Agronomy Research **18**(2), 662–670, 2020
https://doi.org/10.15159/AR.20.118

Study of correlation among ploidy level and steroid glycoalkaloids content in resistance in cultivated and uncultivated potato species from an *in vitro* genebank

D. Zeka[1,*], P. Sedlák[2], V. Sedláková[2], P. Vejl[2], Sh. Fetahu[1], I. Rusinovci[1] and S. Aliu[1]

[1] Department of Plan Production, Faculty of Agriculture and Veterinary, University of Prishtina, Bul. "Bill Clinton" XK10000 Prishtinë, Republic of Kosovo
[2]Department of Genetic and Breeding, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences Prague, Kamýcká 129, Prague 6 – Suchdol CZ165 21, Czech Republic
[*]Correspondence: dukagjin.zeka@uni-pr.edu

Abstract. The present research was carried out with the aim to determine the correlation between ploidy level, steroid glycoalkaloids (SGAs) content and resistance against Late blight (*Phytophthora infestans* (Mont.) de Bary), and Colorado potato beetle (*Leptinotarsa decemlineata* (Say)) in cultivated and wild *Solanum* species preserved in the Potato Gene Bank of Czech Republic. In this study 27 species were included which consist of five cultivated and 22 wild species, with a total of 31 genotypes (four species represented by two accessions). In this study 70.97% of genotypes were evaluated as diploid, 3.23% were triploid, 19.35% tetraploid and 6.45% hexaploid as depicted from counting of chromosomes. The highest concentration, of foliage α-solanine (5,450 mg kg^{-1}) and α-chaconine (9,420 mg kg^{-1}) of dry matter was found in the specie *S. yungasense* 00070, whereas lowest 1.1 mg kg^{-1} and 2.3 mg kg^{-1} in *S. pinnatisectum* 00051, respectively, Tukey's test of one way *anova* was performed for getting significance from the data obtained and found significant variation among species of steroid glycoalkaloids (SGA) content in dry weight at level of $P \leq 0.01$. Leaf damages by *Leptinotarsa decemlineata* under field experiment circumstances were also recorded. *In vitro* study, *S. bulbocastanum PIS 06-17* and *S. bulbocastanum 00240* shown resistant to *P. infestans* upon inoculation of aggressive isolates and strong resistance was observed in *S. stoloniferum 00295*, *S. sucrense 0062* and *S. yungasense 0070.* Nevertheless, there was no correlation of ploidy level, SGA contents and resistance to the CPB (r = 0.00) and late blight (r = 0.076) found in the investigated *Solanum* species.

Key words: *Solanum* species, polyploidy, α-chaconine, α-solanine, resistance.

INTRODUCTION

Genus *Solanum* is one of the largest genera in flowering plants. Ploidy level has been of great importance in the classification and identification of cultivated potatoes (Huamán & Spooner, 2002). Bukasov (1939) was the first who count chromosomes of

the cultivated potatoes and discovered diploids, triploids, tetraploids, and pentaploids and used these data to speculate on their hybrid origins. The evolutionary diversity of the wild species and the comparatively narrow genetic basis of the cultivated potato make *Solanum* species unique materials for breeding (Carputo et al., 2013; Zeka et al., 2015). The potato secondary gene pool consists of the broadest range of wild and primitively cultivated relative species compared to other crop plants (Pavek & Corsini, 2001; Zeka, et al., 2014). Species of the family *Solanaceae* produce a wide spectrum of steroid glycoalkaloids (SGAs). These are secondary metabolites characterized by a bitter taste and toxicity (Friedmann & McDonald, 1997). The two main potato steroid glycoalkaloids are α-solanine and α-chaconine, derived from solanidin, which represent approximately 90 - 95% of total glycoalkaloids. Nevertheless, SGAs are always present in potatoes, albeit in varying amounts, and form the plant's inbuilt protection against insects and disease. The influence of potato genotype on total glycoalkaloids (TGA) content in tubers was significant, but the impact of growing conditions or year are insignificant (Skrabule et al., 2010).

