya i ikh ispol'zovanie v sovremennykh napravleniyakh selektsii» (k 125-letiyu so dnya rozhdeniya N.I. Vavilova)* [Proc. Conf. «World potato genetic resources and their use in modern breeding » (to the 125th birthday of N.I. Vavilov)]. Moscow, 2012: 52-60 (in Russ.).
29. Plaisted R.L. Advances and limitations in the utilization of Neotuberosum in potato breeding. In: *The production of new potato varieties: technological advances.* G.J. Jellis, D.E. Richardson (eds.). Cambridge University Press, Cambridge, 1987: 186-196.
30. Sagredo D.B., Mathias R.M., Barrientos P.C., Acuca B.I., Kalazich B.J., Rojas J.S. Evaluation of a SCAR RYSC3 marker of the Ry_{adg} gene to select resistant genotypes to potato virus Y (PVY) in the INIA potato breeding program. *Chilean Journal of Agricultural Research*, 2009, 69(3): 305-315.
31. Ortega F., Lopez-Vizcon C. Application of molecular marker-assisted selection (MAS) for disease resistance in a practical potato breeding programme. *Potato Research*, 2012, 55: 1-13 (doi: 10.1007/s11540-011-9202-5).
32. Mendoza H.A., Jayashinghe U. Progress in breeding for combined resistance to potato viruses Y, X and leafroll. *Proc. 12th Trienn Conf EAPR.* Paris, 1993: 457-458.
33. Mendoza H.A., Mihovilovich E.J., Saguma F. Identification of the triplex (YYYy) potato virus Y (PVY) immune progenitors derived from *Solanum tuberosum* ssp. *andigena*. *American Journal of Potato Research*, 1996, 73(1): 13-19 (doi: 10.1007/BF02849300).
34. Sakamoto Y., Mori K., Matsuo Y., Mukojima N., Watanabe W., Sobaru N., Tamiya S., Nakao T., Hayashi K., Watanuki H., Nara K., Yamazaki K., Chaya M. Breeding of a new potato variety "Nagasaki Kogane" with high eating quality, high carotenoid content, and resistance to diseases and pests. *Breeding Science*, 2017, 67(3): 320-326 (doi: 10.1270/jsbbs.16168).
35. Fujimatsu M., Hashizume H., Fudan T., Koma Y., Sanetomo R., Ono S., Hosaka K. Harima-

ru: a new potato variety for a local specialty. *Breeding Science*, 2018, 68(2): 284-288 (doi: 10.1270/jsbbs.17109).
36. Valkonen J.P.T., Wiegmann K., Hämäläinen J.H., Marczewski W., Watanabe K.N. Evidence for utility of the same PCR-based markers for selection of extreme resistance to Potato virus Y controlled by Ry_{sto} of *Solanum stoloniferum* derived from different sources. *Annals of Applied Biology*, 2008, 152: 121-130 (doi: 10.1111/j.1744-7348.2007.00194.x).
37. Pavlyuchuk N.V., Voluevich E.A., Makhan'ko V.L., Rusetskii N.V. *Kartofelevodstvo*, 2013, 21(1): 184-192 (in Russ.).
38. Bhardwaj V., Sharma R., Dalamu S.A.K., Baswaraj R., Singh R., Singh B.P. Molecular characterization of potato virus Y resistance in potato (*Solanum tuberosum* L.). *Indian Journal of Genetics and Plant Breeding*, 2015, 75: 389-392 (doi: 10.5958/0975-6906.2015.00062.0).
39. Antonova O.Y., Klimenko N.S., Evdokimova Z.Z., Kostina L.I., Gavrilenko T.A. Finding *RB/Rpi-blb1/Rpi-sto1*-like sequences in conventionally bred potato varieties. *Vavilov Journal of Genetics and Breeding*, 2018, 22(6): 693-702 (doi: 10.18699/VJ18.412).
40. Li W.L., Guo W., Xiao J.P., Bai L., Guo H.C. Germplasm evaluation and molecular selection of potato (*Solanum tuberosum* L.) cultivars with disease resistance in China. *Czech Journal of Genetics and Plant Breeding*, 2017, 53(3): 114-121 (doi: 10.17221/101/2016-CJGPB).
