

Resistance to *Phytophthora infestans* in diploid and tetraploid potato families. 3. Correlations between characters

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Abstract. In four diploid and four tetraploid families correlations were evaluated between resistance to *Phytophthora infestans* of leaflets, tuber slices and whole tubers as well as correlations between three aspects of resistance and maturity or tuber shape regularity. A virulent *P. infestans* isolate was used for inoculations. Only in the family D4 a significant positive correlation was found between all the three aspects of resistance. Genotypes with susceptible leaflets and resistant tuber slices were not identified in any family. In some families genotypes with resistant whole tubers and susceptible tuber slices were found; the family D5 was found to have genotypes in which resistance of leaflets was associated with susceptibility of tuber slices. The resistance to *P. infestans* of leaflets or tuber slices tended to be negatively correlated with both early maturity and regularity of tuber shape.

Key words: *Phytophthora infestans*, potato, resistance.

Introduction

Breeders attempting to develop potato cultivars resistant to *Phytophthora infestans* are interested to know, what is the relation between the resistance in different organs of the plant and what is the relation between resistance to *P. infestans* and other important characteristics of potato cultivars. Reports in this area are not consistent. There is only a weak, positive correlation between resistance to *P. infestans* in foliage and tubers in potato cultivars (ŚWIEŻYŃSKI 1990), but a fairly strong positive correlation between the two characters was

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found in potato families obtained from crossing a resistant parent with a susceptible partner (STEWART et al. 1994). The extent of this correlation was found to depend on the method of resistance evaluation (DEAHL et al. 1974, PIOTROWSKI 1975).

In potato cultivars early maturity is negatively correlated with both, foliage and tuber resistances, the second relation being less pronounced (ŚWIEŻYŃSKI 1990). Nevertheless, in segregating potato families no genotypes were identified in which a high level of tuber resistance would be associated with early maturity (ŚWIEŻYŃSKI et al. 1993).

The main source of resistance to *P. infestans* are wild potato relatives (ROSS 1986). It can be suspected that genes responsible for resistance may be linked to genes determining undesirable characteristics of wild species. The few published reports are not consistent in this respect. CALIGARI et al. (1985) observed no negative effects of selection for resistance to *P. infestans*, but DARSOW and OERTEL (1986) noted that resistant seedlings were on the average inferior in maturity and general tuber appearance.

In some families, obtained from parents utilized in breeding potatoes resistant to *P. infestans*, the variation in leaflet and tuber resistance was analyzed (ŚWIEŻYŃSKI et al. 1997a, b). In the present paper, relations between resistance in leaflets, resistance in tubers, maturity and regularity of tuber shape are evaluated in these families.

Material and methods

Evaluated potato genotypes

Genotypes of diploid (D) and tetraploid (T) families were evaluated together with their parents at the Młochów Research Center. The families were sown in 1991 (evaluated in 1991 and 1992) or in 1992 (evaluated in 1992). Some selected genotypes were tested also in 1993 and finally evaluated in 1994.

In 1991, two diploid (D4 and D5) and three tetraploid families (T5, T6 and T7) were sown. First year seedlings were grown in the field in 1991 and their first tuber progeny was planted with presprouted tubers on 28 April, 1992: from each genotype (1) a 2-hill plot for the evaluation of early tuber yield and tuber shape (planting with medium-size tubers, harvest on 5 August) and (2) two 4-hill plots for the evaluation of vegetative period, tuber resistance and tuber shape (harvest on 9 September). On the basis of the reaction to *P. infestans* in 1992, five groups of genotypes were selected from each family. They had the following characteristics: 1) resistant leaflets and tuber slices,

2) resistant leaflets, susceptible tuber slices, 3) susceptible leaflets, resistant tuber slices, 4) resistant whole tubers, susceptible tuber slices and 5) susceptible leaflets and tuber slices. All these groups, except the last one, were propagated and evaluated in 1993. Virus infection in 1992 reduced the number of genotypes to 58%. If testing in 1993 confirmed the results of 1992, the genotypes were evaluated in 1994. In 1994 the selected genotypes were planted with presprouted tubers on 28 April, each genotype on 15-hill plots in 2 replications; they were harvested on 20 September.