Jansky et al. (2009) found significant effect of ploidy in resistance to CPB; where diploid species were most resistant, followed by hexaploids and than tetraploids. Also she postulated that there was no significant difference among two Endosperm balance number (EBN) and four EBN from each other, but they were more susceptible than the one EBN species.

Phytophthora infestans is responsible for the late blight disease found in potatoes and tomatoes. *P. infestans* belongs to the oomycetes, a diverse group of deeply branching eukaryotic microorganisms (Kamoun, 2003). Due to their filamentous growth habit, oomycetes had been traditionally classified in the kingdom of fungi. Continuous pathogen population studies describing the contemporary *P. infestans* population are essential in order to advise potato breeders and growers accordingly (Runno-Paurson et al., 2016). Late blight has become a particularly devastating disease worldwide during the past few decades (Goodwin et al., 1994; Klarfeld et al., 2009) limiting potato production.

So far, 11 late blight resistance genes from the wild potato speciess *Solanum demissum* were introduced into cultivated potato (Gebhardt & Valkonen, 2001).

The aim of this research was to determinate correlation between ploidy level, steroid glycoalkaloidscontent (SGAs), and resistance against Late blight (*Phytophthora infestans* (Mont.) de Bary) and Colorado potato beetle (*Leptinotarsa decemlineata* (Say)) in cultivated and uncultivated *Solanum* species preserved *in vitro* in Potato Gene Bank of Czech Republic. Moreover, use these plant genetic resources for potato breeding programs and developing new interspecific somatic hybrids highly resistant.

MATERIAL AND METHODS

Plant Material

Twenty-seven of cultivated and uncultivated botanical species of genus *Solanum* were used as biological material in the research. Origin, taxonomy, and genetic background of *Solanum* species are presented in Table 1. The biological material, single clone of 31 genotypes were obtained from *in vitro* preservation gene bank of Potato Research Institute in Havlíčkův Brod Ltd. than genotypes *in vitro* micropropagated and tested in Department of Genetics and Breeding, FAFNR-CULS.

Ploidy level, glycoalkaloid content and resistance to *P. infestans* was analyzed in three random plants with three replication of each genotype, whereas evaluation of resistance to the Colorado potato was done on five plants with three replications in two consecutive years field experiment.

Determination of the Ploidy

The ploidy of all species was determined according to Zlesak et al. (2005) with minor changes in time procedures. Young long roots tips of 5–10 mm sizes were collected for ploidy determination from the greenhouse after four weeks of seedlings. The roots were carefully pre-washed using distilled water. The root tips were treated using 350 µl colchicine 0.3% for 4 hours in room temperature. Fixation of cells was realized by mixture of ethanol 96% and ice acetic acid in ratio of 3:1 in refrigerator (5 °C) overnight and macerated using 1:1 mixture of concentrated HCl and ethanol. Colouring and pressure setting of karyotype was performed on microscopic glass slides as described by (Zlesak et al., 2005), Chromosomes were counted and karotypes documented by means of binocular microscope Olympus BX41TF (Olympus Corporation Tokyo, Japan).

Identification and Quantification of Steroid Glycoalkaloids

The foliage samples were collected and freeze dried for identification and quantification of glycoalkaloids. Total 0.25 g of freeze-dried grinded foliages were used for separation of α–chaconine and α–solanine as described by (Crabbe & Fryer, 1980). Extract were purified on Solid Phase Extraction (SPE) column and analyzed by HPLC-MS/MS method as described by (Friedman & McDonald, 1997). Individual glycoalkaloids were identified by their molecular ions and product spectrum and further quantified using external calibration.

Resistance assessment

Symptoms of potato late blight, and resistance to the Colorado potato beetle was recorded by estimating the percentage of damaged leaf from 3rd week of June month. The evaluation of symptoms was performed at each week interval.

Potato genotypes samples were grown in the CULS experimental field, plot size for each variety was 5 sqm. Plots were arranged three replications in a random design.

