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Over 50 Years of Potato Parental Line Breeding Programme at the Plant Breeding and Acclimatization Institute in Poland

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Abstract

The paper describes the potato parental line breeding programme developed in Poland from the 1960s. The aim of the programme was to create parental forms useful for speeding up the breeding of new potato varieties and getting higher efficiency in directed selection for desired traits. The programme introduced new sources of resistance and quality traits into the Polish breeding pool by conducting research and breeding of tetraploid and diploid parental lines. The programme had significant impact on potato breeding, with 72 Polish potato varieties originating from crossings involving parental lines. These varieties show higher levels of resistance to major pathogens of potato crops, including resistance to Potato virus Y and late blight in starch group. Besides the direct impact on potato breeding, the programme was the stimulus for developing studies focused on potato genotype.

Keywords Diploid potato · Parental lines · Potato breeding · Resistance to pathogens

Introduction

The article is a summary of the programme of potato parental line breeding initiated by professor Kazimierz Świeżyński in 1961, before the Młochów Research Center of the Potato Research Institute was created, and then since 1966 fully developed at this centre for over 50 years. At the time when the programme was started, the most outstanding features of potato production in Poland were the large potato growing area (ca 2.8 million ha) with a harvest of 43 million tonnes a year, which was many times larger than today; the high human consumption (ca. 200 kg/person/year); approximately 50% of potato harvest used for animal feed; and lack of processed products with the

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exception of starch production. Thus, the potato varieties grown at the time were mostly suitable for general use. After World War II, the material foundations of potato breeding, including plant materials, had to be practically rebuilt. Therefore, an urgent need was to increase the scale and speed of variety breeding resulting in new varieties for potato producers.

Tetraploidy of cultivated potato *Solanum tuberosum* L. (*tbr*) hinders the breeding process. During the selection process, the breeder assesses the breeding material in terms of about 50 qualitative, resistance, or agronomic traits, usually independently inherited. It became increasingly difficult to select recombinants in the offspring of tetraploid parents that meet the requirements of the modern variety. Therefore, typically one variety has been selected from around 100,000 clones (Ross 1986) over 11–12 years.

The aim of the programme was to create parental breeding lines useful for speeding up the breeding of new varieties and getting higher efficiency in directed selection for desired traits. According to Świeżyński (1971), the tetraploid parental line (TPL) had to widen the genetic pool available for breeders. TPL is defined as a clone that has high levels of some important traits and after one cross with another partner is able to create the offspring from which a new variety can be selected directly (Świeżyński 1971). It was assumed that all parental lines should be characterized by acceptable tuber yield and tuber appearance and a not too long vegetation period. These basic requirements were the background to some distinguishing traits of specific TPL. The distinguishing traits were related to the specific direction of crop utilization or to specific conditions of its cultivation, such as (1) good cooking quality, (2) earliness in table and starch varieties, (3) high starch and protein content, (4) suitability for light soils with water deficiency, and (5) good processing quality. Taking into account the level of crop cultivation at that time, it was also assumed that future varieties resulting from crossing with TPLs would be characterized by a high level of resistance to important diseases or pests, among which were virus diseases, late blight, storage diseases, and nematodes. These resistances were rare or not identified in the breeding pool available at that time. The programme was realized in two ways using tetraploid and diploid materials. The diploid potatoes were considered the sources of new resistances not present in the pool of tetraploid varieties. However very soon, diploid materials were recognized as valuable source of quality traits as well.

The Selection Scheme

One of the basic ideas in parental line breeding is to develop new breeding lines in the shortest possible time while maintaining the requirement for the most complete and accurate characterization of the traits. In fact, the parental lines were produced in 6-year cycles of pre-breeding (Table 1). The necessary high multiplication rate already at the initial stage of breeding was ensured by the field propagation of the first year seedlings. The individuals of the second vegetative generation were tested in field experiments in which tuber yield, tuber morphology, starch content, and culinary quality were assessed (Domański 2001a, b). Until the mid-1980s, the most advanced tetraploid parental lines were tested in three locations, and for the group of parental lines for light soil cultivation, the field trials in the 4th and 5th year were carried out on sandy, water-

Table 1 Basic (simplified) selection scheme for TPL breeding

Evaluations/testing	Year					
	1 Crossings	2 Field-grown seedlings	3 Vegetative generation	4	5	6
			Seedling's lines	New lines	Young lines	Advanced lines
Agronomic traits in field trials with replications	na	na	na	Yes	Yes	Yes
Viruses resistance#	na	mi	mi	mi/graft	Graft	Graft/aphid
Resistance to LB§	na	na	l	l/t	l/t/f	l/t/f
Resistance to nematodes, wart, and soft rot†	na	na	na	Ro1/D1	Ro1/D1	Soft rot

mi/graft/aphid—mechanical inoculation (resistance to PVX, PVY, or PVM), graft inoculation (resistance to PVY, PVM, and PVS), aphid inoculation (resistance to PLRV)

§ LB l/t/f—testing for resistance to late blight in leaflet test/tuber slice test/field test

† Ro1/D1—testing for resistance to pathotype Ro1 of *Globodera rostochiensis*/pathotype D1 of *Synchytrium endobioticum*

na not applicable at this stage

deficient soil. However, the breeding of tetraploid parental lines for light soils ceased in the mid-1990s due to limited funding.

In the mid-1990s, work commenced on parental lines suitable for processing. The routine selection of such lines (mainly suitable for chipping) involved screening for chipping quality of tubers from various storage condition, namely after 3 months of storage at 10 °C, directly after 5 months of cold storage (4 °C), and after 5 months of storage at 4 °C followed by 2 weeks of reconditioning at 18 °C.