In 1992, two diploid (D7 and D8) and one tetraploid families (T9) were sown. Each family consisted of a large number of genotypes to assess, as far as possible, the whole range of variation in the progeny. To reduce losses caused by viruses in diploid families, young seedlings were inoculated with the viruses PVY and PVM to eliminate susceptible ones. First year seedlings were planted in the field on 21 May and harvested on 6 October. Four groups of first year seedlings were selected for evaluation in successive years. Their respective characteristics are: 1) resistant leaflets and tuber slices, 2) resistant leaflets, susceptible tuber slices, 3) susceptible leaflets, resistant tuber slices and 4) susceptible leaflets and tuber slices. The first tuber progeny was planted and evaluated in 1993. If the results of resistance evaluation in 1992 were confirmed, all the groups, except group 4, were evaluated again in 1994. In 1994 presprouted tubers were planted (15-hill plot in 2 replications) on 28 April and harvested on 20 September. Losses due to virus infection were negligible.

The parents of each family were planted in triplicate and evaluated with the progeny genotypes. The total number of evaluated genotypes in each family is shown on Table 1. The names of parents of these families are given in Table 2 (families sown in 1991) and Table 3 (families sown in 1992). The origin of the evaluated genotypes is given by ŚWIEŻYŃSKI et al. (1997a). The yielding ability of tetraploid parents was on the level of cultivars; that of diploid parents was on the level of *Solanum tuberosum* dihaploids. No early maturing genotypes were present among diploid parents and no first early ones were present among tetraploid parents.

Evaluation of reaction to *P. infestans* in detached leaflets, tuber slices and whole tubers

In families sown in 1991 the evaluation in 1992 consisted of testing 10 leaflets per genotype (2 tests \times 5 leaflets) in the summer and testing 20 tuber slices and 20 whole tubers per genotype (2 tests \times 2 reps. \times 5 slices/whole tubers) in the autumn.

In families sown in 1992 the evaluation in 1992 consisted of testing 6 leaflets per genotype (2 tests \times 3 leaflets) in the summer and 4 tuber slices per genotype (2 tests \times 2 slices) in the late autumn.

In 1994, the evaluation of genotypes selected from families sown in 1991 and 1992 consisted of testing 18 leaflets per genotype (3 tests \times 2 reps \times 3 leaflets) in the summer and 18 tuber slices and 18 whole tubers per genotype (3 tests \times 2 reps \times 3 slices/whole tubers) in the autumn.

All inoculations were made with a virulent fungus isolate MP 245. Testing results are expressed in 9 grade scale (9 = resistant). Dates of individual tests and descriptions of resistance evaluation methods are given by ŚWIEŻYŃSKI et al. (1997a, b).

Evaluation of the length of vegetative period

The number of days from planting to foliage death was determined at weekly intervals on each field plot separately. For genotypes in which foliage was not dead at harvest time, the number of days was extrapolated on the basis of evaluation of foliage senescence before harvest.

Evaluation of early tuber yield and tuber shape regularity

The total tuber yield was determined 14 weeks after planting. Tuber shape regularity was evaluated both at early and at autumn harvests and expressed in a 9-grade scale (9 = regular shape).

Statistical analysis

Correlations were evaluated using Spearman's rank correlation coefficients. The significance of differences between the groups of genotypes and their parents were evaluated with a two sample t-test. Calculations were made with the package MSTAT-C.

Results

Correlations between evaluated characters

Weak correlations were usually found between the evaluated characters. Only in the family D4 significant positive correlations were found between the resistance in leaflets, in tuber slices and in whole tubers (r_s ranged from 0.34 to 0.70). In most families the length of vegetative period tended to be positively correlated and early tuber yield tended to be negatively correlated

Table 1. Rank correlation coefficients (r_s) between various characters, evaluated in 1992

Character	Family							
	D4	D5	T5	T6	T7	D7	D8	T9
Number of evaluated genotypes	52	52	62	43	28	335	247	659
r_s between leaflet resistance and resistance in:								
tuber slices	0.70**	0.09	0.04	0.18	0.27	0.32**	0.46**	-0.01
whole tubers	0.34*	-0.12	-0.06	0.06	-0.14	-	-	-
r_s between resistance in tuber slices and resistance in:								
whole tubers	0.38**	0.26	-0.29*	-0.28	0.15	-	-	-
r_s between the length of vegetative period and resistance in:								
leaflets	0.18	0.04	0.04	0.07	0.28	0.07	0.02	-0.06
tuber slices	0.28*	0.23	0.07	0.20	0.00	-0.03	0.15*	-0.09*
whole tubers	-0.00	0.13	0.17	0.16	0.43*	-	-	-
r_s between tuber yield at early harvest and resistance in:								
leaflets	-0.18	-0.10	-0.14	-0.01	-0.02	-	-	-
tuber slices	-0.11	0.13	-0.17	0.04	-0.24	-	-	-
whole tubers	-0.09	0.01	-0.02	-0.02	-0.50**	-	-	-
r_s between regularity of tuber shape and resistance in:								
leaflets	-0.01	-0.11	-0.21	-0.38*	-0.19	0.05	-0.08	0.05
tuber slices	-0.06	-0.07	-0.16	-0.01	0.20	-0.12*	-0.12	0.08
whole tubers	0.09	0.14	0.14	0.32*	-0.02	-	-	-