In vitro testing of the potato for partial resistance to *P. infestans* (Hodgson, 1961) was followed. *P. infestans* isolates for the reference were received from Department of Plant Protection and maintained as described by Vleeshouwers et al. (1999). Three highly aggressive isolates overcoming *Solanum demissum* genes R1, R2, R3, R4, R6, R7, R10, and R11 recorded from all the inoculums under study. These Isolates were collected from Valečov (Czech Republic) and labelled as 1/3, 2/1 and 4/1. Inoculation of virulent strains were performed in triplicate on 4 weeks old genotypes on the dorsal surface of leafs. Virulence was studied after 72 hours of inoculation under stereomicroscope. The resistant and partially resistant genotypes were again re-evaluated against other aggressive isolates 2/2, 4/2 and 5/3.

Statistical Analyses

Mean results of the α-chaconin, α-salonine and SGA contents between the species were compared by Tukey's test one-way ANOVA at MINITAB 18, whereas analysis of correlation (r) coefficient of SGA and resistance is done using MINITAB 18 and Microsoft® Excel 2007 software's.

Table 1. Origin and taxonomy of *Solanum* species used in this research

Subsections and series	*Solanum* species	2n	EBN[4]	Region of origin	Altitude range, m
subsection *Estolonifera*					
Etuberosa	*brevidens*	24	1	C-S.CHL, S.ARG	< 1,000
subsection *Potatoe*					
super series *Stellata*					
Bulbocastana	*bulbocastanum*	24	1	MEX	1,500–2,300
Pinnatisecta	*pinnatisectum*	24	1	C.MEX	1,800–2,100
Polyadenia	*polyadenium*	24	1	C.MEX	1,900–2,900
Yungasensa	*chacoense*	24	2	BOL, ARG, PRY, URY, PER	0–2,350
	yungasense	24	2	N.BOL-S.PER	1,100–1,900
super series *Rotata*					
Tuberosa (wild)	*berthaultii*	24	2	BOL	2,000–2,800
	gourlai	24	2	C.BOL-NW.ARG	2,100–3,400
	incamayoense	24	2	NW.ARG	2,100-2,800
	leptophyes	24	2	S.PER, N.BOL	2,500–4,000
	microdontum	24	2	ARG, BOL	1,800–3,100
	mochiquense	24	1	N.PER	250–1,750
	sparsipilum	24	2	C.PER-C.BOL	2,400–4,200
	spegazzinii	24	2	NW.ARG	1,900–3,100
	sucrense	48	4	C.BOL	2,500–4,000
	vernei	24	2	NW.ARG	2,200–2,800
	verrucosum	24	2	MEX	2,400–3,200
Tuberosa (cultivated)	*phureja*	24	2	VEN, COL, ECU, PER, BOL	1,600–2,800
	goniocalyx	24	2	N.PER-C.BOL	> 3,000
	stenotomum	24	2	C.BOL-C.PER	3,000–3,800
	x chaucha	36	2	PER, BOL, ARG	1,600–3,800
	andigena	48	4	Andes: ARG-MEX	2,000–3,000
Acaulia	*acaule*	48	2	PER, BOL, NW.ARG	2,600–4,650
Longipedicellata	*fendleri*	24	2	NW.MEX, SW.USA	1,600–2,800
	polytrichon	48	2	C-NW.MEX	1,800–2,500
	stoloniferum	48	2	C.MEX	1,800–3,000
Demissa	*guerreroense*	72	4	SW.MEX	2,600–3,000
	demissum	72	4	MEX, GTM	2,650–3,800

[4] (Source: Spooner & Castillo, 1997; Hijmans et al., 2007).

RESULTS AND DISCUSSION

Solanum species shows ploidy from diploid (2n = 2x = 24) to hexaploid (2n = 6x = 72). Salaman (1926) published first ploidy determination of wild species *Solanum demissum* and *Solanum* x *edinense*. The diploid level in natural occurred (about 80%) wild *Solanum* species (Carputo & Barone, 2005). Hijmans et al. (2007) compiled a total of 5,447 reports of ploidy determination covering 185 of the 187 species.