41. Takeuchi T., Sasaki J., Suzuki T., Horita H., Hiura S., Iketani S., Fujita R., Senda K. DNA markers for efficient selection of disease and pests resistance genes in potato (in Japanese). In: *Hokkaido Nogyo-Shiken-Kaigi-Shiryo 2008*. Hokkaido, 2009: 1-26.
42. Gavrilenko T.A., Klimenko N.S., Antonova O.Yu., Lebedeva V.A., Evdokimova Z.Z., Gadzhiev N.M., Apalikova O.V., Alpat'eva N.V., Kostina L.I., Zoteeva N.M., Mamadbokirova F.T., Egorova K.V. *Vavilovskii zhurnal genetiki i selektsii*, 2018, 22(1): 35-45 (doi: 10.18699/VJ18.329) (in Russ.).
43. Cernák I., Taller J., Wolf I., Fehér E., Babinszky G., Alföldi Z., Csanádi G., Polgár Z. Analysis of the applicability of molecular markers linked to the PVY extreme resistance gene Ry_{sto}, and the identification of new markers. *Acta Biologica Hungarica*, 2008, 59(2): 195-203 (doi: 10.1556/abiol.59.2008.2.6).
44. Heldak J., Bezo M., Stefunova V., Gallikova A. Selection of DNA markers for detection of extreme resistance to potato virus Y in tetraploid potato (*Solanum tuberosum* L.) F_1 progenies. *Czech Journal of Genetics and Plant Breeding*, 2007, 43: 125-134 (doi: 10.17221/2074-CJGPB).
45. Slater T. National potato breeding program: strategic trait development. *Final Report for Horticulture Australia*. Horticulture Innovation Australia Limited, Sydney, 2012.
46. Schwarzfischer A., Behn A., Groth J., Reichmann M., Kellermann A., Songe Y.-S. Markergestützte Selektion in der praktischen Kartoffelzüchtung — Erfahrungen und Perspektiven. *60. Tagung der Vereinigung der Pflanzenzüchter und Saatgutkaufleute Osterreichs 2009*. Raumberg-Gumpenstein, 2010: 81-85.
47. Lindner K., Behn A., Schwarzfischer A., Song Y.-S. Extreme Y-Resistenz im Aktuellen Deutschen Kartoffelsortiment. *Journal Für Kulturpflanzen*, 2011, 63(4): 97-103 (doi: 10.5073/JfK.2011.04.01).
48. Nie X., Chen H., Zhang J., Zhang Y., Yang J., Pan H., Song W.X., Murad F., He Y.Q., Bian K. Rutaecarpine ameliorates hyperlipidemia and hyperglycemia in fat-fed, streptozotocin-treated rats via regulating the IRS-1/PI3K/Akt and AMPK/ACC2 signaling pathways. *Acta Pharmacologica Sinica*, 2016, 37(4): 483-496 (doi: 10.1038/aps.2015.167).
49. Beketova M.P., Rogozina E.V., Chalaya N.A., Khavkin E.E. *Biotekhnologiya rastenii*, 2018, 4: 99-106 (doi: 10.18384/2310-7189-2018-4-99-106).
50. Sharma R., Bhardwaj V., Dalamu D., Kaushik S.K., Singh B.P., Sharma S., Umamaheshwari R., Baswaraj R., Kumar V., Gebhardt C. Identification of elite potato genotypes possessing multiple disease resistance genes through molecular approaches. *Scientia Horticulturae*, 2014, 179: 204-211 (doi: 10.1016/j.scienta.2014.09.018).
51. Biryukova V.A., Shmyglya I.V., Abrosimova S.B., Zapekina T.I., Meleshin A.A., Mityushkin A.V., Manankov V.V. *Zashchita kartofelya*, 2015, 5: 3-7 (in Russ.).
52. Biryukova V.A., Shmyglya I.V., Meleshin A.A., Mityushkin A.V., Manankov V.V., Abrosimova S.B. *Dostizheniya nauki i tekhniki APK*, 2016, 30(10): 22-26 (in Russ.).