The distinctive feature of the parental line breeding programme was applying high selection pressure in the shortest possible time. The selection of genotypes resistant to viruses started at the stage of very young first-year seedlings by applying spray inoculation of some viruses and visual selection before planting in the field (Sieczka 2001a). The selection at this stage was severe, since ca. 10% of field-grown seedlings were collected after visual evaluation of yield and tuber appearance. In the following generations, resistance to pathogens and pests was extensively screened in greenhouse and laboratory tests (Syller 2001; Wasilewicz-Flis 2001; Chrzanowska 2001; Zarzycka 2001; Lebecka 2001; Pietrak 2001; Sieczka 2001b). In the case of virus resistance, such tests were naturally supported by the location of the experimental field in a region with a high viral pressure.

The selection of resistant individuals was based on the identification of genotypes that remained healthy after artificial inoculation with a specific pathogen (Table 1 shows a simplified scheme of selection of resistant genotypes; the details are given by Flis (2017)). However, in the last period of the parental line programme, selection based on the genotype began to replace phenotypic tests, although in some cases, mixed phenotypic and marker-assisted selection was considered best (Flis 2017).

For the diploid programme, the screening and evaluation scheme was essentially the same as for tetraploids, with some modifications such as evaluation in non-replicated field trials at one location.

The best parental lines or advanced lines distinguished only by the desired traits in a specific crossing programme were used in the next cycle of recombination breeding to generate progenies for selecting new lines. This was crucial for rapid development of parental lines with multiple (complex) resistances.

Diploid Parental Line Breeding

In 1968, a diploid parental line (DPL) breeding programme was initiated to complement the TPL programme, and the first diploid seedlings were grown in 1970. The programme was based on the following considerations.

a. Diploid wild and primitive cultivated *Solanum* species are rich sources of resistance and quality traits and widen the genetic variation useful for potato breeding. In addition, many of these species are relatively easily crossed with dihaploids of *S. tuberosum* varieties or breeding lines.
b. The disomic inheritance is much simpler than tetrasomic inheritance.
c. Homozygous parental lines producing non-segregating progenies for desired traits should be easier to achieve in diploids than in tetraploids (Świeżyński et al. 1985).
d. The use of 2*n* gametes (genetically first (FDR) or second (SDR) division restitution) allows the transfer of 2*x* potential to 4*x* level via interploid crosses (4*x*-2*x* or 2*x*-4*x*) (Iwanaga 1982; Zimnoch-Guzowska and Dziewońska 1989).

Diploid Parental Lines (DPL)

The above assumptions determined the methods of diploid exploitation by various research and breeding centres (Chase 1963; Mendinburu and Peloquin 1977; Wenzel et al. 1979). The diploid breeding programme at the Młochów Center was implemented in several stages (Fig. 1). In the early 1970s, preselection was initiated in wild 2*x* *Solanum* species to maximize chosen quality or resistance traits, assuming an increase of homozygosity of the breeding lines. In parallel, the haploidization of several Polish varieties and 4*x* breeding lines was done via pollination with haploid inducers from *S. phureja*. The resulting putative dihaploids were screened for ploidy level and then preselected for agronomic traits and fertility. Next, chosen lines of wild *Solanum* were crossed with the dihaploids of *S. tuberosum*. The next steps involved several consecutive crossing and selection cycles that produced diploid genotypes with increasing complexity of resistance traits, better quality, and reduced negative influences from wild ancestors. After 5–7 cycles of crossing and selection, the DPLs were complex interspecific hybrids. In the last stage of the diploid programme, the switch from 2*x* to 4*x* level was achieved by interploid 4*x*-2*x* crosses, provided the diploid parent produced 2*n* male gametes. The frequency of 2*n* gametes, identified as large pollen grains, was variable among diploid lines and averaged about 22% (Strzelczyk-Żyta et al. 1997). Selected diploids varied in their mechanism of 2*n* gamete formation: FDR or SDR. Due