Our results on investigated genotypes/species confirmed the expected ploidy level (Table 1). In this study 70.97% of genotypes were evaluated as diploid, 3.23% were triploid, 19.35% tetraploid and 6.45% hexaploid as depicted from counting of chromosomes (Fig. 1). We also obtained similar results with other researchers (Spooner & Castillo, 1997; Hijmans et al., 2007).

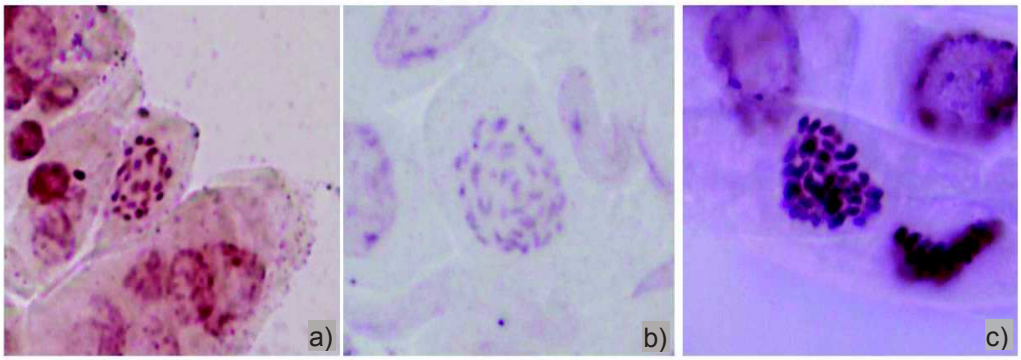


Figure 1. Chromosomes, a) 2n *S. polyadenium 00290*; b) 3n *S. x chaucha 00134 and* c) 4n *S. stoloniferum 00295.*

In this study, the highest concentration, of foliage α-solanine (5,450 mg kg^{-1}) and α-chaconine (9,420 mg kg^{-1}) of dry matter was found in the specie *S. yungasense* 00070, whereas lowest 1.1 mg kg^{-1} and 2.3 mg kg^{-1} in *S. pinnatisectum* 00051, respectively, Tukey's test of one way *anova* was performed for getting significance from the data obtained and found significant variation among species of steroid glycoalkaloids (SGA) content in dry weight at level of $P \leq 0.01$ (Table 2). Solanum glycoalkaloids are known as insect-deterrent activity, which may offer a valuable alternative to synthetic pesticides in providing natural defence against pests, especially CPB. However, in *S. tuberosum* α-solanine and α-chaconine are ineffective against CPB; whereas some accessions of *S. chacoense*, even their total glycoalkaloid content was almost same with other species, showed high resistance to CPB due to their high leptine content (Sinden, et al., 1986). Jansky et al. (2009) postulated that the best sources of CPB resistance seem to be the wild diploid *Solanum* species. Host plant resistance to the CPB has been reported in several other wild *Solanum* relatives (Flanders et al., 1998). Most reports indicated that resistance is due to glandular trichomes or high levels of glycoalkaloids (Jansky et al., 2009). Glandular trichomes provide effective resistance in *Solanum berthaultii* Hawkes (Dimock & Tingey, 1988) and *Solanum polyadenium* Greenm (Gibson, 1976).

