**Tuber flesh colour, enzymatic discolouration, dormancy and late blight resistance of 29 tuber-bearing accessions of *Solanum* spp.**

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**Abstract**

Potato relatives adapted to many different habitats are promising sources of desirable agricultural traits for potato breeding. Wild potato relatives are preserved in different collections around the world, and their detailed description is key to their exploitation in practice. We described 29 seed accessions of 26 *Solanum* species originating from the VIR potato collection (Institute of Plant Industry – VIR, Saint Petersburg, Russia) and preserved in Poland. The description included resistance to *Phytophthora infestans*, tuber flesh colour, enzymatic discolouration and tuber dormancy (sprouting). Up to 13 genotypes were evaluated per accession. The evaluation was repeated in three years for each trait. Two *P. infestans* isolates were used in late blight resistance tests. Among all the tested accessions, five were resistant to both *P. infestans* isolates, including genotype 13\_A2. Twenty-one accessions had white tuber flesh, and 13 accessions showed a lack of or weak enzymatic discolouration. Additionally, we found accessions that were whiter than the standard white-fleshed Polish potato cultivar Irys. In our material, we observed a large variation in the length of the sprouts after storage, indicating differences in the dormancy period length. Four accessions showed a lack of sprouting after 28 weeks of storage at 5 – 6 °C. The tested material is preserved as in vitro plants in the National Centre for Plant Genetic Resources: Polish Genebank (IHAR-PIB, Radzików, Poland), which will facilitate their use in breeding programs.

**Keywords:** germplasm collection, *Phytophthora infestans*, resistance screening, sprouting, *Solanum tuberosum*

**Statements and Declarations**

**Competing Interests:** The authors declare no conflicts of interest.

**Author contribution** M. J. maintained the plant material, prepared inocula of *P. infestans*, collected phenotype data, performed the analyses and wrote the paper; P. S.-D. maintained the plant material and participated in the design of the study; S. S. maintained *P. infestans* cultures and prepared inocula; D. M. introduced and maintained the plant material in in vitro cultures; J. Ś. participated in the design of the study and its coordination and wrote the paper. All authors proofread the manuscript.

**Introduction**

The cultivated potato *Solanum tuberosum* L. is the third most important food crop in the world after rice and wheat in terms of human consumption (Bethke et al. 2017). In 2019, 370 million tons of potatoes were produced in approximately 150 countries over a total area of 17.3 million hectares (FAOSTAT 2021). It belongs to the genus *Solanum*, section *Petota*, which now includes 122 species (Spooner et al. 2014). Wild and cultivated potato relatives originate from America, particularly from Peru, Mexico, Bolivia, Argentina, Venezuela, Colombia and Ecuador. They are adapted to diverse habitats, e.g., cloud forests, deserts, scrub vegetation, mountain pastures, volcanic or loamy soils and many others (Machida-Hirano 2015). Wild potato species differ in their ploidy levels (diploids, triploids, tetraploids, hexaploids) and are very diverse in morphological traits such as plant height, leaf and leaflet shape, flower colour, stolon length and size, colour and shape of tubers (Spooner et al. 2004). This diversity makes potato relatives good sources of resistance against a broad range of pests, diseases, and abiotic stresses, as well as sources of novel alleles affecting tuber quality and agronomic traits (Hawkes 1994). Wild and cultivated potato species have been used by breeders in potato breeding programs for over 150 years (Bethke et al. 2017). They have been widely collected and maintained as botanical seeds, tubers or in vitro plants in genebanks worldwide. The major collections are in South America, North America, Europe and a few countries in Asia. Within the Cornell-Eastern Europe-Mexico (CEEM) Project on Late Blight Control conducted in 1996 – 2000 (Raman et al. 2000), 111 accessions of wild and cultivated potato from the VIR collection (Institute of Plant Industry – VIR, Saint Petersburg, Russia) were preserved at the Plant Breeding and Acclimatization Institute – National Research Institute (IHAR-PIB, Radzików, Poland) in the National Centre for Plant Genetic Resources: Polish Genebank (KCRZG). The VIR potato collection was initiated by Bukasov, Voronov and Juzepczuk in 1925 – 1926 and in 1926 – 1928 by Juzepczuk. They collected and described wild and cultivated potato species discovered in Central and South America (Spooner et al. 2014; Zoteyeva et al. 2012). The goal of this study was to characterize 29 accessions of 26 *Solanum* species originating from the VIR potato collection in terms of traits such as tuber flesh colour, enzymatic discolouration of tuber flesh, tuber dormancy (sprouting) and foliage resistance to *Phytophthora infestans* (Mont.) de Bary.

