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Resistance of Potato Tubers to a Highly Aggressive Isolate of *Phytophthora infestans* in Relation to Tuber Age

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Abstract The goal of these studies was to evaluate the influence of tuber age on the expression of resistance to *Phytophthora infestans* in five selected potato genotypes (three cultivars and two clones) varying in tuber resistance and maturity type, and also to select the best time for testing potato tubers for resistance to blight. Resistance was evaluated by inoculating whole tubers at 13 different times as they progressively aged during growth and storage. Tuber age was expressed as weeks after planting. Tubers were rated from week 13 (late July) until week 43 (late February) for tubers planted on 27–28 April, over three consecutive seasons (2001–2003). Analysis of variance performed on tuber resistance data showed significant effects of genotype, year and tuber age. Significant contributions of genotype × year, genotype × tuber age, year × tuber age and year × genotype × tuber age interactions were also detected. A slight increase in tuber resistance with tuber age was observed for cvs Bzura, Sokół and Irga, while the opposite trend was observed for the clones 97-A-63 and DG 92-227. Changes in tuber resistance with age of tested genotypes were not related to their maturity type. The period of most stable expression of tuber resistance was observed when tubers were tested between the 16th and 28th week after planting.

Keywords late blight · *Solanum tuberosum L.*

Introduction

Phytophthora infestans is the pathogen responsible for late blight on foliage and tubers of potato. Tuber blight often causes serious tuber rot in storage and provides an important means for the pathogen to overwinter (Świeżyński and Zimnoch-Guzowska 2001). Developing and mature tubers may be infected whenever sporangia from lesions on stem and foliage are washed into the soil and come into contact with tubers (Govers 2005). Cox and Large in 1960 (cited in Langton 1972) presented data for England and Wales showing

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that, in years when foliar late blight is widespread, about 2% of tubers are lost due to tuber infection prior to harvesting.

The potato industry's problems with tuber blight have increased along with the changes in the aggressiveness of the *P. infestans* population in North America and in Europe (Lambert and Currier 1997; Peters et al. 1999; Flier et al. 2001). Isolates of the newly established *P. infestans* population in the Netherlands are able to infect potatoes at temperatures ranging from 3 °C to 27 °C, while the old population caused infection at 8 °C to 23 °C (Flier 2001). These changes may also influence development of *P. infestans* on tubers during storage.

Resistance of potato to late blight is even more important in organic potato production, where tubers are more likely to be exposed to infection from blighted plants than in conventional systems. Late blight is termed a fatal threat in organic potato production as it can stop the growing season by the middle of August, as happened in 2003 and 2004 in Finland (Hannukkala and Lehtinen 2005). More attention is paid to the resistance of potato to late blight in foliage than in tubers, although breeding potato for resistance to *P. infestans* in foliage does not always result in increasing the resistance of the tubers. Depending on the material tested, the relationship between resistance of potato to *P. infestans* in foliage and tubers has been described as weak (Świeżyński 1990; Kirk et al. 2001), positively correlated (e.g., in tetraploid populations obtained after crossing of resistant with susceptible parents, correlation ranged from 0.46 to 0.69) (Stewart et al. 1994), and even negatively correlated (Collins et al. 1999). The expression of resistance depends to a large extent on the testing conditions, and thus can be difficult to evaluate (Świeżyński and Zimnoch-Guzowska 2001). A delay between harvest and inoculation dates has sometimes been found to considerably increase the level of tuber resistance. This effect depended on the cultivars tested in studies by Malcolmson (1981), Stewart et al. (1983), and Bjor (1987). In a study by Bhatia and Young (1985), tubers of cultivar Atzimba were highly resistant when recently harvested, but became increasingly susceptible as they aged physiologically; however, tubers of other cultivars – Katahdin, Kennebec and Sebago – remained susceptible. Differences depending on the time of evaluation of tuber resistance were also found in potato genotypes tested by Darsow (1983).

The goal of the this study was to evaluate the relationship between tuber age and resistance of tuber tissue to colonisation by *P. infestans* in five selected potato genotypes varying in the level of tuber resistance and maturity type, and to select the best time for testing potato tubers for resistance to tuber blight.