Table 2. Average steroid glycoalkaloids (SGA) content in dry weight mg kg^{-1}

Order	Species	EVIGEZ Code	Foliar glycoalkaloids content		
			α-chaconin	α-solanin	SGA
1	*S. acaule*	*00030*	7.3^{J}	4.6^{M}	11.9^{K}
2	*S. andigenum*	*00108*	413.0^{I}	152.5^{JK}	565.5^{J}
3	*S. berthaultii*	*00260*	19.3^{J}	8.9^{M}	28.2^{K}
4	*S. bulbocastanum*	*00240*	2.8^{J}	2.9^{M}	5.7^{K}
5	*S. bulbocastanum*	*PIS06-17*	35.5^{J}	23.8^{KLM}	59.3^{K}
6	*S. chacoense*	*00037*	$4,555.0^{E}$	$3,220.0^{C}$	$7,775.0^{E}$
7	*S. chacoense*	*00230*	$6,220.0^{CD}$	$4,500.0^{B}$	$10,720.0^{B}$
8	*S. demissum*	*00250*	7.7^{J}	30.9^{KLM}	38.6^{K}
9	*S. fendleri*	*00275*	56.4^{J}	13.2^{LM}	69.6^{K}
10	*S. goniocalyx*	*00109*	$6,000.0^{D}$	$3,050.0^{D}$	$9,050.0^{D}$
11	*S. gourlai*	*00045*	29.5^{J}	13.1^{LM}	42.6^{K}
12	*S. gourlai*	*00043*	7.9^{J}	10.5^{LM}	18.4^{K}
13	*S. guerreroense*	*00280*	76.1^{J}	15.0^{LM}	91.1^{K}
14	*S. incamayoense*	*00047*	$1,595.0^{F}$	$1,195.0^{G}$	$2,790.0^{G}$
15	*S. leptophyes*	*00048*	$6,715.0^{B}$	$3,025.0^{D}$	$9,740.0^{C}$
16	*S. microdontum*	*00049*	$6,360.0^{C}$	$3,185.0^{C}$	$9,545.0^{C}$
17	*S. mochiquense*	*00050*	695.0^{H}	477.5^{I}	$1,172.5^{I}$
18	*S. phureja*	*00308*	120.0^{J}	62.9^{KLM}	182.9^{K}
19	*S. pinnatisectum*	*00051*	2.3^{J}	1.1^{M}	3.4^{K}
20	*S. polyadenium*	*00290*	70.7^{J}	33.6^{KLM}	104.3^{K}
21	*S. polytrichon*	*00053*	$4,595.0^{E}$	$2,210.0^{E}$	$6,805.0^{F}$
22	*S. sparsipillum*	*00071*	$4,570.0^{E}$	$1,955.0^{F}$	$6,525.0^{F}$
23	*S. spegazzini*	*00060*	66.9^{J}	36.5^{KLM}	103.4^{K}
24	*S. stenotomum*	*00212*	643.5^{HI}	138.5^{JKL}	782.0^{J}
25	*S. stoloniferum*	*00295*	$1,285.0^{G}$	240.5^{J}	$1,525.5^{HI}$
26	*S. sucrense*	*00062*	$1,071.5^{G}$	777.0^{H}	$1,848.5^{H}$
27	*S. vernei*	*00069*	18.1^{J}	10.2^{LM}	$1,848.5^{H}$
28	*S. vernei*	*00234*	5.4^{J}	2.4^{M}	7.8^{K}
29	*S. verrucosum*	*00299*	$4,540.0^{E}$	$2,120.0^{EF}$	$6,660.0^{F}$
30	*S. x chaucha*	*00134*	118.0^{J}	72.5^{KLM}	190.5^{K}
31	*S. yungasense*	*00070*	$9,420.0^{A}$	$5,450.0^{A}$	$14,870.0^{A}$
	Mean		*1,913.61*	*1,034.78*	*2,948.39*
	F		*4,474.80***	*5,763.39***	*5,667.58***
	$LSD_{0.05}$		*113.53*	*56.33*	*156.85*
	$LSD_{0.01}$		*149.19*	*74.03*	*206.15*

*Means that do not share a letter are significantly different according to Tukey's test ($P \leq 0.01$).