The first trait that potato breeders searched for among wild potato species was resistance to *P. infestans*. This pathogen causes late blight, one of the most economically important potato diseases worldwide. Most potato cultivars are susceptible to late blight; therefore, this disease is managed by intensive chemical control. Yield losses and the cost of fungicides used to control the disease are valued at six billion USD globally (Haverkort et al. 2008). Resistance breeding is an alternative to chemical protection against late blight. The first dominant resistance genes, *R1* – *R11*, were identified in the Mexican species *S. demissum* (Black et al. 1953; Malcolmson and Black 1966). Some of these genes were introgressed by crossing and backcrossing into potato cultivars, such as Pentland Ace with gene *R1*; Pentland Dell with genes *R1*, *R2*, and *R3* (Malcolmson 1969); Epoka with genes *R3* and *R4* (Rudkiewicz 1985); and Bzura with an *R2-like* gene (Plich et al. 2015). However, new pathogen strains have been able to rapidly overcome the resistance associated with these genes. A strategy to achieve durable and broad-spectrum resistance against late blight is the pyramidingof *R* genes, which were preferably identified in diverse wild potato relatives (Haverkort et al. 2009; Tan et al. 2010). To date, over 60 *R* genes have been identified from at least 25 *Solanum* species. Nearly 30 of them have been cloned, e.g., *Rpi-blb1, Rpi-blb2*, *Rpi-blb3*, and *Rpi-abpt* from *S. bulbocastanum*; *Rpi-sto1* from *S. stoloniferum*; *Rpi-pta1* from *S. papita*; *Rpi-amr3* from *S. americanum*; *Rpi-mcq1* from *S. mochiquense*; *Rpi-vnt1.1* and *Rpi-vnt1.2* from *S. venturii* (Elnahal et al. 2020; Zheng et al. 2020).

Wild relatives of potato are also a source of both valuable and undesired alleles affecting tuber quality. Hence, thorough morphological characterization is required to improve the exploitation of wild germplasm in breeding programs. One of the important traits for consumers is tuber flesh colour, which has a wide range from white to orange and purple. In various countries, people prefer cultivars with different flesh colours; in some cases, it even depends on the region of country (Jemison et al. 2008). Recently, anthocyanins, which are responsible for red and purple flesh colours, have been valued by consumers as health-promoting compounds with anticancer and immunomodulatory activities (Chandrasekara and Kumar 2016). Other health-promoting compounds, carotenoids, are responsible for a yellow to orange potato flesh colour. Yellow flesh colour is caused by the single dominant allele *Y* at the Y locus, which was mapped on chromosome III from potato (Bonierbale et al. 1988). Orange flesh colour is controlled by allele *Or* at the same locus (Brown et al. 1993), and a number of modifying loci affect the trait, resulting in a wide range of yellow shades and intensities (Haynes 2000).

Another factor influencing tuber quality is enzymatic discolouration (i.e., browning) of freshly cut potatoes. Browning is the major limitation on the shelf life of fresh-cut potatoes for food processing (Cantos et al. 2002). Enzymatic discolouration causes changes in the flavour and a loss of nutritional quality in the tubers (Vitti et al. 2011). Dark pigments (melanins) are formed as a result of the process in which phenolic compounds are oxidized by polyphenol oxidases (PPOs) (Friedman 1997). Prevention of enzymatic browning is mainly based on chemical and physical agents, some of which, such as sulfiting agents, pose a risk to human health. Therefore, breeding new potato cultivars that do not exhibit undesirable browning could be a valuable alternative approach to solve this problem (Werij et al. 2007). A low rate of discolouration has been observed in the wild species *S. hjertingii*, which is related to low PPO activity (Brown et al. 1999). Culley et al. (2002) described that *S. hjertingii* has a truncated version of POT32, one of the major isoforms PPO expressed in potato tuber (Thygesen et al. 1995). Hara-Skrzypiec et al. (2018) identified novel regions important for enzymatic discolouration on chromosomes V, VII, and X within the potato genome, and the presence of Quantitative Trait Loci (QTLs) for this trait located on chromosomes I, III, and VIII was confirmed in a previous study by Werij et al. (2007).

The dormancy of potato tubers is a physiological state after harvest and is useful when the conditions are unfavourable for growth in many regions of the world. Through this resting period, storage of potato tubers becomes possible, and depending on the cultivar, conditions (temperature, humidity and atmospheric composition), geographic location and climate, it may be possible for days, weeks or months (Daniels-Lake and Prange 2007). When the resting period is longer, the tuber quality after storage is better. Earlier sprouting of potato tubers leads to significant economic losses as a result of a loss of water, remobilization of starch and proteins and shrinkage of tubers (Sonnewald 2001). A commonly used method to inhibit potato sprouting is storage of tubers at low temperatures of 3 – 7 °C, but this sometimes results in tissue sweetening (Alamar et al. 2017). Chlorpropham (CIPC) has been a commercially used chemical sprout inhibitor for more than four decades (Mohammed et al. 2015; Source et al. 2005). Because of its negative effects on human health and the natural environment, many countries restrict or prohibit the use of CIPC (Shukla et al. 2019). The EU Commission published Implementing Regulation (EU) 2019/989 on 17 June 2019, which did not renew approval for the use of this active substance. Research is being carried out to find alternative substances that limit sprouting (Shukla et al. 2019). Tuber dormancy is a complex, polygenic trait influenced by many factors. QTLs for tuber dormancy were found on potato chromosomes II, III, IV, V, VII, VIII and X (Bisognin et al. 2018; Freyre et al. 1994; Sharma et al. 2021).

