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NEW SOURCES OF POTATO RESISTANCE TO *PHYTOPHTHORA INFESTANS* AT THE DIPLOID LEVEL

ABSTRACT

New sources of *Phytophthora infestans* (late blight) resistance are studied in two groups of diploids: complex *Solanum* hybrids and clones of pure wild *Solanum* species. In more advanced studies complex hybrids of *Solanum verrucosum, S. phureja* and *S. microdontum* were involved, which were intercrossed in various combinations. In this group, clones with resistance both in leaflets and tubers have been selected. In addition, highly resistant to late blight hybrids are outstanding in chosen quality traits. Resistance to *P. infestans* identified in the advanced hybrids has been successfully transferred into *4x* level with various extent.

The second group of sources recently included in research covers about 110 clones of five wild *Solanum* species (*S. berthaultii, S. kurtzianum, S. michoacanum, S. ruiz–ceballozii* and *S. pinnatisectum)*. In 1999–2003 preselection of leaflets and tuber resistant clones was performed. Selected clones have been simultaneously characterized for male fertility and big pollen grains (*2n*) formation.

Key words: diploids, leaflets, resistance, *Phytophthora infestans, Solanum* spp., tubers

INTRODUCTION

Resistance to late blight is one of the main objectives in majority of potato breeding programs. Lately, more attention has been paid to tuber resistance (Świeżyński and Zimnoch–Guzowska 2001). It was found that resistance of foliage does not protect tubers from infection. More research on tuber resistance to *P. infestans* is desired (Flier *et al.* 2001). Correlation between these two types of resistance is not high and depends on tested material (Świeżyński *et al.* 1997a).

As it is known, there are two ways, complementing each other, of controlling resistance to late blight:

(i) improvement of resistance in grown cultivars by breeding, and
(ii) application of chemical protection.

An intensive search for new sources of resistance to late blight, beyond cultivated selections, has been conducted by many breeders (Colon and

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Budding 1988, Wastie 1991, Louwes *et al.* 1992, Rivera–Pena 1992, Cañizares and Forbes 1995, Colon *et al.* 1995, Ruiz de Galarreta *et al.* 1998, Corsini *et al.* 1999, Ramsay *et al.* 2000, Trognitz *et al.* 2001, Zoteyeva 2001, Budin 2002, Chen *et al.* 2003). Sources of resistance from wild tuber–bearing species have been attempted at *4x* level by breeders.

At the IHAR Młochów breeding for resistance to *P. infestans* has been performed at the tetraploid and diploid level in parallel (Świeżyński *et al.* 1997b). At the diploid level resistance was introduced into *S. tuberosum* hybrids from *S. microdontum, S. phureja, S. verrucosum* and from the hybrid of *S. stenotomum* x *S. phureja*. They were composed with other diploid *Solanum* species in the cycles of recombinant breeding. Lately, evaluation of new sources of resistance to *P. infestans*, so far not used in Młochów, has been done. Initially 36 accessions belonging to 20 *Solanum* species from the N.I. Vavilov All–Russian Research Institute of Plant Industry, St. Petersburg, Russia (VIR collection), and 10 accessions covering 8 *Solanum* species from the Potato Introduction Station, Sturgeon Bay, USA (PI collection), were characterized.

In this paper two groups of new selected diploid sources of resistance to *Phytophthora infestans* and a possibility of applying these sources in cultivar breeding are presented.

MATERIAL AND METHODS

Two groups of diploid potatoes, interspecific hybrids and wild species, were evaluated for resistance to *Phytophthora infestans*.

Diploid interspecific hybrids obtained in recombinant breeding included 22 advanced selections from 1991 and 1992, and 35 young selections from 2001. Resistance of these clones to late blight came from *Solanum microdontum* (PI 265 575, WAC 3220), *S. phureja* Soliman (CCC 1.3), *S. verrucosum* (PI 195 170, PI 275 256, CPC 2644) and from the hybrid of *S. stenotomum* x *S. phureja* (CIP 375186.3/11). Other *Solanum* species, like *S. chacoense, S. gourlayi* and *S. yungasense,* were also introduced into *S. tuberosum* hybrids.