Materials and Methods

The influence of tuber age on the expression of resistance to *P. infestans* was studied in five selected genotypes of various tuber resistance to late blight and maturity type: a mid-late diploid clone (DG 92-227, resistant to *P. infestans* in leaves and tubers); a tetraploid clone (97-A-63, mid-resistant and late); the mid-early cv. Irga (scored 2 in leaves and 4 in tubers), the late cv. Bzura (scored 8 in leaves and 4 in tubers); and the mid–late cv. Sokół (scored 3 and 6 in leaves and tubers, respectively). Scores for foliage and tuber resistance of these cultivars are listed on a scale of 1–9, where 9 is the most resistant according to the Polish Catalogue of Potato Varieties (1996, 1999). Both cv. Bzura and clone 97-A-63 contain *R*-genes derived from *Solanum demissum*. The *R*-gene *Rpi-phu*1 in clone DG 92-227 is derived from *Solanum phureja* (Śliwka et al. 2006).

Tubers were planted during the last week of April (in 2002 and 2003) or the first week of May (in 2001), and harvested in the last week of September in all 3 years of the study. Tuber resistance to *P. infestans* was tested 13 times in each year: every week for 4 weeks, and then every 3 weeks from the last week of July until the last week of February. The first six tests were performed on tubers collected from the field before harvest and the remaining seven tests on tubers kept in storage at 7–9°C.

Evaluation of tuber resistance to colonisation by *P. infestans* was performed according to Björ (1987) with some modifications. The isolate of *P. infestans*, MP 324, race 1.2.3.4.(5).6.7.(8).10.11, was used for inoculation of tubers. The virulence of MP 324 was not fully expressed for factors 5 and 8, as, out of 28 leaflet tests performed at the same time as the tuber inoculations, the leaflets of Black's differential *R5* were infected in seven tests and *R8* in 14 tests. Since the MP 324 isolate was previously maintained for a long time on artificial substrates, it was transferred through susceptible potato slices 2–3 times before the first test date and then maintained on, and collected from, susceptible potato slices during the testing period. The concentration was adjusted to a concentration of 50 sporangia/mm^3, and the inoculum was kept for 2.5 h in a refrigerator and then 0.5 h at 20°C before inoculation. Five tubers of each potato genotype, in two replications, were wounded by small pins, sprayed with *P. infestans* inoculum, and kept in a dark climatic chamber at 16–18°C for 3 weeks. After incubation, tubers were cut longitudinally and disease severity was scored on a scale of 1–9, where 9 = no symptoms (Zarzycka 2001).

Three-factor and two-factor analyses of variance for resistance of tuber tissue to colonisation by *P. infestans* were performed. Genotypes were ranked, and the significance of the deviations of the mean for each date from the general mean for each potato genotype was evaluated using Duncan's Multiple Range test (Milliken and Johnson 1984) using STATISTICA for Windows (Stat Soft, Tulsa, OK; ver. 1997).

Results

In a 3-year evaluation of tuber resistance to *P. infestans* using five potato genotypes, analysis of variance showed highly significant effects of genotype, year, and tuber age on resistance expression (Table 1). The variation among potato genotypes provided the highest contribution to total variation (93.5%). The average resistance score for all tested material was 5.5 in 2001, 5.3 in 2002, and 5.2 in 2003. Tubers of the diploid clone DG 92-227 were

Table 1 Analysis of variance on the resistance to colonisation of potato tubers of different age inoculated with *Phytophthora infestans* for three potato cultivars and two potato clones tested at 13 time points in three growing seasons (2001–2003)

Source	*df*	Mean squares
Genotype	4	146.11***
Year	2	4.11***
Tuber age	12	0.73***
Year × genotype	8	2.11***
Year × tuber age	24	0.54***
Genotype × tuber age	48	2.24***
Year × genotype × tuber age	96	0.39***
Error	195	0.10

*** Significant at $P < 0.001$

Table 2 Tuber resistance to colonisation by *P. infestans* for three cultivars and two clones tested at different age stages in three different years (2001–2003)