Potato cultivation suffers from quantitative and qualitative losses caused by biotic and abiotic stresses. Our study enriches the knowledge about useful traits of wild potato relatives preserved in the KCRZG IHAR-PIB. Well-characterized collections of wild potato species can support changing trends in potato breeding, e.g., minimizing the negative impact on the environment or obtaining potato cultivars with tuber flesh colours attractive to consumers.

**Materials and Methods**

**Plant Materials**

We used 29 seed-preserved accessions of 26 tuber-bearing species stored in the KCRZG IHAR-PIB (Table 1). The selected accessions were from the VIR collection, and the resistance of some of them to *P. infestans*, potato virus X (PVX) and potato virus Y (PVY) was previously described by Zoteyeva et al. (2012). Four accessions (POL003:333119, POL003:333125, POL003:333112, POL003:333071) have not been tested for resistance to *P. infestans* before. To promote germination, seeds were soaked in gibberellic acid (700 ppm) for 24 h at room temperature before sowing. After that, 30 seeds per accession were sown in plastic pots in a greenhouse over two years: 2016 (15 accessions) and 2017 (14 accessions). From one to 30 seedlings per accession were individually transferred into pots. For each accession, one to 13 well-developed plants were grown in a greenhouse until maturity (Table 1). Then, the tubers were collected separately from each plant and stored at 5–6 °C for further evaluation. In the next years, three tubers of each genotype were separately planted in plastic pots. Tubers of the genotypes without sprouts were soaked in thiourea (1%) for 15 minutes to accelerate sprouting (Pietrak 2001).

**Screening for resistance to *P. infestans***

Laboratory detached leaflet/leaf assays (DLAs) were performed in 2017 – 2020 on two different dates and in two replications each year as described by Brylińska and Śliwka (2017). Two Polish isolates of *P. infestans* MP324 and MP1777 (clonal lineage 13\_A2) were used, each isolate in three years (Table 2). Three lateral leaflets (for plants with compound leaves) or one leaf (for plants with simple leaves or with very small, fragile compound leaves from accession numbers POL003:333138, POL003:333155, POL003:333071, POL003:333125) were collected from the middle part of greenhouse-grown, 6-week-old plants from each of the tested genotypes. The leaflets/leaves were placed abaxial side up on wet paper in plastic trays. The inoculum was prepared as described by Sobkowiak and Śliwka (2017). A 30 µl drop of a sporangia suspension with a concentration of 50 sporangia × μl-1 was placed near the midrib on each leaflet. The whole leaves of the four accessions POL003:333138, POL003:333155, POL003:333071, POL003:333125 were sprayed with a sporangia suspension with a concentration of 50 sporangia × μl-1. The inoculated leaflets and leaves were incubated at 16 °C in the dark and under high-humidity conditions (relative air humidity > 80%). The following day, the leaflets and leaves were turned over, adaxial side up, and constant light of approximately 1600 lx was switched on. Scoring was conducted after six days of incubation and was performed on a 1–9 scale, where 9 means no disease symptoms (Brylińska and Śliwka 2017). Each test included standard cultivars Craigs Royal, Bzura, Sárpo Mira, and Biogold; the tetraploid breeding line 04-IX-21 with the *Rpi-phu1* gene; and the diploid breeding lines DG 99-10/36 with the *Rpi-rzc1* gene and DG 99-12/8 with the *Rpi-mch1* gene, which were described by Janiszewska et al. (2021).

**Tuber flesh colour and enzymatic discolouration**

These traits were evaluated 15 weeks after harvest in February 2019, 2020 and March 2021. Tuber flesh colour was determined with two methods. In the first method, flesh colour was scored visually on five tubers per genotype cut in half from the apical to the distal end according to a 1 – 6 scale, where 1 = white, 2 = grey white, 3 = cream, 4 = light yellow, 5 = yellow, 6 = deep yellow. In the second method, the flesh colour was estimated using a Minolta CR-400 colorimeter (Osaka, Japan), and the yellowness index (YI) was calculated for five tubers per genotype according to the formula:

*YIE313*

where C*x* and C*z* are illuminant- and observer-specific constants *X*, *Y*, and *Z* are trichromatic values (ASTM 2005; Hunter and Harold 1987).

Enzymatic discolouration was assessed according to the method described by Hara-Skrzypiec (2017). Five tubers of each genotype were cut in half from the apical to the distal end, and after 4 h, the degree of discolouration was scored according to the colour chart (Dansk Gærings-Industri, Ltd., Copenhagen, Denmark) on a 1–9 scale, where 9 means a lack of discolouration.

Polish potato cultivars Irys with white flesh colour (1), Harpun with cream flesh colour (3) and Bartek with light yellow flesh colour (4) were used as standards in the assessment of tuber flesh colour and enzymatic discolouration.