53. Yermishin A.P., Svitoch O.V., Voronkova E.V., Gukasian O.N., Luksha V.I. Determination of the composition and the allelic state of disease and pest resistance genes in potato parental lines using DNA markers. *Russian Journal of Genetics*, 2016, 52: 498-506 (doi: 10.1134/S1022795416050057).
54. Sainakova A.B., Romanova M.S., Krasnikov S.N., Litvinchuk O.V., Alekseev YA.I., Nikulin A.V., Terent'eva E.V. *Vavilovskii zhurnal genetiki i selektsii*, 2018, 22(1): 18-24 (doi: 10.18699/VJ18.326) (in Russ.).
55. Shanina E.P., Sergeeva L.B., Stafeeva M.A., Klyukina E.M. *Dostizheniya nauki i tekhniki APK*, 2018, 32(12): 47-49 (doi: 10.24411/0235-2451-2018-11213) (in Russ.).
56. Rogozina E.V., Terent'eva E.V., Potokina E.K., Yurkina E.N., Nikulin A.V., Alekseev Ya.I. Multiplex PCR-based identification of potato genotypes as donors in breeding for resistance to diseases and pests. *Agricultural Biology* [*Sel'skokhozyaistvennaya biologiya*], 2019, 54(1): 19-30 (doi: 10.15389/agrobiology.2019.1.19eng).
57. Lopez M., Riegel R., Lizana C., Behn A. Identification of virus and nematode resistance genes

in the Chilota Potato Genebank of the Universidad Austral de Chile. *Chilean Journal of Agricultural Research*, 2015, 75(3): 320-327 (doi: 10.4067/s0718-58392015000400008).
58. Fulladolsa A.C., Navarro F.M., Kota R., Severson K., Palta J.P., Charkowski A.O. Application of marker assisted selection for Potato virus Y resistance in the University of Wisconsin potato breeding program. *American Journal of Potato Research*, 2015, 92(3): 444-450 (doi: 10.1007/s12230-015-9431-2).
59. Luksha V.I., Voronkova E.V., Gukasyan O.N., Ermishin A.P. V sbornike: *Molekulyarnaya i prikladnaya genetika* [In: Molecular and applied genetics]. Minsk, 2012: 82-87 (in Russ.).
60. Levyi A.V., Voronkova E.V., Polyukhovich Yu.V., Ermishin A.P. *Vestsi Natsyyanal'nai akademii navuk Belarusi. Seryya biyalagichnykh navuk*, 2017, 2: 46-54 (in Russ.).
61. Witek K., Strzelczyk-Żyta D., Hennig J., Marczewski W. A multiplex PCR approach to simultaneously genotype potato towards the resistance alleles *Ry-fsto* and *Ns*. *Molecular Breeding*, 2006, 18: 273-275 (doi: 10.1007/s11032-006-9021-6).
62. Lopez-Pardo R., Barandalla L., Ritter E., Ruiz de Galarreta J.I. Validation of molecular markers for pathogen resistance in potato. *Plant Breeding*, 2013, 132: 246-251 (doi: 10.1111/pbr.12062).
63. Milczarek D., Plich J., Tatarowska B., Flis B. Early selection of potato clones with resistance genes: the relationship between combined resistance and agronomical characteristics. *Breeding Science*, 2017, 67: 416-420 (doi: 10.1270/jsbbs.17035).
64. Gavrilenko T.A., Afanasenko O.S., Antonova O.Yu., Rogozina E.V., Khyutti A.V., Shuvalov O.Yu., Islamshina A.R., Chalaya N.A. *Materialy konferentsii RASKHN—RFFI «Orientirovannye fundamental'nye issledovaniya i ikh realizatsiya v APK Rossii»* [Proc. Conf. «Fundamental research and their implementation in Russian agriculture»]. Sergiev Posad, 2009: 94-100 (in Russ.).
65. Rogozina E.V., Shuvalov O.Yu., Antonova O.Yu., Gavrilenko T.A. Interspecific and intraspecific diversity on resistance to Y virus in potato. *Sel'skokhozyaistvennaya biologiya* [*Agricultural Biology*], 2012, 5: 64-69 (doi: 10.15389/agrobiology.2012.5.64rus) (in Russ.).