Significant deviation from null hypothesis at $P = 0.05$ (*) or $P = 0.01$ (**).

with the resistance in leaflets, in tuber slices and in whole tubers, but the relation was seldom statistically significant. Regularity of tuber shape tended to be weakly correlated negatively with resistance in leaflets or resistance in tuber slices, but not with resistance in whole tubers (Table 1).

Effects of selecting potato genotypes differing in reaction to *P. infestans*

Groups of genotypes, differing in reaction to *P. infestans* in 1992, were evaluated in 1992 ('92) and 1994 ('94). The number of genotypes in each group and their mean resistance are given in Table 2 (families sown in 1991) and Table 3 (families sown in 1992).

In all families genotypes with resistant leaflets and tuber slices were found. For testing in 1994, 13 such genotypes in families sown in 1991 and 25 such

Table 2. Genotypes differing in reaction to *P. infestans*, selected from potato families sown in 1991

Family	Selection criteria in 1992									Parents			
	Resistant leaflets and tuber slices		Resistant leaflets, susceptible tuber slices		Susceptible leaflets, resistant tuber slices		Resistant whole tubers, susceptible tuber slices		Susceptible leaflets and tuber slices ¹	♀		♂	
	'92	'94	'92	'94	'92	'94	'92	'94	'92	'92	'94	'92	'94
Leaflet resistance ²													
D4	7.5	8.4	–	–	4.3	–	4.3	6.8	4.0	3.4	4.9	6.4	8.2
D5	8.1	8.4	8.2	7.8	–	–	6.5	8.0	3.7	8.1	8.3	2.9	6.2
T5	7.2	6.8	7.1	–	3.7	–	6.0	6.4	4.3	9.0	6.1	7.2	6.3
T6	7.4	7.6	7.3	6.9	3.3	–	6.6	5.9	4.4	9.0	6.4	9.0	6.2
T7	7.6	6.7	7.2	6.7	4.8	–	6.1	–	3.4	9.0	6.4	7.2	6.3
Mean	7.6	7.6	7.4	7.1	4.0	–	5.9	6.8	4.0	7.7	6.4	6.5	6.6
Resistance in tuber slices ²													
D4	8.1	9.0	–	–	6.6	–	4.1	4.2	4.2	4.4	2.1	7.4	7.6
D5	7.8	8.0	3.7	2.5	–	–	3.8	2.6	3.9	5.4	8.1	3.4	2.6
T5	7.4	7.6	3.4	–	8.0	–	3.3	5.7	3.2	2.4	3.6	7.9	8.6
T6	8.1	8.6	3.8	4.8	8.2	–	3.7	4.6	3.6	4.8	6.4	5.4	7.0
T7	7.4	8.2	4.2	5.8	9.0	–	3.9	–	3.4	4.8	6.4	7.9	8.6
Mean	7.8	8.3	3.8	4.4	8.0	–	3.8	4.3	3.7	4.4	5.3	6.4	6.9
Resistance in whole tubers ²													
D4	8.2	9.0	–	–	7.8	–	7.5	7.1	7.5	8.2	6.4	8.2	8.4
D5	7.9	8.0	7.2	6.1	–	–	7.3	6.8	6.8	7.3	6.7	5.3	4.6
T5	6.0	6.4	6.5	–	5.7	–	6.7	6.3	6.3	6.3	6.5	6.3	6.0
T6	6.8	6.6	6.9	6.4	6.2	–	7.1	7.1	6.9	5.9	5.7	6.8	6.3
T7	6.8	5.8	6.5	6.4	8.4	–	6.8	–	6.8	5.9	5.7	6.3	6.0
Mean	7.1	7.2	6.8	6.3	7.0	–	7.1	6.8	6.9	6.7	6.2	6.6	6.3
Number of genotypes										Names of parents			
D4	13	2	0	0	6	0	19	4	16	DW 84-1457	D2-429		
D5	10	2	22	7	0	0	32	4	13	D3-338	DG 82-198		
T5	19	4	14	0	3	0	20	1	7	T3-436	PS 1300		
T6	8	2	21	1	1	0	26	1	5	T3-423	PS 137		
T7	13	3	6	1	1	0	7	0	2	T3-423	PS 1300		
Total	63	13	63	9	11	0	104	10	43				

¹ the genotypes not evaluated in 1994.