Tuber age (weeks)[a]		13	14	15	16	19	22	25	28	31	34	37	40	43	Mean	
Month		July	August	August	August	September	September	October	November	December	December	January	February	February	Year/overall	
Genotype/ *maturity*	Year															
DG 92-227	2001	8.0	8.0	8.0	8.0	8.0	7.6	8.0	8.0	8.0	8.0	8.0	8.4	7.2	7.9 a	
late	2002	7.6	8.5	9.0	7.9	7.1	7.6	8.0	8.2	8.5	8.1	6.3	6.4	6.2	7.6 b	7.8 u
	2003	8.5	8.6	8.4	8.5	7.9	8.7	8.0	8.0	7.5	7.5	7.4	7.1	6.9	7.9 a	
Cv. Sokół	2001	4.0	4.5	4.7	4.8	5.3	5.1	5.9	5.7	5.6	5.9	6.0	6.1	5.0	5.3 c	
mid-late	2002	5.8	5.7	4.1	4.7	5.3	5.1	5.4	5.1	5.4	5.6	5.7	5.8	5.8	5.3 c	5.2 w
	2003	3.9	4.1	4.1	4.8	4.4	5.2	5.0	5.4	5.3	5.5	5.4	6.0	5.8	5.0 de	
97-A-63	2001	4.7	6.8	6.5	4.8	6.1	5.3	4.8	4.6	4.5	4.8	4.5	4.3	4.7	5.1 d	
late	2002	5.6	6.6	6.2	4.8	4.1	4.9	4.7	4.5	4.1	3.9	4.1	4.6	4.0	4.8 f	5.0 x
	2003	5.4	6.7	6.6	5.2	5.3	5.2	4.6	4.9	4.7	4.4	4.6	4.5	4.0	5.1 d	
Cv. Irga	2001	4.9	4.8	4.7	4.5	4.4	5.9	5.1	4.8	4.9	5.4	5.6	5.5	5.1	5.0 de	
mid-early	2002	4.8	5.0	4.7	5.0	5.2	4.8	4.9	4.8	4.6	5.5	5.4	5.4	5.9	5.1 d	4.8 y
	2003	3.9	4.6	4.9	4.3	3.8	3.6	4.3	4.3	4.8	3.8	5.1	4.8	5.0	4.4 g	
Cv. Bzura	2001	3.7	4.3	2.9	3.2	5.4	3.9	4.3	4.0	5.4	5.5	5.8	5.8	5.0	4.6 g	
late	2002	4.6	4.2	3.7	4.7	4.5	4.2	4.6	5.3	5.2	4.7	5.2	5.7	6.0	4.8 ef	4.4 z
	2003	2.7	3.4	3.8	3.8	3.5	2.7	4.9	3.4	3.8	4.0	4.7	5.1	4.3	3.9 h	
Mean		5.2	5.7	5.5	5.3	5.4	5.3	5.5	5.4	5.5	5.5	5.6	5.8	5.3		

[a] Weeks after planting (the first six tests were performed on tubers collected from the field while the remaining tests were done on tubers from storage); means followed by the same letter do not differ significantly using Duncan's multiple range test at $P = 0.05$

Table 3 Deviations from the 3-year means of tuber resistance to *P. infestans* and ranking of means according to Duncan's multiple range test in three cultivars and two clones of potato tested at 13 age stages over 3 years (2001–2003)

Tuber age (weeks[a])		13	14	15	16	19	22	25	28	31	34	37	40	43
Genotype	Overall mean													
Deviations														
DG 92-227	7.8	0.1	0.5*	0.6*	0.2	−0.2	0.1	0.1	0.2	0.1	−0.0	−0.7*	−0.6*	−1.1*
Cv. Sokół	5.2	−0.6	−0.4	−0.9*	−0.4	−0.2	−0.1	0.2	0.2	0.2	0.5*	0.5*	0.8*	0.32
97-A-63	5.0	0.2	1.7*	1.4*	−0.1	0.2	0.1	−0.3	−0.3	−0.6	−0.6	−0.6	−0.5	−0.8
Cv. Irga	4.8	−0.3	0.0	−0.0	−0.2	−0.3	−0.0	−0.0	−0.2	−0.0	0.1	0.6*	0.4*	0.5*
Cv. Bzura	4.4	−0.6	−0.3	−0.8	−0.4	0.2	−0.7	0.3	−0.1	0.5	0.4	0.9*	1.2*	0.8*
Ranking[b]														
DG 92-227	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Cv. Sokół	b	c	c	c	b	b	b	b	b	b	b	b	b	b
97-A-63	c	b	b	b	b	b	b	c	c	d	d	d	d	c
Cv. Irga	d	c	c	c	b	c	c	c	c	c	c	c	c	b
Cv. Bzura	e	d	d	d	c	c	d	c	d	c	c	c	bc	b

*Significant at $P = 0.05$

[a] Weeks after planting

[b] Ranking concerns only data in columns, same letter indicates the same level of resistance using Duncan's multiple range test at $P = 0.05$

the most resistant to colonisation by *P. infestans*, scoring 7.8 out of 39 tests performed over 3 years. Tubers of cv. Bzura were the most susceptible, scoring 4.4 over the 3 years. The three remaining genotypes, Sokół, 97-A-63 and Irga, scored 5.2, 5.0 and 4.8, respectively, over the 39 tests performed. All these genotypes differed significantly from each other in tuber resistance (Table 2).