66. Kuz'minova O.A., Vologin S.G., Stashevski Z.A., Gimaeva E.A. *Zashchita kartofelya*, 2014, 1: 14-15 (in Russ.).
67. Kuz'minova O.A., Vologin S.G., Stashevski Z., Gimaeva E.A. *Materialy XV molodezhnoi nauchnoi konferentsii «Biotekhnologiya v rastenievodstve, zhivotnovodstve i veterinarii»* [Proc. XV Conf. of young scientists «Biotechnology in crop production, animal husbandry and veterinary medicine»]. Moscow, 2015: 38-39 (in Russ.).
68. Kasai K., Morikawa Y., Sorri V.A., Valkonen J.P.T., Gebhardt C., Watanabe K.N. Development of SCAR markers to the PVY resistance gene Ry_{adg} based on a common feature of plant disease resistance genes. *Genome*, 2000, 43(1): 1-8 (doi: 10.1139/g99-092).
69. Gebhardt C., Bellin D., Henselewski H., Lehmann W., Schwarzfischer J., Valkonen J.P.T. Marker-assisted combination of major genes for pathogen resistance in potato. *Theoretical and Applied Genetics*, 2006, 112(8): 1458-1464 (doi: 10.1007/s00122-006-0248-8).
70. Rizza D.M., Vilary F.L., Torres D.G., Maeso D. Detection of PVY extreme resistance genes in potato germplasm from the Uruguayan breeding program. *American Journal of Potato Research*, 2006, 83(4): 297-304 (doi: 10.1007/BF02871590).
71. Ottoman R.J., Hane D.C., Brown C.R., Yilma S., James S.R., Mosley A.R., Crosslin J.M., Vales M.I. Validation and implementation of marker-assisted selection (MAS) for PVY resistance (Ry_{adg} gene) in a tetraploid potato breeding program. *American Journal of Potato Research*, 2009, 86(4): 304-314 (doi: 10.1007/s12230-009-9084-0).
72. Whitworth J.L., Novy R.G., Hall D.G., Crosslin J.M., Brown C.R. Characterization of broad spectrum potato virus Y resistance in a *Solanum tuberosum* ssp. *andigena-derived* population and select breeding clones using molecular markers, grafting, and field inoculations. *American Journal of Potato Research*, 2009, 86(4): 286-296 (doi: 10.1007/s12230-009-9082-2).
73. Neder D.G., Pinto C.A.B.P., Melo D.S., Lepre A.L., Peixouto L. dos S. Seleção de clones de batata com resistкncia múltipla a pinta preta e aos vírus X e Y. *Ciência Rural*, 2010, 40(8): 1702-1708 (doi: 10.1590/s0103-84782010000800005).
74. Kaushik S.K., Sharma R., Garg I.D., Singh B.P., Chakrabarti S.K., Bhardwaj V., Pandey S.K. Development of a triplex (YYYy) parental potato line with extreme resistance to potato virus Y using marker assisted selection. *The Journal of Horticultural Science and Biotechnology*, 2013, 88(5): 580-584 (doi: 10.1080/14620316.2013.11513009).
75. Tiwari J.K., Pandey S.K., Poonam, Chakrabarti S.K., Gopal J., Kumar V. Molecular markers of Ry_{adg} gene and serological assay reveal potato virus Y (PVY) resistance in the tetraploid Indian potato (*Solanum tuberosum*) germplasm. *Indian Journal of Agricultural Sciences*, 2013, 83: 397-401.
76. Gabriel J., Veramendi S., Pinto L., Pariente L., Angulo A. Associations of molecular markers with diseases resistance, morphological and agronomic characters in potato diploid families (*Solanum tuberosum* L.). *Revista Colombiana de Biotecnologиa*, 2016, 18(1): 17-32 (español).