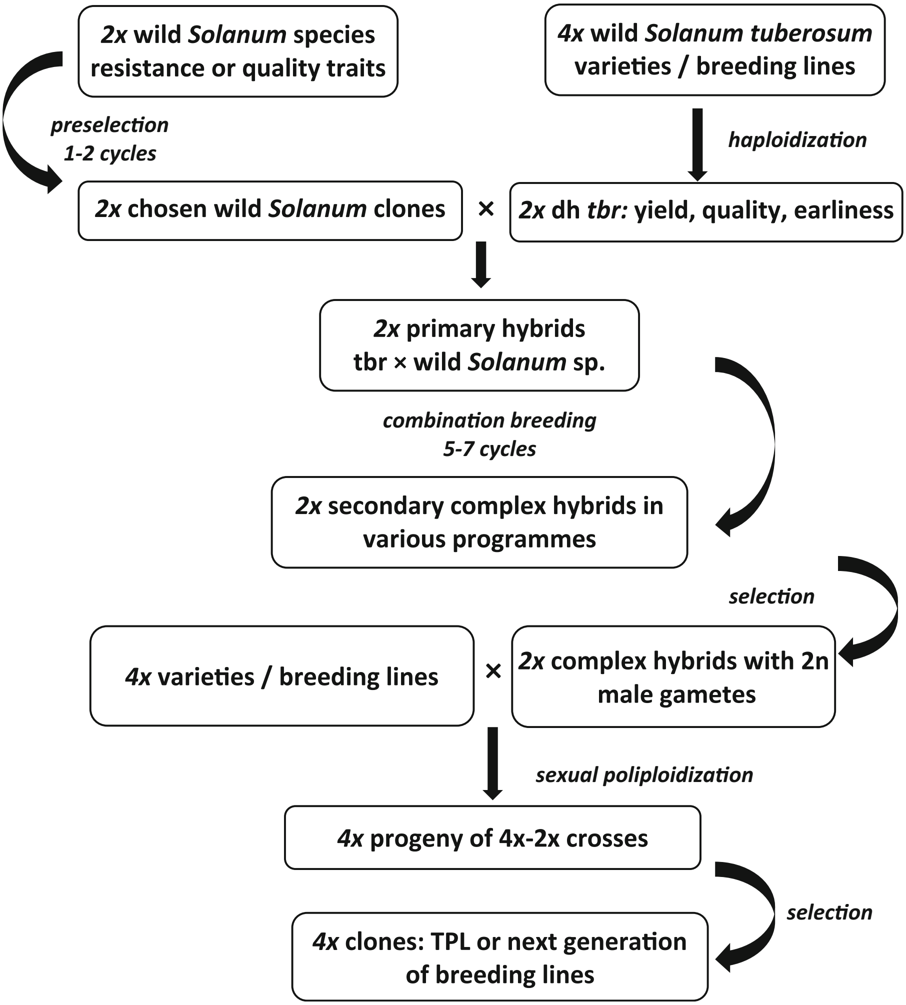

Fig. 1 The scheme of diploid potato breeding and its application at IHAR Młochów Research Center in the years 1970–2013

to inhibited recombination, the gene combinations in interspecific hybrids producing 2*n* gametes by FDR were transferred nearly intact to their progenies in 4*x*-2*x* crosses. This allowed the transmission of both general and specific combining effects to the tetraploid progenies (Mendiburu and Peloquin 1977; Wagenvoort and Zimnoch-Guzowska 1992; Lebecka et al. 2004). It was supported by the significantly higher frequency of desirable 4*x* recombinants found in the offspring of 4*x*-2*x* crosses than those of 4*x*-4*x* crosses (Zimnoch-Guzowska and Wasilewicz 1987; Domański et al. 2000). We recognized as important the necessity to increase the level of seed setting in 4*x*-2*x* crosses, which should facilitate the use of DPLs in breeding programmes of 4*x* varieties.

Directions of Breeding DPL

The directions of diploid programmes were modified over the years (Fig. 2). The oldest ones focused on selection of DPLs with the high starch content of tubers and high starch yield and two supporting subprogrammes: (1) selection of diploids resistant to main potato viruses: potato leafroll virus (PLRV), potato virus Y (PVY), potato virus M (PVM), potato virus X (PVX), and potato virus S (PVS) and (2) diploids resistant to late blight (LB). In 1982, the programmes of DPL breeding for high table value and for chipping quality arose using materials selected for early starch yield combined with resistances to pathogens. Special attention was paid to a support subprogramme with a specific goal for DPLs to enhance ability to form 2*n* gametes. The most recent subprogramme was dedicated to DPLs resistant to the pectinolytic bacteria *Pectobacterium* sp. and *Dickey* sp., the causative agents of blackleg and soft rot of tubers. It has been developed since 1995 and based on high starch diploids (Zimnoch-Guzowska and Łojkowska 1993).

The IHAR diploid programme in 1970s and 1980s was one of the largest in the world (Świeżyński and Zimnoch-Guzowska 1996). In the years 1970–2008, up to 20,000 first-year seedlings and up to 1700 2*x* clones were field grown, with an average of about 7000 seedlings and ca. 800 clones a year. The scale of work was somewhat reduced after 1995 due to the reduction of research funding.

In the programme for high starch content of tubers, several diploid hybrid clones were selected in which starch content reached up to 30% (Zimnoch-Guzowska and Łojkowska 1993). As sources of high starch content in tubers, among others, *Solanum* species of the *Commersoniana* series and *S. verrucosum* have been used. Other goals for starch clones were (1) to shorten vegetation period (by crossings to early yielding dihaploids tbr or diploids), (2) to enhance starch yield through higher tuber yield, and (3) to reduce the content of glycoalkaloids in tubers.

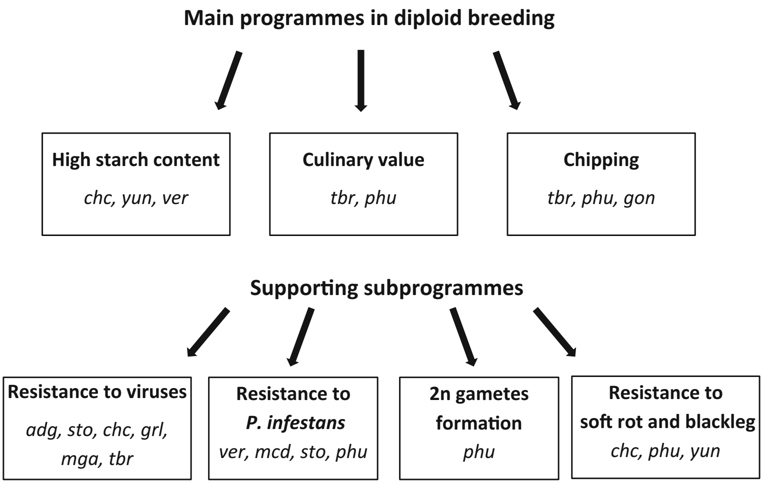

Fig. 2 Main and supporting programmes of DPL breeding at IHAR-PIB and main *Solanum* resources applied (abbreviations of the names of *Solanum* species acc. Huaman and Ross 1985)