² mean of all *P. infestans* resistance tests, performed in 1992 ('92) or 1994 ('94), expressed in a 9-grade scale (9 = resistant).

Table 3. Genotypes differing in reaction to *P. infestans*, selected from families sown in 1992

Family	Selection criteria in 1992							Parents			
	Resistant leaflets and tuber slices		Resistant leaflets, susceptible tuber slices		Susceptible leaflets, resistant tuber slices		Susceptible leaflets and tuber slices ¹	♀		♂	
	'91	'94	'92	'94	'92	'94		'92	'94	'92	'94
Leaflet resistance²											
D7	9.0	8.2	7.7	–	3.0	7.3	1.9	(9.0) ³	8.4	(3.0)	4.9
D8	9.0	8.8	9.0	7.9	2.9	7.1	1.3	(7.0)	8.9	(3.0)	4.9
T9	9.0	6.6	9.0	6.7	2.8	–	2.0	(9.0)	5.5	(9.0)	6.2
Total	9.0	7.9	8.6	7.3	2.9	7.2	1.7				
Resistance in tuber slices²											
D7	9.0	9.0	3.9	–	9.0	9.0	1.9	(6.0)	9.0	(4.3)	2.1
D8	9.0	8.9	2.7	7.9	7.9	8.9	1.3	(6.0)	8.8	(4.3)	2.1
T9	8.4	7.5	1.4	6.7	8.0	–	2.2	(4.0)	6.9	(3.7)	7.0
Mean	8.8	8.5	2.7	7.3	8.3	8.9	1.8				
Resistance in whole tubers²											
D7	–	9.0	–	7.8	–	8.5	–	–	7.9	–	6.3
D8	–	8.9	–	6.8	–	8.0	–	–	8.0	–	6.3
T9	–	7.9	–	5.9	–	–	–	–	5.8	–	6.3
Mean	–	8.6	–	6.8	–	8.2	–				
Number of genotypes							Names of parents				
D7	20	5	11	0	14	4	10	D2-411		DW 84-1457	
D8	38	12	17	4	15	3	12	DG 88-201		DW 84-1457	
T9	18	8	25	7	11	0	17	T3-243		PS 137	
Total	76	25	53	11	40	7	39				

¹ the genotypes not evaluated in 1994.

² mean results of all *P. infestans* tests, performed in 1992 ('92) or 1994 ('94), in a 9-grade scale (9 = resistant).

³ in brackets – results for parents, grown from tubers, are not directly comparable with those for first year seedlings, grown from true seeds.

genotypes in families sown in 1992 were available. This group of genotypes in 1994 was found to be the best in leaflet resistance (7.6 – the mean for families sown in 1991 and 7.9 – the mean for those sown in 1992), resistance of tuber slices (respective values: 8.3 and 8.5) and resistance of whole tubers (respective values: 7.2 and 8.6).

Table 4. Comparison of potato genotypes resistant in leaflets and tuber slices with their parents

Family	No. of resistant genotypes	Vegetative period (days) ¹			Regularity of tuber shape ²		
		resistant genotypes	mid-parent value	difference ³	resistant genotypes	mid-parent value	difference ³
D4	2	147	132	15**	4.4	5.5	-1.1**
D5	2	148	146	2	4.8	5.0	-0.2
T5	4	145	127	18**	5.6	6.2	-0.6**
T6	2	144	138	6	6.1	6.0	0.1
T7	3	145	129	16**	5.8	6.2	-0.4
D7	5	145	138	7	4.8	4.9	-0.1
D8	12	148	142	6	4.6	5.3	-0.7**
T9	8	143	146	-3	6.0	6.0	0.0

¹ \bar{x} of 1992-1994 for families sown in 1991 and \bar{x} of 1993-1994 for those sown in 1992.

² \bar{x} of 1992-1994 in 9-grade scale, 9 = regular shape.

³ significance at P=0.05 (*) or P=0.01 (**), evaluated with t-test.