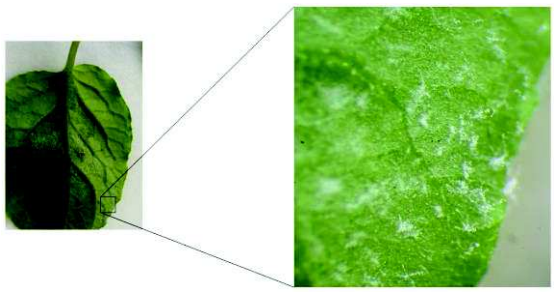
Regarding to the *P. infestans* resistance, in field susceptibility was not recorded; however, under laboratory test *S. bulbocastanum 00240* and *S. bulbocastanum PIS 06-17* were fully resistant upon inoculation of aggressive isolates. Strong resistance observed also in *S. stoloniferum 00295*, *S. sucrense 0062* and *S. yungasense 0070.* The isolates were fully virulent to most of tested species/genotypes and presented in Table 3, Fig. 2).

Table 3. *Solanum* genotypes evaluation of resistance to *Phytophthora infestans*

Order	Species	EVIGEZ Code	Isolates					
			1/3	2/1	4/1	2/2	4/2	5/3
1	*Solanum acaule*	*00030*	+	+	+	+	+	+
2	*S. andigenum*	*00108*	+	+	+	+	+	+
3	*S. berthaultii*	*00260*	+	+	+	+	+	+
4	*S. bulbocastanum*	*00240*	-	-	-	-	-	-
5	*S. bulbocastanum*	*PIS 06-17*	-	-	-	-	-	-
6	*S. chacoense*	*00037*	+	+	+	+	+	+
7	*S. chacoense*	*00230*	+	+	+	+	+	+
8	*S. demissum*	*00250*	+	+	+	+	+	+
9	*S. fendleri*	*00275*	+	+	+	+	+	+
10	*S. goniocalyx*	*00109*	+	+	+	+	+	+
11	*S. gourlai*	*00045*	+	+	+	+	+	+
12	*S. gourlai*	*00043*	+	+	+	+	+	+
13	*S. guerreroense*	*00280*	+	+	+	+	+	+
14	*S. incamayoense*	*00047*	+	+	+	+	+	+
15	*S. leptophyes*	*00048*	+	+	+	+	+	+
16	*S. microdontum*	*00049*	+	+	+	+	+	+
17	*S. mochiquense.*	*00050*	+	+	+	+	+	+
18	*S. phureja.*	*00308*	+	+	+	+	+	+
19	*S. pinnatisectum*	*00051*	+	+	+	+	+	+
20	*S. polyadenium*	*00290*	+	+	+	+	+	+
21	*S. polytrichon.*	*00053*	+	+	+	+	+	+
22	*S. sparsipillum*	*00071*	+	+	+	+	+	+
23	*S. spegazzini*	*00060*	+	+	+	+	+	+
24	*S. stenotomum.*	*00212*	+	+	+	+	+	+
25	*S. stoloniferum*	*00295*	-	+	-	-	-	-
26	*S. sucrense*	*00062*	-	-	+	-	-	-
27	*S. vernei*	*00069*	+	+	+	+	+	+
28	*S. vernei*	*00234*	+	+	+	+	+	+
29	*S. verrucosum.*	*00299*	+	+	+	+	+	+
30	*S. x chacha.*	*00134*	+	+	+	+	+	+
31	*S. yungasense*	*00070*	-	-	+	-	+	-

+ = virulent; - = resistant.

It is interesting to note that diploid genotypes *S. bulbocastanum PIS 06-1* and *S. bulbocastanum* 00240 had low content of foliage SGA but were fully resistant to the late blight, whereas *S. yungasense 0070* showed strong resistance and had very high level of foliage SGA. So, there was a very week correlation (r = 0.076) of foliage SGA contents and resistance to the *P. infestants* (Fig. 3) and less correlation was obtained regarding to the ploidy level and resistance (r = 0.014).



© Zeka, D.