Since 1999 new sources of resistance to late blight, previously not utilized at the IHAR Młochów, have been evaluated. Plant material was obtained from the VIR and PI collections. At the first step about 700 clones of 24 *Solanum* species, presented by 36 accessions from the VIR and 10 accessions from the PI collections, were characterized. The evaluated *Solanum* species were as follows: *S. berthaultii*, *S. candolleanum*, *S. cardiophyllum*, *S. chacoense*, *S. chancayense*, *S. famatinae*, *S. garsiae*, *S. gibberulosum*, *S. kurtzianum*, *S. latisectum*, *S. leptophyes*, *S. marinasense*, *S. michoacanum*, *S. okadae*, *S. parodii*, *S. phureja*, *S. pinnatisectum*, *S. polyadenium*, *S. ruiz–ceballozii*, *S. simplicifolium*, *S. sparsipilum*, *S. spegazzinii*, *S. toralapanum* and *S. vernei* subsp. *balsii*. Of them, 113 clones of five species have been preselected for further studies based on evaluation of resistance to *P. infestans* in leaflet and whole tuber assays and evaluated for chosen quality traits like cold chipping, blackening of tuber flesh and tuber greening (*S. berthaultii* [VIR19986, VIR23047], *S. kurtzianum* [VIR12465, VIR12479, VIR12488, VIR12489, VIR19115, VIR21886], *S. michoacanum* [VIR5763], *S. pinnatisectum* [VIR4459, VIR9174, VIR19157, VIR21955, PI230489] and *S. ruiz–ceballosii* [VIR7370, VIR7381]).

The data on resistance to *P. infestans* presented in the paper are from 2002–2003. A level of resistance was estimated according to Zarzycka (2001a, b). Interspecific hybrids were evaluated using detached leaflet and tuber slice tests, whereas wild *Solanum* species were examined in leaflet and whole tuber tests. Leaflets were collected from the middle part of plants. Six (*Solanum* species) to ten (*Solanum* hybrids) leaflets from each genotype were tested in two replications. Infection of the leaflets was estimated seven days after inoculation. From each genotype, ten double slices, each 10 mm thick, were assessed in two replications. Resistance of tuber slices was evaluated seven days after inoculation. Six tubers from each clone of wild *Solanum* species were assessed in two replications. A rose end of each tuber was wounded with 16 pins, approximately 2 mm long. The tubers were sprayed by inoculum and after 14 days of incubation at 16°C the resistance was estimated. To inoculate the leaflets, tuber slices and whole tubers, inoculum of standard concentration (50 sporangia/mm^3) was used. In each test the *P. infestans* isolate MP 324 was applied. Resistance reaction was evaluated using a 9–grade scale, where 1 = susceptible, 9 = resistant.

Polish potato cultivars Meduza and Irys were used as standards. According to the Polish Catalogue of Potato Varieties (1999), cv. Meduza is resistant in foliage (8.0) and mid–resistant in tubers (5.0), and cv. Irys is susceptible both in foliage and tubers (3.0).

Both interspecific hybrids and wild *Solanum* species were evaluated for fertility and presence of big pollen grains, an indicator of male *2n* gametes (Wasilewicz–Flis and Jakuczun 2001).

RESULTS

Leaflets resistance

All the 22 advanced interspecific hybrids originating from 1991 and 1992 were found to be resistant in leaflets (Table 1). An average rating of resistance for two years in leaflet tests was 8.4. The range of resistance reaction among clones was narrow, and located between 7 and 9 scores. Five clones were scored the highest resistance (9) in two years. The resistance of leaflets of 35 young clones from 2001 was similarly high (Table 1). The two–year mean score was 8.6, with resistance reactions of clones ranging from 7 to 9. In 13 clones no symptoms of infection were observed, and in two years of testing these clones were scored 9. Analysis of variance showed significant differences between the evaluated diploids and standard cultivars. A contrast analysis indicated that in a leaflet assay both old and young selected diploids expressed significantly higher resistance than did cv. Meduza, the resistant standard.