Genotypes with resistant leaflets and susceptible tuber slices were found in 1992 in all families, except D4, but for testing in 1994 only 9 such genotypes in families sown in 1991 and 11 in those sown in 1992 were available. The results obtained in 1994 depended on the family. This is illustrated by data for the families D5 and T9. When being tested in 1994 the genotypes of the family D5 had leaflets resistant (7.8) and tuber slices susceptible (2.5), as susceptible as those in the susceptible parent (2.6). The situation was different with genotypes of this group in the family T9. When tested in 1994 their leaflets were resistant (6.7), but their tuber slices were also resistant (6.7), being similar to those of both parents (6.9 and 7.0) and to those in the group with resistant leaflets and tuber slices (7.5).

Genotypes with susceptible leaflets and resistant tuber slices were found in 1992 in all evaluated families, except D5; for testing in 1994 such genotypes were available only in families D7 and D8. The resistance of their leaflets was relatively high in 1994 (7.3 in D7 and 7.1 in D8). The values did not differ much from respective values in the genotypes with resistant leaflets and tuber slices (8.2 in D7 and 8.8 in D8).

Genotypes with resistant whole tubers and susceptible tuber slices were selected exclusively in the families sown in 1991. For testing in 1994, 10 such genotypes were available in four families. In 1994 the resistance of whole tubers in this group was similar to that of genotypes with resistant leaflets and tuber slices, but the resistance of their tuber slices was much lower. The difference was the most pronounced in the family D5. In this family, out

of four genotypes of this group, three also belong to the group of genotypes with resistant leaflets and susceptible tuber slices (data not presented in tables).

Maturity and tuber shape regularity in potato genotypes with leaflets and tuber slices resistant to *P. infestans*

In most families the resistant genotypes matured later and had a less regular tuber shape, when the mean of such genotypes was compared with the mid-parent value. The differences were statistically significant in some families (Table 4).

Discussion

Poor repeatability of some evaluations of the relation between resistance to *P. infestans* in potato leaflets and tubers

At the preliminary evaluation in 1992, genotypes with susceptible leaflets and resistant tuber slices were found in most families. However, repeated testing did not confirm the presence of such genotypes in any family; e.g. in 1992 many genotypes with resistant leaflets and susceptible tuber slices were found in the family T9, but this result was not repeated at testing in 1994. The likely reason of such results is variation in the expression of resistance to *P. infestans* which was discussed previously (ŚWIEŻYŃSKI et al. 1997a, b).

Relation between resistance to *P. infestans* in potato leaflets, tuber slices and whole tubers

A significant positive correlation between these three aspects of resistance, found in the family D4 confirm the information of STEWART et al. (1994) that potato genotypes may carry genes for resistance to *P. infestans* which are expressed both in foliage and tubers. In the remaining families the relation between these characters was not so close. It indicates the presence of genes differing in expression, depending on the resistance evaluation method.

The detection of genotypes with resistant whole tubers and susceptible tuber slices is consistent with the observation of DURSKA (1975) that there exist such potato cultivars.

No genotypes were found with susceptible leaflets and resistant tuber slices, but in the family D5, genotypes with resistant leaflets and susceptible tuber slices were present. This is an indication, that there are genes for resistance expressed only or stronger in leaflets, but possibly no genes are present, which would be expressed only or stronger in tuber slices. Published data support

this conclusion: SCHICK and HOPFE (1962) and CHADAYEVA (1974) report that genotypes with resistant tubers are also resistant in foliage; PIOTROWSKI (1975) noted that the tuber resistance was usually associated with foliage resistance, the reverse not being necessarily true; ŚWIEŻYŃSKI (1990) found a deficit of potato cultivars with resistant leaflets and susceptible tubers.

Relation between resistance to *P. infestans* and potato maturity

Late maturity is known to be negatively correlated with general resistance in the potato (UMAERUS, UMAERUS 1994). The relation between specific resistance and maturity appears not to be so close (ŚWIEŻYŃSKI et al. 1991). The observed weak relation between resistance and maturity could be due to a large contribution of specific resistance in the evaluated genotypes. This is probably true, as major genes for resistance were found to segregate in the evaluated families (ŚWIEŻYŃSKI et al. 1997a, b). However, this conclusion must be accepted with caution, as instability of resistance expression in many genotypes (ŚWIEŻYŃSKI et al. 1997a, b) and unsuitability of the leaflet test for evaluation of resistance associated with late maturity (SIECZKA 1979) could also contribute to the results obtained.

Relation between resistance to *P. infestans* and potato tuber shape regularity

Some indications were obtained that regularity of tuber shape may be negatively correlated with resistance. The relation was weak and not detectable in all the evaluated families. Nevertheless, the results obtained support the observation of DARSOW and OERTEL (1986) that seedlings resistant to *P. infestans* tend to be inferior in general tuber appearance.

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