**Tuber dormancy (sprouting)**

Sprouting was evaluated 28 weeks after harvest at the end of May 2018, 2019 and 2020. Two weeks before measuring sprouts, the tubers were moved from 5–6 °C to room temperature. One apical potato sprout was measured from 15 tubers of each genotype using electronic callipers CD-15DAX (Mitutoyo Poland Sp. z o.o., Wrocław, Polska).

**Data analyses**

STATISTICA for Windows (StatSoft Polska, Kraków, Poland) was used to perform all the statistical analyses. The effects of interactions on the DLAs, flesh colour, enzymatic discolouration and length of sprouts were estimated by Analysis of variance (ANOVA). In the DLAs, the years of testing for the two pathogen isolates were different (Table 2). Therefore, for the DLAs in ANOVA, we changed from a sigma-restricted model to a type IV sum-of-squares model. Duncan’s multiple range test was used to assess the significance of differences in the DLAs between the standard cultivars. The correlations between the results of resistance to two *P. infestans* isolates, MP324 and MP1777, and between the results of the two methods of flesh colour assessment were determined through calculation of Pearson’s correlation coefficients. The 3-year mean results of the assessment of 276 individual genotypes of 29 accessions are provided in a Supplementary Table. Other information on these accessions, e.g., plant, tuber descriptors and photographs, is available through the G2P-SOL website (<http://www.g2p-sol.eu>).

**Results**

**Resistance to *P. infestans***

The 29 accessions of 26 *Solanum* species were tested for their resistance against two *P. infestans* isolates, MP1777 (clonal lineage 13\_A2) and MP324, as described in Table 2. The tests with each isolate were repeated in three different years. *Phytophthora infestans* isolate MP1777 was virulent towards Black’s differential plants with the *R5* and *R10* genes (Table 2) and more aggressive than isolate MP324, which is illustrated by the reaction of standard cultivars and breeding lines (Fig. 1). The 3-year mean resistance scores of standards were lower for isolate MP1777 than for isolate MP324 and amounted to 2.9–8.8 and 4.1–9.0, respectively. A significant difference in *P. infestans* resistance scores for both isolates was observed for the Biogold cultivar, with mean values of 5.0 (MP1777) and 7.3 (MP324). The 3-year mean resistance scores in the DLAs obtained with both isolates were strongly correlated (Pearson’s correlation coefficient of 0.932 at *p* < 0.001). ANOVA with the 29 accessions of 26 *Solanum* species demonstrated significant effects of accession, year, isolate and all their interactions (accession × year, accession × isolate, year × isolate, accession × year × isolate) on resistance to *P. infestans* (Table 3). Accession had the largest influence on resistance to *P. infestans*.

For 22 accessions, the results obtained with the two *P. infestans* isolates did not differ from each other. Plants of all tested genotypes from five accessions were resistant to *P. infestans* isolates MP324 and MP1777, with 3-year mean resistance scores from 9 to 6 on a 1–9 scale (Fig. 2; Table 4). Segregation of the resistance to both isolates was noted among plants from eight accessions. For nine accessions, 3-year mean scores indicated that all plants were susceptible to *P. infestans* isolates. Differences in the reaction to *P. infestans* isolates MP324 and MP1777 were noted in seven accessions. All plants of accession POL003:333159 of the species *S. papita* were resistant to isolate MP324 but were segregated in terms of their resistance to isolate MP1777. Plants of accession POL003:333108 of species *S. polytrichon* were resistant to isolate MP324 but susceptible to isolate MP1777. In four accessions, the plants of different genotypes were segregated in terms of resistance to isolate MP324, but against isolate MP1777, all were susceptible. In accession PL003:333124 of the species *S. sparsipilum*, all plants were susceptible to *P. infestans* isolate MP324 but were segregated in terms of their resistance against isolate MP1777 (Fig. 2A, B; Table 4).

**Tuber flesh colour and enzymatic discolouration**

Flesh colour was not assessed by a visual method for one accession POL003:333071 of species *S. uyunense* due to the low number of tubers. Colorimeter measurements were not possible due to the small size of the tubers for four accessions (*S. antipovichii* POL003:333099, *S. punae* POL003:333138, *S. uyunense* POL003:333071, *S. acaule* POL003:333155). ANOVA revealed the main effect of accession on flesh colour determined by a visual method and the main effect of accession and year on this trait assessed by a colorimeter (YI) (Table 3). The results obtained by both methods were highly correlated (the Pearson’s correlation coefficient between the 3-year mean results was 0.855 at *p* < 0.001). Twenty-one accessions had white (1) to cream (3) flesh colour determined by the visual method (Fig. 3A). Among seven accessions, segregation from white (1) to yellow (5) flesh colour was observed. No anthocyanin-derived colours were observed in the tested accessions.