Table 1

Two–year mean resistance to *Phytophthora infestans* in selected interspecific hybrids of *Solanum* species (data from the years 2002–2003)

Groups of material	Source of resistance[A]	Resistance in			
		leaflets		slices	
		mean[B]	range[C]	mean[B]	range[C]
22 advanced clones	*mcd, phu, ver*	8.4 a	7.0 – 9.0	6.1 de	4.1 – 8.4
35 young clones	*mcd, phu, stn x phu, ver*	8.6 a	7.0 – 9.0	7.0 d	3.2 – 8.8
cv. Meduza		7.2 b	6.0 – 8.5	5.4 de	4.0 – 7.2
cv. Irys		3.6 c	2.0 – 4.7	3.3 f	1.3 – 4.8

[A] *mcd*, *phu*, *ver*, *stn* × *phu* – *Solanum*: *microdontum*, *phureja*, *verrucosum*, hybrid of *stenotomum* × *phureja*
[B] a, b, c – significance at α > 0.01; d, e, f – significance at α >0.05
[C] scale 1–9, where 1 = susceptible, 9 = resistant

Among the evaluated 88 clones of wild *Solanum* species, many clones were found resistant in leaflet tests (Table 2). Majority of the clones of *S. berthaultii*, *S. michoacanum*, *S. ruiz–ceballozii* and *S. pinnatisectum* showed a low level of infection and were scored more than 6. A number of *S. kurtzianum* clones expressing the resistance in leaflets was relatively smaller, although some of the clones proved to be highly resistant. The average resistance of leaflets shown in two–year observations was the highest in *S. ruiz–ceballozii* (score 7.3) and *S. pinnatisectum* (7.2), and the lowest in *S. kurtzianum* (5.0).

Table 2

Resistance to *Phytophthora infestans* in preselected wild *Solanum* species (mean values for the years 2002–2003)

Plant material	Resistance[A] in					
	leaflets			whole tubers		
	mean	range	number of clones	mean	range	number of clones
S. berthaultii	6.0	1.0 – 8.5	3	6.2	4.6 – 7.3	5
S. kurtzianum	5.0	3.4 – 7.1	19	6.9	1.0 – 9.0	37
S. michoacanum	6.7	4.0 – 9.0	12	7.5	4.7 – 9.0	15
S. pinnatisectum	7.2	1.8 – 9.0	42	7.2	4.1 – 9.0	46
S. ruiz–ceballosii	7.3	1.0 – 9.0	12	7.1	5.3 – 8.3	10
cv. Meduza	7.2	6.0 – 8.5	1	4.8	3.6 – 5.1	1
cv. Irys	3.5	2.0 – 4.7	1	3.9	3.6 – 4.6	1

[A] scale 1–9, 1 = susceptible, 9 = resistant

Standard cvs Meduza and Irys showed the reaction at the expected level (Table 1). In two–year assessing, cv. Meduza, resistant standard, was evaluated on average as 7.2, with a range from 6.0 to 8.5. Cv. Irys, a susceptible standard, was scored 3.6, with variability among tests from 2.0 to 4.7.

Tubers resistance

The clones of interspecific hybrids, both advanced and young, showed quite a high level of tuber resistance in slice tests (Table 1). Two–year means for resistance reaction were 6.1 and 7.0 for old and young clones, respectively. From among 22 advanced clones, 12 were estimated above 6. Twenty–five of 35 young clones were considered resistant in slice tests (score more than 6). Analysis of variance showed significant differences in resistance to late blight between the evaluated diploids and standard cultivars. A contrast analysis of the results obtained in a tuber slices test indicated that young selected diploid clones were significantly higher resistant than cv. Meduza.

Wild *Solanum* species expressed generally high resistance to *P. infestans* in whole tuber tests. From among 113 tested clones, 82 (72%) were found resistant (score higher than 6) (Table 2). Majority of clones of *S. berthaultii*, *S. michoacanum*, *S. ruiz–ceballozii* and *S. pinnatisectum* were tuber resistant. In *S. kurtzianum* accessions wide segregation of tuber resistance, from great susceptibility (scored 1) to high resistance (scored 9), was observed. Nevertheless, the group of tuber resistant clones of *S. kurtzianum* was frequent, as 29 of 37 clones were scored higher than 6.