Significant contributions of genotype × year, genotype × tuber age, year × tuber age and year × genotype × tuber age were also detected. When the averages over years were analysed, a slight increase of tuber resistance with age of stored tubers was observed for three cultivars. Irga from the 34th to 40th week after planting and Sokół and Bzura from the 37th to 43rd week after planting, while a slight decrease in resistance was observed for the clone DG 92-227 from the 37th to 43rd week after planting (Table 3). The same clone (DG 92-227), as well as clone 97-A-63, expressed an increase in resistance at the beginning of the testing period (performed at 1-week intervals, the 14th and 15th week after planting). Expression of resistance to tuber blight in the clone DG 92-227 was stable and high in the first year of testing. However, there was a tendency for decreasing resistance with increasing tuber age in the two subsequent years. Stability of expression of resistance was estimated in two ways: by comparison of a ranking of tested genotypes at each test date with the mean ranking, and by estimation of the significance of deviations of the means from the general means for each genotype tested at each date.

The most stable expression of resistance for all genotypes tested was observed between the 16th and 28th week after planting, when genotype rankings did not differ by tuber age (Table 3). Deviations from the 3-year mean in comparison with the mean of each tuber age for each corresponding genotype were not statistically significant in tests performed on tubers aged between 16 and 31 weeks after planting.

The dynamics of change in tuber resistance was not related to the maturity class of the clones and cultivars. For example, there were two late genotypes, Bzura and 97-A-63, which differed in tuber blight resistance expression tested from July to February. In the clone 97-A-63, resistance increased at the beginning of testing period, and in cv. Bzura resistance increased at the end of the testing period (from the 37th to the 43rd week after planting). Two mid-late maturing genotypes, Sokół and clone DG 92-227, also differed in resistance expression. Sokół expressed decreased resistance in the 15th week, and increased resistance in the 34th–40th week after planting. Clone DG 92-227 showed increased resistance in 14th–15th week after planting and decreased resistance in the 37th–43th week after planting. Cv. Irga, representing the earliest maturity type, mid-early, showed an increase in resistance of tubers at the end of the testing period, i.e., 37–43 weeks after planting.

Discussion

All factors tested in this study (genotype, year and tuber age) were significant in expression of tuber resistance to colonisation by *P. infestans* in potato cultivars and clones. Interactions among all tested factors also proved important. A significant interaction between tuber blight resistance and year of testing was reported by Flier et al. (2001) and Stewart et al. (1996), who also reported a significance interaction between date of harvest and year.

Flier et al. (2001) showed a significant cultivar × isolate interaction, but in our study only one *P. infestans* isolate – the most aggressive isolate from own collection – was used.

Various methods of inoculation reveal various types of resistance. Inoculation of uninjured tubers expresses resistance to infection by the skin (lenticels and eyes) and

cortex, and more closely imitates infection of tubers occurring under natural conditions. In contrast, inoculation of injured tubers, or slices cut from tubers, can reveal resistance of the internal tissue to colonisation and sporulation by the pathogen, which is very important in stored potato tubers (Zarzycka 1990).

Some studies have shown that resistance to initial infection of potato eyes and lenticels of tubers gradually increased as the growing season progressed and the tubers matured (Lapwood 1967; Walmsley-Woodward and Lewis 1977; Malcolmson 1981; Stewart et al. 1983; Bjor 1987). Grinberger et al. (1995) further reported that tuber blight incidence and severity were strongly affected by tuber age: an increase in tuber resistance to blight during vegetation (tested between 48 and 95 days after planting) and in storage (tested between 118 and 208 days after planting) was observed. However, a temporary decrease in resistance was observed for tubers tested between 95 and 118 days after planting.

Different results were obtained when tuber resistance to colonisation by the pathogen was investigated. In a slice test, the resistance of potato tuber tissue remained the same with age in susceptible potato cultivars, but decreased with age of tested tubers in resistant cultivar (Bhatia and Young 1985). Three cultivars evaluated for tuber resistance to colonisation in our study showed a slight increase in resistance with age while the resistance of two genotypes (one highly resistant) slightly decreased. According to Spychalla and Desborough (1990a, 1990b) a gradual increase in the content of unsaturated fatty acids in potato tubers with time in storage lessens membrane permeability and increases concentrations of antioxidants – factors that can contribute to increased resistance to tuber blight.