The yellowness index of the assessed wild potato species was characteristic of white-fleshed potato for 20 accessions, and the maximum value of the 3-year mean was 48.5 (Fig. 3B). Segregation of the 3-year mean yellowness index from white-fleshed to yellow-fleshed potato was observed among five accessions. The standard cultivars had the following 3-year mean yellowness index scores: Irys, 40.5; Harpun, 48.5; and Bartek, 58.4. Ten accessions had a lower value of the 3-year mean yellowness index than the white flesh cultivar Irys.

Consistent results from both methods of tuber flesh colour assessment were observed for 23 accessions, while there were differences between the two accessions. The flesh colour of accessions POL003:333121 of species *S. kurtzianum* and POL003:333149 of species *S. microdontum* determined by visual method segregated between white and light-yellow flesh, but the yellowness index indicated that they all had white flesh (Fig. 3).

Mean enzymatic discolouration of the tested potato accessions evaluated in 2019–2021 is shown in Fig. 3. ANOVA demonstrated significant effects of accession, year and the accession × year interaction on enzymatic discolouration (Table 3). Thirteen accessions showed a lack of or weak enzymatic discolouration, with 3-year mean values of 7–9 on a 1–9 scale. Segregation of mean enzymatic discolouration scores from 9 to 4 was observed for 15 accessions. Accession POL003:333069 of the species *S. parodii* developed the strongest enzymatic discolouration, with a 3-year minimum of 5.5 (Fig. 4). Standard cultivars Irys, Harpun and Bartek showed weak enzymatic discolouration, with a 3-year mean of 8.

**Tuber dormancy (sprouting)**

ANOVA showed significant effects of accession, year and the accession × year interaction on sprouting (Table 3). Four accessions (*S. papita* POL003:333147, *S. fendleri* POL003:333110, POL003:333112, *S. aemulans* POL003:333119) showed a lack of sprouting after 28 weeks of storage (Fig. 5). Sprouts up to 10 mm (3-year mean) were observed for eight accessions. The mean length of sprouts was segregated for the remaining 17 accessions. The longest sprouts (98.3 mm on average) were described for plants of the accession POL003:333141 of species *S. simplicifolium*.

**Discussion**

Among the most important crops in the world, potato has the highest number of wild relatives (Vincent et al. 2013). Screening of collections of wild and cultivated potato species, which are preserved in different gene banks, is a time-consuming and laborious process. The potato genetic resources preserved as seeds are often disordered and unexplored, with variation among individuals within and across accessions and with some species overrepresented and others not adequately represented. Storage of accessions as seeds makes it difficult for breeders to utilize these reservoirs of valuable alleles. To date, characteristics of germplasm collections have been based on populations rather than individuals, without linking individual genotypes to phenotype and genotype data (Bethke et al. 2017). Pérez et al. (2001) tested the late blight resistance of 139 population samples of 51 *Solanum* species, which were preserved as seeds in the International Potato Center (CIP, Lima, Peru). They found all susceptible plants for 22 accessions, all resistant plants for 7 accessions and segregation of resistance for 110 accessions. One hundred ninety-eight accessions of 63 different *Solanum* species from The Commonwealth Potato Collection (CPC, Invergowrie, Great Britain) were mostly preserved as seeds, and few as tubers were examined for resistance to *Globodera pallida* and *G. rostochiensis* by Castelli et al. (2003). They identified 56% and 53% clones resistant to *G. pallida* and *G. rostochiensis*, respectively, among all tested accessions. Khiutti et al. (2015) tested up to three accessions each for 34 wild species preserved as botanical seeds and available from the United States Potato Gene Bank in Sturgeon Bay, Wisconsin, for tuber and foliar resistance to *P. infestans*. They described population samples in terms of taxonomy, ploidy, crossing group, breeding system, and geography, and their results indicated that some of the identified species with foliar and tuber resistance can be easily crossed with cultivars. Bachmann-Pfabe et al. (2019) tested 656 wild potato accessions of 66 *Solanum* species to tuber resistance against *P. infestans* and 749 accessions of 71 *Solanum* species of resistance to *G. pallida*, which were part of the maintained-via-seed wild potato collection of the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK). They anticipated maintenance of genotypes resistant to *P. infestans* and *G. pallida* as in vitro plants. Karki et al. (2021) screened 384 true potato seed accessions of 72 different wild potato species maintained in U.S. Potato GenBank in Sturgeon Bay for resistance to two *P. infestans* isolates (US-23 and NL13316). They discovered 12 species that had never been described as resistant to *P. infestans* and can be used as novel sources of resistance to this pathogen.