A standard cv. Meduza was averagely scored 5.4 in slice tests, with a range from 4.0 to 7.2, and 4.8 in whole tuber tests, with a range from 3.6 to 5.1 (Table 1, 2). Cv. Irys was scored 3.3 in slice tests and 3.9 in whole tuber tests (Table 1, 2). Variation calculated for cv. Irys was 1.3–4.8 in slice tests, and 3.6–4.6 in whole tuber tests.

Thirteen advanced interspecific hybrids resistant to late blight both in leaflets and tuber slices were selected out of 22 clones. In the group represented by young clones from among 35 evaluated ones, 25 clones were found resistant both in leaflets and tuber slices. Among the clones of wild *Solanum* species, 53 were selected as resistant both in leaflets and whole tuber tests.

Male fertility

Twenty of 22 advanced hybrids were male fertile, and 11 were able to form big pollen grains ($2n$). Male fertility in young hybrids was revealed in 30 of 35 tested clones. In this group big pollen grains were found in 20 clones. One hundred and six clones from wild *Solanum* species had fertile pollen grains, but big pollen grains were only produced by 6 clones.

DISCUSSION

Diploid selections from the group of interspecific *Solanum* hybrids were highly resistant to *P. infestans* in leaflets and tuber slices (Table 1).

The ranges of resistance in tuber slices indicated that both resistant and susceptible clones were identified. On the other hand, high two–year means of resistance for slices showed that group of resistant clones was big. It is noteworthy that 13 advanced and 25 young clones, respectively from among 22 and 35 tested ones, combined the resistance in leaflets and tubers. A contrast analysis showed that the resistance in leaflets of old and young group of interspecific hybrids was significantly higher than that of cv. Meduza. As regards the resistance of tuber slices, only 35 young clones appeared to be significantly better than cv. Meduza. Majority of the hybrids presented in the paper (20 old and 30 young clones) were male fertile, so they could be intercrossed at diploid level with donors of other traits. In the group of diploid clones, 29 clones were able to form big pollen grains, thereby making possible a transfer of the resistance into *4x* level in *4x–2x* crosses. Interspecific hybrids, that involve *S. tuberosum* in their origin, show a good level of agronomic traits, similar to that in *4x* selections. Utilization of them in commercial breeding could give quite a short way to obtain required recombinants. At the IHAR Młochów resistance to late blight from *S. stenotomum* x *S. phureja* hybrid has recently been transmitted into *4x* level. The tetraploid progeny lines express the resistance both in leaflets and tubers. In addition, they are mid–early and have good agronomic traits (B. Flis, personal communication). The resistance to *P. infestans* has also been transferred into *4x* level from hybrids of *S. microdontum* and *S. verrucosum*. In 2004 several combinations of tetraploid first–year seedlings have been planted in the field. In our breeding program, *4x–2x* matings between possibly early tetraploid seed parents and the described diploid clones originating from 2001, producing big pollen grains, have been planned. These clones have in their origin mentioned above sources of resistance to late blight: *S. microdontum*, *S. verrucosum* and *S. stenotomum* x *S. phureja*. The advantages of these clones over those earlier transferred into *4x* level are a new configuration of donors of resistance to late blight and a higher level of cultivated characteristics. It should be noted that these clones have also been characterized for resistance to other pathogens and chosen agronomic and quality traits. They seemed to be promising as sources of resistance to *P. infestans* both in leaflets and tubers in combination with other required traits. There were many attempts of introgression of wild *Solanum* species in breeding programs both *via* diploid level and directly at tetraploid level. Resistance to late blight from *S. papita* (*4x*) was successfully introduced into *S. tuberosum* background (Ramsay *et al.* 2000) and the progeny segregated for resistance. In attempts with several wild species Rivera–Pena (1992) found *S. demissum* and *S. iopetalum* to be good sources of resistance, and introduced them into *S. tuberosum.* High resistance to late blight from diploids could be transmitted into *4x* level by using dihaploids forming *2n* gametes (Wastie 1991). Louwes *et al.* (1992) combined resistance of several wild species with dihaploids of *S. tuberosum.* They crossed *S. berthaultii*, *S. circaeifolium*, *S. phureja*, *S. pinnatisectum*, *S. polyadenium* and hybrids of *S. goniocalyx* x *S. tuberosum,* which resulted in 75% of progenies expressing high resistance to *P. infestans* in foliage.

