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BOTTLE NECKS IN BREEDING LATE BLIGHT RESISTANT POTATO

ABSTRACT

The resistance to late blight (LB) is considered as a factor of major importance among resistances to potato pathogens. For four last decades more work has been done on potato resistant to *Phytophthora infestans* than on breeding for resistance to any other potato disease. Many sources of resistance have been known to breeders for many decades, but the results of their utilization are still disappointing. The difficulties in breeding for LB resistance were assessed by 39 participants of the survey organized for the Global Initiative on Late Blight (Zimnoch–Guzowska and Flis 2002), who indicated several major factors hampering progress in this area. The following factors found to be the most important bottle necks are discussed in the paper: (i) identification and utilization of new sources of resistance, not sufficient agronomic value of the used resistance sources; (ii) combination of earliness with LB re–sistance; (iii) complexity of genetic determination of LB resistance; (iv) combination of foliage and tu–ber resistance; (v) screening methods applied for resistance evaluation; (vi) cost of selection for resistance; (vii) lack of molecular markers (MAS) applicable to selection for LB resistance.

Key words: limitations, *Phytophthora infestans*, potato, resistance breeding

INTRODUCTION

Breeding for resistance to late blight (LB), the most devastating fungal disease of potato (*Solanum tuberosum* L.) worldwide, has a long history. Over 150 years ago the Great Irish Potato Famine of 1845–1849 caused millions of deaths and huge emigration from Ireland to the New World. Potato crop, the staple food for inhabitants of Ireland and neighboring countries in those days was totally devastated by *Phytophthora infestans*. Since then, a new potato germplasm has been introduced in Europe. Farmers and breeders started searching for solutions to prevent late blight epidemics by agronomic practices and growing more resistant forms. According to Salaman (1911), breeding for LB resistance was pos–sibly the first scientific attempt of resistance breeding in potato. The cul–tivated potato, like several other species of the genus *Solanum*, originates from the Andean region of South America. *Phytophthora infestans*, the

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LB causal agent, is also thought to originate from this region. Wild *Solanum* species grown in this area were utilized as sources of resistance to *P. infestans* in potato breeding. The LB resistance is considered as a factor of major importance among resistances to potato pathogens. For the last four decades more work has been done on potato resistant to *P. infestans* than on breeding for resistance to any other potato disease. Many sources of resistance have been known to breeders for many de–cades, but the results of their utilization are still disappointing (Świeżyński and Zimnoch–Guzowska 2001).

The importance of LB resistance in potato breeding was pointed out by 23 of 39 potato breeding and research centers participating in 2002 Global Initiative on Late Blight (GILB) survey on screening methods applied and on major factors influencing the progress in breeding for LB resistance (Zimnoch–Guzowska and Flis 2002). The difficulties in breeding potato for LB resistance were assessed by participants of this survey, who indicated several major factors hampering progress in this area. The following fac–tors were found to be the most important bottle necks for getting progress in LB resistance of newly bred cultivars.

IDENTIFICATION AND UTILIZATION OF NEW SOURCES OF RESISTANCE, NOT SUFFICIENT AGRONOMIC VALUE OF THE USED RESISTANCE SOURCES

The practical breeding for LB resistance is based mainly on exploration of already existing resistant cultivars or advanced breeding lines and wild species. Out of 45 listed, nine cultivars were mentioned more than once by surveyed breeders as good resistance sources. In this group of cultivars predominate creations with late maturity (cvs Cara, Bionta, Kuras). Characteristics of maturity and LB resistance of potato cultivars differ when made by various centers (Table 1).

Table 1

Characteristics of maturity and LB resistance of cv. Cara made by various research centers (www.europotato.org)

Maturity	Ref.[A]	Foliage resistance	Ref.[A]	Tuber resistance	Ref.[A]
very late	1, 2	medium	5	low to medium	2
late to very late	3	medium to high	1, 2, 4	medium	5
intermediate to late	4	high	2, 3	high	1, 3
				high to very high	4
				very high	2

[A] Communicated by: 1. Konrad Schuler, 2000; 2. Richard Manchett, 2000; 3. Maureen McCreath, 2000; 4. HZPC, 2000; 5. Stepan Kiru, 1999