Zoteyeva et al. (2012) screened 154 accessions of tuber-bearing *Solanum* species from the VIR collection for resistance in tuber and leaflet tests to *P. infestans* and to the viruses PVX and PVY. They evaluated the resistance of accessions to two *P. infestans* isolates, MP322 in 1998 and MP324 in 1999 and 2000. The results of this work have been exploited to only a limited extent, as two major resistance genes against *P. infestans* have been identified and mapped in this material: *Rpi-rzc1* from *S. ruiz-ceballosii* (Śliwka et al. 2012a) and *Rpi-mch1* from *S. michoacanum* (Śliwka et al. 2012b). The *Rpi-rzc1* gene has been transferred to the tetraploid level of cultivated potato and pyramided on diploid and tetraploid levels with the *Rpi-phu1* gene from *S. phureja* (Stefańczyk et al. 2020). Smyda-Dajmund et al. (2017) introgressed the *Rpi-mch1* gene into the cultivated potato gene pool. One of the reasons for the limited use of material from the work of Zoteyeva et al. (2012) was the loss of clonally propagated and characterized wild potato genotypes. The individual genotypes from our work were preserved as in vitro plants and are available in KCRZG IHAR-PIB, which should have a positive effect on the use of these resources. Smyda-Dajmund et al. (2020) also evaluated the cytoplasm types for all the genotypes of accessions from our work, which will allow more effective exploitation in breeding programs. From the accessions that were tested earlier by Zoteyeva et al. (2012), 25 were screened in this study. In our research, three new species, *S. aemulans* (POL003:333119), *S. uyunense* (POL003:333071) and *S. albicans* (POL003:333125), were added, as well as one new accession of *S. fendleri* (POL003:333112). We tested the accessions with a new *P. infestans* isolate that belongs to the aggressive, resistant to metalaxyl genotype 13\_A2 (MP1777), which rapidly spread throughout Europe between 2005 and 2008 (Cooke et al. 2012). Currently, this genotype is considered as dominant in *P. infestans* populations in countries outside Europe, such as Algeria, India, Turkey, and Pakistan (Dey et al. 2018; Göre et al. 2021; Raza et al. 2021; Rekad et al. 2017). In Poland, we also detected the presence of the 13\_A2 genotype in our research on the *P. infestans* population (Janiszewska et al. 2021). Emerging new strains of the pathogen, for example, by sexual recombination, can change frequently and easily be transported along with wind-borne spores and seed tubers between individual countries. Therefore, it is important to search for new sources of resistance against *P. infestans*. In this study, we identified five accessions (*S. guerreroense* POL003:333096, *S. neoantipovichii* POL003:333117, *S. papita* POL003:333147, *S. microdontum* POL003:333149, and *S. antipovichii* POL003:333099) that were highly or moderately resistant to both *P. infestans* isolates. Our results on resistance to *P. infestans* isolate MP324 for 17 accessions were consistent with those reported earlier by Zoteyeva et al. (2012). Two accessions (POL003:333096 of species *S. guerreroense* and POL003:333069 of species *S. parodii*) were not tested with isolate MP324 by these authors. Moreover, four accessions (*S. papita* POL003:333159 and POL003:333147, *S. microdontum* POL003:333149, *S. polytrichon* POL003:333108) were resistant in our research, but in Zoteyeva et al. (2012), segregation of resistance was observed. In addition, among two accessions (*S. hougasii* POL003:333148, *S. famatinae* POL003:333139) resistance segregated in this work, but both were susceptible in the previous study. The observed differences between our results and those of Zoteyeva et al. (2012) are due to the loss of virulence of the MP324 isolate towards Black’s differential plants with the *R5*, *R8* and *R10* genes.

Our results indicated the presence of new alleles related to a white flesh colour among 29 tested accessions of 26 *Solanum* species because both a visual method of flesh colour assessment and using a colorimeter revealed genotypes that were whiter than the standard cultivar Irys, described in the cultivar catalogue as having a white flesh colour. Among the tested accessions, we identified those that had a white flesh colour and no undesirable browning, which can be desirable traits for breeders (*S. stoloniferum* POL003:333100, *S. guerreroense* POL003:333096, *S. papita* POL003:333147). We also observed large variation in sprouting among the accessions and even within genotypes in the same accession. We noticed accessions lacking sprouts after 28 weeks of storage (*S. papita* POL003:333147, *S. fendleri* POL003:333110, POL003:333112, *S. aemulans* POL003:333119), which can contribute to the identification of new alleles and be used to obtain potato cultivars suitable for long-term storage. Bamberg (2010) even described the occurrence of an eight-year tuber dormancy period in *S. jamesii*. This study provides information on approximately 29 accessions of 26 *Solanum* species originating from the VIR potato collection and preserved in KCRZG IHAR-PIB. Some of these accessions could be an important source of traits related to resistance to *P. infestans*, reduced or no enzymatic discolouration in tubers, a white flesh colour and a long tuber dormancy period.

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**Figures**

**Fig. 1** The results of 3-year mean scores of resistance to *P. infestans* of standards in the DLAs on a 1–9 scale, where 9 is the most resistant. Bars labelled with the same letters (a, b) do not differ significantly according to Duncan’s multiple range test.

**Fig. 2** Box plot of the three-year mean scores of resistance to *P. infestans* in 29 accessions of tuber-bearing *Solanum* spp. A) Mean results of tests with *P. infestans* isolate MP324 obtained in 2018 – 2020. B) Mean results of tests with *P. infestans* isolate M1777 obtained in 2017 – 2019. The mean values of the resistance against *P. infestans* are shown as squares, the box represents standard error, the whiskers indicate minimum and maximum values, circles are outliers and extreme values are marked with an asterisk. Accession number according to KCRZG IHAR-PIB (POL003), followed by a species acronym.