Figure 2. *Phytophthora infestans;* isolate 1/3 in *S. mochiquense 00050.*

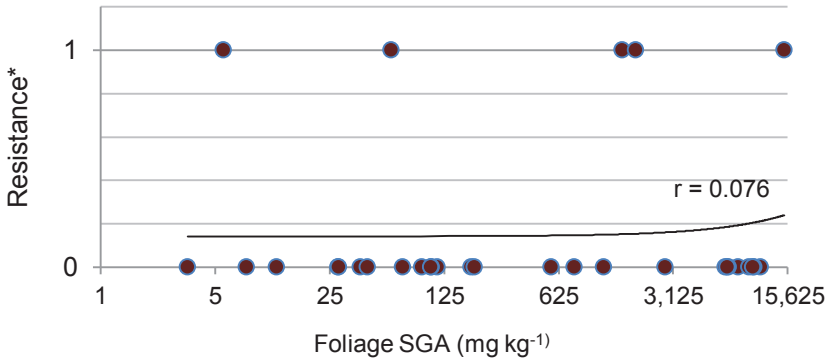


Figure 3. Correlation of foliage (f) SGA of dry weight contents and resistance to the *P. infestans* (**0 – virulent; 1 – resistant*).

CONCLUSIONS

The species under study, preserved *in vitro*, confirmed the anticipated ploidy level. Whereas average amount of foliage SGA was very variable, depending on the species background. However, was no resistance obtained against CPB regardless of EBN, ploidy level or SGA content. Whereas, only two diploid and two tetraploid tested species found resistant against late blight. Based on the results obtained in this study *S. bulbocastanum PIS 06-17, S. bulbocastanum 00240, S. stoloniferum 00295*, *S. sucrense 0062* and *S. yungasense 0070* could be considered for plant breeding of potato, introducing resistance against *P. infestants*. Mechanisms against CPB and late blight are not correlated to the ploidy level neither of SGA content and it's seems to be undetermined.

REFERENCES

Bukasov, S.M. 1939. The origin of potato species. Physis (Buenos Aires) 18: 41–46. In: Huamám, Z., Spooner, D.M. 2002. Reclassification of landrace populations of cultivated potatoes (*Solanum* Sect. *Petota*). *American Journal of Botany* **89**, 947–965.

Carputo, D., Alioto, D., Aversano, R., Garramone, R., Miraglia, V., Villano, C. & Frusciante, L. 2013. Genetic diversity among potato species as revealed by phenotypic resistances and SSR markers. *Plant Genetic Resources* **11**, 131–139.

Carputo, D. & Barone, A. 2005. Ploidy level manipulations in potato through sexual hybridisation. *Annals of Applied Biology* **146**, 71–79.

Crabbe, P. & Fryer, C. 1980. Rapid quantitative analysis of solasodine, solasodine glycosides and solasodiene by high-pressure liquid chromatography. *Journal of Chromatography A* **187**, 87–100.

Dimock, M.B. & Tingey, W.M. 1988. Host acceptance behaviour of Colorado potato beetle larvae influenced by potato glandular trichomes. *Physiological Entomology* **13**, 399–406.

Flanders, K.L., Arnone, S. & Radcliffe, E.B. 1998. The potato: genetic resources and insect resistance, pp. 207 – 239. In: Jansky, S. H., Simon, R., Spooner, D.M. 2009. A test of taxonomic predictivity: Resistance to the Colorado potato beetle in wild relatives of cultivated potato. *Journal of Economic Entomology* **102**, 422–431.

Friedman, M. & McDona, G. 1997. Potato glycoalkaloids: chemistry, analysis, safety and plant physiology. *Critical Reviews in Plant Sciences* **16**, 55–132.