The developments of diploids outstanding in table quality and in chipping quality were the next two main directions of the diploid programme. Additional desirable characters were an ability to form 2*n* gametes and good level of agronomic traits combined with resistances to potato pathogens. All selection and evaluation procedures applied to this group of material were the same as those used for tetraploids (see Table 1). Diploids outstanding in a low accumulation of reducing sugars after cold storage have been selected (Jakuczun et al. 1995). For diploid clones with high table quality, additional attention was paid to the evaluation of blackening of fresh and cooked tuber flesh (Jakuczun and Eising 2003) and tendency of tuber greening under light exposure (Jakuczun and Zimnoch-Guzowska 2006).

The development of diploid lines originating from various late blight resistance sources was the aim of the subprogramme for breeding LB-resistant diploids (Zimnoch-Guzowska 2009). The first selections were based on five sources: *S. verrucosum* (ver PI 1195170 and CPC 2644), *S. microdontum* (WAC 3220), *S. phureja* (Soliman CCC 1.3), and *S. phureja* × *S. stenotomum* carrying *Rpi-phu1* gene (Śliwka et al. 2006). Additional sources introduced into DPL resistant to LB were *S. michoacanum* (including the *Rpi-mch1* gene, acc. Śliwka et al. 2012a) and *S. ruiz-ceballosii* (including the *Rpi-rzc1* gene acc. Śliwka et al. 2012b), obtained from the N.I. Vavilov Research Institute for Plant Industry (VIR), Russia (Zoteyeva et al. 2012).

The oldest 2*x* subprogrammes included the one aimed at the breeding of DPLs with complex resistance to economically important viruses in Poland, i.e., PVY, PRLV, PVM, PVS, and those of lesser importance, such as PVX and PVA. This programme was parallel to the virus-resistant TPL breeding. Within the programme, two different types of resistance to PVM were found in *S. megistacrolobum* and *S. gourlayi* (Dziewońska and Ostrowska 1978; Waś et al. 1980; Świeżyński et al. 1981). In turn, resistance to PLRV was identified in 2*x* clone DW 84-1457 (Dziewońska and Waś 1994). In some cases, the resistance was being selected in dihaploids of resistant 4*x* varieties or breeding lines. The complex virus resistances were subsequently combined with the appropriate agronomic value and other resistances (to wart, nematodes, LB) and finally with the ability to form 2*n* gametes. This group of selected DPLs served as virus resistance sources for other PL programmes.

Tetraploid Parental Line Breeding

The directions of TPL breeding varied during the programme depending on needs of the breeding of new varieties. In the years 1965–1995, parental lines for breeding varieties for fodder and general use accounted ca. 30% of released TPLs, but after 1995, no more were selected. Since the mid-1990s, the growing importance of varieties suitable for processing into chips initiated such direction of TPL breeding. These works were supplemented by the evaluations of general combining ability (GCA) in terms of quality traits, especially the light-coloured chips after cold storage (Domański et al. 2004a; Domański et al. 2004b). All TPLs suitable for processing had at least one parent with positive GCA for light colour of chips (Domański et al. 2002).

The scale of the TPL programme changed over the last 4 decades. Since the initial period of the TPL programme until its full development up to 1990, approximately 60,000 first-year seedlings were grown in the field each year. This number fell to

15,000 in the 1990s and to 5000 at the beginning of the twenty-first century. During the above periods, the average numbers of TPLs issued each year decreased from 18 and 27 in the first 2 decades to 9 and 5 in the last 2 decades. Hence, parental line selection started with ca. 3500 seedling lines at the beginning of the programme and gradually decreased to 2500, then 2000 and 1000 seedling lines in subsequent decades. The reason for this decline was the increasingly limited funding of research work.

Resistance Traits

In practice until the 1990s, the TPL programme was simply the implementation of resistance breeding in its extreme form. The programme focused on resistances to viral pathogens, and resistance to late blight was the other priority. In turn, among the potato viruses, from the beginning in the early 1960s, the most important were PLRV and PVY. PVM was the third virus of agronomic importance in Poland. There was no resistance to PVM in contemporaneously grown varieties, and strong infection pressure with PVM was noted in Poland and Eastern Europe (Kostiw 2002). The fourth virus of interest was PVS. These priorities were in force for over 20 years but changed in the early 1990s, when PLRV began to gradually lose its significance. In contrast, PVY began to spread faster and has created new variants causing increasing problems in seed production up until today (Zimnoch-Guzowska et al. 2013).

The introduction of a resistance into TPLs was preceded by the identification of its sources and subsequent transfer to a more cultivated genetic background. In parallel, there was a period of international exchange of resistance sources with European research centres and the International Potato Center (CIP). The fairly simple genetics underlying the inheritance of most of virus resistances (PVX, PVY, PVM, and PVS) based on major genes helped to introduce these resistances into breeding lines, in various combinations. Since 1989, it has resulted in selection of TPLs having complexes of virus resistance to 4 or 5 viruses (Table 2). The sources of resistance to PVY, PVX, and PVS were the clones of *Solanum stoloniferum*, *S. acaule*, and *S. tuberosum* ssp. *andigena*, which came from the Max Planck Institute in Köln and the Potato Breeding Institute in Gross Luesewitz, Germany. The sources of extreme resistance to PVY and PVX were also obtained from the Scottish Crop Research Institute collection and from the N.I. Vavilov Research Institute for Plant Industry (VIR), Russia. The extremely PVY-resistant clones of *S. stoloniferum* from VIR had a significant impact on TPL breeding, since they were male fertile in contrast to other resistant clones derived from this species (Flis et al. 2005).