Using cultivars as sources of a trait in breeding programs is popular among breeders. However, in the case of resistance to pathogen, this leads to the narrowing of resistance gene pools among cultivars, thereby facilitating the pathogen to overcome resistance expressed in grown cultivars. So, beside this approach, breeders are deeply interested in using wild species as sources of resistance and in searching for newly or rarely used genes governing the LB resistance. Among 39 programs that have been surveyed, 25 are working with wild species, and two, in addition, with transgenes as the sources of resistance. Quite large number of wild or primitive cultivated species was noted by participants of the survey as tested sources of resistance, and among them the species known as donors of *R*–genes predominated. Among 35 species mentioned, thirteen were repeatedly used by breeders: *S. berthaulti*, *S. bulbocastanum*, *S. chacoense*, *S. demissum*, *S. hougasii*, *S. iopetalum*, *S. microdontum*, *S. phureja*, *S. pinnatisectum*, *S. stoloniferum*, *S. tuberosum* ssp. *andigena*, *S. vernei* and *S. verrucosum*.

Introgression of LB resistance from wild species is time–consuming. It is achieved *via* several backcrosses to *S. tuberosum* to eliminate: short–day tendency for tuberization, long stolons, small tuber size, low yield, deep eyes, irregular tuber shape, and high glicoalkaloids content. A few such pre–breeding programs are known in the world to be held on a large scale, and the open question is the need for such an activity on international collaborative platform to speed up the introgression of new sources into cultivated material.

COMBINATION OF EARLINESS WITH LB RESISTANCE

Negative genetic correlation between early maturity and foliage resistance has been noted by many authors (Colon *et al.* 1995, Zimnoch–Guzowska *et al.* 2000) and was also proved by genetic linkage of factors related to both traits evidenced by their map position (Collins *et al.* 1999, Visker *et al.* 2003). Data for late blight resistance and maturity of cultivars registered in the Netherlands, Germany and Poland show the scale of the problem. However, in recent years, some shift towards shortening the vegetation period in set of cultivars with enhanced resistance to late blight has been noticed. The comparison of sets of evaluated cultivars from three listed countries shows that cultivars described as highly resistant (scores 8–9) or highly susceptible (scores 1–3) in foliage are lacking in German set, whereas such groups are noted in the two other countries (Table 2).

Weak positive correlation was observed between tuber resistance and late maturity by Toxopeus (1958) and Świeżyński *et al.* (1991). To overcome the problem in conventional breeding, careful selection against late maturity and for enhanced foliage resistance is recommended by Darsow and Hansen (2004, paper in this issue). Also, selection based on known map position of the Quantitative Trait Loci (QTL) related to lateness and those *R*–genes or QTL which are associated with resistance to late blight (see review by Śliwka 2004) seems to be reasonable. The use of novel sources of resistance via transgenic approach may be a promising way to solve this problem.

Table 2

Foliage resistance to *Phytophthora infestans* and maturity of potato according to varietal assessment (data from three countries)

Maturity	Germany (2002)									Σ
Mid–late to late					5	12	16			33
Mid–early				8	30	25	13			76
Early				2	16	25	9			52
First early				26	7					33
Resistance to LB→	1	2	3	4	5	6	7	8	9	
	susceptible						resistant			
Maturity	The Netherlands (2003)									Σ
Mid–late to late					1	5	1	3	1	11
Mid–early			1	6	13	6	5		1	32
Early		1	13	17	7	3	2	1		44
First early	2	9	6							17
Resistance to LB→	1	2	3	4	5	6	7	8	9	
	susceptible						resistant			
Maturity	Poland (2002)									Σ
Mid–late to late				3	9	11	7	2		32
Mid–early		1	6	9	11					27
Early		1	9	1						11
First early		2	6	1						9
Resistance to LB→	1	2	3	4	5	6	7	8	9	
	susceptible						resistant			

COMPLEXITY OF GENETIC DETERMINATION OF LB RESISTANCE

The species *S. demissum* proved to be an important source of resistance, and by conventional plant breeding in the 1940s and 1950s this source was introduced into commercial cultivars. Major resistance genes identified in this source (*R*–genes) governed race–specific resistance which was widely explored those days (Umaerus and Umaerus 1994). A large number of wild *Solanum* species was utilized by breeders as good sources of resistance. However, majority of them possessed *R*–gene type of resistance. Besides *R*–gene resistance, breeders searched for a more horizontal type of resistance, associated with polygenic background, which was believed to be more stable than the race–specific one. The ideas evolved along with increasing knowledge of the pathogen–host interactions as well as with practical experience.