77. Herrera M. del R., Vidalon L.J., Montenegro J.D., Riccio C., Guzman F., Bartolini I., Ghislain M. Molecular and genetic characterization of the Ry_{adg} locus on chromosome XI from Andigena potatoes conferring extreme resistance to potato virus Y. *Theoretical and Applied Ge-*

netics, 2018, 131(9): 1925-1938 (doi: 10.1007/s00122-018-3123-5).
78. Mori K., Sakamoto Y., Mukojima N., Tamiya S., Nakao T., Ishii T., Hosaka K. Development of a multiplex PCR method for simultaneous detection of diagnostic DNA markers of five disease and pest resistance genes in potato. *Euphytica*, 2011, 180(3): 347-355 (doi: 10.1007/s10681-011-0381-6).
79. Tomczyńska I., Jupe F., Hein I., Marczewski W., Śliwka J. Hypersensitive response to Potato virus Y in potato cultivar is conferred by the *Ny-Smira* gene located on long arm of chromosome IX. *Molecular Breeding*, 2014, 34: 471-480 (doi: 10.1007/s11032-014-0050-2).
80. Sato M., Nishikawa K., Komura K., Hosaka K. Potato virus Y resistance gene, Ry_{chc}, mapped to the distal end of potato chromosome 9. *Euphytica*, 2006, 149: 367-372 (doi: 10.1007/s10681-006-9090-y).
81. *Rossiiskie sorta kartofelya. Katalog* [Russian varieties of potatoes. Catalog]. Cheboksary, 2011 (in Russ.).
82. *Katalog mirovoi kollektsii VIR. Vypusk 809. Kartofel'. Geneticheskaya kollektsiya. 2012 g.* [Catalog of the VIR World Collection. Iss. 809. Potatoes. Genetic collection. 2012 year]. St. Petersburg, 2012 (in Russ.).
83. Vanyagina A.A. *Sorta kartofelya belorusskoi selektsii. Katalog* [Belarusian potato varieties]. Minsk, 2018 (in Russ.).
84. *Sorta kartofelya rossiiskoi selektsii* /Pod redaktsiei E.A. Simakova [Russian potato varieties. E.A. Simakov (ed.)]. Moscow, 2018 (in Russ.).
85. Gavrilenko T., Antonova O., Shuvalova A., Krylova E., Alpatyeva N., Spooner D.M., Novikova L. Genetic diversity and origin of cultivated potatoes based on plastid microsatellite polymorphism. *Genetic Resources and Crop Evolution*, 2013, 60(7): 1997-2015 (doi: 10.1007/s10722-013-9968-1).
86. Milbourne D., Meyer R.C., Colli A.J., Ramsay L.D., Gebhardt C., Waugh R. Isolation, characterisation and mapping of simple sequence repeat loci in potato. *Molecular and General Genetics MGG*, 1998, 259(3): 233-245 (doi: 10.1007/s004380050809).
87. Anisimov B.V., Elanskii S.N., Zeiruk V.N., Kuznetsova M.A., Simakov E.A., Sklyarova N.P., Filippov S.N., Yashina I.M. *Sorta kartofelya, vozdelyvaemye v Rossii. Katalog 2013* [Varieties of potatoes cultivated in Russia. Catalog 2013]. Moscow, 2013 (in Russ.).
88. Simakov E.A., Anisimov B.V., Sklyarova N.P., Yashina I.M., Elanskii S.N. *Sorta kartofelya, vozdelyvaemye v Rossii. Katalog 2005. Ezhegodnoe prilozhenie k gazete «Kartofelevod»* [Varieties of potatoes cultivated in Russia. Catalog 2005. The annual supplement to the newspaper «Kartofelevod»]. Moscow, 2005 (in Russ.).
89. *Katalog mirovoi kollektsii VIR. Vyp. 829. Selektsionnye sorta kartofelya Rossii i SNG* [Catalog of the VIR World Collection. Iss. 829. Selection potato varieties of Russia and the CIS]. St. Petersburg, 2015 (in Russ.).
90. Brigneti G., Garcia-Mas J., Baulcombe D.C. Molecular mapping of the potato virus Y resistance gene Ry_{sto} in potato. *Theoretical and Applied Genetics*, 1997, 94(2): 198-203 (doi: 10.1007/s001220050400).