Two potato clones (DG 92-227, 97-A-63), both possessing *R*-gene(s), showed decreased resistance to blight as tubers aged. This is consistent with the conclusions of others (Chalenko et al. 1980; Allen and Friend 1983) that the expression of *R*-gene-based resistance declines with prolonged tuber storage. A different result was observed for tubers of the *R*-gene(s)-possessing cv. Bzura, in which the resistance of tubers increased with age. The presence of *R*-genes in plants can result in hypersensitive reactions in leaves and in tubers, in leaves only, or in delayed pathogen invasion in tubers (Świeżyński and Zimnoch-Guzowska 2001). The gene *R1* is effective in tubers (Roer and Toxopeus 1961), but efficacy depends on potato genotype and testing conditions (see Świeżyński and Zimnoch-Guzowska 2001). Park et al. (2005) confirmed expression of the *R1* gene in foliage and tubers, and reported that resistance in foliage and tubers is conferred by the same *R*-gene. *Rpi-phu*1, the resistance gene in clone DG 92-227, was highly effective in leaflet, tuber slice and whole tuber tests over 5 years of phenotypic assessment (Śliwka et al. 2006). Tubers of this clone were the most resistant in our study. The clone 97-A-63 and cv. Bzura possess *R*-genes that are expressed in leaves but not in tubers. Expression patterns of *R*-genes for resistance to *P. infestans* may be different in leaves and tubers and the results obtained support this hypothesis.

No clear trends were observed between tuber resistance expression and maturity type. Both the most resistant and the most susceptible genotypes were late maturing. According to Świeżyński (1990), no association between maturity type and tuber resistance was evident in a group of 623 potato cultivars from Germany, Holland, Poland and the former Czechoslovakia.

Tuber resistance to colonisation by *P. infestans* was most stable between the 16th and 28th week after planting (in this experiment between 7 September and 16 November) and this time period may be suitable for testing tuber resistance in potato. The time of highest stability overlaps with the time of stability of tuber resistance to colonisation with *P. infestans* reported in the studies of Bhatia and Young (1985). Their work consisted of eight

tuber tests from the 1st until the 210th day after storage. Uniform results were obtained for 60 days after storage. The authors concluded that the physiological age of potato tuber tissue must be considered when evaluating resistance to *P. infestans*. Bjor (1987) found that differences in planting time of up to 6 weeks did not significantly influence the susceptibility of non-wounded tubers. From a practical point of view, the resistance that is expressed in potato tubers during and prior to harvest, when natural infection can occur, and again at the beginning of storage, when resistance can protect tubers against *P. infestans*, is the most important.

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References

Allen FHE, Friend J (1983) Resistance of potato tubers to infection by *Phytophthora infestans*: a structural study of haustorial encasement. Physiol Plant Pathol 22:285–292

Bhatia SK, Young RJ (1985) Reaction of potato tuber slices to *Phytophthora infestans* in relation to physiological age. Am Potato J 62:471–478

Bjor T (1987) Testing the resistance of potato genotypes to tuber late blight. Potato Res 30:525–532

Chalenko GI, Leontyeva GV, Karavaeva KA, Yurganova LA, Ozeretskovskaya OL (1980) Ustojchivost klubnya kartfelya k vozbuditelyu fitoftoroza v period khraneniya (Resistance of potato tubers to the phytophthorosis agent during their storage). Prikl Biokhim Mikrobiol 16:194–199

Collins A, Collins A, Milbourne D, Ramsay L, Meyer R, Chatot-Balandras C, Oberhagemann P, De Jong W, Gebhardt C, Bonnel E, Waugh R (1999) QTL for field resistance to late blight in potato are strongly correlated with maturity and vigour. Mol Breed 5:387–398

Darsow U (1983) Prüfung unverletzter erntefrischer Kartoffelknollen auf relative Braunfäulerezistenz. Arch Züchtungsforsch 13:357–366

Flier WG (2001) Variation in *Phytophthora infestans*, sources and implications. PhD thesis, Wageningen University, The Netherlands ISBN: 90 5808 420 5

Flier WG, Turkensteen LJ, van den Bosch GBM, Vereijken PFG, Mulder A (2001) Differential interaction of *Phytophthora infestans* on tubers of potato cultivars with different level of blight resistance. Plant Pathol 50:292–301

Govers F (2005) Late blight: the perspective from the pathogen. In: Havenkort AJ, Struik PC (eds) Potato in progress: science meets practice. Wageningen Academic, The Netherlands, pp 245–254