**Fig. 3** Tuber flesh colour of the assessed *Solanum* spp. A) Box plot of the three-year mean results of flesh colour assessed by a visual method in 28 accessions of tuber-bearing *Solanum* spp. on a 1 – 6 scale, where 1 = white, 2 = grey white, 3 = cream, 4 = light yellow, 5 = yellow, 6 = deep yellow. B) Box plot of the yellowness index measured by the Minolta CR-400 colorimeter to estimate the flesh colour of 25 accessions of wild and cultivated potato. The mean values are shown as squares, the box represents standard error, and the whiskers indicate minimum and maximum values, circles are outliers and extreme values are marked with an asterisk. Accession number according to KCRZG IHAR-PIB (POL003), followed by a species acronym.

**Fig. 4** Box plot of mean (2019, 2020, and 2021) enzymatic discolouration in 28 accessions of *Solanum* species assessed according to the colour chart (Dansk Gærings-Industri, Ltd., Copenhagen, Denmark) on a 1 – 9 scale, where 9 means a lack of discolouration. The mean values are shown as squares, the box represents standard error, and the whiskers indicate minimum and maximum values, circles are outliers and extreme values are marked with an asterisk. Accession number according to KCRZG IHAR-PIB (POL003), followed by a species acronym.

**Fig. 5** Box plot of the mean (2018, 2019, 2020) sprout length (mm) in 29 accessions of tuber-bearing *Solanum* spp. measured by electronic callipers. The mean values are shown as squares, the box represents standard error, and the whiskers indicate minimum and maximum values, circles are outliers and extreme values are marked with an asterisk. Accession number according to KCRZG IHAR-PIB (POL003), followed by a species acronym.

**Tables**

**Table 1** The 29 evaluated accessions of *Solanum* species originating from the VIR collection and preserved at the Plant Breeding and Acclimatization Institute—National Research Institute collection

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Species (classification according to Hawkes 1990) | Species three letter code | Accession number VIR RUS001 | Accession number POL POL003 | Number of genotypes | Ploidy | EBN | Place of origin |
| *S. acaule* | acl | 9795 | 333155 | 10 | 4x | 2 | Bolivia |
| *S. aemulans* | aem | 9146 | 333119 | 11 | 3x | 2 | - |
| *S. albicans* | alb | 9814 | 333125 | 10 | 6x | 4 | Bolivia |
| *S. antipovichii* | ant | 2354 | 333099 | 10 | 4x | 2 | Mexico |
| *S. arrac-papa* | arp | 9742 | 333150 | 10 | -a | - | - |
| *S. berthaultii* | ber | 23047 | 333129 | 10 | 2x | 2 | Bolivia |
| *S. dolichostigma* | dls | 7610 | 333114 | 10 | 2x | 2 | Argentina |
| *S. famatinae* | fmt | 4304 | 333139 | 10 | 2x | 2 | Argentina |
| *S. fendleri* | fen | 5671 | 333110 333112 | 10 | 4x | 2 | Mexico |
| 5751 | 11 |
| *S. gibberulosum* | gbb | 2937 | 333103 | 10 | 2x | 2 | Argentina |
| *S. guerreroense* | grr | 18407 | 333096 | 10 | 6x | 4 | Mexico |
| *S. hougasii* | hou | 8818 | 333148 | 10 | 6x | 4 | Mexico |
| *S. kurtzianum* | ktz | 9719 | 333121 333130 | 12 | 2x | 2 | - |
| 2301 | 1 |
| *S. leptophyes* | lph | 5764 | 333113 | 10 | 2x | 2 | Bolivia |
| *S. microdontum* | mcd | 9726 | 333149 | 13 | 2x | 2 | Bolivia |
| *S. neoantipovichii* | nnt | 8505 | 333117 | 10 | 4x | - | Mexico |
| *S. papita* | pta | 8816 | 333147 333159 | 10 | 4x | 2 | Mexico |
| 16888 | 11 |
| *S. parodii* | par | 3701 | 333069 | 10 | 2x | 2 | Argentina |
| *S. polytrichon* | plt | 5347 | 333108 | 10 | 4x | 2 | Mexico |
| *S. punae* | pne | 4263 | 333138 | 10 | 4x | 2 | Peru |
| *S. ruiz-ceballosii* | rzc | 7370 | 333074 | 10 | 2x | 2 | Bolivia |
| *S. simplicifolium* | sim | 5400 | 333141 | 12 | 2x | - | Argentina |
| *S. sparsipilum* | spl | 9808 | 333124 | 10 | 2x | 2 | Bolivia |
| *S. stoloniferum* | sto | 2492 | 333100 | 10 | 4x | 2 | Mexico |
| *S. uyunense* | -b | 4114 | 333071 | 10 | 4x | - | Bolivia |
| *S. verrucosum* | ver | 10556 | 333157 | 11 | 2x | 2 | Mexico |
| a no data, bcode not available (Huamán and Ross 1985) | | | | | | | |