Nowadays, discrimination between types of resistance does not seem to be so strict. Breeders search for effective barriers against this pathogen, including both existing genetic variation and modern techniques of di–agnostics, and for improved methods of creation of resistant genotypes *via* transgenic approach, somatic fusion etc.

Till now five (*R1*, *R2*, *R3*, *R6*, *R7*) of 11 known *R*–genes from *S. demissum* have been mapped on potato genetic map, followed by *R*–genes from *S. bulbocastanum* (*RB, Rblb*), *S. berthaultii* (R_{ber}) and *S. pinnatisectum* (*Rpi1*). They are localized on chromosomes IV, V, VII, VIII, X and XI. In several centers, along with localization of major genes on the map, the extended studies have been conducted on mapping QTL for resistance to late blight and for maturity in several *Solanum* species, being the sources of resistance. QTL for late blight resistance were identified on all the twelve potato chromosomes, with the strongest ones on chromosomes XII, V, III and VIII, whereas QTL for maturity were found on ten of them with the strongest QTL on chromosome V (Śliwka 2004).

Such complexity of genetic determination of resistance to LB and its association with lateness was stated by breeders as a factor hampering progress in resistance breeding.

COMBINATION OF FOLIAGE AND TUBER RESISTANCE

Tuber resistance is an essential component of potato resistance to *P. infestans*, as this pathogen is responsible for tuber rot in storage, and infected tubers of susceptible cultivars provide an important way of its overwintering. Tuber resistance is regarded to be of special importance in foliage resistant cultivars due to the risk of prolonged infection from partly infected foliage (Wastie *et al.* 1991). In organic potato production, when farmers are not able to protect foliage from late blight sufficiently, tuber resistance factor is of growing significance for proper tuber stor–age and reduction of crop losses. For many years breeders were lively interested in getting progress in foliage resistance to *P. infestans,* while tuber resistance was taken into account only occasionally. Recently the situation has changed. Sixty–two percent of the programs surveyed by Zimnoch–Guzowska and Flis (2002) considered tuber resistance to be of equal or higher importance than foliage resistance, while only 38% judged foliage resistance to be more important. The resistance of tubers and foliage is slightly positively correlated, but the strength of this as–sociation depends on plant material under test and a method of assess–ment (Świeżyński 1990, Platt and Tai 1998). The recognized map positions of QTL associated with tuber and foliage resistance confirm that these two characters are governed independently to a large extent. However, when major genes actions are taken into account, joint effects are much stronger (Śliwka, personal communication). Information on none relationship between foliage and tuber resistance has been only sporadic (Stewart *et al.* 1992, Dorrance and Inglis 1998). Some discrep–

ancies in published results indicated strong interactions between such important factors as genetic background of tested material, applied iso–lates and screening methods. From above, the conclusion can be drawn that bred material has to be tested for both traits, when breeder wants to select clones resistant in foliage and tuber.

SCREENING METHODS APPLIED FOR RESISTANCE EVALUATION

The conditions in which tests to assess resistance to *P. infestans* are done can greatly vary between breeding and research programs. This was evidenced in the survey made by Zimnoch–Guzowska and Flis (2002). Large discrepancies are present in tuber resistance assessment, when the same cultivar is assessed at various centers (Świeżyński *et al.* 2001, www.europotato.org).

Foliage and tuber resistance to *P. infestans* of cultivars registered in 2002 in Poland and Germany is presented in (Table 3). It is shown that in Polish register list the group of cultivars with enhanced tuber resis–tance (scored 6 or more) is lacking, while in German list the cultivars with tuber resistance scored 7 or 6 are most frequently represented among listed forms (data from both countries were compared after re–version of German scale). Differences found between the two mentioned register lists might be explained by more severe screening methods used in Poland, or by the differences in the evaluation scale applied.