The sources of resistances to PVM and PLRV were identified in the IHAR collection of diploid potatoes, and the response of resistant genotypes has been accurately recognized (see section on “Diploid Parental Lines” in this paper).

The resistance to LB came from breeding lines developed during the programme, which had *S. demissum* or *S. stoloniferum* in their ancestry. With the beginning of twenty-first century, mid-early clones expressing high resistance to LB were found in the diploid parental line programme using *S. phureja* and *S. stenotomum*. This resistance was successfully transferred to tetraploid breeding lines. Soon in the following years, in diploid clones, the gene *Rpi-phu1* was identified and mapped, and a diagnostic marker linked with the gene was found. Over time, the complexity of created TPLs also increased. TPLs passed on to breeders were characterized for over 30 traits, which

Table 2 Timetable of releasing TPLs with combined resistances to viruses

Year of releasing TPLs	TPLs with resistance combinations
1968	PVY PVX
1977	PVY PVX PVS
1980	PVY PVX PVS (PLRV)
1985	PVY PVX PVM# (PLRV)
1989	PVY PVX PVM# PVS (PLRV)
1993	PVY§ PVX PVM† PVS PLRV

Resistance to viruses (respective gene and source):
PVYgene Ry_{sto}—male sterile *S. stoloniferum*;
PVY§ gene Ry_{fsto}—male fertile *S. stoloniferum*;
PVXgene Rx_{acl}—*S. acaule*;
PVM# gene *Rm*—*S. megistacrolobum*;
PVM† gene *Gm*—*S. gourlayi*;
PVS gene *Ns*—*S. tuberosum* ssp. *andigena*;
(PLRV) elevated level of resistance to PLRV from *S. tuberosum* (various varieties);
PLRV gene *PLRV.4*—diploid clone DW 84-1457

included resistances to pathogens and pests, like resistance to the five main potato viruses (PVY, PLRV, PVM, PVS, PVX), LB, wart, and nematodes. The complex combinations of resistance traits were outstanding features of TPLs. This complexity was particularly common for viral resistances. More than half of TPLs (53%) were resistant to two viruses (predominantly to PVY and PVX), 23% of lines was resistant to three viruses, and 6% of released TPLs was resistant to five viruses. The most important PVY resistance was present in 96% of TPLs.

Impact of Parental Line Breeding

Diploid Parental Lines

The main role of the diploid material was to support the development of TPLs, and this was very effective. The selected DPLs were of various origin and were donors of a number of important quality features related to cooking and chipping ability and increased tuber starchiness (Domański et al. 2004a, 2004b) along with several resistance traits: resistance to PLRV, PVM (Dziewońska and Waś 1994), wart (Plich et al. 2018), late blight (Śliwka et al. 2006), and bacterial soft rot and blackleg (Lebecka et al. 2004). Thus in 1997, about 70% of TPLs grown in Młochów originated from diploids.

However, in 1997, the diploid lines were officially given to Polish breeders as actual parental lines, along with the characteristics of the complex of 30 traits (agronomic traits, quality, and resistances) and recommendation for using them in 4*x*-2*x* crosses. Two diploid clones offered, DG. 88-89 and DG. 88-4556, were a source of good suitability for chipping, due to their low accumulation of reducing sugars in tubers stored at low temperatures. However, due to the difficulties in using DPLs in 4*x*-2*x* crosses, where seed setting was weaker than in 4*x*-4*x* crosses, breeders preferred to obtain tetraploid progenies of 4*x*-2*x* crosses, rather than DPL clone alone.

The 4*x*-2*x* crosses became an element of testing 2*x* clones for their ability to form 2*n* gametes and seed setting efficiency. Furthermore, the 4*x*-2*x* progenies provided evaluations of the 2*x* clones for their breeding value for specific traits (Domański et al. 2000, Domański et al. 2002). In the mid-1980s, along with 2*x*-2*x* crosses, the 4*x*-2*x* crosses were introduced into crossing programmes. In the period of 10 years, 1996–2005, eight 4*x*-2*x* interploid crossing programmes were made with 45 tetraploid parents and 55 tested DPLs (Jakuczun and Wasilewicz-Flis 2006) (Fig. 3). When diploid parents expressed positive GCA effects, tetraploid clones were selected with a higher frequency from 4*x*-2*x* progenies (7.6%) than from 4*x*-4*x* progenies (1.1%). The selection criteria were applied to the set of morphological and quality traits, yield, and resistance to viruses using the method of independent culling levels (Domański et al. 2000, Domański et al. 2010). Furthermore, in some progenies from 4*x*-2*x* crosses, heterosis effects were found both for the total tuber yield and marketable yield (Domański et al. 2006).

Diploid materials have been used in the Młochów Center in studies on genetic background of the most important features of potato resistance and tuber quality. Genetic studies were conducted on diploids to determine inheritance of chosen quality traits: level of glucose, tuber greening, darkening of cooked tuber flesh, and low accumulation of reducing sugars after cold storage. A significant portion of studies on diploids was directed to the inheritance of resistance to main viruses, late blight, bacterial soft rot, and wart disease.