**Table 2** *Phytophthora infestans* isolates used in detached leaflet assays for screening resistance in 29 accessions of 26 *Solanum* species

|  |  |  |
| --- | --- | --- |
| Characteristic | *P. infestans* isolate | |
| MP324 | MP1777 |
| Virulence on Black’s differentials | (1).2.3.4.6.7.(11)a | 1.(2).3.4.(5).(6).7.(10).(11)a |
| SSR genotype | Unique | 13\_A2 |
| Mating type | A1 | A2 |
| Metalaxyl resistance | resistant | resistant |
| Mitochondrial haplotype | IIa | Ia |
| Isolation year | 1997 | 2014 |
| Year of detached leaflet assay | 2018, 2019, 2020 | 2017, 2018, 2019 |
| a Numbers indicate virulence against Black’s differentials (R1 – R11) (Black et al. 1953); numbers in brackets mean that virulence varied between tests | | |

**Table 3** ANOVA for the resistance to *P. infestans*, tuber flesh colour, enzymatic discolouration and tuber dormancy (sprouting) in 29 accessions of 26 *Solanum* species

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Factor/interaction | Degrees of freedom | Sum of squares | F | P |
| Resistance to *P. infestans* |  |  |  |  |
| Accession | 28.0 | 18409.1 | 273.2 | 0.0000 |
| Year | 3.0 | 956.6 | 132.5 | 0.0000 |
| Isolate | 1.0 | 66.8 | 27.8 | 0.0000 |
| Accession × Year | 84.0 | 1962.0 | 9.7 | 0.0000 |
| Accession × Isolate | 28.0 | 433.6 | 6.4 | 0.0000 |
| Year × Isolate | 1.0 | 209.6 | 87.1 | 0.0000 |
| Accession × Year × Isolate | 28.0 | 238.0 | 3.5 | 0.0000 |
| Flesh colour |  |  |  |  |
| Accession | 24.0 | 290.9 | 24.6 | 0.0000 |
| Year | 2.0 | 0.7 | 0.7 | 0.5154 |
| Accession × Year | 48.0 | 7.5 | 0.3 | 0.9999 |
| Flesh colour YI |  |  |  |  |
| Accession | 24.0 | 13267.1 | 31.6 | 0.0000 |
| Year | 2.0 | 1369.0 | 39.1 | 0.0000 |
| Accession × Year | 48.0 | 808.6 | 1.0 | 0.5468 |
| Enzymatic discolouration |  |  |  |  |
| Accession | 24.0 | 256.8 | 12.2 | 0.0000 |
| Year | 2.0 | 53.6 | 30.5 | 0.0000 |
| Accession × Year | 48.0 | 112.3 | 2.7 | 0.0000 |
| Sprouts length |  |  |  |  |
| Accession | 28.0 | 76489.8 | 26.5 | 0.0000 |
| Year | 2.0 | 729.9 | 3.5 | 0.0293 |
| Accession × Year | 56.0 | 13128.0 | 2.3 | 0.0001 |

Table 4 Results of DLAs for resistance against two *P. infestans* isolates in the 29 accessions of 26 *Solanum* species summarized in three categories: susceptible (all individuals with mean score 1-5), segregating (containing both resistant and susceptible individuals), resistant (all individuals with mean score 6-9)

|  |  |  |  |
| --- | --- | --- | --- |
| Accession number  POL003 | Species three  letter code | Resistance to *P. infestans* | |
| MP324 | MP1777 |
| 333155 | acl | susceptible | susceptible |
| 333119 | aem | segregating | susceptible |
| 333125 | alb | segregating | segregating |
| 333099 | ant | resistant | resistant |
| 333150 | arp | susceptible | susceptible |
| 333129 | ber | segregating | segregating |
| 333114 | dls | segregating | susceptible |
| 333139 | fmt | segregating | susceptible |
| 333110 | fen | susceptible | susceptible |
| 333112 | susceptible | susceptible |
| 333103 | gbb | susceptible | susceptible |
| 333096 | grr | resistant | resistant |
| 333148 | hou | segregating | segregating |
| 333121 | ktz | susceptible | susceptible |
| 333130 | susceptible | susceptible |
| 333113 | lph | susceptible | susceptible |
| 333149 | mcd | resistant | resistant |
| 333117 | nnt | resistant | resistant |
| 333147 | pta | resistant | resistant |
| 333159 | resistant | segregating |
| 333069 | par | segregating | susceptible |
| 333108 | plt | resistant | susceptible |
| 333138 | pne | segregating | segregating |
| 333074 | rzc | segregating | segregating |
| 333141 | sim | segregating | segregating |
| 333124 | spl | susceptible | segregating |
| 333100 | sto | segregating | segregating |
| 333071 | *S. uyunense* | susceptible | susceptible |
| 333157 | ver | segregating | segregating |