Gebhardt, C. & Valkonen, J. P. T. 2001. Organization of genes controlling disease resistance in the potato genome. *Annual Review of Phytopathology* **39**, 79–102.
Gibson, R.W. 1976. Glandular hairs of *Solanum polyadenium* lessen damage by the Colorado potato beetle. *Annals of Applied Biology* **82**, 147–150.
Goodwin, S.B., Cohen, B.A. & Fry, W.E. 1994. Panglobal distribution of a single clonal lineage of the Irish potato famine fungus. *Proceedings of the National Academy of Sciences of the USA* **91**, 11591–11595.
Hijmans, R.J., Gavrilenko, T., Stephenson, S., Bamberg, J., Salas, A. & Spooner, D.M. 2007. Geographical and environmental range expansion through polyploidy in wild potatoes (*Solanum* section *Petota*). *Global Ecology and Biogeography* **16**, 485–495.
Hodgson, W.A. 1961. Laboratory testing of the potato for partial resistance to *Phytophthora infestans*. *American Potato Journal* **38**, 259–264.
Huamám, Z. & Spooner, D.M. 2002. Reclassification of landrace populations of cultivated potatoes (*Solanum* Sect. *Petota*). *American Journal of Botany* **89**, 947–965.
Jansky, S.H., Simon, R. & Spooner, D.M. 2009. A Test of Taxonomic Predictivity: Resistance to the Colorado Potato Beetle in Wild Relatives of Cultivated Potato. *Journal of Economic Entomology* **102**. 422–431.
Kamoun, S. 2003. Molecular genetics of pathogenic oomycetes. *Eukaryotic Cell* **2**, 191–199.
Klarfeld, S., Rubin, A.E. & Cohen, Y. 2009. Pathogenic Fitness of Oosporic Progeny Isolates of *Phytophthora infestans* on Late-Blight-Resistant Tomato Lines. *Plant Disease* **93**, 947–953.
Pavek, J.J. & Corsini, D.L. 2001. Utilization of Potato Genetic Resources in Variety Development. *American Journal of Potato Research* **78**, 433–441.
Runno-Paurson, E., Kiiker, R., Aav, A., Hansen, M. & Williams, I.H. 2016. Distribution of mating types, metalaxyl sensitivity and virulence races of *Phytophthora infestans* in Estonia. *Agronomy Research* **14**, 220–227.
Salaman, R.N. 1926. Potato varieties. In: Hijmans, R.J., Gavrilenko, T., Stephenson, S., Bamberg, J., Salas, A., Spooner, D.M. 2007. Geographical and environmental range expansion through polyploidy in wild potatoes (*Solanum* section *Petota*). *Global Ecology and Biogeography* **16**, 485–495.
Sinden, S.L., Sanford, L.L., Cantelo, W.W. & Deahl, K.L. 1986. Leptine glycoalkaloids and resistance to the Colorado potato beetle (Coleoptera: Chrysomelidae) in *Solanum chacoense*. *Environmental Entomology* **15**, 1057–1062.
Skrabule, I., Grauda, D., Mikelsone, A. & Vasariete, A. 2010. Adaptation of glycoalkaloids detection method for evaluation of Latvian potato genetic resources. *Agronomy Research* **8**, 705–710.
Spooner, D.M. & Castillo, R.T. 1997. Reexamination of series relationships of South American wild potatoes (*Solanaceae*: *Solanum* sect. *Petota*): evidence from chloroplast DNA restriction site variation. *American Journal of Botany* **84**, 671–685.
Vleeshouwers, V.G.A.A., van Dooijeweert, W., Keizer, L.C.P., Sijpkes, L., Govers F. & Colon, L.T. 1999. A laboratory assay for *Phytophthora infestans* resistance in various *Solanum* species reflects the field situation. *European Journal of Plant Pathology* **105**, 241–250.
Zeka, D., Sedlák, P., Sedlákova, V., Sharma, K. & Vejl, P. 2015. Phenotype and molecular diversity evaluation of some wild 2n *Solanum* species (super series *Rotata*). *Chilean Journal of Agricultural Research* **75**, 147–151.
Zeka, D., Sedlak, P., Sedlakova, V., Vasek, J., Domkarova, J. & Vejl, P. 2014. cpDNA SSR polymorphism in secondary germplasm of potato maintained in Czech gene bank. *Pakistan Journal of Agricultural Sciences* **51**, 745–750.
Zlesak, D.C., Thill, C.A & Anderson, N.O. 2005. Trifluralin-mediated polyploidization of *Rosa chinensis minima* (Sims) Voss seedlings. *Euphytica* **141**, 281–290.