Grinberger M, Kadish D, Cohen Y (1995) Infectivity of metalaxyl-sensitive and -resistant isolates of *Phytophthora infestans* to whole potato tubers as affected by tuber aging and storage. Phytoparasitica 23:165–175

Hannukkala A, Lehtinen A (2005) Potato late blight-fatal threat in organic potato production. Forskningsnytt 1:10–11

Kirk WW, Felcher KJ, Douches DS, Niemira BA, Hammerschmidt R (2001) Susceptibility of potato (*Solanum tuberosum* L.) foliage and tubers to the US8 genotype of *Phytophthora infestans*. Am J Potato Res 78:319–322

Lambert DH, Currier AI (1997) Differences in tuber rot development for North America clones of *Phytophthora infestans*. Am Potato J 74:39–43

Langton FA (1972) The development of a laboratory method of assessing varietal resistance of potato tubers to late blight (*Phytophthora infestans*). Potato Res 15:290–301

Lapwood DH (1967) Laboratory assessment of the susceptibility of potato tubers to infection by blight (*Phytophthora infestans*). Eur Potato J 10:127–135

Malcolmson JF (1981) Mechanisms of field resistance to potato blight and variability of the pathogen. Scottish Plant Breeding Station, 60th Annual Report 1980–81, pp 110–111

Milliken GA, Johnson DE (1984) Analysis of messy data: volume 1. Designed experiments. Van Nostrand Reinhold, New York

Park T-H, Vleeshouwers VGAA, Kim J-B, Hutten RCB, Visser RGF (2005) Dissection of foliage and tuber late blight resistance in mapping populations. Euphytica 143:75–83

Peters RD, Platt HW, Hall R, Medina M (1999) Variation in aggressiveness of Canadian isolates of *Phytophthora infestans* as indicated by their relative abilities to cause potato tuber rot. Plant Dis 83: 652–661

Polish Catalogue of Potato Varieties (1996) IHAR, Bonin, Poland, pp 1– 147

Polish Catalogue of Potato Varieties (1999) IHAR, Bonin, Poland, pp 1– 200

Roer L, Toxopeus HJ (1961) The effect of *R*-genes for hypersensitivity in potato leaves on tuber resistance to *Phytophthora infestans*. Euphytica 10:35–42

Śliwka J, Jakuczun H, Lebecka R, Marczewski W, Gebhardt C, Zimnoch-Guzowska E (2006) The novel, major locus *Rpi-phu*1 for late blight resistance maps to potato chromosome IX and is not correlated with long vegetation period. Theor Appl Genet 113:685–695

Spychalla JP, Desborough SL (1990a) Fatty acids, membrane permeability and sugars of stored potato tubers. Plant Physiol 94:1207–1213

Spychalla JP, Desborough SL (1990b) Superoxide dismutase, catalase, and α-tocopherol content of stored potato tubers. Plant Physiol 94:1214–1218

Stewart HE, Bradshaw JE, Wastie RL (1994) Correlation between resistance to late blight in foliage and tubers in potato clones from parents of contrasting resistance. Potato Res 37:429–434

Stewart HE, McCalmont DC, Wastie RL (1983) The effect of harvest date and the interval between harvest and inoculation on the assessment of the resistance of potato tubers to late blight. Potato Res 26:101–107

Stewart HE, Wastie RL, Bradshaw JE (1996) Susceptibility to *Phytophthora infestans* of field- and glasshouse-grown potato tubers. Potato Res 39:283–288

Świeżyński KM (1990) Resistance to *Phytophthora infestans* in potato cultivars and its relation to maturity. Genetica Pol 31:99–106

Świeżyński KM, Zimnoch-Guzowska E (2001) Breeding potato cultivars with tubers resistant to *Phytophthora infestans*. Potato Res 44:97–117

Walmsley-Woodward DJ, Lewis BG (1977) Laboratory studies of potato tuber resistance to infection by *Phytophthora infestans*. Ann Appl Biol 85:43–49

Zarzycka H (1990) A comparison of tuber slice and whole tuber tests for the assessment of potato resistance to tuber blight (*Phytophthora infestans* (Mont.) de Bary). Acta Agrobot 43:95–107

Zarzycka H (2001) Assessment of resistance to *Phytophthora infestans* in tuber slices and whole tubers. Plant Breeding and Acclimatization Institute, Radzików, Poland. IHAR Monografie i Rozprawy Naukowe 10a:78–80