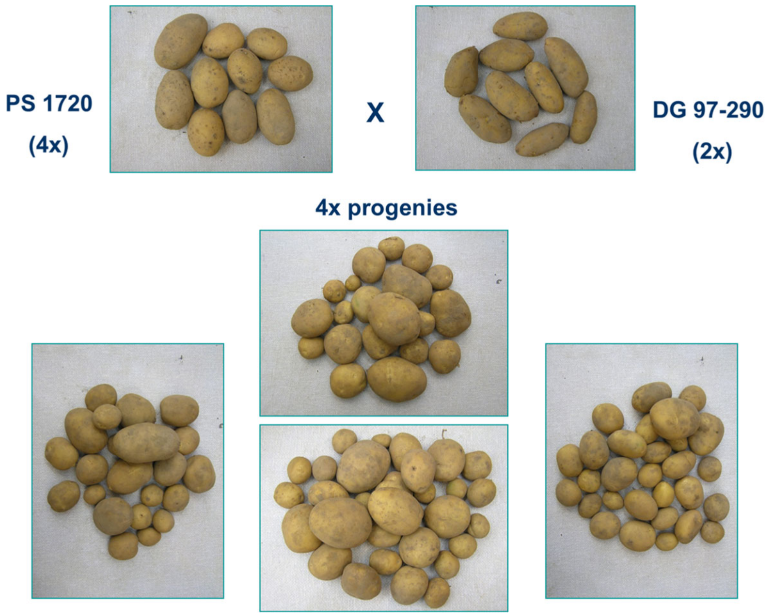

Fig. 3 Tuber appearance of some progeny individuals originating from crossing between tetraploid (PS1720) and diploid (DG97-290) parental lines. PS1720 had good level of cooking and processing quality traits and was resistant to PVY, PVM, PLRV, and wart. DG97-290 had high level of cooking quality combined with resistances to PVX, PLRV, blackleg, and soft rot (2*x* hybrid with 8 *Solanum* species in the origin)

Table 3 List of traits studied in potatoes developed in DPL, names of *Solanum* species exploited, and data on published QTLs/gene localization on the potato genetic maps and their molecular markers

Trait	Resources, *Solanum* species#	QTL/genes mapped to potato genome at IHAR
Resistance to		
Phytophthora infestans	*dms*, *ver*, *mcd*, *mch*, *phu*, *phu-stn*, *rzc*	QTLs (*ver* × *mcd*) (Śliwka et al. 2007); *Rpi-phu1* (Śliwka et al. 2006); *Rpi-mch1* (Śliwka et al. 2012a); *Rpi-rzc1* (Śliwka et al. 2012b)
Potato virus M	*grl*, *meg*	*Gm*, *Rm* (Marczewski et al. 2006)
Potato virus S	*adg*	*Ns* (Marczewski et al. 2002)
Potato virus Y	*sto*, *tbr*, *chc*	*Ry-f*$_{sto}$ (Flis et al. 2005); *Ny-DG* (Szajko et al. 2019)
Potato leafroll virus	*chc*, *yun*, *tbr*, *dms*	*PLRV.1.* (Marczewski et al. 2001); *PLRV.4.* (Marczewski et al. 2004)
Soft rot	Complex hybrids with *tbr*, *chc*, *yun*, *phu*	QTLs (Zimnoch-Guzowska et al. 2000)
Wart	Complex hybrids with predominance of *tbr* and input of *chc*, *grl*, *yun*, *sto*, *acl*, *dms*, *ver*, *mcd*, *phu*	*Sen2* (Plich et al. 2018)
Quality		
Tuber starch content; leaf sucrose content	Complex hybrids with predominance of *tbr* and input of *chc*, *grl*, *yun*, *ver*, *mcd*, *phu*	QTLs (Śliwka et al. 2016)
Low reducing sugars after cold storage	Complex hybrids with predominance of *tbr* and input of *chc*, *grl*, *yun*, *ver*, *mcd*, *phu*	QTLs (Sołtys-Kalina et al. 2020)
Enzymatic discolouration of flesh and black spot bruising	Complex hybrids with predominance of *tbr* and input of *acl*, *chc*, *dms*, *ver*, *mcd*, *grl*, *yun*, *phu*, *stn*	QTLs (Hara- Skrzypiec et al. 2018)
Tuber greening	Complex hybrids with predominance of *tbr* and input of *chc*, *grl*, *yun*, *sto*, *acl*, *dms*, *ver*, *mcd*, *phu*	QTLs (Plich et al. 2020)
Tuber dormancy, shape regularity, eye depth, flesh colour	The 1st set of parents: complex hybrids with predominance of *tbr* and input of *chc*, *ver*, *mcd*, *grl*, *yun*	QTLs (Śliwka et al. 2008)
Traits as above and tuber weight	In the 2nd set of parents input of *acl*, *dms*, *phu*, *stn* in addition	QTLs (Hara-Skrzypiec et al. 2018)

Species abbreviations acc. Huaman and Ross 1985

adg—*S. tuberosum* subsp. *andigena*, *acl*—*S. acaule*, *brd*—*S. brevidens*, *chc*—*S. chacoense CPC 3785*, *GLKS 66.51/6/6*, *PK 133*, *dms*—*S. demissum*, *gon*—*S. goniocalyx*, *grl*—*S. gourlayi INTA 7330*, *INTA7356*; *mcd*—*S. microdontum WAC 3220*, *PI 265575*; *mch*—*S. michoacanum VIR5763*; *meg*—*S. megistracrolobum R.72.554 (MPI)*; *phu*—*S. phureja Soliman CCC 1.3*; *rzc*—*S. ruiz-ceballosi*; *spg*—*S. spegazini*; *sto*—*S. stoloniferum*; *tar*—*S. tarijense*; *ver*—*S. verrucosum PI 195170*; and *CPC 2644*, *yun*—*S. yungasense GLKS 67.107/3R*