Introduction of wild species to breeding programs enriches gene pool with new alleles. To utilize them, more breeding work, as compared with that devoted to presented diploid hybrids, is needed for elimination negative traits related to wildness. At the IHAR Młochów exploitation of new, in our research, sources of resistance to *P. infestans* has been started in 1999. After preselection for resistance to late blight as well as for chosen quality traits, performed within the group of 46 accessions covering 24 *Solanum* species, five species (*S. berthaultii*, *S. kurtzianum*, *S. michoacanum*, *S. pinnatisectum* and *S. ruiz–ceballozii*) from 16 accessions were left for further investigations. The level of resistance to late blight of these five species was evidently higher than that of the other *Solanum* species. Within each species resistant and susceptible clones were identified (ranges), but high two–year means for resistance ratings showed that resistant clones were in prevalence (Table 2). In our studies the resistance to late blight in leaflets and tubers was evaluated, but our main interest was focused on complex resistance. Fifty–three clones of wild species were considered resistant both in leaflets and tubers. They represented five explored species. They flowered intensely and produced fertile pollen grains, but formation of big pollen grains was only sporadic. Clones selected from the evaluated wild *Solanum* species can be crossed with other 2EBN diploids, excluding clones of *S. pinnatisectum* (1EBN). At the IHAR Młochów dihaploids of tetraploid forms were produced as partners for matings with diploid *Solanum* wild species. A crossing program between wild species and dihaploids of *S. tuberosum* has been conducted in 2004. It is the first step of introgression of these sources of resistance to late blight into our diploid program. It is expected that in parallel with late blight resistance also new alleles of quality traits will be introduced into created diploid hybrids. This program is the second set of such a type of crosses after 1970, when preselected clones of various *Solanum* species, among others *S. microdontum* and *S. verrucosum*, were being crossed to dihaploids of cultivars or *4x* breeding lines. This initiated the diploid recombinant breeding at the IHAR Młochów, lasting for about 30 years.

Most of the tested wild *Solanum* species were also evaluated by other researchers. In some cases different results were obtained. Some species characterized in our studies as susceptible were assessed elsewhere as resistant, or *vice versa*. It was rather due to exploring given accessions than to respective species. But it is evident that in some *Solanum* species the occurrence of clones resistant to late blight is higher than that in other species. For example, the good sources of resistance to late blight, intensively explored in breeding, are *S. berthaultii*, *S. microdontum*, *S. verrucosum* (Colon and Budding 1988, Zoteyeva 2001), *S. phureja*

(Cañizares and Forbes 1995, Trognitz *et al.* 2001) or *S. pinnatisectum* (Ruiz de Galaretta *et al.* 1998, Zoteyeva 2001, Chen *et al.* 2003). In turn, *S. kurtzianum, S. michoacanum* and *S. ruiz–ceballozii,* considered by us as resistant to late blight, have not been so widely explored. Zoteyeva (2001) identified genotypes resistant to late blight in tubers and leaves within the species *S. ruiz–ceballozii,* and genotypes resistant in tubers within *S. kurtzianum*. However, Ruiz de Galaretta *et al.* (1998) reported these clones as susceptible to *P. infestans*. Successful selection of resistant clones from above three species, being 2EBN, is important, because they can be directly crossed with other diploids. *S. pinnatisectum* (1EBN), often mentioned as resistant to late blight, needs special techniques like somatic hybridization or bridge crosses (Hermsen and Ramanna 1973) for introducing it into breeding material.

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