Table 3a

Foliage and tuber resistance to *Phytophthora infestans* in potato cultivars registered in Poland, 2002

		Foliage resistance in 1–9 scale									
		1	2	3	4	5	6	7	8	9	Σ
Tuber resistance in 1–9 scale	9										
	8										
	7										
	6										
	5			2	3	3		1	1		10
	4		1	9	6	10	6	5	1		39
	3		1	4	2	3	1				11
	2		2		1						3
	1										
	Σ		4	15	12	16	7	6	2		62

Table 3b

Foliage and tuber resistance to *Phytophthora infestans* in potato cultivars registered in Germany, 2002

Tuber resistance in 1–9 scale	Foliage resistance in 1–9 scale: 1	2	3	4	5	6	7	8	9	Σ
9										
8										
7				20	21	31	16			88
6				13	19	12	13			57
5				2	7	7	4			20
4				1		4	3			8
3					1		1			2
2										
1										
Σ				36	48	54	37			175

EUCABLIGHT, the ongoing UE Concerted Action project, is directed on the creation of agreed sets of standards for agreed conditions of respective assessment methods, that will lead to the creation of joint European database, in which the notes given to cultivars or lines will be of the same or, at least, a very similar meaning.

COST OF SELECTION FOR RESISTANCE

It is difficult to assess the cost of selection for LB resistance, as in routine selection process the elimination of breeding material is done simultaneously according to several criteria. So, the decrease of a number of selected genotypes due to LB resistance is masked by other factors.

It is much easier to estimate the cost of screening for LB resistance. A few examples of costs estimated at various centers for various screening methods are given below.

The total cost of screening of single breeding line evaluated for LB resistance for three years at the IHAR Młochów using various screening methods is 190 . This cost covers two years of field assessment at two locations (the cost of one field screening season is 50), and three years of laboratory tests for both detached leaflets (10 /year) and whole tuber/tuber slices (20 /year).

Own cost of field assessment made at the Plant Research International in Renkum, the Netherlands, is ca 60 e.g. 20 /plot in 3 replicates (Colon, personal communication). In the Mexican program

PICTIPAPA held at Toluca, the place of *P. infestans* origin, the cost of field assessment per single breeding line was estimated at the beginning of 1990s as 200 US$ for private and 50 US$ for public research. Field testing for LB resistance performed at Mont Vermont, USA, has charges varying between years. On average, it is about 50–75 US$. This price covered growing of three reps of five plants in irrigated field, notes for LB development, yield and tuber rot data at harvest, and allozyme characterization of *P. infestans* isolates collected form the trail (Inglis, personal communication).

A comparison of the costs of assessment for LB resistance presented above with the known costs of characterization of other quality or resistance traits strongly suggests that selection for LB resistance is not more costly than selection for other traits done along selection cycle. However, breeders have to accept the additional costs, when screening for LB resistance is included into selection procedures.

LACK OF MOLECULAR MARKERS (MAS) APPLICABLE TO SELECTION FOR LB RESISTANCE

Intensive studies on mapping the potato genome from early 1990s have significantly increased our knowledge on potato genome organization and location on potato genome of several *R*–genes and QTL associated with resistance to *P. infestans*. Up–to–day the selection based on markers (MAS) associated with the LB resistance is not in wide application. The slower progress, as compared with the expected one, in application of MAS is due to different pools of plant material used for mapping or markers studies and for breeding, and also to a narrow specificity of markers identified, which are far from universal application to broad spectrum of breeding pools. Recently, a wide interest is directed to the resistance genes identified in *S. bulbocastanum* source in the USA (Song *et al.* 2003) and Europe (Van der Vossen *et al.* 2002), which to some extent have already been incorporated into breeding material. In the article by Trognitz and Trognitz (2004, this issue) all aspects of using molecular markers in potato selection for resistance to late blight are comprehensively discussed.

FINAL REMARKS

The above reasons inhibiting progress in breeding LB resistant cultivars vary in their importance. It might be stated that three main reasons stimulate activities of breeders and scientists in resistance breeding for LB: (i) losses in ware crop production, (ii) the increase of public interest in organic production, in which chemical crop protection is prohibited, and for which cultivation of LB resistant potato cultivars is the necessity, and (iii) public concern in reduced application of chemi–

cals in potato production, where up to 15–16 sprays, depending on circumstances, are applied under high input production regime.

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