Since the late 1990s, research on 2*x* level was focused on the development of a potato genetic map, chromosomal localization of QTLs, and genes for traits of interest and also on molecular (diagnostic) markers for selection. This programme was partly

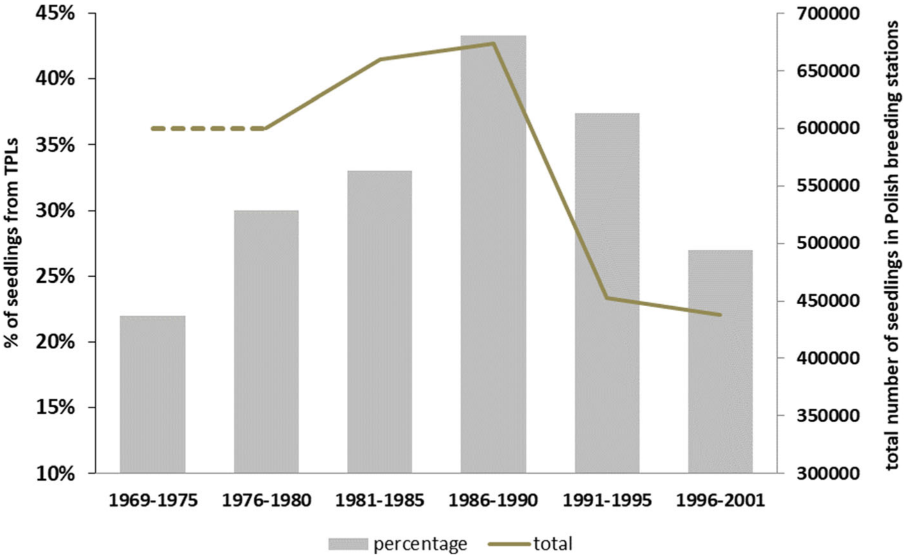

Fig. 4 Participation of seedlings derived from crossing with TPLs in total number of seedlings grown in potato breeding programmes in Poland (dashed line stands for estimated total number of seedlings). Note: Figures are not available after 2001. Since then, Polish breeders have been reluctant to publish data on the scale of their work, as a result of increasing competition from foreign breeding companies

realized in international collaboration to Dr. Christiane Gebhardt from Max Planck Institute. The list of traits studied in diploids, names of *Solanum* species used, and data on published QTLs/gene localization on the genetic maps and molecular markers found are given in Table 3.

Table 4 List of Polish varieties originated from TPLs (**in bold**—varieties currently registered in Poland)

Type	Maturity	Varieties registered in	
		1985–1999	2000–2019
Table	Very early	Malwa	Flaming
	Early	Aksamitka; Lotos	Eugenia; Korona; **Magnolia**; **Owacja**
	Mid early	Barycz; Baszta; Bekas; Tokaj; Triada; Wigry	**Ametyst**; Bursztyn; Etiuda; **Finezja**; **Gardena**; Gawin; Jutrzenka; Legenda; **Malaga**; **Mazur**; **Tajfun**; Wiarus
	Mid late	Arkadia; Beata; Bogna; Danusia	Gustaw; Niagara; Syrena
	Late	Olza	Medea; Soplica; Ursus
Starch	Mid early	Darga; Łucja	**Kaszub**; **Mieszko**; Monsun; **Pasat**; **Rumpel**; **Szyper**; **Widawa**
	Mid late	Brda; Fregata; Grot; **Ikar**; Klepa; Omulew; Vistula	**Amarant**; **Pasja Pomorska**
	Late	**Bzura**; Ceza; Dunajec; Ekra; **Hinga**; Jantar; Koga; Meduza; Nimfy	Gandawa; **Inwestor**; Neptun; **Rudawa**; Sonda; Ślęza; Umiak; Wist

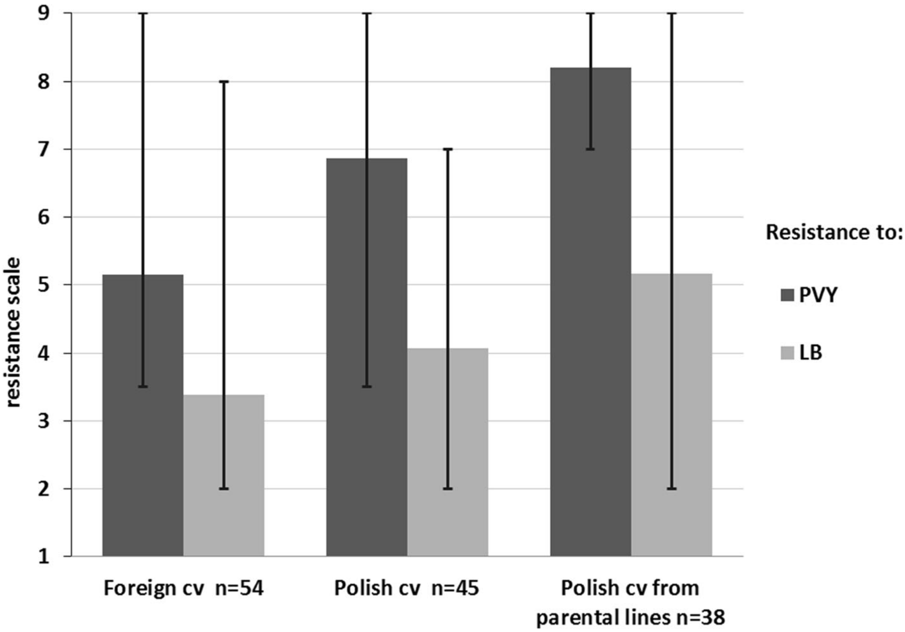

Fig. 5 Resistance to PVY and late blight (LB) in potato varieties registered in Poland for the period 2001–2010 grouped according to their origin. Bars indicate mean resistance values and whiskers indicate range between minimum and maximum of varieties resistances; resistance scale 1–9, where 9 is the most resistant (acc. Boguszewska et al. 2011)

Tetraploid Parental Lines

The programme of parental line breeding significantly influenced the breeding pool in Polish potato breeding companies. The impact on variety breeding was marked by both the number of seedlings derived from crosses with TPLs (Fig. 4) and a significant contribution of ca. 35% of the most advanced breeding lines selected from such seedlings. The programme resulted in the release of 72 varieties in Poland from direct crosses with TPLs (Table 4). In addition to these quantitative effects of the TPL programme on potato breeding, the impact on the genetic composition of varieties released by the breeding companies was equally important. This effect was reflected in the higher level of resistances to LB or PVY that occurs in varieties derived from the TPLs as compared to other registered varieties of non-TPL-related origin (Fig. 5). Also, among varieties from the TPL programme were ones resistant to other viruses such as PVM (e.g., Ametyst, Finezja, Eugenia, Korona), with the gene *Rm*, whose presence was verified by phenotype evaluation and by the identification of appropriate molecular marker (Chrzanowska et al. 2011). Similarly, in some varieties, the gene *Ns* conferring resistance to PVS was identified (e.g., Sonda, Ślęza, Tajfun) (Chrzanowska et al. 2011).

The programme of TPL development had a particularly significant impact on breeding of starch varieties. Starch varieties derived from TPL combine a high level of resistance to LB and a very high starch yield, resulting from both high starch content and high tuber yield. In starch varieties registered after 2000, the resistance to LB in 14 originated from TPLs was rated at 6.1, compared with seven Polish varieties and five foreign ones at 5.3 and 4.8, respectively (in 9 grade scale, where 9 = the most resistant). Among the most LB-resistant varieties still currently grown is variety Bzura, which was registered in 1986 and proved its resistance in field experiments performed in locations most exposed to epiphytosis (e.g., Toluca Valley in Mexico). For starch varieties recorded in Polish National List of Agricultural Plant Varieties in 2001–2019, the mean starch yield in TPL-derived varieties was 9.5 $t{\cdot}ha^{-1}$ as compared to 9.2 $t{\cdot}ha^{-1}$ for other Polish varieties and 8.3 $t{\cdot}ha^{-1}$ in the case of foreign varieties. In this respect, the most outstanding were Sonda (starch yield 10.1 $t{\cdot}ha^{-1}$) and Bzura (9.2 $t{\cdot}ha^{-1}$). The LB- and PVY-resistant starch variety Hinga has been cultivated in Poland and France for years.

From among the various groups of TPLs resulting from targeted selection, the greatest impact on potato breeding in Poland was from TPLs which were evaluated and selected on the basis of field experiments carried out on light soil. These TPLs became the parents of 12 varieties including 6 starch and 6 table ones, including the variety Tajfun which is still recommended for organic farming.

International Exchange

In the parental line breeding programme, materials from foreign collections or breeding programmes were widely used, which was particularly evident in the 1970s and 1980s. However, the use of foreign materials turned into mutual exchange. Breeding materials created during the programme were used by foreign institutions doing research and breeding. The most important was the cooperation with the International Potato Center (CIP), to which some seed samples and tubers of 22 tetraploid and 8 diploid clones were delivered between 1978 and 1994. All these materials were sources of resistance to viruses and/or LB. In the following years, the Młochów Research Center started cooperation with USDA centres and Cornell University, and this resulted in the delivery of some TPLs to the USA. One of the parents of North American variety Defender was a selection from true seeds obtained from the Młochów Research Center and originated from crossing involving a TPL resistant to viruses and LB.

Single tetraploid parental lines were also passed to Germany, Mexico, and Denmark, while diploid lines were sent to breeders or researchers in Canada, Spain, France, Denmark, and Slovakia.

Concluding Remarks

The parental line breeding programme was established to help Polish potato breeding after World War II. Parental lines with improved resistances and quality traits were offered annually to the 11 domestic potato breeding stations that existed in the 1970s to broaden their genetic base. The parental lines themselves were used as resources and not as final products on variety level, as they were outstanding in some features but did not meet all of the criteria of a finished variety, with the exception of variety Bzura. Today, the parental line breeding as described in this paper has been discontinued. The main reason for ending the programme was its high costs and the decreasing importance of potatoes in Polish agriculture. Some breeding work continues, but the development of new breeding lines is being done within the framework of specific projects financed from various sources. These breeding lines usually have special features, e.g., elevated carotenoid content in tubers, suitability for organic cultivation, or combined resistances to late blight from different, not-exploited sources.

The diploid and tetraploid gene pool that was created during the parental development programme is the reservoir of various resistance genes as well as genetic factors determining quality traits. This pool is stored as an in vitro collection of the most valuable genotypes or true seeds from their crosses, or is present in breeding lines that are currently grown in the field.

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